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Key Points:
- Short-term ^{15}N tracer experiment informs tundra plant nitrogen uptake patterns
- Nutrient competition frameworks currently applied in Earth System Models cannot represent observed patterns
- Root biomass, uptake kinetics, and appropriate plant-microbial competition framework are important to predict tundra nitrogen uptake

Supporting Information:
- Supporting Information S1

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Root traits explain observed tundra vegetation nitrogen uptake patterns: Implications for trait-based land models

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Abstract Ongoing climate warming will likely perturb vertical distributions of nitrogen availability in tundra soils through enhancing nitrogen mineralization and releasing previously inaccessible nitrogen from frozen permafrost soil. However, arctic tundra responses to such changes are uncertain, because of a lack of vertically explicit nitrogen tracer experiments and untested hypotheses of root nitrogen uptake under the stress of microbial competition implemented in land models. We conducted a vertically explicit ^{15}N tracer experiment for three dominant tundra species to quantify plant N uptake profiles. Then we applied a nutrient competition model (N-COM), which is being integrated into the ACME Land Model, to explain the observations. Observations using an ^{15}N tracer showed that plant N uptake profiles were not consistently related to root biomass density profiles, which challenges the prevailing hypothesis that root density always exerts first-order control on N uptake. By considering essential root traits (e.g., biomass distribution and nutrient uptake kinetics) with an appropriate plant-microbe nutrient competition framework, our model reasonably reproduced the observed patterns of plant N uptake. In addition, we show that previously applied nutrient competition hypotheses in Earth System Land Models fail to explain the diverse plant N uptake profiles we observed. Our results cast doubt on current climate-scale model predictions of arctic plant responses to elevated nitrogen supply under a changing climate and highlight the importance of considering essential root traits in large-scale land models. Finally, we provided suggestions and a short synthesis of data availability for future trait-based land model development.

1. Introduction

Carbon and nitrogen cycling in terrestrial ecosystems are closely coupled [*LeBauer and Treseder*, 2008], especially in northern arctic regions where nitrogen supply is strongly limited [*Atkin*, 1996; *Elser et al.*, 2007; *Haag*, 1974; *Zhu and Zhuang*, 2013]. In arctic tundra, soil nitrogen availability is typically low due to slow soil nitrogen mineralization [*Nadelhoffer et al.*, 1991], slow nitrogen fixation [*Cleveland et al.*, 1999], and low atmospheric nitrogen deposition [*Bobbink et al.*, 2010]. Limited nitrogen supply generally constrains the production of new plant biomass [*Evans*, 1989] and plays an important role in arctic carbon accumulation and carbon-climate feedbacks [*Baddeley et al.*, 1994; *Weintraub and Schimel*, 2005].

The nitrogen limitation in arctic systems will, however, be perturbed by climate warming in at least two ways: warming will accelerate soil nitrogen mineralization in surface soils [*Rustad et al.*, 2001; *Schmidt et al.*, 2002] and release frozen nitrogen at the permafrost boundary as the active layer thickens [*Keuper et al.*, 2012]. A global meta-analysis concluded that experimental warming enhanced surface soil net nitrogen mineralization by 46% [*Rustad et al.*, 2001], with the highest enhancement in tundra ecosystems [*Jonasson et al.*, 1993]. Globally, warming resulted in ~0.5 g N m^{-2} yr^{-1} additional nitrogen in the surface organic layer (compared with global biological N_2 fixation ~0.45 g N m^{-2} yr^{-1} [*Vitousek et al.*, 2013]), which substantially stimulated plant growth and increased ecosystem carbon storage [*Rustad et al.*, 2001]. Also, the soil that is expected to thaw at the permafrost boundary over the next decades may result in even more plant available nitrogen than from warming in the surface soil. In an study of subarctic peatland soils, consistently higher net nitrogen mineralization and plant nitrogen uptake rates were observed near the permafrost boundary (~50 cm depth) than in the current rooting zone (<15 cm) [*Keuper et al.*, 2012]. The elevated inorganic nitrogen supply at depth came from both direct release of frozen inorganic nitrogen and microbial decomposition of thawed organic nitrogen.

Given that warming will alter nitrogen availability along the entire soil profile, vertically resolved ^{15}N tracer experiments are needed to inform the vertical pattern of plant uptake. The prevailing hypothesis regarding the vertical pattern of plant uptake is that fine-root biomass density, as functionally absorptive tissues, exerts first-order controls on nutrient uptake [*De Baets et al*., 2007; *Vamerali et al*., 2003]. Therefore, the plant nitrogen uptake profile should follow the fine-root biomass density distribution (typically high in shallower soil and low in deeper soil). Evidence from some ^{15}N tracer studies has been consistent with this idea. For example, grass [*Bowman et al*., 2002; *Jumpponen et al*., 2002; *Xu et al*., 2011] and crops [*Andrews and Newman*, 1970; *Kristensen and Thorup-Kristensen*, 2004] take up most soil nitrogen from soil layers where the rooting biomass density is the highest. In contrast, *Liao et al*. [2006] found that three wheat species take up more nitrogen from the middle soil layer (20–70 cm) than from the upper soil layer (0–20 cm), although root biomass density was lower in the middle layer. For tundra ecosystems, the factors controlling plant nitrogen uptake have not been fully evaluated. Therefore, the first objective of this study was to quantify vertical patterns of nitrogen uptake for three dominant arctic tundra species (*Carex aquatilis*, *Eriophorum angustifolium*, and *Salix rotundifolia*) using results from a vertically explicit ^{15}N tracer field experiment.

The observed vertical patterns of plant nitrogen uptake are complicated by soil nutrient competition, i.e., plants dynamically competing for nutrients with microbes [*Schmidt et al*., 2002] and abiotic processes [*Jones et al*., 2005; *Petrone et al*., 2006]. Microbial nitrogen demands are commonly higher in surface soils and lower in subsurface soils, due to strong energy limitation and temperature constraints in the deeper soil [*Fontaine et al*., 2007; *Xu et al*., 2013]. Therefore, roots growing in surface soils face potentially intense competition for nitrogen from microbes. Plants could directly compete with microbial decomposers in surface soils by enabling highly efficient nutrient uptake systems, increasing fine-root density, developing more effective fine roots (i.e., roots with a greater length to mass ratio), or establishing mycorrhizal fungi associations [*Kuzyakov and Xu*, 2013; *Miller and Cramer*, 2005; *Smith and Read*, 2010]. Alternatively, plants can invest carbon to grow fine roots deeper in the soil (where microbial N demand is low) to avoid direct competition with microbes in the surface soil [*Iversen et al*., 2011]. In other words, plant species' distinct competitive functional traits, e.g., maximum rooting depths, root profiles, and uptake kinetics, will determine their vertical uptake pattern under the stress of microbial demand. To better understand the observed plant N uptake patterns, we used a recently developed model (N-COM, nutrient competition) that mechanistically considers competitive interactions among fine roots, microbial decomposers, nitrifiers, denitrifiers, and mineral surfaces by applying the Equilibrium Chemistry Approximation (ECA) [*Tang and Riley*, 2013; *Zhu and Riley*, 2015; *Zhu et al*., 2016]. Our second objective in this study was to use N-COM to understand the complicated competitive interactions and explain the observed plant nitrogen uptake patterns.

Mechanistic consideration of plant-microbe competition is absent in current generation Earth System Models (ESMs), which are used to predict coupling between terrestrial carbon dynamics and climate. Prevailing ESMs with prognostic N cycling did not explicitly account for root traits to represent plant competitiveness but rather applied either a "Relative Demand" [*Thornton et al*., 2007] or a "Microbes Win" [*Gerber et al*., 2010] concept. The Relative Demand concept hypothesizes that plant nutrient competitiveness is dependent on plant nutrient demand. Higher plant demand (e.g., during growing season) will lead to higher competitiveness, regardless of rooting conditions (e.g., root density). The Microbes Win competition hypothesis assumes that microbes always get priority to access the available nutrient pool and plants use the leftover nutrients, without considering the uptake capacity of roots. In contrast, our ECA framework explicitly considers essential root traits and plant-microbe competition mechanism. Our third objective in this study was to evaluate the importance of root traits in modeling plant-microbe nutrient competition and vertical patterns of plant nutrient uptake, by comparing three plant-microbe competition hypotheses: (1) Relative Demand, (2) Microbes Win, and (3) ECA against the ^{15}N data. We hypothesize that models must mechanistically consider essential root traits that control plant-microbe competitive interactions to accurately estimate how much additional N plants can acquire under future warming.

2. Materials and Methods

2.1. ^{15}N Tracer Study

For our modeling analysis, we used data from an ^{15}N uptake study that was conducted as part of the NGEE Arctic project (http://ngee-arctic.ornl.gov) at the Barrow Environmental Observatory in Barrow, AK,

USA [*Iversen et al*., 2016]. The ^{15}N uptake study investigated the vertical patterns of root N acquisition for three dominant vascular plant species: relatively deeply rooted sedges (*Carex aquatilis Wahlenb* and *Eriophorum angustifolium Honck*) and a relatively shallowly rooted deciduous shrub (*Salix rotundifolia Trautv*). The methods from the observational work are described below.

In late July 2013, replicate plots of the three dominant vascular plant species of interest were located in wet tundra near the intensively monitored NGEE Arctic sites (between −156.60481 and −156.60273 longitude and between 71.27687 and 71.27745 latitude). Prior to ^{15}N addition, the initial aboveground biomass of each species was determined by clipping all vascular material to the moss surface in plots that were 9 cm × 9 cm (i.e., small enough to focus on a relatively homogenous patch of each species; 3 species × 4 replicate plots per species = 12 plots total). Vegetation was immediately processed in the laboratory, where it was sorted by species, green leaves, senesced leaves, and stems (attached senesced material was removed from sedge leaves). Plant parts were oven dried at 70°C for more than 48 h, and the mass of living plant parts was summed to determine aboveground biomass per unit ground area.

After clipping, a soil core was manually collected to the permafrost boundary from the center of each plot. Cores were sectioned into 5 cm depth increments in the field (organic and mineral soil layers were treated separately if they fell within a 5 cm depth increment). Each increment was sectioned longitudinally into two halves. One half of the soil was homogenized, large roots and green mosses were removed, and a subsample of soil was extracted with 2 *M* KCl to determine the initial soil depth profile of plant available NH_4-N and NO_3-N (Lachat autoanalyzer, Hach Company, Loveland, CO). Nutrient concentrations were standardized per unit dry soil mass using gravimetric water conversion from samples oven dried for more than 48 h at 70°C. The distribution of total carbon (C) and N throughout the soil profile was determined by elemental analysis (Costech ECS 4010 Elemental Analyzer, Valencia, CA or LECO TruSpec elemental analyzer, LECO Corporation, St. Joseph, MI) on similarly collected and processed soil cores collected in 2012 from the nearby NGEE Arctic Intensive site [*Iversen et al*., 2015b].

Species-specific belowground biomass was determined from the remaining half of the soil from each depth increment. Living roots and rhizomes associated with the target species in each plot were removed from each depth increment using forceps, oven dried at 70°C for more than 48 h, and weighed to determine species-specific living belowground biomass, which was converted to unit ground area using the bulk density of the core depth increments.

After the initial harvest, we injected a solution of $^{15}NH_4Cl$ (at a tracer rate of 200 mg ^{15}N m^{-2}) in the soil beneath newly located 9 cm × 9 cm plots in homogenous species patches. We separately targeted three soil horizons for each species: organic, shallow mineral, or the permafrost boundary (3 species × 3 injection depths × 4 replicate plots per injection depth = 36 plots total). Injections were made in a grid pattern of 16 points per plot to ensure homogenous delivery of the tracer solution at a given soil depth. The organic horizon injections were targeted at 3 cm depth, the mineral horizon injections were targeted at 10 cm depth, and the permafrost boundary injections were targeted at 1 cm above the permafrost boundary (which ranged from 21 to 49 cm depth). One week later, the vegetation in the labeled plots was clipped to the moss surface, and soil cores were taken in the center of each labeled plot. Aboveground and belowground vegetation was processed and quantified as above, and oven-dried, ground plant tissues were analyzed for ^{15}N using continuous-flow isotope ratio mass spectrometry (Integra CN, SerCon, Crewe, UK). Duplicate samples and standards of known ^{15}N concentration were used to ensure the precision and accuracy of the data.

The field experiment provides edaphic and vegetation data collected prior to ^{15}N addition to initialize and drive the N-COM model. Then, the total amount of ^{15}N acquired by the plants after the experimental tracer addition was used to test the predictions from the three nutrient competition concepts (ECA, Relative Demand, and Microbes Win). The major difference among the three competition models is that only ECA explicitly considers essential root traits for plant-microbe competition. Therefore, first, a comparison between the ECA model and the other two models will inform how root traits control plant-microbe competition. Second, the ^{15}N tracer experiment quantifies the vertical distribution of plant N uptake, which is an emergent pattern of plant-microbe competition. By comparing model predictions with different plant-microbe competition hypotheses with the observations, we can evaluate how plant-microbe competition hypotheses affect plant N uptake. Third, since Relative Demand and Microbes Win competition hypotheses

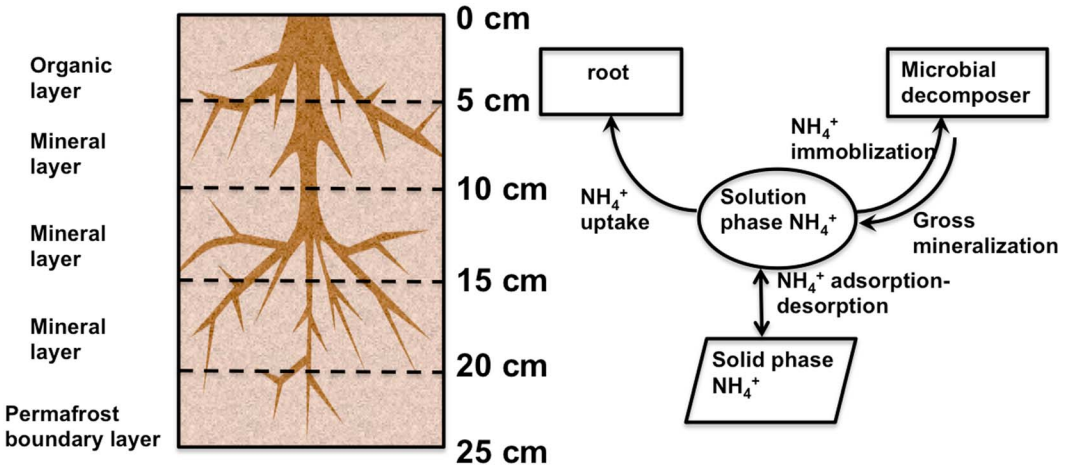

Figure 1. N-COM model setup at Barrow Alaska site. Six soil layers are modeled, with 5 cm depth intervals in each layer. Root distributions were imposed by observations. ^{15}N tracer (at the rate of 200 mg m^{-2}) was applied to the soil, which could be either taken up by microbial decomposers and roots or adsorbed onto mineral surfaces.

are widely used by prevailing ESMs, the discrepancy between these two concepts and observations can inform future modeling efforts.

2.2. N-COM Model Description

N-COM (see supporting information S1 for detailed formulation) is a process-based model originally developed to represent coupled ecosystem carbon, nitrogen, and phosphorus cycles [*Zhu and Riley*, 2015; *Zhu et al*., 2016] based on Equilibrium Chemistry Approximation (ECA) kinetics [*Tang and Riley*, 2013], although its structure is sufficiently generic to include any number of substrates and consumers. The modeling framework mechanistically represents nutrient competition assuming (1) plants and microbes produce specialized nutrient transporter enzymes to react with soil inorganic nitrogen substrates, (2) enzyme-substrate complexes are then formed, (3) these complexes can be transported into cells, and (4) finally, the transporter enzymes are liberated [*Button*, 1985; *Williams and Miller*, 2001]. Thus, the binding of substrates to plant nutrient transporter enzymes inhibits the binding between substrate and microbial nutrient transporter enzymes and vice versa. While nutrient diffusivity limitation may constrain plant uptake by affecting substrate affinity (K_M) [*Tang and Riley*, 2013], we did not consider diffusivity limitation in this study because ^{15}N was directly added in the rooting zone and the spatial scale of the plots were just a few centimeters.

As applied here, N-COM quantifies tundra C and N fluxes in three model layers: organic layer (0–5 cm), mineral layer (5–20 cm), and near the permafrost boundary layer (>20 cm) for *Carex aquatilis*, *Eriophorum angustifolium*, and *Salix rotundifolia* (Figure 1). We focus here on plant $^{15}NH_4^+$ uptake; other nutrient uptake fluxes (e.g., NO_3^-) are described in *Zhu et al*. [2016]. Competition for NH_4^+ occurs among roots, nitrifiers, and microbial decomposers. However, nitrifier activity is typically very small in tundra soils [*Giblin et al*., 1991; *Schimel et al*., 1996]. We therefore assumed in this study that competition only occurred between roots and microbial decomposers. The model does not represent microbial community and diversity (e.g., saprotrophic fungi versus bacteria). Since different microbial functional groups may have different enzymatic kinetics, we also assessed uncertainties stemming from this model simplification in our uncertainty analysis (section 2.4).

Plant NH_4^+ uptake (U) is simulated with explicit consideration of plant-microbe competitive interactions:

$$U = \frac{V_{MAX} C_{froot} [NH_4]}{K_M^{plant,NH_4}\left(1 + \frac{[NH_4]}{K_M^{plant,NH_4}} + \frac{\left[E_{NH_4}^{plant}\right]}{K_M^{plant,NH_4}} + \frac{\left[E_{NH_4}^{mic}\right]}{K_M^{mic,NH_4}}\right)} \quad (1)$$

$$\left[E_{NH_4}^{plant}\right] = \alpha C_{froot} \quad (2)$$

$$\left[E_{NH_4}^{mic}\right] = \beta C_{MIC} \quad (3)$$

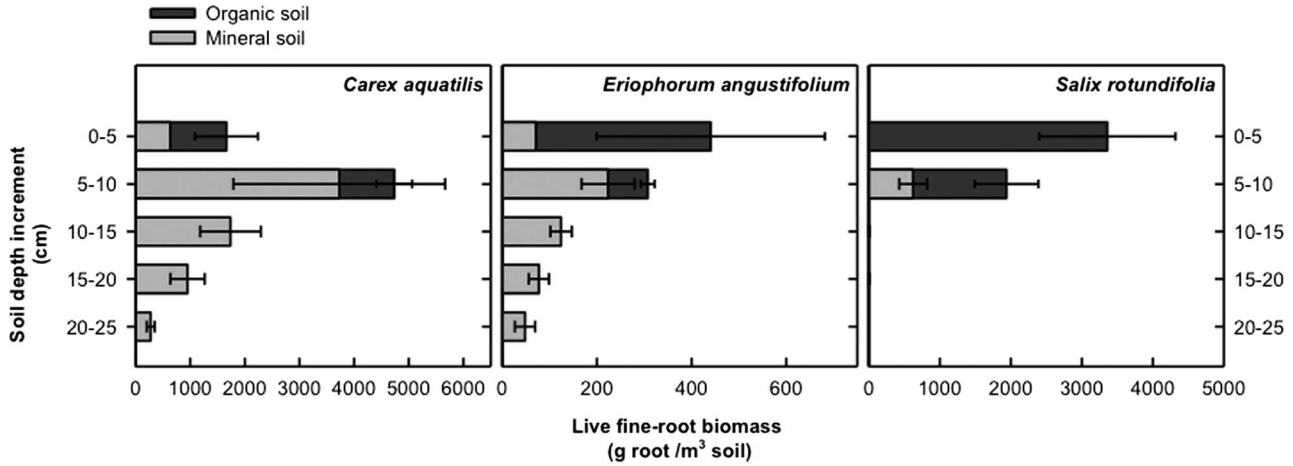

Figure 2. Vertical fine-root biomass distributions of *Carex aquatilis*, *Eriophorum angustifolium*, and *Salix rotundifolia*. *Carex* and *Eriophorum* extend roots to soil horizon near the permafrost boundary layer; *Salix* is shallowly rooted.

where V_{MAX} is the maximum rate of plant NH_4^+ uptake per unit root mass (g N g^{-1} C h^{-1}); $\left[E_{NH_4}^{plant}\right]$ and $\left[E_{NH_4}^{mic}\right]$ are concentrations of plant and microbial nutrient transporter enzymes (g N m^{-3}), respectively, and are assumed to be linear functions (α, β) of fine root biomass (C_{froot}) and microbial decomposer biomass (C_{MIC}), respectively; and K_M^{plant,NH_4} and K_M^{mic,NH_4} are affinity parameters for plant and microbial transporter enzymes to bind with soil solution NH_4^+ (see derivation of solution NH_4^+ based on soil total exchangeable NH_4^+ in supporting information Method S2). K_M for plants and microbes can be considered the concentration of NH_4^+ at which the rate of NH_4^+ uptake is half of the maximum rate (V_{MAX}); a lower K_M indicates greater competitiveness for NH_4^+ acquisition. This equation differs from classic Michaelis-Menten kinetics applied to plant uptake by considering the inhibiting effect of microbial nitrogen demand.

2.3. Characterizing Competitive Parameters for Tundra Vegetation and Microbes

N-COM predictions of plant N uptake are based on root kinetic parameters. Unfortunately, kinetic parameters for the three tundra species (*Carex aquatilis*, *Eriophorum angustifolium*, and *Salix rotundifolia*) were not measured in the ^{15}N tracer study we applied here. We thus derived those parameters from the literature [*Jongbloed et al*., 1991; *Kroehler et al*., 1988; *Leadley et al*., 1997; *McRoy and Alexander*, 1975; *Shaver et al*., 1979; *Smith and Read*, 2010; *Väre et al*., 1992; *Ye et al*., 2015].

For *Carex aquatilis*, V_{MAX} was measured to be 2.75×10^{-4} g N g^{-1} dry weight (DW) leaf h^{-1} in an arctic pond using the ^{15}N tracer technique [*McRoy and Alexander*, 1975]. Given that the root to leaf mass ratio of *Carex aquatilis* is about 2.64 (2.15–3.33, similar to the current study range) [*Shaver et al*., 1979], we estimate $V_{MAX} = 1.04 \times 10^{-4}$ g N g^{-1} DW root h^{-1} (0.83×10^{-4}–3×10^{-4}). Also, K_M was estimated in that study to be 0.01 g N m^{-3} (0.0084–0.0125).

For *Eriophorum angustifolium*, *Leadley et al*. [1997] estimated V_{MAX} to be 0.35×10^{-6} g N cm^{-2} root surface h^{-1} (0.5×10^{-7}–0.5×10^{-6}) by fitting a Michaelis-Menten model to NH_4^+ uptake measurements made in sequentially increasing concentration cuvettes. Assuming plant-specific root area to be 800 cm^2 g^{-1} DW [*Ye et al*., 2015], we estimate $V_{MAX} \sim 2.8 \times 10^{-4}$ g N g^{-1} DW h^{-1} (0.4×10^{-4}–0.4×10^{-3}). K_M was estimated to be 1.4 g N m^{-3} (0.7–3.5) [*Leadley et al*., 1997].

For *Salix rotundifolia*, however, we were unable to find any measured NH_4^+ kinetics parameters. We note that *Salix rotundifolia* is associated with ectomycorrhizal fungi, which have high nitrogen uptake capacity [*Kroehler et al*., 1988; *Väre et al*., 1992]. Mycorrhizal fungi are symbiotic microbes that feed on photosynthates provided by plants and in turn provide nutrients to the plants [*Smith and Read*, 2010]. Therefore, we adopted V_{MAX} (3.05×10^{-4} g N g^{-1} DW h^{-1} (2.94×10^{-4}–3.16×10^{-4})) and a K_M (0.09 g N m^{-3} (0.083–0.097)) from ectomycorrhizal fungi measurements [*Jongbloed et al*., 1991].

Fine-root biomass profiles were measured for these three species (Figure 2) and directly used in the N-COM model. We assumed the root biomass profiles were constant within the week of the ^{15}N labeling. The K_M of

Table 1. Characteristics for *Carex Aquatilis*, *Eriophorum Angustifolium*, and *Salix Rotundifolia* and Tundra Soil, Derived From Literatures[a]

Plant	Max Rooting Depth (cm) [b]	V_{MAX} (g N g^{-1} h^{-1})	K_M (g N m^{-3})	Reference
Carex aquatilis	>20	1.04×10^{-4} [0.83×10^{-4}, 1.3×10^{-4}]	0.01 [0.0084, 0.0125]	*McRoy and Alexander* [1975]
Eriophorum angustifolium	>20	2.8×10^{-4} [0.4×10^{-4}, 0.4×10^{-3}]	1.4 [0.7, 3.5]	*Leadley et al.* [1997]
Salix rotundifolia	~10	3.0×10^{-4} [2.94×10^{-4}, 3.16×10^{-4}]	0.09 [0.083, 0.097]	*Jongbloed et al.* [1991]

Depth Intervals (cm)	Microbial Decomposer Biomass (g C m^{-2}) for Each Depth Interval	Microbial Decomposer K_M (g N m^{-3})	Reference
[0–5, 5–10, 10–15, 15–20, 20–25]	[58, 46, 36, 29, 23]	0.67 [0.39, 0.95]	*Kuzyakov and Xu* [2013] and *Xu et al.* [2013]

[a]Kinetic parameters are reported as mean value and upper and lower boundaries enclosed in brackets.
[b]Also see Figure 2.

soil microbial decomposers (0.67 g N m^{-3} (0.39–0.95)) was taken from a meta-analysis of soil microorganism kinetics parameters [*Kuzyakov and Xu*, 2013]. Microbial decomposer biomass was calculated using total microbial decomposer biomass averaged over the regions covered by tundra biome (up to 1 m depth) and a global dataset of microbial carbon vertical distribution profile [*Xu et al.*, 2013].

2.4. Uncertainty Analysis

Most model parameters were directly taken from field data (e.g., soil bulk density). However, several key model parameters (e.g., root uptake kinetics) were not measured in the field experiment due to logistical constraints, and our derivation of those parameters from literature may have introduced uncertainties. We quantified the uncertainty associated with the unobserved parameters using a Monte Carlo approach. For ECA model simulations, V_{MAX} and K_M were randomly sampled from their observed ranges (Table 1) 500 times for each plant species and for soil microbes. For the Relative Demand and Microbes Win competition models, which do not use kinetics parameters, uncertainty stemmed from the estimate of total plant N demand calculated by dividing plant net biomass production by its C to N ratio. Similarly, we randomly sampled plant net biomass production (supporting information Method S3) 500 times from the literature reported range for each species. Uncertainty ranges associated with the abovementioned parameters are reported as error bars in results and figures.

3. Results

3.1. Competition Model Explains Observed N Uptake Pattern

The three dominant tundra plant species observed here were dramatically different in terms of their maximum rooting depth, vertical rooting profile (Figure 2), and their prescribed root NH_4^+ uptake kinetics (Table 1). However, the distribution of soil NH_4^+ throughout the soil profile was relatively similar across the three plant monocultures (Figure 3), being higher in the organic layer (0–5 cm) and near the permafrost boundary (>20 cm), and lower in mineral soil layers (5–20 cm).

Carex aquatilis is a relatively deep-rooting species (Figure 2: its deepest roots reach the permafrost boundary layer > 20 cm). Moreover, it had the highest total root density of the species, most of which was in the organic and surface mineral layers (0–5 and 5–10 cm). *Eriophorum angustifolium* is also a deep-rooting species (reaches permafrost boundary) (Figure 2). However, its root density was much lower compared with *Carex aquatilis*. *Salix rotundifolia* also has a relatively high density of roots, of which the vast majority are in the upper 10 cm of soil (shallow rooting) and ~90% are in the organic layer (Figure 2). This pattern indicates that *Salix rotundifolia* lacks the ability to access deep soil nutrients (e.g., from thawing near the permafrost boundary) and must directly compete with microbial decomposers in surface soils.

The ^{15}N tracer data show that *Carex aquatilis* took up most of its NH_4^+ from mineral soil layers (5–20 cm) (Figure 4a, blue line), which agrees with its root density profile (Figure 2). Similar to *Carex aquatilis*, *Eriophorum angustifolium* took up most of its NH_4^+ from mineral soil layers (Figure 4b, blue line). However, the observed uptake profile was in contrast to its root density profile (Figure 2). Although roughly equal

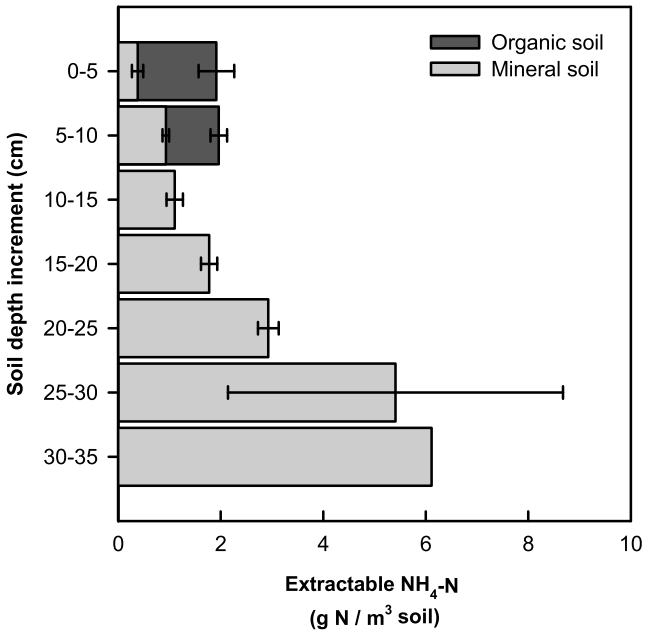

Figure 3. Vertical NH_4^+ distributions in the monocultures of *Carex aquatilis*, *Eriophorum angustifolium*, and *Salix rotundifolia*. Distribution of soil NH_4^+ throughout the soil profile was similar at all three plant monoculture environments. Data are averaged across four plots within a species, and then across the three species. Error bars represent standard deviation.

amounts of roots existed in the organic layer (0–5 cm) and mineral layer (5–20 cm), mineral layer NH_4^+ uptake was tenfold higher than in the organic layer. *Salix rotundifolia* took up 80% of NH_4^+ from the organic layer (Figure 4c, blue line).

Our modeling of plant-microbe competition using the ECA approach in N-COM generally captured the observed vertical patterns of plant N uptake for all three tundra species (Figure 4, green lines). Differences between ECA predictions and observations were small: (1) for *Carex aquatilis*, ECA overestimated plant N uptake near the permafrost boundary (PFB) layer and (2) for *Eriophorum angustifolium*, ECA overestimated plant N uptake at organic layer (top 5 cm soil). Our uncertainty analysis showed that plant-microbe competition was sensitive to the choice of kinetics parameters (error bars in Figure 4, green lines). However, the plant N uptake patterns were conservative even when considering the full range of uncertainties in derived kinetics parameters. Therefore, we conclude that using literature-derived kinetics parameters introduced modest uncertainty in our model analysis but did not undermine the fidelity of the ECA approach.

3.2. Alternative Root Nitrogen Uptake Hypotheses in Models

In addition to the ECA competition hypothesis, two other prevailing hypotheses are employed by ESMs: (1) root nitrogen uptake is based on plant demand and the competition between root and decomposer microbes is scaled with their relative demand (hereafter referred to as the Relative Demand hypothesis, or "RD") (e.g., CLM in CESM [*Koven et al*., 2013; *Thornton et al*., 2007]) and (2) the Microbes Win hypothesis ("MIC"; e.g., LM3 in Geophysical Fluid Dynamics Laboratory [*Gerber et al*., 2010]), which assumes roots are completely outcompeted by microbes and that roots take up nitrogen after microbial demand has been satisfied. Model setup for RD and MIC are described in supporting information Method S3.

Our analyses indicate that RD (Figure 4, cyan lines) and MIC (Figure 4, magenta lines) were inappropriate for all three tundra species. They each predicted substantial nitrogen uptake near the permafrost boundary layer (>20 cm), in contrast to observed uptake. These discrepancies occurred because, in these hypotheses, root uptake in shallow soil layers are either completely suppressed (MIC hypothesis) or largely suppressed by microbial decomposers (RD hypothesis). Therefore, they tend to acquire soil nitrogen from deeper in the soil profile, where microbial competition stress is lower. Both ECA and observations indicate that *Eriophorum* shifts its nitrogen uptake from the organic layer to mineral layer, but not down to the permafrost boundary layer. Overall, by explicitly considering maximum rooting depth, biomass density, and uptake kinetics, ECA is the only hypothesis that captured NH_4^+ uptake patterns for all three tundra species.

4. Discussion

4.1. Trait-Based Plant-Microbe Competition Modeling

For *Carex aquatilis* and *Salix rotundifolia*, the observed NH_4^+ uptake profiles were consistent with the prevailing hypothesis that fine-root biomass density, as functionally absorptive tissues, exerts first-order control on nutrient uptake [*De Baets et al*., 2007; *Vamerali et al*., 2003]. For *Eriophorum angustifolium*, however, the

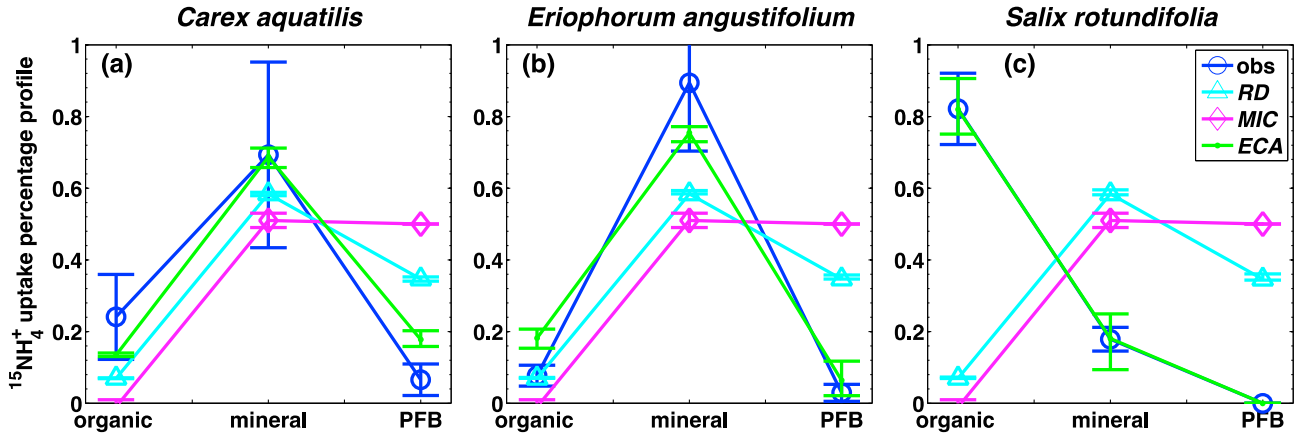

Figure 4. Comparison of NH_4^+ uptake profiles (*x* axis: from organic layer to permafrost boundary (PBF)) between observations (blue lines) and predictions by competition models for (a) *Carex aquatilis*, (b) *Eriophorum angustifolium*, and (c) *Salix rotundifolia*. We considered three alternative competition models: (1) N-COM uses ECA competition (green lines); (2) RD assumes that the plant NH_4^+ uptake is based on demand and profile is proportional to soil NH_4^+ profile (cyan lines); and (3) MIC assumes that microbial decomposers outcompete plants (magenta lines). Error bars represent the associated uncertainty (standard deviation).

observed uptake profile did not follow the prevailing hypothesis. We showed that this pattern resulted from decreased competition between roots and microbial decomposers in mineral soils. The ECA competition hypothesis as integrated in the N-COM model explicitly represents these competitive interactions and accurately predicted the NH_4^+ uptake profile (Figure 4b, green line). The model results indicate that since *Eriophorum angustifolium* is a relatively poor competitor for NH_4^+ (i.e., low affinity, lower root density than the other two species), it shifts its uptake profile deeper in the soil, in order to avoid NH_4^+ competition with microbial decomposers in the organic layer. Root physiology traits suggest that the *Eriophorum angustifolium* root system is less carbon efficient. In particular, compared with *Carex aquatilis*, maintenance and growth respiration per gram of root are higher but root longevity is much shorter for *Eriophorum angustifolium* (1 or 2 years for *Eriophorum*, compared with up to 10 years for *Carex*) [*Billings et al*., 1977; *Shaver and Billings*, 1975]. Although root morphological traits suggest that *Eriophorum angustifolium* has higher root length per gram root biomass [*Eissenstat et al*., 2000], total root density is much lower than *Carex aquatilis* (*Eissenstat et al*. [2000] and this study). Furthermore, the *Eriophorum angustifolium* NH_4^+ uptake pattern is also consistent with the idea that microbial activity and N immobilization are highly limited by carbon availability. Compared with mineral soil layers, relatively higher carbon availability in surface organic layer (compared with subsurface mineral layers) will lead to higher potential of microbial activity and consequently higher microbial N immobilization demand and stronger nitrogen competition between plant and microbe [*Booth et al*., 2005]. Although both gross nitrogen mineralization and immobilization rates are commonly high in surface soils, net immobilization typically occurs because of strong microbial demand [e.g., *Iversen et al*., 2011].

Overall, our ^{15}N tracer measurements and modeling analysis at Barrow, Alaska, showed that plant nitrogen uptake patterns emerge from root and soil biotic competition, which could be predicted by essential root traits (e.g., biomass density and kinetics) and appropriate treatment of microbial competitive interaction. Although not studied here, mineral surfaces are also effective competitors for enzymes [*Sulman et al*., 2014; *Tang and Riley*, 2015], and further research is required to determine when those processes need to be included in nutrient and carbon cycle models.

4.2. Essential Root Traits for Trait-Based Land Model Development

In this study, we showed that an important complication in predicting arctic tundra vegetation species responses to warming is associated with their different root characteristics, which can affect their ability to compete for elevated nitrogen availability throughout the soil profile. In this sense, explicitly considering key root functional traits is particularly important for studying warming-induced fertilization effects on arctic vegetation. Here we highlight the importance of several essential root traits in controlling nitrogen uptake patterns.

First, maximum rooting depth is an important plant functional trait in modeling plant nitrogen uptake and response to arctic warming. More deeply rooted species can access existing and newly thawed deep soil

nitrogen [*Keuper*, 2012]. In addition, roots acclimated to low temperatures in deep soil may have higher nutrient uptake capacity than roots in warmer surface soils [*Chapin*, 1974]. However, nitrogen in deeper soil is available for plant acquisition for a relatively shorter period than nitrogen in near-surface soil because the active layer thaws and increases in thickness throughout the growing season. Shallow-rooting species access soil nitrogen nearer the surface, and do so in the context of stronger microbial competition, but with more abundant soil nitrogen and over longer periods during the growing season. Therefore, different tundra species may respond dramatically differently to climate warming-induced soil nitrogen availability changes. The tradeoffs and ecological significance of plant carbon investments to compete for nitrogen in relatively warm shallow soils with high microbial competition, or to access nitrogen in relatively cold deeper soils with less microbial competition warrant further investigation.

Second, root nitrogen uptake capacity is also an important trait for nutrient competitiveness. Species with low nitrogen uptake capacity (i.e., low V_{MAX}) must develop dense or long-lived roots (*Carex aquatilis*) in order to acquire enough soil nitrogen. For example, *Carex aquatilis*'s fine roots live for multiple years, and the fine-root to leaf biomass ratio can be as large as 16 [*Iversen et al*., 2015b]. In contrast, species with high nitrogen uptake capacity invest less carbon for the growth of relatively short-lived roots (*Eriophorum angustifolium*) [*Eissenstat et al*., 2000].

Third, tundra species with different carbon allocation strategies may contribute differently to carbon-climate interactions. For example, *Carex aquatilis* may fix more carbon per unit additional nitrogen uptake than *Eriophorum angustifolium*, because the former allocate more carbon to grow roots and root C:N ratios are much higher than leaves (C. Iversen, unpublished data, 2016). Carbon costs (growth respiration) of constructing roots are commonly lower than aboveground tissues [*Poorter*, 1994]. In addition, tissue lifespan [*Withington et al*., 2006], decomposability [*Hobbie et al*., 2010], maintenance respiration [*Segal and Sullivan*, 2014], and contribution to soil carbon accumulation [*Hu et al*., 2016] differ among leaves and roots. Integration of these essential root traits into ESMs will improve understanding of how arctic tundra plants will respond to climate warming, through informing the magnitude of warming-induced increases in nitrogen availability on tundra carbon production.

4.3. Data Availability for Trait-Based Land Model Development

Current ESM land models have rudimentary representations of plant traits because of (1) a lack of mechanistic understanding of how those traits control plant and ecosystem biogeochemical processes and (2) a lack of trait data to structure and parameterize large-scale simulations. We have recommended several key traits, which should improve predictions of root nitrogen uptake and how arctic tundra plants may respond to warming-induced elevated nitrogen availability. Some knowledge of the global spatial distributions of several of the aforementioned root traits is available. For root biomass profiles, the first global database was presented by *Jackson et al*. [1996]. *Zeng* [2001] further analyzed those biomass profile data according to Plant Functional Types (PFTs) and derived PFT-based root distribution data needed for large-scale land models. *Schenk and Jackson* [2002] expanded the *Jackson et al*. [1996] data set to include 475 root biomass profiles. However, most of those profile data are from temperate regions (i.e., United States and European countries). Tropical and arctic ecosystems are largely undersampled. Moreover, the PFT-based root distributions have not been updated accordingly.

A global-scale maximum rooting depth data set was synthesized by *Canadell et al*. [1996] and included 253 plant species. They also aggregated maximum rooting depth data based on PFTs, which is readily applicable to large-scale land models. The rooting depth followed the order: forest > shrub > herbaceous plants > crops. However, within-PFT variation was quite large. For example, the maximum rooting depth of tropical species (*Boscia albitrunca*) was 68 m, while the mean of tropical evergreen plant maximum rooting depth was about 15 m. Particularly for arctic tundra, a more detailed rooting depth data set was developed by *Iversen et al*. [2015a]. Tundra maximum rooting depth ranged from 0.7 cm for a deciduous shrub species (*Vaccinium myrtillus*) to 100 cm for a forb species (*Chamerion angustifolium*). In general, evergreen shrub tundra has the shallowest rooting depth (~10 cm). Grass, forb, and deciduous shrub tundra have deeper root systems (~20 cm), and sedge tundra has the deepest roots (~28 cm). This data set casts doubt on land model PFT classifications for arctic tundra. For example, CLM and ALM represent arctic tundra with only two PFTs (arctic grass and shrub), which substantially underrepresents root traits across the wide range of dominant tundra species, including arctic grasses, sedges, forbs, deciduous shrubs, and evergreen shrubs [*Chapin et al*., 1996].

Root nitrogen uptake kinetics traits, including V_{MAX} and K_M, are frequently measured or estimated in laboratory and field experiments. However, these measurements are species specific [*BassiriRad et al*., 1996a; *BassiriRad et al*., 1999; *BassiriRad et al*., 1996b; *Cruz et al*., 1993; *Eltrop and Marschner*, 1996; *Hangs et al*., 2003; *Høgh-Jensen et al*., 1997; *Kronzucker et al*., 1995, 1996; *Leadley et al*., 1997; *Min et al*., 2000]. To our knowledge, a PFT-based kinetics parameters database is still lacking.

5. Conclusions

In this study, a ^{15}N field experiment was conducted to measure plant nitrogen uptake profiles for three dominant tundra species (*Carex aquatilis*, *Eriophorum angustifolium*, and *Salix rotundifolia*) at Barrow, Alaska. A mechanistic model was then used to explain the observed uptake patterns and test hypothesis about plant and microbe soil nutrient competition. Supported by the ^{15}N data and modeling results, we demonstrated that plant nitrogen competitiveness (as represented by root density and kinetics) exert first-order control on plant nitrogen uptake patterns. Our results imply that the prevailing hypothesis that root biomass density always dominates the nitrogen uptake profile [*Andrews and Newman*, 1970; *Bowman et al*., 2002; *De Baets et al*., 2007; *Jumpponen et al*., 2002; *Kristensen and Thorup-Kristensen*, 2004; *Vamerali et al*., 2003; *Xu et al*., 2011], which is coded in some root models [*Leadley et al*., 1997; *McMurtrie et al*., 2012; *Somma et al*., 1998], might be problematic in tundra systems. In addition, the current nutrient competition theories integrated in Earth System Land Models (Relative Demand and Microbes Win) were also unable to represent the observed NH_4^+ uptake patterns. Arctic tundra plant root functional traits responsible for nitrogen uptake are dramatically different among species. Arctic warming will probably enhance soil nitrogen availability in shallow [*Rustad et al*., 2001] and deeper soils [*Keuper*, 2012]. However, the ability of plants to access and compete for this nitrogen is species specific. Thus, we highlighted the importance of considering several key root functional traits related to nitrogen uptake in arctic studies. Furthermore, limited data are globally available on root traits to inform models, especially from arctic ecosystems, and targeted field campaigns are needed to address this limitation.

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