Incorporating Belowground Competition for Nitrogen into Quantitative Models to Predict Ecosystem Productivity and Carbon Storage

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Major Findings:

- Symbiotic, mycorrhizal fungi can receive up to 25-30% of carbon used to fuel tree growth in northeastern forests.
- Conifer-dominated stands allocate more carbon to mycorrhizal fungi than do hardwood-dominated stands.

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http://www.nsrcforest.org

Project Summary

Rationale: Like most plants, trees in northeastern forests require light, nutrients, and water to fuel their growth. Within forests, the composition of tree species and the availability of growth limiting resources, exert a strong influence on how trees allocate the carbon they acquire through photosynthesis, to different components of their growth. For example, recent work in temperate forests has highlighted a tradeoff between carbon allocation to aboveground woody tissues (access to light), and belowground carbon allocation to fine roots (access to soil nutrients). In addition to fine roots, trees allocate carbon belowground to mycorrhizal (root-associated) fungi. Nearly all temperate and boreal forest trees have symbiotic associations with one of two types of mycorrhizal fungi: ectomycorrhizal (ECM) or arbuscular mycorrhizal (AM) fungi. Both types of symbiotic fungi provide trees with soil nutrients and water necessary for growth, and receive photosynthetically-fixed carbon from their tree hosts in return. Although mycorrhizal fungi are crucial for nutrient acquisition, and can receive 20% or more of the carbon used for tree growth, most studies fail to include carbon allocation to mycorrhizal fungi. In part, this is due to the inherent difficulties in accurately quantifying fungal production.

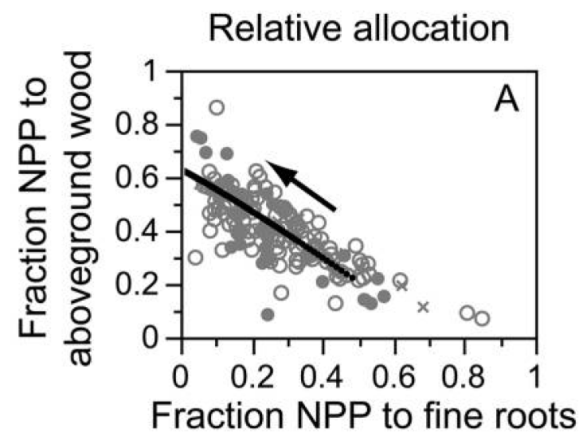
Methods: We took several approaches to quantify production of mycorrhizal fungi, including a carbon budget approach and isotopic techniques. Here we present data on patterns of carbon allocation to aboveground (wood and foliar production), and belowground components (production of fine roots and mycorrhizal fungi), across temperate forest stands spanning a range of nitrogen availability and species composition.

Major Findings: We found that as the proportion of conifers increased, and the availability of nitrogen decreased, both the absolute amount, and the fraction of carbon allocated to foliage, aboveground wood, and fine root growth decreased. In fact, the production of plant components (the sum of foliage, wood, and fine roots), decreased by nearly 100% between hardwood and conifer-dominated stands. While allocation to plant pools decreased, allocation to mycorrhizal fungi significantly increased (by more than 100%), with increasing conifer dominance and increasing soil nitrogen availability. We did not find a strong trade-off between carbon allocation to fine roots and aboveground wood or foliage. Instead, a negative relationship was seen between allocation to mycorrhizal fungi and other plant pools.

Implications for the Northern Forest region: Effort to estimate carbon allocation to mycorrhizal fungi is important for gaining a more complete understanding of how forests in the northeast respond to changes in growth-limiting resources, and will help us to understand how forests (and different species within the forest) will respond to future changes in climate and land management. A better understanding of the tradeoffs between plant and fungal components change with species and nutrient availability will also help predict that magnitude of ecosystem services (e.g. timber production) afforded by northern forests. Data from this project are also being used to modify an existing ecosystem model to include mycorrhizal fungi.

Background and Justification

- Trees allocate carbon assimilated through photosynthesis to above and belowground biomass pools, to acquire light, soil nutrients and water.
- In forest ecosystems, the allocation of photosynthetically-fixed carbon among different biomass pools is driven by the species present, as well as by the availability of growth limiting resources.
- Recent studies in temperate and boreal forests have found that a higher proportion of carbon is allocated belowground to fine roots under nitrogen-limiting conditions, while proportionally more carbon is allocated aboveground to wood (access to light) under nitrogen-rich conditions.
- This shift in tree level carbon allocation patterns primarily reflects a tradeoff between belowground nitrogen (N) limitation and aboveground light limitation, and has important implications for determining C residence time and the magnitude of ecosystem services afforded (e.g. timber production).



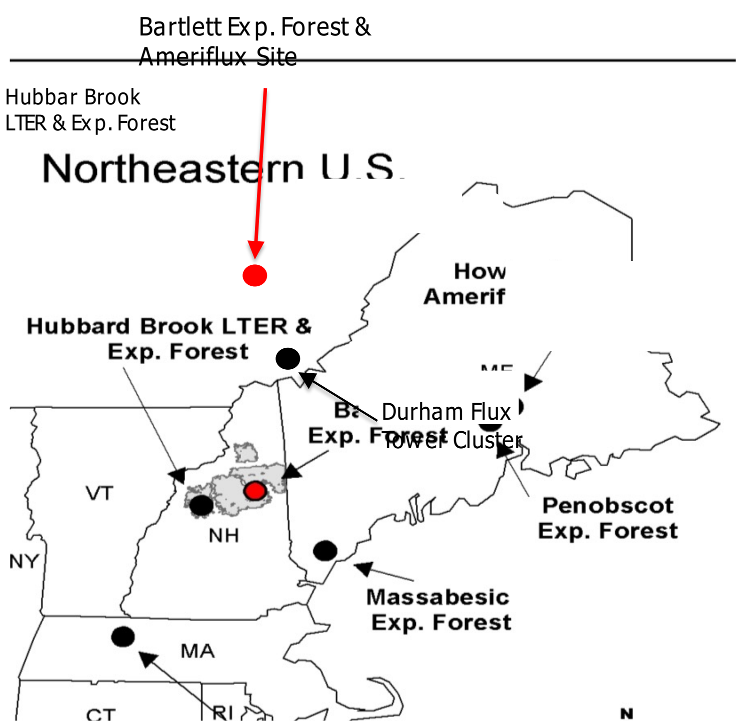
Fraction of plant carbon allocated to wood vs. fine root production (NPP = net primary production), showing a strong trade-off between above and belowground production across a range of forested site. From Dybzinski et al. 2011

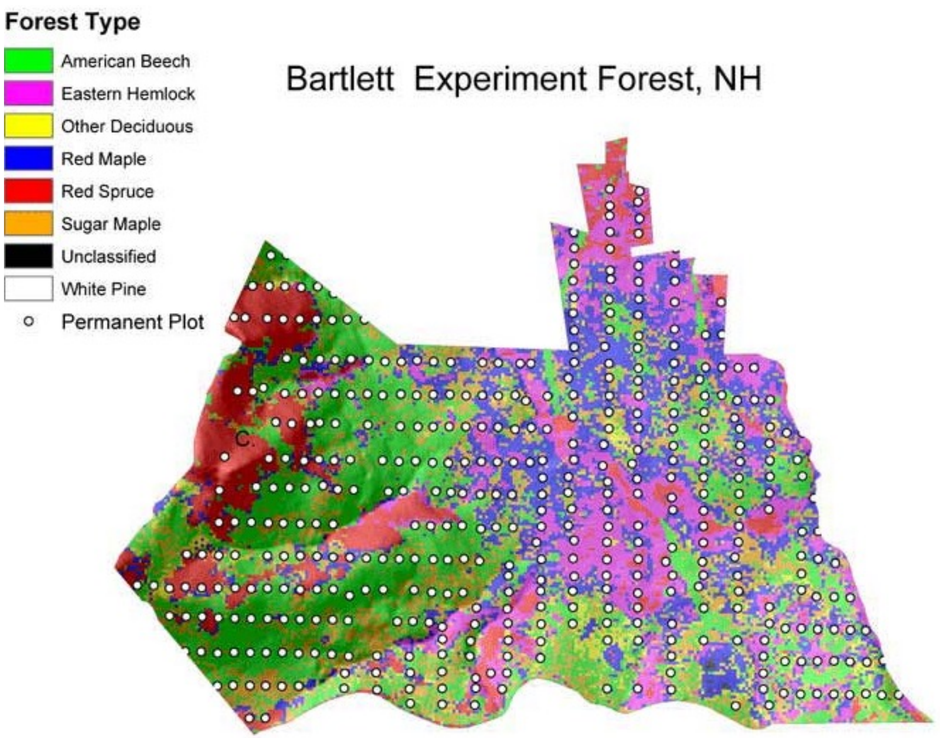
Background and Justification

- In addition to fine roots, trees allocate carbon belowground to mycorrhizal (root-associated) fungi. Nearly all temperate and boreal forest trees have symbiotic associations with one of two types of mycorrhizal fungi: ectomycorrhizal (ECM) or arbuscular mycorrhizal (AM) fungi.
- Both types of symbiotic fungi provide trees with soil nutrients and water necessary for growth, and receive photosynthetically-fixed carbon from their tree hosts in return.
- Although mycorrhizal fungi are crucial for nutrient acquisition, and can receive 20% or more of the carbon used for tree growth, most studies fail to include estimates of carbon allocation to mycorrhizal fungi.
- Here we quantified production of foliage, wood, fine roots, and mycorrhizal fungi across a species and nutrient availability gradient at Bartlett Experimental Forest, NH.

Fine roots (dark brown) colonized by mycorrhizal fungi (whitish). From https://mycorrhizas.info

Research Site:
Bartlett Experiment Forest





Map of New England (left) showing location of Bartlett Experimental Forest (BEF) in relation to other local research sites. Species composition map (right) of BEF.

METHODS to quantify plant production:

We quantified production of foliar, wood, and fine roots using standard approaches. Specifically we used annual collections of foliar litter to estimate foliar production, successive measurements of tree diameter to allometrically estimate wood growth, and year-long ingrowth cores to estimate fine root production.

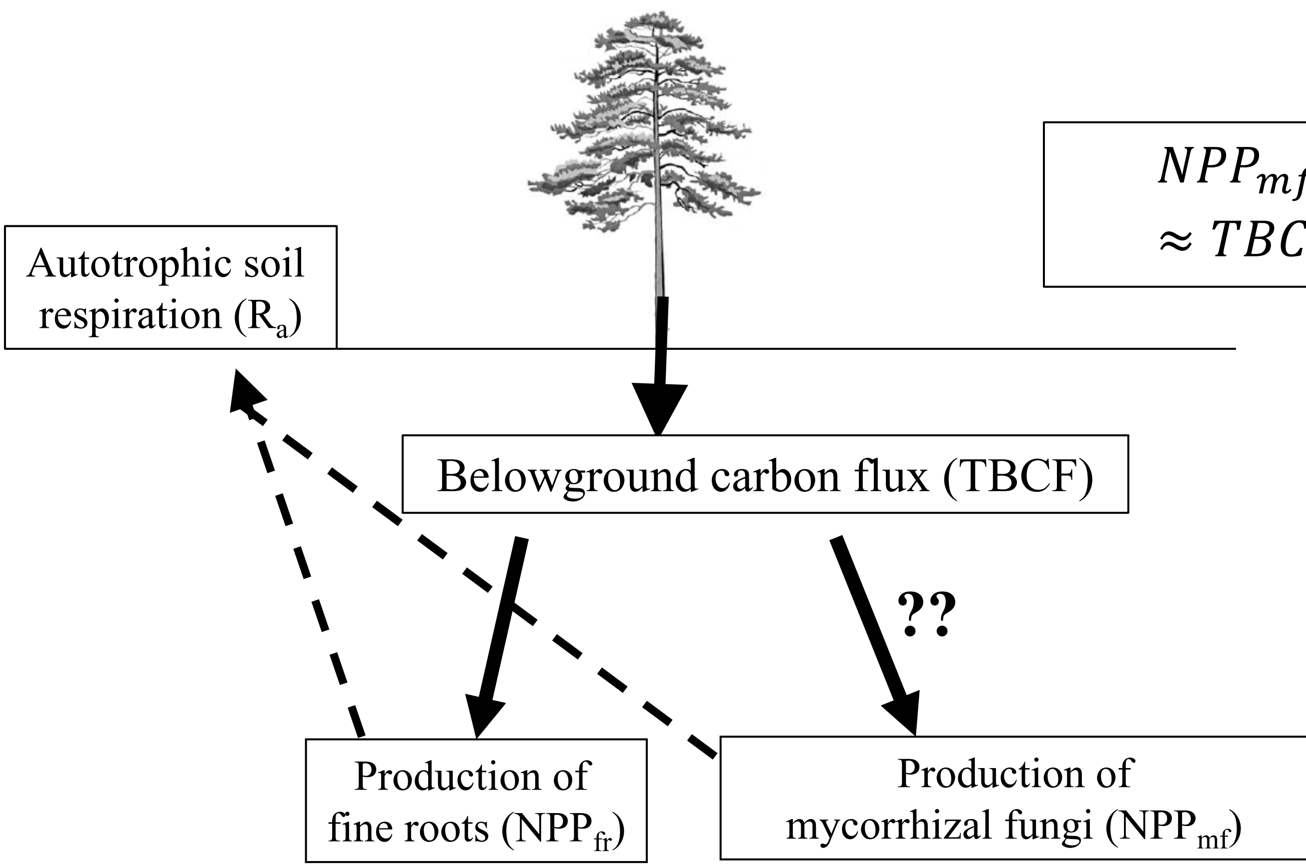
For this work we made use of the following measurements that have taken place annually at BEF since 2004:

- Eddy flux tower estimates of ecosystem carbon fluxes
- 120+ litter baskets to measure foliar litterfall
- 156 soil respiration collars (manual)
- 5 autochamber soil respiration units
- 60 branchfall tarps
- Annual diameter measurements of 1800+ trees
- Annual collection of foliage from 250+ trees for foliar %N
- 225 year-long root ingrowth cores (1 year only; partial year collections from 4 other years)

<u>METHODS</u> to estimate carbon allocation to symbiotic ECM fungi:

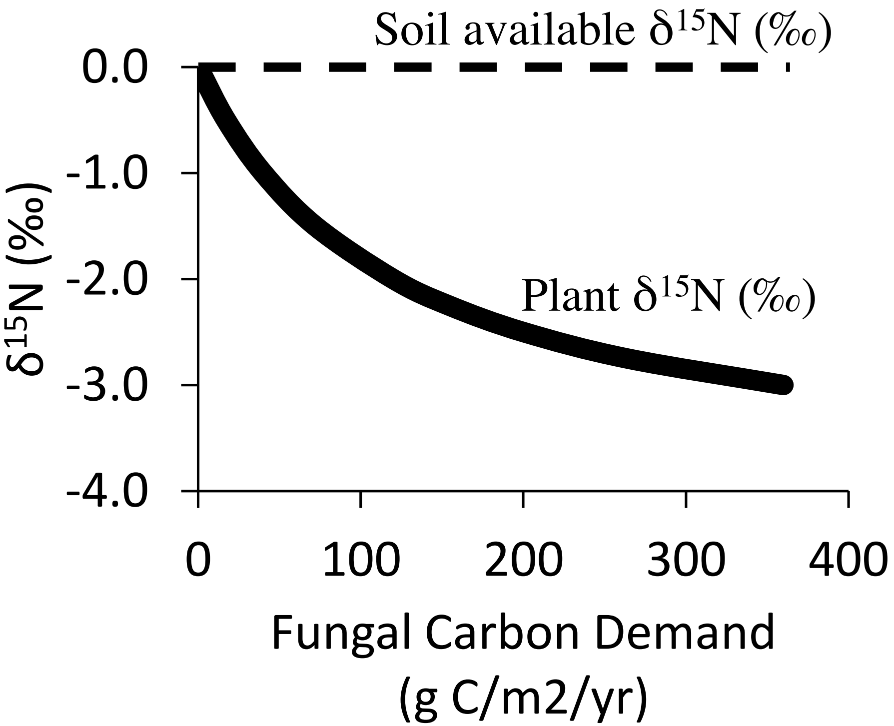
1) **Carbon balance (budgeting approach)**
2) Isotopic Techniques
3) Direct Measures of fungal production

$$NPP_{mf} \approx \text{"}missing\text{"}\ TBCF \approx TBCF - \left(NPP_{fr} + R_a\right)$$



<u>METHODS</u>: Approaches used to estimate carbon allocation to symbiotic ECM fungi:

1) Carbon balance (budgeting)
2) **Isotopic Techniques**
3) Direct Measures of fungal production



Equations to calculate carbon allocation to mycorrhizal fungi using $\delta^{15}N$ (see notes)

1) $$Tr = 1 - \frac{(\delta^{15}N_{AvailN} - \delta^{15}N_{Root})}{\Delta_f}$$

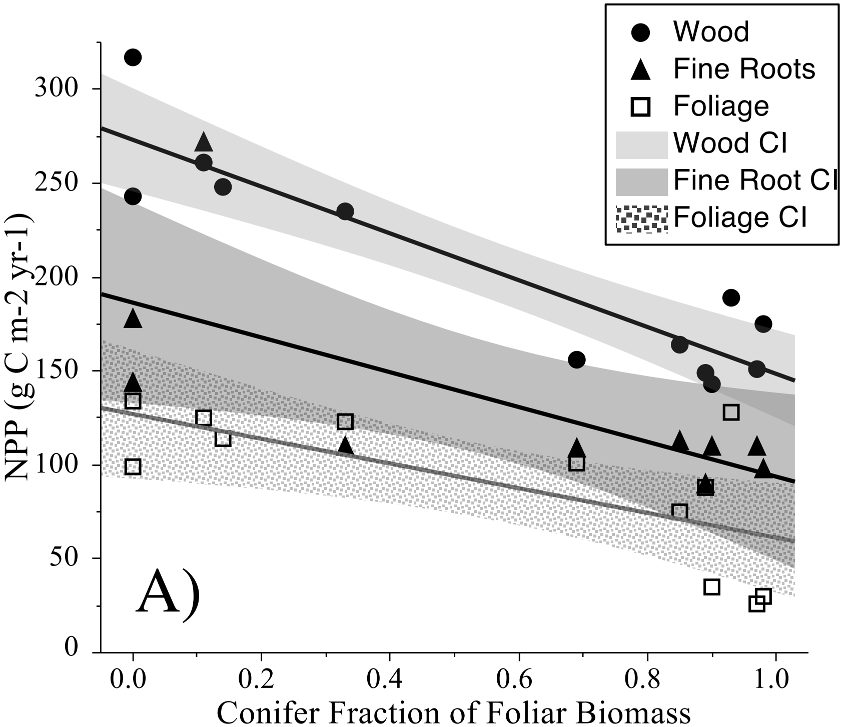
2) $$C_{fungi} = \left(\frac{1}{Tr} - 1\right) \times N_{plant} \times (C:N)_{fungi}$$

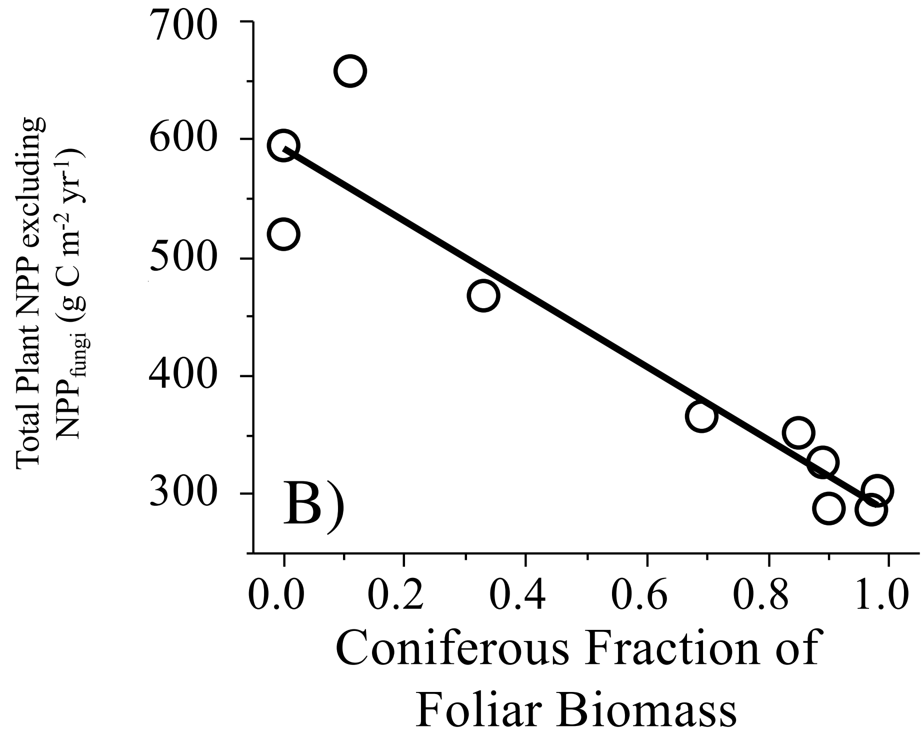
METHODS: Approaches used to estimate carbon allocation to symbiotic ECM fungi:

1) Carbon balance (budgeting)
2) Isotopic Techniques
3) **Direct Measures of fungal production**

Quantitative "Truffle Hunting"

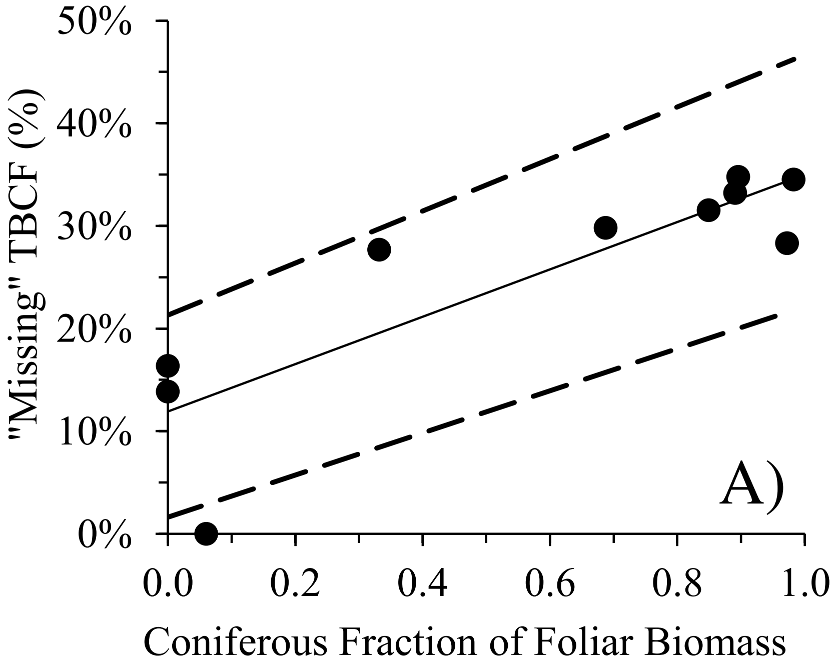
Results

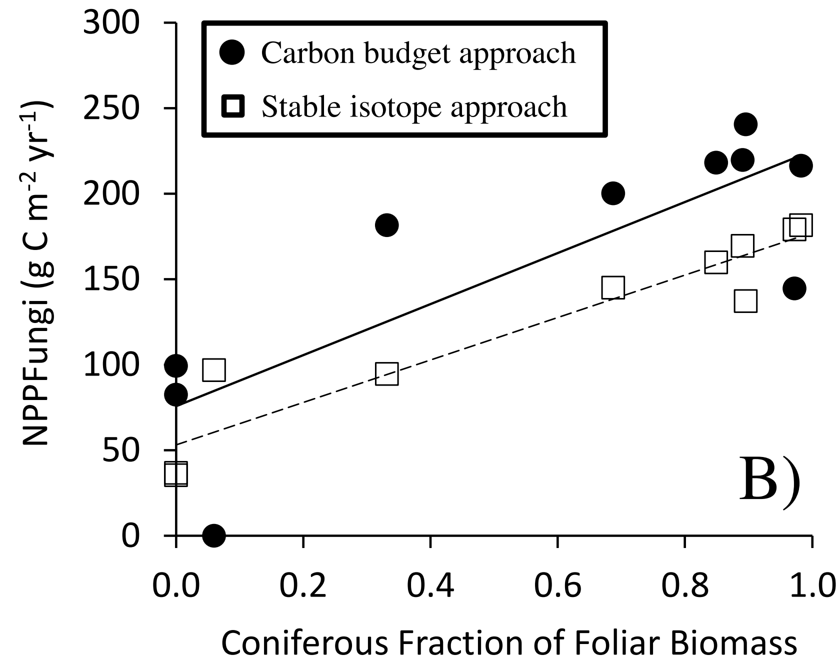




In stands at Bartlett Experimental Forest, production (growth) of foliage, wood, and fine roots all decreased with increasing proportion of conifer species (A). Total plant production (or the sum of foliar, wood, and fine root growth) decreased by 100% across this species gradient (B).

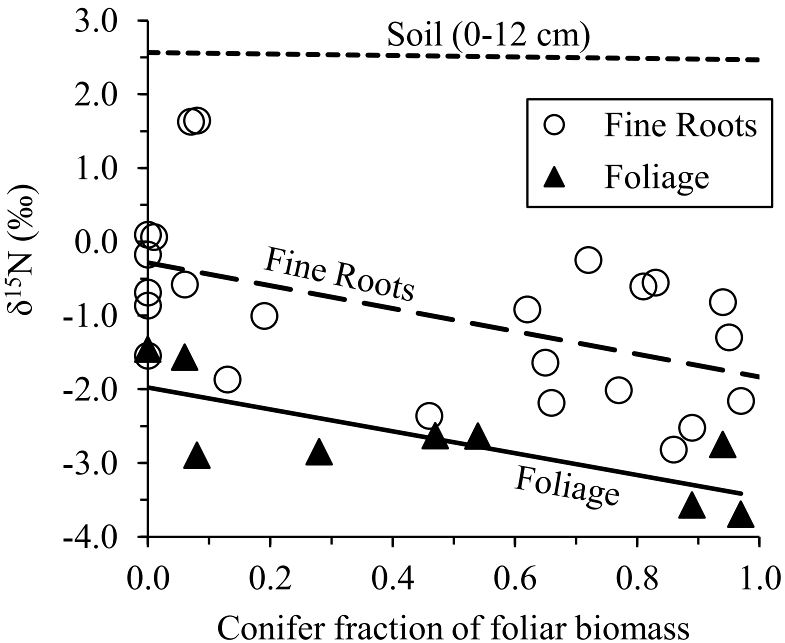
Results

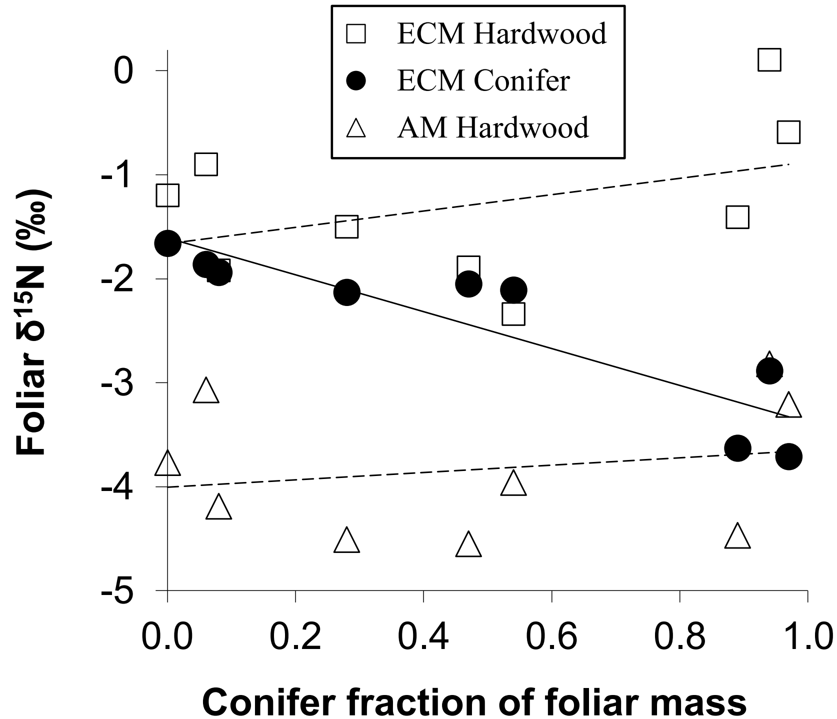




In stands at Bartlett Experimental Forest, the fraction of belowground carbon (TBCF) that was "missing", (which is assumed to be equivalent to production of mycorrhizal fungi), increased with increasing conifer dominance (A). The production (growth) of mycorrhizal fungi increased by over 100% when estimated using either a carbon budget approach or an isotope approach (B).

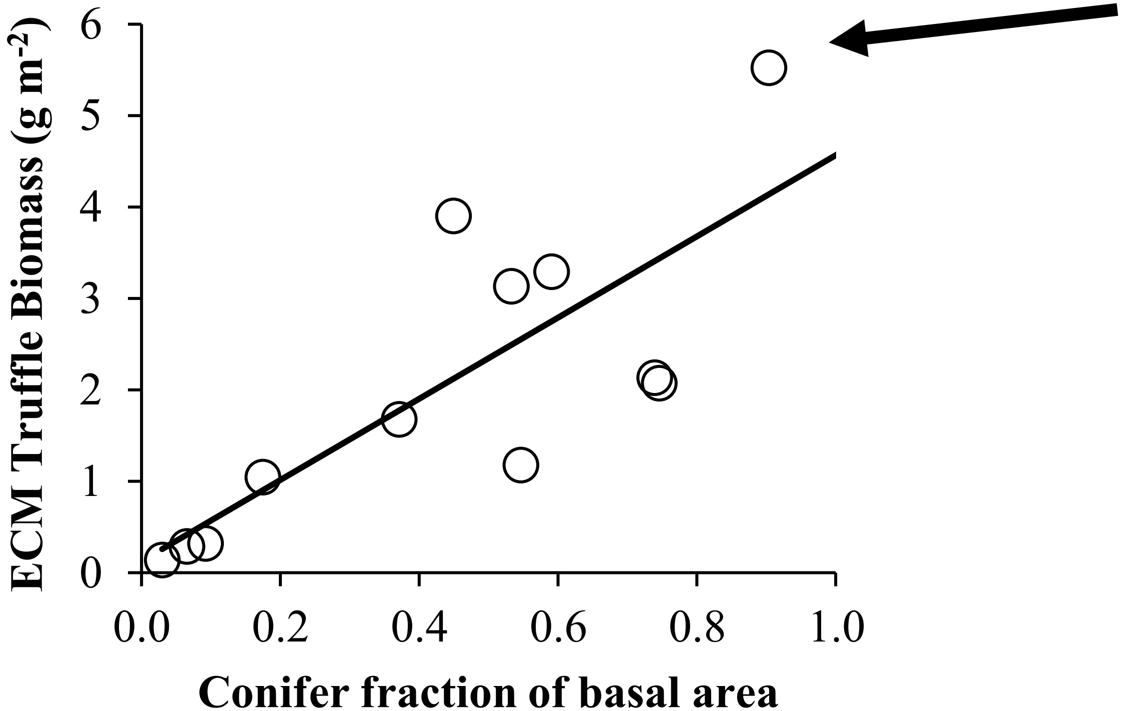
Results





In stands at Bartlett Experimental Forest, the $\delta^{15}N$ of both fine roots and foliage decreased with increasing conifer dominance; consistent with increasing reliance of mycorrhizal fungi at conifer-dominated stands (A). For foliar tissues, this change in $\delta^{15}N$ was seen only in conifer species, suggesting conifer species relied more heavily on mycorrhizal fungi (B).

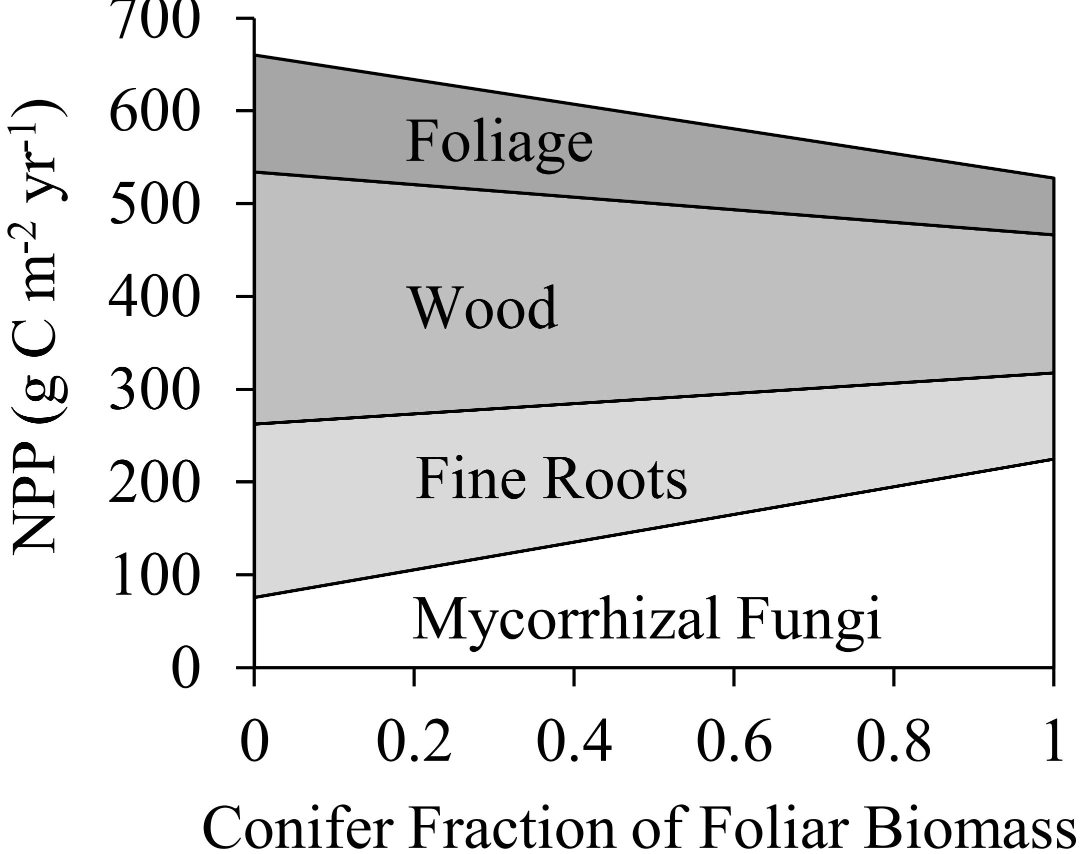
Results



Equivalent to >50,000 truffles per hectare in conifer stands

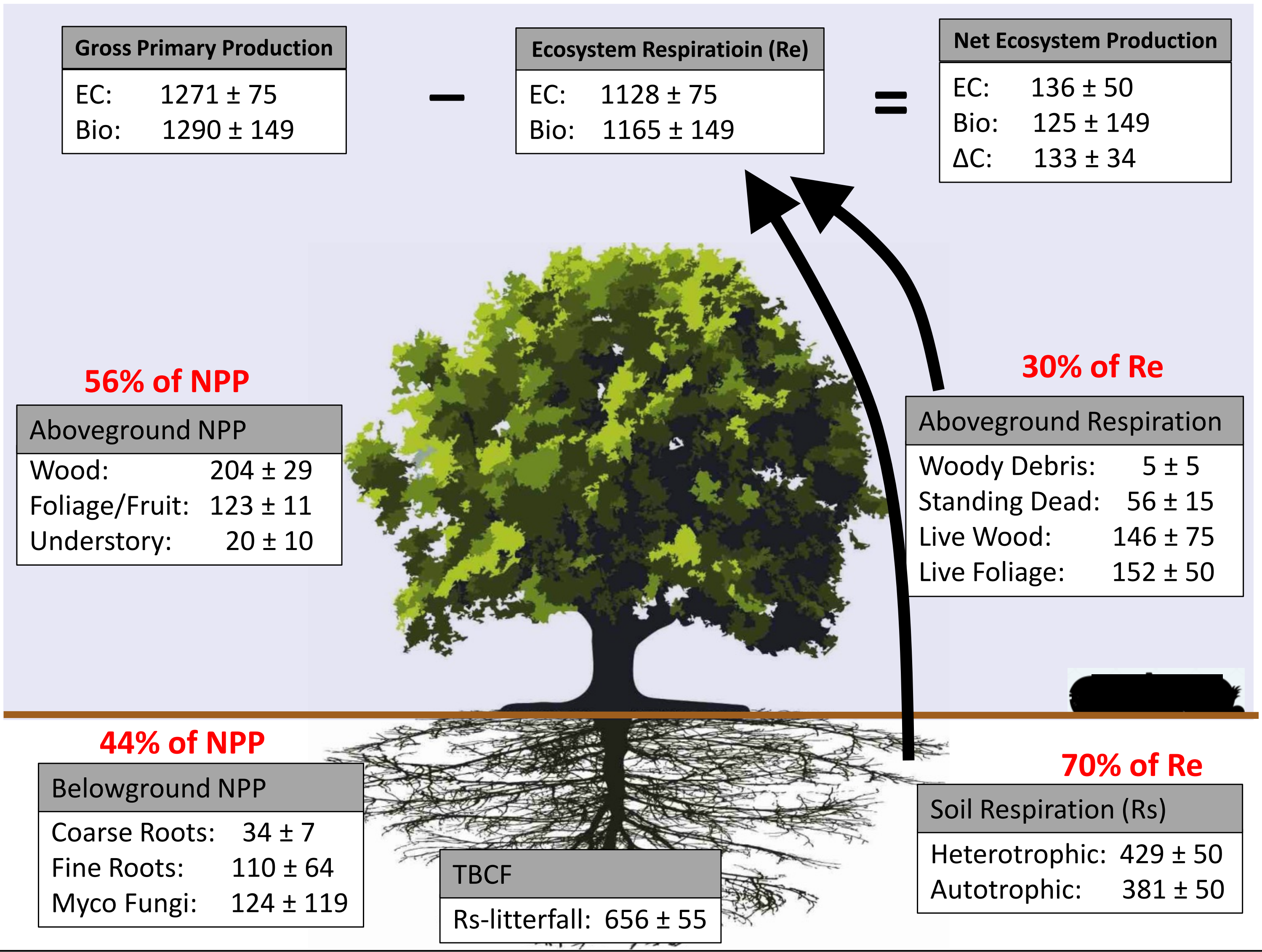
In stands at Bartlett Experimental Forest, quantitative truffle surveys found higher biomass of mycorrhizal (symbiotic) truffles at conifer-dominated stands, with more that 50,000 truffles per hectare in some stands. This direct measure of the abundance of mycorrhizal fungi was consistent with the carbon budget and isotopic approaches.

Results



Patterns of measured foliar, wood, fine root, and mycorrhizal fungi production, across stands with increasing conifer dominance at Bartlett Experimental Forest. The data highlight the contrasting patterns of plant and fungal ecosystem components, with carbon allocation to mycorrhizal fungi increasing, and allocation to plant components decreasing, with increasing conifer abundance.

Results



Ecosystem carbon budget for hardwood-dominated stands within the footprint of the eddy covariance (EC) flux tower at BEF from both EC and biometric (Bio) measurement approaches. Including the production of mycorrhizal fungi helps to close the carbon budget. See notes and Ouimette et al, *in review*

Implications and applications in the Northern Forest region

- Very few, if any other studies, have attempted to quantify both the production mycorrhizal fungi and plant components (foliage, wood, fine roots).
- Results from this study indicate that the production of symbiotic mycorrhizal fungi increased dramatically at low nitrogen, conifer-dominated stands and were supported by large investments of carbon from their plant hosts.
- Quantifying carbon allocated to mycorrhizal fungi is important for reconciling ecosystem carbon budgets, for understanding the ecological strategy of various tree species, and for predicting the magnitude of ecosystems services (e.g. timber production) afforded by northern forests.

Future directions

- Very few, if any other studies, have attempted to quantify the production of plant components (foliage, wood, fine roots), and mycorrhizal fungi.
- Future studies should target a wider range of sites using the carbon budget approach outlined here, to quantify the importance of mycorrhizal fungi at broader scales.
- The data collected here are currently being used to modify/parameterize existing forest ecosystem models and may help to better simulate patterns of forest growth seen in experimental studies (e.g. nitrogen and CO_2 fertilization experiments)

List of products

Publications:

1. Ouimette AP, Ollinger SV, Hollinger D, Richardson A, Keenan T, Vadeboncoeur M, Lepine L. (*in review*). Ecosystem Carbon Fluxes and Their Potential Interannual Drivers in a Temperate Forest Assessed Using Multiple Approaches. *Agricultural Forest and Meteorology Special Issue.*
2. Ouimette AP, Ollinger SV, Hobbie EA, Lepine LC, Rowe R, Stephens R, Vadeboncoeur MA, Tumber-Davila S. *(in prep)*. Changes in carbon allocation to aboveground versus belowground forest components are driven by a trade-off involving mycorrhizal fungi, not fine roots. *New Phytologist*
3. Tumber-Davila SJ. 2013. Quantifying carbon allocation to mycorrhizal fungi by temperate forest tree species across a nitrogen availability gradient. University of New Hampshire Honors Senior Thesis.

List of products

Presentations:

4. Ouimette AP, Ollinger SV, Hollinger D, Richardson A, Keenan T, Vadeboncoeur M, Lepine L. (2017) Comparison of carbon flux estimates using 13 years of eddy covariance data and plot-level biometric measurements from the Bartlett Experimental Forest, New Hampshire. Oral presentation at 2017 Northeastern Ecosystem Research Cooperative Annual Meeting. Saratoga Springs, NY. March 28-29.
5. Ouimette AP, Ollinger SV, Hollinger D, Richardson A, Keenan T, Vadeboncoeur M, Lepine L. (2016) Comparison of carbon flux estimates using 10 years of eddy covariance data and plot-level biometric measurements from the Bartlett Experimental Forest, New Hampshire. Poster presentation at Ameriflux Meeting. Golden, CO. Sept. 21-24.
6. Tumber-Davila SJ, Ouimette A. (2014) Estimates of carbon allocation to ectomycorrhizal fungi in a temperate forest. Poster presentation at AGU Fall Meeting San Francisco, CA December 2014.
7. Ouimette AP (2013) Incorporating Mycorrhizal Fungi into PnET-CN. Oral presentation by PI Ouimette at PnET Workshop, Durham, NH, May 20-22, 2013.
8. Ouimette AP, Ollinger SV, Vadeboncoeur MA, Hobbie EA. (2012) Estimates of carbon allocation to ectomycorrhizal fungi in a temperate forest. Poster presentation at AGU Fall Meeting San Francisco, CA December 2012.
9. Tumber-Davila, Ouimette AP. Poster presentation by McNair student Shersingh Joe Tumber-Davila at UNH McNair Conference, Durham, NH (July 2013)
10. Poster presentation by McNair student Shersingh Joe Tumber-Davila at **Ivy Plus Symposium, Cambridge, MA** (March 2014)
11. Poster presentation by McNair student Shersingh Joe Tumber-Davila at UNH Undergraduate Research Conference, Durham, NH (April 2014)
12. Poster presentation by McNair student Shersingh Joe Tumber-Davila at **McNair Research Symposium, Seattle, WA** (May 2014)

Leveraged/Collaborative Grants:

1. Undergraduate Shersingh Joe Tumber-Davila was awarded funding by the McNair program (stipend, travel, supply money)
2. Ouimette was awarded funding by the UNH Graduate Program for travel (AGU)
3. Ouimette was awarded funding by UNH NRESS Program for travel (AGU)
4. NSRC grant 110227 “An NSRC working group for improved modeling of Northern Forest Ecosystems” provided an opportunity for collaborative work. Specifically Dr. Zaixing Zhou was responsible for creating a new version of PnET that includes mycorrhizal fungi (PnET-Myco) as part of collaborative work between the two NSRC grants.

Support

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