Co-limitation in northern hardwood forest ecosystems: a synthesis of recent studies

T.J. Fahey[a], **M.C. Fisk**[b], **K.E. Gonzales**[c], **J.L. Butt**[b], and **R.D. Yanai** [ORCID][d]

[a]Department of Natural Resources, Cornell University, Ithaca, NY 14853, USA; [b]Department of Biology, Miami University, Oxford, OH 45056, USA; [c]California Department of Fish and Wildlife, Seal Beach, CA 90740, USA; [d]Department of Sustainable Resources Management, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, USA

Corresponding author: **R.D. Yanai** (email: rdyanai@syr.edu)

Abstract

Co-limitation is defined as the coincident limitation of biological activity by multiple resources. According to theories of resource optimization, co-limitation should be common as organisms adjust to changes in the availability of resources in the environment. We review the multi-faceted nature of the co-limitation concept and provide a synthesis of recent experimental studies of co-limitation in northern hardwood forests to illustrate the complexities of nitrogen (N) and phosphorus (P) co-limitation and possible responses to environmental stressors such as acid rain, N deposition, elevated CO_2, land-use, and climate change. In a factorial nutrient addition experiment, cycling of one nutrient changed in response to addition of the other through synergistic interactions and feedbacks between N and P, including microbial recycling, soil enzyme activity, and foliar nutrient resorption; these responses were suggestive of some degree of N–P co-limitation in these forests. After 8 years of treatment, aboveground growth increased in response to either N or P added individually and even more in response to N + P addition, indicating N–P co-limitation. Surprisingly, fine root growth increased in response to nutrient addition, with significantly greater root growth in N + P plots in five successional stands and in N plots in three mature stands. In contrast, fine litterfall did not respond significantly to nutrient addition. Collectively, these results demonstrate the complexity of the interactions between macronutrients in regulating production processes in forest ecosystems.

Key words: Bartlett Experimental Forest, Hubbard Brook Experimental Forest, MELNHE, nitrogen, phosphorus
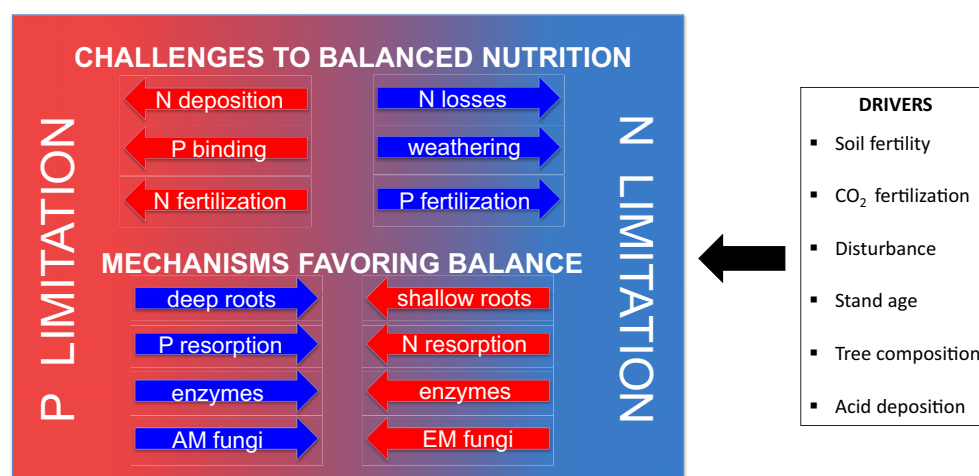
What is co-limitation?

Many biotic and abiotic factors may constrain an organism's growth rate. Such constraints were once conceived as single, one-at-a-time limits to growth. The law of the minimum, popularized by von Liebig, posited that crop production is limited by the soil nutrient in lowest supply relative to the demand of the crop; adding that nutrient to the soil should increase crop yield until some other nutrient becomes more limiting. However, plants have the capacity to change their allocation of biomass, enzymes, and energy to acquire the resources that most limit them, such that limitation of primary productivity by multiple nutrients—co-limitation—is likely much more common than single element limitation. According to resource optimization theory, under constant environmental conditions, plants adjust toward a condition where all resources are equally limiting (Bloom et al. 1985). Thus, maintaining co-limitation involves a dynamic response to limited resources.

Although often conceived in terms of nitrogen (N) and phosphorus (P) limitation of growth in primary producers, co-limitation may apply to other elements (Kaspari and Power 2016) and other resources (e.g., water and light; Farrior et al. 2013) as well as other trophic levels, such as consumers (Sperfeld et al. 2016) and decomposers (Fanin et al. 2016). The concept can be applied beyond growth rate or productivity to other measures of performance such as fitness (Walworth et al. 2016), metabolism (Schreiber et al. 2016) and photosynthesis (Domingues et al. 2010). Co-limitation may also be relevant at scales beyond individual plants, both larger, including communities (Arrigo 2005) or whole ecosystem properties such as consumer-driven recycling of limiting plant nutrients (Sperfeld et al. 2016), and smaller, such as limitation by different nutrients within different plant parts. For example, shoot and root production have been shown to be limited by different nutrients in both lowland tropical forest (Wright et al. 2011) and grasslands (Cleland et al. 2019). Because the acquisition of resources is ultimately limited primarily by energy, the co-limitation concept is ideal for applying to the challenge of linking the energy and nutrient currency of ecosystems (Reiners 1986).

Several categories of co-limitation have been proposed. Independent or additive co-limitation occurs when the response to the combined addition of nutrients is similar to the sum of responses to each nutrient individually (Harpole et al. 2011). In synergistic co-limitation, the response to the combined addition of resources is greater than the sum of the

Environ. Rev. **33**: 1–15 (2025) | dx.doi.org/10.1139/er-2024-0128

1

Fig. 1. Conceptual model of nitrogen (N) versus phosphorus (P) limitation in forests, showing factors that cause systems to deviate from co-limitation by N and P and the mechanisms that favor co-limitation by conserving or acquiring the more limiting nutrient. AM, arbuscular mycorrhizal; EM, ectomycorrhizal.

individual responses (Elser et al. 2007). Serial or sequential co-limitation occurs when organisms respond to addition of a resource only after limitation by another resource has been relieved (Craine et al. 2008). This category has been particularly well demonstrated for N and water in grassland vegetation (Farrior et al. 2013). In practice, these categories may be difficult to distinguish, as serial limitation would look synergistic if experimental nutrient additions were sufficient to relieve limitation by more than one nutrient by the time a response was observed (Davidson and Howarth 2007).

In complex natural ecosystems, a variety of mechanisms can contribute to the maintenance of a co-limited state (Fig. 1). At the physiological level, foliar N concentration regulates the maximum photosynthetic rate (A_{max}) in plant leaves (Wright et al. 2004) through its influence on carboxylation enzyme activity. However, the relationship between foliar N and photosynthetic capacity also depends upon foliar P (Domingues et al. 2010), due to the role of P in electron transport and other processes (Carstensen et al. 2018). Within individual plants, conservation of previously acquired N and P through foliar resorption may be interrelated, influencing soil recycling via litterfall (See et al. 2015; Gonzales 2017). Moreover, a change in the supply of one nutrient may drive a change in availability of the other nutrient, reflecting biochemically dependent co-limitation (Bracken et al. 2015); a classic example is the influence of N supply on the production of phosphatase enzymes (Marklein and Houlton 2012). Shifts in tree species composition also may contribute to maintaining co-limitation at the stand level; in tropical forests, most of the variation in foliar N:P stoichiometry was associated with inter-specific differences within forest communities (Townsend et al. 2007). Such differences may reflect different strategies of trees in relation to nutrient limitation. Overall, it is clear that N and P are linked at a variety of scales.

Co-limitation may depend on trophic levels other than primary producers, such that interactions among various functional components maintain a co-limited state at the whole

ecosystem level. Soil microbial communities exhibit considerable stoichiometric variation arising from differences both in composition (e.g., fungi vs. bacteria) and in plasticity within taxonomic groups (Fanin et al. 2016; Zhang and Elser 2017). Microbes may be co-limited by N and P due to the need to balance the production of high N:P resource acquisition machinery, such as proteins, and low N:P growth machinery, such as ribosomal RNA, in response to changing environmental conditions (Arrigo 2005); because this balance is modulated by C availability, C may be simultaneously co-limiting in combination with N or P (Weintraub and Schimel 2003; Allison and Vitousek 2005). Thus, microbial C use efficiency is sensitive to the availability of mineral nutrients, which is one reason why microbial production of CO_2 decreases with increasing N availability (Manzoni et al. 2012). Therefore, the co-limitation of microbial activity could reinforce patterns of nutrient limitation at broader scales through complex feedback mechanisms associated with organic C quality and nutrient recycling (Wutzler et al. 2017). The consequences for plants of such limitations to heterotrophic microorganisms depend on the process considered (i.e., growth, decomposition, nongrowth activity) because of their implications for nutrient immobilization versus mineralization. Mutualisms and interactions with mycorrhizal fungi add additional complexities (Bergmann et al. 2020), especially when mycorrhizal fungi and plants are limited by different nutrients (Johnson et al. 2003; Li et al. 2019) or when fungi sequester limiting nutrients rather than supplying them to the plant (Nasholm et al. 2013; Hasselquist et al. 2016).

Diagnosing co-limitation in forest ecosystems

As contrasted with many well-studied aquatic ecosystems, determining the status of limitation in terrestrial vegetation can be challenging. The complexity of development, struc-

ture, and allocation processes in vascular plants challenges simplistic formulations about responses to nutrient additions. For example, tree growth responses to nutrient additions may not be instantaneous but instead take time to develop because of changes to belowground allocation and to nutrient recycling feedbacks. Interpreting tree growth responses over time can be further complicated by different responses above- and below-ground (Wright et al. 2011; Shan et al. 2022), and potentially by different limitations of root versus mycorrhizal growth (Johnson et al. 2003).

Several approaches have been taken to assess nutrient co-limitation in forests. The most straightforward and conclusive approach involves experimental additions of nutrients. Ideally such experiments are fully factorial and randomized, applied over a long time period. To avoid problems of pseudo-replication, such experiments should be conducted in multiple locations within a forested region, and the levels of nutrient addition should be moderate to avoid artifacts associated with heavy fertilization. Unfortunately, such studies are very expensive, requiring prolonged high levels of funding. To reach wider generalization, a network of such experiments would be conducted coincidentally across forest biomes, but given the high costs it is not surprising that such a network has not yet been established. The existence of such a network in grasslands reflects in part the much lower costs of treatment and monitoring for nonwoody vegetation (Fay et al. 2015). Meta-analyses can reveal global patterns in ecosystem responses to N and P addition, in spite of disparate experimental designs, such those of above- and below-ground biomass (Li et al. 2016), foliar stoichiometry (You et al. 2021), and microbial activity (Deng et al. 2017), generalizing across responses of tropical, boreal, and temperate forests.

An alternative to direct measurements of forest primary production for evaluating nutrient limitation utilizes the nutrient status of the vegetation (Sullivan et al. 2014). In particular, the mechanisms and dynamics underlying simultaneous limitation by N and P have been elaborated in stoichiometric theory (Elser et al. 1996). To the extent that the stoichiometry of these macronutrients in tissues is fixed, production responses to addition of a single nutrient should be constrained. However, strict homeostasis is not typical in primary producers, and wide variation in N:P ratios is observed both among and within species across natural ecosystems. Foliar N:P ratios have been used to diagnose N or P limitation (Gusewell and Koerselman 2002), but these ratios may not predict growth responses to nutrient addition. Foliar N:P ratios did not predict the response of grassland vegetation (Craine et al. 2008) or hardwood trees (Hong et al. 2022) to N versus P fertilization, likely because foliar nutrient ratios and their responses to limitation differ across species and ecosystems (McGroddy et al. 2004; Cleveland and Liptzin 2007). General thresholds that transcend forest types seem unlikely given the failure of foliar N:P ratios to consistently predict nutrient limitation across multiple ecosystems (Yan et al. 2017).

A fourth approach for diagnosing N and P limitation of forest productivity relies on the nutrient conservation strategy of foliar nutrient resorption. Prior to senescence and shedding of foliage, plants transport a high proportion of the N and P content of the leaves into perennial tissues for storage and re-use the following growing season. Because of the relatively high metabolic cost of resorption, the process may be down-regulated when nutrient availability is high, and many studies have utilized the efficiency of nutrient resorption as an indicator of nutrient limitation (Reed et al. 2012; Vergutz et al. 2012). Du et al. (2020) justified a framework utilizing the ratio of N resorption efficiency to P resorption efficiency (i.e., NRE:PRE) for diagnosing N versus P limitation in global vegetation: NRE/PRE > 1 indicates predominantly N limitation and NRE:PRE < 1 suggests primarily P limitation; and a ratio near 1 indicates either N–P co-limitation or limitation by some other resource. Although these ratios can differ among species within diverse vegetation types, reliance on measurements of the dominant tree species was justified as a reliable standard approach (Du et al. 2024).

Representing N–P co-limitation in a simulation model

Simulation models provide a conceptual representation of nutrient co-limitation in ecosystems. In particular, the Multiple Element Limitation (MEL) model has served to explore the consequences of the theory of co-limitation (Rastetter and Shaver 1992) by simulating interactions among multiple resources in terrestrial ecosystems based on resource optimization theory. The heart of the MEL model is an algorithm that drives vegetation toward an optimal state of co-limitation through the continued reallocation of plant assets (e.g., biomass, enzymes, energy) toward the acquisition of the most limiting resources (e.g., light, water, N, P, CO_2).

The MEL model was parameterized for a northern hardwood forest ecosystem at the Hubbard Brook Experimental Forest (HBEF), New Hampshire (Rastetter et al. 2013). The model predicted that N and P co-limitation would develop following harvest as the cycles of these limiting nutrients gradually re-synchronize, correcting the disruptions associated with high losses of N both during and immediately after harvest (Bormann et al. 1968) as well as from reduced plant uptake of the less limiting nutrients. Thus, the model predicted greater N limitation in early stages of recovery (ca. 0–15 years), greater P limitation in mid-succession (ca. 40 years) and eventually N–P co-limitation in more mature stands (>100 years). These predictions are illustrated by successional changes in forest biomass (Fig. 2) as well as plant effort allocated to acquisition of N, P, and other resources (Rastetter et al. 2013).

These predictions reflect the near-total dependence of forest plants on recycled nutrients and the stoichiometric constraints on resource demand of both plants and soil microbes. Thus, N and P fluxes in the form of plant uptake, litterfall, and nutrient mineralization should approach synchrony. The dependence of forest plants on recycled nutrients in MEL results from the key role played by soil heterotrophs, because microbially mediated mineralization of soil organic matter is the principal source of growth-limiting nutrients. As heterotrophic organisms, most soil microbes (fungi, Bacteria, Ar-

Fig. 2. Woody biomass response to fertilization beginning at stand ages of (*a*) 15, (*b*) 40, and (*c*) 100 years as predicted by the Multiple Element Limitation model applied to our forest type (Rastetter et al. 2013). Vertical lines indicate dates of tree inventory, 4 and 8 years after the onset of fertilization. N, nitrogen; P, phosphorus.
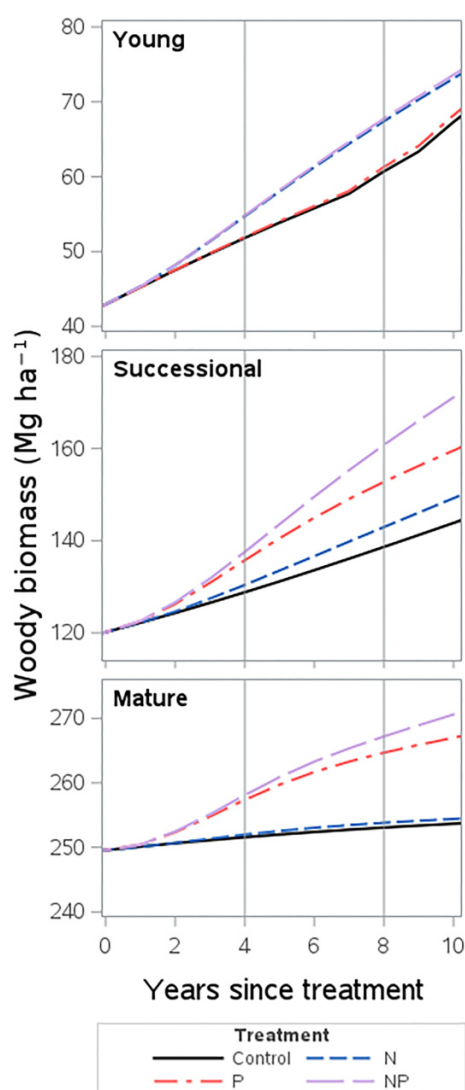
chaea) are limited primarily by energy and by their ability to access organic matter; however, as with understory vegetation, which tends to be light-limited, microbial communities are often co-limited by energy and mineral nutrients. Exactly how this sort of co-limitation of microbial dynamics influences nutrient availability to vegetation depends upon a complex suite of interactions among members of the soil community that also includes mycorrhizal fungi and soil invertebrates. In northeastern deciduous forests, the sensitivity of the response of soil C mineralization to addition of new C resources (cellulose, leaf litter) has been shown to vary in relation to N and P availability (Fisk et al. 2015). Relieving N limitation of microbial carbon-use efficiency can lower rates of mineralization of native soil organic matter, whereas relieving P limitation can increase mineralization of newly added

labile organic matter (Fisk et al. 2015). Thus, the co-limitation of microbial communities by C, N, and P appears to reflect N limitation of microbial biomass synthesis together with P limitation of microbial metabolism (Hartman and Richardson 2013), somewhat analogous to the separate roles of N and P in limiting gross primary production (Domingues et al. 2010).

The feedback between microbial activity and plant nutrient availability also reflects interactions between N and P availability. In the MEL model, this interaction is represented implicitly based on the dependence of N and P mineralization rates on the C:N and C:P ratios of soil organic matter (Rastetter et al. 2013). A classic synergistic interaction is possible, i.e., the available pools of N and P may be co-dependent, with the size of both pools changing simultaneously. Several studies have reported effects of N addition in promoting production of phosphatase enzymes; synthesis of enzymes depends on an adequate N supply (Olander and Vitousek 2000; Marklein and Houlton 2012). Hence, both resin-available P and soil phosphatase activity increased along a N availability gradient in northern hardwoods stands (Ratliff and Fisk 2016). This sort of interaction could be an important microbially mediated mechanism promoting forest ecosystem co-limitation by N and P.

Review and synthesis of recent studies of co-limitation in northern hardwood forests

A more complete understanding of limits to forest productivity and a rigorous validation of the MEL model requires long-term factorial experiments, ideally including timescales of tree species replacement. At three sites in the White Mountains of New Hampshire, an ongoing factorial experiment was devised consistent with the treatments simulated in the MEL model. We further explore the co-limitation concept and its application to the temperate broadleaf deciduous forest ecosystem type by synthesizing key results from this long-term field experiment—Multiple Element Limitation in Northern Hardwood Ecosystems—MELNHE.

Study sites and treatments

The MELNHE study was initiated in 2011 and includes 13 stands (Table 1) spanning a range of ages (25 to >100 years) and native site fertility in the White Mountains of NH, USA (Goswami et al. 2018). The forest stands were located in three sites: nine at Bartlett Experimental Forest (44°2–4′N, 71°9–19′W; elevation 250–500 m); two at Hubbard Brook Experimental Forest (43°56′N, 71°44′W; elevation 500 m), and two at Jeffers Brook (44°2′N, 71°53′W; elevation 730 m; Fig. 3). Tree species composition varied across stands, with the mature (>100 years), second-growth stands typical of the northern hardwood forest type dominated by sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), and American beech (*Fagus grandifolia* Ehrh.). Young and midsuccessional, third-growth stands (<40 years old) were dominated by a variable mixture of red maple (*A. rubrum* L.), striped maple (*A. pensylvanicum* L.), pin cherry (*Prunus pensylvanica* L.f.),

Table 1. Stand descriptions for the Bartlett Experimental Forest, Hubbard Brook Experimental Forest, and Jeffers Brook.

Site	Stand	Forest age	Year cut	Elevation (m)	Basal area (m² ha⁻¹)	Dominant species
Bartlett	C1	Young	1990	570	25.2	*Betula papyrifera, Prunus pensylvanica, Fagus grandifolia*
Bartlett	C2	Young	1988	340	23.4	*Acer rubrum, F. grandifolia, B. papyrifera*
Bartlett	C3	Young	1985	590	30.5	*P. pensylvanica, F. grandifolia, A. rubrum*
Bartlett	C4	Mid-age	1979	410	32.9	*B. papyrifera, Populus grandidentata, P. pensylvanica*
Bartlett	C5	Mid-age	1976	550	27.2	*B. papyrifera, P. pensylvanica, A. rubrum*
Bartlett	C6	Mid-age	1975	460	30.1	*A. rubrum, B. papyrifera, F. grandifolia*
Bartlett	C7	Mature	1890	440	32.1	*F. grandifolia, A. saccharum, Tsuga canadensis*
Bartlett	C8	Mature	1883	330	35.2	*F. grandifolia, A. saccharum, B. alleghaniensis*
Bartlett	C9	Mature	1890	440	32.7	*A. saccharum, F. grandifolia, B. alleghaniensis*
Hubbard Brook	HBM	Mid-age	1970	500	29.5	*B. alleghaniensis, B. papyrifera, A. rubrum*
Hubbard Brook	HBO	Mature	1911–1913	500	33.9	*B. alleghaniensis, F. grandifolia, A. saccharum*
Jeffers Brook	JBM	Mid-age	1974	730	27.9	*B. alleghaniensis, B. papyrifera, A. saccharum*
Jeffers Brook	JBO	Mature	1915–1929	730	35.7	*A. saccharum, B. alleghaniensis, F. grandifolia*

Fig. 3. The Multiple Element Limitation in Northern Hardwood Ecosystems experiment includes two stands at Jeffers Brook, two at Hubbard Brook, and nine at the Bartlett Experimental Forest. Stand names are shown in Table 1. An example of four treatment plots from one stand is shown.
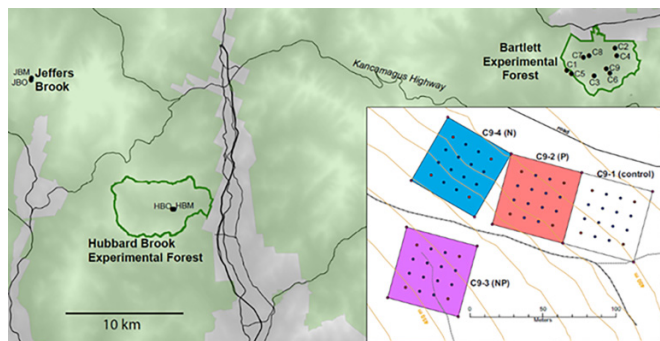
paper birch (*Betula papyrifera* Marsh.), yellow birch, and American beech.

Soils in all stands were formed in glacial drift and are predominantly Spodosols with a range of drainage characteristics (Vadeboncoeur et al. 2012; Table 2). Precipitation is evenly distributed throughout the year and amounts to about 130 cm annually (Richardson and Hollinger 2023). Annual temperatures in this humid, continental climate range from an average low of $-8.5\ ^\circ$C in January to 18.8 $^\circ$C in July (Bailey 2003), but differences in elevation, slope, and aspect across the stands and sites result in slight temperature differences.

At Bartlett, there were three each of young, mid-successional, and mature stands. At both Hubbard Brook and Jeffers Brook, there was one mid-successional and one mature stand. Within each of the 13 stands we positioned four 0.25 ha (50 m × 50 m) treatment plots (except for 30 m × 30 m plots in the mid-successional stands at Hubbard Brook and Jeffers Brook). Each plot was randomly assigned to one of four treatments: control, N addition, P addition, or N + P addition, excluding configurations where an N-treated plot might drain into a non-N plot. Fertilization has been conducted an-

nually since 2011, with N added as granular NH_4NO_3 at a rate of 3 g N m⁻² year⁻¹ and P added as granular NaH_2PO_4 at a rate of 1 g P m⁻² year⁻¹. Measurements are conducted at least 5 m (in the smaller plots) or 10 m from the treatment boundaries to avoid edge effects.

Approaches and measurements

A large suite of measurements has been conducted on a periodic basis within the 52 plots in the MELNHE study pre- and post-treatment. For this report, we provide a broad overview of these approaches with reference to our published studies that describe the methods in greater detail. Soil nutrient availability was measured in the top 10 cm of soil using cation and anion resin strips (Fisk et al. 2014; Goswami and Fisk 2024). Activities of N-acquiring enzymes (alanine aminopeptidase, leucine aminopeptidase, and N acetylglucosidase) and P-acquiring enzymes (acid phosphatase were measured in forest floor and surface mineral soil after 3 and 6 years of treatment) (Shan 2020). All trees > 10 cm in diameter at breast height were tagged, and diameters were measured in 2011, 2015, and 2019, allowing estimation of growth by species in each plot (Goswami et al. 2018; Blumenthal et al. 2025). Foliar nutrient concentrations were measured for the dominant species in each stand in mid-summer by collecting sun-exposed leaves from mid-canopy (Hong et al. 2022), and other foliar traits (specific leaf area, leaf dry matter content, and del 13 C) were also measured (Zukswert et al. 2025a) to characterize the leaf economics spectrum (Wright et al. 2004). Fine litterfall mass was measured with a network of five 0.19–0.23 m² litter traps in each plot. Foliar nutrient resorption was measured by collecting fresh leaf litter of the dominant species during the peak litterfall period in mid-October (Gonzales and Yanai 2019). Fine root biomass was measured in each plot in 2010 and 2015—16 by sorting roots by hand from 10–12 soil cores (5 cm diameter) to 30 cm soil depth in each plot (Shan et al. 2022; Li et al. 2023). Fine root growth was measured using root ingrowth cores in mature stands (C7, C8, C9) in 2014 (Shan 2020), young stands (C1, C2) in 2017 (Li et al. 2023) and in mid-age stands (C5, C6, HBM) in 2022.

Table 2. Soil chemistry in 2009 (pre-treatment) in the Oe, Oa, and upper mineral horizons of reference plots.

	pH (in water)	OM (%)	Bic P (ug/g soil)	N min (ug/g soil/day)	Nitr (ug/g soil/day)	Exch Ca (ug/g soil)
Oe	4.28	77.28	67.64	19.92	0.97	4361.73
Oa	4.02	47.95	53.85	7.31	2.13	1278.10
Mineral	4.59	9.37	13.14	0.45	0.36	125.37

Note: OM, organic matter; N min, potential net N mineralization; Nitr, potential net nitrification; Bic P, bicarbonate-extractable P.

Fig. 4. Resin-available nitrogen and phosphorus in surface soils of 13 forest stands. Each box shows the interquartile range of the 13 replicates, with the mean and median, averaging data from 2012–2021 within each plot.
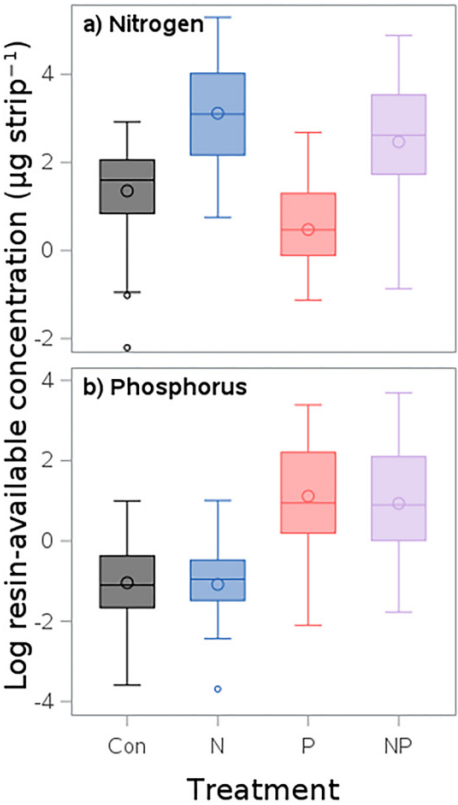
Some findings from the MELNHE experiment

Soil nutrient availability, enzymes, and microbial activity

Resin-available N and P in surface soils increased in response to addition of the same nutrient, as expected (Fig. 4). More complex responses included an effect of adding one nutrient on the availability of the other. Resin-available P did not respond to N addition in young stands but declined in response to N in mature stands, possibly as a consequence of greater root growth in N addition plots of mature stands (Shan et al. 2022; discussed below). Adding P reduced resin-available N ($p < 0.001$ for the main effect of P in a full-factorial ANOVA of N, P, age, and year), shown in Fig. 4 (Goswami and Fisk 2024), with the most pronounced effects in stands with high net N mineralization potentials ($r = -0.54$, $p = 0.05$ in re-

gression) (Goswami and Fisk 2024). These interactions might contribute to the observed increase of N-acquisition enzymes in soils of the P addition plots; notably, an analogous response of phosphatase enzymes in N addition plots was not observed (Shan 2020). Net N mineralization potential did not respond to P addition, despite lower recycling of N in litterfall, and P effects on resin-N availability were likely caused by N uptake (either by roots and mycorrhizae or soil heterotrophs) rather than by lower mineralization inputs (Goswami and Fisk 2024).

Foliar nutrients and other leaf traits

Foliar nutrition has been used as an indicator of N versus P limitation in terrestrial vegetation (Koerselman and Meuleman 1996; Gusewell 2004), although thresholds indicative of co-limitation should be used with caution as some studies have questioned their effectiveness for this purpose (Niinemets and Tamm 2005; Craine et al. 2008), and N:P thresholds have not been established for temperate deciduous forests. Foliar N:P ratios in the same stand can differ markedly among northern hardwood species (Gonzales and Yanai 2019), consistent with broad observations for tropical forests (Townsend et al. 2007). Notably, before treatments were applied, foliar N:P in the northern hardwood forests of the MELNHE study mostly exceeded 20, suggestive of P limitation (Fig. 5; Zukswert et al. 2025a).

Not surprisingly, nutrient additions resulted in increased foliar nutrient concentration of the added nutrient, with a greater response for P than N (Fig. 5; Zukswert et al. 2025a). Thus, foliar N:P ratios declined significantly in response to P addition, generally moving into the suggested N–P co-limitation range, whereas N addition had the opposite effect. However, a wide range of responses was observed in the N + P addition plots, varying markedly among species and stands (Hong et al. 2022), and supporting the sort of interspecific variation observed in tropical forests (Ostertag 2001; Townsend et al. 2007).

The leaf economics spectrum has been employed to characterize the strategies of plants along an axis from conservative to acquisitive (Wright et al. 2004). The key traits in this spectrum include foliar nutrient concentrations and specific leaf area, both of which are expected to increase with higher resource availability, and a shift toward acquisitive strategy, whereas leaf dry matter content decreases. Among the six dominant tree species in our study sites, maples and beech are most conservative, cherry most acquisitive and birches intermediate. A shift in these traits in response to nutrient addition can reflect either or both plasticity within species and compositional shifts driving community-wide responses. After 10 years of treatment, we observed a shift toward more

Fig. 5. Foliar nitrogen (N) and phosphorus (P) concentrations measured from 2014 to 2016 in 10 stands, averaged by species. Dotted lines represent N:P ratios of 10 and 20; the solid lines indicate ratios of 14 and 16.
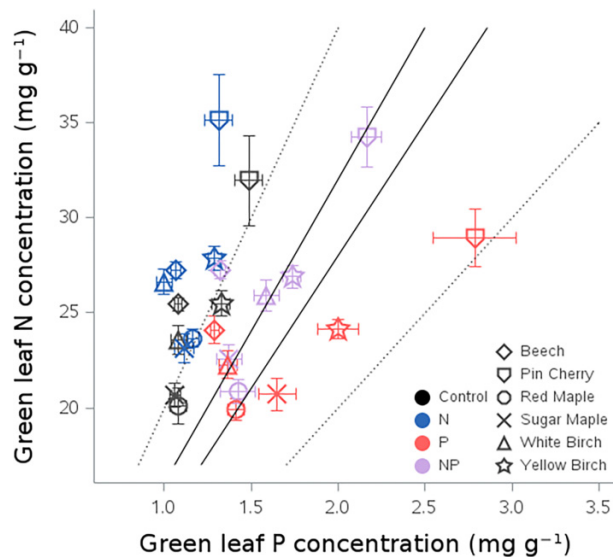
acquisitive strategies in response to nutrient addition, driven primarily by plastic responses within species rather than by changes in species composition (Zukswert et al. 2025a). Some evidence for co-limitation by N and P was indicated by synergistic effects of the addition of one nutrient on foliar levels of the other nutrient at the community level. Such interactions may signal biochemical co-limitation in which the addition of one nutrient increases the availability of the other nutrient (Bracken et al. 2015). Finally, the response of intrinsic wateruse efficiency, as indicated by del 13 C, to nutrient additions did not fit on the same axis of the leaf economics spectrum as the other traits, suggesting a trade-off between water use efficiency (WUE) and nutrient use efficiency (NUE) in these forests (Zukswert et al. 2025a).

Foliar resorption

Plants exhibit a variety of mechanisms that contribute to maintaining N–P co-limitation in the face of environmental changes that promote single nutrient limitation, such as atmospheric N deposition, NO_3- leaching, changing soil pH (Fig. 1). Among the most prominent is foliar nutrient resorption, which reduces the need for root uptake of limiting nutrients. Up to 70% of foliar N and P may be withdrawn prior to leaf abscission, and this resorption process is often responsive to changes in soil fertility, presumably because downregulating resorption reduces energy expenditure (Killingbeck 1996).

We observed such apparent downregulation of N and P resorption: resorption efficiency (% of leaf nutrient content resorbed) and proficiency (litter nutrient concentration) of both N and P decreased with addition of the respective nutrient (Gonzales et al. 2023; Zukswert et al. 2025b). Responses of resorption in the N + P plots were intermediate for both nutrients (Fig. 6; Zukswert et al. 2025a). Intriguingly, we found ev-

idence of a synergistic interaction of N and P resorption after 4 years of treatment in our young stands: N resorption efficiency increased significantly with P additions and vice versa (Gonzales and Yanai 2019). This synergistic response may indicate a degree of N–P co-limitation in these stands. In contrast, in the mid-successional and mature stands P addition suppressed P resorption but N addition had no effect on N resorption (Gonzales et al. 2023). Less N return in litterfall in plots receiving P additions could indicate that N limitation is developing once P limitation is alleviated (Goswami and Fisk 2024). Indeed the response of foliar resorption to nutrient addition increased in magnitude from years 4–6 of treatment to years 10–12 (Zukswert et al. 2025b). This gradual plastic shift in resorption might reflect the effect of biochemically dependent co-limitation as a suite of mechanisms associated with increased supply of one nutrient gradually drives increased availability of the other nutrient (Bracken et al. 2015).

We evaluated the NRE:PRE ratio of the dominant tree species across 10 of the stands as a suggested indicator of N versus P limitation or co-limitation (Du et al. 2020). In general, the NRE:PRE ratio was low (considerably less than 1) in the untreated reference plots, suggestive of P limitation (Gonzales et al. 2023) and coinciding with indications based on live foliar chemistry (see above). Although addition of P shifted the ratio closer to 1, the NRE:PRE still remained less than 1 except for one species, red maple. This species has been characterized as particularly plastic in its response to a variety of environmental changes (Abrams 1998).

Stem growth

After 4 years of treatment, results from the MELNHE experiment provided some tentative support for predictions of the MEL model: trees in mid-successional (35–40 years old) and mature (>100 years) stands exhibited significantly higher diameter growth in response to P addition, whereas trees in young stands (~25 years old) grew marginally faster in response to N addition (Fig. 7; Goswami et al. 2018). Although tree diameter growth was on average greatest in N + P plots, greater growth in response to N + P than to either N or P alone was noted in only 6 of 13 stands and neither synergistic nor additive effects of N + P were detected after 4 years of treatment.

In contrast, after 8 years of treatment the highest basal area growth was observed in the N + P plots (Fig. 7). In stands of all ages, effect sizes in N and in P treatments in a Bayesian analysis exceeded those in controls (effect size 95% credible intervals > 0). Effect sizes for the N + P treatment consistently exceeded those for single nutrient addition plots (effect size 95% credible intervals > 0), indicative of the development of co-limitation under N + P treatment, for total basal area increment (Fig. 7) and for the relative basal area increment of all individual trees (Blumenthal et al. 2025). Note that this delayed detection of N–P colimitation was predicted by the MEL model (Fig. 2).

Fine litterfall mass

Surprisingly, despite increased stem growth in response to nutrient additions, no significant treatment response of fine

Fig. 6. Foliar and leaf litter (*a*) nitrogen (N) and (*b*) phosphorus (P) concentrations measured in 2014–2016, showing the mean and standard error of community-weighted averages across 10 stands. Dashed isolines indicate resorption efficiency.
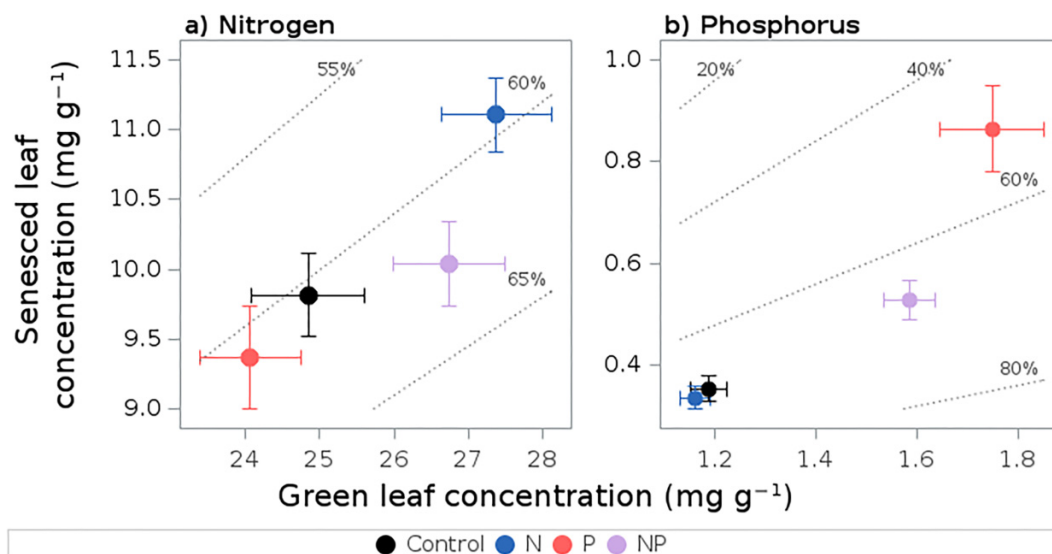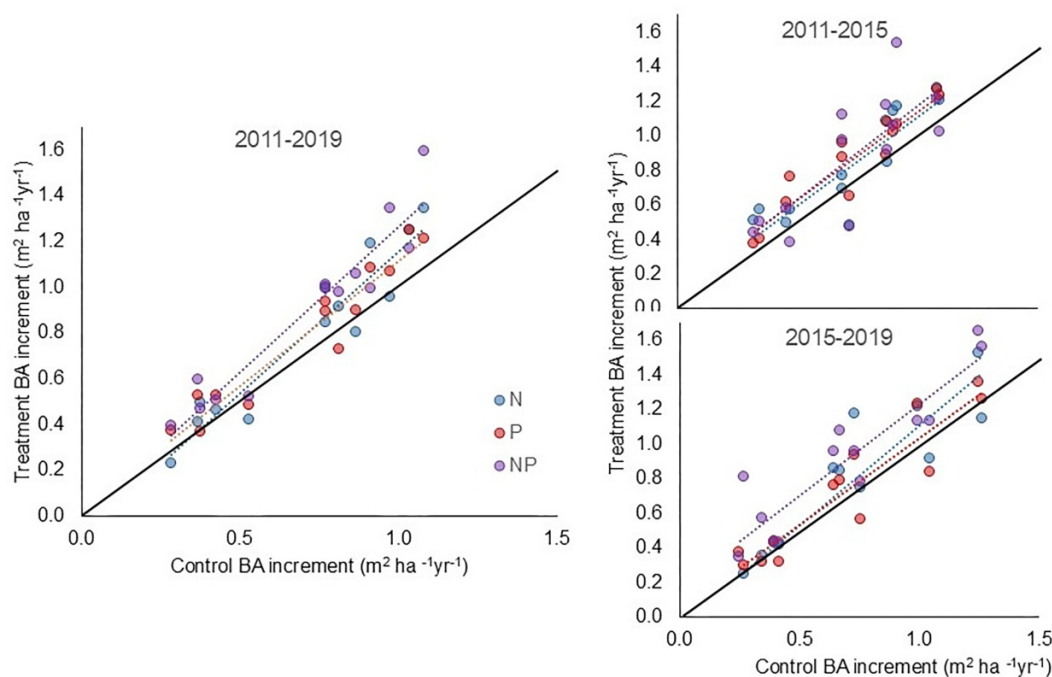

Fig. 7. Basal area (BA) increment of trees > 10 cm DBH in 13 forest stands in treatment plots (N, P, or N + P) versus control plots after 4 and 8 years of treatment. Solid line is the 1:1 line; dotted lines are the best fit to the treatments. N, nitrogen; P, phosphorus.

litter production was observed across the MELNE study (Yanai et al. 2024). In the case of the mature forest stands, this lack of response was not unexpected, because the canopies of these stands were fully developed and leaf area index exceeded 6 (Fahey et al. 2022). In the successional stands, it might have been reasonable to expect that canopy development would be accelerated by nutrient addition, resulting in greater foliar production and litterfall mass. However, canopy closure occurs quite quickly in these pin-cherry dominated stands (Hamburg et al. 2025).

Fine root growth and biomass

Maximal performance in the MEL model is achieved by allocating assets previously acquired by plants to maintain an optimal balance and to facilitate further acquisition of various resources in the face of differing availability or supply. For example, the acquisition of C by foliage and water and nutrients by roots and mycorrhizae can be balanced by the adjustment of root:shoot ratio to assure sufficient light and soil resource capture in the face of competition and soil resource scarcity. Thus, we expected root:shoot growth and biomass

Fig. 8. Fine root ingrowth (<1 mm diameter, 0–30 cm depth) in eight forest stands (two young, three mid-age, and three mature) after 4–8 years of treatment with added N, P, or N + P. N, nitrogen; P, phosphorus.
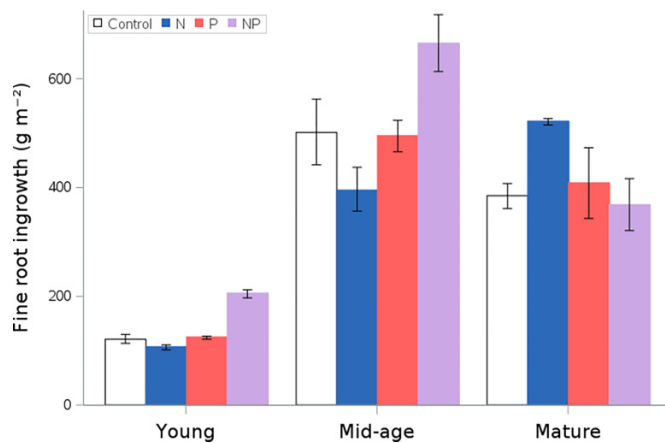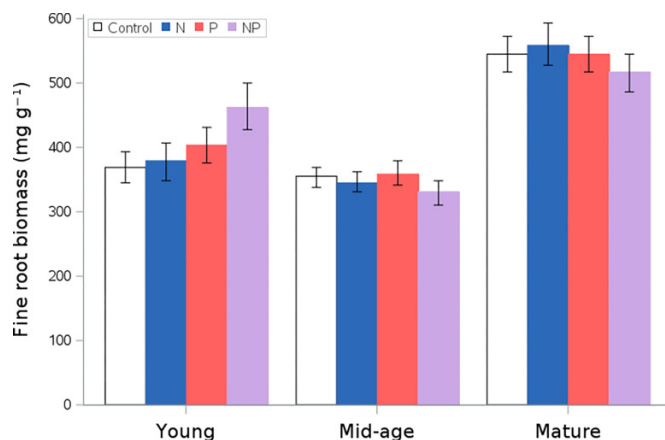

Fig. 9. Fine root biomass (<1 mm, 0–30 cm depth) in 13 forest stands (3 young, and 5 each, mid-age and mature) after 5–6 years of treatment with added N, P, or N + P. N, nitrogen; P, phosphorus.

ratios to decline in response to fertilization, thereby maximizing aboveground growth by increasing proportional allocation of C to shoots, in accordance with the functional balance theory (Thornley 1991).

Surprisingly, we found no evidence that nutrient additions caused a reduction in either root growth (Fig. 8) or standing root biomass (Fig. 9).Measurements of root growth using ingrowth cores after 4 years of treatment indicated significant increases (about 30%) in response to N in three mature stands (C7, C8, C9; Shan et al. 2022; Fig. 8). Notably, this response was primarily associated with increased growth in mineral soil horizons rather than surface organic horizons, consistent with root foraging for P rather than N. In contrast, in five successional stands the highest fine root growth was observed in N + P plots (Fig. 8), averaging 45%–98% more than other treatments in two young stands (Li et al. 2023) and 35%–44% more

than other treatments in three mid-age stands ($p = 0.01$ for the N × P interaction). Taken together with the aboveground growth results, these large root growth responses indicate that allocation to root growth did not decline consistently in response to the nutrient additions and in fact, in most cases, it increased.

Discussion

Co-limitation of aboveground tree growth in northern hardwood forests

Primary productivity in terrestrial ecosystems is commonly limited by the availability of multiple environmental resources (Rastetter and Shaver 1992), and the nature of those limitations is shifting rapidly with global environmental change; hence, a better understanding of the mechanisms of multiple resource co-limitation is needed. N and P are the most commonly limiting soil nutrients and N–P co-limitation also may be common. Previous summaries of studies of nutrient co-limitation (Elser et al. 2007; Harpole et al. 2011) noted that few had been conducted in temperate forest ecosystems. These forests are widespread across the northeastern United States and southeastern Canada on landscapes where soil formation began following deglaciation only about 14 000 years ago. According to the paradigm of P supply from weathering of young soils (Walker and Syers 1976), we expected young, post-glacial soils of these forest ecosystems to be well supplied with P, and N limitation was expected because of limited biological N$_2$ fixation (Roskowski 1980). Indeed, a meta-analysis of 35 fertilization experiments in forests of northeastern U.S. and southeastern Canada indicated that N limitation of aboveground productivity was most common (Vadeboncouer 2010). However, a long history of anthropogenic N addition to the region could have relieved N limitation, resulting in so-called "transactional" P limitation (Vitousek et al. 2010), and some evidence for P limitation was also suggested (Vadeboncouer 2010). The few, short-term factorial fertilization experiments showed little evidence of synergistic (greater than additive) co-limitation (Vadeboncouer 2010). Perhaps this result is not surprising because adding nutrients in the short-term in large amounts to test for limitation disrupts the existing balance among the processes regulating supply, acquisition, and utilization of different resources.

Both the MEL model (Fig. 2) and diagnostic criteria of pretreatment foliar N:P ratios (Fig. 5) predicted a greater response to P than to N in the MELNHE study. Indeed, after 4 years of treatment, our low-level N and P additions to 13 northern hardwood stands provided evidence of transactional P limitation in the mid-successional and mature stands (Goswami et al. 2018) as the highest tree growth was observed in plots receiving added P. However, this response was transient, as additive N and P co-limitation of tree growth in these forests was observed after 8 years (Blumenthal et al. 2025), with the highest cumulative growth in N + P plots (Fig. 7). The MEL model also predicted that evidence of NP co-limitation would develop gradually in mid-successional and mature forest stands (Fig. 2). It is worth noting that pretreatment fo-

Environ. Rev. **33**: 1–15 (2025) | dx.doi.org/10.1139/er-2024-0128

9

liar N:P ratios did not accurately predict growth responses to added N or P (Hong et al. 2022), even though the MELNHE experiment provided the perfect setting for establishing the ratio diagnostic of colimitation (Koerselman and Meuleman 1996).

Synergistic responses

Some strongly synergistic responses in the MELNHE forest stands illustrated how balanced N–P nutrition can be maintained in the face of changes that might be expected to drive nutrient imbalances, such as acid rain, N deposition, or CO_2 fertilization (Fig. 1). In particular, resorption of N and P were co-dependent in early successional stands dominated by pioneer species (birches, pin cherry); N resorption increased in P fertilized stands and vice versa (Fig. 6). This mechanism could contribute to maintaining N–P co-limitation as internal recycling of nutrients would reduce nutrient uptake requirements. From the nutrient supply standpoint, the decline in N availability in response to alleviating P limitation was indicative of the development of N–P co-limitation. Depletion of available pools of one nutrient in response to adding another nutrient is a mechanism that could contribute to the type of sequential co-limitation discussed by Davidson and Howarth (2007), in which alleviating limitation by one nutrient induces secondary limitation by another. Furthermore, a condition of co-limitation that is detectable when N and P are added in large quantities (as in most experiments) may instead appear as a response to one nutrient and then to the other over time under modest rates of fertilization such as ours, due to the time required for the addition of one nutrient to affect the demand for and availability of the other. In our forests, the initial (4 years) tree growth response to P indicated by Goswami et al. (2018) might have been suppressed by the longer-term effects of P addition on available N pools and litterfall N recycling so that eventually N–P co-limitation was revealed only after 8 years of treatment (Blumenthal et al. 2025). However, N + P had a more consistent effect on total basal area increment over the first 4 years of treatment (Fig. 7) than on relative basal area increment of individual trees reported by Goswami et al. (2018).

Nutrient limitation of root growth

We observed clear evidence of increased root growth in response to nutrient addition in these northern hardwood forest stands (Fig. 8). What mechanisms could contribute to this unexpected response? On one hand, nutrient limitation of leaf and shoot growth could be fundamentally different than for root growth because roots have first access to the soil nutrients they absorb. Moreover, leaf growth occurs in a large pulse in early summer creating strong nutrient demand, whereas fine root growth continues throughout the warm season (Tierney et al. 2003). On the other hand, nutrient availability might limit root growth, given that a considerable proportion of the supply of mineral nutrients for root growth comes from recycling from limited storage pools and not from uptake (Millard and Grelet 2010). For exam-

ple, Marschner et al. (1997) estimated that two-thirds of the K demand for growing root tips may be derived from storage rather than immediate root uptake. Assuming that storage pools can be depleted in the face of nutrient limitation, then it is not surprising that N or P could limit fine root growth especially with coincident high nutrient demand in shoots.

In the two youngest stands in the MELNHE study, both fine root biomass and root growth were stimulated by P addition, but significantly higher root growth was observed in response to combined N–P addition than predicted by P alone. (Fig. 8). This result is at odds with the traditional view of plant allocation and suggests an alternate interpretation of plant strategies in these early successional forests. The greater fine root growth response to N + P addition than to P alone suggests the possibility that balanced nutrition is required for maximal growth, an idea that is supported by root accumulation of N under elevated P availability (Blanes et al. 2013). In contrast, in the mature MELNHE stands, N addition stimulated root growth (Shan et al. 2022); moreover, Naples and Fisk (2010) observed that root ingrowth into P-enriched soil cores increased in mature forest sites where N availability is high, suggesting that high N supply can result in imbalanced root P nutrition. Thus, it was only in the successional stages after disturbance (i.e., 25–40 years post harvest) that co-limitation of fine root growth by N and P was observed in these northern hardwood forest ecosystems. What could explain such a pattern? Early in the recovery process following harvest, allocation of plant effort toward acquisition of the light resource is particularly high as the trees grow rapidly in height and build their canopies. At this stage there is intense competition for light among individuals and species. At the same time, the plants must allocate sufficient effort to belowground assets (fine roots, mycorrhizae) to assure adequate supply of soil resources to maintain growth and other physiological functions. Thus, light and soil resources should both be limiting at least until the canopy closes and maximum forest leaf area is attained (typically about 40 years; Aber 1979). An experimental evaluation of co-limitation by light and soil resources in early successional northern hardwood stands (age 12–24 years) indicated that the ability of a highly intolerant tree species, pin cherry, to compete effectively for light with other tree species (*Betula*, *Populus*, *Acer*, *Fagus*) was dependent upon soil resource supply (Fahey et al. 1998); without soil resource augmentation, pin cherry was unable to sustain height growth and was overtopped by species better able to access limited soil resources. Hence, we suggest that N–P co-limitation of root growth in these successional stands reflects in part the combined competition for light and soil nutrients among individual trees and tree species. Notably, fine root biomass increases with stand age in northern hardwoods (Yanai et al. 2006), and the highest values were observed in the five older, mature stands in the MELNHE experiment (Table 1). We surmise that performance in competition for soil resources demands greater investment in roots during the soil occupancy phase; perhaps the higher net C gain by trees in N + P plots allowed such greater investment. This response may be elicited only with balanced N and P nutrition of tree roots.

## Different nutrients limit stem versus root growth

Results from the MELNHE study suggest that co-limitation by multiple nutrients could be associated in part with independent limitation of different plant parts as noted previously for grasslands (Fay et al. 2015). Increased soil nutrient supply would be expected to cause a reduction in belowground carbon allocation and proportionally higher aboveground allocation and shoot growth (Haynes and Gower 1995).

However, co-limitation could complicate this simple expectation if the growth of roots is limited by a different nutrient than that of the shoot. In three mature stands in the MELNHE study, where aboveground growth initially responded mostly to P (Goswami et al. 2018), we observed that N limits root growth, as significantly increased root growth was observed in root ingrowth cores in the N addition plots in these stands (Shan et al. 2022; Fig. 8). Moreover, slightly, though not significantly ($p = 0.31$; Mann et al. 2024) higher fine root biomass was observed in the N-amended plots (Fig. 9). Constraints on root growth by low N availability is a potential mechanism by which N could interact with P limitation. Alleviating N limitation of root construction would allow greater root growth and hence the potential for higher P uptake in these P-limited stands. Moreover, increased mining of apatite P was observed in mature stands where P was not added (Shan 2020). Separate limitation of shoot versus root growth, as observed in lowland tropical forest in Panama (Wurzburger and Wright 2015), could be analogous to the suggestion of independent nutrient limitation of mycorrhizal fungi versus their host plants (Treseder and Allen 2002). According to the stoichiometric framework of Johnson (2010), mycorrhizal colonization should increase in response to added N when P is limiting to the host plant but decline when P is not limiting (Johnson et al. 2003; Blanke et al. 2005). Thus, more C may be allocated to mycorrhizae to compensate for increased P demand resulting from N addition. We suggest that fine root production controls plant uptake of P, and that the initial P limitation of aboveground growth in these mature northern hardwood forests was caused in part by N limitation of root growth.

Microbial and rhizosphere processes

One mechanism by which vegetation could maintain N–P co-limitation is through the activity of roots in supplying organic compounds to rhizosphere soil to facilitate nutrient mineralization and acquisition. This rhizosphere carbon flux comprises as much as 20% of forest C assimilation (Kuzyakov and Domanski 2000; Phillips and Fahey 2005). Although our observations of root growth responses to nutrient addition departed from the expectations based on the functional balance theory (Thornley 1991), represented in the form of effort allocation in the MEL model, it is possible that rhizosphere carbon flux decreased in response to nutrient addition. Although few direct measurements are available, the effect of rhizosphere carbon flux can be evaluated by comparing microbial populations and biogeochemical properties between rhizosphere and bulk soil (Kuzyakov 2002). For example,

Fig. 10. Treatment N and P effect on red maple and yellow birch rhizosphere effects ((rhizosphere-bulk)/bulk) on (*a*) soil processes and (*b*) microbial abundance in three young northern hardwood forests stands. –N, +N, –P, and +P indicate whether plots received these treatments. Significance of differences are indicated with * if $p < 0.05$, ** if $p < 0.01$ (reprinted from Shan et al. (2018) with permission from Elsevier). N, nitrogen; P, phosphorus.
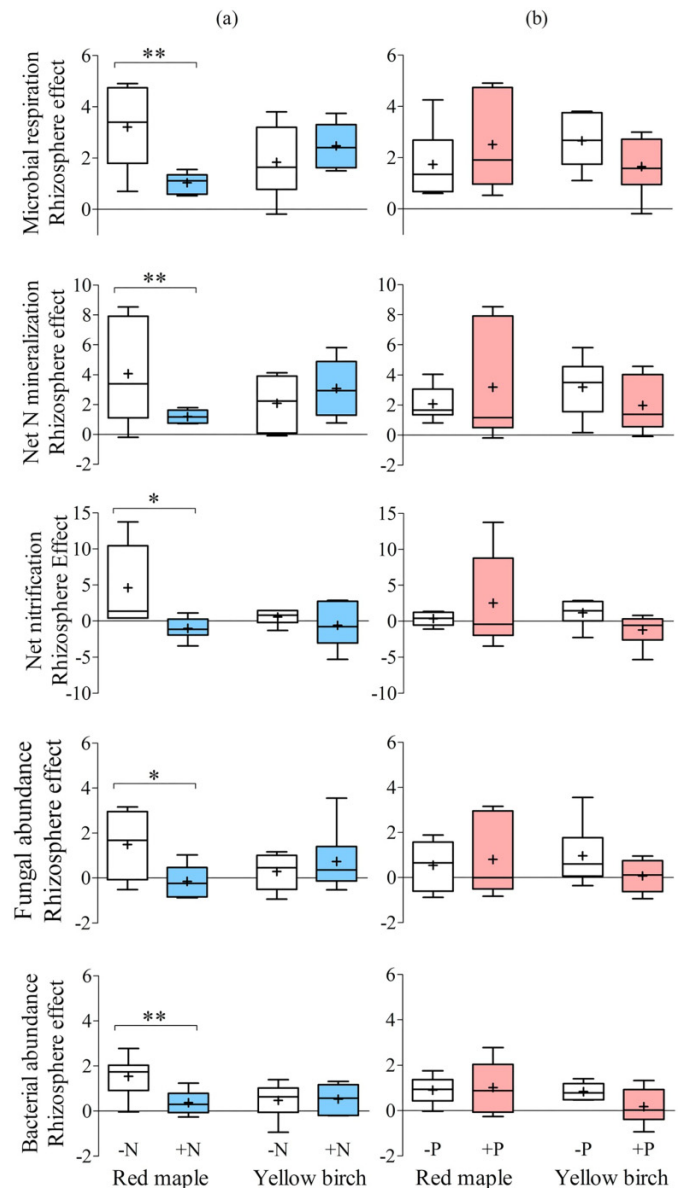
co-limitation would be maintained if N addition promoted P availability in the rhizosphere (e.g., via increased phosphatase activity) and P addition stimulated N mineralization. In the MELNHE study, N addition (but not P addition) had strong effects on rhizosphere processes (Shan et al. 2018; Fig. 10). The responses were strikingly different between maple, which has arbuscular mycorrhizae, and birch, which is ectomycorrhizal; in the former, N addition strongly suppressed rhizosphere effects on microbial activity, whereas in the latter, N addition suppressed both rhizosphere and bulk soil

microbial activity (Fig. 10). These results suggest a possible influence of mycorrhizal type on processes driving N versus P limitation in northern hardwood forests, and they reinforce suggestions of a mycorrhizal-associated nutrient economy (Phillips et al. 2013) and its likely role in the extent of coupling of N and P cycling in deciduous forests (Cheeke et al. 2017). Clearly, more direct measurements of rhizosphere carbon flux and its components are needed in experiments like MELNHE to better understand the complex mechanisms underlying N–P colimitation in forest ecosystems. Notably, none of these complexities has as yet been incorporated into models of forest nutrient dynamics, such as the MEL model.

Conclusions

The complexity of N–P co-limitation is illustrated by the many possible feedbacks among plants, soil microbes, and resource availability and consequent synergistic relationships between N and P supply and demand. In response to low-level nutrient additions in the MELNHE experiment, evidence of N–P co-limitation of tree growth became apparent after 8 years of treatment. We found evidence for both microbially mediated co-dependence of soil N and P availability as well as co-dependent responses of N and P resorption from senescing leaves. Thus, the traditional view of the response of forest carbon allocation to increased nutrient availability—a functional balance theory (Thornley 1991)—may be oversimplified when considered in relation to N–P co-limitation, competition for light resource, and forest successional development. In successional stands, we found strong evidence for N–P co-limitation of root growth (Li et al. 2023; Butt et al. unpublished), suggesting a need for balanced nutrition for maximal root growth. In mature stands, we observed apparent differences between root and shoot nutrient limitation, in which root growth was limited by N (Shan et al. 2022) during the first 4 years of treatment when we detected P limitation of aboveground growth (Goswami et al. 2018), after which, in addition to P limitation, we also detected N limitation and NP colimitation aboveground (Blumenthal et al. 2025). These differences suggest fundamental shifts in root-shoot relations as forests mature and occupancy of both canopy space and soil volume progresses. Such mechanisms would be complementary to the resynchronization of nutrient recycling hypothesized by Rastetter et al. (2013), based on the MEL model as applied to northern hardwood forests. Resolving uncertainty about the relative role of C allocation and nutrient demand in regulating belowground production would improve understanding of the nature of linkages between energy flow and nutrient cycling in terrestrial ecosystems (Reiners 1986). Capturing these complexities in a modeling framework demands a better understanding of the relationships between plant competition and community-wide optimization of performance of both plants and soil microbes.

Acknowledgements

Article information

Copyright

Data availability

Fahey, T.J., S. Li, S. Shan, M. Fisk, R.D. Yanai, and J. Blum. 2023. Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE): Root biomass and growth responses to nitrogen and phosphorus ver 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/c51516c8eca9071862db5becec0f4542.

Fisk, M. 2023. Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE): Net N mineralization at Hubbard Brook Experimental Forest, Bartlett Experimental Forest and Jeffers Brook, central NH USA, 2009–2017 ver 4. Environmental Data Initiative. https://doi.org/10.6073/pasta/826e44994e01aba173fae30115478584.

Fisk, M.C., R.D. Yanai, and T.J. Fahey. 2022. Tree DBH response to nitrogen and phosphorus fertilization in the MELNHE study, Hubbard Brook Experimental Forest, Bartlett Experimental Forest, and Jeffers Brook ver 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/377b1fd44bd88a58e9654ab207e50706.

Fisk, M.C., R.D. Yanai, S.D. Hong, C.R. See, and S. Goswami. 2022. Litter chemistry and masses for the MELNHE N × P fertilization experiment ver 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/8b2975a3a02cbcfb1b0a12ac954576d4.

Hamburg, S.P., R.D. Yanai, and M.A. Vadeboncoeur. 2025. Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE): Leaf area index (LAI), 2004 ver 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/c5aa2fccc8cdd81fa11db6007e9ce959.

Yanai, R.D., M.C. Fisk, M.A. Vadeboncoeur, J.M. Zukswert, T. Mann, A. Young, G. Walsh, M. Morley, and C.R. See. 2024. Mul-

tiple Element Limitation in Northern Hardwood Ecosystems (MELNHE): Litterfall mass 2009–2022 ver 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/e2d437bddf1166a733b0df09c87f89f1.

Yanai, R.D., M. Fisk, and T.J. Fahey. 2024. Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE): Project description, plot characteristics and design ver 2. Environmental Data Initiative. https://doi.org/10.6073/pasta/6cc8a39d052834c030650fb29937bf4f.

Zukswert, J.M., S.D. Hong, K.E. Gonzales, C.R. See, and R.D. Yanai. 2024. Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE): Foliar chemistry 2008–2022 in Bartlett, Hubbard Brook, and Jeffers Brook ver 3. Environmental Data Initiative. https://doi.org/10.6073/pasta/cdf7e7456a8fd43a4e773ad286e4a2ff.

Zukswert, J., K. Gonzales, S. Hong, C. See, B. Quintero, and R.D. Yanai. 2024. Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE): Fresh litter chemistry ver 2. Environmental Data Initiative. https://doi.org/10.6073/pasta/374ae16e29da50e75432871292675e5f.

Author information

Author ORCIDs
R.D. Yanai https://orcid.org/0000-0001-6987-2489

Author contributions
Conceptualization: TJF, MCF, JLB, RDY
Investigation: JLB
Project administration: RDY
Visualization: MCF, KEG, JLB, RDY
Writing – original draft: TJF
Writing – review & editing: MCF, KEG, JLB, RDY

Competing interests
The authors declare there are no competing interests.

Funding information

References

Aber, J.D. 1979. Foliage-height profiles and succession in northern hardwood forests. Ecology, **60**(1): 18–23. doi:10.2307/1936462.

Abrams, M.D. 1998. The red maple paradox. Bioscience, **48**(5): 355–364. doi:10.2307/1313374.

Allison, S.D., and Vitousek, P.M. 2005. Responses of extracellular enzymes to simple and complex nutrient inputs. Soil Biol. Biochem. **37**(5): 937–944. doi:10.1016/j.soilbio.2004.09.014.

Arrigo, K. 2005. Marine microorganisms and global nutrient cycles. Nature, **437**: 309–355. doi:10.1038/nature04159.

Bailey, A.S. 2003. Hydrometeorological database for Hubbard Brook Experimental Forest, 1955–2000 (Vol. 305). US Department of Agriculture, Forest Service, Northeastern Research Station.

Bergmann, J., Weigelt, A., van Der Plas, F., Laughlin, D.C., Kuyper, T.W., Guerrero-Ramirez, N., and Mommer, L. 2020. The fungal collaboration gradient dominates the root economics space in plants. Sci. Adv. **6**(27): eaba3756. doi:10.1126/sciadv.aba3756.

Blanes, M.C., Viñegla, B., Merino, J., and Carreira, J.A. 2013. Nutritional status of Abies pinsapo forests along a nitrogen deposition gradient: do C/N/P stoichiometric shifts modify photosynthetic nutrient use efficiency? Oecologia, **171**: 797–808. doi:10.1007/s00442-012-2454-1.

Blanke, V., Renker, C., Wagner, M., Füllner, K., Held, M., Kuhn, A.J., and Buscot, F. 2005. Nitrogen supply affects arbuscular mycorrhizal colonization of artemisia vulgaris in a phosphate-polluted field site. New Phytol. **166**(3): 981–992. doi:10.1111/j.1469-8137.2005.01374.x.

Bloom, A.J., Chapin, F.S., III, and Mooney, H.A. 1985. Resource limitation in plants-an economic analogy. Annu. Rev. Ecol. Syst. **16**(1): 363–392. doi:10.1146/annurev.es.16.110185.002051.

Blumenthal, N., Stevens, H.M., Goswami, S., Yanai, R.D., Fahey, T.J., and Fisk, M.C. 2025. N and P co-limitation of forest growth in northern hardwood forests. Ecology, In review.

Bormann, F.H., Likens, G.E., Fisher, D.W., and Pierce, R.S. 1968. Nutrient loss accelerated by clear-cutting of a forest ecosystem. Science, **159**(3817): 882–884. doi:10.1126/science.159.3817.882.

Bracken, M.E., Hillebrand, H., Borer, E.T., Seabloom, E.W., Cebrian, J., Cleland, E.E., and Smith, J.E. 2015. Signatures of nutrient limitation and co-limitation: responses of autotroph internal nutrient concentrations to nitrogen and phosphorus additions. Oikos, **124**(2): 113–121. doi:10.1111/oik.01215.

Carstensen, A., Herdean, A., Schmidt, S.B., Sharma, A., Spetea, C., Pribil, M., and Husted, S. 2018. The impacts of phosphorus deficiency on the photosynthetic electron transport chain. Plant Physiol. **177**(1): 271–284. doi:10.1104/pp.17.01624.

Cheeke, T.E., Phillips, R.P., Brzostek, E.R., Rosling, A., Bever, J.D., and Fransson, P. 2017. Dominant mycorrhizal association of trees alters carbon and nutrient cycling by selecting for microbial groups with distinct enzyme function. New Phytol. **214**(1): 432–442. doi:10.1111/nph.14343.

Cleland, E.E., Lind, E.M., DeCrappeo, N.M., DeLorenze, E., Wilkins, R.A., Adler, P.B., and Seabloom, E.W. 2019. Belowground biomass response to nutrient enrichment depends on light limitation across globally distributed grasslands. Ecosystems, **22**: 1466–1477. doi:10.1007/s10021-019-00350-4.

Cleveland, C.C., and Liptzin, D. 2007. C:N:P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? Biogeochemistry, **85**: 235–252. doi:10.1007/s10533-007-9132-0.

Craine, J.M., Morrow, C., and Stock, W.D. 2008. Nutrient concentration ratios and co-limitation in South African grasslands. New Phytol. **179**(3): 829–836. doi:10.1111/j.1469-8137.2008.02513.x.

Davidson, E.A., and Howarth, R.W. 2007. Environmental science: nutrients in synergy. Nature, **449**(7165): 1000. doi:10.1038/4491000a.

Deng, Q., Hui, D., Dennis, S., and Reddy, K.C. 2017. Responses of terrestrial ecosystem phosphorus cycling to nitrogen addition: a meta-analysis. Global Ecol. Biogeogr. **26**: 713–728. doi:10.1111/geb.12576.

Domingues, T.F., Meir, P., Feldpausch, T.R., Saiz, G., Veenendaal, E.M., Schrodt, F., and Diallo, A. 2010. Co-limitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands. Plant Cell Environ. **33**(6): 959–980.

Du, E., Terrer, C., McNulty, S.G., and Jackson, R.B. 2024. Nutrient limitation in global forests: current status and future trends. Future For. 65–74.

Du, E., Terrer, C., Pellegrini, A.F., Ahlström, A., van Lissa, C.J., Zhao, X., and Jackson, R.B. 2020. Global patterns of terrestrial nitrogen and phosphorus limitation. Nat. Geosci. **13**(3): 221–226. doi:10.1038/s41561-019-0530-4.

Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., and Smith, J.E. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol. Lett. **10**(12): 1135–1142. doi:10.1111/j.1461-0248.2007.01113.x.

Elser, J.J., Dobberfuhl, D.R., MacKay, N.A., and Schampel, J.H. 1996. Organism size, life history, and N: P stoichiometry: toward a unified view of cellular and ecosystem processes. Bioscience, **46**(9): 674–684. doi:10.2307/1312897.

Fahey, T.J., Battles, J.J., and Wilson, G.F. 1998. Responses of early successional northern hardwood forests to changes in nutrient availability. Ecol. Monogr. **68**(2): 183–212. doi:10.1890/0012-9615(1998)068%5b0183:ROESNH%5d2.0.CO;2.

Fahey, T.J., Cleavitt, N.L., and Battles, J.J. 2022. Long term variation of leaf abundance in a northern hardwood forest. Ecol. Indic. **137**: 108746. doi:10.1016/j.ecolind.2022.108746.

Fanin, N., Hättenschwiler, S., Chavez Soria, P.F., and Fromin, N. 2016. (A)synchronous availabilities of N and P regulate the activity and structure of the microbial decomposer community. Front. Microbiol. **6**: 1507. doi:10.3389/fmicb.2015.01507.

Farrior, C.E., Tilman, D., Dybzinski, R., Reich, P.B., Levin, S.A., and Pacala, S.W. 2013. Resource limitation in a competitive context determines complex plant responses to experimental resource additions. Ecology, **94**(11): 2505–2517. doi:10.1890/12-1548.1.

Fay, P.A., Prober, S.M., Harpole, W.S., Knops, J.M., Bakker, J.D., Borer, E.T., and Adler, P.B. 2015. Grassland productivity limited by multiple nutrients. Nat. Plants, **1**(7): 15080. doi:10.1038/nplants.2015.80.

Fisk, M., Santangelo, S., and Minick, K. 2015. Carbon mineralization is promoted by phosphorus and reduced by nitrogen addition in the organic horizon of northern hardwood forests. Soil Biol. Biochem. **81**: 212–218. doi:10.1016/j.soilbio.2014.11.022.

Fisk, M.C., Ratliff, T.J., Goswami, S., and Yanai, R.D. 2014. Synergistic soil response to nitrogen plus phosphorus fertilization in hardwood forests Biogeochemistry, **118**(1–3): 195–204. doi:10.1007/s10533-013-9918-1.

Gonzales, K., and Yanai, R. 2019. Nitrogen–phosphorous interactions in young northern hardwods indicate P limitation: foliar concentrations and resorption in a factorial N by P addition experiment. Oecologia, **189**(3): 829–840. doi:10.1007/s00442-019-04350-y.

Gonzales, K.E. 2017. Effects of calcium, nitrogen, and phosphorus fertilization on foliar nutrient dynamics of three northern hardwood tree species. MS Thesis. SUNY College of Environmental Science and Forestry, Syracuse, NY.

Gonzales, K.E., Yanai, R.D., Fahey, T.J., and Fisk, M.C. 2023. Evidence for P limitation in eight northern hardwood stands: foliar concentrations and resorption by three tree species in a factorial N by P addition experiment. For. Ecol. Manage. **529**: 120696. doi:10.1016/j.foreco.2022.120696.

Goswami, S., and Fisk, M.C. 2024. Elevated P availability slows N recycling in northern hardwood forests. For. Ecol. Manage. **570**: 122203. doi:10.1016/j.foreco.2024.122203.

Goswami, S., Fisk, M.C., Vadeboncoeur, M.A., Garrison-Johnston, M., Yanai, R.D., and Fahey, T.J. 2018. Phosphorus limitation of aboveground production in northern hardwood forests. Ecology, **99**(2): 438–449. doi:10.1002/ecy.2100.

Güsewell, S. 2004. N:P ratios in terrestrial plants: variation and functional significance. New Phytol. **164**(2): 243–266. doi:10.1111/j.1469-8137.2004.01192.x.

Güsewell, S., and Koerselman, W. 2002. Variation in nitrogen and phosphorus concentrations of wetland plants. Perspect. Plant Ecol. Evol. Syst. **5**(1): 37–61. doi:10.1078/1433-8319-0000022.

Hamburg, S.P., Yanai, R.D., and Vadeboncoeur, M.A. 2025. Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE): Leaf Area Index (LAI), 2004 ver 1. Environ. Data Initiative. doi:10.6073/pasta/c5aa2fccc8cdd81fa11db6007e9ce959.

Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E., and Smith, J.E. 2011. Nutrient co-limitation of primary producer communities. Ecol. Lett. **14**(9): 852–862. doi:10.1111/j.1461-0248.2011.01651.x.

Hartman, W.H., and Richardson, C.J. 2013. Differential nutrient limitation of soil microbial biomass and metabolic quotients (qCO2): is there a biological stoichiometry of soil microbes? PLoS One, **8**(3): e57127. doi:10.1371/journal.pone.0057127.

Hasselquist, N.J., Metcalfe, D.B., Inselsbacher, E., Stangl, Z., Oren, R., Näsholm, T., and Högberg, P. 2016. Greater carbon allocation to mycorrhizal fungi reduces tree nitrogen uptake in a boreal forest. Ecology, **97**(4): 1012–1022. doi:10.1890/15-1222.1.

Haynes, B.E., and Gower, S.T. 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiol. **15**(5): 317–325. doi:10.1093/treephys/15.5.317.

Hong, D.S., Gonzales, K.E., Fahey, T.J., and Yanai, R.D. 2022. Foliar nutrient concentrations of six northern hardwood species responded to nitrogen and phosphorus fertilization but did not predict tree growth. PeerJ, **10**: e13193. doi:10.7717/peerj.13193.

Johnson, N.C. 2010. Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. New Phytol. **185**(3): 631–647. doi:10.1111/j.1469-8137.2009.03110.x.

Johnson, N.C., Rowland, D.L., Corkidi, L., Egerton-Warburton, L.M., and Allen, E.B. 2003. Nitrogen enrichment alters mycorrhizal allocation at five mesic to semiarid grasslands. Ecology, **84**(7): 1895–1908. doi:10.1890/0012-9658(2003)084%5b1895:NEAMAA%5d2.0.CO;2.

Kaspari, M., and Powers, J.S. 2016. Biogeochemistry and geographical ecology: embracing all twenty-five elements required to build organisms. Am. Nat. **188**(S1): S62–S73. doi:10.1086/687576.

Killingbeck, K.T. 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. Ecology, **77**(6): 1716–1727. doi:10.2307/2265777.

Koerselman, W., and Meuleman, A.F. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. J. Appl. Ecol. 1441–1450. doi:10.2307/2404783.

Kuzyakov, Y. 2002. Factors affecting rhizosphere priming effects. J. Plant Nutr. Soil Sci. **165**(4): 382–396. doi:10.1002/1522-2624(200208)165:4%3c382::AID-JPLN382%3e3.0.CO;2-.

Kuzyakov, Y., and Domanski, G. 2000. Carbon input by plants into the soil. Rev. J. Plant Nutr. Soil Sci. **163**(4): 421–443. doi:10.1002/1522-2624(200008)163:4%3c421::AID-JPLN421%3e3.0.CO;2-R.

Li, L., McCormack, M.L., Chen, F., Wang, H., Ma, Z., and Guo, D. 2019. Different responses of absorptive roots and arbuscular mycorrhizal fungi to fertilization provide diverse nutrient acquisition strategies in Chinese fir. For. Ecol. Manage. **433**: 64–72. doi:10.1016/j.foreco.2018.10.055.

Li, S., Fisk, M.C., Yanai, R.D, and Fahey, T.J. 2023. Co-limitation of root growth by nitrogen and phosphorus in early successional northern hardwood forests. Ecosystems. doi:10.1007/s10021-023-00869-7.

Li, Y., Niu, S., and Yu, G. 2016. Aggravated phosphorus limitation on biomass production under increasing nitrogen loading: a meta-analysis. Global Change Biol. **22**: 934–943. doi:10.1111/gcb.13125.

Mann, T.A., Yanai, R.D., Fahey, T.J., and Reinmann, A.B. 2024. Nitrogen and phosphorus addition affect soil respiration in Northern Hardwood forests. Ecosystems, **27**(6): 765–778. doi:10.1007/s10021-024-00912-1.

Manzoni, S., Taylor, P., Richter, A., Porporato, A., and Ågren, G.I. 2012. Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. New Phytol. **196**(1): 79–91. doi:10.1111/j.1469-8137.2012.04225.x.

Marklein, A.R., and Houlton, B.Z. 2012. Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial ecosystems. New Phytol. **193**(3): 696–704. doi:10.1111/j.1469-8137.2011.03967.x.

Marschner, H., Kirkby, E.A., and Engels, C. 1997. Importance of cycling and recycling of mineral nutrients within plants for growth and development. Bot. Acta, **110**(4): 265–273. doi:10.1111/j.1438-8677.1997.tb00639.x.

McGroddy, M.E., Daufresne, T., and Hedin, L.O. 2004. Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial redfield-type ratios. Ecology, **85**(9): 2390–2401. doi:10.1890/03-0351.

Millard, P., and Grelet, G.A. 2010. Nitrogen storage and remobilization by trees: ecophysiological relevance in a changing world. Tree Physiol. **30**(9): 1083–1095. doi:10.1093/treephys/tpq042.

Naples, B.K., and Fisk, M.C. 2010. Belowground insights into nutrient limitation in northern hardwood forests. Biogeochemistry, **97**(2–3): 109–101. doi:10.1007/s10533-009-9354-4.

Näsholm, T., Högberg, P., Franklin, O., Metcalfe, D., Keel, S.G., Campbell, C., and Högberg, M.N. 2013. Are ectomycorrhizal fungi alleviating or aggravating nitrogen limitation of tree growth in boreal forests?. New Phytol. **198**(1): 214–221. doi:10.1111/nph.12139.

Niinemets, Ü., and Tamm, Ü. 2005. Species differences in timing of leaf fall and foliage chemistry modify nutrient resorption efficiency in deciduous temperate forest stands. Tree Physiol. **25**(8): 1001–1014. doi:10.1093/treephys/25.8.1001.

Olander, L.P., and Vitousek, P.M. 2000. Regulation of soil phosphatase and chitinase activity by N and P availability. Biogeochemistry, **49**(2): 175–191. doi:10.1023/A:1006316117817.

Ostertag, R. 2001. Effects of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. Ecology, **82**(2): 485–499. doi:10.1890/0012-9658(2001)082%5b0485:EONAPA%5d2.0.CO;2.

Phillips, R.P., and Fahey, T.J. 2005. Patterns of rhizosphere carbon flux in sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) saplings. Global Change Biol. **11**(6): 983–995. doi:10.1111/j.1365-2486.2005.00959.x.

Phillips, R.P., Brzostek, E., and Midgley, M.G. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. New Phytol. **199**(1): 41–51. doi:10.1111/nph.12221.

Rastetter, E.B., and Shaver, G.R. 1992. A model of multiple-element limitation for acclimating vegetation. Ecology, **73**(4): 1157–1174. doi:10.2307/1940666.

Rastetter, E.B., Yanai, R.D., Thomas, R.Q., Vadeboncoeur, M.A., Fahey, T.J., Fisk, M.C., and Hamburg, S.P. 2013. Recovery from disturbance requires resynchronization of ecosystem nutrient cycles. Ecol. Appl. **23**(3): 621–642. doi:10.1890/12-0751.1.

Ratliff, T.J., and Fisk, M.C. 2016. Phosphatase activity is related to N availability but not P availability across hardwood forests in the northeastern United States. Soil Biol. Biochem. **94**: 61–69. doi:10.1016/j.soilbio.2015.11.009.

Reed, S.C., Townsend, A.R., Davidson, E.A., and Cleveland, C.C. 2012. Stoichiometric patterns in foliar nutrient resorption across multiple scales. New Phytol. **196**(1): 173–180. doi:10.1111/j.1469-8137.2012.04249.x.

Reiners, W.A. 1986. Complementary models for ecosystems. Am. Nat. **127**(1): 59–73. doi:10.1086/284467.

Richardson, A., and Hollinger, D. 2023. AmeriFlux FLUXNET-1F US-Bar Bartlett Experimental Forest.

Roskowski, J. 1980. Nitrogen fixation in hardwood forests of the northeastern United States. Plant Soil, **54**: 34–44.

Schreiber, F., Littmann, S., Lavik, G., Escrig, S., Meibom, A., Kuypers, M.M., and Ackermann, M. 2016. Phenotypic heterogeneity driven by nutrient limitation promotes growth in fluctuating environments. Nat. Microbiol. **1**(6): 16055. doi:10.1038/nmicrobiol.2016.55.

See, C.R., Yanai, R.D., Fisk, M.C., Vadeboncoeur, M.A., Quintero, B.A., and Fahey, T.J. 2015. Soil nitrogen affects phosphorus recycling: foliar resorption and plant–soil feedbacks in a northern hardwood forest. Ecology, **96**(9): 2488–2498. doi:10.1890/15-0188.1.

Shan, S. 2020. The controls of nutrient limitation on resource allocation belowground. PhD Dissertation. Miami University, Oxford OH USA. Available from http://rave.ohiolink.edu/etdc/view?acc_num=miami1580078025127756 [accessed 2 June 2025].

Shan, S., Devens, H., Fahey, T.J., Yanai, R.D., and Fisk, M.C. 2022 Fine root growth increases in response to nitrogen addition in phosphorus-limited Northern hardwood forests. Ecosystems, **25**: 1589–1600. doi:10.1007/s10021-021-00735-4.

Shan, S., Fisk, M.C., and Fahey, T.J. 2018. Contrasting effects of N and P on rhizosphere processes in two northern hardwood species. Soil Biol. Biochem. **126**: 219–227. doi:10.1016/j.soilbio.2018.09.007.

Sperfeld, E., Raubenheimer, D., and Wacker, A. 2016. Bridging factorial and gradient concepts of resource co-limitation: towards a general framework applied to consumers. Ecol. Lett. **19**(2): 201–215. doi:10.1111/ele.12554.

Sullivan, B.W., Alvarez-Clare, S., Castle, S.C., Porder, S., Reed, S.C., Schreeg, L., and Cleveland, C.C. 2014. Assessing nutrient limitation in complex forested ecosystems: alternatives to large-scale fertilization experiments. Ecology, **95**(3): 668–681. doi:10.1890/13-0825.1.

Thornley, J.H.M. 1991. A transport-resistance model of forest growth and partitioning. Ann. Bot. **68**(3): 211–226. doi:10.1093/oxfordjournals.aob.a088246.

Tierney, G.L., Fahey, T.J., Groffman, P.M., Hardy, J.P., Fitzhugh, R.D., Driscoll, C.T., and Yavitt, J.B. 2003. Environmental control of fine root dynamics in a northern hardwood forest. Global Change Biol. **9**(5): 670–679. doi:10.1046/j.1365-2486.2003.00622.x.

Townsend, A.R., Cleveland, C.C., Asner, G.P., and Bustamante, M.M. 2007. Controls over foliar N:P ratios in tropical rain forests. Ecology, **88**(1): 107–118. doi:10.1890/0012-9658(2007)88%5b107:COFNRI%5d2.0.CO;2.

Treseder, K.K., and Allen, M.F. 2002. Direct nitrogen and phosphorus limitation of arbuscular mycorrhizal fungi: a model and field test. New Phytol. **155**(3): 507–515. doi:10.1046/j.1469-8137.2002.00470.x.

Vadeboncoeur, M.A. 2010. Meta-analysis of fertilization experiments indicates multiple limiting nutrients in northeastern deciduous forests. Can. J. For. Res. **40**(9): 1766–1780. doi:10.1139/X10-127.

Vadeboncoeur, M.A., Hamburg, S.P., Blum, J.D., Pennino, M.J., Yanai, R.D., and Johnson, C.E. 2012. The quantitative soil pit method for measuring belowground carbon and nitrogen stocks. Soil Sci. Soc. Am. J.doi:10.2136/sssaj2012.0111.

Vergutz, L., Manzoni, S., Porporato, A., Novais, R.F., and Jackson, R.B. 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecol. Monogr. **82**(2): 205–220. doi:10.1890/11-0416.1.

Vitousek, P.M., Porder, S., Houlton, B.Z., and Chadwick, O.A. 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. Ecol. Appl. **20**(1): 5–15. doi:10.1890/08-0127.1.

Walker, T.W., and Syers, J.K. 1976. The fate of phosphorus during pedogenesis. Geoderma, **15**(1): 1–19. doi:10.1016/0016-7061(76)90066-5.

Walworth, N.G., Fu, F.X., Webb, E.A., Saito, M.A., Moran, D., McIlvin, M.R., and Hutchins, D.A. 2016. Mechanisms of increased Trichodesmium fitness under iron and phosphorus co-limitation in the present and future ocean. Nat. Commun. **7**: 12081. doi:10.1038/ncomms12081.

Weintraub, M.N., and Schimel, J.P. 2003. Interactions between carbon and nitrogen mineralization and soil organic matter chemistry in arctic tundra soils. Ecosystems, **6**(2): 0129–0143. doi:10.1007/s10021-002-0124-6.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., and Villar, R. 2004. The worldwide leaf economics spectrum. Nature, **428**(6985): 821–827. doi:10.1038/nature02403.

Wright, S.J., Yavitt, J.B., Wurzburger, N., Turner, B.L., Tanner, E.V., Sayer, E.J., et al. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology, **92**(8): 1616–1625. doi:10.1890/10-1558.1.

Wurzburger, N., and Wright, S.J. 2015. Fine-root responses to fertilization reveal multiple nutrient limitation in a lowland tropical forest. Ecology, **96**(8): 2137–2146. doi:10.1890/14-1362.1.

Wutzler, T., Zaehle, S., Schrumpf, M., Ahrens, B., and Reichstein, M. 2017. Adaptation of microbial resource allocation affects modelled long term soil organic matter and nutrient cycling. Soil Biol. Biochem. **115**: 322–336. doi:10.1016/j.soilbio.2017.08.031.

Yan, Z., Tian, D., Han, W., Tang, Z., and Fang, J. 2017. Assessment on the uncertainty of the nitrogen to phosphorus ratio as a threshold for nutrient limitation in plants. Ann. Bot. **120**: 937–942. doi:10.1093/aob/mcx106.

Yanai, R.D., Fisk, M.C., Vadeboncoeur, M.A., Zukswert, J.M., Mann, T., Young, A., et al. 2024. Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE): litterfall mass 2009-2022 ver 1. Environ. Data Initiative. doi:10.6073/pasta/e2d437bddf1166a733b0df09c87f89f1.

Yanai, R.D., Park, B.B., and Hamburg, S.P. 2006. The vertical and horizontal distribution of roots in northern hardwood stands of varying age. Can. J. For. Res. **36**(2): 450–459. doi:10.1139/x05-254.

You, C., Peng, C., Xu, Z., Liu, Y., Zhang, L., Yin, R., et al. 2021. Nitrogen addition mediates the response of foliar stoichiometry to phosphorus addition: a meta-analysis. Ecol. Processes, **10**: 58. doi:10.1186/s13717-021-00329-x.

Zhang, J., and Elser, J. 2017. Carbon:nitrogen:phosphorus stoichiometry in fungi: a meta-analysis. Front. Microbiol. **8**: 1281. doi:10.3389/fmicb.2017.01281.

Zukswert, J.M., Fahey, T.J., Vadeboncoeur, M.A., Hong, D.S., and Yanai, R.D. 2025b. Changes in foliar chemistry and nutrient resorption in northern hardwood forests in response to long-term experimental nitrogen and phosphorus addition. Oikos, e10867. doi:10.1111/oik.10867.

Zukswert, J.M., Vadeboncoeur, M.A., Fahey, T.J., and Yanai, R.D. 2025a. Treatment effects of nitrogen and phosphorus addition on foliar traits in six northern hardwood tree species. Oecologia, **207**: 23. doi:10.1007/s00442-025-05664-w.