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ORIGINAL PAPER

Aboveground nutrients and merchantable wood volume across soil nutrient gradients in managed northern hardwood forests of New England, USA

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Abstract Forest management typically focuses on assessments of aboveground structure and yield, often overlooking the belowground nutrient reservoirs that sustain long-term ecosystem function. While soil nutrient richness is known to influence forest productivity and resilience, the role of base cation availability in shaping aboveground nutrient dynamics and merchantable wood value remains poorly understood in glaciated hardwood forests. This study investigated how soil nutrient richness, tree size class, and tree genus influence aboveground nutrient concentrations, pools, and merchantable wood volume and value across three managed northern hardwood forests in Vermont and New Hampshire, USA, spanning Poor, Moderate, and Rich soil nutrient richness classes. We measured foliar and wood nutrient concentrations (Ca, Mg, K, P) and estimated biomass and timber value across 45 forest plots. Nutrient-rich soils supported the highest foliar and woody nutrient concentrations, particularly for Ca and P, whereas total aboveground nutrient pools were driven primarily by forest structure rather than soil fertility alone. *Acer* and *Fraxinus* dominated aboveground nutrient pools, with *Fraxinus* having the highest wood concentrations of Ca, Mg, K, and P among all genera. Poletimber trees contained the largest wood nutrient pools due to their high collective basal area. Contrary to expectations, merchantable wood volume did not increase with increasing soil nutrient richness, likely reflecting differences in stand age and composition, indicating that soil fertility assessments alone are not sufficient to predict timber yield or stand value. However, merchantable wood value varied across the richness gradient, with the Moderate Forest consistently yielding the highest simulated returns due to a high abundance of *Acer*. These findings highlight the importance of soil fertility in sustaining long-term forest productivity, and suggest that standard pre-harvest assessments of species composition and stand structure should be paired with soil fertility surveys to maintain economic value in nutrient-limited northern hardwood forests.

Keywords Aboveground nutrient pools · Merchantable wood · Timber quality · Soil fertility gradient · Nutrient cycling

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Introduction

Intensive timber harvesting methods, such as whole-tree harvesting and clearcutting can accelerate the export of nutrient-rich components like branches and foliage which reduces long-term soil nutrient pools and limits forest regeneration and growth (Thiffault et al. 2010; Marschner 2012; Achat et al. 2015; Richardson et al. 2017; Ouimet et al. 2021). This removal is especially consequential for nutrients such as Ca, Mg, K, and P that regulate tree structure, metabolism, and stress tolerance (Kaiser 1982; Schachtman et al. 1998; White and Broadley 2003; Wang et al. 2020; Carpenter et al. 2021; Richard et al. 2022; Dukic et al. 2023). Since nutrient-poor soils have limited base cation pools and low buffering capacity, timber harvests remove a disproportionately large amount of nutrient reserves compared to nutrient-rich soils. As a result, these sites are more vulnerable to long-term nutrient depletion and declines in aboveground productivity.

Although some research suggests that removing harvest residue has limited effects on species composition, other work demonstrates that nutrient losses through the soil from harvests can hinder tree growth, particularly high-value species like sugar maple (*Acer saccharum*; Moore et al. 2012; Marlow and Peart 2014; Vadeboncoeur et al. 2014; Achat et al. 2015). These contrasting findings highlight that the consequences of harvesting depend strongly on underlying soil nutrient richness. Nutrient-poor soils are especially sensitive, and even small nutrient exports can lead to declines in soil fertility and tree growth. Over time, soil nutrient limitations may reduce biomass production, species diversity, and economic value with short-term reductions in tree growth estimate at 3–7% following harvest (Carpenter et al. 2021; Richard et al. 2022). Given these harvest-driven nutrient losses, understanding how natural variability in soil nutrient richness influences aboveground nutrient storage is critical for sustainable forest management.

Soil nutrient richness plays a central role in determining forest growth, species composition, and resilience (St Clair et al. 2008; Vadeboncoeur 2010; Lucash et al. 2012; Leak et al. 2014; Achat et al. 2018). In New England, soil nutrient availability and total nutrient abundance vary widely due to differences in parent material, weathering, and historical disturbances (Nezat et al. 2008; Schlesinger and Bernhardt 2013; Rice et al. 2024). The bedrock geology ranges from nutrient-rich metamorphosed rocks such as marble, schist, and shale to nutrient-poor granites and quartzite which produce soils with distinct fertility gradients across the region. These soils, which are largely derived from glacial till and glaciofluvial deposits, have high variability in mineral composition and nutrient content that result in substantial differences in base cation availability (Rice et al. 2024). This heterogeneity influences species distributions and nutrient-use strategies, with *A. saccharum* tending to be more abundant and productive on Ca-rich soils, whereas American beech (*Fagus grandifolia*) is more tolerant of acidic, granite derived soils and often dominates nutrient-poor or repeatedly disturbed stands (Leak and Sendak 2002; Hallett et al. 2006; Schaberg et al. 2006; Siccama et al. 2007; Otto and Watmough 2021; Rogers et al. 2021). Nutrient allocation and storage also differ among tree species and size classes, with smaller trees generally having higher nutrient concentrations and species such as *A. saccharum* being particularly sensitive to Ca depletion and soil acidity (Phillips and Watmough 2012; Achat et al. 2018; Long et al. 2019; Otto and Watmough 2022). Together, these patterns suggest that soil nutrient richness may influence forest composition and structure and therefore shape aboveground nutrient pools and the distribution of biomass across tree size classes.

Despite extensive research on forest nutrient cycling, key gaps remain in understanding how soil nutrient richness influences aboveground nutrient storage and merchantable wood volume, particularly on young, glaciated soils. To address this gap, we measured Ca, Mg, K, and P concentrations in green leaves and branch wood of trees along a natural soil Ca-Mg nutrient richness gradient across three managed northern hardwood forests in Vermont and New Hampshire with similar management histories. Our primary objective was to assess how soil nutrient richness influences aboveground nutrient pools and merchantable wood volume. Specifically, we asked: (1) Does soil nutrient richness affect aboveground nutrient concentrations and pools? (2) Do tree size and genus influence foliar and woody nutrient concentrations and pools? and (3) Does soil nutrient richness, tree size, and genus affect merchantable wood volume and forest value?

For the first research question, we hypothesized that the forest with nutrient-rich soils would exhibit greater aboveground nutrient (Ca, Mg, K, P) concentrations and pools, suggesting that belowground availability controls aboveground uptake. For the second, we hypothesized that certain tree genera, particularly *Acer* and *Betula*, would exhibit increased nutrient uptake with higher belowground availability and during maturation due to luxury uptake. Lastly, we hypothesized that total and genus-specific merchantable wood volume would be greatest in forests with nutrient-rich soils and result in the highest overall economic value among the forests. Overall, this study quantifies the influence of soil nutrient richness on aboveground woody, foliar, and merchantable wood biomass, providing insights for sustainable forest management practices in northern hardwood forests in the northeastern United States (U.S.).

Materials and methods

Study area and soil physicochemical characteristics

This study applies a comparative approach across three managed U.S. New England forests with documented harvest histories: Bartlett Experimental Forest in central New Hampshire, Dartmouth College's Second College Grant in northern New Hampshire, and Dartmouth College's Clement Woodlot in eastern Vermont (Table 1; Fig. S1). These three forests were intentionally chosen because they represent a full range in soil nutrient richness (Poor, Moderate, Rich) that share similar forest types, management histories, and regional climate, which allows for meaningful comparisons across the nutrient gradient. All three forests are located on mountainous landscapes and are dominated in varying proportions by sugar maple (*A. saccharum*), American beech (*F. grandifolia*), yellow birch (*Betula alleghaniensis*), red maple (*Acer rubrum*), and white ash (*Fraxinus americana*) as the primary canopy species. Smaller components of pin cherry (*Prunus pensylvanica*) and striped maple (*Acer pensylvanicum*) were present in more recently harvested areas. These three forests have been managed with similar silvicultural approaches to establish uneven-aged forest structures, which provide a unique set of forests for this study. In Bartlett Experimental Forests, specifically in the sampled compartments (5 and 6), harvesting has occurred through group selection. Historically, harvests were initiated in the 1930s, followed by subsequent cuts in 1951, 1960, and the early to mid-1990s (Yamasaki et al. 2014; Rogers et al. 2021). In Second College Grant, within the management area that we sampled, harvesting has primarily utilized single-tree and group selection harvests over the past several decades. Prior to this period, harvests were largely characterized as targeted removal of conifers in the late 1800s and early 1900s and diameter-limit harvests of hardwood sawlogs in the 1950s (Jevon et al. 2019). Clement Woodlot is the only site that was historically cleared for agricultural uses (sheep pasture) with the forests developing after agricultural abandonment. Clement Woodlot was managed primarily with single-tree and group selection harvests beginning in the 1980s. All three forests were naturally regenerated.

Soils across the three forests range from poorly to somewhat excessively drained Spodosols and Inceptisols developed from glacial till and glaciofluvial deposits. The three forests studied exhibit a natural soil Ca-Mg gradient, with Bartlett Experimental Forest classified as the nutrient "Poor", Second College Grant as the nutrient "Moderate", and Clement Woodlot as the nutrient "Rich" forest. This gradient is due to the range in parent material composition (Ratcliffe et al. 2011; Rice et al. 2024) and is attributed to the variations in parent material compositions. The Rich Forest has a high abundance of amphiboles and sodium

Table 1 Site characteristics for each of the three forests used in this study including the location of each forest, bedrock geology and soil chemical traits. Error is standard error for the mean. Nutrient values were extracted from Rice et al. (2024). MAT = mean annual temperature, MAP = Mean annual precipitation

Forest	Soil nutrient richness‡	Lat (dd)	Long (dd)	MAT§ (°C)	MAP§ (mm)	Soil pH	Base sat. (%)	Total soil Ca (mg/g)	Total soil Mg (mg/g)	Total soil K (mg/g)	Total soil P (mg/g)
Bartlett Experimental Forest	Poor	44.048	− 71.272	5.9	1406	4.11	5.04 ± 0.99	5.91 ± 0.41	3.09 ± 0.29	28.94 ± 1.2	1.18 ± 0.08
Second College Grant	Moderate	44.887	− 71.130	4.1	1196	4.27	19.09 ± 3.0	5.69 ± 0.31	9.49 ± 0.42	10.83 ± 0.49	1.27 ± 0.07
Clement Woodlot	Rich	44.049	− 72.311	5.5	1163	4.92	54.2 ± 5.8	12.96 ± 0.54	27.3 ± 2.2	6.08 ± 0.58	1.24 ± 0.10

‡Soil nutrient richness is based upon Ca and Mg concentrations within parent material.

§PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu, data created 4 Feb 2014, accessed 16 Dec 2020

feldspar, the Moderate Forest is dominated by clay and mica minerals, and the Poor Forest is abundant in potassium and sodium feldspar (Rice et al. 2024). The Poor Forest is predominantly mapped as Marlow Series which is a Coarse-loamy, isotic, frigid Oxyaquic Haplorthod (Soil Survey Staff 2022). The Moderate Forest is mainly mapped as the Peru Series which is a coarse-loamy, isotic, frigid Aquic Haplorthod. The Rich Forest is mapped as predominantly the Colrain Series, a coarse-loamy, mixed, active, frigid Humic Dystrudept although our observations suggest the soil may be an Oxyaquic Eutrudept.

Tree mensuration and sampling

In each forest, we established fifteen circular, 400 m^2 plots (Fig. S1). This standardized plot size ensured compatibility with long-term studies in the region, facilitating data comparison and synthesis (Rogers et al. 2021). To ensure a representative sample within each forest, plots were categorized into three developmental stages (young, intermediate, mature) based on species composition, tree diameter at breast height (DBH), and time since the last record harvest, with five plots per stage.

Within each plot, all trees with a DBH ≥ 10.1 cm were identified to species. Trees were further classified into five size classes based on DBH defined by Luppold and Pugh (2016): sapling (2.5–12.6 cm), poletimber (softwoods: 12.6–23 cm; hardwoods: 12.6–28 cm), small sawtimber (28–33 cm), medium sawtimber (33–40.5 cm) and large sawtimber (> 40.5 cm). Only poletimber and sawtimber trees were considered for merchantable wood volume calculations.

Green leaves and small branches were collected from at least one individual of each of the three most abundant tree species (*Acer*, *Betula*, and *Fagus*) within each of the 15 plots within each forest. If a target species was absent from a plot, samples were collected from the two most frequent tree species present. Sampling occurred in mid-July 2022 from the mid-canopy of healthy trees with full canopies using a Notch Big Shot slingshot with a tethered throw weight. Mid-July was chosen because by this time of the year tree leaves have fully expanded and their nutrient concentrations are stable. A minimum of ten leaves and two small diameter branches were collected from each sampled tree. Healthy trees were defined as those with vibrant green foliage, a full canopy, strong branches free from excessive cracks or breaks, and bark free from excessive cracks, peeling, or signs of disease and insect infestation.

Sample processing and inorganic nutrient analyses

Each branch and green leaf sample was ground to < 2 mm using a Model 4 Thomas Wiley Mill, and a 0.50 g homogenized subsample was ashed at 500 °C for 8 h to remove organic matter, which can reduce the efficiency of the subsequent acid digestion. The ash was then digested with 5 mL of reverse aqua regia (9:1 HNO_3:HCl) at 90º C for 45 min, a procedure recognized as a pseudototal digestion (Quevauviller 1998). For quality control and assurance, every 20 samples were accompanied by a preparation blank, a duplicate sample, and two certified reference materials (NIST 1547a Peach leaves and NIST 1537a Tomato leaves). Digests were then diluted to 50 mL with deionized water, followed by a further dilution of a 3 mL subsample to 15 mL for elemental analysis. Concentrations of inorganic nutrients (Ca, Mg, K, P) were measured using an Agilent 5110 Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES; Agilent Technology, Santa Clara, California, USA). Recoveries for pseudototal digests of Ca, K, Mg, and P in the certified reference materials ranged from 81–112% of their certified values. The coefficient of variation for duplicate samples was < 7% for all elements analyzed. Metal concentrations in the preparation blanks were < 0.1% of their analyte concentrations.

Calculation of biomass, nutrient pools, and merchantable wood

Woody and foliar biomass concentrations and associated nutrient pools

Our analysis focused on six dominant tree genera (*Acer*, *Betula*, *Fagus*, *Fraxinus*, *Prunus*, *Tsuga*). Tree genera that accounted for < 3% of the total basal area across each forest were not analyzed individually but instead were grouped into a single category labeled "Other". The only exception was *Picea,* which comprised 12% of the basal area at the Rich Forest and was not retained as a distinct genus in the analysis. These genera included in the "Other" category were *Abies*, *Amelanchier*, *Malus*, *Ostrya*, *Picea*, *Pinus*, *Populus*, and *Quercus*. Stand age affected composition, with early-successional species such as *P. pensylvanica*, and *A. pensylvanicum* present in younger plots. Basal area was calculated using only live trees. Although standing dead trees were not explicitly excluded, they were rarely present in the plots. Of the 972 trees measured, only one was a snag and no additional standing dead trees were encountered during sampling.

Woody and foliar biomass were estimated for each tree using the allometric equation utilized by Ter-Mikaelian and Korzukhin (1997) with regional and state-specific data for tree species (Eq. 1).

$$M = a(D)^b \quad (1)$$

where M is the oven dried mass (kg) of the biomass component of the tree (stem, branch, or foliage), D is diameter at breast height (cm), and *a* and *b* are regional species-specific parameters that vary depending on the tree component. If *a* and *b* parameters were not published for a specific species, the parameters were used from the most closely related species within the same genus or family.

Branches and green leaf concentrations of Ca, Mg, K, and P were scaled from the digest to a per dry weight concentration prior to statistical analyses and calculation of nutrient pools. If elemental concentrations for a specific species were missing within a plot, values were used from the tree species within the plot that were most closely related based on genera, family, function, and DBH similarities. Further, woody and foliar nutrient pools (expressed in megagrams per hectare, Mg ha^{-1}) were calculated for each element (Ca, Mg, K, P) using the following Eq. 2 and Eq. 3:

$$\text{Wood Nutrient Pool} = \sum \left(M_{wood,i} * C_{wood,i}\right) \quad (2)$$

$$\text{Foliar Nutrient Pool} = \sum \left(M_{foliar,i} * C_{foliar,i}\right) \quad (3)$$

where $M_{wood,i}$ represents the wood (stem + branches) biomass of the *i*th species, and $C_{wood,i}$ represents the total wood nutrient concentration of the i^{th} species. Similarly, $M_{foliar,i}$ represent the foliar biomass of the *i*th species and $C_{foliar,i}$ represent the foliar nutrient concentration of the *i*th species. The sums were calculated for each genus within each of the 15 plots within each forest.

Estimating merchantable wood volume

Total merchantable wood volume and value were calculated for each of the 45 forest plots and summarized by soil nutrient richness. Merchantable wood refers to the estimated volume of usable stem wood suitable for commercial timber products which typically exclude branches and leaves. Only trees with sufficient DBH (> 12.5 cm) were considered merchantable. This threshold reflects the minimum size generally accepted for commercial harvesting. In total, 761 trees met this criterion and were included in the analysis. To calculate merchantable wood volume, first the merchantable height of each tree was calculated based on Ek et al. (1984) using appropriate species-specific coefficients within the northeastern U.S. region. Next, merchantable wood volume was calculated using Honer's equation (Honer et al. 1983), which uses merchantable tree height, DBH, and species-specific regression coefficients. For species without reported coefficients, the coefficients of the most closely related genus were used first, followed by those of the same family.

To estimate the economic value of each merchantable tree, we first calculated the number of 4.88 m (commonly, 16-foot) saw logs that could be cut based on merchantable stem height. Board foot was then estimated using the International ¼ Inch Rule which calculated usable lumber volume based on DBH and log count while accounting for material lost during milling (e.g. a ¼ inch saw kerf). This rule is widely used in the study region and is considered the most accurate for regional timber assessments.

Monte Carlo simulation of timber wood value under variable wood qualities

To estimate the variability in total merchantable wood value across the soil nutrient richness gradient, we conducted Monte Carlo simulations with 10,000 iterations. These simulations were designed to account for uncertainty in wood quality which was not directly assessed in the field (e.g. stem straightness, defects, or rot).

Tree timber value for each tree was calculated by multiplying the estimated board foot by species-specific stumpage prices that were dependent on wood quality. Timber values were obtained from the New Hampshire Department of Revenue Administration using average prices reported for the Northern Region for the period of October 1, 2024 to March 31, 2025 (revenue.nh.gov/taxes-glance/timber-tax; Table 2). For each species, stumpage prices were published as "low" and "high" which we interpreted as proxies for low- and high-quality wood, respectively. To represent mid-quality timber, we used the midpoint between the published low and high values.

We modeled four scenarios to capture a range of plausible wood quality distributions: (1) all wood classifies as pulpwood with value randomized within the reported low and high price range; (2) a fixed distribution of low (23%), mid (36%), and high (41%) quality timber; (3) a fixed distribution including pulpwood (17%) with low (25%), mid (35%), and high (23%) quality wood based on harvest observation reported by Luppold and Pugh (2016); and (4) a randomized distribution of pulpwood and sawtimber quality classifications with proportions drawn from a uniform distribution (0–1) and normalized to sum to one in each iteration. This simulation framework provides a robust estimation of both the mean and range of total merchantable wood values across the soil nutrient richness gradient by explicitly incorporating price uncertainty and variation in wood quality.

Statistical analyses

All statistical analyses were performed in R (R Core Team 2024). To meet assumptions of normality and homoscedasticity, wood and foliar nutrient concentrations and pools (Ca, Mg, K, and P) were log transformed prior to analysis. Linear mixed effects models were used to evaluate the fixed effects of soil nutrient richness, tree size classification, and tree

Table 2 Estimated monetary value for tree species by wood quality for northern New Hampshire, including pulpwood and sawlog values

Species	Pulpwood		Sawlog	
	Low value ($ ton^{-1})	High value ($ ton^{-1})	Low value ($ MBF^{-1})	High value ($ MBF^{-1})
Abies balsamea	$0	$4.41	$120	$175
Acer rubrum	$3.31	$11.02	$100	$225
Acer saccharum	$3.31	$11.02	$225	$450
Betula alleghaniensis	$3.31	$11.02	$150	$300
Betula papyrifera	$3.31	$11.02	$100	$220
Fagus grandifolia	$3.31	$11.02	$30	$120
Fraxinus americana	$3.31	$11.02	$130	$250
Picea glauca	$0	$4.41	$120	$175
Pinus strobus	$0	$3.31	$120	$200
Populus tremuloides	$3.31	$11.02	$30	$120
Quercus rubra	$3.31	$11.02	$200	$425
Tsuga canadensis	$0.55	$5.51	$30	$70

Pulpwood values are reported per metric ton, while sawlog values are reported per thousand board feet (MBF). The values for each species and wood quality were derived from the New Hampshire Department of Revenue Administration's Average Stumpage Value Information for October 1, 2024 to March 31, 2025.

genera on nutrient concentrations and pools while accounting for random variation among plots nested within forest developmental stages. Models were fit using the "lmerTest" and "lme4" packages.

We initially included interaction terms (Richness × Tree Size and Richness × Genus) in the full mixed effects models to test for interactive effects among predictive variables. However, several models produced singular fits or rank-deficiency warnings, which indicated insufficient data structure to reliably estimate interaction terms. Therefore, the final models evaluated only the main effects of soil nutrient richness, tree size classification, and genus. We used a Type III analysis of variance (ANOVA) using the "car" package to test the significance of fixed effects, including interactions. Post hoc pairwise comparisons were conducted using Tukey's Honest Significant Difference (HSD) tests using the "emmeans" package to identify differences among group means.

Model residuals were assessed for normality using the Shapiro–Wilk tests. Statistical comparisons and p-values are based on model adjusted marginal means estimated from the mixed effects models. Raw (unadjusted) means calculated directly from field measurements and biomass estimates are reported in the text and tables because ecological studies commonly present raw means which allows for interpretations and comparisons across other published studies.

Results

Forest genera composition and biomass across nutrient gradients

Forest composition varied distinctly along the nutrient richness gradient (Fig. 1). *Acer* was the most abundant genus across all three forests, but its dominance varied from 21% of stems at the Poor Forest to 63% at the Moderate Forest and 49% at the Rich Forest. The Poor Forest had a higher relative abundance of *Fagus* (27%) compared to the Moderate (15%) and Rich (11%) forests, and was the only forest where *Tsuga* was present. *Betula* comprised 18% of stems at the Poor Forest and 19% at the Moderate Forest but was far less common at the Rich Forest (0.36%). The Rich Forest

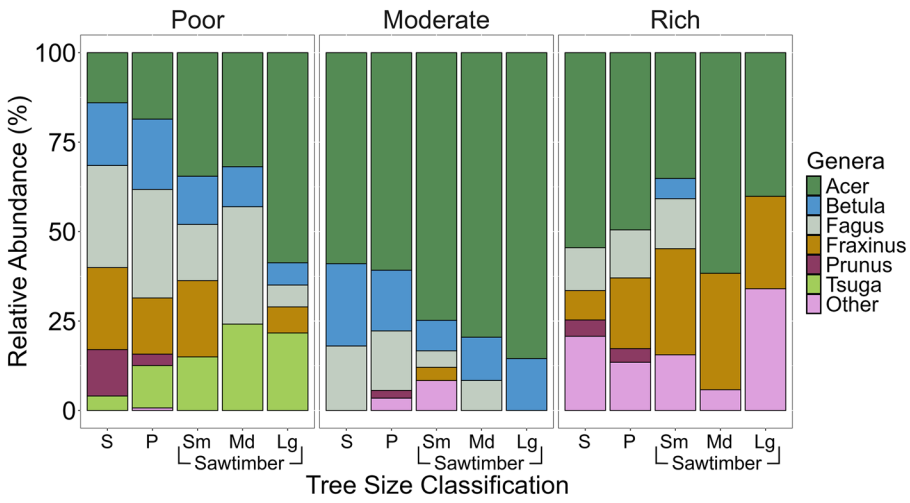

Fig. 1 Relative abundance of six dominant tree genera across five tree size classes along a soil nutrient richness gradient. Tree genera include *Acer*, *Betula*, *Fagus*, *Fraxinus*, *Prunus*, and *Tsuga* while all remaining genera are grouped as "Other". Size classes are ordered from smallest to largest: sapling (S), poletimber (P), small sawtimber (Sm), medium sawtimber (Md), and large sawtimber (Lg). Values present the proportion of total stems within each forest and size class averaged across 15 plots per forest

also had notable presence of *Fraxinus* (19%), which was more than the abundance at the Poor (16%) and Moderate Forests (0.32%).

Stem density declined across the nutrient richness gradient by ~ 28% from Poor to Rich, with 636 stems ha^{-1} at the Poor Forest to 528 stems ha^{-1} at the Moderate Forests and 457 stems ha^{-1} at the Rich Forest (Table S1). Poletimber trees consistently had the highest stem densities across the forests, whereas large sawtimber classes had the lowest. Basal area followed a similar pattern, with the Poor Forest having the highest values (27.0 m^2 ha^{-1}) and the Moderate Forest the lowest (19.3 m^2 ha^{-1}). Within all genera, poletimber had the highest basal area and saplings the lowest.

Diameter distributions were right skewed across the forests, with 62% of stems between 5–20 cm DBH and only ~ 1% exceeding 50 cm (Fig. S2). The Poor Forest had a greater proportion of small diameter trees than the Moderate and Rich Forests, although these differences among forests were not reflected in the larger size classes. Woody biomass was ~ 25–35% higher at the Poor Forest (153 Mg ha^{-1}) than the Rich (120 Mg ha^{-1}) and Moderate Forests (114 Mg ha^{-1}; Table 3). This pattern was consistent across *Acer*, *Betula*, and *Fagus.* Across all forests, poletimber trees contributed the largest proportion of woody biomass, while saplings contributed the least. Foliar biomass followed a similar pattern with the highest values at the Poor Forest (6.62 Mg ha^{-1}) and the lowest at the Rich Forest (4.85 Mg ha^{-1}). The Poor Forest produced 36% more foliar biomass than the Rich Forest, and poletimber trees accounted for the largest share of foliar biomass at each forest.

Effects of soil nutrient richness on aboveground nutrients

Wood nutrient concentrations and pools

Soil nutrient richness significantly influenced wood concentrations of Ca, Mg, K, and P (all $p < 0.01$; Fig. 2). Wood Ca concentrations were ~ 45% higher at the Moderate (8.17 g kg^{-1}) and Rich (8.18 g kg^{-1}) forests than at the Poor Forest (5.65 g kg^{-1}). Wood Mg concentrations peaked at the Moderate Forest (0.93 g kg^{-1}) which was 45% higher than

Table 3 Woody and foliar biomass (Mg ha^{-1}) by tree size class across the soil nutrient richness gradient. Woody biomass includes both the bole and branch components. Woody and foliar biomass were estimated from tree diameters

Woody and foliar biomass (Mg ha^{-1})	Soil nutrient Richness	Tree size classification				
		Sapling	Poletimber	Small Sawtimber	Medium Sawtimber	Large Sawtimber
Woody biomass All genera	Poor	6.56	42.4	17.7	25.5	60.6
	Moderate	4.76	46.2	17.3	28.8	17.4
	Rich	3.38	38.4	14.9	22.8	40.8
Woody biomass *Acer*	Poor	0.68	7.98	6.24	7.62	39.5
	Moderate	2.65	28.0	13.5	22.8	15.0
	Rich	1.75	19.4	5.69	15.2	24.0
Woody biomass *Betula*	Poor	1.19	8.10	2.51	2.97	4.06
	Moderate	1.10	7.55	1.46	3.33	2.38
	Rich	–	–	0.90	–	–
Woody biomass *Fagus*	Poor	2.28	15.9	3.74	11.19	5.33
	Moderate	1.01	9.00	0.94	2.70	–
	Rich	0.47	6.14	2.48	–	–
Foliar biomass All genera	Poor	0.41	1.98	0.70	1.00	2.53
	Moderate	0.28	2.29	0.87	1.32	0.81
	Rich	0.18	1.67	0.59	0.92	1.59
Foliar biomass *Acer*	Poor	0.11	0.46	0.30	0.33	1.82
	Moderate	0.18	1.55	0.72	1.17	0.76
	Rich	0.10	1.06	0.30	0.79	1.20
Foliar biomass *Betula*	Poor	0.06	0.37	0.09	0.10	0.10
	Moderate	0.05	0.28	0.04	0.09	0.06
	Rich	–	–	0.03	–	–
Foliar biomass *Fagus*	Poor	0.11	0.52	0.09	0.25	0.08
	Moderate	0.05	0.29	0.02	0.06	–
	Rich	0.02	0.20	0.06	–	–

Values are presented for all genera combined and for the most common tree genera (*Acer*, *Betula*, *Fagus*)

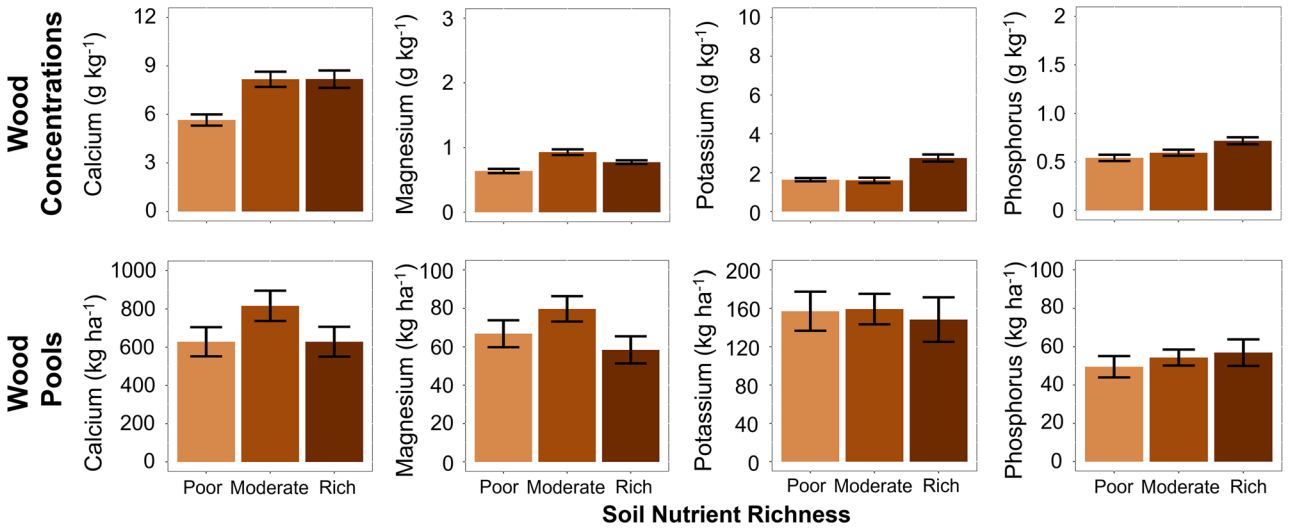

Fig. 2 Mean nutrient concentrations and pools of Ca, Mg, K, and P in wood across the soil nutrient richness gradient. Elemental concentrations are based on branch wood samples from 2022. Pools were scaled from elemental concentrations and tree biomass estimates using diameter at breast height based allometric equations. Bars represent plot level averages ($n = 15$ per forest) with standard error

the Poor Forest (0.64 g kg^{-1}) and 21% higher than the Rich Forest (0.77 g kg^{-1}). Wood K concentrations were highest at the Rich Forest (2.75 g kg^{-1}) which was 68% higher than the Poor (1.64 g kg^{-1}) and Moderate Forests (1.60 g kg^{-1}). Wood P concentrations were 10–20% higher at the Rich (0.72 g kg^{-1}) and Moderate (0.59 g kg^{-1}) forests compared to the Poor Forest (0.54 g kg^{-1}).

Soil nutrient richness also significantly influenced wood pools of Ca, Mg, and P (all $p < 0.01$), but not K ($p = 0.11$; Fig. 2). Wood Ca pools were highest at the Moderate Forest (816 kg ha^{-1}) which was 30% higher than at both the Rich (629 kg ha^{-1}) and Poor Forests (628 kg ha^{-1}). Mg pools followed the same pattern, with the Moderate Forest (79.8 kg ha^{-1}) having 19% more wood Mg than the Poor Forest (66.8 kg ha^{-1}) and 37% more than the Rich Forest (58.4 kg ha^{-1}). Wood P pools were slightly higher at the Rich (56.9 kg ha^{-1}) and Moderate (54.4 kg ha^{-1}) forests than at the Poor Forest (49.6 kg ha^{-1}). Wood K pools varied little among the forests (148–159 kg ha^{-1}) but did not differ significantly.

Foliar nutrient concentrations and pools

Foliar nutrient concentrations varied significantly across the soil nutrient richness gradient (all $p < 0.01$; Fig. 3). Foliar Ca increased by 39% from the Poor Forest (6.98 g kg^{-1}) to the Rich Forest (9.67 g kg^{-1}), with the Moderate Forest falling in between (7.84 g kg^{-1}). Foliar Mg concentrations peaked at the Moderate Forest (2.32 g kg^{-1}) which was about 37% higher than the Rich Forest (1.69 g kg^{-1}) and 48% higher than the Poor Forest (1.57 g kg^{-1}). In contrast, foliar K was highest at the Poor Forest (8.00 g kg^{-1}) which was 29% higher than the Moderate Forest (6.18 g kg^{-1}). Foliar P concentrations were ~ 23% higher at the Moderate (1.33 g kg^{-1}) and Rich (1.31 g kg^{-1}) forests than the Poor Forest (1.02 g kg^{-1}).

Foliar nutrient pools had weaker responses to soil nutrient richness. Foliar Ca pools did not differ significantly among forests and ranged from 21 to 32 kg ha^{-1} ($p = 0.13$). Foliar Mg pools were 27% higher at the Moderate and Poor Forests (both 6.86 kg ha^{-1}) than the Rich Forest (5.40 kg ha^{-1}; $p < 0.01$). Foliar K pools were strongly affected by nutrient richness with the Poor Forest (34.0 kg ha^{-1}) having 54% more K than the Rich (22.1 kg ha^{-1}) and Moderate (22.0 kg ha^{-1}) forests ($p < 0.01$). Foliar P pools did not differ significantly among forests and ranged from 3.61 to 4.53 kg ha^{-1} ($p = 0.25$).

Effects of genus and tree size on aboveground nutrients

Wood nutrient concentrations by genus and tree size classification

Wood nutrient concentrations varied significantly among genera for all nutrients ($p < 0.01$; Fig. 4) whereas tree size class had no detectable effect on concentrations of Ca, Mg, K, or P ($p \geq 0.49$; Fig. S3). *Fraxinus* consistently had the highest wood nutrient concentrations across all four elements. Wood Ca concentrations in *Fraxinus* (8.79 g kg^{-1}) and *Acer* (8.73 g kg^{-1}) were 46–63% higher than those in *Fagus* (5.98 g kg^{-1}) and *Betula* (5.40 g kg^{-1}). *Fraxinus* also had the highest wood Mg concentrations (0.88 g kg^{-1}) which was 6–32% higher than *Betula* (0.83 g kg^{-1}), *Fagus* (0.74 g kg^{-1}), and *Acer* (0.68 g kg^{-1}). Wood K

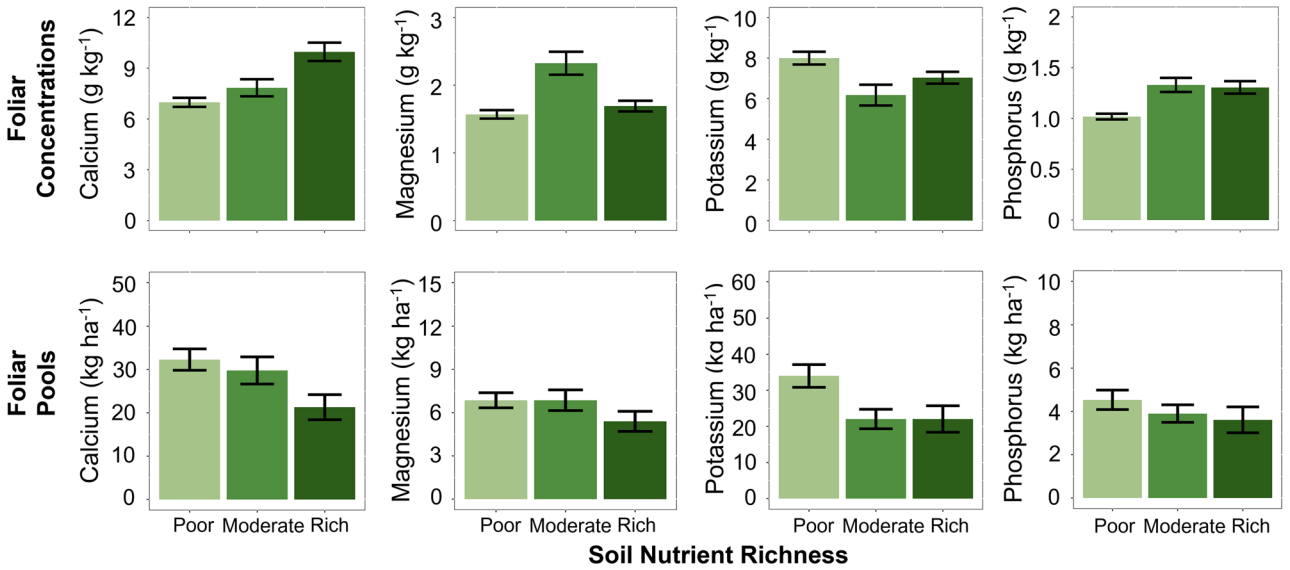

Fig. 3 Mean nutrient concentrations and pools of Ca, Mg, K, and P in foliage across the soil nutrient richness gradient. Elemental concentrations are based on green leaf samples from 2022. Pools were scaled from elemental concentrations and tree leaf biomass estimates using diameter at breast height based allometric equations. Bars represent plot level averages ($n = 15$ per forest) with standard error

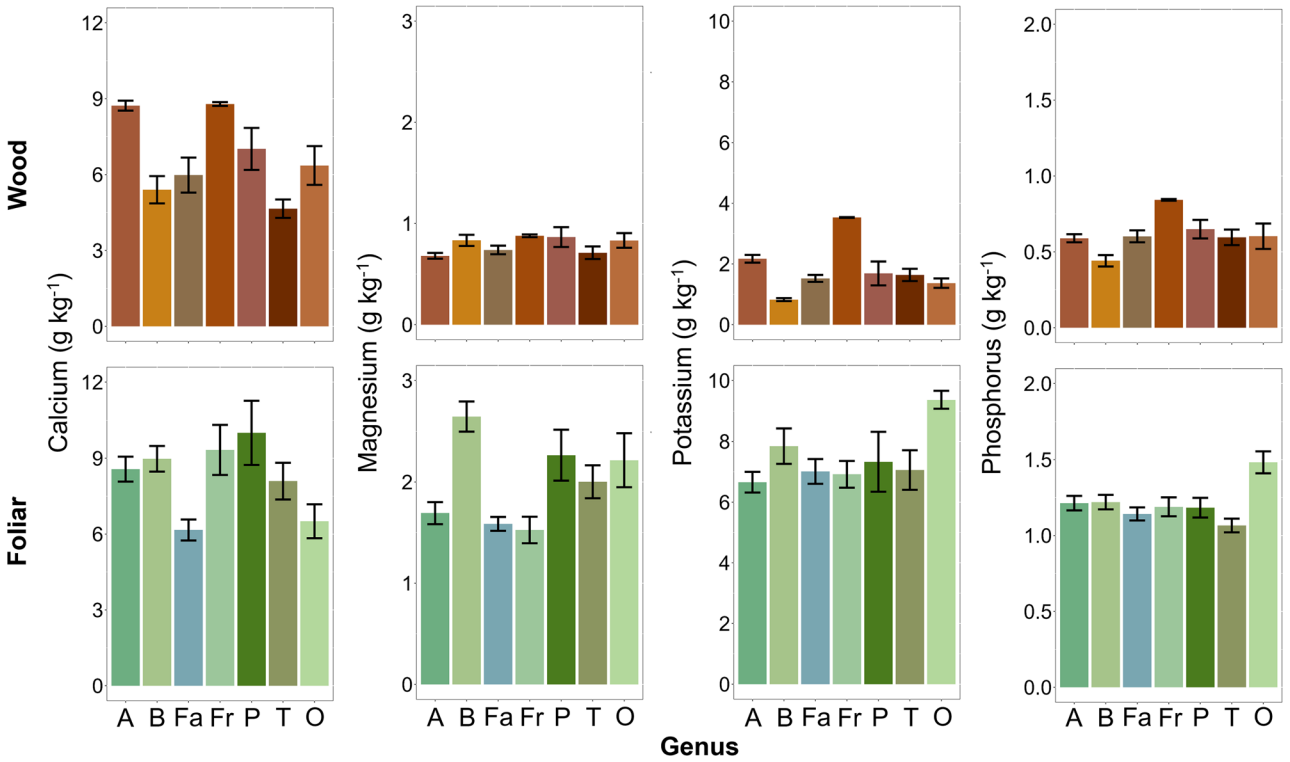

Fig. 4 Mean nutrient concentrations (Ca, Mg, K, P) in wood and foliage across dominant tree genera. Bars represent raw mean values with standard errors calculated from plot-level average for each genus. Since genus presence varied by plot, the number of samples differed among bars. Nutrient concentrations were derived from elemental concentrations of branch wood and green leaf samples from 2022. Genera are abbreviated as follows: "A" for *Acer*, "B" for *Betula*, "Fa" for *Fagus*, "Fr" for *Fraxinus*, "P" for *Prunus*, "T" for *Tsuga*, and "O" for Other

concentrations were 63% higher in *Fraxinus* (3.53 g kg^{-1}) than in *Acer* (2.17 g kg^{-1}) and were 330% higher than in *Betula* (0.82 g kg^{-1}). Wood P concentrations followed the same pattern, with *Fraxinus* (0.84 g kg^{-1}) exceeding all genera by 40–91%.

Foliar nutrient concentrations by genus and tree size classification

Foliar nutrient concentrations varied significantly among tree genera ($p < 0.01$; Fig. 4) but did not differ among tree size classes ($p > 0.77$; Fig. S4). *Fagus* consistently had the lowest foliar nutrient concentrations, and *Betula* among the highest. Foliar Ca concentrations were 44% higher in *Betula* (9.16 g kg^{-1}) than in *Fagus* (6.37 g kg^{-1}) and 8% higher than in *Acer* (8.48 g kg^{-1}). Foliar Mg concentrations were highest in *Betula* (2.64 g kg^{-1}) and *Tsuga* (2.00 g kg^{-1}) which were 10–74% higher than in *Acer* (1.82 g kg^{-1}), *Fraxinus* (1.56 g kg^{-1}), and *Fagus* (1.52 g kg^{-1}). Foliar K was greatest in *Betula* and *Prunus* (both 7.75 g kg^{-1}) which were ~ 15% higher than in *Fagus* (6.81 g kg^{-1}) and *Acer* (6.73 g kg^{-1}). Foliar P concentrations had smaller differences, with *Acer* (1.25 g kg^{-1}) having the highest values and *Fagus* (1.11 g kg^{-1}) and *Tsuga* (1.07 g kg^{-1}) the lowest.

Merchantable wood volumes and values

Merchantable wood volumes

Merchantable wood volume did not vary across the soil nutrient richness gradient ($p = 0.88$) or among tree genera ($p = 0.06$). However, merchantable wood volumes differed strongly by tree size ($p < 0.01$; Fig. 5). Poletimber trees contributed the greatest merchantable wood volume (9150 cm^3 m^{-2}), producing 57–113% more volume than any sawtimber size class. Merchantable volumes did not differ among small (5316 cm^3 m^{-2}), medium (5819 cm^3 m^{-2}), and large sawtimber trees (4290 cm^3 m^{-2}; $p > 0.66$).

When examined at the genus level, soil nutrient richness influenced merchantable wood volume only for *Acer* ($p = 0.03$). *Acer* produced approximately 25% more merchantable wood volume at the Moderate Forest than at the Poor Forest ($p = 0.02$), while volumes at the Rich Forest did not differ from either site ($p = 0.44$). Merchantable volume was not affected by soil nutrient richness for *Betula* or *Fagus* ($p \geq 0.16$). Although tree size class strongly influenced merchantable volume when all genera were combined, size-class effects were inconsistent within individual genera.

Merchantable wood volume had no significant relationship with soil nutrient availability (Fig. S5). Relationships with soil available Ca, Mg, combined Ca + Mg, or total base cation and P availability were weak and not significant ($R^2 \leq 0.15$; $p > 0.10$).

Merchantable wood values

Simulated forest value varied by wood-quality pricing scenario and soil nutrient richness (Fig. 6). When all wood was classified as pulpwood, forest values were uniformly low ($0.05–0.06 m^{-2}) and barely differed among forests. In contrast, scenarios that included higher-value wood grades produced clear differences among forests. Under non-pulpwood

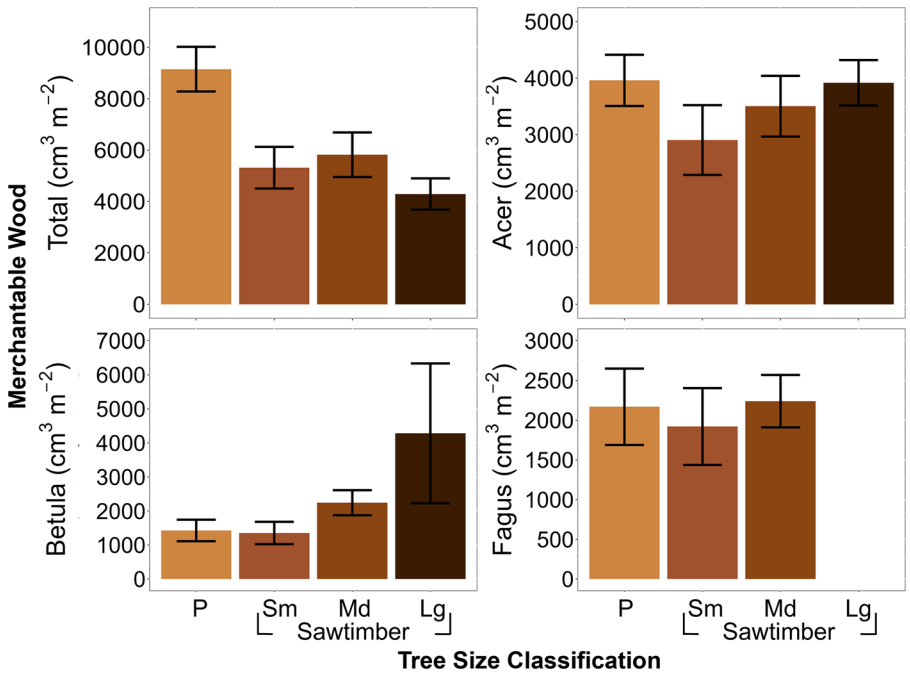

Fig. 5 Merchantable wood volume (cm^3 m^{-2}) across tree size classes and genera. The top-left panel depicts total wood volume across all genera, while the other panels show wood volume for specific genera: *Acer* (top-right), *Betula* (bottom-left), and *Fagus* (bottom-right). Size classes are ordered from smallest to largest: poletimber (P), small sawtimber (Sm), medium sawtimber (Md), and large sawtimber (Lg). Merchantable volume was calculated for poletimber and sawtimber size classes and saplings were excluded. Bars represent mean values with standard error. Volumes were estimated using published equations using diameter measurements

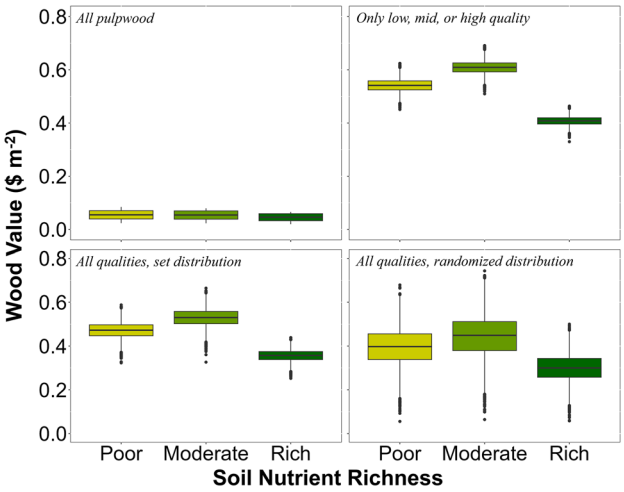

Fig. 6 Simulated merchantable wood value ($ m^{-2}) across the soil nutrient richness gradient under four quality pricing scenarios. Scenarios included: all wood as pulpwood (top-left), only sawtimber qualities (low/mid/high; top-right), a realistic distribution of wood quality based on published values (bottom-left), and randomized wood quality (bottom-right). Bars represent the interquartile range with whiskers that show 1.5×'s the interquartile range

pricing scenarios, the Moderate Forest consistently had the highest simulated value ($1.26 m^{-2}) which was 12–22% higher than the Rich ($1.13 m^{-2}) and Poor ($1.03 m^{-2}) forests. Including all wood grades based on published quality distributions reduced total values slightly but retained the same rank order among forests. The Moderate Forest again had the highest simulated value ($1.09 m^{-2}), followed by the Rich Forest ($0.97 m^{-2}), and the Poor Forest ($0.89 m^{-2}). A randomized quality distribution produced a similar pattern, with the Moderate Forest maintaining the highest value ($0.91 m^{-2}), followed by the Rich ($0.81 m^{-2}) and the Poor Forests ($0.74 m^{-2}).

Discussion

Soil nutrient richness drives tissue nutrient concentrations but not pools

We hypothesized that wood nutrient concentrations and pools would increase with soil nutrient richness. Our findings support this hypothesis for wood Ca, K, and P concentrations which were lowest at the Poor Forest and highest at the Rich, consistent with patterns of nutrient uptake and incorporation into woody biomass (Arthur et al. 1999; Yang et al. 2016; Roy et al. 2021). However, wood Mg concentrations did not follow this gradient. Instead, they peaked at the Moderate Forest which suggests that Mg assimilation may be shaped more by uptake physiology (van der Heijden et al. 2015), internal allocation strategies (Xu et al. 2022; Dalling et al. 2024), and competitive interactions with Ca, K, and manganese (Mn) at the root level (Gransee and Führs 2013; Chen et al. 2018).

The elevated wood Mg concentrations at the Moderate Forest are likely linked to differences in soil texture. The Moderate Forest has higher clay content and cation exchange capacity than the coarser textured Rich and Poor Forests (Rice et al. 2024), which are conditions that enhance Mg retention and plant uptake (Jobbágy and Jackson 2001; Brady and Weil 2016). Finer textured soils also maintain more consistent soil moisture which supports more consistent nutrient acquisition (Kozlowski and Pallardy 1997). While regional studies are limited, similar patterns of higher Mg at intermediate fertility sites have been reported in the White Mountains (Arthur et al. 1999; Yang et al. 2016). Slight concentration differences between our findings and those of earlier studies (e.g. Johnson et al. 2004) may reflect our use of branch wood which generally contains higher nutrient concentrations than bole wood (Oelmann et al. 2010; Choi et al. 2016).

Foliar nutrient concentrations exhibited more complex patterns than those in wood. Foliar Ca concentrations followed the expected nutrient richness gradient, with the highest Ca concentrations observed at the Rich Forest. In contrast, Mg concentrations were highest at the Moderate Forest, likely reflecting its relatively high soil Mg availability (Rice et al. 2024). Foliar K and P concentrations did not align with soil nutrient availability, suggesting that additional factors influence their concentrations. The strong relationship between foliar Ca and soil available Ca indicates a direct link between nutrient availability and foliar nutrient assimilation. However, the decoupling of foliar K and P from soil nutrient availability suggests processes such as the leaching of soluble elements through atmospheric precipitation and internal nutrient cycling play a stronger role in regulating foliar nutrient concentrations (Staelens et al. 2007; Turpault et al. 2021). Foliar nutrient concentrations observed in this study are consistent with those reported for hardwood forests in other portions of the study region (Yang et al. 2016; Hong et al. 2022). While some studies report a strong relationship between soil P availability and foliar P concentrations (Cross and Perakis 2011), our findings do not support this relationship, reinforcing the influence of atmospheric deposition on foliar K and P dynamics. Our findings suggest that luxury uptake of K and P was limited in the managed temperate forests, implying that trees on nutrient-poor sites may rely more on internal cycling rather than direct uptake from the soil. However, we did not measure nutrient resorption or efficiency, and therefore further research is needed to better understand how trees regulate nutrient use under varying soil nutrient conditions. From a forest management perspective, the leaching of these elements from foliage is likely not an issue, as these leached elements are presumed to return to

the forest floor and remain available for plant uptake. In fact, this process may be beneficial by contributing to soil nutrient pools before whole-tree harvests.

Despite differences in tissue concentrations, neither wood nor foliar nutrient pools (Ca, Mg, K, P) followed the nutrient richness gradient. Instead, they reflected total biomass accumulation. The nutrient Poor Forest had the highest woody and foliar biomass which offset lower concentrations and resulted in nutrient pools comparable to or exceeding those at the nutrient Rich Forest (Table 3). Foliar Mg and K pools were lowest at the Rich Forest while Ca pools were highest at the Poor Forest which were driven by differences in foliar biomass rather than concentration. These findings are consistent with other temperate hardwood forests, where nutrient pools often reflect forest structure more than soil chemistry (Rutkowski and Stottlemyer 1993; Palviainen et al. 2007; Dalling et al. 2024).

The unexpected high total biomass at the nutrient Poor Forest suggests that other factors are driving productivity. One possibility is greater N availability due to historical deposition, species traits, or more efficient cycling (Aber et al. 1998; Carter et al. 2017). Additionally, *T.F canadensis* and *F. grandifolia* were dominant at the Poor Forest and are late-successional, shade-tolerant species capable of accumulating biomass even on nutrient-poor soils (Rogers 1978; Halman et al. 2015; Nolet and Kneeshaw 2018). Finally, the Poor Forest was approximately 40 years older than the other two forests and had experienced less recent disturbance which provided more time for biomass to accumulate (Compton and Boone 2000; Després et al. 2017).

Combined, our results emphasize that nutrient concentrations in plant tissues are influenced by soil nutrient availability, while total nutrient pools are more shaped by forest composition, stand structure, and site history. This decoupling has important implications for nutrient exports during harvests and highlights the need to account for site-specific legacies and species traits in forest management planning.

Tree genus but not size affects tissue nutrient concentrations

Tree size classification did not influence wood or foliar nutrient concentrations, but concentrations varied among genera. *Fraxinus* had the highest wood Ca, Mg, K, and P concentrations, while *Betula* and *Fagus* had some of the lowest. In contrast, *Betula* had the highest foliar Ca, Mg, and K concentrations, whereas *Fagus* had the lowest. These results align with regional studies that found *Betula* generally have higher wood and foliar nutrient concentrations than *Fagus* (Park and Yanai 2009; Yang et al. 2016; Hong et al. 2022). The lack of influence of tree size classification on wood nutrient concentrations suggests that nutrient allocation is primarily driven by species- or genus-specific traits rather than size. These differences likely reflect species-specific nutrient uptake efficiencies (Hong et al. 2022; Gonzales et al. 2023), potential plasticity in nutrient acquisition strategies (Mao et al. 2019), mycorrhizal associations (Pena and Tibett 2024), and interspecies competition (Fahey et al. 1998). On nutrient-poor soils, trees may increase nutrient use efficiency by the resorption of more nutrients (Schmidt et al. 2015), may alter their root architecture to improve nutrient acquisition (Mao et al. 2019), or enhance mycorrhizal relationship to optimize nutrient acquisition and to maintain tree productivity (Pena and Tibbet 2024).

Tree size and genus affect tissue nutrient pools

While wood and green leaf nutrient concentrations did not differ by tree size, nutrient pools were highest in poletimber trees due to their greater biomass within each forest. This occurred because nutrient pools are a function of both concentration and biomass, meaning that even if nutrient concentrations remain constant across size classes, trees with more biomass will store greater total amounts of nutrients. Poletimber having the highest biomass among all three forests is most likely a function of natural succession with the ability of an area to hold a large quantity of small trees compared to large trees (Schroeder et al. 1997; Leak and Yamasaki 2010). Similarly, *Acer* had consistently higher wood and green leaf nutrient pools than all other genera, primarily due to its high biomass within each forest rather than inherently higher nutrient concentrations. This pattern has been established in previous studies showing that species with greater biomass accumulation contribute disproportionately to total nutrient pools, and tree size classifications influence total nutrient storage more than nutrient concentrations alone (Rutkowski and Stottlemyer 1993; Palviainen et al. 2007; Dalling et al. 2024). These findings suggest that nutrient export through harvesting will be more strongly influenced by tree size class and species of the removed tree, rather than by differences in wood or green leaf nutrient concentrations. Managing for species with high biomass, such as *Acer* in these forests, could enhance forest nutrient retention, while excessive removal may accelerate soil nutrient depletion.

Forest value reflects species composition more than soil fertility

Merchantable wood volumes were not significantly affected by soil nutrient richness. Instead, tree size classification emerged as the primary driver of merchantable wood volume, with poletimber trees contributing the most volume across the three forests. Additionally, while tree genera did not significantly affect total merchantable volume, *Acer* showed differences in merchantable wood volume depending on tree size classification, whereas *Betula* and *Fagus* did

not. The economic value of merchantable wood was more complex, as tree genera played a crucial role in determining the overall value of the forest.

Despite expectations that the nutrient Rich Forest would yield greater merchantable wood volumes due to improved tree growth, our results indicated no significant relationship between nutrient richness and total merchantable wood. One possible explanation is that factors such as tree age, stand history, and species composition overshadow the influence of soil nutrients. For example, the trees at the Poor Forest are approximately 40 years older than those in the other two forests due to differences in historical management of each forest. Additionally, the presence of *Tsuga* at the Poor site allows for increased stem density leading to higher overall biomass. Over time, the cumulative biomass compensated for its lower nutrient availability, reducing the expected difference in merchantable wood volume. Additionally, factors such as competition (Rozendaal et al. 2020), light availability (Beauchamp et al. 2025), and past disturbances (Després et al. 2017) may have influenced growth patterns, potentially masking any direct effects of soil nutrient richness on merchantable wood volume.

Tree size classification, however, only significantly affected merchantable wood volumes in *Acer*. Poletimber total merchantable wood volumes were significantly higher than the other size classifications. The higher woody biomass in poletimber is the driver for the high total merchantable wood volumes (Table 3). When considering tree genera, *Acer* had differing total volumes of merchantable wood yield. The differences in merchantable wood volume among tree genera further suggests that species or genera specific growth rates and ecological traits influence forest productivity more than soil nutrient richness if adequate soil nutrients are available. Such differences could potentially be due to moisture availability (Stern et al. 2023), species growth rates (Lévesque et al. 2016), shade tolerance (Walters and Reich 1996), and species or genera specific competitive strategies (Coates et al. 2009; Hartmann and Messier 2011).

Our findings aligned with previous research which found that tree size is a dominant factor influencing timber production, whereas soil nutrient availability may play a more indirect role (e.g., through species composition and stand dynamics). Other studies have found that in relatively young stands, the majority of the biomass is stored in smaller trees (Leak and Yamasaki 2010; Taylor et al. 2014; Searle and Chen 2017; Piponiot et al. 2022). The lower overall biomass of larger trees relative to smaller trees is attributed to the faster growth rates and higher stocking densities in smaller trees.

Unlike merchantable wood volumes, soil nutrient richness did have an impact on the economic value of the forest when wood quality was considered. Monte Carlo simulations revealed that wood value varied depending on the assumed distribution of pulpwood, low-, mid-, and high- quality sawtimber. The Moderate Forest had the highest wood value per unit area in three out of the four simulations. The consistently higher value at the Moderate Forest reflects the dominance of high-value *Acer* species which is one of the highest economically valued genera out of the genera present. Other studies have also found that the total valuation of a forest or region is skewed by the abundance of high valued species (Luppold and Bumgardner 2021). Our findings support that species composition and abundances play a critical role in the economic value of a forest and that slight differences in harvesting techniques or management practices can affect the overall economic value of a forest. When wood quality was randomized, the Moderate Forest remained the highest valued, suggesting that moderate soil fertility supports an optimized balance of wood volume, or that forests on relatively young soils can be actively managed to enhance productivity. Although soil nutrient effects may not be immediately reflected in merchantable wood value, this does not imply that these levels of productivity are sustainable over the long-term.

Limitations and future research directions

While this study provides insight into how soil nutrient richness shapes aboveground nutrient concentrations, pools, and wood value, several empirical limitations should be noted. First, we did not measure nitrogen (N) availability or cycling, even though N can interact with Ca and Mg and influence productivity. Therefore, we cannot determine whether unmeasured N dynamics contributed to the lack of a relationship between soil nutrient richness and merchantable wood volume. Second, we did not quantify nutrient resorption, root traits, or mycorrhizal activity which limits our ability to identify the mechanisms driving the observed patterns in tissue nutrient concentrations. Third, our sampling represents a single point in time, so our results do not capture seasonal or interannual variability in biomass or nutrient status.

Phosphorus may be another important limitation. All three forests had exchangeable P concentrations below 5 mg kg^{-1} which is a threshold associated with reduced productivity and wood quality (Gradowski and Thomas 2006; Rice et al. 2024). Since P supports lignification, vascular function, and energy metabolism, low available P could have contributed to the patterns we observed in nutrients and biomass in green leaves and wood. However, we did not directly measure P fluxes, weathering inputs, or wood quality so these relationships remain speculative.

Beyond soil fertility, species composition, soil moisture, and species-specific plasticity in nutrient uptake likely shaped differences among forests. For example, genera such as *Fagus* may maintain biomass accumulation on

nutrient-poor soils through conservative nutrient strategies, while other genera may rely more heavily on active uptake or mycorrhizal associations (Rust and Savill 2000; Tobner et al. 2013). These potential mechanisms were not directly evaluated in this study but could influence nutrient use patterns and productivity.

Future research should quantify belowground processes including N cycling, nutrient resorption, root traits, and mycorrhizal associations, and assess temporal variability in nutrient status to better understand how soil fertility interacts with species and stand structure. Addressing these gaps will improve our ability to predict long-term nutrient sustainability and support forest management strategies that maintain soil fertility while ensuring economic return.

Implications for forest management

The findings of this study highlight several considerations for sustaining forest productivity and soil fertility in actively managed forests, particularly as they relate to harvest planning, species composition, and long-term nutrient monitoring. Soil nutrient richness influenced tissue concentrations but did not predict merchantable wood volume or total aboveground nutrient pools. This decoupling has a direct consequence for harvest planning as soil fertility monitoring alone is not sufficient to assess either the timber yield potential or the nutrient cost of harvesting the timber. Stand age, structural development, and species composition were strong drivers of both volume and value in this study. Therefore, forest managers should consider incorporating routinely collected species-level composition and structural data with soil surveys to evaluate harvest potential, especially when comparing stands across heterogeneous landscapes. Specifically, stands dominated by *Acer* on moderately fertile soils may consistently outperform structurally similar stands on richer soils if *Acer* abundance is lower at the rich site, demonstrated by the Monte Carlo simulations across all four pricing scenarios.

Since nutrient concentrations varied substantially among genera, with *Acer* and *Fraxinus* having the highest wood concentrations and *Fagus* generally the lowest, the nutrient cost of a harvest is determined by which species are removed and not only by the volume removed. Harvesting large *Acer* sawtimber from a nutrient-poor site exports more Ca, Mg, K, and P than *Fagus*, and is compounded if residual leaves and branches are not left behind (Rothstein and Gadoth-Goodman 2023). Maintaining a portion of nutrient-rich genera on nutrient-poor sites may support long-term soil fertility even where commercial pressure favors their removal, and particularly where *Acer* recruitment is already constrained by *Fagus* dominance or repeated disturbance.

Poletimber trees contributed the largest aboveground nutrient pools across all three forests due to their high collective basal area, not just elevated nutrient concentrations in tissue. Therefore, harvests in stands with high poletimber stocking are removing a disproportionate amount of aboveground nutrient reserves even when the individual trees are commercially small. Forest managers working on nutrient-poor sites should consider this when designing thinning prescriptions especially since harvests focusing on poletimber removal have nutrient implications that are not apparent from stem size alone.

Finally, the decoupling we observed between soil nutrient richness, tissue concentrations, and total nutrient pools highlights the importance of monitoring both soil fertility and foliar nutrient status over time. Routine assessments of these indicators would allow forest managers to detect early signs of nutrient depletion, particularly in stands with high biomass accumulation on low-fertility soils. Monitoring foliar Ca in *A. saccharum*, which is sensitive to Ca depletion and soil acidification, may provide an early indication of nutrient stress before it is expressed in radial growth or crown conditions. Integrating these assessments with species composition inventories and stand structure data will support long-term productivity and economic viability in northern hardwood forests, especially on glaciated soils where nutrient availability varies substantially across the landscape.

Conclusion

This study reveals that while forest nutrient richness strongly influences nutrient concentrations in green leaves and wood, total aboveground nutrient pools are more strongly driven by forest structure, biomass distribution, and species composition. Nutrient-rich soils increased nutrient concentrations in leaves, but forest stands on nutrient-poor soils accumulated comparable or greater nutrient pools because of higher overall biomass. These results demonstrate that nutrient concentrations alone do not reflect stand-level nutrient storage. Tree genera differed substantially in nutrient concentrations with *Acer* and *Fraxinus* having the highest concentrations while *Betula* and *Fagus* generally had the lowest. These patterns reinforce that species-specific nutrient acquisition and allocation strategies play a critical role in shaping nutrient cycling across forests with heterogeneous soil fertility and should be considered when harvesting trees.

Merchantable wood volume did not differ across the nutrient richness gradient which indicates that stand age, structural development, and historical management influence wood production more than soil fertility alone. This finding has direct implications on harvest planning as soil fertility alone cannot predict timber yield, and volume-based assessments should be paired with species composition inventories and stand structural data to provide an accurate prediction of the harvest potential. However, merchantable wood value

varied among forests due to differences in species composition specifically, the abundance of high value *Acer*. Therefore, economic return from a stand is more sensitive to the species present than to the productivity of the site determined by the soil fertility.

These findings demonstrate that forests can remain productive and economically valuable across a range of soil nutrient conditions but sustaining productivity requires management that accounts for nutrient exports, species traits, and soil fertility. Since genera differ in foliar and wood nutrient concentrations, the nutrient content of harvest residues is not uniform. Residues from species with high nutrient concentrations, such as *Fraxinus* and *Acer*, contribute disproportionately to the return of nutrients to the soil. On nutrient-poor sites, retaining nutrient-rich residues, limiting whole-tree harvests, and retaining nutrient-rich species can help buffer the loss of soil nutrients. In contrast, nutrient-rich sites may allow for greater harvest intensities if managers monitor changes in species composition and soil fertility. Integrating soil fertility assessments, species composition, and species-specific residue retention into harvest planning supports long-term forest productivity while maintaining economic returns in northern hardwood forests.

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Data availability Data of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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