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Long-term treatments alter acidification, fertility and carbon in soils of the Fork Mountain long-term soil productivity experiment

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Abstract

Historic atmospheric acidic deposition resulting from the combustion of fossil fuels may alter the pools of important nutrients and base cations in sensitive forest soils. This raises concern that chronic acidic deposition, particularly when coupled with intensive forest biomass harvesting, may diminish long-term soil fertility, forest productivity, and carbon storage potential. To address these concerns, the Fork Mountain long-term soil productivity experiment was initiated in 1996 at the Fernow Experimental Forest, West Virginia. The replicated experimental design consists of 16 plots (0.2 ha) that receive one of four treatments: (1) whole-tree harvesting (removal of all aboveground biomass, WT plots); (2) whole-tree harvesting + ammonium-sulfate fertilization (WT + NS plots); (3) whole-tree harvesting + ammonium-sulfate fertilization + dolomitic lime (WT + NS + Lime plots); and (4) untreated reference plots. We present forest floor and soil chemistry responses after ~25 years of treatment and evaluate the temporal changes to illuminate these results. Soil acidification has occurred, and base cation movement through the soil profile was observed, with effective cation exchange capacity increasing slightly in the deepest soil horizon by the end of the 25 years. However, some of our hypotheses were not supported. In particular, soil C did not increase over time with fertilization/soil acidification but was mainly altered by WT harvesting, as were other nutrients. Dolomitic lime provided some amelioration of acidification, but surprisingly, most of the changes in base cations appeared to be the results of Mg, not Ca, likely due to greater tree requirements and uptake of Ca.

1 | INTRODUCTION

Acidic deposition has been an environmental concern for decades, and although somewhat ameliorated in the US by the Clean Air Act amendments of 1990 (Congressional Research

Service, 2022; www.epa.gov/castnet), the long-term effects on forest ecosystems remain a concern globally. Early results from long-term acidification experiments at the US Forest Service Fernow Experimental Forest (FEF) in West Virginia and elsewhere suggest that historic atmospheric acidic deposition resulting from combustion of fossil fuels may deplete the pool of important nutrient and base cations in sensitive forest soils (Adams et al., 2006; Bailey et al., 2005; Fernandez et al., 2003; Fowler, 2014; Gilliam et al., 2020)

Abbreviations: ECEC, effective cation exchange capacity; FEF, Fernow Experimental Forest; LTSP, long-term soil productivity; NS, ammonium-sulfate fertilization; REF, untreated reference; SOM, soil organic matter; WT, whole-tree harvesting.

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and have implications for soil carbon (C) pools (Adams & Angradi, 1996; Eastman et al., 2021). Despite improvements in air quality related to reductions in SO₂ and NO_x (e.g., Mathias & Thomas, 2018), the long-term trajectory of forest soil nutrient and C cycling in response to these reductions is not well understood.

Research on the effects of intensive forest removals on site productivity has been conducted for many years (Powers, 2006; Thiffault et al., 2011). Despite a robust body of research and increasing interest in the bio-economy and intensive harvesting of forest biomass for climate change mitigation (Galik et al., 2021), there is still a need to understand the long-term consequences of and uncertainty surrounding intensive forest removal. Intensive biomass removal can deplete soils of nutrients and exacerbate soil acidification through reductions in soil organic matter (SOM) and buffering capacity (Akselson et al., 2007; Jiang et al., 2018; Thiffault et al., 2011), although effects are highly variable and dependent on forest type, soil genesis, and other factors (Johnson & Curtis, 2001; Nave et al., 2010; Smith et al., 2022).

Decades of chronic acidic deposition, particularly when coupled with intensive forest harvesting, has the potential to strongly diminish long-term soil fertility, forest productivity, and forest C storage potential (Adams, 1999; Eastman et al., 2022; Nave et al., 2010; Yanai et al., 2003). To address these concerns, a study affiliated with the long-term soil productivity (LTSP) study (Powers, 2006) was initiated on the FEF in 1996 and was designed to investigate the interaction of forest biomass removal and acidic deposition on long-term soil fertility and C storage.

Specifically, the Fork Mountain LTSP study evaluates the influence of nutrient removals, both through air pollution-related leaching and through intensive harvest, on long-term forest productivity through examination of nutrient cycling, biomass production, and stand development over time. The treatments consist of: whole-tree harvesting (removal of all aboveground biomass other than the forest floor; WT); whole-tree harvesting in combination with fertilization (WT + NS); and whole-tree harvesting with fertilization and liming (WT + NS + LIME). There is also an uncut, untreated reference (REF). The WT treatment removes nutrients, particularly calcium (Ca) and magnesium (Mg), in aboveground vegetation. Ammonium sulfate fertilizer is being added to mimic elevated acidic deposition (Adams et al., 2004) and increase leaching of nutrients from the soil. The addition of dolomitic lime is to test whether relatively simple amelioration techniques can be used to mitigate soil acidification and base cation loss.

In this paper, we will focus on soil acidification and soil nutrient changes, in particular base cations, carbon, nitrogen (N), and phosphorus (P), during the first 25 years of the experiment (1996–2021). This study and the treatments are ongoing, and as the stands are reaching crown closure, other parts of this effort will evaluate how these soil changes

Core Ideas

- Soil acidification was created through fertilization and whole-tree harvesting.
- Changes in forest ecosystems, including the soils, often require decades to manifest and understand.
- Soil acidification can be mitigated, somewhat, in forest soils.
- The links between soil chemistry, productivity, and diversity required further exploration.

affect forest communities in central Appalachian hardwood forests, including vegetative species composition, structure, diversity, and productivity (Fowler et al., 2015; Storm et al., 2022; Walter et al., 2021).

Herein, we evaluate the effects of the experimental treatments on soil (a) after ~25 years of treatments, from soil samples collected in 2021, and (b) describe the changes in soil nutrients based on repeated sampling to elucidate the processes over time. To evaluate changes due to acidification, we will look at pH, acidity, and aluminum (Al^{3/2+}) concentrations. We hypothesized after 25 years of treatments that the (1) soils would be more acidic than at the beginning of the study in the fertilized plots (WT + NS). We evaluated the base cation content (Ca, Mg, and potassium [K]) and nutrient content (C, N, and P) in response to the treatments. We also hypothesized that (2) soil base cation content would be less in the plots receiving WT + NS relative to other treatments, and (3) elevated N availability from the fertilization would increase belowground C stores in the plots receiving ammonium sulfate fertilizer. We also expected to see temporal trends with acidification increasing throughout the soil profile with time, and that base cations in the WT + NS plots would quickly decrease in the early stages (years 0–10) of experimental applications and remain low over time. Increased soil C storage was expected to occur over longer time periods (10–20 years) and continue to accumulate with further applications (Eastman et al., 2021).

2 | METHODS AND MATERIALS

This LTSP experiment is designed to address the long-term effects of nutrient removals, particularly Ca and Mg, on forest productivity, measured as aboveground biomass, and to allow repeated measures of many important parameters and processes. It is designed as a complete block experiment, with four replications of four treatments, and is blocked by slope position (i.e., each row of four (0.2 ha) plots is one block; see Adams et al., 2004 for a plot map). The treatments in the Fernow LTSP study are: (1) uncut REF plots that were

last harvested around 1910 and that received no experimental manipulation; (2) cut plots (WT) that were subjected to a whole-tree harvest in which all aboveground biomass was removed; (3) cut and fertilized plots (WT + NS) that were whole-tree harvested and that have received annual applications of ammonium sulfate at a rate of 35 kg N ha⁻¹ year⁻¹ and 40.6 kg sulfur (S) ha⁻¹ year⁻¹; and (4) cut, fertilized, and limed plots (WT + NS + LIME) that were treated the same as the WT + NS plots and that also receive dolomitic lime every other year. Whole-tree harvesting occurred in the fall of 1996 and early winter of 1997. Fertilizer treatments began in May 1997 and have since been applied annually in three applications (March, July, and November) to mimic natural deposition patterns. During the period of the study covered in this paper, 840 kg N ha⁻¹ and 974 kg S ha⁻¹ have been added to the plots receiving fertilizer over 24 years. Dolomitic lime was applied every other year, starting in May 1997, usually in March, at a rate of 22.5 kg Ca ha⁻¹ year⁻¹ and 11.6 kg Mg ha⁻¹ year⁻¹, for a total application of 540 kg Ca ha⁻¹ and 278.4 kg Mg ha⁻¹.

2.1 | Site description

The Fork Mountain LTSP site is located within the FEF, in Tucker County, West Virginia (latitude 39° 04' N, longitude 79° 41' W), and located in the Allegheny Mountain subsection of the Appalachian Physiographic Province. The site has a southeast aspect, with slopes ranging from 15% to 31%. Elevation ranges from 798 to 847 m. Soils are classified as Calvin, Berks, or Hazleton series (loamy skeletal, mixed mesic Typic Dystrochrept). At the initiation of this study, trees on this mostly undisturbed forested site were about 85 years old and were typical of a relatively high productivity (red oak site index₅₀ = 80 ft) central Appalachian mixed hardwood forest. This site was last harvested around 1910. However, significant storm damage was recorded in December 2009 (Walter et al., 2021) and October 2012 (Walter et al., 2019), which affected the plots and treatments differentially. Pretreatment conditions are described in detail in Adams et al. (2004).

2.2 | Soil sampling and analyses

In March and April of 1996, soils were sampled from three randomly located quantitative pits per treatment plot. First, a 30.5 cm by 30.5 cm square template was placed on the soil surface, and the surface litter layers (Oi and Oe + Oa horizons, separated) were collected from within the template, by cutting around the edge with a knife, and placed in separate paper bags. The Oe and Oa horizons were aggregated to ensure consistency of sampling. Then the top mineral soil layer (0–15 cm) was removed within the same 30.5 cm × 30.5 cm area, gravels and cobble-sized materials were removed, and

all components were weighed separately; bulk density was calculated for the surface horizon. A bulk density core was collected from the 15–30 cm horizon using an AMS (Art, Manufacturing and Supply, Inc.) soil core bulk density sampler. The soil was removed from the 15- to 30-cm depth, subsampled, and the process repeated for the 30–45 cm layer. These depths approximately correspond with soil horizons (A, AB or BA, and Bw or BC) determined from the soil reconnaissance. Soils were subsampled by depth for nutrient determination. Soil samples were air-dried, passed through a 2-mm (#10) sieve, and stored in plastic bags at room temperature. Each soil sample was then analyzed in duplicate for physical and chemical characteristics at the Virginia Tech Forest Soils Lab, as described in Lusk (1998). Soil pH was determined in distilled water, and exchangeable acidity was determined by extraction with 1 N KCl. Exchangeable base cations were measured by extraction with 1 N NH₄OAc at pH 7.0. Total C was determined by combustion analysis.

Subsequently, soils were sampled for nutrients utilizing the same depths and locations near the three original sample locations every 5 years (2001, 2006, 2011, 2016, and 2021), in spring (April–early June), except the forest floor was not sampled on the treated plots in 2001. Otherwise, the same horizons and depths were used to ensure repeatability and consistency. Soil samples were collected, placed in plastic bags, air-dried, passed through a 2-mm sieve, and analyzed for nutrients at the University of Maine Soil and Plant Testing Laboratory using their Forest Soil Protocol. Soil pH was measured in distilled water. Total N and C were measured by combustion analysis at 1350°C. Exchangeable acidity was extracted in 1 M KCl and measured by titration with 0.1 M NaOH. Exchangeable cations and total extractable phosphorus (P) were extracted in ammonium chloride (NH₄Cl) and measured by ICP-OES (inductively coupled plasma optical emission spectroscopy). Effective cation exchange capacity (ECEC) was calculated by summation of milliequivalent levels of Ca²⁺, K⁺, Mg²⁺, Na⁺, and acidity.

Nutrient content was calculated using the average bulk density (<2 mm fraction) for each plot and mineral soil layer from 1996 (since there were no interim measurements of bulk density) and for the nutrient concentration, yielding Ca, Mg, K, P, and N and C stocks/content in kg ha⁻¹. The O horizon mass, which was measured at each soil sampling for both the Oi and Oe + Oa layers, was used to calculate the nutrient content of these horizons. The O horizon nutrients are not included in the time series due to missing/incomplete data from at least two of the sampling periods.

2.3 | Statistical design

For the 2021 soil chemistry and forest floor mass data, analysis of variance procedures were used. Initial

analyses with all the data from all the horizons/depths revealed that depth/horizon were always highly statistically significant. Therefore, an ANOVA was conducted by horizon/depth (PROC GLM) in SAS (SAS Institute), with a reduced model including the factors treatment and block. Each plot was considered a single replicate. If significant effects for either factor were found, then post hoc Tukey–Kramer tests were run to compare means among treatments or blocks. An α level of 0.05 was used throughout to assess statistical significance, and p -values between 0.05 and 0.10 were considered trends.

For the time series analysis, data for the mineral soil nutrients and forest floor mass were analyzed through a generalized linear mixed effects model (PROC GLIMMIX) in SAS 9.4 (SAS Institute). Year, Treatment, and Horizon were main effects. Year and Block were considered random effects. We utilized a compound symmetry structure to account for variance among treatments and nested random effects due to subsampling. Post hoc means tests were Tukey adjusted to account for multiple comparisons. Due to multiple years of missing data, models for forest floor (O horizon) nutrients would not converge, and the results are not presented here.

3 | RESULTS

3.1 | 2021 Results

Horizon/depth was always a strongly significant main effect for all the variables, so we analyzed all the 2021 data by horizon. Block was generally not a significant effect and will not be presented here.

3.1.1 | Forest floor horizon mass

The mass of the Oi horizon varied significantly with treatment (Table 1; $p = 0.0065$), with the largest mass in the REF plots, followed by WT + NS, and then the WT and WT + NS + LIME (Figure 1). There were no statistically significant differences in the mass of Oe + Oa horizon, due to treatment or block, nor were the effects statistically significant for the total O horizon mass (data not shown).

3.1.2 | Soil acidification

Soil pH was consistently affected by the treatment in all the soil horizons (Table 1), although the treatments had different effects in the O horizons relative to the mineral soil. Specifically, in the O horizons, soil pH was highest in the WT + NS + LIME treatment and significantly greater than the WT + NS treatment and the REF in the Oi layer (Figure 2). How-

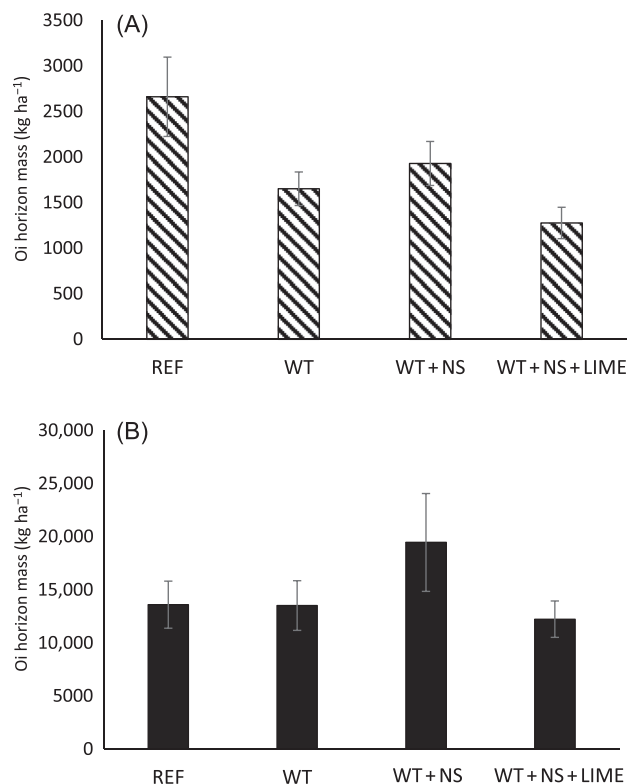


FIGURE 1 Mean mass of O horizons (kg ha^{-1}), 2021 sampling. (A) Mean mass and standard error for the Oi horizon. Bars with letters indicate statistically significant different mass of the Oi horizon among the treatments. (B) Mean mass and standard error for the Oe + Oa horizons. Mean values do not differ significantly among the treatments. Note the differences in the vertical scale of the two graphs. NS, ammonium-sulfate fertilization; REF, untreated reference; WT, whole-tree harvesting.

ever, in the mineral soil, the highest soil pH was in the WT treatment, and it was significantly greater than the WT + NS treatment. Mean soil pH values ranged from 4.5 to 5.5 in the organic horizons and generally were 4.5 or less in the mineral horizons.

Levels of exchangeable acidity followed similar (but inverse) patterns to pH (data not shown). In the O horizons, the lowest levels of acidity were in the WT + NS + LIME treatment, and the highest levels were in the WT + NS treatment plots. In the mineral soil, the effect of treatment on acidity was statistically significant for the 30- to 45-cm depths ($p = 0.0154$), but there was a trend for the 0- to 15-cm and 15- to 30-cm depths ($p = 0.0513$ and 0.0823). However, the pattern was consistent with the highest mean levels of acidity in the WT + NS treatment and the lowest in the WT.

Exchangeable $\text{Al}^{3/2+}$ concentrations varied significantly among the treatments only in the mineral soil horizons (Table 1), although there was a trend ($p = 0.0842$) in the Oe + Oa horizon (Figure 3). At 0–15 and 15–30 cm, the lowest levels of $\text{Al}^{3/2+}$ were consistently found in the WT plots, and the

TABLE 1 Results of general linear model analysis, for 2021 soil chemistry, Fork Mountain long-term soil productivity (LTSP) study, testing for treatment effect.

		pH water		Acidity (cmol kg ⁻¹)		Al ^{2/3+} concentration (mg kg ⁻¹)			
	<i>df</i>	<i>F</i> value	Pr > <i>F</i>	<i>F</i> value	Pr > <i>F</i>	<i>F</i> value	Pr > <i>F</i>		
Oi	3	17.3	<0.0001*	2.8	0.0523**	1.3	0.3006		
Oe + Oa	3	4.1	0.0130*	4.0	0.0142*	2.4	0.0842**		
0–15 cm	3	3.1	0.0372*	2.8	0.0513**	3.1	0.0385*		
15–30 cm	3	3.9	0.0156*	2.4	0.0823**	4.1	0.0122*		
30–45 cm	3	3.9	0.0154*	3.9	0.0154*	3.1	0.0362*		
		Ca content		Mg content		K content		ECEC (cmol kg ⁻¹)	
	<i>df</i>	<i>F</i> value	Pr > <i>F</i>	<i>F</i> value	Pr > <i>F</i>	<i>F</i> value	Pr > <i>F</i>	<i>F</i> value	Pr > <i>F</i>
Oi	3	2.64	0.1130	1.69	0.2375	6.33	0.0134*	1.8	0.1584
Oe + Oa	3	0.39	0.7627	3.79	0.0523**	0.11	0.9547	2.0	0.1254
0–15 cm	3	1.05	0.4178	5.03	0.0256*	0.24	0.8632	3.4	0.0283*
15–30 cm	3	0.87	0.4937	1.75	0.2266	1.92	0.1971	3.3	0.0317*
30–45 cm	3	1.77	0.2232	2.53	0.1224	0.36	0.7827	5.1	0.0045*
		N content		C content		P content		FFMASS (kg ha ⁻¹)	
	<i>df</i>	<i>F</i> value	Pr > <i>F</i>	<i>F</i> value	Pr > <i>F</i>	<i>F</i> value	Pr > <i>F</i>	<i>F</i> value	Pr > <i>F</i>
Oi	3	5.77	0.0176*	7.750	0.0073*	11.72	0.0018*	4.71	0.0065*
Oe + Oa	3	0.22	0.8814	0.11	0.9546	0.08	0.9685	1.15	0.3395
0–15 cm	3	0.26	0.8499	0.33	0.8042	1.35	0.3181		
15–30 cm	3	1.67	0.2424	2.47	0.1286	2.52	0.1237		
30–45 cm	3	0.56	0.6544	0.90	0.4768	0.75	0.5468		

Note: All nutrient contents units are kg ha⁻¹.

Abbreviation: ECEC, effective cation exchange capacity; FFMASS, forest floor horizon mass.

** and * denote significance at $p < 0.10$ and $p < 0.05$, respectively.

highest levels were found in the WT + NS plots. However, at the deepest sampling depth (30–45 cm), the highest level of Al^{3/2+} was in the WT + NS + LIME treatment, and it was significantly greater than the WT.

3.1.3 | Base cations

Calcium content did not vary significantly with treatment after 24 years of fertilizer and lime additions in any horizon/layer (Table 1). However, Mg content showed a trend with treatment in the Oe + Oa horizon ($p = 0.0523$) and was statistically significant in the upper 15 cm of the mineral soil ($p = 0.0256$). In the Oe + Oa, mean Mg contents were highest in the WT + NS + LIME treatment and significantly greater than in the other three treatments (Figure 4). This pattern held in the upper mineral soil (0–15 cm). Potassium content varied with treatment only in the Oi horizon and followed a pattern similar to the mass of the Oi layer (Figure 1), with the highest levels in the REF plots and significantly greater than the WT and WT + NS + LIME (data not shown). The potassium content among the plots that had been whole-tree-harvested did not differ from each other.

ECEC did not differ significantly among the treatments in the O horizons but was significantly affected in all three of the mineral soil depths (Table 1; Figure 5). In the mineral soil, the WT treatment plots exhibited the lowest mean ECEC, which either differed significantly from the REF plots (0–15 cm), the WT + NS (15–30 cm), or the WT + NS + LIME (30–45 cm).

3.1.4 | Soil carbon, nitrogen, and phosphorus

As with forest floor mass, carbon content varied with treatment in the Oi horizon ($p = 0.0073$), but not in the Oe + Oa horizon (Table 1), nor were there significant differences among the treatment means. Total C content was greatest in the Oi layer on the REF plots and was significantly greater than C content on the WT and WT + NS + LIME plots (Figure 6A). For the three WT-harvested plots, C content in the forest floor layers did not vary significantly with treatment, nor did C content vary with treatment in the mineral soils.

The total N content of the Oi horizon varied with treatment ($p = 0.0176$) and was greatest in the REF treatment, but was only significantly greater than the WT + NS + LIME treatment (Figure 6B). P content only varied with treatment in the

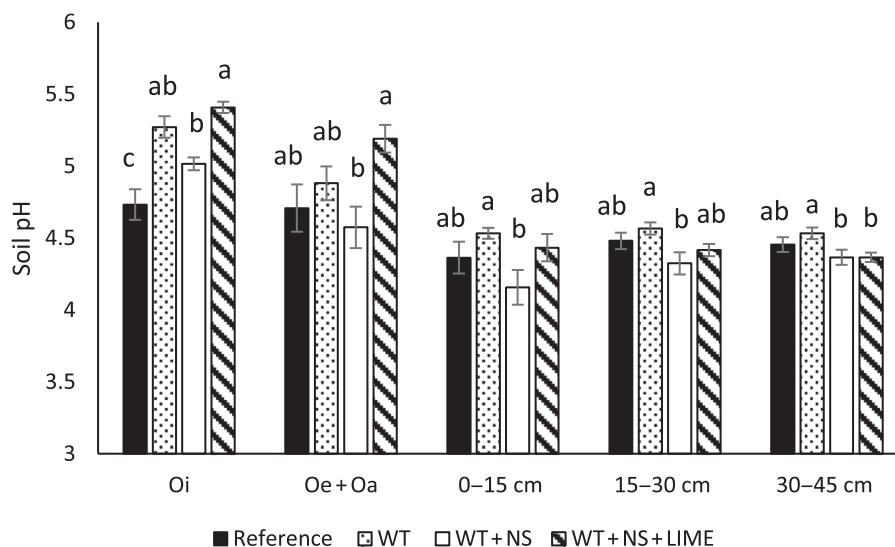


FIGURE 2 Mean soil pH (water), 2021 by layer and treatment. Means within a soil layer with different letters are statistically significantly different at $p = 0.05$. Vertical bars represent standard errors of the mean. NS, ammonium-sulfate fertilization; WT, whole-tree harvesting.

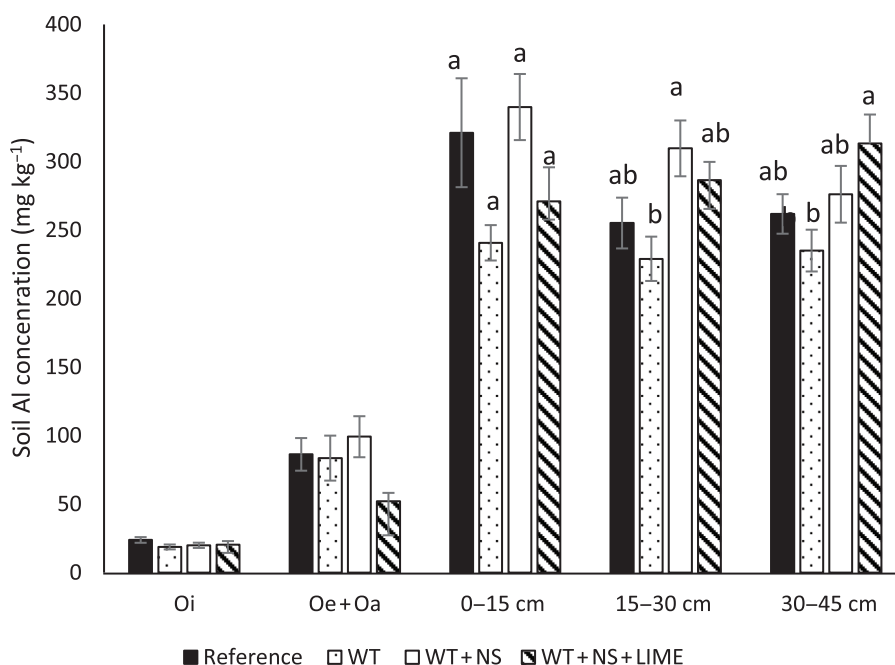


FIGURE 3 Mean soil exchangeable Al concentrations, by soil horizon and treatment, 2021 soil sampling. Means within a soil layer with different letters are statistically significantly different at $p = 0.05$. Vertical bars represent standard errors of the mean. NS, ammonium-sulfate fertilization; WT, whole-tree harvesting.

Oi layer. Content was greatest in the REF relative to the WT and WT + NS + LIME (data not shown). P content was not statistically different among treatments in the mineral soil in 2021.

3.2 | Changes over time

Year and Horizon were highly significant main effects for all the variables we evaluated in the mineral soil (Table 2), and

the interaction was also significant, pointing to changes in soil chemistry among the horizons with time. Treatment was only statistically significant as a main effect for Mg, but the interaction of Treatment $\times$ Horizon was significant for pH, exchangeable acidity and $\text{Al}^{3/2+}$ concentration, Ca, Mg, C, N, and P contents, but not for ECEC or Forest Floor mass. The interaction of Year $\times$ Treatment $\times$ Horizon was only significant for Mg, and ECEC, and as a trend for Al. We evaluate these results graphically to understand the processes of soil acidification, base cation cycling, and soil C and N

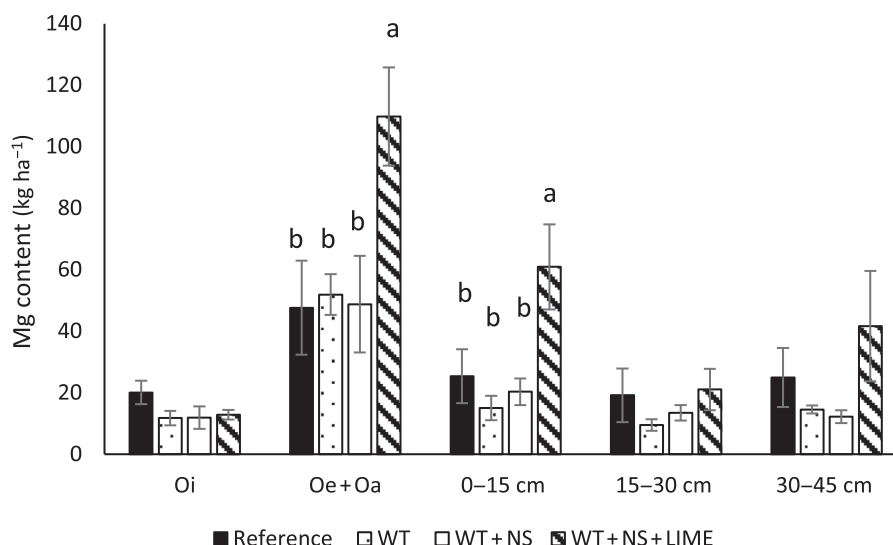


FIGURE 4 Average exchangeable Mg content in forest floor and mineral soil by horizon/depth and treatment, 2021 soil sampling. Means within a soil layer with different letters are significantly different at $p = 0.05$. Vertical bars represent standard errors of the mean. NS, ammonium-sulfate fertilization; WT, whole-tree harvesting.

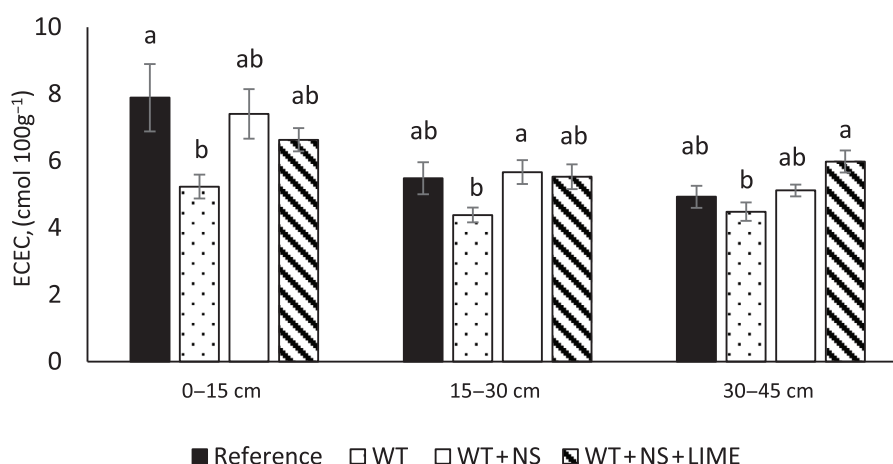


FIGURE 5 Average effective cation exchange capacity (ECEC) of mineral soil, by depth and treatment, 2021 soil sampling. Means within a soil layer with different letters are statistically significantly different at $p = 0.05$. Vertical bars represent standard errors of the mean. ECEC did not vary significantly among treatments for the O horizons, so data are not shown. NS, ammonium-sulfate fertilization; WT, whole-tree harvesting.

cycling. Complete means comparison results can be found in the [Supporting Information](#).

3.2.1 | Forest floor mass

The mass of the Oi layer of the forest floor decreased after the treatments began, even in the REF plots that were not harvested (Figure 7). Mass was around 6000 kg ha^{-1} in 1996 before any treatments began and decreased drastically by 2006 to less than 2000 kg ha^{-1} , before leveling off at around 2000 kg ha^{-1} for the last 15 years. Trends in the mass of the Oi layer among treatments were persistent, although the differences were only significant between the REF plots and the WT-harvested plots in 2021.

The Oe + Oa layer did not experience such large changes in mass due to the initiation of treatments, although the WT and WT + NS + LIME treatments diverged from the REF in 2016. The mass of the Oe + Oa appears to be increasing with time, although the differences are not statistically significant. Total forest floor mass largely reflects the pattern of the Oe + Oa layer.

3.2.2 | Acidification

Soil pH in the 0–15 cm mineral soil horizon rapidly diverged with time since treatments began, with average pH values for the WT + NS treatment dropping from 4.3 to below 4.2 within the first 5 years (Figure 8; Table 2) and ultimately as low as

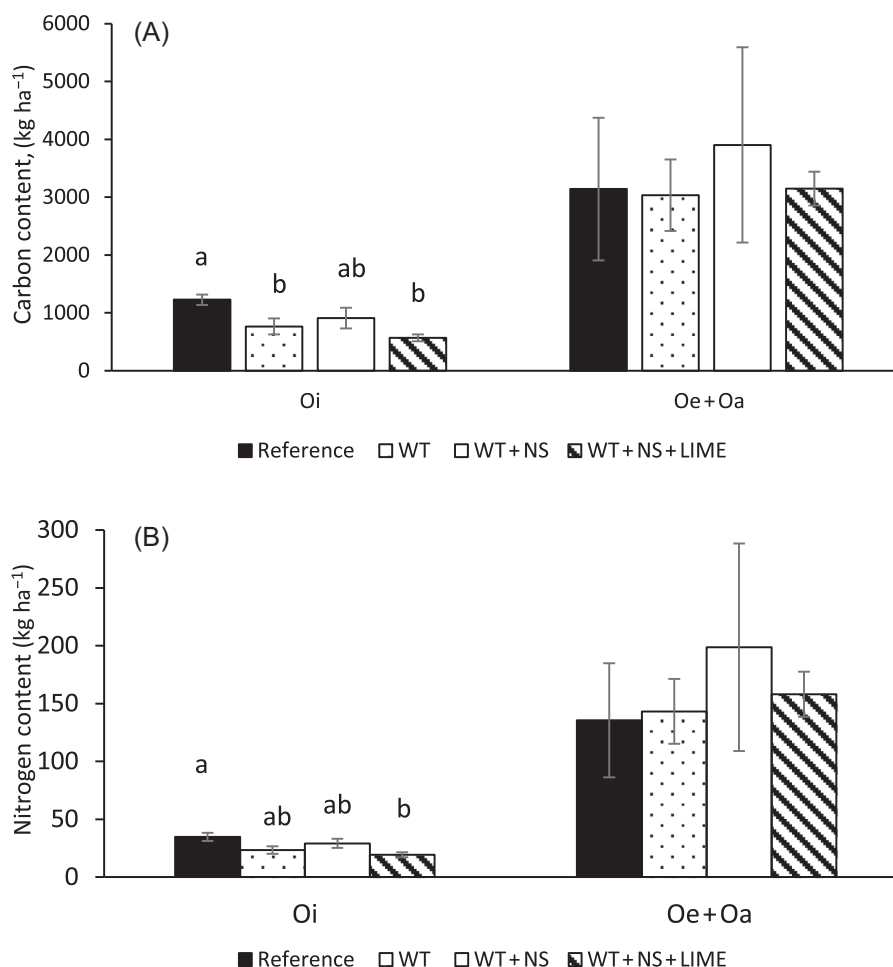


FIGURE 6 Soil content of carbon (A) and nitrogen (B) in the O horizons by treatment, 2021 soil sampling. Means within a soil layer with different letters are statistically significantly different at $p = 0.05$. There were no significant effects of treatment in the Oe + Oa layer or the mineral soil. Vertical bars represent standard errors of the mean. NS, ammonium-sulfate fertilization; WT, whole-tree harvesting.

3.9. Statistically significant differences between the WT + NS and the other treatments were detected in 2006 and continued through 2016. The pattern of WT + NS having the lowest soil pH in the upper horizon was also observed in 2021, but the values were not statistically different because of high variability.

In the deeper mineral horizons (15–30 and 30–45 cm), soil pH levels initially increased through 2006 before declining and returning to approximately pretreatment levels. The differences between the plots receiving fertilizer (WT + NS vs. WT + NS + LIME) were small, and the only significant differences were those between the two fertilized treatments and the non-fertilized plots (WT and REF), pointing to the acidifying effect of the fertilizer. In the non-fertilized plots, soil pH increased initially in all horizons and treatments, except for the 0–15 cm horizon, then decreased slightly over time. Mean pH values were lowest in the 0–15 cm (mean = 4.36) and increased slightly with depth in the mineral soil. While

similar patterns were observed with exchangeable acidity, the only statistically significant effects in exchangeable acidity were detected in the upper mineral horizon (data not shown).

Average exchangeable $Al^{3/2+}$ concentrations increased after treatments began in the WT + NS plots and remained consistently high in the 0–15 cm of the mineral soil (Figure 9). However, these apparent differences among treatments were statistically significant only in 2006, where the levels in the WT plots were significantly less than those in the WT + NS plots. In the 15- to 30-cm depth, a temporal pattern was less obvious. In the deepest 30–45 cm horizon, all mean $Al^{3/2+}$ values decreased from 1996 to 2001 and then increased slightly in 2011 and 2016. However, significant differences were only detected in 2016 and 2021, where the WT values were found to be significantly less than those from the WT + NS + LIME. In 2021, however, the average $Al^{3/2+}$ concentration of the WT plots was significantly less than the WT + NS plots.

TABLE 2 Results of general linear mixed effects model, repeated sampling of soil chemistry, and Fork Mountain long-term soil productivity (LTSP) study.

	NDF	DDF	pH		Acidity		Al ^{2/3+}			
			F	p	F	p	F	p		
Year (Y)	4	48	60.91	<0.0001*	16.94	<0.0001*	16.60	<0.0001*		
Treatment (T)	3	12	2.37	0.1223	1.00	0.4262	0.84	0.4980		
Y × T	12	48	3.47	0.0003*	1.21	0.2892	1.57	0.1107		
Horizon (H)	2	24	89.86	<0.0001*	109.56	<0.0001*	26.83	<0.0001*		
Y × H	8	96	4.17	<0.0001*	5.61	<0.0001*	6.04	<0.0001*		
T × H	6	24	6.00	0.0006*	7.76	0.0001*	5.16	0.0016*		
Y × T × H	24	96	0.79	0.7658	1.06	0.3918	1.43	0.0892**		
	NDF	DDF	Ca		Mg		K		CEC	
			F	p	F	p	F	p	F	p
Year (Y)	4	48	9.56	<0.0001*	17.38	<0.0001*	37.75	<0.0001*	425.73	<0.0001*
Treatment (T)	3	12	1.16	0.3647	7.56	0.0042*	0.78	0.5259	1.35	0.3038
Y × T	12	48	1.43	0.1647	5.40	<0.0001*	1.29	0.2374	2.61	0.0045*
Horizon (H)	2	24	71.88	<0.0001*	89.14	<0.0001*	132.08	<0.0001*	192.45	<0.0001*
Y × H	8	96	5.42	<0.0001*	8.26	<0.0001*	10.63	<0.0001*	26.29	<0.0001*
T × H	6	24	3.16	0.0198*	11.67	<0.0001*	2.09	0.0920**	1.54	0.2066
Y × T × H	24	96	1.08	0.3754	3.57	<0.0001	0.82	0.7319	1.72	0.0219*
	NDF	DDF	C		N		P		Forest floor mass	
			F	p	F	p	F	p	F	p
Year (Y)	4	48	49.68	<0.0001*	38.72	<0.0001*	41.54	<0.0001*	12.56	<0.0001*
Treatment (T)	3	12	1.16	0.3653	0.68	0.5820	2.08	0.1570	1.39	0.2941
Y × T	12	48	1.33	0.2157	0.80	0.6768	1.66	0.1075	3.38	0.0013
Horizon (H)	2	24	328.21	<0.0001*	292.02	<0.0001*	232.06	<0.0001*	229.18	<0.0001*
Y × H	8	96	6.38	<0.0001*	9.21	<0.0001*	6.03	<0.0001*	5.77	<0.0001*
T × H	6	24	7.10	0.0002*	6.67	0.0003*	7.08	0.0002*	1.66	0.1734
Y × T × H	24	96	0.65	0.9156	0.68	0.8931	0.68	0.8596	0.91	0.5863

Note: All nutrient contents units are kg ha⁻¹.

Abbreviations: CEC, cation exchange capacity; DDF, denominator degrees of freedom; NDF, numerator degrees of freedom.

** and * denote statistical significance at $p < 0.10$ and $p < 0.05$, respectively.

3.2.3 | Base cations

The Treatment × Horizon effect was statistically significant for all the bases but not for ECEC. However, the Year × Treatment × Horizon effect was statistically significant for Mg content and for ECEC. The interactions of Year × Horizon and Treatment × Horizon were statistically significant for Ca and Mg, but for K, Treatment × Horizon was a trend (Table 2). The content of these analytes was generally greater in the upper mineral horizon than in the lower two horizons, but there were few statistically significant differences due to treatment. However, in the 0–15 cm horizon, the Ca levels were generally highest in the WT + NS + LIME plots, and they were significantly greater than the other treatments in 2001. In 2016, there was very high variability around the mean of the REF plot, which altered the pattern (Figure 10). In the 15–30 cm horizon, significant differences among treatments were detected

in 2001 and 2006, where Ca was highest in the WT + NS + LIME, which was significantly greater than in all the other treatments. In 2011 and 2021, in the 30–45 cm horizon, mean Ca values from the WT + NS + LIME plots were significantly greater than the other plots. Also, note that Ca content generally declined over time and moved deeper into the soil with time.

The addition of dolomitic lime increased mean soil Mg content, although with different timing in the different horizons (Figure 11). In the 0–15 cm horizon, soil Mg increased from around 25 kg ha⁻¹ in 1996 to around 250 kg ha⁻¹ in 2001 in the WT + NS + LIME treatment, which was significantly greater than in the other treatments including the REF. Thereafter, it decreased to around 150 kg ha⁻¹ in 2006 and to between 50 and 75 kg ha⁻¹ during 2011–2021. Average Mg content remained significantly greater in the WT + NS + LIME treatment in 2006 (relative to the WT + NS and

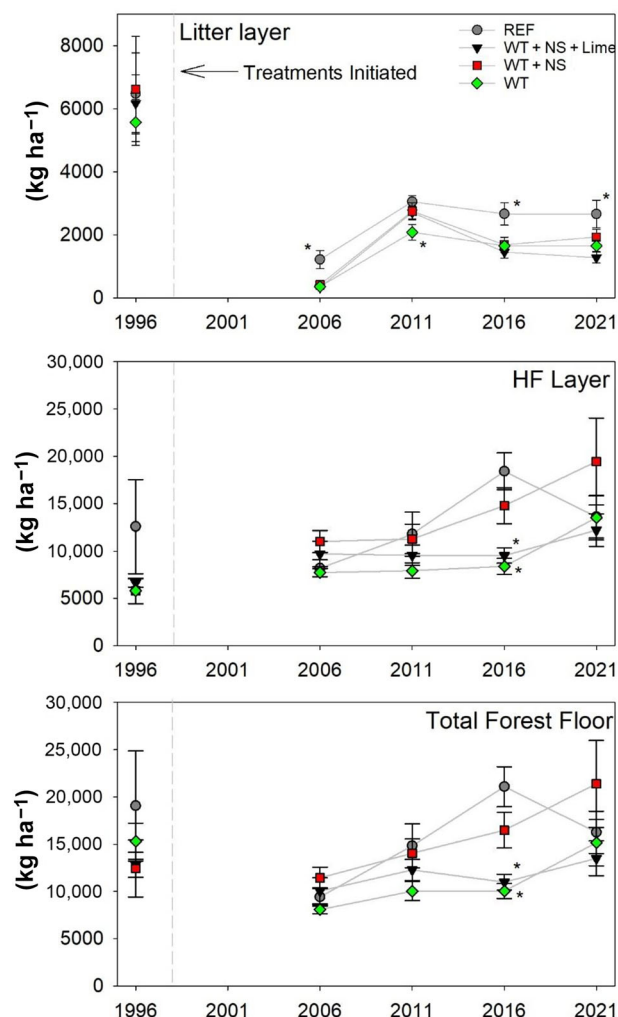


FIGURE 7 Mean forest floor mass from five sampling periods on the Fork Mountain long-term soil productivity (LTSP) study. Treatments were initiated in winter 1996–1997 (vertical bar), and 1996 values represent pretreatment samples. Vertical bars represent standard errors. Black asterisks indicate significant differences from the reference. Red asterisks indicate significant differences between treatments (see [Supporting Information](#) for full means comparisons). NS, ammonium-sulfate fertilization; REF, untreated reference; WT, whole-tree harvesting; HF, is the Humus and Fermentation layers (Oe+Oa horizons).

REF treatments) and in 2016 (relative to the WT treatment), and levels declined during the last 15 years. In the 15–30 cm horizon, significant differences were detected due to the lime treatment in 2001 and 2006 only. In the 30–45 cm horizon, however, average soil Mg content increased in the WT + NS + LIME treatment over time and was significantly greater in 2016 (relative to WT) and 2021 (relative to REF, WT, and WT + NS), reaching $\sim 40 \text{ kg ha}^{-1}$ by 2021.

The pattern of K content over time was an initial increase in mean values in the upper two horizons through 2006 and declining values afterwards, similar to Mg (Figure S1). However, there were few statistically significant differences in soil

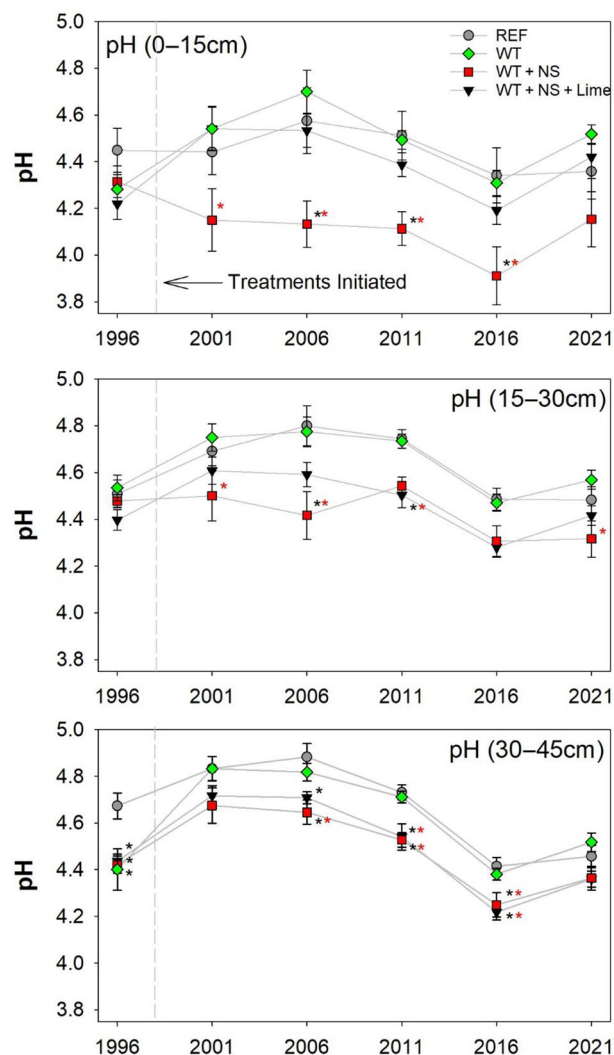


FIGURE 8 Mean soil pH (water) from five sampling periods on the Fork Mountain long-term soil productivity (LTSP) study, at three depths in the mineral soil. Treatments were initiated in winter 1996–1997 (vertical bar), and 1996 values represent pretreatment samples. Vertical bars represent standard errors. Black asterisks indicate significant differences from the reference. Red asterisks indicate significant differences between treatments (see [Supporting Information](#) for full means comparisons). NS, ammonium-sulfate fertilization; REF, untreated reference; WT, whole-tree harvesting.

K content among the treatments in any horizon, and none after 2006. In the 15–30 cm horizon, the WT plots had the lowest mean values, but these differences were not significant in 2001. However, K content was lower in WT + NS than in REF plots in 2006. The only significant differences found in the 30–45 cm horizon occurred in 2006 when WT + NS plots had significantly lower K content than REF.

For ECEC, all the interactions among main effects (Year $\times$ Treatment, Year $\times$ Horizon, Year $\times$ Treatment $\times$ Horizon) were statistically significant (Table 2). Also, note that there were significant differences among the treatment plots prior to the initiation of treatment in all three horizons (Figure 12).

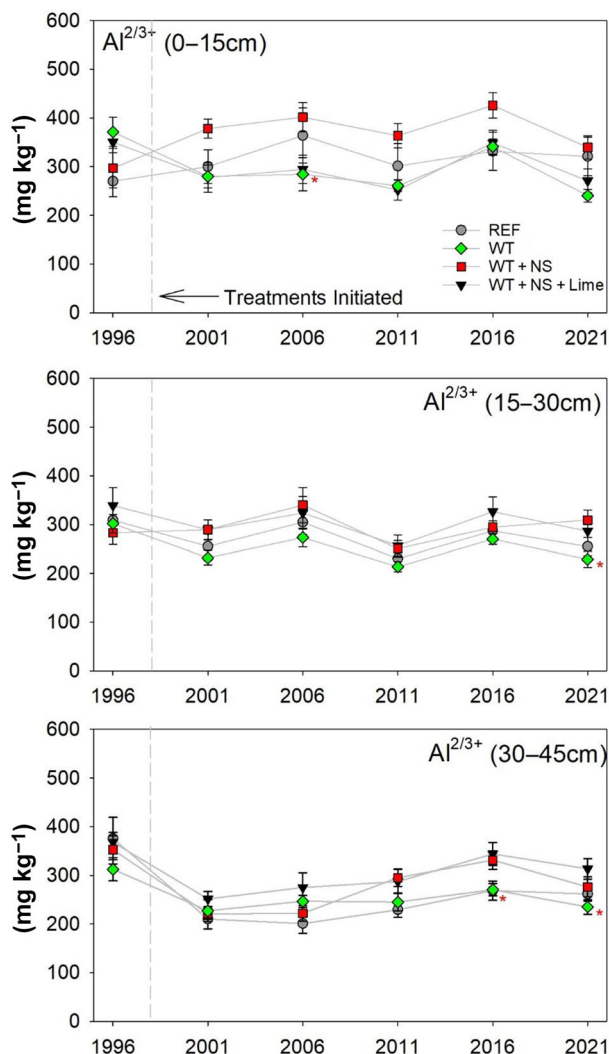


FIGURE 9 Mean extractable Al concentrations from five sampling periods on the Fork Mountain long-term soil productivity (LTSP) study, at three depths in the mineral soil. Treatments were initiated in winter 1996–1997 (vertical bar), and 1996 values represent pretreatment samples. Vertical bars represent standard errors. Black asterisks indicate significant differences from the reference. Red asterisks indicate significant differences between treatments (see [Supporting Information](#) for full means comparisons). NS, ammonium-sulfate fertilization; REF, untreated reference; WT, whole-tree harvesting.

The pretreatment range in mean values was greatest in the 0–15 cm mineral soil. In the lower horizons, the differences were between the REF plots and the other treatments; however, in the upper horizon, the plots chosen to be the WT + NS plots had a significantly higher ECEC relative to the WT + NS + LIME plots. These differences were reported in Adams et al. (2004).

After treatment began, average ECEC values showed inconsistent changes with time (Figure 12). Generally, the mean ECEC for the WT treatments was the lowest, mirroring

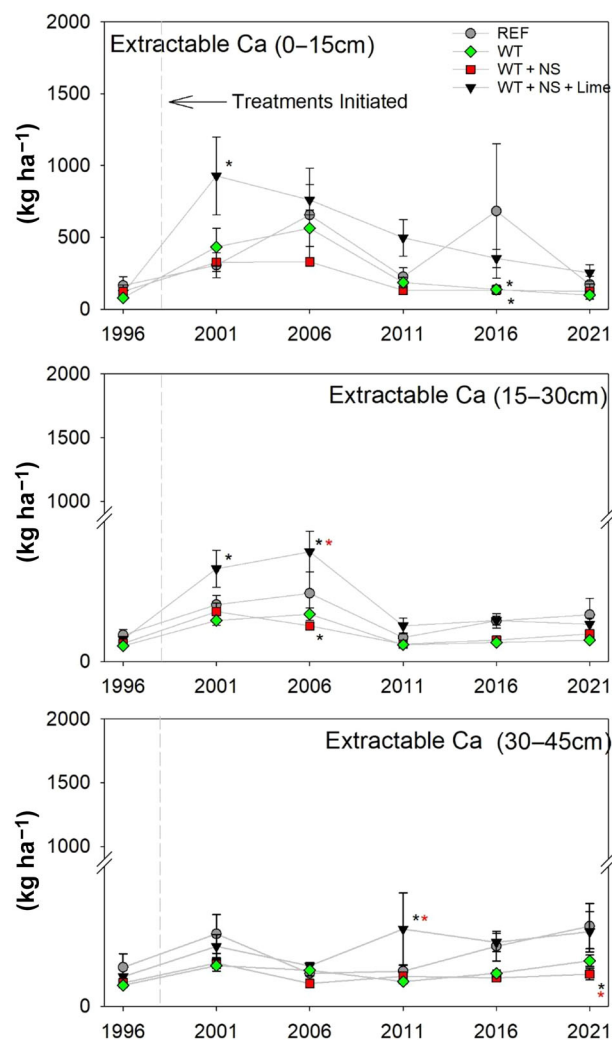


FIGURE 10 Mean extractable soil Ca content from five sampling periods on the Fork Mountain long-term soil productivity (LTSP) study, at three depths in the mineral soil. Treatments were initiated in winter 1996–1997 (vertical bar), and 1996 values represent pretreatment samples. Vertical bars represent standard errors. Black asterisks indicate significant differences from the reference. Red asterisks indicate significant differences between treatments (see [Supporting Information](#) for full means comparisons). NS, ammonium-sulfate fertilization; REF, untreated reference; WT, whole-tree harvesting.

Mg, but not Ca, in all horizons. In the 0–15 cm horizon, the ECEC of the WT plots decreased with time and was significantly less than that of the WT + NS and the REF plots in most years, but the WT + NS + LIME value was only significantly greater in 2001. In the 15–30 cm horizon, mean ECEC was less than in the 0–15 cm horizon, and in 2001, 2006, 2016, and 2021, means comparisons showed that the WT plots had significantly lower ECEC than those plots that had been limed. In the 30–45 cm horizon, values of ECEC increased slightly over time similar to Mg. The plots receiving lime had the highest

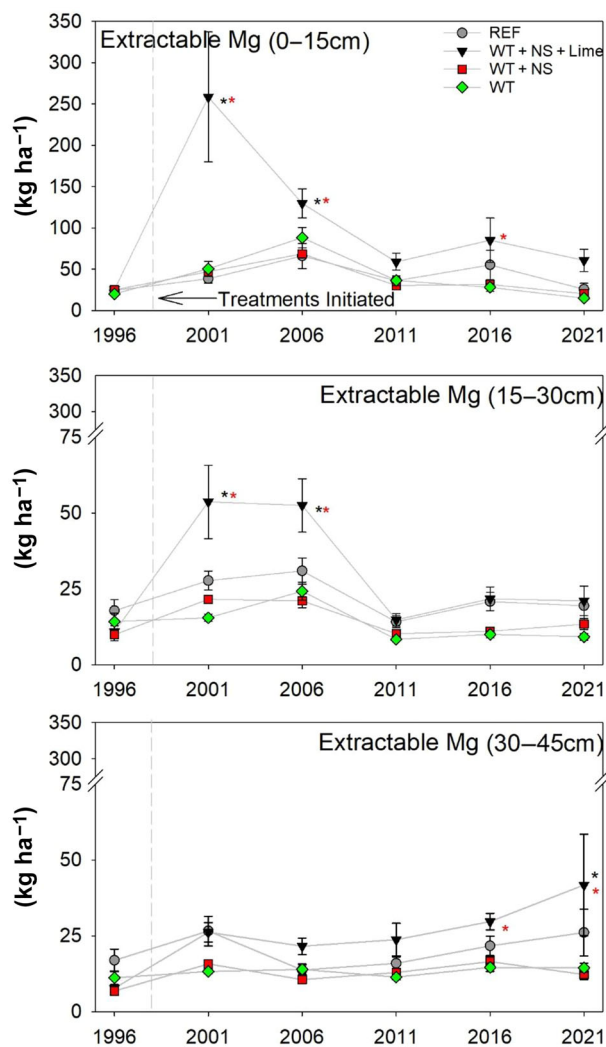


FIGURE 11 Mean soil Mg content from five sampling periods on the Fork Mountain long-term soil productivity (LTSP) study, at three depths in the mineral soil. Treatments were initiated in winter 1996–1997 (vertical line), and 1996 values represent pretreatment samples. Note change in vertical scale in lower two horizons. Vertical bars represent standard errors. Black asterisks indicate significant differences from the reference. Red asterisks indicate significant differences between treatments (see [Supporting Information](#) for full means comparisons). NS, ammonium-sulfate fertilization; REF, untreated reference; WT, whole-tree harvesting.

mean values, which were significantly greater than mean values in the REF plots (2006, 2011, and 2021) or the WT plots (2011, 2016, and 2021).

3.2.4 | Carbon, nitrogen, and phosphorus

Treatment $\times$ Horizon was a significant effect for those variables related to C and N cycling (Table 2), even though treatment was not a significant main effect. Mean total soil C increased dramatically after 1996 through 2006, particu-

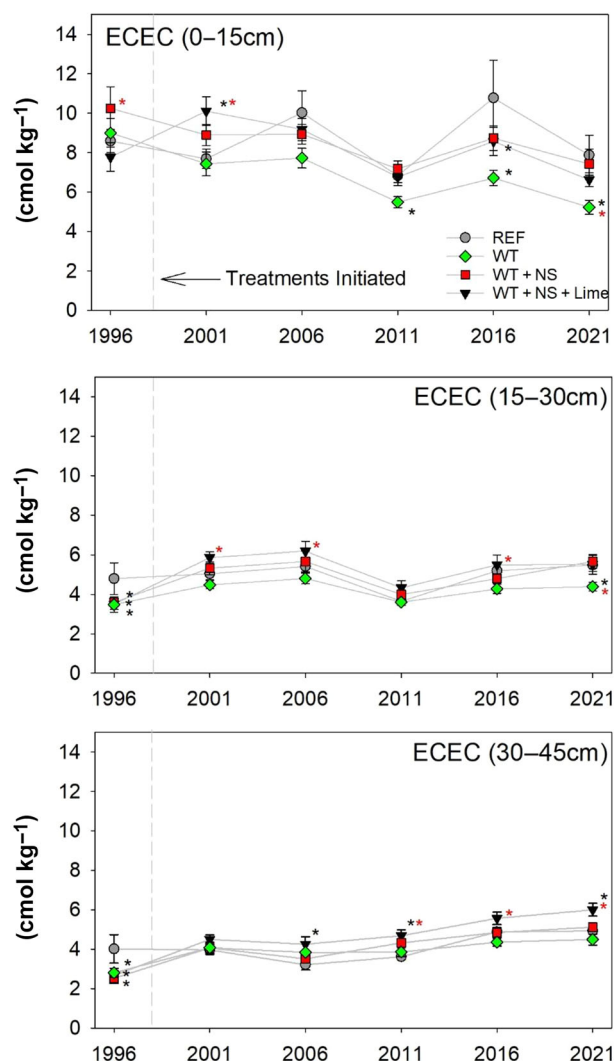


FIGURE 12 Mean effective cation exchange capacity (ECEC) from five sampling periods on the Fork Mountain long-term soil productivity (LTSP) study, at three depths in the mineral soil. Treatments were initiated in winter 1996–1997 (vertical bar), and 1996 values represent pretreatment samples. Vertical bars represent standard errors. Black asterisks indicate significant differences from the reference. Red asterisks indicate significant differences between treatments (see [Supporting Information](#) for full means comparisons). NS, ammonium-sulfate fertilization; REF, untreated reference; WT, whole-tree harvesting.

larly in the top two horizons, and then declined (Figure 13). Values ranged from around 70,000 kg ha⁻¹ in 1996 to almost 150,000 kg ha⁻¹ in the 0–15 cm in the WT + NS treatment plots. Total C decreased with depth in the soil, and a temporal pattern is least obvious in the 30–45 cm horizon. In the 0–15 cm depth, the WT + NS is higher in C content, but significantly so only in 2006 (significantly greater than WT and REF). In the 15–30 cm horizon, the significant differences are generally between the REF and WT-harvested plots in 2001, 2006, 2016, and 2021. In the 30–45 cm horizon, the C content

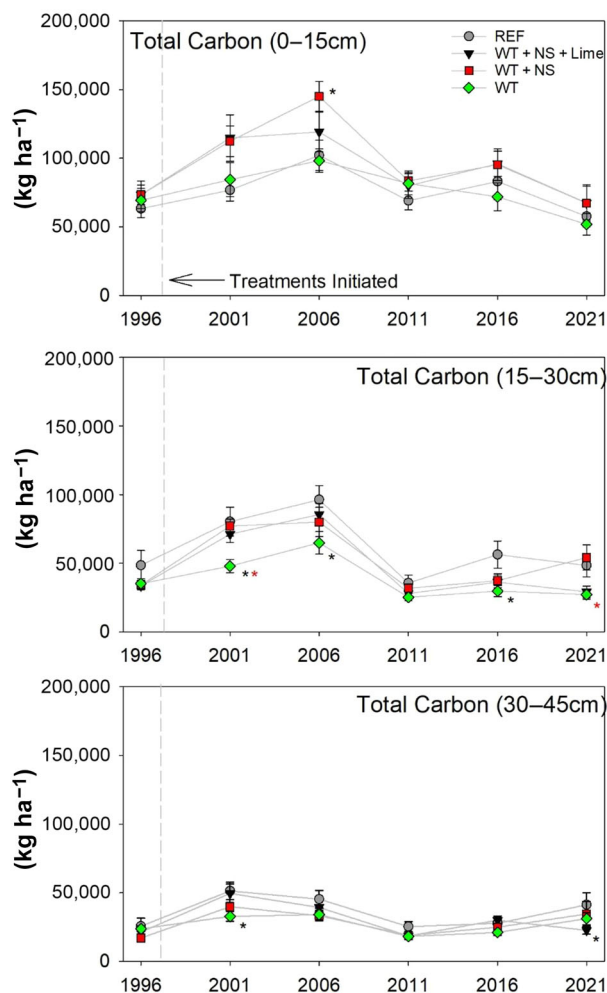


FIGURE 13 Mean soil C content from five sampling periods on the Fork Mountain long-term soil productivity (LTSP) study, at three depths in the mineral soil. Treatments were initiated in winter 1996–1997 (vertical bar), and 1996 values represent pretreatment samples. Vertical bars represent standard errors. Black asterisks indicate significant differences from the reference. Red asterisks indicate significant differences between treatments (see [Supporting Information](#) for full means comparisons). NS, ammonium-sulfate fertilization; REF, untreated reference; WT, whole-tree harvesting.

of the REF plots is only significantly greater than that of the WT plots in 2001 and the WT + NS + LIME in 2021.

The general patterns of total N content with time and depth were similar to soil C, with large increases during the first 10 years and decreases after 2006 (Figure 14), particularly in WT + NS and WT + NS + LIME treatments. This pattern is dampened with soil depth. However, in the 0–15 cm horizon, there were no significant treatment differences in soil N. In the 15–30 cm horizon, the overall pattern is similar, although the effect of the fertilizer is less obvious; significant differences were found between the REF and WT plots in 2001, 2006, and 2016. Only in 2021, soil N is significantly greater in the WT + NS plots than the WT plots. In the 30–45 cm horizon, the

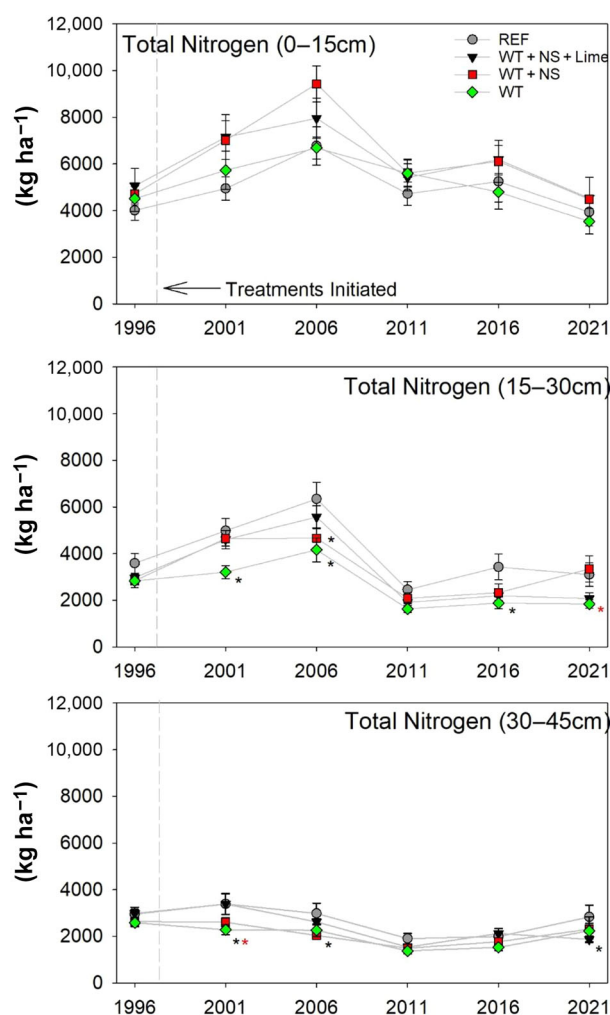


FIGURE 14 Mean total soil N from five sampling periods on the Fork Mountain long-term soil productivity (LTSP) study, at three depths in the mineral soil. Treatments were initiated in winter 1996–1997 (vertical bar), and 1996 values represent pretreatment samples. Vertical bars represent standard errors. Black asterisks indicate significant differences from the reference. Red asterisks indicate significant differences between treatments (see [Supporting Information](#) for full means comparisons). NS, ammonium-sulfate fertilization; REF, untreated reference; WT, whole-tree harvesting.

only significant differences among the treatments are in comparison to the REF plots and WT plots having significantly less N than WT + NS + LIME in 2001.

The interactions of Year $\times$ Treatment, Year $\times$ Horizon, and Treatment $\times$ Horizon were significant in the model for P content over time, and levels of total extractable P generally declined from 2001 through 2021 (Figure 15). In the 0–15 cm layer, in 2001 and 2006, the P content in the WT + NS treatment was significantly greater than the REF, with the REF plot also being significantly less than the WT + NS + LIME in 2001. In the 15- to 30-cm depth, the WT only plots had the lowest values, and they were significantly less than the WT + NS + LIME (2001), the REF (2011), and the WT + NS in

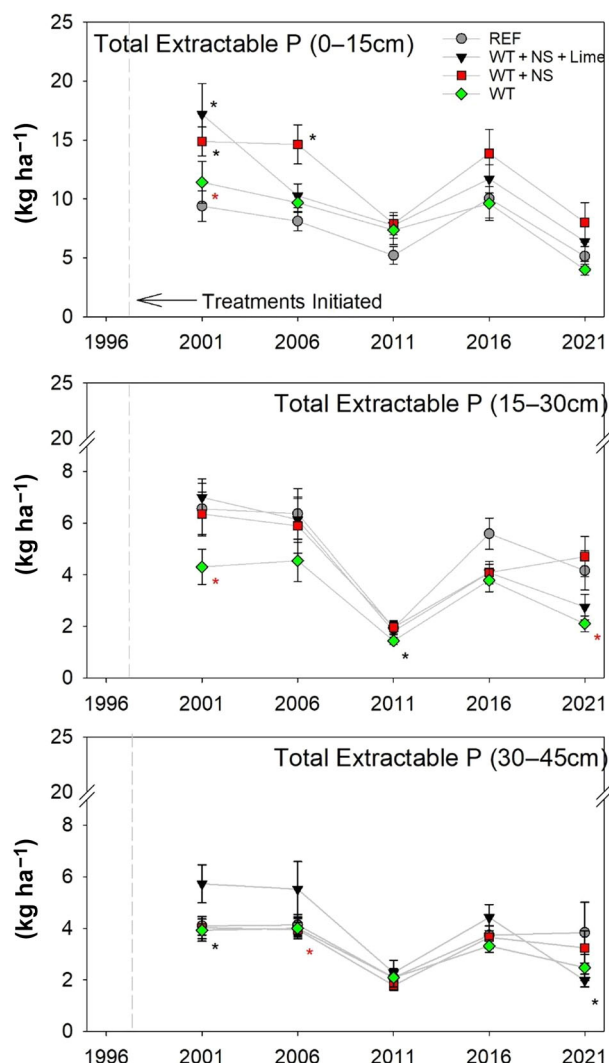


FIGURE 15 Mean total soil N from four sampling periods on the Fork Mountain long-term soil productivity (LTSP) study, at three depths in the mineral soil. Treatments were initiated in winter 1996–1997 (vertical bar). Vertical bars represent standard errors. Black asterisks indicate significant differences from the reference. Red asterisks indicate significant differences between treatments (see [Supporting Information](#) for full means comparisons). NS, ammonium-sulfate fertilization; REF, untreated reference; WT, whole-tree harvesting.

2021. In the deepest layer, the WT + NS + LIME were significantly greater than all the other plots in 2001, than the WT + NS and WT plots in 2006, and significantly less than the REF plots in 2021.

4 | DISCUSSION

The original goal of the Fork Mountain LTSP study was to remove Ca and Mg from the site, through harvesting and acidification via fertilization, to explore how diminished levels of

Ca and Mg in the acidified soil might affect site productivity in these diverse mixed hardwood forests (Adams, 1999; Adams et al., 2004). In this current paper, we evaluated the effects on the soil nutrients and chemistry after 25 years of treatment. We hypothesized that continuous fertilizer additions would result in changes in soil chemistry, particularly soil acidification, and our results support this hypothesis. In samples collected in 2021, the soil was acidified in all soil horizons. Also, significant changes in soil pH and exchangeable acidity occurred rapidly within the first 5 years of fertilizer additions in the upper horizons. The changes in acidity were clearly a response to the addition of ammonium sulfate fertilizer.

We also see a progression of acidity through the soil profile over time, with acidity increasing in the lower horizons at the time that it decreases in the upper 15 cm. Our results compare with those of Fowler (2014), who documented similar results after 10 years in the upper 5 cm of soil of these plots. Such an effect has been documented previously on other studies at Bear Brooks Watersheds in Maine (Fernandez et al., 2003; Patel et al., 2019), on the Fernow Watershed Acidification Study (Adams et al., 2006; Edwards et al., 2002), and elsewhere (McNulty et al., 2017).

However, aluminum levels, another indicator of soil acidification, did not differ among the treatments in the O horizons after 25 years, nor in the mineral soil. Concentrations of $Al^{3/2+}$ were generally highest in the WT + NS soils, with the WT exhibiting the lowest $Al^{3/2+}$ levels, but these differences were only occasionally statistically significant. Fowler (2014) reported increases in resin-available soil $Al^{3/2+}$ in the upper 5 cm of the soil after 10 years, as well as decreased Ca:Al⁺ in soil and foliar Ca:Al in leaves of *Liriodendron tulipifera*. That study concluded that soil acidification and base cation leaching were in their early stages after 10 years of treatments. In our study, in contrast, mineral soil Al levels declined or remained the same after 10 years. However, we sampled deeper horizons in our study and evaluated more of the soil profile (to 45 cm), and we observed other signs of acidification.

We also evaluated base cation concentrations in the soil. In the time series, we do see a pattern of Mg and, to a lesser degree, Ca being leached through the soil profile over time, as has been reported elsewhere (Edwards et al., 2002; San-Clements et al., 2010). Yet base cation levels in the soil after ~25 years of treatment do show differences due to treatments. However, we hypothesized that base cation levels would be lowest in the fertilized plots and lower than those receiving fertilizer plus dolomitic lime. We also expected to see movement of Ca and Mg from the organic and upper soil horizons over the 25 years to deeper horizons, or even evidence of declining levels. Surprisingly, Ca levels were largely unaffected either by the fertilizer or liming treatments, but Mg levels differed in the Oe + Oa and upper mineral soil horizons in 2021 in response to the liming treatment. Also, significant

increases in soil Mg levels were apparent (2001 and 2006), but then declined in the upper two mineral soil horizons. In the lowest mineral horizon, significant differences in Mg content due to liming showed up later (2016 and 2021), suggesting that Mg has moved down through the profile due to leaching. Trends in ECEC reflect Mg, further pointing to the importance of Mg in these soils. We hypothesize that as Mg has a lower exchange affinity relative to Ca and trees take in a much lower quantity of Mg relative to Ca (Ovington, 1959), Mg is more mobile and less is needed by trees, resulting in greater leaching than Ca.

The addition of dolomitic lime appeared to somewhat ameliorate the elevated acidity in the organic horizons by the end of the 25 years, but the effects were less obvious in the mineral soil horizons. Fowler (2014) also reported that the WT + NS + LIME treatment appeared to mitigate the acidification induced by the fertilizer amendments (0- to 5-cm depth). Soil solution data collected from tension lysimeters below the rooting depth also support these results over time (Figure S2). Such changes are largely consistent with the postulated outcomes of acidification from inputs of elevated levels of N and S (J. Aber et al., 1998; Fernandez et al., 2003; McDowell et al., 2004).

We hypothesized that elevated N in the soil from the ammonium sulfate fertilizer treatment would increase belowground C stores, although this might take longer than changes in acidification and base cation content. Nave et al. (2009) reported lags of 15–20 years in soil C response to N additions and that overall soil C pools generally increased only in the mineral soil. Other studies have suggested that elevated N additions can slow decomposition (Adams & Angradi, 1996; Frey et al., 2014; Nave et al., 2009). While we saw initial increases in soil C early on in the top mineral soil horizon, all effects in O horizons were due to harvest removals, and no significant increases in total C content were observed in the soil as a result of the fertilizer treatment, nor did we see significant changes in N content. Soil C and N were relatively unaffected by the fertilizer treatment in the O horizons and in the mineral soil. The only differences are due to harvesting (comparisons between REF and the WT treatments), pointing to the important effect of harvesting on belowground C.

There has been a great deal of research comparing WT harvesting with traditional stem-only harvesting, and Thiffault et al. (2011) evaluated a number of these studies from the northern hemisphere and found little evidence for clear impact of WT harvesting on soil C relative to stem-only harvest. However, in this study, the effects we have detected are the effects of harvesting (which included the removal of all aboveground organic matter other than the forest floor) relative to a non-harvested stand. Nave et al. (2010) reported no significant impacts associated with harvesting intensity on soil C storage in temperate forests across wide gradients of soil and stand type.

Changes in the forest floor mass were only significant for the Oi layer and are likely the result of reduced litter inputs and possibly increased decomposition. Although the plots are 0.405 ha (total area), because they were surrounded on two to four sides by plots that were WT harvested, it is likely that leaf litter inputs decreased even on the REF plots (Figure S3), as a mature canopy was removed from three-fourth of the plots. It is also probable that the microclimate was changed at the ground level, which could have altered decomposition. Finally, the WT harvesting removed all aboveground organic matter (including dead wood), except for the forest floor. Thus, it is likely that the harvesting effect that we observed with some nutrients is due to altered aboveground C inputs. Also, several studies have documented altered decomposition of leaf litter with N additions (Adams & Angradi, 1996; Frey et al., 2014; Pregitzer et al., 2008). We did not directly measure decomposition in this study. However, Eastman et al. (2022) reported that nearly 30 years of fertilizer additions slowed leaf litter decomposition by about 11% and attributed it to changes in the properties of the organic matter.

Most fertilizer addition/acidification studies do not include a harvesting treatment, and this is an important difference in our study. It is also worth noting that a severe windstorm affected the plots in 2009, and Walter et al. (2019) found that the stand damage was greater on those plots receiving WT + NS (fertilization). SanClements et al. (2010) reported that additional litter inputs from an ice storm may have obscured trends in soil chemistry at Bear Brooks Watersheds in Maine. Thus, the harvesting effect in our study might be an organic matter effect/interaction with the acidification process.

The time series show some indications of increased C in the mineral soil early in the study, similar to the results of Eastman et al. (2021) from the Fernow Whole Watershed Acidification Study. However, these differences in soil C were no longer apparent in the upper horizons by around 2011. Fowler (2014) reported after 13 years of fertilization that C storage was greater in plots receiving fertilizer, but primarily in aboveground vegetation growth and to a lesser extent in the forest floor (O horizons), but found no significant changes in allocation to fine roots or mineral soil C. The early increases to total soil C in response to fertilization may be related to increases in vegetative inputs of light/labile soil C fractions, which then decompose rapidly with elevated N inputs with short decadal turnover times (Neff et al., 2002). Walter et al. (2016) showed that the fertilization treatment increased the cover of *Rubus*, which is likely the source of a more labile soil C. Strong vegetative root growth and exudates would also likely promote “priming” of soil C decomposition, thus resulting in short-term C increases that are quickly attenuated by induced decomposition of the heavier pools (Crow et al., 2009; Mazzilli et al., 2014). Heavier, mineral-associated fractions of soil C are then further stabilized with longer turnover times, with the potential for storage dependent upon soil texture/clay

content and clay mineralogy (Richter et al., 1999). Greater insight into the C dynamics and storage potential alterations may be derived by further fractionation of the C pool (e.g., Cotrufo et al., 2019) and should be an important addition to this study. Additionally, fertilization and acidification may have induced dispersion of soil aggregates, with lowered potential for physical protection of soil C (Kemner et al., 2021). Relatedly, declines in soil Ca may also be predictive of less stable soil C (Rowley et al., 2018). These are questions deserving additional attention, in addition to more detailed nutrient budgets incorporating both above- and belowground nutrients.

5 | CONCLUSIONS

Long-term research such as the LTSP study are important for understanding how forest ecosystems respond to a changing climate over the life of a stand. In this paper, we evaluated forest floor and soil chemistry responses 25 years after whole tree harvesting and after 24 years of fertilizer and lime additions to a mixed hardwood forest. Soil acidification has occurred as a result of the ammonium sulfate fertilization, and base cation movement through the soil profile was observed, as predicted. But most of the changes in base cations appeared to be the result of Mg, not Ca, and the addition of dolomitic lime provided some amelioration of the acidification. Also, we did not see the expected increases in C belowground with fertilization and hypothesize that the WT harvesting treatment, and possibly storm damage, may have created an interaction with organic matter inputs that confounded our results. Further detailed budgeting of nutrients is needed to further elucidate the important processes at this site, including aboveground vegetative growth, decomposition, and carbon allocation.

AUTHOR CONTRIBUTIONS

Mary Beth Adams: Conceptualization; data curation; formal analysis; investigation; project administration; resources; writing—original draft; writing—review and editing. **Benjamin M. Rau:** Formal analysis; resources; writing—review and editing. **William T. Peterjohn:** Resources; writing—review and editing. **Zach Fowler:** Investigation; resources; writing—review and editing. **Charlene Kelly:** Formal analysis; investigation; resources; writing—original draft; writing—review and editing.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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