

Ground-layer plant community responses to even-age and uneven-age silvicultural treatments in Wisconsin northern hardwood forests

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Abstract

We evaluated ground-layer plant diversity and community composition in northern hardwood forests among uncut controls and stands managed with even-age or uneven-age silvicultural systems. Even-age treatments included diameter-limit cuttings (20-cm diameter at 30-cm stem height) in 1952 and shelterwood removals in 1964. Uneven-age treatments included three intensities of selection harvest (light, 20.6 m²/ha residual basal area after harvest; medium, 17.2 m²/ha residual basal area; and heavy, 13.8 m²/ha residual basal area) that were applied in 1952, 1962, 1972, and 1982. All treatments were winter logged over snow pack. In 1991, plant diversity and community composition were examined. Species richness for spring ephemerals ranged from 1 to 6 species/150-m², spring ephemeral diversity (Shannon's Index of Diversity) averaged 0.57 ± 0.04 and evenness averaged 0.45 ± 0.03 . Summer flowering species richness ranged from 1 to 18 species/1-m², with an average diversity of 0.71 ± 0.07 and evenness of 0.42 ± 0.03 . We found no significant differences among treatments for any of these variables, although power to detect a difference (at $p = 0.05$) was low in all cases (0.15–0.55) due to high variance and low replication. Community composition was not significantly different among the treatments, for either spring ($p = 0.09$) or summer ($p = 0.79$) flora. Few exotic species were found in any treatment. Lack of exotic invasions and minimal differences in plant diversity or composition among treatments may be due, in part, to the negligible amount of soil disturbance that resulted from winter logging. While other (unmeasured) ecosystem components may differ among these silvicultural treatments, our results suggest that ground-layer plant communities in northern hardwood ecosystems are either resistant to change or have recovered within the 40 years since disturbance in the even-age treatments and within 10 years since disturbance in the uneven-age treatments.

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1. Introduction

Today, the success of silvicultural prescriptions is judged on more than the traditional measures of regeneration responses and growth and yield of commercial tree species. An increasing number of landowners and organizations are managing to sustain a wide variety of ecosystem goods and services. In particular, the sustainability of plant species diversity in the understory is considered an important metric by which to judge the efficacy of silvicultural treatments, because ground flora play a fundamental role in the structure and function of ecosystems (Roberts and Gilliam, 1995) and are sensitive to

environmental changes (Pregitzer and Barnes, 1982; Rubio et al., 1999). Designing silvicultural systems that restore or sustain native and late-successional species diversity, while also meeting goals for timber production, is a growing area of research. Silvicultural systems to meet these objectives are being developed and evaluated for a wide variety of forest ecosystems (e.g. Muir et al., 2002; Seymour et al., 2002; Palik and Zasada, 2003; Aubry et al., 2004).

Silvicultural experiments and surveys of stands that have contrasting management histories can be used to better understand the diversity responses to silvicultural treatments on ground-layer plant diversity and community composition. Some studies have found that ground-layer plant communities in stands managed with uneven-age systems differed little from control forests when assessed 10–15 years after the last treatment (Metzger and Schultz, 1984; Jenkins and Parker,

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1999). In contrast, recent work on ground-layer plant communities in northern hardwoods in Wisconsin and Michigan suggests that uneven-age management using a selection system in second-growth stands, shifted the community from species representative of old-growth conditions to weedy and early successional species (Scheller and Mladenoff, 2002).

Comparisons of plant community responses between unmanaged stands and those managed using even-age silvicultural approaches show increases in species diversity in the first few years after harvest (Outcalt and White, 1981; Gilliam et al., 1995; Halpern and Spies, 1995), followed by recovery to conditions similar to uncut forest by 50–60 years (Hix and Barnes, 1984; Albert and Barnes, 1987; Ruben et al., 1999). A similar pattern of recovery time has been shown in understory species composition of northern hardwoods in Michigan. Species composition showed the greatest difference 4–5 years after even-age and uneven-age harvests, but the composition was similar to controls in all treatments after 50 years (Metzger and Schultz, 1984). There are notable exceptions to this recovery pattern. For instance, Appalachian hardwood plant communities that were clearcut 50 years ago had half the species richness of primary old-growth forest in the same area (Duffy and Meier, 1992). In Michigan, understory species composition of northern hardwoods was significantly different among management regimes that included even-age (clearcut 65–82 years ago), uneven-age (selection entry 12–14 years ago), and control (old-growth) (Scheller and Mladenoff, 2002). However, working in central hardwoods in Indiana, Jenkins and Parker (1999) found that, after 7–26 years, stands managed with even-age and uneven-age approaches did not differ in understory species composition.

Ground-layer plants compositional and spatial patterns are highly sensitive to environmental conditions. One study found that herbaceous understory composition was more affected by site resource availability than by clearcutting (Gilliam et al., 1995). In southern Ontario, soil disturbance patterns from harvesting were related to percent herbaceous species lost, while harvesting intensity was not related (Reader, 1987). A different study found that post-harvest spatial pattern of understory vegetation species was highly related to its location prior to harvest (Hughes and Fahey, 1991).

Many studies compare only even-age stands with uncut control stands, omitting uneven-age treatments. Even among studies of even-age systems, often only clearcut systems are evaluated relative to controls (Gilliam et al., 1995; Hix and Barnes, 1984; Albert and Barnes, 1987; Hughes and Fahey, 1991; Duffy and Meier, 1992; Ruben et al., 1999). Studies examining uneven-age stands often report results after only one selection harvest (e.g. Reader, 1987; Jenkins and Parker, 1999), with little understanding of the long-term implications of multiple (two or more) entries. Additionally, there may be no quantitative data describing the nature of the selection system, to allow an interpretation of likely effects on resources and establishment and growth conditions (e.g. Jenkins and Parker, 1999; Scheller and Mladenoff, 2002). Finally, few studies were designed experiments that included

randomization of treatments (e.g. Metzger and Schultz, 1981, 1984; Reader, 1987).

Our study provides a unique opportunity to examine the effects of uneven-age and even-age silvicultural treatments on ground-layer plant communities after 40 years of management, in a replicated design. We compared ground-layer plant community data from a long-term study of contrasting northern hardwood silvicultural approaches (even-age and uneven-age management and controls in northern Wisconsin, USA). The experimental design included treatment randomization and replication in blocks, with stands and blocks occurring within one ecosystem or habitat type. At the time of plant community sampling, uneven-age selection treatments had been applied four times over a 40-year period, and even-age approaches had been applied once at the beginning of this period. Our objective was to evaluate how ground-layer plant species richness, diversity, and composition differed among contrasting silvicultural approaches and controls after 40 years of management.

2. Methods

2.1. Study site

In 1952, North Central Research Station (formerly known as the Lake States Forest Experiment Station) of the USDA Forest Service installed a “cutting methods” experiment on the Argonne Experimental Forest in northern Wisconsin, USA, in a second-growth, northern hardwood forest that regenerated after clearcutting around 1902. The original intent of the study was to contrast a range of silvicultural treatments (both even-age and uneven-age) for their efficacy at meeting timber production and regeneration objectives. The forest is dominated by sugar maple (*Acer saccharum* Marsh., averaging 63% of overstory basal area), with lesser amounts (4–9% basal area each) of white ash (*Fraxinus americana* L.), yellow birch (*Betula alleghaniensis* Britt), basswood (*Tilia americana* L.), hemlock (*Tsuga canadensis* (L.) Carr), and red maple (*Acer rubrum* L.) (Niese and Strong, 1992). The site supports quality northern hardwood development, with site indices (50 year base) of 19.8 m for sugar maple and yellow birch and 21.3 m for basswood. Soils are predominantly sandy loams of the Argonne-Sarwet series, while the habitat type is largely *Acer/Osmorhiza-Caulophyllum* (Kotar et al., 2002).

2.2. Experimental design

The experiment consisted of a randomized block design with six treatments randomly assigned to 1-ha stands within each of the three blocks. Even-age treatments included diameter-limit cutting and shelterwood. The diameter-limit treatment removed all trees greater than 20-cm diameter at 30-cm stem height in 1952 (39 years before ground-layer plant sampling (see Section 2.3)). Mean (\pm standard error) residual basal area was 5.3 ± 1.7 m²/ha. The shelterwood treatment was cut to 60% crown cover or about 9.2 m²/ha in 1957. The shelterwood overstory was removed in 1964 (27 years before sampling).

Uneven-age treatments included three levels of individual tree selection: (i) light (20.6 m²/ha residual basal area after harvest), (ii) medium (17.2 m²/ha residual basal area), and (iii) heavy (13.8 m²/ha residual basal area). These treatments removed trees larger than 11.7-cm in diameter and were applied four times, 39, 29, 19 and 9 years before 1991, when ground-layer vegetation was sampled. Volume removed from the uneven-age treatments are given in Table 1. Marking in the selection treatments followed the BDq method (Smith et al., 1997).

2.3. Vegetation sampling

In 1991, the cover of ground-layer vegetation (herbaceous, woody, and shrub species below 0.5 m tall) was sampled twice in each treatment and control stand. Sampling occurred midspring to capture spring ephemerals and again midsummer to capture later developing species. The data were collected at five points installed systematically without bias. Minimum distance between points was 35 m. At each point, cover of spring species was recorded in a 10 × 15-m plot (150-m²) and summer flowering species cover was recorded in eight 1-m² plots separate from the 10 × 15-m plot. The 1-m² plot sub samples were arrayed in a 2 × 4 grid centered on the point and oriented in a random direction. Cover classes included rare (1 or 2 individuals), 0.1–1%, 1–5%, 6–15%, 16–25%, 26–50%, 51–75%, and 75–100%. Midpoints of cover classes were used in all calculations.

2.4. Analysis

Plant taxa (USDA, 2005) were divided into three data sets: (1) spring ephemerals, (2) summer flowering species, and (3) summer functional groups (summer flowering species classified by growth habit (Grabner and Zenner, 2002)): (a) exotics, (b) native annual/biennial, (c) native, perennial forbs and ferns, (d) native sedges, grasses, and rushes, (e) native shrubs, (f) native trees, (g) native woody vines and (h) unknowns. The spring ephemeral dataset was not divided into groups because only one group was found (native, perennial forbs and ferns).

Species richness for spring ephemerals was determined by averaging the five 10 × 15-m plots per stand. For the summer flowering species and summer functional group datasets, cover estimates were averaged among the eight 1 m × 1 m plots at each of the five points. The five points in a stand were then averaged to generate a stand-level mean richness value.

Table 1
Average volume (m³/ha) harvested by decade in the uneven-age management treatments

Year	Uneven-age treatments (residual)		
	Light	Medium	Heavy
1951	36.5	46.0	55.1
1961	52.9	61.5	60.0
1971	49.6	51.8	56.8
1981	58.1	46.2	58.1

Diversity was calculated at each of the five points in a stand using the Shannon Index of Diversity (Magurran, 1988),

$$H = - \sum p_i \ln p_i, \quad (1)$$

where H is the diversity and p_i is the cover of species i . The diversity indices for the five points were averaged to generate a stand mean.

Evenness was calculated at each point using Eq. (2) (Magurran, 1988):

$$E_H = H/H_{\max} = H/\ln S, \quad (2)$$

where E_H is the evenness, H the diversity (Shannon Index of Diversity), H_{\max} is the maximum potential diversity, and $\ln S$ is natural log of species richness. Mean stand-level evenness was calculated the same way as diversity, by averaging the five point estimates in each stand.

We used randomized block analysis of variance to test for treatment differences in species richness, diversity, and evenness. If data did not meet the assumptions of homogeneous variance and normality, they were transformed using a power transformation. Each ANOVA was run with PROC MIXED and was tested for retrospective power at an alpha level of 0.05 in SAS (SAS Institute, Inc., Cary, NC, 2003).

Nonmetric multidimensional scaling (NMS) was used to compare composition of ground-layer plant communities among treatments. NMS is effective with ecological data because it does not assume linearity of species responses to gradients (McCune and Grace, 2002). NMS uses rank order information in a dissimilarity matrix that eliminates the “zero truncation” problem in most ordination methods and can use any distance measure. We ran NMS on (1) 18 experimental units (six treatments replicated three times) by cover of nine spring ephemeral species; (2) 18 experimental units by cover of 82 summer flowering species; and (3) 18 experimental units by cover of eight plant functional groups using PC-Ord version 4.36 (MjM Software Design, Gleneden Beach, OR, 1999).

For each ordination, species that occurred in only one experimental unit were deleted. For the summer flowering species analysis, the data matrix was relativized by one to reduce the influence of highly abundant species and improve normality. For the spring ephemerals and summer functional group analyses, the normality of the data was improved by a square-root transformation. A Sørensen distance measure was used for all three data sets. A random seed started each analysis and included 40 runs of real data and 50 runs of randomized data for use in a Monte Carlo permutation procedure (McCune and Grace, 2002). The Monte Carlo permutation procedure is a randomization test that determines if NMS is generating stronger axes than expected by chance. Results of the Monte Carlo test and examination of stress in a scree plot were used to determine dimensionality. Overlays and correlations with axes were run in PC-Ord to interpret the data.

We further tested for treatment differences in community composition (separately within spring ephemerals, summer flowering species, and summer functional groups) using a blocked multi-response permutation procedure (MRPP), a

non-parametric hypothesis test for multivariate differences between groups. MRPP constructs a distance matrix, calculates average within-group distances, and compares these to a Pearson type III continuous distribution of all possible partitions of the data (Peck, 2003). Groups were analyzed by treatment and blocked by replication using PC-Ord. The Euclidean distance measure was used for all analyses. With MRPP, the chance-

corrected within-group agreement (A) statistic describes effect size. A ranges from -1 to $+1$. When $A = -1$, there is less agreement between groups than expected by chance. When $A = 0$, groups are no more or less different than expected by chance, and when $A = 1$, groups are identical. The more positive A is, the more homogeneous groups are and the greater confidence in the p -value, especially when the sample size is small (Peck, 2003).

Table 2
Species identified^a during spring or summer sampling periods

Scientific name	Spring	Summer	Functional Group ^b	Scientific name	Spring	Summer	Functional Group ^b
<i>Acer pensylvanicum</i> L.		X	6	<i>Lonicera canadensis</i> Bartr. ex Marsh.		X	5
<i>Acer</i> spp.		X	6	<i>Lotus corniculatus</i> L.		X	1
<i>Achillea millefolium</i> L.		X	3	<i>Lycopodium annotinum</i> L.		X	5
<i>Actaea</i> spp.		X	3	<i>Lycopodium lucidulum</i> Michx.		X	5
<i>Adiantum pedatum</i> L.		X	3	<i>Lycopodium obscurum</i> L.		X	5
<i>Agrostis hyemalis</i> (Walt.) B.S.P.		X	4	<i>Lycopus</i> spp.		X	3
<i>Amelanchier</i> spp.		X	5	<i>Maianthemum canadense</i> Desf.		X	3
<i>Anemone quinquefolia</i> L.	X	X	3	<i>Mentha</i> spp.		X	3
<i>Aralia nudicaulis</i> L.		X	3	<i>Mitchella repens</i> L.		X	5
<i>Aralia racemosa</i> L.		X	3	<i>Onoclea sensibilis</i> L.		X	3
<i>Arisaema triphyllum</i> (L.) Schott		X	3	<i>Oryzopsis asperifolia</i> Michx.		X	4
<i>Aster macrophyllum</i> L.		X	3	<i>Osmorhiza claytonii</i> (Michx.) Clarke		X	3
<i>Athyrium filix-femina</i> (L.) Roth		X	3	<i>Osmunda cinnamomea</i> L.		X	3
<i>Blephilia ciliata</i> (L.) Benth.		X	3	<i>Osmunda claytoniana</i> L.		X	3
<i>Botrychium virginianum</i> (L.) Sw		X	3	<i>Oxalis montana</i> Raf.		X	3
<i>Brachyelytrum erectum</i> (Schred. Ex Spreng.) Beauv.		X	4	<i>Panax quinquefolium</i> L.		X	3
<i>Bromus</i> spp.		X	4	<i>Parthenocissus quinquefolia</i> (L.) Planch.		X	7
<i>Cardamine concatenata</i> (Michx.) Sw.	X	X	3	<i>Phegopteris connectilis</i> (Michx.) Watt		X	3
<i>Carex intumescens</i> Rudge		X	4	<i>Poa</i> spp.		X	4
<i>Carex leptoneuria</i> (Fern.) Fern.		X	4	<i>Polygonatum biflorum</i> (Walt.) Ell.		X	3
<i>Carex ormostachya</i> Wieg.		X	4	<i>Polygonatum pubescens</i> (Willd.) Pursh		X	3
<i>Carex pensylvanica</i> Lam.		X	4	<i>Polygonum scandens</i> L.		X	3
<i>Caulophyllum thalictroides</i> (L.) Michx.		X	3	<i>Prenanthes alba</i> L.		X	3
<i>Cinna latifolia</i> (Trev. ex Goepf.) Griseb		X	4	<i>Pyrola rotundifolia</i> L.		X	5
<i>Circaea alpina</i> L.		X	3	<i>Ranunculus recurvatus</i> Poir.		X	3
<i>Circaea lutetiana</i> L.		X	3	<i>Ribes</i> spp.		X	5
<i>Cirsium</i> spp.		X	1	<i>Rubus allegheniensis</i> Porter		X	5
<i>Claytonia virginica</i> L.	X			<i>Rubus</i> spp.		X	5
<i>Clintonia borealis</i> (Ait.) Raf.		X	3	<i>Rubus idaeus</i> L.		X	5
<i>Corallorrhiza maculata</i> (Raf.) Raf.		X	3	<i>Sambucus pubens</i> L.		X	5
<i>Cornus alternifolia</i> L. f.		X	5	<i>Sanguinaria canadensis</i> L.	X	X	3
<i>Corylus</i> spp.		X	5	<i>Schizachne purpurascens</i> (Torr.) Swallen		X	4
<i>Cryptotaenia canadensis</i> (L.) DC.		X	3	<i>Smilacina racemosa</i> (L.) Desf.		X	3
<i>Danthonia spicata</i> (L.) Beauv. ex Roemer & J.A. Schultes		X	4	<i>Solidago flexicaulis</i> L.		X	3
<i>Dicentra cucullaria</i> (L.) Bernh.	X			<i>Solidago</i> spp.		X	3
<i>Diervilla lonicera</i> P. Mill.		X	5	<i>Streptopus roseus</i> Michx.		X	3
<i>Dirca palustris</i> L.		X	5	<i>Taraxacum</i> spp.		X	3
<i>Dryopteris carthusiana</i> (Vill.) H.P. Fuchs		X	3	<i>Thelypteris phegopteris</i> (Michx.) Watt		X	3
<i>Elymus hystrix</i> L.		X	4	<i>Tiarella cordifolia</i> L.		X	3
<i>Fragaria virginiana</i> Duchesne		X	3	<i>Trientalis borealis</i> Raf.		X	3
<i>Galium boreale</i> L.		X	4	<i>Trillium</i> spp.	X	X	3
<i>Galium triflorum</i> Michx.		X	3	<i>Uvularia grandiflora</i> Sm.	X	X	3
<i>Gymnocarpium dryopteris</i> (L.) Newman		X	3	<i>Uvularia perfoliata</i> L.		X	3
<i>Hepatica americana</i> Schreb.		X	3	<i>Uvularia sessilifolia</i> L.		X	3
<i>Hieracium</i> spp.		X	3	<i>Viola pubescens</i> Ait.		X	3
<i>Hydrophyllum virginianum</i> L.	X			<i>Viola</i> spp.	X	X	3
<i>Laportea canadensis</i> (L.) Weddell		X	3	<i>Waldsteinia fragarioides</i> (Michx.) Tratt.		X	3

^a Taxa and growth habits were referenced in the USDA Plants Database (USDA, 2005).

^b Summer flowering species were assigned to a functional group by growth habit: 1: exotics; 2: native annual/biennial; 3: native, perennial forbs and ferns; 4: native sedges, grasses, and rushes; 5: native shrubs; 6: native trees, and 7: native, woody vines.

3. Results

3.1. Richness, diversity, and evenness

A total of 94 species were identified. Ground-layer composition consisted of species typically associated with northern hardwood ecosystems (Table 2). Common species included *Athyrium filix-femina* (L.) Roth, *Carex pensylvanica* Lam., *Maianthemum canadense* Desf., *Osmorhiza claytonii* L., and *Viola* spp. Invasive species were few (*Taraxacum* spp., *Cirsium* spp., and *Lotus corniculatus* L.) and rare (<1% of total cover in any one stand).

The spring ephemeral diversity measures were not clearly related to treatment (Fig. 1). Across all treatments, mean spring ephemeral richness was 3.6 ± 0.5 species/150-m², diversity was 0.6 ± 0.1 (on a range of 0–4.5), and evenness was 0.4 ± 0.08 (on a range of 0–1). Treatment differences were not significant (<0.05), however, power to detect a difference (at $p = 0.05$) was low (Table 3).

Summer ground-layer plant diversity measures were not strongly related to treatment. Species richness averaged 4.4 ± 0.5 species/m² overall. There was no significant difference in richness among treatments (Fig. 1, Table 3). Diversity and evenness values also were similar among treatments, averaging 0.7 ± 0.07 and 0.4 ± 0.03 , respectively (Fig. 1), and treatment means were not significantly different for either measure (Table 3). Again, power to detect a difference (at $p = 0.05$) was low for these variables (Table 3).

Diversity measures based on summer functional groups were not clearly related to treatment (Fig. 1). Overall, functional group richness was 1.8 ± 0.1 groups/m², diversity was 0.2 ± 0.04 and evenness was 0.3 ± 0.05 . There was no significant difference among treatments, but power to detect a difference (at $p = 0.05$) was low (Table 3).

3.2. Composition

NMS found a three-dimensional solution for the spring ephemeral data (108 iterations; final stress of 5.4; Monte Carlo test, $p = 0.02$). For ease of interpretation, only two axes of the

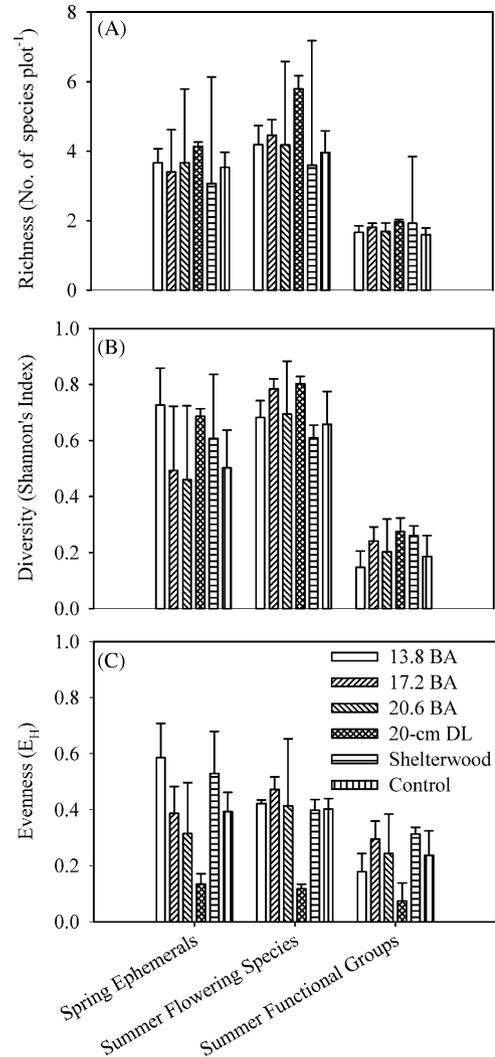


Fig. 1. Diversity measures for spring ephemerals, summer flowering species, and summer functional groups. A. Richness. B. Shannon Index of Diversity. C. Evenness. Values are means + 1 S.E. (N = 3).

NMS ordination are displayed in Fig. 2A. These two axes accounted for 11% of total variation. The third axis accounted for no additional variation. Spring plant communities did not

Table 3
Level of significance and power analysis results for species richness, diversity, and evenness in the spring ephemeral, summer flowering species and summer functional group datasets

Diversity Measure	Dataset	Level of		
		F-value ^a	Significance ^b	Power ^c
Richness	Spring ephemerals	0.62	0.6861	0.153
	Summer flowering species	2.57	0.0955	0.548
	Summer functional groups	0.97	0.4800	0.222
Shannon Index of Diversity	Spring ephemerals	1.00	0.4640	0.228
	Summer flowering species	0.72	0.6227	0.172
	Summer functional groups	0.88	0.5278	0.203
Evenness	Spring ephemerals	1.17	0.3883	0.263
	Summer flowering species	0.35	0.3216	0.274
	Summer functional groups	1.36	0.3168	0.303

^a Numerator degrees of freedom = 5; denominator degrees of freedom = 10.

^b Alpha level = 0.05.

^c Power = 1 - β.

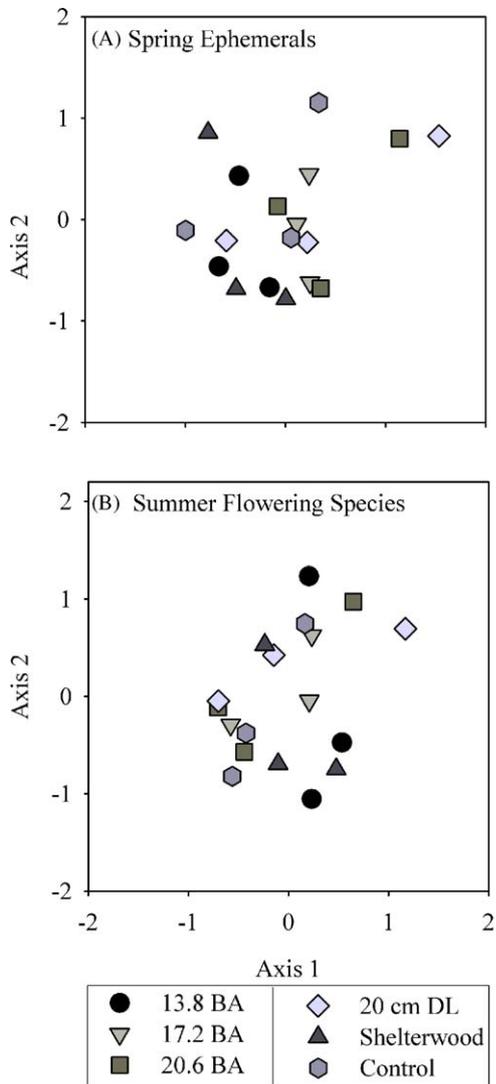


Fig. 2. NMS ordination of ground-layer plant communities for uneven-age (13.8 BA, 17.2 BA, and 20.6 BA), even-age (20-cm DL and Shelterwood), and control treatment stands. A. Spring ephemerals. B. Summer flowering species.

differ appreciably among treatments (Fig. 2A). This was confirmed by a blocked MRPP analysis, which was not significant ($p = 0.09$, $A = 0.09$).

A three-dimensional solution also was found for summer flowering species (130 iterations; final stress of 12.6; Monte Carlo test, $p = 0.02$). The three axes of the NMS ordination for summer flowering species accounted for 68% of total variation among stands. However, after examination of overlays, little of this variation appeared to be related to overstory treatment. Two axes are presented in Fig. 2B, which account for 63% of the variation. Again, the blocked MRPP analysis indicated no significant difference among treatments ($p = 0.79$, $A = -0.01$).

The NMS for summer functional group composition failed to extract a more useful ordination than expected by chance. The Monte Carlo test was not significant for solutions between one- ($p = 0.0784$) and six-dimensions ($p = 0.8235$), suggesting weak data structure and little effect of treatment on community composition. The lack of treatment effect was confirmed by the non-significant MRPP results ($p = 0.27$, $A = 0.02$).

4. Discussion

We found little difference in spring or summer ground-layer plant community richness, diversity, evenness, and composition among stands treated with even-age or uneven-age silvicultural systems or between managed stands and older untreated forest. In our study, time since last harvest for the two even-age treatments has been considerable: 39 years between harvest and ground-layer sampling for the diameter-limit cutting and 27 years since overstory removal in the shelterwood treatment. Given these time spans, ground-layer plant communities may have recovered to levels of richness, diversity, and evenness, as well as composition that are largely indistinguishable from the 90-year-old control forest. Alternatively, the ground-layer plant communities of the study ecosystem may be resistant to change in the face of such disturbances. We cannot distinguish between the two alternatives but hypothesize that the latter is not likely to be the case in the even-age treatments.

Other studies have documented initial change in vegetation in northern hardwoods after disturbance, but the effects of disturbance were temporary. In the Upper Michigan, herbaceous species that require high light environments were present four years after clearcutting but were no longer present 50 years after treatment (Metzger and Schultz, 1984; Albert and Barnes, 1987). We sampled at only one point in time after harvest and found no difference between our even-age and control treatments. However, we cannot discount the possibility of earlier differences among treatments, which would be consistent with studies in other regions (Gilliam et al., 1995; Halpern and Spies, 1995).

In our study, nine years separated the most recent harvest and ground-layer sampling in the selection treatments, much less time than in the even-age treatments. Moreover, the uneven-age treatments were applied four times through the course of the study, compared to once for the even-age treatments. Consequently, frequency of disturbance was higher, but intensity lower, relative to the even-aged treatments. Nonetheless, ground-layer diversity and composition in the selection treatments did not differ from the control or even-age treatments. Moreover, intensity of harvest (i.e. light, medium, or heavy selection) did not result in differences in ground-layer diversity or composition.

Nine years since selection harvest may be sufficient time for ground-layer plant communities to recover to levels and patterns similar to the control, when disturbance to the forest is minimal. Alternatively, ground-layer plant communities may be resistant to change from selection harvesting in northern hardwoods. We cannot distinguish between these alternatives, since we did not follow vegetation development in the years immediately post-harvest; however, the latter explanation is plausible for these treatments, because most of the understory species found in this study are poor seed producers and expand their range slowly and vegetatively (Whitford, 1951; Struik and Curtis, 1962). It is unlikely that species were completely eliminated and then reestablished in the nine years since harvest. Rather, most species likely persisted through the disturbance.

The lack of invasive species, along with rapid recovery or resistance of ground-layer plant communities, suggests limited physical disturbance to the forest floor and surface soil during logging. In a similar study, species composition was influenced more by surface disturbance than by harvest intensity or area cut (Ruben et al., 1999). Moreover, Buckley et al. (2003), found that the physical disturbance from haul roads and skid trails, rather than the silvicultural system, provided conduits for invasive and weedy species, in northern hardwoods in western Upper Michigan. In our study, minimal soil disturbance was observed in the field by Forest Service scientists over the years (Gus Erdmann, personal communication). All logging operations were completed in winter with snow depths of 40–100 cm. In the 1952 harvest, logs were skidded by horses in all treatments. In subsequent harvests, logs were removed with mechanical logging equipment (tractor, tracked Iron Mule, and rubber-tired forwarder). Minimal surface disturbance suggests that perennial plants existing before harvest had little direct physical damage from logging.

We caution that the lack of significant differences among measured variables may be influenced by low statistical power. Power is directly related to replication, alpha level, and effect size, and is indirectly related to variation (Zar, 1996). We had no control over the level of replication ($r = 3$), since the study was established with prior scientists and for other objectives. Effect size and variation were low and high, respectively, resulting in generally low power. Although the use of retrospective power analysis is debatable (Gerard et al., 1998; Johnson, 1999), reporting power when a study has failed to reject the null hypothesis can be useful in reminding the reader that some differences may exist, but were not detected due to design and analysis issues (Peterman, 1990a,b).

Our results contrast with recent work examining understory species diversity and composition in similar northern hardwood forests in Wisconsin and Upper Michigan. Scheller and Mladenoff (2002) found that the richness and diversity (Shannon Index of Diversity) of understory plants (individuals <2 m tall) increased from old-growth forest to managed even-aged forests (clearcut 65–82 years before sampling) to uneven-aged forests managed with selection harvest (most recent harvest 12–14 years before sampling). Moreover, community composition was measurably different with selection management, relative to old-growth conditions and even-age management. In particular, the selection-harvested stands contained more early successional and weedy species, such as *Galeopsis tetrahit* L., *Rubus* spp., and *Schizachne purpurascens* (Torr.) Swallen, compared to old-growth and even-aged stands, which had similar composition. Our stands did not contain these early successional species at the time of sampling.

There are several possible reasons for the differences in results between our study and Scheller and Mladenoff's (2002) study. First, we had only three replications and our stands were relatively small (1 ha). Study design could have influenced our results; however, the study area was embedded in a matrix of intact, mature forest (50 years old in 1952) of the 2630-ha Argonne Experimental Forest. The chance of a weedy invasion from the surrounding forest was minimal because the Experi-

mental Forest has been mostly undisturbed since original harvest 90 years earlier. The treated stands from the Scheller and Mladenoff (2002) study were embedded in a relatively more intensively managed landscape.

Second, the habitat types differed between the two studies. Our study stands were on the *Acer/Osmorhiza-Caulophyllum* habitat type, while the stands in the Scheller and Mladenoff (2002) study were on the *Acer-Tsuga/Dryopteris* and *Acer-Tsuga/Maianthemum* habitat types (Kotar et al., 2002). Both our stands and those in the Scheller and Mladenoff (2002) study were mesic sites, but our stands were on richer soils. Soil nutrient regime differences may have had some influence on propagule availability and species establishment.

Finally, it is possible that season of harvest may have differed between our study and the Scheller and Mladenoff (2002) study, affecting level of soil and forest floor disturbance. Harvesting in all our study stands took place during winter over snow pack and often frozen surface soil conditions. This would have protected many ground-layer plants from direct impacts and would have minimized forest floor and soil disturbance. The season of logging in the Scheller and Mladenoff (2002) study was not recorded. Moreover, the level of disturbance in the form of roads and trails may have been greater in the Scheller and Mladenoff (2002) study, providing the avenues for invasion by exotic and weedy species, as demonstrated by Buckley et al. (2003) in the same area.

Based on their results, Scheller and Mladenoff (2002) suggest that uneven-age management in northern hardwoods may be problematic over the long term if periodic disturbance leads to a change of composition characterized by weedy and early successional species. Our results for three different single-tree selection systems, with a 10-year cutting cycle, suggest that this is not always the case; ground-layer plant communities in the selection treatments were largely indistinguishable from those occurring with even-age management, from the 90-year-old control forest, and from each other. Early successional and weedy species were found in trace amounts in our treatments.

In our study, herbivory by white-tail deer (*Odocoileus virginianus* Zimm.) may have had an influential effect on ground-layer plant communities. The Argonne Experimental Forest is comprised of one-third northern hardwood uplands (used in this study), one-third lowland conifers, and one-third xeric pine ecosystems. Although the hardwoods are not heavily used by deer, the adjacent lowland conifer swamps are used extensively as winter deeryards. According to the Wisconsin Department of Natural Resources, populations in the greater forest area annually ranged from 2 to 15 deer/km² over the course of the study period (Ron Eckstein, Wisconsin Department of Natural Resources, personal communication). Heavy deer browsing has been shown to alter ground-layer plant community structure and composition by changing the trajectory of vegetation development to species that are resilient or avoided by deer (Hobbs, 1996; Horsley et al., 2003). Deer are a natural part of the ecosystem in the study area, but the effects of high population densities on our results are unknown. Further investigation of the feeding habits of the local deer

population could determine if the similarity in composition between the treatments was due to the elimination of species or the alteration of competitive interaction and dominance relationships. We do not have data to assess this but do recognize it as a potential influence that overrides treatment effects in our study.

5. Conclusion

We failed to detect significant differences in ground-layer plant diversity or community composition among five contrasting silvicultural treatments, including diameter-limit cutting (39 years since treatment), shelterwood (27 years since overstory removal), light, medium, and heavy selection (harvests at 39, 29, 19, and 9 years before sampling) stands. Moreover, ground-layer plant communities in treated stands did not differ appreciably from those in control stands (unmanaged forest, 90 years old at time of sampling). Finally, contrary to the findings of other studies, repetitive stand entries under uneven-aged management systems did not lead to dominance by weedy, early-successional species. The lack of treatment differences may reflect adequate recovery time since disturbance, resistance to the disturbances (associated with snow and frozen ground during harvest), the overriding effect of deer herbivory on all treatments, or low statistical power, the later making it difficult to detect treatment effects. Additionally, the small size and position of treatment stands within matrices of mature forest may protect harvested stands from invasion by exotic and weedy species.

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