Nitrogen Acquisition Costs to Plants Reduce Net Primary Production at the Global Scale

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CESM Biogeochemistry Working Group
June 17th 2015, Breckenridge, CO
Motivation

The role of nutrient availability in regulating net ecosystem production and ecosystem C use efficiency

Improving terrestrial C sinks associated with nutrient limitation to climate models and Earth system models

Accurate predictions of the land C sink and nutrient constraints captured by CLM

Plant NPP allocation for N acquisition: up to 20% of NPP to both symbiotic and free-living microbes at the root surface to increase their access to N

BUT, CLM assumes that N is acquired at no C cost to plants!
Scientific Questions

How much N is taken up and what is the global distribution?

How does the C cost of N acquisition vary spatially and temporally?

How sensitive is the land C sink to a dynamic prediction of the C cost of N acquisition?
Methods

The Fixation and Uptake of Nitrogen (FUN) model (Fisher et al., 2010; Brzostek et al., 2014) explicitly includes the C cost for N acquisition.

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


Received 25 June 2009; revised 22 September 2009; accepted 8 October 2009; published 20 March 2010.

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.

Methods

The Fixation and Uptake of Nitrogen (FUN) model (Fisher et al., 2010; Brzostek et al., 2014) explicitly includes the C cost for N acquisition.

Carbon cost of plant nitrogen acquisition: A mechanistic, globally applicable and fixed

Journal of Geophysical Research: Biogeosciences

RESEARCH ARTICLE
10.1002/2014JG002660

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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.
Methods

The Fixation and Uptake of Nitrogen (FUN) model (Fisher et al., 2010; Brzostek et al., 2014) explicitly includes the C cost for N acquisition.

Carbon cost of plant nitrogen acquisition: A mechanistic, globally applicable and fixated

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Key Points:
- Mycorrhizal and simultaneous nitrogen 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

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Citation:

Citation: Fish acquisition: A n
Cycles, 24, GB

Received 3 MAR 2014
Accepted 7 AUG 2014
Accepted article online 11 AUG 2014
Published online 27 AUG 2014

Modeling the carbon cost of plant nitrogen acquisition:

Integration of nitrogen dynamics into the Noah-MP land model v1.1 for climate and environmental predictions

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Received: 11 April 2015 – Accepted: 05 May 2015 – Published: 27 May 2015

Abstract. Climate and terrestrial biosphere models consider nitrogen an important factor in limiting plant carbon uptake, while operational environmental models view nitrogen as the leading pollutant causing eutrophication in water bodies. The community Noah land surface model with multi-parameterization options (Noah-MP) is unique in that it is the next generation land surface model for the Weather Research and Forecasting meteorological model and for the operational weather/climate models in the National Centers for Environmental Prediction. In this study, we add capability to Noah-MP to simulate nitrogen dynamics by coupling the Fixation and Uptake of Nitrogen (FUN) plant model and the Soil and Water Assessment Tool (SWAT) soil nitrogen dynamics. This incorporates FUN’s state-of-the-art concept of carbon cost theory and SWAT’s strength in representing the impacts of agricultural management on the nitrogen cycle. Parameterizations for direct root and mycorrhizal-associated nitrogen uptake, leaf retranslocation, and symbiotic biological nitrogen fixation are employed from FUN, while parameterizations for nitrogen mineralization, nitrification, immobilization, volatilization, atmospheric deposition, and leaching are based on SWAT. The coupled model is then evaluated at the Kellogg Biological Station – a Long-term Ecological Research site within the U.S. Corn Belt. Results show that the model performs well in capturing the major nitrogen state/flux variables (e.g., soil nitrate and nitrate leaching). Furthermore, the addition of nitrogen dynamics improves the modeling of the carbon and water cycles (e.g., net primary productivity and evapotranspiration). The model improvement is expected to advance the capability of Noah-MP to simultaneously predict weather and water quality in fully coupled Earth system models.

Methods

Model Structure

Total N Uptake
- Passive Uptake
  - Transpiration
- Active Uptake
  - Soil N
- Biological N Fixation
  - Root C
  - NPP Optimization
  - Cost Active Uptake
    - Cost BNF
  - Soil Temperature
  - Cost Re-translocation
- Re-translocation
  - Leaf N

CLM provides FUN:
1) Available C
2) Soil mineral N
3) Root Biomass
4) Leaf N
5) Plant C:N ratio
6) Soil layer depth
7) Soil temperature
8) Transpiration

(Fisher et al., 2010)
Methods

(Fun 2.0 model)

(a) C Pools

| C for Growth |
| Net Primary Production |
| C spent on N uptake |

(b) Resistance Network

| Retranslocation |
| Biological N Fixation |
| Arborcular mycorrhizal |
| Ectomycorrhizal |
| Non-Mycorrhizal |

(c) N Pools

| Leaf |
| Atmosphere |
| Soil |

(Fun 1.0)

FUN optimally allocates C to growth and to N uptake as a function of the N needed to support NPP and the integrated C costs across all of the pathways in the resistor network.
Cost of active nitrogen uptake (Cost_{active}) with range of cost of biological nitrogen fixation (Cost_{fix}) versus:

(a) soil nitrogen with low and high root biomass,
(b) root biomass with low and high soil nitrogen
(c) both soil nitrogen and root biomass. (Fisher et al., 2010)
Scatterplot of observed versus predicted 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).

(Fisher et al., 2010)
Stepwise improvement in model predictions of total N uptake across six sites that vary in mycorrhizal association from FUN2.0. The dashed line indicates the 1:1 relationship. (Brzostek et al., 2014)
CLM-Trunk-FUN Coupling

FUN was coupled with CLM4.0-CN, CLM4.5-BGC, and CLM-Trunk-BGC:

- clm_varcon.F90
- CNDriverMod.F90
- pftconMod.F90
- CNFUNMod.F90
- CNVegCarbonFluxType.F90
- CNVegCarbonStateType.F90
- readParamsMod.F90
- CNPhenologyMod.F90
- CNVegStateType.F90
- CNVegNitrogenFluxType.F90
- CNVegNitrogenStateType.F90
- SoilBiogeochemNStateUpdate1Mod.F90
- SoilBiogeochemCarbonFluxType.F90
- NutrientCompetitionCLM45defaultMod.F90
- SoilBiogeochemNitrogenFluxType.F90
- SoilBiogeochemCompetitionMod.F90
The global total uptake is $1.2 \text{ Pg N yr}^{-1}$.

Mycorrhizal represent the dominant pathway followed by retranslocation, direct root uptake, and fixation.
Results

- The high N uptake regions are tropics and mid-latitudes in the north hemisphere.
- The fractions of the mycorrhizal uptake, direct root uptake, retranslocation, fixation, and passive uptake amounts are 64%, 10%, 19%, 7%, and 0.1% of the total N uptake amount, respectively.
Results

How does the C cost of N acquisition vary spatially and temporally?

- Total N uptake does not meet total N demand for most of the year in all biomes.
- Evergreen broadleaf forest has the largest N uptake rate, which is 11 g N m\(^{-2}\) y\(^{-1}\).
- Deciduous needleleaf forest has the most met demand.
Results

How does the C cost of N acquisition vary spatially and temporally?

- C spent on N acquisition is 5.1 Pg C yr\(^{-1}\) globally.
- The mycorrhizal and fixation used C amounts are 1.6 Pg C yr\(^{-1}\) and 2.6 Pg C yr\(^{-1}\), respectively; they are 31% and 50% of the global total used C amount, respectively.
- Grassland spends the most C on N acquisition per unit area; evergreen broadleaf forest spends the least C on N acquisition per unit area.
Results

How does the C cost of acquisition vary spatially and temporally?

- Tropical forests have the lowest C use ratio.
- High-latitude shrubland and arid and semi-arid regions have the highest C use ratio.

\[ C_{use\,\text{ratio}} = \frac{C_{use\,\text{acquisition}}}{C_{available}} \]

where \( C_{use\,\text{acquisition}} \) is the total C used by the four N uptake pathways, and \( C_{available} \) is the difference between GPP and maintenance respiration.
Results

How sensitive is the land C sink to a dynamic prediction of the C cost of N acquisition?

- Global total NPP is down-regulated by 41%.
- The reduced NPP amount peaks at 2°S, and decreases towards the Poles.
- CLM-Trunk-FUN results in NPP decrease in all biomes.
Discussion

**CLM-Trunk-FUN simulated symbiotic BNF**

- CLM-Trunk-FUN predicted symbiotic BNF is 81.1 Tg N yr\(^{-1}\) and 0.53 g N m\(^{-2}\) yr\(^{-1}\).

- Symbiotic BNF is 105.1 Tg N yr\(^{-1}\) (Cleveland et al., 2013) and 0.85 g N m\(^{-2}\) yr\(^{-1}\) on an per unit area basis (Sullivan et al., 2014).
Discussion

We used a new global nutrient limitation product developed from remote sensing (Fisher et al., 2012).

The nutrient limitation and NPP variation patterns at the global scale.

Benchmarking CLM-Trunk-FUN

Figure 2. (a) Map of remote sensing–based nutrient limitation and disturbance at 0.5; (b) remaining undisturbed pixels for comparison without any effect of disturbance. Nutrient limitation is defined as the percentage productivity (or greenness or other proxy) less than what would otherwise be dictated by climatic constraints.
Conclusions

Take Home Messages

• Global total N uptake amount is 1.2 Pg N yr\(^{-1}\).
• N acquisition uses 5.1 Pg C yr\(^{-1}\) globally.
• Mycorrhizal N uptake is the dominant N uptake pathway and BNF is the most expensive N uptake pathway.
• Total N uptake reduces NPP globally by 41%.

Future Work

• NPP downregulation
• Climate impact
Primary Results From CAM-FUN

- The C spent on N acquisition results in temperature decrease in mid- and high-latitude areas and increase in polar regions.

- Global precipitation pattern is also changed with FUN coupled into CLM and CAM.
Acknowledgments

• The US Department of Energy Office of Biological and Environmental Research Terrestrial Ecosystem Science Program

• The US National Science Foundation Ecosystem Science Program

• The technical support from Erik Kluzek at NCAR.
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<th>Name of the PFTs</th>
<th>AM (%)</th>
<th>ECM (%)</th>
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<td>Bare soil (not vegetated)</td>
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<td>100</td>
</tr>
<tr>
<td>Needleleaf evergreen temperate tree</td>
<td>0</td>
<td>100</td>
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<tr>
<td>Needleleaf evergreen boreal tree</td>
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<tr>
<td>Needleleaf deciduous boreal tree</td>
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