Carbon cost of plant nitrogen acquisition: A mechanistic, globally applicable model of plant nitrogen uptake, retranslocation, and fixation

J. B. Fisher,[1] S. Sitch,[2] Y. Malhi,[1] R. A. Fisher,[3] C. Huntingford,[4] and S.-Y. Tan[1]

[1] Nitrogen (N) generally limits plant growth and controls biosphere responses to climate change. We introduce a new mathematical model of plant N acquisition, called Fixation and Uptake of Nitrogen (FUN), based on active and passive soil N uptake, leaf N retranslocation, and biological N fixation. This model is unified under the theoretical framework of carbon (C) cost economics, or resource optimization. FUN specifies C allocated to N acquisition as well as remaining C for growth, or N-limitation to growth. We test the model with data from a wide range of sites (observed versus predicted N uptake r^2 is 0.89, and RMSE is 0.003 kg N m^{-2}·yr^{-1}). Four model tests are performed: (1) fixers versus nonfixers under primary succession; (2) response to N fertilization; (3) response to CO_2 fertilization; and (4) changes in vegetation C from potential soil N trajectories for five DGVMs (HYLAND, LPJ, ORCHIDEE, SDGVM, and TRIFFID) under four IPCC scenarios. Nonfixers surpass the productivity of fixers after ~150–180 years in this scenario. FUN replicates the N uptake response in the experimental N fertilization from a modeled N fertilization. However, FUN cannot replicate the N uptake response in the experimental CO_2 fertilization from a modeled CO_2 fertilization; nonetheless, the correct response is obtained when differences in root biomass are included. Finally, N-limitation decreases biomass by 50 Pg C on average globally for the DGVMs. We propose this model as being suitable for inclusion in the new generation of Earth system models that aim to describe the global N cycle.

1. Introduction

[2] Nitrogen (N) controls plant growth and net primary productivity (NPP) in most terrestrial ecosystems and is tightly coupled with the global carbon (C) cycle [*Lloyd*, 1999; *Magnani et al.*, 2007; *Vitousek and Howarth*, 1991]. With global warming, increasing temperatures from rising atmospheric CO_2 could lead to greater soil decomposition, N mineralization, and N availability, thereby increasing C sequestration in N-limited vegetation [*Melillo et al.*, 1993; *Pastor and Post*, 1988; *Peterjohn et al.*, 1994]. This acts as a negative feedback on climate change, potentially mitigating CO_2 emissions to some extent. Still, other researchers have postulated the opposite: namely a reduction in available N (progressive N limitation) over long-term time scales (decadal) with increasing CO_2 because N becomes "locked up" in increasing vegetation biomass [*Luo et al.*, 2004]. Thus, currently the future role of the land in absorbing a significant fraction of anthropogenic CO_2 is uncertain [*Friedlingstein et al.*, 2006; *Sitch et al.*, 2008], and a large part of that uncertainty is the role of the N-cycle in modulating the exchange of CO_2 between terrestrial ecosystems and the atmosphere [*Hungate et al.*, 2003; *Jenkinson et al.*, 1999; *Melillo et al.*, 1993; *Nadelhoffer et al.*, 1999; *Oren et al.*, 2001; *VEMAP Members*, 1995].

[3] Despite the potential large impact of the N-cycle on climate change, plant N uptake has only recently been developed in some large-scale ecosystem models and associated General Circulation Models (GCMs) [*Ostle et al.*, 2009; *Sokolov et al.*, 2008; *Thornton et al.*, 2007; *Xu-Ri and Prentice*, 2008]. Most of the models included in the last Intergovernmental Panel on Climate Change assessment still lack a mechanistic approach for these processes [*IPCC*,

[1]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK.
[2]School of Geography, University of Leeds, Leeds, UK.
[3]Earth and Environmental Sciences, Los Alamos National Laboratory, Los Alamos, New Mexico, USA.
[4]Centre for Ecology and Hydrology, Wallingford, UK.

2007]. The IPCC models likely predict a greater amount of CO_2 sequestration (and stronger ability of the terrestrial biosphere to slow the rate of growth in atmospheric CO_2 concentration) than would be expected if N-cycle feedbacks were included [*Cramer et al.*, 2001; *Hungate et al.*, 2003; *Sitch et al.*, 2008] because most terrestrial ecosystems are N-limited [*Vitousek and Howarth*, 1991]. One reason for the slow implementation of the N-cycle in Earth system models is that the mechanisms of the terrestrial N-cycle are not very well understood, and the linkages from the enzymatic and kinetic level (i.e., root physiology and cellular processes) to large-scale (global) functioning are difficult to establish. Data are sparse for natural ecosystems, and empirically fitted parameters are not necessarily robust across biomes [*Galloway et al.*, 2004].

[4] Some N uptake models have been empirically constructed for specific crops or agroforestry (e.g., corn, legumes, maize, wheat, Scots pine, Norway spruce, Pendula birch) [*Boote et al.*, 2002; *Drouet and Pag*, 2007; *Hansen et al.*, 1991; *Komarov et al.*, 2003; *Ma et al.*, 2007]. Of the general ecosystem models with a N-cycle, some treat N uptake as a mechanism that simply proceeds at the rate of demand until N has been completely depleted from the soil (e.g., BIOME-BGC, CENTURY, DNDC, GFDL LM3V, HYBRID, SDGVM) [*Friend et al.*, 1997; *Gerber et al.*, 2010; *Miehle et al.*, 2006; *Schimel et al.*, 1996; *Thornton and Rosenbloom*, 2005; *Woodward et al.*, 1998], whereas others include a more theoretically correct form of energetics for C cost assessment [*Dickinson et al.*, 2002; *Rastetter et al.*, 2001; *Vitousek et al.*, 2002; *Vitousek and Field*, 1999; *Wang et al.*, 2007]. The latter set of models is particularly important for modeling C dynamics because N acquisition generally requires C expenditure, which the former set of models does not account for.

[5] *Vitousek and Field* [1999] and *Vitousek et al.* [2002] initially proposed a simple model of N uptake and fixation that introduced the concept of energetic cost for N uptake, particularly the cost difference between fixers (plants that can convert atmospheric N to an available form via symbiotic N-fixing bacteria on their roots, the process of which is called biological N fixation or BNF) and nonfixers. They focused on why fixers do not have a competitive advantage over nonfixers, and how this relates to successional dynamics. Following on this idea, *Rastetter et al.* [2001] developed a model of resource optimization for N acquisition, which allowed for a variable cost of soil N uptake and a switch between fixation and soil N uptake dependent on which process has less energetic cost. This model, which improved the characterization of the energetics, and is arguably the most theoretically rigorous of the N models, is also the most difficult to parameterize due to the added complexity. *Dickinson et al.* [2002] were among the first to integrate a N uptake and fixation model for the NCAR CCM3 GCM based on energetic costs. However, their model relies on many reference values from limited data (i.e., constants from spruce seedlings), which may not apply uniformly well for global assessments.

[6] Our approach is to build upon these advancements in modeling N uptake and fixation. We introduce new con-sistent mathematical submodels of active soil N uptake, leaf N resorption, and BNF all unified under the theoretical framework of C cost economics, i.e., resource optimization. Our main objective is to develop a process-based model of N acquisition that captures these concepts, and yet retains sufficient simplicity that it can be parameterized by generally accessible data. Our model, called Fixation and Uptake of Nitrogen (FUN), specifies C allocated to N acquisition as well as remaining C for growth or N-limitation to growth. It can be run as a stand alone module or coupled to a larger land surface model. For example, we have implemented it within the Joint U.K. Land Environment Simulator (JULES) [*Cox et al.*, 1998] with a new dynamic soil process model that can allow for explicit N-cycle representation in GCM's.

2. Methods

2.1. Model Description

[7] We follow the theoretical framework of *Hopmans and Bristow* [2002] to model N uptake and transport through the roots, and of *Wright and Westoby* [2003] to model retranslocation. N can be acquired by plants through (1) advection (passive uptake), (2) retranslocation (resorption), (3) active uptake, and (4) BNF (see Figure 1 for model schematic). The mathematical formulation of the latter three pathways is entirely new as well as is the C optimization framework.

[8] Advection is the transport of dissolved N in water used by the plant. We include natural diffusion of N into the roots as part of advection because diffused N will interact with the water (except at night or under drought when N demand may be low because NPP is low). Retranslocation is the resorption (both terms are used interchangeably) of N in leaves before senescence or leaf fall (root resorption is minimal [e.g., *Gordon and Jackson*, 2000]). Resorption requires C to synthesize the enzymes and regulatory elements that degrade and remobilize leaf nutrients, and to drive the translocation stream in which the nutrients are suspended [*Holopainen and Peltonen*, 2002; *Wright and Westoby*, 2003]. Active uptake is an ion-specific enzyme-catalyzed process analogous to Michaelis-Menten kinetics [*Michaelis and Menten*, 1913]. Energy demand for ion uptake can consume a substantial amount (as much as 35%) of total respiratory C (that might otherwise be allocated for growth) to move N against concentration gradients [*Marschner*, 1995]. Finally, BNF is performed by bacteria living in symbiosis within root nodules on certain types of plants: many leguminous (family *Fabaceae*) and some actinorhizal (22 genera of woody shrubs or trees in 8 plant families) plants (for global distributions, see *Cleveland et al.* [1999]). The symbiotic bacteria convert atmospheric nitrogen (N_2) to ammonia (NH_3), which is quickly protonated (addition of protons, or hydrogen) into ammonium (NH_4^+) by bacterial enzymes called nitrogenase. The plants can take up the now useable available NH_4^+ and in return supply the carbohydrate energy (from NPP) used to sustain the bacteria and the process.

[9] Our model relies on nine input parameters or drivers (Table 1): (1) NPP (C_{NPP}; kg C m^{-2} s^{-1}), (2) total (coarse
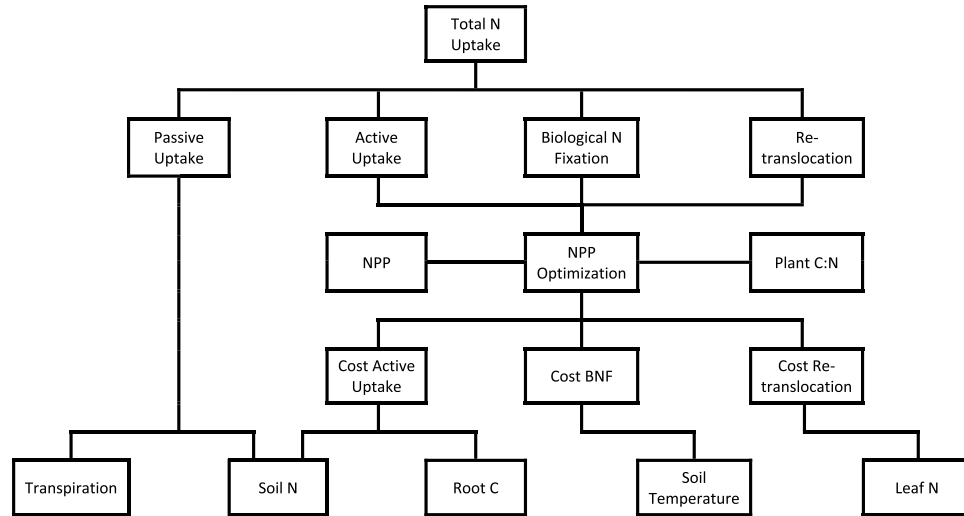
Figure 1. Structure of the Fixation and Uptake of Nitrogen (FUN) model. Total nitrogen uptake is equal to the sum of passive uptake of nitrogen from advection through the transpiration stream (passive uptake), active uptake of nitrogen through respiratory expenditure, resorbed nitrogen from leaves (retranslocation), and/or, if capable, through symbiotic biological nitrogen fixation.

and fine) root biomass (C_{root}; kg C m^{-2}), (3) plant C:N ratio ($r_{C:N}$; kg C kg N^{-1}), (4) leaf N in leaves before senescence (N_{leaf}; kg N m^{-2}), (5) transpiration rate (E_T; m s^{-1}), (6) ability to fix (A_{fix}; TRUE or FALSE), (7) soil water depth (s_d; m), (8) soil temperature (T_{soil}; °C), and (9) available soil N for the given soil layer (N_{soil}; kg N m^{-2}). N_{soil} is assumed immobile and unavailable in dry soil. For simplicity, our model is described here for one soil layer, but can be adapted to multiple soil layers (as in JULES, for instance). Within JULES it is run on a daily time step.

[10] First, N demand (N_{demand}; kg N m^{-2} s^{-1}) is calculated as the N required to maintain the prescribed C:N (whole plant) ratio ($r_{C:N}$), which is updated each time step, as C is accumulated from (positive) C_{NPP}:

$$N_{\text{demand}} = \frac{C_{\text{NPP}}}{r_{C:N}} \qquad (1)$$

[11] The first source of N that the plant depletes is from passive uptake (N_{passive}; kg N m^{-2}·s^{-1}), through the transpiration stream because there is no explicit associated energetic cost and is acquired at no C expenditure to the plant:

$$N_{\text{passive}} = N_{\text{soil}} \frac{E_T}{s_d} \qquad (2a)$$

[12] If this potential uptake exceeds the N_{demand}, then N_{passive} is reduced accordingly:

$$N_{\text{passive}} = \min\left(N_{\text{soil}} \frac{E_T}{s_d}, N_{\text{demand}}\right) \qquad (2b)$$

[13] Likewise, when N_{soil} levels are insufficient to satisfy the potential extraction rate, N_{passive} is constrained by the total extractable N in the soil:

$$N_{\text{passive}} = \min\left(N_{\text{soil}} \frac{E_T}{s_d}, N_{\text{soil}}\right) \qquad (2c)$$

[14] N_{soil} is then updated as the previous time step value minus the N extracted from N_{passive}. Equation (2a) extracts a fraction of water out of the soil layer (E_T divided by s_d) and multiplies it by the concentration of N in that water. Although E_T is biologically and climatologically controlled, E_T will approach zero as s_d approaches zero (E_T will go to zero more quickly as the soil dries out).

[15] If N_{passive} does not satisfy N_{demand}, then the plant must obtain the remaining required N from either retranslocation (N_{resorb}; kg N m^{-2} s^{-1}), active uptake (N_{active}; kg N m^{-2} s^{-1}) or, if capable (i.e., the plant is a fixer; $A_{\text{fix}} =$ TRUE), from BNF (N_{fix}; kg N m^{-2}·s^{-1}). N_{resorb}, N_{active} and N_{fix} are associated with variable C costs to the plant that must be calculated.

Table 1. Model Input Parameters and Drivers

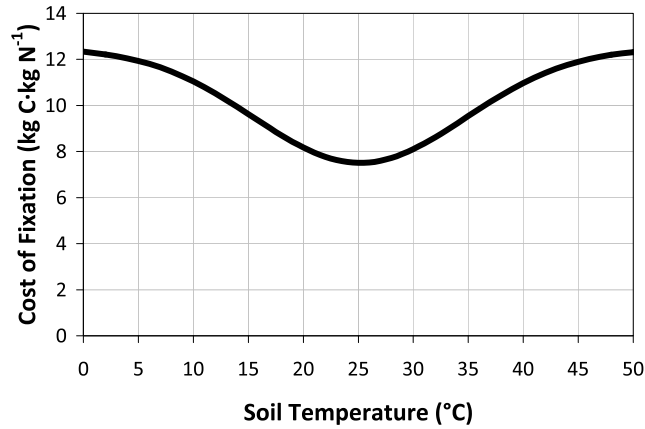| Parameter	Notation	Units
Ability to fix	A_{fix}	TRUE or FALSE
Available soil N	N_{soil}	kg N m^{-2}
Total root biomass	C_{root}	kg C m^{-2}
Leaf N before senescence	N_{leaf}	kg N m^{-2}
Net primary production	C_{NPP}	kg C·m^{-2}·s^{-1}
Plant C:N ratio	$r_{C:N}$	kg C kg N^{-1}
Soil water depth	s_d	M
Soil temperature	T_{soil}	°C
Transpiration	E_T	M s^{-1}

Figure 2. Cost of biological nitrogen fixation (Cost$_{\text{fix}}$) is a function of soil temperature (T_{soil}). Adapted from *Houlton et al.* [2008].

[16] The C cost of fixation (Cost$_{\text{fix}}$; kg C kg N^{-1}) has been observed to range from 8 to 12 kg C kg N^{-1} [*Gutschick*, 1981] as a function of soil temperature (T_{soil}; °C) [*Houlton et al.*, 2008]. We combine the equation of *Houlton et al.* [2008] for normalized nitrogenase activity as a function of T_{soil}

with the observed C cost range as constrained by *Gutschick* [1981]:

$$\text{Cost}_{\text{fix}} = s\left(\exp\left(a + b \cdot T_{\text{soil}}\left(1 - 0.5\frac{T_{\text{soil}}}{c}\right)\right) - 2\right) \quad (3)$$

where *a*, *b*, and *c* (−3.62, 0.27 and 25.15, respectively) are empirical curve-fitting parameters (unitless) given by *Houlton et al.* [2008]; *s* is −5 times the *Houlton et al.* [2008] scaling factor of 1.25(= −6.25), which inverts the *Houlton et al.* [2008] equation and constrains it between 7.5 and 12.5 kg C kg N^{-1} (Figure 2). The units of *s* may be considered kg C kg N^{-1} °C^{-1} for unit consistency.

[17] The calculation of costs associated with N_{active} (i.e., active uptake) requires scaling of root chemistry to more easily measureable plant physiological parameters. For example, *Dickinson et al.* [2002] require many root physiological parameters to calculate this rate. We simplify the calculation of the cost of active uptake (Cost$_{\text{active}}$; kg C kg N^{-1}) as

$$\text{Cost}_{\text{active}} = \left(\frac{k_N}{N_{\text{soil}}}\right)\left(\frac{k_C}{C_{\text{root}}}\right) \quad (4)$$

where k_N and k_c are both 1 kg C·m^{-2} (see section 4 for derivation of k_N and k_C). As N_{soil} approaches zero, the energetic cost required to take it up tends to infinity (Figure 3a).
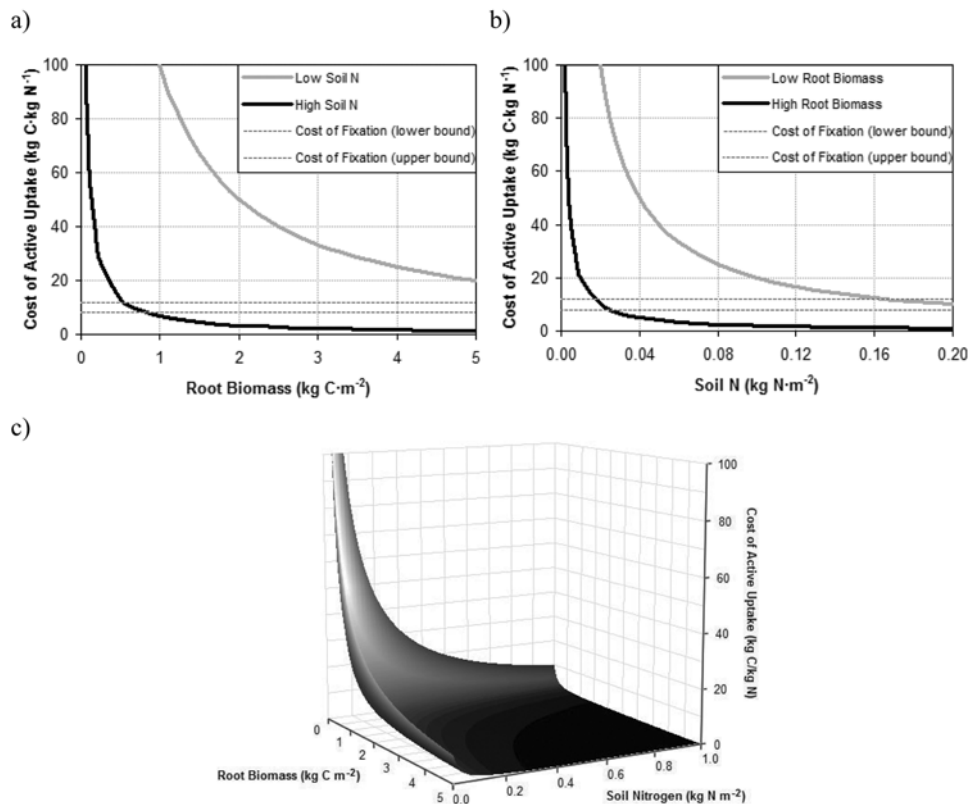

Figure 3. Cost of active nitrogen uptake (Cost$_{\text{active}}$) with range of cost of biological nitrogen fixation (Cost$_{\text{fix}}$) versus (a) soil nitrogen with low and high root biomass, (b) root biomass with low and high soil nitrogen, and (c) both soil nitrogen and root biomass.

Conversely, as N_{soil} approaches its maximum proportion of soil mass, the energetic cost required to take it up tends to zero. Additionally, as C_{root} approaches zero, N_{soil} again becomes infinitely costly to take up [*Bossel*, 1996]; and, as C_{root} fills the soil, N_{soil} becomes increasingly cheaper to take up (Figure 3b). C_{root} is defined as the biomass of both coarse plus fine roots because the cost is dependent on access to N_{soil}, and fine roots (connected to coarse roots) are the principle mechanism for active nutrient uptake [*Jackson et al.*, 1997].

[18] Similarly, the C cost for resorption (Cost$_{resorb}$; kg C kg N^{-1}) is dependent on the N in the leaves (N_{leaf}), but not dependent on distance or access to this N (as is the case with C_{root}). The same logic as Cost$_{active}$ follows; that is, the amount of C required to resorb a unit of N (Cost$_{resorb}$) tends to infinity as the amount of N in the leaf (N_{leaf}) approaches zero, and vice versa. The cost of resorption (Cost$_{resorb}$) in equation form may be expressed as

$$Cost_{resorb} = \frac{k_R}{N_{leaf}} \qquad (5)$$

where k_R is equal to 0.01 kg C m^{-2} (see section 4 for derivation of k_R).

[19] At each time step the plant will compare the different costs of N acquisition (N_{acq}; kg N m^{-2} s^{-1}) and then choose the lowest (Cost$_{acq}$; kg C kg N^{-1}):

$$Cost_{acq} = \min(Cost_{resorb}, Cost_{active}, Cost_{fix}) \qquad (6a)$$

[20] Some of the C_{NPP} will be expended to the cost of either resorption, active uptake or BNF, but some must be retained for growth (C_{growth}; kg C m^{-2} s^{-1}), and all within the constraint of maintaining the $r_{C:N}$. Therefore, the plant must optimize its C_{NPP} expenditure. To calculate the three unknowns: (1) the C retained for growth (C_{growth}), (2) the C expended in N acquisition (C_{acq}), and (3) the N acquired from the C expenditure (N_{acq}), we simultaneously solve the following three equations:

$$C_{growth} = C_{NPP} - C_{acq} \qquad (6b)$$

$$N_{acq} = \frac{C_{acq}}{Cost_{acq}} \qquad (6c)$$

$$r_{C:N} = \frac{C_{growth}}{N_{passive}} + N_{acq} \qquad (6d)$$

[21] In equation (6b), the C available for growth of new tissue (C_{growth}) is the difference between the plant C_{NPP} and the C expended (C_{acq}) by the plant in sourcing N (either through retranslocation: C_{resorb}, active uptake: C_{active}, or BNF: C_{fix}), depending on which source is cheapest (i.e., equation (6a)). In equation (6c), N acquired is by definition equal to the amount of C the plant expends to source this N divided by the unit cost of C expenditure. In the last equation (6d), the C:N ratio should equal the C available for

growth divided by the total N taken up (and also available for growth). The total N uptake (N_{uptake}) is the sum of $N_{passive}$ and N_{resorb} and/or N_{active} and/or N_{fix}.

[22] At each model timestep, N_{soil} is updated again (previously after $N_{passive}$) if there is active uptake. Leaf litter N content is calculated as N_{leaf} minus N_{resorb}. Finally, C is added to the soil through the respiratory costs of active uptake and/or fixation from C_{active} and/or C_{fix}. Photosynthesis is therefore indirectly down-regulated via N-limitation by decreased growth. Under N-limitation, more C_{NPP} will be allocated to N acquisition under increasing costs (i.e., Cost$_{active}$) than retained for growth. Thus, new leaves cannot be grown to replace old leaves. Root and shoot growth may be stunted, thereby causing potential stress in water uptake as well as light competition.

2.2. Model Assumptions

[23] 1. Time step: We run FUN no finer than on a daily time step to match and aggregate the diurnal cycle of photosynthesis, whereby C expenditure at the end of the day translates into the associated N acquisition. Thus, the rates of N fixation, uptake, retranslocation and transport operate on a daily scale.

[24] 2. N storage: Land surface models such as JULES typically specify how vegetation allocates its C resources to growth for competition. An initial store of C is assumed for budburst and, given the relationship between C and N ($r_{C:N}$), implicitly an initial N store.

[25] 3. Chemical form of N: It is unclear how well one can generalize plant preference for uptake of NH_4^+ (ammonium) versus NO_3^- (nitrate) versus dissolved organic N so we assume no preference [*Falkengren-Grerup*, 1995; *Jones et al.*, 2005; *Marschner et al.*, 1991; *Nordin et al.*, 2001]. Better characterization of pH dynamics could inform this assumption.

[26] 4. Rate of BNF: We do not model root nodules, and thus assume that a fixer can fix as much N as demanded, given sufficient C_{NPP} for Cost$_{fix}$, and that the cost varies only with T_{soil} [*Houlton et al.*, 2008], i.e., equation (3). Thus, BNF capacity scales with root biomass (as would NPP to first approximation), and as soon as a BNF-capable plant has roots, it can also have root nodules. However, the production rate and capacity of root nodules are unclear. Both the quantity and size of nodules vary across plant species, and many plants have nodules that are inactive [*Kiers et al.*, 2003; *King and Purcell*, 2001; *Laws and Graves*, 2005; *Newcomb and Tandon*, 1981].

[27] 5. Mycorrhizae: Mycorrhizal symbioses are similar to BNF in that plants provide C to mycorrhizal fungi (rather than bacteria in BNF) that provide N (among other nutrients) from elsewhere in the soil (rather than produced from atmospheric N). However, there is no unifying framework with which to accurately predict/model the amount of N given in exchange for C [*Smith et al.*, 2009]. Because of this knowledge gap, we do not model mycorrhizae. The implications to FUN are that if there are mycorrhizal symbioses, then the mycorrhizae essentially act as extended roots, which would lower Cost$_{active}$. In the absence of mycorrhizal symbioses such as, for example, under high N_{soil} [*Aber et al.*, 1989; *Menge et al.*, 2008], the plant would need to in-

crease root biomass to equalize $Cost_{active}$. Thus, technically the term "root biomass" should be replaced with "effective root biomass" that accounts for the role of symbiotic mycorrhizal biomass, with a mycorrhizae-specific scalar to allow for varying rates of C cost and efficiency by different mycorrhizae. Nonetheless, we may implicitly capture at least a partial effect of mycorrhizae in our treatment of $Cost_{active}$: if there are more roots and/or more N_{soil}, then mycorrhizae may not be needed (requiring little C payment), and $Cost_{active}$ subsequently decreases; oppositely, if there are few roots and/or less N_{soil}, then mycorrhizae may be more needed (and may demand a higher C cost), and $Cost_{active}$ subsequently increases.

2.3. Data Test

[28] We tested the model with data from a range of sites, including four sites from the Free Air CO_2 Enrichment (FACE) experiments [*Finzi et al.*, 2007], three agroecosystem sites from the Special Collaborative Project 179 (SCP179) international workshop data set [*McVoy et al.*, 1995], three tropical montane sites in the Peruvian Andes [*Tan*, 2008], and an ancient woodland in the United Kingdom [*Tan*, 2008]. The latter two data sets were collected specifically to test FUN. It was necessary that all data sets contain measurements over at least two time periods (i.e., NPP, plant/leaf N) to test against N_{uptake}, which is a measure over time (i.e., N_{uptake} equals measured plant N in year 1 minus measured plant N in year 0). The data are described extensively in the cited references. The data were not used to fit or calibrate any parameters in FUN (i.e., purely predictive forward modeling).

[29] The FACE experiments provided data (N = 160 data points from 2 to 3 years for each site) from Chapel Hill, North Carolina, United States (Duke); Oak Ridge National Laboratory, Tennessee, United States (ORNL); Viterbo, Italy (POP-EURO); and, Rhinelander, Wisconsin, United States (RHI). The FACE data had a high level of quality control and subsequently required minimal gap-filling. The SCP data, however, required an estimation of root biomass, which was not included in the original data set. A constant root-to-shoot biomass ratio of 0.17 for the SCP crops was assumed [*Tan*, 2008], though this value likely varies throughout the year [e.g., *Katterer et al.*, 1993]. Additionally, the leaf turnover rate in the SCP data set was unknown. We used the average leaf turnover rate from the Ecosystem Demography (ED) [*Moorcroft et al.*, 2001] model as parameterized to the GLOPNET database [*Wright et al.*, 2004] of 51.5% (34–69%) as a constant turnover percentage.

2.4. Model Experiment 1: Succession

[30] *Vitousek and Howarth* [1991] posed the conundrum of why N-fixers are not more ubiquitous given that they have a substantial competitive advantage over nonfixers wherever N is limiting, and N is limiting in most ecosystems. In fact, fixers are generally observed as dominant early in succession, but not in late succession [*Vitousek and Howarth*, 1991]. It is therefore unclear what mechanisms cause this shift in ecosystem dominance, and whether or not we can adequately represent these ecosystem dynamics mathematically.

[31] We tested FUN under a simplified scenario of primary succession with competition between a fixer and nonfixer following a disturbance that set N_{soil} to zero (e.g., a volcanic eruption or landslide). It was hypothesized that the fixer will dominate (larger C_{growth}) early in succession, but the nonfixer will later dominate [*Vitousek and Howarth*, 1991]. Both the fixer and nonfixer were allowed to exist simultaneously with the same N_{soil} pool (assume no outside additions or losses, and instantaneous return to the soil). N_{soil} was partitioned between the two plants based on their respective C_{root} fractions. We ran the model for 300 simulation years.

[32] Each plant (or cohort or species or functional type) started with the same initial conditions (JULES is not used for this experiment): $C_{NPP} = 0.2$ kg C m^{-2} yr^{-1}, $r_{C:N} = 300$, $T_{soil} = 17°C$ $s_d = 50$ m, $C_{root} = 0.05$ kg C m^{-2}. N_{leaf} (kg N m^{-2}) and E_T (m) scale proportionally with NPP and thus are given as proportions of C_{NPP} (0.1% and 20%, respectively). $r_{C:N}$, s_d and T_{soil} remained constant throughout the simulation. For both the fixer and nonfixer C_{NPP} increased by 2% ($\mu_1 = 0.02$ yr^{-1}) of the previous C_{NPP} allocated for growth (C_{growth}). However, that rate was decreased by a shading effect caused by the growth of the competitor. This shading term is simplistic and should likely follow a Beer's Law exponential-type pattern rather than a linear adjustment. The first difference between fixers and nonfixers was that the nonfixer, assumed to be low-light adapted as a late successional species, was given a 50% ($\mu_2 = 0.50$ yr^{-1}) reduced shading effect, which reduces the running sum of C_{growth} (i.e., total accumulated C_{growth}, or ΣC_{growth}) of the competitor normalized by the maximum accumulated C_{growth} possible given no competition (max$\Sigma C_{growthopt}$):

$$\frac{dC_{NPP,nf}}{dt} = \mu_1 C_{growth,nf}\left(1 - \mu_2 \frac{\sum C_{growth,f}}{\max \sum C_{growthopt,f}}\right) \quad (7a)$$

$$\frac{dC_{NPP,f}}{dt} = \mu_1 C_{growth,f}\left(1 - \frac{\sum C_{growth,nf}}{\max \sum C_{growthopt,nf}}\right) \quad (7b)$$

[33] The second difference was that the nonfixer allocated a constant 25% ($\mu_3 = 0.25$ yr^{-1}) of C_{NPP} to C_{root} [e.g., *Cairns et al.*, 1997], whereas the fixer allocated only 1% ($\mu_4 = 0.01$ yr^{-1}) unless the $Cost_{active}$ was less than $Cost_{fix}$, in which case the fixer allocated 25% as well:

$$\frac{dC_{root,nf}}{dt} = \mu_3 C_{growth,nf} \quad (8a)$$

$$\frac{dC_{root,f}}{dt} = \mu_4 C_{growth,f} \qquad : Cost_{fix} < Cost_{active}$$

$$\frac{dC_{root,f}}{dt} = \mu_3 C_{growth,f} \qquad : Cost_{fix} > Cost_{active} \quad (8b)$$

2.5. Model Experiment 2: N Fertilization

[34] This model experiment takes advantage of a field nutrient manipulation as part of the Peru data set described

previously. In this data set, a portion of the data was from plots fertilized by N. The subsequent soil N in the fertilized plots was on average greater than in the control plots (1.52 versus 1.43 kg N·m^{-2}, respectively) as well as the N uptake (0.0211 versus 0.0194 kg N·m^{-2}, respectively). The model test was therefore to take the data from the control plots, and model (off-line) an increase in soil N to the same levels as was applied in the fertilizer. Would the predicted N uptake subsequently increase to match the measured N uptake in the fertilized plots (N_{acq}; equation (6c))? In other words, we asked what would happen if we applied N to the soil of the controls plots, and then we compared the modeled N uptake response to the actual N uptake response from the N fertilized plots (modeled fertilization versus actual fertilization). It was expected that the control plots were also N-limited, and that the increase in soil N would allow greater N uptake due to a lower Cost$_{active}$.

2.6. Model Experiment 3: CO$_2$ Fertilization

[35] Similar to the N fertilization model experiment, this model experiment takes advantage of the CO$_2$ enrichment focus of the FACE data. In this data set, a portion of the data were from plots exposed to elevated atmospheric CO$_2$ while the remaining data were from plots exposed to ambient levels of CO$_2$. The subsequent NPP in the CO$_2$ fertilized plots was on average greater than in the ambient plots (2.24 versus 1.78 kg C m^{-2}, respectively) as well as the N uptake (0.0107 versus 0.0093 kg N m^{-2}, respectively) due to enhanced photosynthetic capacity [*Finzi et al.*, 2007]. The model test was therefore to take the data from the ambient CO$_2$ plots, and model (off-line) an increase in NPP that matched the increase in NPP in the elevated CO$_2$ plots. Would the predicted N uptake subsequently increase to match the measured N uptake in the CO$_2$ fertilized plots? In other words, we asked what would happen to N uptake in the ambient plots if NPP increased (i.e., due to CO$_2$ fertilization), and then we compared the modeled N uptake response to the actual N uptake response from the elevated CO$_2$ plots (modeled NPP increase versus actual NPP increase). It was expected that an increase in NPP in the ambient plots would lead to greater N uptake due to greater N_{demand}.

2.7. Model Experiment 4: DGVM Vegetation Carbon

[36] With projected increases in atmospheric CO$_2$, DGVMs simulate enhanced plant productivity and subsequent proportional increases in vegetation C. In the absence of a N-cycle, however, it is likely that these models overestimate the amount of NPP globally that can be used for vegetation C because some of that NPP may be allocated to acquiring potentially diminishing supplies of soil N [*Hungate et al.*, 2003; *Luo et al.*, 2004]. It is expected that with the inclusion of a N-cycle, the amount of vegetation C will be less than that expected from the current DGVMs [*Sokolov et al.*, 2008; *Thornton et al.*, 2007; *Xu-Ri and Prentice*, 2008]. Capturing this behavior in global land surface models is important given that many policy decisions regarding future emissions scenarios assume significant natural mitigation (i.e., "drawdown") of atmospheric CO$_2$. Changes to this particular ecosystem "service" will

affect permitted emissions to achieve prescribed levels of stable atmospheric concentrations of CO$_2$.

[37] Here, we used the modeled globally averaged NPP output from five DGVMs [*Sitch et al.*, 2008] (model output available at http://dgvm.ceh.ac.uk/): HYLAND, LPJ, ORCHIDEE, SDGVM, and TRIFFID, under four IPCC Special Report on Emissions Scenarios (A1, A2, B1, B2) [*Nakicenovic et al.*, 2000] to drive FUN given a range of prescribed possible soil N trajectories. For each DGVM we first correlated global NPP to global vegetation C following a linear relationship. This experiment took the DGVM global NPP, subtracted the amount of NPP that was used in FUN for N acquisition, and translated the remaining NPP into the global vegetation C that can be supported by this productivity, using the calculated linear relationship.

[38] Four soil N trajectories were explored: (1) unlimited N_{soil}; (2) constant low N_{soil} (0.1 kg N m^{-2}); (3) progressive N limitation starting at high N_{soil} (1.0 kg N m^{-2}), but decreasing at a rate of 0.04 kg N m^{-2} yr^{-1}; and (4) increasing N availability (0.004 N m^{-2} yr^{-1}) starting at low N_{soil} (0.1 kg N m^{-2}). All other input parameters are held constant: $r_{C:N}$ is 200 [i.e., *Hungate et al.*, 2003], $E_T = 0.5$ m· yr^{-1}, $s_d = 50$ m, $C_{root} = 0.5$ kg C m^{-2}, $N_{leaf} = 0.001$ kg N m^{-2}, and fixers are turned off.

[39] Trajectory 1 was equivalent to the outputs by the C-only DGVMs, i.e., unchanged without FUN. With trajectory 2 it was considered that vegetation is generally N-limited, and the low N_{soil} value is conservatively within the globally observed values [*Post et al.*, 1985]. The first two trajectories assumed no changes in N deposition and N mineralization, and therefore represented the upper and lower bounds of expected vegetation C. Trajectory 3 represented the "progressive N limitation" case where N is gradually locked up in the increasing plant biomass pool. The loss rate was set arbitrarily, but within realistic bounds, so that N_{soil} approached zero near the end of the simulation (year 2100) for visualization. Finally, trajectory 4 represented the scenario where N availability increases through increasing N deposition and/or increased rates of N mineralization in soils in response to warming. The gain rate was set arbitrarily, but within realistic bounds, so that it was symmetric to the loss rate in trajectory 3 (offset by 1 order of magnitude) and that the gain could be easily visualized (as opposed to too abrupt or too gradual an increase).

3. Results

3.1. Data Test

[40] The model performed reasonably well against the data (Figure 4). The r^2 was 0.89, root mean squared error (RMSE) was 0.003 kg N m^{-2} yr^{-1} and the slope of the regression forced through the origin (zero observed N uptake should correspond with zero predicted N uptake) was 1.03 ($p < 0.01$). The greatest variability was in the SCP data due primarily to the assumptions in the gap-filled root biomass and turnover rate. For the FACE data under ambient conditions only, FUN predicted less N uptake than was actually observed, primarily because measured NPP was very low (especially for the Duke and RHI sites). N demand was underestimated for these low values (calculated as
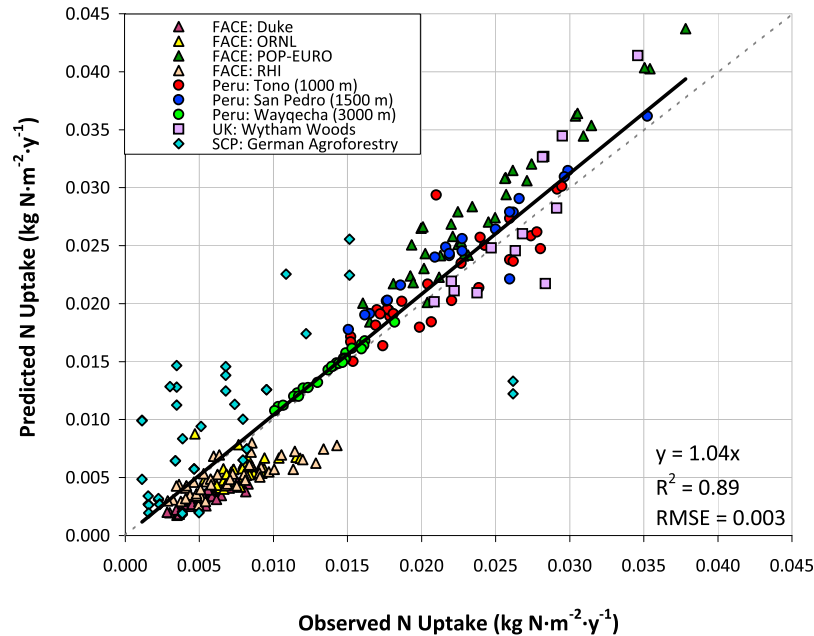
Figure 4. Scatterplot of observed versus predicted nitrogen (N) uptake (FUN) from the Free Air CO_2 Enrichment (FACE) experiments [*Finzi et al.*, 2007], three agroecosystem sites from the Special Collaborative Project 179 (SCP179) international workshop data set [*McVoy et al.*, 1995], three tropical montane sites in the Peruvian Andes [*Tan*, 2008], and an ancient woodland in the United Kingdom [*Tan*, 2008].

$C_{NPP}/r_{C:N}$, i.e., equation (1)) because either NPP was underestimated, the C:N ratio was overestimated or a combination of both.

[41] On average for all of the data, N_{uptake} was 92% of N_{demand} indicating N-limitation of 8%; in other words, 92% of C_{NPP} was used for growth, and N therefore limited growth by 8% of what could have occurred had there been sufficient N. The average $Cost_{active}$ exceeded $Cost_{resorb}$ (11.5 versus 2.7 kg C kg N^{-1}, respectively; for reference, $Cost_{fix}$ would have been on average 9.9 kg C kg N^{-1} if any fixers were present); $Cost_{resorb}$ was less than $Cost_{active}$ 89% of the time, and therefore resorbed N_{leaf} was the first source of N extracted after $N_{passive}$ if N_{demand} remained positive. $N_{passive}$ satisfied all of N_{demand} in only 2% of the data. The cheapest N source after $N_{passive}$ was sufficient to satisfy all of N_{demand} 46% of the time; the other 54% required additional N from the next cheapest N source. On average, $N_{passive}$ alone would have been able to satisfy 18% of N_{demand}; N_{resorb} alone would have been able to satisfy 51% of N_{demand}; N_{active} alone would have been able to satisfy 63% of N_{demand}; and, N_{fix} (if there were fixers) alone would have been able to satisfy 75% N_{demand}.

3.2. Sensitivity Analysis

[42] Here we present the sensitivity of FUN to variation in each input parameter and driver while holding all other inputs constant (Figure 5). The default drivers were set as annual averaged constants as $C_{NPP} = 0.5$ kg C m^{-2}· yr^{-1}, $r_{C:N} = 300$ kg C kg N^{-1}, $E_T = 0.5$ m yr^{-1}, $s_d = 50$ m, $T_{soil} = 17°C$, $C_{root} = 1.0$ kg C m^{-2}, $N_{leaf} = 0.0012$ kg N·m^{-2}

and $N_{soil} = 0.05$ kg Nm^{-2}. The subsequent costs were: $Cost_{resorb} = 8.3$ kg C kg N^{-1}; $Cost_{active} = 20.2$ kg C kg N^{-1}; $Cost_{fix} = 9.0$ kg C·kg N^{-1}. $Cost_{active}$ was therefore somewhat high to create a large difference between $Cost_{active}$ and $Cost_{fix}$ to visualize clear differentiation between fixer ($A_{fix} = $ TRUE) and nonfixer ($A_{fix} = $ FALSE). Similarly, s_d was set somewhat low so that $N_{passive}$ does not overwhelm the contributions from the other uptake mechanisms (again, for visualization purposes). We do not show variation in T_{soil} because it affects only the fixer (constant N uptake for nonfixer across soil temperature). Each parameter varied from zero through and beyond a reasonable range until predicted N uptake reached an infinite state (i.e., plateau at N_{demand}).

[43] The FUN model was most sensitive to C_{NPP} and $r_{C:N}$ due to the effect on N_{demand}, whereas it was less sensitive to changes in E_T and s_d (compare y axes) because N can still be assimilated through N_{resorb}, N_{active} or N_{fix} when $N_{passive}$ is zero. In the sensitivity plot with NPP (C_{NPP}), the fixer can continue to acquire N through N_{fix} as long as C_{NPP} continues to increase (i.e., equation (6b) with "fix" notation). The nonfixer, however, can only take up at a maximum the value of N_{soil} and N_{resorb}. As N_{soil} and N_{resorb} approach zero any increase in C_{NPP} will go to the infinitely increasing $Cost_{active}$ and $Cost_{resorb}$ (i.e., equations (4) and (5)).

[44] Similarly, as $r_{C:N}$ decreased, the N_{demand} increased per unit of C_{NPP} (i.e., equation (1)). As N_{demand} increased, the difference in N uptake by the fixer and nonfixer also increased because the nonfixer was spending increasingly more C_{NPP} per unit of N needed, whereas the fixer spent C
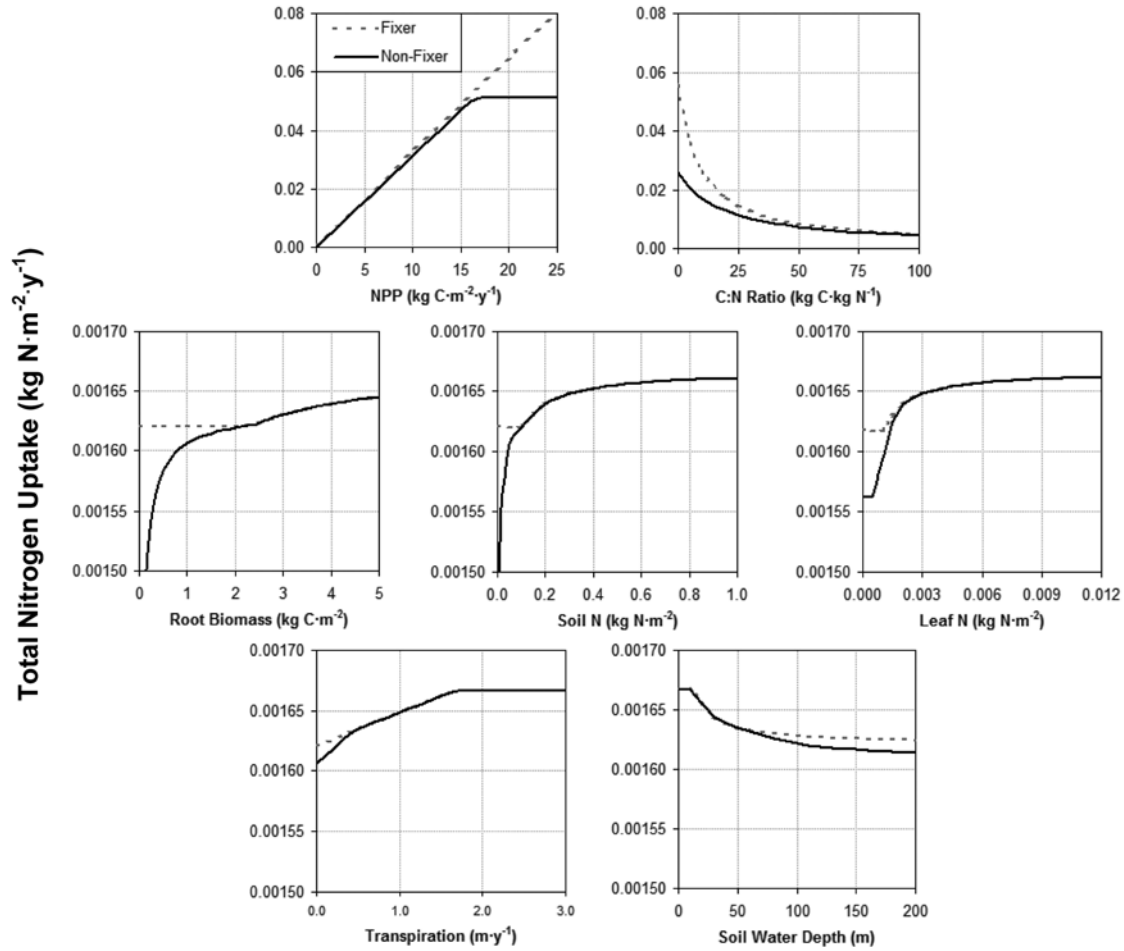
Figure 5. Sensitivity of simulated total nitrogen uptake from FUN (y axis) to variation in each input parameter (x axis) holding all other inputs constant ($C_{\mathrm{NPP}} = 0.5$ kg C m^{-2} yr^{-1}, $r_{C:N} = 300$ kg C kg N^{-1}, $C_{\mathrm{root}} = 0.5$ kg C m^{-2}, $N_{\mathrm{soil}} = 0.05$ kg N m^{-2}, $N_{\mathrm{leaf}} = 0.0012$ kg N m^{-2}, $E_T = 0.5$ m yr^{-1}, $s_d = 50$ m, and $T_{\mathrm{soil}} = 17°$C). Continuous lines (black) correspond to nonfixers, and dashed lines (gray) correspond to fixers. The varied parameter was allowed to increase beyond a reasonable range until total nitrogen uptake reached a steady state (i.e., plateau).

at a constant rate. At a certain point in the decreasing $r_{C:N}$, N_{demand} exceeded N_{soil} plus N_{leaf} and the nonfixer could subsequently take up only as much as the maximum available. In the other direction as $r_{C:N}$ increased, N_{demand} decreased. If N_{demand} was positive, even if marginal, the uptake of N would cost more for the nonfixer because Cost$_{\mathrm{active}}$ was greater than Cost$_{\mathrm{fix}}$ (for this test). Therefore, the fixer would always acquire more N than would the nonfixer until $r_{C:N}$ was so large and N_{demand} low that N_{demand} equaled N_{passive} and active uptake and BNF were zero.

[45] Sensitivity to variation in C_{root} and N_{soil} largely affected Cost$_{\mathrm{active}}$, as described in section 2 (see Figure 3). As C_{root} increased, the plant (i.e., nonfixer) was able to exploit all of the N_{soil} at a minimal cost. Similarly, as N_{soil} increased, enough of it was in contact with the given C_{root} to satisfy N_{demand}. Because Cost$_{\mathrm{active}}$ eventually declined past Cost$_{\mathrm{fix}}$ in both cases a fixer would switch from BNF to active uptake and subsequently follow the nonlinear

reduction in cost. When C_{root} and/or N_{soil} were minimal, however, the fixer would acquire most of the N_{demand} from N_{fix}, but the nonfixer would be able to take up only N_{resorb} at the minimum. A similar pattern occurred for variations in N_{leaf} from analogous mathematical logic.

[46] As evaporative demand E_T increased, total N uptake increased until equaling N_{demand} because N_{passive} required no C_{NPP} expense, assuming N_{soil} was not limiting (i.e., equation (2)). The increase for the fixer was linear because the additional N required was coming from N_{fix} (because Cost$_{\mathrm{fix}}$ < Cost$_{\mathrm{active}}$ in this scenario), which did not vary with decreasing N_{soil} (i.e., equation (3)). The increase for the nonfixer was nonlinear because Cost$_{\mathrm{active}}$ increased as more N was extracted from N_{soil} in N_{passive}. Likewise, the difference in total N uptake between the nonfixer and fixer increased as the cost difference increased. When E_T was zero the plants could satisfy N_{demand} through active uptake or BNF. At the other extreme if E_T was large enough, then
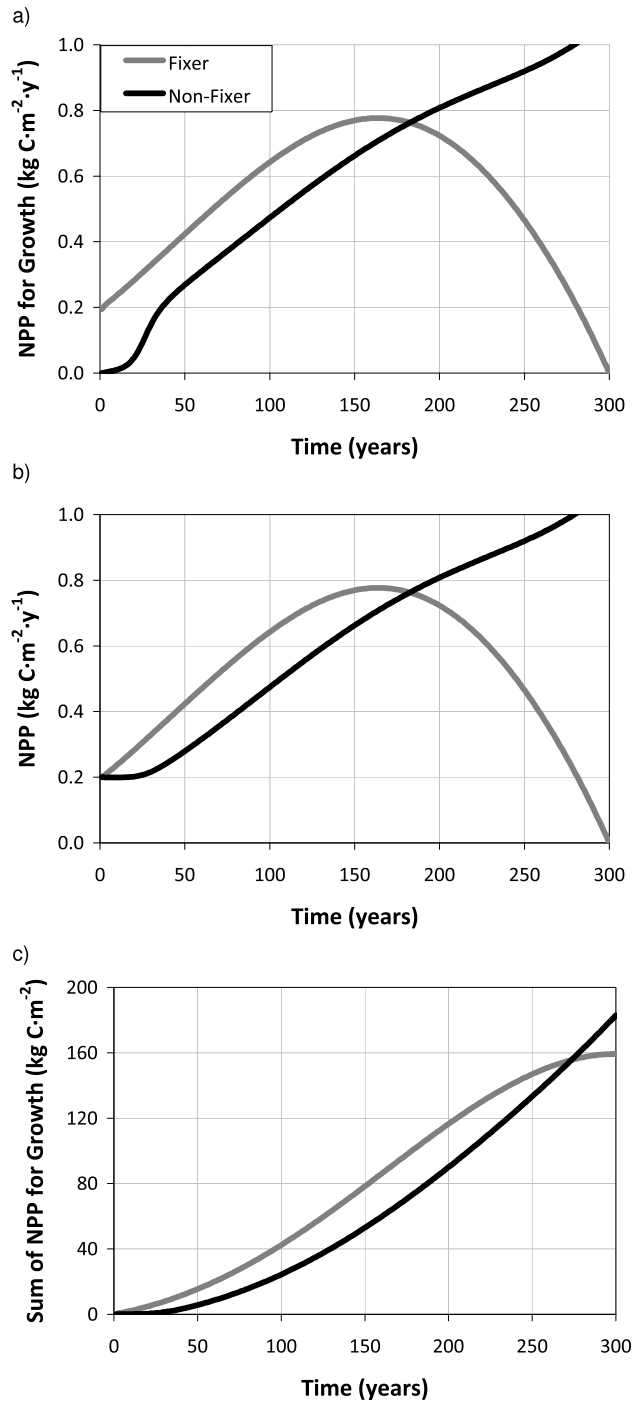
a)

b)

c)

Figure 6. Scenario of primary succession between fixer and nonfixer. (a) Initially, there is no N in the system, and only the fixer can grow by acquiring N through BNF, which eventually returns to the system for the nonfixer. (b) NPP for the nonfixer increases gradually with increasing N uptake, whereas the NPP for the fixer decreases gradually as the nonfixer improves its competitive status. (c) Although the nonfixer has eventually exceeded the fixer in NPP and NPP for growth, it is not until later that the sum of NPP for growth (integration of Figure 6a in time) exceeds that of the fixer.

the plants could use all of the C_{NPP} for growth as advection through transpiration provided all the required N to maintain $r_{C:N}$.

[47] The sensitivity analysis with respect to s_d was somewhat misleading because it allowed for all other inputs or drivers to be held constant. In reality, variation in s_d would not be independent of E_T. Further, available N by definition depends on wet soil and becomes immobilized (decreases in availability) as s_d decreases. If N_{soil} was held constant while s_d decreased, then N_{soil} could be considered more concentrated. Thus, a small amount of E_T would take up a relatively large amount of N_{soil} (i.e., equation (2)). In the opposite direction, if s_d was large then N_{soil} could be considered diluted and $N_{passive}$ became minimal. The difference between the fixer and nonfixer would be due to the higher cost of uptake for the nonfixer.

3.3. Model Experiment 1: Succession

[48] Initially, there was no N in the system, and only the fixer could grow by acquiring N through BNF (Figure 6a). The fixer would not allocate more C_{growth} to roots (assume no other reasons to increase root growth, e.g., water, stability) because there was no N_{soil} and therefore root development for active uptake would be wasted C_{growth} (more efficient to expend C on BNF, i.e., equation (3) versus equation (4)). The fixer continued to grow and photosynthesize (Figures 6b and 6c). Meanwhile, as N_{soil} increased with turnover from the fixer, the nonfixer began to grow and slowly increase its photosynthesis. As N_{soil} continued to increase, $Cost_{active}$ decreased for the nonfixer faster than it did for the fixer because the nonfixer was allocating more C_{growth} to C_{root}. Soon thereafter $Cost_{active}$ was less than $Cost_{fix}$ for only the nonfixer, and the nonfixer was therefore allocating less C_{NPP} for N acquisition than was the fixer: this was the critical point of difference. Further, as the nonfixer increased in growth, the fixer photosynthesized at less than maximal rates due to shading. The C_{NPP} for the nonfixer eventually surpassed that of the fixer as well as the associated C_{growth}. Finally, the overall sum of C_{NPP} for growth for the nonfixer passed that of the fixer. Figure 6 shows continuous increases for the nonfixer, but these would eventually plateau from limitation by other factors (e.g., water availability). We prescribed equal and constant $r_{C:N}$ throughout, but if $r_{C:N}$ was lower for the fixer (it may be that more N is required for fixers in general), then the dynamics of Figure 6 are shifted faster in time. Thus, nonfixers surpassed the productivity of fixers after ~180 years (after ~150 years if $r_{C:N} = 200$ for the fixer), and we were therefore able to adequately represent successional dynamics from mechanistic principles.

3.4. Model Experiment 2: N Fertilization

[49] Under a modeled N_{soil} increase for the control plots, FUN estimated an increase in N_{uptake} (0.0212 kg N·m^{-2}) that was equivalent to the mean actual N_{uptake} (0.0211 ± 0.0012 kg N·m^{-2}) from the fertilized plots (Figure 7). Because these ecosystems were N-limited, the fertilization showed that adding N resulted in increased N uptake. Although this appears intuitive, in fact this would not be the case if NPP was low because N_{demand} would also be low, so
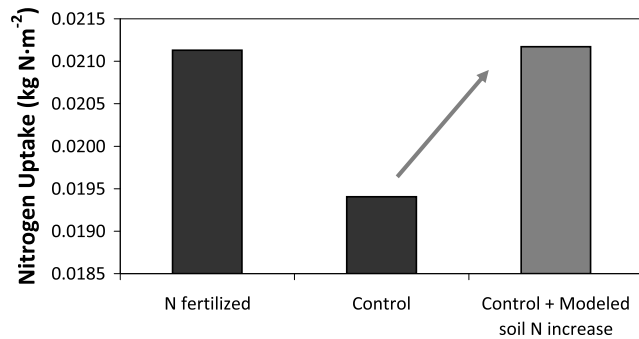
Figure 7. Data from a nitrogen (N) fertilization experiment in Peru show that N uptake in the N fertilized plots was on average larger than that in the control plots (dark bars) because the ecosystems were N-limited. A modeled soil N increase for the control plot data was applied, resulting in a simulated increase in N uptake (light bar) that matched the observed N uptake from the plots that were actually fertilized by N.

an increase in N_{soil} would have little effect. C_{NPP}, C_{root}, $r_{C:N}$, E_T, s_d, and N_{leaf} were not significantly different between fertilized and control plots. It can also be calculated how much N_{soil} should be added to saturate the system so that no additional N will be taken up with increased N_{soil}. The maximum N uptake given saturation was 0.0252 kg N m^{-2} given 40 kg N m^{-2} of N_{soil}, but an uptake of 0.0242 kg N m^{-2} was given at 5 kg N m^{-2} of N_{soil} so the added N uptake decreased exponentially with increasing N_{soil}. Thus, we were able to adequately represent the N uptake response in the experimental N fertilization from the modeled N fertilization. This result provides grounding for determining ecosystem response from changes in N availability from warming, as well as N deposition. Additionally, the exercise may be particularly useful to specifying amounts of fertilizer application for agriculture.

3.5. Model Experiment 3: CO$_2$ Fertilization

[50] Under a modeled NPP increase for the ambient CO$_2$ plots, FUN estimated an increase in N_{uptake} (0.0103 kg N m^{-2}) that was not as large as the mean actual N_{uptake} (0.0107 ± 0.0012 kg N·m^{-2}) from the CO$_2$ fertilized plots (Figure 8). It was therefore evident that something other than NPP was limiting N uptake in the ambient plots.

[51] An initial consideration might suggest that the soil N concentrations were different between the CO$_2$ fertilized and ambient plots. Perhaps there was more soil N in the CO$_2$ fertilized plots from increased decomposition or mineralization acting to increase N_{uptake} [*Finzi et al.*, 2007]. Unfortunately, data were not available for comparison. However, we were able to test this hypothesis in the model environment by taking the data from the ambient plots, and modeling an increase in N_{soil} (similar to Model Experiment 2). N_{uptake} subsequently increased slightly for the ambient plots under higher N_{soil} levels, but still not enough to match the N_{uptake} observed in the CO$_2$ fertilized plots.

[52] A second possibility was that there were differences in leaf N concentrations between the CO$_2$ fertilized and

ambient plots. Greater N_{leaf} in the CO$_2$ fertilized plots could lead to greater N_{uptake} from retranslocation. Data were available for comparison, but there was on average no significant difference in N_{leaf} between ambient and CO$_2$ fertilized plots (0.010 versus 0.009 kg N·m^{-2}, respectively). Similarly, there was on average no significant difference in $r_{C:N}$ between the ambient and CO$_2$ fertilized plots (306 versus 305, respectively).

[53] However, there was a large difference in C_{root} between the ambient and CO$_2$ fertilized plots: 0.173 versus 0.253 kg C·m^{-2}, respectively. The CO$_2$ fertilized trees were allocating this extra C into root biomass as well as aboveground growth. This means that the Cost$_{active}$ was lower for the CO$_2$ fertilized plots, and those trees could subsequently take up more N with less expense to NPP. Given that difference, we took the data from the ambient plots, and modeled an increase in C_{root} to match that from the CO$_2$ fertilized plots. N_{uptake} subsequently increased for the ambient plots under greater C_{root} biomass. In fact, that difference in root biomass plus the difference in NPP between the ambient and CO$_2$ fertilized plots accounted for the entire difference in N_{uptake} between the ambient and CO$_2$ fertilized plots (0.0106 versus 0.0107 kg N m^{-2}, respectively). The results of this experiment are particularly useful for providing a mechanistic model representation of the observations from the CO$_2$ enrichment experiments, which will also help to understand how ecosystems will respond globally to rising CO$_2$ concentration.

3.6. Model Experiment 4: DGVM Vegetation Carbon

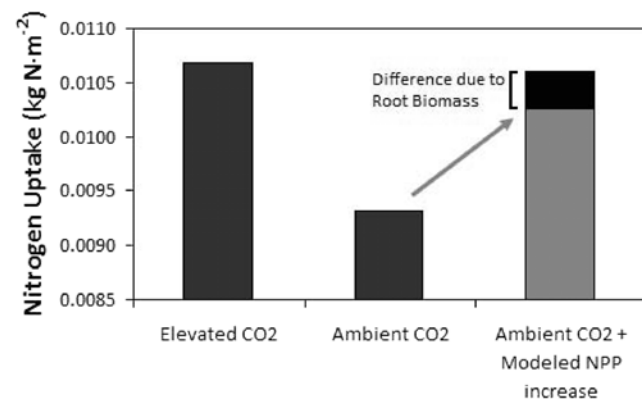[54] The five DGVMs (HYLAND, LPJ, ORCHDEE, SDGVM, and TRIFFID) all estimated increases in NPP and

Figure 8. Data from the Free Air CO$_2$ Enrichment (FACE) experiments show that nitrogen (N) uptake in the elevated CO$_2$ plots was on average larger than that in the ambient CO$_2$ plots (dark gray bars) because NPP was also larger in the elevated CO$_2$ plots [*Finzi et al.*, 2007]. A modeled NPP increase for the control plots was applied (equal to the greater NPP in the elevated CO$_2$ plots), resulting in a moderate simulated increase in N uptake (light bar). Increasing NPP did not fully explain the difference in N uptake between the elevated and ambient CO$_2$ plots. The remaining difference in N uptake was due to differences in root biomass between the elevated and ambient CO$_2$ plots.
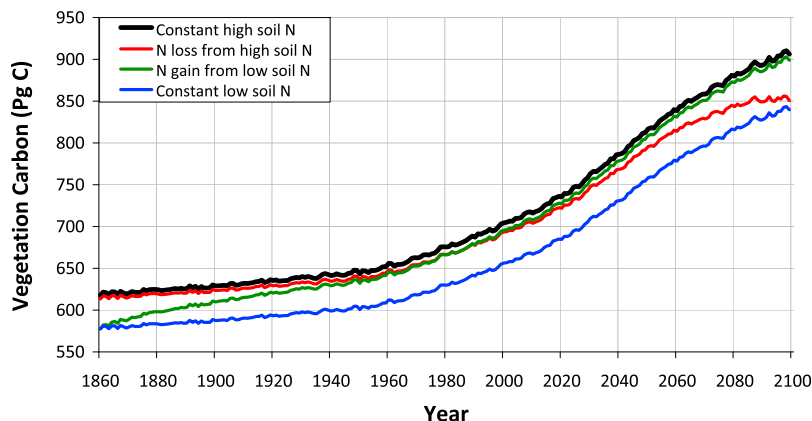
Figure 9. Vegetation C from five DGVMs (HYLAND, LPJ, ORCHDEE, SDGVM, and TRIFFID) is averaged together for the IPCC A1 scenario. Without a N-cycle (black line: constant high soil N), the estimated vegetation C may be considered "potential" that must be scaled down to "actual" on the basis of C allocated to N uptake. Assuming N-limitation, but soil N in equilibrium, vegetation C continues to increase to 2100, but with less C allocated to vegetation C because some is used for N acquisition (blue line: constant low soil N). Two alternate soil N trajectories are shown: (1) progressive N limitation (red line: N loss from high soil N); and (2) increasing soil N with increasing N mineralization from warmer temperatures and/or N deposition (green line: N gain from low soil N).

vegetation C into the future based on the IPCC scenarios (A1, A2, B1, B2) for projected atmospheric CO_2 increase. There were significant differences between in the rates of increase, variability, and magnitude of NPP and vegetation C across the models [*Sitch et al.*, 2008]. For illustrative purposes we reduce the number of figures from five models × four IPCC scenarios × four N_{soil} trajectories to two summary figures: (1) the average model vegetation C for the A1 scenario; and (2) the year 2000 and 2100 vegetation C for each model averaged from all four IPCC scenarios.

[55] Without a N-cycle, the DGVMs on average estimated ~700 Pg of vegetation C in year 2000 increasing to ~900 Pg in year 2100, or an annual global C sink of 2 Pg C yr^{-1} (Figure 9, black line: constant high soil N). It is likely that these values represent overestimates [*Hungate et al.*, 2003], but by how much depends on what we may expect in N_{soil} trajectories (given different soil models). Assuming global N-limitation from low N_{soil} [*Vitousek and Howarth*, 1991], but maintaining equilibrium so that N removal equals N addition, the estimated vegetation C was lower at ~650 Pg C in 2000 and ~850 Pg C in 2100. However, the time series pattern still followed a similar trajectory of increase because of increasing N_{demand}, as well as increasing C to pay for more N_{soil} due to increased photosynthesis from CO_2 fertilization (Figure 9, blue line: constant low soil N).

[56] Two alternate idealized N_{soil} trajectories may occur: (1) progressive N limitation, whereby N_{soil} decreases every year [*Luo et al.*, 2004]; and (2) increasing N_{soil} due to increasing soil decomposition and N mineralization from warmer temperatures and/or increasing anthropogenic N deposition [*Melillo et al.*, 1993; *Peterjohn et al.*, 1994]. In the first instance, we started at a relatively high N_{soil} in year 1860 (vegetation C nearly equal to that without N-cycle: 213 Pg versus 218 Pg) but decreased a constant amount each year until N_{soil} was nearly zero by year 2100 ($N_{soil} = 0.04$ kg

N·m^{-2}). The difference in "actual" versus "potential" vegetation C increased each year, though still maintained an increasing annual vegetation C until year ~2080 when vegetation C started to plateau (Figure 9, red line: N loss from high soil N). The reason why vegetation C was allowed to increase for the most part with decreasing N_{soil} is because NPP was also increasing exponentially so there was progressively more C_{NPP} to pay for linearly diminishing supplies of N_{soil}. However, at a certain point (i.e., year 2080) the exponentially increasing Cost$_{active}$ meant that the vegetation must put nearly all of its C_{NPP} into N acquisition, leaving very little left to add to vegetation C.

[57] With increasing N_{soil} starting from low N_{soil}, however, there was the potential to "catch up" to the potential vegetation C (Figure 9, green line: N gain from low soil N). Still, even with N_{soil} greater than 1 kg N m^{-2} by 2100, the actual vegetation C was ~7.5 Pg less than potential. It is the balance between N deposition/mineralization and progressive N limitation that will determine which trajectory will outweigh the other.

[58] The second summary figure illustrates the individual model differences in vegetation C and N uptake, averaging the IPCC scenarios and giving only the range between low and high N_{soil} at equilibrium (Figure 10). Figure 10 is similar, but not equivalent to that of *Hungate et al.* [2003]. There are a number of observations that can be made from Figure 10. Focusing first on the darker square points (no N-limitation), the vegetation C varied considerably between the models, as was evident in the spread along the x axis. For example, in year 2000 the vegetation C for TRIFFID was 461 Pg, while that of LPJ was 886 Pg; the year 2100 vegetation C for TRIFFID was 489 Pg, while that of HYLAND was 1097 Pg. The year 2000 vegetation C for HYLAND and ORCHIDEE was similar (~800 Pg), but the N uptake was very different: N uptake for ORCHIDEE was
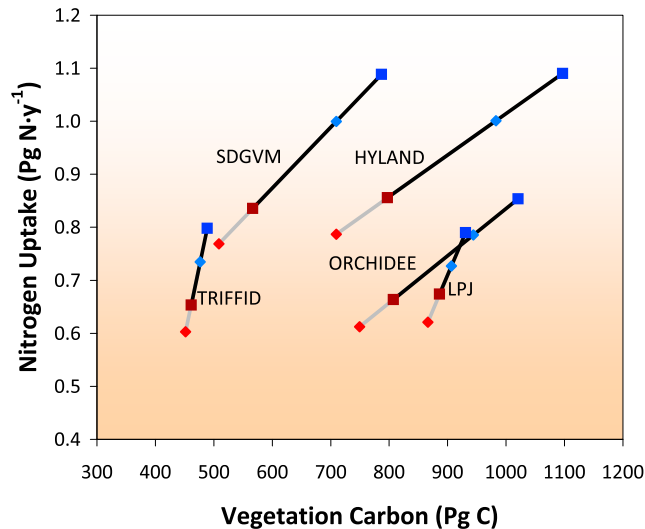
Figure 10. Individual model differences for five DGVMs in vegetation C and N uptake. The red points are values for year 2000, and blue points are for year 2100. The squares represent the models under no N-limitation (high soil N), and the diamonds represent the models under N-limitation (low soil N).

more similar to that of TRIFFID and LPJ, while N uptake for HYLAND was more similar to that of SDGVM. The slopes of the lines reveal how much N uptake was required per unit vegetation C. The slopes may be considered the sensitivity of the vegetation C in the models to N uptake. The slope was steeper for TRIFFID and LPJ than it was for SDGVM, HYLAND and ORCHIDEE. The difference in slopes is due to differences in how much NPP goes to vegetation C for each of the models, which also translates into how much NPP is available for N acquisition, as well as the differences in C:N ratios between the models thus affecting N demand.

[59] Focusing next on the lighter diamond points (N-limitation), both the modeled vegetation C and N uptake decreased for all models given low N_{soil}. HYLAND and SDGVM lost a lot more vegetation C when N-limited than did LPJ and TRIFFID. Nonetheless, the proportional decrease in vegetation C was similar for all the models, though slightly less for HYLAND and TRIFFID (47%) than for LPJ and TRIFFID (49%). This result emphasizes the models that put most of the NPP into vegetation C are more likely to be affected by N-limitation than those where the fate of NPP shifts more toward the soil, and that the C in biomass may be ~50 Pg on average less than what was originally estimated without N-limitation.

4. Discussion

4.1. Implications of the Model Experiments

[60] The overall context of the FUN model is its implementation in a full land-surface model suitable for large spatially explicit scales, and then subsequent implementation in a GCM to refine the existing prediction and impacts of increasing levels of atmospheric greenhouse gas concentrations [*IPCC*, 2007]. Much recent work on DGVMs has focused on plant competition and phenology aspects to specify the global spatial distribution and timing of vegetation C [*Moorcroft et al.*, 2001]. DGVMs will be affected by inclusion of the N-cycle, especially when simulating primary succession. Vegetation may not be able to realistically grow in the DGVMs where there is no N_{soil}, but inclusion of N fixers can solve that problem. However, it may be difficult to remove N fixers later in succession without a logical mechanistic representation of the successional processes [*Vitousek and Howarth*, 1991]. The model experiment of succession showed that FUN can realistically represent primary succession. We showed that fixers generally dominated early on, but were replaced by nonfixers after ~150–180 years. This represents a longer duration than that reported in similar model experiments (~100 years), but different driving data are used between the studies so we cannot conclude that the differences are due to model or data [*Rastetter et al.*, 2001; *Vitousek and Field*, 1999]. The large-scale implications of this difference is that if DGVMs or land surface models prescribe differences between fixers and nonfixers for NPP, stress sensitivity, albedo, water cycling and N demand, then the global drawdown of CO_2 and radiative feedbacks will be altered depending on whether or not fixers are present or nonfixers are present.

[61] The model experiments that took advantage of large-scale manipulation studies in N fertilization (Peru) and CO_2 fertilization (FACE) showed that FUN can be used to understand and inform these data and the responses to the manipulations. If we scale up these measurements globally, we can then ask larger-scale questions such as: How will ecosystems respond to changes in N deposition and CO_2 fertilization? The Peru model experiment was relatively straightforward in that the response from the modeled increase in N_{soil} matched the measured response from the actual N fertilization. The FACE model experiment results were less straightforward in that the modeled increase in NPP did not result in a large enough increase in N uptake to match that from the elevated CO_2 plots. Nonetheless, the model was able to reveal why that discrepancy occurred, namely the affect of changes in root biomass, which is helpful to understand the ecosystem dynamics in response to rising atmospheric CO_2. *Finzi et al.* [2007] indicated that a combination of factors including changes in root production was likely to account for greater N uptake under elevated CO_2. Here, we support and quantify their explanation with our model and independent test of their data.

[62] The DGVM vegetation C model experiment showed not only how FUN can be used with these models, but also the global-scale response ranges for what to expect under different N_{soil} trajectories for the various IPCC scenarios. It illustrated the existing differences in DGVMs [*Sitch et al.*, 2008] as well as how these models might respond to N-limitation. The next step is complete integration of FUN into the DGVMs so that more dynamic, spatially explicit analyses can be performed. Without this next step, it is difficult to draw comparisons between reductions in global vegetation C from 24–64% with the N-cycle from other studies [*Jain et al.*, 2009; *Sokolov et al.*, 2008; *Thornton et*

al., 2007]. Our results show a much more modest reduction of 7%, which is comparable to the 8% reduction from *Zaehle et al.* [2010], but this is only from the plant N acquisition component of the total N-cycle. For a fair comparison, FUN would need to be integrated into those models and tested for its effect.

4.2. Observed Ranges of Drivers

[63] All inputs and drivers significantly affect total N uptake given enough variation in the input or driver, but the amount of variation required to cause a significant change may be unrealistic (Figure 5). C_{NPP} may range from 0–2 kg C·m^{-2} yr^{-1} [*Cao and Woodward*, 1998; *Moorcroft et al.*, 2001], thus full depletion of all N sources is unlikely from unrealistically high C_{NPP} (e.g., 15 kg C·m^{-2} yr^{-1} in Figure 5). The largest differences between fixers and non-fixers with respect to $r_{C:N}$ occurred when N_{demand} was very high because of low $r_{C:N}$ (the fixer could satisfy this unusually high N_{demand} with BNF), but observed $r_{C:N}$ values are rarely that low [*Schindler and Bayley*, 1993].

[64] N_{soil} ranges from 0–1.6 kg N m^{-2} [*Post et al.*, 1985], which changes $Cost_{active}$, and subsequently influences the primary source and amount of N uptake, the amount of C available for growth, and the competitive behavior between fixers and nonfixers. Likewise, C_{root} ranges from 0–1.5 kg C m^{-2} [*Jackson et al.*, 1997] for live fine root biomass, and up to 5 kg C m^{-2} for total standing root biomass [*Jackson et al.*, 1996]. This wide range in root biomass alters the ability with which a plant can access N_{soil}, and is particularly important in lowering $Cost_{active}$ for both nonfixers and fixers. Similarly, N_{leaf} may range from 0.0005–0.01 kg N m^{-2} [*Wright et al.*, 2004], but whether or not a plant chooses to drop a leaf and resorb that N depends on shading, deciduousness, leaf lifespan, and the costs of active uptake or BNF.

[65] Observed annual total rates of E_T of up to 2 m yr^{-1} [*Fisher et al.*, 2008] may lead to $N_{passive}$ as the only source of N necessary to satisfy N_{demand}, but this depends on N_{soil} as well (equation (2)). Given sufficiently large N_{soil} (e.g., fertilized management or N deposition), an increase in E_T may lead to a significant increase in $N_{passive}$, but given low N_{soil}, an increase in E_T will do little to increase N_{uptake}. Under drought conditions, s_d may approach zero, which leads to a decrease in available N_{soil}, but N-limitation may be less important than drought stress at this point. The range in T_{soil} may be from extreme cold to extreme hot, which also influences BNF activity [*Houlton et al.*, 2008], but physiological temperature stress may be more important than increases in $Cost_{fix}$; still, only a slight shift in T_{soil} can cause a switch in competitive ability between N fixers and non-fixers as the balance between $Cost_{fix}$ and $Cost_{active}$ changes to one direction or the other.

[66] Climate change drives changes in the input drivers to FUN. C_{NPP} and $r_{C:N}$ may increase with CO_2 fertilization [*Idso and Kimball*, 1993; *Johnson et al.*, 1997; *Pregitzer et al.*, 1995; *Rastetter et al.*, 1992]. E_T may decrease as regions become drier [*Cox et al.*, 1999, 2000] or due to CO_2 induced stomatal closure [*Gedney et al.*, 2006] or increase as other regions become wetter [*Zhang et al.*, 2007]. N_{soil} may increase with increasing temperatures [*Pastor and Post*, 1988; *Perring et al.*, 2008] or decrease with progressive N limi-

tation if N becomes concentrated in slow decaying pools [*Luo et al.*, 2004].

[67] In the framework of a DGVM, other NPP-limiting factors such as phosphorus, water, light, temperature, pH and trace nutrients may be treated with individual sub-models. FUN may be particularly useful for phosphorus acquisition, as recent research has demonstrated that N is required to acquire phosphorus [*Wang et al.*, 2007]. Herbivory impacts plant growth, and fixers may be more susceptible than non fixers due to higher leaf N concentrations [*Menge et al.*, 2008]. In addition, the priority with which plants allocate C to different processes of tissue turnover, maintenance and N uptake is difficult to predict, and depends on life strategy and response to environmental conditions. Changes in the demands for C caused by altered rates of respiration or turnover (e.g., caused by increasing temperatures) might affect the ability to actively acquire N, as would changes in gross photosynthetic rates (e.g., caused by CO_2 fertilization, as proposed by *Finzi et al.* [2007]).

4.3. A Closer Look at the Cost Functions

[68] The k constants for $Cost_{active}$ and $Cost_{resorb}$ warrant examination. For $Cost_{active}$, root biomass does not necessarily need to be high if N_{soil} is high (given nonlimitation of other factors) [*Aerts et al.*, 1991]. Yet, plants allocate C to root growth in search of N when N_{soil} is low. Closer proximity of roots to N means that less C is required to drive N_{active}. But, what matters more: few roots or little N_{soil} (or, oppositely, a lot of roots versus high N_{soil})?

[69] Consideration is given to the balance between $Cost_{fix}$ and $Cost_{active}$; the intersection point between the two is reasonable given observations of N_{soil} and C_{root}, as well as observed switching between BNF and active uptake [*Jackson et al.*, 1996; *Post et al.*, 1985; *Rastetter et al.*, 2001]. The product of k_N and k_C must equal unity: products of k_N and k_C greater or less than 25% of unity result in both unrealistically high or low costs as well as the loss of a plausible switching point between $Cost_{active}$ and $Cost_{fix}$ (see Figure 3). The function tends to infinity and zero at the low and high ends, respectively, of the global observations for N_{soil} and C_{root}. Nonetheless, the relative weights between the two are undetermined. For instance, k_N could be 0.1 kg C m^{-2} while k_C is 10 kg C·m^{-2}, or vice versa. It is likely that these values are variable depending on root physiology and soil properties. An alternative form of $Cost_{active}$ with a scalar to be determined may be considered as:

$$Cost_{active} = scalar \left(\frac{k_N}{N_{soil}} + \frac{k_C}{C_{root}} \right) \qquad (9)$$

[70] However, given the original formulation of $Cost_{active}$ (equation (4)) and specification for k_N and k_C, the average observed N_{soil} and average C_{root} [*Jackson et al.*, 1996; *Post et al.*, 1985] leads to $Cost_{active} < Cost_{fix}$, which means that fixers on average have no competitive advantage over nonfixers, which is generally true [*Vitousek and Howarth*, 1991]. But, when N_{soil} and C_{root} are smaller than average, for instance in an early successional state, then $Cost_{active} > Cost_{fix}$, and fixers dominate nonfixers, which is generally true [*Rastetter et al.*, 2001]. In some cases, nonfixers and

fixers coexist late in succession with the fixers acquiring N through active uptake ($\text{Cost}_{\text{active}} < \text{Cost}_{\text{fix}}$) [*Crews*, 1999; *Marschner*, 1995]. How did the fixers manage to survive late into succession and switch to active uptake given a disincentive to grow roots? Other incentives to grow roots (i.e., stability, water, phosphorus) paid later dividends in the ability to access later increases in N_{soil} and not suffer a high $\text{Cost}_{\text{active}}$ [*Crews*, 1999].

[71] Similarly, k_R in the cost function for retranslocation (equation (5)) is set based on global observations, but may need a more explicit link to leaf physiology. In a perfectly efficient system, all of the N in an old leaf could be resorbed and put into a new leaf: the plant would therefore require very little new N from the soil. However, plants on average resorb only 50% of leaf N, and this value varies widely not only from species to species but also within the same plant from year to year [*Aerts*, 1996]. This raises the question as to why plants operate such that actual resorption is less than potential resorption?

[72] Much of the literature on retranslocation has focused on inconsistencies with linking soil or leaf N status to the ability of a plant to resorb a maximum amount of leaf N, also referred to as resorption efficiency or proficiency [*Killingbeck*, 1996]. Sometimes the link is strong; other times there is no evidence for the link [*Chapin and Kedrowski*, 1983; *Wright and Westoby*, 2003]. Some have observed a link with shading, leaf lifespan and water stress to resorption rates [*Del Arco et al.*, 1991], but few other studies have supported these observations. In a critical observation, *Chapin and Moilanen* [1991] concluded that resorption efficiency is influenced most strongly by the leaf C flux in a source-sink interaction; this conclusion was not elaborated for more than a decade afterward, although *Aerts* [1996] recommended that future research focus on the biochemical basis of resorption efficiency. *Wright and Westoby* [2003] proposed a theoretical model in which the proportion of resorbed versus soil N uptake is set by the relative cost of acquisition from the two sources. We support this concept, which fits perfectly into the framework of our FUN model, and thus we derive our calculation for $\text{Cost}_{\text{resorb}}$ from their theoretical model.

[73] The intersection point of $\text{Cost}_{\text{resorb}}$ with $\text{Cost}_{\text{active}}$ should be on average where 50% of leaf N is resorbed based on observations [i.e., *Aerts*, 1996]: the first 50% of N_{leaf} is generally less C costly to acquire than is N_{soil}, but the next 50% comes at a greater cost and the plant may then switch to N_{soil} acquisition. For example, *Crane and Banks* [1992] and *Helmisaari* [1992] observed decreased retranslocation rates after N fertilization, which would reduce $\text{Cost}_{\text{active}}$, and therefore the plants would acquire N primarily from the soil and less from retranslocation; plants under nutrient stress draw proportionally more on stores of N [*Chapin et al.*, 1990]. The value of $k_R = 0.01$ kg C·m^{-2} allows $\text{Cost}_{\text{resorb}} < \text{Cost}_{\text{active}}$ when N_{soil} and C_{root} are less than or equal to these average observed conditions (see ranges in section 4.2).

5. Conclusion

[74] To summarize, we introduced a new mechanistic model of plant N acquisition that is robust and simple enough to be applicable to global models. The theoretical framework of the model is based on C cost economics, which allows C to be expended on N acquisition as well as retained for vegetation growth. The model compares reasonably well with data from a range of sites. FUN is able to produce a realistic switching behavior between fixers and nonfixers in primary succession, replicate N uptake responses from N fertilization and CO_2 fertilization experiments (including providing insight into root biomass contributions to the latter), and illustrate a reduction in vegetation C from five DGVMs. This model may be suitable for inclusion in the N-cycle of the new generation of Earth system models.

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J. B. Fisher, Y. Malhi, and S.-Y. Tan, Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK. (joshbfisher@gmail.com)

R. A. Fisher, Earth and Environmental Sciences, Los Alamos National Laboratory, Los Alamos, NM 87545, USA.

C. Huntingford, Centre for Ecology and Hydrology, Maclean Bldg., Crowmarsh Gifford, Wallingford OX10 8BB, UK.

S. Sitch, School of Geography, University of Leeds, Leeds LS2 9JT, UK.