United States Department of Agriculture

Progress Report

Title:	**Soil Nutrient Limitation of Northern Hardwood Forest Productivity: Mechanisms Contributing to N and P co-Limitations**

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Recipient Organization

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Departments

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Non-Technical Summary

The productivity of temperate forests on glaciated soils has been presumed to be nitrogen (N) limited, although theory suggests that ecosystem productivity should be co-limited by multiple nutrients, especially including phosphorus (P). Experimental tests of N vs. P limitation in temperate forests are needed to better understand the capacity of ecosystems to balance the acquisition of limiting resources. In 2011 we began a full-factorial NxP fertilization experiment in 13 stands of young, mid-aged, and mature northern hardwoods in three contrasting sites that span a range of native soil fertility. Surprisingly, early results showed tree growth responding more to P than to N fertilization. We propose to continue these treatments to test whether P limitation will persist, possibly as a consequence of decades of anthropogenic N enrichment, or whether adjustment of effort to acquire N versus P will result in co-limitation. We will measure aboveground and belowground productivity and evaluate shifts in allocation of effort after a decade of nutrient manipulation. Mechanisms that could enable the ecosystem to acquire and conserve N and P and to maintain stoichiometric balance in the face of changing nutrient availability include foliar N and P resorption, differential rooting depth, soil enzymes, mycorrhizae and changes in tree species composition. The Multiple Element Limitation model will be used to integrate data from the various components of the study, advance understanding of nutrient limitation, and extrapolate the results to improve management of forest ecosystems in the face of increasing CO_2, changing climate, and a legacy of atmospheric deposition.

Accomplishments

Major goals of the project

The overall goal of this proposed research is to test and elaborate the theory of temperate forest co-limitation and to evaluate the importance of various mechanisms that may contribute to maintaining co-limitation.

Objective I. Test for limitation or co-limitation of forest productivity

Hypothesis 1: Aboveground productivity is co-limited by N and P.

Prediction: Tree diameter growth and aboveground productivity will be greatest in response to N+P, consistent with theories of co-limitation.

Prediction: Growth responses to either N alone or P alone will exceed those in controls because of the tradeoffs addressed under Objective II.
Alternative Prediction: If only one element were limiting, this would be exhibited by the response to addition of the other element being no different from the control.
Hypothesis 2: Belowground productivity is least under N+P addition.
We will measure three indicators of belowground productivity, because it cannot be measured directly: belowground carbon allocation, fine root biomass, and fine root growth.
Prediction: Belowground productivity will be least in response to N+P, consistent with co-limitation to aboveground growth. Alleviating nutrient limitation should reduce allocation of effort belowground.
Prediction: Belowground responses to additions of either N or P alone will be similar, if N and P are co-limiting, and less than in the controls.
Alternative Prediction: If only one element is limiting, then addition of that element will reduce belowground productivity, while addition of the other element will have no effect.
Objective II. Explore mechanisms that restore balance between N and P limitation
Hypothesis 3: Plant and microbial responses to nutrient limitation act to restore co-limitation.
Prediction: Foliar N resorption will be greatest under P addition, and foliar P resorption will be greatest under N addition.
Prediction: Where N is limiting (P fertilized plots), root exploration and mycorrhizal colonization will be greater in the surface horizons to access N from organic matter. Where P is limiting, root exploration and mycorrhizal colonization will be greater at depth to access slowly-available P and P weathered from soil minerals.
Prediction: Phosphatase enzyme activity will decline in response to P addition and increase in response to N addition, and the activity of enzymes involved in N acquisition (leucine amino peptidase and N-acetyl glucosaminidase) will decline in response to N addition and increase in response to P addition
Hypothesis 4: Changing species dominance will result in species with nutrient requirements and acquisition mechanisms that are more closely matched to N and P supply rates, thus driving the ecosystem toward co-limitation
Prediction: Belowground, AM species will gain dominance when N is added and EM will gain when P is added. Belowground dominance will be indicated by the species composition of fine roots and by mycorrhizal colonization rates.
Prediction: Aboveground, EM species will gain canopy dominance when P is added, whereas AM will gain dominance when N is added. This change will be most pronounced in young stands where tree mortality is high during the self-thinning phase of stand development.
Prediction: In mature stands where tree replacement is very slow, differences in performance by EM vs AM tree species will be reflected in greater stem growth and reproductive output, as opposed to canopy and belowground dominance.
Alternative prediction: Other tree traits, such as maximum shoot growth rate or plasticity in fine root:shoot ratio, play a more important role than mycorrhizal status in determining the outcome of competition among species.
Objective III. Evaluate improved understanding of co-limitation via the MEL model and predict long-term forest response to anticipated future conditions
The MEL model will serve as a means to synthesize results of the project and link those results to the large volume of data already available from northern hardwood forest ecosystems. The underlying question to be addressed in this synthesis is: Do all the data currently available fit together in a self-consistent representation of the linked C, N, P, and water dynamics of northern hardwood forests? If not, why not, and how does the model have to be changed to accommodate the discrepancies? The model will also serve as a means to examine the whole-ecosystem consequences of our experimental results. For example, we expect the results to show differences among our sites and in response to the factorial N and P additions in aboveground and belowground tree biomass and productivity, degree and type of mycorrhizal colonization, and exo-enzyme activity. These changes can be studied in the model by changing the parameterization of the affected processes. In the model, these parameter changes will result in changes in process rates, which will then have effects that propagate all through the system. Do such changes result in ecosystem-level feedbacks that dampen or amplify the direct effects? If the parameter changes can be associated with other dynamics in the model (e.g., increased light use efficiency as the canopy closes), then the parameters can be replaced by equations describing the association, thereby allowing a more dynamic examination of the long-term consequences of our findings. An improved MEL model will allow us to explore the importance of resource limitation to future forest responses to continued anthropogenic N deposition, increasing CO_2, and changing precipitation and temperature scenarios.

What was accomplished under these goals?

Abstracts of three papers submitted during the reporting period summarize our important accomplishments.
1. Shan, S., H. Devens, T.J. Fahey, J. Blum, R.D. Yanai, and M.A. Fisk. Controls by N and P on fine root biomass and growth in northern hardwood forests. Ecology (submitted 5/20/20)
Trees can respond to nutrient limitation by adjusting belowground carbon (C) allocation in multiple ways. At scales smaller than a tree root system, roots can proliferate in response to patches of a growth-limiting nutrient (referred to here as

foraging). At scales of an individual and larger, trees can allocate more C belowground to support higher total root production in response to limitation by a nutrient. We examined fine root responses to nutrient availability at small and large scales as part of a broader nitrogen (N) × phosphorus (P) fertilization study in mature northern hardwood forests where P has been shown to limit aboveground growth. We used root ingrowth cores to test whether fine roots forage for P derived from apatite (a calcium phosphate mineral) at the small patch scale, and to test fine root growth response to large plot-scale nutrient enrichment. We observed fine root foraging for apatite-derived P in plots without P fertilization, but not in plots with P fertilization, as expected due to reduced demand. Surprisingly, fine root growth was not affected by P fertilization at the plot scale. However, N addition at the plot scale did significantly increase root growth. These results suggest that belowground root growth was limited by N, in contrast to aboveground growth, which was previously shown to be limited by P in our study sites. We propose that N limitation of fine root growth is a mechanism by which N availability interacts with P acquisition in northern hardwood forests, contributing to the maintenance of co-limitation of forest production.

2. Young, A.R., R. Minocha, S. Long, J. E. Drake, and R.D. Yanai. 2020. Responses of physical, chemical, and metabolic leaf characteristics to depth within mature sugar maple crowns and to nitrogen and phosphorus addition. Tree Physiology (submitted May 19, 2020)

• The distribution of leaf characteristics within large and complex tree crowns is poorly understood and may depend on both light environment and soil nutrient availability.
• To explore leaf characteristics throughout tree crowns, we collected leaves along a vertical gradient within mature sugar maple crowns in a full factorial nitrogen by phosphorus addition experiment in three forest stands in central New Hampshire, USA.
• Specific leaf area was not sensitive to N or P addition but increased with depth in the crown, reflecting both decreased mass and increased area per leaf. Concentrations of photosynthetic pigments and many elements increased with depth in the crown. Trees that received N had higher concentrations of foliar N and chlorophyll throughout the crown. Nitrogen-treated trees also had higher concentrations of Al, Mn, alanine, glutamate, and valine. Phosphorus addition increased foliar P and B throughout the crown and increased concentrations of chlorophyll and Zn concentrations with depth in the crown.
• Understanding patterns of leaf characteristics through tree crowns is useful not only for modeling crown-level acclimation to increased N and P availability but may also improve field sampling designs. Studies that ignore the vertical gradient miss the opportunity to understand the plasticity of traits within tree crowns.

3. Rice, A.M., Johnson, M.T., Libenson, A.J., and Yanai, R.D. Tree variability limits the detection of nutrient treatment effects on sap flow in a northern hardwood forest. Forest Ecology and Management (submitted April 1, 2020)

The role of nutrient availability in controlling transpiration is not well understood, in spite of the importance of transpiration to forest water budgets. The objective of this study was to determine whether nutrient fertilization influences sap flow rates in northern hardwood forests. We were unable to detect an effect on sap flow from additions of nitrogen, phosphorus, a combination of nitrogen and phosphorus, or calcium silicate in American beech (Fagus grandifolia, Ehr.), red maple (Acer rubrum L.), sugar maple (Acer saccharum Marsh.), white birch (Betula papyrifera Marsh.), or yellow birch (Betula alleghaniensis Britton.). Tree-to-tree variability was high, with coefficients of variation averaging 39% within treatment plots. The minimum difference in sap flow rates detectable with our observed variability and study design ranged from 46% to 352%, depending on the species and year of the study. We analyzed other sap flow studies reported in the literature and found detectable differences ranging from 16% to 78%. Given the high variability in sap flow rates, our power to detect treatment effects would have been improved by collecting pretreatment data as a covariate.

What opportunities for training and professional development has the project provided?

Thomas Mann is graduate student who was partially funded on this grant. He prepared data sets for archiving and is working on a MS thesis, described below.

Alexendrea Rice, a recent graduate student, collected soil samples in our sites and prepared the data for sharing. She also submitted a manuscript on nutrient treatments and water use by trees.

How have the results been disseminated to communities of interest?

Presentations and papers are listed above. We are continuously producing products from this long-term study; the ones completed in this year were funded primarily by the earlier grants from NSF. Thus while federal funding is acknowledged, NIFA funding is not.

What do you plan to do during the next reporting period to accomplish the goals?

We are continuing to fertilize the stands and characterize their responses.

Noah Blumenthal, a grad student at Miami University, is working up the results of tree inventory conducted in August 2019 and describing growth response to N and P addition.

Thomas Mann is measuring respiration and litterfall and will write a paper on below ground carbon allocation in response to nutrient limitation.

Carina Berlineri and Eva Paradiso are characterizing root morphology and mycorrhizal colonization in response to nutrient treatments.

A new student will install litter decomposition bags.

Participants

Actual FTE's for this Reporting Period

Role	Non-Students or faculty	Students with Staffing Roles			Computed Total by Role
		Undergraduate	Graduate	Post-Doctorate	
Scientist	0.3	0	0.1	0	0.4
Professional	0	0	0	0	0
Technical	0.1	0	0	0	0.1
Administrative	0	0	0	0	0
Other	0	0	0	0	0
Computed Total	0.4	0	0.1	0	0.5

Student Count by Classification of Instructional Programs (CIP) Code

Undergraduate	Graduate	Post-Doctorate	CIP Code
0	1	0	01.12 Soil Sciences.

Target Audience

The MELNHE project is communicating to researchers and to managers at the White Mountain National Forest, National Forest System.

Products

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Gonzalez, K.E. and R.D. Yanai. Nitrogen-Phosphorus Interactions in Northern Hardwoods Stands Indicate P Limitation: Foliar Concentrations and Resorption in a Factorial N by P Addition Experiment. December 9, 2019, American Geophysical Union Fall Meeting, San Francisco, CA.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Yanai, R.D. Going Beyond the Valley: MELNHE and the Chronosequence Studies. October 30 2019, Hubbard Brook Committee of Scientists Meeting, Cary Institute of Ecosystems Studies, Millbrook, NY.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Yanai, R.D., M. Fisk, and T.J. Fahey. The first long-term soil N x P manipulation experiment in a temperate forest system. September 3, 2019, International Long Term Ecological Research Network 2nd Open Science Meeting (ILTER), Leipzig, Germany.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Rice, A.M., M. Vadeboncoeur, and R.D. Yanai. Using Soil Nutrient Pools to Explain Ecosystem Processes. November 12, 2019, American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America International Annual Meeting, San Antonio, TX.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Young, A.R. and R.D. Yanai. Detecting foliar nutrient status of northern hardwoods from the sky. August 14, 2019, Ecological Society of America Annual Meeting, Louisville, KY.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Gonzales, K.E., R.D. Yanai, T.J. Fahey, M.A. Johnston, and D. Parry. Nitrogen-phosphorous interactions in northern hardwoods stands indicate P limitation: Foliar concentrations and resorption in a factorial N by P addition experiment. August 16, 2019, Ecological Society of America Annual Meeting, Louisville, KY.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Hong, D., T.J. Fahey, M. Fisk, M.A. Johnston, and R.D. Yanai. The timing of senescence effect foliar P resorption. July 12, 2019, Hubbard Brook Annual Meeting, W. Thornton, NY

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Mann, T.A., K. Bazany, and R.D. Yanai. Baby boomers: Are there any surviving germinants from the recent mast year? July 12, 2019, Hubbard Brook Annual Meeting, W. Thornton, NY.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Victoroff, C., T.R. Horton, R.D. Yanai. Fruiting response of ectomycorrhizal fungi to nutrient additions. July 12, 2019, Hubbard Brook Annual Meeting, W. Thornton, NY.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Abbott, S., T.J. Fahey, R.D. Yanai, A.R. Young, and S. Li. Belowground C Allocation Estimated as Soil Respiration Minus Aboveground Litter Inputs. July 12, 2019, Hubbard Brook Annual Meeting, W. Thornton, NY.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Zukswert, J.A., R.D. Yanai, S. Fraver ,M. Fisk, M. Jurgensen, and C. Miller. Having a stake in nutrient cycling: Effects of N and P addition on wood decay. July 12, 2019, Hubbard Brook Annual Meeting, W. Thornton, NY.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Young, A., R. Minocha, R.D. Yanai. Sugar maple leaf characteristics vary with depth in the crown and nutrient addition. July 12, 2019, Hubbard Brook Annual Meeting, W. Thornton, NY.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Congress, S., B. Fahey and R.D. Yanai. Space Wars: The Fight for Light in the Stands of Bartlett. July 12, 2019, Hubbard Brook Annual Meeting, W. Thornton, NY.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Yanai, R.D. Can We Predict the Biogeochemistry of Catchments? June 5, 2019, Gordon Research Conference, Andover, NH. Invited keynote speaker.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Hong, D.S., K.E. Gonzales, and R.D. Yanai. Foliar analysis of six northern hardwood species indicates nutrient limitation. June 3-5, 2019, LTER Midterm Review, Hubbard Brook, NH.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Shan S, and M.C. Fisk. N and P availability influence species composition of the fine root community in northern hardwood forests. May 28-31, 2019, Soil Ecology Society, Toledo, Ohio.

Type	Status	Year Published	NIFA Support Acknowledged
Conference Papers and	Other	2019	NO

Citation

Shan S, and M.C. Fisk. 2019. N and P availability influence species composition of the fine root community in northern hardwood forests. August 16, 2019, Ecological Society of America Annual Meeting, Louisville, KY.

Other Products

{Nothing to report}

Changes/Problems

We were able to fund the first field season on other grants. We will be spending in earnest beginning with the 2020 field season. We hope to request a no-cost extension to continue our work in 2022. The longer we continue our fertilization treatments the greater is our ability to describe ecosystem responses to nutrient limitation.