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Key Points:

- Develop a process-based C-N coupling approach incorporating dynamic C/N ratios and plant C-N framework for modelling C-N interaction
- Newly developed SSiB5/TRIFFID/DayCent-SOM produces better above-ground terrestrial plant production, GPP and NPP, and LAI compared to observation

Abstract

It is important to adequately represent plant nitrogen (N) biogeochemistry and its respective processes in land surface models. Thus far, various N representations in models lead to uncertainty in estimating model responses to global warming. Through plant and microbial N dynamics, nitrogen availability regulates the capture, allocation, turnover of carbon (C), and photosynthetic capacity. In this study, to fully incorporate these N regulations, we have developed a plant C-N framework by coupling a biophysical and dynamic land model, SSiB4/TRIFFID, with a soil organic matter cycling model, DayCent-SOM, to simulate the impact of nitrogen on the plant growth and C cycling. To incorporate the N limitation in the coupled system, we first developed the parameterization for the C/N ratios. Then, after accounting for daily plant/soil N-cycling, N will not only limit the plant growth when not sufficient, causing the net primary productivity (NPP) to be down-regulated, but will also impact plant respiration rates and phenology. Using this newly-developed model named SSiB5/TRIFFID/DayCent-SOM, we conduct several simulations from 1948 to 2007 to predict the global vegetation distribution and terrestrial C cycling, and the results are evaluated with satellite-derived observational data. The sensitivity of the terrestrial C cycle to N processes is also assessed. In general, the coupled model can better reproduce observed emergent properties, including gross primary productivity (GPP), NPP, leaf area index (LAI), and respiration. The main improvement occurs in tropical Africa and boreal regions, accompanied by a decrease of the bias in global GPP and LAI by 16.3% and 27.1%, respectively.

Plain Language Summary

Adequate representation of Nitrogen cycle representation is crucial for climate models to produce proper responses to elevated atmospheric CO₂ and global warming. This study presents a new approach in coupling Carbon cycle with Nitrogen processes in a newly developed biophysical, dynamic vegetation, and soil biogeochemical model, in which a biogeochemical component represents soil organic matter cycling and estimates the amount of nitrogen available to plants and plant soil nitrogen uptake. A plant Carbon-Nitrogen framework is developed for modeling interactions between carbon and nitrogen process, and regulates photosynthesis, respiration, and plant phenology based on nitrogen availability. Moreover, instead of fixed carbon/nitrogen ratio as done by many land models, a dynamic carbon/nitrogen ratio is introduced based on the nitrogen availability. A series of numerical experiments are carried out to assess whether the carbon/nitrogen framework properly produces satellite-derived monthly mean gross primary productivity, leaf area index, and global nitrogen-limitation patterns. The results show that properly introducing the Nitrogen processes produces lower bias for these variables.

1 Introduction

Land surface processes affect climate (Foley et al., 1998; Ma et al., 2013; Sellers et al., 1986; Y. Xue et al., 2004, 2010) and are influenced by climate (G. B. Bonan, 2008; Liu et al., 2019a; Zhengqiu Zhang et al., 2015), forming complex feedbacks to climate change (Friedlingstein et al., 2006; Gregory et al., 2009). To study these processes, the land surface components of Earth System Models (ESMs) have evolved from only representing biophysical processes (i.e., hydrology and energy cycle) to include terrestrial carbon (C) cycle, vegetation dynamics, and nutrient processes (Dan et al., 2020; Foley et al., 1998; Jiang et al., 2014; Lu et al., 2001; Niu et al., 2020; Oleson et al., 2013; Pan et al., 2017; Sellers et al., 1986; Sitch et al., 2003; Wang et al., 2010a; Yang et al., 2019). Current land surface models have large uncertainties in predicting historical and current C exchanges (Beer et al., 2010; Richardson et al., 2012; Zaehle et al., 2015), which has been criticized for being unjustified from an ecological point of view (Reich et al., 2006) and for overestimating terrestrial C sequestration in the future (Hungate et al., 2003; Thornton et al., 2007). The differences in predictions using land models have been attributed to many factors. The inclusion or exclusion of nutrient limitations on productivity is one of the critical factors. Those C-only models ignore significant nitrogen (N) deficits and therefore overestimate carbon sequestration by ecosystems under climate change (Peñuelas et al., 2013; Zaehle et al., 2015).

Ecosystem N cycling processes are among dominant drivers of terrestrial C-climate interactions through their impacts, mainly N-limitation, on vegetation growth and productivity (Reich et al., 2006), especially in nitrogen-poor younger soils in high latitudes (LeBauer & Treseder, 2008; PeterM. Vitousek & Howarth, 1991), and on microbial decomposition of organic matter (Hu et al., 2001). The need to represent soil organic matter (SOM) cycling and N-limitation to plant

and microbial processes led to the development of CENTURY (W. J. Parton et al., 1988) and DayCent (William J. Parton et al., 2010; William J Parton et al., 1998), which operates at a daily time step and includes soil nitrification/denitrification processes. More recently, the Fixation and Uptake of Nitrogen (FUN) model (Fisher et al., 2010) expands N acquisition to include passive uptake, active uptake, re-translocation, and symbiotic N-fixation through a carbon cost.

The N cycle and its effect on C uptake in the terrestrial biosphere in land surface models (LSMs), the land components of ESMs is a recent progression (Davies-Barnard et al., 2020), and various representations of N processes and N deposition have been included in ESMs (A.A. Ali et al., 2015; Best et al., 2011; Clark et al., 2011; Ghimire et al., 2016; Krinner et al., 2005; Matson et al., 2002; Oleson et al., 2013; Wang et al., 2010b). The latest Coupled Model Intercomparison Project Phase 6 (CMIP6, Eyring et al., 2016) has at least 10 models that incorporate the N cycle (Arora et al., 2020). Among these models, by coupling the terrestrial biogeochemistry model Biome-BGC (Thornton et al., 2007, 2009), the Community Land Model version 4 (CLM4; Oleson et al., 2010) was the first N model for ESMs used in CMIP5. In CMIP6, the CLM5 (Lawrence et al., 2019) implements a C cost basis for acquiring N, derived from the Fixation and Uptake of Nitrogen (FUN) approach (Fisher et al., 2010). The Lund-Potsdam-Jena General Ecosystem Simulator version 4.0 (LPJ-GUESS; Smith et al., 2014) incorporates a SOM cycling scheme adopted from the CENTURY model (W J Parton et al., 1993) to simulate C and N dynamics and produce N-limitation map. The SURFEX (Surface Externalisée, Le Moigne, 2018) also employs CENTURY to simulate soil C and N dynamics. Some modelling studies have reported improvements in simulated C stocks and fluxes by introducing N processes. For instance, by considering the N cycle, the Joint UK Land Environment Simulator version 5.1 (JULES-CN, Wiltshire et al., 2020) found nutrient limitation reduces carbon-use efficiency. With N cycling SURFEX represented the terrestrial carbon cycle in a more realistic way (Le Moigne, 2018). The implementation of CO₂-induced nutrient limitation (CNL, Goll et al., 2012) and a decomposition model (YASSO, Goll et al., 2012) help the JSBACH model (Daniel S. Goll et al., 2017) reduce accumulated land carbon uptake.

A few key N processes, such as N limitation on GPP, the effect of biomass N content on autotrophic respiration, vegetation pool C:N stoichiometry, plant N uptake, ecosystem N loss and biological N fixation, have been introduced into LSMs with various complexity and selected components. This paper mainly focuses on the N limitation effect, which has been presented in current land models with different approaches, including using N to scale down photosynthesis parameter $V_{c,max}$ (Ghimire et al., 2016; Zaehle et al., 2015) or potential gross primary productivity (GPP) to reflect N availability (Gerber et al., 2010; Oleson et al., 2013; Wang et al., 2010a), defining a C cost of N uptake (Fisher et al., 2010), optimizing N allocation for leaf processes (Ashehad A. Ali et al., 2015), and adapting a flexible C/N ratio for N allocation (Ghimire et

al., 2016). In many of these approaches, N limitation is represented as instantaneous down-regulation of potential photosynthesis rates based on soil mineral N availability. Moreover, the plant C/N ratio is a key concept in presenting the C/N interaction. Many land models, however, specify fixed plant C/N ratios for each plant functional type (PFT) (e.g., Best et al., 2011; Clark et al., 2011; Krinner et al., 2005; Oleson et al., 2013; Wang et al., 2010b). However, plant C/N ratios actually change over the plant’s lifecycle as well as with nutrient availability, and flexible plant C/N ratios are not represented in many models.

In this paper, we present a newly developed LSM, in which the N uptake depends on plant demand from a biophysical and dynamic vegetation model SSiB5/TRIFFID (The Simplified Simple Biosphere Model version 5/ the Top-down Representation of Interactive Foliage and Flora Including Dynamics Model, Cox, 2001; Harper et al., 2016; Liu et al., 2019; Xue et al., 1991; Zhan et al., 2003; Zhang et al., 2015) and is limited based on N availability in the soil and C:N stoichiometry in the plant that are produced from the SOM cycling portion of the DayCent model, DayCent-SOM (Gordon B. Bonan et al., 2013; Del Grosso et al., 2000; William J. Parton et al., 2010; William J Parton et al., 1998). A plant C-N framework, which regulates photosynthesis, respiration, and plant phenology, is introduced to couple DayCent-SOM into SSiB5/TRIFFID. This plant C-N framework is central to the newly coupled model, SSiB5/TRIFFID/DayCent-SOM, and includes flexible C/N ratios based on whether the N demands of different plant organs (e.g., leaf, root, and wood) are satisfied. Using this flexible C/N, SSiB5/TRIFFID/DayCent-SOM can simulate the plant resistance and prevent untrue instantaneous down-regulation of potential photosynthesis rates; and a new strategy to present the limitation of N and plant-N-related respiration rates and phenology changes. This model development incorporates DayCent’s strength in parameterizations of symbiotic biological N fixation, N mineralization/immobilization, nitrification/denitrification, N-gas emissions, atmospheric N deposition, and nitrate leaching. The coupled model has been used to conduct multiple global simulation experiments for the 1948 to 2007 time period, and model predictions of GPP, NPP, and LAI have been evaluated against satellite-derived observational data. Model results demonstrate the relative importance of several N processes in the plant C-N framework.

2 Models and Coupling Strategy

2.1 SSiB4/TRIFFID model

The Simplified Simple Biosphere Model (SSiB, Xue et al., 1991; Sun and Xue, 2001; Zhan et al., 2003) is a biophysical model that simulates fluxes of surface radiation, momentum, and sensible/latent heat, runoff, soil moisture and temperature, and vegetation gross primary products (GPP) based on energy and water balance and photosynthesis processes. The SSiB was coupled with a dynamic vegetation model, the Top-down Representation of Interactive Foliage and Flora Including Dynamics Model (TRIFFID), to calculate net primary product (NPP), leaf area index (LAI), canopy height, and PFT fractional cov-

erage according to the C balance (Cox, 2001; Harper et al., 2016; Liu et al., 2019; Zhang et al., 2015). Moreover, the surface albedo and aerodynamics resistances are also updated based on the vegetation conditions. The previous work has improved the PFT competition strategy and plant physiology processes to make the SSiB4/TRIFFID suitable for seasonal, interannual, and decadal studies (Zhang et al., 2015). SSiB4/TRIFFID includes seven PFTs: (1) broadleaf evergreen trees (BET), (2) needleleaf evergreen trees (NET), (3) broadleaf deciduous trees (BDT), (4) C3 grasses, (5) C4 plants, (6) shrubs, and (7) tundra. A PFT coverage is determined by net C availability, competition between species, and disturbance, which includes mortality due to fires, pests, and windthrow. A detailed description and validation of SSiB4/TRIFFID can be found in Zhang et al., (2015); Liu et al., (2019) and Huang et al., (2020).

2.2 DayCent model

DayCent is a daily version of the CENTURY ecosystem model (Parton et al., 1998; Del Grosso et al., 2000). The model simulates major processes associated with C, N, phosphorus (P), and sulfur (S) cycling in a plant-soil system. The model also simulates agriculture land management practices, such as grazing, irrigation, cultivation, residue removal during harvest, organic matter and chemical fertilizer additions, and flooding and drainage. Key processes include decomposition of litter and SOM; mineralization/immobilization and plant uptake of nutrients; N-gas emissions from nitrification and denitrification; and CH₄ oxidation in non-saturated soils (i.e., methanotrophy). Litter and SOM decomposition is controlled by soil moisture, temperature, and pH, and tillage intensity. Model inputs are daily weather data (e.g., maximum and minimum air temperature, precipitation, solar radiation, wind speed, and relative humidity), soil properties, and land management and disturbance data (e.g. fire, biomass harvest, flooding, and storm damage). The DayCent model has been used to simulate NPP, soil organic C, N₂O emissions, nitrate leaching, and CH₄ oxidation in various native and managed systems with extensive validations (Del Grosso et al., 2005; Del Grosso et al., 2000; Parton et al., 2010).

Only DayCent's SOM cycling functions (DayCent-SOM) are coupled with the SSiB5/TRIFFID. DayCent-SOM includes five types of organic C and N pools consisting of two plant litter pools (metabolic and structural) and three kinetically defined organic matter pools, (active, slow, and passive); all organic pools except the passive pool have both above-ground and below-ground counterparts. DayCent-SOM is forced with soil temperature and soil moisture, and plant C and N litter inputs from SSiB4/TRIFFID, computes daily changes to all organic matter and mineral soil pools, estimates losses of N from nitrate leaching and N₂O, NO_x, and N₂ emissions, estimates the amount of inorganic N available to plants (Navail), and updates inorganic N pools based on plant N-uptake. The full description for plant N uptake and soil N dynamics is available in Parton et al. (1994, 1998) and Del Grosso et al. (2000).

2.3 Plant Carbon-Nitrogen (C-N) Interface framework

To represent C/N interactions in SSiB5/TRIFFID/DayCent-SOM, we have developed a plant C-N interface framework to describe N effects on plant physiology: photosynthesis, plant autotrophic respiration, and plant phenology plus a flexible C/N ratio (Fig. 1). This approach takes into account both biophysical and biochemical N processes in plant life activities and is unique among LSMs. The conceptual considerations in developing this framework are presented in this section.

A commonly used parameterization of photosynthetic C assimilation by the terrestrial biosphere in ESMs is represented by the Farquhar, von Caemmerer, and Berry (FvCB) model of photosynthesis (Collatz et al., 1991; Farquhar et al., 1980). Plants require N as essential components of photosynthetic proteins involved in light capture, electron transport, and carboxylation (Evans, 1989). Nitrogen is an important constituent of Rubisco enzyme and mitochondrial enzymes that regulate respiration and adenosine triphosphate (ATP) generation (Makino & Osmond, 1991). One of the most important photosynthetic model parameters, the maximum carboxylation rate by the Rubisco enzyme ($V_{c,max}$) is a key parameter in the FvCB model (Farquhar et al., 1980), and has an extensive range across the models depending on the plant N content (Rogers, 2014). Since N is an important component of Rubisco enzyme, leaf N content will affect $V_{c,max}$ thus GPP. The original FvCB model has not explicitly considered the N effect on the plant C; while in a number of LSMs an empirical relationship is applied to relate $V_{c,max}$ to leaf N content N_{leaf} to generate the effect of N on photosynthesis, e.g., $V_{c,max} = i_v + s_v \times N_{leaf}$, where the intercept (i_v) and slope (s_v) are derived for each PFT based on observations (Kattge et al., 2009; Raddatz et al., 2007). Moreover, for plant N processes, normally, only the relationship between the root N uptake and GPP/NPP is considered to represent the N-limitation on C cycles (Ashehad A. Ali et al., 2015; Fisher et al., 2010; Ghimire et al., 2016). However, because NPP is the difference between GPP and autotrophic respiration, adjusting NPP or GPP only may cause the ratio between NPP and respiration to deviate from reality. Using process-based N-limitation factor produced from DayCent-SOM to modify $V_{c,max}$ (See section 3.3) is an approach in our C-N interface framework and should be a more realistic way to produce the N effect on photosynthesis process.

In the SSiB4/TRIFFID, with the assumed unlimited N availability, fixed C/N ratios and assimilated C determine nitrogen contents of leaf, stem, and root, then respiration, which influences GPP, LAI, and NPP. The C/N ratio is specified based on PFTs. However, there is evidence that plants can adjust their resources and stoichiometric requirements. Changes in N resource availability will result in changes to plant C allocation and partitioning. Studies show plants resorb only about 50% of leaf N on average (Aerts, 1996) to conserve nutrients (Clarkson & Hanson, 1980), and to increase nutrient use efficiency (Herbert & Fownes, 1999; Peter Vitousek, 1982). These processes cause a major internal nutrient flux and changes of C/N ratios to reduce the impact of nitrogen limitation (Talhelm et al., 2011; Vicca et al., 2012). In addition, plant responses, such as plant resistance and self-adjustment, will be limited under fixed C/N ratios,

which affect plant productivity and change litter N content, thus drive changes in the underground biogeochemistry and ultimately C and N uptake and storage (Drewniak & Gonzalez-Meler, 2017). A study on the N deposition effect shows that the increase in foliar N under increased N, would improve model responses because it allows adaptations in the stoichiometry of C and N (Medlyn et al., 2015). The main impact of this will be to decrease C/N ratio in leaves, driving increases in productivity and changes soil and litter N content. A dynamic C/N ratio is employed in our framework to more realistically obtain N states and properly represent the effect of N processes (See section 3.2 for more details).

Nitrogen is not only a dominant regulator of vegetation dynamics, GPP/NPP, and terrestrial C cycles; Reich et al. (2008) demonstrate strong relationships between respiration and N scaling based on observational data from various species. At any normal N concentration, respiration rates are consistently lower on average in leaves than in stems or roots. Therefore, we introduce two parameters for stem and root, respectively, based on PFT to adjust the respiration rate in section 3.4.

Nitrogen also affects plant phenology and can be remobilized to supply spring bud-break or vegetative shoot extension (Kolb & Evans, 2002; Marmann et al., 1997; Millard, 1994; Neilsen et al., 1997). Nitrogen resorption is found during leaf senescence and growth in evergreens (May & Killingbeck, 1992). Because plants need time to turnover, the plant N processes also have a lag effect on plant phenology (Thomas et al., 2015). Phenology in SSiB4/TRIFFID modulates LAI evolution, including leaf mortality, but it is not directly linked to N. Since different N states and supplements will lead to different lags on phenology, we add N impact on plant phenology by introducing a N limitation parameter and will be discussed in section 3.5.

3 The Development of SSiB5/TRIFFID/DayCent-SOM model

3.1 The SSiB5/TRIFFID/DayCent-SOM computational flow

In SSiB5/TRIFFID/DayCent-SOM, SSiB5 provides GPP, autotrophic respiration, and other physical variables such as canopy temperature and soil moisture every 1 to 3 hours for TRIFFID (Fig. 2). TRIFFID accumulates the GPP and respiration from SSiB5 and predicts biotic C, PFT fractional coverage, vegetation height, and LAI every ten days, which are used to update surface properties, such as albedo, roughness length, and aerodynamic/canopy resistances, in SSiB5. The plant C-N framework uses the meteorological forcings (i.e., air temperature and precipitation) and physical variables (i.e., soil moisture and soil temperature) provided by SSiB5 every 1-3 hours and the biophysical properties (vegetation fraction and biotic C) provided by TRIFFID, which is updated every ten days. The plant C-N Interface Framework calculates dynamic C/N ratios, N-limited photosynthesis, N-impacted respiration rate, and N-limited phenology every 1-3 hours. The C loss and potential N uptake are accumulated within one day in the C-N Interface Framework and plant C and N litter fall are transferred to DayCent-SOM at the end of the day. DayCent-SOM calculates inorganic N

available for plant N uptake (N_{avail}) and N losses from nitrate leaching and N-trace gas emissions each day. TRIFFID updates the vegetation dynamics based on C balance on Day 10, using the NPP and PFT competition strategy. The updated vegetation dynamics are transferred to SSiB5 to reflect the N impact on the C cycle.

3.2 Dynamic C/N ratios based on plant growth and soil nitrogen storage

The N availability for new growth limits the C assimilation rate in plant through the C/N ratio, i.e., the model simulated NPP should be no more than $N_{\text{avail}} \times$ C/N ratios. In the original TRIFFID parameterization, the C/N ratios for different plant components (leaf, root, and wood) are fixed based on plant functional types (Cox, 2001). In reality, changes in C/N ratios occur over the lifecycle of the plant and vary with nutrient availability, which are not captured in original SSiB4/TRIFFID models. Based on DayCent's method of determining variable C:N ratios for plants, a linear relationship between C/N ratio (CNR_{actual}) and N_{avail} is introduced to the SSiB5/TRIFFID/DayCent-SOM for each PFT's components (Figure 3, Eq 1).

$$CNR_{\text{actual}} = \begin{cases} CNR_{\text{max}}, & \frac{N_{\text{avail}} - N_{\text{demand,max}}}{N_{\text{demand,min}} - N_{\text{demand,max}}} \times CNR_{\text{min}} + \frac{N_{\text{avail}} - N_{\text{demand,min}}}{N_{\text{demand,max}} - N_{\text{demand,min}}} \times CNR_{\text{max}} \\ CNR_{\text{min}}, & \end{cases} \quad (1)$$

where N_{avail} is the amount of soil mineral nitrogen that was available at the end of the previous day (g N m^{-2}) calculated from DayCent-SOM. The minimum and maximum amounts of nitrogen required ($N_{\text{demand,min}}$, $N_{\text{demand,max}}$) for the potential NPP_p ($\text{g C m}^{-2} \text{ day}^{-1}$) that is obtained from SSiB4/TRIFFID are:

$$N_{\text{demand,min}} = \frac{NPP_p}{CNR_{\text{max}}} \quad (2)$$

$$N_{\text{demand,max}} = \frac{NPP_p}{CNR_{\text{min}}} \quad (3)$$

where CNR_{min} and CNR_{max} are the minimum and the maximum C/N ratio for each PFT's components (Table. 1).

Since the DayCent-SOM only provide the total available nitrogen ($N_{\text{avail, total}}$) for the plant within one grid box, the nitrogen available for each PFT in the grid box and each component for each PFT is calculated as

$$N_{\text{avail}} = N_{\text{avail, total}} * \text{frac}_i * \sum_j \text{Cfrac}_{i,j} \quad (4)$$

where frac_i is the fraction of PFT i in one grid, and $\text{Cfrac}_{i,j}$ is the fraction of total $N_{\text{avail, total}}$ allocated to plant type i, component j, and is determined as

$$\text{Cfrac}_{i,j} = \frac{\text{Growth}_{i,j}}{\sum_j \text{Growth}_{i,j}} \quad (5)$$

where $\text{Growth}_{i,j}$ is the amount of new C allocated to plant type i, component j, and is calculated in TRIFFID.

The potential NPP_p that is allocated to each PFT's components is defined similarly as

$$NPP_p = NPP_i * \sum_j Cfrac_{i,j} \quad (6)$$

where NPP_i is the i th type's potential NPP and is calculated in TRIFFID.

3.3 Effect of nitrogen limitation on photosynthesis based on soil available nitrogen and plant C-N ratio

There are several different ways to represent N-limitation, including using N to scale down photosynthesis (Ghimire et al., 2016; Zaehle et al., 2015), or potential gross primary productivity (GPP) to reflect N-availability (Gerber et al., 2010; Oleson et al., 2013; Wang et al., 2010a), or defining an NPP cost of nitrogen uptake (Fisher et al., 2010). We choose the most physiological way, adjusting $V_{c,max}$ during the photosynthesis process, which regulates both C assimilation and autotrophic respiration, rather than net production (NPP) at the end of the photosynthesis process.

During photosynthesis the assimilation product, GPP, is proportional to the maximum Rubisco carboxylation rate ($V_{c,max}$) which is related to the N concentration.

We therefore introduce a downregulation of the canopy photosynthetic rate based on the available mineral N for new growth (N_{avail}) using a N-availability factor, $f(N)$.

$$V_{c,max-new} = V_{c,max} * f(N) \quad (7)$$

The $f(N)$ is determined by the nitrogen availability:

$$f(N) = \begin{cases} \frac{N_{avail}}{N_{demand,min}} & N_{avail} \leq N_{demand,min} \\ 1 & \text{otherwise} \end{cases} \quad (8)$$

Plants adjust the relative allocations of C and N during N uptake and via N remobilization and resorption to reduce the impact of N-limitation. We assume there is no N-limitation on photosynthesis when $N_{avail} > N_{demand,min}$. We add a linear relationship between $f(N)$ and N_{avail} when N availability is not sufficient for the minimum N demand for new growth. In this approach, a variable ($V_{c,max}$), which is related to the N during the photosynthesis process and affects both C uptake and autotrophic respiration, is adjusted.

In fact, the factor, $f(N)$ can also be applied to NPP and GPP as shown in Equations 9a –b and had been done by the studies as reviewed at the beginning of this section.

$$NPP_{new} = NPP * f(N) \quad (9a)$$

$$GPP_{new} = GPP * f(N) \quad (9b)$$

If NPP is adjusted (Eq. 9a), this is equivalent to adding a photosynthesis N-limitation on plant respiration, which is not reasonable based on plant physi-

ology and may distort the ration of NPP and respiration. In SSiB4/TRIFFID, GPP will be recalculated after determining the potential C achievement. We had tested all of these approaches and find that they all limit the end production (NPP) of the photosynthesis process, but adjusting $V_{c,\max}$ is the most direct and process-based one (See section 6.1 for more discussion).

3.4 Improvement of nitrogen impact on respiration rates based on field observations

Nitrogen affects plant respiration (Reich et al., 2008; Thornely & Johnson, 1990). In the original SSiB4/TRIFFID, the total maintenance respiration is given by Cox (2001):

$$R_{\text{pm}} = 0.012R_{\text{dc}} \frac{N_l + N_s + N_r}{N_l} \quad (10)$$

where R_{dc} is canopy dark respiration, N_l , N_s and N_r are the N contents of leaf, stem, and root, respectively, and the factor of 0.012 is from the unit conversion. Eq. (10) assumed the respiration rates in root and stem have the same dependence on N content as leaf. However, studies (Reich et al., 2008) had shown that the respiration rates at any common N concentration were consistently lower in leaves than in stems or roots on average.

Thus, we introduce two PFT-specific parameters ($\text{Res}A_S$, $\text{Res}A_R$) from field observations (Wang et al., 2006; Yang et al., 1992) to represent root and stem respiration.

$$R_{\text{pm}} = 0.012R_{\text{dc}} \frac{N_l + \text{Res}A_S * N_s + \text{Res}A_R * N_r}{N_l} \quad (11)$$

Since $\text{Res}A_S$ and $\text{Res}A_R$ generally larger than 1, new R_{pm} is larger than the former one, the increased respiration due to the nitrogen limitation will decrease the NPP (= GPP – autotrophic respiration). Notably, the R_{dc} calculation linearly depends on $V_{c,\max}$ thus the introduced N limitation of $V_{c,\max}$ in section 3.3 may contradict the N effect on respiration.

3.5 N-limitation on LAI based on plant phenology

In the original SSiB4/TRIFFID, a parameter p is used to represent the vegetation’s phenological status and to calculate the leaf drop rate and LAI. Studies (Aerts & Berendse, 1988; Thomas et al., 2015) show that leaf turnover and aboveground productivity are related to nutrient availability and that plant N processes can potentially lead to lags on phenology. In TRIFFID, a leaf phenology parameter, p , (Cox, 2001) is introduced to adjust the model-simulated maximum LAI based on carbon balance, LAI (L_{balance}), to actual LAI (L) and produce realistic phenology.

$$L = p \times L_{\text{balance}} \quad (12)$$

and

$$\frac{dp}{dt} = \begin{cases} -\gamma_p & \gamma_{lm} > 2\gamma_0 \\ \gamma_p(1-p) & \gamma_{lm} \leq 2\gamma_0 \end{cases} \quad (13)$$

where leaf constant absolute drop rate $\gamma_p = 20 \text{ yr}^{-1}$, the leaf mortality rate γ_{lm} is a function of temperature T , and the minimum leaf turnover rate $\gamma_0 = 0.25$ (Cox, 2001). This phenology parameter, p , indicates that “full leaf” is approached asymptotically during the growing season, and p is reduced at a constant absolute rate when the mortality rate is larger than a threshold value. Otherwise, p increases but the rate of increase is reduced as the growing season evolves. To reflect the N limitation in SSiB5/TRIFFID/DayCent-SOM, we assume p , is limited by the N availability with the new p determined by

$$p_{\text{new}} = f(N) \times p_{\text{original}} \quad (14)$$

where $f(N)$ is calculated in section 3.3.

4 Data and Experimental design

4.1 data

4.1.1 Meteorological forcing data

The Princeton global meteorological dataset for land surface modeling (Sheffield et al., 2006) was used to drive SSiB4/TRIFFID from 1948 to 2007 at $1^\circ \times 1^\circ$ spatial resolution and 3-hourly temporal interval. This dataset, including surface air temperature, pressure, specific humidity, wind speed, downward short-wave radiation flux, downward long-wave radiation flux, and precipitation, was constructed by combining a suite of global observation-based datasets with the National Center for Environmental Prediction/National Center for Atmospheric Research reanalysis data.

4.1.2 Observation data

To access the climatological status, variation, and trends of simulated LAI, two widely used LAI products were used as references in this study: the Global Inventory Modeling and Mapping Studies (GIMMS) LAI and the Global Land Surface Satellite (GLASS) LAI. GIMMS-LAI is based on the third generation of Normalized Difference Vegetation Index (NDVI3g) from the GIMMS group and an Artificial Neural Network model (Zhu et al., 2013). GIMMS-LAI provides a 1/12-degree resolution, 15-day composites, and spans July 1981 to December 2011. GLASS-LAI is generated from Advanced Very High Resolution Radiometer (AVHRR) (from 1982 to 1999 with 0.05-degree resolution) and MODIS (from 2000 to 2012 with 1 km resolution) reflectance data using general regression neural networks (Xiao et al., 2014). GIMMS and GLASS LAI, and the meteorological forcing data for overlap period 1982 to 2007, were remapped to 1-degree spatial resolution and a monthly temporal interval.

The Model Tree Ensemble (MTE) GPP product (M. Jung et al., 2009) was used as the reference to evaluate simulated GPP. MTE is based-on a machine

learning technique in which the model is trained to predict the five C fluxes at FLUXNET sites driven by observed meteorological data, land cover data, and the remotely-sensed fraction of absorbed photosynthetic active radiation (M. Jung et al., 2009). The trained model was then applied at the grid-scale driven by gridded forcing data. MTE-GPP data was resampled to 1-degree spatial and a monthly temporal resolution.

4.2 Experimental design

4.2.1 Initial condition for equilibrium simulation

There are different ways to initialize the surface condition for the quasi-equilibrium simulation. Following previous SSiB4/TRIFFID study (Zhengqiu Zhang et al., 2015), we set up the initial condition using the SSiB vegetation map and SSiB vegetation table, which are based on ground surveys and satellite-derived information (Dorman & Sellers, 1989; Yongkang Xue et al., 2004; Zhengqiu Zhang et al., 2015) with 100% occupation at each grid point for the dominant PFT and zero for other PFTs, then we ran the SSiB4/TRIFFID model with the climate forcing for 100 years to reach the equilibrium conditions. The vegetation and soil conditions then were used as the initial conditions for the subsequent model runs.

4.2.2 Control run and sensitivity runs

In this study, SSiB4/TRIFFID was applied to produce the global vegetation distribution as the control run (Exp. SSiB4) then the control run was compared to model experimental simulations to assess the sensitivity of C cycle variability and trend to N processes. All the simulations are driven by real-forcing from 1948-2007 (Table 2). In the control run, using the quasi-equilibrium simulation results as the initial condition, the historical meteorological forcing was used to drive SSiB4/TRIFFID from 1948 through 2007. Using the control simulation, we first evaluated the ability of the model to reproduce the climatology and variability of multiple biotic variables by comparing it to multiple observation-based datasets. In addition to the control run, two sets of experiments were conducted to quantify the N process’s main effects on the C cycle. They were designed as follows:

- (1). Nitrogen limitation on photosynthesis (Exp. NIPSN): The same meteorological forcing used for the control (Exp. SSiB4) drives the model, but dynamic C/N ratios and N-limitation on $V_{c,max}$ (Eq. 7) are introduced. The difference between Exp. SSiB4 and Exp. NIPSN indicates the effect of N- limitation on photosynthesis.
- (2). SSiB5/TRIFFID/DayCent-SOM (Exp. SSiB5): The model was driven by the same meteorological forcing used for Exp. SSiB4, but all four N processes, i.e., dynamic C/N ratio, and N impacts on photosynthesis, autotrophic respiration, and phenology, are introduced. The difference between Exp.NIPSN and Exp. SSiB5 indicates the nitrogen effect on autotrophic respiration and phenology, and the difference between Exp. SSiB4 and Exp. SSiB5 indicates the effect

of N dynamics.

Two additional sets of experiments were conducted to quantify the difference in the three N-limitation approach (Eq. 7, 9a, and 9b):

(3). Nitrogen limitation on NPP (Exp. N1NPP): The same meteorological forcing used for the control (Exp. SSiB4) drives the model, but dynamic C/N ratios and N-limitation on NPP are introduced (Eq. 9a). The difference between Exp. SSiB4 and Exp. N1NPP indicates the effect of N- limitation on NPP.

(4). Nitrogen limitation on GPP (Exp. N1GPP): The same meteorological forcing used for the control (Exp. SSiB4) drives the model, but dynamic C/N ratios and N-limitation on GPP are introduced (Eq. 9b). The difference between Exp. SSiB4 and Exp. N1GPP indicates the effect of N- limitation on GPP.

5 Results

5.1 Evaluation of global LAI and GPP

The simulated GPP averaged over 1982-2007 is compared to FLUXNET-MTE GPP (Martin Jung et al., 2011) to examine the impact of model parameterization of N processes on C and ecosystem characteristics. Both SSiB4/TRIFFID (Exp. SSiB4) and SSiB5/TRIFFID/DayCent-SOM (Exp. SSiB5) capture the distribution of global GPP (Fig. 4). The highest GPP occurs in the tropical evergreen forest and decreases with latitude in both the observations and the model. However, Exp. SSiB4's simulated GPP has a negative bias in the Amazon tropical forest and a positive bias in tropical Africa and boreal regions. This simulated global GPP is $1082.36 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Table. 3), higher than the estimate, $862.86 \text{ g C m}^{-2} \text{ yr}^{-1}$ in FLUXNET-MTE (Martin Jung et al., 2011). After introducing all N processes, Exp. SSiB5's GPP prediction, $941.81 \text{ g C m}^{-2} \text{ yr}^{-1}$, is closer to observations compared to Exp. SSiB4, with a 16.3% improvement (Table 3). The GPP bias in tropical Africa and boreal regions is reduced, which shows an improvement in spatial simulation (the spatial correlation coefficient from 0.88 to 0.90, Fig. 4). Despite the general global improvement, the GPP simulation in East Asian semi-arid seems to get worse. SSiB4's simulation there is close to observations and the imposed N-limitation in SSiB5 increases the bias. This issue needs to be further investigated in the regions where the N-limitation is not dominant. Of course, the uncertainty of measurement in these areas also need to be assessed. Further improvements, such as better ecological understanding of plant N dynamics and plant N observations, are necessary in this regional research. In addition, the negative GPP bias in Amazon is increased. This issue will be discussed in section 5.3.

Exp. SSiB5 also improved predictions of LAI compared to the control (Fig. 5). The highest LAI occurs in the tropical evergreen forest and decreases with latitude in both the observations and the model. The simulated LAI in Exp. SSiB4 has a global positive bias. After introducing all nitrogen processes, the positive bias is reduced. Globally, Exp. SSiB5 has an LAI bias of 0.94/1.12 for GIMMS/GLASS, respectively (Table. 4), which is lower than the LAI bias in

Exp. SSiB4 (global bias = 1.26/1.44 for GIMMS/GLASS, respectively), with a 31.1% improvement (compared to GIMMS, Table 4).

It is interesting to notice that despite the global general LAI reduction, the SSiB5 slightly increased LAI estimates in North Africa and India. The N-impacts on phenology and respiration cause a slight change in the vegetation from shrub (N. Africa) or C4 grass (India) to C3 grass in these areas. This contributes to the GPP and LAI increase (Fig. 8). In next sections, we will further identify the effect of N-limitation to each process, such as the photosynthesis process, on simulated GPP and LAI.

5.2 Effects of nitrogen limitation on photosynthesis

In this section, we discuss the results from Exp. NIPSN, which applies Eq. (7) to scale down the $V_{c,max}$. Exp. NIPSN has a lower global GPP bias (128.52 g C m⁻² yr⁻¹) compared to FLUXNET-MTE estimates than Exp. SSiB4 does (219.50 g C m⁻² yr⁻¹) (Fig. 6, Table 3). Exp. NIPSN has a global LAI bias of 1.13 (Fig. 7, Table 4), which is lower than the LAI bias in Exp. SSiB4 (1.26). The largest reductions in LAI bias are in the North American and Eurasian continents.

The highest GPP occurs in the tropical evergreen forest and decreases with latitude in Exp. SSiB4 and the other three model experiments (Exp. NIPSN, Exp. NINPP, Exp. NIGPP). However, compared to FLUXNET-MTE GPP (OBS), the simulated GPP in Exp. NIPSN has the lowest negative bias in the Amazon tropical forest and lowest positive bias in tropical Africa and boreal regions (Fig. 6). Exp. NIPSN had lower global GPP bias (128.52 g C m⁻² yr⁻¹, Fig. 6) compared to FLUXNET-MTE GPP estimates than Exp. NINPP (173.38 g C m⁻² yr⁻¹) and Exp. NIGPP did (154.31 g C m⁻² yr⁻¹). For global LAI, Exp. NIPSN had a bias of 1.13 (Fig. 7), which is lower than the LAI bias of Exp. NINPP (1.17) and Exp. NIGPP (1.15). The Exp. NIPSN approach yields the best results. This is because adjusting $V_{c,max}$ is the most direct and process-based one on physiology, and the most suitable for SSiB5's model structure.

Exp. SSiB5 did not produce the best results everywhere. The Exp. SSiB5 GPP results had a greater negative bias than Exp. NIPSN in East Asian semi-arid area; however, the LAI results improved with SSiB5 for this region. As we address in section 5.1, this issue needs to be investigated with more data and models. By and large, Table 3 and Table 4 show two general things: after introducing N-limitation on photosynthesis, Exp. NIPSN reduces GPP and LAI compared to Exp. SSiB4. After introducing N-impacts on respiration and phenology, Exp. SSiB5 further reduces GPP and LAI compared to Exp. NIPSN in most regions. Since Exp. SSiB4 and Exp. NIPSN overestimate LAI in all areas, N-limitation helps Exp. SSiB5 to produce the best LAI results everywhere. However, SSiB4 doesn't overestimate in all regions. The introduced N-limitation does not guarantee Exp. SSiB5 produces the best results in every region. Since Exp. NIPSN did best at substantially reducing the biases of simulated GPP

and LAI in SSiB5, we finally choose Eq. (7) rather than Eq. (9a) or (9b) to scale down the photosynthesis.

5.3 Attribution of N processes on C cycle

It is interesting to notice that despite the fact that N processes generally reduced the global GPP/LAI in our results, N-limitation on photosynthesis (indicated by Exp. NIPSN – Exp. SSiB4) and the other two N processes (N-impacts on phenology and respiration, indicated by Exp. SSiB5 – Exp. NIPSN) show different regional attributions (Fig. 8, Table 3 and Table 4). Because not only N but also P limitation constrain the magnitude of terrestrial C uptake in response to elevated carbon dioxide and climate change, efforts have been made to identify regions constrained by global nutrient limitation. Some studies (Lauenroth et al., 1978; Owensby et al., 1970) show that N is quite limiting to grassland plant production in temperate systems since 50% increases for dry grasslands and 100% increases for wet grasslands with N fertilizer additions. Du et al. (2020) examined global N and P limitation using the ratio of site-averaged leaf N and P resorption efficiencies of the dominant species across 171 sites, and found a strong latitudinal pattern of N and P limitation. N-limitation prevails in boreal forests, tundra, temperate coniferous forests, and montane grasslands and shrublands, whereas phosphorus (P) has more effect in Mediterranean biomes, grasslands, savannas, shrublands and forests in tropical, subtropical and temperate regions.

The LAI and GPP bias reduction between Exp. SSiB4 and Exp. SSiB5 (Fig. 4f, Fig. 5f) as well as the experiments that examine the impact on N-limitation on different processes should provide a global N-limitation pattern. Our simulations show a strong latitudinal pattern of N-limitation and relatively close agreement with Du et al. (2020) results but provide more comprehensive information. N-limitation on photosynthesis, which is shown in the difference between Exp. SSiB4 and Exp. NIPSN, results in a dominant decrease in tropical Africa and boreal regions (Fig. 8a), but N-impacts on phenology and respiration dominate the decline in GPP in tropical forests (Fig. 8b).

Moreover, there is a transition to N-limitation at higher elevations in some lower-latitude regions (i.e., the Tibetan Plateau) (Du et al., 2020). This pattern is also caught in this study (Fig.8a, Fig. 8c). It should be pointed out that using bias reduction of GPP/LAI to show N limitation pattern may not be sensitive to leaf N and P resorption efficiencies; however, it provides information on spatial heterogeneity and is a tool for comparing nutrient limitation globally to existing assessments based on site nutrient fertilization experiments. Since plant production in the Amazon area and Australia are typically P-limited, this may explain why SSiB5's N-limitation is not very effective in these areas (Fig.8a, Fig. 8c). In the future we will need to add plant-soil P processes to consider both P and N limitation.

6 Conclusions

This study presents improvements in modelling C cycle by introducing plant

N processes into SSiB5/TRIFFID/DayCent-SOM. We have employed DayCent-SOM to calculate the amount of N available to plants and plant soil N uptake, and have developed a plant C-N framework for modeling the C/N interactions. The new model structure in SSiB5/TRIFFID/DayCent-SOM allows us to use dynamic C/N ratios to determine the N-limiting effect on photosynthesis, plant respiration rates, and LAI through phenology. These improvements replace the original fixed C/N ratio model framework that did not include the impact of N on plant growth. In the new SSiB5/TRIFFID/DayCent-SOM model structure, N impacts on GPP are predicted directly with leaf N content, which is affected by V_{\max} , autotrophic respiration, and plant phenology.

We evaluated the model against multiple reference data sets for GPP, LAI, and global N-limitation patterns. SSiB5/TRIFFID/DayCent-SOM has a lower bias for GPP and LAI than the baseline version of SSiB4/TRIFFID. The more realistic representation of dynamic C/N ratios and plant N framework lead to general improvements in SSiB5/TRIFFID/DayCent-SOM's global C cycling predictions. The downregulation of the canopy photosynthetic rate based on the available mineral N for new growth was better and reducing the GPP bias than the downregulation of GPP or NPP directly and was more realistic from the perspective of plant physiology. This coupled model can better reproduce observed state variables and their emergent properties (such as GPP, NPP, LAI, and respiration). The new model can also predict a global pattern of terrestrial N-limitation.

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Author contributions. ZX, YX, MH, and YL designed the coupling strategy between SSiB4/TRIFFID and DayCent-SOM. ZX conducted the simulation with suggestions from YX, WB, and WG. ZX, YX, and MH drafted the text and ZX made the figures. All authors (ZX, YX, WG, MH, WG, PC, and YL) have contributed to the analysis methods and the text.

Data availability. The evaluation/reference data sets from model data discussed in this paper are archived at <https://doi.org/10.5281/zenodo.5126455>

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