

Interactive comment on “Modeling the effects of organic nitrogen uptake by plants on the carbon cycling of boreal ecosystems” by Q. Zhu and Q. Zhuang

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1 Consequences of the assumption that plants take up inorganic N (IN) first and, if not sufficient for survival and growth, absorb amino acids to make up this deficiency

Thanks for pointing out the potential problem about our assumption of plant's preference in acquiring different forms of nitrogen (inorganic N versus organic N). As we know that rooting systems take up different forms of N generally following the order: NH_4^+ > amino acids > NO_3^- (Ohlund and Nasholm, 2001; Thornton and Robinson,

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2005). In some cases, the uptake rate of amino acids may even exceed the uptake rates of NH_4^+ or NO_3^- (Chapin et al., 1993; Kielland et al., 2006). In this study, we made an assumption that plants take inorganic forms of N first (NH_4^+ and NO_3^-) and utilize organic N as supplement when the inorganic N is insufficient. This assumption allows us to evaluate whether the additional amino acid N source and uptake could improve quantification of ecosystem carbon dynamics. We developed a version of ON-TEM to allow organic N to be taken up in addition to inorganic N. Based on the assumption we made, the simulation differences between two versions of TEM can reveal the effects of organic N uptake on carbon dynamics. As is also mentioned by the second reviewer, our assumption is the an appropriate assumption to make, if the primary purpose of the modeling exercise is to determine whether addition of an organic-N uptake module improves performance of the C/N cycling estimates made by the model.

A possible drawback of our assumption is that ON-TEM may underestimate the ratio of organic N to inorganic N uptake by plants. In addition, to date, plant utilizing organic forms of N and its effects on plant production is still an open question. This study is among first attempts to model the impact of organic N uptake on ecosystem carbon cycling. Organic N uptake and its effects on carbon dynamics should deserve more studies.

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2 ON-TEM clearly identified the potential importance of ON as a fraction of total plant N uptake (36-87% for the tundra site; 26-50% in boreal forest). Do these results imply that TEM (-ON) may have underestimated total plant N uptake by an equal magnitude – with sundry effects on GPP and NEP? Moreover, did the increased uptake from ON scale to increased NEP in a reasonable fashion?

The results from ON-TEM simulations show that the organic N uptake accounts for 36-87% and 26-50% of total N uptake in tundra and boreal forest, respectively. In the model, plants will use inorganic forms of N first (NH₄⁺ and NO₃⁻) and utilize organic N as supplement. These organic N uptake ratios imply that original TEM might have underestimated the total N uptake by a similar magnitude.

The underestimation of N uptake in TEM generally could not meet the plant N demand, so plant production will be limited. As a result, TEM simulated GPP and NEP deviated from the observations (Table 5 in the Discussion paper). In contrast, in ON-TEM, soil organic N supply alleviated the limitation of N. The increased N supply is appropriately scaled to increased GPP and NEP, since it results in better estimates of GPP and NEP compared with observations (Table 5 in the Discussion paper).

3 Equation 4 (Model development) describing changes in vegetation nitrogen (as plant IN and ON uptake minus N loss in litter) appears incorrect

It was a typo. The correct equation is:

$$\frac{dN_v}{dt} = NUPTAKE_{AV} + NUPTAKE_{AC} - L_N \quad (1)$$

As is shown in Fig. 1 of the Discussion paper, the vegetation N pool (N_v) has two input fluxes, which are inorganic N uptake (NUPTAKE_AV) and organic N uptake (NUPTAKE_AC); and one output flux of litterfall N (L_N).

4 The sensitivity analysis identified a plant factor (maximum root uptake) as the primary control over plant ON acquisition, rather than the hitherto prevailing idea that edaphic characteristics (e.g., diffusion rates) primarily exert such control (e.g., Tinker and Nye 2000).

Our sensitivity analysis indicates that the organic N uptake was controlled by the maximum root uptake rate (I_{max}). In contrast, some published literatures suggested that organic N availability is controlled by edaphic characteristics, especially diffusion rate (D_e) of nutrient through soil, due to the strong interactions between free amino acid and soil matrix (Jones and Darrah, 1994; Tinker and Nye, 2000; Lipson and Näsholm, 2001; Näsholm et al. 2009).

The differences between our results and the literatures might be due to the method we employed for sensitivity analysis. The adjoint-based sensitivity used in this study is strongly controlled by the “local values” of each specific parameter. This approach quantifies the sensitivity of the model output (here, organic N uptake) to a certain parameter with fixed parameter values. Thus, the calculated model sensitivities might not appropriately represent overall response of the modeled process to the selected parameters. For example, the maximum uptake rate (I_{max}) used in this study might be underestimated, which biases our sensitivity analysis results. Specifically, the maximum uptake rate used in this study is $1.0e-9$ mmol cm⁻² s⁻¹ (Leadley et al., 1997,

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Table A2), which is equivalent to $2.0 \mu\text{mol g}^{-1} \text{h}^{-1}$ (Chapin et al. 1993, Table 1) after unit conversion. Based on a comprehensive survey on plant amino acid maximum uptake rate (Lipson and Näsholm, 2001, Table 2), the I_{max} could range from 0.22 to $45 \mu\text{mol g}^{-1} \text{h}^{-1}$. The value we used ($2.0 \mu\text{mol g}^{-1} \text{h}^{-1}$) is towards the low end of the range. This may be the reason that our analysis indicates the uptake kinetics is a major control.

To address this issue, we have conducted a global sensitivity analysis which considered the whole range of each organic N uptake associated parameters (Table 1). SOBOL technique (Pappas et al., 2013) is used for parameter sampling and sensitivity index calculation. Figure 1 shows the first order sensitivity index of each parameter of interest. Our results show that: (1) the most sensitive parameters are the diffusion coefficient (D_e) and the radius of rhizosphere soil cylinder (r_1); (2) the second most sensitive parameters are the radius of root (r_0) and Maximum root uptake rate (I_{max}). The global sensitivity analysis results are reasonably consistent with published studies, which suggested that organic N availability is controlled by edaphic characteristics (such as diffusion coefficient D_e) due to the strong interactions between free amino acid and soil matrix. We have replaced the local sensitivity results with the global sensitivity results in the revised paper.

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- 5 **One issue of concern regarding the generality of this paper pertains to the source data for parameter estimations (as acknowledged in the text by the authors). Whereas I have no problem allowing models to go forward with moderate amounts of data, or off site data for that matter, I was somewhat perplexed by the absence of ecosystem-specific data employed here. Surely a wide suite of information from the primary literature on arctic and boreal ecosystems could have been accessed: Amino acid concentration data (Kielland 1995; Nordin et al 2001; Weintraub and Schimel 2006; Werdin-Pfisterer et al. 2009), protease activity (Weintraub and Schimel 2006; Kielland et al. 2007), as well as plant uptake kinetics for a variety of species (Kielland 1994, 2006; Persson and Nasholm 2003)**

The adjoint approach for TEM (Appendix A of the discussion paper) was developed to use flux data of GPP, NPP, NEP, and RESP only. Thus, only carbon flux data were used for parameterizing both TEM and ON-TEM. Data sets of amino acid concentrations, protease activity and plant uptake kinetics mentioned by the reviewer are undoubtedly important and potentially helpful for further improving our model. However these data are often sparse and our adjoint approach has not been developed to assimilate these data. We plan to organize more data and further develop ON-TEM to assimilate those data to improve modeling the effects of organic N uptake on carbon cycling in boreal forest and tundra ecosystems.

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Table 1. Upper and lower bounds of the selected parameters for the global sensitivity analysis

Selected parameters	Testing factors	Unit	Upper bound	Lower bound	References
P (Proteolysis rate in soil)	Supply factors	$nmol\ g^{-1}h^{-1}$	55	10	Lipson et al., 2001
R (First order microbial amino acid uptake rate)	Supply factors	h^{-1}	0.43	0.048	Lipson et al., 2001
N_{AC} (Soil amino acid initial concentration)	Supply factors	$nmol\ g^{-1}$	$2.8 \cdot 10^4$	$1.7 \cdot 10^3$	Kielland et al., 2007. ^a
De (First order Fick's law diffusion coefficient)	Soil factors	cm^2s^{-1}	$7 \cdot 10^{-6}$	$5 \cdot 10^{-7}$	Leadley et al., 1997
v0 (Water flux at the root surface)	Soil factors	cms^{-1}	$5 \cdot 10^{-7}$	$1 \cdot 10^{-8}$	Leadley et al., 1997
r0 (the radius of root)	Root factors	cm	0.07	0.0035	Leadley et al., 1997
r1 (the radius of rhizosphere soil cylinder)	Root factors	cm	0.5	0.2	Leadley et al., 1997
I_{max} (Maximum root uptake rate)	Uptake kinetics	$mmolcm^{-2}s^{-1}$	$2.1 \cdot 10^{-8}$	$1 \cdot 10^{-10}$	Lipson and Nasholm, 2001. ^b
Km (Half-saturation constant for root uptake kinetics)	Uptake kinetics	$mmolcm^{-3}$	$1.3 \cdot 10^{-2}$	$1.6 \cdot 10^{-6}$	Lipson and Nasholm, 2001. ^c

^a Given in unit (μgg^{-1}); unit conversion: $\mu gg^{-1} \cdot 10^3 (ng\mu g^{-1})/14 (gmol^{-1}) = nmol\ g^{-1}$

^b Given in unit ($nmol\ g^{-1}h^{-1}$); unit conversion: $\mu mol\ g^{-1}h^{-1} \cdot 10^{-3} (mmol\ \mu mol^{-1})/3600 (sh^{-1}) \cdot MSR (gcm^{-2}) = mmolcm^{-2}s^{-1}$, $MSR = 0.0017 gcm^{-2}$ is mass per unit surface of root (Chapin et al., 1979; Leadley et al., 1997)

^c Given in unit ($\mu molL^{-1}$); unit conversion: $\mu molL^{-1} \cdot 10^{-3} (mmol\ \mu mol^{-1}) \cdot 10^{-3} (Lcm^{-3}) = mmolcm^{-3}$

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