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Changes in forest floor and soil nutrients in a mixed oak forest 33 years after stem only and whole-tree harvest

D.W. Johnson [a,*], C.C. Trettin [b], D.E. Todd Jr. [a]

[a] Natural Resources and Environmental Science, University of Nevada, Reno, NV 89557, USA
[b] USDA Forest Service, 2730 Savannah Highway, Charleston, SC 29141, USA

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ABSTRACT

Vegetation, forest floor, and soils were resampled at a mixed oak site in eastern Tennessee that had been subjected to stem only (SOH), whole-tree harvest (WTH), and no harvest (REF) 33 years previously. Although differences between harvest treatments were not statistically significant ($P < 0.05$), average diameter, height, basal area and biomass were 8–18% lower in the WTH than in the SOH treatment 33 years after harvest whereas they differed by 2% 15 years after harvest. In contrast to results 15 years post-harvest, total forest floor mass and nutrient contents were twofold greater in the WTH than in the SOH treatment at 33 years post-harvest, due largely to differences in Oa horizon mass. Soil total C concentrations increased significantly ($P < 0.05$) over the first 15 years post-harvest in both harvest treatments. Decreases in soil C between 15 and 33 years post-harvest were not statistically significant. Soil total N increased significantly in both harvest treatments over the first 15 years post-harvest. Consistent decreases in soil total N occurred in the WTH treatment between years 15 and 33 post-harvest that bordered on statistical significance whereas total N was stable over that time period in the SOH treatment. The increases and decreases in soil N content cannot be explained by any known processes of N inputs or outputs. Harvest treatment effects on both Ca^{2+} and Mg^{2+} observed at 15 years post-harvest are still observable and significant at 33 years post-harvest, although decreases between 15 and 33 years were found. Treatment effects and changes in soil exchangeable Ca^{2+} and Mg^{2+} are consistent with known inputs from decomposing logging residues, inputs from atmospheric deposition, and increments in forest floor and vegetation. No treatment effects were found for soil extractable P, but steady decreases over time were found. No treatment or time effects were found for soil exchangeable K^+.

1. Introduction

Concern over the effects of intensive forest harvesting on long-term productivity dates back several decades when calculations suggested that nutrient removals by whole-tree harvesting (WTH) might not be sustainable given current nutrient inputs and ecosystem nutrient capital (Boyle et al., 1973; Weetman and Weber, 1972; White, 1974). Although N was most often the limiting nutrient in forests, many early nutrient budget calculations suggested that whole-tree harvesting would cause depletion of other nutrients as well, especially Ca (Alban and Perala, 1990; Boyle et al., 1973; Johnson et al., 1982; Turner and Lambert, 1986; Weetman and Weber, 1972; see also reviews by Federer et al., 1989; Grigal, 2000). In the early 1990s, harvesting effects on forest soil C became a concern because of global C issues. A meta analysis of 73 observations from 26 publications showed that on average, whole-tree harvesting caused a slight (−6%) but significant decline in soil C while sawlog, or stem only harvesting caused a significant increase (+18%), presumably because of differences in inputs from decomposing logging residues (Johnson and Curtis, 2001). Thiffault et al. (2011) recently published a comprehensive review of studies addressing the effects of WTH compared to stem-only harvest (SOH). These authors found that WTH had mixed effects on mineral soil C compared to SOH, with approximately half the studies showing increases and half showing decreases. The effects on forest floor C were more pronounced, however, with 70% of the studies showing negative effects of WTH compared to SOH (Thiffault et al., 2011), as would be expected. The patterns for N were similar: there was a slight tendency toward lower mineral soil total N with WTH compared to SOH (58%) and a much larger negative effect on forest floor N (Thiffault et al., 2011). Of the nutrients reviewed by Thiffault et al. (2011), soil P showed the largest effects of WTH compared

* Corresponding author.
E-mail address: dwj@cabnr.unr.edu (D.W. Johnson).

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to SOH. Seventy-eight percent of the studies reviewed showed a decrease in soil P with WTH compared to SOH, which was in accordance to nutrient budgets which indicated 5–7-fold increases in P removal with WTH compared to SOH. Of the base cations reviewed (Ca, K, and Mg), nutrient budgets suggested the greatest potential for Ca depletion in most cases, although some indicated concern over K and Mg as well. Correspondingly, 70% of the studies reviewed reported a decrease in soil base cation concentrations and contents with WTH compared to SOH. In terms of post-harvest productivity, Thiffault et al. (2011) found that differences in regrowth during early years between WTH and SOH were negligible in most cases, but after 5 years most studies showed slower growth in WTH sites. In summary, Thiffault et al. (2011) noted that they could not "define universal and definitive prescriptive indices of site sensitivity to forest biomass harvesting with the data currently available." They also noted that the data were skewed toward even-aged coniferous forests, and that more studies from uneven-aged deciduous forests, for example, were needed.

In this study, we report the results of vegetation, forest floor and mineral soil resampling 33 years after SOH and WTH in an uneven-aged, mixed deciduous forest located near Oak Ridge, Tennessee. Initial predictions from this site indicated that harvesting removals of Ca would have the most significant effect on ecosystem nutrient budgets. In particular, calculations indicated that WTH removed twice as much Ca as was initially present on the soil exchange sites (to a 45 cm depth) and accounted for 15% of total ecosystem Ca capital including total soil Ca (Johnson et al., 1982). Foliage accounted for 7%, 7%, 23%, and 5% of tree N, P, K, and Ca; thus, although harvesting took place after leaf-fall, it had little ameliorative effects on N, P, and Ca removals. A resampling of the site 15 years after harvest (in 1995) showed no difference in forest regrowth but greater foliar concentrations of K, Ca, and Mg in the SOH than in the WTH treatment (Johnson and Todd, 1998). Contrary to initial predictions, there were no changes in exchangeable Ca^{2+} contents in the WTH soils due to tree uptake. In the SOH site, soil exchangeable Ca^{2+} increased by twofold, which was attributable to Ca release from decomposing logging residues minus Ca uptake by trees. Smaller increases in exchangeable K^{+} and Mg^{2+} were also found in the SOH as compared to the WTH sites. In both WTH and SOH sites, inexplicably large increases in total soil N content were found; these increases far exceeded possible inputs from decomposing logging residues and atmospheric deposition, and no major nitrogen fixing plant species were present (Johnson and Todd, 1998).

In 2013, we sampled vegetation, forest floor, and mineral soils of this site using the same procedures as in the past with the exception of large woody debris inventory. Soil samples from the 1980 and 1995 samplings were available and re-analyzed to avoid the possibility of laboratory bias.

2. Materials and methods

2.1. Site

The study site is located on Dept. of Energy's Oak Ridge Reservation near Oak Ridge, Tennessee. Mean annual precipitation is approximately 1500 mm, and mean annual temperature is approximately 14.4 °C (Johnson et al., 1982). The site was a woodland pasture prior to 1942 when it became part of the Oak Ridge Reservation. Since that time, it has converted to a mixed oak forest. Major species prior to harvest (and currently on the reference watershed) included chestnut oak (*Quercus prinus* L.), black oak (*Quercus velutina* Lam.), northern red oak (*Quercus rubra* L.), white oak (*Quercus alba* L.), tulip-poplar (*Liriodendron tulipifera* L.), red maple (*Acer rubrum* L.), black gum (*Nyssa sylvatica* Marsh.), sourwood (*Oxydendrum arboreum* L.), and hickory (*Carya ovata* L. and *Carya tomentosa* Nutt.). There were also occasional shortleaf pine (*Pinus echinata* Mill.) and sugar maple (*Acer saccharum* Marsh.) in the overstory and occasional sassafras (*Sassafras albidum* Nutt.) and dogwood (*Cornus florida* L.) in the understory. Non-tree understory vegetation (grasses, forbs, etc.) was negligible in this closed canopy forest. Ages of overstory trees ranged from 50 to 120 years at the time of harvest (Johnson et al., 1982).

In 2013, thirty-three years after harvest, chestnut oak, red maple, scarlet oak (*Quercus coccinea* Münchh.), and black cherry (*Prunus serotina* Ehrh.) accounted for approximately 70% of the overstory in both harvested treatments (Fig. 1). Other overstory species included southern red oak (*Quercus falcata* Michx.), white oak, tulip-poplar, loblolly pine (*Pinus taeda* L.), hickory (*Carya* spp.), sugar maple, sourwood, and northern red oak. Understory species included occasional dogwood, sweetgum (*Liquidambar styraciflua* L.), black gum, eastern red cedar (*Juniperus virginiana* L.), white ash (*Fraxinus americana* L.).

Soils are highly-weathered Ultisols derived from dolomite. Soil from ridgetops on nearby Walker Branch Watershed, which lie on the same ridge and soil type as this study, have been shown to reach 30 m in depth (Johnson and Henderson, 1979) and presumably such extremely deep soils are also present on ridgetops of the current study as well. The two dominant series on the site are highly eroded phases of the Fullerton and Bodine series, both Typic Paleudults. Fullerton soils occupy ridgetop and upper slope positions whereas Bodine occupy steeper side slopes and have a greater coarse fragment component. There are also minor inclusions of the Dewey and Dunmore series (Typic Paleudults) in the lowest slope positions (Johnson et al., 1982).

2.2. Treatments

In the spring of 1979 (prior to harvest), five contiguous watersheds ranging in size from 0.25 to 0.54 ha were surveyed and assigned treatments: watersheds 1 and 2 were whole-tree harvested, watersheds 3 and 4 were harvested for sawlogs only, leaving logging residues on site, and watershed 5 was left as an unharvested reference. In the fall of 1980, watersheds 1–4 were clearcut. All above-stump material was removed from watersheds 1 and 2, while only sawlogs (>28 cm dib) were removed from watershed 3 and 4. Each harvested log and tops and non-commercial trees from watersheds 1 and 2 were weighed at the time of harvest (Johnson et al., 1982).

2.3. Sampling

In the spring of 1979, two 10 × 10 m plots were established in each watershed ($n = 4$ for each harvested treatment, $n = 2$ for the reference watershed) for detritus and soil sampling, as per the protocols used for detritus and soil sampling on nearby Walker Branch Watershed (Johnson et al., 2007). Within each 10 × 10 m plot, three 2 × 2 m randomly selected subplots were sampled for forest floor and soil sampling ($n = 12$ for each harvest treatment and $n = 6$ for the reference treatment). Forest floor was sampled by horizon within a 0.25 m^2 circular ring at each sample point. After removal of the forest floor, a 5 cm diameter core was taken at one point within the 0.25 m^2 area for bulk density and soil samples were taken at 0–15, 15–30, and 30–45 cm depths using a bucket auger at another point in the 0.25 m^2 area. In the 1979 sampling, total soil bulk density measurements were obtained by quantitative pit excavations (Johnson et al., 1982), and these data were used to calculate total soil C and other nutrient contents. In both the 1995 and 2013 samplings, the originally established 10 × 10 m plots were relocated and sampled at different randomly-located

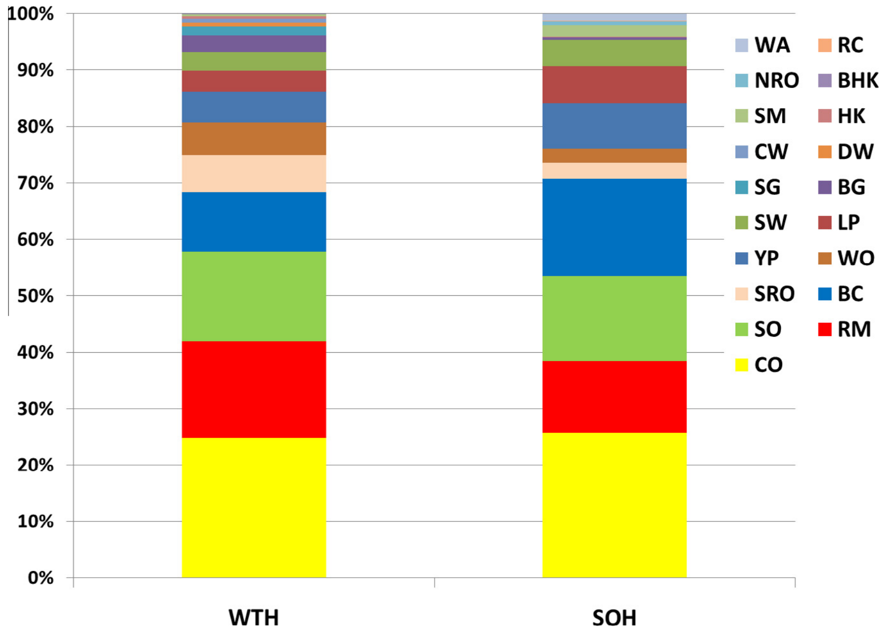

Fig. 1. Species distribution between the two harvest treatments (WTH = whole-tree harvest, SOH = stem only harvest) in 2013, 33 years after harvest according to biomass. None of the differences in species composition were significantly different (Student's *t*-test, $P < 0.05$). WA = white ash (*Fraxinus americana*), NRO = northern red oak (*Quercus rubra*), SM = sugar maple (*Acer saccharum*), CW = cottonwood (*Populus deltoides*), SG = sweetgum (*Liquidambar styraciflua*), SW = sourwood (*Oxydendrum arboreum*), YP = yellow poplar (*Liriodendron tulipifera*), SRO = southern red oak (*Q. falcata*), SO = scarlet oak (*Q. coccinea*), CO = chestnut oak (*Q. prinus.*), RC = eastern red cedar (*Juniperus virginiana*), BHK = butternut hickory (*Carya cordiformis*), HK = other hickory species (*C. ovata* and *C. tomentosa*), DW = dogwood (*Cornus florida*), BG = black gum (*Nyssa sylvatica*), LP = loblolly pine (*Pinus taeda*), WO = white oak (*Q. alba*), BC = black cherry (*Prunus serotina*), and RM = red maple (*Acer rubrum*). There were no significant differences in species composition between the two harvest treatments in 2013.

points for litter and soils in the spring of each year using the same protocols as in the 1979 sampling (Johnson and Todd, 1998).

During the spring of 2013, tree dbh was measured in 6 randomly-located, nested circular plots using the Walker Branch protocols (Harris et al., 1973). The nested plots consisted of three circular concentric plots (0.004, 0.04, and 0.08 ha). The diameter at breast height (DBH, 1.37 m) of trees of 1.5–9-cm diameter was measured within the smallest (0.004-ha) plot, the DBH of trees of 9–24-cm diameter was measured in the next smallest (0.04-ha) plot, and the DBH of trees >24 cm was measured in the largest (0.08 ha) plot. Height of co-dominant trees was also measured within each 0.08 ha plot. Tree biomass and nutrient contents were estimated from the regression equations and nutrient concentrations developed for nearby Walker Branch Watershed (Harris et al., 1973; Johnson et al., 2007, 2008).

Methods of measurement for coarse woody debris (CWD) varied over time. In 1980 (immediately after harvest) and 1995, CWD was measured by destructive sampling of three randomly-located 2 × 2 m subplots within the 10 × 10 cm plots (Johnson and Todd, 1998) whereas in 2013 CWD was estimated using the planar intercept technique described by Brown (1974) within the vegetation sampling plots.

Forest floor and soil samples taken in 2013 were analyzed for loss on ignition (LOI) and mass expressed on an ash-free basis. Forest floor and soil samples from 2013 as well as archived soil samples from 1979 and 1995 were analyzed at Coweeta Hydrological Laboratory. At Coweeta, total C and N in forest floor samples were analyzed on a Flash EA series 1112 NC Elemental Analyzer (Miniat, 2015). Total P, K, Ca, and Mg in forest floor samples were analyzed on a Thermo Scientific iCAP9300 inductively couple plasma spectrometer following dry ashing at 500 °C and dissolution of ash in 5% HNO_3 (Miniat, 2015). Soils from the 2013 sampling as well as those archived from the 1979 and 1995 samplings were analyzed for total C and total N as described above. Soils were analyzed for Bray-extractable P (2 g soil in 0.5 M HCl plus 1 M NH_4F) using a Thermo Scientific iCAP9300 inductively-coupled plasma spectrometer on extracts. Exchangeable K^+, Ca^{2+}, and Mg^{2+} in soils were measured by extraction with 1 M NH_4Cl (10 g soil, 50 ml NH_4Cl) followed by analysis of the extractant on a Thermo Scientific iCAP9300 inductively-coupled plasma spectrometer (Miniat, 2015).

2.4. Statistical methods

Treatment effects on the vegetation, coarse woody debris, forest floor, and soil samples taken in 2013 were analyzed using PROC GLIMMIX in SAS (Statistical Analysis Systems, Cary, North Carolina). Tukey post hoc tests were performed to determine differences among treatments. The effects of sampling year on soil concentrations were also analyzed by treatment using PROC GLIMMIX with Tukey post hoc tests for differences among years. In the latter case, only the soil samples analyzed in 2013 were used to avoid issues with laboratory bias over the years. Some of the original samples were missing from the archived collections and for that reason along with the change in statistical method (PROC GLM in SAS was used in the past), the results of the statistical analyses in the current study did not exactly match those done in the past (Johnson and Todd, 1998). Student's *t*-tests in Microsoft Excel® were used to test for differences in species composition between the two harvested treatments.

3. Results

3.1. Differences among treatments 33 years after harvest

3.1.1. Stand characteristics and distribution of above ground biomass

In the 2013 sampling, average tree diameter, basal area, height, and biomass were smaller in the WTH than in the SOH site, but the differences were not significant at the traditional $P < 0.05$ (Table 1).

Table 1
Stand characteristics and above-ground biomass in 2013. Average and standard errors (among plots) of diameter at 1.37 m, basal area (BA), height of dominant and co-dominant trees, numbers of stems, biomass of trees, coarse woody debris (CWD), and forest floor by horizon in stem only harvested (SOH), whole-tree harvested (WTH), and unharvested stands (REF). *P* values indicate the difference among treatments, PROC GLIMMIX in SAS. Means not sharing the same letter are significantly different, $P < 0.05$.

	REF	SOH	WTH	*P*
Stand characteristics				
Diameter (cm)	27.6 ± 0.4^{b}	14.2 ± 1.3^{a}	13.1 ± 0.9^{a}	<0.01
BA (m^2 ha^{-1})	31.9 ± 7.1^{a}	23.7 ± 1.0^{a}	20.6 ± 2.4^{a}	0.10
Height (m)	31.5 ± 1.9^{b}	20.2 ± 0.6^{a}	16.7 ± 1.4^{a}	<0.01
Stems (# ha^{-1})	544 ± 148^{a}	3722 ± 745^{a}	4324 ± 1513^{a}	0.20
Biomass (Mg ha^{-1})				
Trees	257.5 ± 34.8^{b}	149.3 ± 5.9^{a}	124.4 ± 17.0^{a}	<0.01
CWD	16.5 ± 3.4^{a}	54.4 ± 14.7^{a}	25.9 ± 2.6^{a}	0.10
Forest floor				
Other	2.3 ± 0.6^{a}	1.6 ± 0.4^{a}	2.0 ± 4.1^{a}	0.57
Oi	2.9 ± 0.2^{a}	2.4 ± 0.3^{a}	3.2 ± 0.3^{a}	0.25
Oe	3.7 ± 0.6^{a}	4.0 ± 0.5^{a}	3.7 ± 0.6^{a}	0.90
Oa	1.9 ± 1.3^{a}	2.0 ± 0.8^{a}	10.8 ± 3.5^{a}	0.02
Total	10.8 ± 1.7^{ab}	10.1 ± 1.3^{a}	19.8 ± 3.3^{b}	0.02
Total aboveground	287.3 ± 50.7^{b}	215.7 ± 18.5^{ab}	175.5 ± 17.0^{a}	0.05

As expected, the REF site had greater average diameter, basal area, and height but lower stems per ha than either of the harvested treatments.

The only significant difference in detritus among treatments was in total forest floor mass, which was twofold greater in the WTH than in the REF and SOH treatments (Table 1). These differences were due to the much greater Oa horizon mass in the WTH than in the other treatments. Variability in Oa mass was very high, however: one third of the sampling points in the WTH treatment had no Oa horizon, and half of the SOH and REF sample points had no Oa horizon. Sample points with no Oa horizon were counted as having zero mass when calculating means and standard errors. Total aboveground biomass (including tree, CWD, and forest floor) was significantly greater in the REF than in the harvested treatments because of greater tree biomass in the former.

3.1.2. Forest floor nutrient concentrations and contents

There were no significant differences in nutrient concentrations in the Oi horizons or in the composites of twigs and reproductive parts ("other") 33 years after harvest, but differences did occur in the Oe and Oa horizons. Potassium concentrations were greatest in the Oe and Oa horizons of the WTH treatment, and Ca and Mg concentrations were greatest in the Oa horizon of the WTH treatment (Table 2). Because of differences in Oa horizon mass (and also differences in the concentrations of K, Ca, and Mg), there were significant differences in nutrient contents among the treatments (Fig. 2). In Fig. 2, the probability of treatment effects on total forest floor nutrient contents was statistically significant ($P < 0.05$) and in each case, post hoc tests showed significantly greater nutrient contents in the WTH than in the SOH treatment.

3.1.3. Soil nutrient concentrations

There were no statistically significant differences in soil total C, total N, C:N ratio, or exchangeable K^{+} concentrations in any horizon in the 2013 sampling (Table 3). Extractable P concentrations in the 0–15 cm depth were significantly greater in the REF than in the SOH or WTH treatments, but differences in extractable P at other depths were small and not statistically significant. Exchangeable Ca^{2+} concentrations were significantly lower in the WTH than in the SOH and REF treatments at both the 0–15 and 15–30 cm depths. The same was true at the 30–45 cm depth, but differences were not statistically significant ($P = 0.10$) at that depth. Similarly, exchangeable Mg^{2+} concentrations were significantly lower in the WTH than in the SOH and REF treatments at both the 0–15 and 15–30 cm depths. Unlike the case with Ca^{2+}, however, the pattern did not hold at the 30–45 cm depth, and differences in exchangeable Mg^{2+} were not statistically significant ($P = 0.50$).

3.2. Changes over time

3.2.1. Tree and forest floor biomass

Changes in tree and forest floor biomass over time are depicted in Fig. 3. In 1979 (prior to harvest), a complete inventory of the watersheds showed that tree biomass differed by 10% among the treatments (191.7, 207.1, and 187.7 Mg ha^{-1} in the REF, SOH, and WTH treatments, respectively) (Johnson et al., 1982; Johnson and Todd, 1987) (Fig. 3A). In 1980 (immediately after harvest), tree biomass in both harvest treatments was 0. In 1995 (15 years after harvest), tree biomass in the harvest treatments was virtually identical (2% lower in the SOH than in the WTH) and equaled 22% of that in the REF treatment (Johnson and Todd, 1998). In 2013 (33 years after harvest), as noted above, tree biomass in the SOH treatment was 20% greater than in WTH treatment but differences were not statistically significant ($P < 0.05$) according to Tukey post hoc comparisons. Tree biomass in the SOH and WTH treatments equaled 48% and 58% of that in the REF treatment,

Table 2
Forest floor nutrient concentrations in 2013. Statistically significant differences ($P < 0.05$) are shown in bold. Means not sharing the same letter are significantly different according to Tukey's post hoc tests.

Horizon	Treatment			Prob.	Treatment			Prob.
	REF	SOH	WTH		REF	SOH	WTH	
	Carbon (mg g^{-1})				*Nitrogen (mg g^{-1})*			
Other	408 ± 27	452 ± 16	403 ± 38	0.32	10.1 ± 1	10.4 ± 1.3	9.8 ± 1.1	0.93
Oi	433 ± 19	395 ± 26	430 ± 27	0.48	10.8 ± 1	9.3 ± 0.8	10 ± 1.4	0.65
Oe	393 ± 29	421 ± 13	378 ± 35	0.42	9.4 ± 0.8	9.2 ± 0.7	9.3 ± 0.8	0.99
Oa	311 ± 37	427 ± 21	386 ± 47	0.20	8.4 ± 0.7	9.8 ± 0.5	10.1 ± 1.4	0.41
	Phosphorus (mg g^{-1})				*Potassium (mg kg^{-1})*			
Other	0.50 ± 0.06	0.65 ± 0.07	0.66 ± 0.07	0.39	0.95 ± 0.09	1.12 ± 0.07	1.07 ± 0.14	0.53
Oi	0.74 ± 0.05	0.56 ± 0.06	0.65 ± 0.09	0.23	1.28 ± 0.07	1.21 ± 0.07	1.08 ± 0.11	0.28
Oe	0.55 ± 0.06	0.54 ± 0.04	0.59 ± 0.06	0.77	**1.10 ± 0.05^{ab}**	**0.96 ± 0.06^{a}**	**1.18 ± 0.07^{b}**	**0.03**
Oa	0.47 ± 0.05	0.52 ± 0.04	0.63 ± 0.09	0.19	**0.77 ± 0.16^{a}**	**0.83 ± 0.05^{a}**	**1.40 ± 0.09^{b}**	**0.01**
	Calcium (mg g^{-1})				*Magnesium (mg g^{-1})*			
Other	12.2 ± 1.8	10.2 ± 1.7	14.9 ± 2.1	0.16	1.55 ± 0.18	1.22 ± 0.14	1.54 ± 0.3	0.33
Oi	14.0 ± 1.3	14.0 ± 1.7	10.0 ± 0.7	0.09	1.2 ± 0.14	1.47 ± 0.18	1.43 ± 0.06	0.55
Oe	22.4 ± 1.4	18.5 ± 1.1	15.0 ± 5.7	0.17	1.43 ± 0.12	1.23 ± 0.09	1.28 ± 0.19	0.51
Oa	**10.7 ± 2.6^{a}**	**18.5 ± 2.1^{ab}**	**24.1 ± 2.7^{b}**	**0.02**	**0.73 ± 0.08^{a}**	**1.18 ± 0.04^{b}**	**1.74 ± 0.22^{c}**	**<0.01**

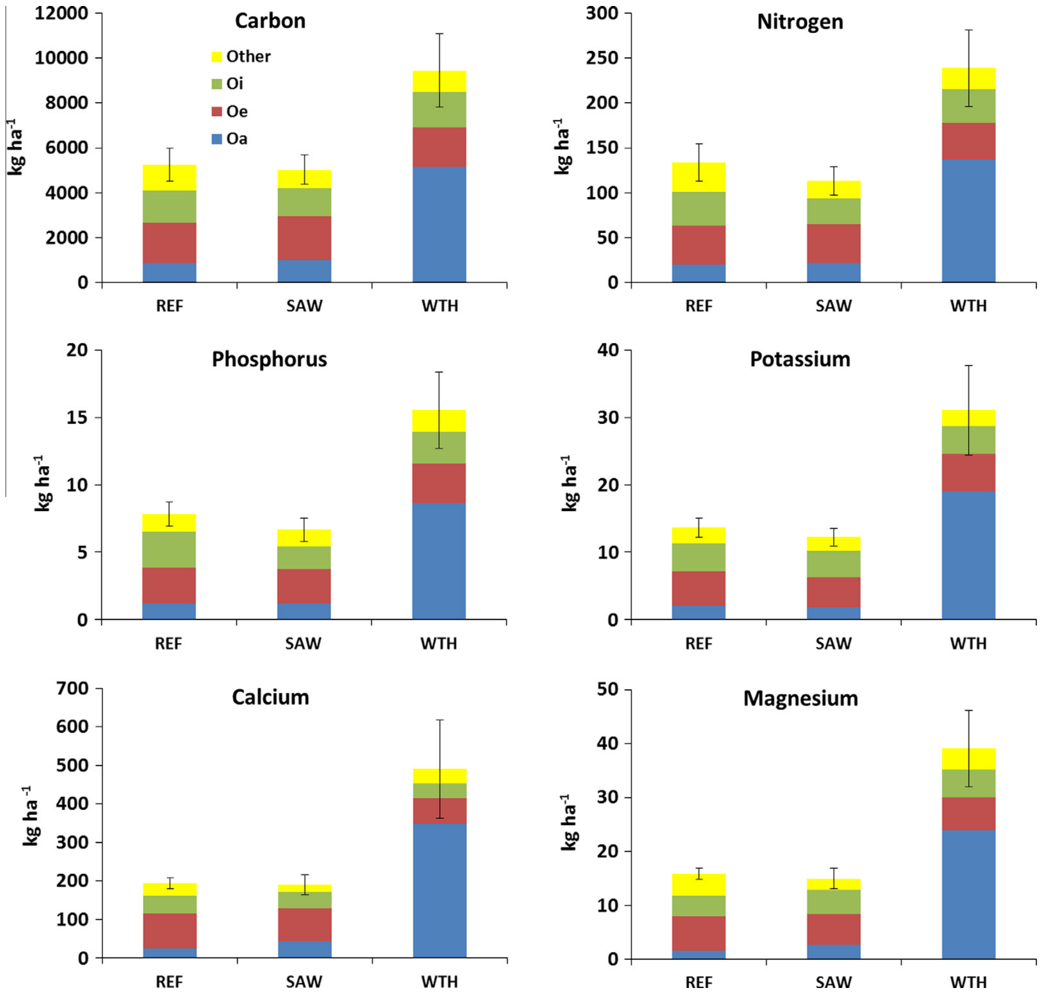

Fig. 2. Forest floor nutrient contents in 2013, 33 years after harvest. REF = reference treatment (no harvest), SOH = stem only harvest, WTH = whole-tree harvest. Error bars indicate standard errors.

Table 3
Soil nutrient concentrations in 2013. Statistically significant differences ($P < 0.05$) are shown in bold. Means not sharing the same letter are significantly different according to Tukey's post hoc tests.

Depth (cm)	Treatment			Prob.	Treatment			Prob.
	REF	SOH	WTH		REF	SOH	WTH	
	Carbon (mg g⁻¹)				*Nitrogen (mg g⁻¹)*			
0–15	21.6 ± 3.3	21.3 ± 1	19.7 ± 1.2	0.65	1.15 ± 0.17	1.17 ± 0.09	0.92 ± 0.07	0.12
15–30	11.3 ± 2.9	10.3 ± 0.8	9.4 ± 0.6	0.34	0.57 ± 0.2	0.53 ± 0.03	0.45 ± 0.03	0.09
30–45	3.9 ± 0.9	7.2 ± 0.9	6 ± 0.5	0.38	0.11 ± 0.07	0.4 ± 0.04	0.32 ± 0.02	0.22
	C:N ratio				*Phosphorus (mg kg⁻¹)*			
0–15	18.7 ± 0.7	18.8 ± 0.4	22.0 ± 1.4	0.05	**17.35 ± 1.93[a]**	**11.48 ± 1.08[b]**	**10.1 ± 0.94[b]**	**<0.01**
15–30	18.3 ± 0.9	19.4 ± 0.9	21.0 ± 1.3	0.12	5.28 ± 0.57	4.63 ± 0.29	5.09 ± 0.49	0.59
30–45	18.7 ± 1.1	18.0 ± 0.7	18.4 ± 0.7	0.95	2.06 ± 0.21	1.89 ± 0.37	2.67 ± 0.52	0.41
	Potassium (cmol$_c$ kg⁻¹)				*Calcium (cmol$_c$ kg⁻¹)*			
0–15	0.21 ± 0.02	0.18 ± 0.02	0.15 ± 0.01	0.12	**1.68 ± 0.3[a]**	**1.13 ± 0.2[a]**	**0.35 ± 0.09[b]**	**<0.01**
15–30	0.11 ± 0.01	0.12 ± 0.01	0.11 ± 0.01	0.77	**0.62 ± 0.2[a]**	**0.58 ± 0.13[a]**	**0.15 ± 0.02[b]**	**0.01**
30–45	0.09 ± 0.01	0.11 ± 0.01	0.12 ± 0.02	0.48	0.39 ± 0.14	0.47 ± 0.12	0.19 ± 0.05	0.10
	Magnesium (cmol$_c$ kg⁻¹)							
0–15	**0.39 ± 0.07[a]**	**0.31 ± 0.06[ab]**	**0.15 ± 0.02[b]**	**0.01**				
15–30	**0.15 ± 0.02[ab]**	**0.16 ± 0.03[a]**	**0.08 ± 0.01[b]**	**0.02**				
30–45	0.14 ± 0.03	0.21 ± 0.06	0.14 ± 0.05	0.50				

respectively. Tree biomass in the REF treatment increased by 28% from 1979/1980 to 1995, but by only 5% between 1995 and 2013.

Forest floor biomass in the SOH treatment was stable (varied by <10%) over the entire sampling period. Forest floor biomass in the WTH treatment was also stable from 1979 through 1995, but then increased by twofold by 2013. Forest floor biomass differed by less than 5% between the SOH and WTH treatments in 1979, 1980, and 1995 but by two fold in 2013. Forest floor biomass in the REF

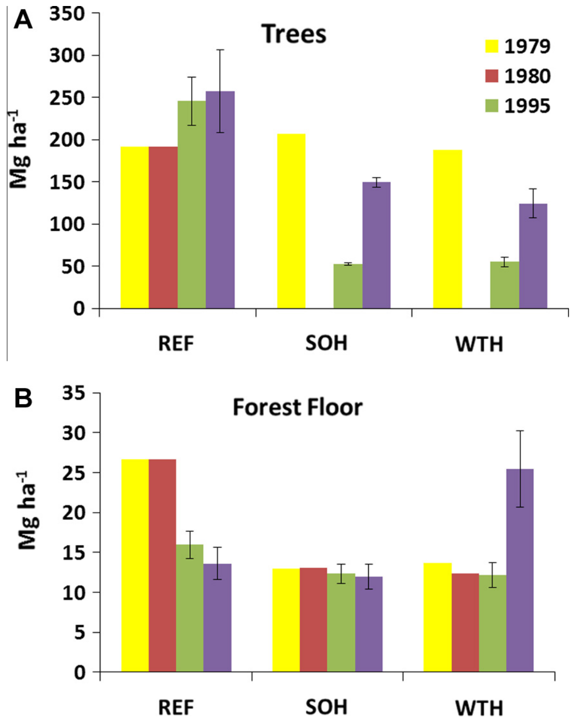

Fig. 3. Vegetation (A) and forest floor (B) biomass in the two harvest treatments before harvest (1979), immediately after harvest (1980), 15 years after harvest (1995), and 33 years after harvest (2013). Values for 1979, 1980, and 1995 are taken from Johnson et al. (1982) and Johnson and Todd (1987, 1998). SOH = stem only harvest, WTH = whole-tree harvest. Error bars indicate standard errors.

treatment was twofold greater than in either of the harvest treatments in 1979, but then decreased by 50% between 1979 and 1995, and by 15% from 1995 to 2013.

Changes in the mass of coarse woody debris biomass (CWD) in the harvested treatments between 1980 and 1995 have been reported previously (Johnson and Todd, 1998), and due to the changes in methodology, direct comparisons between 2013 values and those in past years were not made. As previously reported, CWD biomass in the SOH treatment (55.9 Mg ha^{-1}) was 15-fold greater than in the WTH treatment (3.6 Mg ha^{-1}) immediately after harvest because of the differences in logging residues (Johnson and Todd, 1998). Fifteen years later, CWD in the SOH treatment (10.6 Mg ha^{-1}) had decreased by 80% but was still greater than in the WTH treatment (0.9 Mg ha^{-1}) (Johnson and Todd, 1998). In 2013, CWD biomass in the SOH treatment was over twofold greater than in the WTH treatment but differences were not statistically significant (Table 1).

3.2.2. Soil nutrient concentrations

Changes in soil nutrient concentrations over time can be evaluated more rigorously than those in biomass and detritus because of our ability to re-analyze archived samples from 1979 and 1995 along with those from 2013 in the same laboratory at the same time. Figs. 4–7 depict these changes by depth and Table 4 gives the results of statistical analyses of the effects of time by treatment.

Changes in C concentration over time were significant in the 0–15 cm depths of the SOH and WTH treatments and in the 30–45 cm depth in the SOH treatment (Table 4). In the 0–15 cm depths, this was due to statistically significant increases between 1979 and 1995 in both harvest treatments (Fig. 4A). Decreases in total soil C in the 0–15 cm depth between 1995 and 2013 were observed in both harvested treatments, but these were not statistically significant according to Tukey post hoc tests (Fig. 4A). Previous results for the 0–15 cm depths in both harvest treatments also showed statistically significant increases between 1979 and 1995 (Johnson and Todd, 1998). In the 30–45 cm depth in the SOH treatment this was due to a significant increase between 1995 and 2013 (Fig. 4A).

Changes in N concentration were significant over time in the 0–15 and 15–30 cm depths of the SOH treatment and in the 15–30 and 30–45 cm depths in the WTH treatment (Table 4). In the SOH treatment, concentrations increased between 1979 and 1995 at both the 0–15 and 15–30 cm depths (Fig. 4B). These changes were significant ($P < 0.05$) at the 15–30 cm depth but not the 0–15 cm depth according to Tukey post hoc tests, even though overall P values in the former were statistically significant ($P = 0.03$). Tukey's post hoc P values for the increase in total N in the 0–15 cm depth between 1979 and 1995 in the SOH treatment ($P = 0.0509$) were very close to the traditional cutoff value, however. In the WTH treatment, increases in total N between 1979 and 1995 were statistically significant at both the 15–30 and 30–45 cm depths. The current results are consistent with previous results, which also showed statistically significant soil N increases ($P < 0.05$) between 1979 and 1995 in 0–15 and 15–30 cm depths of the SOH treatment and in the 15–30 and 30–45 cm depths in the WTH treatment (Johnson and Todd, 1998). There were no statistically significant differences in N concentrations between 1995 and 2013 in any treatment according to Tukey post hoc tests, but there was a general pattern of decrease in all depths of the WTH treatment whereas concentrations remained similar in the SOH treatment (Fig. 3B). In the case of the decrease in total N in the 30–45 cm depth between 1995 and 2013 in the WTH treatment, Tukey's post hoc P value ($P = 0.0583$) was very close to the traditional cutoff value, however.

Changes in C:N ratio were significant only at the 30–45 cm depth in the SOH treatment, where there was a decrease between 1979 and 1995, followed by an increase in 2013 (Table 4 and Fig. 5A). Differences between individual years were not significant according to Tukey post hoc tests even though the overall P value ($P = 0.0495$) was slightly below the traditional cutoff value (Fig. 5A). Previous results showed decreases in C:N ratio between 1979 and 1995 in the 15–30 and 30–45 cm depths in both harvest treatments, but results were statistically significant ($P < 0.05$) only in the 15–30 cm depth of the SOH treatment (Johnson and Todd, 1998).

Changes in extractable P were significant in the 0–15 cm depths in all treatments due to large decreases between 1979 and 1995 (Table 4 and Fig. 5B). Changes in extractable P were also significant in the 15–30 cm depth in the SOH treatment due to decreases from 1979 to 2013. Other depths in any treatment. Previous results also showed large decreases in extractable P in the 0–15 cm depths of all treatments between 1979 and 1995 (Johnson and Todd, 1998). However, because the archived 1979 samples were not reanalyzed in the 1995 study, statistical analyses were not performed at that time because of potential errors due to laboratory bias (Johnson and Todd, 1998).

There were no statistically significant changes in exchangeable K^+ over time in any treatment (Table 4 and Fig. 6A). Similarly, previous results showed no statistically significant changes in exchangeable K^+ between 1979 and 1995 in any treatment (Johnson and Todd, 1998)

Changes in exchangeable Ca^{2+} were statistically significant in the 0–15 cm depth of the SOH treatment and in the 15–30 cm depth in the WTH treatment (Table 4). Exchangeable Ca^{2+} increased significantly between 1979 and 1995 in the 0–15 cm depth of the SOH treatment (Fig. 6B), as reported previously (Johnson and Todd, 1998). These increases were attributed to releases of Ca from decomposing logging residues. Previous results

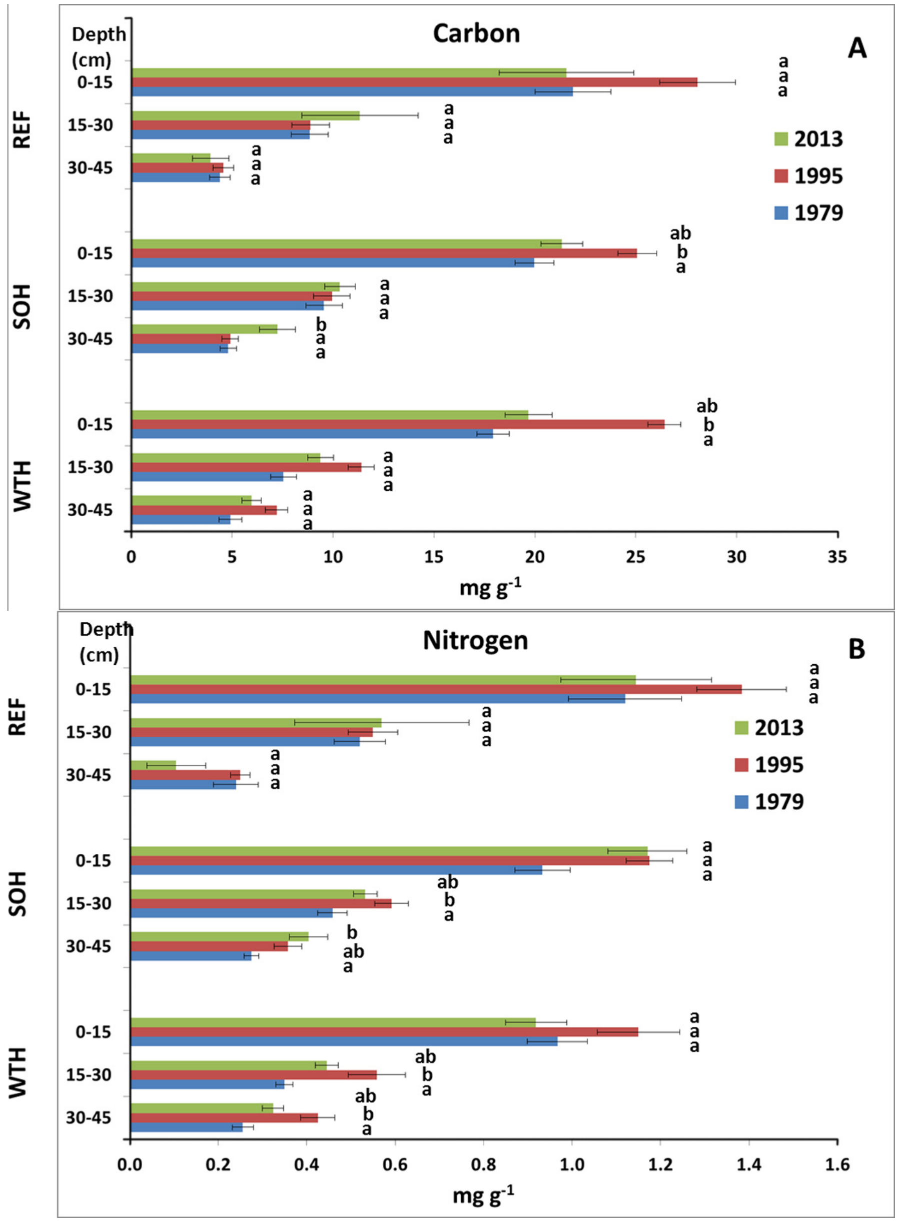

Fig. 4. Total soil C (A) and total soil N (B) before harvest (1979), 15 years after harvest (1995), and 33 years after harvest (2013). REF = reference treatment (no harvest), SOH = stem only harvest, WTH = whole-tree harvest. Values not sharing the same letter within each treatment and depth are significantly different from one another ($P < 0.05$) according to Tukey's post hoc test.

also showed statistically significant ($P < 0.05$) increases in exchangeable Ca^{2+} in the 15–30 cm depth of the SOH treatment (Johnson and Todd, 1998), but the current analyses did not show that change to be statistically significant ($P = 0.19$). In the WTH treatment, exchangeable Ca^{2+} decreased between 1995 and 2013 in all horizons (Fig. 6B). These decreases were significant ($P < 0.05$) in the 15–30 cm depth according to Tukey's post hoc tests, and Tukey's post hoc P for the decrease in the 0–15 cm depth ($P = 0.0556$) was only slightly above the traditional cutoff value.

Changes in exchangeable Mg^{2+} were statistically significant only in the 0–15 cm depth of the SOH treatment (Table 4). Exchangeable Mg^{2+} increased between 1979 and 1995 at that depth and treatment. The P value from Tukey post hoc tests of changes between 1979 and 1995 at that depth and treatment ($P = 0.0541$) was only slightly above the $P < 0.05$ level (Fig. 7). Previous results also showed that the only significant changes in Mg^{2+} were at the 0–15 cm depth of the SOH treatment ($P < 0.01$).

4. Discussion

4.1. Changes in vegetation and forest floor

Mann (1984) reported that average sprout production per stump was greater in the WTH than in the SOH site in the first year after harvest and estimated that sprout biomass was greater in the SOH (679 kg ha^{-1}) than in the WTH and (433 kg ha^{-1}) treatment. Mann (1984) also found some species differences between treatments one year after harvest: maximum heights of stump sprouts on chestnut oak, black oak, and red maple were greater on the SOH than on the WTH site, whereas the reverse was true for tulip-poplar and sourwood. Most species produced more seedlings in the WTH than in the SOH site, a response attributed to the level of site disturbance.

These early differences noted at one year after harvest disappeared at 15 years after harvest, when regeneration biomass was

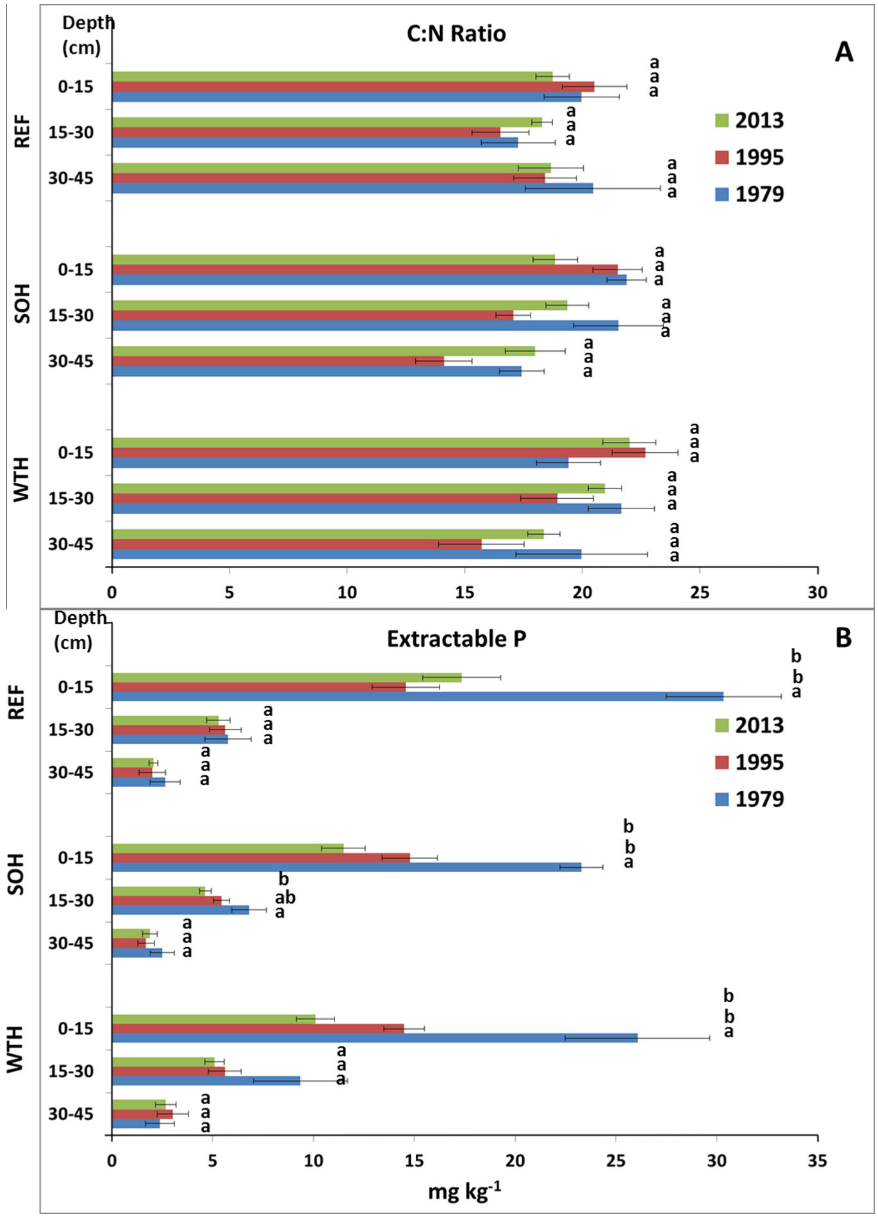

Fig. 5. Soil C:N ratio (A) and extractable P (B) before harvest (1979), 15 years after harvest (1995), and 33 years after harvest (2013). REF = reference treatment (no harvest), SOH = stem only harvest, WTH = whole-tree harvest. Values not sharing the same letter within each treatment and depth are significantly different from one another ($P < 0.05$) according to Tukey's post hoc test.

virtually identical (differed by 2%) in the two harvest treatments (Johnson and Todd, 1998). It appears that differences in biomass may be starting to re-emerge again in 2013 when biomass in the SOH treatment was 20% greater than in the WTH treatment. Differences in 2013 were not statistically significant according to Tukey post hoc tests, however. Thus, no statistically definitive statement about the long-term effects of harvest treatments on tree growth can be made at this time.

A very clear difference between past results and those from the 2013 sampling is evident in the forest floor results. For reasons that are unclear, average mass and nutrient contents in the forest floor in the WTH treatment increased by over two fold between 1995 and 2013 whereas values in the SOH treatment remained relatively stable. This difference was due entirely to differences in Oa horizon mass. As noted earlier, Oa horizons were spotty, with an Oa present on two thirds of the sample points in the WTH treatment and half of the sample points in the SOH and REF treatments. The greater percentage of sample points with zero Oa mass in the WTH treatment was only a minor factor, however: the average Oa mass of sample points with a positive Oa mass was much greater in the WTH treatment (16.3 ± 4.0 Mg ha^{-1}) than in the SOH (4.0 ± 1.2 Mg ha^{-1}) or REF (3.9 ± 1.4 Mg ha^{-1}) treatments. There are of course always concerns as to interpreting boundaries between forest floor horizons; while we feel that this was well controlled for, the fact remains that total forest floor mass in the WTH treatment (19.8 ± 3.3 Mg ha^{-1}) was twice as high as in the SOH treatment (10.1 ± 1.3 Mg ha^{-1}) and REF (10.8 ± 1.7 Mg ha^{-1}) treatment. The differences in forest floor mass between the WTH and SOH treatments in 2013 were not due to differences in understory forbs or grasses, both of which were negligible in both treatments in the 1995 sampling. These differences do not appear to be caused by differences in N concentrations of any forest floor horizon, nor have they caused any differences in forest floor N concentrations among treatments (Table 2). Potassium, Ca, and Mg concentrations are greater in the Oa horizons of the WTH treatment than in the other treatment, but whether this is a cause or an effect of the

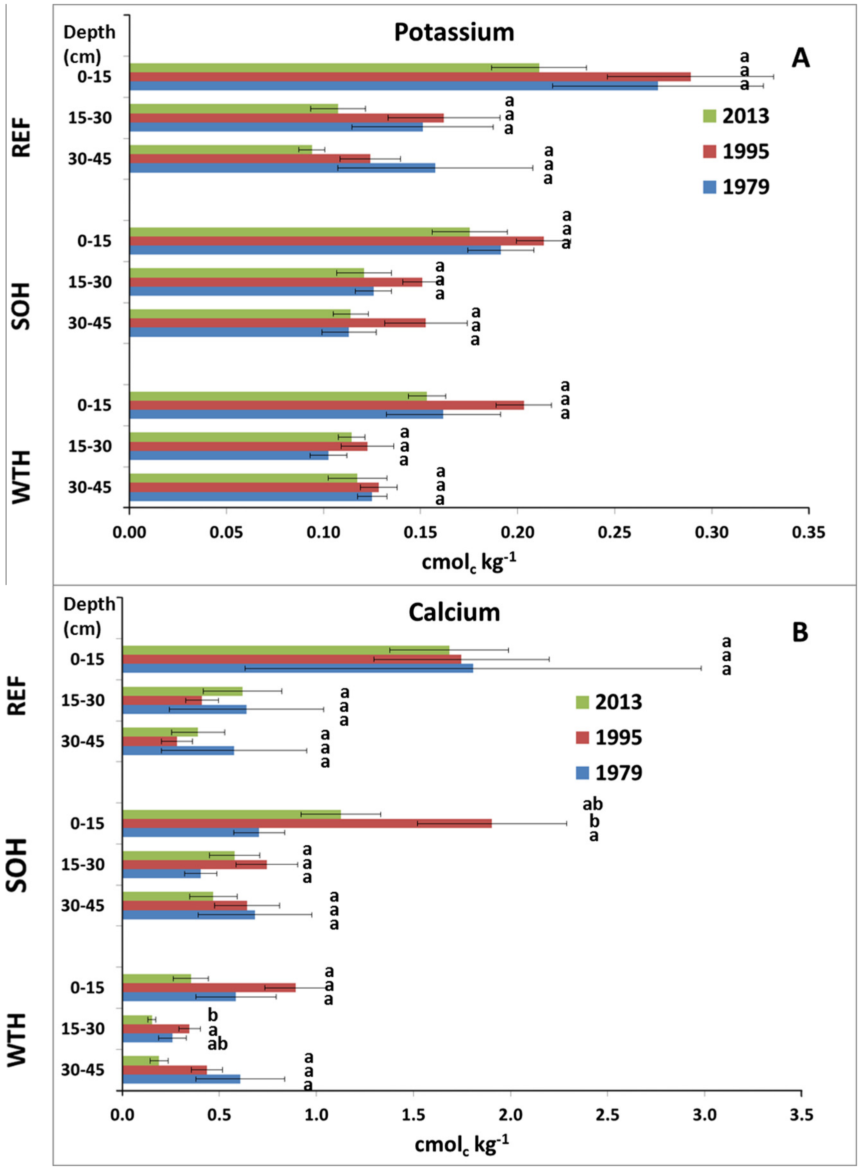

Fig. 6. Soil exchangeable K^+ (A) and Ca^{2+} (B) before harvest (1979), 15 years after harvest (1995), and 33 years after harvest (2013). REF = reference treatment (no harvest), SOH = stem only harvest, WTH = whole-tree harvest. Values not sharing the same letter within each treatment and depth are significantly different from one another ($P < 0.05$) according to Tukey's post hoc test.

differences in Oa horizon mass are unclear. It is clear that the patterns in Oa horizon concentration did not cause increases in mineral soil exchangeable Ca^{2+} or Mg^{2+} concentrations immediately below, the latter of which were significantly lower in the WTH treatment than in the other treatments (Table 3). There were no significant correlations between Oa horizon C, N, P, K, Ca, or Mg concentrations and the concentrations of C, N, Bray P, K^+, Ca^{2+} or Mg^{2+} in surface soils (0–15 cm) beneath. There were significant ($P < 0.05$) correlations between Oa horizon mass and Bray P ($r^2 = 0.63$, $P < 0.01$) and K^+ ($r^2 = 0.24$, $P = 0.03$), but no other significant correlations between Oa mass and other soil nutrients. Causal relationships between Oa mass and soil P and K^+, if any, are unknown, however. It is noteworthy that the pattern in Oa horizon cation concentrations in 2013 is in direct contrast to foliar analyses in 1995, where K, Ca, and Mg concentrations were all lowest in the WTH treatment. As noted earlier, there were no tree species differences between the two harvested treatments in either the 1995 or 2013 samplings. The differences in biomass and species compositions at one year after harvest noted by Mann (1984) may have had some long-term effect on the development of thicker Oa horizons in the WTH treatment, but such an effect, if it occurred, was not manifest at 15 years after harvest. Thus, the reason(s) for the large increase in Oa horizon biomass and nutrient content in the WTH treatment remain(s) unclear. The observed response on this site following harvesting contrasts with the stereotypic response which portrays declines in forest floor organic matter following harvesting followed by a slow recovery (Yani et al., 2003a). Instead, we've observed distinct shifts in the forest floor organic matter content both within a treatment (e.g., REF, WTH) and between treatments that do not align easily with a disturbance response followed by recovery. Clearly the forest floor mass, and especially the Oa horizon, is dynamic, and merits careful consideration to assess the causes of change over time (Yani et al., 2003b).

4.2. Nutrient contents

We sampled bulk density by the core method in the surface depth at each soil sampling point in 1995 and 2013 in order to

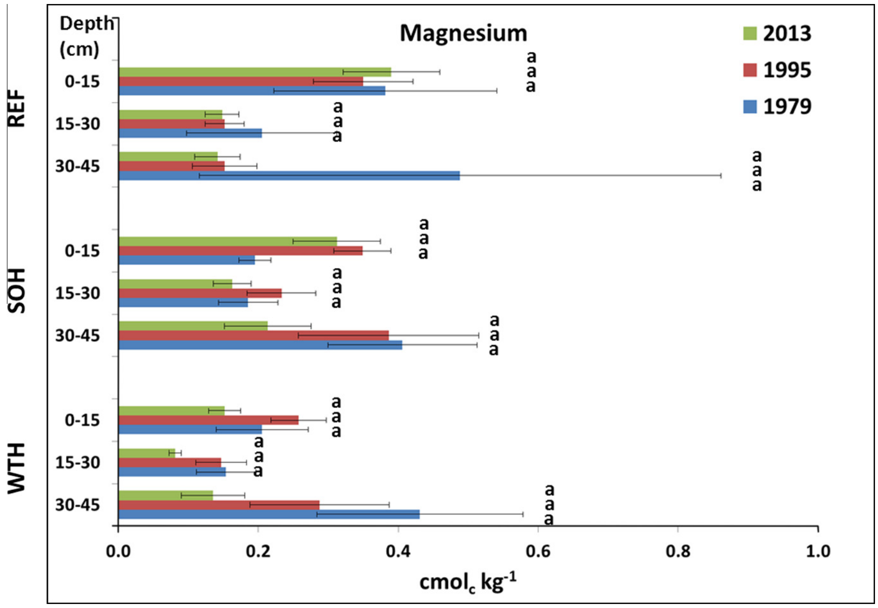

Fig. 7. Soil exchangeable Mg^{2+} before harvest (1979), 15 years after harvest (1995), and 33 years after harvest (2013). REF = reference treatment (no harvest), SOH = stem only harvest, WTH = whole-tree harvest. Values not sharing the same letter within each treatment and depth are significantly different from one another ($P < 0.05$) according to Tukey's post hoc test.

Table 4
Statistical analysis of changes in soil nutrient concentrations over the 1979, 1995 and 2013 samplings using PROC GLIMMIX. Values in bold are $P < 0.05$.

Source	df	REF		SOH		WTH	
		F	*P*	*F*	*P*	*F*	*P*
Carbon							
0–15 cm	2	2.11	0.16	**5.40**	**<0.01**	**4.02**	**0.03**
15–30 cm	2	1.05	0.37	0.28	0.26	1.37	0.27
30–45 cm	2	1.41	0.29	**4.69**	**0.02**	1.13	0.34
Nitrogen							
0–15 cm	2	1.12	0.35	**3.91**	**0.03**	2.48	0.10
15–30 cm	2	0.54	0.59	**4.17**	**0.02**	**6.28**	**<0.01**
30–45 cm	2	0.58	0.59	3.16	0.06	**7.22**	**<0.01**
C:N ratio							
0–15 cm	2	0.56	0.58	3.16	0.06	1.75	0.19
15–30 cm	2	0.58	0.58	2.97	0.07	1.23	0.30
30–45 cm	2	0.27	0.77	**3.37**	**0.05**	1.39	0.27
Bray P							
0–15 cm	2	**14.60**	**<0.01**	**26.79**	**<0.01**	**13.87**	**<0.01**
15–30 cm	2	0.09	0.91	**3.72**	**0.03**	2.55	0.09
30–45 cm	2	0.37	0.70	0.79	0.46	0.72	0.80
Potassium							
0–15 cm	2	1.29	0.31	1.27	0.29	1.83	0.17
15–30 cm	2	1.35	0.29	2.02	0.15	0.96	0.39
30–45 cm	2	1.27	0.31	1.98	0.16	0.25	0.78
Calcium							
0–15 cm	2	0.01	0.98	**5.36**	**<0.01**	2.91	0.07
15–30 cm	2	0.35	0.71	1.76	0.19	**3.27**	**0.05**
30–45 cm	2	0.41	0.67	0.28	0.75	2.61	0.09
Magnesium							
0–15 cm	2	0.07	0.93	**3.19**	**0.05**	1.31	0.48
15–30 cm	2	0.33	0.72	0.79	0.46	1.51	0.23
30–45 cm	4	0.92	0.42	0.93	0.40	2.10	0.13

check for treatment effects. No effects were found in the 1995 sampling, but unfortunately the 2013 samples were disposed of before being sieved and thus cannot be used to evaluate treatment effects or to calculate mass and nutrient contents in the fine earth (<2 mm) fraction (samples for nutrient analyses sieved before analysis with a 2 mm sieve). For this reason, and because the small core cannot account for large coarse fragment contents, we used the 1979 quantitative pit bulk density data to calculate soil C and other nutrient contents, as was the case for the previous paper (Johnson and Todd, 1998).

Soil total C content to a 45 cm depth increased by 11.1, 9.6 and 26.7 Mg ha^{-1} (0.69, 0.60, and 1.67 Mg ha^{-1} yr^{-1}) between 1979 and 1995 in the REF, SOH and WTH treatments, respectively. Previous estimates for soil C content changes between 1979 and 1995 were +9 and +27 Mg ha^{-1} (0.6 and 1.7 kg ha^{-1} yr^{-1}) in the SOH and WTH treatments, respectively (changes in the REF treatment were not reported) (Johnson and Todd, 1998). As noted previously, the changes from 1979 to 1995 could be accounted for by litterfall and root turnover inputs similar to those measured on nearby Walker Branch watershed (90 Mg ha^{-1}) (Johnson and Todd, 1998). Carbon releases from decomposing residues in the SOH treatment over this time period (45 Mg ha^{-1}) were large enough to account for the increases in soil C content in that treatment, but the fact that there was no difference in soil C contents between the harvest treatments in 1995 suggests that most C lost from decomposing residues was lost as CO_2 (Johnson and Todd, 1998).

Calculations of soil N content changes using the 2013 concentration data showed increases of 540, 840 and 1070 kg ha^{-1} (34, 53, and 67 kg ha^{-1} yr^{-1}) between 1979 and 1995 in the REF, SOH and WTH treatments, respectively. Previous estimates were 850 and 1250 kg ha^{-1} (53 and 78 kg ha^{-1} yr^{-1}) in the SOH and WTH treatments, respectively (changes in the REF treatment were not reported) (Johnson and Todd, 1998). As noted previously (Johnson and Todd, 1998), these increases were far greater than could be explained by atmospheric N inputs (150 kg ha^{-1}), release of N from decomposing logging residues (110 kg ha^{-1}) or any other known input. Nitrogen fixing vegetation one year after harvest constituted 2% of herbaceous biomass (23 and 34 kg ha^{-1} in the SOH and WTH treatments respectively) (Mann, 1984) and were entirely absent in 1995 and 2013 (Johnson and Todd, 1998). Between 1995 and 2013, calculated total N changes in the REF, SOH, and WTH treatments were −660, −30, and −819 kg ha^{-1} (−36, −2, and −46 kg ha^{-1} yr^{-1}), respectively. The changes in the REF and WTH sites are unreasonably large compared to N leaching rates measured previously at this site (approximately 2.7 kg ha^{-1} yr^{-1}) (Johnson and Todd, 1987) and forest floor changes (50, −30 and 100 kg ha^{-1} in the REF, SOH and WTH treatments, respectively). We did not obtain permission to harvest trees to measure nutrient concentrations in 2013, but using concentration data from nearby Walker Branch Watershed (Johnson et al., 2007, 2008), we estimate N increments in vegetation at 15, 250, and 190 kg ha^{-1} (0.8, 14, and 11 kg ha^{-1} yr^{-1}) in the REF, SOH, and WTH treatments, respectively. Thus, from these calculations, we can account for only 2% of the decreases in soil N contents between 1995 and 2013 in the REF treatment and 35% of the decreases in the WTH treatment.

Inexplicably large and significant changes in soil total N have also been observed in the more mature forests on nearby Walker Branch Watershed. In that case, a significant decrease in soil N content was observed between 1982 and 1993 (−70.4 kg ha^{-1} yr^{-1}) followed by an increase between 1993 and 2004 (+23.4 kg ha^{-1} yr^{-1}). In that case, the decreases could not be explained by leaching, increments in vegetation and forest floors (both of which were measured over time), or reasonable estimates of errors in sampling depth. In both that study and the previous study on the harvested sites, changes could not be accounted for by differences in sample storage: total N concentrations did not change during sample storage, and total N values by the two methods employed (Kjeldahl and combustion) were nearly identical (Johnson and Todd, 1998). The other possibilities for these changes in N content include denitrification for the decreases and free-living N fixers for the increases; however, we have no information on the role of either processes in this ecosystem.

Previous results indicated that decreases in extractable P content between 1979 and 1995 were greater than could be accounted for by increments in trees and forest floor in the WTH treatment but not in the SOH treatment (Johnson and Todd, 1998). Current estimates of changes in soil extractable P between 1995 and 2013 (+4, −7, and −9 kg ha^{-1} in the REF, SOH and WTH treatments, respectively) can be accounted for by estimated P increments in trees (1, 16 and 11 kg ha^{-1} in the REF, SOH and WTH treatments, respectively) and forest floor (3, −1 and 8 kg ha^{-1} in the REF, SOH and WTH treatments, respectively).

Previous results showed that the increase in exchangeable Ca^{2+} observed in the SOH treatment between 1979 and 1995 (532 kg ha^{-1}) plus the Ca increment in vegetation (264 kg ha^{-1}, totaling 796 kg ha^{-1}) could be accounted for almost exactly by the Ca release from logging residues (690 kg ha^{-1}) plus inputs by atmospheric deposition (130 kg ha^{-1}, totaling 820 kg ha^{-1}) (Johnson and Todd, 1998). The current estimate of soil exchangeable Ca^{2+} decrease in the SOH treatment between 1995 and 2013 (−400 kg ha^{-1}) could be more than accounted for by the increment in vegetation (+750 kg ha^{-1}) and coarse woody debris (+100 kg ha^{-1}, totaling +850 kg ha^{-1}), implying Ca uptake by trees from deeper soil horizons than sampled. Previous results in the WTH treatment showed virtually no change in soil exchangeable Ca^{2+} content between 1979 and 1995 (−9 kg ha^{-1}), implying that Ca increment in trees (+225 kg ha^{-1}) also came from sources deeper than 45 cm (Johnson and Todd, 1998). The current estimate of soil exchangeable Ca^{2+} decrease in the WTH treatment between 1995 and 2013 (−360 kg ha^{-1}) is less than estimates of Ca increments in vegetation (+600 kg ha^{-1}) and forest floor (+320 kg ha^{-1}, totaling 920 kg ha^{-1}) over that period, again implying uptake from deeper sources.

Results from nearby Walker Branch Watershed also showed that Ca release from decomposing logs (a result of natural mortality in that case) could cause measureable increases in soil exchangeable Ca^{2+} below. In that case, decreases in exchangeable Ca^{2+} were found in 7 out of 8 core plots between 1982 and 2004. The exception was a case where Ca release from CWD (a decomposing chestnut oak trunk) apparently caused an increase in soil exchangeable Ca^{2+} (Johnson et al., 2008).

Previous results indicated that the increase in soil exchangeable Mg^{2+} in the SOH treatment between 1979 and 1995 (36 kg ha^{-1}) plus the increment in vegetation (13 kg ha^{-1}, totaling 49 kg ha^{-1}) could be more than accounted for by the release of Mg from detritus (mostly decomposing logging residues) (52 kg ha^{-1}), and inputs from atmospheric deposition (14 kg ha^{-1}, totaling 66 kg ha^{-1}) (Johnson and Todd, 1998). The current estimate of soil exchangeable Mg^{2+} decrease between 1995 and 2013 in the SOH treatment (−48 kg ha^{-1}) could be largely accounted for by increments in vegetation (34 kg ha^{-1}) and detritus (11 kg ha^{-1}, totaling 45 kg ha^{-1}). Previous results indicated that decreases in soil exchangeable Mg^{2+} in the WTH treatment between 1979 and 1995 (−55 kg ha^{-1}) could not be accounted for by increments in vegetation (12 kg ha^{-1}) or detritus (−11 kg ha^{-1}, totaling +1 kg ha^{-1}) and was attributed to leaching. Similarly, decreases in exchangeable Mg^{2+} between 1982 and 2004 on nearby Walker Branch Watershed were attributed to leaching (Johnson et al., 2008).

4.3. Potential sources of error and limitations of the data

Sources of error include bias in either laboratory analyses or field sampling. In the case of soil analyses, laboratory bias was minimized by having analyses of all samples from all years done at the same laboratory at the same time. Previous results have shown that changes in soil concentrations during storage are negligible (Johnson and Todd, 1998). Archived samples from forest floor and coarse woody debris were not available for re-analysis and this is a potential source of error that could have been introduced in calculating changes in forest floor nutrient contents over time. It is doubtful, however, that laboratory bias was a significant factor in calculations of forest floor nutrient content in the WTH treatment compared to the effects of changes in mass alone. Potential errors in measuring O horizon mass include changes in horizon designations over time and variations in judgement as to where Oa horizons end and underlying mineral soil horizons begin. We minimized this source of error by having the same two investigators (Johnson and Todd) present for each sampling (1979, 1995, and 2013) both overseeing the sampling and participating in it. We consider the increase in Oa horizon mass in the WTH treatment in 2013 to be considerably larger than any bias in sampling method over time. In the case of changes in CWD over time, however, the major change in methods between 1995 and 2013 may well have introduced a bias in estimating changes over time. There were no changes in measurement methods for CWD between 1979 and 1995, however (Johnson and Todd, 1998).

In his review of studies where inexplicably large increases in soil N (so-called "occult N") have been reported, Binkley et al. (2000) concluded that most results could be questioned because of inadequate experimental design. An exception to this was our 15 year sampling (Johnson and Todd, 1998) where Binkley et al. (2000) correctly note that while the experimental design was adequate and the reported changes could not be explained by experimental error, the authors of the study (Johnson and Todd) were nevertheless skeptical of the results. The potential effects of field sampling bias on the apparent changes in soil N over time need to be re-examined. Investigator bias was minimal in that the same two researchers (Johnson and Todd) took all soil samples in 1979 and 1995 and either took or closely oversaw soil sampling in 2013. While investigator age may have been a factor in error in sampling, variation in the major investigators and equipment used (5 cm diameter bucket auger) was not. Laboratory bias was eliminated by having both archived and current soil samples analyzed at the same laboratory at the same time, both in the 1995 sampling (Johnson and Todd, 1998) and the 2013 sampling. In a more recent study of soil N changes on nearby Walker Branch Watershed, we have made some theoretical calculations of the possible effects of differences in sampling depth on soil N measurements (Johnson et al., 2007). In the Walker Branch case, calculations of the potential effect of sampling 2 cm too deep in the 0–15 cm depth (the maximum error that we deemed possible in depth of sampling) resulted in maximum of 8% of the value in the 0–15 cm depth and was deemed insufficient to account for the apparent changes in soil N over time in that case. Given the inexplicably large changes in N in this study, we repeated these calculations here. Assuming that the 1979 total N values for the 0–15 cm depth were identical to those in 1995 and we consistently sampled to 17 cm instead of 15 cm in 1979, the 1979 values would be 12–19% higher than those reported and the changes in time would be about one third (28–38%) of those reported and probably not statistically significant. While this could theoretically explain away the problem with the observed "occult N" increases in this case, we consider it unlikely that we sampled too deeply in all samples in 1979, and that field errors in sampling depth, while most certainly real, were random in direction (too shallow, too deep) and amount.

A source of error in calculations of vegetation nutrient increment was the lack of information on nutrient concentrations in 2013 samples. While we did take samples of bark and wood for chemical analyses in 2013, available biomass regression equations did not include independent estimates of bark and wood biomass and thus vegetation nutrient concentration data on 2013 samples could not be used to calculate vegetation nutrient increment. Accordingly, the calculations of increment in biomass and nutrients in trees must be considered approximate. Nevertheless, we felt that even approximate estimates of nutrient increment in vegetation would be helpful in trying to account for observed changes in soils. Also lacking is any information on root biomass and turnover times in these systems, which may have contributed to the observed changes in soil C and other nutrient contents.

A lack of data on changes in bulk density over time is a source of error of unknown magnitude in calculating soil nutrient pools. As mentioned above, bulk density samples were taken at each soil sampling point in 2013, but unfortunately the samples were disposed of before being sieved and thus could not be used to calculate mass and nutrient contents in the fine earth (<2 mm) fraction (samples for nutrient analyses sieved before analysis with a 2 mm sieve). Thus, these calculations must be considered approximate. As for coarse fragment contents, we have data from quantitative pits in 1979 and see no reason that this component (consisting largely of chert) should change over time.

As is the case for any field study of treatment effects or changes in ecosystem C and other nutrient contents over time, there is the issue of pseudo-replication (Hurlburt, 1984). Larger scale studies, including harvesting, wildfire and even planetary science often suffer from pseudo-replication, but that does not necessarily imply that studies with such limitations have no value (Carpenter, 1990; Oksanen, 2001). In this study, as well as many like it, the experimental design was put in place before the issue of pseudo-replication was raised, and thus could not be adjusted to accommodate any suggestions to alleviate the problem. Aside from that, it was not logistically feasible to randomize the harvest treatments among individual watersheds or plots nor was it possible to replicate the entire experiment on similar soils and with similar vegetation as was the case in many similar studies (Johnson, 1995; Johnson et al., 1997; Knoepp and Swank, 1994). Thus, any conclusions reached as to the effects of treatment or changes over time relate to this site only; the reader is referred to reviews of the effects of harvesting and changes in C and other nutrient pools over time that include earlier results from this site as well as many others for more generalized conclusions (e.g., Grigal, 2000; Johnson and Curtis, 2001; Mann et al., 1988; Thiffault et al., 2011).

4.4. Summary and conclusions

Sampling of the REF, SOH, and WTH treatments 15 and 33 years after harvest showed:

1. No statistically significant differences in the biomass of regrowing trees at either 15 or 33 years post-harvest, although differences between treatments widened considerably between 1995 (2%) and 2013 (when biomass in the SOH treatment was 20% greater than in the WTH treatment).
2. Whereas there were no differences in forest floor biomass 15 years after harvest between the SOH and WTH treatments, forest floor mass and nutrient content was over two fold greater in the WTH than in the SOH treatment 33 years after harvest. This difference was due to largely to the development of a spotty but significant increase in Oa horizon mass in the WTH treatment. Concentrations of K, Ca and Mg in the Oa horizons of the WTH treatment were greater than those in the SOH treatment, but concentrations of N and P did not differ. Oa horizon mass was positively correlated with extractable P and exchangeable K^+ in soils immediately below, but there were no other significant correlations between Oa mass and underlying soil nutrient concentrations or between nutrient concentrations in Oa and underlying soils. Cause(s) of this increase in the WTH treatment remain not known.
3. There were no statistically significant treatment effects on soil C, N, or C:N ratios 33 years after harvest, as was also the case 15 years after harvest. Inexplicably large, statistically significant increases in soil N were found over the first 15 years post-harvest, as was the case in past studies. Soil C and N changes between 15 and 33 years post-harvest differed among treatments (lower in WTH, more stable in SOH), but were not statistically significant.
4. Thirty-three years after harvest, extractable P concentrations in surface soils were lower in both harvest treatments than in the REF treatment, but did not differ between SOH and WTH. Soil extractable P concentrations generally declined over time in all treatments.
5. No treatment or time effects on soil exchangeable K^+ were found.
6. Soil exchangeable Ca^{2+} and Mg^{2+} concentrations did not differ between the SOH and WTH treatments before harvest but increased by two fold in the SOH treatment 15 years after harvest due mainly to inputs from decomposing logging residues. This difference persisted at 33 years post-harvest when soil exchangeable Ca^{2+} and Mg^{2+} concentrations were still two- to threefold greater in the SOH than in the WTH treatment.

In summary, changes in soil N over time in all treatments remain to be accounted for and merit further investigation. Recent analysis of ^{15}N in some soil samples suggests the possibility of N fixation (Trettin, unpubl. data), even though a significant presence of N-fixing vegetation was never noted. Further research on ^{15}N patterns over time is planned, and an investigation into the possible role of free-living N-fixers is needed.

Treatment effects and changes in soil exchangeable Ca^{2+} and Mg^{2+} are consistent with known inputs from decomposing logging residues, inputs from atmospheric deposition, and increments in forest floor and vegetation. Harvest treatment effects on both Ca^{2+} and Mg^{2+} observed at 15 years post-harvest are still observable and significant at 33 years post-harvest.

The cause(s) of the large increase in Oa horizon mass and nutrient content in the WTH treatment remain unknown. Species differences were not significant in either the 1995 or 2013 vegetation inventories and differences in N concentration between the WTH and other treatments were small and non-significant. The greater K, Ca, and Mg concentrations in Oa horizons from the WTH treatment might be either a part of the cause of the difference or an effect of it (concentration increases in older organic matter).

Finally, the differences in vegetation 33 years after harvest merit future investigation. The combination of much greater forest floor mass and nutrient contents and lower tree biomass in the WTH compared to the SOH treatment suggest that treatment effects are finally beginning to emerge 33 years after harvest.

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