https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

Biogeosciences Discussions

Nitrogen limitation information retrieved from data assimilation

Song Wang[1,2,3], Carlos A. Sierra[3], Yiqi Luo[4], Jinsong Wang[1,2], Weinan Chen[1,2], Yahai Zhang[3,5], Aizhong Ye[5], Shuli Niu[1,2]

[1]Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Research, Chinese Academy of Sciences, Beijing 100101, China.

[2]College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China.

[3]Department of Biogeochemical Processes, Max Planck Institute for Biogeochemistry, Jena, 07745, Germany.

[4]School of Integrative Plant Science, Cornell University, NY 14853, USA.

[5]State Key Laboratory of Earth Surface Processes and Resource Ecology, Faculty of Geographical Science, Beijing Normal University, Beijing 100875, China.

Corresponding to: Shuli Niu (sniu@igsnrr.ac.cn)

Abstract: Nitrogen (N) limitation greatly constrains terrestrial ecosystem carbon (C) uptake and its response to climate change and elevated carbon dioxide. Hence, accurate assessments of ecosystem N limitation are crucial for predicting C-N feedbacks, and vital for providing guidance for policy making or ecosystem management as well. This study aims to retrieve N limitation information by data model fusion from one field N addition experiment so that we can better understand N controls on the terrestrial C cycle. We estimated two sets of parameters with one C-only model and one coupled C-N model. Our results showed that the estimated leaf photosynthetic efficiency (LPE) and process rates (e.g., senescence and decomposition rates) of organic C from almost all pools were higher with the coupled C-N model than those with the C-only model at the ambient treatment. However, the differences in the LPE and the C exit rates between the coupled C-N model and the C-only model decreased with the increasing N addition rates. Both the C-only and coupled C-N models simulated similar C pool sizes as observed at every N addition treatment with their respective parameter estimates. However, simulated ecosystem C storage and gross primary productivity (GPP) decreased if we ran the coupled C-N model with the parameters estimated by the C-only model. This decrease was larger at the ambient treatment and became smaller with the increase of N addition. In general, we put forward a new method to retrieve N limitation information from observations by data model fusion. This method will make it possible to estimate the

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

global nutrient limitation and benefit ecosystem management and policy making.

Keywords: Data assimilation, nitrogen limitation information, nitrogen addition, model structure, carbon and nitrogen cycles.

1. Introduction

Nitrogen (N) availability is a key limiting factor for growth in many terrestrial ecosystems, and thus important for both ecosystem productivity and the decay of dead organic material (Keeler et al., 2009; Liu et al., 2019; Pregitzer et al., 2010). As a consequence, plant tissue N content is often highly correlated with key metabolic rates such as photosynthesis (Zong et al., 2018) and respiration (Sun et al., 2014), and an important control on the turnover of soil organic matter (Fog, 2008; Keeler et al., 2009). Manipulative N addition experiments and field studies have demonstrated larger plant growth with increasing N deposition (LeBauer and Treseder, 2008; Pregitzer et al., 2010). Hence, the capacity of terrestrial ecosystems to store carbon (C) is limited by its N availability and the C:N stoichiometry of plant tissue (Hungate et al., 2003; Luo et al., 2004), especially under elevated atmospheric CO2 concentrations.

An accurate assessment of ecosystem N limitation is crucial for predicting C cycle and its feedback to climate change, which remain one of the biggest uncertainties in earth system models (Friedlingstein et al., 2022). One important source of uncertainty in predicting C cycle is the degree to which N limits plant growth (Elser et al., 2007; Hungate et al., 2003). Furthermore, the N limitations in plant growth, photosynthetic capacity, and decomposition rates in litter and soil are poorly understood partially because they are very difficult to be measured (Vicca et al., 2018). Some methods have been used to infer nutrient limitation, including fertilization experiments, leaf nutrient resorption efficiency and the thresholds of leaf N:P ratios (Bracken et al., 2015; Du et al., 2020; Sullivan et al., 2014; Tessier and Raynal, 2003). But most of these methods are either very time-consuming and laborious, or have greater uncertainty, although researchers have invested a lot of efforts to use these methods to retrieve nitrogen limitation information in terrestrial ecosystems.

Data assimilation is a statistically rigorous method for estimating the parameter values of a mechanistic model representing rates of transfer of C and N within an ecosystem. Not only does this method allow models to be better calibrated to data, but it also provides great opportunities to understand model parameterization that reflects N-limitation. When data assimilation is applied to calibrate models with

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

specific observations, the information in observations is integrated into the model via a set of specific parameters (Luo and Schuur, 2020). All data assimilation studies indicate that the optimal estimated parameters vary across different treatments of global change experiments (Liang et al., 2018; Luo and Schuur, 2020; Wang et al., 2021; Xu et al., 2006). Because there are always some processes at unresolved scales (processes that can't be represented explicitly) that may potentially interact with processes at resolved scales (processes that can be represented explicitly) to influence model results. Varying parameters is a useful modeling approach, which recognizes that the model need not explicitly incorporate all processes on a resolved scale (Luo and Schuur, 2020). Meanwhile, the estimated parameters are the result of retrieving the ecological information from the specific data set. Hence, many studies used data assimilation to understand ecological processes (e.g., coefficients of plant allocation and litter decomposition) by comparing the posterior probability density functions of parameter values among different experimental treatments or sites (Liang et al., 2018; Wang et al., 2021; Xu et al., 2006).

Therefore, data assimilation provides the great possibility to retrieve N limitation information from observations since the N limitation information is represented in parameterization as a model is calibrated with the observations (Luo and Schuur, 2020). However, when a N cycle module is incorporated into the C-only model, N processes are explicitly represented and simulated. N limitation influences on C processes are no longer accounted by C-related parameter values (Wang et al., 2022). A study using data assimilation technique found that parameter values change with model structures, while simulated ecosystem C dynamics were similar (Wang et al., 2022), but they didn't further explore the nutrient limitation information behind models with different structures and how it influenced the C cycle predictions. Previous studies also tried to use models with or without a nutrient module to represent whether there was the corresponding nutrient limitation (i.e., nitrogen and phosphorus) with data assimilation (Du et al., 2021). But they ignored the fact that the nutrient limitation information in the C-only model and C-nutrient coupling model is consistent because the observations they used for data assimilation were identical. Hence, it's necessary to retrieve information on nutrient limitation by data assimilation.

In this study, we used data assimilation to estimate parameters that reflect N limitation in a C-only model and coupled C-N model from 17 data sets collected at a field N enrichment experiment at an alpine meadow in the Qinghai-Tibet Plateau. The Bayesian probabilistic inversion as the data assimilation

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

method was used in this study to estimate the C cycle associated parameters and simulated C pool dynamics of different ecosystem components under the integral measurement collected at Hong Yuan alpine meadow field site from 2014 to 2020. The specific questions we addressed in this study are: (1) how to retrieve N limitation information from experimental data by data assimilation? (2) how does N limitation influence the predictions of ecosystem C dynamic?

2. Materials and methods

2.1 Site description

The Hong Yuan station was located on the eastern Qinghai-Tibet Plateau (32°84'N, 102°58'E), which is high elevation continental plateau with a frigid temperate monsoon climate. The mean annual precipitation is 747 mm, the mean annual temperature is 1.5℃, the sunshine duration per year is about 2000-2400 hours, and the growing season lasts from April to October. The main vegetation type in this study area is alpine meadow, and the soil type here is subalpine meadow and boggy soil (Song et al., 2014). This area is dominated by *Deschampsia caespitosa* (Linn.) *Beauv., Koeleria cristata* (Linn.) Pers., *Gentiana sino-ornata* Balf. f., *Potentilla anserina* L., and *Anemone rivularis* Buch.-Ham (Quan et al., 2018).

2.2 Data source

Data sets used to drive the Grassland ECOsystem (GECO) model and used to estimate parameters in this study both were from a N addition experiment and a co-located eddy-covariance measurement system. Meteorological variables, such as soil volumetric water content (VWC) and soil temperature (Tsoil) simultaneously measured with the eddy covariance system at a depth of 10 cm every hour. Meanwhile, the photosynthetically active radiation, wind speed, relative humidity, and air temperature used for simulating photosynthesis also come from the continuous observation of the eddy covariance system. The N addition experiment near the Eddy covariance tower used a random block design with six N addition treatments (N0, N2, N4, N8, N16, N32, representing N addition rates of 0, 2, 4, 8, 16, 32 g $N \cdot m^{-2} \cdot year^{-1}$, respectively, with five replications each). The area of each plot is 8 × 8 m, and the distance between adjacent quadrats is 3 m. During the growing season, from May to September every year, N was added once a month. The method of N addition was spraying, and ammonium nitrate (NH_4NO_3, analytical purity, content ≥ 99%) was used as N fertilizer. Gross primary productivity (GPP) and soil respiration

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

(SR) were measured twice a month with static chambers (LI-6400XT, LI-COR Environmental, Lincoln, Nebraska, USA) in plots with different treatments in the growing season from 2014 to 2020. Biometric measurements were made once a year to determine leaf and root biomass, standing and surface litter quality, and microbes, soil C content, N content of leaves and roots, standing litter, surface litter, total N content of microbe and soil, and soil inorganic N concentration in all plots.

The data that used to drive the model includes daily soil moisture, soil temperature, photosynthetically active radiation, wind speed, relative humidity, and air temperature from 2014 to 2020. The data assimilated into the GECO model for parameter estimation include C and N contents in leaf, root, standing litter, surface litter, microbial, soil, and autotrophic and heterotrophic respiration at every N addition treatment (Table S1).

2.3 Model

The GECO model was used in this study (Wang et al., 2021), which has evolved from the Terrestrial ECOsystem (TECO) model (Xu et al. 2006, Shi et al. 2016) with a distinct standing litter pool for grassland ecosystems. The GECO model has both coupled C-N and C-only version. There are seven C and N pools and one more mineral nitrogen pool in the coupled C-N model. The pools are leaf (X1, N1), roots (X2, N2), standing litter (X3, N3), surface litter (X4, N4), fast (X5, N5), slow (X6, N6), passive soil organic matter (SOM, X7, N7) and mineral N pool (Fig. 1). But the C-only model just has the counterpart C pools. In the GECO model, CO_2 in the atmosphere enters the ecosystem by canopy photosynthesis which is simulated by a two-leaf model (Wang et al., 1998). The plant photosynthetic capacity is limited by the leaf N concentration in the coupled C-N model, reflecting plant investment in photosynthetic machinery for light harvesting and carboxylation rates (Leuning et al., 1995; Walker et al., 2015). Leaf photosynthetic efficiency (LPE) limited by foliage N content as a scalar:

$$SNvcmax = \max\left(\min\left(\exp\left(-\frac{CN_{leaf}-CN_{leaf,0}}{CN_{leaf,0}}\right), 1\right), 0\right) \quad (1)$$

where CN_{leaf} is the estimated C:N ratio of foliage and $CN_{leaf,0}$ is the defined C:N ratio of foliage without N limitation. Some of the photosynthates were used for plants' respiration, and the remaining assimilated C was allocated to leaf (X1) and root (X2) pools. Detritus from the dead plants then flowed into the litter pool, which contained standing litter (X3) and surface litter (X4). Some of the subsurface litter was respired by microbes, while the rest was converted to fast SOM (X5) and slow SOM (X6). The CO_2

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

released by the decomposition of soil C eventually re-enters the atmosphere. Similarly, plants uptake N from the mineral soil. Subsequently, the uptaken N is distributed to the plant pools and then transferred to the litter and soil pools. The organic N in the seven pools returns to the soil through microbial mineralization. The GECO model uses a matrix-based 1st-order differential equation approach to describe the process of carbon transfer between ecosystem carbon pools as:

$$\frac{d}{dt}\boldsymbol{X}(t) = \boldsymbol{A}\xi(t)\boldsymbol{K}\boldsymbol{N_s}\boldsymbol{X}(t) + \boldsymbol{b}u(t) \quad (2)$$

$$\boldsymbol{X}(0) = \boldsymbol{X}_0$$

where $\boldsymbol{X} = (x_1\ x_2\ x_3\ x_4\ x_5\ x_6\ x_7)^T$, in which $x_{(t)}$ represents the C pools in leaves, roots, standing litter, surface litter, fast, slow and passive SOM at time *t*. The matrix **A** represents C transfer between pools (Xu et al., 2006). ***K*** is a 7×7 diagonal matrix with diagonal entries. The elements on the diagonal indicate the C processing rates of each pool (i = 1, 2, ..., 7). $\boldsymbol{N_s}$ is a 7×7 diagonal matrix with diagonal entries, elements on the diagonal indicate the N limiting effects on the pools decomposition rates, which is represented by $\boldsymbol{N_s(i)} = \exp((CN0-CN(i))/CN0)$ (i = 1, 2, ..., 7). For the C-only model, there is no any diagonal matrix to represent the N limitation effects. *u* represents the C produced by canopy photosynthesis, which is constrained by equation (1). ***b*** is a vector of partitioning coefficients of photosynthetic products to leaves and roots. $\xi(t)$ is an environmental scalar to account for effects of temperature and humidity on decomposition (Luo et al., 2003).

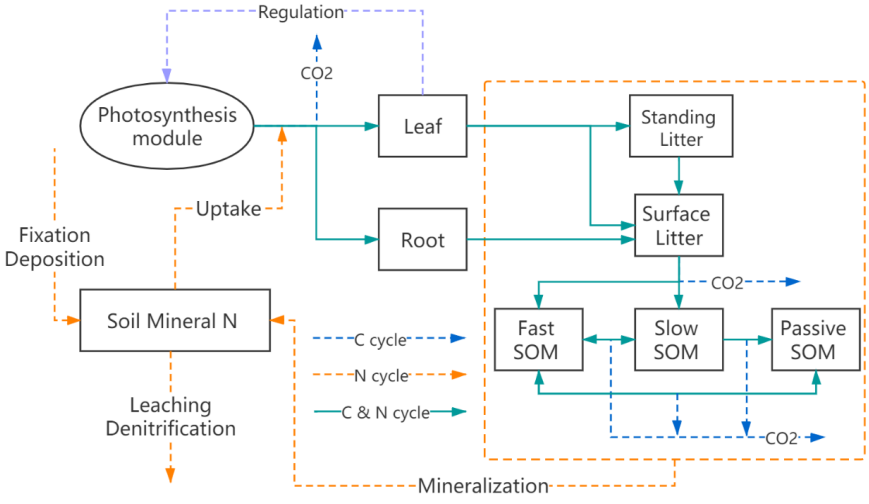

Figure 1 Carbon and nitrogen pools and flux pathways in GECO model. Blue arrows show carbon transfer processes, yellow arrows indicate nitrogen transfer processes, and green arrows represent C and N coupling

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

processes. SOM, soil organic matter.

In the coupled C-N model ,the N processes can be described by this formula:

$$\frac{d}{dt}\boldsymbol{N}(t) = \boldsymbol{A}\xi(t)\boldsymbol{K}\boldsymbol{N_s}\boldsymbol{R^{-1}}\boldsymbol{X}(t) + \kappa_\mu N_{min}(t)\boldsymbol{\pi} \quad (3)$$

$$\mathbf{N}(0) = \boldsymbol{N}_0$$

where $\boldsymbol{N} = (n_1\ n_2\ n_3\ n_4\ n_5\ n_6\ n_7)^T$, in which $n_{(t)}$ represents the N pools in leaves, roots, standing litter, surface litter, fast, slow and passive SOM at time *t*. $\boldsymbol{R}$ is a 7×7 diagonal matrix with diagonal elements indicating the C:N ratio of each pool. $\boldsymbol{\pi} = (\pi_1\ 1\text{-}\pi_1\ 0\ 0\ 0\ 0\ 0)^T$ is an allocation coefficient vector of N from mineral soil to leaves and roots. κ_μ is N uptake rate of plants, $N\min(t)$ is the amount of available N in the soil at time *t*. The dynamic equilibrium of mineral N in soil is determined by the input of mineralization, biological fixation, atmospheric deposition, the output of plant input, leaching, and gaseous N fluxes, which can be described by:

$$\frac{d}{dt}N_{min}(t) = -(\kappa_u + \kappa_L)N_{min}(t) + \boldsymbol{A}\xi(t)\boldsymbol{\varphi_1^*}\boldsymbol{K}\boldsymbol{N_s}\boldsymbol{R^{-1}}\boldsymbol{X}(t) + F(t) \quad (4)$$

$$N_{min}(0) = N_{min,0}$$

In formula (4), κ_μ and κ_L represent rates of N uptake and N loss, respectively. $\boldsymbol{A}\xi(t)\boldsymbol{\varphi_1^*}\boldsymbol{K}\boldsymbol{N_s}\boldsymbol{R^{-1}}\boldsymbol{X}(t)$ represents N mineralization, $\boldsymbol{\varphi_1^*}$ represents mineralization rate, and $F(t)$ represents N input by biological fixation and atmospheric deposition.

In this study, the initial pool sizes of leaves, roots, standing litter, surface litter, fast soil, slow soil, and passive soil pools were constrained using ambient treatment data. The same values used in the ambient treatment were used for initial pool sizes in the N addition treatment, assuming that there was no significant difference between the ambient and supplemental N treatments before treatment began.

Compared with the coupled C-N model, the C-only model doesn't contain any N-cycle process. In this study, the C exit rates of 7 pools, the C allocation coefficients of GPP, and the C transfer coefficients were estimated using both the C-only model and the coupled C-N model. Meanwhile, N-related parameters such as N partitioning coefficient, N uptake, N loss, external N input, initial mineral N pool, and C:N ratios of different ecosystem components were estimated in the coupled C-N model.

2.4 Data assimilation

We used Markov-Chain Monte-Carlo (MCMC) to estimate parameters values of the GECO model. In this method, the targeted parameters are considered as random variables within to a certain prior probability distribution. According to the Bayesian theorem, the prior knowledge about the parameters

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

and the information contained in the data are fused to generate posterior distributions of the parameters (Xu et al., 2006) as

$$P(p|Z) \propto P(Z|p)P(p) \quad (5)$$

In formula 5, *P(p)* and $P(p|Z)$ represent the prior probability density function (PDF) and posterior probability density function (PPDF) of parameters, respectively. $P\ (Z \mid p)$ represents conditional probability density of observation under the prior parameters, which is also called the likelihood function of *p*. We assume that the random error is normally distributed and has a mean of zero, so the likelihood function can be represented as follows:

$$P(Z|p) \propto \exp\left\{-\sum_{i=1}^{17}\sum_{t\in Z_i}\frac{[Z_i(t)-\varphi_i X(t)]^2}{2\sigma_i^2(t)}\right\} \quad (6)$$

In formula 6, $Z_i\ (t)$ and $\varphi_i X(t)$ represent the measured value and simulated values of the observed variable *i* at time *t*, and σ_i is the standard deviation of the observed variable *i*. In this study, *i* from 1 to 17 represents seventeen data sets, which are the C or N contents of leaves, roots, standing litter, surface litter, microbes, mineral soil and heterotrophic respiration, inorganic N in soil, soil mineralization, N uptake by plant and external N input. φ_i is the mapping vector that maps the simulated state variables to the observed data. For example, the observation operator φ is expressed as follows:

Leaf C and N: φ_1 = (1 0 0 0 0 0 0)

Root C and N: φ_2 = (0 1 0 0 0 0 0)

Standing litter C and N: φ_3 = (0 0 1 0 0 0 0)

Surface litter C and N: φ_4 = (0 0 0 0.5 0 0 0)

Microbial C and N: φ_5 = (0 0 0 0 1 0 0)

Mineral soil C and N: φ_6 = (0 0 0 0 1 1 1)

The Metropolis-Hastings (M-H) algorithm was used as the (Hastings, 1970; Metropolis et al., 1953) MCMC sampler. The initial parameter set was randomly selected within the priori parameter ranges. At each iteration, a set of parameters (p_{new}) is proposed based on the accepted parameters from the previous iteration (p_{k-1}). We accept p_{new} only if $R = \frac{P(p^{new}|Z)}{P(p^{k-1}|Z)} \Rightarrow$ a random number between 0 and 1. Otherwise,p_{new} will be rejected, and we let $p_k = p_{k-1}$ to start the sampling of next iteration. The M-H algorithm is repeated until 300,000 sets of parameter values have been accepted, and then all accepted parameter values are used to construct the probability distribution functions (PDFs) (Weng and Luo, 2011; Xu et al., 2006).

3. Results

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

3.1 Model performance on simulating C cycle under different N addition gradients

We selected 100 sets of parameter values from the PPDFs to run the GECO model and simulate the C dynamics from 2014 to 2020 using the C-only model and the coupled C-N model, respectively. The two models simulated the C pools in leaves, standing litter, surface litter, microbes, soil, and GPP well compared to observations under the different N addition treatments (Figure 2 and Figure S1-S2).

Meanwhile, among 19 C-related parameters in both the C-only and coupled C-N models, nine were well constrained by observations according to their posterior PDFs. These nine well-constrained parameters are baseline leaf maximum carboxylation rate, C exit rates of root, leaf, standing litter, surface litter, fast SOM, slow SOM, the allocation coefficients of C to root and leaf under all treatments. While the C exit rate of the passive SOM and the transfer coefficients among pools ($f_{i,j}$) were poorly constrained. In this study, we used the comparison of well estimated parameters between two models to indicate the N limitation in the C cycle processes represented by these parameters, and used the comparison of different C pool sizes between different models to indicate N limitation in the C pools as well.

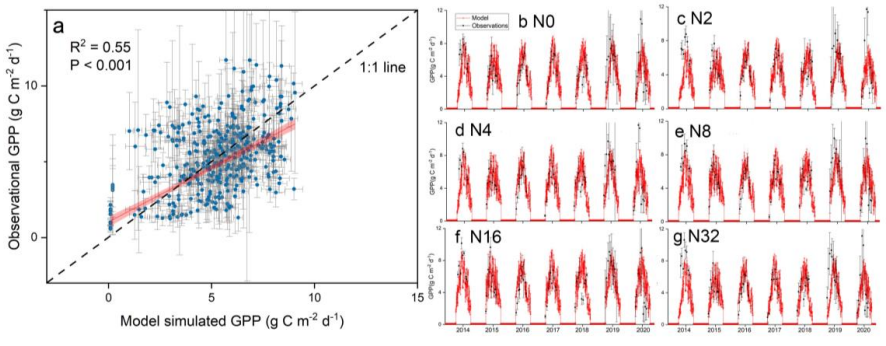

Figure 2 Comparison of observed and model-simulated GPP simulated by the coupled C-N model. A is the overall comparison under different addition rate; b, c, d, e, f, g are the time dynamics of observed (dots) and model-simulated (red lines) GPP simulated by the coupled C-N model under N0, N2, N4, N8, N16, N32 addition rate, respectively.

3.2 Estimated parameters between model structures and N addition treatments

The C-only and coupled C-N models led to different posterior PDFs of these well-constrained parameters under the different treatments (Figures 3 and 4). The leaf photosynthetic efficiency (LPE) was higher in the coupled C-N model than in the C-only model. But changes in estimated parameters between the C-only and coupled C-N models differed with different N addition treatments. The estimated LPE decreased with increasing N addition in the coupled C-N model, but the estimated LPE increased first

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

and then decreased with the increase of N addition in the C-only model. The divergent responses to N addition treatments led to the results that the differences in the LPE between the coupled C-N model and the C-only model got smaller with the increase of N addition rates (Figure 3).

C exit rates of all the pools were higher in the coupled C-N model than in the C-only model at the ambient treatment (Figure 4). And with the increase of N addition rate (from N0 to N8), the differences in the C exit rates of all the pools except the surface litter and fast SOM pools between the coupled C-N model and the C-only model got smaller. But with the continuous increase of nitrogen addition (N16 & N32), the differences of parameters between the C-only model and the coupled C-N model no longer decreased, or even became greater. In general, the N addition effects on these parameters were consistent in the C-only and coupled C-N model. N addition effects on parameterization varied among parameters. C exit rate of the root pool decreased with the N addition rates, whereas the C exit rates of the standing litter, fast SOM and slow SOM pools decreased first and then increased with the N addition rates. For the remaining parameters, N addition didn't significantly change them (Figure 4).

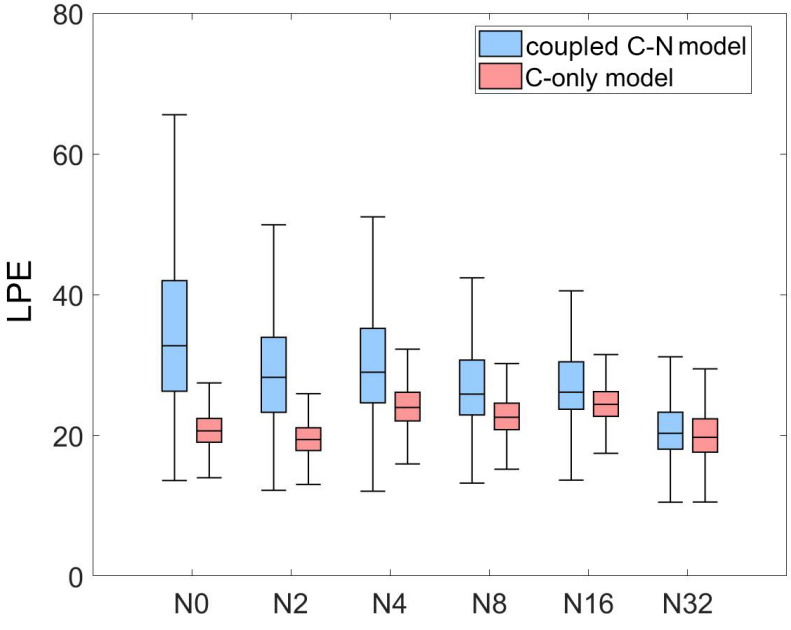

Figure 3 Posterior distributions of estimated leaf photosynthetic efficiency (LPE) of the C-only and coupled C-N models under N0, N2, N4, N8, N16, N32 addition rate, respectively.

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

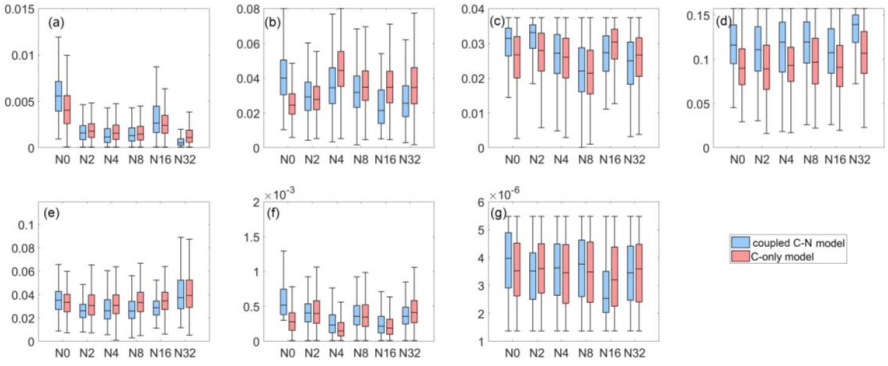

Figure 4 Posterior distributions of estimated key parameters of the C-only and coupled C-N models under different N addition treatments. Baseline senescence rates of fine root (a) and leaf (b); baseline decomposition rates of standing litter (c), surface litter (d), fast SOM (e), slow SOM (f),and passive SOM (g). The red and blue boxes represent the distributions of estimated parameters of the C-only and coupled C-N models, respectively.

3.3 Simulations of C dynamics with the C-only and coupled C-N models

The different ecosystem C pools exhibited divergent responses to N addition treatments in the simulations by both the C-only and coupled C-N models. Simulated passive SOM pools showed no N addition effects (Figure 5g). Except for passive SOM pool, most of the rest carbon pool size increased first and then decreased with the increase of N addition (Figure 5). Simulated leaf and surface litter C pools reached the maximum pool size at N16 treatment (Figures 5a, 5d). Simulated standing litter reached the maximum pool size at N8 treatment (Figure 5c). However, simulated fast and slow SOM C pools reached the maximum pool size at N4 treatment (Figures 5e, 5f). Because the slow SOM C accounts for about 90% of the total soil C and accounts for about 70% of the total ecosystem C, total soil C and ecosystem pools responded similarly with slow SOM under the N addition treatments (Figure 5h, 5i). Meanwhile, simulated GPP also showed a unimodal response with the increase of N addition and the maximum GPP values appeared at N16 treatment in both the C-only and coupled C-N model (Figure 6).

To further elucidate the N effects in the C only model, we tested the response of the coupled C-N model without retuning parameters to compare the N limitation of ecosystem carbon pools and flux due to the addition of N coupling components. The results showed that the simulated ecosystem C storage and GPP decreased if we ran the coupled C-N model with the parameters estimated by the C-only model (Figures 5 and 6). In addition, the decreased simulations by the coupled C-N model with the parameters estimated by the C-only model were greater at the ambient treatment, and the decreases were reduced

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

with the increase of N addition (Figures 5 and 6). However, when the N addition reached at the N8 treatment, the difference between simulations by the coupled C-N model with the parameters estimated by the C-only model and simulations by the coupled C-N model with its count part parameters became very small. Hence, the simulations of the C-only, coupled C-N models and the coupled C-N model with the parameters estimated by the C-only model were consistent at high N addition treatments (Figures 5 and 6).

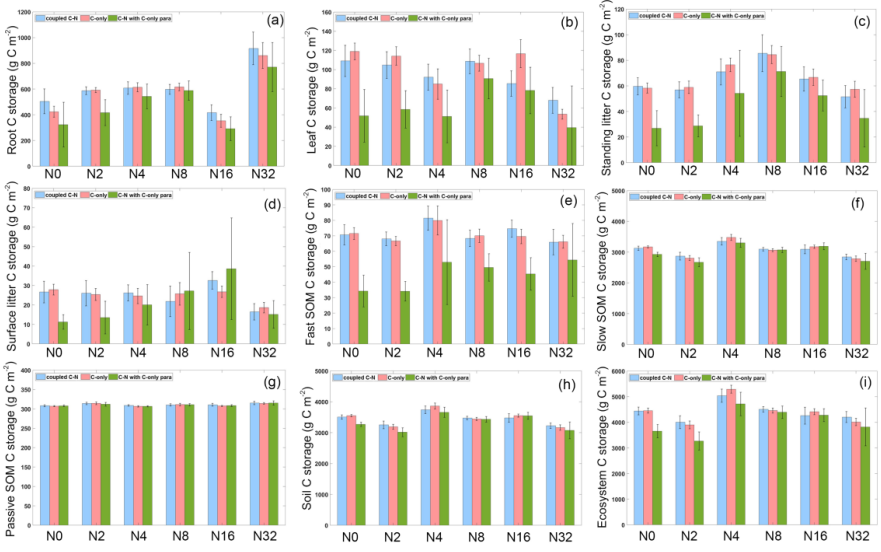

Figure 5 Model simulated ecosystem C storage under different N addition treatments in 2020. They are root (a), leaf (b), standing litter (c), surface litter (d), fast SOM (e), slow SOM (f), passive SOM (g), total soil C storage (g) and total ecosystem (i) simulated by the C-only model with the C only parameters (blue bars), the coupled C-N model with the coupled C-N parameters (red bars) and the coupled C-N model with the C only parameters (green bars) under different N addition rates

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

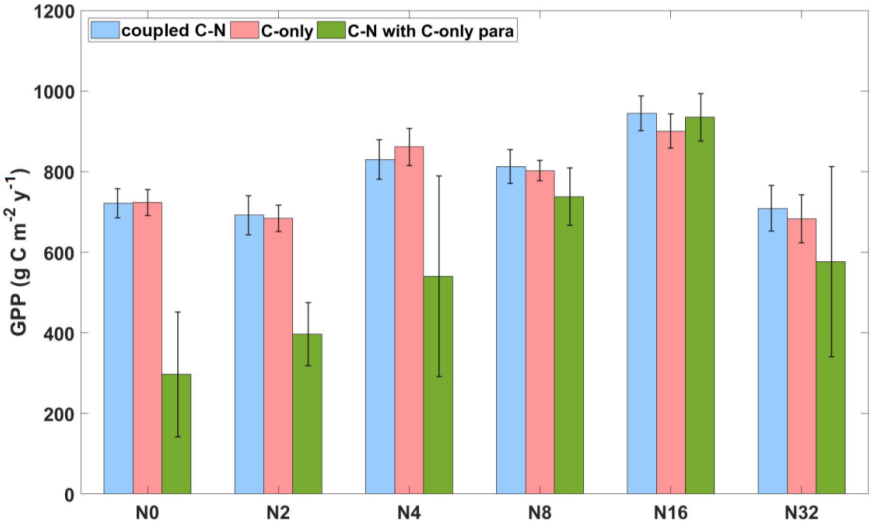

Figure 6 Model simulated GPP under different N addition treatments in 2020. Blue bar is ecosystem C storage simulated by the C-only model with C-only parameters; Red bar is ecosystem C storage dynamic simulated by the coupled C-N model with coupled C-N parameters; Green bar is ecosystem C storage dynamic simulated by the coupled C-N model with C-only parameters.

4. Discussion

4.1 Retrieving N limitation information by data assimilation and its implications

In this study, we used data assimilation to retrieve N limitation information from observations. Our results indicated that N limitation information can be retrieved by the following ways. First, the differences between the parameters estimated by the C-only model and the coupled C-N model with the same observation set. The parameters estimated by models with the data assimilation technique can represent the C cycle processes of an ecosystem, e.g., GPP allocation to leaf and root are represented by two allocation coefficients, and soil decomposition is represented by the soil exit rate. Because in the C-only model, the N-related information contained in the observation is implicitly represented in the estimated parameters. But when a coupled C-N model is calibrated using the same observations, the N-related information is no longer implicitly represented in the C-related parameters (Wang et al., 2022). Second, the differences between the C pool dynamic simulated by the coupled C-N model with parameters from C-only model and the C pool dynamic simulated by the coupled C-N model with its counterpart parameters (Figure 7), because the N limitation information behind parameters estimated by the C-only model can be intuitively expressed by the simulations of ecosystem C pools. And our method in

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

quantifying N limitation degree was confirmed by the N addition gradient in this study.

We highlight two main advantages of our method to retrieve nutrient limitation. On the one hand, by comparing the parameters shift and pools size, we can evaluate the N limitation effect on any specific C cycle processes of an ecosystem. And the N limitation degree can be quantitatively reflected by the differences between estimated parameters or simulated pool size. On the other hand, the data set used for data assimilation is no longer limited to nitrogen addition experiments. All of the observations which contain the basic C and N condition can be used to evaluate the N limitation by a C-only model and the coupled C-N model with data assimilation technique. In addition, there have been studies doing inverse analysis using global data products (Bloom et al., 2016; Yang et al., 2021), it will become possible to estimate the global nutrient limitation distribution by our method with increasing global data products with high reliability.

Due to the important effect of N on ecosystem C dynamics, it is vital to evaluate N limitation degree of an ecosystem. Understanding the N limitation condition at different areas can provide guidance for policy making and ecosystem management. Different managements should be conducted according to their N restriction condition of a specific ecosystem, so as to manage an ecosystem most efficiently. Besides, the N limitation in different C cycle processes and pools were poorly understood because it is hard to measure (Vicca et al., 2018). Our method can retrieve N limitation information of any specific ecosystem C cycle processes or pools, by which we can adjust ecosystem functions and services more accurately by precise management.

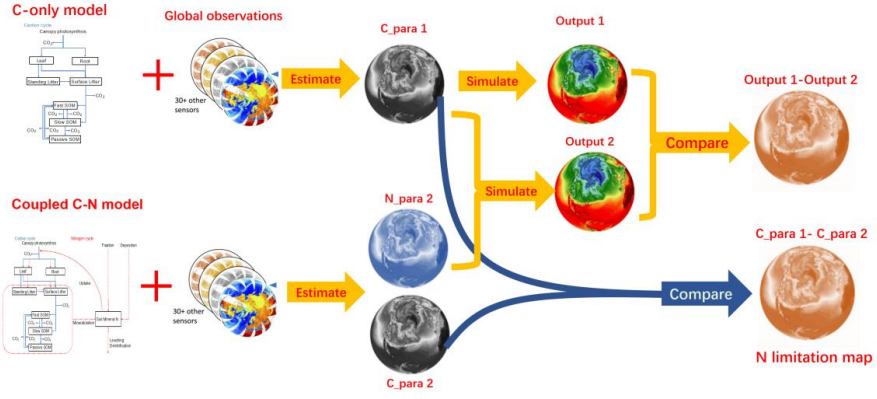

Figure 7. A concept figure about how to map the global N limitation of a specific C pool.

4.2 Retrieve nitrogen limitation information from different C cycle processes

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023


Biogeosciences Discussions

In this study, we used two models: The C-only and coupled C-N models, to retrieve information on N limitation. Our results show that the senescence rate from leaf and root, the decomposition rates of standing litter, surface litter, fast SOM, slow SOM and passive SOM, the allocation coefficients of GPP to leaf, and the LPE were higher in the C-N model than these in the C-only model at the ambient treatment and lower in the N addition treatments (Figures 3, 4 and Figure S3). The N limitation degree was the strongest at the ambient treatment, but the N regulations of C cycle processes are not explicitly simulated and, thus, considered to be unresolved processes in the C-only model (Wang et al., 2022). Hence, the N limitation on photosynthesis was reflected in a smaller value of LPE in the C-only model than that in the coupled C-N model which incorporated a N module into the C model. Because N processes were explicitly simulated in the coupled C-N model, N limitation effects on C processes were no longer accounted by C-related parameter values (Figure 3). Meanwhile, the N limitation degree at the high N addition treatments was much less than that at the ambient treatment (Figure S4). Therefore, differences in the LPE between the coupled C-N model and the C-only model got smaller with the increase of N addition rates (Figure 3), indicating that N limitation degree was reduced or even disappeared with the increase of N addition rates. It needed to be specifically pointed out that we didn't consider any toxic effect at the high N addition treatment because there was usually less N deposition in the real world than in most field experiments (Adams et al., 2021).

Similarly, the senescence rates from leaf and root, the decomposition rates of standing litter, surface litter, fast SOM, slow SOM and passive SOM were regulated by their counterpart C:N ratios (Niu et al., 2010), and this regulation was also reflected in this model (Wang et al., 2022). The N limitation on their senescence rates and decomposition rates were reflected in smaller values in the C-only model than that in the coupled C-N model. Different from LPE, N limitation degree in those variables between the coupled C-N model and the C-only model got similar at the middle N addition rates (N2, N4, N8). Because low-level N additions could alleviate N limitation but high-level N addition would harm plants due to the ionic toxicity (Aber et al., 1998; LeBauer and Treseder, 2008; Niu et al., 2016). That was why the differences in some parameters estimated by the coupled C-N model and the C-only model even got larger at high N addition treatments. However, some other parameters estimated by different models had no significant difference in different N addition treatments. This may be due to the fact that these parameters contain little N limitation information, and therefore these C cycle related processes are not

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

regulated by N processes and can be considered to be resolved processes in both the C-only and coupled C-N models.

4.3 Retrieve nitrogen limitation information from different ecosystem C pools

Although the N limitation information behind many estimated parameters was different, two models simulated similar pool sizes when two sets of parameters were used in accordance with their different structures (Figure 5). This was reasonable as models with different structures were supposed to similarly simulate the dynamics of the same ecosystem under the same conditions (at every N addition treatment). When we incorporated an N module into the C model, N processes are explicitly simulated, estimated C-related parameters no longer contain N processes for the coupled C-N model, and the N limitation information was retrieved from the C-only model as well.

By using the coupled C-N model with parameters estimated by the C-only model to simulate the terrestrial ecosystem C dynamic, the N limitation information behind parameters can be intuitively expressed. Our results showed that GPP, ecosystem C storage in plant and soil pools simulated by the coupled C-N model with the parameters estimated by the C-only model all decreased at the N0 treatment (Figures 5 and 6), but these C pools and GPP change got smaller with the increase of N addition (Figures 5 and 6). These results indicated that the parameters estimated in the C-only model did contain the N limitation information, and the limitation degree reduced with increasing N addition rates. If there was no N limitation in observations, the parameters estimated by either the C-only model or coupled C-N model would not contain any N limitation information. Therefore, the C dynamic simulated by the coupled C-N model with the parameters estimated by the C-only model would be consistent to the result simulated by the C-only model. If there was N limitation in observations, the parameters estimated by the C-only model would contain the N limitation information but the parameters estimated by the coupled C-N model would not. Our results that the C fluxes and pools simulated by the coupled C-N model with the parameters estimated by the C-only model was smaller than that simulated by the C-only model, indicate clear N limitation information. The stronger the N limitation, the greater the decrease of the simulation by the coupled C-N model with the parameters estimated by the C-only model (Figures 5 and 6).

Given that parameter values in their original C-only models were kept or manually tuned for the new models with N processes (Koven et al., 2013; Sokolov et al., 2008; Zaehle and Friend, 2010),

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

predictions by the newly modified ESMs with the N modules mostly predict lower photosynthesis rates, lower C sequestration, and lower ecosystem C storage than their C-only counterpart models. Our results in this study reveal that such predictions of lower C storage with the coupled C-N models than their original models may not reflect reality (Figure 8). In contrast, ESMs may underestimate both future terrestrial C sequestration and the potential C-climate feedback because they overestimate N constraints.

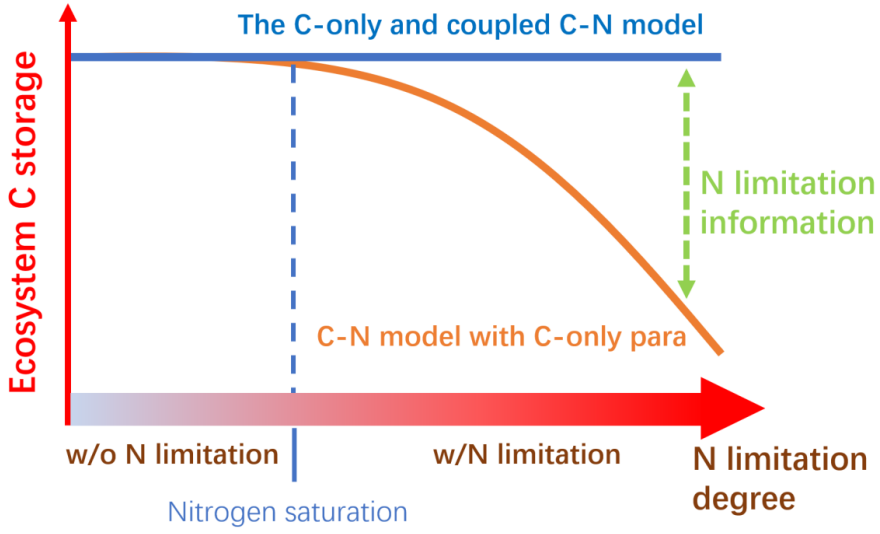

Figure 8 The influence of different N limitation degree on the parameterization of the C-only model and the coupled C-N model. Blue line is the C storage simulated by the C-only model or coupled C-N model with data assimilation, orange line is the C storage simulated by the coupled C-N model with parameters estimated by the C-only model.

5. Conclusion

Based on a 7-year field N addition experiment and data assimilation method, this study carried out an inverse analysis with the C-only model and the coupled C-N model. We found that data assimilation technique could be used to retrieve N limitation information from observations. N limitation information of some C cycle processes can be retrieved by comparing the differences between the parameters estimated by the C-only model and the coupled C-N model with the same observation. N limitation information of the C pools and fluxes can be retrieved by comparing the differences between the C pool dynamic simulated by the coupled C-N model with C-only parameters and the C pool dynamic simulated by the coupled C-N model with its counterpart parameters. In addition, N additions had a unimodal response on most ecosystem component C storage which was mainly determined by their exit rates in

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

this study. In general, we put forward a new method to retrieve N limitation information from observations by data assimilation technique. With the increase of global data products, our method will make it possible to estimate ecosystem nutrient limitation with high reliability and thus provide guidance for policy making or ecosystem management.

Data availability

All additional data produced in this study will be published FigShare (10.6084/m9.figshare.22094111)

Author contribution: SW, JW and SN designed the experiments, evaluated the data and wrote the manuscript. CS, YL were involved in the writing (review and editing) of the paper before submissions. WC collected and arranged data. YZ, AY developed the conceptualization and methodology of this study.

Competing interests: The authors declare that they have no conflict of interests.

Acknowledgments

This study was supported by National Key R & D Program of China (2022YFF0802102) and National Science Foundation of China (31988102)

Reference

Aber, J., W. McDowell, K. Nadelhoffer, A. Magill, G. Berntson, M. Kamakea, et al. 1998. Nitrogen saturation in temperate forest ecosystems - Hypotheses revisited, Bioscience, 48(11), 921-934.

Adams, M. A., T. N. Buckley, D. Binkley, M. Neumann, and T. L. Turnbull. 2021. CO2, nitrogen deposition and a discontinuous climate response drive water use efficiency in global forests, Nat. Commun., 12(1).

Bloom, A. A., J.-F. Exbrayat, I. R. Van Der Velde, L. Feng, and M. J. P. o. t. N. A. o. S. Williams. 2016. The decadal state of the terrestrial carbon cycle: Global retrievals of terrestrial carbon allocation, pools, and residence times, 113(5), 1285-1290.

Bracken, M. E. S., H. Hillebrand, E. T. Borer, E. W. Seabloom, J. Cebrian, E. E. Cleland, et al. 2015. Signatures of nutrient limitation and co-limitation: responses of autotroph internal nutrient concentrations to nitrogen and phosphorus additions, Oikos, 124(2), 113-121.

Du, E., C. Terrer, A. F. A. Pellegrini, A. Ahlstrom, C. J. van Lissa, X. Zhao, et al. 2020. Global patterns of terrestrial nitrogen and phosphorus limitation, Nat Geosci, 13(3), 221-+.

Du, Z., J. Wang, G. Zhou, S. H. Bai, L. Zhou, Y. Fu, et al. 2021. Differential effects of nitrogen vs. phosphorus limitation on terrestrial carbon storage in two subtropical forests: A Bayesian approach, The Science of the total environment, 795, 148485-148485.

Elser, J. J., M. E. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, et al. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

terrestrial ecosystems, Ecol Lett, 10(12), 1135-1142.

Fog, K. J. B. R. 2008. The effect of added nitrogen on the rate of decomposition of organic matter, Biological Reviews, 63(3), 433-462.

Friedlingstein, P., M. O'Sullivan, M. W. Jones, R. M. Andrew, L. Gregor, J. Hauck, et al. 2022. Global carbon budget 2022, 14(11), 4811-4900.

Hastings, W. K. 1970. Monte-Carlo Sampling Methods Using Markov Chains and Their Applications, Biometrika, 57(1), 97-&.

Hungate, B. A., J. S. Dukes, M. R. Shaw, Y. Q. Luo, and C. B. Field. 2003. Nitrogen and climate change, Science, 302(5650), 1512-1513.

Keeler, B. L., S. E. Hobbie, and L. E. Kellogg. 2009. Effects of Long-Term Nitrogen Addition on Microbial Enzyme Activity in Eight Forested and Grassland Sites: Implications for Litter and Soil Organic Matter Decomposition, Ecosystems, 12(1), 1-15.

LeBauer, D. S., and K. K. Treseder. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed, Ecology, 89(2), 371-379.

Leuning, R., F. M. Kelliher, D. G. G. D. Pury, E. D. J. P. C. Schulze, and Environment. 1995. Leaf nitrogen, photosynthesis, conductance and transpiration: scaling from leaves to canopies, Plant Cell Environment, 18(10), 1183-1200.

Liang, J., J. Xia, Z. Shi, L. Jiang, S. Ma, X. Lu, et al. 2018. Biotic responses buffer warming-induced soil organic carbon loss in Arctic tundra, Glob Chang Biol, 24(10), 4946-4959.

Liu, J., X. Li, Q. Ma, X. Zhang, Y. Chen, F. Isbell, et al. 2019. Nitrogen addition reduced ecosystem stability regardless of its impacts on plant diversity, 107(5).

Luo, Y., and E. A. J. G. C. B. Schuur. 2020. Model parameterization to represent processes at unresolved scales and changing properties of evolving systems, 26(3), 1109-1117.

Luo, Y., B. Su, W. S. Currie, J. S. Dukes, A. C. Finzi, U. Hartwig, et al. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide, Bioscience, 54(8), 731-739.

Luo, Y. Q., L. W. White, J. G. Canadell, E. H. DeLucia, D. S. Ellsworth, A. C. Finzi, et al. 2003. Sustainability of terrestrial carbon sequestration: A case study in Duke Forest with inversion approach, Global Biogeochem Cy, 17(1).

Metropolis, N., A. W. Rosenbluth, M. N. Rosenbluth, A. H. Teller, and E. Teller. 1953. Equation of State Calculations by Fast Computing Machines, J Chem Phys, 21(6), 1087-1092.

Niu, S. L., A. T. Classen, J. S. Dukes, P. Kardol, L. L. Liu, Y. Q. Luo, et al. 2016. Global patterns and substrate-based mechanisms of the terrestrial nitrogen cycle, Ecol Lett, 19(6), 697-709.

Niu, S. L., R. A. Sherry, X. H. Zhou, S. Q. Wan, and Y. Q. Luo. 2010. Nitrogen regulation of the climate-carbon feedback: evidence from a long-term global change experiment, Ecology, 91(11), 3261-3273.

Pregitzer, K. S., A. J. Burton, D. R. Zak, and A. F. J. G. C. B. Talhelm. 2010. Simulated chronic nitrogen deposition increases carbon storage in Northern Temperate forests, 14(1), 142-153.

Quan, Q., F. Y. Zhang, D. S. Tian, Q. P. Zhou, L. X. Wang, and S. L. Niu. 2018. Transpiration Dominates Ecosystem Water-Use Efficiency in Response to Warming in an Alpine Meadow, J Geophys Res-Biogeo, 123(2), 453-462.

Song, B., S. L. Niu, L. H. Li, L. X. Zhang, and G. R. Yu. 2014. Soil carbon fractions in grasslands respond differently to various levels of nitrogen enrichments, Plant Soil, 384(1-2), 401-412.

Sullivan, B. W., S. Alvarez-Clare, S. C. Castle, S. Porder, S. C. Reed, L. Schreeg, et al. 2014. Assessing

https://doi.org/10.5194/bg-2023-33
Preprint. Discussion started: 6 March 2023

nutrient limitation in complex forested ecosystems: alternatives to large-scale fertilization experiments, Ecology, 95(3), 668-681.

Sun, Z., L. Liu, Y. Ma, G. Yin, C. Zhao, Y. Zhang, et al. 2014. The effect of nitrogen addition on soil respiration from a nitrogen-limited forest soil, Agr Forest Meteorol, 197, 103-110.

Tessier, J. T., and D. J. Raynal. 2003. Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation, J. Appl. Ecol., 40(3), 523-534.

Vicca, S., B. D. Stocker, S. Reed, W. R. Wieder, M. Bahn, P. A. Fay, et al. 2018. Using research networks to create the comprehensive datasets needed to assess nutrient availability as a key determinant of terrestrial carbon cycling, 13(12), 125006.

Walker, A. P., A. P. Beckerman, L. Gu, J. Kattge, L. A. J. E. Cernusak, and Evolution. 2015. The relationship of leaf photosynthetic traits – Vcmax and Jmax – to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study, Ecology, 4(16), 3218-3235.

Wang, S., Y. Q. Luo, and S. L. Niu. 2022. Reparameterization Required After Model Structure Changes From Carbon Only to Carbon-Nitrogen Coupling, J Adv Model Earth Sy, 14(4), 15.

Wang, S., Q. Quan, C. Meng, W. Chen, Y. Luo, and S. J. J. o. P. E. Niu. 2021. Experimental warming shifts coupling of carbon and nitrogen cycles in an alpine meadow, J Plant Ecol.

Wang, Y. P., R. J. A. Leuning, and F. Meteorology. 1998. A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy. I. Model description and comparison with a multi-layered model, 91(1-2), 89-111.

Weng, E., and Y. Luo. 2011. Relative information contributions of model vs. data to short- and long-term forecasts of forest carbon dynamics, Ecol Appl, 21(5), 1490-1505.

Xu, T., L. White, D. Hui, and Y. Luo. 2006. Probabilistic inversion of a terrestrial ecosystem model: Analysis of uncertainty in parameter estimation and model prediction, Global Biogeochem Cy, 20(2), n/a-n/a.

Yang, H., P. Ciais, Y. L. Wang, Y. Y. Huang, J. P. Wigneron, A. Bastos, et al. 2021. Variations of carbon allocation and turnover time across tropical forests, Global Ecol Biogeogr, 30(6), 1271-1285.

Zong, N., X. Chai, P. L. Shi, and X. C. Yang. 2018. Effects of Warming and Nitrogen Addition on Plant Photosynthate Partitioning in an Alpine Meadow on the Tibetan Plateau, J. Plant Growth Regul., 37(3), 803-812.