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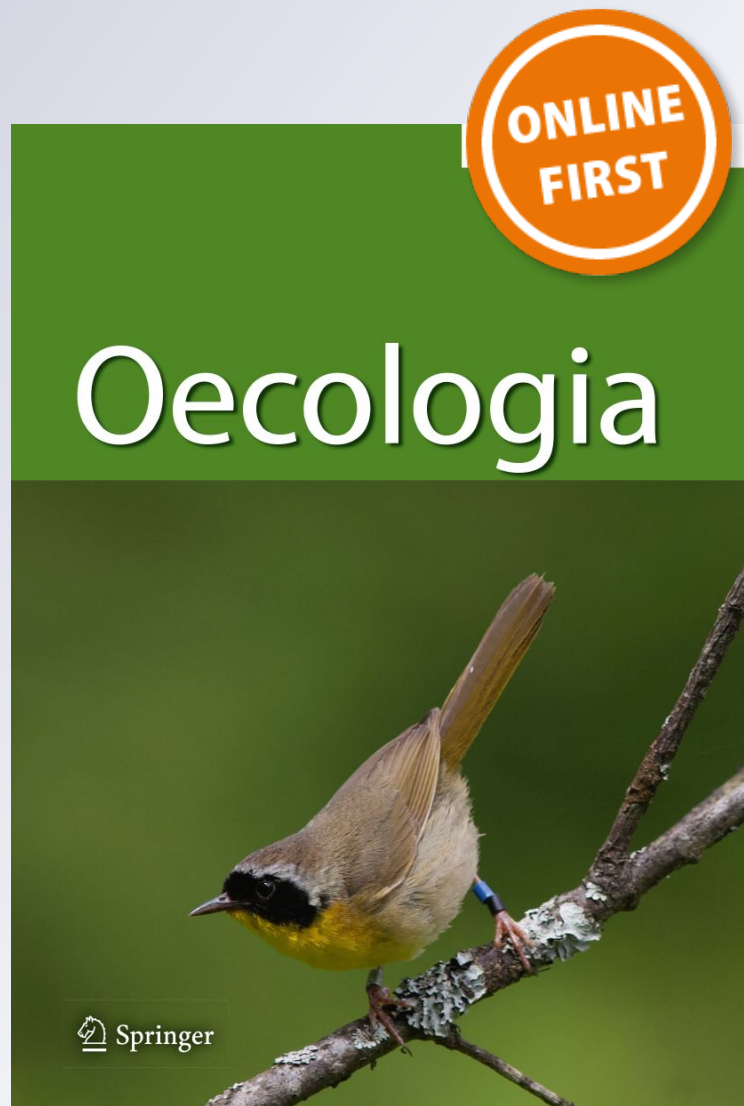
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Nitrogen–phosphorous interactions in young northern hardwoods indicate P limitation: foliar concentrations and resorption in a factorial N by P addition experiment

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Abstract

Resorption, the process of withdrawing foliar nutrients prior to leaf abscission, is one of the most important nutrient conservation mechanisms in trees. Along with foliar nutrient concentrations, foliar resorption can be used to infer nutrient limitation. We collected green and senesced leaves of five species in early successional stands in the White Mountains of New Hampshire. In unmanipulated controls, foliar N:P ratios ranged from 20 to 31 and litter N:P ratios ranged from 19 to 36. These values suggest P limitation, although this forest type has been assumed to be N-limited. Additionally, N:P resorption ratios in control plots were < 1, reflecting proportionately more conservation of P through resorption than N. Four years into a full-factorial N × P fertilization experiment, N and P additions had increased N and P concentrations in leaves; more importantly, P addition reduced N concentration, possibly indicating alleviation of growth limitation by P. Resorption of P was less proficient (indicated by the concentration of an element in leaf litter) with P addition, as expected. Resorption proficiency and efficiency (the proportion of leaf nutrients resorbed) of N increased with P addition, suggesting increased demand for N with alleviation of P limitation. Resorption of P was more proficient and efficient with N addition, consistent with exacerbated P limitation. Temperate forests on glaciated soils are generally thought to be N-limited, but long-term N × P manipulations in this biome are lacking. Our results suggest that decades of anthropogenic N deposition may have tipped the balance to P limitation in these forests.

Keywords Resorption proficiency · Resorption efficiency · Nutrient limitation · Northern hardwoods · Fertilization · Foliar nutrients

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Introduction

Increases in atmospheric nitrogen (N) deposition have profoundly affected the biogeochemistry of forests through changes in pH, net nitrification, and nutrient limitation status (Aber et al. 2003; Elser et al. 2007; Finzi et al. 2011). Since the N and phosphorus (P) cycles are tightly coupled (Chapin III et al. 2011), human-mediated alterations to N cycling affect the degree of P limitation as well (Van Heerwaarden et al. 2003; Marklein and Houlton 2012).

On a global scale, limitation by N or P may be driven by geologic history and soil type (Walker and Syers 1976). Highly weathered soils in the tropics are likely to be more P-limited, and recently glaciated soils in temperate regions are likely to be N-limited (Vitousek and Sanford Jr 1986; Reich and Oleksyn 2004; Vitousek et al. 2010). Foliar nutrient concentrations and, by extension, N:P ratios, are easily quantifiable indicators of plant nutrient status and relative

nutrient limitation. In general, foliar N:P ratios above 20 indicate P limitation, and ratios below 10 indicate N limitation (Güsewell 2004). Ratios > 16 and < 14 indicate P and N limitation in wetlands (Koerselman and Meuleman 1996). Foliar N:P ratios have been found to increase towards the tropics, reflecting the transition to P limitation in highly weathered soils (Reich and Oleksyn 2004; McGroddy et al. 2004). Increases in N:P ratios and shifts towards P limitation have been induced by N fertilization and deposition in Ontario (Gradowski and Thomas 2006), Sweden (Hedwall et al. 2017), and California (Menge and Field 2007).

Limitation status affects nutrient uptake and conservation in plants (Güsewell 2004). Resorption is one of a plant's principal nutrient conservation mechanisms. During this process, nutrients are translocated out of senescing leaves to be stored in other plant tissues, thus reducing nutrient loss in litter and permitting nutrient reuse within the plant (Killingbeck 1996). Nutrient resorption lessens plant dependence on external nutrient supplies (Aerts and Chapin 1999), and thus may confer a competitive advantage under nutrient limitation (Fahey et al. 1998). Resorption is reported in terms of efficiency (the percent difference between nutrient concentrations in green and senesced leaves) and proficiency (the concentration to which nutrients have been reduced in leaf litter). Globally, resorption efficiency averages 54% for N and 50% for P, on a concentration basis (Aerts 1996). Values were found to be somewhat higher, 62% for N and 65% for P, in a study that corrected for mass loss during senescence (Vergutz et al. 2012).

While nutrient resorption would be expected to reflect the demand for the nutrient resorbed, there are reasons to consider the availability of other nutrients. Plants should allocate effort so as to remain simultaneously co-limited by multiple resources (Bloom et al. 1985; Rastetter and Shaver 1992). One implication of this idea is that a nutrient that is not limiting could be directed towards the acquisition or conservation of a more limiting nutrient. For example, excess N can be used to enhance P acquisition through the construction of phosphatase enzymes (Treseder and Vitousek 2001; Naples and Fisk 2010) or P conservation through the production of nuclease enzymes involved in foliar P resorption during senescence (Buchanan-Wollaston 1997). This plasticity in nutrient resorption is an important mechanism of maintaining balanced nutrition or co-limitation.

Co-limitation may occur not only at the individual level, but also at the whole ecosystem level. In species-rich ecosystems, intra- and interspecific variation can contribute to maintaining a state of co-limitation by multiple resources (Niinemets and Kull 2005; Danger et al. 2008; Harpole et al. 2011), due to differences among species in response to limitation. Foliar nutrient concentrations and resorption differ interspecifically, and different species within a single site can exhibit disparate responses to fertilization (Van

Heerwaarden et al. 2003; Davidson et al. 2004; Townsend et al. 2007). Species may be considered to exist along an economics spectrum (Grime 1979; Reich et al. 1997; Wright et al. 2004), in which evolutionary trade-offs result in an inability to both maximize high productivity and minimize nutrient losses (Berendse and Aerts 1987). For example, evergreens limit nutrient losses by maintaining low leaf nutrient concentrations in long-lived leaves, but this limits their potential growth rate (Aerts 1990; Reich et al. 2003; Kobe et al. 2005). Fast-growing, short-lived trees may exhibit a more nutrient-acquisitive strategy and have high foliar nutrient concentrations and high productivity, traits selected for in fertile habitats. In young successional forests, species of contrasting life-history strategies co-occur, affording an opportunity to compare species responses of foliar chemistry and nutrient resorption to N and P manipulation. Pin cherry (*Prunus pensylvanica* L.f.), for example, is a fast-growing, short-lived species in the northern hardwood forest type with high-nutrient concentrations (Fahey et al. 1998); American beech (*Fagus grandifolia* Ehrh.), a shade-tolerant, long-lived species in the same forest type, might be expected to exhibit more conservative strategies (Tripler et al. 2002).

The present study took place in the Bartlett Experimental Forest in the White Mountains of central New Hampshire, USA. Plots in these stands have been fertilized annually in a full N and P factorial design since 2011 in a study of multiple-element limitation in northern hardwood ecosystems (MELNHE; Fisk et al. 2014). Prior to fertilization, observations of foliage and leaf litter in six of these stands indicated that N availability influenced P resorption proficiency and efficiency more than P availability, but P availability did not have a corresponding influence on N resorption (See et al. 2015). The experimental nutrient manipulations in the MELNHE study allow us to test whether these correlations are in fact caused by differences in nutrient availability and not some other factors correlated with nutrient gradients across the landscape.

We characterized foliar N and P and calculated resorption efficiency in five species in one early successional stand in the MELNHE study. In three stands, we compared resorption proficiency of N and P. We predicted that early successional species [pin cherry, white birch (*Betula papyrifera* Marsh.), and red maple (*Acer rubrum* L.)] would have high foliar nutrient concentrations and low resorption efficiency, while shade-tolerant species [American beech and yellow birch (*Betula alleghaniensis* Britton)] would exhibit a more conservative strategy of low leaf nutrient concentrations and high resorption. We hypothesized that foliar N:P ratios in the control plots would reflect N limitation, as predicted for early successional stage species growing on recently glaciated soils (Rastetter et al. 2013) and by responses to fertilization in the northern hardwood region (Vadeboncoeur 2010). We expected that foliar N:P ratios would reflect shifts

in limitation induced by experimental fertilization (higher than the control in the N treatment and lower than the control in the P treatment). We hypothesized that P resorption proficiency and efficiency would be enhanced by N addition. Although the mechanisms for the converse are not clear, we hypothesized that resorption proficiency and efficiency of N would be higher with P treatment. To our knowledge, this is the first full-factorial test of N and P manipulation of nutrient resorption in a temperate forest.

Methods

Site description

The three study stands (C1, C2, and C3) are located in the Bartlett Experimental Forest (BEF) in the White Mountains of New Hampshire. All three are northern hardwood stands regenerated naturally following clearcutting 25–35 years prior to sampling in 2014. Dominant tree species are white birch, American beech, red maple, pin cherry, sugar maple (*Acer saccharum* Marsh.), and yellow birch (Table 1). Soils are well-drained Spodosols (Typic Haplorthods) formed in granitic glacial drift. Soils are described by (Vadeboncoeur et al. 2012, 2014). All three stands are located at similar elevation, 340–590 m above sea level. The climate is humid continental, with an annual average precipitation of 127 cm (Adams et al. 2003). Between 1979 and 2003, wet N deposition in this area was 4–7 kg N ha⁻¹ year⁻¹, but has dropped to about 2–4 kg N ha⁻¹ year⁻¹ since 2008 (NADP Program Office 2017; US Environmental Protection Agency Clean Air Markets Division 2017). Atmospheric deposition of P in this region is negligible, estimated to be ~0.04 kg P ha⁻¹ year⁻¹ (Yanai 1992).

Four treatment plots were established in each stand as part of a larger study on multiple-element limitation and

have been fertilized annually since 2011 in a full-factorial design (Fisk et al. 2014). One plot in each stand has been treated with N alone (30 kg N ha⁻¹ year⁻¹ as NH₄NO₃), P alone (10 kg P ha⁻¹ year⁻¹ as NaH₂PO₄), N and P together (same application rates), or control. Treatment plots measure 0.25 ha (50 m × 50 m) and all measurements are made in the inner 30 m × 30 m, allowing for a 10-m buffer to avoid edge effects.

Foliar collection

Five tree species were sampled in every plot: pin cherry, white birch, yellow birch, red maple, and American beech. Pre-treatment samples were collected in 2009 and 2010 prior to the onset of fertilizer applications in 2011 (Table 2). Post-treatment samples were collected in 2014.

Green leaves were collected in one stand (C2) using pole pruners (pre-treatment) or a shotgun (post-treatment) during the first week of August in 2009, 2010, and 2014. Trees > 10 cm dbh in our plots are tagged; about half of the individuals sampled in 2010 had dbh > 10 cm and thus were tagged. These trees were also chosen for sampling in 2014. Trees sampled in 2014 were > 10 cm dbh and intermediate or dominant in the canopy. Leaves were shot from 2 to 4 trees [3 trees in > 90% of 60 cases (trees × species × plot) in 2014] of each of the five species in each of the four plots. Leaves were collected from sun-exposed portions of the mid to upper canopy from at least two sides of each tree.

Leaf litter was collected from two stands (C1 and C2) in 2009 and 2010, and from three stands (C1, C2, and C3) in 2014. Pre-treatment leaf litter was collected with multiple net traps distributed within each plot (See et al. 2015), while post-treatment litter was collected from the ground. In both cases, litter was collected throughout the plot and, since the experimental unit was the plot, composited before analysis. This sampling method results in a sample representative of

Table 1 Characteristics of the three study stands

| Stand | Last cut | Elevation (m) | Aspect | Slope (%) | Basal area (m ² ha ⁻¹) | | | | | | | |
|-------|----------|---------------|------------|-----------|---|-----|-----|------|------|------|-----|-----|
| | | | | | AB | ASH | PC | RM | SM | STM | WB | YB |
| C1 | 1990 | 570 | Flat to SE | 5–20 | 0.4 | 0.3 | 1.7 | 0.04 | 0.04 | 0.0 | 5.1 | 0.1 |
| C2 | 1988 | 340 | NE | 15–30 | 1.7 | 0.1 | 1.0 | 3.1 | 1.2 | 0.05 | 2.0 | 0.2 |
| C3 | 1980 | 590 | NNE | 8–20 | 5.0 | 0.1 | 3.7 | 3.9 | 1.2 | 0.6 | 2.5 | 1.5 |

AB American beech, ASH ash, PC pin cherry, RM red maple, SM sugar maple, STM striped maple, WB white birch, YB yellow birch

Table 2 Experimental design, including identification of which data were collected pre- and post-treatment

| | Sampling unit | C1 | C2 | C3 |
|---------------------------------|---------------|--------------|--------------|------|
| Green leaves | Tree | | Pre and post | |
| Litter (resorption proficiency) | Plot | Pre and post | Pre and post | Post |
| Resorption efficiency | Plot | | Pre and post | |

the full canopy, while green leaves are sampled from the upper canopy. The variation in nutrient concentrations in foliage due to sampling position was only 12% in an earlier study in northern hardwoods (Yang et al. 2016). In all sampling years, litter was collected in early October following a rain-free period.

In the laboratory, we selected at least ten leaves per tree (green leaves) or per plot (litter) for analysis, avoiding those that showed evidence of disease or damage from buckshot or herbivory.

Foliar analysis

Leaf area was measured on all samples collected post-treatment using a LiCor-3100 Area Meter. Leaves were then oven-dried at 60 °C to constant mass and ground in a Wiley mill to pass a 40-mesh screen. Nitrogen concentrations were determined through combustion in a CN analyzer (FlashEA 1112 analyzer, Thermo Scientific). Apple leaves (NIST 1515) were run as a tissue standard.

Subsamples of 0.25 g were ashed at 470 °C in a muffle furnace and hot-plate digested with 5 mL of 6 N nitric acid. One duplicate sample, one blank, and two replicates of a standard (NIST 1515) were processed with each group of 30–35 samples. The extractant was analyzed by inductively coupled plasma optical emission spectroscopy (ICP-OES; Optima 5300 DV, Perkin-Elmer). During ICP-OES analysis, a blank was run after every ten samples and an in-house quality control after every five; we re-calibrated the machine if > 5% drift was observed in the in-house standards.

For the standard reference material (NIST 1515), recovery of N was within 5% of the certified value for 22 of 24 samples, and within 10% for all samples. For P, recovery was within 10% of the certified value for nine of ten samples, and the relative percent difference (RPD) was $\leq 8\%$ for each pair of duplicate standards. For replicate samples, the mean RPD was 8%. Replicate samples were averaged for subsequent analysis. The element concentrations in all method blanks were < 10% of the lowest measured sample.

Data analysis

Foliar N and P were expressed in units of concentration (mg g^{-1}), content (mg leaf^{-1}), and content per unit leaf area (mg cm^{-2}). Resorption efficiency, the proportion of a nutrient withdrawn from senescing leaves before abscission, was calculated using all three of these approaches. Both resorption per unit leaf area and per unit leaf mass (concentration) may underestimate true resorption since leaves can lose both area and mass during senescence. We found that the direction of effects tended to be consistent regardless of the basis of expression, though the levels of significance and the magnitudes of effects differed. Since we did not have leaf

area information for the pre-treatment data, and were thus unable to compare to post-treatment data using the content per unit leaf area metric, we opted to report concentration-based metrics in this paper. Results for the other metrics may be found on the Hubbard Brook database.

For concentration (mg g^{-1}), there were three post-treatment-dependent variables each for N and P: green leaf concentrations, litter concentrations (i.e., resorption proficiency), and resorption efficiency. The predictor variables were N treatment, P treatment, and tree species. Nitrogen and P treatments were considered main effects in a full-factorial design, such that the NP treatment is represented as an interaction term.

We included all five species in analyses of variance (ANOVA) to test for the effects of nutrient manipulation on the three above-mentioned dependent variables for both N and P (Online Resource 1). Since different numbers of stands were sampled for green leaves and litter, several statistical models were used. Green leaves were collected in just one stand, and the plot was the experimental unit (Table 2). Since leaves were collected from three trees of each species, the individual trees were considered the sampling unit. Though there was no replication of treatment plots across stands, the experimental design permitted analysis of the full factorial of N treatment, P treatment, and species since each treatment was applied to two plots and each species occurred in all four plots.

Litter was collected at the plot level (not attributable to a particular tree) from three stands, which were treated as blocks in a randomized complete block design, resulting in three replicates of each treatment. Though there was no replication within plot for models pertaining to litter, replication at the plot level allowed us to analyze the full factorial of N treatment, P treatment, and species because the same species were in all four plots and the factorial $N \times P$ treatment meant that each nutrient was applied to two plots in each stand.

Since green leaves were collected only in C2, resorption efficiency could be calculated for only one stand (Table 2). Similar to the models for resorption proficiency, the plot was the experimental unit, with one value per species in each plot. We were able to test the main effects of N and P treatments and species, as well as the interaction of N and P treatment, but not the three-way interaction of N, P, and species, because there was no replication of stands or of species within plots.

For green leaf and litter nutrients and resorption efficiency based on concentrations, we also conducted analyses of covariance (ANCOVA) by including the corresponding pre-treatment values as a covariate. The models for litter and resorption efficiency were identical to the ANOVA models, save for the inclusion of the covariate. However, since we were unable to match pre- and post-treatment green leaf concentrations by individual

tree, we had to compare plot-wide means. Therefore, the ANCOVA model we used for green leaves with a covariate was the same as that for resorption efficiency, and was thus simpler than the ANOVA model for green leaves (Table 2). For each dependent variable, we tested for an interaction between the covariate and treatment; none of these was significant at $\alpha=0.05$, indicating no significant differences between the slopes of the lines by treatment and permitting the retention of the covariate in the model. Equal slopes allowed us to standardize by the covariate and test whether there was a difference in treatment means (i.e., higher/lower Y intercepts) while statistically controlling for the confounding effects of pre-treatment differences.

The covariates were included to control for variation among plots not due to treatment, improving our ability to detect treatment effects. We report results both with and without the corresponding covariate for the following reasons. In the case of litter, we had pre-treatment data for only two of the three stands, so the sample size is smaller in the ANCOVA. In the case of green leaves, we could use trees as replicates without the covariate, but because in many cases the same trees were not sampled pre- and post-treatment, we had to use the average for the plot in the ANCOVA. This precluded testing for an interaction between treatments and species, because green leaves were sampled in only one stand.

Tukey's post hoc tests were used to differentiate among treatment means when effects were significant at $\alpha \leq 0.05$. All analyses were performed in SAS 9.4 (Cary, NC).

Results

Green leaf response to N and P additions

Green leaf N and P, measured in five species in one stand, showed the expected single-element response, with 12% higher N concentrations, on average, under N addition (x -axis of Fig. 1; $p=0.01$, main effect of N treatment in ANOVA) and 44% higher P concentrations under P additions (x -axis of Fig. 1b; $p=0.02$, main effect of P). Additionally, green leaf P concentrations were 13% higher with N additions, though this effect was not significant ($p=0.15$, main effect of N). In contrast, green leaf N was 11% lower under P addition (Fig. 1a; $p=0.03$, main effect of P). The effects of N and P together on green leaf nutrient concentrations were the same as the predicted additive effects of N and P separately (i.e., $N \times P$ interactions were not significant for foliar N ($p=0.70$) or for foliar P ($p=0.48$)). Specifically, for green leaf N, since N additions had a positive effect of a similar magnitude as the negative effect of P additions, the average green leaf N concentration in the NP treatment was similar to that in the control, as shown by Tukey's post hoc comparison of means. In contrast, the average green leaf P concentration was highest in the NP treatment, since fertilization with either N or P was associated with higher concentrations of P.

Since green leaves were measured in only one stand (C2), it was important to consider whether the treatment plots differed for reasons not associated with the N and P additions. For N, even when pre-treatment values were included as a predictor (Fig. 2), green leaf N concentrations

Fig. 1 Effects of factorial N and P additions on green and senesced leaf **a** N and **b** P concentrations in one stand (C2). Values are mean \pm standard error of five species: American beech (*Fagus grandifolia*), pin cherry (*Prunus pensylvanica*), red maple (*Acer rubrum*), white birch (*Betula papyrifera*), and yellow birch (*Betula alleghaniensis*). Resorption proficiency is indicated by the litter concentration; resorption efficiency is the departure below the 1:1 line (with values indexed by dotted lines). This figure is available in color in the online version of the journal

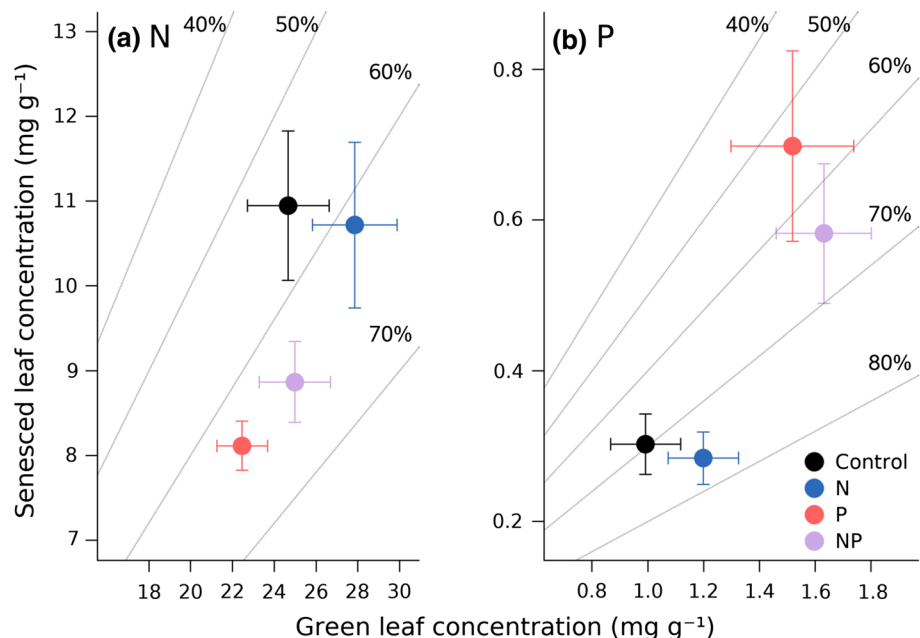
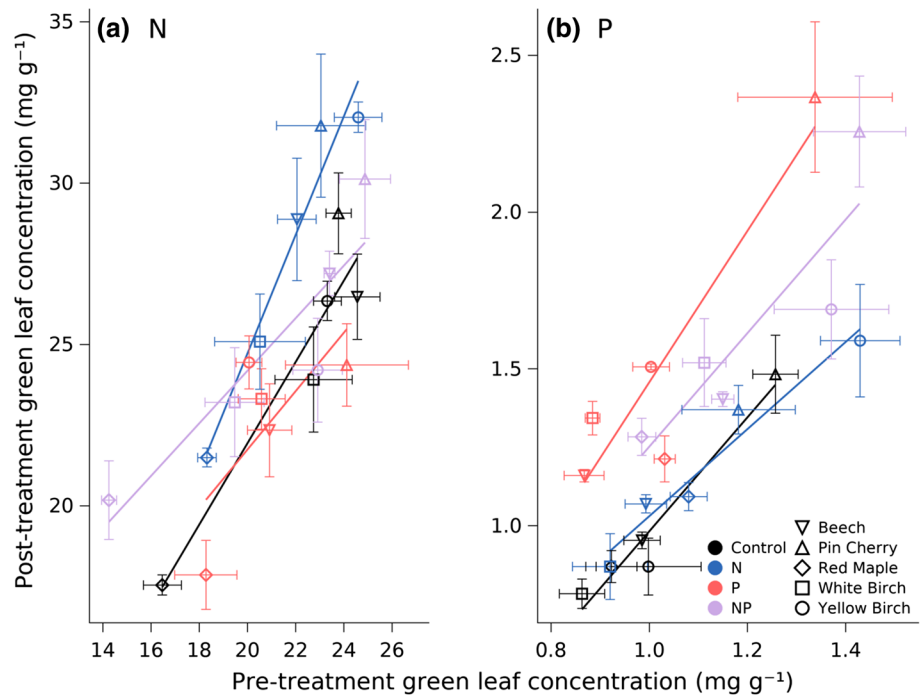


Fig. 2 The effect of treatment on green leaf **a** N and **b** P concentrations in one stand (C2) was analyzed while controlling for pre-treatment differences with ANCOVA. Simple linear regression lines are shown for each treatment with species as replicates. Error bars give the standard error for 3 individuals per species per treatment. Comparing the regression lines shows that green leaf N concentrations were higher with N addition, while green leaf P was increased by P addition. This figure is available in color in the online version of the journal



were 12% higher with N addition ($p=0.003$) and 9% lower with P addition ($p=0.02$), with no significant interaction ($p=0.58$). Likewise, P concentrations in green leaves were still significantly higher with P addition when pre-treatment concentrations were included in the ANCOVA ($p<0.0001$). However, when regression lines were fitted for ANCOVA, the P treatment had the highest adjusted mean P concentration. Nitrogen addition had little effect on green leaf P concentrations standardized by pre-treatment concentrations ($p=0.44$), but the addition of N and P together resulted in P concentrations between those found in the single-element plots ($p=0.12$ for the $N \times P$ interaction).

Species differed in their green leaf concentrations ($p<0.001$ for both N and P); red maple had the lowest average concentrations of both N and P in green leaves (Fig. 2). For N concentrations, all five species responded similarly to both N ($p=0.35$ for the N by species interaction) and P ($p=0.17$, $P \times$ species interaction) additions and the interaction of N and P ($p=0.13$ for $N \times P \times$ species interaction; Fig. 3). For P concentrations, species differed in their response to treatments. Phosphorus concentrations were 38% higher in yellow birch following N addition, but only 10% higher, on average, for the other four species ($p=0.02$, $N \times$ species). The increase in P concentrations following P addition was largest in white birch (73%) and pin cherry (62%), followed by yellow birch (30%), red maple (27%), and American beech (27%) ($p=0.001$, $P \times$ species). There was not a significant difference among species in the

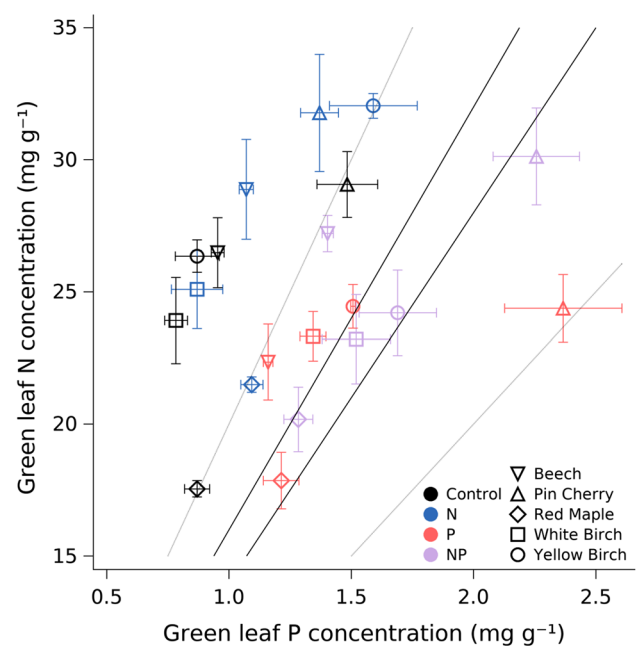


Fig. 3 Effects of factorial N and P additions on green leaf N and P concentrations (species mean \pm standard error, $n=3$) in one stand (C2). Solid lines indicate N:P ratios of 14 and 16, and dotted lines indicate N:P ratios of 10 and 20. Foliar N:P ratios were in the P-limited range in the control and N plots. This figure is available in color in the online version of the journal

interactive effects of $N \times P$ on P concentrations ($p=0.21$ for the three-way interaction; Figs. 2, 3).

Leaf litter and nutrient resorption

A single-element response of increased nutrient concentration with nutrient addition was predicted not only for green leaves, but also for leaf litter (i.e., reduced resorption proficiency). We also expected nutrient resorption efficiency, indicated by comparing green leaf to litter concentrations, to decrease with additions of the same nutrient. The expected single-element relationships were observed for P resorption following P addition in both the ANOVA and ANCOVA models (Figs. 1, 4). In the three stands where litter was collected, litter P concentrations were 40% higher with P addition ($p < 0.001$, main effect of P; Fig. 5), meaning that P resorption proficiency decreased. Phosphorus resorption efficiency (measured in stand C2) also decreased by 24% ($p = 0.01$, main effect of P; Fig. 1), because litter P concentrations increased proportionately more than green leaf P concentrations. Thus, as predicted, P resorption was less proficient and efficient with increased availability of P.

The single-element response was much weaker for N than for P; there was no significant main effect of N addition on litter N concentrations (resorption proficiency) across three stands ($p > 0.37$ for ANOVA and ANCOVA; Figs. 1, 4, 5). Since green leaf N concentrations were elevated by N addition (as described above), N resorption efficiency was 6% higher with N addition in C2, but this effect was also not significant ($p > 0.10$ for ANOVA and ANCOVA; Fig. 1).

We were interested in multiple-element interactions, namely whether addition of N would be associated with increased resorption of P, and vice versa. In the three stands

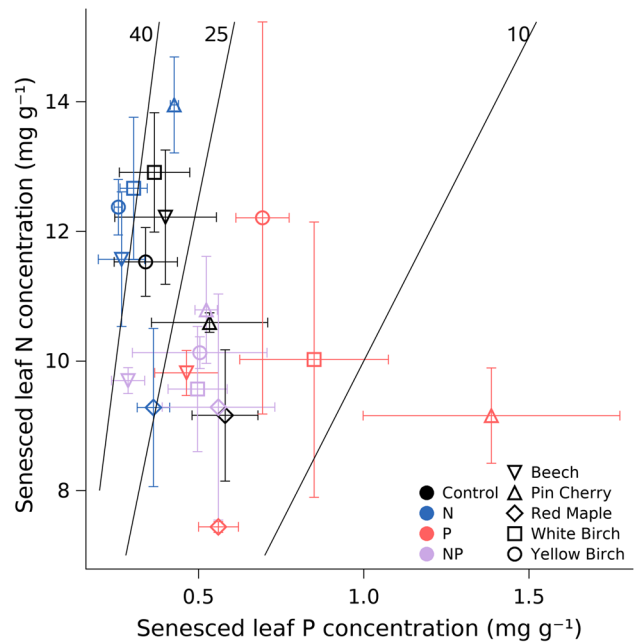
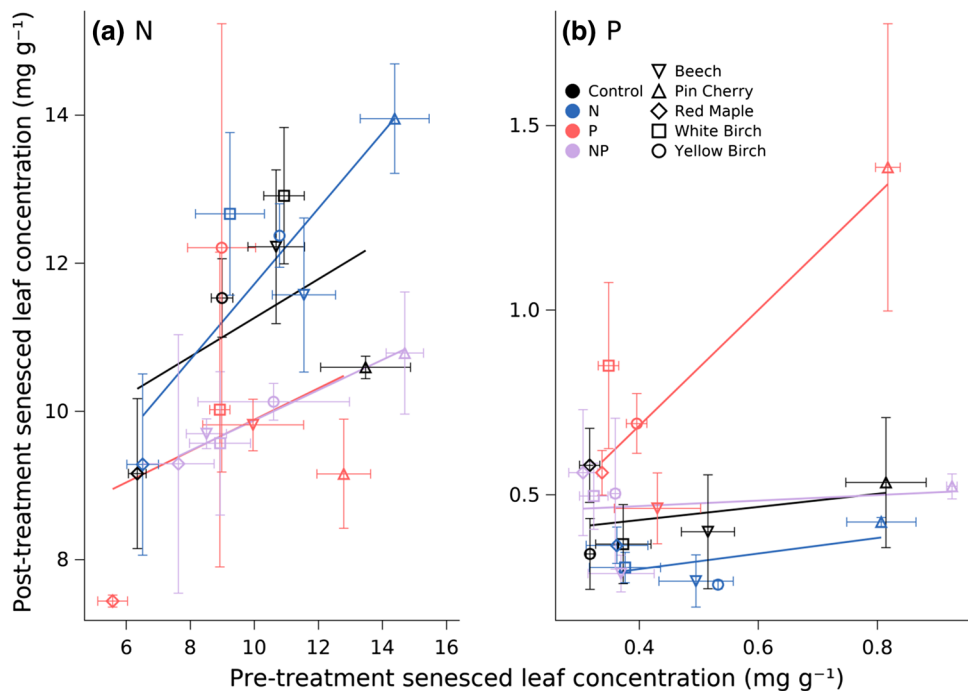


Fig. 5 Effects of factorial N and P additions on plot-wide litter N and P concentrations for five species (mean \pm standard error, $n = 3$ stands). Solid lines indicate N:P ratios of 10, 25, and 40. The effects of treatment on litter N:P ratios were similar to those in green foliage, with trees P-limited in the N and control plots. Additions of P, alone or with N, alleviated the severity of P limitation observed in the control plots. This figure is available in color in the online version of the journal

Fig. 4 Effects of factorial N and P additions on senesced leaf **a** N and **b** P concentrations in two stands (C1 and C2) were analyzed while controlling for pre-treatment differences with ANCOVA. Simple linear regression lines are shown for each treatment with species as replicates. Error bars give the standard error across stands. Comparing the regression lines indicates that trees became more proficient at N resorption with P addition and more proficient at P resorption with N addition. This figure is available in color in the online version of the journal



where litter was collected, N resorption was 18% more proficient with P addition ($p < 0.001$, main effect of P; Fig. 1). Lower litter N concentrations resulted in 9% more efficient N resorption with P additions in stand C2, where both litter and green leaves were sampled ($p = 0.02$, main effect of P in stand C2; Fig. 1). These effects remained even after standardizing by pre-treatment resorption values, increasing our confidence that the observed effects are, in fact, related to nutrient additions: with the pre-treatment covariates, N resorption was 21% more proficient with P addition ($p < 0.001$; Fig. 4) and 8% more efficient ($p = 0.09$).

Similar multiple-element relationships were observed for the proficiency of P resorption with N addition, but were less clear for the efficiency of P resorption. Litter P concentrations in the three sampled stands were 35% lower with N addition ($p = 0.001$, main effect of N; Figs. 1, 4). However, the NP treatment had similar P resorption proficiency as the control (Fig. 4), consistent with P addition reducing P resorption proficiency, as described above. In stand C2, the higher green leaf P concentration with N addition described above, coupled with lower litter P concentrations, resulted in 12% more efficient P resorption with N addition, but this effect was not significant in ANOVA or ANCOVA ($p \geq 0.13$, main effect of N; Fig. 1).

Species were similar in resorption efficiency, measured in stand C2 (Fig. 6). Among the five species, average N resorption efficiency in C2 ranged from 59% in white birch

to 65% in pin cherry ($p = 0.48$, main effect of species; Fig. 6), and average P resorption efficiency ranged from 57% in white birch to 71% in beech ($p = 0.36$). For resorption proficiency, however, which we measured across three stands (Fig. 5), the five species had significantly different litter concentrations ($p < 0.01$ for both N and P, main effect of species), with red maple significantly more proficient at N resorption than pin cherry, white birch, or yellow birch, and yellow birch and American beech significantly more proficient at P resorption than pin cherry. The effect of treatment on resorption proficiency did not differ by species (Fig. 5; $p \geq 0.20$ for litter N, $p \geq 0.15$ for litter P, for the interaction of species with nutrient treatment): litter N concentrations were lower with P addition for all five species. Litter P concentrations were lower with N addition and higher with P addition for all species across three stands, and pin cherry showed the largest response to treatment.

Foliar N:P as an indicator of nutrient limitation

Foliar N:P ratios in the control plots suggest that our study stands were P-limited, averaging 26 for green leaves and 32 for leaf litter. The strong effect of P addition on foliar N and P concentrations was reflected in the N:P ratios: the average green leaf N:P ratio (Fig. 3) was 59% lower with P treatment (main effect of P, $p = 0.003$), but only 5% higher with N treatment (main effect of N, $p = 0.57$). For litter, likewise, the average N:P ratio (Fig. 5) was 80% lower with P addition ($p < 0.001$) and 36% higher with N addition ($p = 0.001$). These patterns remained when we controlled for pre-treatment N:P ratios (Fig. 7): foliar N:P ratios were higher with N addition ($p = 0.04$) and lower with P addition ($p = 0.003$).

Pin cherry and red maple had the lowest green leaf and litter N:P ratios (Fig. 3; $p < 0.001$ for the main effect of species), in the range suggesting co-limitation by N and P. For all five species, the green and senesced leaf N:P ratio was similarly affected by treatment ($p \geq 0.21$, interaction of $N \times P \times \text{species}$).

The N:P resorption efficiency ratio is the ratio of N resorption efficiency to P resorption efficiency; a ratio > 1 signifies proportionately more N resorption than P resorption and < 1 signifies more P resorption than N resorption. The mean N:P resorption efficiency ratio for all species in the control plot was 0.77, indicating proportionately more conservation of P than of N, another sign of P limitation (Fig. 6). When P was added, the N:P resorption efficiency ratio was significantly higher than the control ($p = 0.02$) and > 1 , resulting from an increase in N resorption efficiency and a decrease in P resorption efficiency with P additions (as described above). Clearly, N and P resorption are both responsive to changes in nutrient availability.

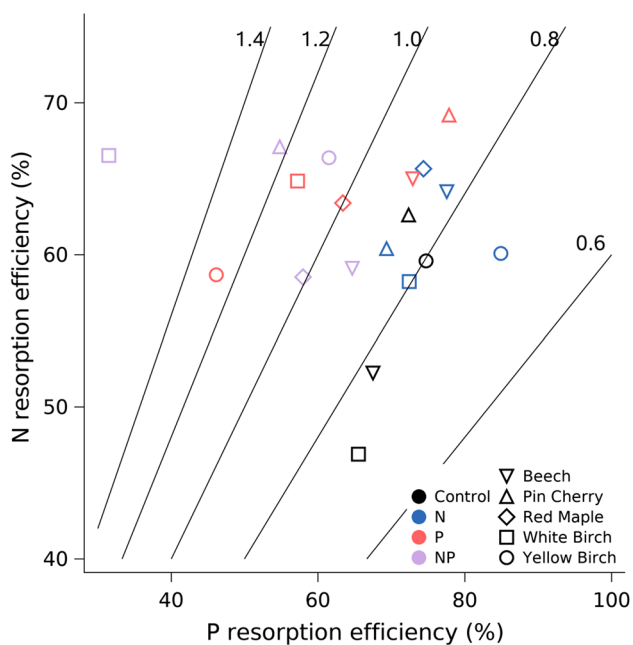


Fig. 6 Effects of factorial N and P addition on species-level N and P resorption efficiency in one stand (C2, $n = 1$). The 1.0 index line indicates equal resorption of N and P. Proportionately, more P than N was resorbed in the N and control plots. This figure is available in color in the online version of the journal

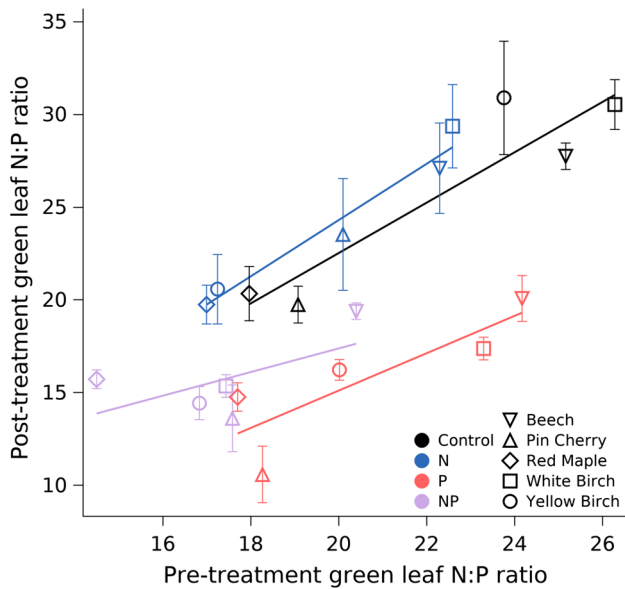


Fig. 7 Effects of factorial N and P addition on post-treatment N:P ratios standardized by pre-treatment N:P ratios (indicated by linear regression lines) in four treatment plots of one stand (C2) for five northern hardwoods species (mean \pm standard error, $n=3$ for post-treatment values). This figure is available in color in the online version of the journal

Discussion

Forests in temperate regions are typically thought to be N-limited (McGroddy et al. 2004; Reich and Oleksyn 2004). However, decades of anthropogenic N deposition in the northeastern United States might be expected to lead to altered biogeochemical cycling, and we found multiple indications of P limitation in our stands. The average N:P ratio of green leaves in the control plot of stand C2 was 26 (Fig. 3), well above published thresholds indicative of P limitation (Koerselman and Meuleman 1996; Güsewell 2004). Proportionately more P than N was resorbed by trees in the control plot, evidenced by N:P resorption ratios < 1 (Fig. 6), which is also consistent with P limitation (Reed et al. 2012). It appears that adding P alleviated the severity of limitation; N:P resorption ratios and green leaf N:P ratios were more affected by the addition of P, alone or with N, than by the addition of N alone (Fig. 3). These indicators are consistent with a recent finding of increased diameter growth of trees in response to P but not N addition in mature stands in our study system (Goswami et al. 2018).

It was not surprising that foliar P concentrations were significantly higher in plots with P additions (the P and NP treatments) (Fig. 1). Similarly, foliar N concentrations were higher in plots treated with N. However, green leaf N concentrations were lower in the P treatment plot. Under P limitation, trees are expected to respond to P additions with increased growth, resulting in a dilution of non-limiting

elements (Vitousek 1984; Haase and Rose 1995; Ostertag 2010). The fact that there was no analogous reduction in foliar P concentration under N addition lends further support to our finding of P limitation in this forest.

Resorption proficiency is the level to which nutrients are reduced in leaf litter (Fig. 1). Not surprisingly, litter P concentrations were highest in the P-treated plots and litter N concentrations were highest in the N-treated plots. In hardwoods, resorption may be considered complete below concentrations of 0.7% N and 0.05% P and incomplete above concentrations of 1.0% N and 0.08% P in leaf litter (Killingbeck 1996). By this definition, P resorption was complete in the control plots, but incomplete in plots with P added. Nitrogen resorption, however, was incomplete in both the control and N plots, suggesting that N is less in demand. The relative completeness of resorption may reflect the relative costs of acquiring nutrients via uptake from external sources versus recycling from internal sources. Trees can afford to rely less on internal recycling through resorption where soil nutrient availability is high. Therefore, incomplete N resorption in the control plots is further evidence that N is not limiting, consistent with green leaf N:P ratios.

Resorption efficiency was calculated only for site C2, as it requires information on nutrient concentrations in foliage as well as in litter. Consistent with studies that have found nutrient resorption to be low when nutrient availability is high (Staaf 1982; Kobe et al. 2005; Hagen-Thorn et al. 2006; Vergutz et al. 2012; Yuan and Chen 2015; Ji et al. 2018), P resorption proficiency and efficiency were reduced in the P and NP treatment plots, due to higher P concentrations in both green leaves and litter (Fig. 1). Since the cost of P uptake should be reduced when P availability is high and P is not limiting, trees can expend effort on other mechanisms for increasing fitness.

The MELNHE experiment allowed us to test not only for single-element resorption responses but also for multiple-element interactions. Functional links between N and P mean that the concentration of one nutrient influences concentrations of the other, within species-specific ranges of N:P ratios (Mohren et al. 1986). Phosphorus resorption in our study sites prior to fertilization was higher in stands with high soil N (See et al. 2015). We found similar results after experimentally manipulating soil N availability: P resorption was most proficient (Fig. 5), efficient (Fig. 6), and complete in the plots fertilized with N. This was driven by both higher green leaf P and lower litter P when N was added.

It was more surprising that we also found evidence for the converse: N resorption was more proficient and efficient in plots treated with P, resulting from lower litter N concentrations (Fig. 1a). The mechanisms for N to facilitate P resorption are clear, because N is required to build the enzymes required to resorb P. It is less clear by what mechanisms available P could be used to improve N resorption, but the

value of resorbed N is greater when P limitation is relieved. Theoretically, plants should distribute effort towards maintaining stoichiometric balance, by increasing acquisition and conservation of the most limiting nutrient (Chapin et al. 2002; Harpole et al. 2011; Rastetter et al. 2013).

Differences among species in nutrient requirements are not surprising, and species are often found to differ in foliar nutrient concentrations (Niinemets and Kull 2005; Hagen-Thorn et al. 2006; Wood et al. 2011; Reed et al. 2012). Though differences among families are not often explicitly reported (but see Townsend et al. 2007), our results generally agree with those of Killingbeck (1996), who reported lower senesced leaf N and P in trees of subclass Rosidae (which includes red maple) compared to those in subclass Hamamelidae (which includes American beech, white birch, and yellow birch). However, pin cherry, a member of the Rosidae, had the highest green leaf N and P concentrations of the five species.

Differences in resorption efficiency and nutrient concentrations among growth forms or functional types may be attributed to different adaptations for increasing nutrient use efficiency, which depends on the mean residence time of a nutrient and the productivity per unit of the nutrient (Aerts 1990). There are trade-offs associated with maximizing either of these quantities. At one end of the spectrum, evergreens maximize nutrient use efficiency through low leaf nutrient concentrations, lower N resorption, a longer leaf lifespan, and a lower potential growth rate compared to deciduous species (Aerts 1996; Killingbeck 1996; Vergutz et al. 2012). We expected that the late successional species in our young forests would exhibit some of these more conservative nutrient strategies and the early successional species would occur at the other extreme, although all our species are deciduous. Indeed, American beech and yellow birch were the most proficient at P resorption, and pin cherry behaved in the manner predicted of a fast-growing pioneer species, with high-nutrient concentrations in both green and senesced leaves. These results suggest that life-history strategy, in addition to phylogeny, is important in explaining species differences in resorption in our forest type.

Species differences in nutrient conservation efficiency may also help predict changes in forest composition in response to changing nutrient availability. Pin cherry exhibited some of the greatest increases in foliar P concentrations in response to P additions (Fig. 3); increased uptake could help pin cherry to outcompete other species or persist longer if P is limiting (Fahey et al. 1998). Such adaptability to changing conditions is likely important for a pioneer species. Changes in available nutrients have been observed to lead to shifts in species dominance and composition in grasses, forbs, and evergreen species (Aerts 1990; dos Santos Jr et al. 2006; Soudzilovskaia et al. 2007; Bai et al. 2010; Venterink and Güsewell 2010). Pin cherry also had the lowest green

leaf N:P ratio. A low N:P ratio is associated with a higher growth rate in plants, because of the role of RNA in protein synthesis (Ågren 2004). Note that the green leaf N:P ratio of red maple was almost as low as that of pin cherry. Red maple was also the most nutrient-conservative species, with low green and senesced leaf N and P concentrations. Low-nutrient requirements and a low N:P ratio may contribute to the unprecedented expansion of red maple across the eastern US (Fei and Steiner 2007) where N deposition has presumably made historically N-limited forests more P-limited. The plasticity we observed in foliar resorption supports the importance of this process to species success in the face of changing nutrient availability.

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Author contribution statement The idea for this study was part of a much larger project led by RDY. KEG joined the project in her final semester as an undergraduate student, collecting samples and processing them. As a graduate student, KEG analyzed the data. KEG and RDY interpreted the results, wrote the paper, and enhanced its value through extended revision.

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