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Herbaceous-Layer Community Dynamics along a Harvest-Intensity Gradient after 50 Years of Consistent Management

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In 1958, a demonstrational cutting trial totaling 22.2 ha was established in a northern hardwood forest in Alberta, MI. Eight different treatments were installed, including four diameter-limit treatments (56 cm, 41 cm, 30 cm, and 13 cm), three single-tree selection treatments with residual basal areas of 21 $m^2 \cdot ha^{-1}$, 16 $m^2 \cdot ha^{-1}$, and 11 $m^2 \cdot ha^{-1}$, and an uncut control. Within each treatment, a 0.4-ha permanent plot was established and subdivided into 0.04-ha square subplots. Harvests have been implemented every ten years with the most recent harvest occurring during the winter of 2008-2009. We quantified ground layer vegetation response before and after the most recent harvest. Nonmetric multidimensional scaling (NMS) ordination showed a very distinct separation between the most intensive management treatment (13-cm diameter-limit treatment) and the uncut control. Compositionally, the diameter-limit treatments moved with greater directionality and magnitude towards the 13-cm diameter-limit treatment following harvest, while compositional change in the residual basal area treatments was less pronounced and lacked strong directionality. Herbaceous species percent cover generally decreased with increasing residual overstory basal area across treatments. Weedy and early successional species were most abundant under lower residual basal area and diameter-limit treatments. Results based on 50 years of continuous management suggest that diameter-limit harvests likely have a greater impact on the herbaceous community than single-tree selection or no management.

Keywords: Northern Hardwood Forests; Uneven-Aged Management; NMS Ordination; Understory Diversity; Diameter-Limit; Single-Tree Selection

Introduction

While overstory dynamics in forested ecosystems have received considerable study (e.g. Nyland, 1996; Oliver & Larson, 1996; Frelich, 2002), herbaceous-layer dynamics in response to natural and anthropogenic disturbance are less well understood, especially given the contribution of this layer to biological diversity and ecosystem function (Gilliam, 2003). Within northern temperate forests in North America, the herbaceous layer often contains the highest species richness (Curtis, 1959; Whittaker, 1967; Whitney & Foster, 1988; Scheiner & Istock, 1994; Gilliam, 2007) and represents a disproportionate amount of the net primary productivity relative to its biomass (DeAngelis et al., 1981).

Land-use often leaves a legacy across a landscape that provides an important historical context for interpreting contemporary vegetation dynamics. The Great Lakes region was once dominated by a vast forest; the United States General Land Office Survey estimated circa 1850 that there were approximately 32.6 million ha of closed-canopy forests with 47% or 15.3 million ha in the hardwood forest type (Frelich, 2002). Widespread logging in the Great Lakes region began in the mid-1800s, with an estimated 20 million ha of forested land harvested in 60 years (Williams, 1989). The rapid pace of commodity driven harvesting and associated slash fires left millions of hectares of cutover and degraded forests (Williams, 1989; Stearns, 1997).

Contemporary forest management in northern hardwood forests in the Great Lakes region has focused on producing sustainable, high quality sawtimber using uneven-aged regeneration harvest methods (e.g., Arbogast, 1953; Arbogast, 1957; Tubbs, 1977) with forest diversity as a lower priority. However, decreases in understory tree diversity have been a common consequence of long-term, uneven-aged management in northern hardwood forests (Leak & Sendak, 2002; Kelty et al., 2003; Neuendorff et al., 2007; Gronewold et al., 2010). Studies in northern hardwood forests have shown varying responses in the herbaceous layer due to uneven-aged management (e.g. Metzger & Schultz, 1981; Crow et al., 2002; Scheller & Mladenoff, 2002; Kern et al., 2006; Wolf et al., 2008; Burton et al., 2009).

Along the border of northern Wisconsin and the Upper Peninsula of Michigan, Scheller and Mladenoff (2002) observed that actively managed uneven-aged northern hardwood stands had significantly greater herbaceous species richness than old-growth northern hardwood stands. Uneven-aged stands received management approximately ten to thirteen years prior to sampling. The greatest percent cover in all herbaceous species groups (ferns, forbs, weeds, graminoids, and shrubs) except

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spring ephemerals was observed in the managed uneven-aged stands. Spring ephemerals may be more sensitive to uneven-aged management due to reoccurring disturbance on the forest floor and in the canopy (Metzger & Schultz, 1981; Scheller & Mladenoff, 2002). However, at the Argonne Experimental Forest in northern Wisconsin, there was no observed difference in spring or summer herbaceous species between areas receiving no management, uneven-aged, or even-aged management nine years after the most recent harvest (Kern et al., 2006). This lack of species composition change between management types (uneven- or even-aged management) was also observed in a central Indiana hardwood study (Jenkins & Parker, 1999).

Land-use history, including timber harvest, is a factor that can affect herbaceous species composition that is often not controlled for in studies, or is unknown (e.g. Scheller & Mladenoff, 2002). In addition, time since harvest may be important in assessing vegetation dynamics. For example, when harvest intensities were controlled in the Argonne Experimental Forest, pre-harvest conditions were not sampled and post-harvest conditions were measured a minimum of nine years after harvest activities (Kern et al., 2006). The lack of pre-harvest data and the delay in sampling could have missed important compositional changes in vegetation that occurred before and after harvest. These compositional changes may be transient; however, repeated short cutting cycles in northern hardwood forests have been hypothesized to create novel herbaceous communities dominated by transient early successional species (Scheller & Mladenoff, 2002).

Few long-term studies of the impact of forest management on the herbaceous layer in northern temperate forests are available (e.g. Kern et al., 2006). One of the longest running and most consistently treated silvicultural trials in the upper Great Lakes region began in 1957 as a demonstrational woodlot at the Ford Forest (Michigan Technological University, Alberta, MI) with the goal of assisting small landowners by providing examples of various management techniques for northern hardwood forests (Bourdo & Johnson, 1957; Reed et al., 1986; Erickson et al., 1990; Bodine, 2000). The consistency of the study offers a unique opportunity to observe the response of the herbaceous layer after 50 years of management. The overstory and understory of the study site are dominated by *Acer saccharum*, and the herbaceous layer adds the majority of species richness and diversity in these stands. Our primary objective was to observe how herbaceous-layer plant communities that have developed under various management approaches respond to contemporary harvesting. We hypothesized that herbaceous species composition and response to harvesting would vary along a gradient of harvest intensity, and that the less intensively managed treatment would have herbaceous communities more similar to the second-growth, uncut control than the more intensively managed treatments.

Methods

Site Description and Study History

The study is located at the Ford Forest, owned by Michigan Technological University and located in Alberta, Michigan (46.66˚N, 88.51˚W; Baraga County). The site once supported a *Pinus strobus*-hardwood forest with the pine resource being removed around 1890 (Bourdo & Johnson, 1957). By 1938, the Ford Motor Company had "selectively logged" the study site and the surrounding area twice before the area was donated to Michigan Technological University in 1954 (Bourdo & Johnson, 1957). Further information about pre-treatment conditions and harvest guidelines can be found in Bourdo and Johnson (1957). The demonstrational woodlot reached its fifth cutting cycle and 50th year of harvest activity during the winter of 2008-2009. Consistent management has occurred over this period with strict adherence to a 10-year cutting cycle (Bourdo & Johnson, 1957).

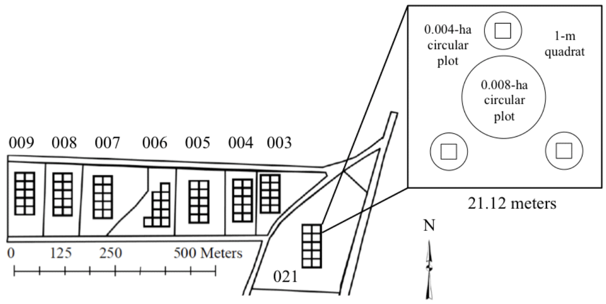
The site's proximity to Lake Superior regulates temperatures; 17.4˚C and –9.8˚C are the average summer and winter temperatures, respectively (Berndt, 1988). Average total precipitation and snowfall are 87.4 cm and 385.5 cm, respectively (Berndt, 1988). The soils of the area are classified as Allouez gravelly coarse sandy loams with slopes generally ranging from 0% - 6% (Berndt, 1988). The original composition of the overstory was mainly *Acer saccharum*, with *Tilia americana*, *Betula alleghaniensis*, and *Ulmus americana* as important associate species. *Acer saccharum* has increased in dominance in all layers of vegetation with uneven-aged management (Reed et al., 1986; Erickson et al., 1990; Bodine, 2000).

Study Design and Data Collection

The study consists of eight different harvest treatments ranging in size from 1.2 to 5.7 ha with a total study area of 22.2 ha. There are four diameter-limit treatments of 56 cm (22 in), 41 cm (16 in), 30 cm (12 in), and 13 cm (5 in); three single-tree selection treatments with residual basal areas of 21 $m^2 \cdot ha^{-1}$ (90 $ft^2 \cdot ac^{-1}$), 16 $m^2 \cdot ha^{-1}$ (70 $ft^2 \cdot ac^{-1}$), and 11 $m^2 \cdot ha^{-1}$ (50 $ft^2 \cdot ac^{-1}$); and an uncut control. Diameter-limit treatments are defined as the removal of any tree of any species over the specified diameter (Helms, 1998). The residual basal area treatments generally focus on the removal of poor quality trees in all size classes (12.7 cm and greater diameter at breast height (1.37 m)) with management generally following a *q*-factor of 1.3 (Schwartz et al., 2005). The maximum residual diameter for trees was set at 61 cm (24 in). The uncut control has not received active management since 1938 with the exception of a sanitation cut to remove *Ulmus americana* in the 1980's. The first harvest occurred during the winter of 1958-1959 when all treatments were harvested. The 21 $m^2 \cdot ha^{-1}$ residual basal area treatment, the 41 cm diameter limit treatment, the 16 $m^2 \cdot ha^{-1}$ residual basal area treatment, and 11 $m^2 \cdot ha^{-1}$ residual basal area treatment have been harvested during the last five cutting cycles (cutting cycle: 10 yrs). The 56-cm diameter-limit treatment, 30-cm diameter-limit treatment, and the 13-cm diameter-limit treatment were cut in four, three, and two of the last five cutting cycles, respectively.

The treatments are not replicated and generally follow a gradient of harvest intensity beginning with the 21 m^2 ha^{-1} residual basal area treatment to the 13-cm diameter-limit treatment (**Figure 1**). Within each treatment a 0.4-ha permanent block was established by Bourdo and Johnson in 1957 (**Figure 1**). The permanent block was subdivided into ten 0.04-ha square subplots. Within each subplot, all overstory species (greater than 11.4 cm in dbh) were identified to species and measured for diameter, height, tree grade, and number of 2.4-m logs or 2.4-m sticks.

During the 1998 pre-harvest sampling, seedling and sapling plots were established in each subplot to quantify the establishment and recruitment of different tree species (Bodine,



Compartment	Treatment
021	Uncut Control
003	21 $m^2 \cdot ha^{-1}$ (90 $ft^2 \cdot ac^{-1}$)
004	56 cm DLH (22 in)
005	16 $m^2 \cdot ha^{-1}$ (70 $ft^2 \cdot ac^{-1}$)
006	41 cm DLH (16 in)
007	11 $m^2 \cdot ha^{-1}$ (50 $ft^2 \cdot ac^{-1}$)
008	30 cm DLH (12 in)
009	13 cm DLH (5 in)

Figure 1.
Ford Forest (Michigan Technological University) silviculture cutting trial designed by Eric Bourdo in 1957. The study totals 22.2 ha which is subdivided into nine different treatments. Within each treatment, there is a 0.4-ha permanent rectangular block which is subdivided into ten 0.04-ha subplots. Within each subplot, one 0.008-ha circular plot used to measure saplings was located in the center. Three 0.0004-ha circular plots used to measure seedlings were set equidistance from the center. At the center of each 0.0004-ha circular plot, a 1-m^2 quadrat was used to estimate herbaceous percent cover. All plot locations are permanently marked. DLH refers to diameter limit harvest.

2000). A 0.008-ha circular plot was established at the center of each subplot to measure sapling density, totaling 10 plots per treatment. Sapling classification was based on both height and diameter: 1) 30.5 cm to 91.4 cm in height, 2) 91.5 cm in height to 2.41 cm dbh, 3) 2.43 cm to 7.49 cm dbh, and 4) 7.5 cm to 11.42 cm dbh. Three circular 0.0004-ha plots were located equidistant from the center of the subplot where seedling density was measured, totaling 30 plots per treatment (**Figure 1**). Seedlings were defined as any woody tree individual less than 30.5 cm height. During the 2008 pre-harvest sampling, additional 1-m^2 quadrats were established to measure the impact each treatment was having on the diversity and composition of the herbaceous layer. At the center of the seedling plots, a 1-m^2 quadrat was placed facing north to estimate percent coverage of herbaceous species, totaling 30 plots per treatment (**Figure 1**). Percent cover was estimated for each species; total percent cover in each quadrat could total more than 100%. Herbaceous species were identified to species except when accurate identification was not possible in the field; in those cases, species were identified to genus. Overstory sampling occurred during July and August of 2008 and 2009. Sampling of all layers of understory vegetation occurred during July in both 2008 and 2009 (pre- and post-harvest, respectively). Data collected from 2008 and 2009 was used for analysis. Lack of pretreatment herbaceous vegetation data (1957) limits our ability to make inferences related to change over time. However, the habitat type is consistent across the treatments (ATD, *Acer-Tsuga-Dryopteris*; Burger and Kotar 2003) with similar species composition across all treatments.

Data Analysis

Nonmetric multidimensional scaling (NMS) ordination was used to examine herbaceous species composition along a gradient of harvesting intensity. NMS was used due to the relaxed assumption of normality and because it does not assume a linear response in species to different gradients (McCune & Grace, 2002). Data were organized at the subplot level; each treatment contained 10 subplots for a combined total of 80 subplots for each year, 2008 (pre-harvest) and 2009 (post-harvest) sampling periods (n = 160). Unknown species were deleted prior to analysis; unknown species were present in only two of the 160 plots used in the ordination. The remaining herbaceous species percent cover data were square-root transformed, which is a common transformation used for percent cover data to reduce the influence of a few samples with high percent cover (Field et al., 1982). Transformed herbaceous species percent cover by treatment and year was arranged in n-dimensional space using PC-Ord Version 5 (McCune & Mefford, 2011). Autopilot mode (slow and thorough) was selected using the Sørensen (Bray-Curtis) distance measurement and a random starting configuration. Two hundred and fifty runs were completed for both the real data and randomized data to determine dimensionality. Correlation analysis in the statistical interface R (R Development Core Team, 2009) was used to test environmental variables used in the ordination for significance.

Summary statistics for each treatment were calculated at the subplot level (n = 10) for overstory tree basal area per hectare, herbaceous percent cover, and seedling and sapling stems per hectare. Species richness (S) and Shannon's diversity index (H') were calculated for the herbaceous layer, seedling, and sapling layers. The herbaceous species richness is the average number of species per 1-m^2 quadrat.

Results

Overstory Composition

The 13-cm diameter-limit harvest was the only treatment not harvested during the winter of 2008-2009; this treatment was last harvested during the winter of 1998-1999. All other actively managed treatments were harvested with the specifications established by Bourdo and Johnson in 1957. As expected, management decreased overstory basal area in all treatments receiving active management (**Figure 2**). The average diameter at breast height (dbh) of trees harvested in the permanent plots of each diameter-limit treatment was 55.4 cm (st.dev = 0.5) for the 56-cm diameter-limit treatment, 31.2 cm (st.dev = 12.8) for the 41-cm diameter-limit treatment, and 31.5 cm (st.dev = 7.3) for the 30-cm diameter-limit treatment. In the 41-cm and 30-cm diameter-limit treatments, a few trees under the minimum diameter were removed due to operability constraints, but there was no tending in the smaller diameter classes. The residual basal area treatments typically removed smaller diameter trees; the average dbh of removed trees was 20.4 cm (st.dev = 10.7) for the 21 $m^2 \cdot ha^{-1}$ residual basal area, 20.2 cm (st.dev = 7.9) for the 16 $m^2 \cdot ha^{-1}$ residual basal area, and 24.4 cm (st.dev = 11.5) for the 11 $m^2 \cdot ha^{-1}$ residual basal area. The diameter-limit treatments generally created larger openings across the treatments, resulting in higher light environments (personal observation).

Herbaceous Species Composition

Fifty-two herbaceous species were observed during both pre- and post-harvest sampling periods. Twelve exotic species were observed, representing 23% of the total species richness (**Table A1**). Slightly more species were observed in the post-harvest

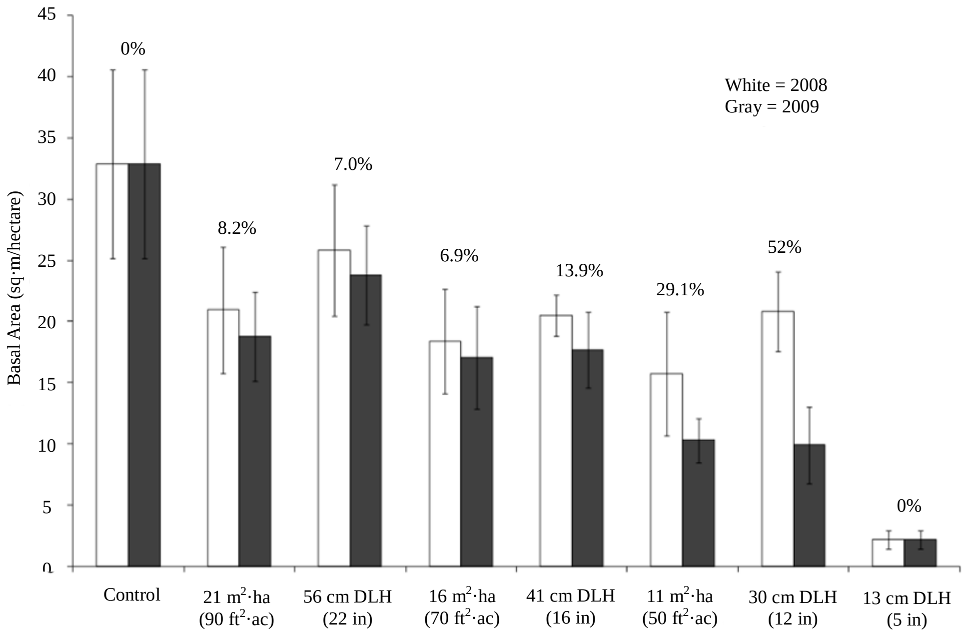


Figure 2.
Overstory basal area per hectare pre- and post-harvest summarized by subplot (n = 10) at the Ford Forest Cutting Trial, Alberta, MI. Percentage above each treatment represents the average decrease in basal area ($m^2 \cdot ha^{-1}$). DLH refers to diameter limit harvest.

period (39 observed in 2009 versus 35 observed in 2008). Of these 52 species, nine species only occurred once during the two years.

Total percent cover of the herbaceous layer in all treatments increased from 2008 to 2009; the greatest increase occurred in the 13-cm diameter-limit treatment, increasing from an average of 15.5% in 2008 to 105.4% in 2009 (**Table 1**). *Dryopteris spinulosa*, *Carex* spp., *Rubus* spp., and *Galeopsis tetrahit* were herbaceous and semi-woody species that showed the greatest increase in average percent cover from 2008 to 2009 (**Table 2**). *Dryopteris spinulosa* consistently increased in percent cover from 2008 to 2009 in all treatments; *Rubus* spp. also increased in all treatments except for the uncut control and the 30-cm diameter-limit treatment (**Table 2**). The largest average percent cover increases for *Dryopteris spinulosa* occurred in the uncut control, 1.9% to 10.3% respectively (**Table 2**). *Rubus* spp. had the largest average percent cover increase in the 13-cm diameter-limit treatment, 6.9% to 56.1% respectively (**Table 2**). *Dryopteris spinulosa* and *Rubus* spp. had high frequencies across all treatments and between years (**Table A2**).

Few species were found in only one treatment which may be due to the proximity of treatments to one another (**Table A3**; **Figure 1**). Herbaceous species co-occurrence in the actively managed treatments generally ranged between 40-60% during both years (**Table A3**). The uncut control and the 13-cm diameter-limit treatment became more dissimilar from 2008 to 2009; a 32% herbaceous species overlap was observed in 2008 vs. 10% herbaceous species overlap in 2009 (**Table A3**). The uncut control and the 13-cm diameter-limit harvest share few species in common. In 2009, only *Dryopteris spinulosa* and *Trillium* spp. were observed in both treatments. The 30-cm diameter-limit treatment had the greatest herbaceous species overlap with the 13-cm diameter-limit treatment in 2008 and 2009, 52% and 46% respectively (**Table A3**).

Herbaceous and Woody Richness (S) and Diversity (H')

On average more herbaceous species were observed in each treatment in 2009 than in 2008 except in the 16 $m^2 \cdot ha^{-1}$ residual basal area treatment and the 13-cm diameter-limit treatment (**Table 1**). There was an average of 8.5 herbaceous species observed in the 13-cm diameter-limit treatment in 2008 and an average of 9.6 herbaceous species observed in the 11 $m^2 \cdot ha^{-1}$ residual basal area treatment in 2009 (**Table 2**). However, diversity of herbaceous species on average decreased from 2008 to 2009 (**Table 2**).

The control contained on average the fewest number of species in each of the understory layers in 2008 and 2009, except for the sapling layer in 2008 (**Table 2**). The 21 $m^2 \cdot ha^{-1}$ residual basal area treatment had on average 2.2 species of seedlings observed (**Table 2**). Diversity was generally low in all layers of the understory for the control (**Table 2**).

Compositional Change in the Herbaceous Layer

The NMS ordination solution was three-dimensional, explaining 84% of the variance in herbaceous community composition, and had a final stress of 13.94 (**Figures 3** and **4**). Axis 2 and Axis 3 were the most informative axes, explaining 37% and 26% of the variation, respectively. Axis 2 and Axis 3 were significantly associated with distance to stream (m), overstory basal area, average diameter of overstory, and sapling Shannon's diversity (**Table 3**). Total seedling density and sapling richness were also significantly associated with Axis 3 (**Table 3**). Total sapling density, seedling richness, seedling Shannon's diversity, overstory richness, overstory Shannon's diversity, percent of *Acer saccharum* seedling, sapling, and overstory layers, and distance from the road are additional variables that were included in the analysis, but did not have a significant effect.

Table 1.
Herbaceous and woody species abundance, richness (S), and Shannon's Diversity Index (H') pre- and post-harvest by treatment at the Ford Forest Cutting Trial, Alberta, MI. Means are ± one standard deviation in parentheses. Seedlings are defined as any woody tree species less than 30.5 cm in height. Saplings are defined as any woody tree species greater than 30.5 cm in height and less than 11.42 cm at dbh. Herbaceous species richness is the average number of species per 1-m^2 quadrat. Herbaceous percent cover, seedling, and sapling stem/hectare are summarized by subplot (n = 10). DLH refers to diameter limit harvest.

	Control		21 $m^2 \cdot ha^{-1}$ (90 $ft^2 \cdot ac^{-1}$)		56 cm DLH (22 in)		16 $m^2 \cdot ha^{-1}$ (70 $ft^2 \cdot ac^{-1}$)		41 cm DLH (16 in)		11 $m^2 \cdot ha^{-1}$ (50 $ft^2 \cdot ac^{-1}$)		30 cm DLH (12 in)		13 cm DLH (5 in)	
2008																
Herbaceous Percent Cover	2.8	(1.9)	6.1	(2.6)	7.1	(2.8)	4.7	(12.2)	6.3	(2.9)	8.6	(2.4)	3.7	(1.4)	15.5	(1.5)
S_{Herb}	1.8	(1.1)	3.9	(0.9)	4.9	(1.0)	5.6	(1.4)	7.9	(1.8)	8.3	(2.4)	6.3	(2.5)	8.5	(1.2)
H'_{Herb}	0.42	(0.40)	1.06	(0.25)	1.28	(0.19)	1.49	(0.3)	1.88	(0.21)	1.77	(0.36)	1.7	(0.42)	1.57	(0.18)
Seedling (stems/ha)	1067	(436)	517	(387)	187	(179)	304	(160)	304	(210)	11	(5)	272	(142)	57	(39)
$S_{Seedling}$	1.4	(0.5)	1.8	(0.4)	1.9	(0.3)	2.2	(0.9)	2.7	(0.7)	2.2	(0.9)	3.1	(0.3)	2.1	(0.7)
$H'_{Seedling}$	0.03	(0.05)	0.2	(0.26)	0.4	(0.26)	0.3	(0.3)	0.57	(0.34)	0.45	(0.3)	0.93	(0.18)	0.55	(0.34)
Sapling (stems/ha)	110	(54)	46	(31)	97	(60)	96	(58)	96	(55)	112	(44)	59	(17)	22	(13)
$S_{Sapling}$	2.4	(1)	2.2	(1.0)	3.2	(0.6)	2.5	(1.1)	3	(0.5)	3.2	(0.6)	3.2	(0.4)	2.7	(0.7)
$H'_{Sapling}$	0.21	(0.21)	0.43	(0.32)	0.68	(0.29)	0.45	(0.27)	0.44	(0.12)	0.63	(0.29)	0.7	(0.32)	0.71	(0.36)
2009																
Herbaceous Percent Cover	14.7	(9.8)	30.3	(25.5)	47.5	(27.9)	17.7	(17.6)	19.9	(15)	41.5	(21.4)	21.9	(15.7)	105.4	(26.7)
S_{Herb}	2	(1.2)	4.8	(1.8)	6.1	(2.3)	5.4	(2.1)	8.1	(2.6)	9.6	(3.2)	7.7	(2.4)	6.7	(1.3)
H'_{Herb}	0.35	(0.36)	0.89	(0.41)	1.05	(0.39)	1.08	(0.41)	1.29	(0.42)	1.37	(0.49)	1.27	(0.42)	1.03	(0.19)
Seedling (stems/ha)	546	(280)	291	(214)	96	(63)	165	(138)	190	(97)	97	(52)	77	(61)	666	(524)
$S_{Seedling}$	1.2	(0.4)	3	(1.1)	3.1	(1.0)	2.9	(1.3)	3.7	(1.0)	3.4	(1.0)	3.2	(1.0)	1.3	(1.0)
$H'_{Seedling}$	0.02	(0.04)	0.5	(0.27)	0.86	(0.29)	0.62	(0.44)	0.89	(0.38)	0.93	(0.33)	0.95	(0.28	0.28	(0.39)
Sapling (stems/ha)	271	(157)	42	(29)	91	(58)	164	(104)	97	(56)	101	(38)	43	(19)	32	(16)
$S_{Sapling}$	3.1	(1.5)	3.3	(1.4)	4.6	(1.1)	4	(0.9)	4.1	(1.1)	4.3	(1.3)	4	(1.3)	3.8	(1.2)
$H'_{Sapling}$	0.15	(0.13)	0.66	(0.26)	0.91	(0.35)	0.55	(0.3)	0.58	(0.24)	0.8	(0.33)	0.93	(0.37)	0.93	(0.2)

Table 2.
Mean percent cover (± one standard deviation in parentheses) of selected herbaceous species pre- and post-harvest at the Ford Forest Cutting Trial, Alberta, MI. All herbaceous species with average percent cover greater than 1% are included. Percent cover is summarized by subplot (n = 10). Full species names are in **Table A1**. DLH refers to diameter limit harvest.

Species Code	Control		21 $m^2 \cdot ha^{-1}$ (90 $ft^2 \cdot ac^{-1}$)		56 cm DLH (22 in)		16 $m^2 \cdot ha^{-1}$ (70 $ft^2 \cdot ac^{-1}$)		41 cm DLH (16 in)		11 $m^2 \cdot ha^{-1}$ (50 $ft^2 \cdot ac^{-1}$)		30 cm DLH (12 in)		13 cm DLH (5 in)	
2008																
carspp					1.1	(0.4)									4	(0.4)
drycar	1.9	(0.5)	1.6	(0.3)	1.6	(0.4)	1.1	(0.3)								
galtet*											2.3	(0.3)				
rubspp			3.2	(0.7)	2.9	(0.5)					1.9	(0.7)			6.9	(0.4)
2009																
adiped									3.4	(3.2)						
carspp							1.5	(1.2)	1.6	(0.7)			3.9	(1.8)	34.9	(4.8)
cautha							1.3	(1.3)			1.5	(0.8)				
drycar	10.3	(3.0)	7.1	(2.0)	8.9	(2.3)	6.2	(2.5)	3.7	(1.4)	1.5	(0.5)	1.4	(0.8)	1.3	(1.3)
elyhys															2.3	(0.5)
galtet*							1.2	(0.6)	2.2	(1.0)	14.6	(4.9)	8.6	(3.4)	4.4	(3.6)
lapcom*											4.3	(1.3)				
loncan	1.3	(1.3)														
oryasp	1.7	(1.3)	1.5	(0.8)	6.3	(2.7)							2.3	(1.3)		
polspp															4.1	(1.7)
ribspp	1.3	(1.2)			2.4	(2.3)	1.9	(1.9)								
rubspp			20.5	(5.5)	25.7	(6.4)	4	(2.5)	5.3	(3.1)	13.7	(4.4)			56.1	(5.1)

*Exotic species.

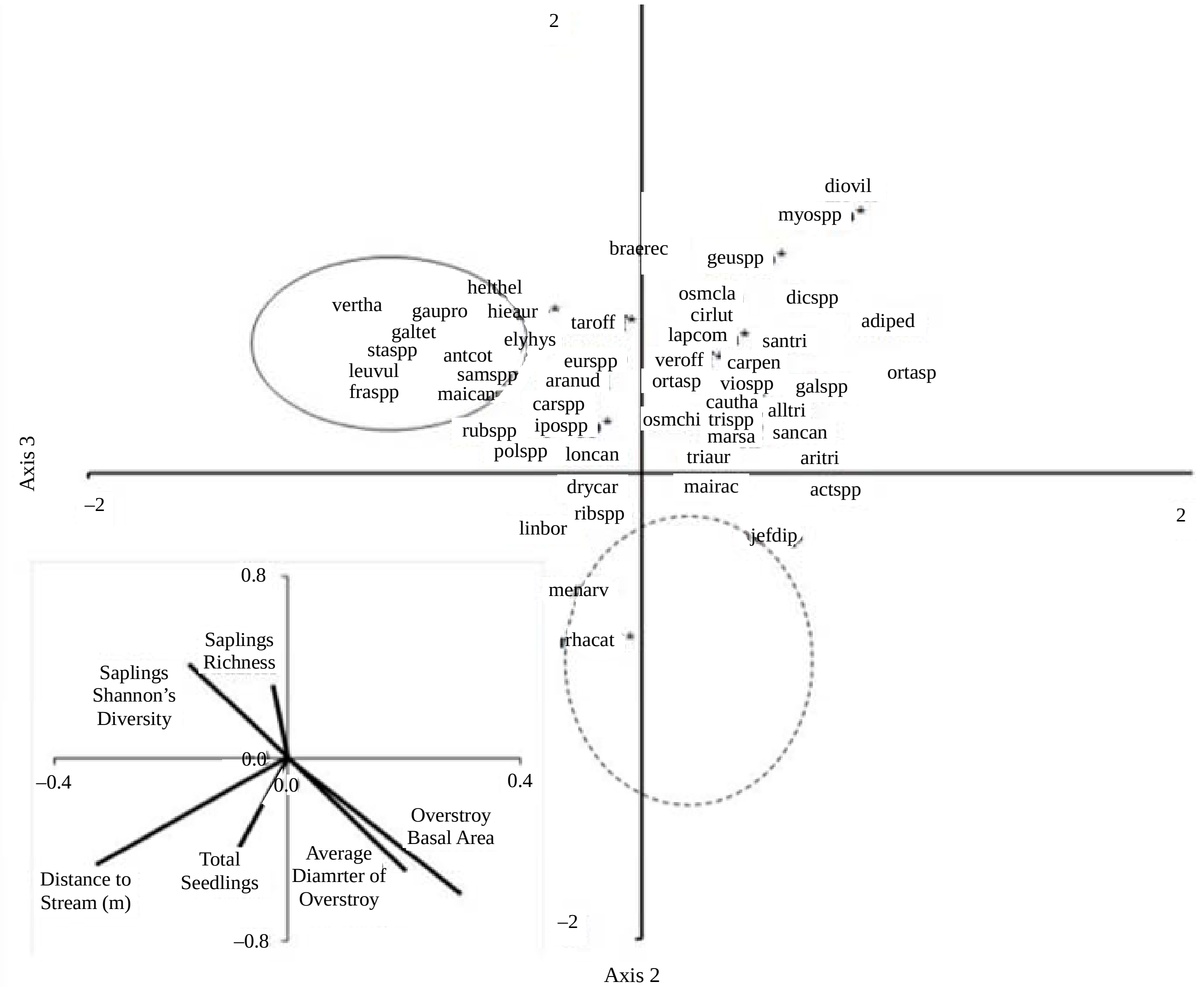


Figure 3.
Non metric multi dimensional scaling ordination of herbaceous species observed in each treatment in 2008 and 2009 at the Ford Forest Cutting Trial, Alberta, MI. Axis 2 explains 37% of the variation while Axis 3 explains 26% of the variation. All species bolded with asterisks are exotic. The solid black ellipsis is associated with the 13-cm DLH. The black dotted ellipsis is associated with the Control. Full species names and additional information can be found in **Table A1**. The insert is the significant environmental variables (p = 0.05) and their relation to ordination space. Additional information about significant environmental variables can be found in **Table 3**.

The uncut control and the 13-cm diameter-limit harvest were used to compare how the actively managed treatments shifted after harvest. These two treatments were used due to the distinct communities that have developed in the last 50 years of management in the 13-cm diameter-limit treatment and presumably due to the lack of active management in the control (**Figures 4(a)** and **(b)**).

The diameter-limit treatments generally shifted compositionally with greater directionality and magnitude towards the 13-cm diameter-limit treatment compared to the residual basal area treatments (**Figures 4(a)-(e)**). Compositional movement in the residual basal area treatments was generally smaller in magnitude and was also more random in direction (**Figures 4(a)**, **(b)**, **(f)** and **(g)**).

Discussion

After 50 years of management, we observed two distinct herbaceous communities in the uncut control and the 13-cm diameter-limit treatments. There was some movement in the herbaceous community between years, which may be due to differences in environmental conditions; no harvesting occurred in either of these treatments between 2008 and 2009. The NOAA National Weather Service station at Alberta, MI recorded lower average temperatures during the months of June and July in 2009 and higher precipitation falling in the form of snow and rain during the months of April, May, and June in 2009 prior to sampling. This increased precipitation and cooler conditions may be one of the main reasons why percent cover of herbaceous species increased in all treatments. In treatments where harvests did occur, increased light levels may have also contributed to increases in percent cover in the herb layer. This movement could also be attributable to the carousel effect; the basic premise of which is that individual species in a plant community are not spatially static through time but rather tend to reoccur in similar locations (van der Maarel and Sykes, 1993). In a closed canopy forest in Stockholm, Sweden understory species composition changed little within the forest be-

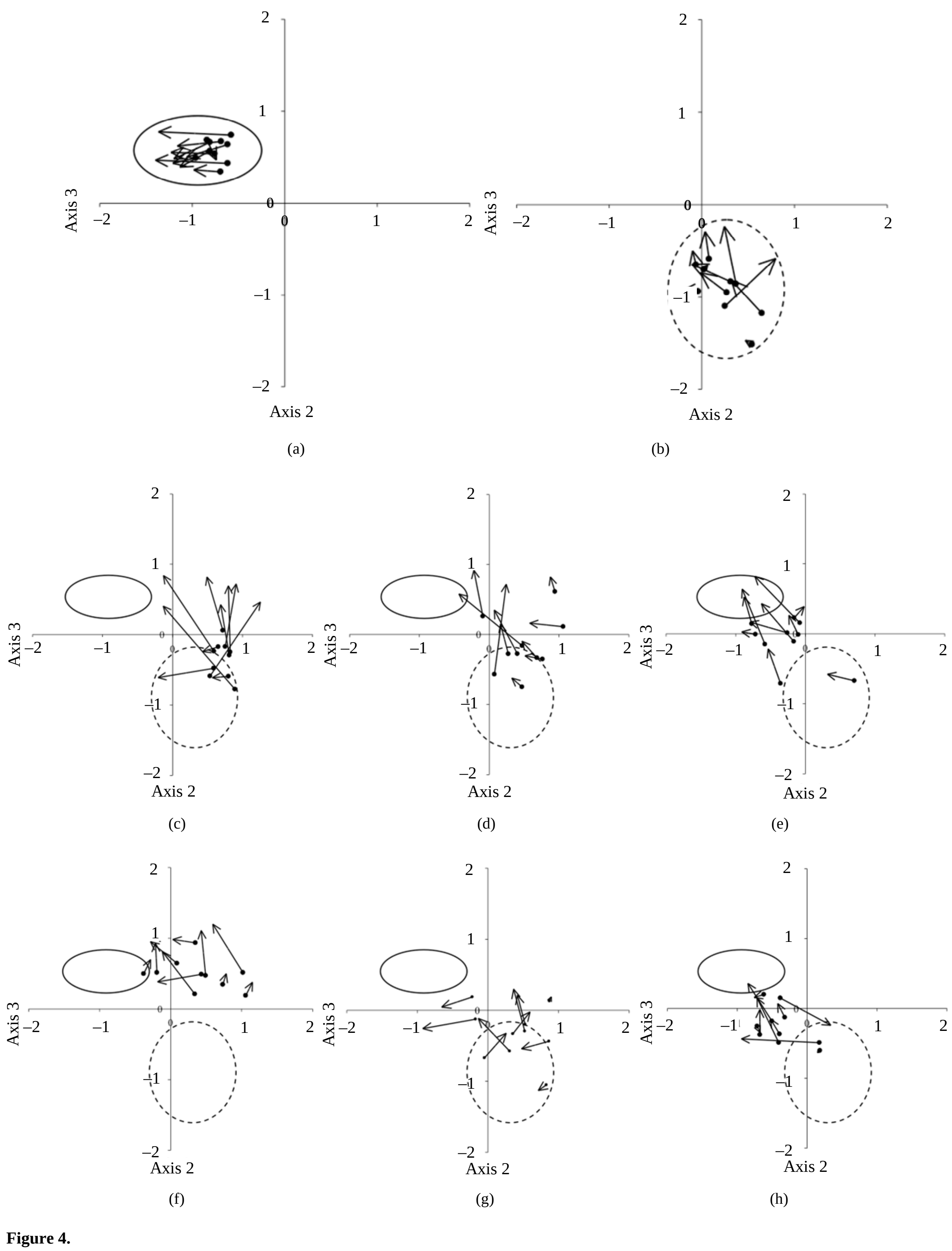


Figure 4.
Non metric multi dimensional scaling ordination of pre- and post-harvest conditions for each treatment at the Ford Forest Cutting Trial, Alberta, MI: (a) 13-cm DLH (diameter-limit harvest); (b) Control; (c) 30-cm DLH; (d) 41-cm DLH; (e) 56-cm DLH; (f) 11 $m^2 \cdot ha^{-1}$ residual; (g) 16 $m^2 \cdot ha^{-1}$ residual; and (h) 21 $m^2 \cdot ha^{-1}$ residual. Axis 2 explains 37% of the variation while Axis 3 explains 26% of the variation. Dots represent 2008 conditions and arrows represent direction and magnitude of change following harvests in 2009. Longer arrows represent greater difference in the plant community pre- and post-harvest. The solid black ellipsis is associated with the 13-cm DLH. The black dotted ellipsis is associated with the Control. Significant environmental variables can be found in **Table 3**.

Table 3.
Important environmental attributes associated with the ordination axes of the NMS used in **Figures 3** and **4** at the Ford Forest Cutting Trial, Alberta, MI. Environmental variables that were significantly ($p = 0.05$) correlated to Axis 2 or Axis 3 were included. The relative location in ordination space is graphed in the inset in **Figure 3**.

	Axis 1				Axis 2				Axis 3			
	r	r^2	*p* value		r	r^2	*p* value		r	r^2	*p* value	
Average Diameter of Overstory	0.517	0.267	<	0.001	0.196	0.038		0.013	0.48	0.23	<	0.001
Distance to Stream (m)	0.345	0.119	<	0.001	0.317	0.1	<	0.001	0.454	0.206	<	0.001
Overstory Basal Area	0.551	0.304	<	0.001	0.286	0.082	<	0.001	0.58	0.337	<	0.001
Saplings Richness	0.06	0.004		0.451	0.026	0.001		0.749	0.308	0.095	<	0.001
Saplings Shannon's Diversity	0.348	0.121	<	0.001	0.162	0.026		0.04	0.392	0.154	<	0.001
Total Seedlings	0.17	0.029		0.032	0.08	0.006		0.313	0.382	0.146	<	0.001

tween 1970 and 1993; however, within permanent plots, species composition was not static (Fröborg & Ove, 1997). The carousel effect has not been studied extensively in forest communities; future monitoring of permanent plots, such as those established in this cutting trial, will allow for a more robust assessment of this effect.

Compositional changes amongst the 13-cm diameter-limit harvest and the control were generally small. The control treatment was generally associated with greater overstory basal area and larger average diameter of overstory trees compared to the 13-cm diameter-limit harvest, which was associated with greater richness and diversity in the sapling layer. The uncut control was dominated mainly by a shade tolerant fern, *Dryopteris spinulosa,* and *Acer saccharum* seedlings and saplings. The composition of the 13-cm diameter-limit treatment was mainly dominated by shade intolerant, exotic species such as *Galeopsis tetrahit*, *Hieracium aurantiacum*, *Taraxacum officinale*, and *Veronica officinalis.*

In the 13-cm diameter-limit treatment, *Rubus* spp. did not change in frequency but did increase in percent cover. This increase in percent cover may have contributed to the absence of the exotic species *Anthemis cotula*, and *Hieracium aurantiacum* during the 2009 sampling period, all of which are considered intolerant. *Rubus* spp. has been shown to delay tree regeneration and herbaceous establishment in some northern hardwood forests (Shields and Webster, 2007). Holmes and Webster (2010) observed in hemlock/hardwood forests a difference in the herbaceous community in deer access and deer exclusion plots; plots without fencing (deer access) were generally dominated by weedy and exotic species. However, interactions between *Rubus* spp., deer herbivory, and tree regeneration are often complex and vary regionally (Horsley and Marquis, 1983). Teasing out the effects of management (past and present) and herbivory on long-term forest dynamics are extremely complex and often do not have simple answers (Hester et al., 1996; Gill, 1996).

Following a winter harvest, the diameter-limit treatments had herbaceous communities that were more similar to the 13-cm diameter-limit harvest than the control. The directionality and magnitude of compositional change was consistent across all diameter-limit treatments. This trend, however, was not observed in the residual basal area treatments. These results did not support our original hypothesis that harvest intensity, in terms of the percent overstory basal area removed, would be the main factor influencing herbaceous composition. However, changes in light availability may be contributing to changes in the herbaceous community (e.g. Shields & Webster, 2007).

This trend in shifting herbaceous communities after management is consistent with a meta-analysis of vascular plants in Europe (Paillet et al., 2009). Paillet and colleagues (2009) identified that species richness was generally higher in managed forests than unmanaged forests. This trend in greater species richness was also observed by Scheller and Mladenoff (2002) in northern hardwood stands located along the border of northern Wisconsin and the Upper Peninsula of Michigan. They observed an increase in species richness in actively managed stands, both even-aged and uneven-aged, compared to old-growth stands. Some of the greatest differences in the light environment, herbaceous abundance, and herbaceous diversity they observed occurred between uneven-aged and old-growth stands. The control in our study is not considered old-growth. However, our control and the even-aged stands in the Scheller and Mladenoff (2002) study share many similarities and had a distinctly different herbaceous community than the uneven-aged stands. The largest environmental difference that Scheller and Mladenoff (2002) observed in even-aged and old growth stands was the amount of coarse woody debris. As vegetation dynamics continue to occur in our control, a more heterogeneous environment may occur in the understory which may allow for the development of a herbaceous layer having more old-growth qualities.

This shift in herbaceous species composition between different harvest intensities, even-aged and uneven-aged management was not observed at the Argonne Experimental Forest in northern Wisconsin (Kern et al., 2006). The Argonne Experimental Forest includes two diameter-limit treatments, 20-cm and 30-cm, that were harvested 39 years before vegetation sampling; three single-tree selection treatments with residual basal areas of 20.6 $m^2 \cdot ha^{-1}$, 17 $m^2 \cdot ha^{-1}$, and 13.8 $m^2 \cdot ha^{-1}$ harvested nine years before vegetation sampling; a shelterwood harvest; and a control. The differences between studies may be largely due to the difference in exotic species. Within the Argonne, only three exotic species were observed and all were considered rare. At the Ford Forest Cutting Trial, on the other hand, twelve exotic species were observed and some were rather common (e.g., *Galeopsis tetrahit*). There are a number of potential reasons that these two studies have produced seemingly divergent responses. First, propagules may not have been as common in the surrounding landscape at the time of harvest or simply failed to invade the site due to barriers to movement or limited availability. This is a likely casual mechanism since the Ford Forest Cutting Trial is proximate to a state highway and numerous haul roads. Roads are widely recognized vectors for the spread of exotic species and Buckley et al. (2003) observed that haul roads were one of the primary ways that introduced species enter forested stands in the Upper Peninsula. Second, the exotic species in question may be transient and disappear after a suitable recovery period, while remaining dormant in the seedbank for extended periods (Thompson and Band, 1997). Short cutting cycles (10 years) at the Ford Forest Cutting Trial may allow these species to persist and spread more readily than the longer cutting cycles at the Argonne Experimental Forest. Third, the pool of potential invaders may be increasing with time. Consequently, recently applied treatments may be more susceptible to invasion than older studies were. Continued treatment of these and other silvicultural trials along with more consistent monitoring of herbaceous-layer dynamics would help to shed additional light on the resiliency of forest plant communities to anthropogenic disturbance and changes in exotic propagule pressure. Though our results demonstrate the initial response of the herbaceous community to these treatments, the real strength of this study will be in following the response of the herbaceous community over time in response to long-term, consistent silvicultural treatment.

Management Implications

As our understanding of forest ecosystem function expands, the term *sustainable management* will continue to include more complex processes especially with an uncertain climate future. It is hypothesized that more diverse forest communities may be more resilient to climate change (reviewed by Hooper et al., 2005). In a review by Folke et al. (2004), they noted that human actions can reduce ecosystem resilience through top-down effects (loss of functional groups of species), bottom-up effects (environmental changes such as climate change and pollutants), and changes to disturbance regimes. Scheller and Mladenoff (2002) hypothesize that traditional uneven-aged management with short cutting cycles may be creating herbaceous communities dominated by early successional and exotic species. Managers will need to experiment with traditional and non-traditional techniques to retain and/or enhance native diversity in all layers of the forest ecosystem. Diameter-limit harvesting is one traditional technique that may have a greater effect on the structure of the overstory (Bohn et al., 2011) and in our study caused a greater shift in the herbaceous layer than traditional single-tree selection management.

Consistent management in northern hardwood forests is rare. The Ford Forest Cutting Trial was intended to be a demonstrational forest where scientists and managers could observe the results of consistent management. Following 50 years of treatment, divergent responses in the herbaceous layer are becoming apparent along a gradient of harvest intensity. Continual monitoring of these treatments will allow future scientists and managers to observe the long-term effects of forest management on vegetation dynamics.

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Appendix

Table A1.
Complete species list, both scientific and common names, and general characteristics of each species found at the Ford Forest Cutting Trial, Alberta, MI. USDA Plant Database was used for scientific nomenclature.

Species Code Name	Scientific Name	Common Name
actspp	*Actaea* L. *spp*	Baneberries
adiped	*Adiantum pedatum* L.	Northern maidenhair Fern
alltri	*Allium tricoccum* Aiton	Wild leek
antcot*	*Anthemis cotula* L.	Mayweed
aranud	*Aralia nudicaulis* L.	Wild sarsaparilla
aritri	*Arisaema triphyllum* (L.) Schott	Jack-in-the-pulpit
braerec	*Brachyelytrum erectum* (*Schreb.* ex *Spreng.*) *P. Beauv.*	Bearded shorthusk
carpen	*Cardamine pensylvanica*Muhl. ex Willd.	Pennsylvania bittercress
carspp	*Carex* L. spp.	Sedge
cautha	*Caulophyllum thalictroides* (L.) Michx.	Blue cohosh
cirlut	*Circaea quadrisulcata* (Maxim.) Franch. & Savigny var. canadensis (L.) H. Hara	Enchanter's nightshade
dicspp	*Dicentra* Bernh. spp.	Bleeding Heart
diovil	*Dioscorea villosa* L.	Wild yam
drycar	*Dryopteris spinulosa* (*O.F. Müll.*) *Watt*	Spinulose shield fern
elyhys	*Elymus hystrix* L.	Rye grass
eurspp	*Eurybia* (Cass.) Cass spp.	Aster
fraspp	*Fragaria* L. spp.	Strawberry
galspp	*Galium* L. spp.	Bedstraw
galtet*	*Galeopsis tetrahit* L.	Bristlestem hempnettle
gaupro	*Gaultheria procumbens* L.	Wintergreen
geuspp*	*Geum* L. spp.	Avens
helhel	*Heliopsis helianthoides* (L.) Sweet	Smooth oxeye daisy
hieaur*	*Hieracium aurantiacum* L.	Orange hawkweed
ipospp*	*Ipomoea* L. spp.	Morning glory
jefdip	*Jeffersonia diphylla* (L.) Pers.	Twinleaf
lapcom*	*Lapsana communis*	nipplewort
leuvul*	*Leucanthemum vulgare* Lam.	Oxeye daisy
linbor	*Linnaea borealis* L.	Twinflower
loncan	*Lonicera canadensis* Bartram ex Marsh.	American fly honeysuckle
maican	*Maianthemum canadense* Desf.	Canada mayflower
mairac	*Maianthemum racemosum* (L.) Link	False Solomon's seal
matstr	*Matteuccia struthiopteris*(L.) Torado	Ostrich fern
menarv	*Mentha arvensis* L.	American wild mint
myospp*	*Myosotis* L. spp.	Forget-me-nots
oryasp	*Oryzopsis asperifolia* Michx.	Rough leaf rice grass
osmchi	*Osmorhiza chilensis* Hook. & Arn.	Mountain sweetroot
osmcla	*Osmorhiza claytoni* (Michx.) C.B. Clarke	Sweet cicely
polspp	*Polygonatum* Mill spp.	True Solomon's seal
rhacat*	*Rhamnus cathartica* L.	Common buckthorn
ribspp	*Ribes* L. spp.	Gooseberry
rubspp	*Rubus* L. spp.	Raspberry
samspp	*Sambucus* L. spp.	Elderberry
sancan	*Sanguinaria canadensis* L.	Bloodroot
santri	*Sanicula trifoliata* E.P. Bicknell	Long-fruited snakeroot
staspp	*Stachys* L. spp.	Lamb's ears
taroff*	*Taraxacum officinale* F.H. Wigg.	Dandelion
triaur	*Triosteum aurantiacum* E.P. Bicknell	Orangefruit horse-gentian
trispp	*Trillium* L. spp.	Trillium
veroff*	*Veronica officinalis* L.	Common speedwell
vertha*	*Verbascum thapsus* L.	Common mullein
viospp	*Viola* L. spp.	Violet

*Exotic species.

Table A2.
Frequency of occurrence of herbaceous species pre- and post-harvest by treatment at the Ford Forest Cutting Trial, Alberta, MI. Herbaceous species are summarized at the subplot level (n = 10). DLH refers to diameter limit harvest.

Species Code Name	Control		21 $m^2 \cdot ha^{-1}$ (90 $ft^2 \cdot ac^{-1}$)		56 cm DLH (22 in)		16 $m^2 \cdot ha^{-1}$ (70 $ft^2 \cdot ac^{-1}$)		41 cm DLH (16 in)		11 $m^2 \cdot ha^{-1}$ (50 $ft^2 \cdot ac^{-1}$)		30 cm DLH (12 in)		13 cm DLH (5 in)	
	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009
actspp	-	-	-	-	-	-	-	-	-	-	10	-	10	-	-	-
adiped	-	-	-	-	-	-	-	-	20	20	-	-	-	-	-	-
alltri	-	-	-	-	-	10	-	-	-	10	20	60	10	20	-	-
antcot*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	-
aranud	-	-	-	-	10	10	-	10	-	-	-	-	-	-	-	-
aritri	-	-	-	-	-	10	20	20	30	10	30	10	30	-	-	-
braerec	-	-	-	-	-	10	-	-	-	-	-	10	-	-	-	-
carpen	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-
carspp	40	-	70	40	80	50	80	60	100	70	90	80	100	100	100	100
cautha	-	-	-	-	-	-	10	10	20	20	50	40	-	-	-	-
cirlut	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-
dicspp	-	-	-	-	-	-	-	-	-	10	-	10	-	10	-	-
diovil	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-
drycar	80	90	100	90	80	80	90	90	80	80	80	70	60	40	10	10
elyhys	-	-	-	20	-	-	-	10	-	40	-	50	-	40	-	90
eurspp	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-
fraspp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20
galspp	-	-	-	-	-	-	-	-	10	-	-	-	-	20	50	20
galtet*	-	-	40	60	60	50	80	60	90	100	100	100	90	80	100	30
gaupro	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-
geuspp*	-	-	-	-	-	-	-	-	-	20	-	20	-	-	-	-
helhel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-
hieaur*	-	-	-	10	-	-	-	-	-	-	10	-	-	-	50	-
ipospp*	-	-	-	-	-	-	20	-	-	-	-	-	20	-	80	-
jefdip	-	-	-	-	-	-	10	-	60	-	-	-	-	-	-	-
lapcom*	-	-	10	20	20	20	10	20	10	70	90	90	40	40	80	-
leuvul*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20
linbor	-	-	20	-	10	-	-	-	-	-	-	-	-	-	-	-
loncan	-	10	-	-	-	10	-	-	-	-	-	-	-	-	-	-
maican	10	-	-	-	-	10	-	-	-	-	-	-	10	10	10	40
mairac	-	10	-	10	-	10	-	-	-	30	-	-	-	10	-	-
matstr	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-
menarv	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
myospp*	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-
oryasp	-	30	-	50	-	70	-	60	-	20	-	50	-	70	-	-
osmchi	-	-	-	-	-	-	-	-	-	10	-	10	-	20	-	-
osmcla	-	-	-	-	-	-	-	-	30	-	-	-	-	-	20	-
polspp	-	-	10	30	30	10	30	10	50	30	20	30	50	40	-	100
rhacat*	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-
ribspp	30	20	10	10	-	20	-	10	10	10	-	20	50	30	10	-
rubspp	-	-	90	90	90	90	60	50	60	70	70	80	10	60	100	100
samspp	-	-	-	10	-	30	-	10	-	-	10	10	-	-	-	10
sancan	-	-	-	20	50	50	50	60	80	70	50	80	60	60	20	30
santri	-	-	-	-	-	-	-	-	10	10	20	-	-	-	-	-
staspp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-
taroff*	-	-	-	10	10	10	-	-	20	-	40	30	20	20	70	60
triaur	-	-	-	-	-	-	-	-	10	10	-	-	-	-	-	-
trispp	10	10	30	10	20	30	60	40	60	20	80	50	20	40	10	20
veroff*	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	10
vertha*	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-
viospp	10	30	-	-	20	20	40	30	40	60	40	40	50	30	70	-

*Exotic species.

Table A3.
Percent of herbaceous species co-occurrence between treatments in 2008 and 2009 at the Ford Forest Cutting Trial, Alberta, MI. DLH refers to diameter limit harvest.

2008	Control	21 $m^2 \cdot ha^{-1}$ (90 $ft^2 \cdot ac^{-1}$)	56 cm DLH (22 in)	16 $m^2 \cdot ha^{-1}$ (70 $ft^2 \cdot ac^{-1}$)	41 cm DLH (16 in)	11 $m^2 \cdot ha^{-1}$ (50 $ft^2 \cdot ac^{-1}$)	30 cm DLH (12 in)	13 cm DLH (5 in)
Control	-	33	27	37	25	25	47	32
21 $m^2 \cdot ha^{-1}$ (90 $ft^2 \cdot ac^{-1}$)	33	-	53	44	38	38	53	32
56 cm DLH (22 in)	27	53	-	53	45	45	53	39
16 $m^2 \cdot ha^{-1}$ (70 $ft^2 \cdot ac^{-1}$)	37	44	53	-	60	52	61	39
41 cm DLH (16 in)	25	38	45	60	-	52	52	46
11 $m^2 \cdot ha^{-1}$ (50 $ft^2 \cdot ac^{-1}$)	25	38	45	52	52	-	59	36
30 cm DLH (12 in)	47	53	53	61	52	59	-	52
13 cm DLH (5 in)	32	32	39	39	46	36	52	-
2009	Control	21 $m^2 \cdot ha^{-1}$ (90 $ft^2 \cdot ac^{-1}$)	56 cm DLH (22 in)	16 $m^2 \cdot ha^{-1}$ (70 $ft^2 \cdot ac^{-1}$)	41 cm DLH (16 in)	11 $m^2 \cdot ha^{-1}$ (50 $ft^2 \cdot ac^{-1}$)	30 cm DLH (12 in)	13 cm DLH (5 in)
Control	-	29	33	28	29	20	29	10
21 $m^2 \cdot ha^{-1}$ (90 $ft^2 \cdot ac^{-1}$)	29	-	57	63	50	58	59	20
56 cm DLH (22 in)	33	57	-	61	45	57	58	44
16 $m^2 \cdot ha^{-1}$ (70 $ft^2 \cdot ac^{-1}$)	28	63	61	-	54	63	50	41
41 cm DLH (16 in)	29	50	45	54	-	62	57	30
11 $m^2 \cdot ha^{-1}$ (50 $ft^2 \cdot ac^{-1}$)	20	58	57	63	62	-	59	40
30 cm DLH (12 in)	29	59	58	50	57	59	-	46
13 cm DLH (5 in)	10	20	44	41	30	40	46	-

