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A new theory of plant–microbe nutrient competition resolves inconsistencies between observations and model predictions

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Abstract. Terrestrial plants assimilate anthropogenic CO₂ through photosynthesis and synthesizing new tissues. However, sustaining these processes requires plants to compete with microbes for soil nutrients, which therefore calls for an appropriate understanding and modeling of nutrient competition mechanisms in Earth System Models (ESMs). Here, we survey existing plant–microbe competition theories and their implementations in ESMs. We found no consensus regarding the representation of nutrient competition and that observational and theoretical support for current implementations are weak. To reconcile this situation, we applied the Equilibrium Chemistry Approximation (ECA) theory to plant–microbe nitrogen competition in a detailed grassland ¹⁵N tracer study and found that competition theories in current ESMs fail to capture observed patterns and the ECA prediction simplifies the complex nature of nutrient competition and quantitatively matches the ¹⁵N observations. Since plant carbon dynamics are strongly modulated by soil nutrient acquisition, we conclude that (1) predicted nutrient limitation effects on terrestrial carbon accumulation by existing ESMs may be biased and (2) our ECA-based approach may improve predictions by mechanistically representing plant–microbe nutrient competition.

Key words: ¹⁵N tracer; earth system model; grassland; microbial N uptake; nutrient competition model; nutrient competition theory; plant N uptake; plant–microbe competition.

INTRODUCTION

Nutrients, especially nitrogen (N) and phosphorus (P), affect terrestrial ecosystem carbon cycling through their regulation of plant and soil microbial activity (Elser et al. 2007, Norby et al. 2010, Reich and Hobbie 2013). Natural terrestrial ecosystems are often nitrogen and (or) phosphorus limited (Vitousek 1984, Elser et al. 2007, LeBauer and Treseder 2008), with a general consensus that temperate and boreal ecosystems are commonly N limited (Tateno and Chapin 1997, Reich et al. 2006, Norby et al. 2010, Zhu and Zhuang 2013) while tropical forests are phosphorus limited (Cleveland et al. 2002, Davidson et al. 2004, Vitousek et al. 2010, Wright et al. 2011). In both cases, strong competition occurs between plants and microbes (Merckx et al. 1987, Bottner et al. 1999, Hu et al. 2001, Kuzyakov 2002, Dijkstra et al. 2010, 2013) so that (1) actual nutrient uptake by individual consumers is often less than their demand due to limited supply and (2) uptake of a nutrient by one consumer (e.g., plants) suppresses the functioning of other consumers (e.g., soil microbial decomposers).

Furthermore, as CO₂ concentrations increase, nutrient competition between plants and microbes is expected to intensify. Because elevated CO₂ concentrations fertilize plant carbon productivity, plants will require more soil

nutrients to facilitate enhanced photosynthesis and for tissue construction (Norby et al. 2010, Reich and Hobbie 2013). On the other hand, enhanced carbon assimilation dilutes tissue nutrient concentrations (Long et al. 2004, Norby and Iversen 2006) and lowers litter quality (i.e., higher litter C:N ratio). Decomposing lower quality litter implies that soil microbes may need to immobilize nutrients to maintain their stoichiometric balance (Hu et al. 2001, Manzoni et al. 2010). In addition, under elevated CO₂ conditions, available nutrients will progressively move from fast cycling tissues (e.g., leaves) to slow cycling tissues (e.g., wood), which induces progressive nutrient limitation (Luo et al. 2004) that further exacerbates nutrient limitations. Although increased external nutrient inputs (e.g., deposition, parent material weathering) and accelerated nutrient mineralization rates under warming soil conditions may enhance soil nutrient availability (Melillo et al. 2002) and partly ease plant–microbe nutrient competition, these additional nutrients may be insufficient to satisfy the enhanced plant nutrient demands (Hungate et al. 2003, Wieder et al. 2015).

To investigate nutrient competition and its effects on the terrestrial carbon cycle, different theories of plant–soil nutrient competition have been developed and implemented in Earth System Models (ESMs). However, theoretical justification and observational support for these theories are rarely discussed, which may have resulted in large biases in modeled nutrient and carbon cycling (Zhu and Riley 2015, Niu et al. 2016). To reconcile this inconsistency between theory, observations, and models, we

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focus on one overarching question in this study: Is there an observationally consistent, theoretically supported, and mathematically robust theory that is simple enough to implement in ESMs while accurately representing plant–microbe competition for nutrients?

To answer this question, we first survey four existing nutrient competition theories (CT1–CT4) and their implementation in ESMs (Table 1). In *Results*, we discuss in detail these four competition theories: CT1, no direct competition; CT2, microbial decomposers outcompete plants; CT3, competition depends on pore-scale soil fertility heterogeneity; and CT4, plant–microbe relative demand controls competition. Then we describe a new theory of nutrient competition (CT5) based on Equilibrium Chemistry Approximation (ECA) kinetics (Tang and Riley 2013, Zhu et al. 2016). We test our new theory together with other existing competition theories against

a unique observational data set of N competition in a grassland ecosystem.

MATERIAL AND METHODS

Data collection

To inform the development of ESM land models, observations have to satisfy two criteria. First, observations should capture plant and microbe competition at the whole-soil level, because the significance of microsite heterogeneity diminishes at this spatial scale. Second, measurements should target short-term nutrient uptake, thus enabling relatively clear separation of the instantaneous competitive interactions from other ecosystem dynamics that occur over longer time scales (e.g., microbial turnover and release of nutrients for plant uptake, changing plant

TABLE 1. Theories of plant and microbe nutrient competition.

Competition theory	Rationale	Ecosystem model implementation	Sources
Existing theory			
CT1. No competition	<ol style="list-style-type: none"> (1) Plants are nutrient limited; microbial decomposers are carbon limited. (2) Plants rely on inorganic nitrogen; microbial decomposers rely on organic nitrogen. 		Van Veen and Kuikman (1990), Berg (2000), Harrison et al. (2007)
CT2. Microbial decomposers outcompete plants	<ol style="list-style-type: none"> (1) Microbial decomposers are ubiquitous. (2) Microbial decomposers release inorganic nitrogen as “waste product” during soil organic matter decomposition. 	<ol style="list-style-type: none"> (1) Separately simulate plant and microbial decomposer nutrient uptake. (2) If soil inorganic nutrient is limited, immobilization is satisfied prior to plant uptake. 	Harmsen and Van Schreven (1955), Nadelhoffer et al. (1985)
CT3. Competition depends on pore-scale soil fertility heterogeneity	<ol style="list-style-type: none"> (1) Plants do not completely lose the competition. (2) Existence of plants exacerbates microbial nutrient limitation and suppress microbial immobilization at both microsite and whole-soil scales. 	Explicit modeling of microsite scale soil fertility heterogeneity, nutrient diffusion, root–microbe interactions (~mm spatial scale).	Hodge et al. (2000), Hu et al. (2001), Schimel et al. (1989), Wang and Bakken (1997)
CT4. Plant–microbe relative demand controls competition	<ol style="list-style-type: none"> (1) Plant nutrient demand is a proxy of nutrient uptake capacity. (2) Expedient approach to implement competition in large-scale models. (3) No need to introduce parameters describing nutrient uptake and competition. 	<ol style="list-style-type: none"> (1) Separately simulate plant and microbial decomposer nutrient uptake. (2) If soil inorganic nutrient is limited, both fluxes are down regulated proportional to demand. 	Thornton et al. (2007), Goll et al. (2012)
New theory			
CT5. Plant and microbe traits control competition	<ol style="list-style-type: none"> (1) Plants and microbes have specialized nutrient transporter enzymes to acquire soil nutrients. (2) Nutrient uptake rates are controlled by nutrient transporter enzyme abundances and enzyme–substrate affinity, both of which can be related to competitor traits. 	Treat plants, decomposing microbes, and nutrients as a coupled reaction network. Simulate plant and microbial nutrient uptake simultaneously by considering competitive interactions.	Tang and Riley (2013), Zhu and Riley (2015), Zhu et al. (2016)

allocation). To our knowledge, the only experiment that meets these two criteria was conducted in an alpine meadow ecosystem with homogeneous vegetation cover using a ^{15}N tracer (Xu et al. 2011). In this experiment, the investigators randomly selected 90 10 cm diameter microplots within a 25×25 m area and added 0.32 g N/m^2 in the form of $^{15}\text{N-NH}_4^+$ or $^{15}\text{N-NO}_3^-$ with three soil depths treatments. ^{15}N was injected at 2.5 cm, 7.5 cm, and 12.5 cm depth for 0–5, 5–10, and 10–15 cm treatments, respectively. The isotopic tracer was sampled 24 and 48 hours later, which informed partitioning of added nitrogen between microbes and plants. Furthermore, the grassland system has a very high rooting density, which allows us to isolate competitive interactions in the root zone from transport limitations so that observed competition patterns are directly comparable with theoretical models (see more explanation in *Discussion* and Appendix S2). For our model evaluation, we extracted the data points from Fig. 4 of Xu et al. (2011) using the matlab script GRABIT (*available online*).²

Competition theories and models

Below we first describe the theoretical underpinnings of the nutrient competition theories that we identified from the literature. Then we describe the rationale that leads to the new competition theory based on the Equilibrium Chemistry Approximation (ECA) kinetics. We then describe the strategy for quantitative evaluation of the different theories.

Existing nutrient competition theories.—Among the four existing theories surveyed, the traditional Nutrient Competition Theory (CT1; Table 1) assumes that plants and microbes do not compete for nutrients. This theory presumes that plants can assimilate carbon directly from the atmosphere but rely on nutrients released from soil microbial activity, so plants are carbon (C) rich but nutrient limited (Caldwell et al. 1992, Whitmarsh 1999). Conversely, because soil microbes decompose soil organic matter to obtain carbon and nutrients (Van Veen and Kuikman 1990, Berg 2000), they are relatively nutrient abundant but carbon limited (as confirmed by some soil priming experiments [Nottingham et al. 2009, Pascault et al. 2013], ^{14}C labeling studies [Farrell et al. 2014], and C/N/P factorial fertilization experiments [Allen and Schlesinger 2004]). A second reason ecologists hypothesize that plants and microbes do not compete is that microbes can directly use organic N during decomposition (e.g., monomers), while plants primarily use inorganic N (Harrison et al. 2007). However, depending on their carbon use efficiency (Schimel and Weintraub 2003, Manzoni et al. 2010) and biomass stoichiometric imbalances against substrates (i.e., soil organic matter; Harrison et al. 2007), microbes do

immobilize inorganic nutrients and thus directly compete with plants, creating the first contradiction against the CT1 theory. Further, plants may also utilize some low molecular weight amino acids through mycorrhizal fungi associations (Chapin et al. 1993, Näsholm et al. 1998) or direct root uptake (Chapin et al. 1993), which creates a second contradiction to the theory. However, no existing ESMs apply CT1 to represent nutrient competition (Table 2).

The second theory (Competition Theory 2 [CT2; Table 1) posits that microbial decomposers out-compete plants in nutrient acquisition. This theory assumes that microbial nutrient uptake is extremely efficient (Perakis and Hedin 2001), and microbes assimilate as much nutrients as they can during decomposition, provided they are not carbon (energy) limited. When carbon is limited, mineral nutrients are released as a “waste product” (Harmsen and Van Schreven 1955). This concept leads to the classic idea that plants can only use “leftover” nutrients after microbial demands are satisfied (Schimel and Bennett 2004), which is why measured net mineralization rates (not gross mineralization rates) are commonly used as a proxy for plant-available nutrients (Nadelhoffer et al. 1985). However, no evidence exists to support its validity at the whole-soil or ecosystem level. In contrast, ^{15}N labeling studies have demonstrated that plants can continuously acquire inorganic nutrients, even when both plants and microbes are nutrient limited (Marion et al. 1982, Jackson et al. 1989, Yevdokmov and Blagodatsky 1993). Other observations indicate that plants may even suppress microbial nutrient uptake (Wang and Bakken 1997, Hu et al. 2001).

CT2 has been applied in several ESMs. HadGEM2 (Bradbury et al. 1993, Smith et al. 2010) and GFDL (Gerber et al. 2010, Lee et al. 2014) assume that soil microbial decomposers always outcompete plants and have priority for available nutrients (i.e., microbial immobilization first, then plant uptake). IPSL (Zaehle and Friend 2010) and BNU-ESM (Ji et al. 2014, Xu and Prentice 2008) also assume that microbial immobilization has priority, but apply this priority to the estimated gross mineralization flux in the current model time step, as opposed to the nutrient pool.

The third competition theory (Competition Theory 3 [CT3; Table 1) applies the emerging perspective that plant–microbe nutrient competition depends on the spatial heterogeneity of soil nutrient fertility, and therefore plants do not completely lose the competition at the whole-soil or ecosystem level. In a heterogeneous soil medium, inorganic nutrients move from nutrient-rich microsites (net mineralization) toward nutrient-limited microsites (net immobilization), with roots potentially intercepting the nutrients (Schimel et al. 1989, Wang and Bakken 1997, Hu et al. 2001, Schimel and Bennett 2004). CT3 has been integrated into very fine-spatial scale (on the order of millimeters) models that explicitly consider the role of microsite soil nutrient heterogeneity, nutrient diffusion, root–microbe interactions (Korsaeth et al.

² <https://www.mathworks.com/matlabcentral/fileexchange/7173-grabit>

TABLE 2. Summary of nitrogen processes and competition representations in Earth system models (ESMs).

Models	Land component	Plant N uptake	Soil N immobilization	Competition	Sources
BNU-ESM	CoLM + BNU-DGVM	$N_{\text{demand}} \times N_{\text{stress}}$	no gross mineralization and immobilization, net mineralization is directly calculated	microbial decomposers outcompete plants (CT2)	Ji et al. (2014), Xu and Prentice (2008)
CESM	CLM4.5-BGC/CLM4-CN/ CLM4-CNP	$N_{\text{demand}} \times N_{\text{stress}}$ or $N_{\text{require}} \times \min\{N_{\text{stress}}, P_{\text{stress}}\}$	C fluxes between soil organic matter pools scaled by their soil C:N ratios	relative demand (CT4)	Koven et al. (2013), Yang et al. (2014)
IPSL	ORCHIDEE (now O-CN)	$f_{\text{max}} \times C_{\text{root}} \times [N_{\text{av}}] \times f_T \times f_{\text{NC}}$	C fluxes between soil organic matter pools scaled by their soil C:N ratios	microbial decomposers outcompete plants (CT2)	Li et al. (2000), Zaehle and Friend (2010)
GFDL	LM3 (now LM3-TAN)	$V_{\text{max}} \cdot C_{\text{root}} \cdot \frac{[N_{\text{pl}}]}{K_M + [N_{\text{pl}}]}$	C fluxes between soil organic matter pools scaled by their soil C:N ratios	microbial decomposers outcompete plants (CT2)	Gerber et al. (2010), Lee et al. (2014)
HadGEM2	JULES (now JULES+ECOSSE)	$N_{\text{demand}} \times f_T$	C fluxes between soil organic matter pools scaled by their soil C:N ratios	microbial decomposers outcompete plants (CT2)	Bradbury et al. (1993), Smith et al. (2010)
MPI-ESM	JSBACH (now JSBACH-CNP)	$N_{\text{demand}} \times \min\{N_{\text{stress}}, P_{\text{stress}}\}$	C fluxes between soil organic matter pools scaled by their soil C:N ratios	relative demand (CT4)	Goll et al. (2012)
NorESM	CLM-CN	$N_{\text{demand}} \times N_{\text{stress}}$	Carbon fluxes between soil organic matter pools scaled by their soil C:N ratios	relative demand (CT4)	Thornton et al. (2007), Bentsen et al. (2013)

Notes: N_{demand} and N_{stress} are nitrogen demand (calculated by potential NPP and plant C:N ratio) and nitrogen down-regulation factor (nitrogen supply divided by plant nitrogen demand); f_{max} and K_M are maximum uptake rate and affinity parameter; $[N_{\text{av}}]$, $[NH_4^+]$, and $[NO_3^-]$ are soil free nitrogen, ammonium, and nitrate concentrations; C_{root} is root biomass; and f_T and f_{NC} are soil temperature and plant NC status factors, respectively.

2001, Raynaud and Leadley 2004), and microbe–microbe competition (Kaiser et al. 2014). In these models, plants do not completely lose the competition with microbes because they can take advantage of fine-scale spatial gradients between immobilizing and mineralizing microbes. The emergent responses from these models indicate that nutrient diffusion rates, sink strength (i.e., root uptake kinetics), and competitor spatial distributions are the most important factors affecting plant competitiveness. However, these models' fine spatial resolution is not directly applicable to ESMs. In ESMs, each soil column is assumed to be a well-mixed environment of nutrients and competitors. Such an assumption is currently necessitated, at least, by limited computational power and observations. Although ESM spatial resolutions likely will become finer, simulating microsite-level soil heterogeneity will remain impractical in the near future. In addition, a model based on CT3 may have high explanatory value but low predictive value, because it requires fine resolution observations of soil heterogeneity (nutrient, microbes, and roots).

The fourth nutrient competition theory (Competition Theory 4 [CT4]; Table 1) has been applied in several ESMs. In these ESMs, plant nutrient demand is simulated based on potential Net Primary Production (NPP) in the absence of nutrient constraints and the plant C to N ratio (C:N); an analogous approach is taken for microbial nutrient demand. When soil nutrient supply is insufficient to satisfy these demands, both plant and microbial demands are reduced in proportion (a reduction factor) to their respective demands (Goll et al. 2012, Yang et al. 2014). The actual NPP is then calculated by rescaling NPP demand with the reduction factor. This “relative demand” theory implicitly assumes that the consumer (plant or microbe) with higher demand will be relatively more competitive. While being simple, the CT4 predicted plant nutrient uptake is mechanistically inconsistent with measurements (McFarlane and Yanai 2006, Hawkins et al. 2014), although Goll et al. (2012) argued that the “demand-driven” approach requires fewer model parameters. The ESMs that apply CT4 include CLM-CN and NorESM (Thornton et al. 2007, Bentsen et al. 2013, Koven et al. 2013, Yang et al. 2014), CLM-CNP (Yang et al. 2014, 2016), and JSBACH-CNP (in MPI-ESM [Goll et al. 2012]).

The ECA-based nutrient competition theory.—The final competition theory (CT5) is based on the concept of substrate–enzyme interactions (Tang and Riley 2013) applied to multiple nutrients and consumers (Zhu and Riley 2015, Zhu et al. 2016). Substrate–enzyme kinetics theory has been extensively applied to model enzyme mediated processes (Farquhar et al. 1980, Grant et al. 2010, Tang and Riley 2013); however, its potential to represent plant and microbe nutrient competition is under-appreciated. Previous work that used the Michaelis-Menten equation to calculate nitrogen uptake (Hunt 1977, Coughenour 1984) only considered one carrier enzyme and one substrate at a time. To our

knowledge, this study is the first that successfully extends classic enzyme kinetics theory to reconcile inconsistencies between observed plant and microbe nutrient competition and predictions from existing ESM competition theories.

The substrate–enzyme view of plant nutrient uptake (Bassirirad 2000, Williams and Miller 2001) posits that first, extra-cellular enzymes, primarily produced by microbes, degrade polymers into monomers and inorganic nutrients, and second, plants produce nutrient transporter enzymes (E) specialized for each mineral nutrient (S) (e.g., ammonium, NH_4^+ ; nitrate, NO_3^- ; phosphate, PO_x ; Fig. 1). These plant-membrane-bound transporter enzymes react with substrates and form complexes (C), which are then transported into the root cell, after which the transporter enzymes are freed for the next substrate acquisition. Similar uptake mechanisms have been identified for microbes (Button 1985, 1998, Allison 2012, Stone et al. 2012). This “nutrient carrier enzymes mediating uptake” conceptual framework allows us to extend the classic enzyme kinetics theory to represent plant–microbe competition based on the Equilibrium Chemistry Approximation (ECA) theory (Zhu et al. 2016) and functional traits of the organisms. The same idea has provided the theoretical basis for the classic Michaelis-Menten (MM) type representation of nutrient uptake (Williams and Miller 2001, Näsholm et al. 2009) (e.g., used by O-CN [Zaehle and Friend 2010] and LM3 [Gerber et al. 2010]). However, classic enzyme theory and the resulting MM kinetics only consider one carrier enzyme and one substrate at a time, making them theoretically unable to

represent competitive interactions among multiple consumers (enzymes) for multiple substrates.

The novelty of the ECA approach is that it systematically considers multiple nutrient carrier enzymes and substrates together, and provides a rigorously derived and theoretically supported mathematical solution (Tang and Riley 2013). It is also more accurate than the MM kinetics for cases involving only one carrier enzyme and one substrate (Tang 2015). No current ESMs apply the ECA theory, although we are integrating it into the ACME Land Model (ALM; Zhu and Riley 2015). This work represents our first attempt to demonstrate its utility for plant–microbe nitrogen competition.

Formulation of CT2 and CT4 models.—For CT2 and CT4, we assume that microbial N demand is proportional to microbial biomass density (see detailed discussion in *Formulation of the CT5 (ECA) model*). In both theories, plant N demand is calculated as alpine meadow NPP (Wang et al. 2010) divided by plant C:N ratio (Wang and Moore 2014; constant throughout the short-term experiment). Because the plant and microbial N demands are estimated prior to competition, the actual N uptake used for metabolics activities or biomass production is usually smaller than demand. Specifically, the microbial and plant N demands are

$$\text{UP}_{\text{mic}} = a \cdot C_{\text{mic}} \quad (1)$$

$$\text{UP}_{\text{plant}} = b \quad (2)$$

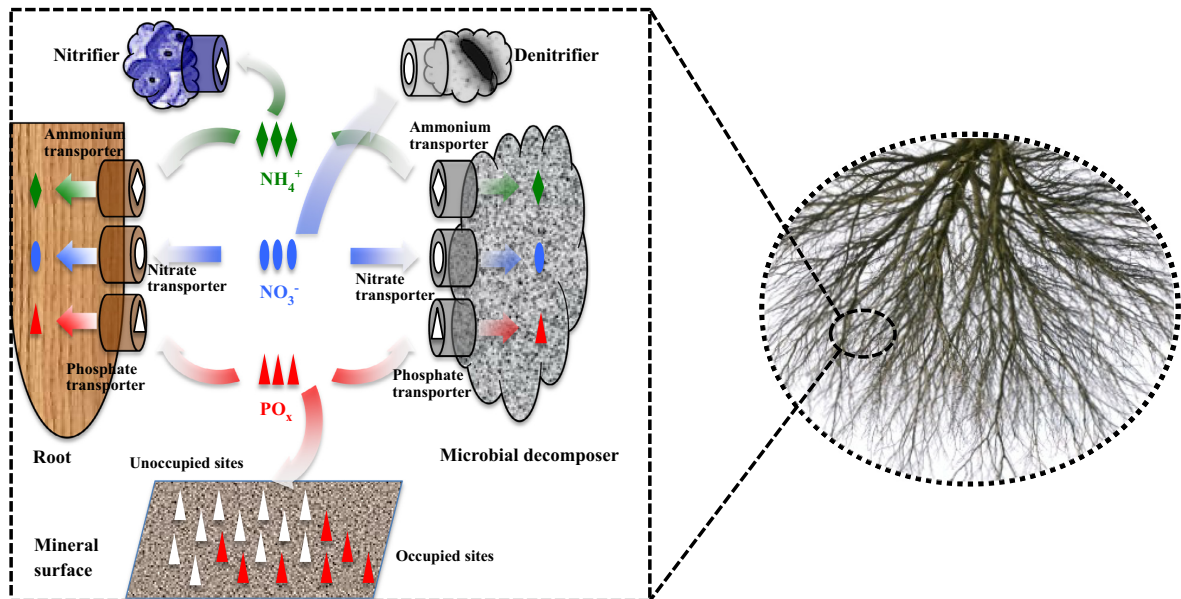


FIG. 1. Illustration of soil nutrient competition: (1) plants, microbial decomposers, and nitrifiers compete for NH_4^+ ; (2) plants, microbial decomposers, and denitrifiers compete for nitrate; (3) plants, microbial decomposers, and mineral surfaces compete for phosphate. This new competition paradigm is based on the competitor–substrate reaction network. Each competitor has its own specialized transporter enzyme to take up a particular nutrient molecule. In this study, the modeling framework is applied to NH_4^+ and NO_3^- competition between plants and microbial decomposers. [Color figure can be viewed at wileyonlinelibrary.com]

where a scales microbial biomass density to microbial nitrogen uptake (UP_{mic} [$g\ N\cdot m^{-3}\cdot h^{-1}$]) and b is nitrogen uptake by plant (UP_{plant} [$g\ N\cdot m^{-3}\cdot h^{-1}$]), calculated by NPP dividing by plant C to N ratio. Since the observed nitrogen competition patterns were reported in terms of nitrogen partitioning between plants and microbes (Xu et al. 2011), we modeled the nitrogen partitioning to enable direct comparison with observations. The CT2 model assumes that microbial decomposers always out-compete plants, leading to the following predicted nitrogen partitioning

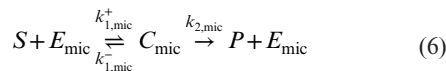
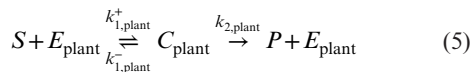
$$\frac{UP_{mic}}{UP_{plant}} = \frac{a \cdot C_{mic}}{[S] - a \cdot C_{mic}} \quad (3)$$

where $[S]$ is the total nitrogen supply ($g\ N/m^3$). Since the CT4 model assumes that microbe and plant competitiveness are proportional to their demand, CT4 predicts that

$$\frac{UP_{mic}}{UP_{plant}} = \frac{a \cdot C_{mic}}{b} \quad (4)$$

Formulation of the CT5 (ECA) model

The CT5 approach assumes plant and microbial nutrient uptake follow substrate-enzyme kinetics



where k are the reaction rates. Superscripts $+$ and $-$ indicate forward and backward reactions, respectively. Subscripts $_{plant}$ and $_{mic}$ represent the specialized enzymes produced by plants and microbial decomposers, respectively. Eqs. 1 and 2 are single substrate and single enzyme reaction networks (Michaelis and Menten 1913). When combined, competitive interactions occur between consumers (i.e., plants and microbes). For example, if substrates were limiting, binding between S (g/m^3) and E_{plant} (g/m^3) would inhibit binding between S and E_{mic} (g/m^3). Compounds and enzymes that interact with abiotic agents such as mineral surfaces will also affect the relative interactions between the various nutrient consumers (Fig. 1). In this short-term study, we assume that NH_4^+ in the aqueous and adsorbed phases equilibrate rapidly, and therefore the total amount of NH_4^+ available for competitors will be relatively unaffected by mineral surface interactions.

To account for the competitive interactions in a manner appropriate for ESMs (i.e., without explicitly resolving the kinetics), we compute the ECA kinetics (Tang and Riley 2013, Zhu and Riley 2015, Zhu et al. 2016) based nutrient uptake by plants (UP_{plant}) and soil microbes (UP_{mic}) as

$$UP_{plant} = k_{2,plant} \frac{E_{plant}[S]}{K_M^{plant} \left(1 + \frac{[S]}{K_M^{plant}} + \frac{[E_{plant}]}{K_M^{plant}} + \frac{[E_{mic}]}{K_M^{mic}} \right)} \quad (7)$$

$$UP_{mic} = k_{2,mic} \frac{E_{mic}[S]}{K_M^{mic} \left(1 + \frac{[S]}{K_M^{mic}} + \frac{[E_{plant}]}{K_M^{plant}} + \frac{[E_{mic}]}{K_M^{mic}} \right)} \quad (8)$$

In Eqs. 7 and 8, we have assumed a well-mixed soil environment (but nevertheless with an assumed pore structure as characterized by pedotransfer functions in an ESM). For equal levels of enzymes, the model will predict that plants are less competitive than microbial decomposers, because the observed affinity parameter (K_M) is typically higher (thus lower affinity) for plants than microbes (Kuzaykov and Xu 2013). The model also allows the competitiveness of plants and microbes to be dynamic (E_{plant} and E_{mic} are scaled by root and microbial biomass). Microbial transporter enzyme density could also be affected by stoichiometric imbalance between microbial decomposer and soil organic matter (Manzoni et al. 2008). However, microbial C to N stoichiometry variability is relatively narrow (7.4–8.1; Xu et al. 2013), and in similar alpine grassland ecosystems vertical profiles of soil C to N ratios show little variation (Heman et al. 2016). Thus, we do not consider the stoichiometric imbalance effect in this study. Root biomass profile is calculated based on the observed range (Xu et al. 2011) and its vertical distribution (Zeng 2001). Microbial biomass is set by the observed total biomass (Xu et al. 2011) and a typical vertical profile for grassland ecosystems (Xu et al. 2013). By scaling nutrient transporter enzyme abundance with root biomass density, the model structure recognizes that plant root density affects competitiveness. As a result, plant roots can out compete microbes if the root density is sufficiently high (e.g., in the topsoil).

Therefore, taking together Eqs. 3 and 4, the ECA approach calculates the observed uptake ratio as

$$\frac{UP_{mic}}{UP_{plant}} = \frac{k_{2,mic} \cdot [E_{mic}] \cdot \left(K_M^{plant} + [S] + [E_{plant}] + \frac{[E_{mic}] \cdot K_M^{plant}}{K_M^{mic}} \right)}{k_{2,plant} \cdot [E_{plant}] \cdot \left(K_M^{mic} + [S] + \frac{[E_{plant}] \cdot K_M^{mic}}{K_M^{plant}} + [E_{mic}] \right)} \quad (9)$$

We applied two approaches to estimate the parameters for this model: (1) using literature values based on measurements in other systems and (2) using a Bayesian inversion approach (Appendix S1) to estimate parameters based on the observations. Our hypothesis was that the observed competitive pattern would be predicted by approach 1, and the accuracy of the competitive pattern would be improved by approach 2.

We assumed that plant and microbe nutrient transporter enzyme abundances (E_{plant} , E_{mic} [g/m^3]) are proportional to their biomass ($[E_{plant}] = f_{plant} \times C_{plant}$ and $[E_{mic}] = f_{mic} \times C_{mic}$). For approach 1, we set the scaling factors $f_{plant} = 1.25 \times 10^{-5}$ (Zhu et al. 2016) and $f_{mic} = 0.05$ (Tang and Riley 2013). K_M^{plant} and K_M^{mic} are set to $1.2\ g\ N/m^3$ and $0.18\ g\ N/m^3$ for NH_4^+ ; $1.8\ N/m^3$ and $0.41\ N/m^3$ for NO_3^- (Høgh Jensen et al. 1997, Kuzaykov and Xu 2013). $[S]$ is the observed N content $0.32\ g\ N/m^2$ (Xu et al. 2011).

The reaction rate k_{plant} is 10.8 h^{-1} for NH_4^+ and 8.9 h^{-1} for NO_3^- . The reaction rate k_{mic} is 0.32 for NH_4^+ and 0.26 for NO_3^- . These values are derived from the observed maximum uptake rates ($\text{VMAX}_{\text{plant}}$ is $9.7 \mu\text{mol}\cdot\text{g root}^{-1}\cdot\text{h}^{-1}$ for NH_4^+ and $8 \mu\text{mol}\cdot\text{g root}^{-1}\cdot\text{h}^{-1}$ for NO_3^- (Høgh Jensen et al. 1997); VMAX_{mic} is $48 \mu\text{mol}\cdot\text{g root}^{-1}\cdot\text{h}^{-1}$ for NH_4^+ and $39 \mu\text{mol}\cdot\text{g root}^{-1}\cdot\text{h}^{-1}$ for NO_3^- (Kuziyakov and Xu 2013)).

RESULTS

Modeling nutrient competition in a grassland ecosystem

We compared observations from the ^{15}N tracer study with three model structures for competition: CT2 (microbial decomposers outcompete plants), CT4 (plant–microbe relative demand controls competition), and CT5 (ECA). We were unable to build a model based on CT3 for the study site due to a lack of detailed information about soil N heterogeneity, root architecture, and N diffusion and mass flow rates. Further, such a complex model structure would currently be computationally intractable for ESM applications, although below we discuss a possible intermediate-complexity approach based on CT3 concepts that could be integrated with CT5 in an ESM land model.

The CT2 model predicts that topsoil plant ^{15}N uptake is very small due to large microbial nutrient demand (i.e., little “left-over” nutrient for plants). In contrast, because of lower microbial nutrient uptake at depth, there are more “left-over” nutrients and plant ^{15}N uptake is relatively higher, although root biomass density decreases with depth. Therefore, there is an increasing microbial to plant ^{15}N uptake ratio with increasing root biomass for the CT2 model (Fig. 2, green line).

For relative-demand-based competition (CT4), the predicted microbial nutrient uptake declines with depth, because topsoil litter substrates are nutrient depleted and microbial biomass declines sharply with depth (Xu et al. 2013). However, in this calculation, the whole plant nutrient demand (NPP divided by plant C:N ratio) is fixed. This constraint implies that microbial decomposers are more competitive in the topsoil than they are in subsoil, while plant competitiveness (as measured by relative N demand) remains constant across the soil profile. Therefore, the predicted ratio of microbial to plant ^{15}N uptake increases with increasing root biomass (Fig. 2, red line).

The CT2 and CT4 models were unable to match the observed nitrogen partitioning between microbes and plants. Comparing CT2 and CT4 in the topsoil, CT2 predicted a much higher ratio of the microbe to plant ^{15}N uptake, because plants do not completely lose the competition in the relative demand approach (CT4). Importantly, in our evaluation, both CT2 and CT4 resulted in nutrient competition profiles qualitatively opposite to those observed. We also confirmed that no combination of parameters for either CT2 or CT4 could

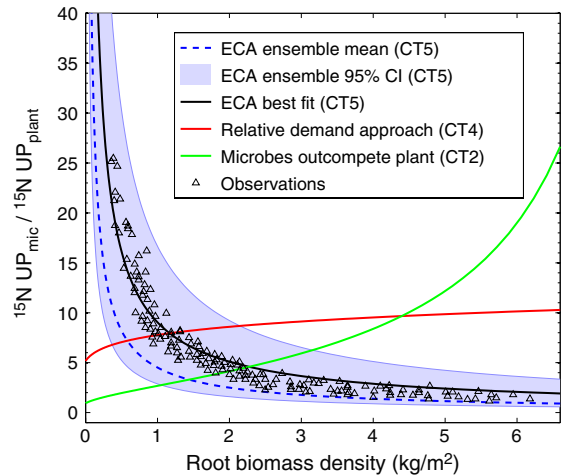


FIG. 2. Observed plant and microbe competition pattern (triangles) compared with (1) relative demand competition theory (CT4; red line); (2) “microbes outcompete plant” competition theory (CT2; green line); and (3) the new competition theory based on equilibrium chemistry approximation (ECA) kinetics (CT5). The blue dashed line is the mean of ECA ensemble predictions using literature-derived parameters from other grassland systems. The shaded area shows 5–95% percentiles of those ECA ensembles. The black line shows the best parameter fit ECA model for the observations at this site. Only the ECA competition theory captures the shape and magnitude of the observed competitive environment. Also see Appendix S2: Fig. S2a, which clarifies plant–microbe competition pattern when plant N uptake was small; Appendix S2: Fig. S2b, which is scatter plot of model–data comparison and associated root mean square errors. [Color figure can be viewed at wileyonlinelibrary.com]

reproduce the qualitative shape of the observed competitive relationship because, for both CT2 and CT4 models, the target variable $\text{UP}_{\text{mic}}/\text{UP}_{\text{plant}}$ is proportional to microbial biomass (high in topsoil and low in subsoil). Shaping parameters (a or b) only affect the steepness of $\text{UP}_{\text{mic}}/\text{UP}_{\text{plant}}$, but not the general trend.

The ECA approach (CT5) explicitly considers the substrates (nitrogen molecules) and enzymes (nitrogen carrier enzymes) competitive interactions throughout the profile. It captures the general competition pattern using literature-derived parameters from other ecosystems (Fig. 2, blue line and shaded area), and qualitatively and quantitatively captures the competition pattern using parameters derived for this site (Fig. 2, black line and shading for 95% CI).

DISCUSSION

Comparing model predictions with ^{15}N observations

The ECA representation of nutrient competition (CT5) provides a theoretical and modeling construct that resulted in very good comparison with the nitrogen uptake partitioning. These predictions demonstrate that (1) integrated across the soil profile, plants were less competitive than microbial decomposers; (2) plant

competitiveness against microbes is a spatially distinct property and there is no simple coefficient that can scale their “competitiveness”; (3) the ECA framework offers a theoretically consistent approach to continuously update individual competitiveness; (4) plant competitiveness is controlled by functional and structural traits (e.g., root biomass density, enzyme-substrate affinity); and (5) in the topsoil, plants might out-compete microbes and consequently suppress microbial nutrient uptake.

Of course, applying the ECA competition to ESMs comes at the cost of introducing new parameters and additional uncertainty associated with those parameters. However, the ECA approach does not necessarily increase overall model uncertainty (considering structural and parametric uncertainty). In fact, ECA competition largely reduced the uncertainty in global-scale predictions by considering essential processes that govern system dynamics (Zhu and Riley 2015). We argue that an analogous result occurred in this analysis, i.e., that the uncertainty reduction in model structure overwhelmed uncertainty associated with new model parameters. In addition, most of the ECA parameters are kinetic parameters, which can be directly measured or optimized (Zhu and Zhuang 2014, 2015), implying that targeted experiments and model calibration could further reduce parameter uncertainty.

Improving models of short-term nutrient competition

Nutrient competition constantly occurs between plants and microbes in natural terrestrial ecosystems and it will likely intensify under climate change (e.g., because of the likely higher nutrient demand under elevated CO₂; Hu et al. 2001). Therefore, two fundamental questions arise: (1) what controls the partitioning of limited nutrient resources between plants and microbes and (2) how should short-term competition be modeled?

Regarding the first question, we highlight the very few observations available to quantitatively partition nutrient acquisition by plants and microbes, and contend that such observations are critical to improve carbon-climate feedback predictions. As we showed here, the detailed ¹⁵N tracer experiment used in this study allowed us to evaluate the existing and newly developed plant–microbe N competition hypotheses, because the experiment was conducted at the plot scale and ¹⁵N was directly injected in the rooting zone (substantially reducing diffusion constraints; Appendix S2). Thus, most of the observed plant N uptake pattern reflected the direct competition between roots and microbes, via nutrient carrier enzymes quantity and quality.

Regarding the second question, we show here that plant and microbial nutrient uptake can be mechanistically explained as different nutrient transporter enzymes reacting with soil nutrients in a competitive manner. By linking plant root and microbial biomass density to nutrient transporter enzyme abundances, our new competition theory produces qualitatively correct competition

patterns with literature-derived parameters from other ecosystems, and is easy to calibrate for specific ecosystems. Further, the linkage of nutrient competition with plant and microbial traits will allow a model to represent the competitors’ dynamic allocation of resources to acquire necessary nutrients.

However, more work is required to determine how to better represent coupled microbe–plant nutrient competition and transport limitations. For example, we have previously shown (Tang and Riley [2013]; their equation 27) that one can apply a homogenous soil environment assumption (which implies some soil pore structure for substrate transport) and include the substrate diffusivity constraint in the ECA competition parameters. In this approach, the diffusivity constraint can be directly integrated into the substrate affinity (K_M) parameter. The “effective” K_M would be higher than the affinity measured, e.g., in a hydroponic chamber (which would not have diffusive constraints). We hypothesize that our calibrated K_M value, which led to an excellent match with the observations (Fig. 2), effectively accounted for this extra diffusive constraint on nutrient uptake.

A second approach would be to explicitly consider fine-scale soil fertility heterogeneity, explicitly represent nutrient movement (Nye and Tinker 1977, Gerber and Brookshire 2014), and apply the ECA framework at high resolution throughout the rhizosphere and bulk soil. However, to test, develop, and apply such a model requires (1) fine-scale measurements of soil nutrient concentrations, microbial activity, and rhizosphere properties and dynamics; (2) model representation of horizontal and vertical root architecture and microbial activity; (3) effective nutrient diffusivities; and (4) potentially, computational resources beyond what is practical in current ESMs. Yet, there is potential value in this approach if we can produce a reduced order version of the fine-scale model (Pau et al. 2014, 2016) that is reasonable and applicable to ESMs.

A third approach, of intermediate complexity, would be to simplify the spatial heterogeneity of root architecture, soil nutrient distributions, and nutrient transport. Roots could be conceptually clustered in the center of the soil column, where nutrients would become depleted and competition between microbes, roots, and abiotic processes would occur. Nutrients would diffuse and advect (Leadley et al. 1997) from the bulk soil toward the root zone. The “radius of influence” concept that defines a root influencing zone (Gerber and Brookshire 2014) could be used to simplify heterogeneity, with CT5 competition applied to this root influencing zone. More model development, large-scale application, and model-data comparisons are needed to justify such an approach.

As we argued above, the choice of nutrient competition theory used by ESMs faces a dilemma between necessary model simplification and accurate process representation. Our goal is to rigorously represent nutrient competition in ESMs with a simple framework that is consistent with theory and appropriate observational constraints while

not unduly sacrificing accuracy. We conclude that our ECA nutrient competition approach meets this goal, because it is simple enough to apply to climate-scale prediction and is based on reasonable simplifications to the complex nutrient competition mechanisms occurring in terrestrial ecosystems.

Limitations and future work

In this study, we only evaluated nutrient competition at a grassland site. Our recent work suggested that ECA is also applicable to tropical forest (Zhu et al. 2016a) and arctic tundra (Zhu et al., 2016b). However, a full comparison requires more observations in different ecosystems covering different climate regimes. ECA competition theory could support the inclusion of mycorrhizal fungi in ESMs (Treseder 2016) by expanding the consumer-substrate network (i.e., adding mycorrhizae as an additional consumer) and recognizing that mycorrhizal nutrient uptake is also mediated by nutrient transporter enzymes (Jongbloed et al. 1991). Although we do not consider mycorrhizal fungi association in this study due to lack of observations, it is possible that this omission may have contributed to the bias between the uncalibrated ECA model (Fig. 2, blue dashed line) and observations.

CONCLUSIONS

In conclusion, our modeling analysis and comparison with detailed field observations demonstrate that predicted plant and microbe competition and the resulting nutrient acquisition are very sensitive to the assumed functional form of competition. Among existing theories, we argued that CT2 (microbial decomposers outcompete plants) and CT4 (plant–microbe relative demand controls competition) are conceptually flawed and do not represent the observed nutrient competition. However, CT3 (competition depends on pore scale soil fertility heterogeneity) is a mechanistic approach that can represent millimeter scale soil heterogeneity and is supported by fine-scale measurements (Schimel et al. 1989). Unfortunately, a model based on CT3 may have high explanatory value but low predictive value, because it requires fine resolution observations of soil heterogeneity (nutrient, microbes, and roots) and its implementation requires resolving three-dimensional dynamics. Therefore, CT3 is not directly applicable to ESMs and is not currently feasible due to limited data availability. Our new ECA-based approach simplifies the complex nature of plant and microbe nutrient competition by linking competitiveness to competitor functional and structural traits (e.g., biomass density profile, affinity) and accurately represents the whole-soil level competition pattern. Importantly, these functional and structural traits are practically measured in the field.

Future researches are needed to evaluate the ECA competition at various different ecosystems.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/eap.1490/full>

DATA AVAILABILITY

Data associated with this paper have been deposited in a Dryad digital repository <https://doi.org/10.5061/dryad.7449j>