Synergistic soil response to nitrogen plus phosphorus fertilization in hardwood forests

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Abstract Plant and microbial processes exert control on the stoichiometry of available nutrients, potentially influencing forest ecosystem responses to nitrogen enrichment and other perturbations that alter resource availability. We tested whether an excess of one nutrient influenced the available pool of another, to learn the net outcome of various feedbacks on mineralization and uptake processes. We examined nitrogen and phosphorus availability (assayed with buried ion-exchange resin strips) in the first year of fertilizing northern hardwood forests with 30 kg/ha N, 10 kg/ha P, or N and P together. Fertilizing with a single nutrient raised the availability of the added nutrient and had no detectable effect on availability of the other nutrient. However, resin-available N was raised substantially more by adding N+P than it was by adding N alone. This effect of N+P must be the result of either reduced biotic uptake of N or increased mineralization of N, and suggests that N loss following forest disturbances will be enhanced in cases where the availability of both N and P are increased. That P interacts with N to enhance N availability, by whatever mechanism, could help explain observations of N and P co-limitation in ecosystems and calls attention to the need to carefully elucidate mechanisms underlying co-limitation of forest productivity.

Keywords Co-limitation · Fertilization · Nitrogen · Northern hardwood forest · Nutrient availability · Phosphorus

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Introduction

The balance of available nutrients in terrestrial ecosystems depends upon feedbacks between soil nutrient availability and the processes of nutrient recycling. The importance of coupling among nutrient cycles is well recognized (Finzi et al. 2011), with interactions between soil N and P likely to influence biogeochemical response to natural and anthropogenic change. In forest ecosystems, the influence of nutrient availability on plant and soil processes can feed back to increase the availability of soil nutrients and accelerate nutrient recycling (for example, Hart et al. 1997; Vitousek 2004). Feedbacks to nutrient availability can also reduce availability and slow nutrient recycling (for example, Flanagan and VanCleve 1983; Fisk and Fahey 2001). The possible contribution of N and P interactions in these feedbacks is not commonly considered but could influence their outcomes, especially in response

to any disturbance that does not affect nutrients in stoichiometric proportion (Rastetter et al. 2013). Hardwood forests experience a suite of perturbations (i.e., insect irruptions, ice storms, drought stress, soil frost, acid deposition, forest harvest) that could alter nutrient interactions in a manner that maintains the stoichiometry of available nutrients and thus contributes to resilience in forest productivity, or that exaggerates differences in availability among nutrients and thus promotes nutrient loss.

There are a variety of ways in which excess of one nutrient could influence the availability of the other through changes in mineralization and uptake processes. One example is an enzymatic feedback, via allocation of resources by decomposer organisms to different enzymes depending on availability of N, P, and C (Allison et al. 2011), analogous to resource optimization processes in plants (Bloom et al. 1985). Principles of resource allocation suggest that adding one nutrient will increase availability of the other by shifting enzyme expression, and will thereby promote better balance in availability between N and P. For instance, added N can promote the activity of phosphatase enzymes (Olander and Vitousek 2000; Treseder and Vitousek 2001; Marklein and Houlton 2012) and hence increase P mineralization. For the same reasons, we would expect P additions to promote the production of N-mineralizing enzymes (Olander and Vitousek 2000).

Alternatively, adding one nutrient could reduce available pools of another by promoting uptake of the second nutrient. For example, where N limits microbial growth, adding N should increase microbial uptake of P, because the stoichiometry of soil microorganisms is thought to change little relative to available N and P resources (Cleveland and Lipzin 2007). The same could be true for plants if the addition of one nutrient promotes growth and uptake of other nutrients. However, plants will likely respond to additions of nutrients far more slowly than microbes, with effects taking some years to develop.

The net outcomes of these feedbacks to nutrient availability are important for interpreting how forest ecosystems respond to change and develop over time. This may be especially relevant in northern hardwood forest ecosystems of the northeastern US, where N enrichment, soil acidification, and management practices can all influence soil processes and alter limitations to forest productivity (Aber et al. 2003; Fiorentino et al. 2003; Rastetter et al. 2013). We examined N and P interactions in northern hardwoods in a factorial N×P fertilization experiment that has the long-term goal of examining nutrient limitation or co-limitation of forest productivity in northern hardwoods, with co-limitation referring to productivity responses to added N+P that exceed those to either nutrient added alone. We chose to focus on N and P, because of evidence for N limitation, P limitation, and N and P co-limitation of primary productivity in northern hardwoods (Vadeboncoeur 2010), with evidence in some cases suggesting stronger P limitation in younger forests (Naples and Fisk 2010; Rastetter et al. 2013). We conducted our study in the Bartlett Experimental Forest (BEF), NH, which is typical of northern hardwoods throughout the region and has the advantage of multiple distinct stands of different ages. We included early-, mid-, and late successional forests, in a total of nine different forest stands, to represent a wide range of site conditions and to include variability in ecosystem development related to forest management.

We hypothesized that adding an essential nutrient (N or P) affects the availability of the other nutrient, and asked whether the direction of that effect is influenced more by enhancing mineralization (and hence availability) or by enhancing biotic uptake of that nutrient, or whether there is no net effect. If a net effect is detected, the direction of that effect should indicate whether nutrient feedbacks to mineralization and uptake processes contribute to balance in the relative availability of N and P, or exaggerate differences in availability between the two nutrients. The nutrient additions in the first year likely affected soil microbial and plant root-associated processes but were not yet likely to influence nutrient mineralization processes via plant-mediated changes in above- or belowground litter supply or its chemistry. Hence, this first year was an ideal time to test direct effects of nutrients on microbial and plant root processes.

Methods

Our study sites were in northern hardwood forest at the Bartlett Experimental Forest (BEF), NH, with elevations of 330–590 m and slopes of 5–30 %. The overstory in our mature forest sites was dominated by American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton), and sugar maple

(*Acer saccharum* Marsh) with some ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.), and white birch (*Betula papyrifera* Marsh). Soils were mostly Spodosols (typic and aquic Haplorthods) overlying glacial till, with thick organic surface horizons.

We studied nine forest stands, three each of mature (>100 years), intermediate (30–35 years), and young (21–26 years) age. The intermediate and young stands originated following clearcut harvest, and forest composition was typical of early-successional hardwood forests of the region, with pin cherry (*Prunus pensylvanica* L.f.), white birch, yellow birch, red maple, and beech common in the overstory. Sugar maple is generally a late successional species in this region (Leak 1991) and was occasionally present in the younger stands. Native soil fertility varied across our study sites as a consequence of distribution of glacial tills, contributing to some variation in overstory species composition especially in late succession (Leak 1991). These soils had low pH, varying from 4.2 to 4.9 in the surface 10 cm of the mineral soil of the different forest stands. Clay content in the B horizon varied from 14 to 18 % and sand content varied from 48 to 67 % across stands. Organic matter concentrations varied across sites from 73 to 85 % in the Oe horizon, 42 to 64 % in the Oa horizon, and 6.9 to 10.7 % in the top 10 cm of the mineral soil.

In each of our nine stands we established four 50×50 m plots. Pre-treatment soil properties and net N mineralization potentials were analyzed on soil samples collected from three of the four plots per stand in the mid-age and mature stands in the first week of July, 2008, and in all plots of all nine stands in the last week of June, 2009. In each plot we extracted ~ 30 soil cores (2 cm diameter) to a depth of 10 cm in the mineral horizon and separated Oe, Oa, and mineral horizons. Samples were composited by horizons within each plot. Each sample was homogenized and inorganic N was extracted from an initial subsample and also from a second subsample after 21 days incubation in the laboratory at 20 °C. Subsamples were shaken in 2 M KCl ($\sim 1{:}5$ soil mass:extractant volume) and extracts were filtered through Whatman #1 paper after ~ 18 h settling time. We used a phenolate–hypochlorite method to quantify NH_4^+ (method 351.2, US EPA 1983) and a cadmium reduction method to quantify NO_3^- (method 353.2, US EPA 1983) in extracts. Net N mineralization was estimated as the difference in KCl-extractable NH_4^+ and NO_3^- between initial and incubated soil subsamples.

Fertilization treatments were initiated in spring, 2011. We randomly assigned control, N addition, P addition, and N+P addition treatments to each of the four plots within a stand. We adjusted treatment locations in a few stands where N addition was initially assigned to a plot upslope of control or P addition, to ensure that added N would not be transported from one plot to another. We assumed that P would not be mobile. In mid May and early July 2011 we fertilized all plots, adding N as pelletized NH_4NO_3 and (or) P as powdered NaH_2PO_4, for a total of 30 kg/ha of N and 10 kg/ha of P. The level of P was high relative to N to account for potential fixation in soil. Fertilizer was spread by hand evenly over 2.5×10 m^2 sub-plots. We imitated our fertilizer spreading procedure (without fertilizer) in control plots to ensure similarities among plots in any short-term disturbance to the forest floor.

We used anion exchange resin strips (Ionics AR-204-SZRA; Maltz Sales) to quantify resin-available PO_4^- and NO_3^-, and cation exchange resin strips (Ionics CR67-HMR; Maltz Sales) to quantify resin-available NH_4^+ in soils of our plots. Strips (2×6 cm) were prepared by rinsing in weak HCl and deionized (DI) H_2O and then soaking in 1 M NaCl (cation strips and anion strips for NO_3^-) or alternating rinses in DI H_2O and 0.5 M $NaHCO_3$ (anion strips for PO_4^-). All strips were rinsed with DI H_2O immediately prior to placement in the field. Resin strips adsorb ions in soil solution that come in contact with the surface of the resins; therefore, we assume that the resin-available pools of N and P are similar to soil solution pools that are available to plant roots and other soil biota.

In late July, 2 weeks after the second treatment application, we deployed resin strips in the Oa horizon by inserting them under the blade of a knife used to cut the surface organic horizon at a 30°–45° angle. This time period was chosen to be as close as possible to the peak period of N mineralization in northern hardwoods (July, Bohlen et al. 2001) yet still allow time for fertilizers to dissolve, move into soil, and be available for biotic uptake in soil after application. Six strips per plot were deployed for each nutrient. Strips were retrieved after 14 days and rinsed in DI H_2O prior to extraction for nutrient analyses. The Ameriflux network site at the BEF recorded 26 mm of rainfall during the time of resin strip incubation, distributed relatively evenly over four events, and a total of

21 mm in the month prior to incubation (http://ameriflux.ornl.gov/fullsiteinfo.php?sid=75).

Anion exchange resins were extracted by shaking rinsed strips in 30 mL of 1 M KCl for NO_3^- and 30 mL of 0.5 M HCl for PO_4^- for 1 h each. Cation strips were extracted by shaking rinsed strips in 30 mL of 1 M KCl for 1 h. NH_4^+ and NO_3^- concentrations were analyzed as described above. Extract P concentration was analyzed by the ammonium-molybdate-ascorbic acid method (Murphy and Riley 1962).

We quantified pH of Oe and Oa horizon samples collected in July 2012. Four 5-cm diameter cores were collected in each of four quadrats per plot and pooled within plots. pH was measured in 1:5 soil mass:water volume slurries, with constant stirring.

Resin-strip data were log-transformed prior to analyses to meet assumptions of normality of the residuals. Treatment effects on resin-available NH_4^+, NO_3^-, total inorganic N (NH_4^+ plus NO_3^-) and PO_4^- were tested using a mixed-effects model with treatment and forest age as fixed effects, forest stand as a random effect, and treatments nested within stands (Proc Mixed, SAS 9.2, Cary, NC, USA). Differences in resin-available nutrients between specific treatments were tested with Tukey differences of least square means. We described the interaction of added P and N by comparing the difference in resin-available nutrient between the N+P and N treatments, with the difference between the P and control treatments. We did this using contrast analysis to test the null hypothesis that, for a resin-available nutrient, (N+P) – N = P – Control. Relationships among soil variables were explored using Proc Corr in SAS.

Results

Our treatments increased resin-available P and inorganic N ($NH_4^+ + NO_3^-$) relative to controls (Fig. 1A, B; $t = -4.49$, $P < 0.001$ for P; $t = -4.59$, $P = 0.001$ for N). The N treatment effect was also significant for NH_4^+ ($t = -5.37$, $P < 0.0001$) and for NO_3^- ($t = -3.81$, $P = 0.03$) alone. Adding one nutrient alone did not detectably affect the availability of the other nutrient relative to controls ($t = 1.18$, $P = 0.64$ for P response to N addition; $t = -0.05$, $P = 1.0$ for total N response to P addition; similar lack of significance for NH_4^+ or NO_3^- response to P addition). Forest age had
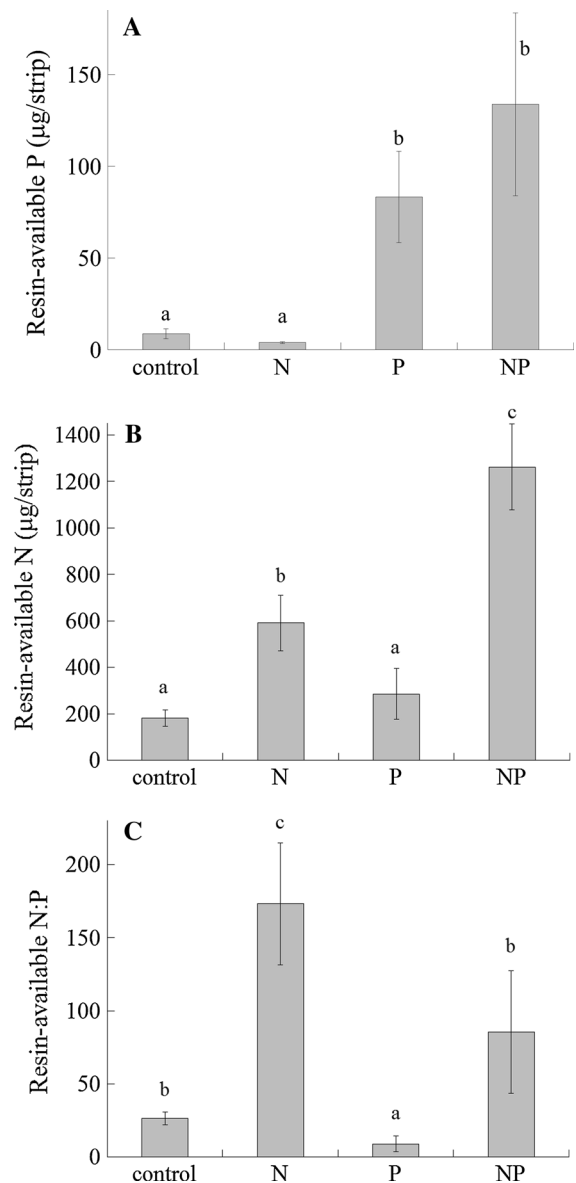

Fig. 1 Resin-available P (A), N ($NO_3^- + NH_4^+$; B), and the ratio of N:P (C) in control and fertilized plots in nine forest stands (three each of young, mid-age, and mature forest). Resin strips were incubated in the Oa horizon for 2 weeks beginning in late July, 2011. *Error bars* are standard error of the mean; $n = 9$. Treatments with the *same letter* do not differ significantly

no consistent effect on resin-available nutrients but there was an age by treatment interaction for NO_3^- ($F = 2.54$, $P = 0.048$), with larger N effects on NO_3^- in young forests (Fig. 2A). Resin-available NH_4^+ did not differ significantly among forest ages or exhibit an age by treatment interaction (Fig. 2B).
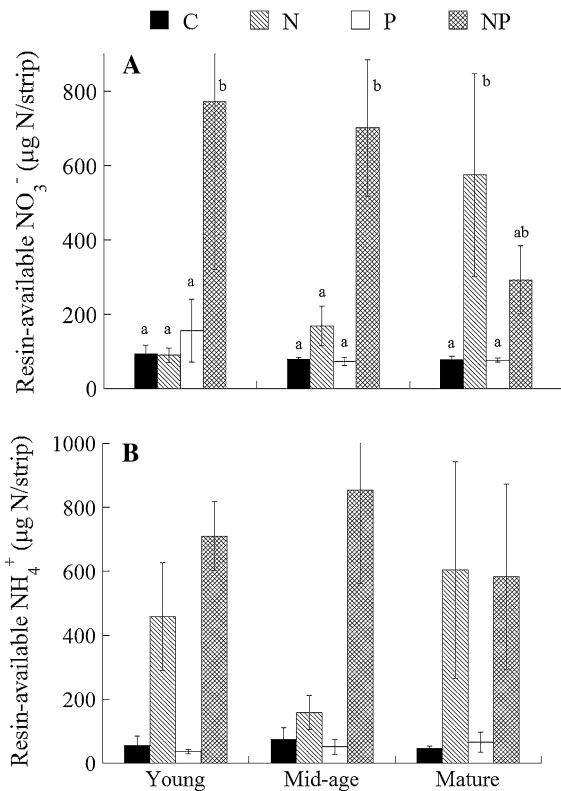
Fig. 2 Resin-available NO_3^- (**A**) and NH_4^+ (**B**) in control and fertilized plots in young, mid-age, and mature forest stands. Resin strips were incubated in the Oa horizon for 2 weeks beginning in late July, 2011. *Error bars* are standard error of the mean; $n = 3$ stands per forest age group. For NO_3^-, treatments with the *same letter* within each forest age do not differ significantly. Significance is not shown for NH_4^+ because there was no age × treatment interaction; see text for treatment differences

A more notable result was the greater effect on resin-available N of N+P addition compared to N addition alone (Figs. 1B, 2A). Resin-available inorganic N was substantially higher in N+P compared to N treatments ($t = -3.29$, $P = 0.02$) and resin-available NH_4^+ was marginally higher in N+P compared to N treatments ($t = -2.50$, $P = 0.08$). The NO_3^- response depended on forest age, with higher NO_3^- in N+P compared to N treatment in young ($t = -3.43$, $P = 0.04$) and mid-age (-4.67, $P = 0.01$) but not mature forests (Fig. 2). Similarly, the contrast analysis detected an interactive effect of N+P, with an enhancement of N availability when both N and P were added, compared to the effect on N availability when only P was added. This effect was significant for total inorganic N ($F = 5.24$, $P = 0.03$) and NH_4^+ ($F = 5.16$, $P = 0.03$), and for

NO_3^- in young ($F = 6.34$, $P = 0.02$) and mid-aged ($F = 5.04$, $P = 0.03$) but not mature forests.

We did not detect differences in resin-available P between P-only and N+P treatments. Coefficients of variation for the different treatments indicated more spatial heterogeneity for P than for N, varying from 30 to 43 % for resin-available P, compared to only 6–13 % for resin-available N. Hence, while N+P treatments did not appear to increase resin-P availability markedly more than adding P alone, larger numbers of resin strips would be required to detect more modest effects of N+P versus P.

Resin-available N:P ratios varied widely across stands in control plots, from 5 to 45 (mass basis). N addition significantly raised resin-available N:P ($t = -3.76$, $P = 0.005$) and P addition reduced resin-available N:P ($t = 3.86$, $P = 0.004$) (Fig. 1C).

N mineralization potentials varied across forest stands in a pattern that was consistent between 2008 and 2009 in mid-age and mature forest stands (young stands were not sampled in 2008) (Table 1). Resin-available N in control plots was significantly related to N mineralization in the Oe horizon across the nine forest stands ($R = 0.78$, $P = 0.01$). This correlation suggests that resin-available N provides a good index of mineralization rates across our sites. Site-level variation in ambient N availability also appeared to strongly influence resin-available N:P ratios, which in control plots were correlated with resin-available N ($R = 0.90$, $P = 0.001$) and with net N mineralization in the Oe horizon ($R = 0.89$, $P = 0.001$; Fig. 3). Resin-available P contributed to the pattern of N:P ratios, but in a less linear fashion compared to N. Resin-available P was especially high (12–27 µg/strip/day) at the three sites with lowest N:P (and the lowest N mineralization, in one young and two mature stands; Fig. 3) and was lower and less variable (3–6 µg/strip/day) in the remaining sites.

Soil pH was not affected by fertilization treatments, and in the Oe horizon averaged 4.79 (±0.12 standard error of the mean) in controls, 4.83 (±0.05) in +N, 4.70 (+0.08) in N+P, and 4.85 (+0.10) in +P plots. pH was slightly lower in the Oa horizon, averaging 4.33 (±0.14) in controls, 4.19 (±0.08) in +N, 4.29 (+0.10) in N+P, and 4.20 (+0.09) in +P plots.

Discussion

Fertilization treatments can cause abrupt changes in the soil environment. We added relatively low levels of

Table 1 Pretreatment N mineralization potentials in the Bartlett Experimental Forest, NH, measured in early July 2008, and late June 2009

Stand	Year clear-cut	Age group	Net N mineralization (μg N/g/day)					
			Oe horizon		Oa horizon		B horizon	
			2008	2009	2008	2009	2008	2009
C1	1990	Young		15.9 (1.24)		9.9 (2.11)		0.34 (0.053)
C2	1988	Young		16.8 (0.75)		6.2 (1.53)		0.31 (0.037)
C3	1985	Young		30.7 (4.67)		9.1 (1.01)		0.46 (0.043)
C4	1979	Mid-age	20.5 (1.81)	18.1 (1.67)	5.3 (0.50)	7.8 (0.94)	0.56 (0.148)	0.38 (0.077)
C5	1976	Mid-age	19.6 (0.94)	23.1 (3.00)	5.2 (0.99)	8.8 (0.97)	0.54 (0.083)	0.45 (0.077)
C6	1975	Mid-age	28.9 (5.54)	36.9 (10.08)	5.9 (1.25)	7.9 (0.43)	0.68 (0.076)	0.49 (0.044)
C7	NA	Mature (>100 years)	10.9 (1.06)	10.2 (2.21)	4.6 (0.67)	4.5 (0.48)	0.64 (0.037)	0.36 (0.034)
C8	NA	Mature (>100 years)	9.7 (3.14)	8.9 (1.69)	4.1 (1.04)	4.1 (0.25)	0.72 (0.148)	0.27 (0.045)
C9	NA	Mature (>100 years)	16.2 (2.77)	17.4 (3.21)	7.7 (1.43)	8.3 (1.37)	0.77 (0.180)	0.38 (0.051)

$n = 4$ plots per stand, standard errors of the mean are in parentheses
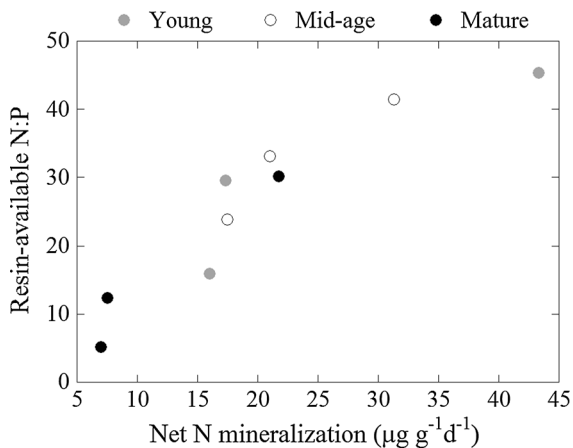
NA not applicable

Fig. 3 Relationship between resin-available N:P and net N mineralization in the Oe horizon in control plots of young, mid-age, and mature forest stands. Resin strips were incubated in the Oa horizon for 2 weeks beginning in late July, 2011; net N mineralization was quantified in lab incubations in mid-summer 2009

nutrients (30 kg/ha N, 10 kg/ha P), with the intention of causing moderate increases in nutrient availability with minimal shock to the system. Elevated resin-availability of the added nutrient indicated that our treatments exceeded the short-term biological and chemical immobilization capacities of these soils. Hence, the added nutrient appears to have alleviated potential limitation of soil organisms even at these relatively low levels of addition.

We did not find support for the hypothesis that adding one nutrient alone would alter the resin-availability of the other. It is possible that the added nutrient had no effect on the processing of the other, or that the effect of the added nutrient on both mineralization and uptake of the other caused a net neutral effect. If N limits microbial growth, as suggested by the overflow metabolism hypothesis (Schimel and Weintraub 2003), then we would expect decomposer microbes and mycorrhizal hyphae to take up more P in response to a relief from N limitation, and thus reduce available P. At the same time, if microbes optimize allocation to produce different enzymes depending on relative costs and benefits (Allison et al. 2011), then adding N or P should increase mineralization of the other nutrient, especially if organic substrates are available (Allison and Vitousek 2005). The lack of directly comparable methods for measuring N and P mineralization limits our ability to examine the mechanisms underlying this result by testing effects on mineralization processes. Nevertheless, we can conclude that neither mineralization nor uptake processes were obviously dominant in the response by one nutrient to an excess of the other.

The marked response of N availability to added N+P appears to be a synergistic effect; it was higher than the effect of N treatment alone (especially in early- and mid-successional forests) and there were not significant effects on N following P treatment alone. The effect is largely related to the increase in

NO_3^- when P was added with N (Fig. 2A). The more obvious response by NO_3^- than by NH_4^+ and in young and mid-age compared to mature stands is consistent with higher nitrification potentials in early-successional compared to mature forests of this region (Fisk and Fahey 1990). Minick et al. (2011) found that adding P enhanced gross nitrification rates in mature northern hardwoods at the nearby Hubbard Brook Experimental Forest, and suggested that high microbial NO_3^- immobilization prevented a net nitrification response. It is possible in early successional forests that P also promotes gross nitrification, and that this affects net nitrification as well because immobilization potentials are lower.

The age-related pattern of NO_3^- response to N+P addition also corresponds to that of resin-available N:P in control plots. Simultaneously low N and high P contributed to the very low resin-available N:P in two mature stands (Fig. 3), and it was only in these stands (C7 and C8) that the N+P treatment did not elicit higher resin-available N than did the N treatment alone (data not shown). Hence, it is likely that the synergistic effect of N+P on resin-available N depended on relatively low ambient availability of P.

We suggest several possible explanations that deserve attention to better understand the apparent effects of N+P addition on resin-available N. First, it is possible that adding N+P together reduced microbial immobilization of N to cause higher resin-available N pools, more so than did adding N or P alone. Suppression by N+P of rhizosphere C inputs could be one mechanism contributing to lower microbial N uptake. Lower microbial immobilization may also contribute to a P effect on net nitrification, as suggested by Minick et al. (2011). Second, the synergistic effect of N+P on N availability could arise from changes in N use for enzyme production, if N uptake declines as a consequence of lower demand for N to produce N- and P-mineralizing enzymes. This explanation is consistent with the meta-analysis by Marklein and Houlton (2012), which showed that addition of N+P reduced phosphatase activity in the ecosystems that were represented in their analysis (grasslands and tropical forest but not temperate forest). Any reduction in phosphatase production should reduce plant and microbial demand for N because of the high N cost of phosphatase production, thereby contributing to the high N availability that we observed. This explanation is also consistent with our observation that the response by resin-available N to added N+P did not exceed that to N alone in the two mature forests where, under ambient conditions, resin-available P was relatively high. In this case, allocation to phosphatase enzymes under ambient conditions may have been low enough that adding P did not reduce it further. Although N could potentially be reallocated to C-mineralizing enzymes, this would pertain only to heterotrophic microorganisms, while a high proportion of phosphatase could be produced by plant roots (Marklein and Houlton 2012).

A third possible explanation for increased resin-available NH_4^+ is displacement from the exchange complex by Na from the NaH_2PO_4 fertilizer. This effect was likely very small. We estimate a range across our sites of 1.33–2.45 eq/m^2 exchange (summing Ca, K, Mg, Na) in the Oa and B horizons (Vadeboncoeur et al. unpublished). Adding 10 kg/ha/year of P as NaH_2PO_4 adds 0.03 eq/m^2/year of Na, only 1–3 % (depending on the forest stand) of existing exchange capacity in the Oa and mineral soil to the bottom of the B horizon. This estimate excludes Oe horizon exchange capacity, which we did not measure, making the contribution of added Na relative to soil available pools even <1–3 %.

Quantitative comparisons of N and P availability are challenging for practical reasons, because of a lack of comparability of methods for measuring nutrient mineralization, and for conceptual reasons, because of a lack of comparability of pools. Our results show that resin strips provide useful relative comparisons between N and P, but it remains uncertain whether this method is similarly efficient in quantifying these two nutrients. For example, the strong effect of N relative to P on resin-available N:P in control plots raises the possibility that resin strips more efficiently detect variation in the availability of N. It is possible that P desorbs from resins over time. While we would not expect this effect to be large in these organic horizons, compared to potential desorption in a mineral soil, it could nevertheless contribute to underestimating available P. It is also possible that high uptake of P where N availability is relatively high consistently reduces the levels of resin-available P, such that the influence of biotic uptake contributes to an unexpectedly wide variation in resin-available N:P across sites. While we did not find support for our hypothesis that adding one nutrient would reduce availability of the other, the relationship between N mineralization and resin N:P in control soils could be

interpreted as support for the effect of N availability on resin-available P, over longer time periods that are likely subject to different controls than the shorter-term response to fertilization.

Our results have implications for effects of short-term changes in soil resource availability arising from various disturbances in hardwood forests. For example, nutrient availability can be elevated following ice storms (Houlton et al. 2003), soil freezing (Mitchell et al. 1996; Groffman et al. 1999), and forest harvest (Fisk and Fahey 1990). Insect defoliations can also alter nutrient recycling processes (Lovett et al. 2002), potentially affecting nutrient availability. We did not find evidence that soil processes will respond to elevated available nutrient pools, of the sort that might arise from these types of short-term disturbances, in a direction that contributes to balanced nutrient availability. Instead, the synergistic effect of N and P on available N pools that we found suggests soil feedbacks to elevated N and P could enhance N losses by further elevating N availability, especially in early successional forests with relatively high potential for nitrification.

Nutrient interactions appear less likely to increase N losses following disturbances that elevate N but not P. Disturbance would be expected to elevate N more than P availability if P mineralization declines after harvest because of low plant demand; P mineralization is driven more by biotic demand than as a byproduct of C mineralization (McGill and Cole 1981). In addition, rapid adsorption of available P on soil surfaces is expected in this soil type after disturbances that reduce plant uptake (Wood et al. 1984; Yanai 1998), which would also reduce availability of P relative to N. Concurrent measures of N and P responses to disturbances in hardwood forests are not common but would be useful for interpreting disturbance effects.

Comparing our short-term nutrient responses to fertilization with measurements made following several years of treatment, allowing for plant-mediated feedbacks to develop, will be relevant to questions of longer-term responses. For example, available nutrient pools under chronic N enrichment depend not only on direct effects of nutrients on microbial metabolism and activity, but also on the changes in plant tissue chemistry and C allocation that develop over time in response to plant uptake. Contrasting with our results, 8 years of fertilizing young forests in central NH with N, P, K, and micronutrients reduced net N mineralization and did not increase soil inorganic N pools, suggesting that nutrient recycling feedbacks functioned to conserve N in these ecosystems (Fahey et al. 1998; Fisk and Fahey 2001). In the present experiment, we will follow responses to continued treatment to examine changes over time in the relative effects of direct versus plant-mediated effects on nutrient availability.

A synergistic effect of N and P on N availability could contribute to observations of co-limitation of forest productivity, in which productivity response to added N+P exceeds productivity response to addition of either nutrient alone. Nutrient co-limitation of productivity appears to be prevalent in many ecosystems (Elser et al. 2007; Harpole et al. 2011). While temperate forests were not well represented in these analyses, subsequent analysis of northern hardwood forests suggests co-limitation in these systems as well (Vadeboncoeur 2010). The additive or synergistic promotion of forest productivity by N and P together could originate at many levels, from soil availability to nutrient uptake mechanisms to biochemical controls of the photosynthetic process (Saito et al. 2008; Ågren et al. 2012). From a stoichiometric perspective, we expect N and P to be co-limiting because of the simultaneous need by plants for N-rich enzymes and for P-rich phospholipids and nucleic acids. However, our results support the possibility that productivity responds synergistically to N+P because a single nutrient (N) is limiting at the biochemical level, but the second nutrient (P) interacts in soil to promote availability of the first limiting nutrient. Empirical studies of the mechanisms of co-limitation are scarce (Davidson and Howarth 2007), and our results illustrate the need to consider N and P interactions in soil as a mechanism that could drive some of the synergy in forest production response. Furthermore, the likelihood that N+P causes only a transient increase in N availability (prior to full effects of plant allocation feedbacks) adds to the argument by Davidson and Howarth (2007) that timing is important to interpreting co-limitation responses.

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