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Nutrient and regeneration responses to biomass harvesting and prescribed fire in a northern mixedwood forest

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ABSTRACT

Biomass harvesting is common across the northeastern United States, yet plant and soil responses in the years-to-decades after harvest are poorly understood. We assessed regenerating species composition and foliar and soil element concentrations after clearcutting with whole-tree harvesting, stem-only harvesting, and stem-only harvesting with prescribed burning in spruce-fir-hardwoods in Maine, U.S.A. We made measurements 50 years after the first treatment (applied 1964–65) and within 10 years after the second treatment (applied 2018), providing one of the longest evaluations of biomass harvesting in naturally regenerated temperate forests. In 2014, 50 years after the first treatment, there were few detectable differences in the composition of advance regeneration, or foliar and soil element concentrations among treatments; parent material was the primary driver of soil element variation. However, after the second repeated treatment, advance regeneration shifted toward early-successional species for at least seven years, and soil element concentrations of ammonium, phosphorus, potassium, and sulfur were elevated when prescribed burning was recently applied and the water table was shallow. These findings suggest that biomass harvesting with or without prescribed fire in spruce-fir-hardwoods has limited, transient effects on nutrients, though persistent shifts in overstory species as a result of intensive forest management may result in stand type conversions with ecological and economic implications.

1. Introduction

Many communities in the northeastern United States are economically reliant on forests for timber production (Daigneault and Gendron, 2025). Yet, tree removal methods vary and can leave different amounts of residual biomass (e.g., slash) on site, altering regeneration patterns and plant nutrient status (Brüllhardt et al., 2022; Clarke et al., 2021). For example, whole-tree harvesting removes the entire aboveground portion of the tree, including most branches and leaves. In northeastern forests, whole-tree harvesting is a common timber production method, accounting for 50–80 % of total production (Leon and Benjamin, 2012). In whole-tree harvesting, felled trees are typically grappled to a landing for processing, after which tree tops and branches are chipped or, if there is no biomass market, may be returned to machinery trails for site protection. In contrast, stem-only harvesting removes only the stem of the tree, processing felled trees at the stump and leaving branches and leaves to decompose on-site (Conway, 1982; Soman et al., 2020). The decision to use whole-tree or stem-only harvesting on commercial forestland is ideally based on silvicultural objectives, but is often determined by equipment availability. For example, the majority of logging crews in the northeastern state of Maine, where most of the commercial forestland in the region is located, are currently operating whole-tree harvesting equipment (Bailey et al., 2020). Where stem-only harvesting is applied, it is sometimes followed by prescribed burning (SOHB) of slash to clear debris, remove fuels, mobilize nutrients, and/or control the herbaceous layer (Knapp et al., 2009; Poulos, 2015; Weber and Taylor, 1992).

Harvesting exposes the forest floor to light and disturbs soil, creating

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conditions that can favor fast-growing early-successional species. Harvesting also physically removes carbon (C), nitrogen (N), and other nutrients from the ecosystem, and may further alter plant and soil nutrient status by accelerating decomposition through microclimate changes and soil disturbance, or by reducing plant uptake from severed roots. Previous studies in temperate mixedwoods (hardwood-softwood mixtures) have found lower foliar concentrations of some elements, particularly calcium (Ca), potassium (K), and magnesium (Mg), after intensive harvest (Johnson and Todd, 1998; Thiffault et al., 2006), consistent with broader evidence for both loss and mobilization of soil nutrients, particularly inorganic forms of N, phosphorus (P), and base cations (Mann et al., 1988; Thiffault et al., 2011; Tritton et al., 1987; Vos et al., 2023; Weetman and Webber, 1972). Few studies in the northeastern U.S. have attempted to quantify changes to soil nutrient concentrations after biomass removal and site treatments. Studies conducted at the Hubbard Brook Experimental Forest in New Hampshire and Weymouth Point in Maine applied whole-tree and/or stem-only harvests in the 1970s, finding that harvesting had the potential to decrease pH (Johnson et al., 1991) and cause losses of ions into streamwater (Dahlgren and Driscoll, 1994; Hornbeck et al., 1986; Likens et al., 1970). A study in three stand-age chronosequences (1–120 years) in New York, New Hampshire, and Massachusetts also identified long-term depletion of base cations and micronutrients in soil, attributed to the uptake of regenerating forest (Richardson et al., 2017).

Many observed losses attenuated over time. For example, at Hubbard Brook Experimental Forest, researchers observed an increase in soil nutrients mobilized into streamwater after whole-tree harvesting that was most pronounced during the second year after harvest, followed by a decline to near reference concentrations in 4–5 years (Dahlgren and Driscoll, 1994; Hornbeck et al., 1986). Similarly, the Weymouth Point study identified elevated concentrations of nitrate (NO_3-N) and Ca within the first three years after whole-tree harvest (Briggs et al., 2000), but after 35 years most measurements of plant and soil response did not differ across treatments, including forest floor and mineral soil C, N, extractable nutrients (Smith et al., 2022a), tree growth, and nutrient uptake (Smith et al., 2022b). Most long-term biomass removal studies in the northeastern U.S. did not quantify treatment effects after 20–35 years, and none tested the effects of repeated treatment or post-harvest burning.

Post-harvest burning can shift species composition in softwood and mixedwood forests of the Northeast, introducing pioneer species such as aspens (*Populus* spp.), birches (*Betula* spp.), and red maple (*Acer rubrum* L.), though spruce-fir (*Picea-Abies*) and northern hardwoods may re-establish as a subcanopy and increase in composition over time (Little, 1974). Burning also transforms the forest floor and can rapidly mobilize soil nutrients. Studies across diverse ecosystems have shown that burning significantly influences soil properties (Boerner et al., 2009; Certini, 2005). In particular, fire often temporarily increases availability of N, P, and exchangeable cations (Agbeshie et al., 2022), as well as soil pH due to the volatilization of organic acids and the deposition of alkaline ash (Kennard and Gholz, 2001; Pereira et al., 2019; Scheuner et al., 2004). Despite these well-documented effects elsewhere, such controlled studies remain scarce for northeastern forest soils.

Long-term trends in forest composition and productivity may be determined by management treatments, but they are also shaped by environmental conditions. In particular, previous studies of northeastern forests have noted that treatment effects on soil element concentrations covary with soil drainage class, although there is not enough data to identify consistent patterns in the direction or magnitude of effect (Briggs et al., 2000; Czapowskyj, 1979). Similarly, the role of parent material in shaping long-term soil conditions and subsequent plant productivity outcomes is well-known from a theoretical perspective (Jenny, 1941), and studies in the Northeast have established that soils derived from glacial till, glaciofluvial, and marine sediments can vary systematically in their physical and chemical characteristics (Marek and Richardson, 2020; Puhlick et al., 2019; Rice et al., 2024).

Studies that have explored relationships between harvesting and prescribed burning together have primarily been conducted in western North America and the southern Appalachia region of the U.S. (Brodie et al., 2024; Hood et al., 2020; Liu et al., 2024; Schwilk et al., 2009). Yet, with growing concerns about wildland fire in the Northeast (Gao et al., 2021) and the potential for increased use of prescribed burning for fuels management, it is increasingly important to evaluate potential management strategies that include prescribed burning.

A U.S. Forest Service biomass harvesting and prescribed burning experiment with repeated treatments on the same experimental units was established on a low-productivity site in 1964–65 at the Penobscot Experimental Forest in Maine (Fig. 1). Dominant conifers in the studied forest, i.e., red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), eastern hemlock (*Tsuga canadensis*), and northern white-cedar (*Thuja occidentalis*), are generally slow-growing and reliant on moist substrates for successful germination and survival. In contrast, associated hardwoods, e.g., red maple, paper and grey birch (*Betula papyrifera* and *B. populifolia*), and aspen spp., regenerate prolifically from seeds, root suckers, or cut stumps and grow rapidly in large openings. Studies of foliar (Czapowskyj, 1979) and soil (Czapowskyj et al., 1977) nutrient concentrations were made in 1973, eight years after treatments, and of aboveground stand structure and stocking (Muñoz Delgado et al., 2019) in 2014, 50 years after treatments. These studies describe a lack of treatment effect on soil and foliar nutrients after eight years, and a lasting shift from spruce-fir dominance to northern mixedwood (spruce-fir-hardwoods) 50 years after harvest. Foliar and soil nutrients 50 years after first treatment, short-term effects of treatment re-application, and the trajectory of ecosystem responses inferred from the combined findings of this 60-year-old study have not previously been reported.

To address these gaps, our study has three objectives that together aim to better understand the impacts of biomass harvesting with and without prescribed burning on a low-productivity temperate mixedwood forest one to 50 years after three management treatments (stem-only harvest, whole-tree harvest, and stem-only harvest with prescribed burning) are applied. We aim to 1) quantify the effect of management treatments on regenerating species composition, 2) measure the impact of management on foliar and soil element concentration, and 3) understand the relative impact of treatments vs. site characteristics on short- and long-term ecosystem responses.

Based on the silvics of dominant species, we hypothesized that all harvesting treatments would shift regenerating species composition toward sprouting and shade-intolerant hardwoods, and that this shift would be more pronounced following harvest plus burning than harvest alone. We further hypothesized that, given prior findings from this and related experiments (Briggs et al., 2000; Muñoz Delgado et al., 2019), foliar and soil element concentrations would not differ detectably from unharvested controls 50 years after the first treatment. However, after the second treatment, we expected that harvesting-induced element mobilization would accelerate losses, resulting in lower plant-available foliar and soil element concentrations in harvested than in unharvested stands (Dahlgren and Driscoll, 1994; Hornbeck et al., 1986). Finally, we hypothesized that both foliar and soil elements would be elevated where the water table is shallow and where soils are derived from glaciomarine parent material (Czapowskyj, 1979; Puhlick et al., 2019).

2. Methods

2.1. Study site

The study site is located in the Penobscot Experimental Forest (PEF) in Bradley, Maine, in the northeastern U.S. (44° 51' 56.754" N, 68° 38' 12.1812" W). The PEF is in a transition zone between eastern broadleaf and boreal forest types within the Acadian Forest region (Noseworthy and Beckley, 2020). The PEF has a mixedwood composition, composed of spruce (*Picea spp.)*, balsam fir (*Abies balsamea)*, eastern

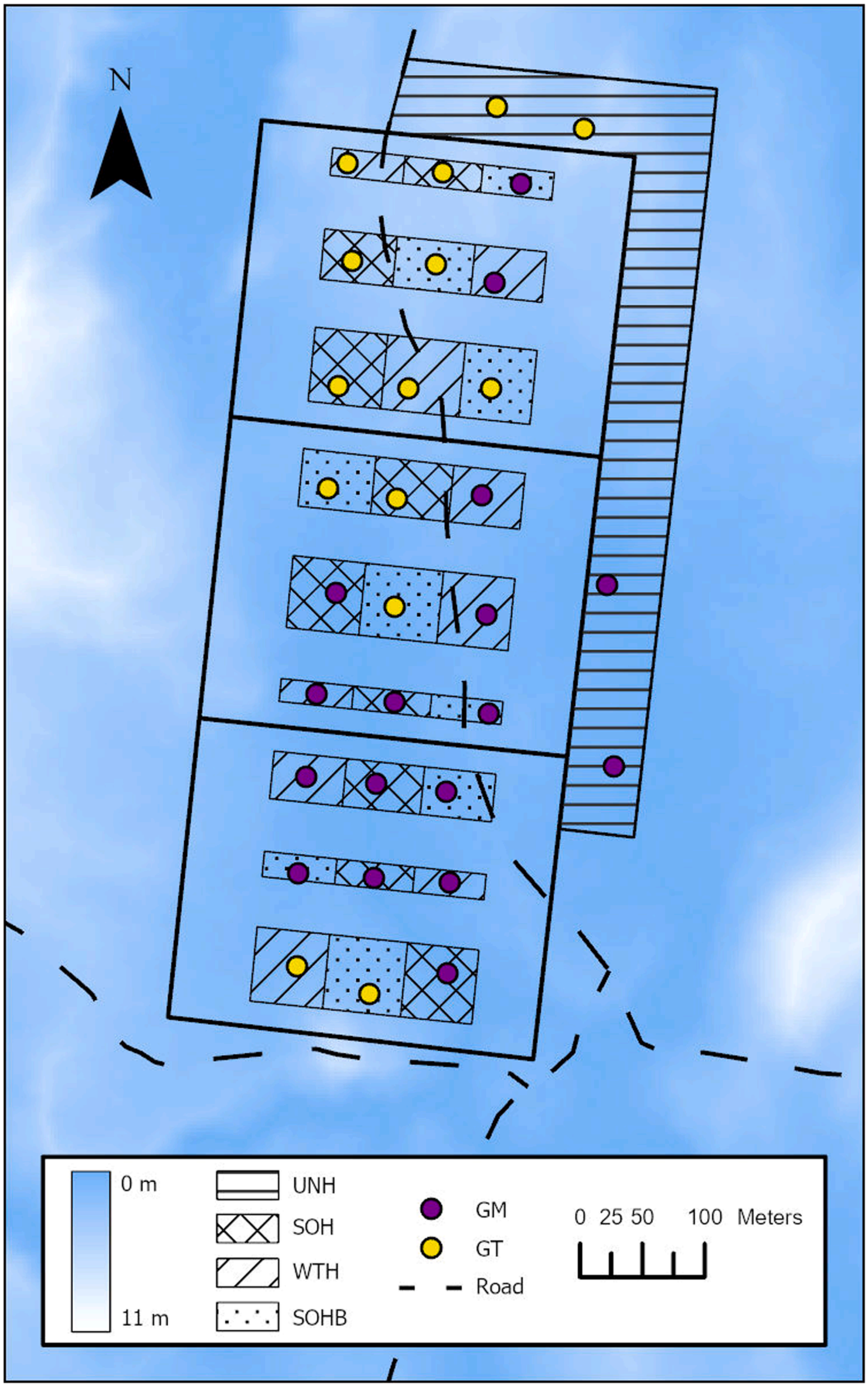

Fig. 1. Map of study area in Penobscot Experimental Forest, Bradley, Maine, U.S. Experimental units are located within three replicate blocks with randomly assigned treatments that include: stem-only harvesting (SOH; crosshatch), stem-only harvesting with burning (SOHB; dotted), and whole-tree harvesting (WTH; diagonal lines), and an unharvested reference area (UNH; horizontal lines). Permanent sample plots are indicated by circular symbols. Symbol color signifies whether the underlying parent material at the plot is glaciomarine (GM; purple symbols) or glacial till (GT; yellow symbols). Blue shading represents the LiDAR-estimated depth to the water table in meters (UNB Forest Watershed Research Center, 2014), with darker shading indicating a shallower water table. Dashed lines indicate gravel roads.

hemlock (*Tsuga canadensis*), and other softwoods and hardwoods with prolific natural regeneration (Brissette, 1996). Elevation on the PEF ranges from 29 to 77 m (m; Dibble, 2014). From 2000–2024, mean annual precipitation for the PEF was 118 centimeters (cm) with an average minimum and maximum monthly temperature of 3.0 °C and 14.0 °C, respectively (Fick and Hijmans, 2017). Soil properties vary throughout the study area, with soils derived from either glacial-till or marine sediments. In the southern portion of the study area, soils can be characterized as an association of Typic Epiaquepts, Aeric Epiaquepts, and Aquic Haplorthods (Scantic-Lamoine-Colonel series). The northern portion of the study area can be characterized as Typic Haplorthods (Danforth series; Soil Survey Staff, 2025). The study area was never cleared prior to this experiment but was repeatedly partially harvested between the 1700s and late 1800s, resulting in an uneven-age structure with trees ranging from new germinants to more than 150 years old in the 1960s (based on data collected in other PEF stands; (Seymour and Kenefic, 1998). Currently, rotations for naturally regenerated even-aged spruce-fir stands in the region range from 50 to 80 years, though this varies with dominant species and management objectives.

In management unit 33 (MU33) of the PEF, a 26-ha replicated experiment was initiated in 1964–65 with three treatments across 27 fixed-area experimental units (EUs) within three 7.2-ha replicate blocks, making up a randomized complete block design (Fig. 1). Within each block, three treated strips 60-m, 40-m, and 20-m wide were oriented east-west and separated by 40-m wide buffer strips, except for the northern- and southern-most buffer strips which are half that width. Each strip contained three 60-m long EUs between 60-m end buffers. The three treatments were clearcutting with whole-tree harvest (WTH, i.e., slash removed), stem-only harvesting (SOH, i.e., slash left on site), and SOH with post-harvest prescribed burning of logging residues (SOHB). Harvesting occurred over the winter of 1964–65. All trees ≥ 1.3 cm dbh were felled, delimbed in-woods with chainsaws (in SOH and SOHB treatments), and extracted using a cable skidder. In fall 1965, the SOHB experimental units were burned. The first treatments, applied in 1964–65, were monitored intermittently for 10 years (Bjorkbom and Frank, 1968; Czapowskyj, 1979; Czapowskyj et al., 1977; Rinaldi, 1970).

In 2014, the study was re-opened (Fig. 2). The original reference, which had been harvested in 1978–79 (Frank, 1979; Frank and Lawlor, 1978), was replaced with an area of comparable size in an adjacent unmanaged stand (Fig. 1). We established 31 permanent sample plots across the study area: four in UNH and nine each in WTH, SOH, and SOHB. Each plot consists of nested 0.02- and 0.008-ha circular plots with a common center for measuring overstory trees (defined as stems ≥11.4 cm dbh) and saplings (defined as stems ≥1.3 cm dbh but <11.4 cm dbh). Three 4-m^2 sub-plots are located at 0°, 90°, and 180° true north on the periphery of each 0.02-ha plot for measuring seedlings (defined as stems 15 cm tall to <1.3 cm dbh). Global positioning system (GPS) locations of all plot centers installed in 2014 onwards were obtained using a Trimble GeoXH GPS unit and differentially corrected through post-processing in GPS Pathfinder version 5.85 (Trimble Navigation, Sunnyvale, California, USA). Plots were randomly placed at least 5 m from the edge of the EU.

Overstory and sapling data were collected on a subset of 23 plots in 2014–15 (four UNH, seven WTH, six SOH, and six SOHB) and on all 31 plots in subsequent inventories, except saplings in 2025, which were measured on 29 plots. Seedling data were collected on sub-plots within sampled plots at each inventory except 2025. Soil and foliar element data were collected on a subset of 16 plots in 2014 (four UNH, seven WTH, and five SOH); no element data were collected in SOHB at that time. Soil element and pH data were collected on all 31 plots in 2018. In February-March of 2018, the original harvest treatments were re-applied to each EU in MU33. All trees ≥ 1.3 cm dbh were felled using a feller-buncher, delimbed with an in-woods stroke delimber (in SOH and SOHB treatments), and extracted using a grapple skidder. In September 2018, the SOHB experimental units were re-burned. For a timeline of treatments and measurements, see Fig. 2.

2.2. Forest composition and regeneration

Regeneration of seedlings and saplings was measured using sampling protocols from Waskiewicz et al. (2015). Seedlings were measured in June 2014, July 2018, and June 2019; saplings were measured in May 2014 and May 2025 (Fig. 2). Seedlings were tallied by species in the following height classes: ≥ 15 cm to < 30 cm, ≥ 30 cm to < 60 cm, ≥ 60 cm to < 1.4 m, and ≥ 1.4 m tall but < 1.3 cm dbh. Small saplings 1.3 cm ≤ dbh < 6.4 cm were tallied by species and 2.5-cm dbh class in the 0.008-ha nested sub-plot. Large saplings 6.4 cm ≤ dbh < 11.4 cm were tallied in the 0.02-ha plot, except in May 2025. At that time, all saplings 1.3 cm ≤ dbh < 11.4 cm were tallied in the 0.008-ha nested sub-plot by species and 2.5-cm dbh classes. Diameter at breast height measurements were made with calipers. Though trees ≥ 11.4 cm dbh were measured in May 2014, those data were described in Muñoz Delgado et al. (2019) and are not included in the present study. After the second treatment, there were no saplings or overstory trees (stems ≥ 1.3 or 11.4 cm dbh) at time of the July 2018 or June 2019 inventories, and no overstory trees (stems ≥ 11.4 cm dbh) at the time of the May 2025 inventory. There are thus no data for stems of those sizes associated with those inventories.

2.3. Foliar and soil measurements

2.3.1. Foliar elements

Foliar samples were collected in August 2014 from 16 plots: four

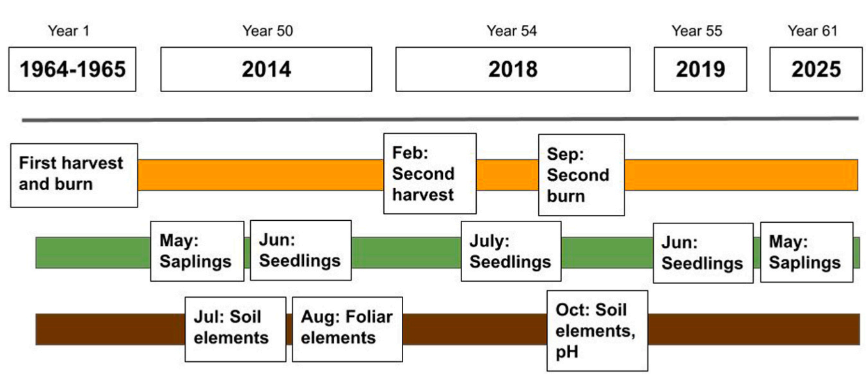

Fig. 2. Timeline of treatments and measurements. The orange timeline represents harvest and burn treatment applications (1964–1965, February 2018, and September 2018). The green timeline represents measurement of seedlings (June 2014, July 2018, and June 2019) and saplings (May 2014 and May 2025). The brown timeline represents measurement of foliar elements (Aug 2014), soil elements (July 2014 and Oct 2018), and pH (Oct 2018). Time periods represented are not to scale.

UNH, five SOH, and seven WTH. SOHB plots were not sampled at that time. Within each plot, four dominant overstory trees—two red maple and two balsam fir—were selected based on crown class (Nyland, 2016), except in one plot where two red maple and no balsam fir were selected. These species were chosen for their prevalence across the study area at the time of sampling. Foliar samples were collected from the upper one-third of each canopy using pole pruners, targeting current-year foliage and intact leaves free of insect and disease damage. Foliar tissue samples were washed, dried at 60 °C for two weeks, and ground in a Wiley mill passing through a 20-mesh screen. To estimate foliar aluminum (Al), boron (B), calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), phosphorus (P), and zinc (Zn), samples were dry-ashed at 550 °C using a muffle furnace, extracted with 50 % hydrochloric acid (HCl), and quantified using inductively coupled plasma emission spectroscopy (ICP). Foliar N was measured via direct combustion on a LECO-CN−2000 analyzer. Foliar element chemical analyses were carried out by the Maine Agricultural and Forest Experiment Station Analytical Laboratory in Orono, Maine following documented quality assurance (Agricultural and Forestry Experiment Station, 2016) and analytical protocols (The Northeast Coordinating Committee for Soil Testing (NECC-1312), 2025).

2.3.2. Soil elements

Differences in plant-available soil elements across treatments were assessed using ion exchange resin membranes (IERMs; General Electric Company, now Suez Water Technologies and Solutions), an approach similar to D'Orangeville et al., (2014), Johnson et al., (2005), and Littke et al. (2024). Sampling occurred at a distance equal to 10 times the dbh of each selected tree, positioned on a magnetic southern (~180°) aspect. The cation exchange membranes (CEM; Model CR67HMR) were saturated with sodium (Na^+) as the counter ion, and the anion exchange membranes (AEM; Model AR204SZRA) were saturated with chloride (Cl^-). CEMs and AEMs were stored at 4 °C throughout field implementation for quality assurance. IERMs were inserted beneath the organic horizon at a 45° angle and remained in situ for two weeks (Cooperband and Logan, 1994; Reinmann, 2006) in mid-July 2014 and October 2018. In 2014, 16 plots were sampled (identical to foliar element plots: four UNH, seven WTH, and five SOH) with four sampling locations per plot, except in one plot where there were two sampling locations. In 2018, 31 plots were sampled (four UNH, nine WTH, nine SOH, and nine SOHB) with three sampling locations per plot

Field-implemented CEMs and AEMs were cut in half for extraction. One half was placed in a 125 mL Erlenmeyer flask containing 30 mL of 2 N potassium chloride (KCl) for extraction of nitrate-nitrogen (NO_3–N) and ammonium-nitrogen (NH_4–N), and sealed with a deionized water–rinsed rubber stopper. The other half was extracted with 30 mL of 0.2 N HCl to recover Ca, K, Mg, and P. Blank extraction solutions of both 2 N KCl and 0.2 N HCl were included randomly within each batch (16–36 samples) for quality assurance. All flasks were shaken for one hour at low speed using a wrist-action shaker. Extracts were filtered through Whatman No. 42 filter paper under light suction and collected into labeled 60 mL containers. Nitrate- and ammonium-nitrogen were determined colorimetrically, and Ca, K, Mg, and P were quantified by ICP. After extraction, resin halves were air-dried and weighed to normalize element concentrations to mg kg^{-1} of dry resin. Similar to foliar element analyses, soil element chemical analyses were carried out by the Maine Agricultural and Forest Experiment Station Analytical Laboratory in Orono, Maine (Agricultural and Forestry Experiment Station, 2016; The Northeast Coordinating Committee for Soil Testing (NECC-1312), 2025).

2.3.3. Soil pH

Soil pH was assessed in October 2018 in 0.01 M calcium chloride ($CaCl_2$) at a 1:4 and 1:2 soil volume:$CaCl_2$ solution for the organic and mineral horizons, respectively. Soil for pH analysis was collected at the same plots as IERM samples. One organic and one mineral horizon sample per plot were extracted separately from within a 15.2 × 15.2 cm frame. Only the O_a and O_e sublayers were extracted for the organic horizon. Mineral soil beneath the E horizon, if present, was sampled to collect approximately 50 cm^3 of soil. Samples were air dried, then each organic soil sample was sieved using a 0.6-cm sieve and each mineral soil sample was sieved using a 2-mm sieve prior to analysis. Assessment of pH was completed by the U.S. Forest Service, Northern Research Station laboratory in Durham, New Hampshire.

2.3.4. Site characteristics

Cartographic depth-to-water table (DTW) at each plot location was estimated using light detection and ranging (LiDAR) (Murphy et al., 2011; UNB Forest Watershed Research Center, 2014). For a subset of 23 plots (four UNH, seven WTH, six SOH, and six SOHB), parent material was assessed 3.1 m from the plot border at true north. Using soil maps derived from Web Soil Survey (WSS; Soil Survey Staff, 2025) as a reference, parent material was visually confirmed or corrected in the field, by identifying defining properties such as soil texture, water movement, and presence of coarse fragments in the soil. For remaining plots, parent material was assessed geospatially using the WSS soil map classification at each plot location.

2.4. Statistical analysis

Our analysis approach uses comparisons to unharvested stands rather than repeated measures to infer treatment effects. We chose this approach because certain measurements (e.g., foliar elements, pH) were only collected either before or after the second treatment. Further, longitudinal analysis using data collected in the 1960s-1970s was not possible because original raw data were lost, though qualitative comparison to published findings from the decade after the first treatment allows us to infer potential long-term trends and differences between effects of one versus two treatments.

To test for differences in seedling and sapling stem density among treatments in each sampling year, we fit one-way ANOVAs to the log-transformed plot-level density with treatment as the only fixed effect and the unharvested reference as the baseline. To assess the effect of treatments and environmental covariates on foliar elements, soil elements, and pH, we used linear mixed models (LMMs) fit to log-transformed response variables. We first removed values that were more than five standard deviations from the mean of data as outliers, a very conservative assumption meant only to remove extreme errors (Barnett and Lewis, 1994). In foliar element, soil element, and pH data, we detected and removed two, six, and zero outliers, respectively. Subsamples collected within each plot were averaged to the plot level prior to analysis. We log-transformed response variables prior to analysis because foliar and soil data are right-skewed. We assessed log-normality using simulated residual plots and Q-Q plots. We fit two models to each response variable, one to test the relative effect of treatments and site characteristics on foliar and soil response variables, and another to test for pairwise treatment effects for each foliar or soil element separately. For the first model, we fit a LMM with the foliar or soil response variable from a given sampling year (i.e., 2014 or 2018) as the dependent variable; treatment, depth-to-water (DTW) table, parent material (PM), and horizon (if pH) as additive fixed effects; and element identity (e.g., nitrogen, calcium, phosphorus) as the random effect. Strip width was not found to be statistically significant in prior analyses and is partially accounted for by plot-level averaging. Including Block as a random intercept did not improve model fit and was thus dropped. In order to select the best model, we used a backward stepwise elimination procedure (Zuur et al., 2009), by first fitting models with all possible fixed effects, including interaction effects, and then removing the least-significant term sequentially until only significant fixed effects remained, while retaining random effects.

We developed five models to estimate 1) balsam fir foliar elements measured in 2014, 2) red maple foliar elements measured in 2014, 3) soil elements measured in 2014, 4) soil elements measured in 2018, and 5) pH measured in 2018. The best model according to AIC was 1) DTW only, 2) treatment only, 3) PM only, 4) treatment and DTW, and 5) treatment and horizon. However, herein we will present all model summary tables with additive fixed effects (treatment, DTW, PM, and horizon if applicable) included for consistency (Table 1).

For the second model, we tested for differences in element concentrations and pH across treatments by fitting linear models with the log-transformed response variable from a given sampling year (i.e., 2014 or 2018) as the dependent variable; DTW, PM, or horizon (if pH) as additive fixed effects; and a treatment by element identity (e.g., nitrogen, calcium, phosphorus) interaction effect. This model was used to calculate estimated marginal means and Sidak-adjusted pairwise contrasts (α=0.05) for each element.

Non-significant effects are reported alongside the minimum detectable difference (MDD), defined as the smallest difference that could be detected at 80% power with a α= 0.05 error rate using a pooled within-group standard deviation from a one-way ANOVA comparing the treatment in question with the unharvested control (sensu Yanai et al., 1999). ANOVAs were fitted to the log-transformed response variable. We compare observed fold-changes (treatment mean / unharvested control mean) with upper and lower MDD thresholds, which are symmetric on the log scale (MDD upper = MDD fold-change; MDD lower = 1/MDD fold-change). A difference is detectable if the observed fold-change exceeds the upper threshold or falls below the lower threshold. Linear mixed models were fitted using lmer (lme4 v.2.0–1) with Satterthwaite degrees of freedom for F-tests (lmerTest v.3.2–1; Satterthwaite, 1946). Model assumptions were checked using DHARMa simulated residuals and Q-Q plots (DHARMa v.0.4.7). Estimated marginal means and pairwise contrasts were calculated using emmeans (v.2.0.3). All analyses were conducted in R version 4.5.2. (R Core Team, 2025).

3. Results

3.1. Forest composition and regeneration

Fifty years after the first treatments in 2014, advance regeneration (seedlings and saplings) in all plots consisted primarily of balsam fir with low densities of other species, including birches, oaks (*Quercus spp.*), eastern white pine (*Pinus strobus*), and red maple (Figs. 3, 4a). Regenerating seedlings and saplings after the second harvest and burn treatments, however, had more early-successional species than unharvested plots for at least seven years. Four-to-five months after the second harvest in 2018, early-successional species including aspen species, birch species, and red maple were regenerating in both the WTH and SOH plots. Early-successional species also appeared seven-to-ten months after the SOHB plots were re-burned in September of 2018 (Fig. 3, Figure S1). Whole-tree harvest resulted in the largest number of estimated seedlings per square meter (Fig. 3), particularly of quaking aspen (*Populus tremuloides*), gray birch (*Betula populifolia*), and paper birch (*Betula papyrifera*) (Figure S1). Sapling regeneration data collected in 2025, seven years after the second harvest and burn, shows a similar near-term difference in regenerating species, with few saplings in unharvested plots and ingrowth of early-successional species across harvested plots, including bigtooth aspen (*Populus grandidentata*), quaking aspen, red maple, and gray birch (Fig. 4). Stem density of seedlings and saplings did not differ significantly among treatments in 2014

Table 1

Linear mixed models predicting a) balsam fir and b) red maple foliar element concentration with element identity as a random effect in 2014, soil element concentration with element identity as a random effect in c) 2014 and d) 2018, and e) pH. We report estimates back-transformed from the log-scale to geometric means and 95% confidence intervals, t-values, degrees of freedom (df), and p-values. SOH = stem-only harvest, SOHB = stem-only harvest with burning, DTW = depth-to-water table, and PM = parent material, GT = glacial till. Significance is highlighted as follows: $p \leq 0.1$ (·), $p \leq 0.05$ (*), $p \leq 0.01$ (**), $p \leq 0.001$ (***), or $p \leq 0.0001$ (****).

	Estimate	95% confidence intervals		df	t-value	p-value
a) Balsam fir foliar element concentration in 2014						
Intercept	275.58	51.74	1467.91	10.06	6.58	≤ 0.001***
Treatment (WTH)	0.97	0.87	1.07	150	−0.63	0.53
Treatment (SOH)	0.97	0.87	1.09	150	−0.46	0.65
DTW	1.05	1.01	1.10	150	2.21	≤ 0.05*
PM (GT)	1.11	0.97	1.27	150	1.56	0.12
b) Red maple foliar element concentration in 2014						
Intercept	312.31	54.14	1801.7	10.07	6.42	≤ 0.001***
Treatment (WTH)	0.83	0.74	0.93	161	−3.18	≤ 0.001***
Treatment (SOH)	0.88	0.77	1.00	161	−1.95	≤ 0.05*
DTW	1.00	0.95	1.05	161	−0.12	0.91
PM (GT)	1.11	0.95	1.29	161	1.30	0.20
c) Soil element concentration in 2014						
Intercept	65.63	15.46	278.61	8.76	5.67	≤ 0.001***
Treatment (WTH)	0.92	0.66	1.28	131	−0.48	0.63
Treatment (SOH)	1.15	0.78	1.69	131	0.71	0.48
DTW	1.04	0.90	1.20	131	0.56	0.58
PM (GT)	0.61	0.39	0.94	131	−2.23	≤ 0.05*
d) Soil element concentration in 2018						
Intercept	222.89	57.76	860.05	7.26	7.85	≤ 0.001***
Treatment (WTH)	1.86	1.18	2.93	205	2.66	≤ 0.01**
Treatment (SOH)	1.95	1.23	3.11	205	2.83	≤ 0.01**
Treatment (SOHB)	3.9	2.46	6.18	205	5.79	≤ 0.001***
DTW	0.82	0.73	0.93	205	−3.21	≤ 0.001***
PM (GT)	1.09	0.76	1.57	205	0.46	0.64
e) pH in 2018						
Intercept	3.61	3.21	4.06	55	21.67	≤ 0.001***
Treatment (WTH)	1.1	0.97	1.24	55	1.58	0.12
Treatment (SOH)	1.1	0.98	1.25	55	1.63	0.11
Treatment (SOHB)	1.48	1.31	1.67	55	6.48	≤ 0.001***
Horizon (Mineral)	0.9	0.84	0.96	55	−3.05	≤ 0.001***
DTW	0.95	0.92	0.99	55	−2.91	≤ 0.01**
PM (GT)	1.02	0.93	1.12	55	0.42	0.67

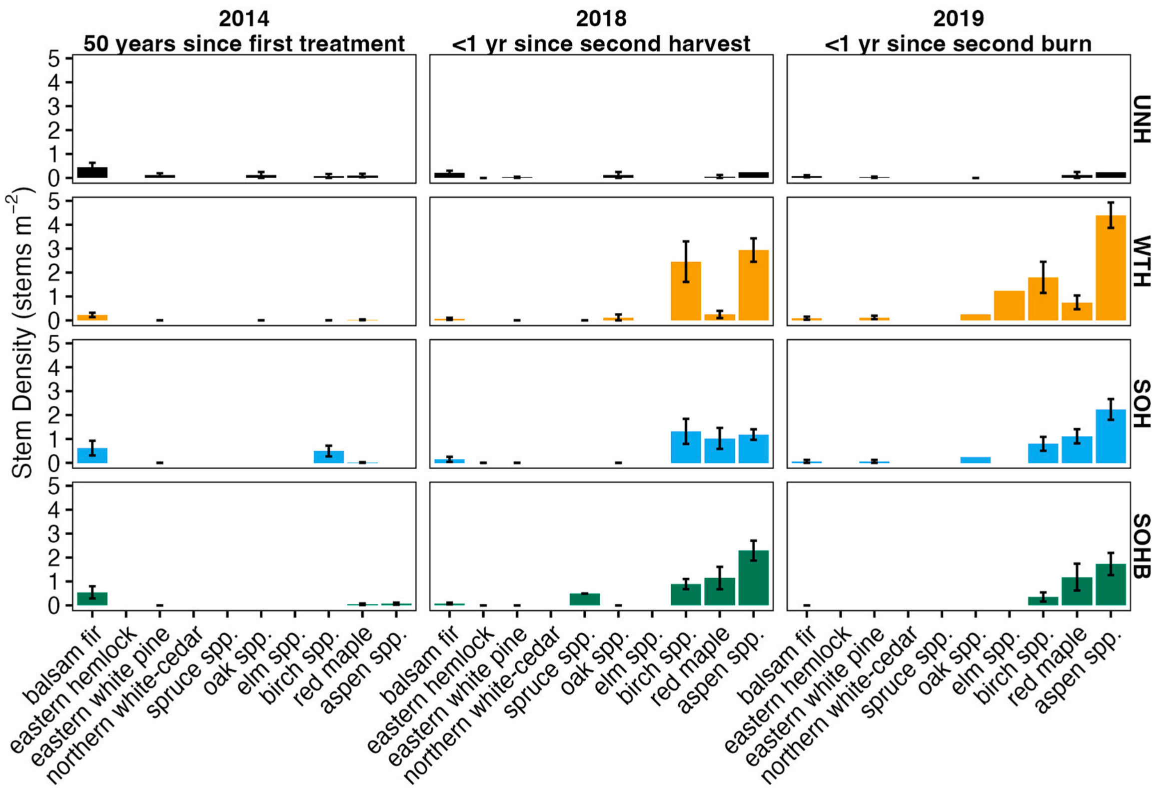

Fig. 3. Stem density (stems m^{-2}) of seedlings greater than 15 cm in height in the study area in June 2014 (50 years after first harvest and burn treatments; n = 4 UNH, n = 7 WTH, n = 6 SOH, n = 6 SOHB), July 2018 (<1 year after second harvest; n = 4 UNH, n = 9 WTH, n = 9 SOH, n = 9 SOHB), and June 2019 (<1 year after second burn; n = 4 UNH, n = 9 WTH, n = 9 SOH, n = 9 SOHB). UNH: unharvested, WTH: whole-tree harvest, SOH: stem-only harvest, SOHB: stem-only harvest with burning. Error bars are standard errors across replicate plots. Four plots had no seedlings recorded in 2014 (1 SOH, 2 WTH, 1 SOHB), and two plots had no seedlings recorded in 2019 (1 UNH, 1 SOHB).

(seedlings: $F_{3,15} = 1.48$, $p = 0.26$, saplings: $F_{3,19} = 0.07$, $p = 0.97$) but was higher than the unharvested reference in all treatments except for saplings in the SOHB treatment after the second harvest (seedlings 2018: $F_{3,27} = 13.07$, $p < 0.0001$, seedlings 2019: $F_{3,25} = 16.31$, $p < 0.0001$, saplings 2025: $F_{3,25} = 9.08$, $p < 0.001$). Seedlings were most commonly found at a height ≥ 30 cm but < 1.4 m (Figure S2), and while saplings in 2014 (before the second harvest) appeared to be distributed fairly evenly across measured size classes, saplings in 2025 appeared concentrated in the smaller size classes (e.g., dbh <6.4 cm; Figure S3).

3.2. Foliar and soil measurements across treatments

We did not detect any differences in balsam fir foliar element concentrations among treatments in 2014, 50 years after the first harvest; the range of observed fold changes from control means (0.63–1.0) was within the range of undetectable fold changes (median lower MDD = 0.7, median upper MDD = 1.5, Table S1) (Fig. 5, Table 1a). Balsam fir foliar element concentration was significantly affected by DTW. However, we did detect differences among treatments in red maple foliar Al, B, and Mn concentrations (Fig. 5, Table 1b), although the observed fold changes for Al and Mn were within the range of undetectable fold changes (Table S1). We do not have data to assess short-term changes in foliar element concentration after treatments were re-applied in 2018–2019.

Harvesting treatments did not significantly alter plant-available soil elements 50 years after first harvest (i.e., 2014, Fig. 6, Table 1c). Less than one year after the second harvest (i.e., 2018), potassium (K) concentrations were significantly elevated in SOH compared to UNH plots, but we did not detect differences in other elements (Fig. 6, Table 1d). With respect to the effects of prescribed burning, plant-available soil element concentrations were greater in SOHB relative to UNH one month after the second treatment (Table 1d), specifically NH_4-N, P, K, and sulfur (S) (Fig. 6). Other soil elements, particularly Ca and Mg, also tended to have higher concentrations in harvested and burned treatments, but pairwise comparisons were not significantly different. In 2014, observed fold changes (range: 0.5–2.6) were within the range of undetectable changes (median lower MDD = 0.3, median upper MDD = 3.8), but in 2018 observed fold changes (range: 0.4–15.4) exceeded minimum detectable fold changes (median lower MDD = 0.2, median upper MDD = 4.9) for detected effects in all but one case. Sulfur concentration in SOHB plots was significantly elevated compared to unharvested plots despite the observed fold change (5.3) falling within the range of undetectable differences (0.1–10.4; Table S1).

The relative importance of management treatments, depth-to-water table, and parent material on foliar and soil elements differed depending on the time since management treatments were applied. Fifty years after the first treatment (2014), parent material was the only site characteristic that explained variation in soil elements, with elevated element concentrations in glaciomarine-derived soils compared to glacial till soils (Table 1c). Parent material did not explain variation in soil elements one year after the second treatment; rather, soil element concentrations were elevated in plots where prescribed burning was applied and where the water table was shallower (Table 1d).

Soil pH < 1 year after the second harvest did not significantly differ among harvest-only treatments (i.e., UNH, SOH, WTH; Fig. 7, Table 1e). The second burn (i.e. SOHB) was applied one month before soil elements were measured; for this treatment pH was strongly elevated in both the organic and mineral horizons relative to UNH. Organic and mineral horizon pH values were within 0.4 units of each other for all treatment groups except for SOHB. The average organic horizon pH of recently burned soil was 1.1 units higher than the average pH of the underlying mineral soil.

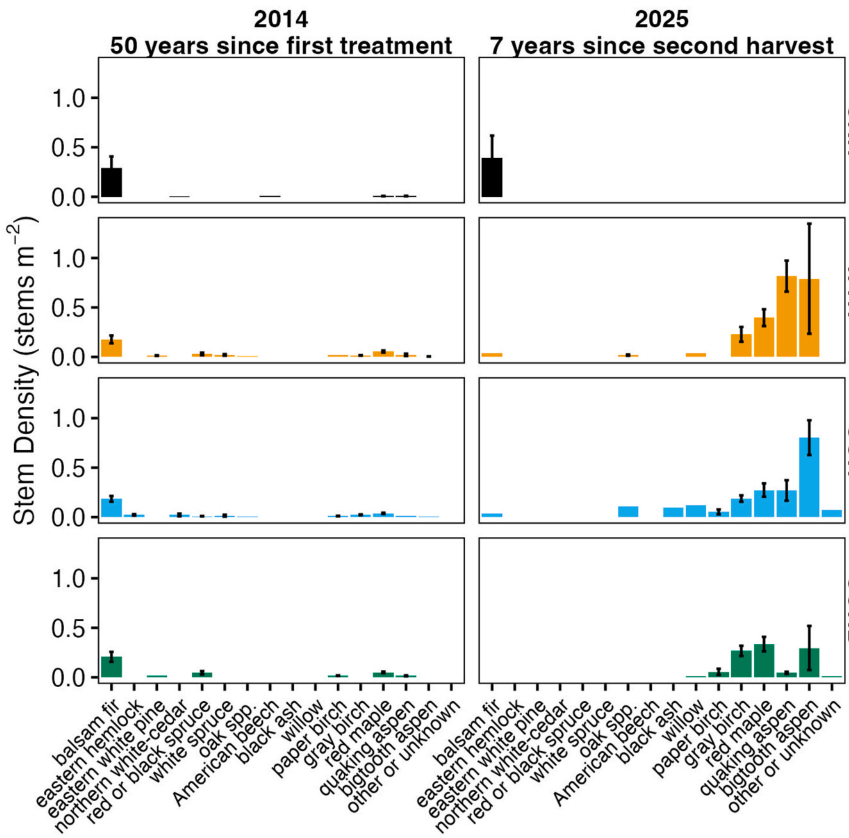

Fig. 4. Stem density (stems m^{-2}) of saplings collected in May 2014 (50 years after first harvest and burn treatments; n = 4 UNH, n = 7 WTH, n = 6 SOH, n = 6 SOHB) and May 2025 (seven years after second harvest and burn treatments; n = 3 UNH, n = 9 WTH, n = 8 SOH, n = 9 SOHB) in the study area. UNH: unharvested, WTH: whole-tree harvest, SOH: stem-only harvest, SOHB: stem-only harvest with burning. Error bars are standard errors across replicate plots.

4. Discussion

The findings of this study suggest that biomass harvesting with or without prescribed fire did not detectably change some indicators of site productivity (regenerating species composition, foliar element concentration, plant-available soil elements, and pH) 50 years after first treatment, but may temporarily affect site productivity indicators in the first decade after treatment, partially supporting our hypotheses about the transient nature of these disturbance effects. Although we found some evidence for changes within the first decade after the second treatment (as did previous researchers after the first treatment, e.g., Czapowskyj, 1979; Czapowskyj et al., 1977), these changes were not detectable in 2014, 50 years after the first treatment, suggesting that either treatment effects persist for years but not decades or that treatment effects are lower than detectable thresholds.

All methods of harvest and site preparation (i.e. slash removal or burning) shifted regenerating species composition to early-successional species for at least seven years, supporting our first hypothesis (Fig. 3, Fig. 4). Our observations are consistent with species composition shifts recorded after the first treatment in 1965 (Table 2), which found that hardwoods increased from 15% to 23% of stems ha^{-1} before treatment to 25–100% of stems ha^{-1} between four and 10 years after treatment (Bjorkbom and Frank, 1968; Czapowskyj, 1979; Czapowskyj et al., 1977, 1976; Rinaldi, 1970). This compositional change indicates a shift in forest type from spruce-fir dominance prior to the first harvest in 1964 to northern mixedwood (spruce-fir-hardwoods). This observed shift to more nutrient-demanding sprouting and pioneer species (e.g., red maple and aspen) is broadly consistent with other studies in this forest type following intensive silvicultural treatments (e.g. clearcutting; Barrette et al., 2024; Westveld, 1928). Despite this change in species composition, there were no consistent differences in year 50 between harvesting systems (i.e., stem-only vs whole-tree harvest) in stand structure and stocking (Muñoz Delgado et al., 2019), and no evidence of foliar or soil nutrient loss associated with harvesting (this study).

Data are not available for foliar elements on burned plots in 2014, 50 years after the first treatment, or for any treatment after the second harvest in 2018, so we cannot determine the effect of prescribed burn treatments or of more than one harvesting treatment on this attribute. Studies from forests of other regions (i.e., southern Canada and southeastern U.S. mixedwoods) found mixed evidence for altered foliar elements after harvest (Treasure et al., 2019), with some studies noting lower concentrations of some foliar elements after whole-tree harvest compared to stem-only harvest (particularly Ca, K, and Mg; Johnson and Todd, 1998; Thiffault et al., 2006). In our study area, Czapowskyj (1979) noted the potential effect of soil drainage, treatment, or an interaction of the two variables, on foliar element concentrations of young balsam fir trees eight years after first treatment in 1964-65.

In 2014, fifty years after first treatment, we did not observe differences between treatments in balsam fir foliar elements. We did observe lower foliar red maple Al and Mn concentrations in stem-only harvested plots, and lower B in whole-tree harvested plots, compared to unharvested plots. There are many potential mechanisms to explain these changes. For example, because B is a rock-derived nutrient, soil organic matter serves as its primary reservoir, and soil organic matter may be depleted in whole-tree harvested plots compared to control plots. If the slash deposited on stem-only harvested plots creates a more moist upper soil environment, it is possible that Al and Mn are preferentially mobilized. However, data are insufficient to make inferences about the strength of, and mechanisms underlying, these differences. Similar to Czapowskyj (1979), we also observed a small effect of soil water status (DTW) on balsam fir foliar elements, although the coefficient of this effect implies that a deeper water table is linked to a greater

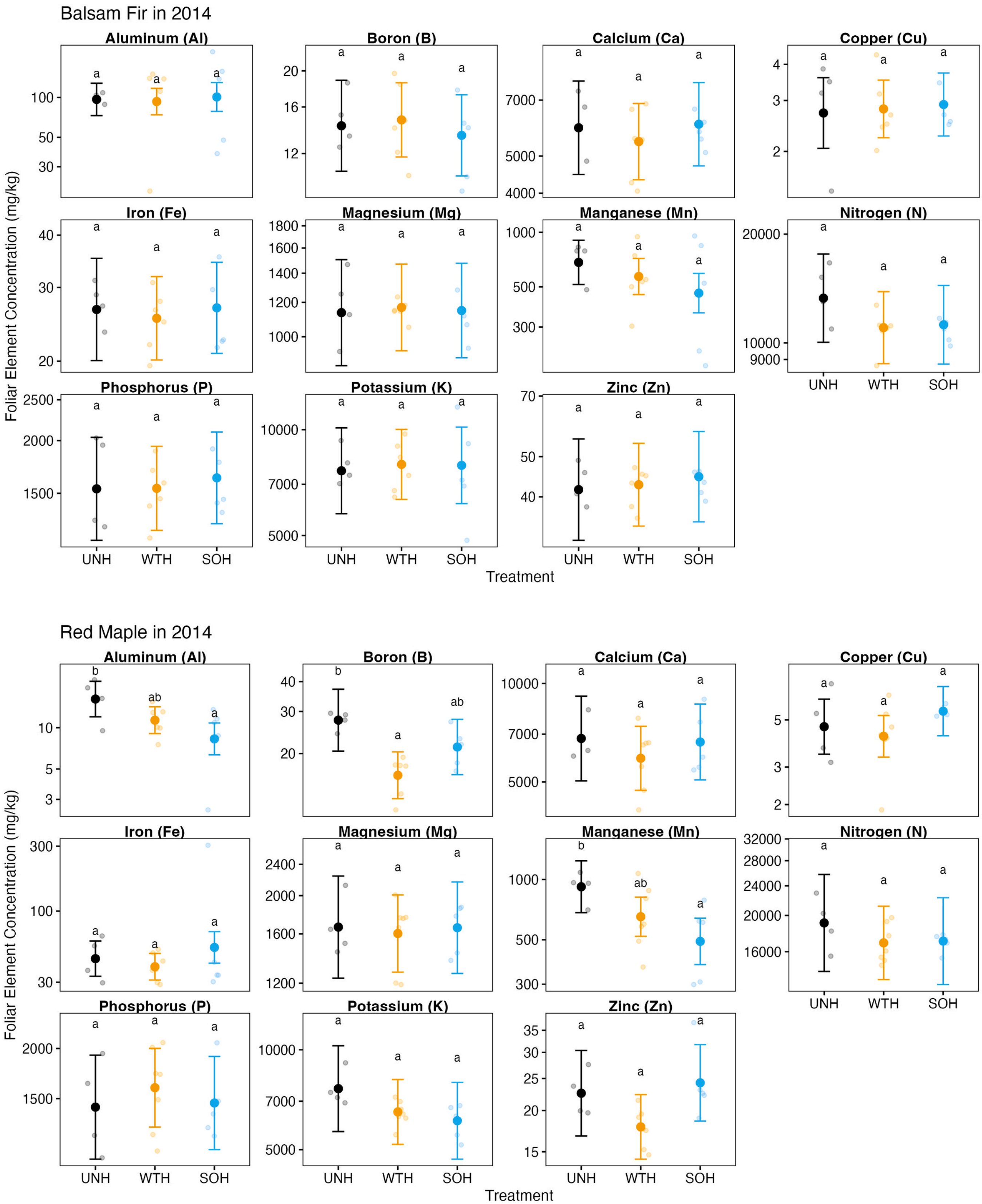

Fig. 5. Estimated marginal means of foliar element concentration in mg/kg for 11 elements assessed across treatment plots on balsam fir (upper) and red maple leaves (lower) in August 2014. Semi-transparent jittered points are observations. UNH: unharvested reference, SOH: stem-only harvest, WTH: whole-tree harvest. Error bars are 95% confidence intervals across replicate plots (n = 4 UNH, n = 7 WTH, n = 5 SOH). Treatments sharing a letter are not significantly different using Sidak-adjusted pairwise comparisons (α = 0.05).

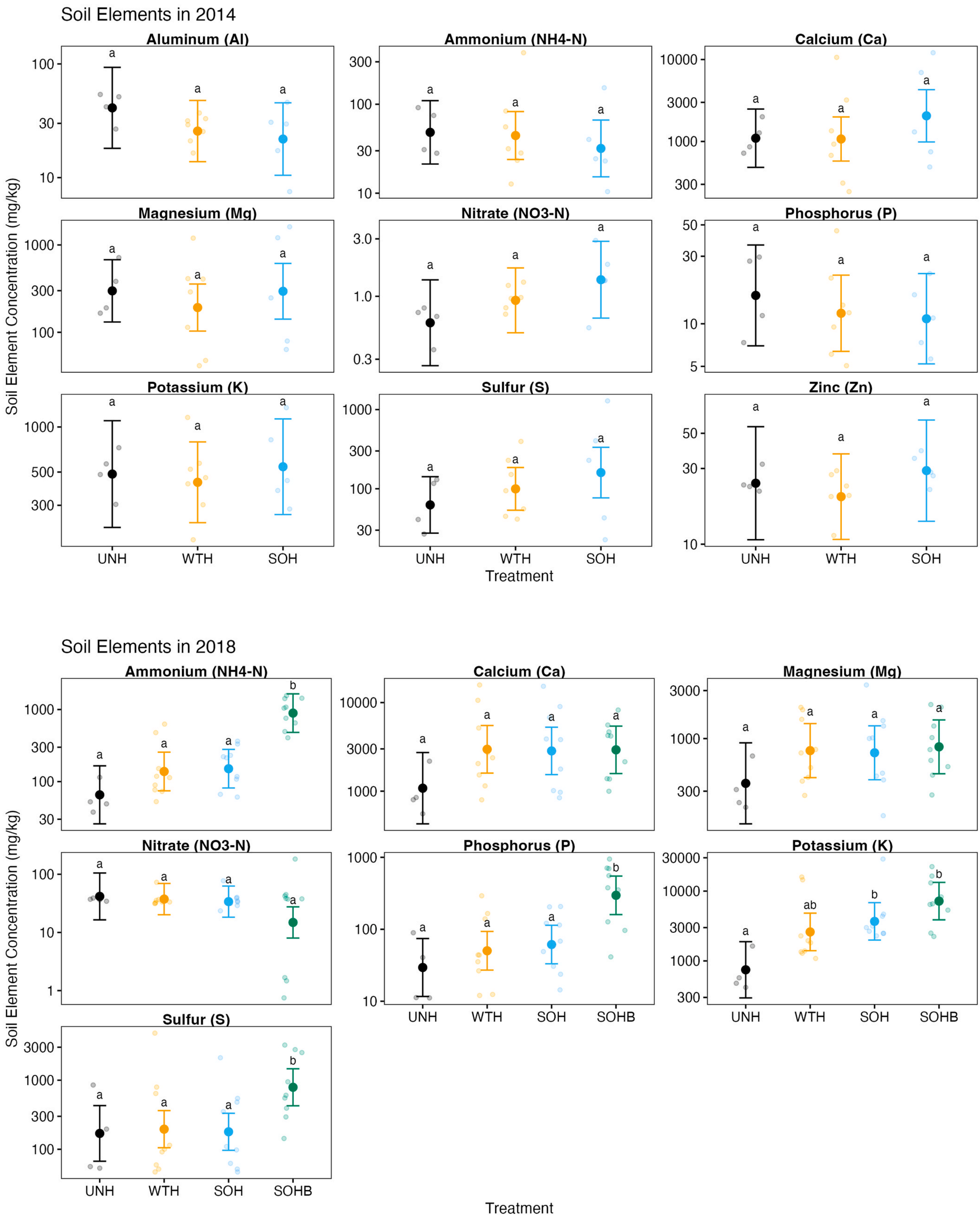

Fig. 6. Estimated marginal means of soil element concentrations in mg/kg of dried ion-exchange resin membrane in the four harvest and burn manipulation treatments in the study area in 2014, 50 years after harvest and burning (upper) and 2018, one year after second harvest and burning (lower). Semi-transparent jittered points are observations. UNH: Unharvested, WTH: whole-tree harvest, SOH: stem-only harvest, SOHB: stem-only harvest with burning. Treatments sharing a letter are not significantly different using Sidak-adjusted pairwise comparisons ($\alpha = 0.05$). Error bars are 95% confidence intervals across replicate plots ($n = 4$ UNH, $n = 9$ WTH, $n = 9$ SOH, $n = 9$ SOHB).

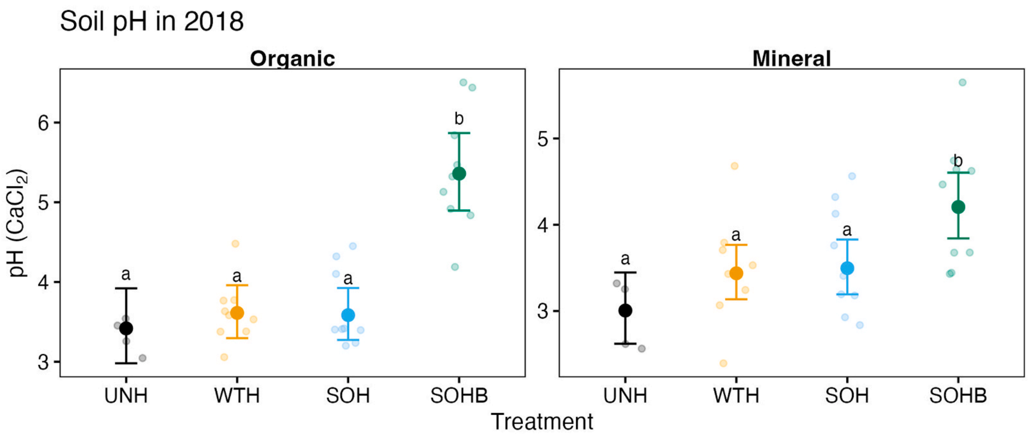

Fig. 7. Estimated marginal means of organic and mineral horizon pH ($CaCl_2$) for each treatment after second harvest and burn. Semi-transparent jittered points are observations. UNH: Unharvested, WTH: whole-tree harvest, SOH: stem-only harvest, SOHB: stem-only harvest with burning. Error bars are 95% confidence intervals across replicate plots (n = 4 UNH, n = 9 WTH, n = 9 SOH, n = 9 SOHB). Treatments sharing a letter are not significantly different using Sidak-adjusted pairwise comparisons (α = 0.05).

Table 2
Summary of differences across treatments < 1 year, 3–10 years, or 50 years after the first and second treatments. The superscript letter indicates whether findings are from this study (a) or from previous studies on the same experimental units (b-f). References are listed at the bottom of the table. WTH = whole-tree harvest, SOH = stem-only harvest, SOHB = stem-only harvest with burning. NA = indicates future sampling intervals for which the response variable has not yet been measured.

Feature	Time since treatment	After 1st treatment	After 2nd treatment
Overstory composition	**< 1 year**	No trees due to harvest[fg]	No trees due to harvest[a]
	10 years	Hardwood composition increased relative to pre-treatment after 10 years[e]	NA
	50 years	Hardwood composition increased relative to pre-treatment, but no difference in stand productivity[b]	NA
Seedling composition	**< 1 year**	Data not available	Regenerating seedlings were early-successional hardwoods (aspen, birch, maples)[a]
	3–4 years	Increase in young hardwoods across all treatments[f]	Not measured
	50 years	No detectable difference between treatments, balsam fir dominated[a]	NA
Sapling composition	**< 1 year**	None due to harvest	None due to harvest
	3–7 years	Increase in young hardwoods across all treatments[f] Softwoods over 15 cm tall failed to establish in SOHB, occurred in small numbers in WTH, and exceeded pre-cut in SOH[f]	Saplings are early-successional hardwoods (aspen, birch, maple)[a]
	50 years	Primarily balsam fir[a]	NA
Foliar elements	**< 1 year**	Not measured	Not measured
	8 years	Only Fe affected by treatments[c] Drainage class explains variation[c] Parent material not investigated[c]	NA
	50 years	Minor difference between treatments[a]	NA
Soil elements	**< 1 year**	Not measured	K elevated by SOH, otherwise no detectable difference between harvest treatments[a] NH4-N, P, K, S elevated by SOHB[a] Depth-to-water table explains variation[a]
	8 years	Ca, Mg, K elevated by harvest and burning[d] No difference in N, P, and other soil elements[d] Drainage class and parent material explains variation[d]	NA
	50 years	No detectable difference between treatments[a] Parent material explains variation[a]	NA
pH	**< 1 year**	Not measured	Elevated by SOHB in both horizons[a]
	8 years	Elevated by SOH and WTH in the organic horizon[d] Elevated by SOH in the mineral horizon for poorly drained sites[d]	NA
	50 years	Not measured	NA

a (This study)
b (Muñoz Delgado et al., 2019)
c (Czapowskyj, 1979)
d (Czapowskyj et al., 1977)
e (Czapowskyj et al., 1976)
f (Rinaldi, 1970)
g (Bjorkbom and Frank, 1968)

concentration of nutrients in leaves (Table 1). Though we did not observe an effect of depth to the water table or parent material on red maple foliar elements, there may be unmeasured climate, seasonal (Tian et al., 2025), or biological predictors that would explain variation in foliar element concentration and warrant future investigation. Both depth to the water table and parent material can feasibly constrain foliar element concentration. A lack of available water may limit nutrient uptake to absorptive fine roots (Schlesinger et al., 2016), while stands on marine-sediment-derived soils were shown in previous work at the PEF to have a higher site quality index compared to glacial-till-derived soils (Puhlick et al., 2019).

Studies of whole-tree and stem-only harvesting in naturally regenerated forests have observed limited declines of some soil element concentrations 5–20 years after intensive harvest (e.g., clearcutting with whole-tree harvesting compared with stem-only harvesting) (Johnson and Todd, 1998; Papaioannou et al., 2018; Thiffault et al., 2006). However, as with foliar elements above, there are typically multiple elements tested in these studies with only a few significant differences identified. Considering all data reported, a conservative interpretation of these studies is either that most soil elements did not change after harvest over the long term, or that we do not have enough evidence of change due to the heterogeneity of soil element concentrations and the large sample size needed to achieve statistical power. There is more robust evidence of soil element loss when considering rates of loss measured from soil solution chemistry, where order of magnitude losses are often observed after whole-tree harvest in the northeastern U.S. (Briggs et al., 2000; Dahlgren and Driscoll, 1994). However, these effects are typically limited to the first 3–5 years after harvest. In another study in Maine, even though harvesting induced losses of soil elements observable from solution chemistry, the total loss of nutrients (N, P, K, Ca, Mg) from the site was < 5% of total nutrient stock (Briggs et al., 2000; Smith et al., 2022a). Thus, even when nutrient losses measurably increase after harvesting in the short term, these changes may not detectably affect long-term nutrient availability due to the large size of the soil nutrient pool.

In the present study, we observed no effect or a small effect of either whole-tree or stem-only harvest on short- or long-term soil element concentrations. Eight years after first treatment in 1964, forest floor and soil element concentrations did not vary substantially across treatments (Czapowskyj et al., 1977). Though we did not find significant differences between unharvested and harvested plots for most soil elements measured < 1 year after the second harvest, this may be a result of undersampling rather than a lack of true effect. In Fig. 6, element concentration values tended to be higher in harvested plots relative to unharvested plots, but high variability in these data limited our ability to draw conclusions. Minimum detectable difference ranges of soil elements were larger than those of foliar elements and pH, and in some cases, 10- or 12-fold changes would have been required to detect a difference (Table S1). We detected these changes when treatment effect sizes were sufficiently large, such as when prescribed burning was recently applied. Yanai et al. (1999) found that a loss of ~19% in forest floor Ca concentration would have been required to be statistically detectable at the intensively sampled Hubbard Brook Experimental Forest. Given our experimental design and high spatial variability of soil element concentrations, driven in part by heterogeneity in water table and parent material, we cannot rule out that modest but meaningful differences in elements occurred below detectable thresholds.

There was limited evidence for elevated pH in harvest-only treatments. In our study, pH values tended to be higher in harvested plots, but this effect was not significant. Czapowskyj et al. (1977) noted that pH values were elevated on stem-only harvest plots on poorly drained sites in our study area. Possible explanations for elevated pH after harvest include the sudden absence of root exudation containing organic acids (Oburger et al., 2009), changes in soil microclimate and nitrification rates (Hornbeck, 1992), or mobilization of elements from decomposing harvest residues or severed plant roots (McGivney et al., 2019). Together the studies summarized in Table 2 suggest that there has been no detectable or persistent loss of stand productivity after harvesting in this northern mixedwood stand.

The second (2018) stem-only harvest with prescribed burning was the only treatment with significantly higher available soil NH_4-N, P, K, S, and pH relative to reference plots, with variation in element concentrations explained by both treatment and water table depth. Disturbance-related elevation of soil nutrients may support the growth of regenerating species, but a portion of these mobilized nutrients can be lost to leaching (Houle et al., 2009), depending on the redox conditions of the soil (Anas et al., 2026). After the first treatment in 1965, Czapowskyj et al. (1977) found limited evidence of higher available soil Ca, Mg, and K in clearcut areas (whole-tree harvesting, stem-only harvesting, and stem-only harvesting with burning) relative to unharvested forest 8 years after the first treatment in our study area, with variation explained by both drainage class and parent material. Fifty years after the first treatment, we observed no consistent difference in soil elements in clearcut plots relative to unharvested plots, and variation in element concentration was only explained by parent material (Table 1c). These findings suggest that over 0–10 year timescales, prescribed burning and soil water availability can mobilize soil macro- and micro-nutrients into plant-available forms, but productivity over multi-decadal timescales appears to be primarily controlled by parent material, supporting our final hypothesis that both foliar and soil elements would be elevated where the water table is shallow and where soils are derived from glaciomarine parent material.

Our findings suggest that one biomass removal treatment did not induce lasting detectable changes in nutrient dynamics at our study site, though studies of repeated harvest suggest that multiple applications of high-intensity treatments can change forest productivity in lasting ways (Kaarakka et al., 2014; Rogers et al., 2017), and therefore merit further study. There were lasting changes in overstory species composition following biomass removal, i.e., a shift toward greater dominance of sprouting and early-successional hardwoods that persists into the overstory (Muñoz Delgado et al., 2019), though composition of regeneration established beneath the canopy in year 50 suggests potential recovery of softwood dominance, primarily balsam fir. This finding is consistent with Barrette et al. (2024), who found that clearcutting can trigger successional setbacks and delay composition recovery by up to a century. Repeated application of clearcutting, as in the present study, further delays that recovery.

Spanning six decades from the first harvest in 1964–1965 to sapling remeasurement in 2025, the present study provides a rare assessment of response to repeated biomass harvesting in the studied ecosystem, with findings (from the published literature) within 10 years after the first harvest and (from our remeasurement) 50 years after the first harvest and within 10 years after the second harvest. The similarity in response after the first (Bjorkbom and Frank, 1968; Czapowskyj, 1979; Czapowskyj et al., 1977, 1976; Rinaldi, 1970) and second treatments, coupled with our finding that earlier-reported differences were no longer detectable after 50 years, suggest that post-second-treatment responses will similarly resolve. We cannot rule out that undetected short- and long-term treatment effects exist at smaller fold changes than our experimental design can detect, but ongoing re-inventory and re-analysis can strengthen or challenge the theory that harvesting and prescribed burning effects are transient. Future studies could follow forest productivity measurements in the study area and quantify the ecosystem-level changes in C and N stocks, as well as fuels across management treatments – relevant for estimating both potential C sequestration and fire risk mitigation for northern mixedwood forests.

In conclusion, biomass harvesting and prescribed burning in a low-productivity temperate spruce-fir forest as applied in this study did not detectably change regenerating species composition, or foliar and soil nutrition 50 years later. However, immediately after both the first and second treatment, changes in regenerating species composition and some plant-available soil elements were detectable, and (in the case of the first treatment) resulted in lasting changes in overstory composition. We also found that the site characteristics explaining differences in soil elements changed over time, with depth-to-water table explaining variation in soil elements < 1 year after the second treatments, but parent material explaining variation 50 years after the first treatments, suggesting that short-term trends in soil nutrient status are shaped by management and soil water availability, but long-term trends in soil nutrient status are shaped by edaphic conditions that change only over geologic time. As such, these findings provide a framework for considering how soil-site relationships change over time when interpreting productivity outcomes of biomass harvesting and prescribed burning.

CRediT authorship contribution statement

Rose Z. Abramoff: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation. **Ivan J. Fernandez:** Writing – review & editing, Supervision, Resources, Methodology. **Laura S. Kenefic:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Muñoz Delgado Bethany L.:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Data curation, Conceptualization.

Declaration of Competing Interest

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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123980.

Data availability

All experimental data generated in this study are publicly available at the following DOI: doi: 10.2737/RDS-2026-0033. Ancillary datasets used in select analyses are cited where referenced in the text.

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