FOLIAR NUTRIENT RESORPTION IN A NORTHERN HARDWOOD FOREST

by

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Abstract

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Previous studies have attempted to link the foliar resorption of P to soil P availability with mixed results. Based on resource optimization theory, we propose that in an N and P co-limited system, foliar resorption of P may be linked to N availability. Here we compare the community-level foliar chemistry of six hardwood tree species to soil chemistry across 18 plots in Bartlett Experimental Forest, New Hampshire. Estimates of soil N content in the rooting zone were strongly correlated with estimates of P resorption efficiency in four of the six tree species sampled. Plot-level averages of P resorption efficiency, with species weighted by their contribution to litter mass, were even more stongly correlated (P<0.01). If N availability drives biological P conservation, it could provide a crucial mechanism for the coupled cycling of N and P in forest ecosystems.

Key Words: northern hardwood forests, resorption, retranslocation, co-limitation, resource optimization, N cycling, P cycling, coupled cycles,

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1: Introduction

History

Since the early 20th century, researchers have been studying the seasonal variability of plant tissue nutrient concentrations. In 1926, French scientist R. Combes published two essays showing that in *Quercus* and *Fagus* species, decreases in foliar N at the time of senescence corresponded to a similar increase in stem and root N content (Combes 1926, Ryan 1979). It wasn't until the 1960s, however, that Taylor and May showed experimentally that the N from leaves was indeed being moved to roots. They observed that peach (*Prunus persica*) root N concentrations increased after senescence, and since each tree was transplanted mid-growing season into an N-free medium, this change could not be attributed to N uptake (Taylor and May 1967). Since then, a number of studies have explored the physiological and biochemical mechanism of resorption, and even more have focused on its ecological implications.

Foliar nutrient resorption can be defined as the movement of nutrients out of leaf tissue into other tissues during senescence. This phenomenon has also been called foliar translocation (Tilton 1977, Hill 1980), retranslocation (Chapin and Kedrowski 1983), or reabsorbtion (Lajtha 1987). Resorption is nearly ubiquitous among perennial plants, regardless of form or life history. Because senescent leaf tissue constitutes the largest annual nutrient loss in most plants, the process of resorption is one of the most important nutrient conservation mechanisms at both the organismic and ecosystem levels (Ryan and Borman 1982).

Physiology of Nitrogen and Phosphorus resorption

Biochemically, resorption begins with the catabolism of macromolecules, followed by the conversion of the catabolites to a transportable form, and finally the transport of nutrients out of

cells via phloem (Mae 2004). A large portion of the nutrients conserved through resorption originate in the chloroplasts, which are estimated to contain upwards of 80% of total leaf N (Mae et al. 1993). Research on the degradation of chloroplasts has therefore become a topic of focus for physiologists interested in senescence and leaf nitrogen economics. Many of these studies have been conducted using agricultural crops (see review by Hortensteiner and Matile 2004).

Up to 90% of the N resorbed annually is thought to originate from chloroplast proteins (Morita 1980). Chloroplast DNA is one of the first molecules to disappear from the leaf as the plastid begins to degrade (Inada et al 1998). This is followed by the degradation of chloroplast proteins, of which RuBisCO is by far the most plentiful protein degraded (Gepstein 1988), and has been shown to contribute 40% of resorbed nitrogen in rice plants (Makino et al. 1984). In the thylakoid membrane, the pigment-protein complexes associated with chlorophyll are broken down after chlorophyll catabolism has occurred (Matile 1992). Following the catabolism of macromolecules within the leaves, transport of the nutrients into stem and root tissues occurs primarily via the phloem (Bollard 1960).

Chapin and Kedrowski (1983) estimated that the hydrolysis of proteins into amino acids accounted 82-91% of total nitrogen resorbed in their study. While most N is thought to overwinter as amino acids and proteins, the specific type of storage proteins and location within the plant varies by species. Numerous studies have investigated the storage form and location of N using ¹⁵N tracers (see review by Millard and Grelet 2010). Unfortunately, due to a lack of stable P isotopes less is known about the transport and storage of phosphorus.

In a study of boreal tree species in Alaska, Chapin and Kedrowski (1983) attributed 40-47% of resorbed P to the breakdown of DNA and RNA, and 26-38% to hydrolyzed phospholipids. The study found an increase in winter stem concentrations of phospholipids,

nonhydrolyzable P esters, and nucleic acids, suggesting that these are the chemical forms in which P is stored. This seasonal increase in stem tissue phospholipid concentration had been previously documented (Chapin et al. 1982), and is thought to not only function as a storage mechanism, but also to help prevent frost damage in many trees.

Resorption as an Ecosystem Process

Resorption is important as a conservation mechanism in not just individuals, but as an ecosystem-level process. Nutrients resorbed by perennial plants are not returned to the forest floor in the fall, and therefore are not at risk of being lost from the system. Ryan and Bormann (1982) estimated that in a 5 year old stand at the Hubbard Brook Experimental Forest, 35.6 kg/ha/yr of N and 2.6 kg/ha/yr of P were resorbed annually. This equates to 57.4% of biological nitrogen uptake and 40.6% of biological phosphorus uptake. Nutrient resorption also affects the carbon cycle by controlling substrate quality for decomposition (Vitousek 1984).

Due to its importance as an ecosystem process, nitrogen resorption is included in most ecosystem models, either explicitly as a variable, or implicitly through litterfall nutrient concentrations. Out of 21 models reviewed by Vergutz et al (2012), however, P resorption was only represented in one (Wang et al 2007). This omission is due in large part to the fact that most ecosystem models still do not include P, although this is rapidly changing as questions are being raised about the coupling of C, N, and P cycles (Goll et al. 2012, Rastetter et al. 2013). The desire to model P cycling (and resorption) in ecosystems will likely increase as global N inputs continue to increase and phosphorus becomes increasingly limiting (Elser 2011, Elser and Bennett 2011).

Factors Affecting Resorption Efficiency

Many environmental factors have been shown to affect resorption efficiencies. Nutrients move out of the leaves until abscission, and physical removal of leaves before the plant drops them naturally leads to incomplete resorption. In one experiment, Chapin and Moilanen (1991) glued leaves to the stems of birch, and found that extending the time leaves stay attached past when they would have abscised naturally did not lead to increased resorption efficiency. Senescence occurs gradually over the course of weeks, and early leaf fall due to external events can cause incomplete resorption, evidenced by higher nutrient concentrations in litterfall. This has been most commonly seen in cases of early frost (Wang et al 2010). Resorption efficiency of both N and P have been shown to decline during drought (Minoletti and Boerner 1993, Marchin et al 2010). Light availability also plays a role. When leaves are shaded during senescence they have lower resorption efficiencies of N and P (Chapin and Moilanen 1991). This suggests that the energetic cost is high enough that plants require energy obtained through photosynthesis during senescence for the maximum potential resorption of these nutrients.

Over the past 30 years, there have been over a hundred published studies comparing resorption to various estimates of site nutrient status. Most of these studies have used nutrient manipulations or naturally occurring gradients to address the hypothesis that plants will resorb more of a nutrient when it is in low supply. There is now plenty of evidence supporting this hypothesis on a global scale, but many individual studies have shown no correlation. Both Aerts (1996) and Killingbeck (1996) published summaries of these field experiments. These reviews established a few global trends: evergreen shrubs and trees have lower resorption efficiencies for N than deciduous ones (Aerts 1996), leaf nutrient status rarely correlates with resorption efficiencies (Aerts 1996), nitrogen fixing plants resorb less nitrogen (Killingbeck 1996).

Since these reviews were published, the number of resorption measurements from individual studies around the world has continued to grow. More recently a number of papers have been produced that combine estimates from these studies to analyze resorption efficiency trends on a global level. Two review papers have now shown that globally, higher fresh foliar concentrations lead to lower resorption efficiencies (Kobe et al. 2005, Vergutz et al. 2012). Another analysis showed that N resorption increases with latitude, but decreases with mean annual precipitation and temperature (Yuan and Chen 2008). This same study found the opposite to be true of P resorption efficiency, which decreases with latitude, an increases with temperature and precipitation. Reed et al. (2012) demonstrated this same global trend by using the ratio of N resorption to P resorption to climate and latitude. Reed (2012) suggested that the N:P resorption ratio could be a new tool to estimate the relative N and P limitations of a site, and demonstrated this in a tropical forest. Since then, the use of N:P resorption ratios was also shown to correlate with levels of N addition in a grassland system (Lu et al 2013).

Nutrient Co-limitation

In 1839, Carl Sprengel posited that productivity in agricultural systems is solely limited by the nutrient in shortest supply (Sprengel 1839). This was soon popularized by Justus von Leibig in 1842, and became known as Leibig's law of the minimum (von Leibig 1842)--. This single-element model of nutrient limitation was extended to non-agricultural ecosystems as the field of ecology developed in the twentieth century.

Using a chronosequence in New Zealand, Walker and Syers (1976) developed the first coherent model addressing how ecosystem-level nutrient limitation changes as soils age. As the ultimate source of ecosystem nitrogen is atmospheric, N was predicted to accumulate over time, while bedrock-derived P would tend to deplete and become chemically unavailable over time.

Therefore, younger soils will tend to be nitrogen limited, while older soils will be phosphorus limited. Evidence for this theory has mounted over the years (see special issue of Plant and Soil edited by Turner and Condron, 2013).

A classic demonstration of Walker and Syers' model was the Hawaiian chronosequence where Crews et al. (1995) showed a shift from N limitation to P limitation with age through changes in both soil and foliar nutrient concentrations. The model may not hold as well in more xeric systems. While total P declined with increasing soil age in a Jordana desert chronosequence spanning over 20,000 years, there was no relationship between soil age and available P measured via resin bags, or with plant tissue P concentrations (Lajtha and Schlessinger 1988).

While the Walker and Syers model of pedogenesis is still widely accepted, global metaanalyses have recently shown that most terrestrial systems are not solely limited by N or P, but rather co-limited by both (Elser et al. 2007). As the name implies, co-limitation requires that two or more nutrients are simultaneously limiting, although they can be limiting to different degrees. This idea of simultaneous limitation is what sets co-limitation theory apart from traditional concepts of nutrient limitation.

Strictly speaking, Leibig's law of the minimum allows for two elements to be in nearly equal demand, such that a small addition of one creates limitation by the other (see Davidson and Howarth 2007), but this scenario still rests upon the notion that only one element is truly limiting at any given time. If one element at a time were completely limiting, a treatment response could only be seen to one element at a time. Even if the second limiting element was in nearly equal demand, no growth response would be expected. In a paper on the nature of co-limitation, Harpole et al. (2011) made an important distinction between independent and simultaneous

limitation. They define simultaneous limitation as a special case of Leibig's law in which two or more elements are required together such that they could be considered a single resource. In this case, a growth response would not be expected from the addition of either element alone. In the case of independent co-limitation, one would expect to observe a growth response when either nutrient is added.

Full factorial N and P additions often show treatment responses to additions of either N or P, and a much larger synergistic response when both are added (Elser et al. 2007, Vadeboncoeur 2010). This response can be explained at the organismal level through resource optimization theory, which predicts that plants will alter their morphology and physiology to ensure that all resources are equally limiting (Bloom et al 1985, Chapin et al. 1987, Gleeson and Tilman 1992).

Plants have many strategies for optimizing their nutritional needs, such as allocating carbon towards root growth or mycorrhizal associations (Tilman 1990, Fransson and Johansson 2010). Species can not only optimize nutrient uptake, but also increase their nutrient use efficiency (Vitousek 1982, Pastor and Bridgham 1999). Finally, plants can minimize nutrient losses through conservation mechanisms. Because many of these optimization methods are used to obtain multiple elements at once (rooting, mycorrhizal associations) or involve internal tradeoffs (allocating nitrogen for phosphatase), it can be difficult to make inferences about a site's nutrient limitations without nutrient manipulation experiments (Gleeson and Tilman 1992).

The most commonly used indicator of the relative N and P limitations of a site are biomass N:P ratios, commonly expressed as the ratio of concentrations on a per unit mass basis (Koerselman and Mueleman 1996). While meta-analyses from fertilization experiments around the world have shown that the community-level N:P ratio reflects community-level nutrient

limitations, the optimal ratio varies by system (Koerselman and Mueleman 1996, Gusewell 2004). There are also interspecific differences in N:P ratios, which may reflect the relative importance of N and P to the nutrition of the species (Weand et al 2010).

Evidence from a recent study suggests that while N:P ratios are a good estimator of nutrient availability, they do not necessarily reflect the nutrient limitations for a given species (Sorrell et al. 2011). Another paper found no shift in foliar N:P ratios across a regional N deposition gradient in the northeastern United States (Crowley et al 2012). Instead of foliar N:P ratios, Sorrell et al. (2011) recommend using estimates of plant conservation (such as resorption) to estimate nutrient limitation.

Soil nitrogen drives phosphorus resorption in a co-limited system:

evidence from a northern hardwood forest.

Abstract

Previous studies have attempted to link the foliar resorption of P to soil P availability with mixed results. Based on resource optimization theory, we propose that in an N and P co-limited system, foliar resorption of P may be linked to N availability. Here we compare the foliar chemistry of six hardwood tree species to soil chemistry across 18 plots in Bartlett Experimental Forest, New Hampshire. Estimates of soil N content in the rooting zone were correlated with estimates of P resorption efficiency in four of the six tree species sampled. Community-level averages of P resorption efficiency, with species weighted by their contribution to litter mass, were even more strongly correlated (P<0.01). Previous research into the coupled cycling of N and P has focused primarily on N availability as a driver of P uptake in soils. Evidence that soil N availability is driving P resorption provides another mechanism for plants to maintain their stoichiometric balance of these elements, and provides further evidence that N availability drives P conservation at the ecosystem level.

Introduction

Over the last century, humans have more than doubled the amount of reactive nitrogen in the biosphere. A major question in ecology is how ecosystems will respond to the increasing biological demand for P as N availability increases (Vitousek et al 2010, Marklein and Houlton 2011, Cleveland et al. 2013). Resource optimization theory predicts that organisms will invest their internal resource supplies to reflect environmental availability of multiple limiting resources (Bloom et al. 1985). In the case of limiting nutrients such as N and P, this means organisms will allocate their stores of internal nutrients and energy towards maintaining

stoichiometric balance (Rastetter et al. 2013). To date however, many of the biological mechanisms for P conservation in response to changes in the environmental availability of N:P remain unclear.

Nutrient resorption, defined as the withdrawal of nutrients from leaves to other plant tissues prior to abscission (Killingbeck 1986), is the largest nutrient conservation mechanism in perennial plants. Resorption is most commonly reported as resorption efficiency, which is the percentage of the difference between litterfall concentration and the concentration in green leaves. Resorption efficiencies vary between species and within populations. This variation has been the subject of many ecological studies around the world (see datasets compiled by Kobe et al. 2005, Vergutz et al. 2012).

Due to its importance as a conservation mechanism, many researchers have compared N and P resorption with measures of nutrient limitation such as site nutrient availability or leaf nutrient status, often returning conflicting results. The simplest hypothesis is that the resorption of an element should increase as the element's environmental availability decreases. Across a global gradient, P resorption is higher in regions with older, more weathered soils (Richardson et al. 2008), but the relationship between resorption and soil nutrients in more localized studies has not been as clear. While studies at some sites have shown the expected inverse correlation between nutrient resorption efficiency and soil availability, many more have found no relationship, and some have even reported increases in resorption efficiency with increasing availability (see review by Aerts 1996).

The relationship between leaf nutrient status and resorption is as variable as the relationship between soil nutrient availability and resorption. It was recently demonstrated that globally, leaves with high concentration of a nutrient have lower resorption efficiencies for that nutrient

(Kobe et al. 2005, Vergutz et al. 2012), however this trend is often not seen within individual systems (see review by Aerts, 1996). This implies that at more localized scales, the relationship between resorption and the nutrient status of leaves or soils may be too complex to be explained with a single element model.

We hypothesized that in an N and P co-limited system, the resorption of N or P could be driven by the availability of both N and P. Fertilization studies of northern hardwood forests suggest that their productivity is co-limited by both nitrogen and phosphorus (Vadeboncoeur 2010). We tested our hypothesis by comparing the N and P resorption efficiencies in a northern hardwood forest to the foliar N:P ratio of fresh leaves, and to estimates of soil N and P content obtained from quantitative soil pits.

Methods

Site description

This study took place in the Bartlett Experimental Forest in the White Mountains of New Hampshire. Soils are well drained Spodosols underlain by granitic bedrock, and have been previously described (Park et al. 2007, Vadeboncoeur et al. 2012). Like most of the surrounding region, these sites have a history of logging and stands are even-aged. Here we present data from 18 previously established plots from six stands, ranging in age from 21-126 years at the time trees were sampled (table 1).

Within each stand, three 30 x 30m plots were established. Dominant tree species in the younger stands included American beech (*Fagus grandifolia*), white birch (*Betula papyrifera*), red maple (*Acer rubrum*) and pin cherry (*Prunus pensylvanica*). Older stands were dominated by American beech, sugar maple (*Acer saccharum*), and yellow birch (*Betula alleganiensis*). Mid-

aged stands included a mixture of all species, along with bigtooth aspen (*Populus grandidentata*).

Soil nitrogen and phosphorus

Each sampling plot contained 0.71x0.71m quantitative soil pits excavated in 2004 (Vadeboncoeur et al. 2012). From these pits, all material was excavated from the Oa horizon, then to increments of 0-10cm and 10-30cm in the mineral soil. Each depth increment was weighed in the field. The Oa horizon was dried and sieved to 6 mm in the laboratory. Mineral soils were sieved to 12 mm in the field, then air dried and further sieved to 2mm in the laboratory. Homogenized subsamples from each depth were then analyzed for nutrient concentrations.

Four distinct soil P fractions were determined using a series of sequential extractions modified from the procedure outlined by Nezat et al. (2007). Soluble and exchangeable P was extracted for 24 hours in 1M NH₄Cl, followed by a 24 hour extraction in 30% H₂O₂ to oxidize organic P, then a 24 hour 1M HNO₃ extraction for apatite-bound P in contact with the solution. Apatite is the primary source of P from mineral weathering in this system. Finally, samples were digested in concentrated HNO₃ at 150° C for 3 hours to estimate the amount of apatite P in silicate minerals. The P concentration of each extract was determined using inductively coupled plasma optical emission spectroscopy (ICP–OES, PE-3300DV, PerkinElmer, Norwalk, CT). Total soil nitrogen concentration was determined using a carbon-nitrogen elemental analyzer (CE Instruments Model NC2100).

For each pit, nutrient content was calculated for each depth increment by multiplying dry soil mass by nutrient concentration. Pit content for total N and all four P fractions was then calculated by summing the Oa, 0-10cm, and 10-30cm contents. Total P content was estimated as

the sum of all four P fraction contents, although our leaching procedure was unable to access apatite inclusions in more refractory silicate minerals. We chose to report total content across depths to avoid issues of autocorrelation, because multiple depths in the same pit are not statistically independent of each other, and because all three depths are within the rooting zone in these stands (Park et al. 2007).

Foliar nutrient sampling

Fresh leaves were collected in the first week of August 2009 and 2010. Up to five trees of the dominant species in each plot were sampled using a pole pruners or shotgun, depending on tree height. Between 20-30 leaves were collected from sun-exposed areas of the mid-canopy of each tree. All leaves belonging to the same individual were combined and analyzed for nutrient concentrations.

Freshly fallen litter was collected from all plots in autumn 2009 and 2010 for nutrient analysis. Net traps were hung at three locations within each plot to catch falling litter. Senesced leaves were collected between rain events to minimize leaching. Litter from each species in each trap was analyzed for nutrient concentrations.

To obtain foliar P concentrations, 0.25g of sample was oven dried at 60°C, ashed in a muffle furnace at 470°C, and digested in 6N HNO₃ before analysis with ICP-OES (PE-3300DV, PerkinElmer, Norwalk, CT). Foliar N concentrations were determined using a carbon nitrogen elemental analyzer (Thermo Electron Corporation, EA1112 elemental analyzer).

Litterfall mass sampling

In each plots, five baskets with a collection area of 0.234m² were used to estimate the relative species contribution to litterfall mass. Each 30mx30m square plot was divided into nine 10mx10m square subplots, with baskets in each of the four corner subplots, and one in the

center. Litter baskets were emptied November 3-5, 2009, and contents were sorted to species. Species masses for each basket were recorded after oven drying at 60°C.

Data analysis

We used plot as our experimental unit in all analyses, because soil pits were not replicated with each plot. We averaged all trap concentrations to calculate a single nutrient concentration for each species. Plot-level fresh foliar nutrient concentrations were calculated for each species by taking the average of all individuals within a plot. Resorption efficiencies were calculated on a dry mass basis as the percent difference between fresh foliage and senesced litter nutrient concentrations. For each species, resorption efficiencies were calculated as the average of efficiencies measured in 2009 and 2010.

To aggregate species, we calculated plot-level resorption efficiency, weighting the resorption efficiency of each species by the percentage of mass that species contributed to the total litter basket mass. When weighting resorption efficiencies, we excluded the litterfall masses of poorly represented species in our plots, so that the sum of the study species totaled 100%. Plot level estimates of foliar N:P ratios were also weighted in a similar manner.

To control for the potential influence of stand, all plot-level comparisons were calculated using a general linear model treating stand as a random effect using Proc GLM in SAS statistical software (SAS Institute Inc. Cary, NC).

Results

Soil N content was positively correlated with P resorption efficiency in four of the six species we sampled, supporting our hypothesis of multiple element interactions (Fig. 1d). The correlation was significant in sugar maple, American beech, yellow birch and white birch. There was no detectable correlation between soil P content and N resorption efficiency (Fig. 1a). Across all plots resorption efficiencies did not vary significantly between species, with the exception of pin cherry, which had lower resorption efficiency (p<0.001) and higher litter concentrations (p<0.001) than the other five species.

The results for individual species also showed some evidence supporting the single element hypothesis for nitrogen resorption. There was a marginally significant decline in nitrogen resorption for sugar maple and yellow birch with increasing soil N content (p<0.1)(Fig. 1b). We did not see this trend when comparing soil pit P to P resorption for any species (Fig. 1c). In fact, American beech showed a marginally significant (p<0.1) positive correlation between P resorption and soil P.

When species-level resorption estimates were weighted by litterfall mass to yield communitylevel resorption efficiencies for each plot, the correlation between P resorption and soil N was stronger than it was for any individual species (Table 2). When this comparison was made at the stand level by averaging the three plots within each stand, the relationship was even stronger (Fig. 2). At the plot level, P resorption was also positively correlated with soil carbon content, and the soil content of labile P (Table 2). The relationship between P resorption and these other variables was not as strong, however and may reflect relationships between soil organic matter and N (R = 0.9, p<0.001) and soil organic matter and available P (R=0.64, p<0.01).

Our analysis returned no relationship between community-level N resorption and any of the soil nutrient pools estimated (Table 2). The range in P resorption efficiencies (37-80%) was also much larger that the range in N resorption efficiencies (47-65%) suggesting that P resorption is a more plastic trait among the trees in this system.

Foliar N:P in our plots reflected the total N:P content of the soil pits, demonstrating that this plant-soil stoichiometric relationship is detectable within the Bartlett Experimental Forest (Fig.

3). While the resorption patterns we observed appeared to be driven primarily by soil N, foliar N:P ratios were significantly correlated with both soil N and many of the P fractions. Interestingly, foliar N:P was more strongly correlated with the refractory P fractions than with the overall ratio of soil N:P content (Table 2).

The amount of N resorbed relative to P also varied significantly with soil N content. Higher nitrogen plots resorbed proportionately less nitrogen than phosphorus (Table 2). The trees that had the lowest N:P concentrations during the summer resorbed proportionately more nitrogen than phosphorus in the fall (R = 0.5, p<0.01; Fig. 4). This relationship was strongly driven by one plot in particular, C8 plot 3, which had the lowest soil N content of any of the plots measured.

Discussion

The strong correlation between P resorption and soil N content in the rooting zone suggests that N availability plays a role in regulating this process. This is supported by recent evidence from a grassland, where some species responded to N additions with increasing P resorption efficiency (Lu and Han 2010). Multiple element regulation of P resorption may help to explain the positive correlation seen between P resorption and available phosphorus, which is counterintuitive from a single-resource conservation standpoint, but has been shown in other studies as well (ie. Boerner 1986, Chapin and Shaver 1989, Sabate et al. 1995). Because both N and P pools tend to increase with organic matter, an increase in P resorption due to soil N availability would also result in a correlation between P resorption and labile P supply.

A possible mechanism for the regulation of P resorption by soil N could be production of the nitrogen-rich enzymes required for resorbing P. For example the phospholipases required for the breakdown of the phospholipid bilayer of leaf cells, and have been shown to increase in

concentration during the onset of senescence (Brady 1973). Phospholipids are a major form of overwinter P storage in trees (Chapin and Kedrowski 1983), which unlike nucleic acids (another form of overwinter storage), do not contain N. If we assume some degree of plasticity in the production of these enzymes, resource optimization theory would predict that C and N allocation towards phospholipases and other enzymes involved in P resorption would reflect the relative physiological demand for N and P.

Under conditions where both elements are in similar demand, it would be essential that mechanisms be in place to regulate N and P stoichiometry. The theory that N availability is driving P resorption provides a mechanism, and offers insight into why P resorption was so much more variable than N resorption in our stands. Indeed, P resorption efficiency decreased as the stoichiometric balance of foliar N:P in leaves approached N limitation (Table 2). This can best be seen by comparing the ratio of N resorption to P resorption as it relates to fresh foliar N:P (Fig. 4). Here, the two plots with the lowest fresh foliar N:P ratios are resorbing proportionately more N than P. Foliar N:P ratios greater than 16 are an often cited threshold for P limitation (Koerselman and Meuleman 1996). This threshold corresponds remarkably well to a shift in our plots towards higher N resorption relative to P resorption.

The only plot with foliar N:P ratios below 14, generally thought of as the threshold for N limitation, has a ratio of N:P resorption that is almost twice the mean of the other plots (Fig. 4). This was due to a decrease in P resorption efficiency, which in this plot was more than 2 standard deviations lower than the mean, while N resorption remained relatively constant. Repeated diameter measurements show that between 2004 and 2011, this plot had the highest growth rate of any of our 18 plots (S. Goswami, *personal communication*), which combined with the higher foliar N:P ratios in the other plots suggests at least some degree of P limitation across

most of this landscape. This is consistent with a study in the Catskills (NY) that found high N:P ratios in understory vegetation determined to be primarily P limited after nutrient additions (Tessier and Raynal 2003), but contradicts a regional meta-analysis of fertilization experiments which showed the Northeastern US to be primarily N limited (Vadeboncoeur 2010).

The range of N and P availability in our sites was considerably lower than gradient studies that have been conducted elsewhere (Chapin and Moilenen 1991, Vitousek 1998, Richardson et al. 2008). Many of these gradients exist across soil chronosequences that span millions of years, with sites geographically much farther apart than our plots. That we were able to detect correlations between community-level foliar dynamics and soil chemistry within a single forest points to the importance of fine-scale variability in co-limited systems, as well as the tight stoichiometric balance of nutritional demands in undisturbed forests. Our results may also reflect the importance of reporting nutrient availability in terms of content instead of concentration in rocky soils.

To date, research on ecosystem P conservation in response to increased N availability has focused primarily on soil P acquisition mechanisms such as phosphatase production (Marklein and Houlton 2011). While our results are observational, they suggest that N availability may be directly regulating P resorption in this system. Currently, P resorption is estimated to supply roughly 40% of global plant demand for P (Cleveland et al 2013). In most forests, litterfall is the single largest annual P flux, and therefore a crucial component to ecosystem models (Vergutz et al. 2012, Rastetter et al. 2013). Further research is warranted, since a P resorption response to increasing N availability could provide a key mechanism for the coupled cycling of N and P in many terrestrial systems.

Chapter 3: Summary

Since the industrial revolution humans have more than doubled the amount of bioavailable nitrogen on earth. Nitrogen and phosphorus are tightly cycled in forest ecosystems, and relative biological demand is in close stoichiometric balance. Theory predicts that the communities in these forests will respond to increases in N supply by increasing effort towards the acquisition and conservation of P.

The results presented here suggest that soil N content affects foliar P resorption in a northern hardwood forest. Resorption is a major source of nutrient conservation for perennial plants, and therefore ecosystems. The idea that N availability increases P conservation via resorption provides a mechanism for how plants maintain their N:P stoichiometry. This would have major implications for the coupling of ecosystem N and P cycles, and should potentially be included in ecosystem models.

Our results also demonstrate relationships between soil stoichiometry, leaf stoichiometry, and resorption within a relatively small study area. These differences were seen within a single forest, and sometimes even among plots within a single stand. This points to the close balance between supply and demand for N and P in this system, and raises questions about spatial patterns of nutrient limitation across landscapes. Future research should include nutrient additions to see if experimentally increasing N availability leads to increases in P resorption. Further research should also focus on how much of the plasticity in resorption rates is found within individuals versus within populations, as this could be important to predicting how forests will respond to continuing N deposition.

Figures and Tables

		U					
	Clear-						
Site	cut	Latitude	Longitude	Elevation (m)	Aspect	Slope	Species Composition
		44º 02'					
C1	1990	Ν	71° 19' W	570	SE	5-20%	PC, WB, BE, RM, ASH
		44º 04'				15-	
C2	1988	Ν	71° 16' W	340	NE	30%	BE, RM, PC, WB, YB
		44º 03'				20-	WB, BA, BE, PC, YB,
C4	1978	Ν	71° 16' W	410	NW	25%	RM
		44º 02'				13-	YB, BE, RM, WB, PC,
C6	1975	Ν	71° 16' W	460	NNW	20%	SM
		44º 03'					
C8	1883	Ν	71° 18' W	330	NE	5-35%	BE, SM, YB, RM
		44º 03'				10-	
C9	~1890	Ν	71° 17' W	440	NE	35%	SM, BE, YB

Table 1. List of site characteristics in Barlett Experimental Forest. Species composition is listed in order of decreasing basal area.

Notes: species codes are: PC (Prunus pennsylvanica), RM (Acer rubrum), WB (Betula papyrifera), BE (Fagus grandifolia), YB (Betula alleghaniensis), SM (Acer saccharum), BA (Populopus grandidentata)

	Phosphorus	Nitrogen		
	resorption	resorption	N:P resorption	Foliar
	efficiency	efficiency	efficiency ratio	N:P ratio
Carbon	0.59**	0.22	-0.51*	0.46**
Nitrogen	0.69**	0.22 -0.55**		0.29**
Exchangeable P	0.43*	0.46	-0.18	-0.13
Organic P	0.45*	0.002 -0.42*		0.18
Exchangeable + Organic				
Р	0.50*	0.11	-0.41 *	0.13
Apatite P	0.27	0.006	-0.08	-0.29*
Exchangeable, Organic				
and Apatite P	0.31	0.02	-0.12	-0.27*
Armored P	-0.29	0.015	0.44*	-0.55**
All fractions	0.16	0.02	0.05	-0.41**
Soil N:P (all fractions)	0.18	0.18	-0.22	0.50**

Table 2. Pearson correlation coefficients comparing soil nutrient contents with plot-level resorption and foliar N:P ratios.

Notes: Soil pit contents used in the analysis were estimates of total pit content (g/m^2) from the Oa horizon to 30cm depth in the mineral soil. Foliar chemistry is the plot mean of all species weighted by contribution to plot litterfall mass. P values for significance were determined using a generalized linear model which treats stand as a random effect.* denotes significance at $\alpha < 0.05$, ** denotes significance at $\alpha < 0.01$.



Fig. 1. Scatterplots of the relationship between soil nutrient content and nutrient resorption for six hardwood species. Soil contents were calculated from the Oa horizon to 30cm mineral soil. Phosphorus content is the sum of exchangeable and organic pools. Error bars show the standard error of resorption efficiency across 2 years. Solid lines represent significance at p<0.05, and dashed lines represent significance at p<0.1.



Fig. 2. Soil nitrogen content from the Oa to 30cm depth is strongly correlated with phosphorus resorption efficiency at the stand level ($r^2=0.93$, P<0.01). Error bars represent the standard error across 3 plots.



Fig. 3. The ratio of nitrogen to phosphorus soil content from the Oa to 30cm depth is reflected in the ratio of plot level foliar N:P ratios ($r^2=0.25$, P<0.01). Soil phosphorus content was calculated as the sum of four sequential leaches.



Fig. 4. The ratio of N resorption efficiency to P resorption efficiency is negatively correlated with fresh foliar N:P concentrations ($r^2=0.4$, p<0.01). When the foliar N:P ratio of a plot drops below the commonly cited phosphorus limitation threshold of 16, trees begin to resorb proportionately more nitrogen than phosphorus.

References

- Aerts, R. 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? Journal of Ecology **84**:597-608.
- Bloom, A.J., F.S. Chapin, and H.A. Mooney. 1985. Resource limitation in plants: an economic analogy. Annual Review of Ecology and Systematics. **16**:363-392.
- Bollard, E.G. 1960. Transport in the xylem. Annual Review of Plant Physiology 11:141-166.
- Brady, C.J. 1973. Changes accompanying growth and senescence and effect of physiological stress. Pages 317-351 *in* G.W. Butler and R.W. Bailey, editors. Chemistry and biochemistry of herbage. Volume 2. Academic Press, London, England.
- Chapin, F. S., 111, J. M. Follett, and K. F. O'Connor. 1982. Growth, phosphate absorption and phosphorus chemical fractions in two Chionochloa species from high and low-phosphate soils. Journal of Ecology 70:305-321.
- Chapin, F.S., and R.A. Kedrowski. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumnal retranslocation in evergreen and deciduous taiga trees. Ecology **64**:376-391.
- Chapin, F.S., G.R. Shaver, and R.A. Kedrowski. 1986. Environmental controls over carbon, nitrogen and phosphorus fractions in *Eriophorum vaginatum* in Alaskan tussock tundra. Journal of Ecology **74**:167-195.
- Chapin, F.S., A.J. Bloom, C.B. Field, and R.H. Waring. 1987. Plant responses to multiple environmental factors. BioScience **37**:49-57.
- Chapin, F.S., and L. Moilenan. 1991. Nutritional controls over nitrogen and phosphorus resorption from Alaskan birch leaves. Ecology **72**:709-715.
- Combes, R. 1926. Etude de la migration autumnale des substances azoteez chez le Chene, par l'analyze de plants entieres. Comptes Rendus de l'Académie des Sciences. **182**:984-987.
- Combes, R. 1926. La migration des substances azotees chez la Hetre au cours du jounissement autumnal. Comptes Rendus de l'Académie des Sciences. **182**:1169-1171.
- Crews, T., K. Kitayama, J. Fownes, D. Herbert, D. Mueller-Dombois, R. Riley and P.M. Vitousek. 1995. Changes in soil phosphorus fractions and ecosystem dynamics across along soil chronosequence in Hawaii. Ecology **76**:1407-1424.
- Crowley, K.F., B.E. McNeil, G.M. Lovett, C.D. Canham, C.T. Driscoll, L.E. Rustad, E. Denny, R.A. Hallett, M.A. Arthur, J.L. Boggs, C.L. Goodale, J.S. Kahl, S.G. McNulty, S.V. Ollinger, L.H. Pardo, P.G. Schaberg, J.L. Stoddard, M.P. Weand, K.C. Weathers. 2012. Do nutrient limitation patterns shift from nitrogen toward phosphorus with increasing nitrogen deposition across the northeastern UnitedStates? Ecosystems 15: 940-957

Elser, J.J., M.E.S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J.T. Ngai, E.W. Seabloom, J.B. Shurin, and J.E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecology Letters 10:1135-1142.

Elser, J.J., and E. Bennett. 2011. A broken biogeochemical cycle. Nature. 478: 29-31.

Elser, J.J. 2011. A world awash with nitrogen. Science. 334:1504-1505.

- Fransson P. M. A., Johansson E. M. (2010). Elevated CO2 and nitrogen influence exudation of soluble organic compounds by ectomycorrhizal root systems. FEMS Microbiol. Ecol. 71, 186–196.
- Gepstein, S. 1988. Photosynthesis. In *Senescence and aging in plants* (L.D. Nooden and A.C. Leopold, Eds.), pp 85-109. Academic Press, San Diego.
- Gleeson, S.K. and D. Tilman. 1992. Plant allocation and the multiple element hypothesis. American Naturalist **139**:1322-1343.
- Goll D.S., V. Brovkin, B.R. Parida, C.H. Reich, J. Kattge, S. Zaehle, P.B. Reich, P.M. van Bodegom, and Ü. Niinemets. 2012. CO₂-induced nutrient limitation on land carbon cycling in projections with a model of combined carbon, nitrogen and phosphorus cycling. Biogeosciences 9:3173-3232.
- Güsewell, S. 2004. N: P ratios in terrestrial plants: variation and functional significance. New Phytologist **164**:243-266.
- Hill, J. 1980. The remobilization of nutrients from leaves. Journal of Plant Nutrition. 2:407-444.
- Hortensteiner S., and P. Matile. 2003. How leaves turn yellow: catabolism of chlorophyll. Pages 189-199 *in* L.D. Nooden, editor. Plant cell death: processes. Academic Press, San Diego, California, USA.
- Inada, N., A. Sakai, H. Kuroiwa, and T. Kuroiwa. 1998. Three-dimensional analysis of the senescence program in rice (*Oryza sativa L.*) coleoptiles-Investigations of tissues and cells by fluorescence microscopy and electron microscopy. Planta **206**:585-597.
- Killingbeck, K.T. 1986. The terminological jungle revisited: making a case for use of the term resorption. Oikos **46**:263-264.Killingbeck, K.T. 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption efficiency. Ecology **77**:1716-1727
- Kobe, R.K., C.A. Lepczyk, and M. Iyer. 2005. Resorption efficiency decreases with increasing green leaf nutrients in a global data set. Ecology. **86**:2780-2792.
- Koerselman, W., and A.F.M. Meuleman. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. Journal of Applied Ecology **33**:1441-1450.

- Lajtha, K. 1987. Nutrient reabsorbtion efficiency and the response to phosphorus fertilization in the desert shrub *Larrea tridentata*. Biogeochemistry **4**:265-276.
- Lajtha, K. and W.H. Schlesinger. 1988. The biogeochemistry of phosphorus cycling and phosphorus availability along a desert soil chronosequence. Ecology **69**:24-39.
- Lu X.T., S.C. Reed, Q. Yu, N.P. He, Z.W. Wang, and X.G. Han. 2013. Convergent responses of nitrogen and phosphorus resorption to nitrogen inputs in a semiarid grassland. Global Change Biology **19**:2775-2784.
- Mae, T., H. Thomas, A.P. Gay, A. Makino, and J. Hidema. 1993. Leaf development in *Lolium temulentum*: photosynthesis and photosynthetic proteins in leaves senescing under different irradiances. Plant Cell Physiology **25**:333-336.
- Mae, T. 2004. Leaf senescence and nitrogen metabolism. Pages 157-168 *in* L.D. Nooden, editor. Plant cell death: processes. Academic Press, San Diego, California, USA.
- Makino, A., T. Mae, and K. Ohira. 1984. Relation between nitrogen and ribulose-1,5biphosphate carboxylase in rice leaves from emergence through senescence. Plant Cell Physiology **25**:429-437.
- Makino, A., and B. Osmond. 1991. Effects of nitrogen nutrition on nitrogen partitioning between chloroplasts and mitochondria in pea and wheat. Plant Physiology **96**:355-362.
- Marchin R.M., H. Zeng, W.A. Hoffmann. 2010. Drought-deciduous behavior reduces nutrient losses from temperate deciduous trees under severe drought. Oecologia **163**: 845–854.
- Marklein, A.R., and B.Z. Houlton. 2012. Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial ecosystems. New Phytologist **193**:696-704.
- Matile, P. 1992. Chloroplast senescence. Pages 413-440 *in* S.P. Long and B.G. Drake, editors. Crop photosynthesis: Spatial and temporal determinants. Academic Press, Amsterdam, Netherlands.
- Millard, P., and G.A. Grelet. 2010. Nitrogen storage and remobilization by trees: ecophysiological relevance in a changing world. Tree Physiology **30**:1083-1095.
- Minoletti, M.L., and R.E.J. Boerner. 1993. Seasonal photosynthesis, nitrogen and phosphorus dynamics, and resorption in the wintergreen fern *Polystichum acrostichoides* (Michx.) Schott. Bulletin of the Torrey Botanical Club:397-404.
- Morita, K. 1980. Release of nitrogen from chloroplasts during leaf senescence in rice (*Oryza sativa* L.). Annals of Botany **46**:297-302.

Nezat, C.A., J.D. Blum, R.D. Yanai, and S.P. Hamburg. 2007. A sequential extraction to

determine the distribution of apatite in granitoid soil mineral pools with application to weathering at the Hubbard Brook Experimental Forest, NH, USA. Applied Geochemistry. **22**:2406–2421.

- Park, B.B., R.D. Yanai, M.A. Vadeboncoeur, and S.P. Hamburg. 2007. Estimating root biomass in rocky soils using pits, cores, and allometric equations. Soil Science Society of America Journal. 71:206-213.
- Pastor, John, and Scott D. Bridgham. 1999. Nutrient efficiency along nutrient availability gradients. Oecologia **118**:50-58.

Peltzer D.A., D.A Wardle, Allison, W.T. Baisden, R.D. Bardgett, O.A. Chadwick, L.M. Condron, R.L. Parfitt, S. Porder, S.J. Richardson, B.L. Turner, P.M. Vitousek, J. Walker, L.R. Walker. (2010) Understanding ecosystem retrogression. Ecological Monographs **80**:509-529

- 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 Application **23**(3):621-642.
- Ratliff, T.J. 2012. Nitrogen and Phosphorus Availability in Forests of Varying Ages in the Bartlett Experimental Forest White Mountains, New Hampshire. MS Dissertation, Miami University, Ohio, USA.
- Reed, S. C., A. R. Townsend , E.A. Davidson, and C.C. Cleveland. 2012. Stoichiometric patterns in foliar nutrient resorption across multiple scales. New Phytologist **196**:173-180.
- Richardson, S.J., R.B. Allen, and J.E. Doherty. 2008. Shifts in leaf N:P ratios during resorption reflect soil P in temperate rainforest. Functional Ecology **22**:738-745
- Ryan, D. F. 1979. Nutrient resorption from senescing leaves: a mechanism of biogeochemical cycling in northern hardwood forest ecosystem. PhD. Dissertation, Yale University, Connecticut, USA.
- Ryan, D. F., and F. H. Bormann. 1982. Nutrient resorption in northern hardwood forests. BioScience:29-32.
- Sabete, S., A. Sala, and C.A. Gracia. 1995. Nutrient content in *Quercus ilex* canopies: seasonal and special variation within a catchment. Plant and Soil. **168-169**, 297-304.
- Sorrell B.K., C. Chague-Goff, L.M. Basher, and T.R. Partridge. 2011. N:P ratios, delta(15)N fractionation and nutrient resorption along a nitrogen to phosphorus limitation radient in an oligotrophic wetland complex. Aquatic Botany **94**:93-101.
- Sprengel, C.P. 1839. Die Lehre vom Dünger oder Beschreibung aller bei der Landwirthschaft gebräuchlicher vegetablilischer, animalischer und mineralischer Düngermaterialien, nebst Erklärung ihrer Wirkungsart. Leipzig, 1839

- Taylor, B.K., and L.H. May. 1967. The nitrogen nutrition of the peach tree. II. Storage and mobilization of nitrogen in young trees. Australian Journal of Biological Science **20**:389-411.
- Tessier, J.T., and D.J. Raynal. 2003. Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. Journal of Applied Ecology **40**:523-534.
- Tilman, David. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos:3-15.
- Tilton, D.L. 1977. Seasonal growth and foliar nutrients of *Larix laricina* in three wetland ecosystems. Canadian Journal of Botany **55**:1291-1298.
- Turner, B.L., and L.M. Condron. 2013. Pedogenesis, nutrient dynamics, and ecosystem development: the legacy of T.W. Walker and J.K. Syers. Plant and Soil **367**:1-10.
- Vadeboncoeur, M.A. 2010. Meta-analysis of fertilization experiments indicates multiple limiting nutrients in northeastern deciduous forests. Canadian Journal of Forest Research **40**:1766–1780.
- Vadeboncoeur, M.A., S.P. Hamburg, J.D. Blum, M.J. Pennino, R.D. Yanai, and C.E. Johnson. 2012. The quantitative soil pit method for measuring belowground carbon and nitrogen stocks. Soil Society of America Journal. 76:2241-2255.
- Vergutz, L., S. Manzoni, A. Porporato, R.F. Novais, and R.B. Jackson. 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecological Monographs **82**:205-202.
- Vitousek, P.M. 1982. Nutrient cycling and nutrient use efficiency. American Naturalist:553-572.
- Vitousek, P.M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology **65**:285–298.
- Vitousek, P.M. 1998. Foliar and litter nutrients, nutrient resorption, and decomposition in Hawaiian *Metrosideros polymorpha*. Ecosystems. **1**:401-407.
- Von Liebig, J. 1842. Animal Chemistry, or Organic Chemistry in its Application to Physiology and Pathology. Johnson Reprint Corporation, New York, USA.
- Walker, T.W. and J.K. Syers. 1976. The fate of phosphorus during pedogenesis. Geoderma. **15**: 1-19.
- Wang, Y. P., B. Z. Houlton, and C.B. Field. 2007. A model of biogeochemical cycles of carbon, nitrogen, and phosphorus including symbiotic nitrogen fixation and phosphatase production. Global Biogeochemical Cycles 21:GB1018.

- Wang, W., S. You, Y. Wang, L. Huang, and M. Wang. 2010. Influence of frost on nutrient resorption during leaf senescence in a mangrove at its latitudinal limit of distribution. Plant Soil 342:105-115.
- Weand, M.P., M.A. Arthur, G.M. Lovett, F. Sikora, K.C. Weathers. 2010. The phosphorus status of northern hardwoods differs by species but is unaffected by nitrogen fertilization. Biogeochemistry **97**:159-181
- Yuan, Z. Y., and Han YH Chen. 2009. Global-scale patterns of nutrient resorption associated with latitude, temperature and precipitation. Global Ecology and Biogeography **18**:11-18.

Appendices

Below are scatterplots of soil nutrient content and foliar nutrient resorption efficiency by species. Content was calculated by summing the content estimates for all three depth increments (Oa, 0-10cm, 10-30cm mineral soil). Phosphorus leaches were as follows:

Leach 1: overnight in 1N NH₄Cl at 20°C Leach 2: overnight in 30% H₂O₂ at 20°C Leach 3: overnight in 1N HNO₃ at 10°C Leach 4: 3 hours in concentrated HNO₃ at 150°C

















































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SOCIETY MEMBERSHIPS

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PROFESSIONAL EXPERIENCE

State University of New York College of Environmental Science and Forestry 2012-2013 Graduate Teaching Assistant

EFB797 A History of Ecosystem Thought (Instructor): Designed and taught a graduatelevel seminar on the history of ecosystem ecology (Fall 2013)

FCH153 General Chemistry II (Teaching Assistant): Set up labs, give pre-lab lectures, oversee 2 lab sections, grading lab reports, proctoring exams (Spring 2012, 2013)

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State University of New York College of Environmental Science and Forestry 2011-2012

Graduate Research Assistant

Duties: Assisting with design, implementation, and logistics of a large scale fertilization experiment in the White Mountains, hiring summer interns, scheduling large (12 person) field crew working on all aspects of the project, data management, training technicians in field and lab techniques, managing datasets, coordinating with PIs, vendors, etc.

Fieldwork included: Tree, herb, and germinant inventories, fertilizer application, soil respiration measurements, minirhizotron imaging, soil sampling, collection of fresh foliage and litter

University of Massachusetts, Amherst, MA 2011 (Lynn Adler Lab) Project Manager

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University of Minnesota, Minneapolis, MN 2010

Cedar Creek Ecosystem Science Reserve Intern

Duties: maintaining vegetation plots, constructing scaffolding, taking soil C02 flux measurements, conducting vegetation surveys, database maintenance, assisting with prescribed burns, vegetation sampling, biomass sorting and weighing, small mammal trapping, collecting root and soil cores, developing an independent research project

University of Wisconsin, Madison, WI 2010 (David Mladenoff Lab) Research Technician

Duties: taking soil and wood respiration measurements, laser mapping forest Plots using PDA (ArcPad), vegetation surveys, taking moisture/temperature Readings of soil and CWD, installing resin probes, maintaining deer exclosures, installing C02 flux collars, soil sampling

Dartmouth College, Hanover, NH 2010 (Rebecca Irwin Lab) Field Technician

Duties: locating old and new *Gelsemium sempervirens* plants, mapping field sites, taking flower measurements, trapping and preserving pollinators, taking soil samples, emasculating flowers, collecting stamen

Duke University, Durham, NC 2009 (Jim Clark Lab) Research Technician

Duties: conducting vegetation surveys, building animal exclosures, taking TDR measurements, coring trees/analyzing cores, taking canopy photos, collecting and sorting seeds, constructing warming chambers, wiring thermistors, data entry, data management

PRESENTATIONS ("*" denotes presentation given by another author)

Ecological Society of America Annual Meeting, Minneapolis, MN August 5, 2013

See, C.R., J Hayward, R.D. Yanai, M.B. Green, D.I. Moore. Uncertainty due to gapfilling in long-term hydrologic datasets. (Presented as part of Organized Oral Session)

*Ecological Society of America Annual Meeting, Portland, OR August 8, 2012

Bae, K., R.D. Yanai, S.P. Hamburg, J.D. Blum, M.A. Arthur, M.A. Vadeboncoeur, **C.R. See**, C.R. Levine. Sustainable forest harvest requires calcium supply from soil pools: Ecosystem budgets for second-growth northern hardwoods in New Hampshire. (Poster Presentation)

*Ecological Society of America Annual Meeting, Minneapolis, MN August 9, 2012

Tremblay, H.A., **C.R. See**, R.D. Yanai. Soil nitrate production in lawns and adjacent forests in the White Mountains, NH. (Poster Presentation)

Hubbard Brook Cooperator's Meeting, Hubbard Brook Experimental Forest, NH July 9, 2013

See, C.R., R.D. Yanai, and B.A. Quintero. Community-level conservation of Phosphorus increases with soil Nitrogen availability. (Oral Presentation)

*Hubbard Brook Cooperator's Meeting, Hubbard Brook Experimental Forest, NH July 9, 2013

Warner, C.A., and **C.R. See**. Connecting science to local kids: arthropod communities. (Oral Presentation)

Northeastern Natural History Conference, Springfield, MA April 14, 2013

See, C.R., R.D. Yanai, M.C. Fisk. Foliar N:P ratios and resorption efficiencies provide evidence of nutrient co-limitation in a northern hardwood forest. (Poster Presentation)

Syracuse University Life Sciences Symposium, Syracuse, NY March 22, 2013

See, C.R., and R.D. Yanai. Foliar N:P ratios and resorption efficiencies provide evidence of nutrient co-limitation in a northern hardwood forest. (Poster Presentation)

UMass Symposium on Plant-microbe Interactions, Amherst, MA October 6, 2012

See, C.R., H.A. Tremblay, R.D. Yanai. Lawns vs forests: the effect of suburbanization on microbial nitrogen processes in the White Mountain region of New Hampshire. (Poster Presentation)

LTER All Scientists Meeting, Estes Park, CO September 10, 2012

See, C.R., R.D. Yanai, J.L. Campbell, D.P. Moore, E. Matsuzaki, G.E. Likens. A proposed cross-site comparison of missing data in long-term hydrologic datasets. (Poster Presentation)

*LTER All Scientists Meeting, Estes Park, CO September 10, 2012

Fisk, M.C., T. Ratliff, S. Goswami, C.R. See, B. Naples, M.A. Vadeboncoeur, R.D. Yanai, T.J. Fahey. Examining nutrient co-limitation in a northern hardwood forest. (Poster Presentation)

*LTER All Scientists Meeting, Estes Park, CO September 10, 2012

Goswami, S., C.R. See, M.C. Fisk. Evidence for species-specific nutrient limitation of growth efficiency in northern hardwoods. (Poster Presentation)

Ecological Society of America Annual Meeting, Portland, OR August 8, 2012

See, C.R., R.D. Yanai. One of these squares is not like the other: why it's hard to find replicate forest plots at any scale. (Oral Presentation)

*Ecological Society of America Annual Meeting, Portland, OR August 8, 2012

Yanai, R.D., J.L. Campbell, S.L. Ladeau, K.C. Weathers, **C.R. See**, M.B. Green. Quantifying uncertainty in precipitation estimates. (Oral Presentation)

*Ecological Society of America Annual Meeting, Portland, OR August 6, 2012

Bae, K., R.D. Yanai, S.P. Hamburg, J.D. Blum, M.A. Arthur, M.A. Vadeboncoeur, **C.R. See**, C.R. Levine. Sustainable forest harvest requires calcium supply from soil pools: Ecosystem budgets for second-growth northern hardwoods in New Hampshire. (Poster Presentation)

Hubbard Brook Cooperator's Meeting, Hubbard Brook Experimental Forest, NH July 11, 2012

See, C.R., R.D. Yanai, and B.A. Quintero. Surprising variation in nutrient availability and nutrient resorption. (Oral Presentation)

*Hubbard Brook Cooperator's Meeting, Hubbard Brook Experimental Forest, NH July 11, 2012

Yanai, R.D., C.R. Levine, **C.R. See**, J.L. Campbell, M.B. Green, S.L. LaDeau. Certain progress in uncertainty analysis. (Oral Presentation)

*Hubbard Brook Cooperator's Meeting, Hubbard Brook Experimental Forest, NH July 11, 2012

See, C.R. and H.A. Tremblay. The grass is always greener (than the forest): Is it the nitrate? (Oral Presentation)

*Hubbard Brook Cooperator's Meeting, Hubbard Brook Experimental Forest, NH July 11, 2012

Goswami, S., M.C. Fisk, **C.R. See**. Can leaf mass explain species growth rates in northern hardwood stands? (Oral Presentation)

SUNY-ESF Spotlight on Research, Syracuse, NY April 12, 2012

See, C.R., R.D. Yanai. Using leave-one-out cross validation to quantify uncertainty in filling data gaps: rain gauges at the Sevilleta NWR.

New York Society of American Foresters Annual Meeting, Syracuse, NY January 26, 2012

See, C.R., R.D. Yanai, and B.A. Quintero. Nitrogen and phosphorus resorption efficiency ratios vary with stand age in northern hardwood forests. (Poster Presentation)

Rochester Academy of Science Annual Meeting, Rochester, NY October 29, 2011

See, C.R., R.D. Yanai, and B.A. Quintero. Nitrogen and phosphorus resorption efficiency ratios vary with stand age in northern hardwood forests. (Poster Presentation)

Hubbard Brook Cooperator's Meeting, Hubbard Brook Experimental Forest, NH July 5-6, 2011

See, C.R., R.D. Yanai, and B.A. Quintero. Young and old stands differ in N vs. P resorption from leaves, consistent with MEL model predictions. (Oral Presentation)

ADDITIONAL EXPERIENCE

Manuscript Reviewer for Environmental Management

LTER Synthesis Working Group: Quantifying Uncertainty in Atmospheric Deposition May 21-23

Assisted with the logistical planning and organizing of an LTER funded synthesis working group held at HJ Andrews experimental forest. Presented on gap filling methods, and assisted with writing final report submitted to the LTER network office.

Statistical Workshop: Likelihood and Bayesian Approaches to Data Analysis for Ecologists

May 29-June 2, 2012

Attended workshop taught by Dr. Juan Morales on Bayes approaches to ecology. Workshop focused on applications in R and Winbugs.

Quantifying Uncertainty in Ecosystem Studies (QUEST)

Ongoing assistance with the QUEST Research Coordination Network, including: website upkeep, communicating with authors, workshop/event planning, writing event summaries.

Chainsaw Safety Certification: Game of logging, level 1