

Decades of atmospheric deposition have not resulted in widespread phosphorus limitation or saturation of tree demand for nitrogen in southern New England

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Received: 4 March 2008 / Accepted: 11 January 2009 / Published online: 11 February 2009
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Abstract It is commonly assumed that nitrogen (N) is the primary mineral resource limiting the productivity of temperate forests. Sustained inputs of N via atmospheric deposition are altering the N status of temperate forests raising the possibility that nutrients such as phosphorus (P) are increasingly limiting productivity. The objective of this study was to determine whether P availability limits tree growth alone or in combination with N. This study was conducted in two forest types common throughout the New England landscape of the northeastern United States; in sugar maple and white ash dominated stands growing on base rich parent material characterized by rapid rates of N cycling and high N availability, and in red oak–beech–hemlock dominated stands growing on base-poor parent material characterized by slow rates of N cycling and low N availability. Starting in 2004, N and P were added to replicate plots in each forest type in factorial combination at a rate of 150 and 50 kg ha⁻¹ year⁻¹, respectively. Diameter growth rates of all trees >10 cm DBH were measured in 2005 and 2006 using dendrometer bands and converted into units of basal area increment (BAI) and wood production. Following 2 years of fertilization, basal area increment in the sugar maple–white ash forests remained strongly N limited. Fertilization with P did

not significantly increase BAI alone, although both N and P fertilization tended ($P < 0.10$) to increase diameter growth in white ash. Wood production in the N-fertilized plots increased by 100 g C m⁻² year⁻¹, roughly doubling production in the non-fertilized plots. In the red oak–beech–hemlock stands, there was no overall effect of N or P fertilization on BAI or wood production because BAI in some species was stimulated by fertilization with N alone (e.g., black cherry, red oak), while in other species BAI was unaffected (e.g., red maple, beech) or negatively affected by fertilization with N or P (e.g., eastern hemlock). Given that BAI in several tree species responded to fertilization with N alone and that only one species responded to P fertilization once N was added, this study suggests that decades of atmospheric N deposition have not (yet) resulted in widespread P limitation or saturation of tree demand for N.

Keywords Nitrogen · Phosphorus · Temperate forest · Nutrient limitation · Productivity

Introduction

Biogeochemical theory predicts that on geologically young soils the availability of nitrogen (N) should control forest composition and productivity to a greater extent than phosphorus (P, Walker and Syers

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1976; Crews et al. 1995; Vitousek and Farrington 1997). Young soils have had little time to accrue N through atmospheric deposition or fixation. Consequently, the availability of N for plant growth is low relative to potential demand. By contrast, young soils are thought to contain a relatively large quantity of P in primary minerals. Since some primary minerals can be weathered rapidly (e.g., apatite), it is generally assumed that the supply of P to plants meets or exceeds biotic demand constrained by low N availability.

Soils throughout northeastern North America are geologically young, dating to about 15,000 years BP (Larson and Stone 1980). Consistent with biogeochemical theory, N plays a major role in controlling the productivity of the forests occupying these soils (Mitchell and Chandler 1939; Ward and Bowersox 1970; Safford 1973; Fahey et al. 1998; Magill et al. 2000, 2004). Comparable data on P limitation are rare, yet several lines of evidence suggest that greater attention should be placed on the potential for P limitation in temperate forests. Phosphorus is rapidly assimilated by vegetation once it has been mineralized from soil organic matter (Yanai 1992), and prior to tissue senescence P is as efficiently retranslocated from leaves as is N (Killingbeck 1996) both of which suggest that efficient P cycling is important to tree growth in subsequent years. Fertilization studies conducted in the 1970s suggest P limitation of tree growth in some hardwood species (Auchmoody and Filip 1973; Lea et al. 1979; Auchmoody 1982). More recently, variations in foliar P concentrations have been correlated with diameter growth rates in sugar maple (*Acer saccharum*, Gradowski and Thomas 2006). Similarly, P deficiency is thought to be an important driver of regional declines of sugar maple in eastern Canada (Bernier and Brazeau 1988; Pare and Bernier 1989).

Adding to the interest in P limitation is atmospheric deposition of N. Throughout the northeastern US atmospheric deposition ranges from 5 to >15 kg N ha⁻¹ year⁻¹ (Ollinger et al. 1993; Holland et al. 2005). There is credible evidence to suggest that the N status of northeastern US forests has been altered by enhanced rates of atmospheric N deposition (Aber et al. 2003) and net ecosystem production in European forests appears to be positively correlated with comparable rates of atmospheric N deposition (Magnani et al. 2007). If atmospheric N deposition has increased N availability in northeastern US forests

then primary production in this region may be increasingly limited by the availability of P (Elser et al. 2007).

The objective of this study was to determine whether some combination of N and P availability limits the rate of canopy tree growth in hardwood-conifer forests of southern New England. To address this objective, two forest types with different rates of N cycling were fertilized with factorial additions of N and P: (1) sugar maple and white ash (*Fraxinus americana*) dominated stands characterized by rapid rates of mineralization and nitrification (Finzi et al. 1998a; Goodale and Aber 2001; Lovett et al. 2004; Finzi and Berthrong 2005), and on a regional basis show signs of N saturation (Lovett et al. 2000; Goodale and Aber 2001); and (2) oak (*Quercus rubra*)–beech (*Fagus grandifolia*)–hemlock (*Tsuga canadensis*) forests that are characterized by slow rates of N mineralization and nitrification (Finzi et al. 1998a; Lovett et al. 2004; Finzi and Berthrong 2005), low N availability and few signs of N saturation (Magill et al. 2004). Based on between-site differences in the rate of N cycling and N availability for tree growth, this study tested the hypothesis that (1) P additions would increase diameter growth in high N-availability sugar maple–white ash stands, (2) that N additions would increase diameter growth in the low N availability oak–beech–hemlock stands, and (3) that N and P additions would increase growth rates above those observed in plots fertilized by only a single nutrient in both forest types (Elser et al. 2007).

Methods and materials

Study sites

This research was conducted in the towns of Norfolk and North Canaan, CT (42°N, 73°15'W). The oak–beech–hemlock stands were located in the Great Mountain Forest on the Canaan Mountain plateau at elevations of 300–500 m. In the mid to late 1800s, the Great Mountain Forest was logged for charcoal production (Winer 1955). The oak–beech–hemlock stands studied here are ~120 years old. The soils at the Great Mountain Forest are derived from glacial till overlying mica-schist bedrock. The soils are inceptisols classified as Typic Dystrochrepts (Hill et al. 1980). Red oak, beech and hemlock comprise

16, 17, and 12% of the stands basal area, respectively. The other dominant species in the stand are red maple (*Acer rubrum*) and black cherry (*Prunus serotina*) each comprising 17% of the basal area in the stand. Although no single species is dominant, for brevity the stands within this site are simply referred to as oak–beech–hemlock stands.

The sugar maple–white ash stands were located in the Housatonic State Forest at 300 m elevation. Trees were harvested from the Housatonic State Forest and served as fuel for the Beckley blast furnace. The furnace was in operation until 1919 when forest harvest ended resulting in sugar maple–white ash stands that are ~80 years old today. The soils on this site are derived from glacial till overlying dolomite. The soils are mesic inceptisols classified as Aquic Eutrochrepts (Hill et al. 1980). Sugar maple and white ash comprise 27 and 41% of the stand basal area, respectively. Other important species include big tooth aspen (*Populus grandidentata*) and shag-bark hickory (*Carya ovata*) both of which comprise 9% of the stand's basal area, as well as paper birch (*Betula papyrifera*) which comprises 6% of the stands' basal area, although their distribution within the forest is patchy. Soil properties of each site are summarized in "Appendix". Mean annual temperature in this area is 7°C. Mean annual precipitation is 1330 mm.

Foliage sampling

Early in 2003, twelve 20 × 20 m plots were located in each forest type. At each site, the 12 plots were divided into three blocks of four plots each. The blocks were separated from one another by 50–200 m. Within a block, the four plots were separated by a minimum of 10 m. In June of 2003, all trees >10 cm DBH within each plot were identified to the species level. Live foliage samples were collected from five dominant tree species in each plot using a 20-gauge shotgun. Every effort was made to collect leaves from sunlit portions of the canopy but some shade leaves may have also been included in the sample. Thirty leaves were collected from each tree in each plot. The samples were brought back to the laboratory, dried at 60°C for 4 days, ground and analyzed for N and P using the Kjeldahl digestion procedure of Lowther (1980) followed by colorimetric analysis on an

autoanalyzer (Lachat QuickChem FIA + 8000 Series, Zellweger Analytics, Milwaukee, WI).

Aboveground litterfall was also collected within each plot. In June of 2003, two litter baskets (42 cm × 56 cm) were located within plot. Leaf litter was collected bimonthly throughout the year with the exception of October and November when it was collected bi-weekly. The litter was oven dried for 4 days at 60°C, sorted to species, weighed, ground and analyzed for its N and P content using the Kjeldahl procedure of Lowther (1980). These samples were used to quantify aboveground litterfall, the flux of N and P in litterfall (i.e., litterfall mass multiplied by the N or P concentration in litter), and an index of N- and P-use efficiency based on the ratio of litterfall mass and the nutrient content of litterfall (Vitousek 1982).

Soil sampling

Nitrogen and Phosphorus availability in the soil was measured in 2003 only. N availability was measured in June, in samples collected from the surface organic horizon and in 15 cm increments to a depth of 30 cm in the mineral soil. The rate of potential net N mineralization was used as an index of N availability (Binkley and Hart 1989). To calculate net mineralization, the concentration of inorganic N was measured in two replicate 30 g sub-samples of soil taken from every sample. Similarly, two replicate 30 g sub-samples of soil were incubated for 28 days at 22°C under field-moist conditions in 250 ml polyethylene bottles (Binkley and Hart 1989). Soils were extracted in 2 M KCl, shaken for 1 h, filtered through a Whatman #1 filter and the supernatant frozen until analysis. The concentration of NH_4^+ and NO_3^- in the initial and incubated samples was measured on an autoanalyzer (Lachat QuickChem FIA + 8000 Series, Zellweger Analytics, Milwaukee, WI). The rate of potential net mineralization was calculated as the difference between the concentration of inorganic N in the incubated and initial samples.

Phosphorus availability was measured using two techniques. First, the flux of plant-available inorganic P was measured in the field by placing duplicate ion-exchange resin bags at the interface between the O horizon and the mineral soil horizon in the oak–beech–hemlock stands, and at 7.5 cm depth in the mineral soil

of the sugar maple–ash stands. The resin bags were constructed of nylon stocking with 10 g of resin per bag. The resins were deployed from June to August of 2003. After incubation in the field, the resins were extracted in the lab in 0.5 M NaHCO₃ for 1 h, filtered and analyzed for PO₄³⁻ on an autoanalyzer via reaction with ammonium molybdate.

Second, the concentration of available P was measured as 0.5 M NaHCO₃ extractable PO₄³⁻ in the soil samples from which N data were collected (Schoenau and Karamanos 1993). In addition to bicarbonate-extractable P, the distribution of P among several different forms in the soil was quantified using a modification of the Hedley fractionation procedure (Tiessen and Moir 1993). This phosphorus fractionation scheme recognizes plant-available forms of P (bicarbonate inorganic P, Pi, and organic P, Po), less-readily-plant-available but non-occluded P bound to the outer surfaces of iron and aluminum minerals (NaOH Pi and Po), P in primary minerals (dilute HCl Pi), occluded P (hot HCl) and the residual P fraction (sulfuric acid digestion, Lawrence and Schlesinger 2001). This method has been discussed extensively in the literature (e.g. Cross and Schlesinger 1995) and for brevity the major methods are omitted here. Importantly, the resin Pi extraction was skipped, so this fraction was assumed to be recovered in the bicarbonate Pi pool (Lawrence and Schlesinger 2001). P fractions were measured in triplicate 0.5 g sub-samples of soils separately for the 0–15 and 15–30 cm depth increments.

N and P fertilization experiment

Nitrogen and P fertilizers were added in factorial combination in each forest type in 2004 and 2005. One plot in each of the blocks was randomly assigned a fertilizer treatment: control, +N, +P, +NP. Hence for each forest type, each fertilizer treatment was replicated three times. Nitrogen was added as NH₄NO₃ fertilizer at a rate of 150 kg N ha⁻¹ year⁻¹. Phosphorus was added as triple-superphosphate at a rate of 50 kg P ha⁻¹ year⁻¹. The N and P fertilizers were applied in May, June and July, with each plot receiving 1/3 of the total fertilizer application per month. Fertilizer was applied in solid form. In 2004, we deployed four ion exchange resins bags (IERS) into each plot to measure the availability of N and P in the control and fertilized plots at a depth of 7 cm in

the soil. As described above, 2 M KCl and 0.5 M NaHCO₃ was used to extract inorganic N and P from two replicate resin bags per plot, respectively.

During the summer of 2003, all trees >10 cm DBH were fitted with a dendrometer band. The dendrometer band was made of stainless steel tape looped around the bole of the tree at 1.4 m height from the ground surface. The dendrometer bands were allowed settle during the 2003 growing season. At the end of the 2003, 2004, and 2005 growing seasons the linear distance between hole punches along each dendrometer band was recorded and then converted to a rate of diameter growth in units of mm year⁻¹. To account for differential growth rates between small and large diameter trees, the growth datum for every tree was converted into basal area increment (BAI) with units of cm⁻² year⁻¹. This measure of BAI enabled us to measure species-level responses to N and P fertilization. With the exception of red oak, species-level analyzes were only conducted when a species was found in a least two of the three replicate plots per treatment. Red oak is abundant in these forests but only a single tree was found in a plot where both N and P were added together. Rather than excluding red oak from this study, the data analysis simply determined whether there was a main effect of N or P fertilization on BAI. Whole-forest responses to N and P fertilization were assessed by summing the BAI of each tree in a plot and scaling to an area basis (i.e., cm² ha⁻¹ year⁻¹). Finally, the diameter growth rate data were converted into aboveground woody biomass C accumulation (g C m⁻² year⁻¹) based on allometric relationships published in Jenkins et al. (2004) with a dry matter C concentration of 50%.

Data analysis

The 20 × 20 m plot was considered a statistical replicate ($n = 24$). Between forest type differences in foliar N and P concentrations, aboveground litterfall, N and P fluxes in litterfall and N- and P-use efficiency were analyzed by 1-way ANOVA with site as the main effect. Variations in the concentrations and fluxes of the different N and P pools in the soil were analyzed by 2-way ANOVA with site and soil horizon as main effects. When the site × soil horizon interaction term was statistically significant, we used 1-way ANOVA to test for differences among

sites within a given soil horizon (Underwood 1997). Variations in basal area increment and aboveground wood production were analyzed by 2-way ANOVA with N and P fertilization as main effects. All data were assessed for homogeneity of variance and normality. When necessary, the data were log transformed to conform to model assumptions.

Results

Foliar and litter N and P

Between forest types, there were no differences in the average concentration of N or P in live foliage (Table 1). Foliar N-to-P ratios were significantly lower in the sugar maple–ash stand than in the oak–beech–hemlock stand. Foliar N concentrations (herein foliar [N]) varied significantly among species. Foliar [N] was highest in ash, red oak and beech (2.2–2.9%), intermediate in sugar maple (2.0%) and lowest in hemlock (1.3%, Table 2). Foliar P concentrations were highest in hemlock and ash (~0.16%), intermediate in oak and beech (0.13–0.15%) and lowest in sugar maple (0.12%, Table 2). Foliar N-to-P ratios were highest in sugar maple and beech (16.3–16.7), intermediate in oak and ash (14.6–15.3) and lowest in hemlock (8.7).

Aboveground litterfall and the N flux in litterfall was not significantly different between forest types (Table 3). The flux of P in litterfall was significantly lower in the sugar maple–ash stand than in the oak–beech–hemlock stand. N-use efficiency (litterfall

Table 1 The weighted average concentration (% ± 1 SE, mass basis) of N and P in the foliage of the dominant tree species in the two forest types (see “Study sites” in the “Methods and materials” section for the list of species)

Foliar property	Forest type	
	SM–WA	O–B–H
Nitrogen	2.16 (0.06)	2.31 (0.10)
Phosphorus	0.14 (0.01)	0.13 (0.02)
N:P Ratio*	15.4 (0.42)	17.8 (0.31)

Superscript symbols indicate significant differences among sites at * $P < 0.05$. Weighting of a species contribution to the site mean was based on relative abundance

SM–WA sugar maple white ash stand, O–B–H oak–beech–hemlock stand

Table 2 The average concentration (% ± 1 SE, mass basis) and ratio of N and P in foliage of the dominant tree species in each forest type

Species	Nitrogen	Phosphorus	N:P
Sugar maple	2.00 ^b (0.04)	0.12 ^c (0.01)	16.7 ^a (0.34)
White ash	2.29 ^a (0.09)	0.16 ^a (0.01)	14.6 ^b (0.68)
Red oak	2.22 ^{ab} (0.05)	0.15 ^{ab} (0.01)	15.3 ^{ab} (0.50)
Beech	2.21 ^{ab} (0.04)	0.13 ^{bc} (0.01)	16.8 ^a (0.46)
Hemlock	1.32 ^c (0.12)	0.16 ^a (0.03)	8.66 ^c (0.77)

Values within a column with different superscript letters indicate significant difference among species ($P < 0.01$)

mass/N flux in litterfall) was not significantly different between sites. P-use efficiency (PUE) was significantly higher in the sugar maple–ash stand (Table 3).

Soil N and P

The rate of net N mineralization declined with depth in the soil (Table 4). At both depth increments in the mineral soil the rate of net N mineralization was significantly greater in the sugar maple–ash stand than in the oak–beech–hemlock stand (Table 4). The majority of the mineralized N was found in the organic horizon in the oak–beech–hemlock stands. The accumulation of inorganic P on ion exchange resins was significantly greater in the oak–beech–hemlock stands than in the sugar maple–ash stands (Table 4).

Table 3 The mean (± 1 SE) rate of aboveground litterfall ($\text{g m}^{-2} \text{ year}^{-1}$), the flux of N and P in litterfall (g N or $\text{P m}^{-2} \text{ year}^{-1}$), and NUE and PUE in each forest type (litterfall/N or P flux in litterfall)

Property	Forest type	
	SM–WA	O–B–H
Litterfall	325 (12)	302 (13)
N flux	2.90 (0.11)	2.69 (0.17)
P flux*	0.19 (0.01)	0.26 (0.02)
NUE	113 (3)	124 (13)
PUE*	1807 (84)	1427 (203)

Superscript symbols indicate significant differences among sites at * $P < 0.05$

SM–WA sugar maple white ash stand, O–B–H oak–beech–hemlock stand

In comparison to the sugar maple–ash stands, non-occluded inorganic P pools were significantly larger in the oak–beech–hemlock stands (Table 5). By contrast, occluded organic-P in the concentrated HCl pool and total P in the residual fraction were significantly higher in the sugar maple–ash stands. There were no other differences in the distribution of organic and inorganic P in mineral soils to a depth of 30 cm (Table 5).

N and P fertilization experiment

Averaging across both forest types, fertilization with N significantly increased the flux of inorganic N to resin bags ($1,896 \mu\text{g N g}^{-1}$ resin 90 days^{-1}) 22-fold above that measured in the control plots ($82 \mu\text{g N g}^{-1}$ resin 90 days^{-1}). Similarly, the plots fertilized with P had 32-fold greater inorganic-P availability ($2,426 \mu\text{g P g}^{-1}$ resin 90 days^{-1}) than the control plots ($83 \mu\text{g N g}^{-1}$ resin 90 days^{-1}).

Basal area increment increased significantly in both sugar maple and white ash (Fig. 1a). There was no effect of P fertilization alone on basal area increment in either species, although there was a non-significant ($P < 0.10$) increase in BAI in white ash when both N and P were added together. The species-level responses scaled directly to that observed at the plot-scale. Fertilization with N alone significantly increased BAI ($\text{cm}^2 \text{ ha}^{-1} \text{ year}^{-1}$) and wood biomass production (Fig. 2). Fertilization with N and P tended to increase BAI and biomass production, but in neither case was this response statistically significant.

Table 4 The average (± 1 SE) net production of mineral N and the accumulation of P on ion exchange resins at each study site

Property	Forest type	
	SM-WA	O-B-H
Net mineralization ($\text{g N m}^{-2} 28 \text{ d}^{-1}$)		
Organic horizon	–	0.57 (0.07)
0–15 cm*	1.03 (0.06)	0.03 (0.01)
15–30 cm*	0.12 (0.17)	0.04 (0.10)
Total*	1.15 (0.20)	0.64 (0.03)
P flux ($\mu\text{g P g}^{-1}$ resin 90 days^{-1})*	6.0 (0.3)	160.1 (70.1)

SM-WA sugar maple white ash stand, O-B-H oak–beech–hemlock stand

Superscript symbols indicate significant differences among sites at * $P < 0.05$

Table 5 Results of the P fractionation procedure

	Forest type	
	SM-WA	O-B-H
Bicarbonate (“plant-available P”)		
Pi	20.4 (3.7)	19.4 (4.6)
Po	82.4 (25.1)	75.6 (29.4)
NaOH (“non-occluded P”)		
Pi***	152.9 (33.3)	342.3 (64.6)
Po	560.7 (55.6)	526.0 (69.1)
Dilute HCl (“primary mineral P”)		
Pi [†]	207.7 (60.2)	231.6 (27.5)
Concentrated HCl (“occluded P”)		
Pi	24.3 (9.7)	17.5 (2.6)
Po***	545.5 (93.8)	208.1 (79.2)
Residual (“occluded P”)**		
P*	191.6 (61.9)	130.3 (24.6)

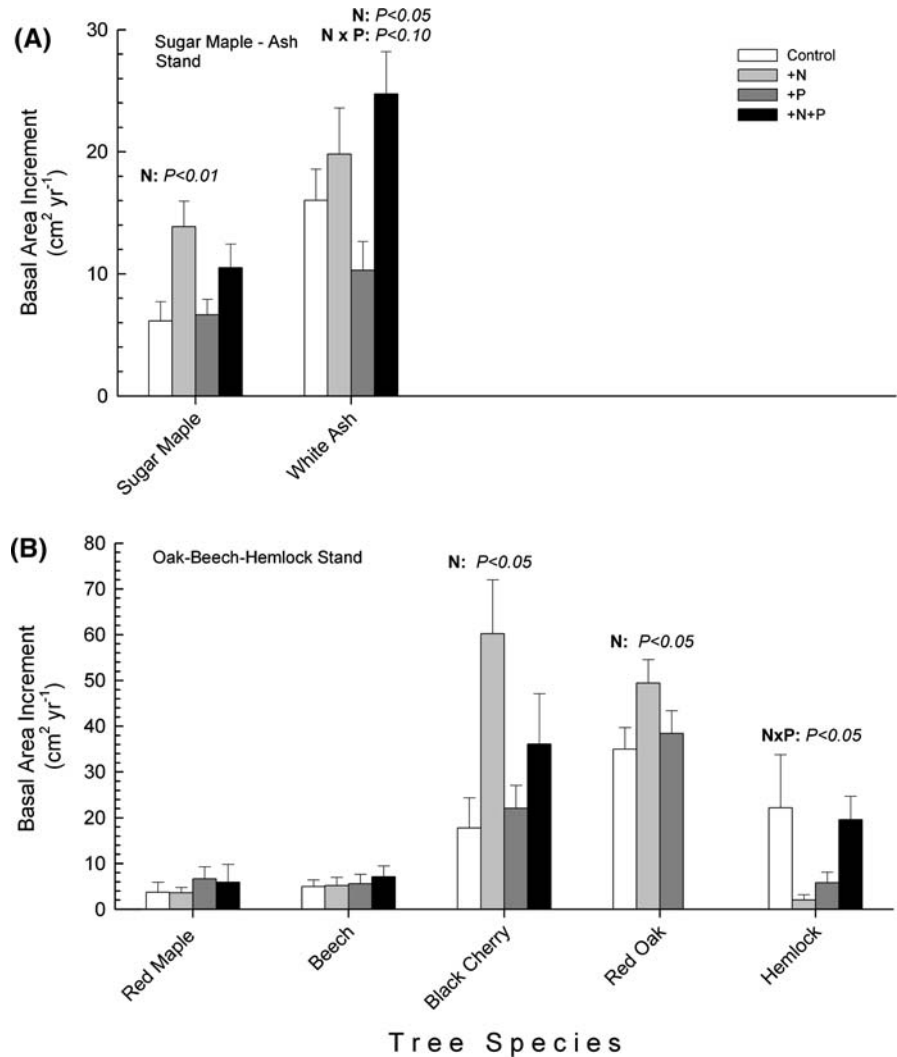
Each value is the average concentration ($\mu\text{g g}^{-1}$) of P in the top 30 cm of mineral soil at each site. Superscript symbols indicate significant differences among sites at: [†] $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$

Fertilization had varying effects on tree growth in the oak–beech–hemlock stand. The basal area increment of red maple and beech were unaffected by fertilization with N or P. Basal area increment in black cherry and red oak increased in response to N fertilization. Basal area increment was significantly lower with N or P fertilization in hemlock, whereas fertilization with N and P together returned basal area increment to levels observed under non-fertilized conditions (Fig. 1b). The aggregation of the positive, neutral and negative responses of tree species to fertilization resulted in no effect of N or P addition on plot-scale BAI or woody biomass production (Fig. 2).

Discussion

Fertilization with N increased basal area increment in four of the seven tree species studied here (Fig. 1). The increase in basal area increment with N fertilization occurred at both research sites, despite significant differences in N and P availability at the two sites (Table 4; Finzi and Berthrong 2005). There was no significant increase in diameter growth in response to P fertilization alone, and only a suggestion that P limitation occurred once N limitation was removed (e.g., white ash, Fig. 1). Thus in contrast to

Fig. 1 The basal area increment ($\text{cm}^2 \text{ year}^{-1} \pm 1 \text{ SE}$) of the dominant tree species in the **a** sugar maple–white ash stands and **b** oak–beech–hemlock stands. Within a site and species the superscript letters “N” and “P” indicate a significant effect of N or P fertilization” respectively, followed by the level of statistical significance. Bars with no statistical information are not statistically different from one another



the initial hypotheses linking N availability with the response of tree growth to the addition of P, growth remains primarily N limited in hardwood-conifer stands of southern New England.

The interpretation of the data presented here is subject to two constraints. First, this was a short-term fertilization experiment documenting the response of tree growth to 2 years of N and P fertilization. The logic was that short-term responses to fertilization with N and/or P would indicate which soil resources were primarily limiting the rate of tree growth, the main objective of this study. As a consequence, too little time may have elapsed for aboveground growth to respond to enhanced nutrient availability, so there is no way to determine whether the lack of a response

to fertilization by species like red maple and beech reflects insufficient time since fertilizer application or other types of ecological interactions such as limitation by other resources (e.g. water, calcium) or the effect of disease on tree growth (e.g., beech bark disease, Latty et al. 2003). Fertilization with N and P did however significantly increase nutrient supply at 7 cm depth in the soil (see “Results”), and at least four of the seven species responded to N fertilization, including species with determinate growth that might be expected to show a delayed response to fertilization (e.g., sugar maple). Moreover, other fertilization experiments have observed significant responses of tree growth to N and P fertilization over similarly short time scales in hardwood-conifer forests in the

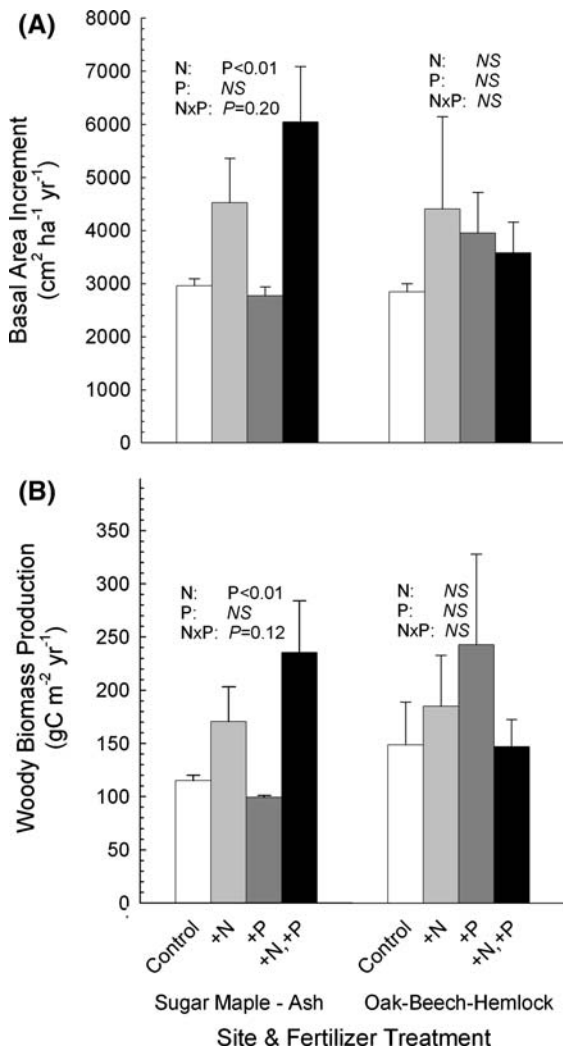


Fig. 2 The mean (± 1 SE) **a** basal area increment ($\text{cm}^2 \text{ha}^{-1} \text{year}^{-1}$) and **b** woody biomass production ($\text{g C m}^{-2} \text{year}^{-1}$), in the sugar maple–white ash and oak–beech–hemlock stands in response to factorial additions of N and P

northeastern US (Lea et al. 1979; Auchmoody 1982). Thus, the responses observed in this study are likely to be indicative of the degree to which N and P are limiting tree growth, at least in the stands studied here and possibly in other stand throughout New England.

Second, the two types of forests were located on two different soil parent materials. The sugar maple–ash forests were located on soils derived from glacial till overlying dolomitic bedrock. The oak–beech–hemlock forests were located on soils derived from glacial till overlying mica-schist bedrock. There are

large differences in soil pH and base cation availability between sites (“Appendix”), and responses to N and P fertilization may be confounded with these factors. For example, the observation that white ash growth was jointly limited by N and P availability may be unique to the high pH soils on which these trees were grown; the rate of P occlusion by iron and aluminum decreases as soil pH increases (Schlesinger 1997), so it is possible that the applied P was available for longer periods of time. Nevertheless the inference drawn from this work should have regional implications. Throughout the New England landscape, sugar maple reaches its greatest abundance on moderately high pH, base rich soils, and oak–beech–hemlock stands are typically found on strongly acidic soils with parent material similar to that of the study sites in northwestern CT (Siccama 1971; van Breemen et al. 1997; Finzi et al. 1998b; Hall et al. 2002). Thus even if soil parent material predisposes trees to respond uniquely to N versus P additions, those responses should apply broadly across the New England landscape and possibly elsewhere.

Consistent with previous studies at this and other sites in the region, N availability was higher in the sugar maple–ash stands compared to the oak–beech–hemlock stands (Table 4; Finzi et al. 1998a, b; Lovett et al. 2004; Finzi and Berthrong 2005). By contrast plant-available P was significantly lower (Table 4), resulting in lower fluxes of P in litterfall and significantly higher PUE (Table 3). Compared to the oak–beech–hemlock stand, high N availability in sugar maple–ash stands is correlated with fast rates of litter decomposition and narrow soil C-to-N ratios that result in rapid rates of mineralization and nitrification (Melillo et al. 1982; Pastor et al. 1984; Finzi and Berthrong 2005). Lower availability of P in the sugar maple–ash stand appears to be due to greater P bound to occluded forms in the soil (Table 5) and the lack of a surface organic horizon where plant-available pools of P can be high (Pare and Bernier 1989). Given high N availability but low P availability it was notable that fertilization with P alone had no effect on the basal area increment of the trees at this site (Fig. 1a). Gradowski and Thomas (2006) found that the growth rate of sugar maple was positively correlated with soil-P availability in Ontario, and Pare and Bernier (1989) found that low P availability in the soil was correlated with declines in sugar maple abundance in Quebec.

Moreover, the concentration of P in sugar maple foliage in this study (0.12%) is within the range of values suggestive of P deficiency by Pare and Bernier (1989) in Quebec. In contrast to this study, correlations between foliar P and sugar maple growth and health have been observed in highly acidic forest soils. Low soil pH, low base cation availability and high concentrations of exchangeable aluminium in the soil are also associated with slow rates of growth and canopy dieback in sugar maple (e.g., Wilmot et al. 1995, 1996), and in general, low pH is correlated with low P availability due to sorption by aluminum (Lindsay and Vlek 1977; but see Pare and Bernier 1989). Thus correlations between P availability and growth or tree health observed in other studies may be related to a correlation between P availability and other factors that have been shown experimentally to affect the growth of sugar maple.

In the sugar maple–ash stands studied here, glacial till overlies dolomitic bedrock resulting in forest soils with a high pH (~5.8) and base cation availability (“Appendix”). The results of this study suggest that the growth of sugar maple and white ash in high pH, high base saturation, low aluminum availability soils remains primarily limited by the availability of N despite decades of atmospheric-N deposition (Ollinger et al. 1993; Holland et al. 2005). The results of this study also suggest that the high PUE efficiency observed in these stands reflects an intrinsic capacity of sugar maple and ash to use P efficiently, at least relative to the tree species in the oak–beech–hemlock stands (Table 3). Hence, comparative analysis of N and P availability or NUE and PUE are not necessarily diagnostic of the relative strength of N versus P limitation (cf. Verhoeven et al. 1996). Interestingly, Lea et al. (1979) found that diameter growth in 70 years old sugar maple trees fertilized in 1975 was N limited not P limited, even though these trees were found on strongly acidic soils. Comparing Lea et al. (1979) to studies suggesting increasing P limitation in acid soils today (Pare and Bernier 1989; Gradowski and Thomas 2006) raises the possibility that the last three decades of N deposition (i.e., 1975 to present) may have shifted nutrient limitation of sugar maple growth from N to P on soils more acidic than those studied here.

The response of basal area increment to fertilization in the oak–beech–hemlock stands was also

inconsistent with the initial hypotheses. Nitrogen availability in these stands is low compared to that in the sugar maple–ash stands yet diameter growth showed no response to N or P fertilization (Fig. 2). In part this reflected the species-specific nature of the response to fertilization (Fig. 1b). Black cherry and red oak responded positively and significantly to N fertilization, red maple and beech growth were unaffected by N fertilization, and hemlock growth was suppressed. Hence the aggregation of these positive, neutral and negative responses to N fertilization resulted in no site-level indication of N limitation despite its occurrence in two of the five abundant species at this site. Moreover, the addition of P to plots treated with N resulted in no additional growth increment in any species (Fig. 1b).

There are few experiments that have applied factorial combinations of N and P for a similar set of species, so there are very few data against which this study can be compared. Auchmoody (1982) fertilized young stands of black cherry seedlings and saplings originating from a clear cut and found that growth increased in response to N additions alone, and to P additions once N was added. In this study, diameter growth of adult black cherry trees increased in response to fertilization with N with no indication of P limitation. Consistent with the findings here (Fig. 1b); Lea et al. (1979) found no effect of N or P fertilization on the growth of beech in a 70 years old stand in the Adirondacks of New York. They did however find that P fertilization increased diameter growth in red maple, a response that was not observed in this study.

The results of this study run somewhat counter to those presented in Elser et al. (2007). Using meta-analysis techniques to analyze the response of ecosystems to factorial additions of N and P, they demonstrated that N and P together limited primary production in marine, freshwater and terrestrial ecosystems. Within terrestrial ecosystems their analysis included a “forest–shrubland” category, which in contrast to their global analysis, exhibited only limitation by P. Importantly, there were no studies of temperate forests included in the Elser et al. (2007) analysis, either because no such data exist or because they have not been published. In this study P limitation was only observed in white ash trees, and then only after N limitation was removed, not vice versa as suggested by the Elser et al. (2007) ‘forest–

shrubland' analysis. This and other studies suggest widespread N limitation in temperate forests (e.g. Magill et al. 2000; LeBauer and Treseder 2008), thus substantial caution needs to be practiced when broadly applying the Elser et al. (2007) model for nutrient limitation.

The results of this study also run counter to those presented in Magnani et al. (2007) who found a significant correlation between the rate of wet N deposition and net ecosystem production across European forests. Assuming that all N deposition is taken up on an annual basis, their analysis suggests that approximately 725 g C are taken up on an annual basis for every gram N in wet deposition (470 g C g N^{-1} if dry deposition is included, de Vries et al. 2008). These very wide C-to-N ratios could only be supported if the N taken up from atmospheric deposition were allocated to the production of wood rather than leaves or fine roots, which typically have C-to-N ratios between 50:1 and 100:1. In this study, fertilization with N increased woody biomass production by $100 \text{ g C m}^{-2} \text{ year}^{-1}$ (Fig. 2). If we assume that the wood in this ecosystem has a relatively low C-to-N ratio of 250:1 (i.e., a high N cost), the increase in wood production in response to fertilization would require an additional $0.4 \text{ g N m}^{-2} \text{ year}^{-1}$. Given strong physical sinks for N in the soil and losses of N through denitrification, it is not surprising that plants take up only a small fraction of N inputs via atmospheric deposition (Nadelhoffer et al. 1999; Van Breemen et al. 2002; Davidson et al. 2003; Magill et al. 2004). In this study however, N fertilizer was applied at an annual rate of 15 g N m^{-2} , ten times greater than the annual rate of N deposition (Ollinger et al. 1993), yet <3% of the fertilizer N inputs was taken up. This level of uptake rivals that observed in whole-system ^{15}N tracer experiments under ambient and N fertilized conditions (e.g., Nadelhoffer et al. 1999; Magill et al. 2004) as well as that measured in European fertilization and inventory studies (De Vries et al. 2006; Hyvonen et al. 2008). Thus, this study in combination with data from a large literature raises substantial doubts about the accuracy of the relationship between N deposition and net ecosystem production reported by Magnani et al. (2007).

Conclusion

Based on 2 years of tree growth following factorial additions of N and P, there was substantial evidence for N limitation of tree growth in two southern New England forests, but only limited evidence for P limitation. The large increase in diameter growth in response to N fertilization in the sugar maple–ash forests is notable given that variations in P availability are correlated with diameter growth in sugar maple stands growing on acid soils Pare and Bernier (1989); Gradowski and Thomas 2006). Moreover, on a regional basis sugar maple stands exhibit symptoms of N saturation as indicated by high, aseasonal rates of NO_3^- losses in stream water (Lovett et al. 2000). The results of this study suggest that NO_3^- losses may not be occurring because the availability of N is in excess of biotic demand but rather because high rates of nitrification in stands dominated by sugar maple (Finzi et al. 1998a; Finzi and Berthrong 2005) coupled with low rates of NO_3^- uptake (Templer and Dawson 2004) predispose these watersheds to lose a highly mobile species of N. Future studies comparing sugar maple growth in response to factorial additions of N and P will play an important role in determining the degree to which N versus P limitation of growth varies between base rich and base poor soils, and in assessments of whether NO_3^- losses from sugar maple-dominated watersheds reflects N saturation or other ecological processes (i.e., high inherent rates of nitrification).

Acknowledgments Thanks the Great Mountain Forest Corporation and the State of Connecticut, Department of Environmental Protection, Natural Area Preserves Program for permission to work in their forestlands. Thanks also to Jody Bronson who helped with the logistical support for this research at the Great Mountain Forest. Edward Brzostek set up and fertilized the research plots and also made repeated dendrometer band measurements; his help was invaluable. Christy Goodale, Matthew Weand and Ruth Yanai provided helpful comments on an earlier draft of this manuscript. This research was supported by the USDA-CSREES (2001-00782).

Appendix

See Table 6.

Table 6 Selected properties of each study site

Property	Research site	
	Oak–beech–hemlock	Sugar maple–ash
Basal area (m ² ha ⁻¹)	44.8 (4.0)	40.0 (3.6)
Soil texture		
% Sand	44.7 (3.2)	46.6 (1.6)
% Silt*	45.1 (1.7)	35.2 (1.5)
% Clay*	10.2 (2.8)	18.3 (1.1)
pH ^a		
0–15 cm**	3.76 (0.13)	5.69 (0.10)
15–30 cm**	4.38 (0.10)	5.95 (0.09)
Organic horizon mass (g m ⁻²)	3110 (249)	–
Bulk density (g cm ⁻³)		
0–15 cm*	0.72 (0.04)	0.95 (0.05)
15–30 cm*	0.99 (0.03)	1.11 (0.06)
Exchangeable bases ^b (Ca + Mg, mol _c m ⁻²)		
O horizon	0.21 (0.03)	–
0–15 cm***	0.20 (0.05)	7.99 (1.35)
15–30 cm***	0.09 (0.03)	5.74 (0.94)
Total***	0.50 (0.09)	13.7 (2.20)
Total C ^c (g m ⁻²)		
O horizon	1151 (106)	–
0–15 cm*	7840 (397)	6255 (660)
15–30 cm	3464 (659)	3045 (643)
Total**	12455 (818)	9300 (1287)
Total N ^c (g m ⁻²)		
O horizon	46 (4)	–
0–15 cm*	392 (9)	491 (41)
15–30 cm	290 (25)	298 (31)
Total	728 (34)	789 (71)
Total P ^d (g m ⁻²)		
O horizon	3.1 (0.1)	–
0–15 cm*	167 (17)	290 (28)
15–30 cm	212 (18)	241 (43)
Total	383 (28)	531 (69)

Each observation is the mean (± 1 SE) of samples collected from four replicate plots per site. Row means with a different superscript letter are significantly different at, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$

^a Measured in 0.1 M CaCl₂

^b Measured in 1 M NH₄OAc

^c Measured by direct combustion on an element analyzer

^d Measured by copper-sulfate, sulfuric acid Kjeldahl digestion

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