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Ten-year response of the herbaceous layer to an operational herbicide-shelterwood treatment in a northern hardwood forest

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ABSTRACT

Shelterwood seed cutting in conjunction with herbicide site preparation has proven effective at regenerating Allegheny hardwood forests, but the long-term impact of this silvicultural system on herbaceous vegetation has not been determined. From 1994 to 2004, we studied the impacts of operational herbicide site preparation using glyphosate plus sulfometuron methyl herbicides in the context of a shelterwood seed cut. Our study took place on 10 partially cut sites on the Allegheny National Forest in northwestern Pennsylvania. Half of each site received herbicide and half did not in a split-plot design with repeated measures. Fences were erected after year six because deer impact had increased. Resilience of individual species and the community were determined using measures of percent cover by species or species groups and indices of diversity and similarity comparing post-treatment to pre-treatment conditions and controls. In the short term, abundance of all species was reduced and there were four fewer species on average in treated areas. No species was eliminated by herbicide across all sites in the long term. Graminoids were more abundant on treated plots after year six. Targeted ferns remained less abundant on treated than control plots after 10 years. Species richness recovered within 4 years following treatment. Shannon Diversity and Shannon Evenness were greater in treated than in control plots over the full study period, but the differences were not significant in any single year. The richness-based Jaccard index of similarity did not differ between control and treatment plots after year two, while relative abundance influenced indices showed significant differences through year eight. Results suggest that herbaceous layer vegetation is resilient to the disturbance created by herbicide-shelterwood treatments.

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1. Introduction

The herbaceous layer plays a significant role in the structure and function of forest ecosystems as the site of intense competition following disturbance (Gilliam, 2007). Both competitive and complementary interactions among understory plants determine successional trajectories of trees. In forest management, it is possible to manipulate the understory environment through overstory and understory vegetation removal to prepare an appropriate regeneration niche, or combination of factors that determine the success of individual plants and species following a disturbance (Grubb, 1977). Egler (1954) proposed that management could be used to control the initial floristics allowing for overstory stability, or at least promoting overstory resilience, and even suggested killing the root systems of undesired species with herbicides. This is essentially what is accomplished in the silvicultural use of shelterwood cutting and broadcast, non-selective herbicide application.

Forest understory plants that interfere with re-establishment of overstory species following disturbance often become dominant as a result of long-term selective herbivory, which can apply selective pressure to an ecosystem (George and Bazzaz, 1999, 2003; Royo and Carson, 2006). For example, in northern hardwood forests with a history of high-intensity browsing by white-tailed deer (*Odocoileus virginanus*), species like striped maple (*Acer pensylvanicum* L.), American beech (*Fagus grandifolia* Ehrl) and the rhizomatous hayscented (*Dennstaedtia punctilobula* (Michx.) T. Moore) and New York ferns (*Thelypteris noveboracensis* (L.) Nieuwl.) often dominate the understory shrub and herb layers (Marquis and Brenneman, 1981; Tilghman, 1989; Horsley et al., 2003). The aggressive hayscented fern can prevent establishment and development of other understory plants in addition to impeding tree seedling establishment and therefore must be removed (Horsley, 1993; Horsley and Marquis, 1983; George and Bazzaz, 2003). Rhizomatous ferns cannot be effectively removed mechanically or with prescribed fire. Therefore, the only effective removal method for interfering ferns is through use of herbicides. An EPA approved tank mix (mixture of herbicides in water) of the herbicides glyphosate and sulfometuron methyl is an

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effective, economical and safe means of accomplishing this task (Horsley, 1981, 1988, 1990).

Recovery of species diversity following treatment with herbicides presents a more difficult challenge than natural disturbance or cutting because in addition to changes in light reaching the forest floor, nearly all individuals with aboveground parts exposed during application of the herbicide are potentially killed. A new cohort of vegetation must become established as opposed to simply adding species or individuals. A shelterwood seed cut is used to establish a new even-aged community under the protection of older trees, in two or more successive harvests leaving some older trees as a seed source (Nyland, 2002). In many shelterwood treated forests, the use of herbicides in silvicultural site preparation is critical to successful establishment of desired tree species prior to final overstory removal (Nyland, 2002).

The use of herbicides to manage for overstory resilience is a controversial topic because of negative public perception of spraying chemicals in the forest (Guynn et al., 2004). Despite the widespread use of this novel disturbance in some regions, it has received limited study in terms of impacts on non-target organisms (Lautenschlager and Sullivan, 2004). Most studies in hardwood-dominated ecosystems at the time this study began focused on tree species and showed increased diversity following forest management treatments (Mc Minn, 1992; Gove et al., 1992; Wang and Nyland, 1993; Niese and Strong, 1992; Stout, 1994). Research on herbaceous vegetation has been conducted mostly with single herbicides in conifer plantations and generally shows species recovery following application (Boateng et al., 2000; Harrington and Edwards, 1999; Miller et al., 1999; Sullivan et al., 1996, 1998). There is a lack of knowledge on impacts of herbicide use in hardwood forests that depend on natural regeneration, and in particular where control of multi-layered interfering vegetation requires a tank mix of herbicides (Guynn et al., 2004; Tatum, 2004).

This paper is part of a multidisciplinary study of herbicide impacts on non-target organisms. Our paper focuses on the long-term effects of a one-time tank mix herbicide application (glyphosate and sulfometuron methyl) on the herbaceous layer in partially cut (shelterwood seed cut) stands. We answered the following question: is the herbaceous community resilient to operational application of this herbicide mix; that is, do such treatments have negative long-term impacts on herbaceous species diversity? We compared species composition and community similarity (pre-treatment versus post-treatment) to determine whether the understory herb community is resilient to herbicide application. The hypotheses tested by our study are: (1) all herbaceous species persist through treatment with herbicides, (2) indices of evenness and diversity are unchanged by treatment, and (3) community similarity is high within treatments through time and between control and treated communities.

2. Methods and materials

2.1. Study sites

This study was conducted from 1994–2004 at ten 80–90 year old stands on the unglaciated portion of the Allegheny Plateau in northwestern Pennsylvania (Fig. 1). Stands were all northern hardwood forests with ⩾25% overstory basal area in black cherry (*Prunus serotina* Ehrh.), which represents a subtype often called Allegheny hardwoods (Marquis and Ernst, 1992). All stands were continuously forested, with last major harvesting occurring in the early 1900s (Marquis, 1975). The unglaciated Allegheny High Plateau section is a landscape with relatively flat to gently rolling plateaus dissected by deep stream valleys (Hough and Forbes, 1943). Study sites ranged from 6.5 to 8 ha, and were all on plateau-tops where elevations range from 500 to 700 m above sea level (Cerutti, 1985; Kopas, 1985; Whitney, 1990). Mean annual temperatures for the region range from 6 to 9.5 °C, depending on aspect and exposure with average precipitation ranging between 100 and 110 cm annually (Cerutti, 1985; Kopas, 1985). Soils of the region are derived from parent materials of sandstones and shales (Aguilar and Arnold, 1985; Whitney, 1990). Within the ten stands, soils of well-drained to moderately well-drained sites were primarily acidic, gray-brown ultisols of the Cookport (aquic fragiudults) or Hartleton (mesic typic hapludults) series, or in some cases acidic gray, brown or red inceptisols of the Hazelton (typic dystrochrept) series (Hough and Forbes, 1943; Aguilar and Arnold, 1985; Cerutti, 1985; Kopas 1985; Whitney, 1990).

Black cherry and red maple (*Acer rubrum* L.) accounted for the largest proportion of basal area at each site (Table 1). Five sites had received a shelterwood seed cut (60% residual basal area) within the previous 5 years, while the other five sites were uncut, but in need of a shelterwood seed cut to increase understory light. The seedling and sapling layers were dominated by abundant, small (<15 cm.) black cherry and red maple, mostly overtopped by larger American beech, striped maple, and birch (*Betula lenta* L. and *Betula allegheniensis* Britton) up to 4.5 m tall. The dominant herbaceous layer species was hay scented fern. All ten sites were chosen for treatment with herbicides to make understory species composition more diverse. Two treatment sequences were tested in this study: (1) a shelterwood seed cut followed by herbicide application within five years; and (2) herbicide application, followed by a shelterwood seed cut after the following growing season.

A tank mix of herbicide (1.7 kg ai ha^{-1}. glyphosate (Roundup®) and 0.1 kg ai ha^{-1} sulfometuron methyl (Oust®) in 38 L H_2O per hectare) was applied to half of each study site between mid-August and mid-September 1994. Treated portions were selected randomly. Herbicide was applied using an air blast mist blower capable of reaching 4.5 m high in the understory. Sites assigned to the herbicide then shelterwood method sequence were cut during the dormant season of 1995/1996. A goal of this experiment was to determine the impacts of operational treatments, rather than simply experimental treatments.

Site selection criteria excluded areas of extremely high levels of deer browsing, and there were new game laws promising to reduce regional deer density, so a decision was made not to fence study areas to exclude deer. As the study progressed, however, changes to game laws were not effective and deer impact at some study sites became a major barrier to seedling height development. To mitigate the highly variable deer impact across sites, woven wire fences 2.4 m high were erected to exclude deer in May 2001. Landowners would do this operationally if the seedling cohort was in danger of being impacted negatively by deer. Fences surrounded both treatments, thus allowing for continued comparisons among treatments.

2.2. Field sampling

Pre-treatment data were collected in 1994. Data were collected after herbicide application in 1995 and again after cutting (where required) in 1996. Additional data were collected every 2 years from 1998 through 2004. Plant inventories were conducted in mid-May to include spring ephemerals, and again in mid-July to more accurately assess abundance (as percent cover) of plants that reach maturity later in the growing season (Ristau et al., 2001; Yorks and Dabydeen, 1999). Percent cover was estimated visually by species using 30 temporary 4-m^2 (1.13 m radius) circular sample plots located systematically to ensure uniform coverage of the entire area. The exact plot locations were different at each visit by design to avoid damage to plants caused by repetitive sampling; it

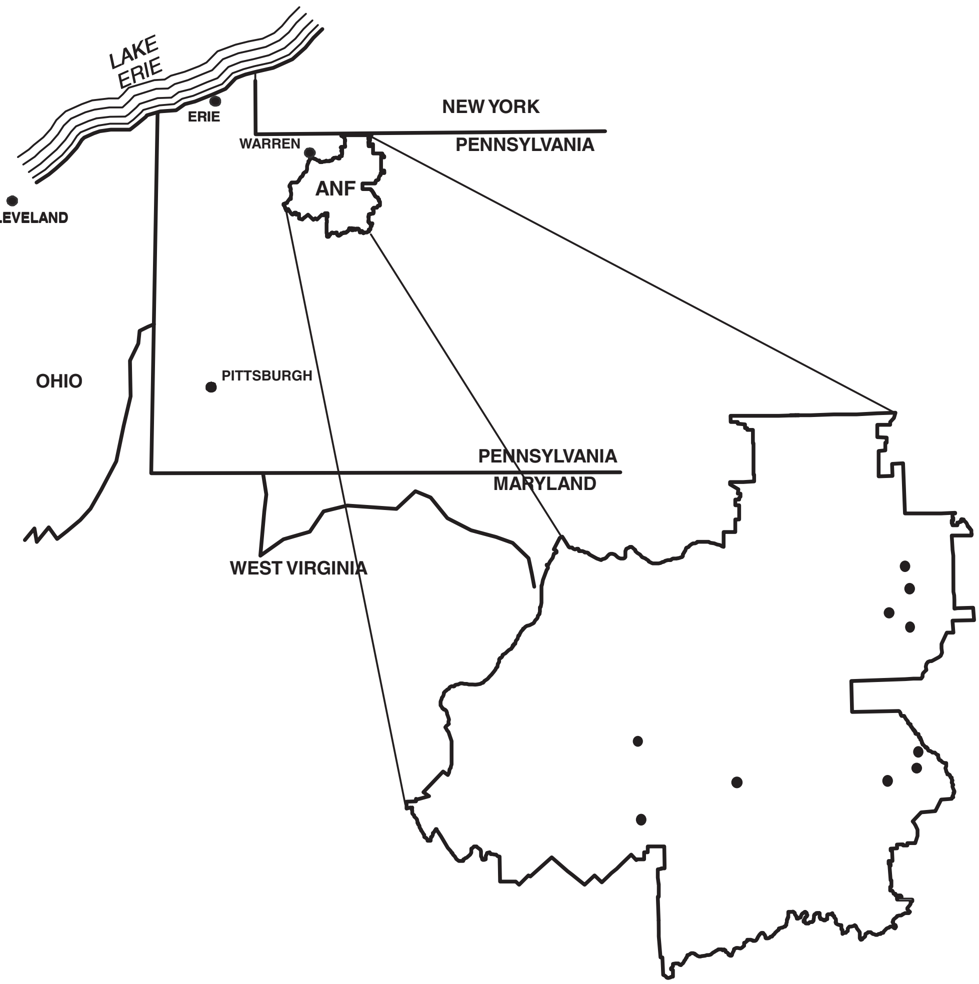

Fig. 1. Study plot locations on the Allegheny National Forest in Northwestern Pennsylvania.

Table 1
Species composition and cutting sequence at the 10 study sites. For sequence, H–S is herbicide followed by shelterwood method, and S–H is shelterwood method followed by herbicide. Treatment status is designated as C for control and H for herbicided. Diameters are mean diameter across all species. RD is relative density and is a measure of crowding. BC = black cherry, SM = sugar maple, RM = red maple, AB = American beech, EH = Eastern hemlock. Other includes yellow-poplar, cucumber magnolia and black birch. Coordinates are latitude and longitude of site center.

						Percent basal area					
Site	Treatment & Sequence		Diameter (cm)	RD(%)	Total BA (m^2/ha)	BC	SM	RM	AB	EH	Other
Blacksnake run (N 41° 45′ 13″, E 78° 47′ 18″)	H—S	C	72	72	30.1	44	12	18	12	10	1
		H	91	91	41.3	55	6	26	7	6	0
Blood run (N 41° 36′ 29″, E 79° 09′ 03″)	S—H	C	48	48	25.3	88	9	2	1	0	0
		H	49	49	26.6	87	6	4	0	0	1
Forest road 185 (N 41° 33′ 59″, E 78° 45′ 22″)	H—S	C	64	64	26.6	31	10	35	11	10	1
		H	60	60	25.0	37	0	34	23	2	0
Forest road 185F (N 41° 34′ 28", E 78° 45′ 14")	S—H	C	63	63	28.7	66	2	19	9	4	0
		H	66	66	30.5	71	8	13	4	0	0
Meade run (N 41° 44′ 22", E 78° 45′ 08")	S—H	C	72	72	35.6	63	4	19	7	5	0
		H	75	75	34.2	62	5	19	8	1	0
Pigeon (N 41° 33′ 10″, E 79° 00′ 26″)	S—H	C	70	70	27.3	29	11	49	4	5	0
		H	68	68	26.4	33	11	44	5	6	0
Seldom seen corners (N 41° 30′ 44″, E 79° 10′ 04″)	S—H	C	59	59	27.3	48	4	24	11	0	12
		H	71	71	33.3	59	0	17	16	0	7
Thundershower run (N 41° 48′ 30″, E 78° 45′ 28″)	H—S	C	80	80	31.5	37	18	41	3	0	1
		H	89	89	36.5	59	9	15	14	1	1
Turnup run (N 41° 47′ 01″, E 78° 44′ 58″)	H—S	C	83	83	30.1	53	21	3	17	0	3
		H	88	88	31.2	51	24	4	17	0	2
Wolf run (N 41° 35′ 02″, E 78° 44′ 23″)	H—S	C	80	80	34.0	70	14	9	5	1	0
		H	58	58	28.5	69	5	14	3	6	1

often was necessary to manipulate dense fern cover (often 80–90%) typical of these sites (Horsley, 1994) to observe the plants growing beneath the fern. Temporary plots increase the variability and limit the inference to net rather than gross change with time, but were a compromise between strict spatial plot location and potential plot damage due to sampling. Spring and summer samples were combined by making an overall species list and using the maximum percent cover for each species across the two sample times, thus not penalizing a species for differences in cover due to life cycle.

Plants up to a height of 1.5 m within or with parts leaning into the plot were identified and the percentage of the plot covered by each species was recorded. Percent cover was chosen as a measure of abundance because many herbaceous plants are clonal, making it difficult to distinguish between discrete individuals (Magurran, 1988; Whitford, 1949). We estimated percent cover visually in 1% intervals up to 5%, then by 5% intervals up to 100%. Because plants occurred in overlapping layers, the total cover on a plot could exceed 100%. Species present on the plot, but not fully covering 1% of plot area, were recorded as 1% cover to indicate their presence. Species abundance was represented as the mean cover of 30 plots for each treatment unit. A total of 71 herbaceous layer plant taxa were identified across all years and sites in the study. Plants were grouped into four life forms (forbs, graminoids, pteridophytes, and shrubs). Several plant species occurred in only one year in small abundance and were therefore grouped into an "other" category within their life form.

Woody species were evaluated separately using the same 30 temporary 4-m^2 (1.13 m radius) sample plots used for herbaceous plants during the mid-July inventory, and in the same years. All stems were counted by species and height class (<1 m and >1 m). All nomenclature follows Gleason and Cronquist (1991).

2.3. Data analysis

Resilience of the herbaceous community was assessed by comparing attributes in herbicided and non-herbicided sites through time and to pre-treatment conditions. Additional analyses included calculating several diversity indices for each location and treatment using the SP-INDEX computer program (Ristau et al., 1995). Diversity indices used included species richness per site (∼4 ha area), mean species richness per 4-m^2 plot, Shannon diversity, Shannon evenness, and the Berger-Parker index (Magurran, 1988). Cumulatively these indices measure all of the attributes of alpha diversity including dominance and evenness. Community similarity measures (Jaccard, Chao-Jaccard and Morisita-Horn) were calculated to compare herbicide treated sites to control sites at each sample time using the program EstimateS (Colwell, 2004). In addition to comparison of treated and control sites, similarity measures were used within a treatment to compare similarity of pre-treatment species assemblage to each time post-treatment.

We used the MIXED procedure in SAS (SAS Institute, 2008) to assess differences among treatments and time. Mixed-model analysis of variance with repeated measures was conducted with locations (10) and year (8) as random variables, and treatment (2) as a fixed variable. The model included all two-way interactions. Data for each diversity index were analyzed separately. Pair-wise comparisons of least squares means with the Tukey–Kramer adjustment were used to test for differences in diversity. A p-value of $\leqslant$0.05 was considered significant in all tests in the analyses of variance, and Tukey-adjusted contrasts.

3. Results

3.1. Abundance responses

In the pre-treatment tally, woody species were dominated by *A. rubrum*, *P. serotina*, *B. lenta*, *Prunus pensylvanica, A. pensylvanicum,*

Table 2
Mean abundance (thousands of stems per hectare) of tree regeneration species encountered. Standard errors of the mean are shown in parentheses. Bold numbers within a species for a given time period and height class are significantly different at $p < 0.05$.

Species	Pre-treatment (1994)			Short-term (1996)		Long-term (2004)	
	Height	Control	Herbicided	Control	Herbicided	Control	Herbicided
Acer pensylvanicum L.	<1 m	1.1 (.5)	1.3 (0.6)	0.8 (0.4)	0.4 (0.2)	0.9 (0.3)	2.1(1.0)
	>1 m	0.1 (0.06)	0.2 (0.1)	0.09 (0.04)	0	0.6 (0.4)	0.5 (0.3)
Acer rubrum L.	<1 m	87.9 (2.1)	66.2 (17.3)	**47.2 (11.9)**	**16.2 (5.7)**	**35.3 (5.8)**	**139.2(17.8)**
	>1 m	0.008 (0.008)	0	0	0	0.2 (0.1)	0.3(0.2)
Acer saccharum Marsh.	<1 m	0	0	0.02 (0.01)	0.008 (0.008)	0.03 (0.03)	0.2(0.1)
	>1 m	0	0	0	0	0	0
Amelanchier arborea (Michx. f.) Fern.	<1 m	0.6 (0.2)	0.7 (0.3)	0.7 (0.3)	0.1 (0.06)	0.9 (0.4)	0.3 (0.1)
	>1 m	0	0	0	0	0	0
Betula lenta L.	<1 m	10.9 (3.4)	12.4 (3.6)	**8.9 (3.8)**	**0.6 (0.3)**	**2.7 (0.8)**	**9.2 (2.2)**
	>1 m	0.6 (0.3)	1.0 (0.5	0.5 (0.3)	0.008 (0.008)	2.2 (1.2)	1.0 (0.7)
Fagus grandifolia Ehrh.	<1 m	2.6 (0.5)	2.8 (0.5)	**1.7 (0.3)**	**0.09 (0.03)**	3.2 (0.9)	1.6 (0.3)
	>1 m	0.6 (0.2)	0.5 (0.1)	0.5 (0.2)	0	**1.8 (0.4)**	**0.4 (0.1)**
Ilex montana (T.&G.) A. Gray	<1 m	0.09 (0.07)	0.1 (0.1)	0.1 (0.07)	0.04 (0.04)	0.2 (0.1)	0.1 (0.08)
	>1 m	0	0	0	0	0	0
Liriodendron tulipifera L.	<1 m	0.1 (0.06)	0.05 (0.03)	0.008 (0.008)	0.008 (0.008)	0.3 (0.2)	0.5 (0.3)
	>1 m	0	0	0	0	0	0
Magnolia acuminata (L.) L.	<1 m	0.2 (0.1)	0.08 (0.04)	0.1 (0.07)	0.03 (0.02)	0.4 (0.2)	0.3 (0.2)
	>1 m	0	0	0	0	0.02(0.02)	0
Prunus pensylvanica L.f.	<1 m	5.8 (4.4)	1.9 (1.0)	**0.3 (0.2)**	**0.09 (0.05)**	**0.2 (0.2)**	**1.5 (0.5)**
	>1 m	0	0	0	0	0.03 (0.03)	0.01 (0.01)
Prunus serotina Ehrh.	<1 m	179.1 (33.0)	172.3 (30.2)	**56.1 (13.4)**	**29.2 (11.3)**	**92.9 (11.6)**	**333.0 (42.7)**
	>1 m	0	0.07 (0.07)	0	0	0.03 (0.03)	0.6 (0.5)
Tsuga canadensis (L.) Carr.	<1 m	0.2 (0.06)	0.2 (0.1)	0.2 (0.1)	0.1 (0.06)	0.09 (0.04)	0.3 (0.2)
	>1 m	0	0	0	0	0	0
Others[a]	<1 m	0.1(0.1)	0.2 (0.2)	0.1 (0.08)	0.05 (0.05)	0.2 (.1)	0.1 (0.1)
	>1 m	0	0	0	0	0	0

[a] Others include: *Aralia spinosa* L., *Crataegus* L. spp., *Fraxinus americana* L., *Hamamelis virginiana* L., *Ostrya virginiana* (Miller) K. Koch, *Pinus strobus* L., *Quercus rubra* L., *Sorbus americana* Marsh., and *Ulmus* L. spp.

Table 3
Mean abundance of taxa found over 10 years. Values in parentheses are standard errors of the mean. Values shown in bold indicate a significant difference between herbicided and unherbicided plots at $p < 0.05$. Values for a species within a year followed an asterisk (*) indicate that herbicided plots are different from pre-treatment levels. Season refers to the growing season portion when aboveground parts are present. Response refers to the pattern describing how herbicides affected the species recovery.

Species	Season/Response	Pre-treatment (1994)		Short-term (1996)		Long-term (2004)	
		Control	Herbicided	Control	Herbicided	Control	Herbicided
Forbs							
Aster spp.	Summer/unaffected	0.1 (0.05)	<0.01 (0.02)	<0.01 (0.01)	<0.01 (0.01)	<0.01 (0.01)	<0.01 (0.03)
Claytonia virginica L.	Ephemeral/unaffected	0.5 (0.48)	0.3 (0.23)	0.2 (0.11)	0.1 (0.05)	0.0	<0.01 (0.01)
Coptis trifolia (L.) Salisb.	Summer/unaffected	0.2 (0.10)	0.1 (0.06)	<0.01 (0.02)	0.0	0.1 (0.07)	0.1 (0.12)
Erythronium americanum Ker-Gawl.	Ephemeral/unaffected	6.0 (2.24)	5.2 (2.16)	**9.2 (2.54)**	**4.2 (1.38)**	3.3 (1.53)	4.2 (1.86)
Maianthemum canadense Desf.	Summer/deer indic.	0.6 (0.31)	0.7 (0.34)	0.6 (0.33)	0.6 (0.51)	**0.7 (0.17)**	**2.5 (1.08)***
Medeola virginiana L.	Summer/deer indic.	0.4 (0.14)	0.5 (0.08)	0.3 (0.08)	0.5 (0.17)	**0.6 (0.11)**	**1.8 (0.38)***
Mitchella repens L.	Summer/unaffected	0.1 (0.04)	0.2 (0.06)	0.1 (0.05)	0.2 (0.05)	0.1 (0.04)	0.4 (0.11)
Oxalis montana Raf.	Summer/vegetative	5.6 (3.72)	4.7 (2.16)	**2.4 (1.29)**	**0.1 (0.04)***	1.2 (0.32)	0.9 (0.27)*
Panax trifolius L.	Ephemeral/unaffected	0.2 (0.06)	0.2 (0.09)	0.2(0.05)	0.2(0.08)	0.1 (0.03)	0.2 (0.13)
Rubus hispidus L.	Summer/unaffected	<0.01 (0.02)	<0.01 (0.02)	<0.01 (0.02)	<0.01 (0.01)	0.1 (0.07)	0.2 (0.14)
Solidago spp.	Summer/unaffected	0.0 (0.01)	<0.01 (0.01)	0.0	0.0	0.1 (0.05)	<0.01 (0.02)
Trientalis borealis Raf.	Summer/unaffected	0.1 (0.03)	0.2 (0.08)	0.1 (0.04)	0.1 (0.06)	0.1 (0.04)	0.1 (0.04)
Trillium spp.	Summer/deer indic.	0.1 (0.05)	0.2(0.06)	0.1(0.04)	0.1 (0.03)	**0.2 (0.08)**	**0.4 (0.14)**
Uvularia sessilifolia L.	Summer/deer indic.	**0.2 (0.05)**	**0.3 (0.12)**	0.2 (0.05)	0.2(0.04)	**0.4 (0.15)***	**1.2 (0.38)**
Viola spp.	Summer/seed bank	1.9 (0.43)	2.6(0.56)	**1.3 (0.24)**	**0.7 (0.15)***	**1.4 (0.65)**	**2.3 (0.74)**
Other forbs	Various	<0.01 (0.01)	<0.01 (0.01)	0.1 (0.07)	<0.01 (0.02)	0.2 (0.17)	0.1* (0.04)
Graminoids							
Brachyelytrum erectum Beauv.	Summer/vegetative	6.0 (3.12)	5.9 (2.21)	3.3 (1.24)	0.5* (0.09)	2.0 (0.95)	4.9 (2.05)
Carex spp.	Summer/seed bank	2.6 (0.61)	2.5 (0.47)	1.5 (0.36)	0.9* (0.18)	**1.6 (0.83)**	**4.7* (0.88)**
Danthonia compressa Austin ex Peck	Summer/seed bank	1.9 (1.05)	2.8 (0.96)	1.9 (1.20)	1.3 (0.51)	**0.1 (0.08)**	**3.8 (1.28)**
Other graminoids	Various	0.3 (0.16)	0.1 (0.06)	0.3 (0.07)	0.4 (0.26)	0.1 (0.12)	0.5 (0.37)
Pteridophytes							
Dennstaedtia punctilobula (Michx.) T. Moore	Summer/vegetative	26.6 (6.52)	27.7 (7.63)	**13.8 (3.73)**	**0.4* (0.13)**	17.0 (7.40)	12.4* (3.75)
Dryopteris intermedia (Muhl. ex Willd.) Gray	Summer/vegetative	7.6 (1.99)	6.6 (1.69)	**4.0 (1.16)**	**0.2* (0.04)**	**9.2 (2.36)**	**1.5* (0.45)**
Lycopodium annotinum L.	Evergreen/unaffected	0.9 (0.72)	1.1 (0.91)	0.2 (0.12)	0.6(0.39)	1.0 (0.67)	0.7 (0.44)
Lycopodium clavatum L.	Evergreen/unaffected	0.1 (0.05)	<0.01 (0.03)	0.0	<0.01 (0.01)	0.0	0.0
Lycopodium complanatum L.	Evergreen/unaffected	0.3 (0.17)	0.3 (0.22)	0.3 (0.26)	0.3(0.32)	0.3 (0.12)	1.1 (0.76)
Lycopodium lucidulum Michx.	Evergreen/unaffected	2.2 (0.91)	2.3 (0.90)	1.7 (0.80)	1.2* (0.47)	1.4 (0.72)	1.0* (0.49)
Lycopodium obscurum L.	Evergreen/unaffected	5.7 (3.07)	3.5 (1.57)	4.5 (1.92)	2.6 (0.95)	5.9 (2.39)	8.5* (2.90)
Thelypteris noveboracensis (L.) Nieuwl.	Summer/vegetative	10.0 (3.09)	11.1(6.36)	**5.3 (1.95)**	**<0.01 (0.01)***	5.6 (2.02)	1.1 (0.50)*
Other Pteridophytes	Various	0.0	<0.01 (0.01)	<0.01 (0.04)	0.0	0.1 (0.07)	0.0
Shrubs							
Rubus spp.	Summer/deer indic.	2.2 (0.74)	3.5 (1.36)	2.2 (0.80)	0.5 (0.13)	**3.9 (1.18)**	**9.9 (2.84)***
Other shrubs	Various	0.0	0.0	<0.01 (0.01)	0.0	0.0	0.0

F. grandifolia with only *A. pensylvanicum*, *B. lenta*, and *F. grandifolia* reaching heights above one meter (Table 2). The short-term response of woody species to herbicide application was significantly reduced numbers of seedlings on herbicided plots versus control plots for *A. rubrum*, *B. lenta*, *F. grandifolia*, *P. pensylvanica*, and *P. serotina* (Table 2). In the long term, herbicided plots contained more seedlings of *A. rubrum*, *B. lenta*, *P.* pensylvanica and *P. serotina*. Numbers of stems greater than one meter for these same species were higher than pre-treatment; however differences from control plots were not significant. Number of *F. grandifolia* stems greater than one meter was significantly lower in the long term for herbicided plots versus control plots.

Forb species composition included spring ephemerals *Claytonia caroliniana* Michx, *Erythronium americanum* Ker Gawl., and *Panax trifolius* L. (Table 3). Abundances of these plants varied year to year, but were similar in treated and control plots in terms of average cover. *E. americanum* and *Oxalis montana* Raf. were the most abundant forbs pre-treatment. *Erythronium* remained the most abundant forb after treatment though significantly lower in abundance than the control in the short term. *Oxalis* was slow to recover to its pre-treatment abundance following herbicide application (Table 3). Common summer understory plants *Coptis trifolia* (L.) Salisb., *Maianthemum candense* Desf., *Medeola virginiana* L., *Mitchella repens* L., *Uvularia sessilifolia* L., *Trillium* spp. (mostly *Trillium undulatum* Willd.), *Trientalis borealis* Raf., and *Viola* spp. (mostly *Viola mackloskeyi* Lloyd and *V. blanda* Willd.) had low abundances from a trace to 3% cover on average (Table 3). Following fencing to exclude deer, *Maianthemum canadense* and *M. virginiana* were significantly higher in abundance than pre-treatment.

Graminoid cover was dominated by *Brachyeletrum erectum* (Schreb.) P.Beauv., *Carex* spp. and *Danthonia compressa* Austin (Table 3). On control plots, abundances of these species decreased gradually through time as woody overstory seedlings developed, on treated plots their abundance was greatly reduced in the short-term, but four years after herbicide was applied, *D. compressa* and *Carex* spp. abundances exceeded pre-treatment levels. *B. erectum* recovered its pre-treatment abundance, but did not exceed it; however there was a steady decline in its abundance on control plots; treated plots had 2.5 times as much *Brachyeletrum* as control plots by the end of the study.

The pteridophytes group includes both club mosses and ferns. Rhizomatous ferns were one of the herbicide targets and as such they had high initial abundances. *D. punctilobula*, *Dryopteris intermedia* (Muhl. Ex Willd.) Gray, and *T. noveboracensis* cumulatively covered 44% of the ground on average pre-treatment (Table 3). Following herbicide, the three species covered less than 1% on average. Among the three ferns, *D. punctilobula* was the quickest to recover its abundance. By the end of the experiment, *Dennstaedtia* coverage recovered to about half its pretreatment level. Club moss abundance was unaffected by the herbicide application though there was some year to year variability of mean cover by *Lycopodium lucidulum* Michx. and *Lycopodium obscurum* L. on both treated and control plots.

The most abundant shrub species was *Rubus allegheniensis* Porter, with a few individuals of other shrubby *Rubus* spp. in some years. Because small *Rubus* plants are difficult to distinguish, they are all reported collectively in the *Rubus* spp. category except *Rubus hispidus* L. which is included with forbs. *Rubus* abundance declined following herbicide application and recovered slowly until fencing to exclude deer. After fencing, the abundance of *Rubus* on herbicide-treated plots increased to more than 2 times its pre-treatment levels (Table 3).

3.2. Diversity responses

Preliminary analyses showed no differences in species composition or diversity among the two treatment sequences of cutting then herbicide versus herbicide then cutting, so all subsequent analyses combined the two sequences. The Berger-Parker diversity index, a measure of domination of a site by a single species, was significantly higher on control plots than treated plots in 2000 and 2002; the overall effect of treatment, year or their interaction was not significant (Table 4, Fig. 2). Species richness had significant year ($p < 0.001$), treatment ($p = 0.035$) and year by treatment interaction ($p < 0.001$) effects (Table 4, Fig. 2). For the first 2 years after treatment, treated plots had lower richness than control plots but those differences were no longer present four years after treatment. On control plots richness never differed among years. Shannon evenness had a significant treatment effect in the overall model (Table 4, Fig. 2). There were no significant differences between treatments in any one year, though herbicided plots had higher evenness than pretreatment 2, 4, 6, and 10 years after treatment. There was no difference in evenness on control plots compared to pre-treatment in any year. Shannon diversity, a measure that combines species richness and evenness into one index, had a significant treatment effect (Table 4, Fig. 2). However, there were no differences in Shannon diversity on treated versus control plots

Table 4
Analysis of variance results for a mixed model with repeated measures. Results are for overall model for each of four diversity measures.

Source of variation	df	Berger-parker		Species richness		Shannon diversity		Shannon evenness	
		F	p	F	p	F	p	F	p
Stand (Random)	9	1.23	0.109	1.61	0.054	1.46	0.072	1.27	0.101
Treatment (Fixed)	1	3.00	0.117	6.14	**0.035**	5.17	**0.049**	9.24	**0.014**
Stand * Treatment	9	1.54	0.182	0.05	0.481	1.37	0.085	1.25	0.105
Year (Fixed)	7	1.93	0.093	6.07	**<0.001**	1.67	0.146	1.67	0.147
Year * Treatment	7	1.74	0.129	8.04	**<0.001**	1.59	0.168	0.53	0.786
Error	54								

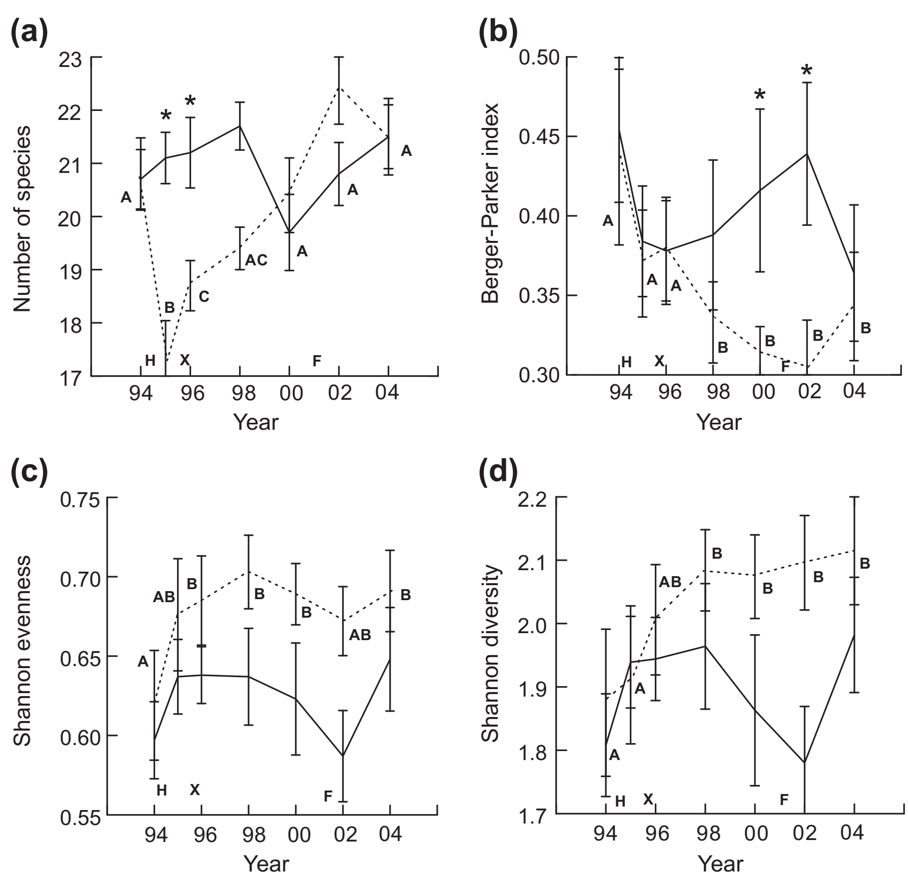

Fig. 2. Species richness (a), dominance (b), Shannon evenness (c), and Shannon diversity (d) by treatment (solid lines are control, and dashed lines are herbicided plots) through time. Error bars are standard error of the mean. Within a given year, an asterisk indicates significant difference between treated and control plots at $p < 0.05$. For treated plots, years followed by the same letter are not significantly different from each other at $p < 0.05$. On the graphs, H indicates the year herbicide was applied, X indicates the year cutting was done, and F indicates the year fences were erected to exclude deer.

in any single year. On treated plots Shannon diversity was higher than pretreatment from 4 years after treatment onward.

3.3. Community similarity

Diversity indices can be the same for two communities with different species present, because species identity is not considered in calculations. Community similarity measures look at species overlap and abundance distribution similarity among assemblages. To measure recovery of species composition, we used community similarity measures (Fig. 3). The Jaccard index is a measure of species overlap and only showed differences due to treatment immediately after herbicide application (Fig. 3a). Chao-Jaccard (Fig. 3b) and Morisita-Horn (Fig. 3c) are sensitive to abundance shifts and both decreased following treatment, and did not recover over the course of the study. The Chao-Jaccard index on treated plots in 2004 was no longer different from the control plots by 2004, but was still different from pre-treatment values (Fig. 3b). Morisita-Horn is known to be affected by the abundance of the most dominant species, which in this case was the targeted hayscented fern.

Recovery of species following herbicide site preparation followed four main response patterns (Table 3, Fig. 4): vegetative reproduction, seed bank germination, unaffected (survival in place), and species known to be indicators of deer browsing (Kirschbaum and Anacker 2005). Vegetative species were the slowest to recover (Fig. 4a). Seed bank species were the earliest group to show a high rate of recovery (Fig. 4b). The unaffected group showed no differences due to treatment over time, though both herbicided and control plots saw increased abundance following fence construction (Fig. 4c). Before fence erection, the deer indicators group resembled the unaffected group, however after fencing these species increased in abundance dramatically (Fig. 4d). All groups showed some increase in coverage after fencing, but the deer indicators group increased to three times their pre-treatment level.

4. Discussion

4.1. Impacts on individual species

Herbicides can be used to promote tree regeneration similar to what would have naturally developed without decades of high intensity deer browsing (Marquis and Brenneman, 1981). In the current study, site preparation with herbicides resulted in a diverse community of tree seedlings, but height growth was restricted until deer were excluded. Fencing after year six did not alter plant species composition.

We found the herbaceous community to be quite resilient following herbicide site preparation. No species was lost from any site at any sampling period. Our findings are consistent with earlier reports that herbicide site preparation in conifer forests may alter abundance but does not eliminate any species (Miller and Miller, 2004; Freedman et al., 1993; Litt et al., 2001; Sullivan and Sullivan, 2003; Guiseppe et al., 2006). The impact of a single application of herbicide on the herbaceous community was short-lived. Over the ten year study period, species diversity improved and dominance by *D. punctilobula* and other browse resistant species was reduced.

Targeted species such as the ferns were slowest to recover. We found that in addition to the rhizomatous ferns, some other species that depended heavily on vegetative reproduction also were slow to recover; e.g. *Oxalis acetosella* and *L. lucidulum*. Roberts and Zhu (2002) found loss of sixteen species in stands disturbed by clearcutting including *O. acetosella, M. repens*, and *C. trifolia*, all found in our study. They attributed species loss to slow growth and reproductive rates, and to clonal growth, ant dispersal and gravity

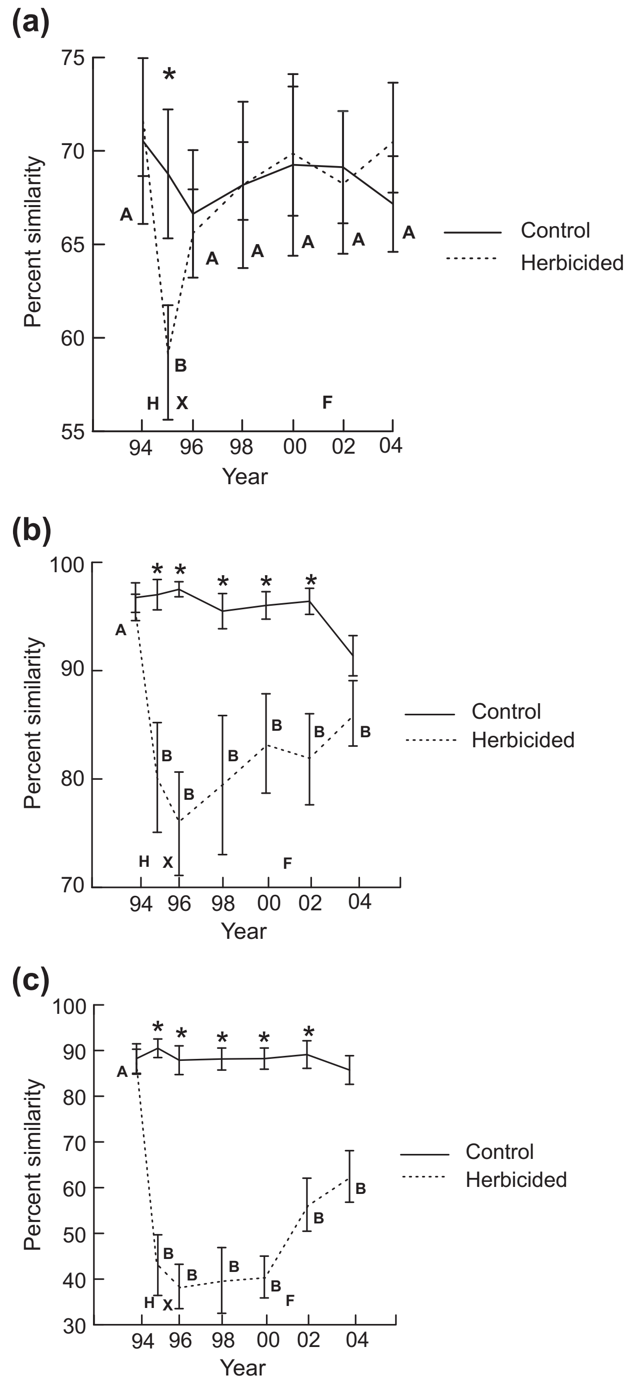

Fig. 3. Community similarity represented by the Jaccard (a), Chao-Jaccard (b), and Morisita-Horn (c), similarity indices by treatment (solid lines are control, and dashed lines are herbicided plots) through time. Each sample year is expressed as similarity to pre-treatment levels. Error bars are standard error of the mean. Within a given year, an asterisk indicates significant difference between treated and control plots at $p < 0.05$. For treated plots, years followed by the same letter are not significantly different from each other at $p < 0.05$. On the graphs, H indicates the year herbicide was applied, X indicates the year cutting was done, and F indicates the year fences were erected to exclude deer.

dispersal making re-colonization slower. In our study, *Oxalis* and *L. lucidulum* remained below pre-treatment abundance levels after 10 years. For these two species, disturbance by herbicide has a similar impact to disturbance by clearcutting, though no species were completely lost.

The survival in place response pattern included spring ephemerals *C. caroliniana*, *E. americanum*, and *P. trifolius* that were not

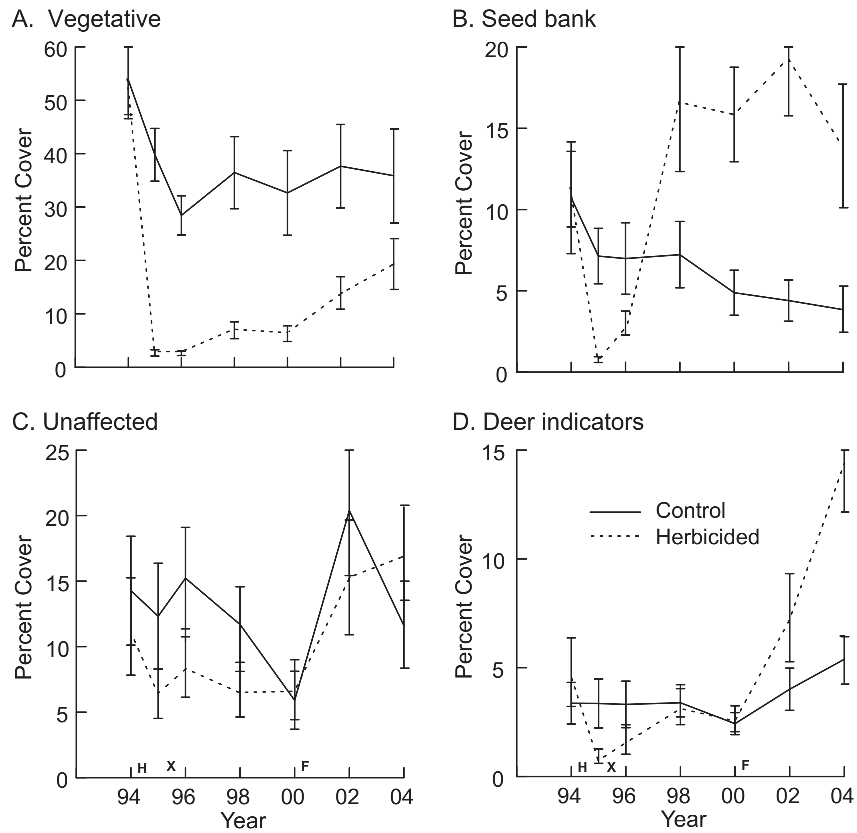

Fig. 4. Abundance of species categorized by recovery mechanisms. Responses shown are by treatment (solid lines are control, and dashed lines are herbicided plots) through time. Deer indicators, apparent seed bank species, those unaffected by herbicide (spring ephemerals and others), and species that rely extensively on vegetative reproduction. An H indicates the year herbicide was applied, X indicates the year cutting was done, and F indicates the year fences were erected to exclude deer.

above ground when herbicide was applied and therefore did not show any negative effects, even with the soil residual activity of sulfometuron methyl. There was high variability in spring ephemeral cover among years due to variable weather patterns in early spring. Additional mechanisms or plant traits that may have allowed for species survival in place include protective waxy coatings on some of the *Lycopodium* species, as well as presence of some refugia or legacies (Drever et al., 2006) where patches missed by the herbicide sprayer allowed species, patterns, or structures to persist within the disturbed area, including seeds, rhizomes, and roots.

Graminoids, the violets, and *Rubus* all decreased initially after application of herbicides, but increased to abundances much higher than pretreatment levels by two to four years after treatment. Other researchers have seen similar responses from these species groups. Harrington et al. (1998) showed an increase in grass, forb, and shrub cover after herbicide. In a study by Freedman et al. (1993), there was an initial decrease in abundance of herbs, but by the end of the second growing season there was recovery including raspberry and other angiosperms. These quickly recovering species are consistent with a buried seed response pattern. Increased light and soil temperature, or perhaps a quick flux of nitrate nitrogen, allowed for germination of buried seed and those small plants became established (Auchmoody, 1979). When grasses and sedges become extremely dense they can present an additional barrier to seedling development (Horsley, 1990). Timing of overstory removal and fence erection can have a major impact on whether or not this seed bank response results in an overabundance of graminoids because of differences in establishment times for seedlings.

Deer browsing early in the growing season also may have served as a mechanism for survival. Denslow (1980, 1985) suggested that presence of intermediate disturbances in a forest maintains a stable species diversity level with sites that are richest in species being adapted to the most commonly created disturbance. In Pennsylvania forests, the most common chronic disturbance is deer browsing. Many herbaceous layer plants that are still somewhat abundant in these deer-altered forests have below-ground storage organs such as bulbs or corms. Yearly shoots provide enough nourishment to the storage organ to allow a new shoot to emerge each year, but not enough for sexual reproduction to occur. This repeated browsing may have allowed individual plants to survive herbicide by not having foliage present to receive the herbicide. Well-known indicators of deer impact (Kirschbaum and Anacker, 2005) such as *M. canadense*, *Trillium* spp., *M. virginiana*, *Rubus* spp., and perhaps *U. sessilifolia* were reduced by herbicide initially, and then recovered slowly until deer were excluded. Removal of deer by fencing allowed both vegetative expansion and sexual reproduction of these species. Expansion of deer indicator plants continued. Some other species had an initial increase after fencing, but their response began to slow after two years. In areas where deer pressure is low, ferns often are out-competed by a dense layer of *Rubus*, through which many hardwoods are able to grow (Horsley and Marquis, 1983; de la Cretaz and Kelty, 2002).

Our findings are consistent with other studies of herbaceous layer response to disturbance. Roberts and Zhu (2002) found that, after clearcutting, species were either lost, decreased in cover and frequency, increased cover and frequency, or were new colonizers of the stands. Halpern (1989) reported that herbaceous plants commonly use two patterns of secondary succession following disturbance. Species either survive the disturbance or colonize following disturbance; long-term changes in diversity then occur slowly through gradual expansion and decline of species. No species were lost in our study, but several decreased in cover and frequency or colonized.

4.2. Community resilience following herbicide application

Short-term losses in species richness were recovered by six years after herbicide site preparation. Dominance, measured by the Berger-Parker index, was significantly reduced on treated sites compared with control sites by six years after treatment. Removal of ferns that dominated the understory led to greater species evenness based on cover, as shown by a significantly higher Shannon evenness index post-treatment than pre-treatment levels in most years. The decline in evenness on control plots was due to increases in cover that occurred following partial harvesting of the overstory. Following canopy disturbance, ferns and other species expand their coverage. In the presence of high deer impact, the unpalatable ferns expand while other species decline in cover (Horsley et al., 2003). Shannon diversity, which combines number of species and their proportional abundances, was heavily influenced by the shifts in dominance and evenness, which explain the trend of higher diversity in treated versus control plots observed with this index. Consistent with other research, we found no long term differences in diversity, and recovery of diversity began within the first few years after treatment (May et al., 1982; Sullivan et al., 1998; Mac-Kinnon and Freedman, 1993; Bell and Newmaster, 2002). Plateau-top Allegheny hardwood forests are resilient in terms of individual species persistence and species richness, and Shannon diversity and evenness can be increased by herbicide and shelterwood treatments.

4.3. Similarity

Perhaps a better method for comparing post-treatment species composition to pre-treatment is through the use of similarity measures. Like diversity indices, some similarity measures emphasize species richness and overlap of species between communities, while others emphasize or incorporate abundance. The Jaccard index, which looks at similarity of species composition without regard for abundance, showed an initial decline in similarity to pre-treatment species, which was likely due to the loss of species that were slower to recover after disturbance, including targeted species (e.g. ferns). The Chao-Jaccard index and the Morisita-Horn index include abundance in their calculations. Both show that treated sites never returned to pretreatment community composition, but rather changed their successional trajectory in favor of a more diverse species mix. Trajectory changes were heavily influenced by the dominant species like hayscented fern, which were targeted by the herbicide treatment. There were no losses of species across the study, but abundance shifts did result in altered species relative abundances on treated sites. Forest managers use the herbicide and shelterwood treatments to cause this abundance shift and establish a diverse mix of woody species to ensure that the species composition after harvest affords the best opportunities for the future including both timber and ecological objectives. Our study shows that this treatment achieves these objectives without compromising non-target herbaceous layer species composition.

4.4. Recovery mechanisms

The lack of observed differences in species composition using similarity and diversity measures of pre- versus post-treatment periods of treated sites, and the lack of difference between treated and control sites, suggest that the understory is indeed resilient to disturbance created by herbicide application. We observed, on average, a 40% canopy removal (shelterwood seed cutting to 60% residual), 90% understory removal through herbicide application, and an approximately 20% forest floor disturbance (from logging and spray equipment). Roberts (2004) predicted recovery mechanisms following several disturbance types based on these overstory, understory and soil disturbance axes. According to that model, vegetation response to shelterwood – herbicide application should be similar to a low intensity (cool) fire with more light available, and that surficial vegetative reproduction (shallow rhizomes and stolons) and seed bank should be the primary recovery sources (Roberts 2004). We did in fact observe these sources to be important, although shallow rhizomes and stolons often were killed by herbicide. Operational application of herbicides nearly always includes patches of refugia that can serve as sources of vegetative expansion. Non-target plant species differed in their ability to recover from the intense understory disturbance caused by herbicide application. Some species were unaffected by the herbicide application either due to their ephemeral phenology or the waxy coatings that protected the plants.

Management to promote tree regeneration using herbicides as a tool makes it possible to reduce the competition from vegetation layers left as a legacy of decades of deer over-browsing. Despite this extreme and novel disturbance event, the non-targeted herbaceous layer was resilient with a six year return time to complete pre-treatment species composition. Properly used, herbicides with short residence times in the soil represent an opportunity for ecosystem restoration. Managing to mitigate deer legacy effects or invasive species represents a challenge that warrants the use of herbicides. Results from this study are consistent with others in showing that understory plant communities are resilient to herbicide site preparation. Under the herbicide with shelterwood cutting scenario we studied, the non-target understory plants were resilient.

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