Canadian Journal of
Forest Research

Cross-site comparison of ecosystem nutrient cycling in hardwood and conifer forests on contrasting soils

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Abstract

In the northeastern United States, both hardwood and conifer forests have developed on sites with contrasting soils, allowing an examination of the effect of site and forest type on ecosystem nutrient cycling. We measured biomass production and nutrient fluxes in northern hardwood and conifer stands at three sites differing in soil fertility. We found that leaf, root, and wood concentrations of calcium (Ca), magnesium (Mg), and potassium reflected differences in soil base cation availability, while concentrations of nitrogen (N) and phosphorus (P) were more consistent across sites. Nutrient uptake was calculated as the sum of litterfall, net throughfall (throughfall minus precipitation), root turnover, and accumulation in perennial tissues (wood). We propose a novel metric of nutrient cycling, the nutrient retention fraction (NRF), defined as the proportion of annual nutrient uptake retained in biomass accretion. Because the NRF is unitless, it can be compared across nutrients; Ca and Mg had the highest NRF and P the lowest ($p = 0.05$). Across sites and elements, NRFs were lower for conifers (5.0 ± 0.6%) than for hardwoods (7.2 ± 0.5%), associated with their lower productivity. Nutrient-use efficiency (biomass production divided by nutrient uptake) tended to be high where foliar concentrations indicated low availability of that nutrient. Nutrient retention of N and P was higher where availability of the other element was high, which could be a mechanism contributing to N and P co-limitation.

Key words: Hubbard Brook, Sleepers River, Cone Pond, ecosystem budget, NUE

Introduction

Forests provide a key ecosystem service in their regulation of the carbon cycle, and primary production is central to this service (Malhi et al. 2002). The productivity of forests is under threat worldwide for myriad reasons, including changes in soil resource availability (Fernandez-Martinez et al. 2014). Soil fertility constrains the primary productivity of most forests. In humid, cold temperate regions such as northeastern North America where soil moisture is usually adequate, mineral nutrients are more likely to be limiting than water, and nitrogen (N) availability has been regarded as the primary factor controlling forest productivity under pristine conditions (Lebauer and Treseder 2008). However, human activities have altered soils to the extent that other nutrients may be limiting or co-limiting forest productivity, due to atmospheric N deposition (Driscoll et al. 2001), soil base cation depletion by acid deposition (Driscoll et al. 2001), and repeated forest harvest and land-use changes (Hamburg et al. 2003). Forest fertilization experiments suggest that productivity of various northeastern forests is limited by N (Finzi 2009; Vadeboncoeur 2010) or phosphorus (P) (Goswami et al. 2018), co-limited by N and P (Vadeboncoeur 2010; Blumenthal et al. 2025), or limited by base cations, especially calcium (Ca) (Long et al. 2009; Battles et al. 2014*b*) or potassium (K) (Heiberg and White 1951; Nowak et al. 1991). An improved understanding of the responses of forest production to changing soil fertility is needed to guide management decisions.

Building on the assumption that the traits of plants have evolved to alleviate resource scarcity (Bloom et al. 1985), early work suggested that the efficiency of nutrient use in plant production should be inversely related to the rate of supply of that nutrient (Miller et al. 1976). A variety of indices of nutrient-use efficiency (NUE) have been devised to evaluate this hypothesis, especially for N and P, with some conflicting results (Vitousek 1982; Berendse and Aerts 1987; Knops et al. 1997). Analogous to water-use efficiency (WUE $= \frac{\text{carbon assimilation}}{\text{water loss or uptake}}$), the most straightforward expression for NUE relates net primary productivity to plant nutrient uptake

(Stanhill 1986) (NUE $= \frac{\text{carbon assimilation}}{\text{nutrient loss or uptake}}$) (Hawkesford et al. 2016). This ratio can also be viewed as the product of nutrient productivity (carbon assimilation per unit nutrient stock) and residence time of the nutrient in vegetation (Berendse and Aerts 1987). Several mechanisms could contribute to high forest NUE. Some of these relate to retention of absorbed nutrients, such as low leaching of foliar nutrients in throughfall and high resorption of nutrients prior to tissue senescence (Aerts 1996). Others relate to the efficiency of production, such as the rate of carbon assimilation relative to foliar nutrient concentrations, the proportion of absorbed nutrients allocated to foliage, and lifespans of foliage (Gray 1983). However, trade-offs among traits could limit the ability of plants to maximize NUE on low fertility sites (Berendse and Aerts 1987); for example, high mean photosynthetic rate per unit leaf N may be incompatible with high residence time of foliar N. Knops et al. (1997) indicated that NUE was either unrelated to site fertility or even maximized in intermediate and high fertility sites.

The evidence that the productivity of humid forests may be limited by different or multiple soil nutrients on different sites presents a challenge to traditional approaches to the characterization of NUE. The biogeochemical cycles of the macronutrients N, P, Ca, magnesium (Mg) and K differ with respect to mechanisms that control NUE. For example, foliar resorption of P is more plastic than that of N (See et al. 2015). Little or no resorption of Ca occurs from senescing foliage, while retention of K in foliage is poor due to its ionic state (Likens et al. 1994). The allocation of the various macronutrients to foliage versus roots also differs markedly for functional reasons; K and P are disproportionately represented in foliage in comparison to N, with Ca being intermediate (Whittaker et al. 1979). New approaches to characterizing nutrient cycling that recognize these differences might provide useful insights into the nature of forest responses to nutrient limitation.

We propose a novel metric for evaluating forest nutrient cycling, the nutrient retention fraction (NRF), defined as the proportion of annual nutrient uptake retained in perennial tissues (NRF $= \frac{\text{nutrient accumulation}}{\text{nutrient uptake}}$). High NRF can result from efficient nutrient use—high productivity per unit nutrient uptake (NUE)—but also from inefficient use, such as low nutrient resorption from heartwood. NRF is thus related to, but distinct from, NUE. Because both the numerator and the denominator of NRF are in units of annual nutrient fluxes per unit area, this index is unitless, which means that NRF can be compared across nutrients, reflecting the stoichiometry of litterfall, throughfall, and root turnover—and thus nutrient uptake.

The purpose of this study was to construct ecosystem nutrient budgets and compare NUE and NRF in a suite of northern hardwood and conifer ecosystems at three research sites on soils with markedly different soil base cation status in the northeastern USA. Aboveground and belowground productivity, previously reported from these stands, exhibited a two-fold and a four-fold range, respectively, and root production (estimated as biomass times turnover) was significantly higher in sites with higher soil base cations (Park et al. 2008). We compiled information on nutrient cycling in these stands to compare tissue concentrations, estimate nutrient fluxes in the hardwood and conifer stands across the fertility gradient, and evaluate both the efficiency of nutrient use and the accumulation of nutrients indicated by NRF.

We expected that the differences in biogeochemical behavior among the macronutrients would result in contrasting patterns in the degree to which they are cycled through vegetation relative to incorporation into new tissues. We hypothesized that NUE would reflect differences in nutrient availability across the sites, as indicated by foliar nutrient concentrations and soil stores. We hypothesized that NRF would differ by element in ways that reflect their biogeochemical behaviors. For example, we predicted that more mobile nutrients, such as K, would exhibit relatively lower NRF due to high turnover, and that the most limiting nutrients, N and P, would show higher NRF than nonlimiting nutrients. Finally, we predicted that conifers would have higher NRF than hardwoods, because of high nutrient retention in long-lived foliage and thus low nutrient turnover.

Methods

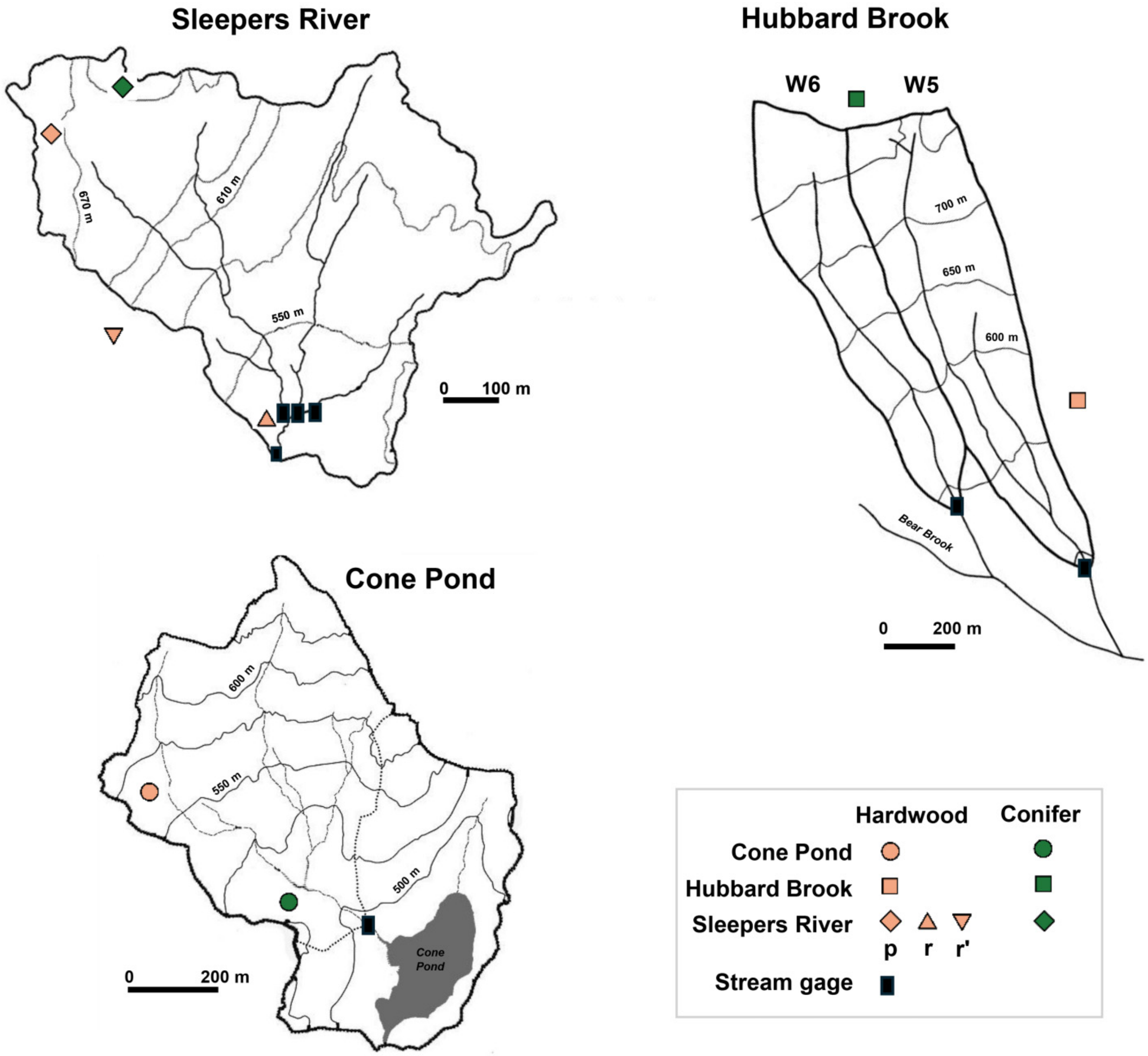
Site descriptions

We studied productivity and nutrient cycling in three sites in the northeastern USA, Cone Pond, Hubbard Brook, and Sleepers River (Fig. 1), which differ in parent material and soils but are similar in many other respects (Park et al. 2008). The climate at all three sites is humid continental, with mean annual precipitation ranging from 1150 to 1370 mm·year^{-1}. Monthly air temperature ranges from –9 to 20 °C. Latitude ranges from 43.90 N (Cone Pond) to 44.48 N (Sleepers River) and the sites are separated by at most 65 km. Elevations of our study plots ranged from 514 to 750 m (Table 1).

The vegetation includes both hardwood and conifer stands at each site (Table 1). The dominant hardwoods include sugar maple (*Acer saccharum* Marsh.); yellow birch (*Betula alleghaniensis* Britton); American beech (*Fagus grandifolia* Ehrh.), especially at Cone Pond and Hubbard Brook; and white ash (*Fraxinus americana* L.) at the richer stands at Sleepers River. Conifer stands include red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* (L.) Mill.) at all sites, eastern hemlock (*Tsuga canadensis* (L.) Carr.) at Cone Pond, and an admixture of white birch (*Betula papyrifera* Marsh.) and yellow birch at Hubbard Brook and Sleepers River. The forests are mature and near steady-state for live biomass at all sites, the most relevant disturbances being harvesting ∼1910 and hurricane blowdown in 1938 (Hubbard Brook), harvesting ∼1929 (Sleepers River), and a hurricane in 1810 followed by extensive fire ∼1820 (Cone Pond).

All three sites have sandy loam soils developed in glacial till developed from schist and granite. Shallow soils and exposed bedrock are much more prevalent at Cone Pond than at the other two watersheds. The prevalence of shallow soils has a strong influence on runoff chemistry (Bailey et al. 2019). Both Cone Pond and Hubbard Brook are underlain by noncalcare-

Fig. 1. Maps of the three study sites showing the locations of the sampled forest stands. Each site has one hardwood and one conifer stand, except that Sleepers River has three hardwood stands, designated p (poor) and r and r′ (rich). Contours show elevations in meters above sea level. The Cone Pond boundary depicts the larger watershed including the pond, whereas the gaged study watershed is a smaller area upstream of the gage. (Reprinted from Byung Bae Park et al. (2008) with permission from Springer Nature.)



ous schists whereas Sleepers River is underlain by calcareous schist. Soils were characterized by genetic horizon in 2003 (Fig. 2; Table 1) as described in detail by Park et al. (2008); these data are published (Bailey 2024*a*, 2024*b*; Shanley et al. 2025). Stream chemistry reflects these differences in soils and bedrock, with a stream pH of 4.4 at Cone Pond, 5.0 at Hubbard Brook, and 7.6 at Sleepers River (Hornbeck et al. 1997). Stream water Ca export was 3.6 at Cone Pond, 7.1 at Hubbard Brook, and 140 kg/ha/year at Sleepers River (Hornbeck et al. 1997).

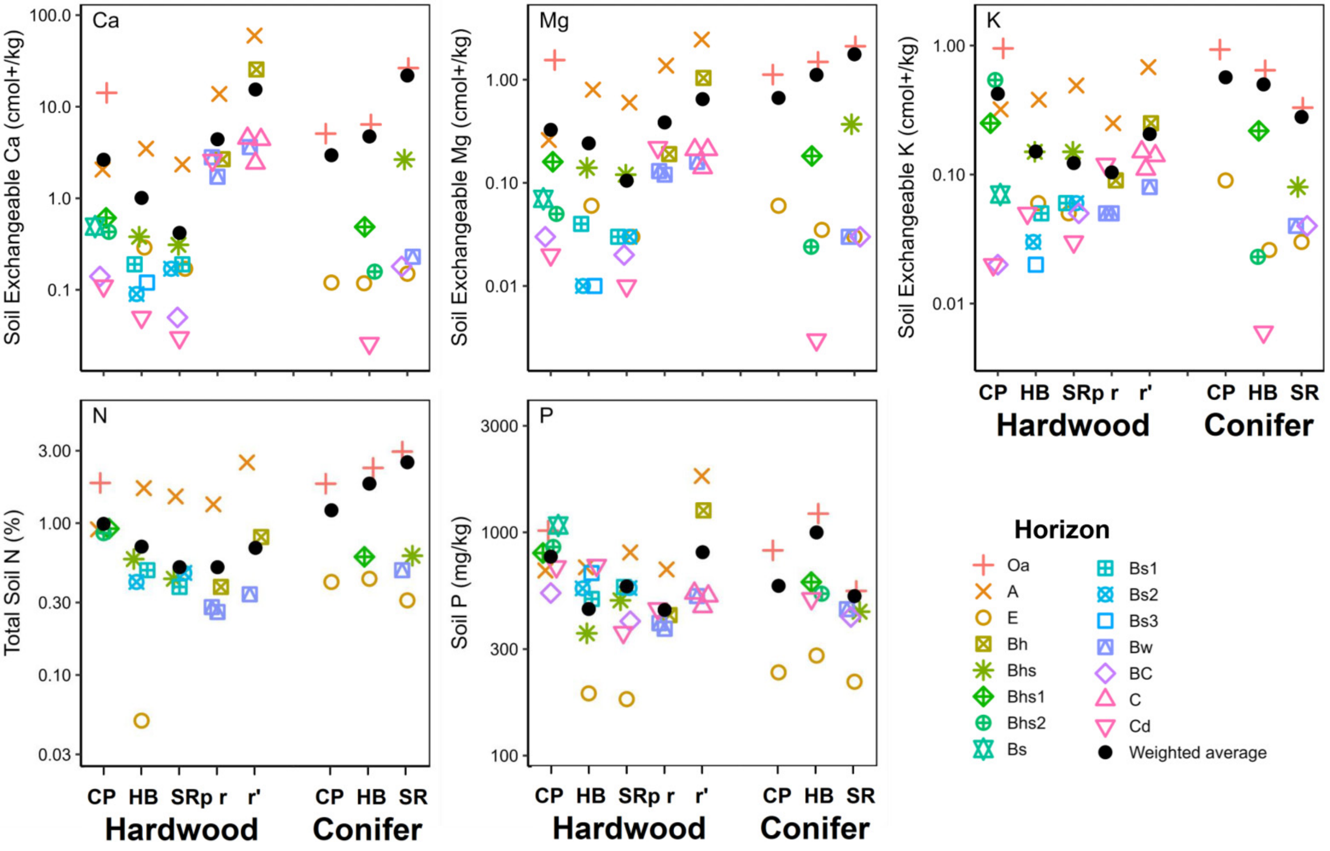
The layout of sample plots in the various sites has been described in detail (Park et al. 2008). Briefly, previously established research plots were used for sampling in each stand, and plot layout (i.e., plot size and shape) differed among sites. At Sleepers River, three hardwood stands and one conifer stand were studied, each with a 0.1 ha plot. The conifer stand and one of the hardwood stands (the “poor” hardwood stand, SRp) were located on better drained sites with less groundwater influence while the other two hardwood stands (the “rich” stand, SRr, and a second rich stand, SRr′) were on less well drained sites influenced by high pH and high Ca in groundwater, resulting in striking contrasts in soil base cation status (Table 1); soil N and P concentrations were more uniform (Fig. 2). At Hubbard Brook Experimental Forest, measurements were taken in and around the reference watershed (W6) where intensive, long-term inventories of tree growth were available in both northern hardwood and conifer stands (Battles et al. 2014*a*, 2014*b*). At Cone Pond, hardwood and conifer stands were surveyed with several 0.04 ha plots (Park et al. 2008).

Table 1. Characteristics of stands in the three sites.

Site	Forest type	Elevation (m)	Dominant species based on basal area	Hor	pH	Ca Mg K (cmol+/kg)			N (%)
Cone Pond	Hardwood	578	*Fagus grandifolia*, *Acer saccharum*, *Betula alleghaniensis*	A	2.9	2.1	0.26	0.32	0.9
				Bhs	3.5	0.6	0.16	0.25	0.9
	Conifer	514	*Tsuga canadensis*, *Picea rubens*, *Abies balsamea*, *A. rubrum*	Oa	2.9	5.1	1.12	0.93	1.8
				E	3.0	0.1	0.06	0.09	0.4
Hubbard Brook	Hardwood	610	*A. saccharum*, *F. grandifolia*, *B. alleghaniensis*	A	3.2	3.5	0.80	0.38	1.7
				Bs	3.9	0.2	0.04	0.05	0.5
	Conifer	770	*P. rubens*, *A. balsamea*, *B. alleghaniensis*, *B. papyrifera*	Oa	2.8	5.4	1.49	0.64	2.3
				Bhs	3.3	0.5	0.18	0.22	0.6
Sleepers River	Hardwood (poor)	653	*F. grandifolia*, *P. rubens*, *B. alleghaniensis*	A	4.7	2.3	0.60	0.49	1.5
				Bs	4.1	0.2	0.03	0.06	0.4
	Hardwood (rich)	543	*T. canadensis*, *P. rubens*, *B. alleghaniensis*	A	3.9	13.8	1.37	0.25	1.3
				Bw	4.6	1.7	0.13	0.05	0.3
	Conifer	666	*P. rubens*, *A. balsamea*, *A. rubrum*, *B. alleghaniensis*, *B. papyrifera*	Oa	2.9	26.4	2.11	0.33	3.0
				Bhs	3.4	2.7	0.37	0.08	0.6

Note: Dominant species are listed in declining order of basal area. Soils characteristics are given for the Oa (conifer) or A (hardwoods) horizon and the mineral soil horizon closest to 15 cm depth. Forest composition and soil characteristics are reported in more detail by Park et al. (2008), Bailey (2024*a*, 2024*b*), and Shanley et al. (2025).

Fig. 2. Soil nutrient concentrations by horizon in hardwood and conifer stands at Cone Pond (CP), Hubbard Brook (HB), and Sleepers River (SR). SR has three hardwood stands, designated p (poor) and r and r′ (rich). At some stands, multiple Bh, Bs, and C horizons were distinguished (Bailey 2024*a*, 2024*b*; Shanley et al. 2025). The average concentrations were weighted by the observed density of roots by depth in each stand. Note varying log scales.



As described below, soils, foliage, and roots were sampled across all three sites by uniform methods within a short time period (2000–2003) by the same investigators. Biomass increment (up to 2002–2003, depending on the site) and root turnover (2003–2005) were also characterized at about that time. The greatest discrepancies in methods and timing were for throughfall and litterfall. Litterfall, which is the larger flux for most elements, is remarkably consistent over time (Knapp and Smith 2001, including data from Hubbard Brook).

Tissue nutrient concentrations

Leaves

In each stand, foliage was sampled from three to six healthy dominant or codominant trees of the principal species (Yanai et al. 2025). A mid-crown sample of sun-exposed leaves was obtained from each tree during the last 2 weeks of August 2000, 2001, or 2002. Foliage samples were collected by shooting small branches from the periphery of the crown with a shotgun. Samples were ground and oven dried at 70 °C, then digested using a microwave-assisted acid digestion procedure (EPA Method 3052 1996) and analyzed for aluminum (Al), P, K, Ca, Mg, and manganese (Mn) by inductively coupled plasma (ICP) spectroscopy. A NIRSystems spectrophotometer was used to measure N concentrations (Bolster et al. 1996). National Institute of Standards and Technology pine needles were used as a reference standard. Recovery of certified elements ranged from 90% for Al to 108% for Ca. Repeatability of determinations for both standards and duplicate samples, expressed as the relative difference (maximum value minus minimum value expressed as a percentage of the mean) was usually less than 3%; the relative difference for duplicate samples was 6%.

Roots

Fine roots (<2 mm in diameter) were sampled in 2003, as described by Park et al. (2008). Four soil cores were collected to 35 cm depth from each of five plots in each stand, corresponding with the minirhizotron locations used to measure root turnover (described below). The cores were divided into increments by depth, and composited by depth increment. Roots were picked from the cores, and live roots were divided into 0–0.5, 0.5–1, and 1–2 mm diameter classes. Dead roots 0–2 mm were not divided by size class. The sorted roots were oven-dried at 65 °C and weighed. The distribution of root biomass with depth has been reported in detail (Park et al. 2008). Roots from all depths were combined by diameter class within each plot for analysis of tissue chemistry. For each diameter class, two samples, each a composite of two plots, were analyzed from each stand.

Before chemical analysis, roots were agitated in a plastic container with deionized water for 10 s to remove soil and organic particles from the surface of the roots. Nutrient losses during brief washing are not a significant source of error (Böhm 1979). Washed samples were ground in a Wiley mill using a 1 mm screen. A subsample was ground using a Wig-L-Bug and analyzed using a carbon-N elemental analyzer (Model NC2001). Another subsample was ashed at 470 °C, and the ash was weighed; we report root biomass on an ash-free basis. The ash was then digested in 6 N HCl. Concentrations of P, K, Ca, Mg, and K were determined by ICP emission spectroscopy (Perkin Elmer Optima 3300DV ICP-optical emission spectrometry (OES)). Other elements we measured (Al, Mn, iron, copper, and zinc) are reported in the associated data package (Yanai et al. 2025).

Wood and branches

Unlike leaves and roots, wood and branches were sampled by methods that differed among sites. At Hubbard Brook, tree tissues were first sampled in 1966 (Likens and Bormann 1970). Light-colored bole wood was sampled separately from heartwood or darkwood; we used the values for lightwood, which best correspond to the wood samples taken at Cone Pone and Sleepers River. We used more recent data from sugar maple, yellow birch, and American beech logs collected in 1990 and 1991 (Johnson et al. 2014), from red spruce, balsam fir, and paper birch cored in 1994 (Arthur et al. 1999), and from red maple, ash, and red spruce trees (Scanlon et al. 2022) cored by Matt Vadeboncoeur from 2011 to 2017, because these were reported with greater precision than the earlier data. The branch data, however, are entirely from Likens and Bormann (1970).

Tree tissues were sampled at Cone Pond in the summer of 1990 (Bailey et al. 1996). Two trees of each of three hardwood species (sugar maple, yellow birch, and American beech) were sampled in the area of the hardwood plots and two trees of each of three conifer species (red spruce, balsam fir, and eastern hemlock) were sampled near the conifer plot. Branches were collected from the mid-crown with a telescoping pruner. Wood samples 8–10 cm long were collected with a 13 mm diameter increment borer. Two replicate samples were collected for each tissue type from each tree. These samples were ground in a Wiley mill to 40 mesh, oven dried at 70 °C, and 0.1 g of each sample digested in a block digester at 400 °C with H_2SeO_3, H_2SO_4, and H_2O_2 (Issac and Johnson 1976, as modified by Hislop et al. 1998). Cations (Ca, Mg, and K) were measured on a Smith-Hieftje 12 Flame Atomic Absorption Spectrophotometer (Thermo Jarrell Ash Co.) and N and P were measured on an autoanalyzer (Technicon Industrial Method No. 329-74 W/A). Four wood samples that were below detection for P were analyzed again in 2019 by the methods used for foliage.

Wood samples were collected at Sleepers River in September 2010 by coring four trees of the major species in the conifer stand and the “poor” and “rich” hardwood stands; the cores were composited by stand and species before analysis. Branches were not sampled at Sleepers River. The wood samples were analyzed for N by using a Thermo Scientific Flash EA 1112 Elemental Analyzer (Thermo Fisher Scientific, Delft, the Netherlands). For Ca, Mg, K, and P, samples were ashed at 470 °C and digested in 6 N nitric acid. The solutions were filtered, diluted to 50 mL, and analyzed using ICP-OES (PE-3300DV, Perkin Elmer, Shelton, CT).

Nutrient fluxes

Litterfall and throughfall

At Hubbard Brook, litterfall was first measured in 1968–1969 (Gosz et al. 1972). We used these data for the conifer stand. We collected hardwood litterfall from 1998 to 1999 and 2001 to 2003 from intensive plots located to the west of W6 (Battles et al. 2014*b*) and measured litter chemistry by methods described for leaves. Throughfall was measured from 1989 to 1992 at Hubbard Brook in the same plots for the growing season only (defined as 1 June to 30 September at all three sites) (Lovett et al. 1996). These early measurements did not include P, which was measured in throughfall for five events in 2007 in hardwood and conifer stands (Fuss 2009) and scaled up to growing-season fluxes. Note that throughfall N fluxes at all the sites exclude the organic fraction.

At Sleepers River, litterfall was collected from 2002 to 2004 in each stand. Litterfall was collected for chemical analysis in 2004 and these concentrations were applied to the average mass. Throughfall was collected in 2003 and 2004 for the growing season only. Ammonium was not reported, but Ryan et al. (2021) found that NH4 was generally below the detection limit of 0.01 ppm. P was not measured in those samples but was measured for multiple events in 2017–2018 near the "rich" stand and scaled up to the growing season. For the stands without throughfall P estimates, we used the average throughfall N:P (3.6) for the three stands with throughfall P measurements to estimate throughfall P.

At Cone Pond, litterfall and throughfall were collected for 3 years, from 1991 to 1993. P was not measured, but estimated from N flux, as at Sleepers River. At this site, throughfall was collected year-round, which was used to estimate dormant-season fluxes at the other sites. In the conifer stand, 61% of throughfall nutrient flux, on average (for NO_3, Ca, Mg, K) occurred in the dormant season, which was close to the value of 63% in the open, whereas a smaller fraction (51%, on average) fell in the dormant season in the hardwood stand, due to greater canopy leaching in the growing season. We used these ratios to estimate dormant-season throughfall fluxes in the other sites, for conifer and hardwood stands, respectively.

Net throughfall is the relevant flux for estimating nutrient uptake by trees, which was calculated as the difference between gross throughfall and open precipitation.

Root turnover

Fine root (<1 mm in diameter) production was based upon measured fine root biomass (described above) and minirhizotron observations of fine root turnover, as reported by Park et al. (2008). The minirhizotron measurements were conducted with a network of five tubes in each stand for 1 year of observations following a conditioning period of at least 1 year. This estimate was augmented with values for 1–2 mm roots, by assuming a turnover rate of 0.2 per year (Fahey et al. 2012). Nutrient turnover in roots was calculated as the product of root biomass turnover and root nutrient concentration. Note that these estimates exclude turnover of large woody roots, which we did not measure at our sites and which remains poorly described globally.

Nutrient accumulation, turnover, and uptake

Annual nutrient accumulation in aboveground live biomass was calculated as the product of accumulation of aboveground live biomass (based on allometric estimates; Park et al. 2008) and the nutrient concentrations in wood, because about 90% of aboveground biomass accumulation is in wood, the rest being mostly bark (Whittaker et al. 1974). Because not every species was sampled in every stand, concentrations for minor species were estimated by substituting values from congeneric or similar species at similar stands. For the second "rich" stand at Sleepers River, where wood was not sampled, we used concentrations from the first "rich" stand.

Nutrient turnover was calculated as the sum of nutrient fluxes in litterfall, net throughfall (throughfall minus precipitation), and root turnover.

Nutrient uptake was calculated as the sum of annual nutrient accumulation in live biomass plus annual nutrient turnover.

Nutrient-use efficiency and nutrient retention fraction

We report NUE as conventionally defined, as a ratio of biomass production to nutrient use (annual nutrient uptake). For biomass production, we used annual biomass increment plus annual turnover of ephemeral tissues (litterfall plus fine roots < 2 mm diameter).

We also report a novel metric, the NRF, in units that can be compared among nutrients. The NRF compares nutrient accumulation in living biomass to nutrient uptake; for this fraction, both the numerator and denominator are in units of annual nutrient flux.

Data analysis

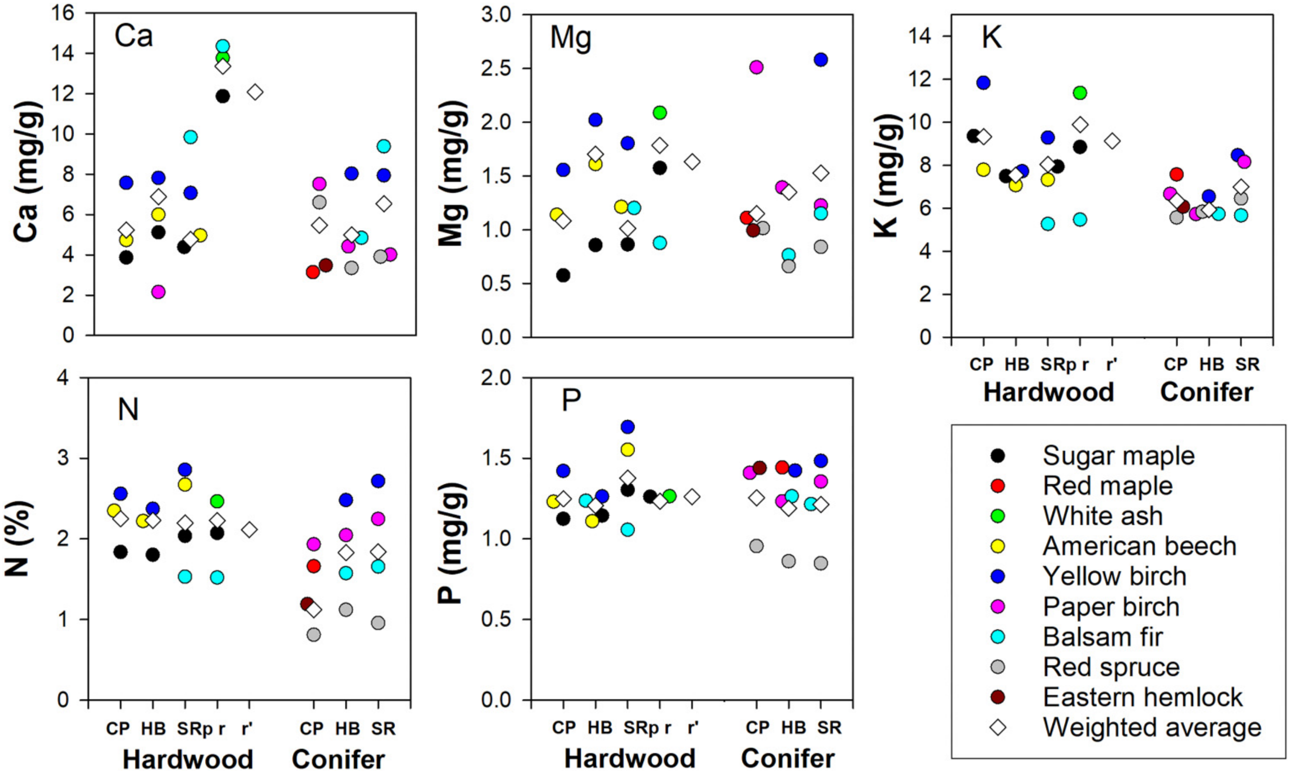
All analyses were performed using R version 4.3.2 (R Core Team 2023). We used analyses of variance (ANOVAs) to test for differences across the three sites (Cone Pond, Hubbard Brook, and Sleepers River) and two forest types (hardwood and conifer) in the following response variables: mass and nutrient fluxes in litterfall, mass and nutrient fluxes in root turnover, nutrient uptake, NUE, and NRF.

Nutrient fluxes were evaluated separately for each element, while NRF included element (Ca, Mg, K, N, P) as an additional factor. An interaction term between site and forest type was included unless the P value for this term was >0.20 (Stehman and Meredith 1995). Main effects of site and forest type and their interactions were explored graphically using the "effects" package (Fox and Weisberg 2019). Main effects were considered significant and reported at $P \leq 0.10$.

To generate a single estimate of soil nutrient availability for each element for each stand, we weighted soil concentrations by the fraction of fine root (<2 mm) biomass density in each horizon described by linear regression as reported by Park et al. (2008). For foliar concentrations, we weighted species by the proportion of basal area reported by Park et al. (2008).

We used linear regression to describe, for each nutrient, the relationships between nutrient cycling variables (nutrient turnover, NUE, and NRF) and the availability of the same nutrient (soil nutrient status and foliar nutrient concentrations). For N and P, we also tested relationships between nu-

Fig. 3. Nutrient concentrations of leaves by species in hardwood and conifer stands at Cone Pond (CP), Hubbard Brook (HB), and Sleepers River (SR). Foliage was collected at the poor (p) and rich (r) hardwood stand at SR. The average foliar concentration for each stand was weighted by the basal area of species at that stand, using estimates from other stands or species for the species not sampled at a particular site.



trient cycling variables (NUE and NRF) and the availability of the opposite nutrient (in soil and foliage). Linear regression was performed using “geom_smooth” with the method “lm” in the “ggplot2” package (Wickham 2016). Model fit and coefficient significance were assessed using the “summary” function.

Statistical power was low, with only one nutrient budget for each combination of site and forest type, with the exception of the multiple hardwood stands at Sleepers River. We describe only the most significant effects in the text; details of insignificant effects can be found in Yanai et al. (2025).

Results

Tissue nutrient concentrations

Foliage

Foliar nutrient concentrations exhibited two- to three-fold variation across stands and species (Fig. 3). For most elements, the variation across sites within species was greater than the variation within sites across species, except for Ca, which had high variability for both (coefficients of variations of 33% for both sources).

As expected, conifers generally had lower foliar nutrient concentrations than hardwoods. Foliar Ca was particularly high in the base-rich stand at Sleepers River. K in hardwood foliage was higher at Cone Pond than the other sites; there was less difference in K concentrations of foliage among the conifers. Among the macronutrients, P exhibited the lowest variation among species and stands.

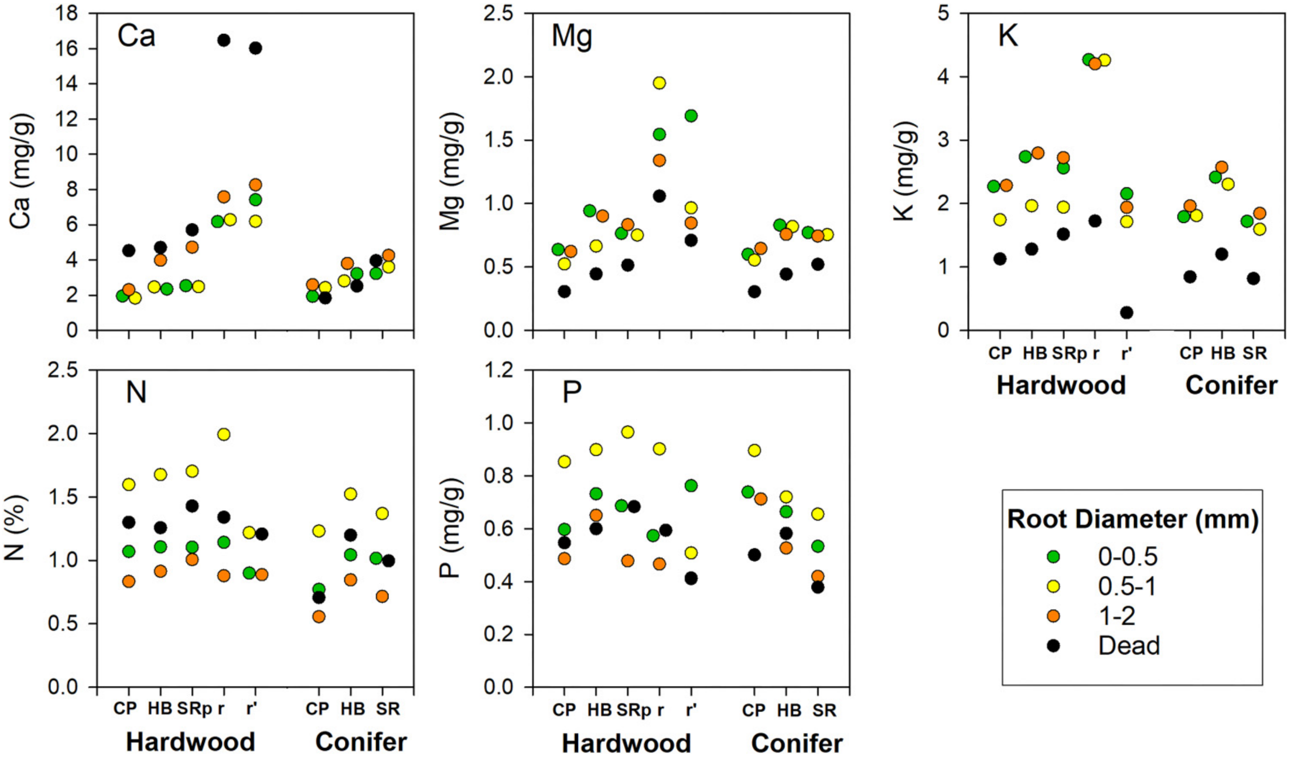
Roots

Differences in root chemistry across sites were consistent with the patterns observed in leaves: the base cations Ca, Mg, and K reflected the nutrient gradient, with the highest concentrations in roots observed at the base-rich Sleepers River stands (Fig. 4). Variation in root chemistry among stands was lower for N and P than for base cations.

Root chemistry varied considerably among diameter classes. Specifically, Ca, Mg, and K were higher in coarser roots (1–2 mm in diameter), while these roots had the lowest concentrations of N and P. Surprisingly, the finest roots (<0.5 mm) were often intermediate in concentration between the 0.5–1 mm roots and the 1–2 mm roots. For N and P, the 0.5 1 mm diameter class had the highest concentrations at all the sites.

Dead roots were not distinguished by species or by size class. For N and P, dead root concentrations were consistent with a weighted average of live root concentrations, which supports our assumption that nutrient resorption from senescing roots is negligible. Dead roots contained high concentrations of Ca but low concentrations of Mg and especially K, compared to live roots. The high concentrations for Ca in dead roots at the base-rich stands at Sleepers River are

Fig. 4. Nutrient concentrations of roots by diameter class in hardwood and conifer stands at Cone Pond (CP), Hubbard Brook (HB), and Sleepers River (SR). SR has three hardwood stands, designated p (poor) and r and r′ (rich).



surprising; these two stands have high water tables and dead roots may absorb more Ca from upwelling groundwater than live roots.

Bole wood and branches

Concentrations of nutrients in wood (Fig. 5) were lower than those in leaves and roots by about an order of magnitude for all five elements. Unlike leaves and roots, base cation concentrations in bole wood were not particularly high in the base-rich stands at Sleepers River. Concentrations of N and P in wood were generally lower in the conifers than the hardwoods, and N concentrations in wood were highest at Sleepers River. White ash and American beech exhibited consistently higher K concentrations in wood than sugar maple or yellow birch, the other dominant hardwoods.

Nutrient concentrations in tree branches (Fig. 6) were mostly similar across the two sites at which they were measured, except for N and Ca. Because branches were sampled at Hubbard Brook in 1965 and at Cone Pond in 1990, the differences we report may reflect change over time in the trees or in the analytical methods, in addition to differences across sites. Specifically, N concentrations were higher at Cone Pond than at Hubbard Brook, which is in the expected direction of change over time, given 25 additional years of elevated N deposition from air pollution. Calcium concentrations were also higher at Cone Pond in 1990 than at Hubbard Brook in 1965.

Branch chemistry was not used in comparing nutrient cycling among stands in this study, because it was not measured at Sleepers River. Instead, we used wood concentrations to characterize the accretion of nutrients in perennial tissues. Nutrient concentrations in branches were consistently higher than in bole wood, which means that nutrient accumulation in trees was systematically underestimated in our budgets. Differences between branch and wood concentrations were greatest for P and smallest for K (Figs. 5 and 6).

Nutrient fluxes

Litterfall and throughfall

Litterfall fluxes of Ca, Mg, and K generally increased along the nutrient gradient, being highest in the “rich” stands at Sleepers River (Fig. 7). Litterfall fluxes of nutrients were generally smaller in conifer stands ($p = 0.001$ for the main effect of forest type in ANOVA), consistent with lower litterfall mass, notably so for K ($p = 0.06$) and P ($p = 0.09$). Litterfall flux of K was especially high in Sleepers River hardwoods ($p = 0.19$ for the interaction of site and forest type).

Throughfall was rich in K concentrations relative to other elements (Fig. 7), as is commonly observed. Magnesium fluxes in throughfall were a smaller fraction of nutrient uptake than for K but greater than for Ca. Throughfall tended to increase in Ca ($p = 0.03$) and Mg ($p = 0.02$) along the gradient, and throughfall fluxes of these elements were higher in conifers than hardwoods ($p = 0.04$ for Ca, $p = 0.03$ for Mg). Net throughfall fluxes of N were negative, meaning that N was removed by the forest canopy; precipitation had more N than

Fig. 5. Nutrient concentrations of wood by species in hardwood and conifer stands at Cone Pond (CP), Hubbard Brook (HB), and Sleepers River (SR). The average wood concentration for each stand was weighted by the basal area of species at that stand, using estimates from other stands or species for species not sampled at a particular site.

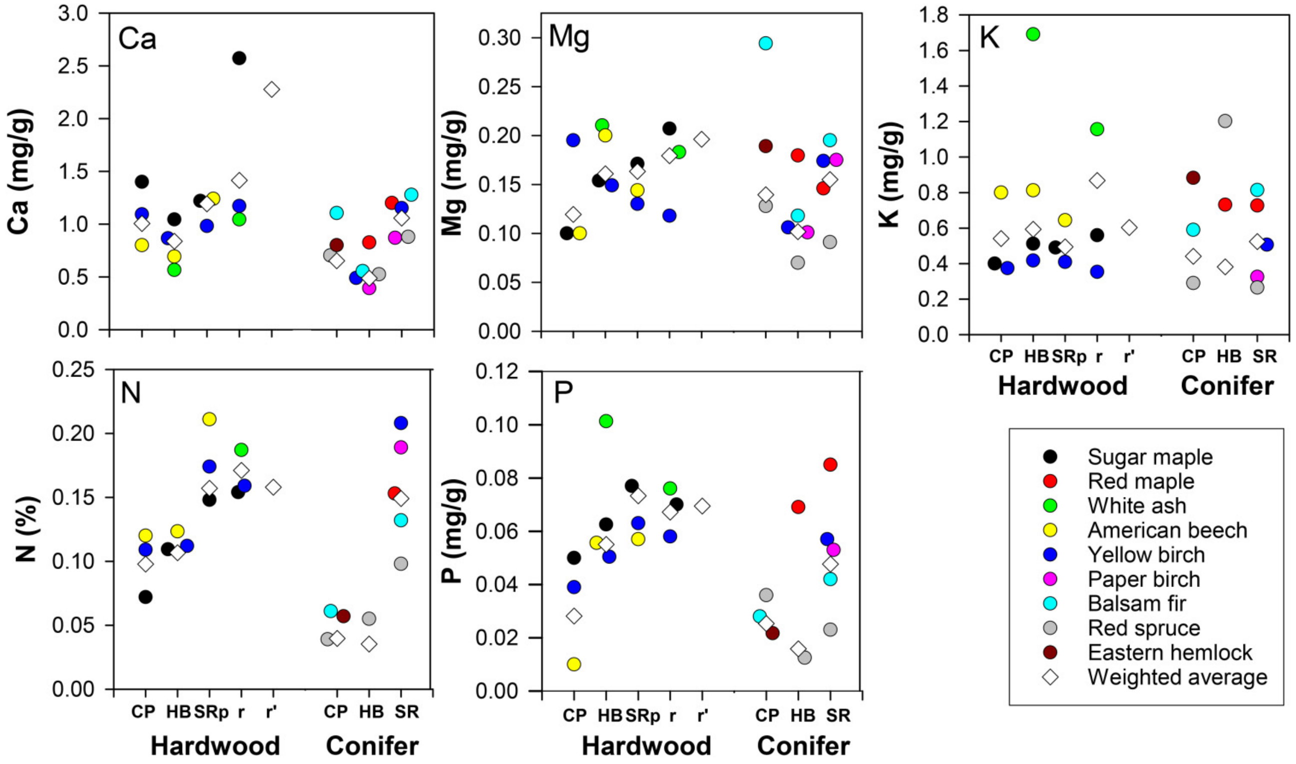


Fig. 6. Nutrient concentrations of branches by species in hardwood and conifer stands at Cone Pond (CP) and Hubbard Brook (HB). Branches were not sampled at Sleepers River.

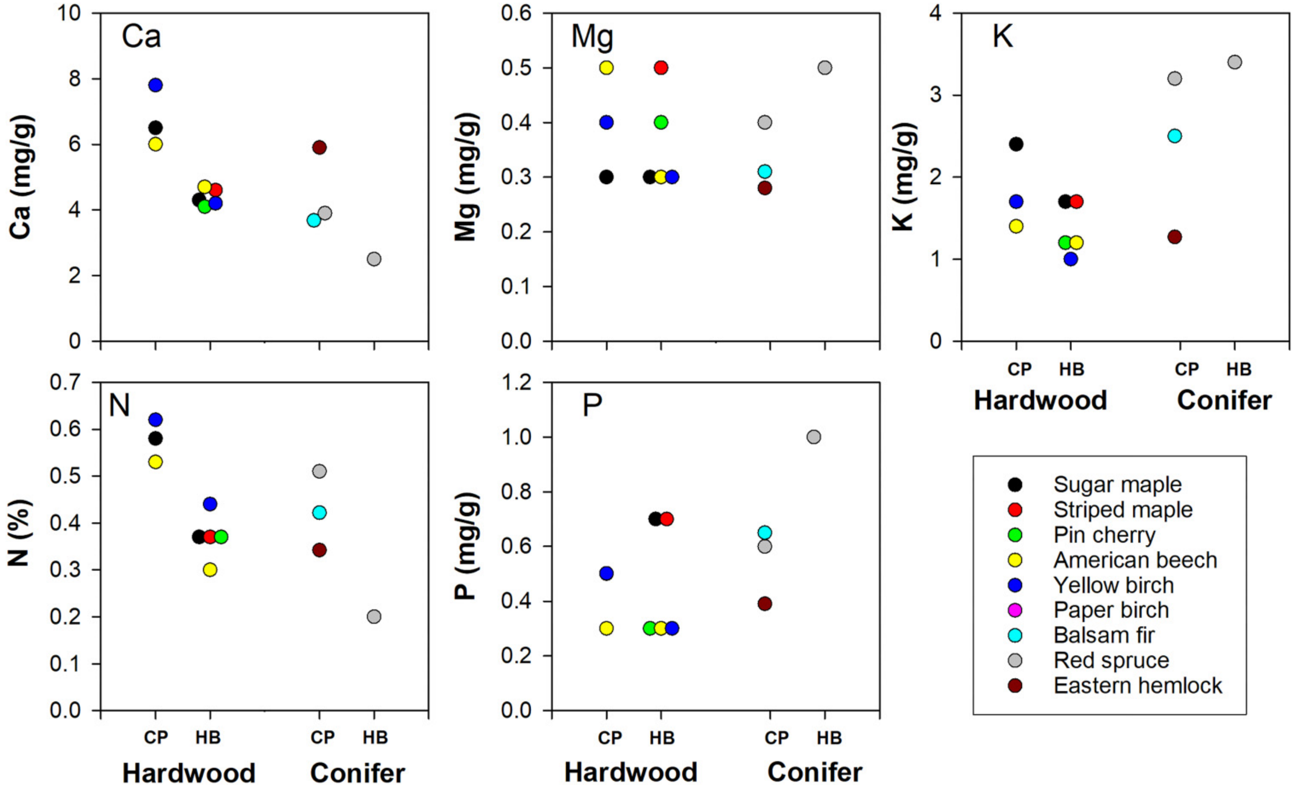
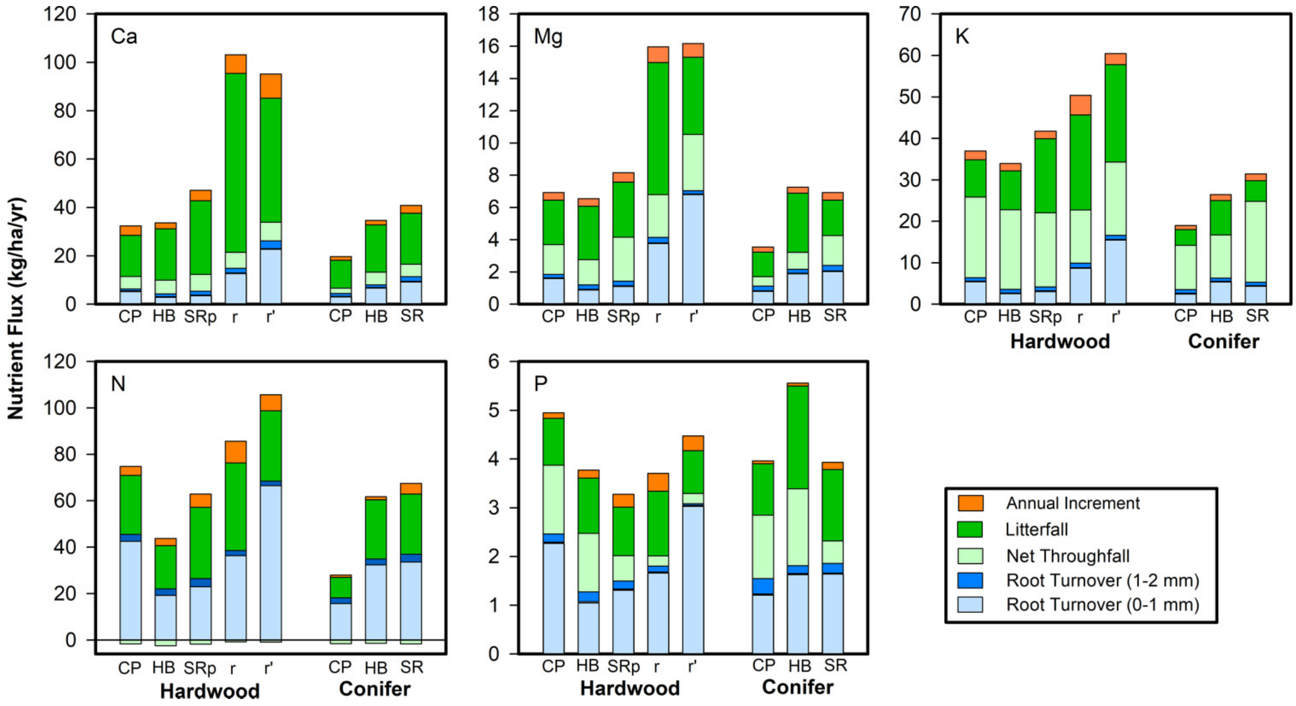


Fig. 7. Nutrient fluxes in woody increment, leaf litter, throughfall, and root turnover in hardwood and conifer stands at Cone Pond (CP), Hubbard Brook (HB), and Sleepers River (SR). SR has three hardwood stands, designated p (poor) and r and r′ (rich). The sum of these fluxes is annual nutrient uptake. Nitrogen is lower in throughfall than in precipitation and thus the net throughfall flux is negative.



did the throughfall beneath the canopy. However, organic N was not measured in throughfall.

Root turnover

Patterns across sites in nutrient turnover in roots (Fig. 7) reflect differences in biomass, nutrient concentration, and turnover rate. Fine root biomass (<2 mm in diameter) was relatively consistent across sites: the highest live root biomass was at the second Sleepers River "rich" hardwood stand (1.8 $\mathrm{Mg \cdot ha^{-1}}$) and the lowest was at the Hubbard Brook hardwood stand (0.6 $\mathrm{Mg \cdot ha^{-1}}$). The turnover rate of fine roots < 1 mm in diameter was more variable and related neither to the nutrient gradient nor to forest type. Three stands had low turnover rates: 0.29 $\mathrm{year^{-1}}$ for Hubbard Brook hardwoods, 0.32 $\mathrm{year^{-1}}$ for the poor Sleepers River hardwoods, and 0.28 $\mathrm{year^{-1}}$ for Cone Pond conifers, while four had turnover rates twice as high: 0.59 and 0.63 $\mathrm{year^{-1}}$ for hardwoods at Cone Pond and the Sleepers River rich stand and 0.64 and 0.68 $\mathrm{year^{-1}}$ for conifers at Hubbard Brook and Sleepers River (Park et al. 2008). As previously reported, the resulting estimates of biomass turnover were highest at the rich hardwood sites at Sleepers River (Park et al. 2008). These sites also had high concentrations of base cations in roots (Fig. 4), resulting in high nutrient turnover in roots; for N and P, where root concentrations were more consistent across sites, variation reflected differences in root lifespan.

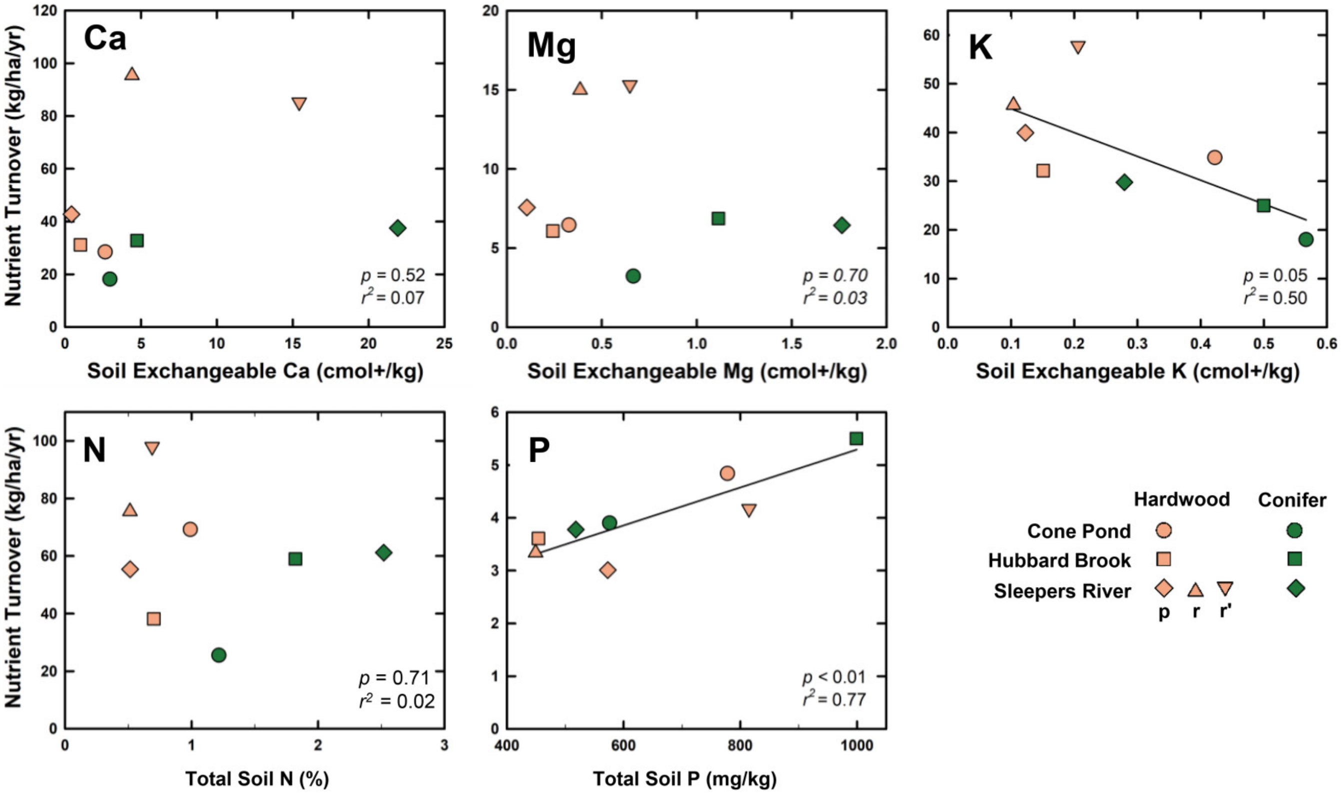
Nutrient accumulation, turnover, and uptake

Nutrient accumulation in perennial tissues (based on concentrations in wood) was generally higher for the hardwood than conifer stands (Fig. 7) reflecting both higher forest growth rates, as previously reported (Park et al. 2008) and wood nutrient concentrations (Fig. 5).

Nutrient turnover was described as the sum of the nutrient fluxes in litterfall, net throughfall, and root turnover (Fig. 7). Nutrient turnover of Ca and Mg varied the most across stands, due to their high fluxes in litterfall and root turnover in the base-rich stands at Sleepers River. Phosphorus turnover was the most consistent across stands, with a coefficient of variation of 14%, compared to 26% and 23% for Ca and Mg. Hardwoods and conifers differed consistently in nutrient turnover only for K; hardwoods had higher K turnover than conifers ($p = 0.05$).

We expected high nutrient turnover where soil nutrient availability was high, and this was the case for P ($R^2 = 0.77$, $p = 0.004$) but not for other elements (Fig. 8). We observed an inverse relationship between soil exchangeable K and K turnover ($R^2 = 0.50$, $p = 0.05$), because the conifer stands (and Cone Pond hardwoods) had high soil K but low nutrient turnover. Although the base-rich stands at Sleepers River had the highest turnover of Ca, Mg, K, and N, the soils at these stands were not higher in all these elements. Note that soils were characterized at one representative pit per stand; foliage was collected from between 9 and 15 trees per stand and thus may better represent fertility differences.

Fig. 8. Nutrient turnover in relation to soil chemistry in hardwood and conifer stands at Cone Pond, Hubbard Brook, and Sleepers River. Sleepers River has three hardwood stands, designated p (poor) and r and r′ (rich). Nutrient turnover is the sum of nutrient fluxes in litterfall, throughfall, and root turnover.



Nutrient uptake was estimated as the sum of nutrient accumulation in live biomass increment and the turnover of nutrients in litterfall, net throughfall (canopy leaching), and fine roots (Fig. 7). Nutrient accumulation in live aboveground biomass was a relatively small proportion of total uptake, and thus statistical contrasts were similar to those for nutrient turnover. Net throughfall flux was a large proportion of total uptake for K and Mg, a smaller proportion for Ca and nil or negative for N—a slight net retention of precipitation N in the canopy was noted previously by Lovett et al. (1996) at Hubbard Brook. Root turnover varied markedly among stands and nutrients, as described above. As a percentage of total nutrient uptake, fine root turnover was particularly high for N and P (43%–67% for N, 32%–69% for P, depending on the stand) and low for Ca and K (12%–29% for Ca, 10%–27% for K). In total, estimated uptake of macronutrients exhibited the greatest range across sites for Ca and Mg, being particularly high at the base-rich stands at Sleepers River. The smallest variation among stands was observed for P; N and K were intermediate (Fig. 7).

Comparisons of nutrient cycling indicators across stands and elements

Nutrient-use efficiency

Nutrient-use efficiency was estimated for each stand and macronutrient as the ratio of net primary production to nutrient uptake (Table 2). The use efficiency of Ca and Mg declined along the nutrient gradient ($p = 0.06$ for Ca and $p = 0.05$ for Mg for the main effect of site in ANOVA), because the turnover of these elements increased along the gradient (Fig. 7) proportionally more than productivity increased; therefore, nutrient use was less efficient at high nutrient availability. Not surprisingly, the use efficiency of Ca and Mg was higher in the base-poor than the base-rich hardwood stands at Sleepers River.

As expected, nutrient use was generally more efficient where weighted average foliar nutrient concentrations indicated low availability of the nutrient (Fig. 9), most significantly for Ca ($p = 0.01$) and Mg ($p = 0.06$). Surprisingly, P use efficiency was not high where foliar P was low (Fig. 9); instead, it was high where foliar N was high ($R^2 = 0.38$, $p = 0.11$), which could reflect greater demand for P where N is less limiting.

NUE was not significantly higher where soil nutrient availability was low ($p \geq 0.20$ in regression). In fact, K-use efficiency was highest where soil K was high ($R^2 = 0.49$, $p = 0.05$).

Nutrient retention fraction

We explored a novel metric, the NRF, to facilitate comparison among nutrients (Table 2; Fig. 10). We defined NRF as nutrient accretion in perennial tissues as a fraction of nutrient uptake.

Table 2. Nutrient-use efficiency and nutrient retention fraction in hardwood and conifer stands used to examine the effect of site and forest type on ecosystem nutrient cycling.

Nutrient-use efficiency (kg/ha/year of wood production divided by kg/ha/year of nutrient uptake)						
		Ca	Mg	K	N	P
Hardwood	**CP**	121	564	106	54	790
	HB	87	449	87	71	780
	SRp	77	444	87	59	1105
	SRr	53	343	109	65	1477
	SRr′	45	269	72	41	972
Conifer	**CP**	113	627	117	84	561
	HB	107	510	140	61	666
	SR	75	444	98	47	784
Nutrient retention fraction (%)						
		Ca	**Mg**	**K**	**N**	**P**
Hardwood	**CP**	12.1	6.7	5.7	5.2	2.2
	HB	7.3	7.2	5.1	7.6	4.3
	SRp	9.2	7.2	4.3	9.3	8.1
	SRr	7.5	6.1	9.4	11.0	9.9
	SRr′	10.4	5.3	4.3	6.6	6.7
Conifer	**CP**	7.4	8.7	5.2	3.3	1.4
	HB	5.2	5.2	5.4	2.2	1.1
	SR	8.0	6.9	5.1	7.0	3.7

Note: CP, Cone Pond; HB, Hubbard Brook; SR, Sleepers River. Sleepers River has three hardwood stands, designated p (poor) and r and r′ (rich).

Elements differed consistently in NRF ($p = 0.01$ for the main effect of element in ANOVA), ranging from a high of 8.4 ± 0.8% for Ca to a low of 4.7 ± 1.2% for P and 5.1 ± 0.7% for K (mean ± SE across the eight stands). Hardwoods had higher NRFs (7.2 ± 0.5%) than conifers (5.0 ± 0.6%) ($p = 0.003$), consistent with woody increment being higher on average in hardwoods (4.1 Mg/ha/year) than conifers (3.0 Mg/ha/year). Sleepers River tended to have the highest NRFs, across all elements, and Hubbard Brook had the lowest ($p = 0.08$).

Unlike NUE, NRF did not generally decrease with increasing foliar concentration of the respective nutrient ($p > 0.23$ in regression) and for N, retention went up with foliar N ($R^2 = 0.39$, $p = 0.10$). While not significant, the interactions of N and P availability and retention were in the expected direction, with N retention high where foliar P was high ($R^2 = 0.15$, $p = 0.34$) and P retention high where foliar N was high ($R^2 = 0.33$, $p = 0.14$), suggesting co-limitation by N and P.

Soil nutrient availability was not a good predictor of NRF ($p \geq 0.20$). Again, soils were collected at only one location per stand and thus might not be expected to represent site fertility as well as the weighted average foliar concentrations of many trees (Fig. 2).

Discussion

Forested ecosystems are exposed to chronic environmental stresses, including soil acidification and changing nutrient availability, which affect long-term productivity and nutrient cycling (Fernandez-Martinez et al. 2014). Because of the long time scales and large spatial scales of forest responses and feedbacks, it is difficult to assess the effects of environmental change on forest ecosystems using experimental manipulations. Naturally occurring gradients provide an alternative approach, though it can be difficult to isolate the intended independent variable from other important differences among the selected study sites. We worked in three northern forest sites that are similar in climate and vegetation cover, each including both hardwood and conifer stands, but that differ in soil characteristics, which allows testing of patterns relative to the gradient both within and across forest types. We previously reported that belowground production was significantly higher in sites with higher Ca, higher base saturation, and lower Al availability in soils (Park et al. 2008). Including additional nutrient cycling information from these stands made it possible to test whether nutrient turnover was highest in sites with high nutrient availability, resulting in reduced efficiency.

NUE has been variously defined, always with some measure of production in the numerator and some measure of nutrient use in the denominator (Miller et al. 1976; Vitousek 1982; Aerts and Chapin 1999). The conventional definition of NUE, the ratio of biomass to nutrient content, gives units that are the inverse of nutrient concentration, which naturally differ by element, and thus comparing nutrient cycling across elements reflects the differences in concentrations of nutrients in plant tissues. Defining NRF as the fraction of nutrient uptake retained in perennial tissues allows nutrient cycling to be compared across elements.

If ratios of elements were constant across tissue types, then NRF, as defined here, would be constant across elements in each system. Tissues, however, differ in their stoichiometry (Figs. 1–4). Because wood is low in P relative to roots and leaves, the annual accumulation of P was low compared to P uptake (Fig. 10). Because throughfall is high in K, turnover was high compared to other elements. For Ca, Mg, K, and N, NRFs were similar, with 6.5%–7.6% of annual uptake being retained in perennial tissues. However, these elements differed in patterns of nutrient cycling (Fig. 7). For Mg and especially for Ca, leaf turnover (litterfall) was the largest component of nutrient uptake. For N and P, in contrast, root turnover was greater than leaf turnover, due to high leaf resorption (Huang et al. 2023) and limited resorption by fine roots (Yuan et al. 2011).

The relatively low NRFs that we observed for P (Fig. 10) reflect the exceptionally low P concentrations in sapwood (Fig. 5). Patterns and controls on the macronutrient content of wood are not well studied. In general, wood chemistry tends to vary more among tree species than across sites within species (Fig. 5; Dalling et al. 2024). Although nutrient concentrations are presumably much higher in the living cells of sapwood ray parenchyma tissues than the dead vessel xylem elements, no relationship was observed between wood nutrient concentrations and proportional ray abundance across 22 tropical tree species (Kotowska et al. 2020). In the case of P, it seems that very effective resorption occurs during cell division and differentiation of xylem from cambium (Ding et al. 2020), since the metabolically active cambial cells presum-

Fig. 9. Nutrient-use efficiency as a function of foliar nutrient concentration (weighted average of the species at each site).

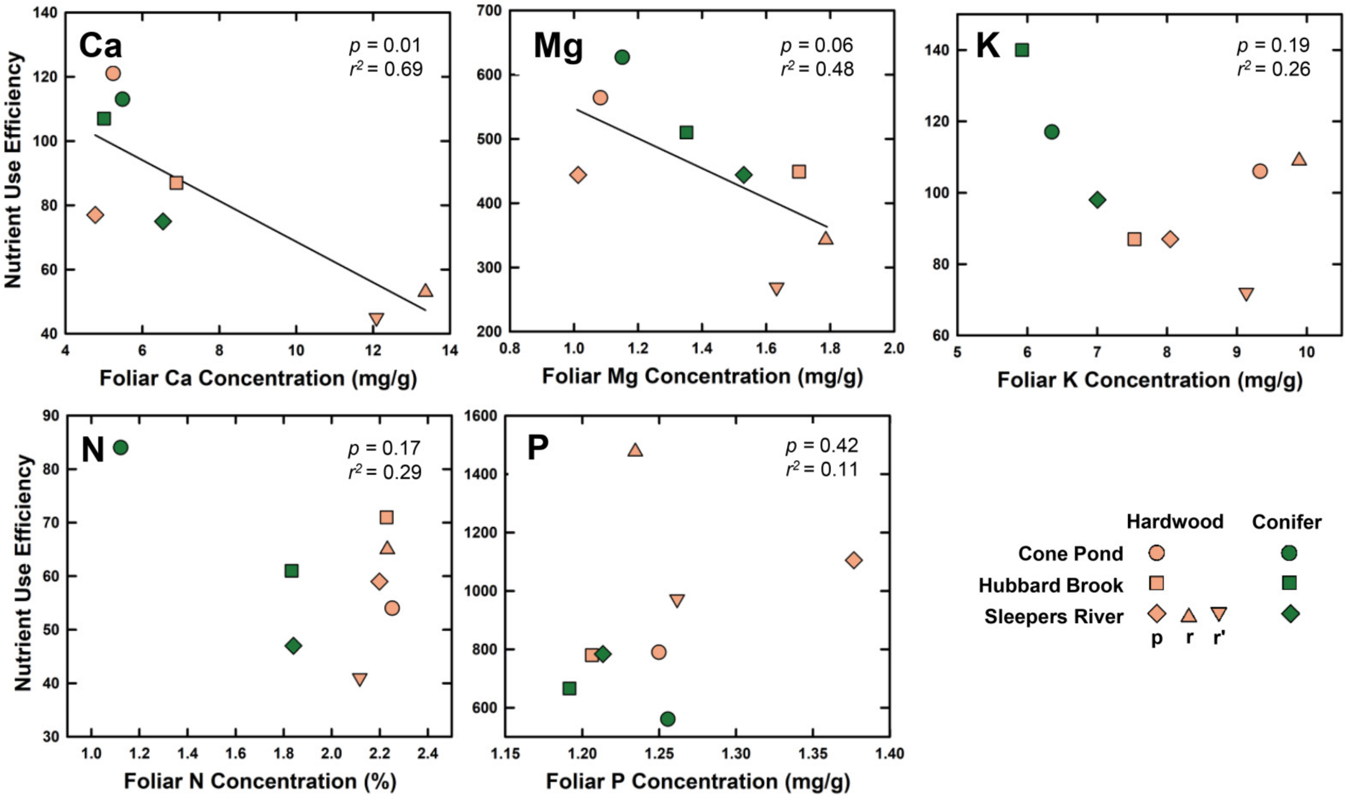
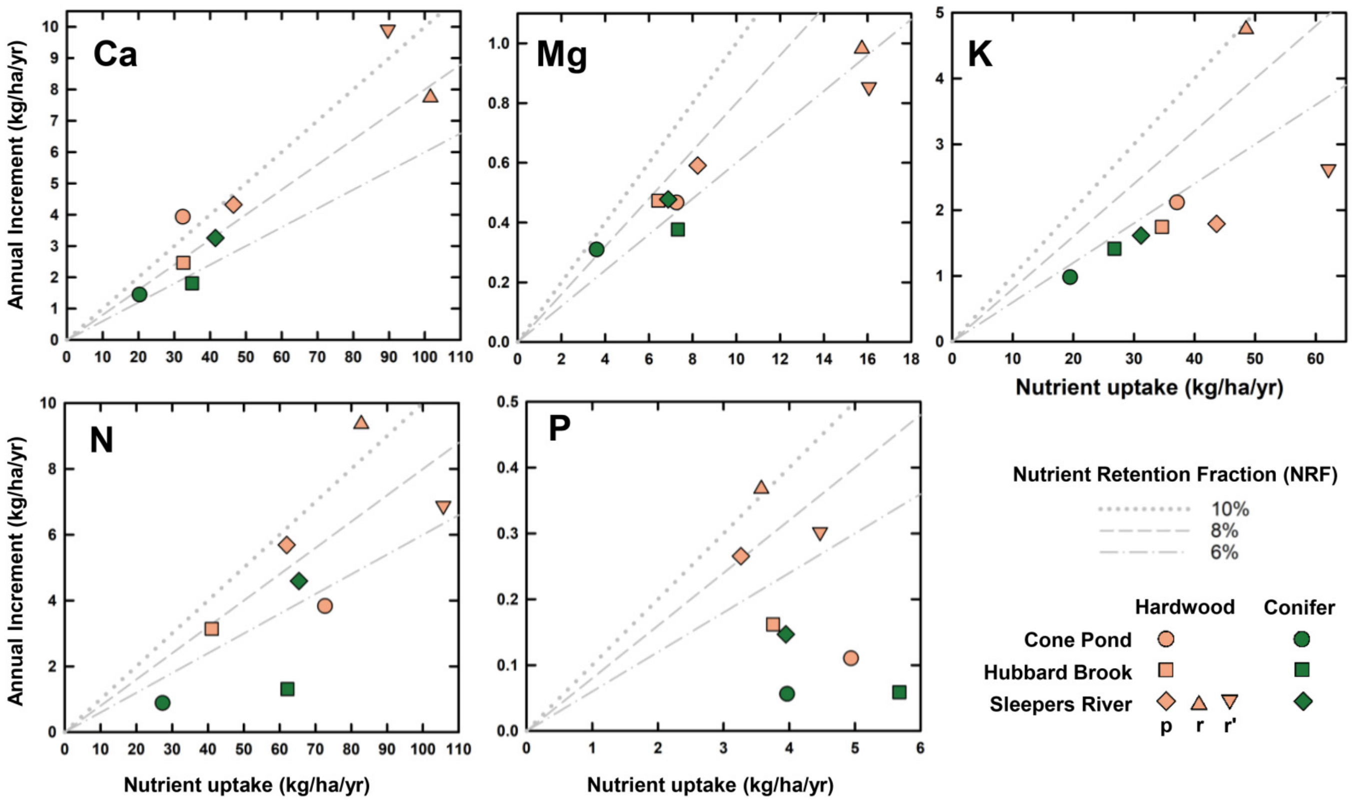


Fig. 10. The nutrient retention fraction (NRF) is the fraction of nutrient uptake retained in perennial tissues. For reference, 6%, 8%, and 10% NRF are indicated with dotted lines.



ably contain very high concentrations of P. Additional work on this crucial process in the internal recycling of nutrients is needed. Internal remobilization during heartwood formation (Dalling et al. 2024) could contribute significantly to the supply of nutrients to growing wood, although the reverse may also occur—for example, Ca concentrations of maple heartwood can be several-fold higher than in sapwood (Likens and Bormann 1970; Arthur et al. 1999).

Although many research reports have been presented from Sleepers River (Shanley et al. 1995, 2015, 2022) and Cone Pond (Hornbeck et al. 1997), this paper presents the first summary of internal nutrient cycling from these sites. In contrast, many forest ecosystem nutrient budgets have been presented for Hubbard Brook (Bormann et al. 1977; Whittaker et al. 1979; Yanai 1992, Yanai et al. 2013), differing over time due to declining net growth as the forests mature (Fahey et al. 2005) and also due to improved observations, particularly for fine root turnover and nutrient concentration.

Even more accurate budgets than those presented here could be constructed where more information is available. For example, we ignored nutrient accumulation belowground in woody roots, and we applied a constant rate of root turnover to 1–2 mm diameter roots. Most importantly, our estimates of aboveground nutrient accumulation in perennial tissues relied on wood nutrient concentrations only, because branches and bark were not analyzed at Sleepers River. At Cone Pond and Hubbard Brook, using the concentrations available for branches (Fig. 6) and bark (Likens and Bormann 1970; Yanai et al. 2025) would result in higher estimates of nutrient accumulation, with the magnitude of the correction depending on the proportion of bark and branches. Notably, wood concentrations were lowest relative to bark and branches for P, consistent with the low NRF we observed for P (Fig. 10).

Questions involving multiple nutrients are particularly interesting. We observed higher P retention fraction in stands with higher foliar N concentrations, consistent with a greater demand for P where N is less limiting. Similarly, N retention fraction was high where foliar P was high. This sensitivity of nutrient conservation to the availability of the other element suggests colimitation by N and P in these forests (Fahey et al. 2025). Resorption of P during leaf senescence, which contributes to P cycling efficiency by reducing the loss of P in litterfall, reflected naturally occurring differences across stands in N availability in hardwood forests similar to ours (See et al. 2015). In a factorial N by P fertilization experiment, both N and P resorption efficiency were increased by addition of the other nutrient (Zukswert et al. 2025), suggesting that plasticity of resorption is an important mechanism of nutrient conservation. If nutrient cycling can become more efficient when nutrient supplies are low, then forest harvesting may be sustained for more rotations than currently predicted (Vadeboncoeur et al. 2014). The efficiency of wood production by trees relative to their nutrient use is important to sustainable production of forest biomass in the face of societal pressure for biomass energy to substitute for fossil fuels.

The seminal work on NUE by Vitousek (1982) was based on leaf production and nutrient concentrations in leaf litter, which are easy to measure compared to biomass and nutrient accumulation in wood and roots. Our analysis shows that the inclusion of other ecosystem components and fluxes can give a more refined view of nutrient use and nutrient turnover. Because these other fluxes are more difficult to obtain, the number of sites and stands reported here is small, and thus the power to detect patterns, for example, between NUE and nutrient availability, is low. The continual growth of information on ecosystem nutrient budgets should make it possible to test additional hypotheses about nutrient controls of productivity with greater statistical power.

Acknowledgements

Many researchers assisted with sample collection and sample analysis, with those from the early years lost in the mists of time. Recent rescue assistance filling in missing data came from Dan Hong, Jenna Zukswert, and Matt Vadeboncoeur; Charan Venkataswamy wrestled tissue chemistry data. Bill O'Neill, Griffin Walsh, Pilar Lyons, and Mary Hagemann made endless versions of SigmaPlot figures. Alex Young and Alex Rice began the conversion of our spreadsheet calculations to R Markdown. Don Ross and Kevin Ryan analyzed samples from Sleepers River. Scott Bailey and Kara Gonzales provided guidance and feedback. This project was funded by the Northeastern States Research Cooperative, the National Science Foundation, the NSF Long-Term Ecological Research program, and the Korea Forest Service. JBS was funded by the USGS Ecosystems Land Change Science program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This article is a contribution to the Hubbard Brook Ecosystem Study.

Article information

History dates

Received: 26 February 2025
Accepted: 17 September 2025
Accepted manuscript online: 3 November 2025
Version of record online: 12 January 2026

Notes

This paper is part of a collection celebrating Tim Fahey's career and contributions to forest ecology.

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Data availability

Data generated and analyzed during this study are available in the following repositories:

Bailey, S.W. 2024. Cone Pond Watershed: Soil Profiles (Pedons), 1988-2023 ver 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/0ca11f1f7f5ae6692b036c5f88c507bf.

Bailey, S.W. 2024. Hubbard Brook Experimental Forest: Soil Profiles (Pedons), 1995-2022 ver 2. Environmental

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Shanley, J.B., Chalmers, A.T., Bailey, S., Sebestyen, S.D., Aspelin, N., and Bruch E.R., 2025. Soil Descriptions and Chemistry at W-9 Catchment, Sleepers River Research Watershed, Danville, Vermont, USA. U.S. Geological Survey data release, ScienceBase, https://doi:10.5066/P13YASAK.

Yanai, R.D., J.B. Shanley, J.E. Beidler, R.A. Hallett, B.B. Park, T.G. Siccama, and T.J. Fahey. 2025. Ecosystem nutrient cycling in northern hardwood and conifer stands at Cone Pond, Hubbard Brook, and Sleepers River ver 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/8bb6c7ed61c696535547b3e009ecf8f6.

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Writing – review & editing: RDY, JBS, BBP, TJF

Competing interests

The authors declare there are no competing interests.

Funding information

Funding was provided by Northeastern States Research Cooperative, the USGS Ecosystems Land Change Science program, the National Science Foundation DEB-0235650, NSF Long-Term Ecological Research DEB-0423259, and the Korea Forest Service S210606L0101104.

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