Forest Ecology and Management 504 (2022) 119809

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Harvest impacts to stand development and soil properties across soil textures: 25-year response of the aspen Lake States LTSP installations

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ARTICLE INFO

Keywords:
Aspen
Long-term soil productivity
Biomass
Compaction
Biomass removal

ABSTRACT

In addition to long-standing concerns about sustaining forest productivity, maintaining forest ecosystems under changing conditions and emerging threats has become increasingly important when planning forest management. With the aim of understanding effects of management on both productivity and recovery, we quantified the 25-year impact of varying degrees of organic matter (OM) removal and soil compaction on above-ground biomass, soil carbon and nutrients, soil bulk density, and stand development in aspen-dominated forests in the upper Lake States region of the US. Treatment impacts were assessed at three different sites with comparable overstory composition, but with varying soil texture, site quality, and climate. Across all sites, soil C and N generally decreased with increasing OM removal, and bulk density increased with increasing compaction; 25-year observations indicate recovery of bulk density at the surface (0–10 cm) but not at deeper portions of the soil profile. At the most productive site (loamy soils) with favorable initial soil porosity, severe compaction decreased mean aboveground biomass (-46%), particularly of trees (-73%). Biomass at 25 years did not differ among organic matter removal treatments (e.g. stem-only harvest), but a greater increase in soil C occurred with stem-only harvest relative to whole-tree harvest plus forest floor removal. In contrast, at a less productive site with sandy soils poorly buffered to nutrient and C removals, whole-tree harvest reduced biomass by 25% (tree biomass declined 35%) relative to stem-only harvest while compaction treatments did not differ in effects on biomass production, soil C or soil N. On clay soils, compaction treatments did not significantly impact biomass production, but whole-tree harvest plus forest floor removal reduced tree biomass by 47% relative to whole-tree harvest alone. Assessment of mean relative density indicates canopy closure has not yet occurred at the least productive site (clay soils) or the more severely disturbed stands at the intermediate site (sandy soils), suggesting the possibility for treatment impacts not yet discernible to become more pronounced as stands develop and nutrient uptake continues in the future. Our results align with concepts of soil quality and texture-specific limitations to growth, underlying a need to understand key soil limitations when considering forest management impacts to aboveground structure and productivity.

1. Introduction

Concerns over the potential for forest harvest practices to impact site productivity have existed for decades (Powers et al., 1989). In particular, there has been much focus on the potential for increased biomass removal (variously referred to as removal of organic matter, woody residues, slash, logging debris, etc.; Nave et al. 2010, Thiffault et al. 2011) and soil compaction (Cambi et al., 2015; Greacen and Sands, 1980) to limit tree growth through nutrient and organic matter losses and reduced soil porosity (Nambiar, 1990; Powers et al., 1989). Despite numerous studies over the past 50 years, there remains uncertainty about the long-term consequences of harvest impacts on productivity as responses vary depending on forest type, site quality, time since disturbance, and land use history (Powers et al., 2005; Thiffault et al., 2011).

Emerging threats associated with global environmental change add urgency to the need to balance management intensity and utilization with the maintenance of forest ecosystem services. More productive ecosystems may inherently have greater resistance (Steiner et al., 2006) and less productive ecosystems may be more susceptible to negative

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https://doi.org/10.1016/j.foreco.2021.119809
Received 29 January 2021; Received in revised form 8 October 2021; Accepted 18 October 2021
Available online 8 November 2021
0378-1127/

impacts from disturbance, both natural and anthropogenic (Pringle et al., 2007). This suggests greater caution may be prudent when managing lower quality, less productive sites. On poorly buffered nutrient-poor soils, particularly where harvests have already occurred one or more times, intensive biomass removal (e.g. whole-tree harvest) can reduce soil nutrient availability and tree growth (Helmisaari et al., 2011; Morris et al., 2014; Walmsley et al., 2009). In contrast, forests with greater nutrient availability may be more resistant to negative impacts associated with residue removal, at least in terms of standing biomass (Roxby and Howard, 2013; Smolander et al., 2010), supporting the idea that more productive ecosystems have greater capacity for recovering fully and more quickly (Franklin et al., 2002; Larson et al., 2008).

Ecosystem productivity is also influenced by soil porosity and its effects on gas exchange, available water, and root development (Nambiar, 1990; Powers et al., 1989). A reduction in soil porosity following soil compaction can reduce ecosystem productivity, with the effects most pronounced where porosity loss corresponds with an impact to related soil properties such as available soil water (Gomez et al., 2002). Increased soil bulk density can also physically limit successful seedling establishment and root growth of many tree species (Kozlowski, 1999), and where trees regenerate via root suckers, as is frequently the case with aspen species, soil compaction can have a variety of impacts. Wounding of aspen roots sometimes increases initial sucker densities (Fraser et al., 2004), but it also frequently reduces the density and growth of regeneration by degrading soil conditions for roots or directly damaging them (Shepperd, 1993). Compaction resulting from harvest operations has been observed to generally reduce root density and volume and to decrease the abundance of fine roots (Renkema et al., 2009; Shepperd, 1993; Zenner et al., 2007) and is particularly detrimental for species like quaking aspen that concentrate root growth and suckering in the upper soil profile (Farmer, 1962; Wolken et al., 2010).

In addition to measurements of biomass production, individual tree characteristics, and soil properties, the rate of stand structural development, or the time it takes for a stand to develop structural characteristics associated with different stages of development (e.g. Oliver et al. 1996, Franklin et al. 2002), provides a measure for assessing recovery following disturbance (e.g. Larson et al. 2008). Stand development is influenced by seed availability, the capacity for vegetative regeneration, and site quality with more productive sites generally developing more quickly (Franklin et al., 2002; Ryan et al., 2008). Slower development, evidenced by a longer period of recruitment during the stand initiation stage and before canopy closure occurs, suggests lower site quality (Larson et al., 2008). It follows that differences in the rate of development of stands regenerated by harvests of varying severity within a relatively homogenous site can serve as an indicator of disturbance impact on site quality. Additionally, the status of stand development has implications for the demand on below-ground resources. For example, the negative impacts of removing nutrients through intensive practices such as whole-tree harvesting may not become evident in forest soils until 10–20 (or more) years after harvest as vegetation recovers and nutrient uptake increases (Mason et al., 2012; Thiffault et al., 2011).

The Long-Term Soil Productivity (LTSP) program was initiated in 1989 to evaluate the effects of increasing biomass removal and soil compaction on forest productivity (Powers, 2006). Over 100 LTSP studies have been installed across a wide range of ecosystems and site (soil) conditions, ultimately representing many of the dominant forest types that occur across North America (Powers, 2006). Originally designed to determine whether common management practices threatened long-term sustainability of forests (in order to inform compliance with the National Forest Management Act; Powers, 2006), the LTSP program essentially set up an experiment to determine how much harvest-related disturbance forests can absorb without substantive change. While the basic questions underlying the LTSP program were developed over 30 years ago, they remain relevant today. Increasing concern related to climate change has renewed interest in sourcing renewable, bioenergy feedstocks from forests (Becker et al., 2009; Berger et al., 2013; Janowiak and Webster, 2010; Millar et al., 2007), which may lead to more frequent harvests, increased logging residue removal, and increased potential for soil compaction. Additionally, changing climate has the potential to alter operating conditions such that risks of soil compaction are increased. For example, warming winter temperatures may limit the establishment of soil frost, leading to a decrease in soil strength and increases in soil compaction during winter harvesting (Kolka et al., 2012; Rittenhouse and Rissman, 2015; Wolf et al., 2008). Given this, the LTSP framework provides an opportunity to address key sustainability issues we face now and into the future.

In the present study, we assessed the impact of organic matter removal and soil compaction on woody biomass production, stand development, soil C and nutrients, and bulk density after 25 years at three LTSP sites dominated by aspen species in the Upper Lake States regionThe three LTSP sites span a gradient in soil texture (sand, loam, clay) that corresponds with differences in site productivity. For all sites, we hypothesized that more extreme biomass removal and greater soil compaction would lead to lower above-ground biomass production and slower recovery, in terms of stand development. We also hypothesized that increasing biomass removal would result in a greater reduction in soil nutrients across sites. Lastly, we expected responses to the two experimental factors (organic matter removal and compaction) to vary by soil texture, with biomass removal having greatest effects where initial nutrient pools are low (sand texture) and soil compaction having greatest effect where initial pore size distribution is most favorable to growth (e.g., higher available water in a loam texture).

2. Methods

2.1. Study areas

We present 25-year results based on data collected from three USDA Forest Service installations of the LTSP study distributed across the Laurentian Mixed Forest Province in aspen-dominated forests. These were located on the Chippewa National Forest (CNF) in Minnesota, USA, and the Ottawa (ONF) and Huron-Manistee (HMNF) National Forests in Michigan, USA. Aspen species (*Populus tremuloides* at all three sites and *P. grandidentata* at CNF and HMNF) dominated all stands prior to harvest, accounting for over 50% of overstory basal area. Associated, less abundant species varied among the sites and included sugar maple (*Acer sacharum*), American basswood (*Tilia americana*), balsam fir (*Abies balsamea*), eastern white pine (*Pinus strobus*), white spruce (*Picea alba*), and northern red oak (*Quercus rubra*). Sites spanned a gradient in soil texture and differed in climate (Table 1). Potential productivity (site index) was greatest at the CNF installation, intermediate at HMNF, and lowest at ONF (Table 1). Consistent with the original intent of the LTSP study, we compared responses across sites that vary in quality for the dominant tree species, in this case aspen (Powers, 2006; Stone, 2001).

2.2. Experimental design

This study utilized a complete factorial design with two factors. The first factor was organic matter removal and included three levels: 1) stem-only harvest (SOH), which consisted of the removal of merchantable stems, as well as all shrubs, but with retention of harvest residues (non-merchantable tops and branches) on site, 2) whole-tree harvest (WTH), which consisted of the removal of all above-ground portions of trees, as well as shrubs, with no retention of harvest residues on site; and 3) whole-tree harvest plus forest floor removal (FFR), which consisted of the removal of all above-ground biomass (trees, shrubs, forest floor). The second factor was compaction and included three levels: 1) no additional compaction above background levels typical of a winter harvest (C0), moderate compaction (C1, target increase of 15% in soil bulk density), and heavy compaction (C2, target increase of 30% in soil bulk density) (Stone, 2001). All treatment combinations were replicated

Table 1
Site information. Mean soil C and nutrients are based on pre-treatment observations at 0–30 cm depth (Slesak et al. 2017). Standard error is provided in parentheses.

	Chippewa (CNF) Minnesota, USA	Huron-Manistee (HMNF) Michigan, USA	Ottawa (ONF) Michigan, USA
Location	47°180 N, 94°310 W	44°380 N, 83°310 W	46°370 N, 89°120 W
Site index for *P. tremuloides* (m, 50 years)	23	19	17–18
Pre-treatment overstory composition (most abundant species in order of decreasing abundance by basal area)	quaking aspen, sugar maple, American basswood	quaking aspen, bigtooth aspen, northern red oak	quaking aspen, balsam fir, white spruce,
Precipitation (cm/yr)	64	77	75
Mean annual temperature (C)	3.8	6.2	4.5
Soil classification	Frigid Haplic Glossudalfs	Frigid Entic Haplorthods, Frigid Typic Udipsamments	Frigid Vertic Glossudalfs
Soil texture (% sand, silt, clay)	silt loam (45/51/4)	sand (93/6/1)	clayey (23/27/50)
Bulk density (Mg m^{-3})	1.24	1.12	1.19
Total C (Mg/ha)	50.3 (10.2)	36.7 (5.2)	62.3 (8.5)
Total N (Mg/ha)	2.7 (0.6)	1.5 (0.7)	3.8 (0/8)
Ca (kg/ha)	1750 (550)	400 (140)	7010 (1650)
Mg (kg/ha)	260 (60)	50 (10)	1870 (420)
K (kg/ha)	220 (40)	100 (20)	740 (140)
P (kg/ha)	300 (80)	110 (40)	70 (20)
Harvest year	1993	1994	1992

three times at the CNF and HMNF sites. Replication at the ONF differed slightly, in part because of recent impacts from beaver. The ONF installation does not have the SOH/C2 treatment but includes five replicates of the WTH/C0 treatment, two replicates of SOH/C1, two replicates of FFR/C2, and three replicates of the remaining treatment combinations. At all three installations, treatments were applied to 0.25 ha plots, consisting of a 40 m X 40 m measurement plot surrounded by a 5 m buffer.

2.3. Data collection

Overstory trees (diameter $\geq$ 10 cm), saplings and seedlings (height $>$ 15 cm and diameter $<$ 10 cm), and woody shrubs (defined by species) were sampled in nine 1.78 m radius (10 m^2) circular subplots per 40 m X 40 m measurement plot. In these plots, the species and diameter (at 15 cm for stems $<$ 2.5 cm at breast height (1.37 m) or at breast height for larger stems) was recorded for all woody stems. Change (Δ) in sapling and tree densities between 20 and 25 years after harvest was calculated to assess the status of tree recruitment to the canopy, a process associated with stand development. Once recruitment of trees to the canopy halts, presumably because the canopy has closed and resources are limited, an even-aged stand enters the stem exclusion stage of stand development, characterized by increasing competition among trees and greater demand on below-ground resources (Oliver et al., 1996). All other data reported were sampled during year 25.

Soils were sampled during the summer in the year preceding harvest (i.e., pretreatment) and at 25 years after treatment implementation. In each treatment plot, soil samples were collected at 5 locations before harvest, and at 9 locations in year 25. Soil samples were collected with a stainless-steel corer (6.35 cm diameter; 190.5 cm^3 volume) using an internal plastic sleeve to a depth of 30 cm. Cores were transported to the laboratory and separated into forest floor and 10 cm mineral soil depth increments. Forest floor was dried at 70 °C for 24 h, weighed to determine mass per unit area, and then composited for nutrient analysis. Mineral soil was dried to 105 °C until constant mass was attained, weighed to determine total mass per unit volume (i.e., bulk density), sieved to pass a 2 mm mesh, weighed again to determine fine fraction mass per unit volume, and then composited by depth increment for nutrient analysis.

2.4. Soil analysis

We derived pretreatment nutrient estimates from archived soils that were analyzed previously as reported in Slesak et al. (2017). The analytical techniques and equipment used for the pretreatment samples are identical to those used for the 25-year analysis reported here. Total forest floor and mineral soil C and N were measured on 1-g pulverized subsamples with dry combustion using a LECO Dumas combustion technique on a Fisons NA1500 NCS Elemental Analyzer (ThermoQuest Italia, Milan, Italy). The Mehlich method (Mehlich, 1984) was used to extract mineral soil P, Ca, Mg, and K, and extract concentrations were measured with inductively coupled plasma spectroscopy (Varian Vista MPX, Varian, Palo Alto, CA, USA). Concentrations were converted to a mass basis using the fine fraction (<2mm) mass estimate. All estimates are reported on an oven dry (105 °C) basis.

2.5. Data summary and analysis

Above-ground biomass for all overstory stems (DBH $\geq$ 10 cm) was estimated using species-specific allometric equations (Jenkins et al., 2004; Table A1). We also quantified the relative density of each stand to allow (in combination with the status of recruitment) an assessment of the rate of stand development. Relative density (RD) is an index of current stand density compared with the maximum possible for a given species (Drew and Flewelling, 1979; Reineke, 1933) or species mixture (Woodall et al., 2005) and can be used to quantify competition within a forest stand independent of site quality and age. It can also be used as an indicator of stand development as a relative density of 0.15 approximates the timing of canopy closure, depending on the stand density index used (Drew and Flewelling, 1979; Jack and Long, 1996). To estimate relative density, we first quantified the stand density index (SDI) as follows:

$$\mathrm{SDI} = \sum sph\left(\frac{DBH_i}{25}\right)^2$$

where DBH_i is the mid-point of the *i*th diameter class (cm) and sph_i is the number of stems per hectare in the *i*th diameter class (Jack and Long, 1996; Reineke, 1933).

Next, because we were working with mixed species stands rather than a single species, we used an equation informed by species' specific gravity (a biological trait related to growth rates and tolerance of competition) to estimate the maximum SDI:

$$SDI_{99} = -2098.6*SG_m + 2057.3$$

where SDI_{99} is the statistical expectation of the 99th percentile maximum SDI and SG_m is the mean specific gravity for a forest stand, given the species composition (Woodall et al., 2005). Relative density was then calculated as SDI/SDI_{99} for each forest stand.

Forest floor and mineral soil mass estimates of C and N were summed for analysis across depths, and mass estimates of extractable macronutrients were summed across mineral soil depth increments only. We assessed treatment effects using the change in soil C and nutrient pools over time to account for differences that may have existed in those pools prior to treatment (Homann et al., 2008). Change in soil C and nutrient content were calculated as the difference between pretreatment estimates and the 25-year post-treatment measurement periods, with negative values indicating absolute losses and positive values indicating gains. Treatment effects on total bulk density were assessed using the same approach as used for soil C and nutrients, with the exception that treatment effects were evaluated by depth increment within each site. Changes in total bulk density were calculated as the difference between pretreatment and the 25th year after treatment, with negative values indicating recovery to densities lower than pretreatment and positive values indicating continued impact with densities higher than pretreatment.

For all analyses, each site was analyzed independently in SAS (SAS Institute, Inc. 2013) with a probability level of 0.1 for type I error, because of low statistical power associated with the level of replication and high inherent variability in some of the variables (Kurth et al., 2014). The influence of organic matter removal and compaction on relative density, change (Δ) in sapling and tree densities between 20 and 25 years after treatment, above-ground standing woody biomass (all tree and shrub species, height > 15 cm), sapling biomass (DBH < 10 cm), tree standing biomass (DBH ≥ 10 cm), shrub biomass, and change in soil C and nutrient pools was tested with mixed-effects ANOVA using the SAS MIXED procedure. When significant, pre-treatment values were included as covariates in analyses of change in soil C and nutrient content. Block was included as a random effect while OMR and CPT were treated as fixed effects. Type III sums of squares were used to account for the unbalanced design at the Ottawa NF.

Confidence intervals were developed for the mean change in soil C and nutrients within a treatment to independently assess if any change over time was significantly different from zero. Residuals were inspected visually to ensure assumptions for ANOVA had been met. Tukey-adjusted multiple comparisons were used to distinguish between treatment pairs, where warranted.

3. Results

3.1. Above-ground biomass production

The response of woody above-ground biomass, as a measure of productivity over the 25-year period, indicates significant treatment effects that varied by site and were largely associated with differences in tree biomass (Figs. 1 and 2). On the highest productivity site with silt-loam soils (CNF), significant treatment effects were associated with soil compaction where the no additional compaction (C0) treatment had the greatest overall standing biomass and the greatest tree biomass, while C1 and C2 reduced productivity by 46 percent and 73 percent, respectively (Fig. 1). The effect of organic matter removal was not significant, and there was no interaction between compaction and organic matter removal for any of the variables assessed (Table 2).

In contrast, treatment effects observed on the intermediate productivity site with sandy soils (HMNF) were largely associated with the organic matter removal treatment. The removal of harvest residues associated with WTH and FFR negatively impacted total standing biomass (-25 and −26 percent, respectively) and tree standing biomass (-39 and −35%, respectively) relative to the SOH harvest. In addition, FFR had lower shrub biomass than WTH, but the contribution of shrub

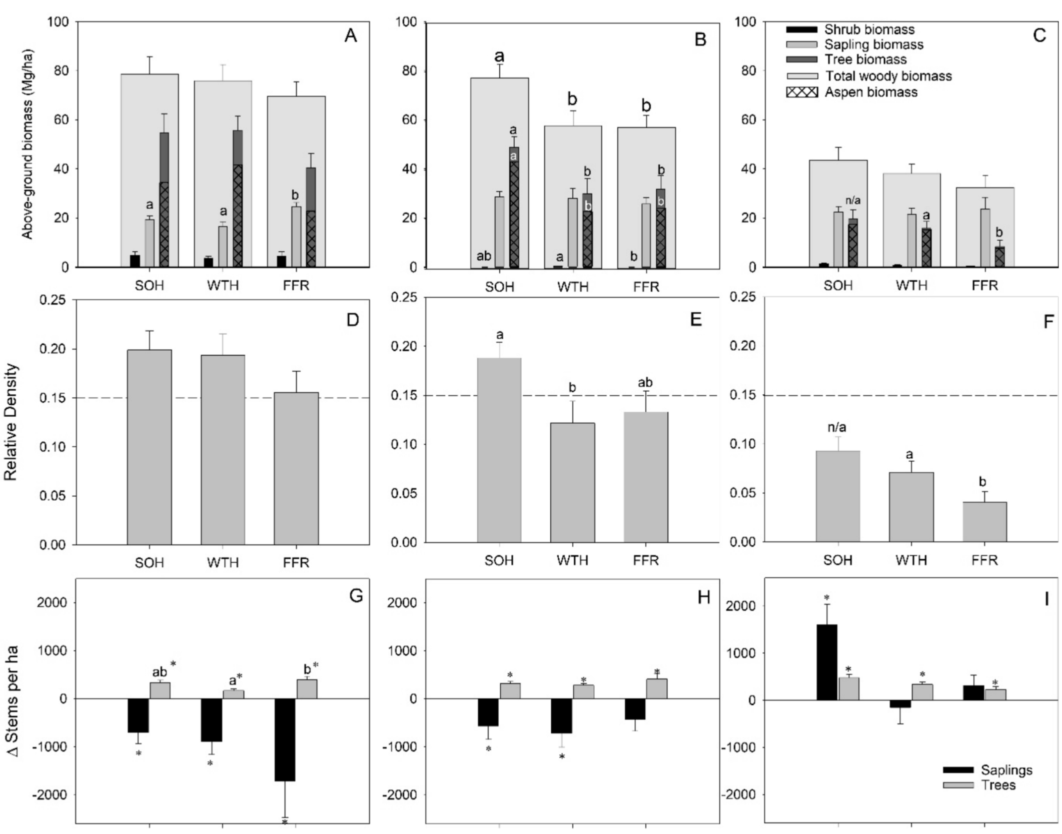

Fig. 1. Vegetation response (forest above-ground biomass and structure) to compaction 25 years after treatment at the Chippewa (panels A, D, G), Huron (panels B, E, H), and Ottawa (panels C, F, I) National Forest LTSP sites. Lower-case letters indicate differences among levels of compaction (C0 - no additional, C1- moderate, C2 - heavy) following Tukey-adjusted pairwise comparisons ($p < 0.10$), where mixed effects ANOVA indicated differences among treatments. In panels D-F, a relative density of 0.15 approximates canopy closure and is marked with a dashed line. Panels G, H, and I show the change (Δ) in sapling and tree densities that occurred between years 20 and 25 after treatment, and an asterisk (*) indicates Δstems per ha ≠ 0. Decreases in sapling densities indicated above have been corrected to account for recruitment into the next largest ("tree") size class (DBH ≥ 10) such that a negative Δ indicates mortality. Error bars indicate standard error for all species in each category. Standard error is not indicated for aspen (*P. tremuloides* and *P. grandidentata,* combined, in panels A-C).

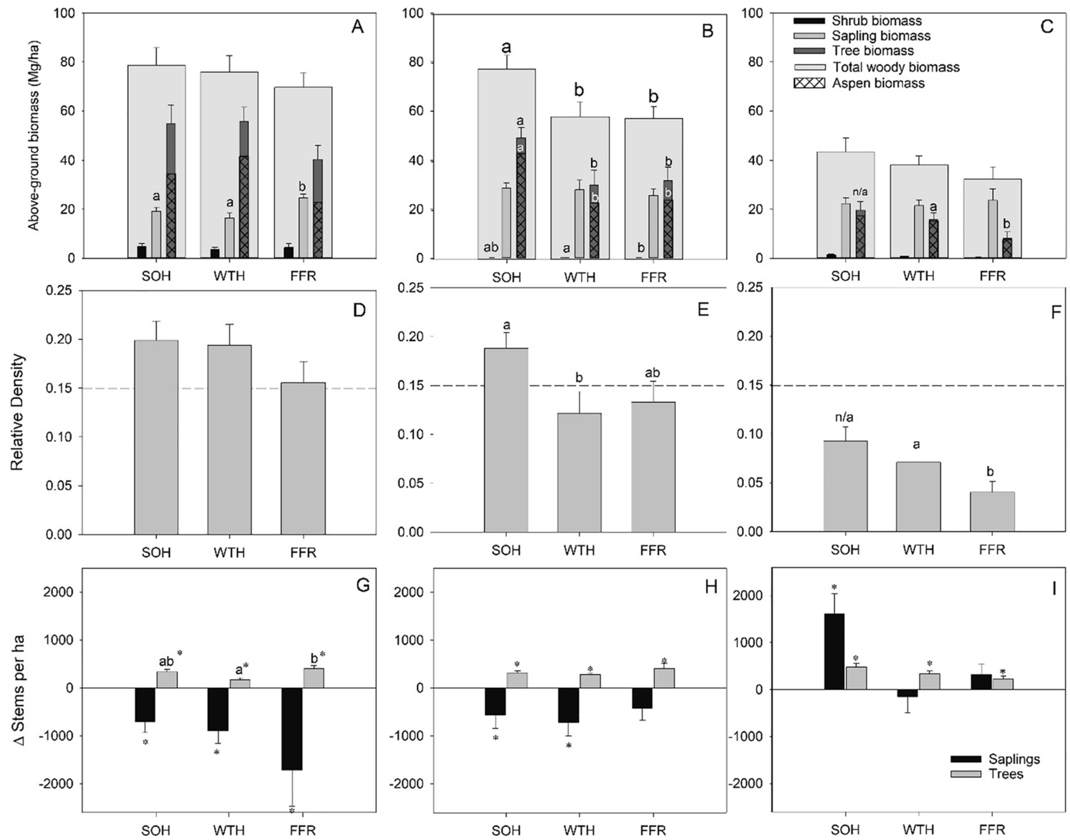

Fig. 2. Vegetation response (forest standing biomass and structure) to organic matter removal treatments 25 years post-harvest at the Chippewa (panels A, D, G), Huron (Panels B, E, H), and Ottawa (Panels C, F, I) National Forests. Lower-case letters indicate differences between levels of organic matter removal (SOH - stem-only harvest, WTH- whole-tree harvest, FFR – whole-tree harvest and forest floor removal) following Tukey-adjusted pairwise comparisons ($p < 0.10$) where mixed effects ANOVA indicated differences among treatments. A relative density of 0.15 approximates canopy closure and is marked with a dashed line in panels D, E, and F. Panels G, H, and I show the change (Δ) in sapling and tree densities that occurred between 20 and 25 years post-harvest, and an asterisk (*) indicates Δstems per ha ≠ 0. Decreases in sapling densities indicated above have been corrected to account for recruitment into the next largest ("tree") size class (DBH ≥ 10) such that a negative Δ indicates mortality. Error bars indicate standard error for all species in each category. Standard error is not indicated for aspen (*P. tremuloides* and *P. grandidentata,* combined, in panels A-C).

Table 2
ANOVA results showing effects of organic matter removal and compaction on standing biomass and forest structure for the Chippewa (high quality), Huron (intermediate quality), and Ottawa (low quality) Lake States LTSP installations.

Effect	df	Total Woody Biomass		Tree biomass		Sapling biomass		Shrub biomass		Relative density	
		F	p-value	F	p-value	F	p-value	F	p-value	F	p-value
Chippewa											
OMR	2	0.83	0.452	1.94	0.175	6.20	**0.009**	0.10	0.905	1.62	0.227
CPT	2	3.87	**0.0412**	3.15	**0.069**	1.65	0.221	1.83	0.191	**5.12**	**0.018**
OMR × CPT	4	1.09	0.3924	0.75	0.573	0.66	0.6313	0.15	0.961	0.78	0.551
Huron-Manistee											
OMR	2	3.44	**0.056**	4.52	**0.027**	0.27	0.769	3.33	**0.060**	**3.38**	**0.058**
CPT	2	0.27	0.764	1.40	0.274	1.27	0.305	1.72	0.208	1.38	0.277
OMR × CPT	4	0.63	0.646	1.09	0.391	0.59	0.676	0.91	0.478	0.98	0.442
Ottawa											
OMR	2	1.38	0.281	2.81	**0.092**	0.16	0.852	5.47	**0.017**	**3.23**	**0.068**
CPT	2	0.88	0.434	0.27	0.766	0.78	0.478	1.68	0.220	0.47	0.636
OMR × CPT	3	1.90	0.172	0.53	0.666	1.50	0.254	0.04	0.990	0.72	0.555

biomass to total aboveground biomass was very low (Fig. 2). There were no significant differences among compaction treatments on above-ground production.

Finally, at the lowest productivity site (clay soils, ONF), there were no significant differences among either organic matter removal or compaction treatments on total standing biomass. However, a 22 percent reduction in tree biomass was observed following the FFR treatment relative to SOH (Fig. 2).

3.2. Stand development

The impact of treatments on the rate of stand development followed trends similar to those reported for standing biomass. At CNF (most productive site), mean relative density was highest in stands receiving the no additional compaction (C0) treatment and lowest with heavy compaction (C2) where it was < 0.15, suggesting the most heavily compacted stands had not yet reached canopy closure (Fig. 2). Mean relative density was also near canopy closure (mean = 0.155) in the FFR treatment where a greater number of stems recruited from smaller size classes (DBH < 10 cm) to the overstory (DBH ≥ 10 cm) between 20 and 25 years after treatment compared with whole-tree harvest stands where recruitment had slowed by year 20 (Fig. 2).

At HMNF (mid-productivity site), SOH led to the fastest rate of development, with mean relative density exceeding 0.15, unlike the WTH and FFR treatments (Fig. 2). Neither relative density nor Δ sapling or tree densities differed among compaction levels indicating little to no effect of compaction on stand development. Forest growth occurred most slowly at ONF, the lowest productivity site, overall (Fig. 2). Changes in sapling and tree densities did not differ among treatments at this site, but none of the stands have reached canopy closure (relative density > 0.15), and unlike CNF and HMNF where losses in sapling densities were broadly observed across treatments, saplings continued to recruit between 20 and 25 years in some stands at the ONF (Figs. 1 and 2).

3.3. Soil C and nutrients

There was a significant effect of organic matter removal on soil C and N at CNF and ONF LTSP sites (Table 3). Effects of organic matter removal on C showed similar patterns across sites, ΔC decreased (greater reductions in soil C or lesser increases in soil C, relative to pre-treatment) with increasing organic matter removal (Fig. 3). At CNF and ONF sites, there were significant differences in Δ soil C between the SOH and FFR treatments resulting from a significant increase with SOH at CNF and a significant increase in SOH coupled with a significant decrease in FFR at ONF. The increase in ΔC with SOH at CNF (Fig. 3) can be attributed to increases in forest floor mass and its effect on forest floor C content (Tables 3 and 4). There were no significant differences in ΔC among treatments at the HMNF (Fig. 3), but C was significantly decreased with FFR (i.e., change < 0) (Tables 3 and 4).

Soil nitrogen generally increased over the 25-year period, with the exception of the FFR treatment at CNF and ONF where change in soil N did not differ from zero (Fig. 3). In both cases, the increase in soil N generally decreased with increasing level of OM removal, with significant differences between the SOH and FFR treatments at CNF (high productivity, silt loam) and significant differences between the WTH and FFR treatments at ONF (low productivity, clay). There was no apparent difference in soil N among treatments on the sandy soils at HMNF.

There was no effect of OM treatments on extractable soil cations and P at any site, and no effect of compaction on any element with one exception. In that instance, at HMNF, the change in extractable soil K was significantly lower in the C0 treatment compared to both C1 ($p = 0.071$; diff. = -13.9 kg ha^{-1}; 90% CI:-26.7, −1.1) and C2 ($p = 0.098$; diff. = -13.4 kg ha^{-1}; 90% CI:-26.8, −0.1). Regardless of treatment, extractable soil Ca and Mg increased over the 25-year time period at the high and intermediate productivity sites (Table B1). Extractable soil P significantly decreased across all treatments over the 25-year time period across all sites (Table B1). The decreases were relatively large, averaging 24% (CNF), 36% (HMNF), and 37% (ONF) across all treatments relative to the pretreatment extractable soil P pool (Table 1).

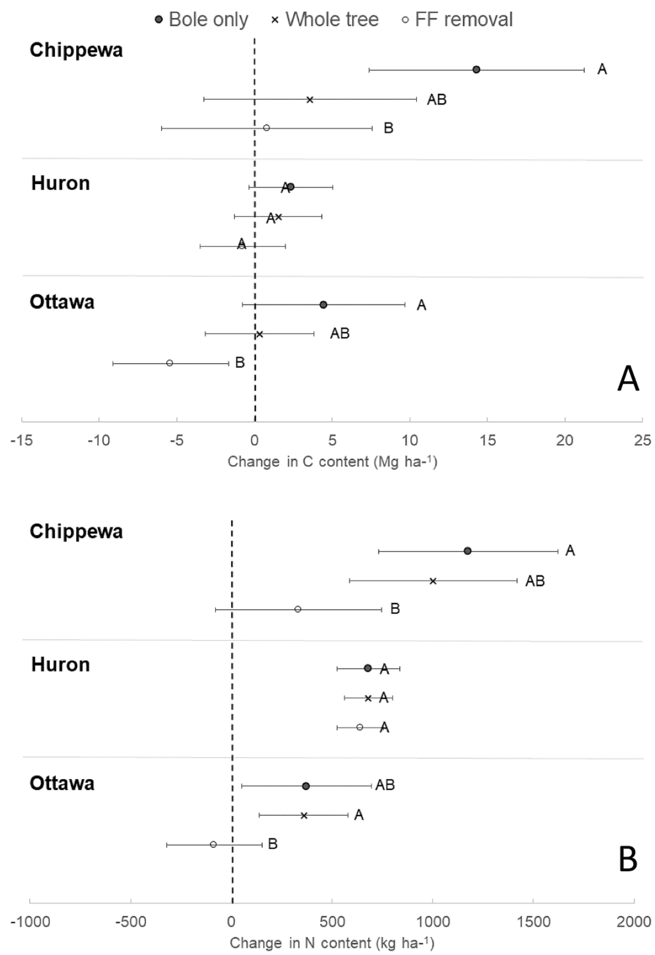

Fig. 3. Change in soil carbon (panel A) and nitrogen (panel B) by organic matter removal treatment at each of the Lake States aspen LTSP sites. Values within a site containing different letters are significantly different. Error bars are 90% confidence intervals for mean treatment values. Intervals which do not overlap the zero line are significantly different from zero.

3.4. Soil bulk density

General patterns of treatment effects on bulk density were similar across sites, where the 0–10 cm depth increment showed full recovery with densities less than pretreatment values at CNF and ONF (silt loam

Table 3
F Statistic probabilities for effects of organic matter removal and compaction on soil properties for the Chippewa, Huron, and Ottawa LTSP installations. Bold text indicates a statistically significant effect ($p < 0.1$).

Effect	C	N	Ca	K	Mg	P	FF mass	FF C	FF N
Chippewa									
CPT	0.350	0.993	0.914	0.210	0.403	0.958	0.309	0.340	0.318
OMR	**0.066**	**0.061**	0.352	0.862	0.696	0.570	**0.071**	**0.058**	**0.065**
CPT × OMR	0.442	0.772	0.350	0.334	0.616	0.950	0.364	0.395	0.307
Huron									
CPT	0.512	0.507	0.858	**0.057**	0.348	0.350	0.201	0.122	0.192
OMR	0.469	0.965	0.414	0.414	0.703	0.390	0.252	0.272	0.232
CPT × OMR	0.947	0.967	0.655	0.139	0.799	0.980	0.915	0.882	0.872
Ottawa									
CPT	0.144	0.234	0.541	0.432	0.646	0.342	0.463	0.549	0.518
OMR	**0.032**	**0.054**	0.887	0.741	0.431	0.453	0.803	0.820	0.979
CPT × OMR	0.826	0.287	0.287	0.297	0.214	0.618	0.220	0.245	0.249

Table 4
Forest floor mass, C content, and N content 25 years after organic matter removal treatment for the Chippewa, Huron, and Ottawa LTSP installations. Means with different letters at the Chippewa site are significantly different; there were no treatment effects at the Huron and Ottawa sites.

Treatment	Mass (Mg ha^{-1})	C content (Mg ha^{-1})	N content (Kg ha^{-1})
Chippewa			
MBH	36.2 (7.0) a	14.3 (2.7) a	600 (119) a
WTH	19.2 (7.0) ab	7.1 (2.7) ab	316 (119) ab
FFR	12.3 (7.0) b	4.7 (2.7) b	186 (119) b
Huron			
MBH	10.4 (0.9)	4.5 (0.4)	138 (11)
WTH	10.4 (0.9)	4.6 (0.4)	130 (11)
FFR	9.5 (0.9)	4.0 (0.4)	114 (11)
Ottawa			
MBH	Non-est[1]	Non-est	Non-est
WTH	12.1 (1.9)	3.8 (0.5)	138 (21)
FFR	12.2 (2.2)	3.8 (0.5)	141 (24)

[1] Non established estimates because of lack of replication.

Table 5
F statistic probabilities for the effect of organic matter removal and soil compaction on the change in soil bulk density between pretreatment and 25-year measurement periods. Bold text indicates statistically significant differences ($p < 0.1$).

Effect	Chippewa	Huron	Ottawa
10 cm depth			
OMR	0.452	0.242	**0.001***
CPT	0.142	0.503	0.152
OMR × CPT	0.488	0.551	0.124
20 cm depth			
OMR	0.172	0.797	0.912
CPT	**0.002**	**0.001**	0.112
OMR × CPT	0.479	0.703	0.747
30 cm depth			
OMR	0.144	0.968	0.686
CPT	0.229	0.131	**0.059**
OMR × CPT	0.712	0.852	0.224

* FFR > SOH and WTH, but all higher than pretreatment values.

and clay soils) and no different than pretreatment values at HMNF (sandy soils), but deeper depths still had bulk densities significantly higher than pretreatment levels (Fig. 4, Table 5). In addition, change in bulk density generally increased with increasing level of compaction, but differences among treatments were only significant at the 10–20 cm increment at CNF and HMNF and at 20–30 increment at ONF (Table 5). Responses at ONF (clay soils) deviated from general trends in two ways; recovery in the 0–10 increment increased with increasing level of compaction, and changes were not significantly different from 0 at the 10–20 and 20–30 cm increments (i.e., recovery occurred at those depths).

4. Discussion

Results from this study supported our general hypothesis that more severe disturbance in the form of heavier compaction or greater biomass removal would slow stand development, reduce above-ground biomass production, and/or generally lead to decreases or lesser increases in soil C and N (but not P or macronutrients) depending on the site. We also observed different responses to the main factors among the three sites included in this study, confirming that site characteristics such as soil texture influence response to disturbance. As discussed further below, compaction treatments and associated increases in soil bulk density had the most pronounced effect on silt-loam soils whereas the loss of additional organic matter through whole-tree harvesting and/or forest floor removal was most impactful on nutrient-poor, sandy soils.

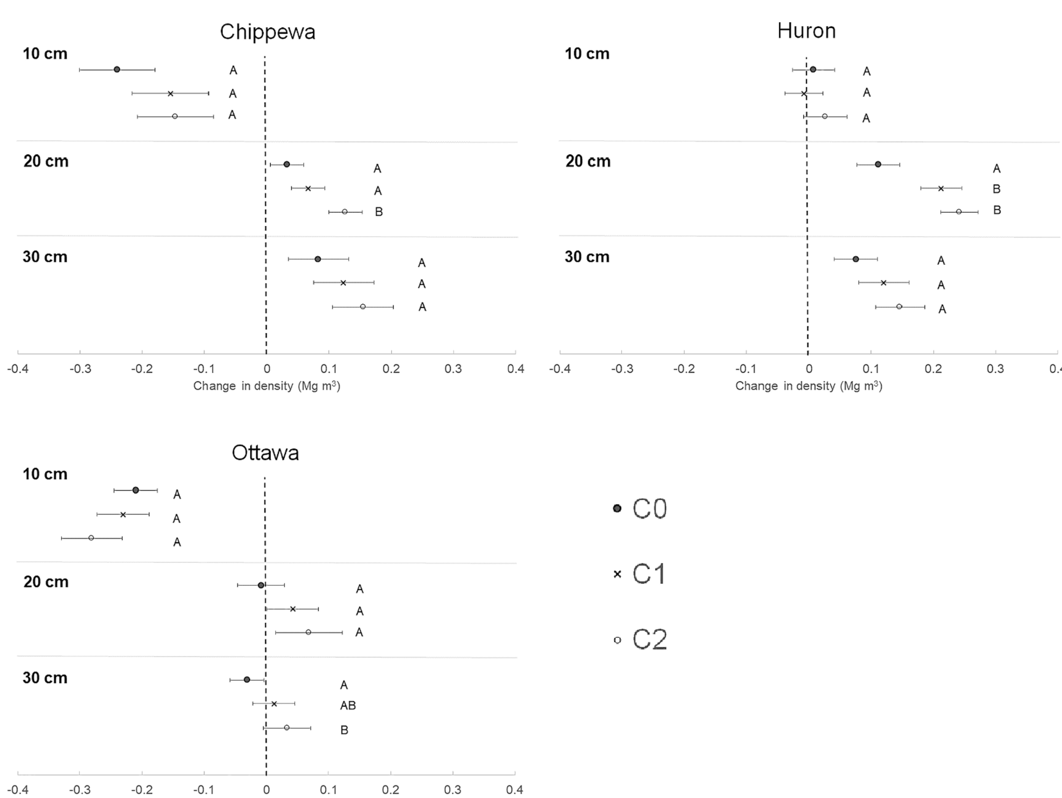

Fig. 4. Change in bulk density by site, treatment, and depth increment. Negative values indicate lower bulk density than pretreatment; positive values indicate higher bulk density than pretreatment. Error bars are 90% confidence limits. Bars which do not overlap the zero line are significantly different from zero.

Consistent with observations in other temperate forests, the additional removal of harvest residues (whole-tree harvest) and of the forest floor did not negatively impact 25-year above-ground standing biomass at our most productive site (Powers et al., 2005; Thiffault et al., 2011). That said, the removal of the forest floor does appear to have slowed stand development at this site. Greater biomass in the sapling size class relative to other treatments and the continued (greater) increase in density of tree stems suggest recruitment is ongoing and stands had not yet entered the stem exclusion stage at 25 years. While the silt-loam soil had large enough nutrient pools to sustain increased organic matter removals without negative impacts to vegetation at 25 years, compaction reduced above-ground biomass in overstory trees 18% and 34% for moderate and heavy compaction, respectively. Loamy textured soils appear to be particularly vulnerable to damage from compaction, despite common assumptions that it is finer-textured soils (such as the clay soils at ONF) that should be least resistant (Steber et al., 2007). This vulnerability likely arises from a pore size distribution that is more susceptible to compaction in loam soils, resulting in a loss of available water holding capacity, reduced aeration, and ultimately a reduction in productivity. The lack of recovery in soil bulk density at depths>10 cm suggests impacts to productivity are likely to continue into the future. Alternatively, it is possible that soil compaction reduced aspen suckering directly through damage to roots (Stone and Kabzems 2002) resulting in an overall decrease in density (and biomass) rather than a change to soil porosity per se, but this does not explain the reduction in height observed early in the study (Stone and Kabzems 2002). Compaction has likely impacted tree regeneration and growth in multiple ways, and additional study, such as assessments of stress response, may provide the data needed to determine mechanisms more precisely. In terms of OM removal, observed reductions in soil C, soil N, forest floor mass, forest floor C, and forest floor N, as well as evidence of potentially slower stand development at the CNF site, together suggest severe forest floor removal could alter long-term forest ecosystem productivity and function in the future.

Forests at HMNF, the intermediate site, are constrained by both nutrient and water availability because of the sandy-textured soils. These soils exhibited greater resistance to compaction with no discernible impacts to above-ground biomass despite increases in bulk density, although earlier assessments indicated potential impacts to functional diversity (Curzon et al., 2016). These results contrast with others that have indicated a possible benefit of soil compaction to tree growth on sandy textured soils (Gomez et al., 2002; Ponder et al., 2012). In contrast, above-ground biomass and relative density were both negatively impacted by whole-tree harvest, likely because the sandy soils are more poorly buffered compared to the silt loam soil at the CNF. The establishment and growth of aspen suckers is heavily influenced by initial growing conditions (Frey et al. 2003, Wolken et al. 2010), and it is not clear whether soil nutrient status or water limitation were the drivers of the reduced productivity we observed following WTH (with or without the addition of forest floor removal). Soil N has recovered following all three OMR treatments at this site, but some of the increase in N could be from decomposition of preexisting belowground OM which was not quantified (Powers et al. 2005, Slesak et al. 2017). In contrast, mineral soil C and forest floor mass remain lower than pre-harvest levels. The reduction in carbon and organic matter coincides with evidence of reduced productivity above-ground, particularly following whole-tree harvest (and whole-tree harvest plus forest floor removal). Removing harvest residues with both of those treatments has had a long-term negative impact on total standing biomass, tree biomass, and the rate of stand development.

The impacts of organic matter removal and compaction on forest response at ONF (clay-textured soils) are less clear. This absence of definitive impacts may be attributed to the slower recovery at ONF where trends in recruitment and mean relative density indicate canopy closure has not occurred. It is also possible that neither nutrient availability nor water are most limiting to growth, but rather other factors such as soil aeration or soil temperature are more important drivers of productivity. Despite having finer texture, clay soils appear to be more resistant to compaction at greater depths than soils with sandier or loamier texture, as was reflected in the changes to bulk density we observed (Fig. 4). The removal of the forest floor at this site resulted in lower soil C and soil N, and as stand development progresses, differences in total standing biomass among treatments may become more evident. Mean above-ground biomass associated with the forest floor removal treatment was 25% lower than the mean observed for stem-only harvest, but variability and lower replication (plots impacted by beaver were excluded) reduced the statistical power and differences were not significant.

One objective driving recent investigations of the relationship between productivity and ecosystem sustainability is the potential value such knowledge may have for prioritizing forest stands for different uses, e.g. more intensive management practices such as whole-tree harvest (Mason et al., 2012) versus restoration of composition and structure (Larson et al., 2008). As observed elsewhere, our results confirm that more productive sites may be more resistant to negative impacts and recover more quickly as indicated by higher relative density and a faster rate of stand development, particularly following the most severe treatments.

Despite the evidence of recovery we report, caution should be exercised even for productive sites as our results also suggest declines in P across the study, regardless of treatment. P-loss in these and similar, temperate forests has not been a wide-spread concern, in part because it has been widely assumed that nitrogen is most limiting (Tamm, 1991) and nutrient budget models have predicted multiple rotations would be necessary before P-limitation occurred (e.g. Vadeboncoeur et al., 2014; Wilhelm et al., 2013). Yet, a substantial amount of available P is held in above-ground biomass (Yanai, 1998), including in aspen-dominated ecosystems (Alban et al., 1978), and removal of additional residues with whole-tree harvest results in significantly more P being removed from a site compared to stem-only harvest (Klockow et al., 2013). Additionally, recent work suggests that both N and P might limit tree growth simultaneously (e.g. Harpole et al., 2011), and P is actually limiting in temperate forests in northeastern North America long believed to be N-limited (Gonzales and Yanai, 2019; Goswami et al., 2018).

The eventual (and gradual) emergence of a soil P reduction 25 years after harvest affirms the value of long-term research as embodied by the LTSP program. Continued assessment of our LTSP installations over the long-term has clarified other impacts as well. Early results from all three sites suggested that a greater degree of disturbance impacted vegetation response relative to conventional practices, but relationships were weak (not statistically significant) and a few trends have changed over time. For example, observations after four to five years at the HMNF indicated compaction of sandy soils might have had a positive effect on mean aspen sapling height and biomass (Stone, 2001; Stone et al., 1999), but this perceived benefit has diminished over time and is no longer apparent. Forest floor removal initially increased the density of aspen regeneration at the CNF (Stone and Kabzems 2002), but that effect has also faded with time (Curzon et al., 2020). On the other hand, initial observations of reduced stem densities in response to greater compaction observed on silt-loam soils at the high productivity site (Stone 2001) have persisted 25 years after treatment (Curzon et al., 2020) and are evident in our assessment of relative density and standing biomass. Also, early non-significant observations that suggested the possibility of reduced sapling biomass on sandy soils (Stone et al., 1999) have become more pronounced over time with the whole-tree harvest and forest floor removal treatments both reducing 25-year total standing biomass by over 25% relative to stem-only harvest. Likewise, the differences in soil C and N among organic matter removal treatments reported here were not observed during previous sampling periods (Slesak et al., 2017).

5. Conclusions and applications to management

With this paper, we provide a rare, mid-rotation assessment of harvest impacts on soil properties, stand development, and above-ground biomass in aspen-dominated forests of the Lake States region. Forest response is driven by specific site conditions (e.g. loamy soils are prone to damage from compaction and sandy soils are more vulnerable to productivity losses following whole-tree harvest), but even the combination of whole-tree harvest, forest floor removal, and severe compaction at the most productive site (CNF) yielded greater mean biomass production and faster recovery (CNF) than less disturbed stands at the least productive site (ONF); therefore, these sites may have greater capacity for recovering from severe harvest disturbance such as the additional removal of residues for bioenergy feedstocks. At the same time, our observations of P losses regardless of treatment also support other emerging work that suggests P-limitation may become a more pressing concern in the future and deserves consideration. Study-wide, the most severely disturbed stands, those showing greater impacts from treatments, have not yet reached the stem exclusion stage when competition and resource demands intensify, particularly at HMNF and ONF. Lastly, this work provides additional evidence that site characteristics (beyond productivity alone) matter for determining response to these treatments; precautions should be taken to protect loam-textured soils (such as those at the CNF) from soil compaction, and whole-tree harvest should be avoided on sandy soils that are less nutrient rich and have lower water-holding capacity (Flinn et al., 1980; Janowiak and Webster, 2010; Thiffault et al., 2011; Vangansbeke et al., 2015).

CRediT authorship contribution statement

Miranda T. Curzon: Conceptualization, writing, analysis. **Robert A. Slesak:** Conceptualization, writing, analysis. **Brian J. Palik:** Conceptualization. **Julia K. Schwager:** Writing, analysis.

Declaration of Competing Interest

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

Acknowledgements

The authors gratefully acknowledge the efforts of many USDA Forest Service scientists and technicians who have contributed to the LTSP study over the last 25 years, particularly Douglas Stone and David Alban who initiated the Lake States aspen installations as well as John Elioff, Josh Kragthorpe, and Doug Kastendick whose efforts collecting and maintaining data over many years have made this research possible. We also appreciate the suggestions made by the editorial team and two anonymous reviewers whose time and comments helped improve the original manuscript. This research was supported by the USDA Forest Service, Northern Research Station and the National Institute of Food and Agriculture McIntire-Stennis Cooperative Forestry Research Program (IOW05567).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119809.

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