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Harvest residue removal and soil compaction impact forest productivity and recovery: Potential implications for bioenergy harvests

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ABSTRACT

Understanding the effects of management on forest structure and function is increasingly important in light of projected increases in both natural and anthropogenic disturbance severity and frequency with global environmental change. We examined potential impacts of the procurement of forest-derived bioenergy, a change in land use that has been suggested as a climate change mitigation strategy, on the productivity and structural development of aspen-dominated ecosystems. Specifically, we tested the effects of two factors: organic matter removal (stem-only harvest, whole-tree harvest, whole-tree harvest plus forest floor removal) and soil compaction (light, moderate, and heavy) over time. This range of treatments, applied across three sites dominated by aspen (*Populus tremuloides* Michx.) but with different soil textures, allowed us to characterize how disturbance severity influences ecosystem recovery.

Disturbance severity significantly affected above-ground biomass production and forest structural development with responses varying among sites. At the Huron National Forest (sandy soils), the removal of harvest residues reduced above-ground biomass production, but no negative effect was observed following whole-tree harvest at the Ottawa and Chippewa National Forests (clayey and loamy soils, respectively) relative to stem-only harvest. Maximum diameter and the density of stems greater than 5 cm DBH exhibited negative responses to increased disturbance severity at two sites, indicating that structural development may be slowed. Overall, results suggest that disturbance severity related to procuring harvest residues for bioenergy production may impact future productivity and development, depending on site conditions and quality.

1. Introduction

Forests have been suggested as a supply of alternative sources of energy feedstocks for offsetting fossil fuel consumption (Millar et al., 2007; Becker et al., 2009; Aguilar and Saunders, 2010; Buford and Neary, 2010); however, increases in demand for forest-derived bioenergy feedstocks could translate to an increase in harvest-related disturbance severity and frequency with associated ecological impacts (Berger et al., 2013). At the same time natural disturbance events (windthrow, fire, etc.) and stressors (e.g. drought) may also increase in frequency and severity as climate change progresses (Dale et al., 2001; Turner, 2010). Uncertainty regarding how ecosystems will respond to changes in disturbance, both natural and anthropogenic, poses a serious challenge to the development of long-term sustainable forest management and conservation strategies (Dale et al., 2001; Joyce et al., 2009).

Given the uncertainty surrounding ecosystem responses to potential increases in disturbance, sustainable forest management requires a better understanding of how disturbance severity affects forest productivity and successional development. Generally, forest development occurs more quickly on more fertile sites (Franklin et al., 2002; Larson et al., 2008; Ryan et al., 2008; Hardiman et al., 2011), but disturbance itself can degrade site quality through depletion of nutrients and changes in the understory environment (Stoeckeler, 1948; Thiffault et al., 2011). Also, increased disturbance severity or compound disturbance events may push ecosystems outside the range of natural variation (Paine et al., 1998; Lindenmayer et al., 2004). These changes in disturbance severity may favor the establishment and growth of dense understory layers (Royo and Carson, 2006) as has been observed in white spruce forests (Eis, 1981) and, to some extent, with trembling aspen (*Populus tremuloides* Michx.; Landhausser and Lieffers, 1998) in boreal regions. Such an understory can interfere with the establishment of tree species historically adapted to a site, thus slowing or changing forest developmental trajectories (Royo and Carson, 2006).

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Results from studies examining the effects of harvest residue removal to date have varied depending on site quality, time since disturbance, and forest type. In nutrient-poor forests, removal of harvest residues (i.e., slash) can reduce nutrient availability and tree growth (Walmsley et al., 2009; Helmisaari et al., 2011; Morris et al., 2014); however, negative effects may not be detected in some cases until 10–20 years following harvest (Egnell and Valinger, 2003; Helmisaari et al., 2011; Mason et al., 2012; Vanguelova et al., 2010). Findings from Long Term Soil Productivity (LTSP) study sites in boreal aspen and black spruce forests suggest that while tree densities may not respond negatively to the removal of harvest residues, tree height can be detrimentally impacted (Kabzems, 2012; Morris et al., 2014). Even where site productivity appears to recover, the reduction in above-ground biomass caused by initial post-harvest declines in site productivity can persist for over 30 years (Egnell, 2011). On richer sites the effects are more difficult to discern (Smolander et al., 2008, 2010; Roxby and Howard, 2013). Fully assessing ecosystem response to disturbance requires quantifying severity in terms of not only the death or removal of biomass, but also impacts to soil given the pervasive influence harvest-related soil disturbance may have on forest community development (Halpern, 1988; Roberts, 2007). The design of the LTSP study network allows assessing these different effects in a way applicable to bioenergy harvests.

Studies that consider impacts to soil, herbaceous biomass, shrub biomass, and other ecological response variables, will increase understanding of the potential long-term impacts that increased levels of feedstock harvests may have on ecosystem structure and function. For example, quantifying productivity in non-tree plant species concurrently with tree species can elucidate competitive interactions among different guilds and the processes behind community disturbance responses (Grewal, 1995; Royo and Carson, 2006). Additionally, the rate of post-disturbance structural development gives an indication of engineering resilience (hereafter 'resilience'; Larson et al., 2008), which represents the length of time required for a system to return to its pre-disturbance state (Holling, 1996). If disturbance severity influences species composition, structural development, and resilience, then anticipated impacts on future functions will vary similarly, as will the degree to which forest stands accommodate different management objectives (Schwenk et al., 2012).

We examined how aspen-dominated forests growing on three different soil textures across the northern Lake States region respond to a gradient of disturbance severity created through different combinations of biomass removal and soil compaction. We show how above-ground productivity and structure respond to experimentally-controlled variations of stand-replacing disturbance and that responses vary across a range of sites. The responses to differing disturbance severities are used to demonstrate how forests may respond to bioenergy feedstock procurement of differing severity and whether some sites may be more resilient to such practices. Because of potential nutrient losses and greater departure from natural disturbance, we hypothesized that above-ground productivity would decrease with increasing disturbance severity across all sites. We also expected that structural development following the most severe disturbance would lag behind less severely impacted stands because of lowered site quality, which is known to be directly tied to the rate of structural development (Franklin et al., 2002; Ryan et al., 2008). These hypotheses were tested using experimental sites associated with the LTSP network, established in the early 1990s. Three LTSP installations in the Lake States located within the Chippewa, Ottawa, and Huron-Manistee National Forests, provide the opportunity to assess how forests dominated by the same species but distributed across a landscape respond to different levels of disturbance severity over 15 years.

2. Methods

2.1. Study sites

The study includes three sites within the Laurentian Mixed Forest Province extending from northern Minnesota, USA to Lower Michigan, USA. Each site was dominated by aspen (*P. tremuloides* Michx.) prior to harvest. The Chippewa National Forest (Chippewa) installation (47°18′N, 94°31′W) occurs on silty loam Frigid Haplic Glossudalfs, receives approximately 64 cm precipitation each year, and is the most productive of the three sites (site index 23 m height at age 50 (SI_{50}) for aspen; Voldseth et al., 2011). Important species prior to harvest included aspen (Curtis Importance Value = 58%), sugar maple (*Acer saccharum* Marshall, 11%) and basswood (*Tilia americana* L., 9%). In terms of relative biomass, aspen maintained a similar dominance 15 years after harvest (52.0%). The Huron-Manistee site (Huron; 44°38′N, 83°31′W) has a SI_{50} of 19 m for aspen (Stone, 2001). Soils are sandy, classified as Frigid Entic Haplorthods and Frigid Typic Udipsamments and annual precipitation is approximately 75 cm (Voldseth et al., 2011). Before harvest important species in addition to aspen (57%) included big-toothed aspen (*P. grandidentata* Michx., 31%) and white pine (*Pinus strobus* L., 4%). Site-wide species composition was similar 15 years post-harvest with aspen (41.8%) and big-toothed aspen (34.1%) dominating, followed by red oak (11%). The Ottawa National Forest installation (Ottawa; 46° 37′ N, 89° 12′ W) occurs on clayey Frigid Vertic Glossudalfs. This site receives approximately 77 cm precipitation annually and has a SI_{50} of 17–18 m for aspen (Voldseth et al., 2011; Stone, 2001). Following aspen (50%), balsam fir (*Abies balsamea* [L.] Mill., 33%) and white spruce (*Picea glauca* [Moench] Voss, 14%) dominated prior to harvest. Aspen abundance was comparatively greater 15 years post-harvest (87.5%) with balsam fir (4.7%) and white spruce (0.01%) making up smaller components than pre-harvest levels.

2.2. Experimental design

The severity of disturbance has been quantified in terms of organic matter removal and soil compaction, two factors likely affected during the procurement of biofuel feedstocks from forests. These two factors, each with three levels, were crossed using a factorial design resulting in nine treatments examined over time.

The three organic matter removal levels are named according to the traditional harvest method they most closely resemble. These levels included: (1) stem-only harvest (SOH), in which shrubs and merchantable tree boles were removed leaving behind harvest residues (branches and non-merchantable tops); (2) whole-tree harvest (WTH) in which all aboveground portions of trees and shrubs were removed; and (3) whole-tree harvest plus forest floor removal (FFR) in which the forest floor was removed in addition to all above-ground woody biomass. Shrubs such as hazel (*Corylus cornuta* Marshall and *C. americana* Walter) often grow densely in this region and can inhibit tree regeneration, so they were removed from all treated plots at the time of harvest. WTH is a best approximation of the harvest practices associated with biomass feedstock procurement, given the focus of these harvests on removing materials, such as tree tops, and tree limbs which normally would be left on site after traditional harvests. Some states and countries have developed guidelines that recommend removal of only a portion of harvest residues for use in bioenergy production (i.e. MFRC, 2007); this study, as it was originally designed in the 1990s, only allows assessment of extremes within the range of residue levels that might be removed as bioenergy feedstocks.

The compaction levels included no additional compaction above normal levels associated with conventional harvesting (C0),

moderate compaction (C1), and heavy compaction (C2). Moderate compaction and heavy compaction were intended to increase soil bulk density by 15% and 30%, respectively, over levels normally associated with harvesting (Stone, 2001). Actual results varied slightly by soil texture and depth (Voldseth et al., 2011). Plots at the Ottawa, Chippewa, and Huron National Forests were harvested during winter in 1991, 1992, and 1993, respectively. Stands regenerated naturally, mostly through root suckers and stump sprouts. At the Chippewa installation, late season snow delayed the compaction application for 10 plots, so aspen seedlings were planted to compensate for any suckers damaged during treatment. The majority of these seedlings died due to the high level of compaction. Harvest operations are described in detail by Stone (2001).

Treatments were applied to 0.16 ha plots (40 m × 40 m) as well as to 5 m buffers surrounding these plots (0.25 ha total area) and generally replicated three times at each location. Treatment implementation at the Ottawa differed slightly from the other sites with five replicates of the WTH/C0 treatment, two replicates of SOH/C1, and only one replicate with SOH/C2. Woody vegetation was sampled in four 1.26 m radius (5 m^2) circular subplots per plot at Chippewa and Ottawa 5 years following harvest. During the 10 and 15 year sampling periods at these sites and all three sampling periods at the Huron NF, nine 1.78 m radius (10 m^2) circular subplots per plot were sampled. For each individual stem at least 15 cm tall, species and diameter at 15 cm were recorded. In each measurement year, a random azimuth and distance (range of 1 to 3 m) from a permanent sample point center was used to determine the location of five 1 m^2 clip-plots per treated plot for sampling above-ground herbaceous vegetation. Clip-plot locations in subsequent years were constrained to be at least 1 m from the previous sample location. Herbaceous vegetation was clipped at the peak of the growing season (late July or early August), oven-dried at 60° C for 48 h, and weighed to determine biomass.

2.3. Analysis

Above-ground biomass of woody species was calculated 5, 10, and 15 years post-harvest with species-specific allometric equations developed using material from several locations across the Lake States, including the Chippewa and Ottawa National Forests (Perala and Alban, 1994). Woody species that can occupy dominant canopy positions in closed canopy conditions at some stage of development in these forests were classified as 'trees'. The 'shrubs' category comprised all remaining woody species except for the genus *Rubus* which was included with herbaceous plants during sampling. Live standing biomass at each measurement period was used as a surrogate for net aboveground productivity in our analyses.

Three attributes were used to assess forest structural development in response to organic matter removal and compaction over time. These included density of stems and quadratic mean diameter, two conventional measures of forest structure. Additionally, we analyzed the maximum basal diameter (maxBD) as a response variable. Larger diameter trees and greater variability in tree diameter are both commonly used to describe structural development, particularly when comparing the structure of managed forests to that of old-growth (i.e. Larson et al., 2008; Silver et al., 2013). The forests sampled for the present study are young, so "large" trees are absent, but the diameter of the largest trees present in each stand provides some indication of structural development at this early stage.

Diameter was measured at a height of 15 cm (basal diameter, BD) in the field with diameter at breast height (DBH, 1.4 m) measured for only a subset of stems. To enable comparison with other studies DBH was estimated using the following equation:

$$\mathrm{DBH} = 0.88 * \mathrm{BD} - 0.254 \ (r^2 = 0.9476, p < 0.0001) \quad (1)$$

where DBH is diameter at breast height (cm) and BD is basal diameter (cm).

The influence of organic matter removal and compaction on productivity and structure was assessed with mixed-model repeated measures ANOVA using the SAS MIXED procedure (SAS Institute, Inc., 2010). The statistical model used was as follows:

$$Y_{ijkl} = \mathrm{OMR} + \mathrm{CPT} + \mathrm{TIME} + (\mathrm{OMR} * \mathrm{CPT}) + (\mathrm{OMR} * \mathrm{TIME}) + (\mathrm{CPT} * \mathrm{TIME}) + (\mathrm{OMR} * \mathrm{CPT} * \mathrm{TIME}) + e_{ijkl} \quad (2)$$

where OMR is organic matter removal, CPT is compaction, TIME is the number of years since harvest, and Y_{ijkl} is above-ground biomass, stem density, or diameter at the *i*th level of OMR, the *j*th level of CPT, the *k*th level of time, and the *l*th level of plot. Plots were included as random effects while OMR, CPT, and TIME were treated as fixed effects. Type III sums of squares were used for all analyses to account for the unbalanced design at the Ottawa NF. Each site was analyzed separately because soil texture, the main characteristic distinguishing them, was not replicated. Some response variables required power transformations to meet ANOVA assumptions for equal variances among groups and normally distributed residuals. Tukey-adjusted multiple comparisons were used to distinguish among effects of factor levels where warranted.

3. Results

3.1. Biomass production

Both main factors and their interaction (OMR * CPT) resulted in significant differences in total above-ground biomass at all three sites (Table 1). Removing harvest residues did not negatively affect total standing biomass at the Chippewa or Ottawa sites (Fig. 1). In fact, with the addition of light compaction (C1) both WTH (23.894 ± 4.367 Mg/ha) and FFR (24.329 ± 5.498 Mg/ha) yielded higher total above-ground biomass at Chippewa compared with SOH (11.426 ± 2.360 Mg/ha; Fig. 1). Similarly at Ottawa, WTH resulted in higher biomass when combined with C1 (23.183 ± 6.525 Mg/ha) or C2 (14.867 ± 3.801) compared to FFR (9.402 ± 3,235 and 10.554 ± 3.520 Mg/ha, respectively) with SOH intermediate (Fig. 1). In contrast, removing residues did result in decreased total above-ground biomass at the Huron site (sandy soils) except when compaction was most severe (C2) in which case the biomass among OMR severity levels did not differ (Fig. 1, Appendix A).

With respect to compaction, no trends in total standing biomass were consistent among the sites. Total biomass declined with increasing CPT at Chippewa (Fig. 1). At Ottawa, the intermediate compaction level (C1) appears to increase total biomass, but only when combined with SOH or WTH (Fig. 1). At Huron, there were no significant differences among CPT levels when OMR was held constant even though CPT was a significant factor by itself (Table 1, Appendix A) and biomass appears to increase with an increase in compaction above C0 (Fig. 1).

When total biomass is divided into its component guilds, responses to disturbance again varied by site. Trees consistently dominated the biomass pools. Accordingly, trends in tree biomass followed those reported above for total above-ground biomass (Fig. 1). Shrub biomass increased with increasing disturbance at Chippewa. Shrub biomass at this site was greatest following FFR (FFR > SOH, WTH; $p = 0.0397$, 0.0004). Increasing compaction also resulted in greater shrub biomass (Fig. 1), but the CPT factor was not significant by itself. Because of the TIME * CPT interaction, we analyzed shrub biomass independently for the 15 year sampling period, and compaction did have a significant effect ($F = 5.54$,

Table 1
Summary of type III tests of fixed effects for aboveground biomass in different pools over 15 years following biomass harvest. The response variable "herbaceous biomass" refers to the percent of total biomass constituted by herbaceous species. Abbreviations for the factors are as follows: organic matter removal, OMR; compaction, CPT. Results are reported for LTSP installations at the Chippewa National Forest, Minnesota (CH), the Huron-Manistee National Forest, Michigan (HM), and the Ottawa National Forest, Michigan (OT). Effects with $p \leqslant 0.05$ are shown in bold.

	Source	df	Above-ground biomass		Tree biomass		Shrub biomass		Herbaceous biomass	
			F	*P*-value	*F*	*P*-value	*F*	*P*-value	*F*	*P*-value
CH (loamy)	OMR	2	**3.86**	**0.0272**	**8.73**	**0.0005**	**8.95**	**0.0004**	0.61	0.5496
	CPT	2	**45.92**	**<0.0001**	**131.92**	**<0.0001**	0.83	0.4404	**89.81**	**<0.0001**
	TIME	2	**154.97**	**<0.0001**	**148.56**	**<0.0001**	**58.73**	**<0.0001**	**72.94**	**<0.0001**
	OMR * CPT	4	2.49	0.0543	**4.15**	**0.0053**	2.41	0.0605	**3.17**	**0.0209**
	OMR * TIME	4	1.17	0.3338	0.19	0.9418	0.19	0.9423	0.17	0.9516
	CPT * TIME	4	1.81	0.1409	2.01	0.1063	**5.62**	**0.0008**	2.04	0.1019
	CPT * OMR * TIME	8	0.47	0.8728	0.28	0.971	0.33	0.9514	0.33	0.9514
HM (sandy)	OMR	2	**7.59**	**0.0013**	**6.94**	**0.0021**	**11.58**	**<0.0001**	2.45	0.0961
	CPT	2	**3.51**	**0.037**	**3.22**	**0.0478**	1.34	0.2701	2.58	0.0856
	TIME	2	**83.94**	**<0.0001**	**67.17**	**<0.0001**	1.24	0.2976	**23.14**	**<0.0001**
	OMR * CPT	4	**2.71**	**0.0395**	2.3	0.0707	1.2	0.3199	1.64	0.1767
	OMR * TIME	4	0.09	0.9857	0.05	0.9946	0.1	0.9805	0.33	0.8551
	CPT * TIME	4	0.03	0.9985	0.05	0.9945	0.1	0.9819	0.2	0.9377
	CPT * OMR * TIME	8	0.07	0.9997	0.04	1	0.17	0.9938	0.12	0.9983
OT (clay)	OMR	2	**12.12**	**<0.0001**	**10.06**	**0.0002**	**5.16**	**0.0091**	**11.14**	**<0.0001**
	CPT	2	**5.51**	**0.0069**	**3.56**	**0.0358**	**4.27**	**0.0195**	**8.23**	**0.0008**
	TIME	2	**144.53**	**<0.0001**	**79.41**	**<0.0001**	**10.71**	**0.0001**	**9.16**	**0.0004**
	OMR * CPT	4	**5.18**	**0.0014**	**6.06**	**0.0005**	**3.16**	**0.0215**	**7.73**	**<0.0001**
	OMR * TIME	4	0.77	0.5519	0.65	0.6281	0.78	0.542	1.47	0.2243
	CPT * TIME	4	0.17	0.9518	0.03	0.9987	0.42	0.7938	0.08	0.9885
	CPT * OMR * TIME	8	1.26	0.2839	0.94	0.4956	2.03	0.0617	1.87	0.0863

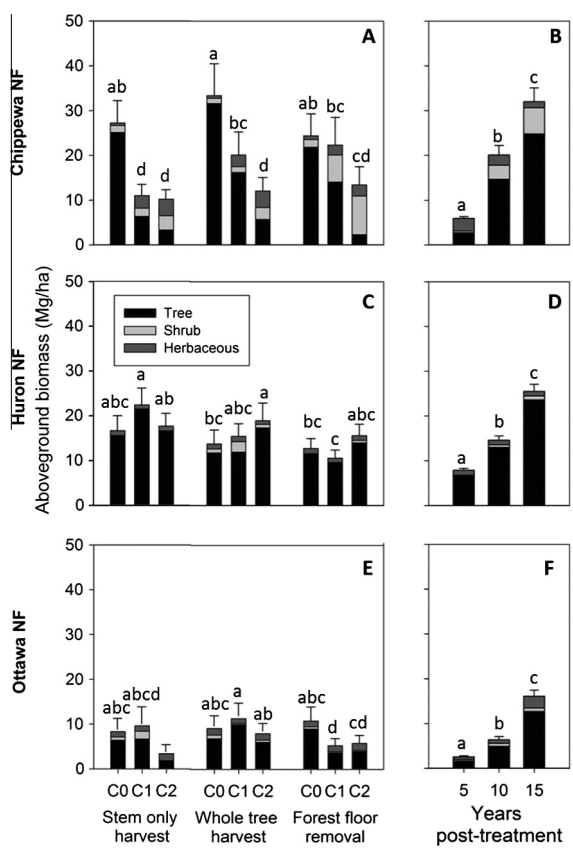

Fig. 1. Total above-ground biomass including trees, shrubs, and herbaceous plants at Chippewa (panel A), Huron (panel C), and Ottawa (panel E). Panels on the right (B, D, F) show corresponding trends in above-ground biomass across treatments over time. Treatments are abbreviated as follows: C0, no compaction; C1, minimal compaction; C2, moderate compaction. Bars indicate standard error. No standard error or significance is shown for the SOH/C2 treatment at Ottawa because this treatment was not replicated.

$p = 0.0133$) with shrub biomass greater following C2 than C0 ($p = 0.0126$). In contrast, shrubs exhibited a negative response to greater disturbance at Ottawa. Where heavy compaction occurred shrub biomass decreased with increasing organic matter removal (SOH > WTH, FFR; $p = 0.0404$, 0.0533). When combined with WTH, increasing compaction also decreased shrub biomass (C0 > C1, $p = 0.0301$). At Huron, WTH may have favored shrub biomass (Fig. 1), but the effects were not significant. Likewise, herbaceous biomass showed no relationship to the disturbance severity associated with either factor. However, at both the Chippewa and Ottawa locations, increasing compaction increased the proportion of biomass allocated to herbaceous plants (C1, C2 > C0 at both sites; Fig. 1, Appendix A). At Ottawa, FFR increased herbaceous biomass over WTH when in combination with increased compaction (C1 or C2, Appendix A).

Most biomass measures varied significantly with time (Table 1, Appendix B). The only exception was shrub biomass at the Huron site which constituted a very small proportion of total above-ground biomass (Fig. 1). Tree biomass increased over time at all three sites. At the Chippewa site, in particular, shrub biomass was greater where severe compaction decreased tree biomass at the 15 year sampling period (Fig. 1). Herbaceous biomass decreased over time at Chippewa NF, but continued to increase up to 15 years after harvest at Ottawa NF.

3.2. Structure

Both main factors and their interaction significantly influenced diameter at the Chippewa and Ottawa sites (fine-textured soils) whereas at Huron (sandy soils) only OMR and the OMR * CPT interaction were significant effects (Table 2). Holding OMR constant at SOH, increasing compaction (C1 or C2) reduced the mean for the largest diameter trees (maxBD) at Chippewa (Fig. 3). Increased compaction also reduced max diameter when combined with FFR (Fig. 3, Appendix A). Maximum diameter increased at Chippewa following WTH compared to SOH, but only in combination with intermediate compaction (C1; Fig. 3, Appendix A). Similarly, at Huron maxBD was greater following SOH compared with WTH

Table 2
Summary of type III tests of fixed effects for forest structural attributes following biomass harvest. Abbreviations are as follows: organic matter removal, OMR; compaction, CPT; maximum basal diameter (99th percentile), BDmax; quadratic mean diameter, QMD. Results are reported for LTSP installations at the Chippewa National Forest, Minnesota (CH), the Huron-Manistee National Forest, Michigan (HM), and the Ottawa National Forest, Michigan (OT). Effects with $p \leqslant 0.05$ are shown in bold.

	Source	df	BDmax		QMD		Stem density	
			F	*P*-value	*F*	*P*-value	*F*	*P*-value
CH (silty loam)	OMR	2	**5.04**	**0.01**	**11.4**	**<0.0001**	**3.67**	**0.032**
	CPT	2	**23.76**	**<0.0001**	**9.99**	**0.0002**	**53.55**	**<0.0001**
	TIME	2	**205.1**	**<0.0001**	**150**	**<0.0001**	**21.22**	**<0.0001**
	OMR * CPT	4	**3.18**	**0.0204**	2.34	0.067	0.17	0.9521
	OMR * TIME	4	0.71	0.5878	2.44	0.0585	0.22	0.9267
	CPT * TIME	4	0.83	0.5117	**0.92**	**0.4612**	0.46	0.766
	OMR * CPT * TIME	8	0.23	0.9834	0.33	0.9509	0.23	0.9828
HM (sandy)	OMR	2	**8.86**	**0.0005**	**3.43**	**0.0398**	0.95	0.3934
	CPT	2	0.1	0.2571	1.73	0.1871	0.61	0.549
	TIME	2	**216.2**	**<0.0001**	**53.4**	**<0.0001**	**10.57**	**0.0001**
	OMR * CPT	4	**3.77**	**0.0091**	0.86	0.4953	2.6	0.0858
	OMR * TIME	4	0.64	0.6372	0.02	0.9994	0.08	0.9874
	CPT * TIME	4	0.09	0.9842	0.14	0.9685	0.15	0.9628
	OMR * CPT * TIME	8	0.08	0.9997	0.06	0.9999	0.09	0.9994
OT (clay)	OMR	2	**6.51**	**0.0031**	**12.7**	**<0.0001**	**3.56**	**0.036**
	CPT	2	**9.03**	**0.0004**	2.83	0.0685	0.79	0.4579
	TIME	2	**259.8**	**<0.0001**	**231**	**<0.0001**	**71.92**	**<0.0001**
	OMR * CPT	4	**3.88**	**0.0081**	**4.56**	**0.0032**	**2.59**	**0.0481**
	OMR * TIME	4	0.37	0.8281	0.96	0.4368	0.67	0.6165
	CPT * TIME	4	0.31	0.8686	1	0.419	**3.44**	**0.0147**
	OMR * CPT * TIME	8	0.78	0.6223	1.08	0.3983	1.83	0.0941

and FFR when combined with C1 ($p = 0.0396$, $p < 0.0001$; Appendix A). At the Ottawa site, pairwise comparisons yielded no significant differences in diameter attributable to OMR severity levels even though the main effect was significant in the model (Table 2).

At Chippewa NF, both the CPT factor and CPT * TIME interaction significantly affected stem density. Holding TIME constant, density decreased with increasing compaction (C0 > C1 > C2, $p < 0.05$) during each time period. At the Ottawa site, both OMR and the OMR * CPT interaction showed a significant effect on tree stem density over time (Table 2), but no pairwise comparisons between OMR levels emerged as significant. An assessment of trees >5 cm DBH in the last sampling period alone (15 years post-harvest) confirms the significant effect of OMR on density ($F = 6.12$, $p = 0.0106$). The greatest stem densities occurred following WTH, but significant differences only emerge when that treatment is combined with intermediate compaction (C1: WTH > FFR, $p = 0.0077$; Fig. 2). At the Huron NF, neither main factor affected tree stem densities over time when all diameters are considered (Table 2). However, if analysis is limited to stems $\geqslant$5.0 cm DBH 15 years post-harvest, OMR does have an effect ($F = 5.30$, $p = 0.0163$) with densities significantly greater when harvest residues are retained (SOH > WTH, FFR; $p = 0.0380$, 0.0245).

As would be expected, tree diameter and stem density changed significantly over time at all three sites. At Chippewa stem density did not differ significantly between years 5 and 10, but did decrease substantially by year 15 (Y5, Y10 > Y15; $p = 0.0068$, 0.0325). At Ottawa NF, OMR * TIME was significant, so changes over time were assessed while holding OMR constant. Only with WTH did densities differ among years (5 > 15, $p = 0.0089$). At Huron NF, stem density decreased between 5 and 10 years post-harvest, but year 15 did not differ from year 10 (5 > 10, 15; $p < 0.0001$). Both measures of diameter (QMD and maxBD) increased over time at all sites (Y15 > Y10 > Y5, $p < 0.0001$).

4. Discussion

Across sites, standing biomass was generally greatest where both diameter (QMD and maxBD) and density were also greatest (Fig. 3). Treatment effects varied among sites, but within sites these three aspects of structure responded to disturbance severity in concert. At Chippewa and Ottawa, the removal of harvest residues did not detrimentally impact total above-ground standing biomass or diameter growth. At the Huron installation, however,

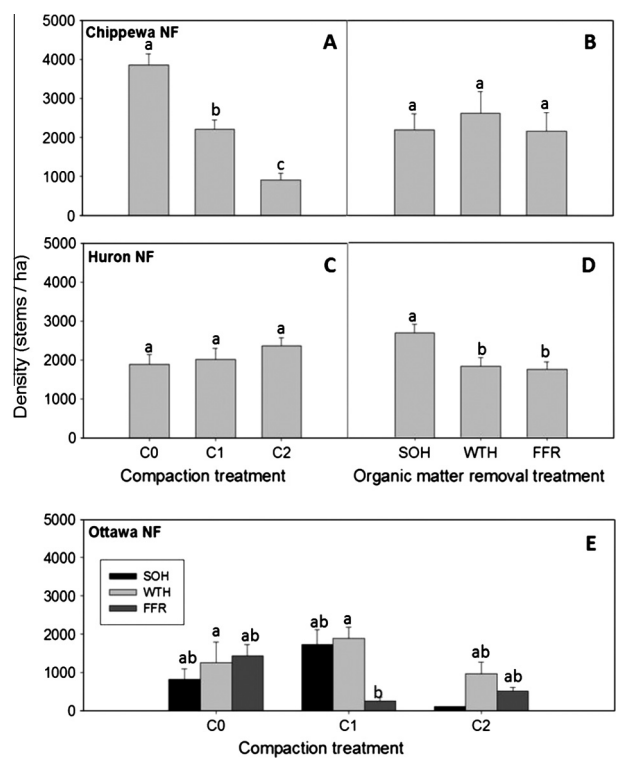

Fig. 2. Density of trees greater than 5 cm DBH 15 years following harvest. For the Chippewa and Huron National Forests, there was no significant effect of OMR * CPT, so means are presented for each factor individually. Panels A and B show mean density according to levels of compaction and organic matter removal, respectively, at Chippewa NF. Panels C and D show mean density by levels of compaction and organic matter removal, respectively, at Huron NF. A significant OMR * CPT interaction was observed at Ottawa NF, so means are presented for each individual factorial combination for this site in panel E. Bars indicate standard error and letters indicate where significant differences among treatments occur. No standard error or significance is shown for the SOH/C2 treatment in Panel E because there was no replication for this treatment.

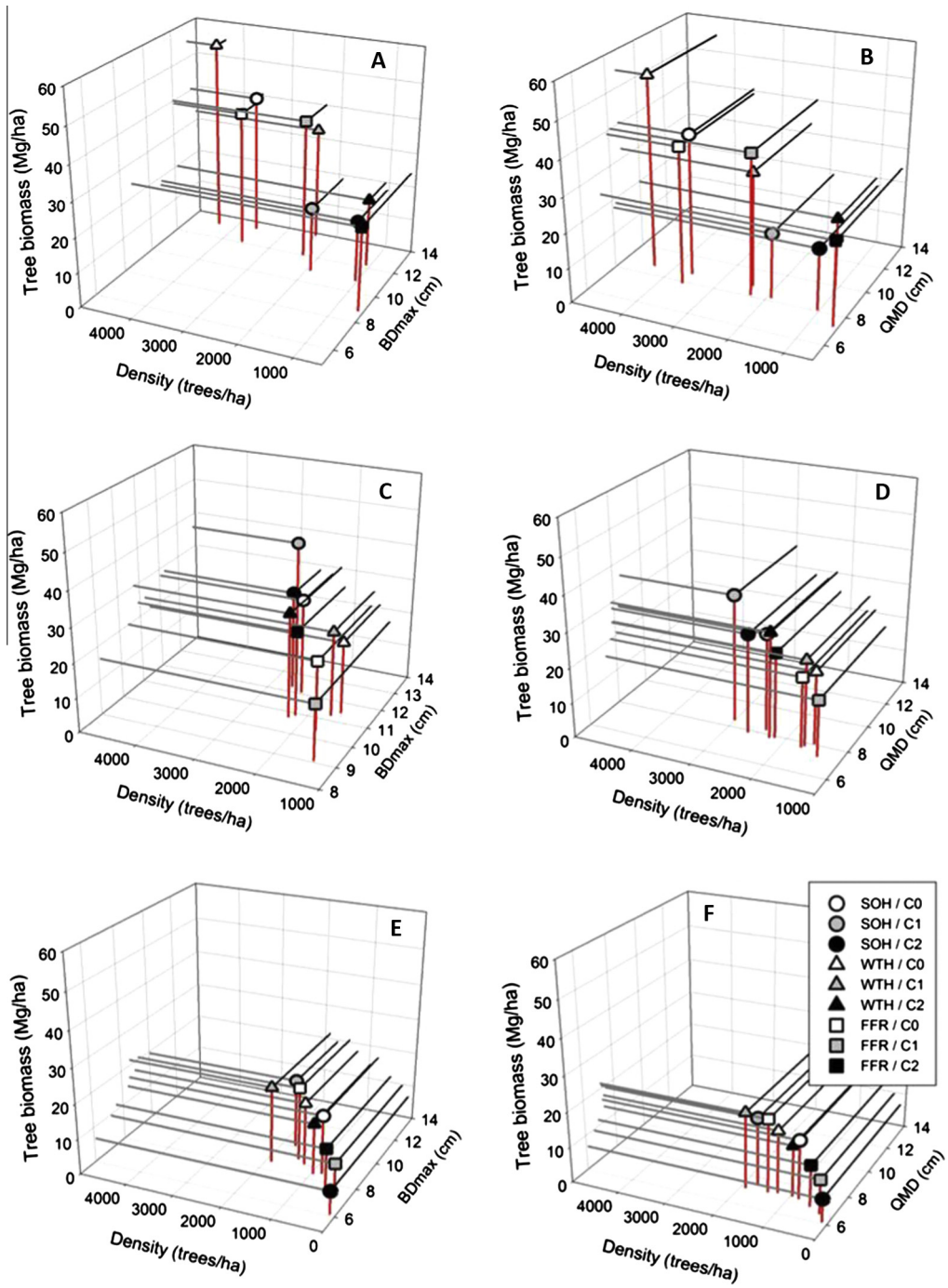

Fig. 3. The relationships among tree biomass, tree stem density, and diameter 15 years following harvest at Chippewa (panels A and B), Huron (panels C and D), and Ottawa (panels E and F) study sites. A tree was defined as having diameter at breast height > 5.0 cm. Symbol shape (circle, square, triangle) corresponds to the OMR factor (SOH, stem-only harvest, WTH, whole-tree harvest, FFR, forest floor removal). Symbol color (white, grey, black) indicates the CPT factor level (C0, no compaction; C1, minimal compaction; C2, moderate compaction).

standing biomass, diameter growth, and tree density all declined with increasing organic matter removal (Fig. 3).

The short period of time (15 years) since stand-replacing disturbance somewhat limits assessment of structural development, but even at this early stage, severe compaction at Chippewa and Ottawa and severe organic matter removal (FFR) at all three sites appeared to delay the accumulation of larger trees (Appendix B). At the Ottawa NF, the temporal trend in stem density gives some indication of structural development. In contrast to the other two sites, stem density declined little over time at this site except where WTH occurred (Appendix B). As a stand develops, there is generally a predictable decline in stem densities due to self-thinning processes, so a delay in decreasing densities may indicate slower structural development in general compared to the other sites. While removing harvest residues (WTH) may improve growing conditions for species (like aspen) that regenerate through root suckers and hasten development compared with SOH, the additional loss of nutrients associated with removing the forest floor (FFR) may have had a negative effect.

One advantage of looking at the effects of soil compaction and harvest removal over time rather than exclusively at an 'endpoint' is a greater ability to discern the processes affecting changes in the

main variables of interest, such as above-ground biomass. At the Chippewa, those stands most severely impacted in terms of soil compaction showed an increase in shrub biomass 15 years post-harvest that coincided with decreased tree biomass relative to other treatments. Because the shrub response to compaction did not emerge until 15 years had passed (Fig. 1), we can infer that the original disturbance negatively impacted tree regeneration in a direct way, possibly through damage to aspen root systems because of rutting (Bates et al., 1993). Shrubs have likely increased over time in response to that original impact on trees rather than directly outcompeting trees because of some advantage conferred immediately following the disturbance (Royo and Carson, 2006). It should cause concern that the most severe disturbance treatment (FFR/C2) results in a community dominated by shrubs 15 years after harvest with no indication of return to the pre-disturbance composition or structure (Fig. 1).

While the lack of replication prevents statistical comparisons among soil textures in our analysis, other studies have observed different responses depending on soil texture (Powers et al., 2005; Morris et al., 2014) or general site quality (Page-Dumroese et al., 2000; Thiffault et al., 2011) and this may contribute to the differences we observed. With the addition of compaction (C1 or C2), removing harvest residues resulted in higher aboveground biomass at the Chippewa and Ottawa sites despite evidence that K decreased with increasing organic matter removal at Chippewa (Voldseth et al., 2011). The soils at Chippewa and Ottawa are considered more nutrient-rich than at Huron, so it may be that where nutrients are not already limiting, the effect of retained harvest residues on the microenvironment can hinder tree establishment and growth. In other regions where forest regeneration depends more on sexual reproduction or planting than the aspen-dominated forests discussed here, harvest residues and litter tend to benefit seedling germination and growth by decreasing soil moisture loss and mitigating extreme conditions in the microenvironment (Gray and Spies, 1997; Roberts et al., 2005; Walmsley et al., 2009; Thiffault et al., 2011) or by reducing competing vegetation (Stevens and Hornung, 1990; Roberts et al., 2005). Additionally, harvest residues eventually provide valuable substrate for species that require decaying woody debris for seedling germination (Shields et al., 2007; Marx and Walters, 2008; Cornett et al., 2001). When the dominant species can regenerate vegetatively through root suckering and is managed using a coppice system, as with aspen in this study, these effects may not prove beneficial for total aboveground biomass production. Instead, the decrease in soil surface temperatures that results from shading by woody debris or dense understory cover (Zabowski et al., 2000) can potentially shorten the growing season and decrease annual growth rates in aspen (Zasada and Schier, 1973; Grewal, 1995; Landhausser and Lieffers, 1998; Fraser et al., 2002).

Forest regrowth and productivity at Huron was negatively impacted by increasing severity of residue removal even though only the two extremes (SOH and FFR) differed significantly once the interaction of main effects was considered. Because sandy soils tend to be of poorer nutrient quality, the detrimental impact of residue removal might be explained by an associated loss of nutrients (Federer et al., 1989; Thiffault et al., 2011). While mineral soil C and N pools have not exhibited a response to OMR over 15 years at this site (Kurth et al., 2014) an analysis of soil cations 10 years after harvest indicated a significantly lower concentration of Ca associated with FFR when compared to SOH 10–20 cm below the surface (Voldseth et al., 2011). This supports concerns expressed in other studies about the potential for Ca losses with residue removal following harvest of aspen and other species that store large amounts of Ca in their tissue (Alban, 1982; Silkworth and Grigal, 1982; Federer et al., 1989). Additionally, the higher levels of fine and coarse woody debris following SOH may alter the microenvironment by reducing exposure and increasing soil moisture (Gray et al., 2002; Roberts et al., 2005; Walmsley et al., 2009), thus increasing biomass production compared to FFR. Leaving residues on site (SOH) increased total above-ground biomass over other OMR treatments except when the most severe compaction treatment (C2) was held constant (Fig. 1, Appendix A). The increase in compaction resulting from C2 would be expected to decrease soil pore space and increase water-holding capacity (Greacen and Sands, 1980; Powers, 1999; Stone, 2001), which may have equalized the moisture-retaining effects of SOH relative to WTH and FFR. The positive (but insignificant) relationship between greater biomass production and increasing compaction (Fig. 1) indicates that water may be limiting as has been observed in other LTSP studies on sandy soils (Powers, 1999; Powers et al., 2005), providing some support for this hypothesis.

An analysis of bulk density 10 years after harvest at each site indicates that the soils at Huron and Chippewa had started to recover from the compaction treatments (Voldseth et al., 2011). However, no significant differences in bulk density at the Ottawa site (clay soils) were observed between sampling periods immediately following harvest and 10 years post-harvest (Voldseth et al., 2011). Based on these trends, we suspect that the responses to compaction observed in biomass production and structure at the Chippewa site, even 15 years post-harvest, were largely realized immediately after treatment. Wet conditions were present when compaction was applied, so damage to aspen root systems may have occurred, which combined with effects of compaction on conditions for seedlings and sprouts during their first growing season, may have generated differences that are still evident 15 years later. At the Ottawa site, however, it is not possible to distinguish between these effects and how continued compaction might affect hydrology, gas exchange, or other processes that influence forest growth.

Some studies have concluded that richer sites should not experience nutrient deficiencies that limit regeneration following WTH (Boyle et al., 1973; Silkworth and Grigal, 1982) with any nutrients lost via harvesting having little noticeable effect on productivity. Recent research indicates that soil disturbance has greater potential to negatively impact net primary productivity than stand mortality or dead wood removal (Peters et al., 2013). Our results at the Chippewa and Ottawa sites align with these findings at present, but as has occurred in other studies, negative effects on productivity may manifest later in stand development (Egnell and Valinger, 2003; Mason et al., 2012).

5. Conclusions

The LTSP network provides a unique opportunity to study the medium-term ecological effects of removing harvest residues. This is particularly important as interest in using those residues for bioenergy production increases and organizations develop management guidelines in anticipation of potential impacts. Our results demonstrate that increased disturbance severity resulting from the removal of harvest residues for bioenergy feedstocks may have a negative effect on structural development and, at least on some sites, above-ground biomass production. While no intermediate levels of harvest residue removal were tested, this study does affirm the need for management guidelines that include provisions for retaining living and dead tree biomass following harvest and for minimizing soil disturbance. Further research should investigate the effects of retaining a portion of residues across a range of sites.

Additionally, our results highlight the importance of accounting for site differences when developing guidelines intended to mitigate impacts from bioenergy feedstock procurement. Such considerations have been integrated by some regional site-level

guidelines (Herrick et al., 2009); however, most recommendations generically apply to all site types (e.g., MFRC, 2007). While removing residues may improve the growing environment on fine-textured soils for species that regenerate vegetatively as occurred at the Chippewa and Ottawa sites, care should be taken to minimize soil disturbance as reductions in tree biomass may occur and, if the disturbance is severe enough, shrubs may increase in dominance. On poorer, sandy soils such as those at the Huron NF, the removal of harvest residues may not be appropriate both because of potential for nutrient losses as well as reductions in moisture availability, particularly in light of projections for more severe and more frequent drought conditions in the future.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.05.056.

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