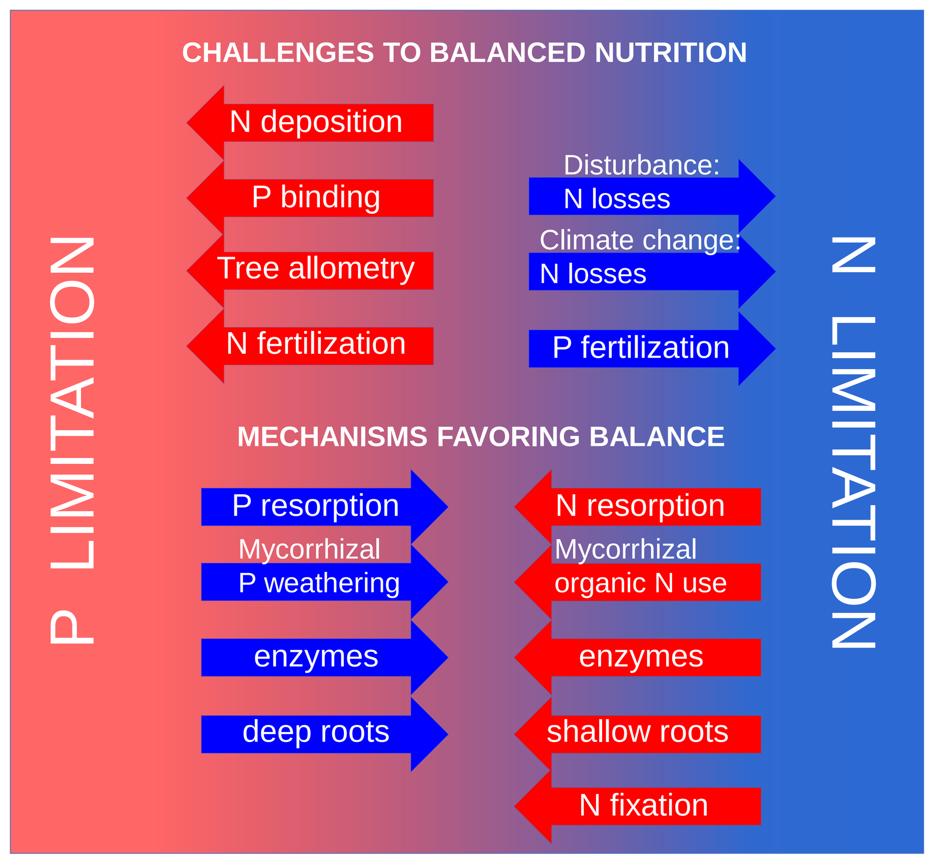
Nitrogen Versus Phosphorus Limitation: A Factorial Fertilization Experiment in Temperate Hardwood Forests

Ruth D. Yanai[1], Kara E. Gonzales[1], Shinjini Goswami[2], Shiyi Li[3], Melany C. Fisk[2] and Timothy J. Fahey[3]
[1]SUNY-ESF, Syracuse, NY; [2]Miami University of Ohio, Oxford, OH; [3]Cornell University, Ithaca, NY

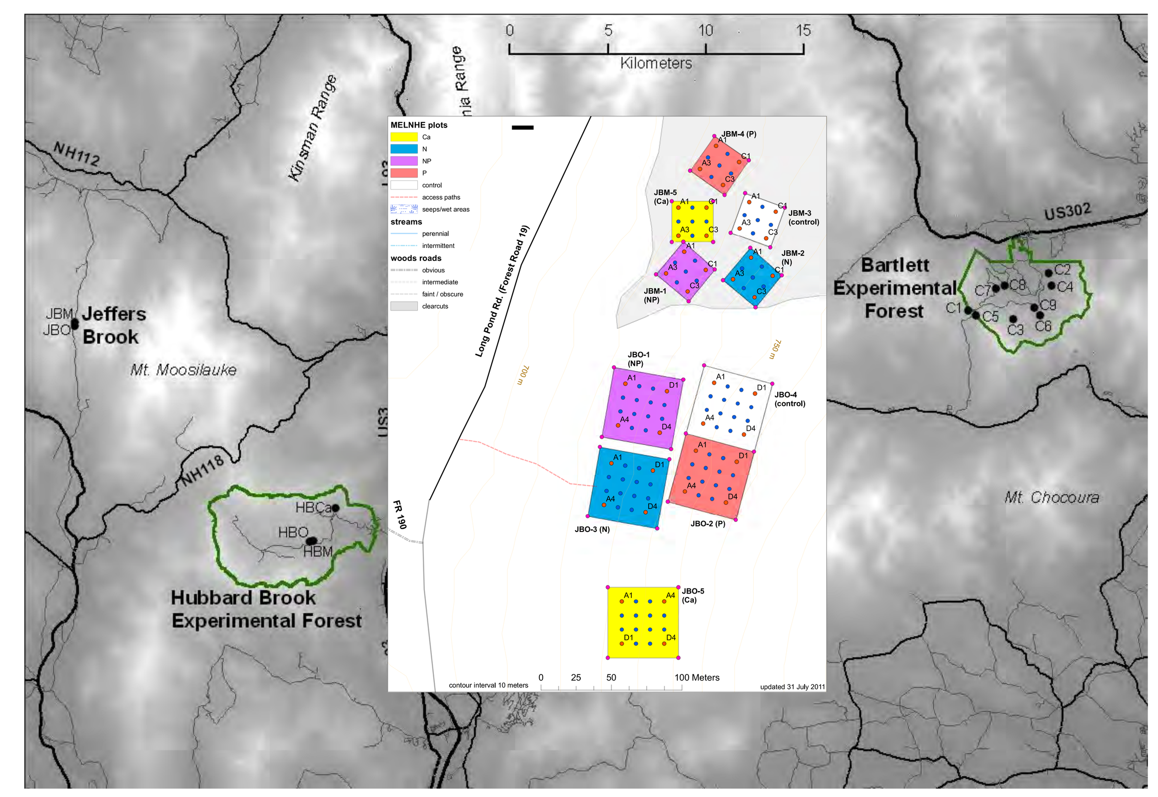


Conceptual model of N vs P limitation in forests, showing factors that cause systems to deviate from co-limitation by N and P and the mechanisms that favor co-limitation by conserving or acquiring the more limiting nutrient.

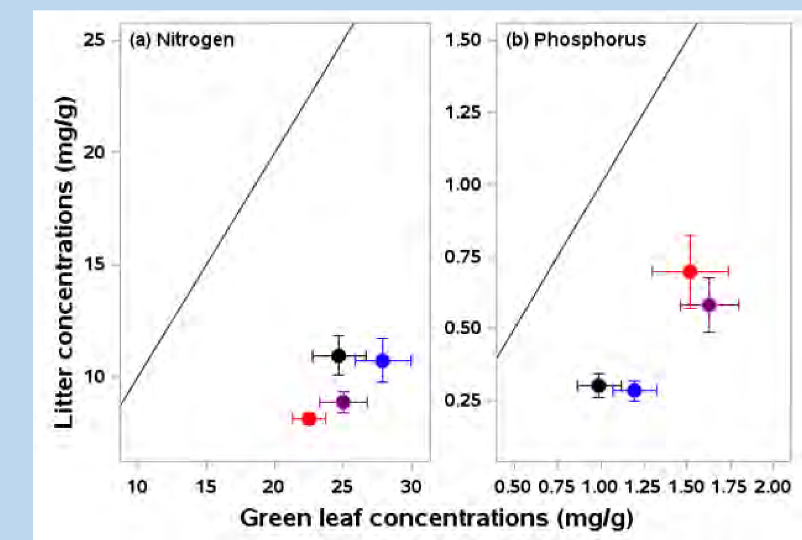
The MELNHE Experiment

Experimental tests of N and P limitation in temperate forest systems are few, and those few have been short- term with very high rates of fertilization. In 2011 we began long-term low-level additions of N, P, and N+P in 13 forest stands distributed across three sites in the White Mountain National Forest of New Hampshire. At Bartlett Experimental Forest (BEF), which is underlain by granite, we have three young, three mid-aged, and three mature stands. At both Hubbard Brook Experimental Forest (HB), on granodiorite, and Jeffers Brook (JB) on amphibolite (metamorphosed basalt), we have one mature and one mid-aged forest stand. Each stand has four plots treated annually with N (30 kg N/ha/yr as NH4NO3), P (10 kg P/ha/yr as NaH2PO4), both N and P, and control. These relatively modest rates are designed to alter site fertility while minimizing artifacts associated with high doses of fertilizer. These treatments allow us to test for NP co-limitation and to challenge balanced forest nutrition and thereby induce mechanisms that maintain co-limitation, such as those represented in the Multiple Element Limitation Model (MEL).

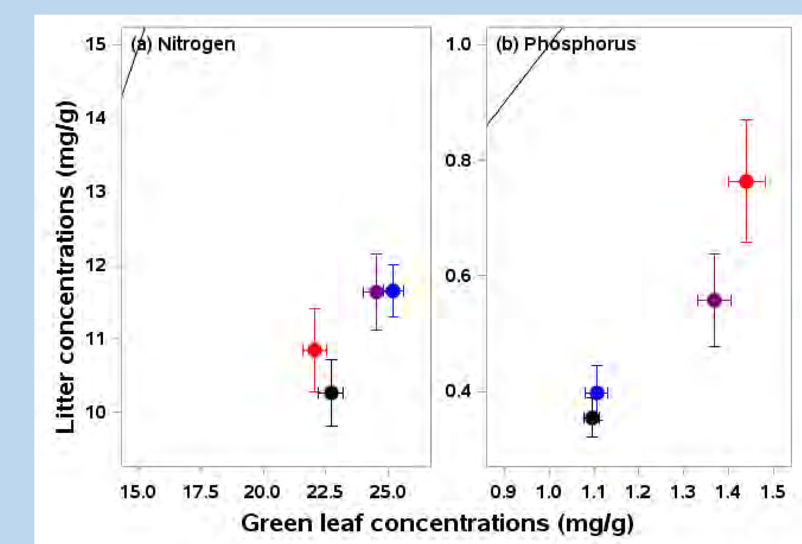
Nutrient Manipulations in Stands of Different Ages in Three Sites



Foliar N and P Resorption

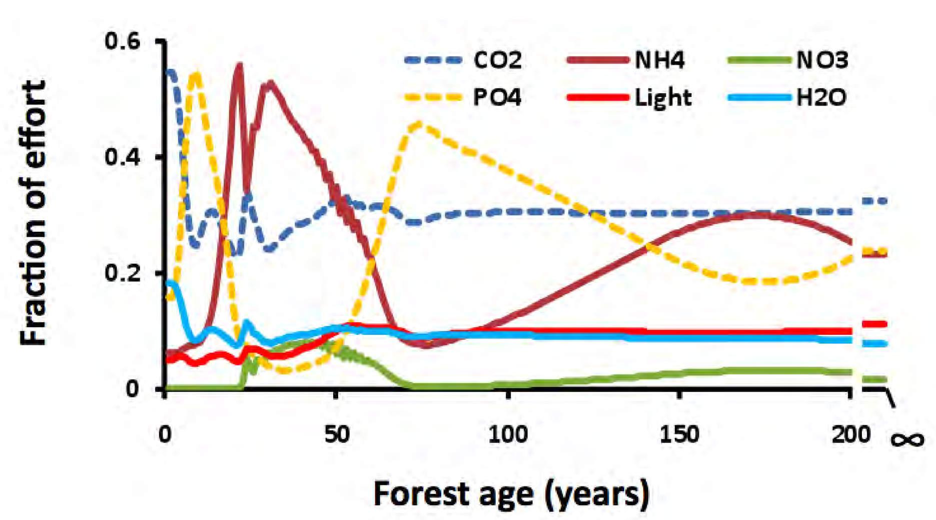


Nutrient resorption from senescing leaves is indicated by the change from green leaf concentrations (shot from the upper canopy in August) and litter concentrations (collected during leaf fall). Departures below the 1:1 line indicate the degree of nutrient resorption. In 2014, in one young stand at Bartlett (C2), P addition increased N resorption and N addition increased N resorption, across all species.

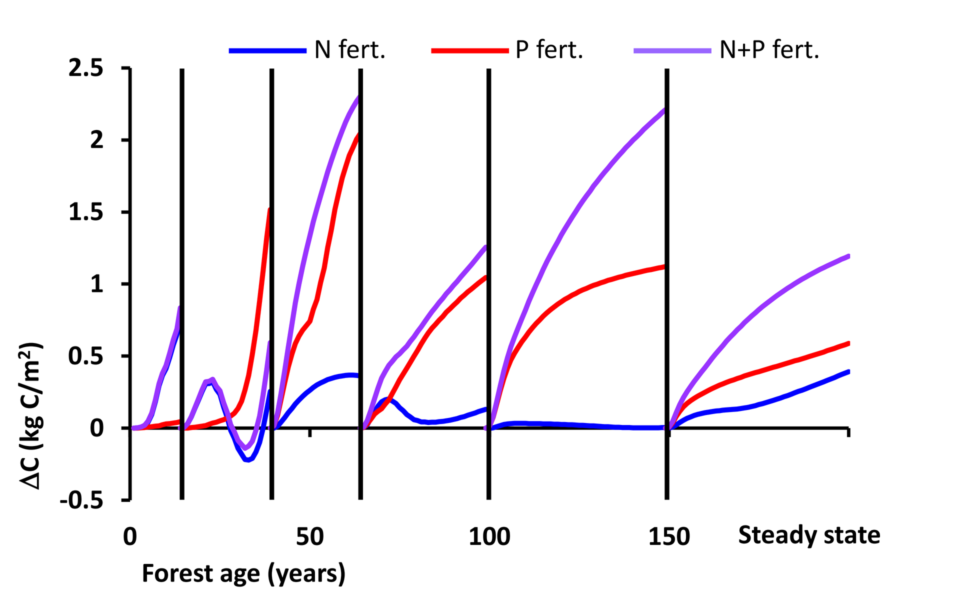


In 2015, in eight additional stands, P resorption was less with P addition and N resorption was less with N addition, but there were not significant interactions with N and P.

MEL simulates effort allocated to acquisition of resources

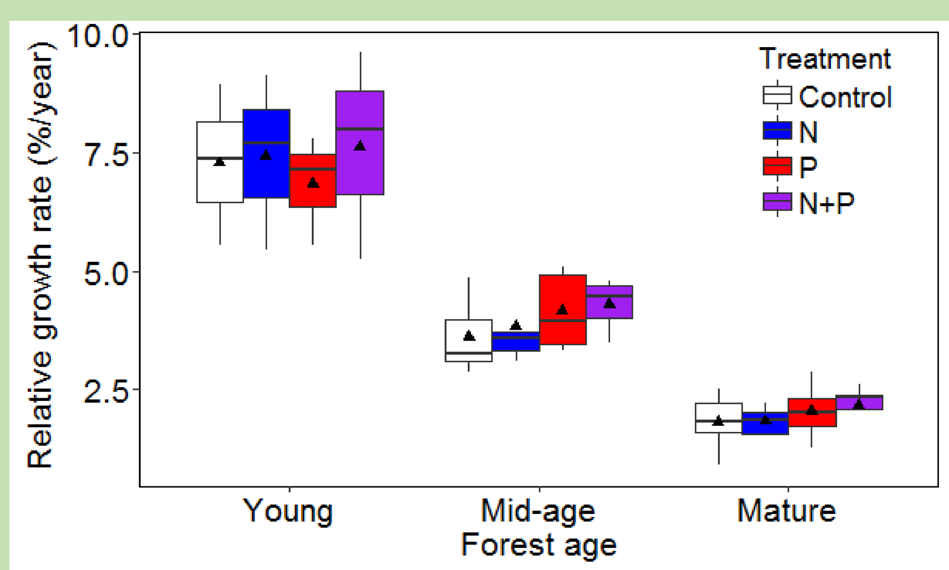


We simulated experimental additions of N (30 kg/ha/yr), P (10 kg/ha/yr) or both at ages 0, 20, 60 and 150 yrs.



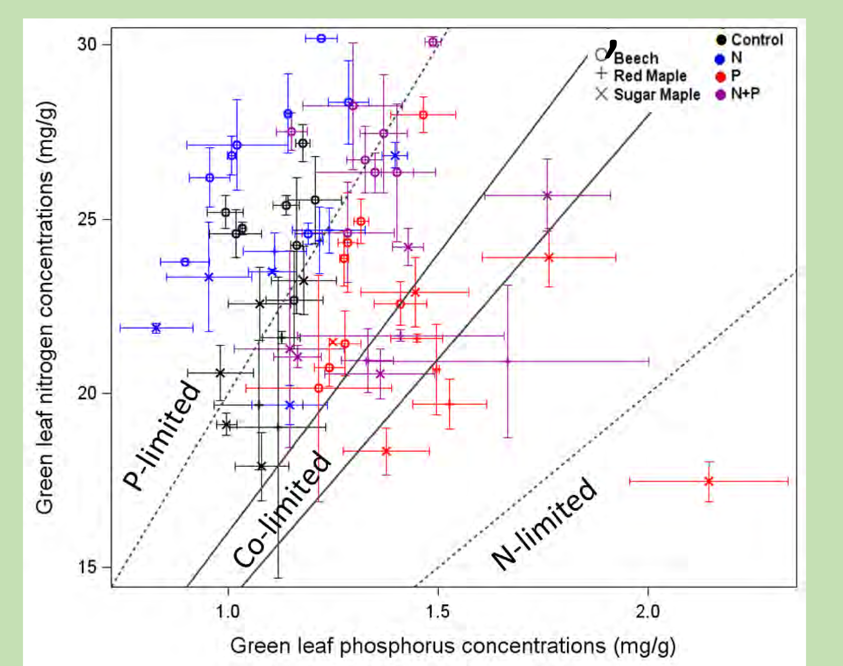
The greatest growth response is to N&P. Limitation shifts from P to N to P and back to N over the course of succession.

Tree Diameter Growth



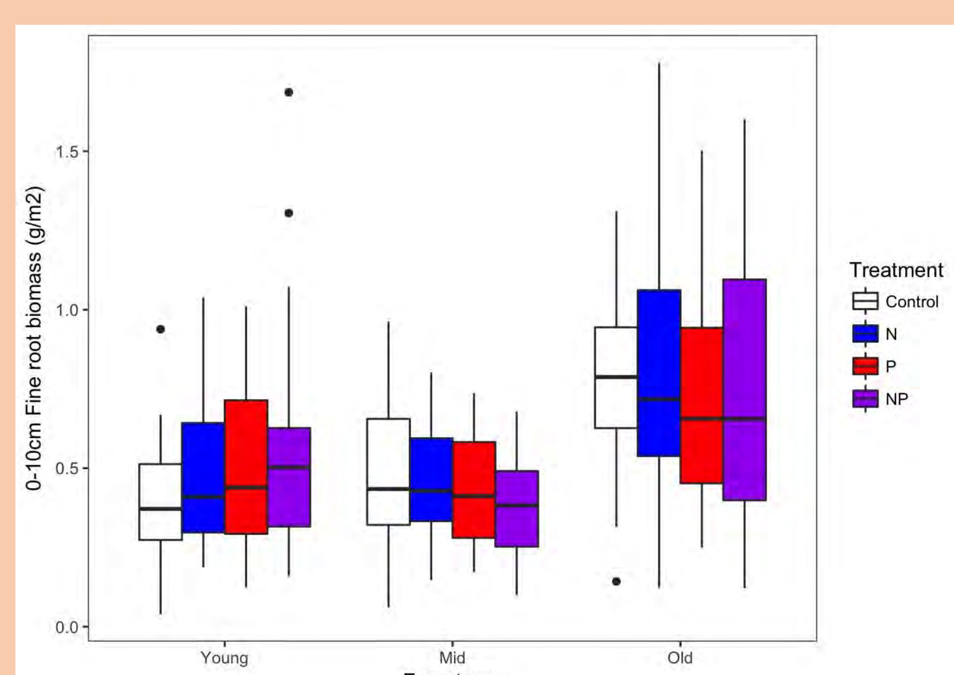
Tree growth (relative basal area increment) from 2011 to 2015 responded significantly to P ($P=0.02$) but not to N ($P=0.73$), there was not a significant N x P interaction. Growth increased by 13% in mid-aged and 15% in mature stands under P addition (P and NP treatments).

Foliar N and P



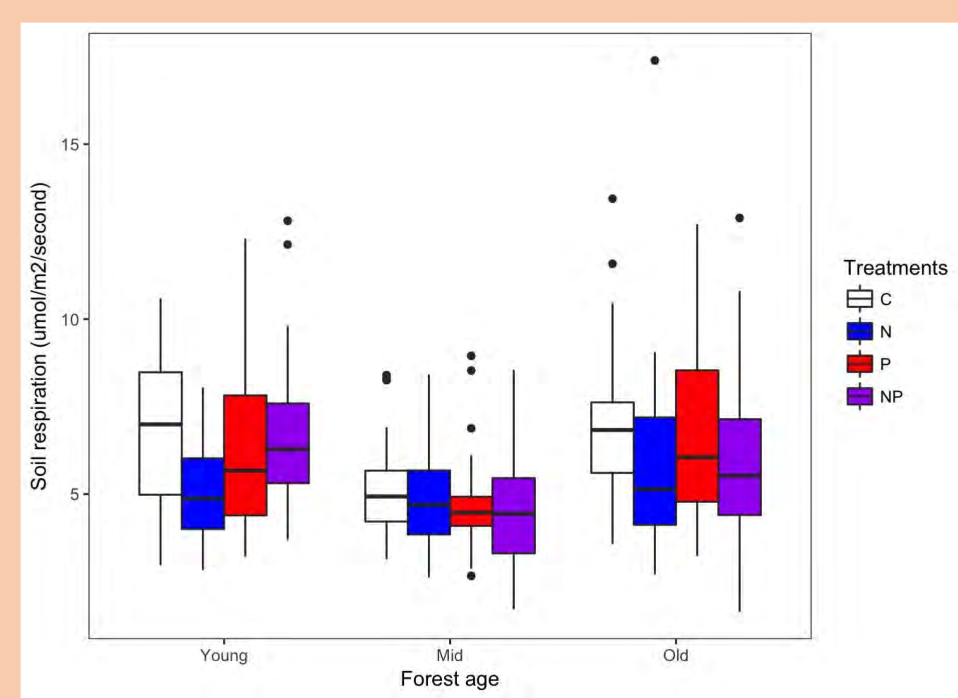
Foliar P and N in 2015 for maple and beech in mid-aged and mature stands. N:P ratios between 14 and 16 are considered to indicate co-limitation (Güsewell 2004). Those below 10 and above 20 indicate N and P co-limitation, respectively (Koerselman and Meuleman 1996).

Fine Root Biomass



There was no significant effect of treatment on fine root biomass by 2015-2016, although we expected to see reduced allocation to root growth under P addition, corresponding to greater carbon allocation aboveground (see figure above). N ($p=0.59$); P ($p=0.91$); NxP ($p=0.72$). Older stands have greater fine root biomass than younger stands ($p=0.03$).

Soil Respiration



Soil respiration in 2016 was significantly reduced by N addition ($p = 0.02$). There was no effect of P ($p=0.50$) and the interaction of NxP was also not significant ($p=0.30$). We did not expect belowground carbon allocation by roots to be reduced by N addition, but this result is consistent with a depression of decomposition rates.

Summary

Foliar N:P in the untreated mid-age and mature stands indicate that most of our sites are P-limited rather than N- limited. Consistent with P limitation, plots receiving P moved into the co-limited range, and those receiving N were even more P limited after 5 years of treatment, according to their foliar N:P ratios. Tree growth responded more to P addition than to N addition in mid-aged and mature stands ($P=0.02$). These results are surprising because temperate forests on glaciated soils have been presumed to be N limited, but they are consistent with predictions of the MEL model, parameterized for our experimental conditions. Given the evidence for P limitation to aboveground growth, we expected to find reduced root biomass under P addition. Instead, we found that roots increased in response to NP in the two young stands. Roots marginally decreased in response to P in the old stands. Perhaps root turnover was reduced by P addition, consistent with reduced microsite depletion; greater root biomass need not reflect greater investment belowground. A better understanding of the capacity of ecosystems to balance the acquisition of limiting resources is needed to manage ecosystems in the face of continuing environmental change.

Bibliography

Kang, H., T.J. Fahey, K. Bae, M.C. Fisk, R.E. Sherman, R.D. Yanai, and C.R. See. 2016. Response of forest soil respiration to nutrient addition depends on site fertility. *Biogeochemistry* 127:113–124.
Bae, K., T.J. Fahey, R.D. Yanai, and M.C. Fisk. 2015. Soil nitrogen availability affects belowground carbon allocation and soil respiration in northern hardwood forests of New Hampshire. *Ecosystems* 18(7):1179–1191.
See, C.R., R.D. Yanai, M.C. Fisk, M.A. Vadeboncoeur, B.A. Quintero, and T.J. Fahey. 2015. Soil nitrogen affects phosphorus recycling: foliar resorption and plant–soil feedbacks in a northern hardwood forest. *Ecology* 96:2488–2498.
Fisk, M.C., T.J. Ratliff, S. Goswami, and R.D. Yanai. 2014. Synergistic soil response to nitrogen plus phosphorus fertilization in hardwood forests. *Biogeochemistry* 118: 195–204.
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. *Ecol. Appl.* 23: 621–642.

Join us if you want to work with MELNHE!

www.esf.edu/melnhe/ rdyanai@syr.edu 315-345-7412