Ecology, 99(2), 2018, pp. 438–449

Phosphorus limitation of aboveground production in northern hardwood forests

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Abstract. Forest productivity on glacially derived soils with weatherable phosphorus (P) is expected to be limited by nitrogen (N), according to theories of long-term ecosystem development. However, recent studies and model simulations based on resource optimization theory indicate that productivity can be co-limited by N and P. We conducted a full factorial N × P fertilization experiment in 13 northern hardwood forest stands of three age classes in central New Hampshire, USA, to test the hypothesis that forest productivity is co-limited by N and P. We also asked whether the response of productivity to N and P addition differs among species and whether differential species responses contribute to community-level co-limitation. Plots in each stand were fertilized with 30 kg $\mathrm{N \cdot ha^{-1} \cdot yr^{-1}}$, 10 kg $\mathrm{P \cdot ha^{-1} \cdot yr^{-1}}$, N + P, or neither nutrient (control) for four growing seasons. The productivity response to treatments was assessed using per-tree annual relative basal area increment (RBAI) as an index of growth. RBAI responded significantly to P ($P = 0.02$) but not to N ($P = 0.73$). However, evidence for P limitation was not uniform among stands. RBAI responded to P fertilization in mid-age ($P = 0.02$) and mature ($P = 0.07$) stands, each taken as a group, but was greatest in N-fertilized plots of two stands in these age classes, and there was no significant effect of P in the young stands. Both white birch (*Betula papyrifera* Marsh.) and beech (*Fagus grandifolia* Ehrh.) responded significantly to P; no species responded significantly to N. We did not find evidence for N and P co-limitation of tree growth. The response to N + P did not differ from that to P alone, and there was no significant N × P interaction ($P = 0.68$). Our P limitation results support neither the N limitation prediction of ecosystem theory nor the N and P co-limitation prediction of resource optimization theory, but could be a consequence of long-term anthropogenic N deposition in these forests. Inconsistencies in response to P suggest that successional status and variation in site conditions influence patterns of nutrient limitation and recycling across the northern hardwood forest landscape.

Key words: aboveground productivity; co-limitation; nitrogen; northern hardwoods; nutrient fertilization; phosphorus.

Introduction

Availability of mineral nutrients constrains primary productivity in many ecosystems. Because phosphorus is obtained from weathering and nitrogen is fixed by biota, ecosystem theory has suggested that productivity should be limited by N on young soils and P on older soils (Walker and Syers 1976, Vitousek 2004); thus, forest productivity on young, glacially derived soils is expected to be N limited. However, evidence of a greater response to N and P together than to either alone across terrestrial and aquatic ecosystems (Elser et al. 2007) raises questions about controls of ecosystem productivity. Resource optimization theory suggests that plants adjust their physiology to minimize limitation by any single resource, allocating effort to acquire the more limiting resources such that eventually plant growth is co-limited by multiple resources (Bloom et al. 1985, Chapin et al. 1987, 2002). However, there are limits to what plants can do to obtain limiting resources, and even when they are capable of achieving co-limitation, it may take time to adjust the allocation of effort when resource availability changes, as with forest succession or atmospheric deposition.

Some previous fertilization studies conducted in the northeastern United States support the idea that productivity in these forests is primarily N limited (Safford 1973, Magill et al. 2000, 2004, Finzi 2009), whereas others indicate P limitation or N and P co-limitation (Lea et al. 1979, Auchmoody 1982, Safford and Czapowskyj 1986). Meta-analyses suggest that productivity in most ecosystems is N and P co-limited (Elser et al. 2007,

Manuscript received 23 January 2017; revised 15 November 2017; accepted 17 November 2017. Corresponding Editor: Anthony W. D'Amato.

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Harpole et al. 2011), but temperate forests were not well represented (4 out of ~100 terrestrial studies) in those meta-analyses. The Multiple Element Limitation model (MEL; Rastetter et al. 2013) suggests, from a theoretical perspective, that N-P co-limitation should eventually prevail as forests develop after large-scale disturbance. A recent meta-analysis for the northeastern United States showed evidence for both N and P limitation (Vadeboncoeur 2010), though few previous studies in this region have had the factorial design necessary to test co-limitation.

Co-limitation can arise from several different mechanisms such as those outlined in the framework by Harpole et al. (2011). Co-limitation by N and P could be "synergistic" when the response to N and P added together (N + P) is greater than the sum of the responses to each nutrient added alone, "additive" when the response to N + P is equal to the sum of the individual responses, or "sub-additive" when the N + P response is less than the sum of the single nutrient responses. In contrast, when the response to the secondary limiting nutrient occurs only after alleviating limitation by the primary limiting nutrient, "sequential" limitation (Davidson and Howarth 2007, Craine 2009) can also give rise to apparent N-P co-limitation.

One instance of additive co-limitation is "community-level" co-limitation that can occur when some species respond primarily to N and others to P (Arrigo 2005). Species traits can influence ecosystem productivity by altering the availability or use of limiting resources (Chapin and Shaver 1985, Chapin et al. 1986, 1987). Tree species can modify their local environment through particular life history and physiological traits, such as shade tolerance, mycorrhizal associations, litter chemistry, and canopy interception (Augusto et al. 2002, Reich et al. 2005, Lang and Polle 2011). Different species in a forest ecosystem can also be limited by different resources as a consequence of traits influencing nutrient acquisition, conservation, and use efficiency. For example, northern hardwood forests have mixtures of tree species that form either ectomycorrhizal (ECM) or arbuscular mycorrhizal (AM) associations, and changes in N or P availability may have differential effects on the growth of AM vs. ECM trees. Therefore, it is important to determine whether individual species that differ in their life history traits and resource use respond differently to the addition of N, P, and N + P, thereby influencing nutrient co-limitation at the ecosystem level, when responses of all species are summed.

Understanding the dynamics of nutrient limitation is especially important in managed and anthropogenically altered ecosystems because nutrient inputs and outputs differ from the conditions under which these systems developed. Managed forests have been subject to nutrient removal due to biomass removal and post-disturbance nutrient export (Federer et al. 1989). Additionally, forest ecosystems in the northeastern United States have been exposed to long-term anthropogenic N deposition, which has altered soil properties and nutrient cycling processes (Fenn et al. 1998, Aber et al. 2003). Simultaneously, acid deposition has accelerated leaching loss of base cations (Bailey et al. 1996, Likens et al. 1996, 1998, Lawrence et al. 1997), promoting soil acidification and possibly altering soil P availability (Fiorentino et al. 2003). Biomass removal coupled with high NO_3^- leaching and increased potential for soil P immobilization when total plant nutrient uptake is low during forest regeneration (Fisk and Fahey 1990, Yanai 1992). As a consequence, forest harvest can decrease N and P availability in these forests (Bormann and Likens 1979) and disrupt the N:P balance (Rastetter et al. 2013). The MEL model predicted a shift from N to P limitation as northern hardwood forests recover from harvesting disturbance, until recycling of N and P become stoichiometrically balanced (Rastetter et al. 2013). Hence, our understanding of nutrient co-limitation would benefit from the study of nutrient dynamics at different stages of succession in a managed forest landscape comprised of multiple stand ages. Furthermore, management effects and changes with succession should be considered in the broader context of anthropogenic effects. In these forests, it appears that anthropogenic enrichment of N could lead to transactional limitation by P (Vitousek et al. 2010), wherein the slow transfer of P from primary mineral form into biotically recycling pools is insufficient to balance high N inputs, leading to P limitation of productivity (Mohren et al. 1986, Aber et al. 1989, Stevens et al. 1993, Vitousek et al. 2010).

A conclusive test of whether productivity in northern hardwood forests is limited by a single nutrient or is co-limited by N and P requires a large-scale, long-term ecosystem study evaluating forest response to a full factorial N × P treatment. We initiated a fertilization experiment in 13 northern hardwood forest stands in three sites in central New Hampshire in 2011. Our main goal was to test the hypothesis that northern hardwood forest productivity is co-limited by N and P, in which case we would expect tree growth to increase in response to addition of N and P together more than to either nutrient alone. We asked the following questions: (1) Is tree growth co-limited by N and P or is growth limited singly by either N or P? (2) Does the limiting nutrient differ with time since large-scale disturbance (forest harvest)? (3) Does the growth of different tree species respond to different nutrients?

METHODS

We studied 13 northern hardwood forest stands at three different sites located on soils formed in glacial drift in central New Hampshire, USA (Table 1): nine at the Bartlett Experimental Forest (BEF) and two each at Hubbard Brook Experimental Forest (HBEF) and Jeffers Brook (JB). Climate in the study region is humid continental with mean temperatures of −9°C in January and 19°C in July (at 450 m elevation). The mean annual precipitation is approximately 140 cm evenly distributed throughout the year. During the study period mean

TABLE 1. Characteristics of 13 northern hardwood forest stands in central New Hampshire, USA.

Stand	Forest age	Year clearcut	Elevation	Aspect	Slope (%)	Pre-treatment (2011) basal area (m^2/ha)
BEF-C1	young	1990	570	SE	5–20	25.1
BEF-C2	young	1988	340	NE	15–30	23.4
BEF-C3	young	1982–1985	590	NNE	8–20	30.4
BEF-C4	mid-age	1979	410	NE	20–25	32.4
BEF-C5	mid-age	1976	550	NW	20–30	27.2
BEF-C6	mid-age	1975	460	NNW	13–20	29.9
BEF-C7	mature	1890	440	ENE	5–10	32.1
BEF-C8	mature	1883	330	NE	5–35	34.6
BEF-C9	mature	1890	440	NE	10–35	32.7
HB-mid	mid-age	1970	500	S	10–25	28.9
HB-mature	mature	1911	500	S	25–35	33.9
JB-mid	mid-age	~1975	730	WNW	25–35	27.9
JB-mature	mature	1915	730	WNW	30–40	35.6

Note: Aspects are SE, southeast; NE, northeast; NNE, north-northeast; NNW, north-northwest; ENE, east-northeast; S, south; WNW, west-northwest.

July–August temperature was approximately 1°C higher than the long-term mean (1901–2000; NOAA 2017) and mean July–August precipitation was 10 cm higher than the long-term mean (1901–2000; NOAA 2017), consistent with long-term climate change in the region (Hamburg et al. 2013). The maximum inter-annual variability in climate during the study duration was 0.8°C in temperature and approximately 6 cm in precipitation. Also, the summers in the years 2012 and 2014 were relatively dry. Soils are Typic and Aquic Haplorthods overlying glacial drift (deposited approximately 14,000 yr ago) originating primarily from granitic rock at BEF, granodiorite and schist at HBEF, and amphibolite at JB. The soils have thick surface organic horizons (~5 cm average depth; Vadeboncoeur et al. 2012*a*) with low pH, varying from 4.1–4.7 (Ratliff and Fisk 2016). More detailed descriptions of soil chemistry from quantitative pits can be found in Vadeboncoeur et al. (2012*a*, 2014).

These 13 forests stands included three each of young (21–25 yr), mid-age (30–40 yr), and mature (>100 yr) forests at BEF and one mid-age and one mature each in HBEF and JB (Table 1). Forest age is given as the time between clear-cut harvest and the year 2011 when treatments began. Young, mid-age, and mature forest ages were chosen to represent different stages of stand development in which nutrient demand might differ (Rastetter et al. 2013). We note that the mature stands are primarily "second growth" whereas the young and mid-age stands are primarily "third-growth" in terms of historical clear-cutting. Forest composition is typical of northern hardwood stands in each age class (Fig. 1). Mature forests were dominated by sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghniensis* Britton), with occasional white ash (*Fraxinus americana* L.), white birch (*Betula papyrifera* Marsh.), and red maple (*Acer rubrum* L.). Mid-age forests were generally dominated by white birch, yellow birch, and American beech, followed by pin cherry (*Prunus pensylvanica* L.f.), red maple, and bigtooth aspen (*Populus grandidentata* Michx.). Pin cherry, white birch, and red maple dominated the young forests. Species composition of northern hardwood forests in this region varies owing to differences in native soil fertility associated with mineralogy and texture of glacial tills and variation in hydrology and soil development (Leak 1991), as well as to past management (Vadeboncoeur et al. 2012*b*). Stand basal areas and stem size distributions show typical successional changes during stand development (Fig. 2).

Four 50 × 50 m plots were established in each stand (except for two stands, HB-mid and JB-mid, where plots

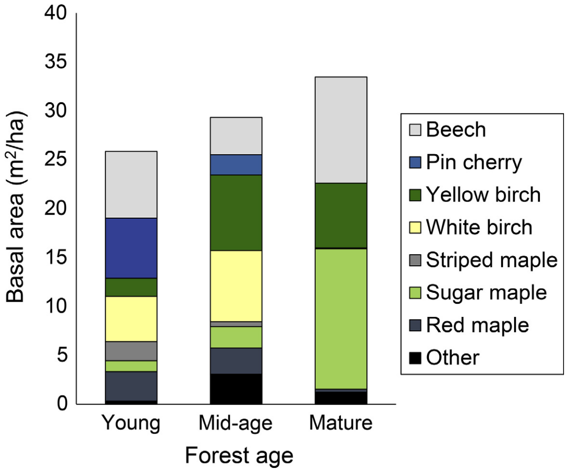

FIG. 1. Basal area of live trees by species in 2011 in young, mid-age, and mature forest stands. Species constituting <15% of the forest basal area include white ash (*Fraxinus americana*), bigtooth aspen (*Populus grandidentata*), quaking aspen (*Populus tremuloides*), balsam fir (*Abies balsamea*), eastern hemlock (*Tsuga canadensis*), northern red oak (*Quercus rubra*), and red spruce (*Picea rubens*), and have been combined and presented as the category "Other."

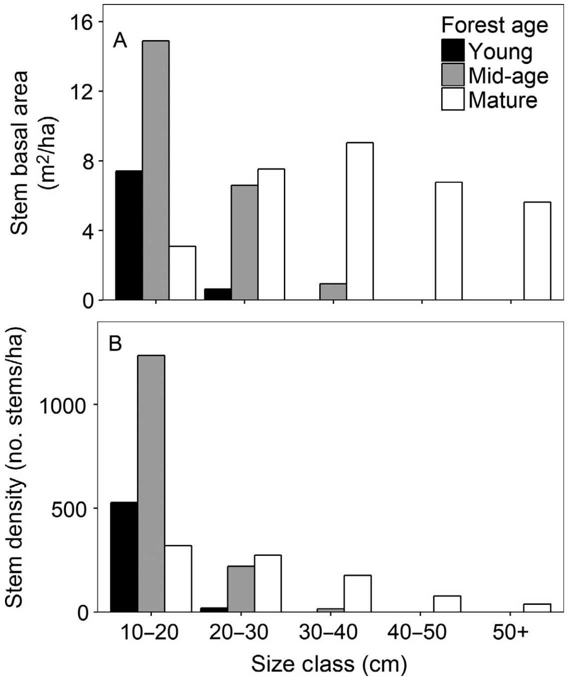

FIG. 2. (A) Basal area and (B) stem density of live trees ≥10 cm DBH by size class in young, mid-age, and mature forest stands.

were 30 × 30 m, limited by the extent of the even-aged stand), and randomly assigned to control, N, P, and N + P fertilizer treatments. Fertilizer was applied to the entire 50 × 50 m plot; measurements were made in the inner 30 × 30 m area (20 × 20 m in the smaller plots). Nutrient additions began in spring 2011. N was added at a rate of 30 $kg \cdot ha^{-1} \cdot yr^{-1}$ as pelletized NH_4NO_3 and P was added at a rate of 10 $kg \cdot ha^{-1} \cdot yr^{-1}$ as powdered or granular NaH_2PO_4. N and P were applied twice (early June and mid-July) in the first three years and once (early June) annually thereafter. Fertilizer was pre-weighed for 2.5 × 10 m sub-plots and spread evenly by hand.

Fertilization successfully elevated in-situ resin-available N and P in 2011, the first year of treatment (Fisk et al. 2014), and we repeated this assay of soil nutrient availability in 2015. We incubated ion-exchange resin strips (2 × 6 cm) in situ during the last two weeks of July 2015, approximately one month after fertilization, following the same method as Fisk et al. (2014). We used cation exchange resin strips (Ionics CR67-HMR; Maltz Sales, Foxboro, Massachusetts, USA) to quantify NH_4^+ and anion exchange resin strips (Ionics AR-204-SZRA; Maltz Sales, Foxboro, Massachusetts, USA) to quantify PO_4^{3-} and NO_3^-. Cation strips and anion strips for NO_3^- were prepared by rinsing in HCl and deionized (DI) H_2O followed by soaking in 1 mol/L NaCl. Anion strips for PO_4^{3-} were prepared by alternating rinses in DI H_2O and 0.5 mol/L $NaHCO_3$. All strips were rinsed with DI H_2O immediately prior to placement in the field. Eight strips per plot were deployed for each nutrient by inserting under the blade of a knife into the organic horizon at a 30°–45° angle from horizontal. Strips were retrieved after 14 d and rinsed in DI H_2O prior to extraction for nutrient analyses. Absorbed NO_3^- and NH_4^+ were extracted with 1 mol/L KCl and PO_4^{3-} was extracted with 0.5 mol/L HCl. Concentrations of NO_3^- and NH_4^+ in the extracts were quantified using an autoanalyzer (Quikchem 8500, Lachat Instrument, Milwaukee, Wisconsin, USA). Concentrations of PO_4^{3-} were analyzed with the ammonium-molybdate-ascorbic acid method (Murphy and Riley 1962).

Leaf litterfall mass and nutrient concentrations were quantified in 2012 in all but one young and one mid-age stand and litterfall mass was also quantified in 2014. Leaf litter was collected in five litter traps (each with a collection area of 0.23 m^2) per plot, approximately weekly throughout the autumn. Litter mass was quantified after oven-drying to constant mass at 60°C. Litter in 2012 was finely ground, ashed at 470°C, digested in 6 mol/L HNO_3, and P concentrations were analyzed using ICP-OES. Nitrogen concentrations were analyzed on a Flash 2000 NC soil analyzer (ThermoScientific, Waltham, Massachusetts, USA).

Forest composition and basal area (Table 1) were quantified in all 52 plots in August of 2011 (in the first year of treatment) and in August 2015, four growing seasons later. All trees ≥10 cm diameter at breast height (DBH) were measured in each plot. Stems <10 cm DBH accounted for the majority of total basal area in young stands but the absence of repeated measurements on individually identified trees, combined with mortality during the study period, precluded estimation of growth in young trees belonging to this size class. We calculated the annual relative basal area increment (hereafter, RBAI) of each ≥10.0 cm DBH stem as follows: $RBAI = ((1+((BA_P-BA_I)/BA_I))^{(1/n)}-1)$, where BA_P = 2015 stem basal area, BA_I = 2011 stem basal area, and n = number of growing seasons of growth observed (four). We also estimated relative density of our stands with species-specific equations developed by Ducey and Knapp (2010) for northeastern U.S. mixed-species forests. These equations estimated relative density of a stand using stem numbers, diameters, and species-specific wood density, which is a functional trait that can affect tree allometry and biomass accumulation relative to tree volume in mixed species forests (Ducey and Knapp 2010, Woodall et al. 2015). Hence, this estimate of relative density is intended to indicate the potential for further biomass accumulation in a forest stand.

Data analysis

We tested treatment effects on resin-available N and P, litter N and P, average-per-plot RBAI, and individual species RBAI using a linear mixed-effects model (nlme package in R; Pinheiro et al. 2016) with treatment (N or P addition) and forest age as fixed effects and forest site (BEF, HBEF or JB) and stand (nested within forest site) as random effects. Forest plot was used as a unit of replication ($n = 52$). This factorial approach compares response variables in plots with N addition (i.e., N and N + P plots) to those with no N addition (i.e., control and P plots) and plots with P addition to those with no P addition, and also tests the interaction between N and P additions. We used post-hoc Tukey comparisons of least-squares means to test the differences between addition of N + P and either N or P alone. We considered P values <0.05 to be significant but also report trends for which P values were between 0.05–0.10.

Nutrient limitation was inferred if RBAI in treated plots exceeded that in control plots following N and P fertilization. A higher response to N + P added together than to either nutrient alone would indicate N and P co-limitation of aboveground growth. A statistically significant N × P interaction would indicate synergistic co-limitation, whereas a significantly higher response to N + P together than to either nutrient alone would indicate additive co-limitation. Additive co-limitation could be interpreted as sequential if one nutrient, but not the other, elicited a response when added separately.

The RBAI for individual species was analyzed for species that occurred in more than 60% of the total 52 study plots, using the same approach as for the average-per-plot RBAI. Community-level co-limitation would be inferred if co-limitation were detected at the ecosystem (plot) level and species were limited by different nutrients. Species were also segregated by mycorrhizal association (AM [maples, cherries, and ash] or ECM [beech, birches, oak, basswood, and conifers]) to test for differences in RBAI between these two groups and in group response to treatment.

Because RBAI varied in relation to tree diameter, within a forest age class, we tested for differences in pre-treatment plot-average DBH. We detected no differences in pre-treatment DBH among treatments within each of the forest age classes. Species also did not differ in their pre-treatment plot-average DBH or number of individuals per plot between treatments across our stands, with the exception of white ash, eastern hemlock and yellow birch in the mature stands; however, these three species did not show any growth response to either N or P. Therefore, differences in size distributions among plots, overall or within individual species did not bias our interpretation of tree increment responses to nutrient addition.

RESULTS

Ecosystem-level responses

Treatments successfully elevated nutrient availability. Resin-available N in the organic soil horizon (forest floor) was higher in plots receiving N compared with those receiving no N ($P = 0.001$) and resin-available P was higher in plots receiving P vs. no P ($P = 0.02$). There was no N × P interaction on resin-available N ($P = 0.29$) or P ($P = 0.88$). Litter N concentrations were higher in plots receiving N compared with those receiving no N in 2012, after two years of treatment ($P = 0.01$) and litter P concentrations were higher in plots with P vs. no P ($P < 0.0001$). There were no N × P or forest age interactions on litter nutrient concentrations.

Litterfall mass differed by forest age in 2012 ($P = 0.03$) but not in 2014, and did not respond to treatments in either year ($P \geq 0.65$ in 2012; $P \geq 0.26$ in 2014; Table 2). There were no N × P or forest age interactions for litter mass.

Across all 13 stands, RBAI of trees ≥10.0 cm DBH responded to P but not to N fertilization (Table 3), with 7% greater RBAI, on average, in plots receiving P vs. no P (Table 4). The aboveground growth response to N + P was greater than that to N or P alone in six out of 13 stands, but was lower than that in response to N or P alone in four stands and was similar in the remaining three stands. We did not detect N-P co-limitation. There was not a significant N × P interaction (Table 3), and RBAI in the N + P plots was not greater than that in P plots ($P = 0.80$ for the comparison of least-square means). RBAI was marginally greater in plots receiving N + P compared with those receiving N ($P = 0.08$), consistent with a P effect.

RBAI was highest in young, intermediate in mid-age, and lowest in mature forest stands (Fig. 3), consistent with the pattern of relative density, which averaged 0.27 in young, 0.71 in mid-age, and 0.88 in mature stands. Although there was not a significant interaction between forest age and N or P addition, responses to P differed among forest ages (Fig. 3A). RBAI was higher in plots receiving P vs. no P, by 13% in mid-age stands ($P = 0.02$) and by 15% in mature stands ($P = 0.07$), but was not higher in plots receiving P vs. no P in young stands (−2%; $P = 0.53$; Table 4). Addition of N did not

TABLE 2. Resin-available N and P in 2015, litterfall N and P concentrations in 2012, and litterfall mass in 2012 and 2014.

Treatment	Resin N (μg/strip)	Resin P (μg/strip)	Litterfall N (mg/g)	Litterfall P (mg/g)	Litterfall mass (g/m^2) 2012	Litterfall mass (g/m^2) 2014
Control	84.4 (28.4)	7.2 (1.7)	14.5 (0.6)	0.46 (0.03)	300 (8)	281 (8)
N	257.6 (70.6)	9.0 (2.7)	15.5 (0.6)	0.48 (0.29)	296 (9)	271 (15)
P	24.8 (34.1)	14.7 (2.6)	13.9 (0.5)	0.60 (0.03)	287 (10)	272 (13)
N + P	123.7 (34.1)	17.3 (3.5)	14.7 (0.6)	0.55 (0.03)	294 (13)	269 (14)

Notes: Standard errors of the mean are in parentheses; $n = 9$ stands for resin-available nutrients and $n = 11$ stands for litterfall. Resin strips were incubated for 14 d.

Table 3. Ecosystem-level (all species) and individual species-level results of mixed effects model showing the main effects of nutrient addition on the annual relative basal area increment (RBAI; % per year) of trees ≥10 cm DBH.

Predictor	Degrees of freedom	*F*	*P*
Ecosystem-level RBAI			
Forest age	2,8	39.83	**≤0.001**
N	1,36	0.23	0.73
P	1,36	9.07	**0.02**
N × P	1,36	0.09	0.67
White birch RBAI			
Forest age	1,4	31.22	**≤0.01**
N	1,21	0.003	0.91
P	1,21	8.45	**0.02**
N × P	1,21	0.80	0.28
Beech RBAI			
Forest age	2,5	23.16	**≤0.01**
N	1,24	0.11	0.57
P	1,24	0.23	0.14
N × P	1,24	0.09	0.32
Sugar maple RBAI			
Forest age	2,5	7.10	**0.03**
N	1,27	0.67	0.42
P	1,27	0.90	0.35
N × P	1,27	0.49	0.49
Yellow birch RBAI			
Forest age	2,6	11.56	**<0.01**
N	1,27	0.12	0.73
P	1,27	0.19	0.67
N × P	1,27	0.35	0.56

Note: Significant *P* values are highlighted in boldface type.

Table 4. Differences in annual relative basal area increment (RBAI) between plots receiving and plots not receiving the nutrient (i.e., N vs. no N) in each stand and means in all stands and in the BEF.

	Difference in RBAI (%)	
Stand	Plots receiving N vs. no N	Plots receiving P vs. no P
Young		
BEF-C1	12.0	−3.7
BEF-C2	8.2	0.6
BEF-C3	−3.8	−1.5
Mid-age		
BEF-C4	7.7	15.5
BEF-C5	−10.0	31.4
BEF-C6	3.8	14.7
HB-mid	24.5	16.5
JB-mid	3.2	−3.9
Mature		
BEF-C7	−21.5	19.5
BEF-C8	3.3	8.2
BEF-C9	20.6	21.9
HB-mature	4.5	14.9
JB-mature	39.2	10.2
All sites		
All stands	7.1 (4.3)	11.1 (3.0)
Young (n = 3)	5.5 (4.8)	−1.5 (1.2)
Mid-age (n = 5)	5.8 (5.5)	14.8 (5.6)
Mature (n = 5)	9.3 (10.1)	14.9 (2.6)
BEF site only		
All stands	2.3 (4.2)	11.8 (3.9)
Young (n = 3)	5.5 (4.8)	−1.5 (1.2)
Mid-age (n = 3)	0.5 (5.4)	20.5 (5.4)
Mature (n = 3)	0.8 (12.2)	16.5 (4.2)

Note: Standard errors of the mean are in parentheses.

affect the RBAI of trees in any age class ($P \geq 0.63$). In mid-age and mature stands, comparisons of the mean responses at BEF with those including all three sites indicate a slightly stronger productivity response to P at BEF than at HB or JB, and a stronger productivity response to N at HB and JB compared with BEF (Table 4).

The RBAI response to P addition was not universal and although the response to N was not significant across all stands, there were stands in which N plots had higher RBAI, especially in mature forest (Table 4). The lack of uniform responses within forest age classes (Table 4) suggests variation in the nutrient to which growth responded.

Species-level responses

White birch, which is an ECM species, was the only species for which we detected significant responses to treatment (P = 0.02 for P and P = 0.91 for N, Table 3). White birch RBAI was greater, by 13%, in plots receiving P vs. no P, but did not respond to N. White birch RBAI differed among forest age classes (Table 3), and the nutrient to which growth responded changed with forest age. The RBAI of white birch was 26% greater in plots receiving P vs. no P in mid-age stands (Fig. 4A, $P < 0.001$) and was 17% greater in those receiving N vs. no N in young stands (Fig. 4B, P = 0.02), but did not respond significantly to P in young stands.

For beech, another ECM species, we did not detect an RBAI response across all stands to either nutrient (P = 0.14 for P and P = 0.57 for N, Table 3). However, the RBAI of beech was lower by 18% in plots receiving P compared to no P in young stands (P = 0.06), and higher in the mid-age (15%; P = 0.09), and mature stands (27%, P = 0.03; Fig. 5A). In contrast, N fertilization did not affect beech RBAI in any forest age class (Fig. 5B). Growth responses to treatments were not detected in any other species. Yellow birch and sugar maple, the two other dominant species in these forests, did not respond to either nutrient (Table 3).

RBAI differed among tree species ($P < 0.001$; Table 5), and between arbuscular mycorrhizal and ectomycorrhizal tree species. The RBAI of ECM tree species was slightly but significantly greater than those of the AM species across all of our stands (7%; $P < 0.001$) and the pattern of higher RBAI by ECM species was consistent among all three age classes (Table 5). The RBAI of

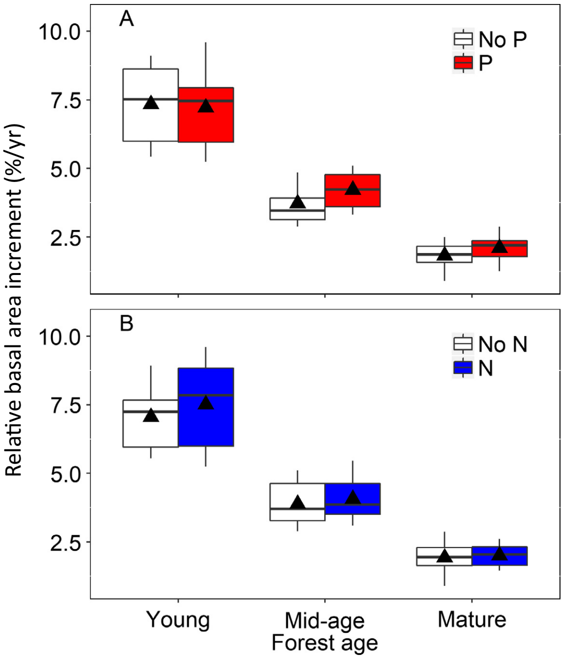

FIG. 3. Annual relative basal area increment (per tree) of live ≥10 cm DBH trees in plots receiving (A) P vs. no P and (B) N vs. no N in young, mid-age and mature forest stands. Boxes represent the interquartile range and whiskers represent the 5th and 95th percentile, with the horizontal line showing the median and the triangle the mean value.

ECM species was 13% higher in plots receiving P compared to no P (*P* = 0.06), and 4% higher in plots receiving N vs. no N (*P* = 0.08) across all stands.

DISCUSSION

Ecosystem-level responses

We found evidence for P limitation of forest growth across a suite of northern hardwood forest stands in central NH, USA. In contrast, limitation by N was not detected, and the response to N + P addition together was not consistently greater than that to the single most limiting nutrient. Phosphorus limitation of growth on these relatively young, glacially derived forest soils was unexpected given the presence of apatite minerals as a P source in these soils (Blum et al. 2002). The P content of apatite in the B horizon at these sites is typically at least an order of magnitude greater than that of aboveground biomass P (Vadeboncoeur et al. 2014). In our forests, historical anthropogenic N enrichment (Likens and Lambert 1998, Driscoll et al. 2003) may have contributed to P limitation by increasing the supply of N relative to P. Although there is evidence that adding N can accelerate P cycling by stimulating extracellular phosphatase enzyme activity (Olander and Vitousek 2000, Treseder and Vitousek 2001, Gress et al. 2007), inputs to P pools from mineral weathering or from very slowly recycling biotic pools may not be sufficient to maintain balance with enrichment from previously high N inputs (Richter et al. 2006, Schaller et al. 2010, Vadeboncoeur et al. 2014). Such a nutritional imbalance owing to N enrichment may have alleviated N limitation of productivity in these ecosystems, inducing a transactional limitation of productivity by P (Vitousek et al. 2010).

The average response to P after four years of treatment was modest (Fig. 3), even though the relatively low rates of fertilization in our factorial N × P experiment were successful in elevating soil nutrient availability and litterfall nutrient cycling (Table 2). The lack of strong overall response to P was partly a consequence of stand age. Growth in mature forest responded relatively weakly to P, consistent with high relative density (0.88); fully stocked stands would be expected to be limited more by light than by nutrients. It is possible that fertilization enhanced canopy expansion more than diameter growth, but the lack of response of leaf litter production (Table 2) suggests that any canopy response was small. The most marked increase in RBAI in response to P addition occurred in the mid-age forests, where the lower relative density (0.71) suggests greater potential for growth and, therefore, nutrient limitation. Phosphorus limitation in the mid-age stands at BEF is consistent with higher root growth in response to localized P additions in the same stands (Naples and Fisk 2010).

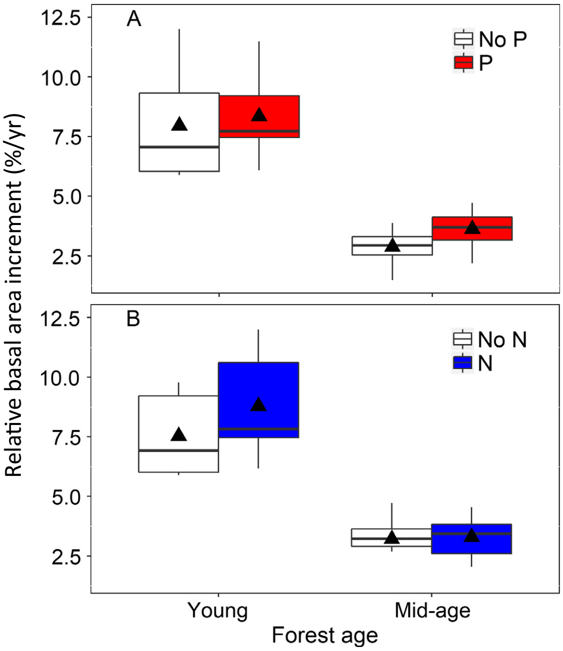

FIG. 4. Annual relative basal area increment (per tree) of live ≥10 cm DBH white birch trees in plots receiving (A) P vs. no P and (B) N vs. no N in young and mid-age forest stands. Boxes represent the interquartile range (25–75%) and whiskers represent 5% and 95% percentile, with the horizontal line as the median and the triangle as the mean.

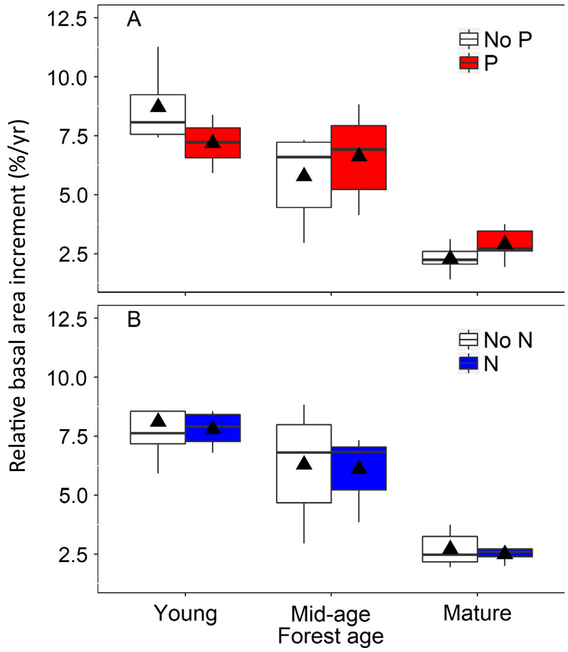

FIG. 5. Annual relative basal area increment (per tree) of live ≥10 cm DBH beech trees in plots receiving (A) P vs. no P and (B) N vs. no N in young, mid-age, and mature forest stands. Boxes represent the interquartile range (25–75%) and whiskers represent 5% and 95%, with the horizontal line as the median and the triangle as the mean.

In young stands, the average RBAI suggested N rather than P limitation of growth, but variation was high and significant effects were not detected. Successional transitions in the young forests included high mortality of both pin cherry and beech, which probably contributed to the high variation in growth among individuals and species. Furthermore, the contrasting nutrient responses by white birch (positive response to N and slightly positive response to P, Fig. 4B) and beech (negative response to both N and P, Fig. 5A) in the young stands complicated the overall response. The relatively low number of stems >10 cm DBH in these young stands also constrained our ability to detect significant treatment effects.

Our results also show that nutrient limitation may vary among forests of this region. In the mid-age and mature forests, broad-scale spatial variation in the response to fertilization contributed to the relatively weak overall effects of P (Table 4). This variation must be interpreted with caution because of the lack of within-stand replication; however, these results are consistent with variation in nutrient limitation among stands as assessed by nutrient-amended root ingrowth cores (Naples and Fisk 2010). Whereas P limitation appears most common across all but the youngest stands in our study, the variation across stands suggests that these forests are close to the threshold between P and N limitation, especially in mature forests.

If nutrient limitation in these forests is indeed relatively close to a state of either N or P limitation, it is surprising that we did not find more obvious evidence of N and P co-limitation of aboveground productivity. The lack of a significant N × P interaction does not support synergistic co-limitation, and the lack of a greater response to N + P addition together than to P alone suggests that there was not additive co-limitation. In the absence of a significant growth response to N alone, the slightly higher RBAI ($P = 0.08$) that was observed when N + P was added together compared to N alone suggests either a primary effect of P, or weak evidence for sequential P followed by N limitation. It is possible that alleviation of limitation by one nutrient induces plant allocation responses, such as changes in fine root growth and mycorrhizal colonization, that will take time to develop before inducing secondary limitation by the other nutrient. If so, this sequential co-limitation response should be evident in future divergence

TABLE 5. The type of mycorrhizal association and the mean annual relative basal area increment (RBAI) of the major tree species in young, mid-age, and mature northern hardwood forest stands after four years of nutrient fertilization.

		RBAI (% per year)		
Species	Representation†	Young	Mid-age	Mature
Arbuscular-mycorrhizal species				
Sugar maple (*Acer saccharum* Marsh.)	41	3.9	3.6	1.1
Red maple (*Acer rubrum* L.)	29	6.7	4.3	1.9
Pin cherry (*Prunus pensylvanica* L.f.)	29	3.6	1.6	-
White Ash (*Fraxinus americana* L.)	13	11.2	5.7	2.0
Striped maple (*Acer pennsylvanicum* L.)	10	4.1	1.4	-
Ectomycorrhizal species				
American beech (*Fagus grandifolia* Ehrh.)	44	7.2	5.4	2.6
Yellow birch (*Betula alleghniensis* Britton.)	42	6.6	4.6	2.1
White birch (*Betula papyrifera* Marsh.)	32	8.2	3.4	-
Eastern hemlock (*Tsuga canadensis* (L.) Carriere)	13	4.8	1.9	2.7

Note: Species present in <10 out of 52 plots are not presented here.
†Number of plots out of 52 possible.

of productivity between fertilization with single nutrients and N + P together.

Species-level responses

Species-level effects are potentially important for interpreting nutrient limitation of productivity. Within an ecosystem, community composition can be driven by limiting nutrients (John et al. 2007), and conversely, community composition can influence the availability or use of limiting nutrients via the traits of individual species (Chapin and Shaver 1985, Chapin et al. 1986, 1987). For example, in some tropical forests, variation in nutrient use and uptake among tree species can cause the primary limiting nutrient to differ among species, thereby contributing to community-level co-limitation of productivity by N and P (Gehring et al. 1999, Menge et al. 2008, Baribault et al. 2012, Waring et al. 2015). Northern hardwood forests are moderately diverse (Lovett et al. 2004), and component species differ in tissue nutrient ratios and nutrient acquisition and conservation strategies (Schwarz et al. 2003, Bigelow and Canham 2007, See et al. 2015), and are segregated along axes of soil nutrient availability (Finzi et al. 1998). We did not find that differences in life history traits associated with successional status corresponded with differences in limiting nutrients, as both white birch (early successional, rapid growth) and beech (late successional, slow growth), responded to P. However, mycorrhizal type may have mediated nutrient responses, as both of the species that responded to P are ECM. RBAI was high for all ECM species, but varied more among AM species (Table 3). RBAI of ECM species were 13% higher in plots receiving P compared to no P ($P = 0.06$), and 4% higher in plots receiving N vs. no N ($P = 0.08$) across all stands. ECM fungi tend to specialize in N acquisition (Smith and Read 2008), with substantial C cost to the host plant (Hobbie 2006), whereas AM fungi, which lack extracellular enzyme production for decomposition, are associated with conditions of higher soil NO_3^- availability (Phillips et al. 2013), and may be more essential for P acquisition. Hence, if ECM species more effectively acquire N when P availability is enhanced, then AM species may be more prone to secondary N limitation under these conditions. Alleviating N limitation is known to shift fungal functional groups (Lilleskov et al. 2002), and can reduce ECM colonization, although responses vary among ecosystems (Treseder 2004). Fertilizer-induced declines in mycorrhizal C costs are likely to allow reallocation to aboveground growth more for ECM than for AM tree species, but less is known about colonization or functional group responses to P availability in forest systems. Our results indicate the need to evaluate ECM species responses under P-limiting conditions, and also to examine species-level nutritional responses to better evaluate these mechanisms.

One exception to the greater growth response to P was the response of white birch to N in the youngest stands (Fig. 4B). Enhanced growth by this species in response to N contributed to the slightly higher average RBAI response to N for all species combined in the young forests (Fig. 3B). Increased RBAI in response to N addition were consistent with pre-treatment observations of high N resorption by white birch foliage in young stands (See et al. 2015). Thus, white birch appeared to be limited primarily by N at age 20–25 yr and by P at age 30–40 yr, suggesting the possibility of a shift in nutrient limitation early in succession, which provides tentative support for predictions of the MEL model of N limitation in early stages of recovery post-harvest (Rastetter et al. 2013). The competition for canopy dominance in young forests promotes aboveground allocation in early successional, shade-intolerant species such as white birch and pin cherry (Fahey et al. 1998). Our results also suggest a shift from belowground allocation for acquisition of N vs. P, with a relatively high demand for N to support aboveground growth during early succession, to an increase in P limitation as early successional species decline and forests transition to middle age with higher relative density and higher relative importance of slower-growing species such as beech and maple.

The response by beech differed between young and mid-age forests, in this case from a negative (but non-significant) to a significantly positive effect of P on growth (Fig. 5A). Beech is a relatively slow-growing, shade-tolerant, "resource-conservative" species and could therefore be expected to be less responsive to changes in nutrient availability (Eskelinen and Harrison 2015). The negative response of beech to P fertilization in young forests could arise from the faster-growing species outcompeting beech for light under conditions of higher nutrient availability. In the mid-age stands, where early successional species are less important (Fig. 1), the trend toward increased beech growth in response to both N and P additions (Fig. 5) raises the possibility that this species is co-limited in the mid-age forests. While it may be surprising that a species with conservative traits such as beech showed the strongest response to P addition in mature forests, this pattern is consistent with pre-treatment observations of greater P conservation by beech via foliar resorption compared to other species in mature stands (See et al. 2015).

Conclusions

After four years of fertilizing 13 northern hardwood stands of varying ages, we found evidence for P limitation in most mid-age and mature stands but no clear indication of widespread N limitation or N × P co-limitation. It is possible that P limitation of productivity has developed as a consequence of the legacy of anthropogenic N deposition in this region, consistent with the idea of anthropogenically induced transactional P limitation (Vitousek et al. 2010). At the same time, the broad extent of our study reveals important spatial variation in P vs. N limitation, which cautions against generalizing about regional nutrient limitation. Observing longer-term responses to our treatments will be valuable for assessing whether sequential co-limitation develops as P limitation is alleviated by treatment and biotic demand for N increases. Species-specific responses were generally consistent with whole-ecosystem responses, but highlighted interesting shifts in limitation by N vs. P as young forests mature.

Acknowledgments

We are indebted to Steve Hamburg for field site selection and setup. We thank Craig See and Adam Wild for outstanding work in the field, and two anonymous reviewers for insightful comments on the manuscript. The Bartlett and Hubbard Brook Experimental Forests are operated and maintained by the USDA Forest Service Northern Research Station, Newtown Square, Pennsylvania, and Hubbard Brook is part of the Long-Term Ecological Research (LTER) network, which is supported by the National Science Foundation. This work is a product of MELNHE (www.esf.edu/melnhe/), and was supported by grants from the National Science Foundation.

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