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Key Points:

- Mycorrhizae and simultaneous uptake are added to FUN, a plant nitrogen model
- Mycorrhizal trade-offs improve predictions of leaf nitrogen retranslocation
- Competition for nitrogen increases uptake costs in mixed mycorrhizal systems

Supporting Information:

- Tables S1 and S2, Figures S1 and S2, and Appendix S1
- Appendix S2

Correspondence to:
E. R. Brzostek,
edbrzost@indiana.edu

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Modeling the carbon cost of plant nitrogen acquisition: Mycorrhizal trade-offs and multipath resistance uptake improve predictions of retranslocation

Edward R. Brzostek[1], Joshua B. Fisher[2,3], and Richard P. Phillips[1]

[1]Department of Biology, Indiana University, Bloomington, Indiana, USA, [2]Jet Propulsion Laboratory, California Institute of Technology, Pasadena, California, USA, [3]Joint Institute for Regional Earth System Science and Engineering, University of California at Los Angeles, Los Angeles, California, USA

Abstract Accurate projections of the future land carbon (C) sink by terrestrial biosphere models depend on how nutrient constraints on net primary production are represented. While nutrient limitation is nearly universal, current models do not have a C cost for plant nutrient acquisition. Also missing are symbiotic mycorrhizal fungi, which can consume up to 20% of net primary production and supply up to 50% of a plant's nitrogen (N) uptake. Here we integrate simultaneous uptake and mycorrhizae into a cutting-edge plant N model—Fixation and Uptake of Nitrogen (FUN)—that can be coupled into terrestrial biosphere models. The C cost of N acquisition varies as a function of mycorrhizal type, with plants that support arbuscular mycorrhizae benefiting when N is relatively abundant and plants that support ectomycorrhizae benefiting when N is strongly limiting. Across six temperate forested sites (representing arbuscular mycorrhizal- and ectomycorrhizal-dominated stands and 176 site years), including multipath resistance improved the partitioning of N uptake between aboveground and belowground sources. Integrating mycorrhizae led to further improvements in predictions of N uptake from soil ($R^2 = 0.69$ increased to $R^2 = 0.96$) and from senescing leaves ($R^2 = 0.29$ increased to $R^2 = 0.73$) relative to the original model. On average, 5% and 9% of net primary production in arbuscular mycorrhizal- and ectomycorrhizal-dominated forests, respectively, was needed to support mycorrhizal-mediated acquisition of N. To the extent that resource constraints to net primary production are governed by similar trade-offs across all terrestrial ecosystems, integrating these improvements to FUN into terrestrial biosphere models should enhance predictions of the future land C sink.

1. Introduction

Terrestrial biosphere models are increasingly being used to simulate how future climate forcing will impact the carbon (C) balance of terrestrial ecosystems. Terrestrial biosphere models estimate net primary production using first principles based on environmental constraints (e.g., temperature and soil moisture) and in more recent versions, based on resource constraints [*Ostle et al.*, 2009]. In most of the world's ecosystems, nitrogen (N) is the resource that limits plant growth [*LeBauer and Treseder*, 2008; *Vitousek and Howarth*, 1991]. Accordingly, the current generation of terrestrial biosphere models now includes representations of simplified N cycles and coupled C-N cycles [*Sokolov et al.*, 2008; *Thornton et al.*, 2007; *Zaehle et al.*, 2010a]. However, as these models have come of age, key areas of uncertainty have emerged. For one, plant N uptake is often incorrectly represented as a mechanism that occurs until plants use all of the available soil N with no metabolic or acquisition cost in terms of C to the plant [*Lawrence et al.*, 2011; *Zaehle et al.*, 2010b]. It is well known that plant N uptake consumes a substantial proportion of C from net primary production that would otherwise be allocated to growth (globally, 50 Pg C [*Fisher et al.*, 2010]) and in the current terrestrial biosphere models, there is no consideration of dynamic belowground allocation by plants in response to changing resource availability [*Ostle et al.*, 2009]. Additionally, most terrestrial biosphere models do not dynamically predict retranslocation rates and assume that a constant fraction of N is retranslocated [*Thornton et al.*, 2007; *Zaehle and Friend*, 2010], despite evidence to the contrary [*Aerts*, 1996; *Chapin and Kedrowski*, 1983; *Kobe et al.*, 2005]. These limitations call into question the degree to which these models can project the future land C sink in ecosystems varying in fertility and subject to changes in nutrient availability.

Perhaps the largest uncertainty in the current generation of terrestrial biosphere models is whether the omission of explicit plant-microbial interactions, which are increasingly being recognized as dominant drivers of C-N couplings [*Johnson et al.*, 2013; *Phillips et al.*, 2013], is limiting the predictive ability of the models. Plants, for example, alter the patterns of C allocation to nutrient-scavenging and nutrient-mining microbes such as mycorrhizal fungi, and C transferred to the fungi can exceed 20% of net primary production, with mycorrhizae supplying over half of the N needed to support net primary production [*Hobbie*, 2006; *Hobbie and Hobbie*, 2008; *Hogberg and Hogberg*, 2002; *Parniske*, 2008]. Nearly all land plants associate with one of two types of mycorrhizal fungi, both of which offer differing trade-offs to the plant in their C cost and ability to provision soil N. Arbuscular mycorrhizal fungi primarily act as scavengers for soil nutrients by increasing the surface area-to-volume ratio of the fungal-root system [*Marschner and Dell*, 1994]. This strategy reflects the fact that arbuscular mycorrhizal plants often occupy more fertile sites [*Chapman et al*., 2006]. By contrast, ectomycorrhizal fungi are able to produce enzymes to mobilize N locked up in soil organic matter, a strategy that is advantageous in sites where greater retranslocation keeps soil fertility low, but also requires greater C expenditure to gain N [*Read and Perez-Moreno*, 2003]. There have been previous efforts to model C and nutrient transfers between mycorrhizae and plants. These models have shown that the mobilization of nutrients from soil organic matter by ectomycorrhizal fungi enhances soil carbon stocks [*Orwin et al*., 2011], plants reduce carbon allocation to arbuscular mycorrhizal or ectomycorrhizal fungi as nutrient availability increases [*Johnson et al*., 1997; *Meyer et al*., 2010], and plants can optimize C allocation to arbuscular mycorrhzal fungi to maximize growth benefits [*Fitter*, 1991]. However, the majority of these efforts have focused solely on arbuscular mycorrhizal or ectomycorrhizal fungi or are highly complex with a large suite of parameters that has precluded their assimilation by terrestrial biosphere models.

The Fixation and Uptake of Nitrogen (FUN) [*Fisher et al*., 2010] model provides a mechanistic framework to assess the impacts of both arbuscular mycorrhizal and ectomycorrhizal uptake strategies on coupled C-N cycles that can be easily assimilated by terrestrial biosphere models due to the limited input parameters (FUN is already coupled to the Community Land Model (CLM) [*Lawrence et al*., 2011] and the Joint UK Environmental Land Simulator (JULES) [*Clark et al*., 2011], with development plans for coupling into the Land surface Processes and eXchanges model (LPX) [*Prentice et al*., 2011] and the Jena-Diversity model (JeDi) [*Pavlick et al*., 2013] as well). FUN uses an optimal allocation scheme to maximize plant growth by allocating C to the uptake pathway with the cheapest C cost: retranslocation of N from leaves, trading C for soil N, or N fixation. Some simplifications and assumptions were made with the original FUN model that we refine and build on, in addition to the inclusion of mycorrhizae. We refined the model by addressing the assumption that total soil N and not mineral N is a proxy for plant-available N and the lack of simultaneous uptake from all three pathways in the original model. To update the serial nature of the uptake pathways, we included a parallel resistance uptake framework. Parallel resistance networks have commonly been used to model the transport of water from the soil through the plant into the atmosphere with the rate of water transport governed by the integrated resistance across every interface [*Sperry et al*., 1998; *Steudle and Peterson*, 1998; *Williams et al*., 1996]. Here we take a similar approach with the total plant nutrient uptake governed by the integrated resistance across a suite of potential N uptake pathways. Building upon these refinements, our primary research objective was to investigate whether mycorrhizal trade-offs improved the ability of the FUN model to predict (1) how much C is invested by the plant in N uptake, (2) how much N is transferred to storage upon leaf senescence, and (3) how the balance between soil N uptake and retranslocation of N from leaves shifts along fertility gradients.

2. Materials and Methods

2.1. FUN Model Description and Refinements

The original FUN model (herein FUN 1.0) uses a theoretical C economics framework to optimally allocate C to maximize net primary production and N uptake while maintaining C:N ratios and minimizing the C cost of N uptake [*Fisher et al*., 2010]. FUN can be readily coupled into existing terrestrial biosphere models because it has only nine model inputs that are simulated by the majority of existing terrestrial biosphere models (Table S1 in the supporting information). In sections 2.1.1 to 2.1.4, we briefly describe the four pathways for N uptake in the original model and highlight the refinements we have made to address model limitations (Figure 1). All of the FUN equations used to calculate the cost for each pathway as well as those used to optimize C allocation and a description of the model inputs are included in the Appendix S1 and Table S1 in the supporting information, respectively.

2.1.1. FUN 1.0 Uptake Pathways

FUN 1.0 has four pathways for plant uptake of N: N passive, active uptake, retranslocation, and biological N fixation [*Fisher et al*., 2010]. N passive is a free (i.e., no C cost) N source for the plant and represents the uptake of soluble N through the transpiration stream. The amount of N passive is dependent upon the transpiration

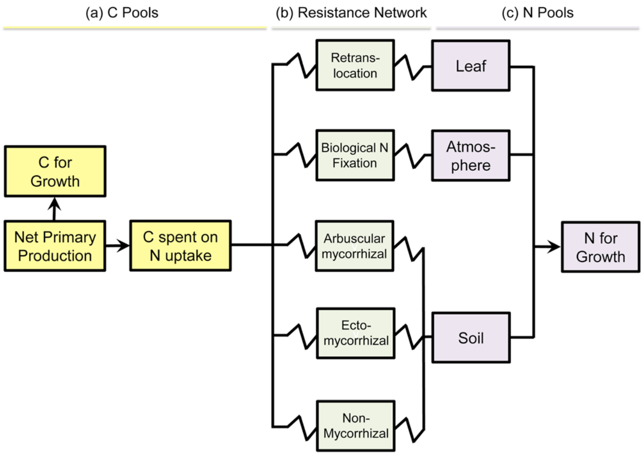

Figure 1. Conceptual diagram of FUN 2.0 model. (a) FUN optimally allocates C to growth and to N uptake as a function of the N needed to support net primary production and the integrated C costs across all of the pathways in the (b) resistor network. The amount of C spent on each pathway depends on the resistance through that pathway with the cost of nonmycorrhizal, ectomycorrhizal, and arbuscular mycorrhizal uptake depending upon soil N and fine root biomass (i.e., availability and access), the cost of biological N fixation depending on soil temperature, and the cost of retranslocation depending on the amount of foliar N. (c) The C spent on each pathway then returns N back to the plant to support growth from either the soil, atmosphere, or leaf N pool.

rates and the amount of dissolved N in soil solution. Active N uptake encompasses the energy required to move N into root cells and although not directly modeled does indirectly include the C exuded by roots to soil microbes. The cost of active uptake is modeled as a function of root biomass and soil N availability, with the cost increasing as root biomass and/or soil N decreases. Retranslocation is the removal of N from leaves prior to senescence with its cost increasing as leaf N decreases. Due to a lack of data on rates of root retranslocation of N at the sites, we did not include it in the model, but we acknowledge that it may be an important process to include in the future [*Freschet et al.*, 2010; *Kunkle et al.*, 2009]. Biological N fixation is the conversion of atmospheric N into mineral forms by symbiotic rhizobium that inhabit root nodules in exchange for plant C and also by free-living N fixers in the rhizosphere. The cost of biological N fixation is based on well-established measurements and constrained as a function of temperature [*Houlton et al.*, 2008]. In the new versions of FUN presented here, biological N fixation is enabled for all ecosystems to reflect the contribution of free-living N-fixing bacteria in the rhizosphere to plant nutrition [*Hayat et al.*, 2010]. Previously in FUN 1.0, biological N fixation was switched on or off, but we have updated FUN 2.0 to include biological nitrogen fixation on at all times, although it only becomes a factor when soil N levels are very low. We assume that free-living fixation has the same cost function as symbiotic fixation but acknowledge that they may differ.

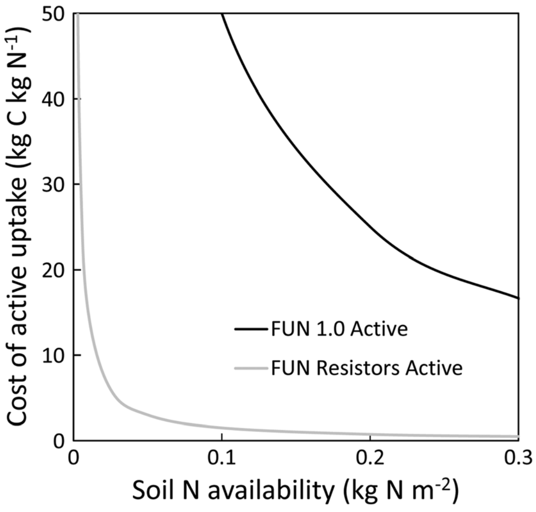

Figure 2. Comparison of active uptake cost functions between FUN 1.0 and FUN Resistors. Root biomass is held constant at 0.2 kg C m^{-2}. At a reasonable empirical level of N mineralization of 0.01 kg N m^{-2} yr^{-1}, FUN Resistors predicts a cost of 15 versus 500 kg C kg N^{-1} in FUN 1.0.

2.1.2. Revised Soil N and Root C Inputs

FUN 1.0 calculates the cost of active uptake using total soil N and includes coarse root C (i.e., those greater than 2 mm in diameter) in the root C pool. However, the majority of N in soil organic matter is not readily available to plants because of physical and chemical protection [*Nannipieri and Eldor*, 2009; *Schulten and Schnitzer*, 1998]. We have modified FUN 2.0 to use mineral N (i.e., the sum of NO_3^- and NH_4^+) to represent plant available N forms. This reflects that the mineralization of organic N into NO_3^- and NH_4^+ is highly correlated with net primary production and is also on the same order of magnitude as annual plant N demands [*Reich et al.*, 1997]. While there is evidence for species preferences for NH_4^+ or NO_3^- [*Harrison et al.*, 2007], we make the assumption that the costs are equivalent because evidence for differential costs is lacking with these preferences often thought to reflect the relative abundance of these forms in soil [*Gallet-Budynek et al.*, 2009]. For root C, we have excluded coarse root C from this pool due to the dominance of fine roots

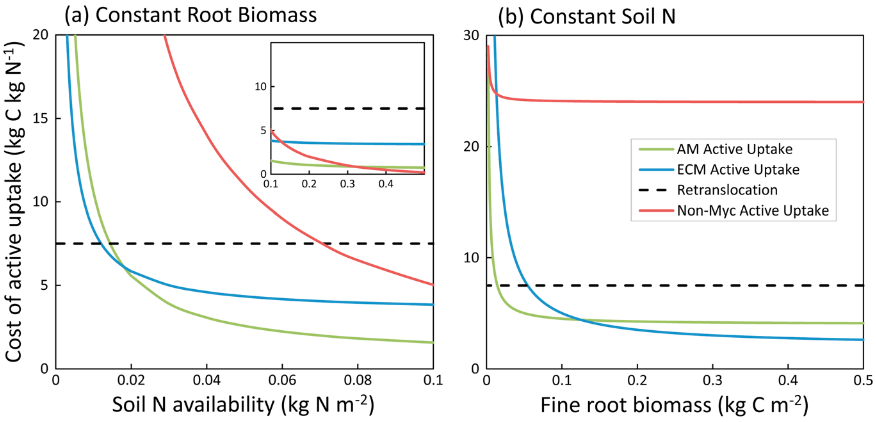

Figure 3. Response of the active uptake cost of arbuscular mycorrhizal (AM), ectomycorrhizal (ECM), and nonmycorrhizal pathways to changes in soil N and root biomass. (a) Under constant root biomass (0.1 kg C m^{-2}), uptake switches from ECM to AM as soil N increases. Inset in Figure 3a shows that at higher levels of soil N that nonmycorrhizal uptake is advantageous. (b) Under constant soil N (0.025 kg N m^{-2}), uptake switches from AM to ECM as fine root biomass increases.

(<2 mm diameter) in nutrient and water uptake due to their greater root length and surface area [*Eissenstat*, 1992]. Essentially, the model uses fine root biomass as a proxy for absorptive surface area and access to soil N. Thus, we have modified the parameters that govern the cost equations accordingly in the revised model (herein FUN Resistors; Figure 2, see Table S2 in the supporting information for parameter values).

2.1.3. Simultaneous N Uptake

We developed a resistance framework in FUN Resistors to allow all of the uptake pathways to occur simultaneously in parallel. In FUN 1.0, the pathways were switched on or off in serial with respect to the cheapest cost. This led to one pathway dominating uptake at the expense of the others and in some cases, the total depletion of some pools due to time step mismatches. To allow for simultaneous uptake, we coded a resistor framework which treated the N uptake pathways as resistors in parallel using Ohm's law:

$$\mathrm{N_{uptake}} = \mathrm{C_{acq}}/\mathrm{Cost_{acq}} \tag{1}$$

where nitrogen uptake ($\mathrm{N_{uptake}}$) is analogous to current, the cost is analogous to integrated resistance ($\mathrm{Cost_{acq}}$), and the C available to spend on N acquisition ($\mathrm{C_{acq}}$) is analogous to the potential difference. $\mathrm{Cost_{acq}}$ is calculated as the integrated resistant across all cost pathways:

$$1/\mathrm{Cost_{acq}} = 1/\mathrm{Cost_{fixation}} + 1/\mathrm{Cost_{active}} + 1/\mathrm{Cost_{resorb}} + 1/\mathrm{Cost_{n}} \tag{2}$$

Thus, $\mathrm{N_{uptake}}$ flows through each pathway at a rate determined by its resistance (i.e., cost) and the $\mathrm{C_{acq}}$. Importantly, new uptake pathways such as phosphorus uptake or the retranslocation of nutrients from roots could be easily added to the resistance network ($\mathrm{Cost_n}$).

2.2. Inclusion of Mycorrhizal Trade-Offs Into FUN

We developed a simple framework to include differential costs of active N uptake between ectomycorrhizal, arbuscular mycorrhizal, and nonmycorrhizal plants (Figure 3). This modeling framework builds upon the refinements in FUN Resistors (herein FUN 2.0). In contrast to FUN 1.0, a sum instead of a product is used in these cost equations:

$$\mathrm{Cost_{active}} = (K_\mathrm{N}/\mathrm{soil\ N}) + (K_\mathrm{C}/\mathrm{fine\ root\ C}) \tag{3}$$

This formulation enables the cost function to respond differentially to a change in either of the function parameters: K_N and K_C which control the cost as a function of soil N and root C, respectively. We simulated the ability of arbuscular mycorrhizal fungi to act as scavengers by reducing K_C relative to that of ectomycorrhizal fungi, effectively increasing the extent of the mycorrhizal-root system (parameters AK_C and AK_N; Table S2 in the supporting information). We simulated the ability of ectomycorrhizal fungi to use enzymes to mobilize N by reducing K_N relative to that of arbuscular mycorrhizal fungi (parameters EK_C and EK_N; Table S2 in the supporting information). The arbuscular mycorrhizal and ectomycorrhizal cost parameters were chosen so that the thresholds in nitrogen availability and root biomass, where arbuscular mycorrhizal or ectomycorrhizal fungi are

Table 1. Validation Site Characteristics[a]

Site	Acronym	Location	Latitude, Longitude	Dominant Tree Species	%ECM	Data References
Oak Ridge National Laboratory FACE	ORNL	Oak Ridge, TN	35°54′N, 84°20′W	*Liquidambar styraciflua*	0	*Johnson et al.* [2004] and *Finzi et al.* [2007]
Poplar FACE	POPFACE	Viterbo, Italy	42°22′N, 11°48′E	*Populus alba, Populus nigra, Populus euramericana*	0-50[a]	*Lukac et al.* [2003], *Hoosbeek et al.* [2006], and *Finzi et al.* [2007]
Duke Forest FACE	Duke	Durham, NC	35°58′N, 79°05′W	*Pinus taeda*	100	*Finzi et al.* [2006] and *Finzi et al.* [2007]
Rhinelander FACE	Rhinelander	Rhinelander, WI	45°40′N, 89°37′W	*Populus tremuloides; Betula papyrifera*	100	*Reich et al.* [1997] and *Finzi et al.* [2007]
Hubbard Brook Experimental Forest	HBEF	Woodstock, NH	43°56′N, 71°45′W	*Acer saccharum, Betula alleghaniensis*	20-90[a]	*Bohlen et al.* [2001], *Fahey et al.* [2005], and *Groffman et al.* [2011]
Morgan Monroe State Forest	MMSF	Martinsville, IN	39°19′N, 86°25′W	*Acer saccharum, Liriodendron tulipifera, Quercus alba*	40	*Ehman et al.* [2002], *Dragoni et al.* [2011], and *Brzostek et al.* [2014]

[a] The percentage of ectomycorrhizal trees varies as a function of species or elevation at the site.

more beneficial to the plant (Figure 3), mirror empirical shifts in the abundance of arbuscular mycorrhizal and ectomycorrhizal fungi and plants across fertility and latitudinal gradients [*Allen et al*., 1995; *Lilleskov et al*., 2001, 2002; *Phillips et al*., 2013]. This framework results in arbuscular mycorrhizal and ectomycorrhizal plants being more competitive at low root biomass or soil N, respectively (Figure 3). Nonmycorrhizal plants were simulated to be more costly than arbuscular mycorrhizal or ectomycorrhizal plants at low levels of soil N, because roots have limited ability to produce enzymes and have a lower surface area-to-volume ratio than fungal hyphae (Figure 3) [*Paungfoo-Lonhienne et al*., 2008]. At higher levels of soil N (inset Figure 3), the nonmycorrhizal strategy was modeled to be more beneficial, because the cost-to-benefit ratio of supporting mycorrhizae increases with a decline in limiting nutrients [*Johnson et al*., 1992, 2008; *Olsson et al*., 2010; *Phillips and Fahey*, 2007].

In addition to adding new mycorrhizal cost equations, incorporating mycorrhizal trade-offs necessitated other model refinements. We added a new input parameter to the model that describes the percentage of aboveground biomass that is composed of arbuscular mycorrhizal or ectomycorrhizal plants in each replicate experimental plot across all of the sites (i.e., % ectomycorrhizal (%ECM); Table S1 in the supporting information). For mixed plots, we then assume that net primary production, leaf N, and root biomass C are divided between arbuscular mycorrhizal and ectomycorrhizal plants depending upon their contribution to aboveground biomass. This separates the mixed plots into their ectomycorrhizal and arbuscular mycorrhizal fractions and allowed us to run the model for these mycorrhizal fractions in parallel. For example, in the ectomycorrhizal fraction of a plot, arbuscular mycorrhizal root uptake is turned off. However, the other pathways are modeled to occur based upon the divided input parameters. Importantly, we assumed that nonmycorrhizal uptake occurs for both fractions to reflect that not all roots of mycorrhizal plants are colonized. Finally, to generate model estimates at the replicate plot scale with the plot size varying for each site, we then integrate the modeled output for the ectomycorrhizal and arbuscular mycorrhizal fractions. When coupled to terrestrial biosphere models, the classification of each plant functional type within a grid cell as ectomycorrhizal, arbuscular mycorrhizal, or mixed along with the ectomycorrhizal/arbuscular mycorrhizal split will occur at the resolution of the larger model.

2.2. Model Validation

We validated the ability of all three model versions (i.e., FUN 1.0, FUN Resistors, and FUN 2.0) to predict observed total N uptake, retranslocation, and soil N uptake across a range of ecosystems. Importantly, these sites vary in mycorrhizal association ranging from ectomycorrhizal dominated to mixed to arbuscular mycorrhizal dominated, including four sites from the Free Air CO_2 Enrichment (FACE) experiments, one AmeriFlux site, and one site from the Long-Term Ecological Research (LTER) network. The four FACE experiment sites include (1) a sweet gum plantation at Oak Ridge National Laboratory, TN; (2) a loblolly pine forest at the Duke Forest, NC; (3) an aspen, birch, maple plantation in Rhinelander, WI; and (4) a poplar coppice plantation in Viterbo, Italy. The two natural forest sites are a sugar maple-oak-dominated forest at the Morgan-Monroe State Forest AmeriFlux site, IN, and a sugar maple-birch forest at the LTER site in Hubbard Brook, NH. The sites were chosen because they possessed detailed C and N budgets that included the model inputs (e.g., soil N mineralization, leaf N, and net primary production) and outputs for validation (e.g., retranslocation and soil N uptake). For all of the sites, there are multiple years of data and also replicate plots which result in a total of 176 site years for validation. The site characteristics and data sources are presented in Table 1, and the model inputs and outputs for each site are presented in Appendix S2 in the supporting information.

In the model, N demand is calculated as the product of the plant C-to-N ratio and net primary production. This exactly mirrors how total N uptake is calculated in the empirical N budgets. Further, N uptake from the soil is then calculated as the difference in the N required to support net primary production and retranslocation [*Finzi et al*., 2007]. Given these limitations of the empirical data, we primarily focus on the model predictions of the C costs of N uptake, retranslocation, and the balance between the different pathways.

For the new %ECM input parameter, we calculated the contribution of ectomycorrhizal and arbuscular mycorrhizal plants to standing biomass using known mycorrhizal associations for species at each site or site-specific colonization data [*Lukac et al*., 2003; *Phillips et al*., 2013]. We ran the model at an annual time step given the temporal resolution of the empirical data. We present the results of the original model to highlight how the step by step refinements made here impact model predictions.

We performed two additional model experiments to highlight the benefits of mycorrhizal versus nonmycorrhizal strategies across all of the different sites. In the first experiment, we ran the model using the ambient mycorrhizal strategy and at three levels of soil N availability from 0.001 kg N m^{-2} to ambient to 0.2 kg N m^{-2}. We then ran the model with only the nonmycorrhizal active pathway turned on at the same three levels of soil N and compared the C costs. In the second experiment, we focused on how shifting mycorrhizal association from all arbuscular mycorrhizal to ambient to all ectomycorrhizal impacted the C costs at the mixed mycorrhizal sites at the same three levels of soil N (i.e., Poplar FACE (POPFACE), Hubbard Brook Experimental Forest (HBEF), and Morgan Monroe State Forest (MMSF)).

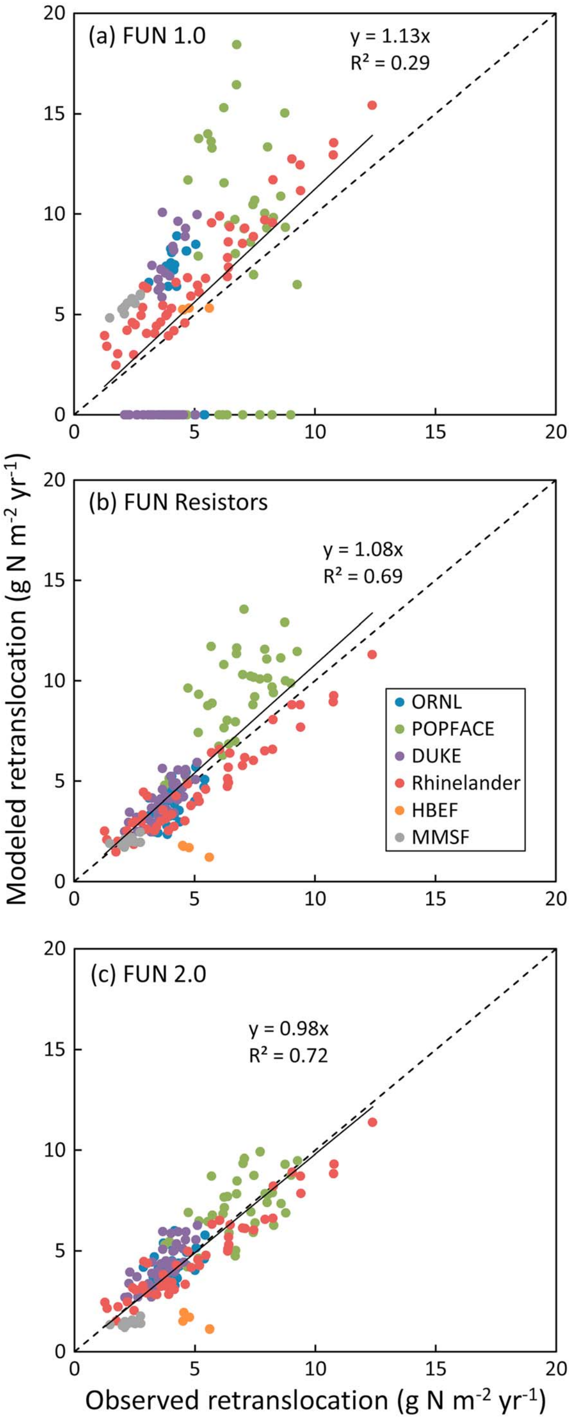

Figure 4. Stepwise improvement in model predictions of retranslocation across six sites that vary in mycorrhizal association from (a) FUN 1.0 to (b) FUN Resistors to (c) FUN 2.0. The dashed line indicates the 1:1 relationship. Sites and mycorrhizal association: Oak Ridge National Laboratory (ORNL; 100% AM), Poplar FACE (POPFACE; 0 to 50% ECM), Duke FACE (DUKE 100% ECM), Rhinelander FACE (100% ECM), Hubbard Brook Experimental Forest (HBEF; ~58% ECM), and Morgan Monroe State Forest (MMSF, 40% ECM).

3. Results

3.1. Total N Uptake

All three versions of the model performed well in predicting variability of observed total N uptake with $R^2 > 0.98$ (Figure S1 in the supporting information). This high R^2 reflects the reliance of the calculations of the empirical N budgets and N demand in the model on the C-to-N ratio of plant tissues and net primary production. However, there was an initial under prediction bias in FUN 1.0 (slope = 0.84); this bias was reduced stepwise moving to FUN Resistors (slope = 0.85) and FUN 2.0 as the carbon cost across the models decreased, which enabled more N uptake (slope = 0.93; Figure S1 in the supporting information). The largest difference between the three models was in predicting the N uptake observed at the POPFACE site, which had the highest net primary production, N demand, and observed N uptake. FUN 1.0 and FUN Resistors predicted N uptake that was only 81% and 86% of that observed on average across site years, respectively. By contrast, FUN 2.0 predicted much greater uptake that was 94% of the observed values.

3.2. Retranslocation

There was much greater variability between the FUN versions in their ability to predict retranslocation than total N uptake (Figure 4). FUN 1.0 performed poorly in predicting retranslocation across all of the site years ($R^2 = 0.29$, slope = 1.13; Figure 4a). At many sites, FUN 1.0 either overpredicted or did not predict any retranslocation. Retranslocation efficiencies greater than 95% were predicted by FUN 1.0 for 52 site years. Further, no retranslocation of leaf N was predicted for nearly 60 site years (Figure 4a). The inclusion of simultaneous uptake from all four pathways in FUN Resistors improved predictions by removing the all or nothing uptake of foliar N by retranslocation in FUN 1.0 ($R^2 = 0.69$, slope = 1.08; Figure 4b). There were not any site years where FUN Resistors predicted no retranslocation or predicted efficiencies greater than 95% (mean = 56%, standard deviation = 13%, min = 13%, max = 94%).

The addition of mycorrhizal pathways in FUN 2.0 resulted in the best model performance ($R^2 = 0.72$, slope = 0.98; Figure 4c). FUN 2.0 also predicted a narrower range of retranslocation efficiencies which reduced model bias (mean = 54%, standard deviation = 13%, min = 12%, max = 80%). Similar to the predictions of total N uptake, there was a progressive decrease in the model bias in predicting retranslocation with each model version. The biggest difference in performance between FUN 2.0 and FUN Resistors was observed for sites that have a mixture of both arbuscular mycorrhizal and ectomycorrhizal trees (POPFACE, MMSF, and HBEF) with FUN 2.0 predicting less retranslocation for these sites than FUN Resistors.

3.3. Soil N Uptake

The variability between the versions in the predicted amount of N taken up from the soil through active uptake and biological N fixation mirrored that of retranslocation (Figure S2 in the supporting information). This similarity in the results and high agreement in the new FUN model versions is due to the reliance of the empirical estimate for soil N uptake on retranslocation and N demand. Due to plant N demand being totally but unrealistically satisfied by retranslocation for some sites in FUN 1.0, particularly at the Rhinelander and Duke sites, FUN 1.0 predicted no uptake from the soil for 56 site years (Figure S2a in the supporting information). For those site years where FUN 1.0 predicted no contribution of retranslocation (Figure S2a in the supporting information), the entirety of plant N demand was met through soil N uptake. This switching between the cheapest uptake pathways results in a poor agreement between the predictions of FUN 1.0 and the observed data (Figure S2a in the supporting information).

Both versions of the model that allowed simultaneous uptake from all the pathways to occur improved the model predictions of soil N uptake (Figures S2b and S2c in the supporting information). The R^2 increased from 0.67 in FUN 1.0 to 0.91 and 0.96 in FUN Resistors and FUN 2.0, respectively. The increase in model performance from FUN Resistors to FUN 2.0 was primarily driven by the increase in the rates of soil N uptake predicted for the POPFACE site and resulted in a reduction in the bias in FUN 2.0 (Figure S2c in the supporting information).

3.4. Balance Between Pathways

The overall contribution of each pathway in meeting N demand showed clear distinctions between model versions (Figure 5). Across the vast majority of site years, FUN 1.0 predicted that either active uptake or retranslocation dominated (Figure 5a). In those site years where uptake from both pathways occurred, it is only when the leaf N or soil N pool was exhausted that FUN 1.0 switched to another pathway. By contrast, in FUN Resistors and FUN 2.0, there were no instances where only one pathway occurred (Figures 5b and 5c). FUN Resistors predicted less active uptake and a greater contribution of biological N fixation and retranslocation to overall plant uptake than FUN 2.0 (Figures 5b and 5c). At the HBEF mixed site, all the versions of FUN consistently predicted higher rates of soil N uptake and lower rates of retranslocation than observed. This site also had the lowest ratio of net primary production-to-soil N availability.

In FUN 2.0, uptake of N from the soil dominated in mixed and arbuscular mycorrhizal sites, whereas retranslocation was more important than soil N uptake at the ectomycorrhizal sites (Figure 5c). In the mixed sites, the contribution of the arbuscular and ectomycorrhizal pathways mirrored the aboveground dominance of these traits (Figure 5c). Also, in those sites with both pathways (POPFACE, HBEF, and MMSF) and at the arbuscular mycorrhizal dominated site (Oak Ridge National Laboratory (ORNL)), there was less reliance on biological N fixation and more nonmycorrhizal uptake (Figure 5c). At the ectomycorrhizal sites with low soil N, nonmycorrhizal uptake contributed less to overall N uptake (Figure 5c).

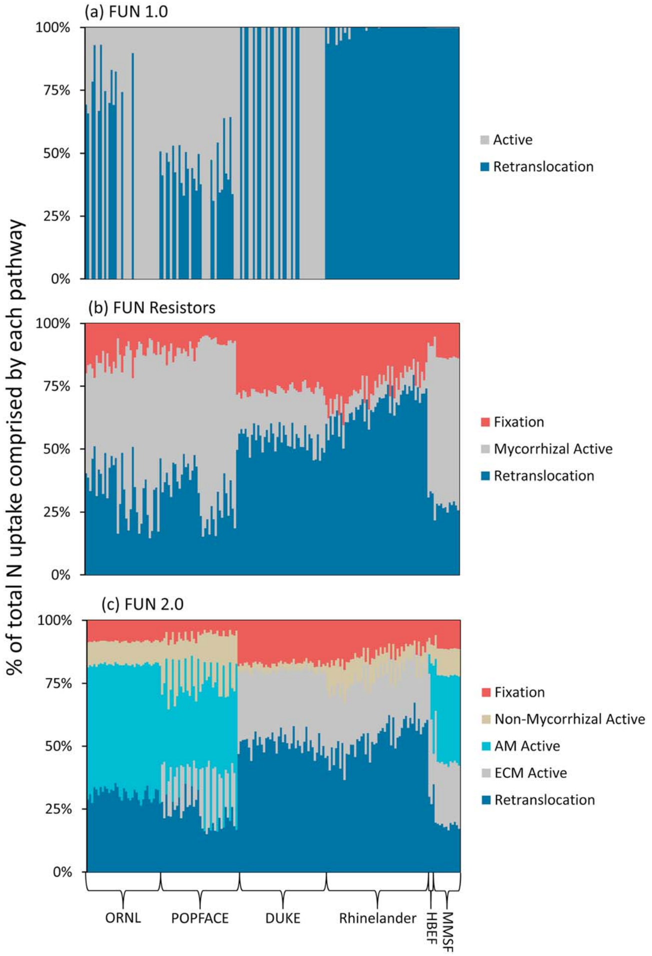

Figure 5. Shifts in the percentage of N uptake composed of each pathway predicted by (a) FUN 1.0, (b) FUN Resistors, and (c) FUN 2.0 (see Figure 4 for site descriptions).

3.5. C Cost of N Acquisition

Across all of the sites, the C cost of N acquisition was lowest (relative to net primary production) for FUN 2.0 and highest for FUN Resistors (Table 2). The Rhinelander site with the lowest net primary production, lowest root biomass, and second lowest soil N availability had the highest relative cost. By contrast, HBEF had the lowest C cost primarily due to high ratio of soil N availability to net primary production. POPFACE was the only site where FUN 1.0 predicted the highest C cost, primarily due to N uptake not meeting N demand (Figure S1 in the supporting information).

Table 2. Percent of NPP (SE) Allocated to N Acquisition

Site	FUN 1.0	FUN Resistors	FUN 2.0
ORNL	9.96 (0.76)	12.29 (0.61)	5.12 (0.10)
POPFACE	18.70 (0.99)	13.00 (0.68)	5.79 (0.27)
Duke	6.93 (0.23)	19.09 (0.29)	8.43 (0.14)
Rhinelander	20.91 (0.70)	34.15 (0.81)	14.37 (0.44)
HBEF	4.27 (0.01)	6.87 (0.74)	4.42 (0.53)
MMSF	4.26 (0.07)	8.29 (0.13)	4.29 (0.07)

In FUN 2.0, the ectomycorrhizal sites (Rhinelander and Duke) with the lowest soil N availability had the highest C cost per unit N compared relatively to other mixed mycorrhizal or arbuscular mycorrhizal sites (Table 3). However, at ambient and low levels of N, the mycorrhizal strategy of the site was more advantageous than a solely

Table 3. C Expended on Each of the Pathways in FUN 2.0 and the C Expended for Each Unit of N[a]

Site	Fixation	ECM-Active	AM-Active	Nonmycorrhizal	Resorb	Total C Expended	C Expended/N Acquired
ORNL	4.83 (0.21)	0	28.96 (1.13)	5.16 (0.17)	17.17 (0.53)	56.12 (1.98)	4.09 (0.03)
POPFACE	6.36 (0.52)	16.42 (2.07)	29.16 (1.70)	18.22 (1.55)	21.68 (1.17)	91.83 (4.14)	3.12 (0.20)
Duke	11.80 (0.40)	18.18 (0.31)	0	1.69 (0.03)	33.51 (1.17)	65.17 (1.82)	8.00 (0.07)
Rhinelander	8.53 (0.25)	15.85 (0.37)	0	5.32 (0.17)	33.53 (1.13)	63.23 (1.32)	7.82 (0.26)
HBEF	2.25 (0.51)	7.71 (1.07)	6.52 (1.62)	2.10 (0.22)	7.12 (1.49)	25.69 (3.11)	4.58 (0.59)
MMSF	4.95 (0.13)	11.19 (0.28)	14.85 (0.39)	4.63 (0.12)	8.01 (0.24)	43.62 (1.11)	5.70 (0.02)

[a] All values are in g C m^{-2} yr^{-1} except for C expended/N acquired which is in g C g N^{-1}. Values are mean (SE).

nonmycorrhizal strategy (Figure 6a). Only at high levels of N, approaching well-fertilized agricultural fields was nonmycorrhizal uptake cheaper than mycorrhizal uptake. Finally, the hypothetical nonmycorrhizal plants at each of the sites would need to increase root biomass by 0.2 kg C m^{-2} in order to have the same cost of C uptake as the ambient mycorrhizal strategies.

Competition between ectomycorrhizal and arbuscular mycorrhizal plants led to the mixed mycorrhizal plots having higher C costs at their ambient mycorrhizal association than with either a full arbuscular mycorrhizal or ectomycorrhizal strategies for all levels of soil N (Figure 6b). Further, the arbuscular mycorrhizal strategy had the lowest cost at high N, and the ectomycorrhizal strategy had the lowest cost at low N (Figure 6b).

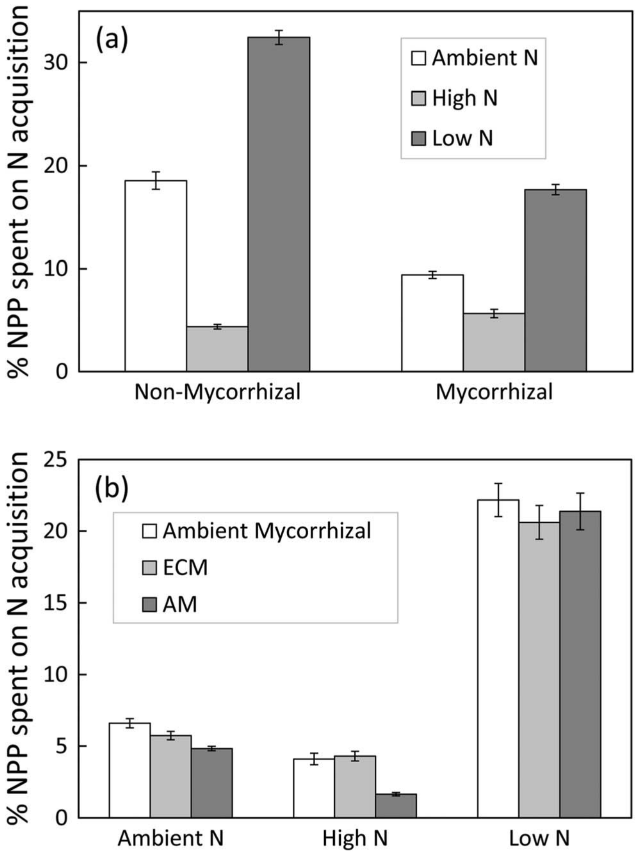

Figure 6. Sensitivity of the percentage of net primary production (NPP) spent on N acquisition to shifts in soil N and mycorrhizal strategy in FUN 2.0. (a) In the nonmycorrhizal simulations, both the arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) pathways were turned off for each site. In the mycorrhizal simulations, the ambient AM and ECM classifications were used for each site. (b) The impacts of shifting mycorrhizal association and N availability at only the mixed mycorrhizal sites (i.e., POPFACE, HBEG, and MMSF) are shown. The bars represent the mean ± SE across all of the sites in Figure 6a and the mean ± SE across the mixed mycorrhizal sites in Figure 6b.

4. Discussion

The current generation of terrestrial biosphere models has simplistic representations of N cycling that do not prescribe a C cost to N uptake or integrate the trading of photosynthate C for soil N between roots and symbiotic fungi, critical to nutrient cycling in nearly all ecosystems [*Thornton et al.*, 2007; *Zaehle and Friend*, 2010]. Here we describe a robust framework that current terrestrial biosphere models can use to address this need. We show that the integration of mycorrhizal trade-offs between arbuscular mycorrhizal and ectomycorrhizal fungi into the FUN model improves the predictions of the balance of N uptake between senescing leaves and soil across six forested sites that vary in mycorrhizal association (Figures 4 and 5). Importantly, we also predict that plant-C transfers to the soil to access N represent ~3–11% of net primary production, an amount that is directly within empirical estimates [*Hobbie*, 2006; *Hogberg and Hogberg*, 2002; *Parniske*, 2008]. Given recent research showing that plant-C transfers

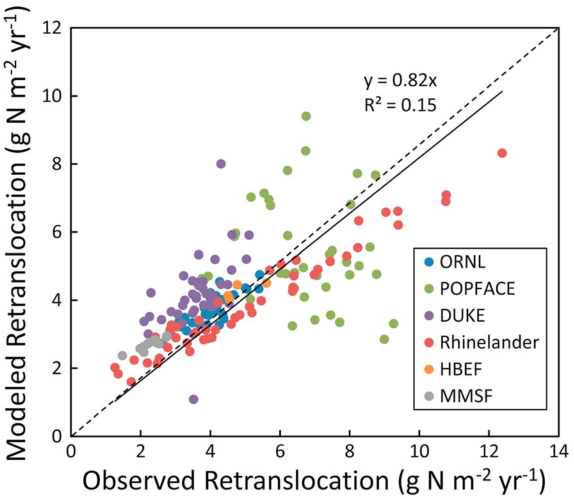

Figure 7. Modeled versus observed retranslocation assuming that a constant fraction of N is retranslocated from leaves upon senescence. CLM assumes that 51% of the canopy leaf N pool for deciduous sites and then assumes that 77% is retranslocated from the evergreen sites using differences in leaf longevity and the C-to-N ratio of leaf litter between the plant functional types. This framework is commonly used in many terrestrial biosphere models. The dashed line indicates the 1:1 relationship.

to the soil increase microbial decomposition (i.e., priming effect [*Kuzyakov et al*., 2000; *Cheng et al*., 2014]), FUN 2.0 offers current land surface models a framework to evaluate how priming influences the response of plant N uptake and soil C stocks to global change.

4.1. Retranslocation Implications

Retranslocation impacts aboveground processes by meeting a significant fraction of a plant's annual N requirement [*Aerts*, 1996] and belowground processes by representing the largest input of N to soils on an annual basis [*Vitousek*, 1982]. However, retranslocation is often assumed to remove a constant fraction of the N in senescing leaves in terrestrial biosphere models [*Thornton et al*., 2007; *Zaehle and Friend*, 2010], which we show is a poor assumption across the validation sites used here (Figure 7). Thus, the ability of FUN 2.0 to accurately predict the total amount of N retranslocated from leaves has important implications for terrestrial biosphere models (Figure 4). Outside of plant N nutrition, there is the potential for a downstream feedback on soil N cycling given that retranslocation directly impacts N inputs to soils and indirectly impacts N outputs through plant N uptake. Further, recent research is challenging the view that the retranslocation of N from fine roots is negligible [*Aerts*, 1990; *Freschet et al*., 2010; *Gordon and Jackson*, 2000; *Kunkle et al*., 2009], a paradigm shift that can be quickly assimilated by the cost-benefit framework of FUN 2.0.

At the mechanistic level, FUN 2.0 provides a unifying framework for the disparate drivers that have been proposed to control retranslocation. Leaf longevity, leaf habit, and greenleaf nutrient status have all been proposed as drivers governing retranslocation rates across nutrient or productivity gradients [*Chapin and Kedrowski*, 1983; *Delarco et al*., 1991; *Killingbeck*, 1996; *Kobe et al*., 2005]. By unifying these drivers, FUN 2.0 dynamically and accurately predicts retranslocation, even interannual variability at the majority of sites (Figure 4). There are two main reasons why FUN 2.0 works. The first is that retranslocation is not simply modeled as a function of one driver (e.g., leaf N or soil N availability) but instead reflects the integrated balance between a suite of N uptake pathways that vary in their costs and benefits (Figure 5). The second reason is that FUN 2.0 couples the traits and soil syndromes of ectomycorrhizal and arbuscular mycorrhizal trees (i.e., root C allocation and soil N availability [*Phillips et al*., 2013]) with the benefits of their mycorrhizae representing a significant improvement over previous cost-benefit efforts to predict retranslocation [*Fisher et al*., 2010; *Wright and Westoby*, 2003].

4.2. Trading Plant C for Soil N

FUN 2.0 predicted that trees and soil microbes maintain an active "marketplace" with roots trading ~3–11% of net primary production with soil microbes to satisfy 35–80% of annual plant N demand (Table 3 and Figure 5). The predicted fraction of net primary production allocated to N uptake was well within empirical estimates of root exudation and C allocation to mycorrhizae in forests [*Brzostek et al*., 2013; *Hobbie*, 2006]. The estimated value of ~3.5% of net primary production allocated to acquiring N from the soil at the MMSF site is strikingly similar to an independent estimate of the amount of net primary production allocated to root exudation at a nearby forest in southern Indiana (~2.5% of net primary production; Yin et al., In review). In general, the fraction of net primary production allocated to soil N uptake increased as net primary production decreased with the greatest relative C expenditure at the Rhinelander site that had the lowest net primary production and root biomass (Table 2; see Appendix S2 in the supporting information). Ectomycorrhizal stands tended to have a higher C cost per unit of N taken up than arbuscular mycorrhizal stands due to low levels of available soil N (Table 3). Despite these higher ectomycorrhizal costs, the ambient mycorrhizal strategy was always more advantageous than a nonmycorrhizal strategy at low and ambient soil N, reflecting the costs of building and maintain roots compared with mycorrhizae (Figure 6a). Thus, it was only at higher levels of soil N, that a nonmycorrhizal strategy was advantageous (Figure 6a). These results are in line with both latitudinal gradients in mycorrhizal association and soil N availability [*Allen et al.*, 1995; *Schimel and Bennett*, 2004] and declines in mycorrhizal colonization with fertilization [*Johnson et al.*, 2008; *Phillips and Fahey*, 2007].

The competition between ectomycorrhizal and arbuscular mycorrhizal fungi increased C costs, with the model sensitivity analysis showing that moving from a mixed to a fully arbuscular mycorrhizal or ectomycorrhizal mycorrhizal strategy reduced C costs (Figure 6b). This reflects the model assumption that ectomycorrhizal and arbuscular mycorrhizal roots compete for the same soil N pool, which is a potential area for model improvement given evidence for partitioning between N forms (i.e., amino acids, NO_3^-, and NH_4^+) by roots of different plant species [*McKane et al.*, 2002].

4.3. Site-Level Variation

The addition of the resistor network, simultaneous uptake through all pathways, and mycorrhizal trade-offs improved model predictions across all of the sites (Figures 4 and 5). However, the best model improvement was seen for those sites with both ectomycorrhizal and arbuscular mycorrhizal trees. For these mixed sites, FUN 2.0 predicted greater soil N uptake at the expense of retranslocation (i.e., POPFACE, MMSF, and HBEF; Figures 4 and 5) suggesting that competition between arbuscular mycorrhizal and ectomycorrhizal trees for the same soil resources increases ecosystem uptake of soil N. These results from FUN 2.0 are supported by empirical data that show enhanced ecosystem function with a greater diversity of plant traits [*Isbell et al.*, 2013]. While nutrient partitioning may mitigate some of the competitive arms race between ectomycorrhizal and arbuscular mycorrhizal trees for soil resources [*McKane et al.*, 2002], these results of the model indicate that the carbon cost of soil N uptake is likely highest in mixed mycorrhizal systems (Figure 6b). Regardless of this balance between competition and partitioning, it appears that incorporating mycorrhizal trade-offs is of greatest importance in mixed mycorrhizal systems that dominate temperate forests [*Phillips et al.*, 2013].

4.4. Key Model Assumptions

As with any ecosystem model, the new developments presented here for the FUN model required that we make conservative assumptions. With respect to model predictions, the model is most sensitive to the assumptions we made regarding the cost parameters controlling arbuscular mycorrhizal, ectomycorrhizal, and nonmycorrhizal uptake. However, the role of arbuscular mycorrhizal fungi as scavengers that can indirectly stimulate decomposition and ectomycorrhizal fungi as active agents of decomposition through the synthesis of enzymes is supported by the empirical literature [*Cheng et al.*, 2012; *Talbot et al.*, 2008; *Veresoglou et al.*, 2012]. In addition, the cost parameters were calibrated to represent realistic switching between when ectomycorrhizal and arbuscular mycorrhizal uptake would be advantageous (Figures 2 and 3) [*Allen et al.*, 1995; *Phillips et al.*, 2013; *Schimel and Bennett*, 2004]. Given the ability of this framework to accurately partition N uptake among pathways (Figure 5), the assumptions that underlie the inclusion of mycorrhizae in FUN 2.0 warrant further research. While previous research has attempted to link the C cost of mycorrhizae with the N benefit to the plant [*Correa et al.*, 2011; *Johnson et al.*, 1997; *Nilsson and Wallander*, 2003], FUN 2.0 raises important testable questions on how this cost-to-benefit ratio varies across fertility and productivity gradients: (1) Is ectomycorrhizal uptake always more advantageous than arbuscular mycorrhizal uptake in sites with low-nitrogen availability? (2) Does the percentage of net primary production allocated belowground increase as soil N availability declines? In particular, experimentally enhancing nitrogen availability in ectomycorrhizal and arbuscular mycorrhizal stands within the same forest to control for abiotic effects would provide a direct test of the switch points in nitrogen availability where FUN predicts ectomycorrhizal or arbuscular mycorrhizal uptake to be advantageous.

4.5. Future Model Improvements

Net primary production can also be limited by phosphorus (P) or colimited by N and P in many ecosystems [*Elser et al.*, 2007; *Fisher et al.*, 2012; *Walker and Syers*, 1976], highlighting the critical need to integrate P dynamics into ecosystem models. The optimal allocation framework used by FUN enables it to be easily retooled to integrate P dynamics. To incorporate P, the model would need to optimally allocate C (and possibly N) to P uptake in addition to growth and N uptake. Mycorrhizal trade-offs could also be parameterized to reflect dominance of arbuscular mycorrhizal fungi in P-limited ecosystems [*Allen et al*., 1995]. Compiling the necessary empirical data to test this model would be the key challenge, as the empirical data on plant tissue concentration and soil cycling of P are not nearly as rich or diverse as N [*Wang et al*., 2010; but see *Yang et al*., 2013, 2014].

As currently formulated, the mycorrhizal and nonmycorrhizal uptake pathways encompass a suite of different processes including C used to move N forms across cell membranes, C exuded to free-living microbes, and C directly transferred to mycorrhizae in exchange for N. The inclusivity of the active uptake process in the model reflects the difficulties in empirically separating the C spent and N gained from each of these pathways [*Hobbie*, 2006; *Phillips et al*., 2008]. An important consequence for terrestrial biosphere models however is that active uptake results in C transferred to soil organic matter leading to cascading effects on soil organic matter stabilization (i.e., priming). Moving forward, once our ability to empirically separate these processes in the field evolves, FUN has the flexibility to parse out these pathways by adding them to the resistor network.

Integrating the mycorrhizal trade-offs of FUN 2.0 into terrestrial biosphere models will require the ability to map arbuscular mycorrhizal and ectomycorrhizal plant distributions. For many ecosystem types, classification will be straightforward because they are dominated almost solely by arbuscular mycorrhizal or ectomycorrhizal plants (i.e., grasslands versus evergreen needleleaf forests). In mixed ecosystems, like temperate forests, this is currently not possible, but recent advances in mapping tree species in temperate forests suggests that remote sensing of known ECM or arbuscular mycorrhizal trees is feasible [*Kokaly et al*., 2009; *Plourde et al*., 2007; *Ustin and Gamon*, 2010]. Additionally, there are likely structural changes that need to be made to existing terrestrial biosphere models to fully couple FUN 2.0. For example, N demand during senescence periods in deciduous systems will need to be modified in terrestrial biosphere models to reflect the stored N needed for leaf out the following year. Finally, many plants in tundra and boreal systems that have high soil organic matter content and low mineral N availability associate with ericoid fungi [*Allen et al*., 1995]. Fully extending FUN 2.0 to the global scale will require incorporating ericaceous dynamics in these ecosystems.

4.6. Conclusion

The FUN 2.0 framework is transformative because it offers current terrestrial biosphere models a robust framework to evaluate how the trading of C for soil N between roots, mycorrhizal fungi, and free-living microbes impacts the size of the land C sink. Importantly, this framework accurately partitioned N uptake between the retranslocation and the soil and predicted belowground C allocation rates that are well within empirical estimates (Figure 5 and Table 3). While existing soil models are well equipped to examine how plant C inputs influence soil organic matter decomposition (i.e., priming effect), the rate of C transfer by roots to microbes is commonly prescribed as a constant fraction of net primary production [*Cheng et al*., 2014]. FUN bridges the gap between terrestrial biosphere models and these soil models by dynamically predicting the amount of C allocated by plants to mycorrhizal fungi and free-living microbes that control the soil nutrient marketplace. Given the magnitude of these C and N transfers [*Hobbie and Hobbie*, 2008; *Rillig*, 2004], representing mycorrhizae and priming at a global scale is critical to reducing uncertainty in the response of the land C sink to global change.

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