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Modeling the effects of organic nitrogen uptake by plants on the carbon cycling of boreal ecosystems

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Abstract

Boreal forest and tundra are the major ecosystems in the northern high latitudes in which a large amount of carbon is stored. These ecosystems are nitrogen-limited due to slow mineralization rate of the soil organic nitrogen. Recently, abundant field studies have found that organic nitrogen is another important nitrogen supply for boreal ecosystems. In this study, we incorporated a mechanism that allowed boreal plants to uptake small molecular amino acids into a process-based biogeochemical model, the Terrestrial Ecosystem Model (TEM), to evaluate the impact of organic nitrogen uptake on ecosystem carbon cycling. The new version of the model was evaluated at both boreal forest and tundra sites. We found that the modeled organic nitrogen uptake accounted for 36–87 % of total nitrogen uptake by plants in tundra ecosystems and 26–50 % for boreal forests, suggesting that tundra ecosystem might have more relied on the organic form of nitrogen than boreal forests. The simulated monthly gross ecosystem production (GPP) and net ecosystem production (NEP) tended to be larger with the new version of the model since the plant uptake of organic nitrogen alleviated the soil nitrogen limitation especially during the growing season. The sensitivity study indicated that the most important factors controlling the plant uptake of organic nitrogen were the maximum root uptake rate (I_{\max}) and the radius of the root (r_0) in our model. The model uncertainty due to uncertain parameters associated with organic nitrogen uptake at tundra ecosystem was larger than at boreal forest ecosystems. This study suggests that considering the organic nitrogen uptake by plants is important to boreal ecosystem carbon modeling.

1 Introduction

Terrestrial ecosystems play an important role in cycling carbon between land and the atmosphere through photosynthesis, plant respiration and soil respiration (Heimann et al., 1998; Melillo et al., 1993). The major terrestrial ecosystem processes associated

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with carbon cycling are significantly constrained by the carbon (C) and nitrogen (N) interactions (Berendse and Aerts, 1987; Lin et al., 2000; Tateno and Chapin, 1997). In N infertile environments, plants have a low access to N and there is a high C/N ratio in the litter. The high C/N ratio litter slows down N mineralization, decreasing available N in the soil and limiting the plants ability to assimilate carbon. The nitrogen limitation effect on carbon cycling has also been confirmed by the elevated CO₂ studies (Norby et al., 2010; Reich et al., 2006a, b). The feedback between carbon and nitrogen cycles could reduce the CO₂ fertilization effect and thus strongly affect the plant carbon productivity. Therefore, the nitrogen cycling is critically important to carbon cycling especially in the regions where the N availability is limited (e.g. McGuire et al., 1992; Sokolov et al., 2008).

The existing terrestrial nitrogen cycling models are based on two assumptions. The first one is that plants are only able to utilize inorganic forms of nitrogen (e.g., Black, 1993). As a result, soil organic nitrogen needs to be mineralized (e.g., to NH₄⁺, NO₃⁻) by microbes before being taken by plants. Microbial activity decomposes the organic compounds and produces ammonia or nitrate as byproducts that plant is able to assimilate (Harmsen and Van Schreven, 1955). The second one is that plants compete poorly against microbes in acquiring inorganic nitrogen; microbes decompose soil organic matter (SOM) for survival and assimilate as much inorganic nitrogen product as they can, meaning the plant can only access leftover inorganic nitrogen after microbes have met their demands. The leftover nitrogen is defined as net mineralization, which is a central component in terrestrial nitrogen cycling (Schimel and Bennett, 2004). Based on this assumption, net mineralization indicates the maximum amount of inorganic nitrogen that is ready to be used by plants or to be leached out from the ecosystem.

These two classical nitrogen cycling assumptions have been challenged for decades. The discrepancy between net mineralization nitrogen and plant uptake nitrogen has been observed over a variety of ecosystem types (e.g., Chapin et al., 1988; Dyck et al., 1987). Some studies found that organic nitrogen is also an important source of plant nitrogen (Bennett and Prescott, 2004; Schimel and Chapin, 1996), in nitrogen-limited

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ecosystems, such as arctic tundra (Chapin et al., 1993), boreal forest (Nasholm et al., 1998), and alpine tundra (Lipson et al., 2001; Lipson and Monson, 1998). Some other researches, however, explain the additional nitrogen uptake as a result of the enhanced competitive capability of plants against microbes to acquire inorganic nitrogen with the help of mycorrhizae (Hodge et al., 2000a, b). Although some studies argue that amino acids are actually taken up by the plant through a mycorrhizal symbiont rather than directly absorbed by plant root (e.g., Jones et al., 2005), it is an accepted fact that both mycorrhizal and non-mycorrhizal plants from various ecosystems are able to use organic forms of nitrogen (Chapin et al., 1993; Lipson and Nasholm, 2001; Nasholm et al., 1998, 2009), bypassing the classical pathway of purely using inorganic nitrogen.

The mycorrhizae have a symbiotic relationship with terrestrial plants that allows for the absorption of organic nitrogen from the soil and helps to transport this nitrogen into plant roots; in return, the mycorrhizae obtain carbon from their photo-symbiont for their own growth and respiration (Hobbie et al., 2006; Smith and Read, 1997). Mycorrhizae survive on the plant, which provides them with a relatively large amount of carbon, instead of relying on carbon from decomposing soil organic matter (SOM). As a result, mycorrhizae are relatively carbon-rich, and they potentially have more extra energy available to produce bio-expensive enzymes, which are used to break down organic nitrogen such as amino acids or even some proteins. Some studies indicated that around half of the plant-utilized nitrogen is provided through this mycorrhizal fungi pathway in the arctic tundra (Hobbie et al., 2006; Kielland, 1994). Non-mycorrhizal plants are also capable of directly accessing the organic form of nitrogen in nitrogen poor environments (e.g., Chapin et al., 1993; Persson et al., 2003). Such organic uptake involves two important factors, one is the concentration of simple organic nitrogen compounds, usually amino acids, in the soil near the root surface, and the other is uptake kinetics. Simple organic compound could be directly used by plants, while complex organic compounds uptake requires bio-expensive enzymes such as those produced by mycorrhizal fungi. It has been estimated that nearly 60% of the nitrogen uptake by plants is from free amino acids in the arctic tundra (Chapin et al., 1993). Therefore, amino

acids taken up by non-mycorrhizal plants become an important issue when modeling nitrogen cycling in arctic ecosystems (Leadley et al., 1997).

Most biogeochemical ecosystem models assume that inorganic nitrogen is the only N source for plant (e.g., McGuire et al., 1992; Parton et al., 1993; Potter et al., 1993; Raich et al., 1991; Running and Coughlan, 1988; Running and Gower, 1991; Zhuang et al., 2010). However, it has been increasingly recognized by the terrestrial ecosystem research community that simple organic nitrogen compounds are potentially an important source for plant nitrogen uptake (Bennett and Prescott, 2004; Chapin et al., 1993; Nasholm et al., 1998; Schimel and Chapin, 1996). Plants compete poorly against microbes in acquiring amino acids. However, in general, plants are still able to acquire enough amino acids because the soil amino acid production is about an order of magnitude higher than plant N demand (Lipson et al., 1998, 1999). A plant organic and inorganic nitrogen uptake kinetics model for arctic ecosystems was constructed to determine uptake controlling factors (Leadley et al., 1997). It modeled the root uptake using Michaelis–Menten uptake kinetics. In this model, the soil amino acid supply rate estimation was however still lacking. Lipson hypothesized that soil amino acid concentrations can be empirically modeled based on the soil proteolysis rate and the rate of amino acid uptake by microbes, in addition to temperature and moisture effects (Lipson et al., 2001). This empirical model quantitatively estimates the amino acid supply rate, which potentially provides an important parameter for the plant root uptake kinetics model (Leadley et al., 1997).

In this study, we coupled an organic nitrogen uptake algorithm into an existing process-based Terrestrial Ecosystem Model (TEM; Melillo et al., 1993; Raich et al., 1991; Zhuang et al., 2003) by incorporating root uptake kinetics (Leadley et al., 1997) and soil amino acids transformation (Lipson et al., 2001). We hypothesize that both organic nitrogen (amino acids) and inorganic nitrogen are important nitrogen supplies and have strong effects on terrestrial carbon cycling. The model was applied to quantify the amount of the organic nitrogen uptake for both tundra and boreal forest ecosystems. We also examined how the modeled carbon dynamics will be affected by

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this new nitrogen uptake algorithm in the model. The estimated carbon fluxes were compared with observations to show if the model predictability is improved by incorporating the nitrogen uptake mechanism into ecosystem carbon modeling.

2 Method

2.1 Overview

In this study, we first coupled the mechanisms of organic nitrogen uptake into TEM (hereafter refer to as ON-TEM). We then used the adjoint version of TEM (Zhu and Zhuang, 2013) to parameterize both original TEM and ON-TEM using AmeriFlux observation data of NEP and GPP. More details about adjoint-TEM parameterization method are presented in Appendix A. Third, we compared TEM and ON-TEM simulations of ecosystem carbon and nitrogen fluxes. Fourth, since organic nitrogen uptake module parameters are directly derived from previous studies, we conducted an uncertainty analysis to examine how uncertain parameters affect simulated organic nitrogen uptake in boreal ecosystems. Finally, sensitivity studies of ON-TEM are conducted to evaluate the importance of several key parameters in controlling organic N uptake dynamics. The importance of these parameters associated with different processes of organic nitrogen uptake is ranked.

2.2 Model development

The Terrestrial Ecosystem Model (TEM; Melillo et al., 1993; Raich et al., 1991; Zhuang et al., 2001, 2002, 2003, 2010) quantifies terrestrial carbon and nitrogen fluxes and their pool sizes across space and time, driven by spatially explicit data including surface characteristics (soil texture, plant functional type, elevation) and climate (precipitation, air temperature, incident radiation). Carbon (C) and nitrogen (N) interactions were refined by incorporating nitrogen availability (NA) scaling factor in calculating GPP and NPP (McGuire et al., 1992). They concluded that the nitrogen limitation is weak in

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tropical and temperate forests, but much stronger in boreal forest and tundra ecosystems. Here we further improve the nitrogen cycling representation in TEM by coupling a mechanism that plants can take up amino acids in boreal ecosystems. The new version of TEM is formulated as follows:

$$\frac{dC_V}{dt} = GPP - R_A - L_C \quad (1)$$

$$\frac{dC_S}{dt} = L_C - R_H \quad (2)$$

$$\frac{dN_V}{dt} = NUPTAKE_{AV} - NUPTAKE_{AC} - L_N \quad (3)$$

$$\frac{dN_S}{dt} = L_N - NETMIN - PROTEOLYSIS + NUPTAKE_{MI} \quad (4)$$

$$\frac{dN_{AV}}{dt} = NETMIN - NUPTAKE_{AV} \quad (5)$$

$$\frac{dN_{AC}}{dt} = PROTEOLYSIS - NUPTAKE_{MI} - NUPTAKE_{AC} \quad (6)$$

ON-TEM consists of six pools including carbon in vegetation (C_V), carbon in soil (C_S), nitrogen in vegetation (N_V), large organic nitrogen compounds in soil (N_S), inorganic nitrogen in soil (N_{AV}) and amino acids in soil (N_{AC}). Twelve fluxes represent the exchange of carbon and nitrogen in the system, which are gross primary production (GPP), autotrophic respiration (R_A), litter carbon production (L_C), litter nitrogen production (L_N), heterotrophic respiration (R_H), net mineralization (NETMIN), inorganic nitrogen uptake by plant (NUPTAKE_{AV}), the nitrogen uptake by plants from amino acids pool (NUPTAKE_{AC}), organic nitrogen compound proteolysis (PROTEOLYSIS) and its uptake by microbes (NUPTAKE_{MI}). Compared with the previous version of TEM (Zhuang et al., 2003, 2010), Eq. (6) was revised to model amino acids pool and fluxes (Fig. 1).

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Following Lipson et al. (2001), the changes in the amino acid pool are modeled as the balance of three components including soil proteolysis, microbial uptake and plant uptake (Fig. 1). Soil proteolysis is estimated with an exponential function of temperature:

$$\text{PROTEOLYSIS} = P \cdot e^{\frac{\ln(PQ10)}{Q10} \cdot T} \quad (7)$$

where P is the seasonal mean proteolysis rate, T is soil temperature, PQ10 is the temperature Q10 parameter on proteolysis. Microbial uptake is modeled as a function of temperature and soil moisture:

$$\text{NUPTAKE_MI} = R \cdot N_{AC} \cdot e^{\frac{\ln(RQ10)}{Q10} \cdot T} \cdot \text{MOIST} \quad (8)$$

where R is the seasonal mean amino acid uptake rate, N_{AC} is amino acid pool size; RQ10 is the temperature Q10 parameter on the microbial amino acid uptake. MOIST represents the moisture effect on uptake rate, which is modeled with a third order polynomial function of soil moisture:

$$\text{MOIST} = \text{AMOIST} \cdot M^3 + \text{BMOIST} \cdot M^2 + \text{CMOIST} \cdot M + \text{DMOIST} \quad (9)$$

where M is soil moisture content. AMOIST, BMOIST, CMOIST, and DMOIST are third-order, second-order, first-order and zero-order coefficients, respectively. The AMOIST, BMOIST, CMOIST, and DMOIST define an empirical relationship between soil water content (M) and its effect on microbial amino acid uptake rate. These parameter values are derived from Lipson et al. (2001).

To model the amount of amino acid taken up by plants (NUPTAKE_AC), we adopted algorithms from existing nitrogen root uptake kinetics models (Barber and Cushman, 1981; Itoh and Barber, 1983; Leadley et al., 1997). These algorithms assume that nitrogen compounds are moved towards the root surface and would be actively taken up as long as they touch the root surface (Fig. 2). The uptake mechanism is described with Michaelis–Menten kinetics. The nitrogen flow is determined by both mass flow and compound concentration gradient induced diffusion. The soil surrounding the rooting

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system is divided into many thin sub-cylinders starting from the root surface to the outer boundary of the rhizosphere. For the i th sub-cylinder, the change in the number of exchangeable amino acid molecules with time ($\frac{\Delta N(i)}{\Delta t}$) is formulated as:

$$\frac{\Delta N(i)}{\Delta t} = 2\pi l \Delta(rF_d) + 2\pi l \Delta(rF_m) + \pi l \Delta(r^2) S(i) \quad (10)$$

$$\Delta(rF_d) = r(i+1) \cdot F_d(i+1) - r(i) \cdot F_d(i) \quad (11)$$

$$\Delta(rF_m) = r(i+1) \cdot F_m(i+1) - r(i) \cdot F_m(i) \quad (12)$$

$$\Delta(r^2) = r(i+1)^2 - r(i)^2 \quad (13)$$

where Δ denotes change of a variable, l is the length of root, and $r(i)$ is the radius of i th sub-cylinder. $F_d(i)$ is the flux due to diffusion, $F_m(i)$ is the flux due to mass flow and $S(i)$ is the amino acid supply rate at the surface of i th sub-cylinder (Fig. 2). $S(i)$ defines how many amino acid molecules are produced within the rhizosphere, while $F_d(i)$ and $F_m(i)$ define how many amino acid molecules are transported towards the root surface. The concentration of soil amino acid N_{AC} is the leftover amino acid, since microbes have already taken enough organic nitrogen through the process of NUPTAKE_MI in Eq. (8).

The change in the exchangeable concentration of amino acids (ΔC) in the i th sub-cylinder is ($\Delta C(i) = \frac{\Delta N(i)}{\pi l \Delta(r^2)}$). The denominator is the sub-cylinder volume. We assume the change of actual amino acid concentration (ΔC_1) is proportional to the change of exchangeable amino acid concentration ($\Delta C_1(i) = \frac{\Delta N(i)}{b \pi l \Delta(r^2)}$). The proportion parameter b is a constant. Then we have:

$$\frac{\Delta C_1(i)}{\Delta t} = \frac{2\Delta(rF_d) + 2\Delta(rF_m) + \Delta(r^2) S(i)}{b \Delta(r^2)} \quad (14)$$

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The diffusion F_d is calculated using the first order Fick's law; the mass flow F_m is estimated by water flow:

$$F_d(i) = -D_e b \frac{C_1(i-1) - C_1(i)}{\Delta r} \quad (15)$$

$$F_m(i) = C_1(i)v(i) \quad (16)$$

where D_e is the effective diffusion coefficient of a nutrient through the soil medium, $v(i)$ is the volume of water moving across the cylinder boundary. We assume that the total water flux at any boundary must be equal to the flux at the root surface, so we have: $v(i) = v_0$. At the surface of root, the amino acid uptake rate I_n is modeled with Michaelis–Menten kinetics:

$$I_n = I_{\max} \frac{(C_1(1) - C_{\min})}{K_m} + (C_1(1) - C_{\min}) \quad (17)$$

where $C_1(1)$ is the soil solution amino acid concentration at the root surface, and C_{\min} is the $C_1(1)$ at which root uptake is zero. Initializing the amino acid concentration with C_0 , and assuming that all the soil sub-cylinders are homogeneous, resulting in $C_1(i) = C_0$ ($i \in [1, n]$). With the boundary condition $F_d(n+1) = 0$ and $F_m(n+1) = 0$, the differential Eq. (6) can be numerically solved. To conserve organic nitrogen in the system, we assume (1) there is no leaching of amino acids; (2) the modeled amino acid uptake is the “potential” nitrogen uptake. Plant takes inorganic nitrogen first, and if inorganic nitrogen is not enough for plant survival and growth, it would use amino acids to meet its demand. The rest of the amino acids (“potential” amino acid uptake minus actual amino acid uptake) will be distributed back into soils.

2.3 Data

The climate forcing data are monthly averaged reanalysis climate data from NCEP, including air temperature, cloudiness and precipitation (Kalnay et al., 1996) from 1948

to 2010. The global averaged atmosphere CO₂ concentration data are observations at Mauna Loa, Hawaii (Conway et al., 1994; Masarie and Tans, 1995). We use the monthly gap-filled (level-4) AmeriFlux NEP and GPP to parameterize and validate the TEM with an adjoint version of TEM (Zhu and Zhuang, 2013). The information of four sites covering wet tundra and boreal forest ecosystems are documented in Table 1.

2.4 Parameterization

We first parameterized TEM using its adjoint version (Zhu and Zhuang, 2013) for an arctic tundra site and a boreal forest site. Model parameters (Table 2) were calibrated in such a way that: (1) the simulated carbon fluxes get close to observations; (2) the optimal parameters are within their prior range so that they are ecologically meaningful. US-Brw (−156.6°, 71.32°) site has low growing temperature, short growing season, frozen soil and shallow water table depth. We classified this site as “wet/moist tundra” in the TEM vegetation classification scheme. The GPP and NEP data of 1999 were used to parameterize the model and the 2001 data were used for model evaluation. Site UCI_1998 (−99.95°, 56.63°) with a boreal climate that is extremely cold in winter and mild to warm in summer was classified as evergreen conifer forest (IGBP classification; Loveland and Belward, 1997). This site was classified as “boreal forest” ecosystem in TEM. GPP and NEP data from 2002 to 2005 were assimilated into TEM. The optimized parameters were then applied to two other boreal forest sites including UCI_1989 (−98.96°, 55.92°) and UCI_1850 (−94.48°, 55.88°) to verify model parameterization.

Next, we parameterized ON-TEM for arctic tundra and boreal forest using the same approach and the same observational data. ON-TEM introduced a new nitrogen pool, three new fluxes (Fig. 1) and several new parameters (Table 3). Initial value of the amino acid pool size (N_{AC}) was derived from the measured seasonal mean amino acid pool size at an alpine site (Lipson et al., 2001). The soil amino acid transformation-related parameters (e.g., Soil proteolysis Q10 (PQ10)) were estimated based on a study on a typical amino acid Glutamate (glu). The glu is used as representative amino acid

type in estimating the parameters, because the microbial uptake of glu is similar to many other amino acids types (Lipson et al., 1999). Thus, the obtained parameters could be used for modeling general amino acid uptake by plants without specifying the types of amino acids. One difference is that Lipson et al. (1999) study focused on alpine tundra soils, while our focus was on arctic tundra and boreal forest. The differences in both climate and soil conditions between alpine tundra and boreal forests might introduce uncertainty in estimating amino acid availability in soils. Therefore we conducted an uncertainty analysis on these parameters. The root uptake kinetics-related parameters were derived from a modeling study at an arctic sedge site (Table 3; Leadley et al., 1997). Only parameters listed in Table 2 are optimized for ON-TEM. Parameters listed in Table 3 are directly derived from previous studies, which are fixed in ON-TEM. As a supplement, we conducted an analysis to investigate how much uncertainties in model outputs are induced by the uncertainty in these parameters from Table 3.

2.5 Sensitivity study

A sensitivity analysis focusing on organic nitrogen uptake dynamics will help identify which process of organic nitrogen uptake is more important in regulating carbon cycling. We grouped the factors and processes in controlling organic nitrogen uptake into four categories (Table 4): (1) amino acid supply factors including the amino acid pool changes due to proteolysis and microbial uptake; (2) soil factors including the Fick's law diffusion coefficient for amino acids through soils and the soil buffer capacity; (3) the root factors, such as the radius of root, the radius of the soil cylinder surrounding the root as well as the water flux at root surface; and (4) the plant uptake kinetics factors including the maximum and half-saturation root uptake rate of Michaelis–Menten kinetics. The sensitivity study was conducted by using the adjoint ON-TEM to calculate the sensitivities of fluxes (e.g., nitrogen uptake) with respect to model parameters (e.g., I_{\max}). The units of parameters are different and also the values of parameters vary over several orders of magnitude. Therefore, the sensitivity was normalized to unit-less

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values using Eq. (18).

$$S_i = \frac{\frac{\partial \text{ON}_{\text{up}}}{\partial p_i} \cdot \left| \frac{p_i}{\text{ON}_{\text{up}}} \right|}{\sum_{j=1}^n \left(\left| \frac{\partial \text{ON}_{\text{up}}}{\partial p_j} \cdot \frac{p_j}{\text{ON}_{\text{up}}} \right| \right)} \quad (18)$$

p_i refers to different parameters of interest in Table 4. ON_{up} denotes the amount of organic nitrogen used by plant. In the numerator of Eq. (18), we multiplied the sensitivity of simulated organic nitrogen uptake to a specific parameter $\left(\frac{\partial \text{ON}_{\text{up}}}{\partial p_i} \right)$ with a scaling factor $\left(\left| \frac{p_i}{\text{ON}_{\text{up}}} \right| \right)$ to make the sensitivity be unit-less and comparable among different parameters. The numerator, in other words, could be interpreted as the percentage change of organic nitrogen uptake $\left(\frac{\partial \text{ON}_{\text{up}}}{|\text{ON}_{\text{up}}|} \right)$ due to the percentage change of parameter $\left(\frac{\partial p_i}{|p_i|} \right)$. We then normalized the sensitivity by dividing a summation of all the numerators calculated for different parameter p_i . The normalized sensitivity S_i is a criterion to rank the importance of these parameters (Brun et al., 2001).

2.6 Uncertainty analysis

The organic nitrogen uptake parameters' values (Table 3) are from other studies (Leadley et al., 1997; Lipson et al., 2001). This might introduce a great deal of uncertainties to the coupled model simulations. To quantify the influence of uncertainties from the organic nitrogen uptake associated parameters in ON-TEM, we conducted an uncertainty analysis with ensemble simulations. Each ensemble used a set of parameters that were independently sampled from the parameter space. Specifically, we assumed the organic nitrogen uptake parameters (p) were distributed within $[0.9p, 1.1p]$, in which a $\pm 10\%$ of parameter uncertainty was enforced. The parameters were sampled uniformly from the range $[0.9p, 1.1p]$. For each parameter we had 100 samples. And only one parameter was perturbed each time. Thus we obtained a large number

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of parameter sets. Each parameter set represented a model with a unique uncertainty in parameter space, and was used to simulate carbon and nitrogen fluxes of GPP, NEP, organic nitrogen uptake and total nitrogen uptake for the analysis.

3 Results and discussion

3.1 TEM and ON-TEM simulations at site-level

Optimized parameters were greatly different after we incorporated the organic nitrogen uptake kinetics into TEM. For example, at the tundra site US-Brw, the parameter C_{MAX} (the maximum rate of photosynthesis) was $341.4 \text{ gCm}^{-2} \text{ month}^{-1}$ for ON-TEM and $399.3 \text{ gCm}^{-2} \text{ month}^{-1}$ for TEM. K_I (Half saturation constant for PAR used by plants) and K_C (Half saturation constant for $\text{CO}_2\text{-C}$ uptake by plants) were $72.4 \text{ Jcm}^{-2} \text{ day}^{-1}$ and $144.4 \mu\text{LL}^{-1}$ for ON-TEM and $33.2 \text{ Jcm}^{-2} \text{ day}^{-1}$ and $53.0 \mu\text{LL}^{-1}$ for TEM, respectively. Original TEM required a higher carbon photosynthesis rate and lower half saturation constants so that it is able to produce higher carbon fluxes (e.g., GPP, NEP) under the same nitrogen-limited environmental conditions.

The optimal parameters were estimated for both TEM and ON-TEM (Table 3). We ran both TEM and ON-TEM (1) at the US-Brw site in 2001 using parameters calibrated with US-Brw data in 1999; (2) at the UCI_1989 and UCI_1850 sites using parameters calibrated at the UCI_1998 site to evaluate the goodness of models and parameters. Model results were compared with observational GPP and NEP (Fig. 3a–d). TEM assumes that plants can only utilize inorganic nitrogen in the soil, and the inorganic nitrogen is usually limited in boreal ecosystems. As a result, TEM underestimated GPP and NEP especially during the growing season (June, July, August and September). Although TEM had a higher C_{MAX} and lower half saturation points for $\text{CO}_2\text{-C}$ uptake and photosynthetic active radiation compared with ON-TEM, it is still unable to produce the observed carbon fluxes during the growing season. It indicated that TEM tended to underestimate GPP and NEP because of the nitrogen limitation rather than

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the underestimated C_{MAX} or overestimated K_I/K_C . In contrast, ON-TEM was able to produce relatively higher carbon fluxes and captured the seasonal variation and magnitude of both GPP and NEP. However, ON-TEM still underestimated NEP, although the underestimations were not as much as those from TEM. In general, ON-TEM reproduced AmeriFlux observations better than TEM (both linear regression R^2 and slope are closer to one) (Table 5). We also found that both TEM and ON-TEM simulate GPP better at boreal forest sites (R^2 : 0.93, 0.81, 0.79 for ON-TEM and 0.87, 0.76, 0.77 for TEM) than at the tundra site (R^2 : 0.60 for ON-TEM and 0.54 for TEM). Both ON-TEM and TEM were able to better simulate GPP than NEP. That is because GPP is much easier to constrain than NEP. GPP has only one process being involved. When modeling NEP, both plant respiration and soil respiration in addition to plant photosynthesis are involved.

The promise of ON-TEM is that plants will take up organic forms of nitrogen when inorganic nitrogen is limited. Organic nitrogen plays a less significant role in boreal forests than it does in tundra (Chapin et al., 1993; Nasholm et al., 1998), since the inorganic nitrogen in tundra soils is much more limited. Our model simulations indicated that, at tundra sites, organic forms of nitrogen accounted for 36–87% of the total nitrogen uptake; for boreal forests, organic nitrogen only accounted for 26–50% of the total uptake (Table 6). Overall, the total amount of organic nitrogen used by boreal forest was $0.45 \text{ g N m}^{-2} \text{ month}^{-1}$ averaged for four months at all three sites, which was greater than that by tundra averaged for four months at US-Brw ($0.15 \text{ g N m}^{-2} \text{ month}^{-1}$).

3.2 Sensitivity study

To understand the effects of controlling factors on plant uptake of organic nitrogen in ON-TEM, we conducted a sensitivity analysis. The organic nitrogen uptake module parameters were grouped into four categories. We found that the magnitudes of the normalized sensitivities were slightly different (Fig. 4), and the order of parameters' sensitivity was similar at the two distinct sites ($I_{max} \approx r_0 > P \approx R \approx K_m > \text{others}$). The most sensitive parameters were the root uptake kinetics factor of I_{max} and the root

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factor of r_0 . The normalized sensitivities for I_{\max} and r_0 were around 40%. The second most sensitive parameters were the root uptake kinetics factor of K_m and the nitrogen supply factors including the first-order soil organic nitrogen proteolysis (P) rate and the first-order amino acid uptake rate (R). The normalized sensitivities were 5–10%.

5 ON-TEM was less sensitive to soil factors, such as Fick's law diffusion coefficient for amino acids (D_e) and water flux at the root surface (v_0); their sensitivities were trivial compared with e.g. I_{\max} .

I_{\max} , P and r_0 were positively correlated to plant uptake of organic nitrogen. A higher maximum uptake rate (I_{\max}) generates a more organic nitrogen uptake. The higher the proteolysis rate, the more available soil organic nitrogen is ready to be transported towards the root surface, if the microbial uptake rate of amino acid does not change. The r_0 is the radius of the root, if we fix the amount of roots in a the soil, the larger the root radius is, the more total amount of organic nitrogen will reach the root surface and be ready to be taken up. The efficiency of organic nitrogen uptake can also be enhanced by lowering the half-saturation constant for root uptake kinetics. Therefore, sensitivity by 15 by K_m was negative. The soil organic nitrogen supply rate could also be improved by decreasing the rate of organic nitrogen uptake by microorganisms. As a result, R was also negatively correlated with plant uptake of organic nitrogen. The model was insensitive to soil organic nitrogen initial concentration (N_{AC}), that is because the actual pool size of organic nitrogen depends on the instantaneous soil proteolysis rate and microbe uptake rate rather than the initial estimation. The instantaneous proteolysis and microbial amino acid uptake rates are so high that the existent organic nitrogen pool are quickly replaced by newly produced organic nitrogen and the initial pool of organic nitrogen is quickly turned over (e.g., Kielland et al., 2007).

3.3 Uncertainty analysis

The organic nitrogen uptake module is the essential component of ON-TEM. It provides the potential amount of organic nitrogen taken up by plants. We conducted an uncertainty analysis using ON-TEM at US-Brw and UCI_1998 site, aiming to quantify the

uncertainties in modeling carbon and nitrogen fluxes associated with uncertain organic nitrogen uptake module parameters. We allowed the selected ten model parameters (Table 4) to randomly vary with a magnitude of $\pm 10\%$, and compared the changes in carbon and nitrogen fluxes.

5 We found that, at both boreal ecosystem sites, the changes of the two nitrogen fluxes induced by the changes of parameters were large (Fig. 5). It meant that the uncertainty in organic nitrogen uptake module had a strong effect on the system nitrogen dynamics. However, for carbon fluxes, only at the tundra site the parameters uncertainty affected GPP and NEP, not at the boreal forest site. Our analysis indicated that, in boreal forests,
10 the amount of organic nitrogen provided by the soil exceeded the actual need of organic nitrogen by the plant. The changes in the selected model parameters alter the organic nitrogen supply, but had trivial influence on the actual uptake.

4 Summary and concluding remarks

15 In this study, we incorporated an organic nitrogen uptake mechanism into the process-based terrestrial ecosystem model (TEM) to develop a new version of TEM (ON-TEM). We used the AmeriFlux GPP and NEP data to parameterize and verify both versions of the model. We found that ON-TEM simulations were more consistent with the observations in comparison with the original TEM. ON-TEM could better quantify carbon cycling of boreal ecosystems considering organic nitrogen uptake. In ON-TEM simulations, organic nitrogen contributed 36–87 % and 26–50 % of total nitrogen uptake at the tundra and boreal forest sites, respectively, suggesting that tundra ecosystem might
20 more relied on the organic form of nitrogen than boreal forest. These results were consistent with the findings of Nasholm et al. (1998), which stated that at least 42 % nitrogen uptake was from organic form of nitrogen for trees in boreal forests. Further, we explored the sensitivity of modeled organic nitrogen uptake to parameters. We found that, for tundra and boreal forests, the root uptake kinetics factor of I_{\max} and root radius r_0 were the most sensitive factors. Root uptake kinetics parameter K_m , the first-order
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soil organic nitrogen proteolysis rate (P), and the first-order microbial amino acid uptake rate (R) were the second most sensitive parameters. However, the organic uptake dynamics was insensitive to soil organic nitrogen initial concentration (N_{AC}). Finally, we conducted an uncertainty analysis on the organic nitrogen uptake module. We found that the uncertainty in organic nitrogen uptake module parameters had larger impacts on tundra carbon dynamics than it on boreal forest carbon dynamics. We conclude that modeling the effects of organic nitrogen uptake on ecosystem carbon cycling is an important step towards incorporating more detailed organic nitrogen dynamics into ecosystem models.

This study has several limitations. First, ON-TEM has not been incorporated with the mycorrhizae effects in the context of organic nitrogen uptake while a number of studies (e.g., Kielland et al., 1994) indicate that the mycorrhizae play a significant role in the process of plant taking up soil organic nitrogen. Second, we adopted the parameters from other studies (Leadley et al., 1997; Lipson et al., 2001), this might introduce additional uncertainty. Our analysis indicated that such uncertainty was small at boreal forest sites, but was large at the tundra site. Third, we had not specified the type of amino acid species that are used by plants in ON-TEM. For different ecosystem soils, the plant might take up different types of organic nitrogen. So modeling the effects of different organic nitrogen compounds is needed for future studies. In addition, the algorithms of soil proteolysis and organic nitrogen uptake by microbes have not explicitly included the substrate limitation effects. For instance, it has been found that the soil proteolysis rate was positively correlated with soil extractable protein content and the total soil nitrogen (Raab et al., 1999).

Appendix A

Adjoint-TEM parameterization method

The parameterization of the Terrestrial Ecosystem Model was conducted with an adjoint method (Zhu and Zhuang, 2013). The adjoint data assimilation method adjusts model parameters through minimizing the misfits between the model and data over the time-space domains. A cost function (J in Eq. A1) measuring the model-data misfit is defined as a summation of two parts including the difference between model parameters and their prior knowledge (Eq. A2) the difference between model simulations and observations (Eq. A3):

$$J = J_{\text{prior}} + J_{\text{obs}} \quad (\text{A1})$$

$$J_{\text{prior}} = \sum_{i=1}^m \frac{1}{8} \left[\frac{1}{(\sigma_i^l)^2} \left(|p_i - p_i^l| - (p_i - p_i^l) \right)^2 + \frac{1}{(\sigma_i^u)^2} \left(|p_i - p_i^u| + (p_i - p_i^u) \right)^2 \right] \quad (\text{A2})$$

$$J_{\text{obs}} = \frac{1}{2} (f(p_i) - y)^T R^{-1} (f(p_i) - y) \quad (\text{A3})$$

J_{prior} constrains the updated parameters within their prior empirical ranges (Table 2) so that they are physically reasonable (Schartau et al., 1999). p_i^l and p_i^u are upper and lower limits of parameter p_i . A parameter that is smaller than its lower limit or larger than its upper limit follows a normal distribution with standard deviation of σ_i^l or σ_i^u respectively. J_{obs} penalizes the updated parameters if model outputs ($f(p_i)$) is deviated from observations (y). R is the error covariance of observations.

The Adjoint-TEM is an adjoint version of TEM model (Errico, 1997; Giering and Kaminski, 1998) that estimates the gradient of target variables (e.g. GPP) with respect to control variables (e.g. model parameters of interest) at each numerical step. By backward integration of these intermediate gradients $\left(\frac{\partial g_i}{\partial g_{i-1}} \right)$, the gradient of cost

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function with respect to model parameters ($\nabla_p J$) could be calculated with Eq. (A4):

$$\nabla_p J = \left(\frac{\partial g_1}{\partial p} \right)^T \cdot \dots \cdot \left(\frac{\partial g_i}{\partial g_{i-1}} \right)^T \cdot \dots \cdot \left(\frac{\partial g_n}{\partial g_{n-1}} \right)^T \cdot \left(\frac{\partial J}{\partial g_n} \right)^T \quad (\text{A4})$$

where $\left(\frac{\partial g_i}{\partial g_{i-1}} \right)^T$ is the transpose of Jacobian matrix. In the Jacobian matrix $\left(\frac{\partial g_i}{\partial g_{i-1}} \right)$, g_i is a vector of output variables at i th numerical step and g_{i-1} is a vector of input variables at $i - 1$ th numerical step.

The gradient of cost function with respect to model parameters ($\nabla_p J$) indicates the decreasing direction of the cost function. Therefore, the model parameters could be updated as:

$$p_{\text{new}} = p_{\text{old}} - a \cdot \nabla_p J \quad (\text{A5})$$

where a is the step size. The new model parameters (p_{new}) then could be used to update cost function (Eqs. A1–A3) and the gradient of cost function with respect to model parameters (Eq. A4). Iteratively, model parameters are optimized when the $\nabla_p J$ is smaller enough, or model outputs $f(p)$ is close enough to observational data y .

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Table 1. Information of AmeriFlux sites used in the study.

ID	Vegetation type	Available data	PI	Reference
US-Brw	Wet Tundra	1999, 2001	Oechel W. C.	Owen et al. (2007); Eugster et al. (2000)
UCI_1998	Boreal forest	2002–2005	Goulden M. L.	Goulden et al. (2011); Bond-Lamberty et al. (2004)
UCI_1989	Boreal forest	2001–2005	Goulden M. L.	Goulden et al. (2011); Wang et al. (2003)
UCI_1850	Boreal forest	2002–2005	Goulden M. L.	Goulden et al. (2011); Saito et al. (2009)

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Table 2. Optimized parameters in TEM and ON-TEM.

ID	Acronym	Definition	Units	Prior range	TEM Tundra	ON-TEM Tundra	TEM Boreal forest	ON-TEM Boreal forest
1	C_{\max}	Maximum rate of photosynthesis C	$\text{g C m}^{-2} \text{ month}^{-1}$	[50, 1500]	399.3	341.4	853.8	568.7
2	K_j	Half saturation constant for PAR used by plants	$\text{J cm}^{-2} \text{ day}^{-1}$	[20, 600]	33.2	72.4	215.5	289.5
3	K_C	Half saturation constant for CO_2 -C uptake by plants	$\mu\text{L L}^{-1}$	[20, 600]	53.0	144.4	286.0	531.6
4	ALEAF	Coefficient A to model the relative photosynthetic capacity of vegetation	None	[0.1, 1.0]	0.8066	0.8179	0.4452	0.4987
5	BLEAF	Coefficient B to model the relative photosynthetic capacity of vegetation	None	[0.1, 1.0]	0.5148	0.4663	0.4216	0.4061
6	CLEAF	Coefficient C to model the relative photosynthetic capacity of vegetation	None	[0.0, 0.5]	0.0300	0.0287	0.3369	0.3228
7	RAQ10A0	Leading coefficient of the Q10 model for plant respiration	None	[1.350, 3.3633]	3.2661	2.3566	1.4041	1.8011
8	KDC	Heterotrophic respiration rate at 0 °C	$\text{g g}^{-1} \text{ month}^{-1}$	[0.0005, 0.007]	0.000686	0.001377	0.001928	0.001694
9	RHQ10	Change in heterotrophic respiration rate due to 10 °C temperature change	None	[1, 3]	2.04	2.01	1.96	2.03
10	K_R	Logarithm of plant respiration rate at 0 °C	None	[-7.5, -1.5]	-1.5228	-5.7254	-1.9854	-2.0106

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Table 3. New parameters introduced in ON-TEM.

Variables parameters	Variables and parameters description	Units	value	reference
Soil amino acids transformation related				
N_{AC}	Soil amino acid initial concentration	nmol g^{-1}	265	Lipson et al. (2001)
P	Proteolysis rate in soil	$\text{nmol g}^{-1} \text{h}^{-1}$	32.8	Lipson et al. (2001)
R	First order microbial amino acid uptake rate	h^{-1}	0.111	Lipson et al. (2001)
RQ10	Soil microbial amino acid uptake Q10	–	2.57	Lipson et al. (2001)
PQ10	Soil proteolysis Q10	–	1.98	Lipson et al. (2001)
AMOIST	Coefficient of moist effect on microbial amino acid uptake rate	–	4.82	Lipson et al. (2001)
BMOIST	Coefficient of moist effect on microbial amino acid uptake rate	–	–9.78	Lipson et al. (2001)
CMOIST	Coefficient of moist effect on microbial amino acid uptake rate	–	6.93	Lipson et al. (2001)
DMOIST	Coefficient of moist effect on microbial amino acid uptake rate	–	–0.69	Lipson et al. (2001)
Root uptake kinetics related				
r_0	Radius of root	cm	0.04	Leadley et al. (1997)
r_1	Radius of rhizosphere soil cylinder	cm	0.35	Leadley et al. (1997)
C_{\min}	Soil solution concentration at which root uptake is zero	mmol cm^{-3}	0.0	Leadley et al. (1997)
D_e	First order Fick's law diffusion coefficient	$\text{cm}^2 \text{s}^{-1}$	1.0e^{-6}	Leadley et al. (1997)
b	Soil buffer capacity	–	3.	Leadley et al. (1997)
I_{\max}	Maximum root uptake rate	$\text{mmol cm}^{-2} \text{s}^{-1}$	1.0e^{-9}	Leadley et al. (1997)
K_m	Half-saturation constant for root uptake kinetics	mmol cm^{-3}	2.0e^{-5}	Leadley et al. (1997)
v_0	Water flux at the root surface	cm s^{-1}	5.0e^{-8}	Leadley et al. (1997)

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Table 4. Organic N uptake controlling parameters grouped into four different categories.

Testing Factors:			
Supply factors:	P (Proteolysis rate in soil)	R (First order microbial amino acid uptake rate)	N_{AC} (Soil amino acid initial concentration)
Soil factors:	D_e (First order Fick's law diffusion coefficient)	B (Soil buffer capacity)	v_0 (Water flux at the root surface)
Root factors:	r_0 (the radius of root)	r_1 (the radius of rhizosphere soil cylinder)	
Plant uptake kinetics:	I_{max} (Maximum root uptake rate)	K_m (Half-saturation constant for root uptake kinetics)	

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Table 5. Statistics interpretation for model-data fitting (in Fig. 3) including the linear regression slope, the Pearson Correlation Coefficient (R^2) and the significance of the Pearson Correlation Coefficient (p value).

Site	GPP R^2 (p value)	GPP slope	NEP R^2 (p value)	NEP slope
ON-TEM vs. AmeriFlux				
US-Brw	0.60(0.019)	0.95	0.64(0.012)	0.74
UCI_1998	0.93($< 10^{-5}$)	1.17	0.29(0.022)	0.67
UCI_1989	0.81($< 10^{-5}$)	0.98	0.56($< 10^{-5}$)	0.60
UCI_1850	0.79($< 10^{-5}$)	0.93	0.64($< 10^{-5}$)	0.61
TEM vs. AmeriFlux				
US-Brw	0.54(0.034)	0.57	0.58(0.024)	0.37
UCI_1998	0.87($< 10^{-5}$)	0.98	-0.082(0.28)	0.30
UCI_1989	0.76($< 10^{-5}$)	0.83	0.26(0.022)	0.37
UCI_1850	0.77($< 10^{-5}$)	0.76	0.27(0.031)	0.31

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Table 6. The amount of organic nitrogen uptake and inorganic nitrogen uptake by plant during growing season (June, July, August and September) at four sites, modeled by ON-TEM.

Site	ID	Jun	Jul	Aug	Sep
Organic nitrogen uptake ($\text{gN m}^{-2} \text{ month}^{-1}$)					
1	US-Brw	0.28 ± 0.067	0.14 ± 0.062	0.13 ± 0.062	0.037 ± 0.011
2	UCI_1998	0.28 ± 0.1	0.48 ± 0.08	0.49 ± 0.09	0.45 ± 0.016
3	UCI_1989	0.46 ± 0.006	0.48 ± 0.001	0.48 ± 0.001	0.46 ± 0.012
4	UCI_1850	0.46 ± 0.006	0.48 ± 0.002	0.48 ± 0.002	0.47 ± 0.001
Inorganic nitrogen uptake ($\text{gN m}^{-2} \text{ month}^{-1}$)					
1	US-Brw	0.04 ± 0.08	0.24 ± 0.01	0.23 ± 0.01	0.035 ± 0.005
2	UCI_1998	0.79 ± 0.08	0.99 ± 0.01	0.87 ± 0.04	0.66 ± 0.032
3	UCI_1989	0.46 ± 0.06	0.89 ± 0.05	0.66 ± 0.12	0.53 ± 0.085
4	UCI_1850	0.47 ± 0.06	0.91 ± 0.05	0.67 ± 0.13	0.54 ± 0.092

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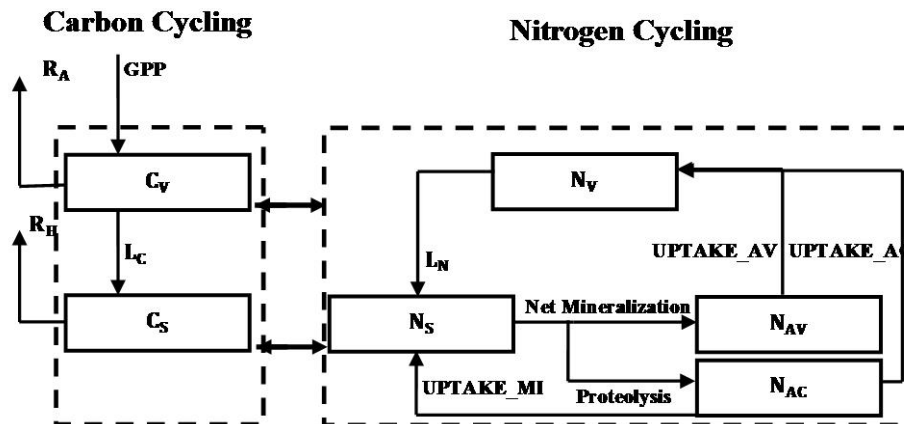


Fig. 1. ON-TEM model diagram: arrows are carbon or nitrogen fluxes; the boxes are state variables. Originally, TEM comprises five state variables: vegetation carbon (C_V), soil organic carbon (C_S), vegetation nitrogen (N_V), soil organic nitrogen (N_S) and soil inorganic nitrogen (N_{AV}). Here an amino acid pool (N_{AC}) is added. Soil nitrogen has two pathways to be taken up by plants: (1) Nitrogen is mineralized by soil microbes into inorganic form, NH_4^+ , NO_3^- or (2) Nitrogen undergoes proteolysis into amino acids and is taken up by the plant.

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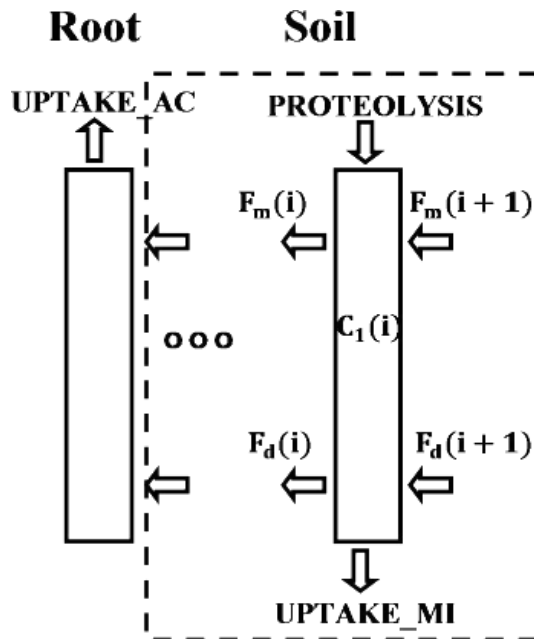


Fig. 2. Schematic representation of modeling amino acid transportation in soil and uptake by plant: The root's surrounding soil is divided into many thin sub-cylinders. This is a vertical slice picture of i th sub-cylinder from the root surface. $C_1(i)$ is concentration of amino acid in soil solution in the sub-cylinder. $F_m(i)$ and $F_d(i)$ are mass flow and diffusion of amino acid. The supply rate of amino acid is calculated by the discrepancy between proteolysis and microbial uptake (Lipson et al., 2001).

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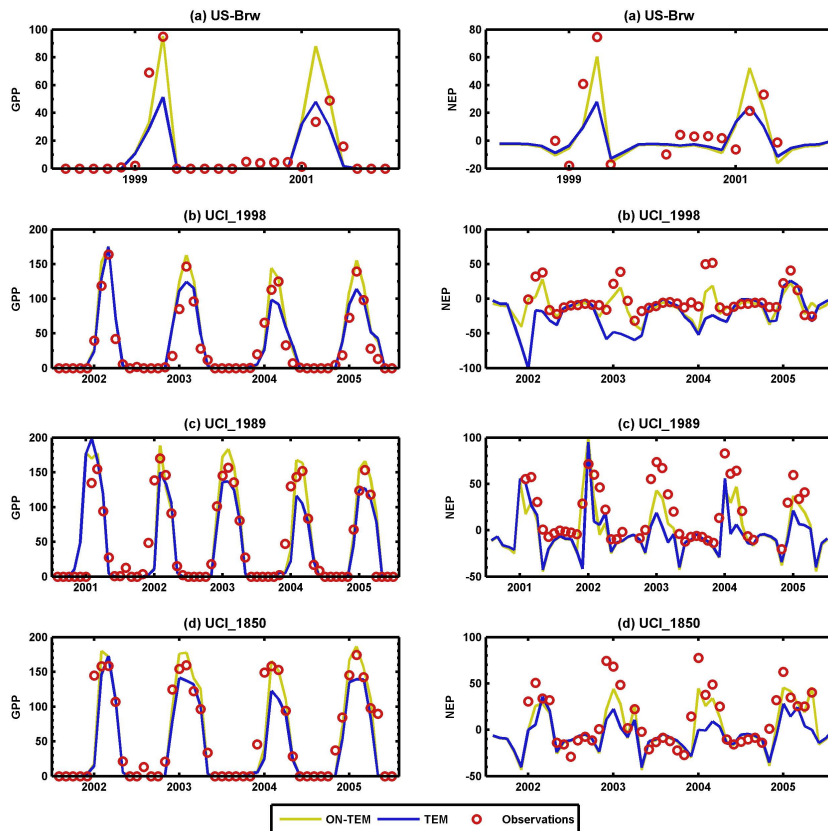


Fig. 3. GPP and NEP ($\text{gCm}^{-2}\text{month}^{-1}$) simulated by ON-TEM, considering the organic nitrogen uptake process were represented by the yellow lines. In comparison with the TEM (blue lines), ON-TEM simulations (yellow lines) are generally more consistent with the observations (red circles). (a–d) are the tundra site US-Brw, the boreal forest sites UCI_1998, UCI_1989 and UCI_1850, respectively.

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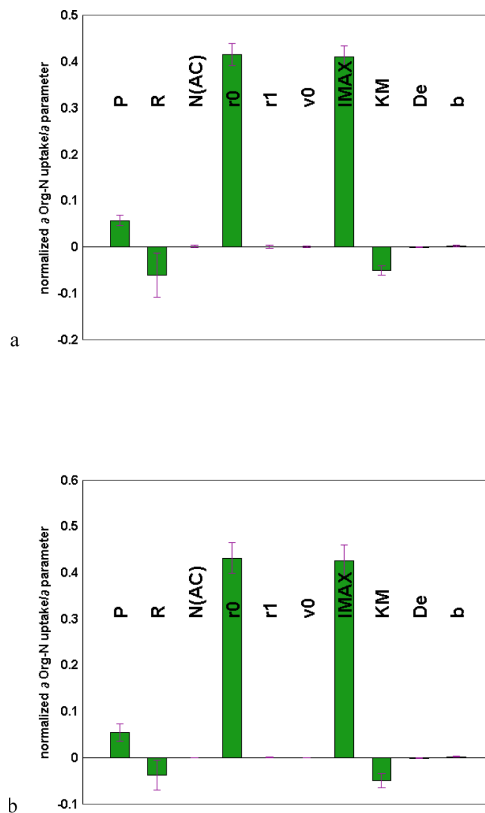



Fig. 4. The normalized sensitivity of organic nitrogen uptake by plants with respect to each individual controlling parameters, shown in terms of mean (green bars) and standard deviation (red error bars) at two sites where we conducted the model sensitivity analysis. **(a)** is for the tundra site US-Brw; and **(b)** is for the boreal forest site UCI_1998.

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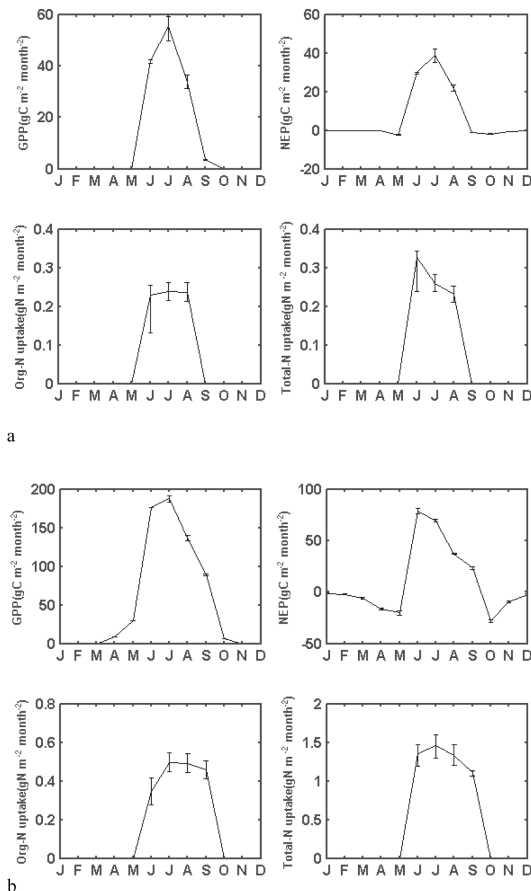


Fig. 5. Uncertainty analysis of the organic nitrogen uptake module-related parameters, showing the ensemble simulations mean, upper and lower bounds. GPP, NEP, the organic nitrogen uptake and the total nitrogen uptake are illustrated. **(a)** is the tundra site US-Brw and **(b)** is the boreal forest site UCI_1998.

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