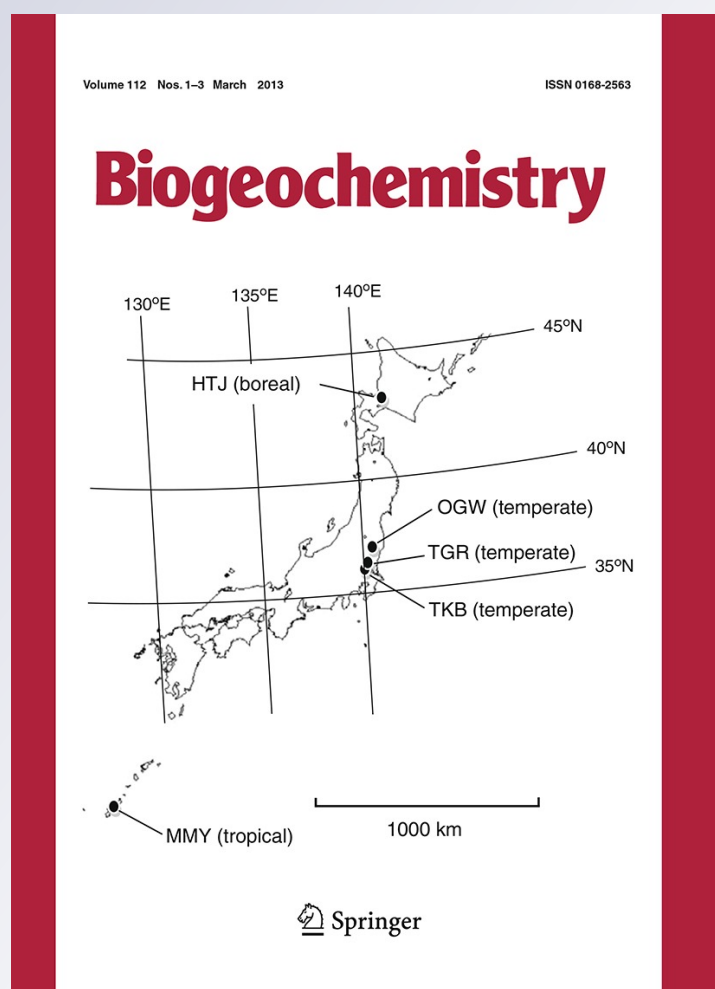# Interactive effects of disturbance and nitrogen availability on phosphorus dynamics of southern Appalachian forests

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Interactive effects of disturbance and nitrogen availability on phosphorus dynamics of southern Appalachian forests

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Abstract Understanding the main and interactive effects of chronically altered resource availability and disturbance on phosphorus (P) availability is increasingly important in light of the rapid pace at which human activities are altering these processes and potentially introducing P limitation. We measured P pools and fluxes in eighteen mixed forest stands at three elevations (low, mid, high) subjected to increasing atmospheric N deposition, where hemlock (*Tsuga canadensis*) was absent or declining due to infestation by the exotic hemlock woolly adelgid (*Adelges tsugae*). While total soil P was similar across the study area, phosphorus fractionation revealed distinct differences in the distribution of soil P fractions as elevation and N availability increased. Soils from high elevation plots where N availability was greatest had 139 % larger organic P pools and 55 % smaller residual and refractory P pools than soils from low elevation plots with less N availability, suggesting that increased N availability has driven the depletion of recalcitrant P pools by stimulating biotic demand and sequestration. These differences in P distribution among fractions influenced how tree mortality affected P dynamics. At high elevations, plots containing declining hemlocks had significantly greater foliar P concentrations and fluxes of P from the forest floor than reference plots at similar elevations, whereas at low and mid-elevations there were no consistent differences between plots. Across all elevation classes, hardwood foliar N:P ratios were lower in plots with declining hemlocks. Collectively, these results suggest that increased N availability enhances bioavailable P, which is sequestered in vegetation until disturbances liberate it.

Keywords Exotic insects · Hemlock · Phosphorus fractionation · N and P co-limitation

Introduction

Phosphorus (P) is critical to biotic function and essential to the development and maintenance of ecosystems (Buendia et al. 2010; Crews et al. 1995; Porder and Hilley 2011; Richter et al. 2006; Turner and Engelbrecht 2011; Vitousek et al. 2010; Walker and Syers 1976; Wardle et al. 2004). Decades of research show that geochemical processes regulate P availability over centuries and millennia, with soil age, parent material mineralogy, and climate explaining most of the variation in the long-term distribution of soil P (Buendia et al. 2010; Porder and Hilley 2011;

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Treseder and Vitousek 2001; Vitousek et al. 2010; Walker and Syers 1976). In contrast, ecological processes mainly influence P availability over the short term, potentially resulting in proximate nutrient limitation over individual growing seasons, years, or decades (Cross and Schlesinger 1995; Vitousek et al. 2010; Wardle et al. 2004). Because of the transitory and more localized nature of these effects on P availability (Austin and Vitousek 1998; Richter et al. 2006; Vitousek et al. 2010; Wardle et al. 2004), biological and ecological processes have generally received less attention compared to geochemical processes.

Human activities are substantially altering ecological processes that can influence P availability; as a result, such pathways may exert greater control on P pools and fluxes than previously appreciated. Human-enhanced nitrogen (N) deposition, for example, has chronically increased the supply of N to terrestrial and aquatic ecosystems (Vitousek et al. 1997). Recent evidence suggests these inputs could induce P limitation (Elser et al. 2007; Gress et al. 2007), while others have found no indication that increased N availability leads to increased P limitation (Finzi 2009; Groffman and Fisk 2011; Weand et al. 2010). Two mechanisms could account for anthropogenically driven P limitation: (1) increased N availability could stimulate primary productivity, thereby increasing biotic P demand; or (2) low soil pH driven by acidic N deposition could cause mobilization of soil aluminum (Al) and iron (Fe) which bind P, resulting in increased P sorption and decreased P availability (Sherman et al. 2006). An important assumption underlying the first mechanism is that recalcitrant P fractions are not bioavailable. However, recent studies suggest that over time strong biotic sinks can drive the transfer of P from recalcitrant to labile pools. Comparing P fractions of archived soils from aggrading forests, Richter et al. (2006) found that biotic P demand drove the depletion of slowly cycling inorganic P pools, thereby maintaining the labile soil P fraction and overall P availability. Fertilization studies also support this finding, showing that increased N availability stimulates microbial and root production of the extracellular enzyme phosphatase, which cleaves ester-P bonds in soil organic matter and increases local P availability (Finzi 2009; McGill and Cole 1981; Olander and Vitousek 2000; Treseder and Vitousek 2001; Vitousek et al. 2010; Wang et al. 2007; Weand et al. 2010).

Human alteration of disturbance regimes also has the potential to change P turnover and availability. Most, if not all, ecosystems experience disturbance (White 1979); however, land conversion and introductions of non-native species are occurring at unprecedented rates and modifying disturbance frequency, extent and intensity (Levine and D'Antonio 2003; Turner 2010). Disturbances can positively or negatively affect P availability. Those that interrupt the nutritional demands of vegetation without removing biomass or soil (e.g., windthrow, pest or pathogen outbreaks) can initially rejuvenate available P pools due to reduced uptake, although the rapid successional biomass production that often occurs after disturbance events may sequester much of the newly available P (Wardle et al. 2004). Conversely, disturbances that remove large amounts of fertile soil and/or biomass (e.g., landslides, logging, agricultural land conversion) can lead to P loss and possibly P limitation (Bormann et al. 1974; Frizano et al. 2002; Matson et al. 1997).

Anthropogenic N enrichment and disturbance can co-occur, yet few studies have considered how they might interact to affect P availability. If greater N supply increases the pool of bioavailable P, the impact of disturbance on ecosystem P cycling might be much greater in areas subjected to high rates of atmospheric N deposition. Moreover, because many ecosystems appear to be co-limited by N and P (Elser et al. 2007), vegetation response to disturbance might vary substantially and further alter nutrient cycling patterns.

The objective of this study was to evaluate how interactions between N availability and forest disturbance, specifically the decline of eastern hemlock (*Tsuga canadensis*) due to exotic invasion by the hemlock wooly adelgid (HWA; *Adelges tsugae*), influence P availability in the southern Appalachian Mountains. We hypothesized that in response to disturbance, forest stands receiving greater N deposition, and having potentially larger bioavailable P pools, would experience larger perturbations to P pools and fluxes than areas with lower rates of N deposition. Nitrogen deposition varies over relatively short distances within the southern Appalachians due to differences in precipitation caused by orographic lift. Previous work demonstrates that differences in vegetation and N deposition along these gradients produce substantial variation in N availability across the southern Appalachian landscape (Knoepp et al.

2008). Although many studies have investigated the effects of tree mortality on carbon (C) and N cycles (Jenkins et al. 1999; Knoepp et al. 2011; Nuckolls et al. 2009), changes in P pools and fluxes remain poorly understood. Invasive pests and pathogen outbreaks are a reoccurring issue in North America (Lovett et al. 2006), and ecosystem response to invasions and the consequences regarding P, an ultimate limiting nutrient (Vitousek et al. 2010), are critical to the understanding of forest ecosystem dynamics.

Methods

Site description and plot selection

This study was conducted at the Coweeta Hydrologic Laboratory, a USDA Forest Service Experimental Forest in the southern Appalachian Mountains of western North Carolina, USA. HWA was first documented in the Coweeta basin in 2003, with extensive infestation and onset of hemlock decline by 2005 (Nuckolls et al. 2009). Tree mortality can occur in as little as 4 years (McClure 1991), and mortality of nearly half of the eastern hemlocks found within Coweeta Hydrologic Laboratory was observed in 2011 (Ford et al. 2011). All hemlocks measured in this study were visually estimated to have 95–100 % canopy loss. Annual precipitation varies with elevation, with stands receiving $\sim$1,800 mm at low elevations and $\sim$2,400 mm at high elevation. Rainfall is evenly distributed throughout the year with >100 mm occurring in most months. The growing season extends from early May to early October. Mean monthly temperatures are highest in June through August ($\sim$20 °C) and lowest in December through January ($\sim$5 °C) (Knoepp et al. 2008). Soils at Coweeta are mostly Inceptisols or Ultisols, classified as Mesic or Humic Hapludults, or Typic Humudepts. Parent material consists of high-grade metamorphic rocks (i.e., mica gneiss, mica schist) and metasedimentary rocks (i.e., metasandstone, phyllite, shale). See Table 1 for additional site details.

We established six 20 m × 20 m (0.04 ha) plots at each of three elevation classes (low, mid, high). Increasing elevation was associated with increasing levels of wet bulk atmospheric N deposition, ranging from 3.40 ± 0.06 (mean ± 1 SE) kg N ha^{-1} in low elevation plots to 4.44 kg N ha^{-1} at high elevation

plots (Table 1). Dry deposition and cloud water deposition were not estimated for these sites, but are likely to increase substantially with elevation in mountainous terrain (Lovett et al. 1997; Weathers et al. 2006). Within each elevation class, three of six plots contained dead or dying eastern hemlock trees (declining hemlock; DH), the remaining three plots had a similar composition of mixed hardwoods and were used as reference (REF) (n = 18 plots total). There were no stands containing hemlock unaffected by HWA. We selected only areas lacking or with very small amounts of *Rhododendron maxima* to avoid biasing nutrient cycling measurements (Boettcher and Kalisz 1990).

Foliage and forest floor sampling

To characterize the vegetation in each plot, we measured the basal area of all trees ≥2.5 cm diameter at DBH (1.37 m above the forest floor) and identified them to species with the exception of *Carya* spp., which were identified to genus. We collected foliage samples from the mid-crown of the three dominant hardwood species per plot (determined by percent of total plot basal area) between 21 July 2010 and 4 August 2010 using a sling-shot and/or pole pruner ("Appendix"). Within each plot, three to five individuals per species were sampled; if fewer individuals of a species existed in the plot, less than three were sampled. Samples were composited by species for each plot, air dried, and ground to <1 mm using a Wiley mill, then a sub-sample was taken for chemical analysis. Total P was determined by ashing a subsample at 480 °C, digesting in HNO_3 acid, and analyzing by inductively coupled plasma atomic emission spectrophotometry (JY Ultima ICP-AES; Horiba Jobin–Yvon, Edison, NJ). Total N was determined by combustion on an Elementar Flash EA 1112 CN analyzer (Thermo Scientific, Waltham, MA). Similar to Ollinger et al. (2002), we scaled foliar P concentration to the plot-level by computing the sum of foliar P concentrations among all species, weighted by the relative foliage mass of each species within a plot ("Appendix"). This weighting technique allowed for comparison of concentration patterns with respect to elevation class and disturbance despite differences in species composition and their abundances across plots. We calculated foliar N:P molar ratios for each species sampled and averaged these values by plot.

Table 1 Site characteristics for HWA-infested (DH) and reference (REF) plots at low (L), mid- (M), and high (H) elevations

Site	Dominant vegetation	Elevation (m)	pH	Wet N deposition (kg N ha^{-1} 9 mol^{-1})	Total live basal area (m^2 ha^{-1})	Soil series
DH-L	*Acer rubrum, Betula lenta, Ilex opaca, Liriodendron tulipifera, Nyssa sylvatica, Oxydendrum arboreum, Quercus alba*	710–716	4.15 4.18	3.45 ± 0.06	26.6 ± 7.2	Saunook series, Cullasaja-Tuckasegee complex
REF-L	*A. rubrum, B. lenta, Carpinus caroliniana, Fagus grandifolia, L. tulipifera, Q. alba, Q. velutina*	698–715	4.33 4.43	3.40 ± 0.06	49.0 ± 9.3	Evard-Cowee complex, Fannin series
DH-M	*A. rubrum, B. lenta, Carya* spp., *L. tulipifera, N. sylvatica, O. arboreum*	917–934	4.17 4.24	3.96 ± 0.20	31.3 ± 6.2	Evard-Cowee complex, Cullasaja-Tuckasegee complex
REF-M	*A. rubrum, Carya* spp., *L. tulipifera, O. arboreum, Q. coccinea, Q. velutina, Robinia pseudoacacia*	924–943	4.18 4.31	4.12 ± 0.22	37.5 ± 4.2	Evard-Cowee complex, Cullasaja-Tuckasegee complex
DH-H	*A. pensylvanicum, A. rubrum, B. alleghaniensis, F. grandifolia, Q. rubrum*	1,402–1,433	3.95 4.15	4.44	52.5 ± 7.9	Plott series
REF-H	*A. pensylvanicum, A. rubrum, A. saccharum, B. alleghaniensis, O. virginiana, Prunus serotina*	1,411–1,423	3.98 4.16	4.44	45.5 ± 6.8	Plott series

Values for pH, wet nitrogen (N) deposition, and basal area are means ±1 SE

pH in 0.1 M CaCl$_2$ at 0–10 cm and 10–30 cm depths; only one rain gauge was used at high elevations

Forest floor (O horizons + wood) was sampled on all plots during March 2010 for determination of total mass and C, N and P concentration. Five samples per plot were collected with a 0.09 m^2 quadrat and separated into Oi, Oe, and Oa horizons and wood (<10 cm diameter). Samples were weighed, processed and analyzed for P concentration by ICP-AES and for total C and N as described above.

Soil sampling

We collected composite soil samples from each plot in June 2010. Samples were collected at depths of 0–10 cm and 10–30 cm using a 2.0 cm diameter soil probe, and were made up of 20–25 individual samples. Samples were stored in plastic bags, and placed on ice during transport to the laboratory the same day. Soil samples were air-dried and sieved (<2 mm) prior to sub-sampling for chemical analysis. Bulk density (g soil cm^{-3}) of both coarse fragment and <2 mm fractions was determined for soils on each plot by collecting five 4.3 cm diameter soil cores per plot;

these data were used to calculate soil nutrient pools in kg ha^{-1}. Soil chemical analyses included total C and N by combustion (as above), dilute hydrochloric and sulfuric acid extractable PO$_4$ (Brown et al. 2009; Olsen and Sommers 1982), and 0.01 M CaCl$_2$ soil pH. Organic P was determined by ignition using the modified Saunders and Williams method (Olsen and Sommers 1982). Soil samples were muffled at 550 °C for 7 h, and both muffled and unmuffled samples were extracted overnight in 0.5 M H$_2$SO$_4$ and analyzed for total P by ICP-AES. Organic P was calculated by subtracting unmuffled from muffled P concentrations.

We further characterized soil P availability at both depths by sequential soil fractionation using the method developed by Psenner et al. (1988) modified for forest mineral soils (SanClements et al. 2009). Briefly, we sequentially extracted one gram soil samples into the following P fractions: (1) 1 M NH$_4$Cl, pH 7, at 25 °C for 1 h was considered the exchangeable fraction (P$_{NH4Cl}$); (2) 0.11 M NaHCO$_3$–Na$_2$S$_2$O$_4$ at 40 °C for 30 min was considered P adsorbed to reducible metal hydroxides, thought to

be primarily Fe-bound P (P_{BD}); (3) 0.1 M NaOH at 25 °C for 16 h extracted P predominately associated with Al and some Fe hydroxides as well as organic P ($P_{NAOH-25}$); (4) 0.5 M HCl at 25 °C for 16 h extracted acid-soluble primary mineral P, considered to be apatite-P (P_{HCl}); and (5) 1 M NaOH at 85 °C for 24 h to dissolve refractory and residual P ($P_{NAOH-85}$); the sum of all P fractions equaled total P (P_{SUM}). All extractions were centrifuged at $3,000 \times g$ for 15 min and filtered through Whatman 42 filter paper (Whatman Inc., Clifton, New Jersey, USA). Extractions were then repeated with an agitation time of 1 min to rinse samples, prior to extracting the next fraction. All extracts were analyzed by ICP-AES.

To characterize P fluxes, we installed ion-exchange resin lysimeters in each plot. We constructed resin lysimeters following the approach of Susfalk and Johnson (2002). Briefly, we placed 25 g of mixed-bed resin (Rexyn #R208-500) into a 2-cm PVC coupling between two Nitex® nylon sheets, which were then sandwiched between two layers of nutrient-free silica play sand. Four resin lysimeters were randomly located throughout each plot just below the forest floor and four below the major rooting zone (heretofore "mineral soil lysimeters"). To place the four mineral soil lysimeters, we dug two 50 cm deep pits with two channels extending perpendicularly from the bottom. One resin lysimeter was placed at the end of each channel. Channels were deep enough to ensure the soil column above the lysimeters remained undisturbed. Initial placement of all resin lysimeters was randomized by maintaining a distance of $\sim$ 1–2 m away from any tree trunk or shrub. Fresh resin lysimeters were deployed in the field during 2010 for three consecutive 100-day periods beginning April 10, July 23, and October 27, corresponding with the early growing season, late growing season, and fall/winter season in this region. Others have found that resin absorption capacity is maintained over longer time periods (i.e., 1 year), even under high exogenous inputs (i.e., N and P fertilization) (McIsaac et al. 2010). Nonetheless, deployment of fresh resins ensured that resin absorption capacity was not exceeded. At the time of collection, resin lysimeters were stored in individual plastic bags, and kept cool during transport to the laboratory.

We characterized plot-level soil N availability with ion-exchange resin bags (Binkley and Matson 1983). Bags made from nylon stockings were filled with 20 g of resin (Rexyn #R208-500) approximately 1 week prior to field installation and kept refrigerated in plastic bags until installation. In each plot, we installed five resin bags by removing five randomly located soil cores (0–5 cm depth) with a bulb planter and placing a single resin bag at the base of each core; the intact soil core and forest floor were then replaced. Resin bags were collected on the same schedule as the resin lysimeters, and new resin bags were placed adjacent to the previous location. Resin from lysimeters and nylon bags was extracted within a week of collection from the field, by shaking resins for 1 h in 100 mL of 2 M KCl. The resin/KCl mixture was filtered through 0.7 μm Whatman filter paper and frozen until analysis. Extracts were analyzed colorimetrically for NH_4–N using the phenolate method, NO_2–N + NO_3–N using a cadmium column reduction, and PO_4 (dissolved reactive phosphorus; DRP) on a Lachat QuikChem 8000 (Hach Company, Loveland, CO). Following correction for lab and field blanks, we determined the mass of N and P in the resin by multiplying extract concentration by the volume of KCl used for extraction. Flux was further calculated by dividing N and P mass by lysimeter collection area (20.4 cm^2).

Statistical analyses

Samples with a single collection date (foliage, forest floor, composite soil samples) were analyzed using ANOVA with elevation (low, mid, high) and disturbance (DH, REF) as main and interactive effects. We used Tukey's HSD test to identify significant differences between groups within class variables and the Slice Statement to evaluate simple main effects of fixed variables within interactions. For resin-based data with repeated collection dates, we used plot means for each temporal period and determined changes over time with a repeated measures statement using an unstructured variance–covariance matrix in a linear mixed model with plot (elevation × disturbance) as the subject. Data were logarithmically transformed as necessary to meet assumptions of normal distribution and equal variance. All analyses were done in SAS v.9.2 (SAS Institute Inc., Cary, NC, USA).

Results

The abundance of hemlock in our plots varied significantly across the elevation gradient. Hemlock

abundance in low elevation plots was 23–56 % of total plot basal area, while mid- and high elevation plots had 13–52 % and 5–8 % hemlock, respectively. As a result, disturbance intensity was not equivalent across plots, with high elevation (i.e., high N deposition) plots experiencing the lowest disturbance intensity.

Foliar and forest floor pools

At the plot-level, the concentration of P in live foliage varied significantly with elevation ($F_{2,18} = 19.8$, $p < 0.01$; Fig. 1a). Averaged over disturbance categories, mean foliar P concentrations were greater in high elevation plots (0.75 g P kg foliage^{-1} $\pm$ 0.14 SE) than in mid- and low elevation plots (0.16 $\pm$ 0.10 and 0.02 $\pm$ 0.005, resp.) (Tukey's HSD: $p < 0.01$). Disturbance also affected plot-level foliar P concentrations ($F_{1,12} = 5.37$, $p < 0.05$), such that DH plots generally had greater foliar P than REF plots (Fig. 1a). However, the degree of difference between DH and REF plots varied with elevation. Analysis of simple effects of disturbance within each elevation class
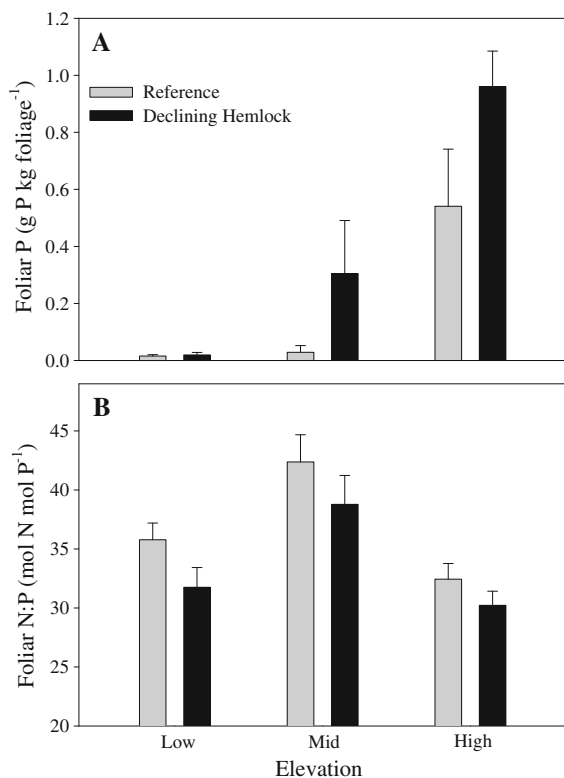
indicated foliar P was significantly greater in DH than REF plots at high elevations ($F_{1,6} = 5.80$, $p = 0.03$) but not at mid- or low elevations. Foliar N:P ratios also varied by elevation ($F_{2,54} = 14.4$, $p < 0.01$), but nonlinearly, such that mid-elevation plots had significantly greater N:P ratios (mean $\pm$ SE: 40.5 $\pm$ 1.7) than low (33.9 $\pm$ 1.2) and high elevation plots (31.3 $\pm$ 0.9). In contrast, disturbance had a strong, consistent effect across all elevations, such that foliar N:P ratios were significantly lower in DH plots compared with REF plots ($F_{1,54} = 5.08$, $p = 0.03$) (Fig. 1b). The interaction term, disturbance by elevation, was not significant, providing no evidence that the influence of disturbance on foliar N:P ratios varied with elevation.

The mass of P in the forest floor (Oi + Oe + Oa + wood) was significantly greater in high elevation plots than in low and mid-elevation plots (elevation: $F_{2,18} = 21.2$, $p < 0.01$; Tukey's HSD: $p < 0.01$) (data not shown). Concentrations of P in forest floor horizons showed similar patterns; P concentration increased with elevation in Oi ($F_{18,2} = 15.5$, $p < 0.01$), Oe ($F_{18,2} = 5.09$, $p = 0.02$), and Oa horizons ($F_{18,2} = 24.8$, $p < 0.01$), as well as in decaying wood ($F_{18,2} = 8.63$, $p < 0.01$) (Table 2). In contrast, disturbance had no effect on forest floor P mass or concentration and did not interact with elevation.

Soil pools

Nitrogen availability increased with elevation, as indexed by resin bags (Fig. 2a). High elevation plots had 2.69 $\pm$ 0.42 (SE) mg inorganic N (NO_3–N + NH_4–N) per bag compared to 0.52 $\pm$ 0.08 mg in mid- and 0.30 $\pm$ 0.07 mg in low elevation plots ($F_{54,2} = 10.3$, $p < 0.01$). There was no effect of disturbance and no elevation $\times$ disturbance interaction. Soil C at 0–10 cm depth also increased with elevation (Fig. 2b); high elevation plots had 11.9 $\pm$ 0.44 %C compared to 5.07 $\pm$ 0.65 %C in mid- and 4.02 $\pm$ 0.17 %C in low elevation plots ($F_{18,2} = 78.7$, $p < 0.01$).

Total P pools (P_{SUM}) were not significantly different across the basin in surface or deep soils (Fig. 3). All soils tested had P_{NH4Cl} below detection limits and low amounts of the second extracted fraction, P_{BD}. A dilute acid extraction was conducted to assess plant-available P. This method extracts a greater relative amount of Fe phosphate compounds than other

Fig. 1 Foliar phosphorus concentration weighted by the foliage mass of each species within a plot (**a**) and foliar N:P ratios (**b**)

Table 2 Total soil nitrogen (N) at 0–10 cm depth, and forest floor mass and phosphorus concentration for HWA-infested (DH) and reference (REF) plots at low (L), mid- (M), and high (H) elevations

	Soil N (Mg ha^{-1})	Forest floor						
		Total mass (g m^{-2})	Carbon** (Mg ha^{-1})	C:N molar ratio***	Phosphorus concentration (µg g^{-1})			
					Oi**	Oe*	Oa**	Wood*
DH-L	1.64 (0.14)	858 (246)	15.1 (6.05)	62 (3.2)	658 (88.7)	606 (39.4)	842 (68.9)	199 (50.6)
REF-L	1.43 (0.17)	409 (96.9)	5.59 (0.40)	55 (2.2)	488 (114)	825 (63.2)	N/A	280 (7.10)
DH-M	1.52 (0.35)	450 (90.1)	7.57 (0.95)	48 (4.8)	595 (55.3)	713 (43.7)	737 (37.5)	315 (45.1)
REF-M	1.34 (0.14)	536 (179)	9.48 (1.91)	45 (3.5)	423 (33.3)	664 (47.0)	752 (70.6)	287 (14.3)
DH-H	2.45 (0.39)	1,411 (506)	20.9 (1.38)	29 (2.1)	955 (138)	1,012 (72.92)	1,254 (143.7)	379 (54.9)
REF-H	2.97 (0.10)	1,407 (553)	18.4 (2.21)	26 (0.7)	958 (39.1)	949 (193)	1,563 (111.6)	445 (52.7

Values are means (±1 SE)

Significant main effect of elevation (* $\alpha \leq 0.05$, ** $\alpha \leq 0.01$, *** $\alpha \leq 0.0001$). No effect of disturbance or any interactions were observed
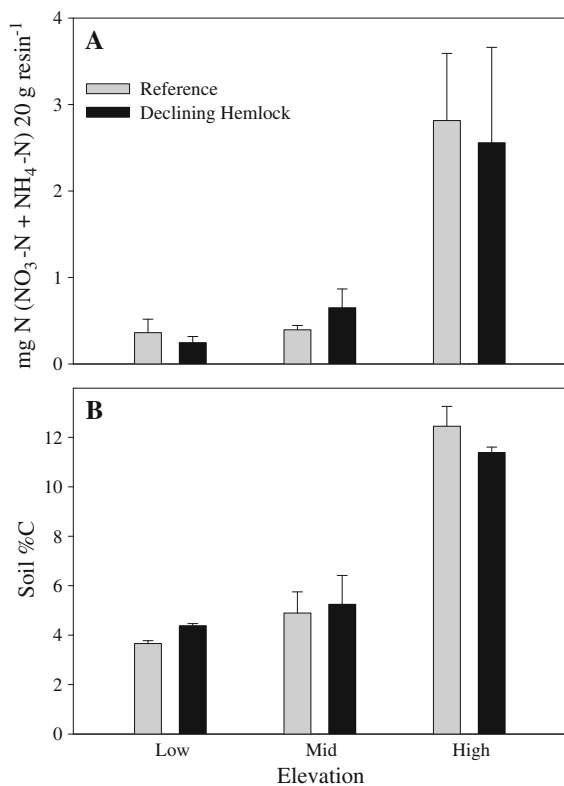
Fig. 2 Nitrogen availability as indexed by resin bags (**a**) and surface soil (0–10 cm) carbon (**b**)

extractions used as an index of P availability and has a good correlation with plant growth responses to P (Brown et al. 2009; Olsen and Sommers 1982). In the top 10 cm, low elevation plots had an average of 6.10 ± 1.02 (SE) kg P ha^{-1} compared to 5.00 ± 0.73 in mid- and 3.66 ± 0.48 kg P ha^{-1} in high elevation plots. Although plant-available P decreased with elevation in the top 10 cm, the trend was not significant, and there was no decrease in the 10–30 cm depth (low: 7.77 ± 0.42; mid: 7.36 ± 1.12 kg P ha^{-1}; high: 8.01 ± 0.73 kg P ha^{-1}). There was also no difference in plant-available P with disturbance and no interaction of the main effects.

Overwhelmingly, the largest pool of soil P was in the $P_{NaOH-25}$ fraction, where P is bound to Al, Fe, or in organic form. This fraction varied significantly but non-linearly with elevation in both the top 10 cm ($F_{2,18} = 6.26$, $p = 0.01$) and the 10–30 cm depth ($F_{2,18} = 4.09$, $p = 0.04$), such that mid-elevation plots had significantly less P stocks in this fraction than low and high elevation plots (Fig. 3). There were no differences observed with disturbance and no elevation × disturbance interaction at either depth in the $P_{NaOH-25}$ fraction. The P_{HCl} fraction, representing primarily mineral P (from apatite), declined slightly
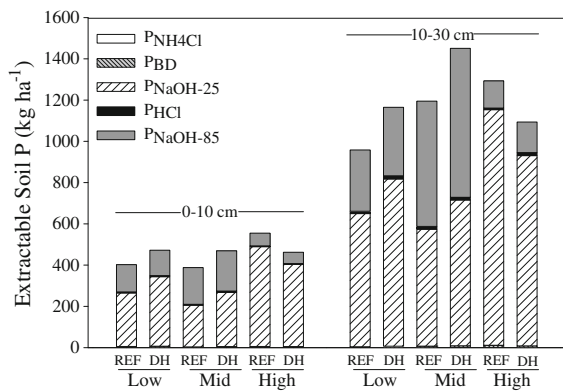
Fig. 3 Soil phosphorus (P) in plots with declining hemlock (DH) and reference (REF) plots containing a similar composition of hardwoods in western North Carolina. A modified version of Psenner P fractionation (SanClements et al. 2009) was performed on soil from two depths at each of these vegetation types at three elevations

Fig. 4 Total and inorganic phosphorus (P) (organic P by subtraction) from a sulfuric acid extraction of the top 10 cm of soil in declining hemlock (DH) and reference (REF) plots at low (L), mid- (M), and high (H) elevations in western North Carolina

with elevation at both depths, but the decrease was not significant, nor was the elevation × disturbance interaction. Surface soil P_{HCl} fraction did not vary with disturbance; however, in deeper soils, DH plots had slightly more P_{HCl} than REF plots ($F_{1,18} = 4.15$, $p = 0.06$) (Fig. 3).

The second largest fraction was $P_{NaOH-85}$, the residual and recalcitrant pool of soil P which is generally thought to be unavailable to plants. At both depths, the size of $P_{NaOH-85}$ fraction differed significantly with elevation (0–10 cm: $F_{2,18} = 17.2$, $p < 0.01$; 10–30 cm: $F_{2,18} = 17.7$, $p < 0.01$) and soils from high elevation plots had significantly smaller $P_{NaOH-85}$ pools than soils from low and mid-elevation plots (Tukey's HSD: $p < 0.01$) (Fig. 3). Disturbance had no effect on the size of this fraction and did not interact with elevation at either depth.

The majority of the P in these soils was organic. Organic P increased significantly with elevation ($F_{2,18} = 56.0$, $p < 0.01$), but did not vary between disturbance types (Fig. 4). However, there was a significant elevation × disturbance interaction ($F_{2,18} = 4.23$, $p < 0.05$). High elevation REF plots had significantly larger organic P pools than DH plots at the same elevation ($F_{1,6} = 10.4$, $p < 0.01$). The high elevation REF plots had 47 % larger pools of organic P in soils than DH plots, while there were no differences with disturbance at mid- or low elevations.
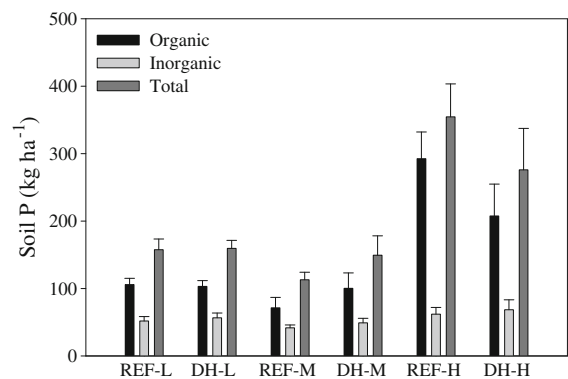
Forest floor and mineral soil fluxes

Averaged over the entire sampling period, flux of DRP from the forest floor increased with elevation ($F_{2,54} = 4.97$, $p = 0.03$). High elevation DH plots had significantly greater DRP flux than REF plots ($F_{1,18} = 4.38$, $p = 0.05$), but DRP flux did not differ at low or mid-elevations (Fig. 5). Fluxes varied substantially with temporal period ($F_{2,54} = 57.3$, $p < 0.01$); greater fluxes were observed during the late growing season compared to the early growing season (Tukey's HSD: $p = 0.06$) and the fall/winter period (Tukey's HSD: $p < 0.01$), consistent with leaf senescence and decomposition. Within temporal periods and elevation classes, we observed significantly greater fluxes of DRP from forest floors in DH plots compared to REF plots only at high elevations and only during the late fall/winter period ($F_{1,6} = 6.88$, $p = 0.02$) (Fig. 5); other trends were not statistically significant.

There was little flux of DRP from the mineral soil across all sites (<0.21 kg ha^{-1} 9 mol^{-1}) and there were no main effects of elevation or disturbance. Temporal period explained substantial variation in mineral soil DRP flux ($F_{2,54} = 12.2$, $p < 0.01$), which was greatest in the period characterizing the late growing season (Fig. 5). Closer inspection of DRP patterns within temporal periods showed that, during the late growing season and fall/winter period, flux from the mineral soil was generally greater in DH plots than REF plots at high elevations but not at other elevations (Fig. 5). However, these trends were not

Fig. 5 Dissolved reactive phosphorus (DRP) flux for forest floor and mineral soil lysimeters in plots with declining hemlock and reference hardwood plots for each temporal period (early growing season, April–July 2010; late growing season, July–October 2010; fall/winter, October 2010–February 2011) across all elevation classes
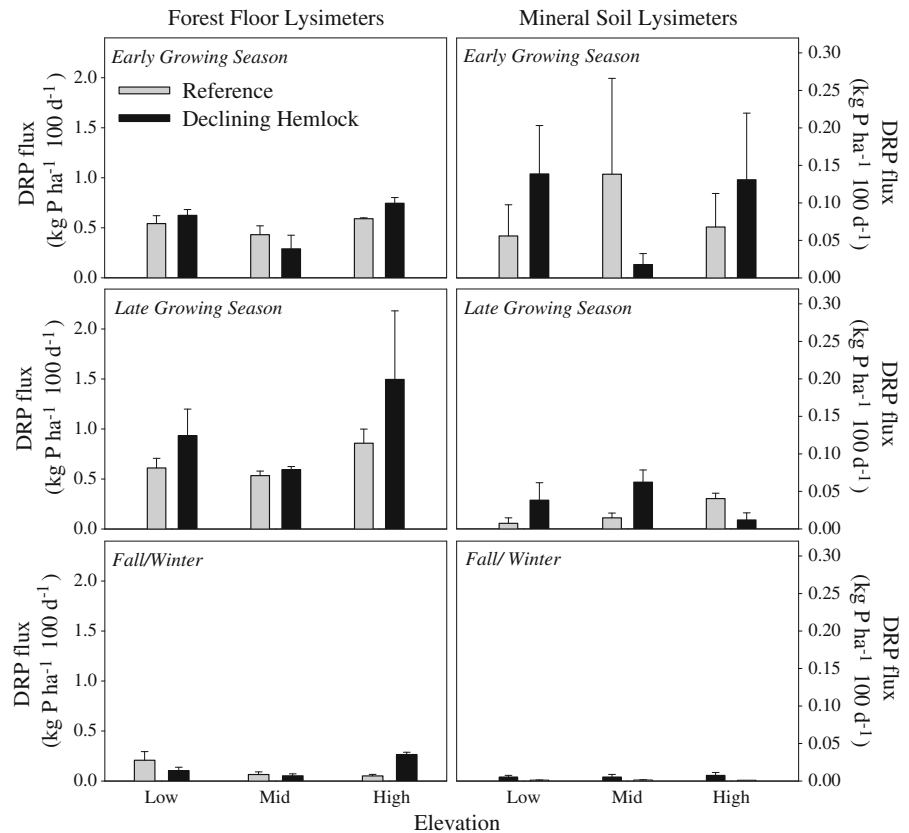
statistically significant (late growing season: $F_{1,6} = 2.91$, $p = 0.11$; fall/winter: $F_{1,6} = 4.24$, $p = 0.06$).

Discussion

We observed distinct differences in soil P fractions as N availability increased. Soils from high elevation plots where N availability was greatest had 139 % larger organic P pools and 55 % smaller residual and refractory P pools than soils from low elevation plots with less N availability. These patterns are consistent with the hypothesis that increased N availability drives the redistribution of P from recalcitrant mineral pools to organic pools; however, other mechanisms could have produced similar patterns. For example, cooler temperatures could decrease mineralization, resulting in greater organic P pools at higher elevations. Differences in parent material could also account for differences in soil P fractions, although this would not account for differences between mid- and high elevation plots as these had similar parent materials.

Regardless, differences in P fractions influenced how tree mortality affected P dynamics. At high elevations, DH plots had significantly greater foliar P concentrations and fluxes of P from the forest floor than REF plots at similar elevations, whereas at low and mid-elevations there was no significant effect of disturbance. These findings suggest that increased N availability enhanced bioavailable P, which was sequestered in vegetation and soil organic matter and released following disturbance.

The mechanisms by which enhanced N might drive restructuring of soil P remain equivocal. Previous studies show that increased N availability can stimulate extracellular phosphatase activity which cleaves ester-P bonds in soil organic matter and can increase local P availability (Finzi 2009; McGill and Cole 1981; Olander and Vitousek 2000; Treseder and Vitousek 2001; Vitousek et al. 2010; Wang et al. 2007; Weand et al. 2010). This finding supports the hypothesis that biotic P demand drives the mobilization of P from pools traditionally considered occluded or recalcitrant. Recently, Richter et al. (2006) concluded that biotic P

demand of aggrading pine forests in the southeastern US accounted for the depletion of slowly cycling organic and inorganic P pools, which maintained or even increased biomass P, labile soil P, and overall P availability over nearly five decades. Using the Hedley fractionation procedure, they identified three potential long-term sources of bioavailable P: a Ca-associated inorganic fraction (an HCl-extracted fraction), an Fe/Al oxide-associated inorganic fraction (an NaOH-extracted fraction), and an organic fraction (an NaOH-extracted fraction); these pools were enriched by fertilization and liming during the late 1800s through the early 1900s (Richter et al. 2006). Direct comparison among fractions is difficult because, unlike Richter et al. (2006), we did not distinguish between organic and inorganic P within each fraction. Still, we observed depletion in similar pools (P_{HCl}) with increased elevation, as well as in the $P_{NaOH-85}$ fraction, which is associated with residual and recalcitrant P. Depletion of the $P_{NaOH-85}$ fraction in our study may have developed as a result of the chronic and long-term nature of elevated N availability in our study ecosystem together with the lack of exogenous P inputs. However, another possible mechanism explaining soil P reallocation among fractions could be the coupled release of P when Fe/Al oxide-associated fractions are freed by low soil pH levels associated with long-term elevated N. Sherman et al. (2006) showed that N additions increased P availability in surface soils via acidification-induced mobilization at the Bear Brook Watershed in Maine. Interestingly, P mobilization at Bear Brook was accompanied by accelerated vegetative uptake of P, higher foliar P concentrations, and a positive growth response in hardwood stands (Elvir et al. 2003; Sherman et al. 2006), which suggests that the biota rapidly responded to changes in P availability.

In our study, hemlock decline was associated with increased hardwood foliar P concentrations and forest floor fluxes at high elevations but not at mid- or low elevations, which suggests that disturbance and N availability interact to affect P availability. Previous studies indicate that disturbance can increase available P by liberating P from the forest floor and reducing plant uptake (Fitzhugh et al. 2001; Frizano et al. 2002; Wardle et al. 2004; Yanai 1998), whereas disturbance often has no effect on the concentration of P in soil solution due to the strong P-sorption capacity of the mineral soil (Wood et al. 1984; Yanai 1991). We observed similar patterns; disturbance increased P flux

from the forest floor but not from the mineral soil. We found no difference in forest floor P content between disturbed and reference plots. One possible explanation for this is that trees readily retranslocate P prior to leaf senescence. Recent work shows that deciduous species retranslocate P in proportion to its bedrock concentration, i.e., higher retranslocation is associated with lower P stocks (Castle and Neff 2009). Post leaf drop, P may also have been rapidly reincorporated into microbial or plant biomass or soluble P may have leached from litterfall prior to sampling the forest floor. Indeed, forest floor DRP flux was greatest in disturbed plots during the late growing season, consistent with the timing of litter fall. Had forest floor been sampled throughout the year, differences in forest floor P content may have been detected. Regardless, the relatively larger forest floor DRP flux in disturbed plots at high elevations suggests P is cycling more rapidly in plots experiencing hemlock decline than in reference plots.

Stoichiometric relationships supported the hypothesis that disturbance increased P availability in this system. Foliar N:P ratios were consistently lower in disturbed than in reference plots across all elevations. The effects of N availability on stoichiometry were less straightforward, and there is evidence that foliar nutrient patterns were confounded by landscape position and its effects on soil P stocks. Foliar N:P was significantly greater in mid-elevation plots compared to low and high elevation plots, which had similar foliar N:P values averaged over disturbance group. The mid-elevation plots were located on side-slopes, whereas low elevation plots were located largely in riparian areas and high elevation plots were located on ridges. Therefore, soil P stocks may have been depleted in mid-elevation plots due to greater rates of soil and forest floor movement and enhanced in low elevation plots due to colluvial deposits. Soil %C was roughly similar in low and mid-elevation plots, suggesting that incorporation of organic matter is similar in both of these locations regardless of their slope position. This interpretation agrees with our finding that mid-elevation plots had the lowest stocks of $P_{NaOH-25}$, while this pool was similar in low and high elevation plots. Collectively, these results suggest that N:P ratios are conserved across different levels of soil nutrient availability (as measured by traditional extractions) provided P stocks are sufficient. Neff et al. (2006) reached a similar conclusion

for cold desert communities, finding that dominant plant species have the capacity to maintain foliar chemistry ratios despite large underlying differences in soil nutrient availability.

Our data provide no evidence that higher N availability has resulted in P limitations in the southern Appalachians. Total soil P based on summed Psenner fractions did not vary with elevation in the 0–10 cm or 10–30 cm depths, nor did the dilute acid extraction of P, an index of plant-available P. These findings are consistent with those of other studies examining effects of N availability on P dynamics. Weand et al. (2010) studied forest plots in the Catskill Mountains of New York that had been fertilized with N for 10 years, examining how P characteristics differed among tree species and/or responded to simulated N deposition. Foliar, litterfall, and root P concentrations, as well as soil P availability and biotic P sufficiency differed by species but were unaffected by N fertilization (Weand et al. 2010). Similarly, Finzi (2009) evaluated basal area growth of sugar maple/white ash stands with high N availability and oak/beech/hemlock stands with low N availability in New England and their response to fertilization with N and P. Several tree species responded to fertilization with N alone and only one species responded to P fertilization once N was added, suggesting that decades of atmospheric N deposition have not resulted in widespread P limitation or saturation of tree demand for N (Finzi 2009).

Differences in soil N availability are likely a function of differing vegetation and the impact on organic matter composition (Knoepp and Swank 1998), however it also may be a result of atmospheric N deposition in this system. It is possible that deposition received over the study period may not have been sufficient to induce P limitation. Levels of total wet N deposition were much smaller (3.40–4.44 kg ha^{-1} 9 mol^{-1}) than those reported by Mohren et al. (1986) (>50 kg N ha^{-1} year^{-1} in the Netherlands) who found evidence that increased N availability leads to P limitation. Likewise, Tessier and Raynal (2003) studied N:P ratios in the Catskill Mountains, and found signs of P limitation in the understory vegetation due to a decade of high N deposition which averaged 6.40 kg ha^{-1} annually. However, we did not estimate dry deposition and cloud water deposition for these sites, and these are likely to increase substantially with elevation in mountainous terrain (Lovett et al. 1997; Weathers et al. 2006).

Differences in stand composition among studies may also account for the different findings. Weand et al. (2010) found that hardwood species vary in the degree to which they rely on internally stored and recycled P versus P obtained from the soil. In their study, single-species plots of beech, birch, and maple trees had average concentrations of foliar and litter P, while oak plots had the greatest concentrations of foliar, litter, and available soil P, as well as the least P retranslocation (Weand et al. 2010). These oak-dominated plots had the highest concentration of inorganic P and high proportions of P bound in organic fractions, suggesting that P turnover may be relatively rapid and support the status of oaks as a "P-rich" species (Weand et al. 2010). Our plots contained these species, but several others as well (Table 1, "Appendix"), whose P cycling traits are not as well known.

Data collected at the same sites show that mixed hardwoods in disturbed plots at high elevations had significantly greater growth rates post-HWA infestation compared to those at low and mid-elevations, whereas prior to infestation growth rates were comparable (C.E. Block, unpublished data). This suggests that nutrients liberated by hemlock decline increased site productivity at high elevations. Observed increases in foliar N and decreases in subsurface N leaching further suggest that hemlock decline alleviated P limitation and stimulated N uptake at high elevations (C.E. Block, unpublished data). Nutrient limitation, however, cannot be evaluated solely on the basis of ratios of foliar nutrients, and N and P addition studies are needed to understand the impacts of disturbance on productivity under conditions of chronically elevated N inputs.

Appendix

See Table 3.

Table 3 Dominant hardwood species sampled in each plot in declining hemlock (DH) and reference (REF) stands at low (L), mid (M), and high (H) elevations within and around Coweeta Hydroloic Laboratory in western North Carolina

Site	Plot	Species	Foliar %N	Foliar %P	Foliar N:P (mol N mol P^{-1})	Total species basal area within a plot (m^2)	Relative basal area (spp BA total plot BA^{-1}) (%)
DH-L	1	*Acer rubrum*	2.02	0.138	32	0.55	4.54
		Oxydendrum arboreum	1.81	0.135	30	1.09	9.09
	2	*Betula lenta*	2.50	0.146	38	6.19	46.8
		Liriodendron tulipifer	2.13	0.170	28	3.17	23.9
		Nyssa sylvatica	1.64	0.153	24	0.14	1.05
	3	*Ilex opaca*	1.17	0.069	38	0.40	6.07
		Liriodendron tulipifer	1.99	0.135	33	0.81	12.4
		Quercus alba	2.12	0.150	31	0.79	12.7
REF-L	1	*Acer rubrum*	1.51	0.115	29	1.43	17.4
		Fagus grandfolia	1.94	0.113	38	0.75	9.14
		Quercus alba	2.22	0.135	36	4.67	56.8
	2	*Acer rubrum*	1.87	0.120	35	1.35	26.5
		Betula lenta	2.56	0.164	35	0.60	11.8
		Carpinus caroliniana	1.94	0.118	36	1.97	38.3
	3	*Liriodendron tulipifer*	2.76	0.137	45	5.46	52.0
		Quercus alba	2.16	0.143	33	0.79	7.49
		Quercus velutina	2.02	0.127	35	2.43	23.1
DH-M	1	*Carya* spp.	2.19	0.101	48	1.44	18.9
		Nyssa sylvatica	1.71	0.106	36	1.20	15.8
		Oxydendrum arboreum	2.01	0.094	47	0.64	8.46
	2	*Betula lenta*	2.28	0.133	38	0.31	4.22
		Carya spp.	1.91	0.101	42	0.66	9.06
		Liriodendron tulipifer	2.25	0.126	40	2.41	33.3
	3	*Acer rubrum*	1.54	0.134	25	1.00	5.80
		Carya spp.	2.18	0.116	42	1.05	6.14
		Liriodendron tulipifer	2.40	0.172	31	6.10	35.5
REF-M	1	*Acer rubrum*	1.90	0.140	30	0.56	11.3
		Liriodendron tulipifer	2.15	0.111	43	1.14	22.8
		Oxydendrum arboreum	1.90	0.100	42	1.01	20.2
	2	*Acer rubrum*	1.74	0.086	45	1.04	16.7
		Liriodendron tulipifer	2.15	0.106	45	2.75	44.0
		Quercus velutina	2.64	0.086	68	0.41	6.62
	3	*Acer rubrum*	1.54	0.096	36	1.99	33.8
		Carya spp.	2.15	0.094	50	0.36	6.03
		Quercus coccinea	1.97	0.091	48	0.90	15.3
DH-H	1	*Acer rubrum*	1.54	0.120	28	2.22	10.7
		Fagus grandfolia	2.09	0.142	33	11.90	57.2
		Quercus rubra	2.08	0.137	34	4.62	22.2
	2	*Acer pensylvanicum*	2.04	0.177	26	0.03	0.12
		Betula alleghaniensis	2.44	0.172	32	18.50	82.6
		Quercus rubra	2.53	0.193	29	0.72	3.24
	3	*Acer pensylvanicum*	1.90	0.158	27	1.05	3.98
		Betula alleghaniensis	2.41	0.198	27	23.02	86.8
		Quercus rubra	2.83	0.174	36	0.57	2.16

Table 3 continued

Site	Plot	Species	Foliar %N	Foliar %P	Foliar N:P (mol N mol P^{-1})	Total species basal area within a plot (m^2)	Relative basal area (spp BA total plot BA^{-1}) (%)
REF-H	1	*Acer pensylvanicum*	2.04	0.144	31	1.14	8.82
		Betula alleghaniensis	2.44	0.146	37	9.83	76.3
		Prunus serotina	2.89	0.181	35	0.24	1.84
	2	*Acer saccharum*	2.15	0.151	31	0.77	4.44
		Betula alleghaniensis	2.07	0.176	26	14.23	82.3
		Ostrya virginiana	2.43	0.143	38	1.47	8.52
	3	*Acer rubrum*	1.87	0.146	28	1.30	13.0
		Betula alleghaniensis	2.20	0.154	32	0.86	8.64
		Prunus serotina	2.18	0.140	34	3.38	33.8

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