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Research article

Changes in foliar chemistry and nutrient resorption in northern hardwood forests in response to long-term experimental nitrogen and phosphorus addition

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Northern hardwood forests have long been assumed to be primarily nitrogen limited, but may often be co-limited by multiple elements. Nutrient limitation can be inferred through responses of foliar and litter chemistry to nutrient addition over time. We compared community-level foliar and litter chemistry and resorption efficiency in a long-term, factorial nitrogen (N) and phosphorus (P) fertilization study across 10 forest stands at three sites in New Hampshire, where N and P were added annually. We measured N, P, calcium (Ca), magnesium (Mg), and potassium (K) in foliage from codominant trees and in fresh litter in 2008–2010 (pretreatment) and again in 2014–2016 and 2021–2022. Foliar N and P concentrations indicated co-limitation in 2014–2016 based on reduced concentrations of one nutrient following addition of the other, suggesting a dilution effect. In 2021–2022, an interactive effect of N and P addition was observed: foliar P concentrations were lower under N+P addition, consistent with dilution following a greater growth response to N+P than to P addition, which was observed by 2015–2019. Changes in litter N and P concentrations with N and P addition mirrored those in foliar N and P. Resorption efficiency of N and P decreased with addition of these respective nutrients and P resorption efficiency was higher in the N+P treatment than the P treatment. Foliar Ca and litter Ca and K decreased with N addition but increased with P addition. Results indicated N and P co-limitation and revealed biogeochemical interactions among N, P and base cations.

Keywords: foliage, litter, nitrogen, phosphorus, resorption

Introduction

Primary production in temperate forests has long been assumed to be mostly nitrogen (N) limited (Vitousek and Howarth 1991). In the late 20th and early 21st centuries, however, more evidence emerged suggesting that temperate forests could be



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limited by phosphorus (P) due to the composition of the parent material, loss of P through leaching and erosion, and anthropogenic effects (Vitousek et al. 2010, Peñuelas et al. 2013). Co-limitation by N, P and calcium (Ca) has also been observed in temperate forests in the northeastern United States (Vadeboncoeur 2010), perhaps in part due to a long history of elevated N deposition owing to anthropogenic activity (Holland et al. 2005). These observations support resource optimization theory suggesting that plants and ecosystems should tend towards limitation by multiple elements and allocate relatively more resources towards acquiring nutrients that are in greater demand, thereby optimizing resource allocation and nutrient uptake (Bloom et al. 1985, Rastetter and Shaver 1992). Nutrient limitation of plant production in temperate forests, therefore, is more complex than once assumed.

A principal mechanism of nutrient conservation in forests is foliar resorption, in which a high proportion (60–70%; Brant and Chen 2015) of foliar N and P content is translocated from leaves to perennial tissues prior to abscission. While energetically costly (Killingbeck 2004), resorption reduces the requirement for root uptake of N and P from soil; therefore, resorption tends to be greater in environments with low soil fertility (Brant and Chen 2015). Two measures of resorption are often used: resorption efficiency, which is the proportion of leaf nutrient content resorbed, and resorption proficiency, which is the nutrient concentration remaining in senesced leaves following resorption (Killingbeck 1996). Both measures of resorption are effective, indirect indicators of plant nutrient limitation (Killingbeck 1996, Han et al. 2013, Ostertag and DiManno 2016, Hong et al. 2022). Addition of a limiting nutrient usually results in increased foliar concentrations and reduced resorption of that nutrient (Yuan and Chen 2015) and decreased foliar concentrations of non-limiting nutrients due to a dilution effect (Jarrell and Beverly 1981, Bracken et al. 2015). For example, if addition of N to soil results in increased N uptake and foliar N concentrations, then net photosynthesis could be enhanced given the strong relationship between photosynthetic rate and foliar N concentration (Field and Mooney 1986). The increased organic matter production would dilute the concentration of any other nutrient, such as P, for which uptake does not increase proportionally.

Nutrient co-limitation of plant production can be indicated by foliar nutrient concentration. When interpreting changes in foliar chemistry following nutrient addition at the community level, a decrease in the concentration of one nutrient with addition of the other and vice versa could reflect the net outcome of dilution that occurs when different species or individuals within a community are limited by different nutrients; this is an example of ‘community co-limitation’ (Fig. 1; Bracken et al. 2015). Alternatively, an increase or no change in the concentration of one nutrient with the addition of another nutrient could indicate ‘biochemically dependent co-limitation’ (Fig. 1; Saito et al. 2008, Bracken et al. 2015). For example, the addition of N can stimulate the production of N-rich phosphatases, which

make more P available, increasing the concentration of foliar P along with increases in foliar N (Marklein and Houlton 2012). Interactive responses to N and P (i.e. super-additive or sub-additive effects of adding both nutrients) can also indicate co-limitation (Harpole et al. 2011).

Nutrient co-limitation of plant production can also be indicated by litter nutrient concentration (i.e. resorption proficiency) and resorption efficiency. Nutrient resorption is expected to increase for one nutrient with the addition of another, limiting nutrient (Yuan and Chen 2015). For example, if N is limiting, P concentrations in litter should decrease with N addition. Resorption efficiency is also expected to decrease with addition of the nutrient in question but increase if another, more limiting nutrient is added (Fig. 1; Han et al. 2013, Yuan and Chen 2015). Resorption proficiency (leaf-litter nutrient concentration) has been found to be more strongly influenced by changes in nutrient availability than is resorption efficiency, perhaps because the nutrient concentrations in litter are traits that can be more directly acted upon by natural selection than the proportion of nutrients resorbed (Killingbeck 1996, Wright and Westoby 2003).

Foliar concentrations of calcium (Ca), potassium (K), and magnesium (Mg) may be influenced by N or P availability. Decreases in foliar Ca, Mg and K concentrations with N or P addition could arise in part from dilution, as described above, or from changes in the availability of other nutrients in the environment, such as a decrease in soil base cations (e.g. Ca, Mg, K) as a result of soil acidification (Lucas et al. 2011, Tian and Niu 2015). These nutrient cycles could also be coupled, meaning that changing the availability of one nutrient changes the availability of the other in the ecosystem (Fiorentino et al. 2003, Finzi et al. 2011, Marklein and Houlton 2012). For example, adding Ca to the forest floor at Hubbard Brook increased concentrations of foliar P, indicating that Ca addition increased rates of soil P cycling, likely due in part to increases in soil pH as a result of Ca addition (Fiorentino et al. 2003). Resorption does not substantially alter Ca, Mg or K concentrations in leaf litter: foliar Ca and Mg are not often resorbed (Berg and McClaugherty 2008), and K is easily leached (Schreeg et al. 2013, Sardans and Peñuelas 2015), which complicates resorption calculations.

The Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE) study, the longest running N × P factorial fertilization study in a temperate forest ecosystem, was developed to investigate N and P co-limitation in northern hardwood forests. This study in New Hampshire, USA, in which fertilization began in 2011, provides a unique opportunity to confirm whether changes in foliar and litter chemistry and in resorption efficiency over time are consistent with nutrient limitation inferred from measurements of plant production. The forest stands in the MELNHE study vary in stand age, which enables comparison across differences in species composition. Treatments induced changes in soil N and P availability (Fisk et al. 2014). Tree diameter growth was reported to respond more to P than N addition by 2015 (Goswami et al. 2018), though co-limitation was observed by 2019 (Blumenthal et al. unpubl.). Limitation by

Single or Co-limitation	Type	Nutrient added	Foliar N	Foliar P	Resorption of N	Resorption of P
Co-limitation	Community Co-limitation	N	↑	↓	↓	↑
		P	↓	↑	↑	↓
		N+P	↑	↑	↓	↓
	Biochemical Co-limitation	N	↑	↑ or =	↓	↓ or =
		P	↑ or =	↑	↓ or =	↓
		N+P	↑	↑	↓	↓
Single nutrient limitation	N Limitation	N	↑	=	↓	=
		P	↓	↑	↑	↓
		N+P	↑	↑	↓	↓
	P Limitation	N	↓	↑	↑	↓
		P	=	↑	=	↓
		N+P	↑	↑	↓	↓

Figure 1. Different types of nutrient limitation and how nutrient addition is hypothesized to change foliar chemistry and resorption under these conditions. Up arrows indicate that the variable will increase with the added nutrient under the specified type of limitation, down arrows indicate that the variable will decrease, and equal signs indicate that the variable is not expected to change.

P was indicated by analyses of foliar and litter N and P measured both in the youngest stands in the MELNHE study in 2014 (Gonzales and Yanai 2019) and in eight stands in *Acer* (maple) species and American beech *Fagus grandifolia* in 2015 (Gonzales et al. 2023). Given that foliar and litter nutrient concentrations suggested a greater response to P addition and tree growth seemed to be P-limited at first and then shifted to co-limitation, we sought to determine whether foliar and litter nutrient concentrations after 10 years would have also changed to reflect co-limitation.

The objective of this study was to quantify the effects of low-level N and P additions on foliar chemistry and nutrient resorption over the first decade of the MELNHE experiment in northern hardwood forests. Foliage and freshly fallen leaf litter were collected by species before treatment from 2008–2010, after treatment from 2014–2016, and most recently in 2021–2022. Community-weighted means of foliar and litter nutrient concentrations and resorption efficiency of N and P were calculated and used to assess community-level responses to changes in nutrient availability; this approach

integrates species-level responses to changes in nutrient availability and reflects changes in nutrient concentrations and relative abundance of species (Lepš et al. 2011). Responses of foliar nutrients, litter nutrients, and resorption efficiency were used to determine whether these northern hardwood forests exhibited evidence of co-limitation by N or P or single nutrient limitation (Fig. 1).

Methods

Site description

Green foliage and freshly fallen leaf litter were collected in 10 even-aged northern hardwood forest stands in the MELNHE study. Six stands were located at the Bartlett Experimental Forest in Bartlett, NH (44°03'N, 71°17'W): stands C1, C2, C4 and C6 were mid-successional, third-growth forests (most recently harvested between 1975 and 1990) and stands C8 and C9 were late-successional, second-growth forests

(harvested between 1883 and 1890). Two stands were located at Hubbard Brook Experimental Forest in Woodstock, NH (44°02'N, 71°53'W): stand HBM was mid-successional (last harvested in 1970) while HBO was late-successional (harvested in ~ 1910). Two stands were located at Jeffers Brook in Benton, NH (44°02'N, 71°53'W): stand JBM was mid-successional (last harvested in ~ 1975), while JBO was late-successional (harvested in ~ 1915, Table 1). Mean annual precipitation at Hubbard Brook was around 1400 mm (Campbell et al. 2010), mean air temperature in January was -9°C, and mean air temperature in July was 18°C (USDA Forest Service 2022).

Dominant tree species in the late-successional stands included American beech *F. grandifolia*, sugar maple *A. saccharum* and yellow birch *Betula alleghaniensis*. The youngest stands (C1 and C2) were dominated by white birch *B. papyrifera*, pin cherry *Prunus pensylvanica* and red maple *A. rubrum*; mid-successional stands consisted of a mix of all species, with *P. pensylvanica* dropping out over the course of the study (Table 1, Fig. 2). Soils were primarily well drained or moderately well drained Spodosols and Inceptisols on glacial till (Vadeboncoeur et al. 2014). Bedrock and parent material differed across sites, with Jeffers Brook underlain by amphibolite, Hubbard Brook by granodiorite and schist, and Bartlett by granite; thus these sites were expected to represent a range of soil conditions across the region, with Jeffers Brook having higher soil fertility than Hubbard Brook or Bartlett. Background atmospheric N deposition from 2008 through 2022 was about 9 kg N ha⁻¹ year⁻¹ (NADP 2024).

In each stand in the MELNHE study, we established four 50 × 50 m treatment plots, consisting of a 30 × 30 m inner measurement area with a 10 m buffer (except HBM and JBM, which had a 20 × 20 m measurement area with a 5 m buffer to accommodate treatment plots in areas of similar species composition and uniform management history). Plots have been treated annually since 2011 with N (30 kg N ha⁻¹ year⁻¹

as NH₄NO₃), P (10 kg P ha⁻¹ year⁻¹ as NaH₂PO₄), both N and P, or neither, as an untreated control. The 3:1 ratio of N to P added to these plots is lower than N:P ratios typically seen in foliage, indicating that more P was added to the plots relative to plant demand compared to N; this higher rate of P addition was chosen to account for the high P adsorption capacity of sesquioxides in these soils (Wood et al. 1984).

Foliar sampling and processing

Foliage was collected from the four treatment plots in each of 10 stands in the MELNHE study using a shotgun (Youngentob et al. 2016) in late July and early August in all three sampling periods: 2008–2010 (pre-treatment), 2014–2016 (after ~ 5 years of treatment), and 2021–2022 (after ~ 10 years of treatment). Leaves were sampled from at least two sunlit portions of the canopies of dominant or codominant trees. All dominant species were sampled from all 10 stands in 2008, 2009 and 2010. In 2014, all dominant species in C2 were sampled. In 2015, only *F. grandifolia*, *A. saccharum* and *A. rubrum* were sampled across all stands, while in 2016, *P. pensylvanica*, *B. alleghaniensis* and *B. papyrifera* were sampled across all stands. All six species were sampled in 2021 at Hubbard Brook and Jeffers Brook and in 2022 at Bartlett (Table 1). Leaves that had little to no damage or disease were selected for chemical analysis. If necessary to choose among damaged leaves, leaves with minor herbivory or intact margins were preferred over leaves with skeletonization or disease. All leaves were processed with petioles included.

Foliar samples collected from 2008 to 2015 were frozen after collection, then oven-dried at 60°C, ground with petioles included to pass a 20 mesh screen, ashed in a muffle furnace and hot-plate digested with 5 ml of 6N nitric acid before being diluted to 20% with deionized water and analyzed for P, Ca, Mg and K using inductively coupled plasma optical emission spectroscopy (ICP-OES; Optima 5300 DV,

Table 1. Characteristics of sampled MELNHE stands, including stand age, the year it was last cut, elevation, aspect, slope, and species sampled. Species symbols are taken from the US Department of Agriculture PLANTS database (Soil Conservation Service 1982): ACRU (*Acer rubrum*), ACSA3 (*Acer saccharum*), BEAL2 (*Betula alleghaniensis*), BEPA (*Betula papyrifera*), FAGR (*Fagus grandifolia*), and PRPE2 (*Prunus pensylvanica*). Species are listed in order of proportion of total basal area, from most abundant to least in each stand.

Site	Stand	Successional		Elevation			Sampled species	
		sage	Year cut	(m)	Aspect	Slope (%)	2014–2016	2021–2022
BEF	C1	mid	1990	570	SE	5–20	BEPA, PRPE2, FAGR, ACRU	BEPA, PRPE2, FAGR, BEAL2
	C2	mid	1988	340	NE	15–30	ACRU, FAGR, BEPA, PRPE2, BEAL2	ACRU, FAGR, BEPA, PRPE2, BEAL2
	C4	mid	1979	410	NE	20–25	BEPA, ACRU, FAGR, BEAL2, PRPE2	BEPA, ACRU, FAGR, BEAL2
	C6	mid	1975	460	NNW	13–20	ACRU, BEPA, BEAL2, FAGR, PRPE2	ACRU, BEPA, BEAL2, FAGR
	C8 C9	late late	1883 1890	330 440	NE NE	5–35 10–35	FAGR, ACSA3, BEAL2 ACSA3, FAGR, BEAL2	FAGR, ACSA3, BEAL2 ACSA3, FAGR, BEAL2
HB	HBM	mid	1970	500	S	10–25	BEAL2, BEPA, ACRU, ACSA3, FAGR	BEAL2, BEPA, ACRU, ACSA3, FAGR
	HBO	late	~1910	500	S	25–35	BEAL2, FAGR, ACSA3	BEAL2, FAGR, ACSA3
JB	JBM	mid	~1975	730	WNW	25–35	BEAL2, BEPA, ACSA3, PRPE2	BEAL2, BEPA, ACSA3
	JBO	late	~1915	730	WNW	30–40	ACSA3, BEAL2, FAGR	ACSA3, BEAL2, FAGR

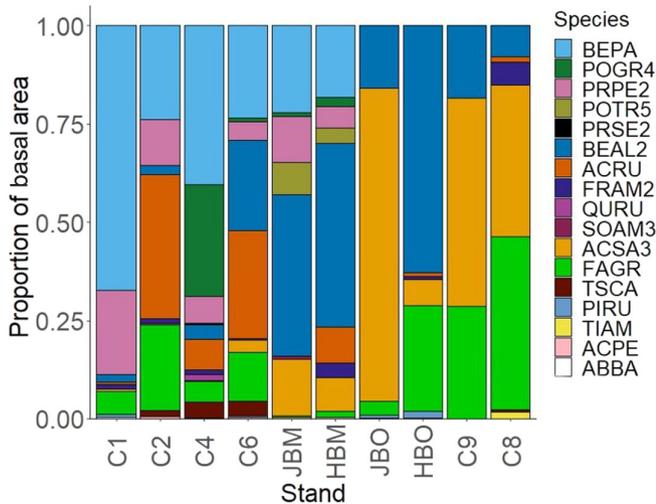


Figure 2. Proportion of basal area by species of trees greater than 10 cm in diameter in each stand in 2015. Species include *Abies balsamea* (ABBA), *Acer pensylvanicum* (ACPE), *A. rubrum* (ACRU), *A. saccharum* (ACSA3), *Betula alleghaniensis* (BEAL2), *B. papyrifera* (BEPA), *Fagus grandifolia* (FAGR), *Fraxinus americana* (FRAM2), *Picea rubens* (PIRU), *Populus grandidentata* (POGR4), *P. tremuloides* (POTR5), *Prunus pensylvanica* (PRPE2), *Quercus rubra* (QURU), *Sorbus americana* (SOAM3), *Tilia americana* (TIAM) and *Tsuga canadensis* (TSCA). Species are grouped by shade tolerance, with shade intolerant at the top (BEPA to PRSE2), intermediate shade tolerant in the middle (BEAL2 to SOAM3), and shade tolerant at the bottom (ACSA3 to ABBA). Within shade-tolerance groups, species are ordered from greatest to least basal area across the study sites. Stands are ordered from youngest to oldest from left to right.

Perkin-Elmer; Gonzales and Yanai 2019, Hong et al. 2022). Foliar samples collected in 2016 were frozen, oven-dried, ground with petioles included to pass a 40 mesh screen, then 0.25 g subsamples were digested with 10 ml of concentrated nitric acid using a MARS 6 microwave digestion system (CEM), then diluted to 20% with deionized water and analyzed using ICP-OES. In 2021 and 2022, sample handling procedures were modified to accommodate measurements of physical leaf characteristics (Zukswert et al. 2025a). Leaf samples were refrigerated after collection and processed within a week. Samples were oven-dried at 60°C and ground to pass a 40 mesh screen, then 0.25 g of oven-dried foliage from each sample was digested in 10 ml concentrated nitric acid using a MARS 6 microwave digestion system (CEM), diluted to 20% with deionized water, and analyzed using ICP-OES. Nitrogen concentrations in subsamples of ground foliage (3.5–4.5 mg) from 2008 through 2016 were measured via combustion in a CN analyzer (FlashEA 1112 analyzer, Thermo Scientific) and in subsamples from 2021 through 2022 were measured using a mass spectrometer (Isoprime VisION, Elementar). Standard reference material (NIST 1515) recovery averaged $99.0 \pm 3.4\%$ (mean \pm SD) for N, $103.2 \pm 3.9\%$ for P, $101.1 \pm 4.8\%$ for Ca, $100.3 \pm 4.7\%$ for K, and $101.0 \pm 4.6\%$ for Mg (Zukswert et al. 2024a). Duplicates of samples collected in 2021–2022 differed by $3.3 \pm 3.6\%$ for P, $4.1 \pm 4.7\%$ for

Ca, $2.7 \pm 3.0\%$ for K, $4.5 \pm 3.6\%$ for Mg, and $9.1 \pm 6.9\%$ on average for N (no N duplicate data are available for 2014–2016; Zukswert et al. 2025b).

For a subset of 20 trees (at least three of each species sampled) in 2021, we processed both a ‘damaged’ and ‘undamaged’ sample to characterize how foliar damage affects concentrations of N, P, Ca, K and Mg. We detected a slight decrease in Ca and Mg concentrations in the damaged samples, but no effects on N, P or K (Supporting information).

Leaf litter sampling and processing

In rain-free periods during peak litterfall in early to mid-October between 2009 and 2022, fresh leaf litter was collected from the same species and stands in which foliage had been sampled the previous summer. In 2009 and 2010, litter was collected from nets suspended ~ 1 m above the ground (12 mm polypropylene mesh deer netting). In 2014–2016 and 2021–2022, recently fallen litter was collected haphazardly from the ground; between 9 and 30 leaves were collected per species per plot. In 2021–2022, freshly senesced leaves free of damage and disease were selected to visually match the sunlit-leaves collected for foliage (Van Heerwaarden et al. 2003), sun leaves being thicker and smaller than shade leaves. Because we aimed to select leaf litter that more closely matched the foliar samples from 2021 and 2022, which were primarily sunlit leaves sourced near the top of the trees, these litter samples are not representative of all leaf litter falling at the plot scale.

Litter samples were processed in the same way as the corresponding foliage samples (See et al. 2015, Gonzales and Yanai 2019). In all years, subsamples of ground litter (3.5–4.5 mg) were analyzed using a CN analyzer (FlashEA 1112 analyzer, Thermo Scientific). Standard reference material (NIST 1515) recovery was within $102.2 \pm 4.8\%$ on average for N, $102.4 \pm 7.4\%$ on average for P, $101.4 \pm 5.0\%$ on average for Ca, $99.6 \pm 6.3\%$ on average for K, and $103.7 \pm 5.0\%$ on average for Mg (Zukswert et al. 2025c). Duplicates were $5.0 \pm 6.0\%$ different on average for P, $4.4 \pm 4.0\%$ different for Ca, $5.5 \pm 11.5\%$ different for K, and $4.4 \pm 4.3\%$ different for Mg, and $6.0 \pm 5.0\%$ different on average for N in 2021–2022 (N duplicate data for 2014–2016 were not available; Zukswert et al. 2025c).

Data analysis

To explore the effects of N and P fertilization on foliar and litter chemistry, we ran linear mixed-effects models for each of the five nutrients measured in foliage and litter and for resorption efficiency of N and P. Models were run in R (www.r-project.org) using the ‘lme4’ (Bates et al. 2015) and ‘lmerTest’ packages (Kuznetsova et al. 2017). Species-level models of foliar and litter nutrient concentrations and resorption efficiency for *F. grandifolia*, *A. saccharum*, *B. alleghaniensis* and *B. papyrifera* are available in the Supporting information but were not interpreted in depth in this study. Models for *A. rubrum* and *P. pensylvanica* were not constructed due to small sample size (i.e. *A. rubrum* and

P. pennsylvanica were sampled in fewer than half the stands; Table 1), but differences in nutrient concentrations among plots were visualized graphically (Supporting information). Resorption efficiency was corrected for organic matter loss during resorption using a standard mass-loss correction factor for deciduous angiosperms (0.784; Vergutz et al. 2012)

We ran linear mixed-effects models at the community level using community-weighted means. We ran separate models for the data from 2014–2016 and from 2021–2022, meaning that we ran 20 models of community-weighted values in total. Community weighted means for each plot (CWM_{Total}) were calculated using

$$CWM = \sum_1^n p_{ij} \cdot x_{ij}$$

where n is the number of species, p is the proportion of basal area of that species i occupies in the ‘community’ (plot) j , and x is the mean trait value of species i in plot j . Fixed effects of these models were N, P, the interaction of N and P, stand age, site, and mean pre-treatment CWM_{Total} for that nutrient. Stand was a random effect. Site was used as a fixed effect because sites were initially selected for the experiment based on presumed differences in soil fertility. Site is confounded with sampling year, however, and thus serves primarily as a blocking factor. Site was removed from overfit models when doing so removed the singularity or enabled convergence; these models included CWM_{Total} litter P in 2014–2016 and CWM_{Total} litter Ca in 2014–2016 and 2021–2022 (Table 4). Post hoc tests were conducted when interactions were present to compare differences in least squares means among treatments; we used the ‘diffsmeans’ function within the ‘lmerTest’ R package, specifying Satterthwaite degrees of freedom, and report the values and corresponding t test statistic.

In the pre-treatment sampling period, a few species that were collected as foliage in the previous summer were not collected as litter because they did not fall into the nets during the sampling interval. These observations were imputed. Pre-treatment concentrations of N in leaf litter were imputed for four plot-species combinations (out of 167; 2%) and pre-treatment concentrations of Ca, P, K and Mg were imputed for 12 plot-species combinations (7%) using the ‘predictive mean matching’ method from the ‘mice’ (‘multiple imputation by chained equations’) package in R (www.r-project.org, Buuren and Groothuis-Oudshoorn 2011). Similarly, concentrations of Ca, P, K and Mg were imputed for four plot-species combinations (out of 168, 2%) in the 2016 litter.

To explore whether significant differences in community-weighted means were due to differences in species composition or within-species variation, we calculated interspecific CWM values (CWM_{Inter}). These values use the overall mean value of each species and convey the contribution of differences in species abundance to CWM_{Total} , and the contribution of intraspecific (within species) variation to CWM_{Total} (CWM_{Intra} ; Lepš et al. 2011). We ran linear mixed-effects models with the same fixed and random effects as the

CWM_{Total} models. CWM_{Inter} was calculated the same way as CWM_{Total} except that one study-wide species mean concentration was used instead of plot-specific means. Resulting differences among CWM_{Inter} were attributed to differences in species abundances across plots. Pre-treatment CWM_{Inter} was used as a covariate in these models. CWM_{Intra} was calculated by subtracting CWM_{Inter} from CWM_{Total} (Lepš et al. 2011), and pre-treatment CWM_{Intra} was also included as a covariate in models. Site was removed from overfit models when doing so removed the singularity or enabled convergence: these models included the following CWM_{Intra} models: foliar N (2021–2022), foliar P (2021–2022), litter P (2014–2016), litter Ca (2021–2022), litter K (2021–2022), and PRE (2014–2016; Supporting information). Post hoc tests were conducted when interactions were present, comparing differences in least squares means among treatments.

For six of the 2021–2022 models, stand effects were zero, which resulted in a singularity, functionally resulting in the testing of site and age at the plot level, rather than stand level. This is a form of pseudoreplication (Hurlbert 1984) and could result in the reporting of factors as significant when they are not. Stand age was not significant ($p > 0.05$) in any of these six models, but site was significant in the foliar P CWM_{Total} model; this result should be interpreted with caution. To test the effects of outliers, the CWM_{Intra} foliar K model from 2021–2022 was run with and without stand HBO. No transformations improved the normality of residuals for the model of CWM_{Intra} foliar N measured in 2021–2022 or the models of CWM_{Inter} for foliar N and P measured in 2014–2016, so the results of these models must be interpreted with caution.

Resorption efficiency of N and P were calculated for each species in 2014–2016 and in 2021–2022 using concentrations of nutrients in foliage and litter using the following equation (Vergutz et al. 2012)

$$NuRE = \left(1 - \frac{Nu_{sen} \times MLCF}{Nu_{gr}} \right) \times 100$$

where NuRE is the resorption efficiency of a nutrient, Nu_{sen} is the concentration of the given nutrient in senesced leaves (leaf litter), Nu_{gr} is the concentration of the nutrient in green foliage, and the MLCF is the mass loss correction factor (0.784 for deciduous angiosperms; Vergutz et al. 2012). These species-level resorption efficiencies were then used to calculate the CWM_{Total} , CWM_{Inter} , and CWM_{Intra} for N and P resorption efficiency. We ran linear mixed-effects models for each of these six CWM resorption efficiency variables with fixed effects including N, P, the interaction of N and P, site, stand age, and pre-treatment CWM, with stand as a random effect. Models for CWM_{Total} and CWM_{Intra} N resorption efficiency measured in 2021–2022 were run with and without stand C9 to compare the results with and without outliers. The model for CWM_{Intra} P resorption efficiency measured in 2021–2022 was run with and without C2 to compare results with and without outliers. Stand-level random effects for the P resorption efficiency model run with and without C2 were

zero; consequently, site and stand age were tested at the plot level instead of stand level and were interpreted with caution.

For all linear mixed-effects models run in this study, results were considered statistically significant if $p < 0.05$ and marginally statistically significant if $p < 0.10$. We interpreted both significant and marginally significant results.

Results

Foliar nutrients

Community-weighted foliar N increased with N addition and decreased with P addition by a similar magnitude in both 2014–2016 and 2021–2022. Specifically, CWM_{Total} N was 2.81 ± 0.4 mg g⁻¹ higher on average with N addition in 2014–2016 ($p < 0.01$; Table 2), 2.64 ± 0.55 mg g⁻¹ higher on average with N addition in 2021–2022 ($p < 0.01$; Table 3), 0.83 ± 0.4 mg g⁻¹ lower with P addition in 2014–2016 ($p = 0.02$; Table 2), and 1.2 ± 0.5 mg g⁻¹ lower with P addition in 2021–2022 ($p = 0.04$; Table 3, Fig. 3). These changes, and all other changes in foliar nutrient CWM_{Total} with N or P addition, were driven primarily by changes in CWM_{Intra} over time (Supporting information).

Community-weighted foliar P increased over time with P addition, but not by as much in the N+P treatment. CWM_{Total} P was 0.48 ± 0.03 mg g⁻¹ higher on average with P addition in 2014–2016 ($p < 0.01$ for the main effect of P; Table 2) and 0.10 ± 0.03 mg g⁻¹ lower on average with N addition in 2014–2016 ($p < 0.01$ for the main effect of N; Table 2), with no interaction between N and P ($p = 0.36$; Table 2). In 2021–2022, however, CWM_{Total} P was 0.9 ± 0.1 mg g⁻¹ higher on average with P addition alone than with no nutrient addition ($t = -13.01$, $p < 0.01$), but was only 0.6 ± 0.1 mg g⁻¹ higher with N+P addition than with no nutrient addition ($t = -8.52$, $p < 0.01$; Table 3, Fig. 3). With N addition, CWM_{Total} P was 0.04 ± 0.07 mg g⁻¹ lower than in the control treatment, but this difference was not statistically significant ($t = 0.53$, $p = 0.60$). Foliar P was higher, on average, at Hubbard Brook than at Bartlett Experimental Forest or Jeffers Brook both in 2014–2016 ($p = 0.046$; Table 2, Fig. 3) and in 2021–2022 ($p < 0.01$; Table 3, Fig. 3).

Community-weighted foliar Ca decreased with N addition and increased with P addition in both sampling periods. CWM_{Total} Ca was 0.57 ± 0.2 mg g⁻¹ lower with N addition in 2014–2016 ($p < 0.01$; Table 2) and 0.86 ± 0.3 mg g⁻¹ lower with N addition in 2021–2022 ($p < 0.01$; Table 3, Fig. 3). CWM_{Total} Ca was 0.60 ± 0.2 mg g⁻¹ higher with P addition in 2014–2016 ($p = 0.01$; Table 2) and 0.97 ± 0.3 mg g⁻¹ higher with P addition in 2021–2022 ($p < 0.01$; Table 3, Fig. 3). CWM_{Total} Ca was greater at Jeffers Brook than in Hubbard Brook or Bartlett Experimental Forest in 2014–2016 ($p = 0.01$; Table 2); no site-level differences were detected in 2021–2022 ($p = 0.95$; Table 2, Table 3, Fig. 3).

Community-weighted foliar K and Mg decreased with N addition in some sampling periods. CWM_{Total} K did not differ with nutrient addition in 2014–2016 but decreased with N

Table 2. The 3-to-5-year (2014–2016) foliar nitrogen, phosphorus, calcium, potassium, and magnesium responses to nutrient addition, site, and stand age, analyzed with linear mixed-effects models. The response variables are community-weighted means (CWM_{Total}). Sums of squares (SS) and numerator (Num) and denominator (Den) degrees of freedom (DF) are displayed. Fixed effects were N addition, P addition, stand age, pre-treatment foliar CWMs, site, and the interaction of N and P. Stand was a random effect. p values for significant results are in bold.

Fixed effect	SS	Num. DF	Den. DF	F	p
Nitrogen					
N	78.58	1	27	63.22	< 0.01
P	6.81	1	27	5.48	0.03
Age	0.49	1	8	0.39	0.55
Pre-N CWM	20.73	1	27	16.68	< 0.01
Site	0.53	2	7	0.21	0.81
N × P	0.64	1	27	0.52	0.48
Phosphorus					
N	0.10	1	26	13.41	0.01
P	2.26	1	26	307.93	< 0.01
Age	0.03	1	5	4.26	0.09
Pre-P CWM	0.11	1	22	14.48	< 0.01
Site	0.09	2	5	5.83	0.046
N × P	0.01	1	26	0.88	0.36
Calcium					
N	3.20	1	26	8.07	< 0.01
P	3.53	1	26	8.92	< 0.01
Age	0.01	1	5	0.03	0.87
Pre-Ca CWM	9.04	1	27	22.83	< 0.01
Site	9.05	2	6	11.42	0.01
N × P	0.01	1	26	0.03	0.87
Potassium					
N	0.18	1	27	0.33	0.57
P	1.12	1	27	2.09	0.16
Age	0.01	1	7	0.02	0.88
Pre-K CWM	15.59	1	23	29.11	< 0.01
Site	0.28	2	6	0.26	0.78
N × P	0.21	1	26	0.40	0.53
Magnesium					
N	0.10	1	27	4.10	0.053
P	0.02	1	27	0.73	0.40
Age	0.005	1	7	0.19	0.68
Pre-Mg CWM	0.995	1	14	40.22	< 0.01
Site	0.12	2	6	2.45	0.17
N × P	0.00	1	27	0.06	0.81

addition in 2021–2022; it was 0.58 ± 0.3 mg g⁻¹ lower on average ($p = 0.03$; Table 3, Fig. 3). CWM_{Total} Mg, however, was slightly lower with N addition in 2014–2016 ($p = 0.053$; Table 2), but did not differ with nutrient addition in 2021–2022 ($p = 0.15$; Table 3, Fig. 3).

For all five nutrients in all CWM calculations, pre-treatment concentrations were positively correlated with the concentrations measured during the treatment period ($p \leq 0.02$; Table 2, 3, Supporting information). Community-weighted P concentrations were 0.05 mg g⁻¹ higher in mid-successional stands than in late-successional stands in 2014–2016 ($p = 0.09$), otherwise, nutrient concentrations did not substantially differ with stand age ($p \geq 0.23$; Table 2, 3, Fig. 3).

Table 3. The 10-to-11-year (2021–2022) foliar nitrogen, phosphorus, calcium, potassium and magnesium responses to nutrient addition and stand age, analyzed using linear mixed-effects models. The response variables are community-weighted means (CWM_{Total}). Sums of squares (SS) and numerator (Num) and denominator (Den) degrees of freedom (DF) are displayed. Fixed effects were N addition, P addition, stand age, pre-treatment foliar CWMs, site, and the interaction of N and P. Stand was a random effect. *p* values for significant results are in bold.

Fixed effect	SS	Num. DF	Den. DF	F	<i>p</i>
Nitrogen					
N	69.49	1	27	23.32	< 0001
P	13.62	1	27	4.57	0.04
Age	2.50	1	7	0.84	0.39
Pre-N CWM	19.83	1	15	6.65	0.02
Site	9.80	2	6	1.64	0.27
N × P	1.32	1	27	0.4	0.51
Phosphorus					
N	0.28	1	32	12.54	0.01
P	5.47	1	32	243.13	< 0.01
Age	0.03	1	32	1.28	0.27
Pre-P CWM	0.15	1	32	6.68	0.02
Site	0.41	2	32	9.08	< 0.01
N × P	0.17	1	32	7.69	0.01
Calcium					
N	7.19	1	32	10.16	< 0.01
P	9.24	1	32	13.05	< 0.01
Age	1.05	1	32	1.48	0.23
Pre-Ca CWM	30.01	1	32	42.37	< 0.01
Site	0.07	2	32	0.06	0.95
N × P	0.11	1	32	0.16	0.69
Potassium					
N	3.25	1	25	5.09	0.03
P	0.38	1	25	0.59	0.45
Age	0.72	1	5	1.13	0.33
Pre-K CWM	7.57	1	21	11.86	< 0.01
Site	0.54	2	5	0.42	0.68
N × P	0.12	1	25	0.18	0.67
Magnesium					
N	0.75	1	32	2.20	0.15
P	0.00	1	32	0.11	0.74
Age	0.00	1	32	0.01	0.91
Pre-Mg CWM	2.43	1	32	72.28	< 0.01
Site	0.13	2	32	1.92	0.16
N × P	0.02	1	32	0.57	0.46

Litter nutrients

Community-weighted litter N increased with N addition and decreased with P addition in both 2014–2016 and 2021–2022 sampling periods. Specifically, CWM_{Total} N was $1.29 \pm 0.3 \text{ mg g}^{-1}$ higher on average with N-addition in 2014–2016 ($p < 0.01$; Table 4) and $1.58 \pm 0.3 \text{ mg g}^{-1}$ higher in 2021–2022 ($p < 0.01$; Table 5, Fig. 4). Litter CWM_{Total} N was $0.64 \pm 0.3 \text{ mg g}^{-1}$ lower with P addition in 2014–2016 ($p = 0.03$; Table 4) and $0.59 \pm 0.3 \text{ mg g}^{-1}$ lower in 2021–2022 ($p = 0.05$; Table 5, Fig. 4). These differences in litter N with nutrient addition, and all other differences in CWM_{Total} litter nutrients with N and P addition, were driven primarily by changes in CWM_{Intra} (Supporting information). Pre-treatment N was

positively correlated with litter N in 2021–2022 ($p < 0.01$; Table 5) but not 2014–2016 ($p = 0.13$; Table 4, Fig. 4). No differences due to stand age or site were detected ($p \geq 0.20$; Table 4, 5).

Community-weighted litter P, like foliar P, increased in the P-addition plots over time, but not by as much in the N+P as for P alone. CWM_{Total} P was $0.62 \pm 0.09 \text{ mg g}^{-1}$ higher in the P-addition plots than in the control plots in 2014–2016 ($t = -7.02$, $p < 0.01$) and $1.95 \pm 0.14 \text{ mg g}^{-1}$ higher in 2021–2022 ($t = -14.2$, $p < 0.01$), but only $0.19 \pm 0.09 \text{ mg g}^{-1}$ higher in the N+P plots than in the control plots in 2014–2016 ($t = -2.2$, $p = 0.04$) and only $0.95 \pm 0.1 \text{ mg g}^{-1}$ higher in 2021–2022 ($t = -7.3$, $p < 0.01$). Litter P did not differ between the control and N plots in 2014–2016 ($t = 0.06$, $p = 0.95$) or in 2021–2022 ($t = 0.18$, $p = 0.85$; Fig. 4). Pre-treatment litter P was not correlated with post-treatment litter P in 2014–2016 nor 2021–2022 ($p \geq 0.39$), and no differences due to stand age or site were detected ($p \geq 0.26$; Table 4, 5).

Community-weighted litter Ca was not detectably affected by N or P addition in 2014–2016 ($p \geq 0.11$; Table 4), but in 2021–2022, CWM_{Total} Ca decreased by $1.08 \pm 0.4 \text{ mg g}^{-1}$ with N addition ($p = 0.01$) and increased by $1.24 \pm 0.4 \text{ mg g}^{-1}$ with P addition, on average ($p < 0.01$; Table 5). CWM_{Total} Ca was $2.35 \pm 0.7 \text{ mg g}^{-1}$ higher in Jeffers Brook than Bartlett and $1.96 \pm 0.7 \text{ mg g}^{-1}$ higher in Jeffers Brook than Hubbard Brook (Fig. 3). In 2014–2016, litter Ca was higher in late-successional stands than mid-successional stands ($p = 0.04$; Table 4, Fig. 3), but it did not differ with age in 2021–2022 ($p = 0.48$; Table 5, Fig. 4). Pre-treatment litter Ca was correlated with litter Ca in both sampling periods (Table 4, 5, Fig. 4).

Community-weighted litter K was not detectably affected by N or P addition in 2014–2016, but in 2021–2022, CWM_{Total} K was $0.83 \pm 0.2 \text{ mg g}^{-1}$ higher in the P-addition plots ($p < 0.01$), though not detectably affected by N addition ($p = 0.54$; Table 5, Fig. 4). Litter K was highest in Bartlett Experimental Forest in 2014–2016 ($p = 0.09$; Table 4) and in 2021–2022 ($p = 0.08$; Table 5). Litter K did not differ with stand age ($p \geq 0.24$) and was positively correlated with pre-treatment K only for 2021–2022 ($p < 0.01$; Table 5).

Community-weighted litter Mg did not differ with N or P addition in either 2014–2016 ($p > 0.12$; Table 4, Fig. 3), but was lower with N addition in 2021–2022 ($p = 0.098$; Table 5, Fig. 4). Litter Mg was lower in Jeffers Brook than in Hubbard Brook and Bartlett in 2014–2016 (Table 4, Fig. 4). Litter Mg was higher at Jeffers Brook in 2021 than at Hubbard Brook in 2021 and Bartlett in 2022 (Table 5, Fig. 4). Litter Mg was not influenced by stand age ($p > 0.11$; Table 4, 5, Fig. 4) and was positively correlated with pre-treatment litter Mg for both 2014–2016 ($p < 0.01$; Table 4) and 2021–2022 ($p < 0.01$; Table 5).

N and P resorption efficiency

Community-weighted N resorption efficiency (NRE) did not differ with nutrient addition in the 2014–2016 sampling

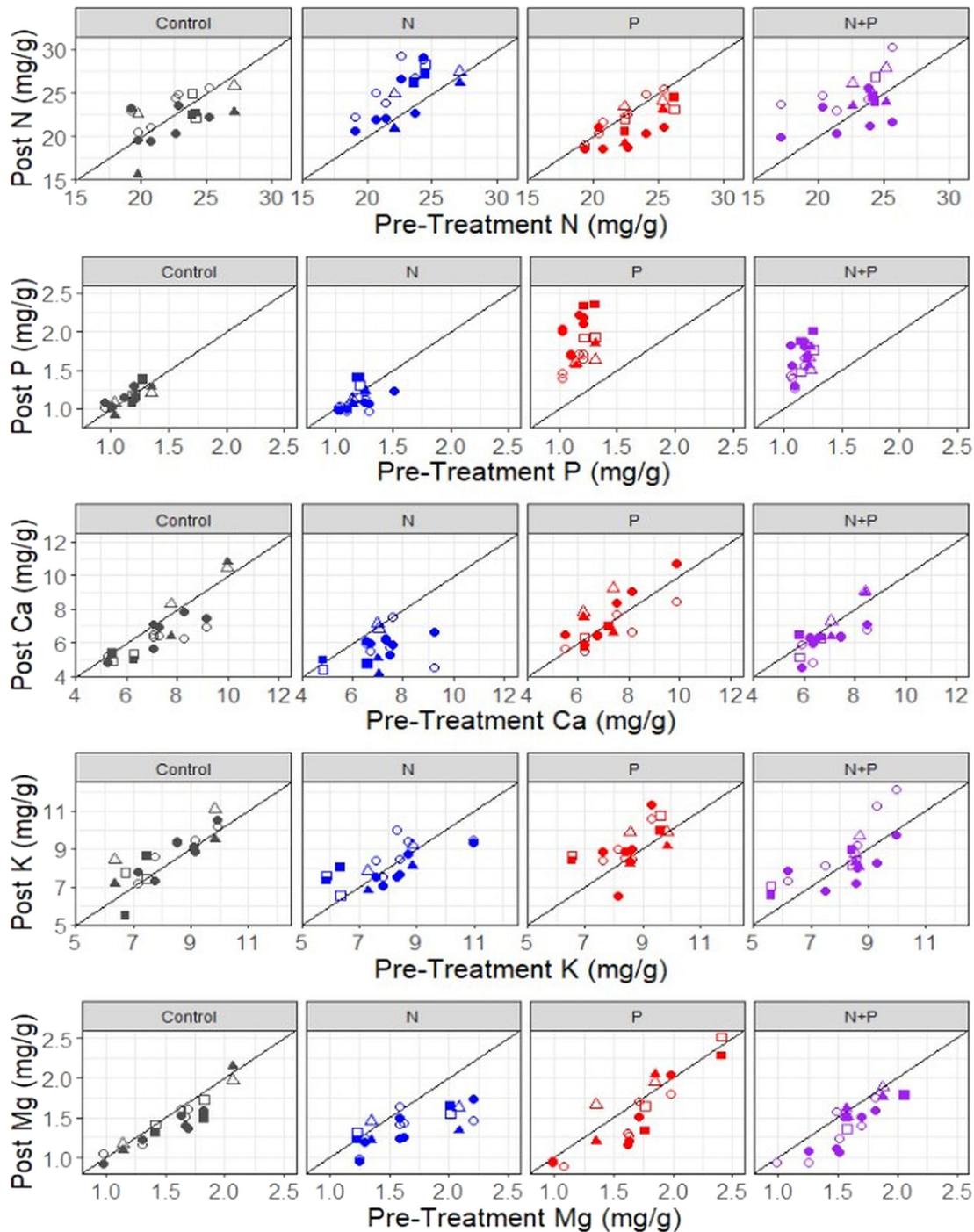


Figure 3. Foliar N, P, Ca, K and Mg concentrations measured before nutrient addition in 2008–2010 ('Pre-treatment') and after in 2014–2016 and 2021–2022 ('Post'). Each point is a plot, and values are community-weighted means. Circles represent Bartlett plots, squares represent Hubbard Brook plots, and triangles represent Jeffers Brook plots. Empty shapes are values from 2014–2016 and filled shapes are values from 2021–2022. Control plots are gray, N plots are blue, P plots are red, and N+P plots are purple.

period but decreased with N addition in 2021–2022 (Table 6, 7, Fig. 5). CWM_{Total} NRE was $2.6 \pm 1.1\%$ lower (expressed in absolute %) on average with N addition ($p=0.02$), and $2.2 \pm 0.9\%$ lower when excluding outlier stand C9 ($p=0.03$; Table 7, Fig. 5). These changes in NRE were driven by changes in CWM_{Intra} (Supporting information). NRE did

not differ across sites or with stand age and was correlated with pre-treatment NRE only in 2021–2022 ($p < 0.01$; Table 6, 7, Fig. 5).

In both sampling intervals, community-weighted P resorption efficiency (PRE) was lower in the P-addition compared to the control plots but did not differ with N

Table 4. The 3-to-5-year (2014–2016) litter nitrogen, phosphorus, calcium, potassium and magnesium responses to nutrient addition, stand age, and site, analyzed using linear mixed-effects models. Response variables are community-weighted means (CWM_{Total}). Sums of squares (SS) and numerator (Num) and denominator (Den) degrees of freedom are displayed. Fixed effects were N addition, P addition, stand age, pre-treatment litter CWMs, site, and the interaction of N and P. Stand was a random effect. p values for significant results are in bold and marginally significant results are in italics.

Fixed effect	SS	Num. DF	Den. DF	F	p
<i>Nitrogen</i>					
N	16.10	1	27	21.64	< 0.01
P	4.07	1	26	5.48	0.03
Age	0.93	1	8	1.25	0.30
Pre-N CWM	1.78	1	30	2.39	0.13
Site	0.80	2	7	0.54	0.61
N × P	1.76	1	27	2.37	0.14
<i>Phosphorus</i>					
N	0.46	1	26	11.86	< 0.01
P	1.63	1	27	41.82	< 0.01
Age	0.00	1	8	0.05	0.83
Pre-P CWM	0.03	1	32	0.75	0.39
Site	Excluded				
N × P	0.43	1	26	11.11	< 0.01
<i>Calcium</i>					
N	3.71	1	27	2.69	0.11
P	2.69	1	28	1.95	0.17
Age	8.53	1	7	6.19	0.04
Pre-Ca CWM	4.65	1	14	3.37	0.09
Site	Excluded				
N × P	0.74	1	26	0.54	0.47
<i>Potassium (ln)</i>					
N	0.21	1	27	2.79	0.11
P	0.01	1	27	0.13	0.72
Age	0.12	1	7	1.60	0.24
Pre-K CWM	0.07	1	32	0.96	0.33
Site	0.56	2	6	3.62	0.09
N × P	0.01	1	26	0.18	0.67
<i>Magnesium</i>					
N	0.06	1	27	2.34	0.14
P	0.07	1	29	2.54	0.12
Age	0.09	1	6	3.52	0.11
Pre-Mg CWM	1.44	1	9	53.6	< 0.01
Site	0.74	2	6	13.87	0.01
N × P	0.05	1	27	1.83	0.19

addition. CWM_{Total} PRE in 2014–2016 was $22.0 \pm 3.7\%$ lower (expressed in absolute %) in the P-addition plots than in the control plots ($t = 5.99$, $p < 0.01$), but did not differ among the control, N, and N+P plots (Fig. 5). In 2021–2022, PRE did not differ between the control and N plots ($t = -0.12$, $p = 0.90$), but was $65.4 \pm 5.2\%$ lower in the P-addition plots than in the control plots ($t = 12.6$, $p < 0.01$), and $38.8 \pm 5.2\%$ lower in the N+P plots than in the control plots ($t = 7.43$, $p < 0.01$; Table 6, 7, Fig. 5). CWM_{Total} PRE differed by site in 2014–2016 but not in 2021–2022; specifically, Jeffers Brook had a higher PRE than the other two stands ($p = 0.03$; Table 6, Fig. 5). These differences were driven by changes in within-species variation (Supporting information).

Table 5. The 10-to-11-year (2021–2022) litter nitrogen, phosphorus, calcium, potassium, and magnesium responses to nutrient addition, stand age, and site, analyzed using linear mixed-effects models. Response variables are community-weighted means (CWM_{Total}). Sums of squares (SS) and numerator (Num) and denominator (Den) degrees of freedom (DF) are displayed. Fixed effects were N and P addition, stand age, pre-treatment litter CWMs, site, and the N × P interaction. Stand was a random effect. p values for significant results are in bold and marginally significant results are in italics.

Fixed effect	SS	Num. DF	Den. DF	F	p
<i>Nitrogen</i>					
N	24.54	1	27	28.99	< 0.01
P	3.46	1	27	4.09	0.053
Age	1.70	1	8	2.01	0.20
Pre-N CWM	20.29	1	17	23.97	< 0.01
Site	1.60	2	7	0.95	0.44
N × P	1.86	1	27	2.20	0.15
<i>Phosphorus</i>					
N	2.36	1	27	25.33	< 0.01
P	21.45	1	27	230.37	< 0.01
Age	0.14	1	6	1.55	0.26
Pre-P CWM	0.04	1	23	0.44	0.52
Site	0.31	2	6	1.69	0.27
N × P	2.10	1	27	22.55	< 0.01
<i>Calcium</i>					
N	11.27	1	26	7.58	0.01
P	14.69	1	27	9.88	< 0.01
Age	0.85	1	6	0.57	0.48
Pre-Ca CWM	57.54	1	14	38.70	< 0.01
Site	Excluded				
N × P	0.01	1	25	0.00	0.95
<i>Potassium</i>					
N	0.19	1	26	0.39	0.54
P	6.74	1	26	13.85	< 0.01
Age	0.83	1	6	1.71	0.24
Pre-K CWM	9.16	1	11	18.82	0.01
Site	4.45	2	5	4.57	0.08
N × P	1.41	1	26	2.89	0.101
<i>Magnesium</i>					
N	0.13	1	27	2.94	0.098
P	0.02	1	28	0.35	0.56
Age	0.10	1	6	2.21	0.19
Pre-Mg CWM	0.84	1	14	18.78	< 0.001
Site	0.58	2	6	6.53	0.03
N × P	0.00	1	27	0.01	0.93

Discussion

Long-term responses of community-weighted foliar N and P to experimental additions of N and P indicated co-limitation more often than N or P limitation alone. In 2014–2016, changes in CWM_{Total} foliar N and P after ~ 5 years of nutrient addition were consistent with community co-limitation in that foliar N concentrations were suppressed by P addition and vice versa. In 2021–2022, however, after ~ 10 years of treatment, foliar N was suppressed by P addition, but foliar P was not affected by N addition alone, which indicates P limitation. There was, however, an interaction between N and P, such that foliar P was lower under the addition of both N and P than P alone. This interaction is consistent in part

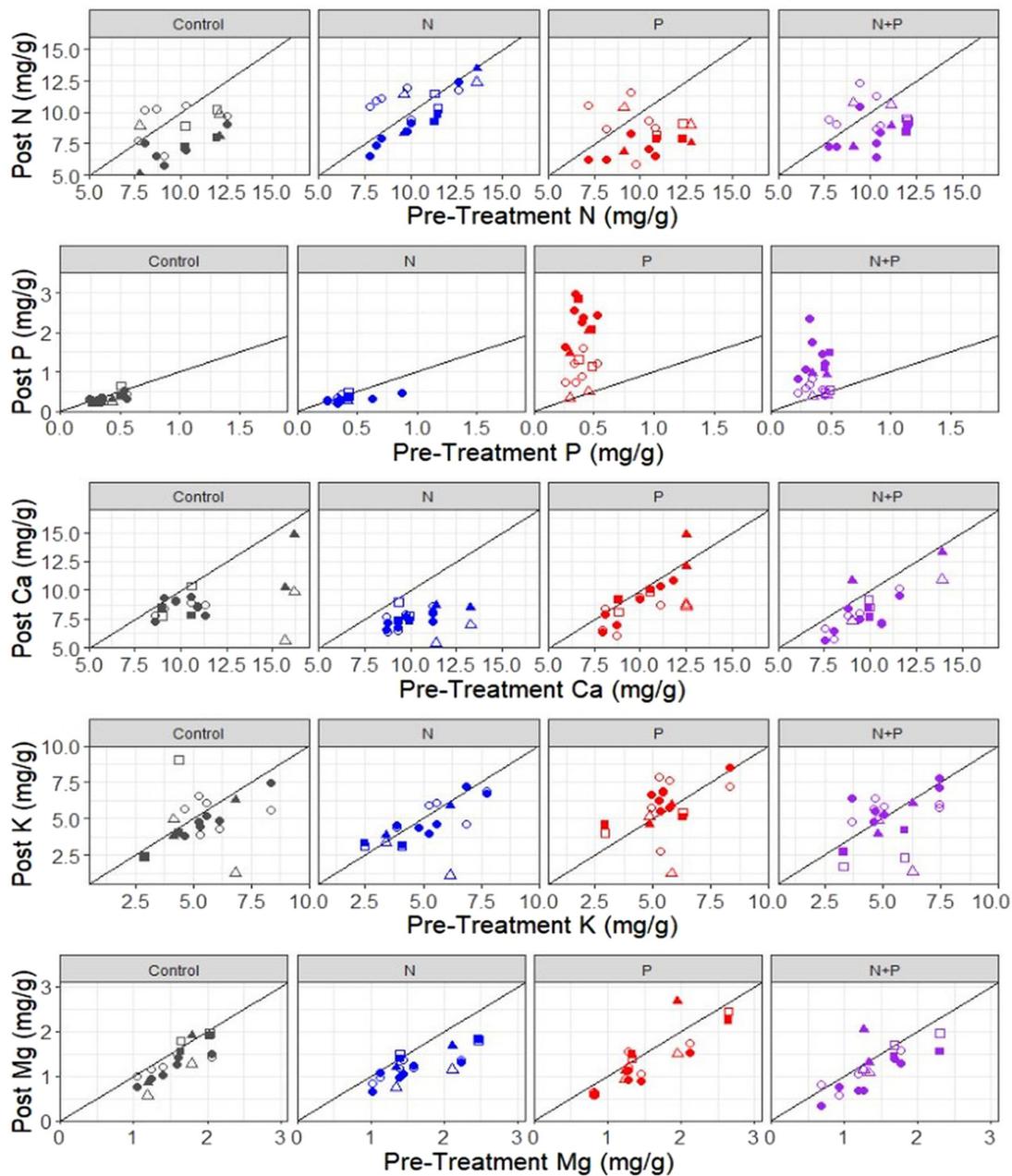


Figure 4. Litter N, P, Ca, K and Mg concentrations measured before nutrient addition in 2008–2010 ('Pre-treatment') and after in 2014–2016 and 2021–2022 ('Post'). Each point is a plot, and values are community-weighted means. Circles represent Bartlett plots, squares represent Hubbard Brook plots, and triangles represent Jeffers Brook plots. Empty shapes are values from 2014–2016 and filled shapes are values from 2021–2022. Control plots are gray, N plots are blue, P plots are red, and N+P plots are purple.

with biochemically dependent co-limitation, in which both elements increase the availability of the other when added (Bracken et al. 2015). There are several mechanisms by which N addition could increase P uptake in trees; some of these mechanisms include increased fine root production and turnover (Ma et al. 2021) and increased phosphatase production (Marklein and Houlton 2012). Indeed, before fertilization, phosphatase activity was higher in the MELNHE stands with greater N availability (Ratliiff and Fisk 2016). Moreover, in three late-successional MELNHE stands, an increase in

fine root growth was observed in response to N addition (Shan et al. 2022). Therefore, the increase in foliar P with N addition was probably associated with these mechanisms and could have offset decreases in foliar P due to dilution. When P was added in addition to N, the sufficiency of P in this treatment would presumably have reduced the value of these P-acquisition strategies, leading to a possible dilution effect as growth increased with the addition of both N and P. This result is consistent with results of a meta-analysis of responses of foliar N and P to nutrient addition

Table 6. The 3-to-5-year (2014–2016) N resorption efficiency (NRE) and P resorption efficiency (PRE) responses to nutrient addition, stand age, and site, analyzed using linear mixed-effects models. The response variables are community-weighted means (CWM_{Total}). Sums of squares (SS) and numerator (Num) and denominator (Den) degrees of freedom (DF) are displayed. Fixed effects were N addition, P addition, stand age, pre-treatment (2008–2010) resorption efficiency CWMs, site, and the interaction of N and P. Stand was a random effect. p values for significant results are in bold.

Fixed effect	SS	Num. DF	Den. DF	F	p
NRE					
N	3.88	1	26	0.34	0.57
P	3.02	1	26	0.26	0.61
Age	27.70	1	7	2.42	0.17
Pre-NRE CWM	7.96	1	29	0.70	0.41
Site	10.49	2	6	0.46	0.65
N × P	28.11	1	26	2.45	0.13
PRE					
N	673.06	1	27	9.98	< 0.01
P	1588.91	1	27	23.56	< 0.01
Age	1.41	1	6	0.02	0.89
Pre-PRE CWM	55.87	1	21	0.83	0.37
Site	895.20	2	6	6.64	0.03
N × P	830.83	1	27	12.32	< 0.01

(Ostertag and DiManno 2016) and with the latest tree inventory results, which indicated greater diameter growth in the N+P treatment than with N or P addition alone (Blumenthal unpubl.). This result did not quite suggest biochemically dependent co-limitation; rather, these results suggest that N addition may have increased acquisition of P, but P addition did not seem to affect acquisition of N. These results were driven by within-species variation (i.e. CWM_{Intra} analyses were significant but CWM_{Inter} analyses were not), indicating that these changes were due to changes in nutrient concentration in foliage with nutrient addition and not due to differences in species composition among plots or to changes in relative species abundance in plots over time.

Table 7. The 10-to-11-year (2021–2022) N resorption efficiency (NRE) and P resorption efficiency (PRE) responses to nutrient addition, stand age, and site, analyzed using linear mixed-effects models. The response variables are community-weighted means (CWM_{Total}). Sums of squares (SS) and numerator (Num) and denominator (Den) degrees of freedom (DF) are displayed. Fixed effects were N addition, P addition, stand age, pre-treatment (2008–2010) resorption efficiency CWMs, site, and the interaction of N and P. Stand was a random effect. The NRE model was re-run without C9 to remove an outlier; these results are shown in parentheses. p values for significant results are in bold and for marginally significant results are in italics.

Fixed effect	SS	Num. DF	Den. DF	F	p
NRE					
N	67.11 (41.33)	1	26 (23)	5.88 (5.73)	0.02 (0.03)
P	0.03 (6.27)	1	26 (23)	0.00 (0.87)	0.96 (0.36)
Age	23.41 (0.05)	1	7 (7)	2.05 (0.01)	0.20 (0.94)
Pre-NRE CWM	122.68 (61.45)	1	32 (28)	10.75 (8.51)	< 0.01 (0.01)
Site	28.61 (28.09)	2	6 (6)	1.25 (1.95)	0.35 (0.22)
N × P	9.22 (24.80)	1	26 (23)	0.81 (3.44)	0.38 (0.08)
PRE					
N	1857.8	1	26	13.90	< 0.01
P	26 692.3	1	26	199.71	< 0.01
Age	109.8	1	5	0.82	0.40
Pre-PRE CWM	48.5	1	22	0.036	0.55
Site	362.3	2	5	1.36	0.34
N × P	1646.7	1	26	12.32	< 0.01

A slightly higher CWM_{Total} P concentration in foliage in mid-successional stands than late-successional stands in 2014–2016 but not in 2021–2022 could reflect a change in species composition, as mid-successional stands initially had more pin cherry, which had higher foliar P concentrations (Supporting information), but many of these trees died between 2014–2016 and 2021–2022 (Fisk et al. 2022). The significant stand age effect for CWM_{Inter} P in 2014–2016 but not 2021–2022 further confirms this hypothesis (Supporting information). The same pattern was observed in CWM_{Total} Ca concentration in litter, and given the relatively high litter Ca concentrations in *Prunus pensylvanica* compared to late-successional species (Supporting information) and significance of stand age in CWM_{Inter} in 2014–2016 but not 2021–2022 (Supporting information), the same explanation may pertain. We did not detect any other effects of successional stage in this study.

Both foliar N and P increased with the addition of these respective nutrients. Foliar P was 41% higher under P addition in 2014–2016 and then 64% higher in 2021–2022, whereas foliar N was 12% higher under N addition in 2014–2016 but only 14% higher in 2021–2022, despite the continued addition of N. One possible interpretation is that N addition led to an increase in foliar biomass that could lead to increases in foliar N content but not concentration, whereas P concentrations may have continued to increase over time following P addition through ‘luxury consumption’ (van den Driessche 1974, Van Wijk et al. 2003). Indeed, N addition has been shown to increase canopy leaf area (Cramer et al. 2000, Zhang et al. 2018), which would contribute to greater foliar N content even in the absence of increased foliar N concentration. Forthcoming analyses of long-term leaf litter production will quantify the importance of this mechanism in the MELNHE study.

Other possible explanations for the greater increase of foliar P with P addition over time than foliar N to N addition could relate to the differences in N and P fertilization

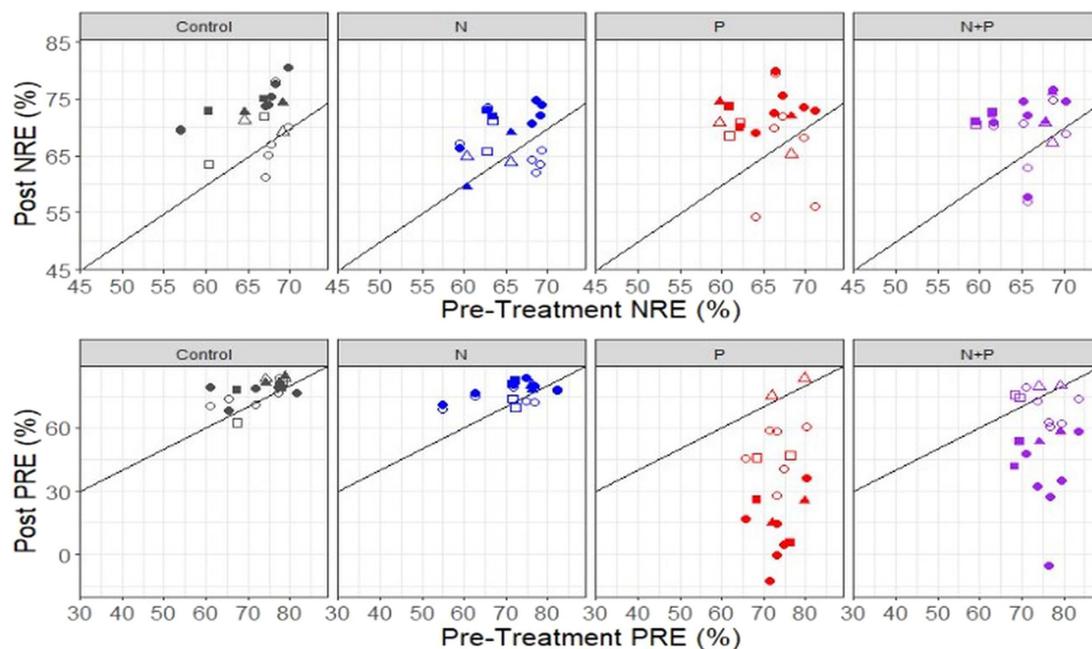


Figure 5. N resorption efficiency (NRE, %) and P resorption efficiency (PRE, %) measured before nutrient addition in 2008–2010 ('Pre-treatment') and after in 2014–2016 and 2021–2022 ('Post'). Each point is a plot, and values are community-weighted means. Circles represent Bartlett plots, squares represent Hubbard Brook plots, and triangles represent Jeffers Brook plots. Empty shapes are values from 2014–2016 and filled shapes are values from 2021–2022. Control plots are gray, N plots are blue, P plots are red, and N+P plots are purple.

treatments. Nitrate is more easily leached than is phosphate and N can also be denitrified (Mulvaney et al. 1997); thus, more of the applied N than P was likely lost from the ecosystem. Additionally, because the adsorption of P to iron- and aluminum-containing minerals, primarily in soil B horizons, makes P unavailable to plants (Wood et al. 1984), we added more P than N relative to plant demand. In our study, the fertilizer N:P ratio was 3:1, which is much more narrow than the ratios seen in plants; pre-treatment foliar N:P averaged 20:1 in the MELNHE study. Adding more P relative to demand than N could explain greater luxury consumption of P in the P-addition plots than N in the N-addition plots.

Changes in concentrations of N and P in leaf litter with nutrient addition resembled changes in foliar N and P. We expected that the resorption proficiency would decrease in the other nutrient following the addition of a limiting nutrient (Killingbeck 1996). A global meta-analysis of foliar and litter N and P concentrations in N and P-addition studies (Yuan and Chen 2015) revealed responses similar to ours: 1) increase in litter N with N addition, and no interaction between N and P; 2) greater increase in litter P with P addition; and 3) smaller increase in litter P with P addition when N and P were added together. The decrease in CWM_{Total} litter N with P addition in both 2014–2016 and 2021–2022 could indicate P limitation, whereas the lack of a decrease in CWM_{Total} litter P with N addition could indicate increased P availability stimulated by N addition. The lower litter P concentrations in N+P compared to P plots could indicate possible N limitation. In this way, the litter N and P results complement the

foliar N and P results, further suggesting co-limitation, and they can be explained by the same mechanisms.

Community-weighted NRE decreased over time with N addition, and community-weighted PRE decreased over time with P addition. We did not observe an increase in resorption efficiency of the other nutrient with the addition of either nutrient, as we had expected (Yan et al. 2018). A lack of an observed effect of nutrient addition on resorption of the other nutrient is consistent with results from a meta-analysis of N and P addition studies, which also showed a clearer response to nutrient addition of resorption proficiency (leaf litter concentration) than of resorption efficiency (Yuan and Chen 2015). Phosphorus resorption efficiency decreased by less with N+P addition than with P addition alone, though, which could be consistent with a dilution effect following greater overall tree growth in response to the addition of both N and P than P addition alone. Notably, community-weighted NRE decreased over time with N addition, and community-weighted PRE decreased over time with P addition, indicating a gradual down-regulation of resorption with cumulative nutrient loading.

Particularly striking was the much greater response of P than N resorption (both proficiency and efficiency) to nutrient additions (Fig. 4, 5) indicating greater plasticity of P resorption. Greater variability of P than N resorption has been widely observed (Aerts et al. 2012, Han et al. 2013) and partly attributed to basic differences in their cellular biochemistry. Most foliar N is in the form of chloroplast proteins which are readily catabolized by proteases and transported

as amino acids. In contrast, P is found in a wide variety of organic compounds – nucleic acids, lipids and esters – as well as inorganic forms, and each is catabolized by different pathways to mobile forms (Estiarte et al. 2022). This variety of P fractions and their degradation pathways may help explain the higher variation in P resorption, and it has been suggested that downregulation of PRE involves a lower percentage of a residual fraction being resorbed when P availability is high (Estiarte et al. 2022).

Previous analyses of N and P resorption (Gonzales and Yanai 2019, Gonzales et al. 2023) in the MELNHE study indicated that these stands were primarily P-limited, rather than co-limited, which was consistent with earlier reports of P limitation of tree growth (Goswami et al. 2018). The previous resorption studies, however, focused on a subset of stands (Gonzales and Yanai 2019) or only two species, rather than the community (Gonzales et al. 2023). Because the current study included data from more stands and species, and represents a sample with greater functional diversity across more site conditions, it is perhaps not surprising that CWM concentrations and resorption efficiencies indicated different nutrient limitation status. A re-analysis of the tree growth data from 2015 is also more consistent with co-limitation during the 2014–2016 sampling period than P limitation (Blumenthal et al. unpubl.), which was also reflected in foliar nutrient concentrations across more stands and all dominant species (Hong et al. 2022). In this way, indications of nutrient limitations from the most comprehensive analyses of foliar and litter nutrient concentrations in MELNHE are consistent in both 2014–2016 and 2021–2022 with the latest analyses of the tree inventory data, which all provide evidence for co-limitation of N and P.

The decrease in community-weighted foliar Ca and K with N addition could provide further evidence for N limitation in these forests, if these decreases are interpreted as a dilution effect. It is important to also consider the potential acidifying effect of ammonium nitrate, which has been associated with decreases in soil base cation concentrations (Lucas et al. 2011, Tian and Niu 2015, Moore and Houle 2023). A meta-analysis of N-addition studies showed significant acidifying effects of N addition rates exceeding 50 kg ha⁻¹ year⁻¹ (Tian and Niu 2015), but not for the 30 kg ha⁻¹ year⁻¹ rate applied in the MELNHE plots. Soil base cation concentrations and pH were measured in MELNHE plots in 2017, while pH in the top 10 cm of the mineral soil decreased by 0.2 following N addition between 2009 and 2017 (Fisk 2022), concurrent decreases in exchangeable soil Ca and K concentrations were not observed (Walsh 2022). Therefore, while ammonium nitrate may have acidified the soil by 2021–2022, there is little evidence for this in the soil data we have to date and there is evidence for N limitation, which would also be consistent with a decrease in Ca and K due to a dilution effect (Hong et al. 2022).

The increase in foliar and litter Ca with P addition was perplexing, particularly if P is also limiting and might be expected to have a diluting effect on Ca (Jarrell and Beverly 1981). Increases in Ca or soil pH in previous P-addition

studies (Reinbott and Blevins 1994, Siedliska et al. 2021) could be due to the Ca contained in many P fertilizers. We use monosodium phosphate instead of conventional P fertilizer to avoid adding the Ca contained in all superphosphate products. However, an increase in Ca concentrations in foliar tissues has also been observed following the addition of iron phosphate (Li et al. 2004) and monosodium phosphate (Nichols and Beardsell 1981), suggesting that phosphate itself may somehow influence foliar Ca concentrations. Our results therefore suggest a synergistic coupling of Ca and P that warrants further investigation.

The increase in litter K with P addition is also unexpected and might suggest a coupling of K and P. The incorporation of P into phospholipid bilayers and susceptibility of K to leaching might suggest a connection between cell membranes and leachability of K. Because it doesn't form covalent bonds, K easily passes through cell membranes (Schreeg et al. 2013, Sardans and Peñuelas 2015). Phosphorus nutrition of plants can influence the permeability of phospholipid bilayer cell membranes; in particular, plants grown in low-P soils had more permeable cell membranes than those grown in soils with higher P availability (Knowles et al. 2001). It may be that P addition increased membrane impermeability, decreasing the loss of K through leaching in P-treated litter. Examining how the different foliar P pools (Tsuji et al. 2017) change with P addition, and whether P addition in this study led to an increase in the lipid fraction, would help confirm this hypothesis.

Higher foliar Ca and litter Ca at Jeffers Brook compared to Hubbard Brook and Bartlett Experimental Forest is likely due to differences in soil parent material, as Jeffers Brook was chosen for its presumed higher soil fertility. Other site differences, such as the higher foliar P at Hubbard Brook (Rangely schist), higher litter K at Bartlett Experimental Forest (Conway and Osceola granites), and changes in which site had the highest foliar and litter Mg, are more difficult to explain. Note that Hubbard Brook and Jeffers Brook were sampled in 2021 but Bartlett was sampled in 2022, which means that these apparent differences might be due to the year of sampling. Interannual variation in foliar nutrient concentrations may occur due to changes in soil water driven by interannual differences in precipitation (Moore and Ouimet 2006, Braun et al. 2020). Unfortunately, it was not possible to sample all the sites in a single year.

In conclusion, our results provide further evidence to support the hypothesis that these northern hardwood forests are co-limited by N and P, illuminate possible mechanisms by which this co-limitation is achieved, and reveal biogeochemical linkages among several macronutrients. The 2014–2016 reduction of foliar N and P to the addition of the other nutrient clearly indicated community co-limitation. The 2021–2022 results also indicated co-limitation, but the response of foliar and litter P to N addition was more consistent with biochemical co-limitation. The effects of N+P on foliar P and PRE in 2021–2022 indicated a potential dilution effect consistent with greater tree growth with N+P addition than with N or P addition alone in the MELNHE study (Blumenthal et al.

unpubl.). Decreases in foliar Ca with N addition and increases in foliar Ca with P addition suggest interactions with N and P cycling that are worth investigating further.

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Jenna M. Zuskwert: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Visualization (lead); Writing - original draft (lead); Writing - review and editing (equal). **Timothy J. Fahey:** Conceptualization (equal); Funding acquisition (supporting); Investigation (supporting); Writing - review and editing (equal). **Matthew A. Vadeboncoeur:** Conceptualization (equal); Funding acquisition (supporting); Investigation (supporting); Writing - review and editing (equal). **Daniel S. Hong:** Conceptualization (equal), Data curation (support), Investigation (support), Methodology (support), Writing - review and editing (equal). **Ruth D. Yanai:** Conceptualization (equal); Funding acquisition (lead); Investigation (supporting); Writing - review and editing (equal).

Data availability statement

Data are available from the Environmental Data Initiative: foliar data: <https://doi.org/10.6073/pasta/ef3696a753150d0a420fd9009f73b1e9>, and litter data: <https://doi.org/10.6073/pasta/f52a613213855e4b4a03fa4a0e2f2922>

Supporting information

The Supporting information associated with this article is available with the online version.

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