

The Role of Mycorrhizae in Water Use in Northern Hardwoods: Is Transpiration Optimized for Uptake of Limiting Nutrients?

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Proposal Status: This is a first submission.

Project Summary

Transpiration is a key ecohydrologic process that requires better understanding, especially considering the need to manage forests under future climates and altered nutrient regimes. Forest fertilization alters transpiration for reasons that are not well understood. This project will use a set of previously established, replicated, nitrogen, phosphorus, and calcium treatments in New Hampshire to provide insight into the mechanisms behind observed effects of nutrient availability on transpiration.

Current models of forest hydrology generally consider evapotranspiration to be a function of vegetation type, atmospheric evaporative demand, and water availability. The role of nutrient availability in determining plant water use has not been adequately explored, and our focus on the role of mycorrhizal fungi in this relationship is novel. The fungal measurements in fertilized plots will also provide evidence of how both ectomycorrhizal and arbuscular mycorrhizal communities reorganize after N, P, or Ca addition. Further, this project will test whether water use and plant and fungal responses are consistent with nutrient optimization theory, using a combination of model simulations and field measurements of nutrient uptake capacity.

The role of mycorrhizal networks in water use has not been comprehensively addressed, and Ca and P have been relatively little studied compared to N in terms of their effect on mycorrhizal communities in forested ecosystems. Testing the optimality of water use will contribute to resource optimization theory. This study will contribute to graduate and undergraduate student training and produce theses and articles in peer-reviewed journals.

Justification

Transpiration moves soil water to the atmosphere, constituting a major flux in the global water cycle (Jasechko *et al.* 2013) and influencing rates of biogeochemical processes sensitive to soil moisture, such as decomposition (Cook and Orchard 2008), denitrification (Groffman and Tiedje 1989), and the consequent fluxes of greenhouse gases to the atmosphere. Improved understanding of forest transpiration is needed to predict forest ecosystem services, water yield, and feedbacks to the climate system.

Many studies have observed changes in transpiration following changes in nutrient availability. At the Hubbard Brook Experimental Forest in New Hampshire, a calcium silicate addition resulted in reductions in streamflow, suggesting a 20 to 25% increase in transpiration (Green *et al.* 2013). Sap flow or transpiration has also been observed to increase in response to additions of nitrogen, phosphorus, or Ca in eucalypts (Hubbard *et al.* 2004), conifers (Phillips *et al.* 2001, Samuelson *et al.* 2008), and tropical forests (da Silva *et al.* 2008). Preliminary measurements in one of our study stands showed that red maples responded to N fertilization with increased transpiration (Hernández-Hernández 2014). Understanding these effects will be important to predicting forest response to increasing N availability caused by human activities (Galloway *et al.* 2004) and subsequent Ca depletion (Likens *et al.* 1996).

Previous studies of transpiration responses to nutrient additions used tree characteristics as explanatory variables. None of them addressed the possible role of mycorrhizal fungi, although the mycelial networks of mycorrhizal fungi extend beyond the plant root systems and are known to mediate delivery of water and nutrients to trees (Smith and Read 2008). The primary goal of this project is to provide information about the role of mycorrhizae in the response of trees to changes in nutrient availability, which has not previously been studied.

Arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) plants might be expected to affect plant water use differently in response to nutrient additions. Some EM fungi produce extensive and long-distance mycelial networks, extending for meters, with vessel-like rhizomorphs active in bulk transport of water (Duddridge *et al.* 1980, Agerer 2001). Lamhamedi *et al.* (1992) showed decreased water stress in seedlings associated with strains of an EM fungus that had greater numbers of hyphae and diameter of rhizomorphs. In contrast, AM mycelial networks are much less extensive and the AM fungi (Glomeromycota) do not form organized structures such as rhizomorphs; mass flow of water through

AM networks may be negligible (Kothari *et al.* 1990). AM plants showed no differences in water depletion in a hyphal compartment whether they were well watered or water-stressed or whether the hyphae were severed from the hosts (George *et al.* 1992). Without water flow through hyphae, AM-associated roots continue to take up water directly even when well colonized because the fungi do not form a sheath that inhibits flow of water directly into the root. In contrast, EM roots are ensheathed by a fungal mantle that physically interferes with direct water uptake by the plants; water uptake is mediated by the hyphae.

An alternative explanation for nutrient-induced changes in transpiration is that transpiration is altered to optimize acquisition of limiting resources. Transpiration determines the velocity of water uptake at the root surface, which affects nutrient uptake (Yanai 1994). The uptake of some nutrients is more sensitive to transpiration rates than others; the velocity of water uptake at the root surface is most important when soil buffering and diffusion rates are low (Williams and Yanai 1996). Thus, optimal stomatal behavior, for example, could reflect the benefit incurred for nutrient uptake (Cramer *et al.* 2009).

Previous Work, Present Outlook, and Future Prospects

Our proposed research will be conducted in mixed EM and AM hardwood stands at the Bartlett Experimental Forest, Hubbard Brook Experimental Forest, and the Jeffers Brook Forest. Substantial prior research in these six stands (Table 1) makes it possible for us to achieve our goals in just 2 years.

Table 1. Published and preliminary findings to date, including indicators of nutrient limitation.

- Pre-treatment root ingrowth cores implying that the most limiting nutrient may vary by stand (Naples and Fisk 2010).
- Pre-treatment characterization of among-stand variation in soil nutrients (Vadeboncoeur *et al.* 2012, 2014), weathering rates (Schaller *et al.* 2010), root biomass (Yanai *et al.* 2006, Park *et al.* 2007), and aboveground biomass and nutrient stocks (Fatemi *et al.* 2011).
- An improved version of the Multiple Element Limitation (MEL) model based in part on data from these stands, predicting changes in limiting nutrients and shifts in optimal allocation with stand age and management (Rastetter *et al.* 2013).
- A stand-scale nutrient depletion model evaluating sustainable harvest removals for forest management and biomass production (Vadeboncoeur *et al.* 2014).
- Pre-treatment variation in foliar nutrient resorption (See 2013) and soil respiration (Bae 2013) showing significant effects related to site, stand age, and nutrient availability.
- Post-treatment responses of foliar chemistry and sugar content of maple sap (Wild 2014).
- A demonstration that fertilizing with P affects demand for and availability of N (Fisk *et al.* 2014).
- Nutrient uptake capacity (this proposal) can indicate nutrient limitation (Harrison and Helliwell 1979)
- Ongoing monitoring of soil chemistry and microbial responses, foliar chemistry, root production, soil respiration, and aboveground productivity, with tree inventory scheduled for 2015.

Preliminary measurements of sap flow in our mature stands in response to Ca addition were consistent with a greater sensitivity of EM species (beech and birch) than AM (maple) (Figure 1), while maple was the species that showed a significant increase in water use in response to N addition in one of our young stands (Hernández-Hernández 2014). More research is needed to determine whether these differences represent general patterns, but this difference is consistent with a greater benefit of transpiration to N uptake predicted by optimality theory. This result is also consistent with a greater contribution of AM fungi to P uptake than N uptake (Smith and Read 2008), resulting in greater sensitivity of their hosts to N addition.

The proposed project will contribute to future prospects of funding from NSF LTREB (Long-Term Research in Environmental Biology), USDA NIFA RENRE (Renewable Energy, Natural Resources, and Environment) and other sources (NSRC, DOE), as described below under Future Funding Plans.

Objectives and Hypothesis

This project will provide insight into the effects of nutrient availability on transpiration, as part of a larger project examining the hydraulic pathway from soil water to mycorrhizal fungi and roots, through stems and leaves to the atmosphere. Our partners will measure sap flow, soil moisture, water-use efficiency, hydraulic conductivity of coarse roots and stems, and leaf area, stomatal density, and stomatal conductance, using the same trees that we will study. Our objectives focus on the root and fungal partners in EM and AM symbioses, addressing the proximate causes of the effects of nutrients on plant water use. We will also learn whether water use is optimal for uptake of limiting nutrients.

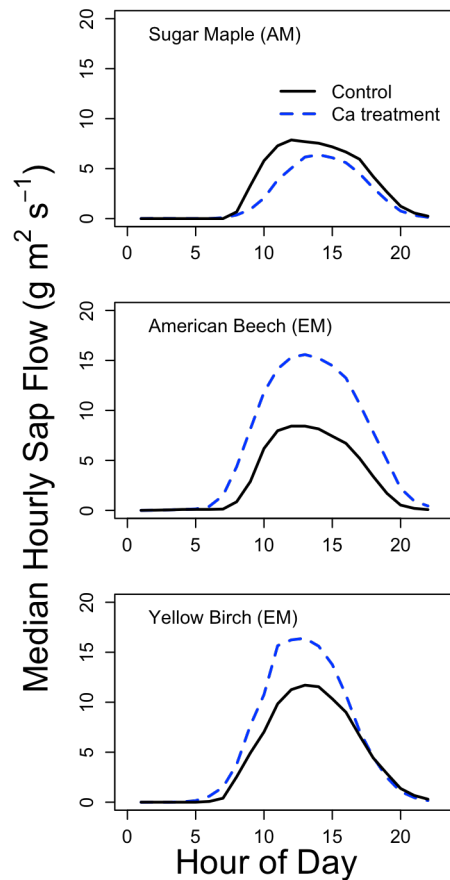


Figure 1. Median hourly values of sap flow were higher following Ca addition for EM but not AM species (3 trees of each species in each treatment at each of our 3 sites). Differences were significant for sugar maple and beech (Mann-Whitney). The data were collected over a 45-day period during the growing season of 2013 (Zahor 2014).

Objective 1: Measure mycorrhizal fungal characteristics that may respond to nutrient additions.

H1: Mycorrhizal colonization of EM and AM roots of trees and seedlings will respond differently to N, P, and Ca additions.

H2: Fungal richness, diversity, and hyphal density in soil and in ingrowth bags will respond to N, P, and Ca additions, reflecting niche partitioning in the functional role of EM fungi.

Objective 2: Measure nutrient uptake capacity at the root surface and construct and parameterize a model of nutrient uptake and transpiration based on our measurements.

H1: Nutrient uptake capacity will be explained by tree species and the mycorrhizal colonization of roots, which will be measured on the roots used in uptake experiments.

H2: Nutrient uptake capacity will reflect nutrient limitation by trees, with the greatest uptake capacity for the most limiting nutrient in each plot.

H3: Water use (measured by our collaborators) will be higher in plots in which uptake of the limiting nutrient is improved by increased uptake of water by roots, as determined by modeling nutrient uptake as a function of nutrient uptake capacity and other variables.

Procedures

Site and treatments: We will test our hypotheses by making measurements in an ongoing plot-scale fertilization experiment in the White Mountains of New Hampshire. Three sites are included to provide experimental replication: Jeffers Brook, Hubbard Brook, and Bartlett Experimental Forest. We will study a mature (>100 yr old) and a successional (30-45 years old) stand at each site (Table 1).

Table 2. Stand characteristics, including AM and EM tree species present in the canopy.

location	stand	yr.cut	elev (m)	aspect	slope (%)	EM species in canopy				AM species in canopy				
						beech	y.birch	w.birch	hemlock	s.maple	r.maple	str.maple	cherry	ash
Bartlett	C6	1975	460	NNW	13-20	x	x	x	x	x	x	x	x	x
Bartlett	C8	1883	330	NE	5-35	x	x		x	x				x
Hubbard	HBM	1971	500	S	10-25	x	x	x		x	x	x	x	x
Hubbard	HBO	1910	500	S	25-35	x	x		x	x				x
Jeffers	JBM	1985	730	WNW	25-35	x	x	x		x		x	x	
Jeffers	JBO	1900	730	WNW	30-40	x	x		x	x	x			

Each stand has four 50 m x 50 m plots treated since 2011 with N (30 kg N/ha/yr as NH₄NO₃), P (10 kg P/ha/yr as NaH₂PO₄), or Ca (1000 kg Ca/ha in the form of CaSiO₃) and a control. The rate of N addition was chosen to simulate chronic N pollution; the P addition was chosen to be comparable to the N

addition, accounting for immobilization by soils. The rate of Ca addition was chosen to restore the Ca losses estimated to have been caused by acid rain (Green et al. 2013).

Indicators of nutrient limitation: We will have data on the response to nutrient additions of aboveground productivity, determined by stand inventory and litter production (Table 1), to identify which nutrient is most limiting in each of our stands. At the plot level, we will have data on enzymes involved in N and P acquisition, which indicate microbial demand, root ingrowth cores containing N, P, and Ca, which indicate plant demand, and foliar nutrient resorption (See 2013). Nutrient uptake capacity (this proposal) is another candidate indicator of nutrient limitation (Harrison and Helliwell 1979).

Roots and fungal partners of trees: Field measurements will be conducted over two field seasons to use limited equipment and labor most effectively and also to reduce our chances of observing these forest plots during one abnormally wet or dry year. We will measure root abundance, AM and EM colonization of roots, and fungal community composition from EM host roots in the four treatments (N, P, Ca, Control) in all six stands, using the same roots involved in nutrient uptake experiments (described below), which will be from the same trees used in sap flow measurements. In Year 1, we will focus our tree measurements on five beech (EM, present in all plots) and five red or sugar maples (AM; species dominance varies by stand) in each plot. In Year 2, in addition to repeating our measures on beech and maple, we will measure a second species of each mycorrhizal type (yellow or white birch for EM, and white ash, cherry, or striped maple for AM), again as species composition allows (Table 2).

Mycorrhizal fungal colonization (AM and EM hosts) will be quantified following Brundrett *et al.* (1996), and we will record the presence of arbuscules, vesicles and Glomeromycota hyphae in the AM roots. EM fungal community composition from the roots of EM hosts will be assessed using molecular techniques (Gardes and Bruns 1996, Horton and Bruns 2001); techniques for species identification of AM fungi from roots have not yet been fully developed. Plant species will be confirmed with molecular techniques from the EM root tips following Dulmer et al. (2014).

Seedling study: Seedlings will be used as bait for mycorrhizal fungi to provide an indication of effects of N, P, and Ca additions on the mycorrhizal community. American beech (EM) and sugar maple (AM) will be germinated in autoclaved quartz sand in growth bags designed to accommodate the growth of the seedling roots in the upper 15 cm of soil where the majority of mycorrhizal activity is expected. The bags will be prepared from mesh screens with a pore size of 45 μm , allowing hyphal but not root

ingrowth from the surrounding soil (Wallander *et al.* 2001). Ten seedling bags for each species will be installed vertically into the ground in the spring of 2015 in all the treatment plots of the mature stands in each of the three sites (10 seedlings x 4 treatments x 3 sites = 120 seedling bags for each mycorrhizal type, 240 total). Our studies of seedling survival show low survivorship of recent germinants in the denser shade of the younger stands, thus the seedling study will be implemented in the mature stands. Seedlings will be thinned to one per bag and harvested after 2 years. Mycorrhizal colonization (AM and EM) and EM community assemblages will be measured as described above. To gain a more complete sampling of the fungi in the bags, DNA will also be extracted from the sand using a Powersoil DNA extraction kit (MoBio, Carlsbad CA) and sequenced using the Illumina MiSeq platform following Smith and Peay (2014) at the SUNY Microarray Core facility. We will focus on sequences that indicate mycorrhizal taxa in our initial screening of the sequences.

Nutrient uptake capacity of fine roots will be measured using intact root branches in the field (Lucash *et al.* 2005, 2007). Uptake rates of cations and anions will be measured by depletion from simulated soil solutions (Rennenberg *et al.* 1996, Gessler *et al.* 1998, Lucash *et al.* 2005, 2007). Target concentrations of the simulated soil solution will be determined from a saturated paste slurry (Carter and Gregorich 2008) of bulked soil samples collected from each of the three research sites. Each root will be exposed to the concentrations, the observed concentration and 5 and 10 times greater, to allow determination of uptake kinetics as a function of solution concentration, as required by the model.

Root branches will be excavated and gently washed free of adhering soil. To conduct the uptake experiments, each root branch will be placed in a 50 ml vial with 27 ml of fresh solution (we use a smaller vial to displace volume, improving the ratio of root surface to solution volume). The vials will be aerated using a system of tubing, clamps, and battery-operated fish pumps and covered with Parafilm to prevent contamination. Bubbling also serves to prevent the formation of depletion zones near root surfaces. After two hours of exposure, the solution samples will be filtered, returned to the lab, and frozen until they can be analyzed for anions and cations by autoanalyzer and ICP spectroscopy. The root branches will be severed from the tree at the end of the experiment, weighed fresh, and cut into pieces and photographed. The photographs will be analyzed for length using a line-intercept method (Tennant 1975). Uptake rates can thus be described per unit mass or surface area. We will identify the fungi from the EM roots following the molecular approach described above.

Nutrient uptake modeling: These observations will provide the parameters necessary to model nutrient uptake at the root surface (Yanai 1994), allowing us to describe the degree to which increased transpiration increases nutrient uptake (Williams and Yanai 1996). Nutrient uptake models simulate the movement of solutes to the root surface and the uptake of nutrients into the root. We use a steady-state model of nutrient uptake (Nye and Tinker 1977, Yanai 1994), because it allows the values of the parameters to vary over time. The parameters required by the model are the root length and diameter, the root length density (root length per unit soil volume), the average soil solution concentration, the buffer capacity, and the effective diffusion coefficient. The latter can be calculated from the soil moisture content and the tortuosity, a function of soil texture (Van Rees *et al.* 1990). We will supply the model with transpiration rates, soil moisture, and uptake kinetics measured in this project; root length, rooting density, and soil solution and solid phase concentrations are available from previous measurements. We will also parameterize the model for uptake by fungal hyphae (Yanai *et al.* 1995).

Data Analysis and Hypothesis Testing for Objective 1: Fungal characteristics

The response of mycorrhizal fungi to nutrient additions will provide novel data, especially for P and Ca additions, which have been little studied relative to N. Mycorrhizal colonization (root length with hyphal structures, proportion of root tips with a fungal mantle) of root branches and seedlings and the density of hyphae in soils and ingrowth seedling bags will be analyzed by ANOVA blocked by stand for each host species with nutrient treatment as the explanatory variable. Species richness and diversity of EM fungi on root systems of seedlings and mature trees and in soils and ingrowth seedling bags will be analyzed at the plot level, blocked by site and stand. We will use ordination analysis (e.g., principal component analysis, non-metric multidimensional scaling) and phylogenetic dispersion patterns to explore the role of nutrient additions on the composition of fungal communities.

Data Analysis and Hypothesis Testing for Objective 2: Nutrient uptake

We will fit nutrient uptake kinetic parameters (I_{max} and K_m) by non-linear regression to observations of uptake at the three nutrient concentrations exposed to each root; alternatively, a linear model (α) may be a better fit (Yanai 1994). Nutrient uptake capacity so determined, for each nutrient and tree species, will be the dependent variables in an analysis of the importance of nutrient treatment (N, P, Ca, control) and the fungal status of the roots used in these measurements (Objective 1).

We will model nutrient uptake rates as a function of measured soil solution concentration, root length per unit soil volume, nutrient uptake capacity, and water uptake rates. We will relate nutrient uptake for each nutrient and tree species to water uptake (represented in the model as the radial velocity of water uptake at the root surface) at the plot level, because root length and nutrient availability are characterized at the plot level. For each nutrient and tree species, we will then test the hypothesis that transpiration is increased in treatments in which uptake of a limiting nutrient is most increased by water uptake. In mathematical terms, we will compare dU_i/dv , the change in uptake of element i predicted by the model to result from a change in the velocity of water uptake, to the growth response of that species in response to addition of element i (or other indicator of nutrient limitation, Table 1). This information will inform future improvements to the MEL model (Rastetter *et al.* 2013).

Benefits to Society and Broader Significance

Forest management has been a primary focus of the McIntire-Stennis Program since its inception. Nutrients regimes are changing, due to N pollution and Ca depletion by acid rain. Understanding the consequences of forest nutrition on water use relates to the need to predict water yield; understanding the effects of plant allocation to mycorrhizal symbionts is key to managing sustainable forest production.

The results of this study will be publishable in high-impact, peer-reviewed journals, and they will likely have influence on other researchers in the field even before they are published, through our informal networks and presentations at meetings. The project will thus advance discovery and understanding, in addition to training students at all levels (we have Research Assistantships for High School Students, funded by NSF, which broaden the participation of underrepresented groups, in this case African-Americans and Asian-Americans). Finally, investments in the long-term nutrient manipulation experiment enhances the infrastructure for future research and education, and the addition of Horton to the Hubbard Brook Committee of Scientists is an addition to intellectual infrastructure.

Probable Duration and Timetable

We will begin data collection in the summer 2015, before the project starts. Field work will be completed in summer 2016.

	Study Activity	2015	2016	2017
Modeling, data synthesis, and writing will extend through the second academic year.	Measurements on sugar maple and beech	X	X	
	Measurements on other AM and EM trees		X	
	Seedling study	X	X	
	Molecular work on fungal communities	X	X	X
	Nutrient uptake - transpiration modeling		X	X
	Data synthesis and writing		X	X

Budget Justification

Salary is budgeted for one graduate student, Jerome Barner, who has already been involved in preliminary experiments with nutrient uptake and the collection and preparation of roots for this study.

Travel to the field sites is budgeted at \$1000/year. Attendance at professional meetings will be covered by other sources, including quarterly meetings of the Hubbard Brook Committee of Scientists and the annual meeting of Bartlett cooperators.

Laboratory supplies are budgeted at \$4000 including reagents, filters, vials, and other consumables for nutrient uptake experiments and supplies for identifying the mycorrhizal symbionts with PCR-based techniques. We are requesting \$2500 for kits, reagents and sequencing runs on the Illumina MiSeq platform (Upstate Medical University Microarray facility) and \$1,000 to cover the costs of constructing the ingrowth bags, buying seed, and additional consumables needed for clearing, staining and viewing mycorrhizal colonization of roots (slides, coverslips, stains, etc.). Analytical and Technical Services are budgeted at \$6000 for analysis of solutions in the nutrient uptake experiments.

ESF Personnel and Cooperators at Other Institutions

Ruth Yanai will lead the project and coordinate relations with the field project in New Hampshire, including continuing the fertilization treatments and measuring nutrient limitation. **Tom Horton** will direct the laboratory activities, including measurements of colonization rates (EM and AM hosts) and molecular identification of EM fungi.

Collaborators working on water use and tree physiology include Heidi Abjornsen and Matt Vadeboncoeur (University of New Hampshire) and Mark Green and Michele Pruyn (Plymouth State University), who are seeking funding from other sources.

Future Funding Plans

The proposed research benefits from a previous NSF grant to Yanai (DEB-0949324). The current grant will run out in 2015. Supporting this project from 2015-2017 will strengthen a future request to NSF for funding for Long-Term Research in Environmental Biology (LTREB), which requires a 6-year record of research activity and producing transformative results.

Identifying functional groups of fungi important for the acquisition of N, P, and Ca will make it possible to pose more targeted research questions in future proposals, including massive sequence datasets for powerful views into fungal communities (e.g. Next Gen sequencing).

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- Wallander, H, LO Nilsson, D Hagerberg, and E Bååth. 2001. Estimation of the biomass and seasonal growth of external mycelium of ectomycorrhizal fungi in the field. *New Phytol* 151(3):753-760.
- Wild, AD. 2014. Soil nutrients affect sweetness of sugar maple sap. MS Thesis. Syracuse, NY: SUNY College of Environmental Science and Forestry.
- Williams, M, and RD Yanai. 1996. Multi-dimensional sensitivity analysis and ecological implications of a nutrient uptake model. *Plant Soil* 180(2): 311-324.
- Yanai, RD. 1994. A steady-state model of nutrient uptake accounting for newly grown roots. *Soil Sci. Soc. Am. J* 58(5), 1562-1571.
- Yanai, RD, TJ Fahey, and SL Miller. 1995. Efficiency of nutrient acquisition by fine roots and mycorrhizae. *In: Smith, W.K. and T.M. Hinckley, Eds., Resource Physiology of Conifers, pp.* 75-103. Academic Press, New York.
- Yanai, RD, BB Park, and SP Hamburg. 2006. The vertical and horizontal distribution of roots in northern hardwood stands of varying age. *Can. J. For. Res.* 36: 450-459
- Zahor, LE. 2014. The impact of calcium on transpiration in an acid rain impacted forest. Ms Thesis. Plymouth, NH: Plymouth State University

Budget

2015-2016 McIntire-Stennis Program

Title: "The Role of Mycorrhizae in Water Use in Northern Hardwoods: Is Transpiration Optimized for Uptake Limiting Nutrients?"

Project Period: 08/15/2015 to 9/30/2017

Yanai-Horton:MS-15-16 rev: 11/10/14

Budget Category	FY 2014 8/15/15 - 9/30/15	FY 2015 10/1/15 - 9/30/16	FY 2016 1/1/16 - 9/30/17	Total
Salaries & Wages				
Principal Investigator				
Ruth Yanai @ 10% AY	0	0	0	0
Co-Principal Investigator(s)				
Thomas Horton @ 5% AY	0	0	0	0
Hourly Personnel (Non-Student)	0	0	0	0
Subtotal	0	0	0	0
Graduate Assistants	2,154	16,000	16,480	34,634
Student Assistants (Hourly)	0	0	0	0
Total Salaries & Wages	2,154	16,000	16,480	34,634
Employee Benefits:				
Regular Employees @ 43.5%, 44%, 44.5%	0	0	0	0
Graduate Students @ 14%, 15%, 16%	302	2,280	2,513	5,095
Undergrad Students @ 5.0%	0	0	0	0
Total Salaries, Wages & Benefits	2,456	18,280	18,993	39,729
Equipment	0	0	0	0
Supplies & Materials	0	4,500	3,000	7,500
Travel	0	1,000	1,000	2,000
Other Direct Costs				
Computer Time	0	0	0	0
Equipment Rental	0	0	0	0
Analytical & Technical Services	0	3,000	3,000	6,000
Publication Costs	0	0	0	0
Total Project Budget	2,456	26,780	25,993	55,229

Responses to Previous Reviews

This is a first submission.

Record of Success with Previous McIntire-Stennis Funding

My first McIntire-Stennis award, with Ralph Nyland, was titled **“New measures of spatial variability in uneven-aged stands: distinguishing sustainable from exploitative cutting practices.”** This project supported Kimberly Bohn, PhD in 2006, now an Associate Professor at the University of Florida. I have not pursued this line of research, but Ralph Nyland has, along with John Wagner and David Newman.

- Bohn, K.K., R.D. Nyland, and R.D. Yanai. 2011. Comparing selection-system and diameter-limit cutting in uneven-aged northern hardwoods using computer simulation. *Canadian Journal of Forest Research* 41:963-973.
- Bohn, K.K., R.D. Yanai, and R.D. Nyland. Spatial structure of residual trees after simulated treatments of selection system silviculture and diameter-limit cutting in uneven-aged northern hardwood stands (in preparation)
- Nyland, R.D. 2009. Diameter-limit Cutting and Exploitation. A webinar in the ForestConnect Internet Seminar Series, sponsored by Cornell Cooperative Extension. 18 February 2009
- Nyland, R.D. 2008. Sustainable Forest Management in Today’s Acadian Forests sponsored by Unama’ki Institute of Natural Resources at Membertou, Nova Scotia. 8-9 July 2008
- Nyland, R.D. 2008. Exploitive or Responsible Forestry? Diameter-limit Cutting, High-Grading, Selective Harvesting – How Your Forests Can Recover from These Practices. A workshop in East Rupert, Vermont, sponsored by the Bennington County Sustainable Forest Consortium. 20 August 2008
- Bohn, K.K. and R.D. Yanai. 2006. Effects of different partial cutting treatments on structural dynamics in uneven-aged northern hardwood stands. *Ecol. Soc. Am.* Memphis, Tennessee, August 2006.
- Bohn, K.K. and R.D. Yanai. 2005. Spatial distribution of trees in northern hardwoods after simulated selection system silviculture and diameter-limit cutting. *Ecol. Soc. Am. Annual Meeting*. Montreal, Quebec, August 2005.
- Bohn, K.K., R.D. Nyland, and R.D. Yanai. 2005. Residual Spatial Structure of Uneven-aged Northern Hardwoods After Simulated Selection System Silviculture or Diameter-limit Cutting. Diameter-limit Cutting in Northeastern Forests Conference. University of Massachusetts. Amherst, MA. May 23-24, 2005.
- Bohn, K.K., R.D. Nyland, and R.D. Yanai. 2005. Residual Overstory Variability in Uneven-aged Northern Hardwoods Managed with Selection System Silviculture versus Diameter-Limit Cutting. New York Society of American Foresters Winter Meeting. Liverpool, NY. February 3, 2005.

My second McIntire-Stennis award, with Tom Horton, was titled **“Sustainable nutrient supply after forest harvest: Characterizing the fungal link from soils to roots.”** This project supported Franklin Diggs, who defended his thesis in January, 2014; he has two papers in preparation. This project marked the entry of Horton in the MELNHE project; he has since collaborated on two pre-proposals to NSF Ecosystem Science and one full proposal, which is currently in review.

- Diggs, F., R.D. Yanai, and T. Horton. 2013. Mycorrhizal guilds decline similarly with depth in two northern hardwood forests. Minneapolis, MN—Ecological Society of America Annual Meeting, August 8, 2013. Contributed Oral Session 89-5.
- Diggs, F.D., R.D. Yanai, T.R. Horton. 2012. Variance in mycorrhizal colonization in stands of mixed hosts. Rochester, NY—Rochester Academy of Science, November 10, 2012.
- Diggs, F., R. Yanai, and T. Horton 2011. Mycorrhizae distributions by depth in northern hardwood ecosystems. Rochester, NY—Rochester Academy of Science Meeting, October 29, 2011.
- Diggs, F., R. Yanai, and T. Horton 2011. Mycorrhizae distributions by depth in northern hardwood ecosystems. New York Society of American Foresters Winter Meeting, January 26, 2012.

Ruth D. Yanai

Professional Preparation

Yale College	Geology and Geophysics	B.A., 1981.
Yale Graduate School	Forest Ecology	M.S. 1985, M. Phil. 1987, Ph.D. 1990.
Boyce Thompson Institute for Plant Research	Plant and Soil Modeling	1991.

Appointments

Sabbatical Fellow, Ecosystems Center, Marine Biological Laboratory. Woods Hole, MA. 2008.
 Professor, SUNY-ESF. 2007 – present.
 Visiting Professor, University of Tokyo, Graduate School of Agricultural and Life Sciences. 2006.
 Associate Professor, SUNY-ESF. 1999 – 2007.
 Assistant Professor, SUNY-ESF. 1994 - 1999.
 Senior Research Associate, Boyce Thompson Institute for Plant Research. 1994.
 Research Associate, Boyce Thompson Institute for Plant Research. 1992 -1993.
 Postdoctoral Associate, Boyce Thompson Institute for Plant Research. 1991.
 Research Support Specialist, Cornell University. 1989-1990.
 Fulbright Fellow, Edinburgh University and Institute of Terrestrial Ecology, 1987-1988.
 Secondary School Teacher, The Putney School, Putney Vermont. 1982-1983.
 Research Assistant, Geology and Geophysics, Yale University. 1981-1982.

Five Publications Most Closely Related to the Proposed Project

Yanai, R.D., M.C. Fisk, T.J. Fahey, N.L. Cleavitt, and B.B. Park. 2008. Identifying roots of northern hardwood species: patterns with diameter and depth. *Can. J. For. Res.* 38: 2862-2869
 Yanai, R.D., B.B. Park, and S.P. Hamburg. 2006. The vertical and horizontal distribution of roots in northern hardwood stands of varying age. *Can. J. For. Res.* 36: 450-459.
 Yanai, R.D., J.D. Blum, S.P. Hamburg, M.A. Arthur, C.A. Nezat, and T.G. Siccama. 2005. New insights into calcium depletion in northeastern forests. *J. For.* 103:14-20.
 Yanai, R.D., T.J. Fahey, and S.L. Miller. 1995. Efficiency of nutrient acquisition by fine roots and mycorrhizae. In: Smith, W.K. and T.M. Hinckley, Eds., *Resource Physiology of Conifers*, pp. 75-103. Academic Press, New York.
 Yanai, R.D. 1994. A steady-state model of nutrient uptake accounting for newly-grown roots. *Soil. Sci. Soc. Am. J.* 58:1562-1571

Five Other Significant Publications

Yanai, R.D., M.A. Vadeboncoeur, S.P. Hamburg, M.A. Arthur, M.A. Fuss, P.M. Groffman, T.G. Siccama, and C.T. Driscoll. 2013. From Missing Source to Missing Sink: Long-Term Changes in a Forest Nitrogen Budget. *Environmental Science & Technology.* 47(20):11440-11448.
 Rastetter, E. B., R. D. Yanai, R. Q. Thomas, M. A. Vadeboncoeur, T. J. Fahey, M. C. Fisk, B. L. Kwiatkowski, and S. P. Hamburg. 2013. Recovery from disturbance requires resynchronization of ecosystem nutrient cycles. *Ecological Applications* 23:621–642. <http://dx.doi.org/10.1890/12-0751.1>
 Yanai, R.D., J.J. Battles, A.D. Richardson, E.B. Rastetter, D.M. Wood, and C. Blodgett. 2010. Estimating uncertainty in ecosystem budget calculations. *Ecosystems* 13(2): 239-248.
 Fisk, M.C. , R.D. Yanai, and N. Fierer. 2010. A molecular approach to quantify root community composition in a northern hardwood forest: testing effects of root diameter and species. *Can. J. For. Res.* 40(4): 836-841
 Yanai, R.D., K.J. McFarlane, M.S. Lucash, J.D. Joslin, and S.E. Kulpa. 2009. Nutrient uptake by Engelmann spruce and subalpine fir at two Colorado subalpine forests. *Forest Ecol. Manag.* 258(10): 2233-2241.

Synergistic Activities

- Workshop, Preparing Manuscripts for Publication: Ecological Society of America Annual Meeting, Montreal, Quebec, Aug. 9, 2005; San Jose, CA, Aug. 7, 2007; Milwaukee, WI, Aug. 5, 2008; American Society of Agronomy Annual Meeting, Seattle, Washington, Nov. 2, 2004; Salt Lake City, UT, Nov. 8, 2005; Indianapolis, IN, Nov 14, 2006; New Orleans, LA, Nov. 6, 2007; Houston, TX, Oct. 7 2008; Pittsburgh, PA, Nov. 3, 2009; Long Beach, CA, Nov. 2, 2010. Forestry and Forest Products Research Institute, Tsukuba, Japan, July 28, 2006; April-May, 2007; Chiba Experimental Forest, Tokyo University, Japan, July 25, 2006; Kyoto University, Graduate School of Agriculture, Kyoto, Japan, July 14, 2006; Marine Biological Laboratory, Woods Hole, MA, Dec. 8, 2008
- Workshop, *Estimating uncertainty in ecosystem budgets*. Michigan State University - Department of Forestry, East Lansing, MI, Feb. 20, 2009; Ecological Society of America meeting, Aug. 2, 2009, Albuquerque, NM; Agronomy Society of America Meeting, Nov. 1, 2009, Pittsburgh, PA; Université Laval, Centre de foresterie de Laurentides & Le Centre d'Étude de la Forêt, Québec, QC, Oct 13, 2010
- Steering Committee, ESF Women's Caucus, providing informal and formal programs for students, staff and faculty and for girls interested in careers in science, 1994-present. Instructor of a graduate seminar at ESF: FOR 797 Women in Scientific and Environmental Professions, 1999-2002.
- Panelist, Climate Change Mitigation and Adaption in Agriculture, USDA NIFA Competitive Programs, Sept 21-24, 2010.
- Moderator, *Forest Stress* session, Workshop on Comparison of Forest-Soil-Atmosphere Models, Leusden, The Netherlands, May 10-14, 1993; session on *Management impacts on forest hydrology, biogeochemistry and water quality (C-14)*, 2010 IUFRO conference, Seoul, Aug. 25, 2010; *COS 38, Soil Ecology* session, 2010 Ecological Society of America annual meeting in Pittsburgh, PA, Aug. 3, 2010.

Current and Pending Research Funding

Yanai, R.D., and M.J Mitchell. Long-term ecological research at the Hubbard Brook Experimental Forest," 2011-2016. National Science Foundation, overall grant to Cornell University is \$5 million, the ESF subcontract is \$330,000, and my share is \$240,000. 1/1/2011-12/31/2016.

Yanai, R.D. Collaborative Research: Nutrient co-limitation in young and mature northern hardwood forest. National Science Foundation. \$905,961 with \$529,987 in collaborative awards to Marine Biological Laboratory, Miami University, University of Michigan, Cornell. 7/01/10- 6/30/15.

Yanai, R.D., J.L. Campbell, M.B. Green, C. Daly, R. Hooper, J. Clark, D.deB. Richter, and M.E. Harmon. RCN: Quantifying Uncertainty in Ecosystem Studies (QUEST). NSF. \$500,000. 1/1/13-12/31/18.

Lapenas, A.G., et al. Aphid-like Biosensors for Ecosystem Studies: NANAPHID Proof of Concept. SUNY 4E, subcontract to SUNY Albany. 2014. \$16,503, of total \$135,000

Yanai, R.D. Forest Health GIS Program. NYS DEC. \$389,624. 7/1/2010-9/30/2014

Yanai, R.D., and C.T. Driscoll. The importance of measuring mercury in wood. ESF Seed Grant. \$5700, 7/1/13-6/30/15.

Yanai, R.D., and T.R. Horton. Collaborative Research: IDBR: Type A: The NANAPHID: A novel aphid-like nanosensor network for real-time measurement of carbohydrates in live plant tissue. NSF. \$16503, with \$59,816 for the ESF component. Other institutions: SUNY Albany, SUNY College of Nanoscale Science and Engineering, Boston University. 2/1/15-1/31/17 (pending).

Yanai, R.D., and C.T. Driscoll. Quantifying Mercury in Forest Biomass. NSRC Theme Two Pre-Proposal. \$78,235. 7/1/15-6/31/17 (pending).

Thomas R. Horton

Professional preparation

Postdoctoral Institution: Oregon State University, Ectomycorrhizal Ecology, 1997 – 2001.

Graduate Institution: University of California, Berkeley, Ph.D. Plant Pathology, 1997.

Graduate Institution: San Francisco State University M.A., with honors: Biology: Ecology and Systematic Biology, 1992.

Graduate Institution: Humboldt State University, Single Subject Teaching Credential in Biology, with a Supplementary Authorization in English, 1987.

Undergraduate Institution: Humboldt State University, B.A. Biology, 1986.

Appointments

Associate Professor, Mycology, State University of New York, College of Environmental Science and Forestry, Syracuse, New York, 2007 – present.

Assistant Professor, Mycology, State University of New York, College of Environmental Science and Forestry, Syracuse, New York, 2001 – 2007.

Biology Teacher, Logan High School, Union City, California, 1987 - 1989.

Products – 5 most relevant to the proposed project (mycorrhizal communities and nutrient dynamics; Student authors italicized)

Dulmer KM, LeDuc SD, Horton TR (2014) Ectomycorrhizal inoculum potential of northeastern US forest soils for American chestnut restoration: results from field and laboratory bioassays. *Mycorrhiza* 24: 65-74.

Horton TR, *Hayward J, Tourtellot SG, Taylor DL* (2013) Uncommon ectomycorrhizal networks: richness and distribution of *Alnus*-associating ectomycorrhizal fungal communities. *New Phytologist* 198: 978-980.

LeDuc SD, Lilleskov EA, Horton TR, Rothstein DE (2013) Ectomycorrhizal fungal succession coincides with shifts in organic nitrogen availability and canopy closure in post-wildfire jack pine forests. *Oecologia* 172: 257-269.

Lilleskov EA, Hobbie EA, Horton TR (2011) Conservation of ectomycorrhizal fungi: exploring the linkages between functional and taxonomic responses to anthropogenic N deposition. *Fungal Ecology* 4: 174-183.

Lilleskov EA, Fahey TJ, Horton TR, Lovett GM (2002) Nitrogen deposition and ectomycorrhizal fungal communities: a belowground view from Alaska. *Ecology* 83: 104 - 115.

Products – 5 additional products

D'Amico KM, Horton TR, Maynard CA, Stehman SV, Oakes AD, Powell WA (in press) Comparisons of ectomycorrhizal colonization of transgenic American chestnut with that of the wild type, a conventionally bred hybrid, and related fagaceae species. *Appl Environ Microbiol* 81:000 – 000. doi:10.1128/AEM.02169-14.

Hayward J, Horton TR, Pauchard A, Nuñez MA (accepted) A single ectomycorrhizal fungal species can enable a *Pinus* invasion. *Ecology*.

Nuñez MA, *Hayward J, Horton TR, Amico GC, Dimarco RD, Barrios-Garcia MN, Simberloff D.* (2013) Exotic Mammals Disperse Exotic Fungi That Promote Invasion by Exotic Trees. *PLoS ONE* 8(6): e66832

Nuñez MTA, Horton TR, Simberloff D (2009) Lack of belowground mutualisms hinders Pinaceae invasions. *Ecology* 90:2352-2359.

Horton TR, Bruns, TD (2001) The molecular revolution in ectomycorrhizal ecology: peeking into the black-box. *Molecular Ecology* 10: 1855-1871.

Synergistic activities

Teaching: I bring a strong microbial ecology perspective in my General Ecology course, reaching over 230 students each fall. I also teach advanced courses in Mycorrhizal Ecology (EFB 428/628) and Advanced Mycology: Basidiomycetes to about 25 students in alternate years. I also teach a variety of graduate seminars focused on mycorrhizal ecology. I developed the Mycorrhizal Ecology course from scratch starting in 2001 and as one colleague suggested when I gave an invited talk at the University of Guelph, he was not aware of any other course in mycorrhizal ecology taught on a regular basis. Last year I was awarded the Weston Award for Excellence in Teaching by the Mycological Society of America.

Development and refinement of research tools/databases. I have made important contributions publishing and testing PCR-based methodologies (contributed to the sequence database in Bruns et al. 1996 -- In 2000 I increased the original database from 152 to 175 taxa, available at <http://nature.berkeley.edu/brunslab/>). I have also contributed to the critical analysis of the methodologies (Horton and Bruns 2001; Horton 2002; Bidartondo et al. 2008; Horton Arnold and Bruns 2008). Horton and Bruns (2001) has been cited over 600 times according to Google Scholar.

Transfer of knowledge – student training in my lab: current graduate students: I have trained two PhD students (1 latina), 11 MS (including 6 females) and 4 MPS students (all female). I accept 2-3 undergraduate students per semester in my lab seeking research experience and have had three REU students (2 female). I have also trained many graduate students from labs of colleagues across campus at ESF and from other Universities including UNH, Rutgers, Duke, Michigan State University, University of Wyoming, Yale, and SU. Most students have published at least one paper from their work in my lab work in high impact journals such as *Agriculture and Environmental Microbiology*, *Ecology*, *Molecular Ecology*, *New Phytologist*, *Oecologia*, and *PLoS One*. I am at the tail end of a project in which I am the sole editor of a contributed author volume under Springer's *Ecological Studies* series tentatively titled, "Mycorrhizal Networks."

Professional service: various committees with Mycological Society of America including chairing the program committee for the annual meeting in Kentucky (2010) and currently serving on the awards committee; scientific Advisor for the Mianus River Gorge Preserve. 2006 – present; Chair, Lowe/Wilcox Mycology graduate fellowship committee, SUNY-ESF, 2009 – present; faculty advisor for the Central New York Mycological Society, 2001 – present; organize the annual Mushroom Festival with CNYMS members, Beaver Lake Nature Center, 2009 – present; editorial board for *Mycorrhiza*; reviews for various journals and funding agencies including serving on USDA and NSF panels.