RESPONSE OF THE UNDERSTORY TO LOW INTENSITY PRESCRIBED BURNING OR MECHANICAL AND HERBICIDE TREATMENT IN A NORTHERN MESIC EASTERN WHITE PINE (*PINUS STROBUS* L.) FOREST IN THE MENOMINEE NATION, WISCONSIN.

by

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ABSTRACT

This study describes understory effects four and five growing seasons following four low intensity prescribed burns and three mechanical and herbicide treatments. Two, 150 year old northern mesic eastern white pine (*Pinus strobus* L.) dominated stands were sampled to compare effects of mechanical and herbicide (M+H) treatments that occurred in late 2002 and low intensity prescribed burns that occurred in 2003. Vegetation was sampled in spring and summer of the fourth and fifth growing seasons after the treatments. Density and composition of saplings; average cover, richness and diversity of understory vegetation; and density and composition of arboreal seedlings were calculated in treated units and controls. The propagule bank of the burn units was also sampled in the fourth growing season following the burns. Comparisons were made with pre-treatment data collected using the same methods pre-treatment and for three growing seasons post treatment. The control treatment had significantly greater density of saplings per hectare than burn and M+H treatments (p =0.01). Understory richness, diversity and average cover were greatest on prescribed burn treatments. There were not significant effects on richness or cover in different burn intensities. Propagule bank richness and density were not significantly affected by the burn, although composition was altered. Arboreal seedling density was greater on M+H treatments but 77% of the regeneration was red maple (*Acer rubrum* L.) at the end of the study period. The M+H treatments were more severe than prescribed burns, but did not result in the most desirable regeneration. Results of this study show that there are important differences in disturbance effects on the understory and propagule bank for at least five growing seasons following prescribed burning and herbicide and mechanical treatment.

DEDICATION

I dedicate this thesis to my daughter Hannah.

ACKNOWLEDGEMENTS

The path to becoming a graduate student on this project was long and winding; I would not have arrived here without the encouragement of Lynn Markham and John DuPlissis.

Many people worked on this study before me, including Betsy Galbraith, who wrote a thesis on the pre-treatment understory condition, and students who assisted in data collection during 2001 through 2004. Dr. James Cook had the foresight to design and continue the study.

Without the continued cooperation of the Menominee Nation and Menominee Tribal Enterprises, the field work for this study would not have been possible. Ron Waukau was especially helpful in assisting with field locations and logistics. I appreciate having access to the lands of the Menominee to conduct this study. Spending two summers in the magnificent forests of the Menominee was a once in a lifetime opportunity. Not only did I learn about understory plants and forest structure, I also developed a deeper appreciation for, as Rachel Carson said, the “beauties and mysteries of the earth”.

Contributions to this study came from many sources. Funding came from the McIntire-Stennis Research Program. I am extremely grateful to the Advanced Opportunity Program via Ron Strege as well as the CNR Graduate Committee at UWSP for generous contributions toward my tuition for two semesters, and while I was writing this thesis. My fellow graduate students assisted me by giving me advice, discussing concepts and asking important questions about my study. Mary Bartkowiak, who has become a wonderful friend to me, provided much organizational support as well as many hours of field, greenhouse, and plant identification expertise. David Vogel provided a great deal of dependable field and greenhouse assistance as well as data entry and error checking help. P.J. Koehler and Shelly Samet both did an excellent job in the field during the second season. Jon Hardy helped a great deal with planning the greenhouse portion of this study. Thank you also to the greenhouse staff including Brian Bale, Erin Johnson, Joe, and Laurel. Dr. Bob Freckmann and Dr. Emmet Judziewicz were steadfast plant identification experts. Both volunteered a great deal of time and were willing to identify specimens and germinants in the greenhouse on a moment's notice. Dr. Michael Demchik, Dr. Eric Anderson, and Dr. Paul Doruska assisted with data analysis questions. My graduate committee, Dr. Emmet Judziewicz and Dr. Michael Demchik provided guidance, asked many helpful questions, and spent many hours reading drafts of this thesis. Dr. Kama Almasi was also a source of guidance before her departure from UWSP in 2007. Dr. James Cook, my advisor, committee chair, and now friend, spent many hours facilitating my learning as we conducted this project. A true mentor, he cared as much that I understood concepts and methods, as that the project was conducted carefully, with consistency and professionalism. James provided encouragement and guidance at every step in the process. The work on this study and thesis would not have been nearly as enjoyable without James' humor, nor would it have been as beneficial to my education without his practice of free and critical thinking.

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PREFACE

Two journal article style manuscripts focusing on separate aspects of this study comprise the main portion of this thesis. One chapter compares effects of the prescribed burn versus the mechanical and herbicide treatment on understory vegetation. The second chapter compares effects of the prescribed burn on the understory and propagule bank. Since the chapters are written in the style of two different journals, the writing style and format of the literature cited will differ. For continuity, an abridged literature review section encompassing the overall study is included before the two manuscripts. The manuscript chapters provide additional details related to the respective topics. A short discussion encompassing both manuscripts concludes the thesis.

INTRODUCTION

This thesis is an effort to quantify and compare the effects of two disturbances on the understory of two northern mesic forests in northeastern Wisconsin.

Disturbance is integral to the ecology of Great Lakes forests, including northern mesic, eastern white pine (*Pinus strobus*) forests in northeastern Wisconsin. Disturbance types, their size, intensity and resulting severity, and cycles on which they occur are collectively known as a disturbance regime (White 1979). Fire and large scale blowdown were the major elements of the historic disturbance regime in northern Wisconsin. The historic fire regime of Great Lakes area white pine forests included large (400 to 4000 hectares), severe, crown or surface fires on intervals of 200 to 300 years with low intensity fires at 20 to 40 year intervals (Canham and Loucks 1984, Heinselman 1981). Native American burning practices also had a role in pre-settlement disturbance regimes (Brown and Smith 2000). Complete canopy wind-throw also occurred in northeastern Wisconsin on over 4800 hectares annually, with an estimated return interval of 1210 years (Canham and Loucks 1984). The ultimate effects of the high intensity fire and large scale windthrow, which created favorable conditions for regeneration, were often sizeable areas of even aged eastern white pine forests (Maisurrow 1941). Several other relatively minor disturbances are part of the historic and current disturbance regime, including herbivory, insect and disease infestation, ice storms, and flooding. Less is known about effects of the more frequent low intensity fires, but they are thought to have prevented development of understories of balsam fir (*Abies balsamea* (L.) Miller), white spruce

(*Picea glauca* (Moench) Voss), northern white cedar (*Thuja occidentalis* L.), red maple (*Acer rubrum*) and other shade tolerant invaders that could out-compete young white pine (Heinselman 1981).

With respect to fire, the historic disturbance regime has been alterred because of: marginalization of Native Americans, and population increase and distribution, and land use practices which result in fire suppression. Some have claimed the decline in white pine in some parts of Wisconsin can be attributed to the interruption of the historic fire regime (Nowacki et al. 1990). However, lack of influence by fire does not render historic disturbances obsolete in contemporary resource management. Silviculture and ecological restoration often consider the historic disturbance regime for a particular region and attempt to mimic effects of those disturbances (Roberts 2004). For example, the shelterwood system, in use on our study sites, is commonly used to regenerate white pine in northeastern Wisconsin. The substantial overstory harvesting mimics the increased light that would have occurred following moderate severity natural disturbances (Wendel and Smith 1990, Nyland 2002). Site preparation treatments such as prescribed burning, herbicide application, mechanical soil scarification, chopping, mowing or crushing vegetation, or some combination of the above (Nyland 2002), clear competing vegetation and may scarify the soil. Depending on the severity of these treatments, conditions are created comparable to what may have existed following a severe stand replacing fire or a low intensity fire. Intermediate treatments to release seedlings can be thought of as mimicking the low intensity fires that killed shade tolerant competitors (Burgess and Wetzel 2000, Nyland 2002, MacKenzie et al. 2005, Hauessler et al. 2004).

In addition to the ultimate effects these treatments have on arboreal seedling regeneration and composition, many other effects occur in the understory, including changes in composition, cover, and richness of understory vegetation. The understory is essential to understanding an ecosystem and its regeneration processes because it cycles a significant amount of nutrients, constitutes a large amount of biodiversity, influences arboreal seedling survival, and contributes greatly to wildlife habitat (Giliam and Roberts 2003). Following a disturbance, understory dynamics including forest structure, light and moisture availability, substrate, nutrient cycling, and propagule availability illustrate the degree of severity.

There are few studies of disturbance-effects on the understory of white pine forests in the Great Lakes region (Neumann and Dickman 2001, Cook et al. 2008). Several studies have compared effects of different severities of mechanical and/or herbicide treatments or of prescribed burning or wildfires on understory properties (McGee et al. 1995; Nuzzo et al. 1996; Burgess and Wetzel 2000; Neumann and Dickman 2001; Hauessler et al. 2004; Lee 2004; Kemball et al. 2005; Newmaster et al. 2007). In general, soil temperatures and nutrient and water availability increase with treatment severity, at least in the short term (Burgess and Wetzel 2000, Hauessler et al. 2004; Newmaster et al. 2007). Burning, chopping, crushing, or herbicide application increase light, water and nutrient availability, as well as soil temperature, because there is less vegetation taking up these resources and casting shade. Burning releases nutrients from litter and other fuels often causing a short term increase in availability (Ahlgren and Ahlgren 1960). After mechanical treatments, nutrient availability can increase in the short term as litter and duff are incorporated into the soil, and over a longer time period as saplings and shrubs decay and release nutrients (Nyland 2002). Soil temperature in burns can increase temporarily through conduction of heat, although usually this effect is not significant unless the fire is very intense (Flinn and Pringle 1983). Reduction of litter and duff depth according to intensity, and the resulting black ground layer are contributors to increased soil temperatures. The former of these also applies to mechanical treatments because the insulation of the litter and duff layer are usually heavily disrupted and the soil is more exposed. Soil microorganisms, including mycorrhizal fungi, which are important in tree and understory vegetation growth, can also be impacted by burning (Smith et al. 1999) or mechanical and herbicide treatment. Fire and mechanical and herbicide treatment tend to result in increased understory species richness, diversity and cover. Often this includes a short term increase in annuals and biennials and increase in biomass or cover (Henderson and Statz 1995; Nuzzo et al. 1996; Neumann and Dickman 2001; Elliott and Knoepp 2005; Kemball et al. 2005)

In general, understory response is roughly proportional to degree of severity (Roberts 2004). However, few studies have compared prescribed burning to M+H treatment. Using the framework of Roberts' disturbance severity model, we can attempt to quantify and better understand the effects of these two disturbances for this forest community. Roberts' model of disturbance severity classifies disturbances based on the amount of forest canopy removed, understory vegetation removed, and forest floor disturbed. To varying degrees, disturbance effects can play an important role in silvicultural management that attempts to incorporate the historic disturbance regimes that a species or ecosystem is adapted to. With this study, I hope to further clarifiy effects of disturbance in this forest community.

CHAPTER 1:
EFFECTS OF BURNING VERSUS MECHANICAL AND HERBICIDE TREATMENT ON SAPLINGS, UNDERSTORY, AND SEEDLING REGENERATION IN A NORTHERN MESIC EASTERN WHITE PINE (*Pinus strobus* L.) FOREST IN MENOMINEE INDIAN RESERVATION, WISCONSIN.

ABSTRACT

While site preparation treatments are common in a shelterwood system, there is little research comparing prescribed burning to herbicide and mechanical treatment in the Lake States. Our main questions were: i) in this northern mesic white pine forest does prescribed burning or mechanical and herbicide treatment following an establishment cut have more severe impact on understory and sapling layer vegetation? ii) which treatment is more effective for promoting eastern white pine regeneration? A prescribed burn treatment or mechanical and herbicide treatment (M+H) were conducted on two similar ~150 year old stands of northern mesic white pine forest in the Menominee Indian Reservation, northeastern Wisconsin. Treatments occurred 8 to 10 years after establishment cuts that were part of a shelterwood system. Vegetation was sampled before and for five growing seasons after the treatments. We calculated density and composition of saplings; average cover, richness and diversity of understory vegetation; and density and composition of arboreal seedlings in burn, M+H and control treatments. The control treatment had significantly greater density of saplings per hectare than burn and M+H treatments ($p = 0.01$). Understory richness, diversity and average cover were greatest on prescribed burn treatments. Arboreal seedling density was greater on M+H treatments but 77% of the regeneration was red maple (*Acer rubrum* L.) at the end of the

study. We conclude that the M+H treatments were more severe than prescribed burns, but did not result in the most desirable regeneration.

INTRODUCTION AND LITERATURE REVIEW

Eastern white pine is a dominant species of much of the Great Lakes forests where its stand establishment historically depended on fire and windthrow (Heinselman 1981, Maissurow 1941). At present, the shelterwood system is commonly used to regenerate managed eastern white pine or mixed white pine forests in the Lake States and Canada (Wendel and Smith 1990). Although many variations exist, the shelterwood is a common even-aged method where the overstory is removed in two or more stages allowing seedlings to regenerate in the increased light available before the entire overstory is removed.

Often some type of site preparation is necessary near the time of the first removal cut (also called the establishment cut) to achieve a suitable seed bed for regeneration and reduce competition (Burgess and Wetzel 2000, Nyland 2002). Site preparation treatments can include prescribed burning, herbicide application, mechanical soil scarification, chopping, mowing or crushing vegetation, or some combination of the above (Nyland 2002). These treatments affect litter and duff depth, soil temperature, and soil microorganisms and nutrient and water availability to differing degrees depending on the severity of disturbance. In turn these treatments can determine composition and diversity of understory vegetation, arboreal seedling establishment, and ultimately overstory species (MacKenzie et al. 2005, Hauessler et al. 2004). The reaction of the understory to site preparation methods is important to understanding collective effects of M+H treatment on the community. The understory contains a large amount of biodiversity and plays an important role in nutrient cycling, arboreal seedling survival, and wildlife habitat (Giliam and Roberts 2003).

Several studies have compared effects of different severities of mechanical and/or herbicide treatments on understory properties such as depth of litter and duff, soil temperature, soil nutrient and water availability, and understory richness, cover and composition. In general, understory diversity, solar radiation, soil temperatures and nutrient and water availability increase with site preparation treatment severity, at least in the short term (Burgess and Wetzel 2000, Hauessler, et al. 2004; Newmaster et al. 2007). Chopping or crushing of vegetation increases light availability and soil temperature, as well as water and nutrient availability, because there is less vegetation taking up these resources; these conditions tend to improve seedling regeneration. Some types of mechanical treatment also churn the soil, which can overturn the litter and duff layer and make nutrients more available in the soil (Nyland 2002). Soil scarification using a brush rake resulted in significantly greater oak seedling densities and significantly lower red maple densities three years later (Zaczek 2002). A comparison of different mechanical treatments in northern British Columbia found that the change in microclimate, including soil temperature and water availability, was the most important factor leading to increased tree growth (MacKenzie et al. 2005).

Herbicide application does not alter litter and duff depth directly but can cause warming of the soil due to increased light. Application of glyphosate has been found to reduce tall shrubs or saplings and thereby increase the richness of the herb layer for 10 years after treatment (Boateng and Bedford 2000). The decreased uptake of water and nutrients can also improve availability for desirable species (Elliot 2005).

Light prescribed burning can somewhat reduce the litter layer but does not reduce the duff depth. This treatment also generally results in an increase in nutrient and water availability as well as soil temperature, in part because small diameter trees and shrubs are killed. In general fire tends to result in increased species diversity, a short term increase in annuals and biennials, and increase in biomass or cover (Henderson and Statz 1995).

While there are many studies investigating the effects of different intensities of prescribed burning, there are few comparing effects of prescribed burning as a site preparation method to M+H treatment. Specific questions of this study were: a) Does mechanical and herbicide treatment serve as a more or less severe treatment (as indicated by sapling density, understory cover, richness, and diversity, and arboreal seedling density) than prescribed low intensity fire? b) Does M+H treatment provide better regeneration for eastern white pine than prescribed low intensity fire?

METHODS

Study Site

The study sites are two stands approximately eight kilometers apart in a northern mesic eastern white pine dominated forest in the Menominee Nation, northeastern Wisconsin (44°56'N, 88°40' W). Elevation is approximately 300 meters above sea level. Average growing season is approximately 133 days per year with an average summer temperature of 20° Celsius and an average winter temperature of -8° C. Average precipitation is approximately 81.76 cm (Mitchell 2004). The soils of both stands consist of deep glacial deposits of loamy alluvium which are moderately well drained, not subject to erosion, and have a moderate nutrient level. The historic disturbance regime of the study site is believed to have included large scale (greater than 405 ha) windthrow and a mixed fire regime including severe large-scale crown or surface fires at intervals of 200 to 300 years, with low intensity fires at intervals of 20 to 40 years (Heinselman 1981, Canham and Loucks 1984, Abrams 2001). Age of dominant white pines on both sites is approximately 150 years old (as of 2007).

Compartment 219 (Burns and 2 controls)

The site is nearly level to gently sloping (less than 6% slopes). Soils are fine sandy loams and some fine sands over sandy outwash overlying the granitic Wolf River batholith. The taxonomic classification of the dominant soil series is sandy mixed, frigid Typic Haplorthods (Mitchell 2004). Although the site is dominated by eastern white pine, its Kotar habitat type is *Acer saccharum-Tsuga canadensis-Fagus grandifolia-Dryopteris spp.* according to Menominee Tribal Enterprises (Ron Waukau, pers. comm. 6/06/08). As of 2001, basal area of the stand was 22 m^2/ha of white pine and 3.5 m^2/ha of hardwoods including sugar maple (*Acer saccharum* Marshall), red maple (*Acer rubrum*), northern red oak (*Quercus rubra* L.), American beech (*Fagus grandifolia* Ehrh.), bitternut hickory (*Carya cordiformis* (Wangenh.) K.Koch), and yellow birch (*Betula alleghaniensis* Britton). The subcanopy includes American elm (*Ulmus Americana* L.), ironwood (*Ostrya virginiana* (Mill.) K.Koch.), and alternate leaved dogwood (*Cornus alternifolia* L.f.). The site experienced two shelterwood cuts 18 and 14 years ago as part of regular management by Menominee Tribal Enterprises. An herbicide and mechanical treatment was conducted on the site 18 years ago (Table 1).

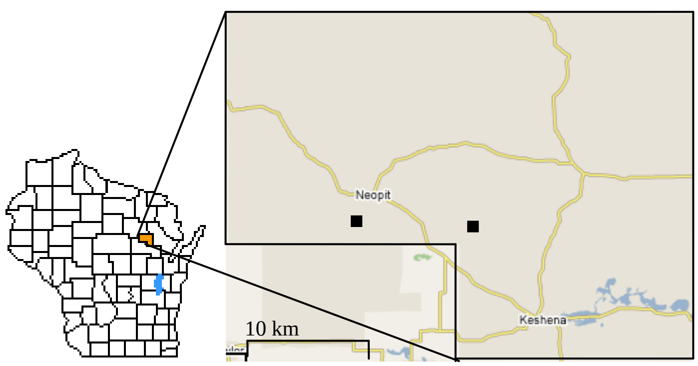
Compartment 344 (M+H and 4 controls)

The M+H and the remaining control units have slopes ranging from nearly level to slopes of 6 - 15%. Soil parent material is silty or loamy alluvium over sandy or loamy glacial till and is considered very bouldery. The taxonomic classification of the dominant soil series, Kennan silt loam, is coarse-loamy mixed, superactive, frigid Typic Glossudalfs (Mitchell 2004). Although the site is dominated by eastern white pine its Kotar habitat type is *Acer-Tsuga-Maianthemum* according to Menominee Tribal Enterprises (Ron Waukau, pers. comm. 6/06/08). A shelterwood cut to 11m^2 basal area was completed in 1989 (Table 1). In 2001 basal area of white pine was 25.8 m^2/ha and 4.2 m^2/ha of hardwoods; the composition was similar to Compartment 219. In 2001 there were not significant differences in overstory composition, basal area, sapling density, understory composition or arboreal seedling density between this site and Compartment 219 (Galbraith 2005).

Table 1. Stand history of M+H, burn, and control units

Year	Compartment 344 -M+H and 4 controls		Compartment 219 - Burns and 2 controls	
~1862	Stand establishment		Stand establishment	
1988			34.4 m^2 basal area/ha	
Mar. 1989			Harvest to 60-70% crown closure(cc), 26.4 m^2 BA/ha	
Sep. 1989	39 m^2 basal area/ha		M+H treatment: 3.5 liter glyphosate/ha and double pass Bracke scarifier	
Winter 1991	Harvest to 60-70% cc, 30 m^2 BA/ha, no site preparation		Regeneration failure: mostly maple, beech, balsam	
1993			Harvest to 50% cc, 23 m^2 BA/ha, no site prep	
	M+Hs	controls	burns	controls
Sep. 2002	M+H treatment: 3.5 liter glyphosate/ ha and double pass Bracke scarifier. 29.2 m^2 BA/ha	No treatment 30.6 m^2 BA/ha	27.5 m^2 BA/ha	24.6 m^2 BA/ha
Apr. 2003			Low intensity prescribed burns	No treatment
Summer 2003	30.6 m^2 BA/ha	31 m^2 BA/ha	26.3 m^2 BA/ha	24.6 m^2 BA/ha

Figure 1. Approximate location of study sites in Menominee County, Wisconsin (indicated by black squares). Maps courtesy Wisconsin online and Google maps.

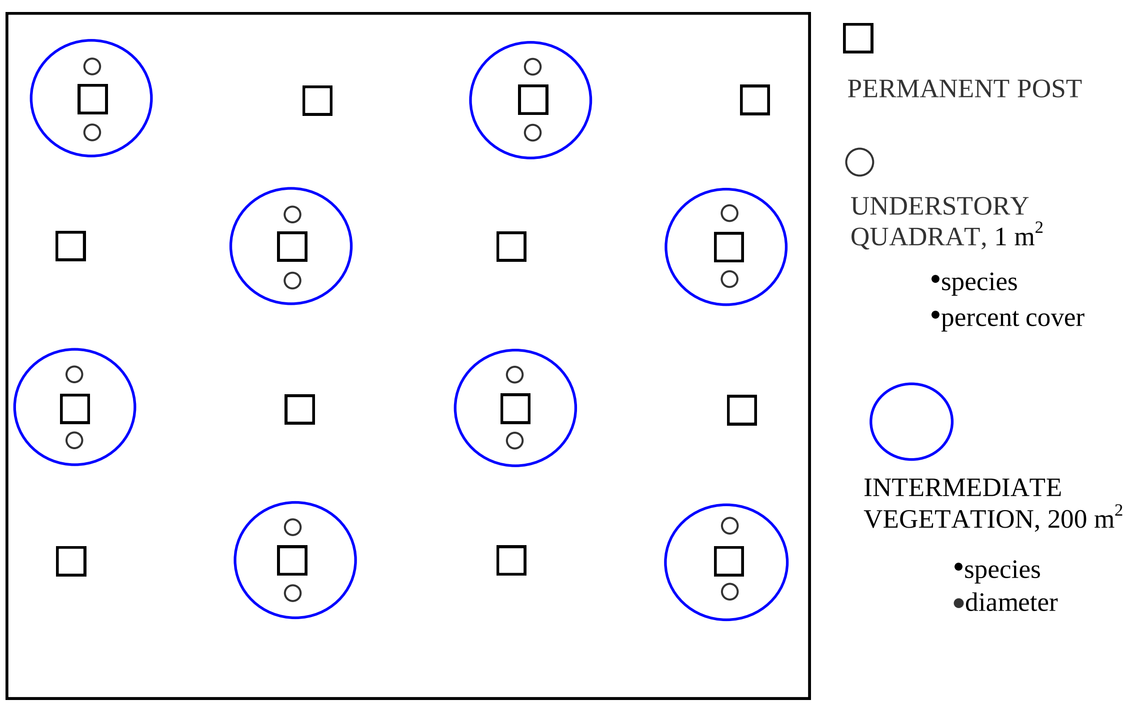


Unit Layout and Treatments

Treatment units are within the above described compartments, which are located in the south-central part of the county (Figure 1).   Compartment 344 contains three mechanical and herbicide treated units and four control units: two near the treated units and two one km away.   Compartment 219 contains four burn units and two control units nearby. Treatment and control units are 0.81 hectares. In each unit a 15.2 by 15.2 meter grid of 16 permanent metal posts guided sampling (Figure 1). There is a 10.06 meter buffer between the boundary of the unit and the outer row of posts and a minimum 20-meter untreated buffer between units within compartments.

Observations of understory vegetation were taken from eight, paired, one-square-meter circular quadrats placed in reference to eight of the 16 posts (Figure 2). The sapling layer was sampled in 200 m^2 quadrats around selected posts.

Figure 2. Treatment unit layout (not to scale)



M+H treatment

In September 2002, three 0.8 hectare units in compartment 344 were treated with 3.5 liters per hectare of glyphosate. The following October the same units were mechanically treated with a Bracke-scarifier using the double-pass method (pers. comm., Dan Pubanz via Dr. James Cook, University of Wisconsin-Stevens Point, July 30, 2002).

Prescribed burn treatment

Four units in Compartment 219 were burned in April 2003. A strip head fire ignition pattern with five to 10 meters between strips was used. Conditions during the burns were: nine days since last rain event, air temperature of 14 to 18°C, wind zero to 11.3 kph, and relative humidity 27 to 40 percent averaging 31 percent. There was high variability in fuel loads between units. The fires burned only the surface of the forest floor and spread slowly. Average flame length was 0.78 m (0.3 – 1.4) and flamefront intensity was 153 kWm^{-1}, which indicates a low intensity fire (Cook et al. 2008).

Since the M+H treatment occurred at the end of the growing season and the burn treatment occurred just prior to the beginning of the next growing season, we characterize growing seasons since treatment in all units equivalently.

Field sampling

In each 0.81 hectare unit, percent cover of herbaceous and woody vegetation ($\leq$1.37 m tall) and counts of arboreal seedlings were recorded in 16, one m^2 quadrats during spring and summer 2006 and 2007. In 2007, stems of sapling size vegetation ($\geq$1.37 m tall but less than 20.3 cm dbh with a tree-like form, in the mid-story or lower) were recorded in 200 m^2 plots centered on the same eight posts where the understory was sampled. Sample size for saplings was eight plots in burn units and four plots in M+H and control units. Spring sampling dates were May 22 – June 22 and summer dates were August 6 - August 23. Understory, seedling and sapling sampling had previously been completed on the same quadrats in spring and summer 2002-04 (Galbraith 2005, Cook et al. 2008).

Data Analysis

For each 0.81ha unit, average sapling density per hectare was calculated based on the 200 m^2 plots. In each unit we calculated average percent cover of understory layer using mid-point of cover classes, understory species richness, diversity using the Shannon index, and average arboreal seedling density based on data from 16, one m^2 quadrats.

Multi-Response Permutation Procedure (MRPP) (PC-ORD version 5.0), was used to test for significance of each variable between burn, M+H, and control treatments. MRPP is a non-parametric, permutation-based method of testing the hypothesis of no difference between two or more pre-existing groups. MRPP compares distances among all possible permutations of data points between groups to test this hypothesis. For additional information on MRPP, see Zimmerman et al. (1985) or McCune and Grace (2002).

Sorenson's index was used to compare species similarity of the understory in burn and control units four and five growing seasons (grss) post treatment. It was also used to compare post-burn propagule bank composition to post-burn understory composition. Sorenson's index, also called Bray-Curtis coefficient, is a proportion coefficient; it can be represented by the overlap between the area under two curves (McCune and Grace 2002). The index gives a percent dissimilarity; subtracting the result from one gives percent similarity which was used in our comparisons.

RESULTS

Pre-treatmet

Sapling densities, although variable among units, were not significantly greater in burns or M+H units than controls pre-treatment. In spring and summer 2002, there were not significant differences in understory richness, diversity, or percent cover between burn and control units. The understory in the burns was on average 31% similar to the understory of the controls (Galbraith 2005). Arboreal seedling density did not differ significantly between any of the treatments.

Sapling layer

Density

The only significant difference in sapling density between pre- and post-treatment was in the control units (A = 0.677, p = 0.003, Table 2). The increase in sapling density in the burns was non-significant compared to controls. Density of saplings almost doubled in the burns between 2001 and 2007. However, sapling density in control units increased by over four times the 2001 level (Figure 3). In M+H units sapling density increased slightly compared to pre-treatment and was significantly less than controls(A= 0.6896, p = 0.0095) five grss post-treatment (Table 2). See Appendix 1 for unit level densities.

Table 2. *A*-(Chance corrected within group agreement) and *p*-values for MRPP tests comparing sapling densities between treatments and years. ^Pre-treatment data were reported in Galbraith 2005.

Pre vs. post-treatment	***A***	***p***
Burns	0.0619	0.2012
M+Hs	-0.1000	0.6351
Controls	0.6375	0.0033*
Pre-treatment^		
M+Hs vs. Controls	-0.0618	0.7054
Burns vs. Controls	-0.00039	0.3946
M+Hs vs. Burns	0.15053	0.0767
Post-treatment		
M+Hs vs. Controls	0.6671	0.0108*
Burns vs. Controls	0.1222	0.1391
M+Hs vs. Burns	0.1098	0.1493

Figure 3. Average saplings per hectare averaged by treatment in 2001 and 2007. Error bars represent standard error of the mean. 2001 data previously reported in Galbraith 2005 and Cook et al. 2008.

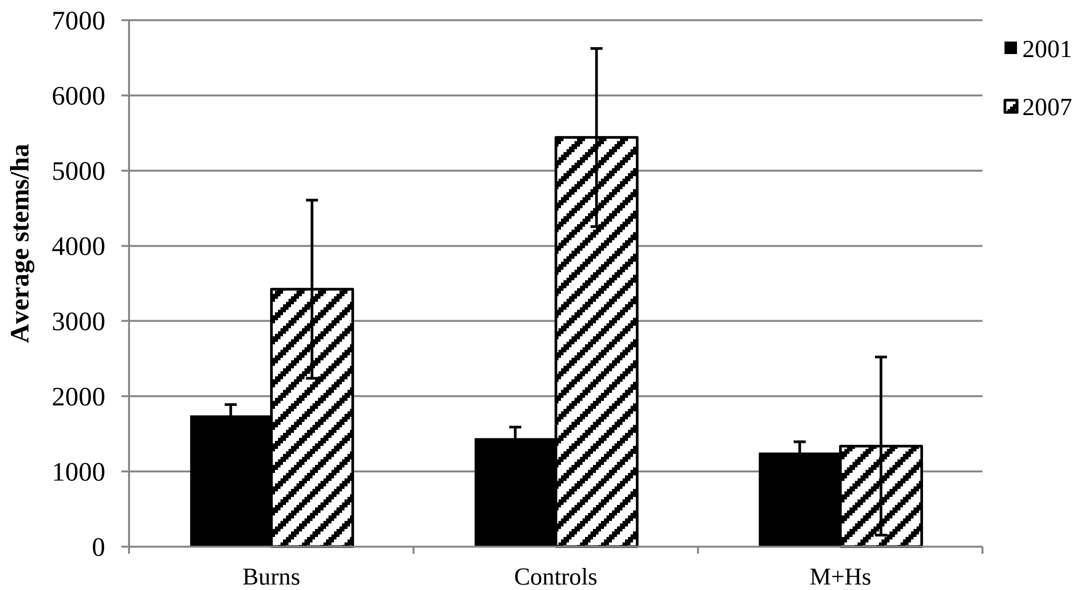


Figure 4. Five most abundant species of saplings pre- and post-treatment. See Appendix 2 for composition and density of all species in sapling layer.

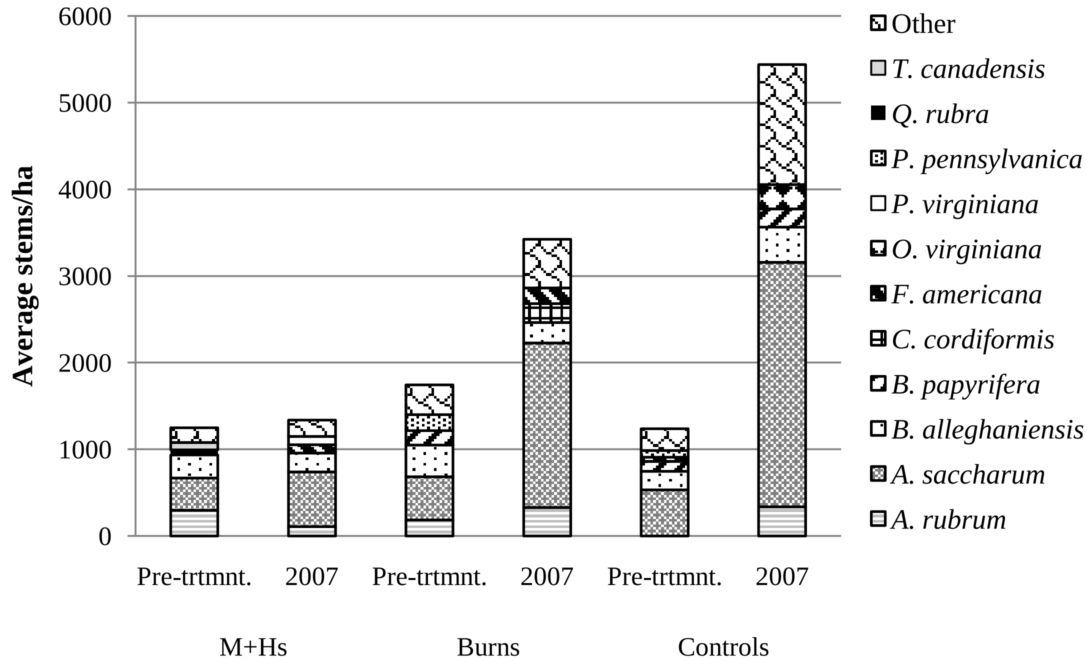
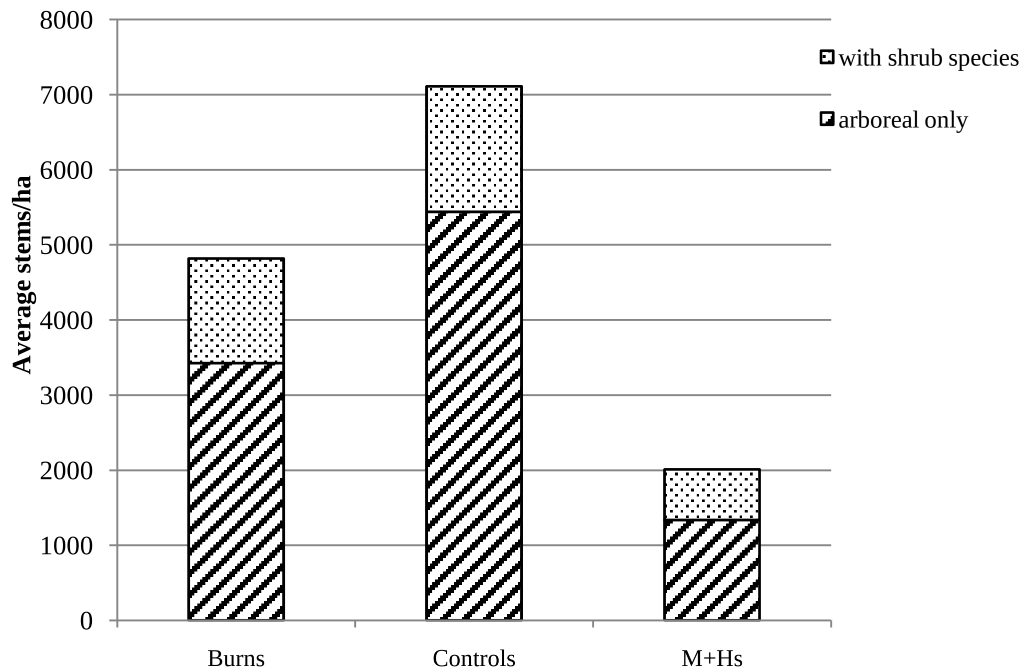


Figure 5. Average saplings per hectare by unit and treatment in 2007 with and without shrub species.



Composition

Sugar maple was the most abundant species in the sapling layer in all three treatments before and after treatment, increasing between 2002 and 2007 (Figure 4). Following the trend of density, the greatest magnitude of increase in sugar maple was in the control units, from 532.3 to 2818.8 stems/ha (Appendix 2). Red maple was also in the top five most abundant species for all treatments and time-periods, except in controls in 2002. Treatment effects on red maple were opposite for burns and M+Hs. Red maple saplings increased by 43% in burn units but decreased by 63% in M+Hs. Yellow birch was the only other consistently abundant species, staying almost the same in M+Hs, decreasing in the burns, and increasing in density but decreasing in relative abundance in controls.

In M+H units hemlock decreased while white ash (*Fraxinus americana* L.) increased. In burns, pin cherry (*Prunus pensylcanica* L.f.) decreased while bitternut hickory increased to almost 10% of saplings. In controls ironwood became more abundant than pin cherry by 2007.

Quantitative comparison with pre-treatment data for the abundance of shrub species meeting the criteria of sapling was not possible; however, it was noted that *Corylus cornuta* Marshall, *Hamamelis virginiana* L., and *Sambucus racemosa* L. made up very little of the sapling layer in 2002. When these shrub species are included in the 2007 count, *Hamamelis* and *Corylus* are in the top five of all treatments. *Corylus cornuta* is the second most abundant species in the burns while *Hamamelis* takes this position in the M+Hs and controls (Figure 5).

Understory

Diversity and cover

Five growing seasons following the treatments, burn units had significantly greater ($p \leq 0.02$) richness and average percent cover in spring and summer (Table 3, Figure 6). M+H units had lower values than burns for all three variables but significantly greater values than controls for richness in spring 2007 ($p=0.04$), and average cover in spring ($p=0.036$) and summer 2007 ($p=0.0038$) (Table 4).

Fern and clubmoss cover increased in burns and controls, but decreased in M+Hs. Cover of perennial forbs increased in controls, greatly increased in burns but decreased and were just recovering to pre-treatment level by 2007 in M+Hs (Table 3).

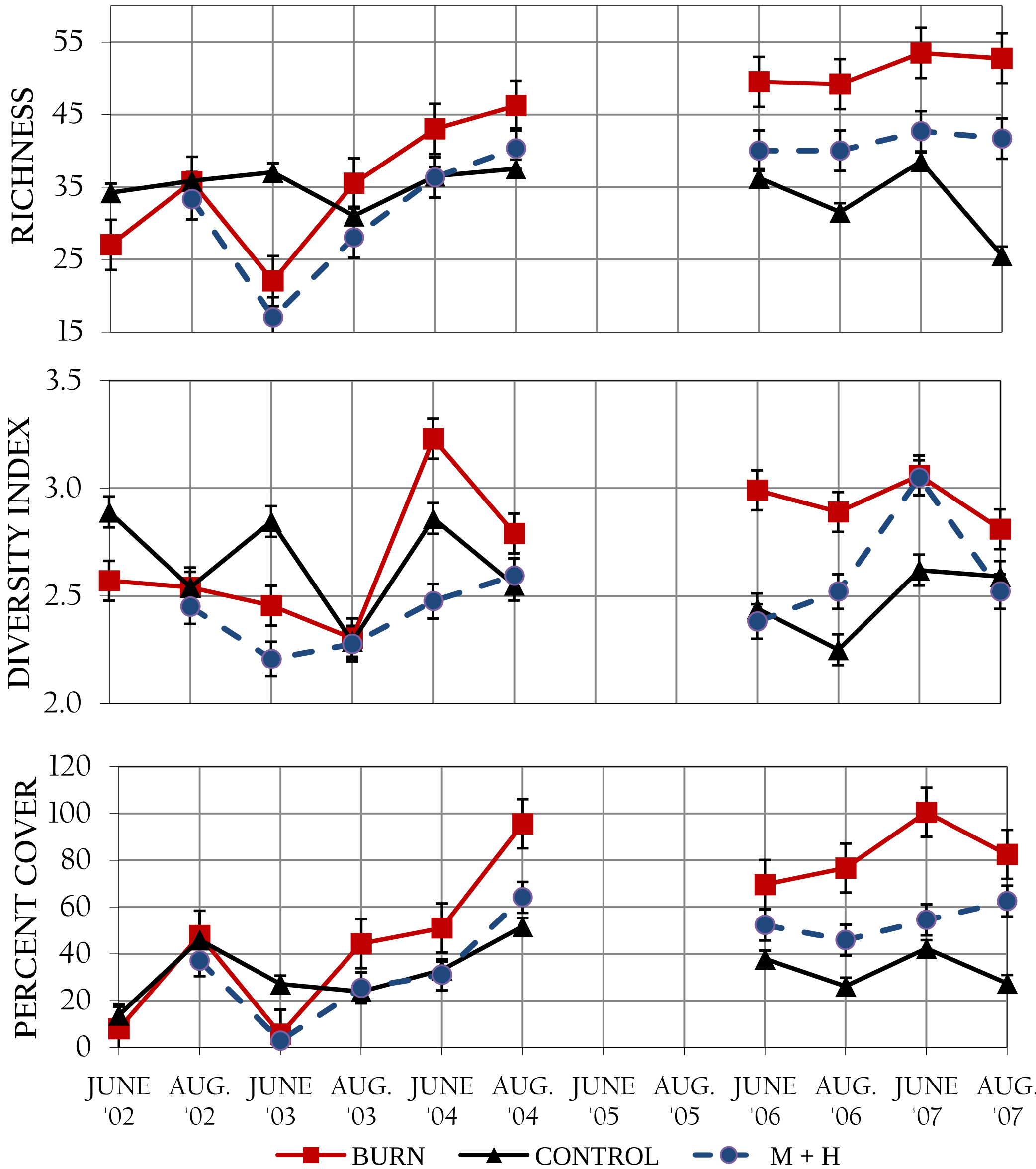
Table 3. Average percent cover of life forms, richness, and diversity averaged by treatment, pre-treatment and four and five growing seasons post-treatment. *2002 values previously reported in Cook et al. 2008 and Galbraith 2005.*

	Average Percent Cover									Richness	Diversity (Shannon index)
	Ferns & clubmoss	Grasses	Carex & Juncus	Rubus	Forb-annual	Forb-perennial	Shrub	Tree	Total		
SPRING											
M+H n=3											
02 spring											
06 spring	0.531	0.344	5.25	16.82	0.063	7.01	5.21	9.51	44.74	39.3	2.54
07 spring	0.927	0.344	4.96	21.39	0.094	6.69	7.3	12.77	54.48	41.7	2.57
Burns n=4											
02 spring	0.164	0.47	0.429	1.24	0.03	3.57	1.15	0.89	7.9	27	2.572
06 spring	8.74	0.601	4.95	15.15	3.91	19.30	4.66	12.29	69.6	49.5	2.991
07 spring	12.86	0.54	6.27	27.11	3.30	26.49	9.25	16.90	102.7	53.5	3.062
Controls n=6											
02 spring	1.38	0.35	0.927	1.009	0.039	5.51	1.63	2.89	13.75	34.2	2.89
06 spring	10.38	0.173	0.41	3.6	0.194	7.37	2.61	12.68	37.5	36.2	2.44
07 spring	13.49	0.29	0.47	1.94	0.13	10.01	4.26	11.68	42.3	38.5	2.59
SUMMER											
M+H n=3											
02 summer	8.76	1.08	4.53	6.92	0	6.28	6.73	2.58	36.89	32	2.49
06 summer	0.75	0.438	4.01	21.51	0.094	4	5.39	8.58	44.78	38.7	2.53
07 summer	0.95	0.22	7.26	25.75	0	6.03	7.67	14.29	62.17	39	2.52
Burns n=4											
02 summer	10.23	0.539	4.467	5.86	0.143	12.42	4.32	9.90	47.9	35.7	2.539
06 summer	10.64	0.59	5.68	23.84	2.42	16.45	5.03	11.99	76.64	49.2	2.878
07 summer	12.54	0.45	5.52	29.84	1.23	15.09	7.25	17.49	89.41	50.5	2.811
Controls n=6											
02 summer	9.152	0.725	2.681	15.09	0.229	4.97	4.287	8.76	45.9	35.8	2.54
06 summer	10.42	0.218	0.75	2.94	0.117	3.89	1.06	6.71	26.11	31.5	2.25
07 summer	11.16	0.44	0.77	2.13	0.04	4.15	2.15	8.66	29.48	33	2.37

Table 4. *A*-(chance corrected within group agreement) and *p*-values from MRPP tests of richness, diversity, and average percent cover between burns, M+Hs and controls four years following treatments. * indicates significance at 95% confidence level, *p*-value after Bonferroni correction is 0.0167.

	A	***p***
RICHNESS		
Spring 2007		
M+Hs vs. Controls	-0.0991	0.9206
Burns vs. Controls	0.2769	0.0193*
M+Hs vs. Burns	0.2358	0.0784
Summer 2007		
M+Hs vs. Controls	0.2240	0.0419*
Burns vs. Controls	0.3019	0.0234*
M+Hs vs. Burns	0.0483	0.2697
DIVERSITY		
Spring 2007		
M+Hs vs. Controls	-0.0531	0.6692
Burns vs. Controls	0.0899	0.1106
M+Hs vs. Burns	0.3475	0.0095*
Summer 2007		
M+Hs vs. Controls	-0.0130	0.4667
Burns vs. Controls	0.0355	0.3178
M+Hs vs. Burns	-0.0967	0.6623
AVERAGE PERCENT COVER		
Spring 2007		
M+Hs vs. Controls	0.1858	0.0362*
Burns vs. Controls	0.6834	0.0014*
M+Hs vs. Burns	0.5682	0.0128*
Summer 2007		
M+Hs vs. Controls	0.5519	0.0038*
Burns vs. Controls	0.6804	0.0018*
M+Hs vs. Burns	0.2903	0.0832

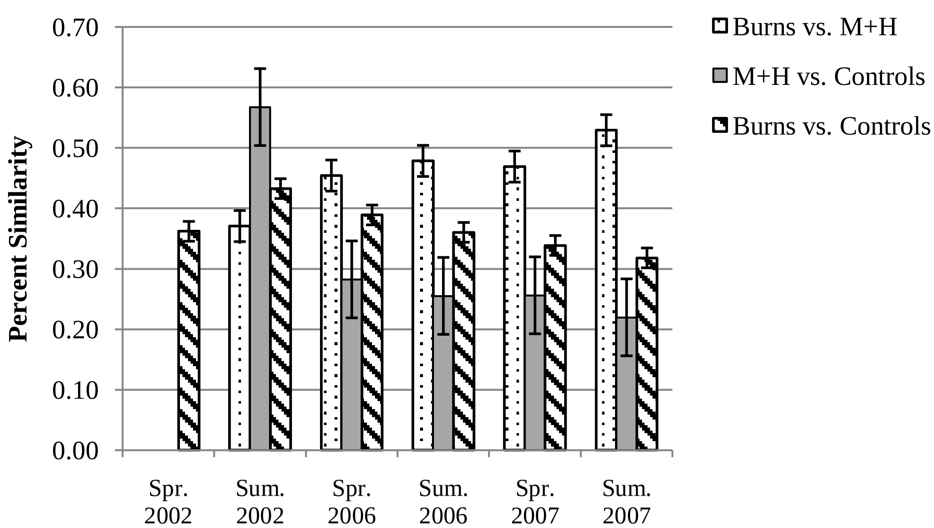
Figure 6. Richness, diversity, and average percent cover in M+H, burn, and control treatments 2002 to 2007. *2002-2004 data previously reported in Galbraith 2005 and Cook et al. 2008.*



Similarity

Pre-treatment (summer 2002) the understory of burn and M+H units were 37% similar to each other (Galbraith 2005). At this time burns had about the same level of similarity to the controls, but M+Hs were more similar to the controls. Five growing seasons following treatments burns and M+H units were 47% and 53 % similar in spring and summer respectively, following a trend of increasing similarity since spring 2006. Similarity of burns to controls followed a reverse trend, becoming less similar from spring 2006 to summer 2007. Similarity of M+H to controls also followed this trend (Figure 7). See Appendix 3 for understory species list.

Figure 7. Percent similarity of understory vegetation between treatment by time period and year. *Error bars are standard error*.



Arboreal seedlings

Four years following treatments, density of arboreal seedlings was greater on M+H units than burn (43%) and control (42%) units (Figure 8). Composition of seedlings changed over time due to the treatments. In M+Hs pre-treatment (summer 2002), red maple was 14.5% of arboreal seedlings. By summer 2007, 77% of arboreal seedlings in M+Hs were red maple. In burn units sugar maple was the dominant arboreal species pre treatment and four years post treatment, although red maple slightly increased. White ash and pin cherry seedlings also increased in burns. In control units red maple was the dominant species in 2002; over the four years red maple decreased while sugar maple increased (Figure 9). White pine seedlings did not comprise a significant proportion of seedlings during any time periods (Table 5, Appendix 6).

Figure 8. Average density of arboreal seedlings per hectare in burns, controls, and M+H units 2002 through 2007. *Error bars are standard error. 2002-2004 data previously reported in Cook et al. 2008.*

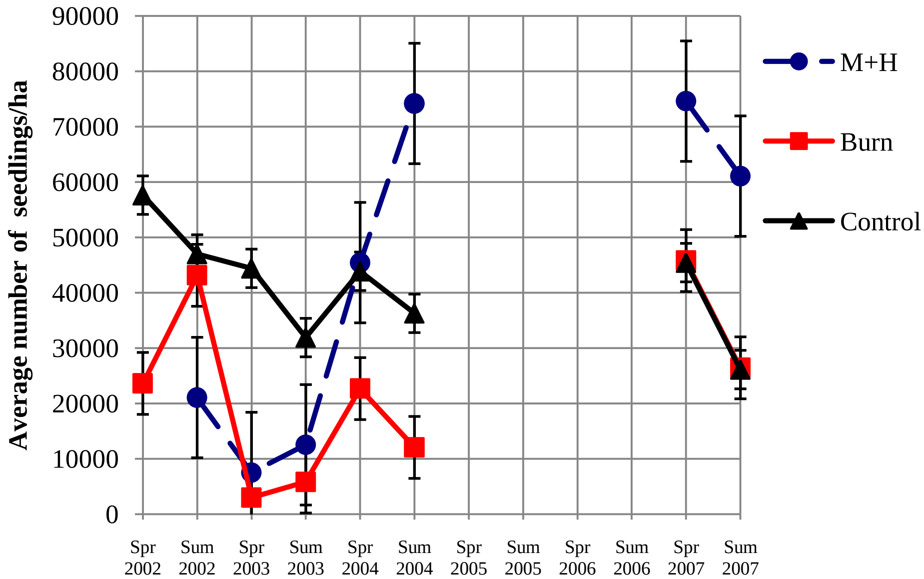


Table 5. Average seedlings per hectare of eastern white pine pre-treatment and four years post-treatment

	Spr. 2002	Sum. 2002	Spr. 2007	Sum. 2007
M+Hs	no data	2500.00	208.33	416.67
Burns	156.25	937.50	312.50	625.00
Controls	625.00	937.50	104.17	312.50

Figure 9. Relative composition of five most abundant arboreal seedlings in M+H, burn and control units pre and five grss post-treatment. See Appendix 6 for composition and density of all seedlings. 2002 data previously reported in Galbraith 2005 and Cook et al. 2008.

a. M+H units

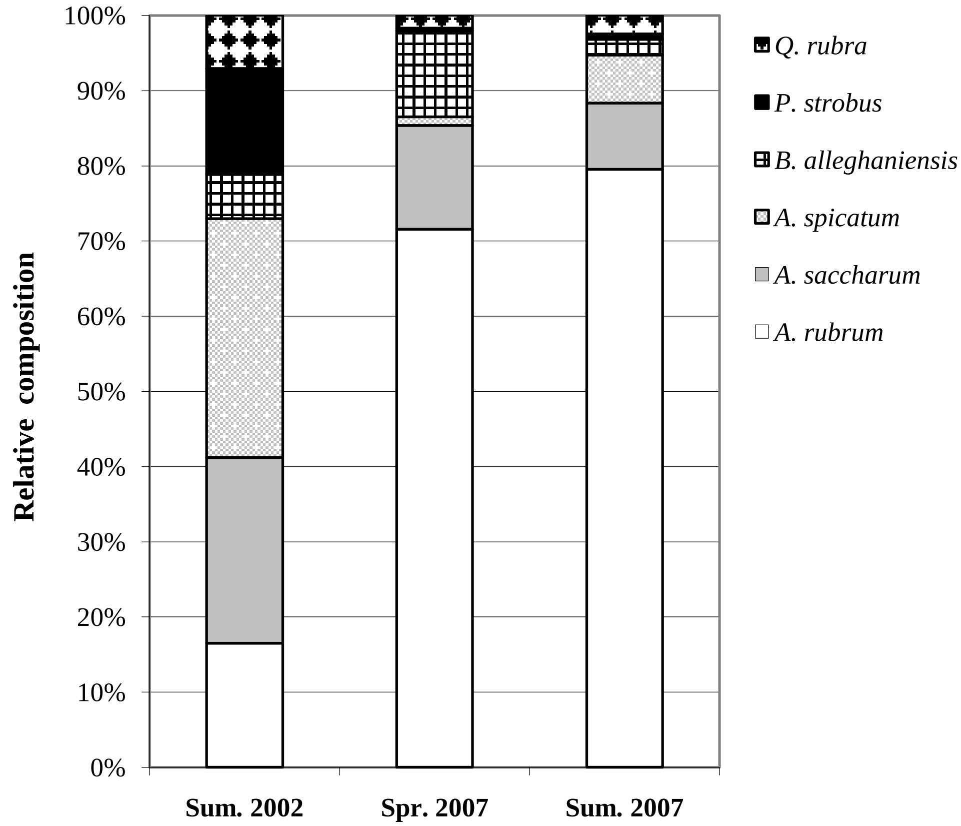


Figure 9. continued.

b. Burn units

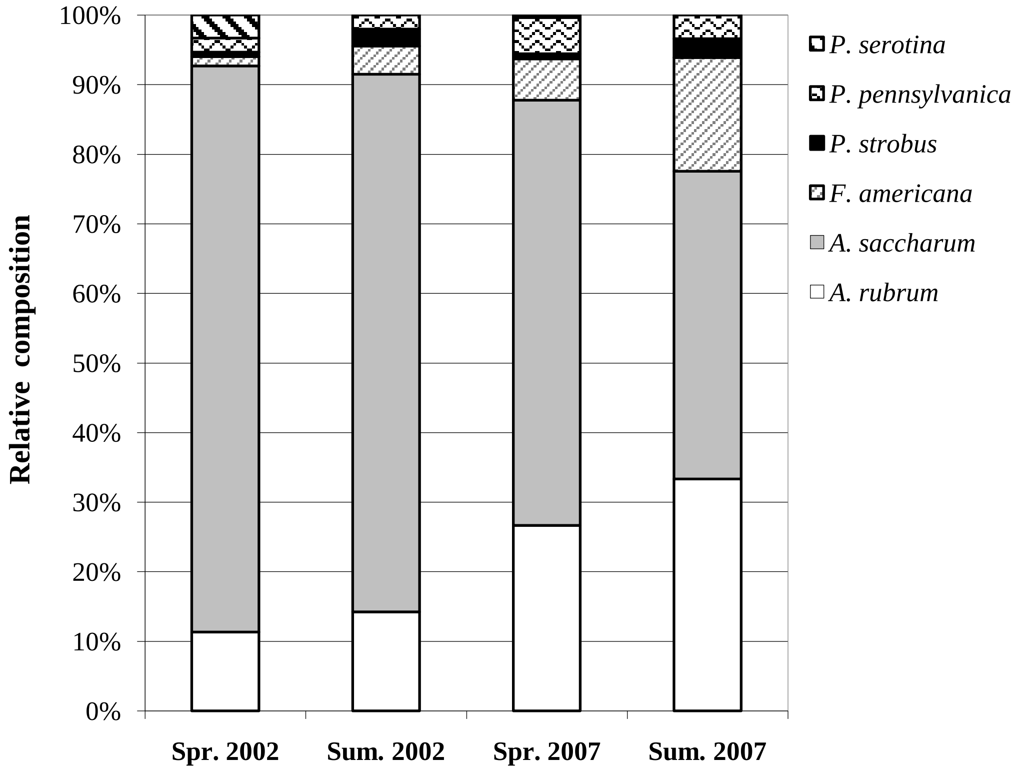
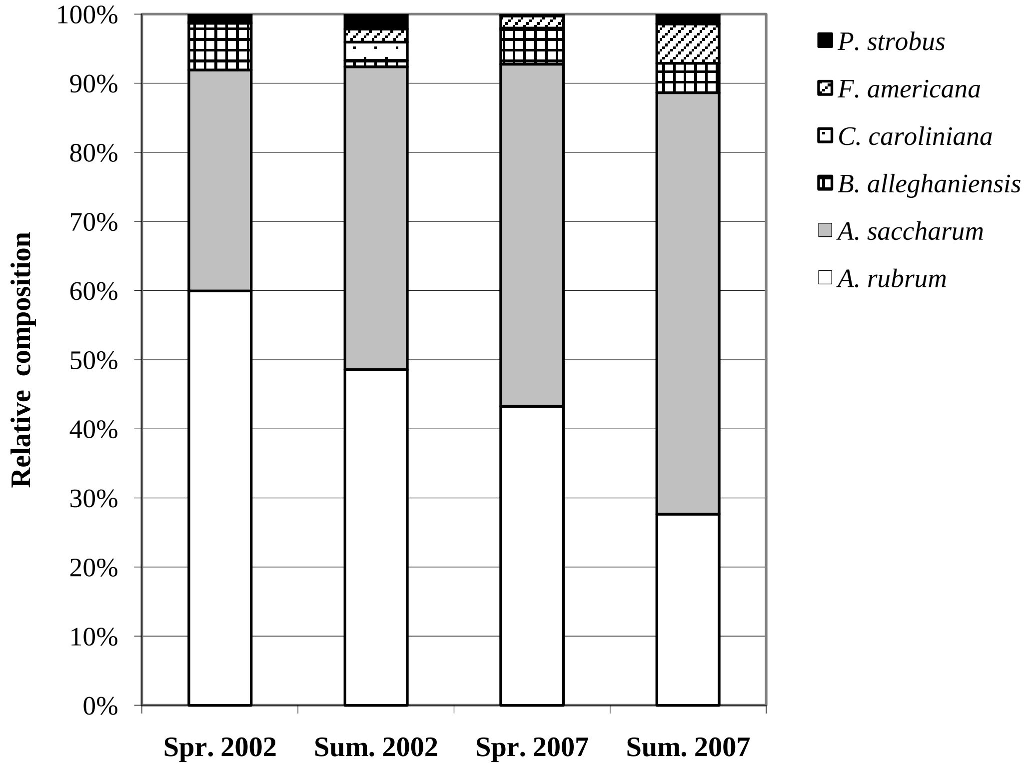


Figure 9. continued.

c. Controls



DISCUSSION

Compared to burn and control units the M+H treatment was clearly the most severe disturbance to saplings. Sapling density was significantly lower in M+H treated units than control units when arboreal species were considered. Qualitatively, this difference remained when shrub species were included in density (Figure 4). Sapling density of control treatments illustrates the need for some type of site preparation in this northern mesic forest; an establishment cut without site preparation resulted in a dense hardwood sapling layer in controls.

Sapling composition also may indicate severity of the treatments. Composition of burn units shared similarities with controls such as a large increase in sugar maple, and an increase in red maple. The increase in red maple in the burns may at first seem surprising because red maple is killed by low intensity fire, especially in spring burns (Hodgkins 1958, Walters and Yawney 1990). However red maple is known to sprout vigorously (Scheiner et.al. 1988) and in 2004, 88% of the red maple saplings in burns were sprouts (Cook 2005). In the M+H units there was a small amount of sprouting. The decrease in red maple in M+H units, especially since it can be resistant to herbicide (Lyman and Kuhns 1989), indicates the M+H treatment was more severe than the burn.

When shrub species, including witch hazel and beaked hazelnut, are factored into sapling density, it appears that both the M+H and burn treatments greatly reduced the density of shrub species compared to the controls. However, M+H units had the lowest sapling density, which supports the hypothesis that this treatment had the greatest severity. Density of witch hazel was greater in the M+Hs than in the burns but burns had greater density of beaked hazelnut than controls. The burn and M+H treatments both must have some confounding effect on shrub species.

The prescribed burn treatment may be less desirable in terms of this site's commercial forestry potential. The amount of red maple sprouts could be a concern; trees of this species that develop by sprouts can have poor form or can pre-maturely rot at the base. The prevalence of red maple could also be a concern because this species is often of less value economically. The density of witch hazel and beaked hazelnut, greater in burn units in absolute terms, is another contrast between burns and M+H units. These species could out-compete desirable hardwoods or white pine seedlings for light and other resources (McGee 1970).

Severity levels of the treatments indicated by sapling densities are matched by the seedling densities. Controls had the highest density of saplings and *Corylus* and *Hamamelis* in summer 2007, but the lowest seedling density. Concurrently the M+H units had the lowest sapling density and greatest seedling density. The greater density of seedlings on M+H units indicates that this treatment had greater severity. The mechanical treatment may have provided a more suitable seedbed compared to the burn treatment. It was noted in the year of treatment that the burn resulted in approximately 30% forest floor disturbance and the M+H resulted in approximately 55% forest floor disturbance (Cook 2005). Furthermore, there was probably more light available in the M+Hs due to lower sapling density. However, the large increase in red maple seedling regeneration in the M+Hs could be a negative impact of the M+H treatment depending on management objectives.

Richness, diversity and cover of the understory are more complicated in indicating treatment severity. In general, understory diversity, soil and water temperatures, solar radiation and nutrient availability increase with site preparation treatment severity, at least in the short term. The burn treatment stimulated the understory to a greater degree than the M+H treatment. This does not necessarily contradict our initial conclusion that the M+H treatment was more severe. Newmaster et al. (2007) found in a study comparing mechanical treatments that the most severe treatment resulted in the lowest species diversity five years after treatments. Peltzer et al. (2000) found that biomass of understory species declined with disturbance intensity. Even though the M+H treatment likely resulted in greater light and water availability (Burgess and Wetzel 2000, Hauessler, et al. 2004; Newmaster et al. 2007), reasons for greater increase in richness, diversity and cover in the burn units include differences in nutrients, coarse woody debris, microtopography, and soil compaction. Both the burn and the M+H treatment likely resulted in increased nutrient availability. However, even though the number of grss following treatment was the same, the M+H treatment occurred after the growing season. Nutrients made available by churning may have been leached from the soil over the winter whereas the burns, which occurred as the growing season began, made nutrients immediately available to understory plants (Wein and MacLean 1983, Schwemlein and Williams 2007). Coarse woody debris increased in M+H units. However, more saplings died in M+H units, and they were either lying on the forest floor or at 45° or greater angle. The volume and arrangement of this debris could have affected the magnitude of response by the understory due to shading or decreasing available space to grow. The impact of the soil disruption by the Bracke scarifier and soil compaction by the tractor that pulled it could contribute to the understory response as well. Ramovs and Roberts (2003) found that microhabitats of understory plants were more disrupted as disturbance severity increased in mechanical site preparation. Soil compaction was also found to affect the height of all plant groups in a five year study in a central hardwood forest (Ponder 2008).

Another indication of severity effect on the understory is composition as indicated by changes in similarity indices and life forms. While richness, cover, and diversity were leveling off in both treatments by summer 2007, the similarity in composition continued to decrease in response to both treatments, especially in M+H units. Additional data are needed to determine how long this effect will persist. However, the greater decrease in similarity of M+Hs to controls compared to that of burns to controls seems to support Alban's et al. (1994) conclusion that heavier disturbed areas take longer to return to pre-disturbance composition. The decrease of fern and clubmoss cover in M+Hs is consistent with several studies finding declines of fern and clubmosses following mechanical treatment (Hauessler et al. 2004, Newmaster and Bell 2002, Newmaster et al. 2007). The decrease in cover of perennial forbs was due mostly to a reduction in cover for many species rather than loss of species. The first grs post-treatment 10.5 and 14.5 species were lost in spring and summer. Perennial forbs lost in M+H units in summer were: *Aralia nudicaulis* L., *Aster macrophyllus* L., *Aster* spp., *Circaea alpina* L., *Coptis trifolia* (L.) Salisb., *Gaultheria procumbens* L. These species are shade tolerant, suited to mesic conditions, produce few seeds and several re-produce by shallow, thin rhizomes (Newmaster et al. 2007). The combination of smothering, herbicide induced mortality and greater light availability in the M+H treatment, contrasted with less forest floor disturbance and greater probability to re-sprout in the burn treatment, likely contributed to the contrast in cover of perennial forbs between treatments. There were fewer differences in cover of grasses, sedges, *Rubus* spp, and annual forbs between the two treatments. The small effect on grass cover matches a study of vegetation five growing seasons following mechanical and herbicide treatment (Sutherland and Foreman 2000). However the increase by sedges contrasts with other studies finding no increase (Sutherland and Foreman 2000, Bell and Newmaster 2002, Forrester and Bohn 2007).

Based on sapling and seedling density as well as some characteristics of understory response, the M+H treatment is a more severe site preparation method for this northern mesic white pine forest than prescribed burning. Five grss following treatment, sapling density of M+Hs was significantly lower than controls and qualitatively much lower than the burn treatments. During the same period seedling density increased greatly on the M+Hs while it decreased in burns and controls. Although richness, diversity and cover of the understory were greater in burns than M+Hs, cover of life forms had some important differences. The decrease in the fern/clubmoss and annual forbs and gradual recovery of perennial layer compared to burns, indicates differential effects on these life forms. These understory effects are important factors in evaluating the effects of a site preparation treatment.

Given the above discussion, the M+H treatment may appear preferable for white pine regeneration, yet the prescribed burn treatments had a higher stocking level. However, white pine seedlings were only 2% of arboreal seedlings in the burns in summer 2007 with other hardwood species dominating. Silviculturally neither of these treatments would be considered successful for white pine regeneration.

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CHAPTER 2

FIRE EFFECTS ON SAPLINGS, UNDERSTORY, AND PROPAGULE BANK OF A NORTHERN MESIC EASTERN WHITE PINE FOREST FOUR AND FIVE GROWING SEASONS AFTER A LOW INTENSITY PRESCRIBED BURN

ABSTRACT

Two approximately 150 year old northern mesic eastern white pine dominated stands were sampled to compare effects of a low intensity prescribed burn that occurred in 2003. The historical fire regime is believed to have included severe surface or crown fires every 200 to 300 years with low intensity surface fires at 20 to 40 year intervals. Fire, in proportion to intensity, influences nutrient cycling, vegetation structure, composition and diversity. These factors can vary at small scales and in turn affect regeneration, successional processes, wildlife habitat and more. A study of the first two growing seasons post burn found average sapling mortality of 63%, and significant increases in cover, richness, and species density in burn units (Cook et al. 2008). This study describes four and five growing season post-burn effects of four low intensity prescribed burns on understory vegetation and soil propagule bank. We found sapling density decreased as a result of the burn, but was not significantly lower than control units by five growing seasons afterward. Analysis by Multi Response Permutation Procedure (MRPP) indicated that species density and percent cover of understory vegetation were significantly greater in burned than control areas during spring and summer five growing seasons post-burn. Propagule bank richness and density were not significantly affected by the burn, although composition was altered. Intensity varied at a

small scale but there did not appear to be significant effects on richness or cover in different burn intensities. Results of this study show that low intensity fire has an important role of stimulating understory and propagule bank dynamics which lasts at least five growing seasons.

INTRODUCTION & LITERATURE REVIEW

Fire is an important ecological process in much of the Great Lakes forests, where historically high intensity stand-replacing fires every 200 to 300 years were the major factor in establishment of eastern white pine (*Pinus strobus* L.) forests (Maisurrow 1941; Heinselman 1981). Low intensity fires are also thought to have burned on approximately 20-40 year cycles as part of the fire regime. The reaction by the understory of a northern mesic eastern white pine forest to low intensity fire is important to understand how this ecosystem functions. The understory, including the soil propagule bank, cycles a significant amount of nutrients, constitutes a large amount of biodiversity, influences arboreal seedling survival, and contributes greatly to wildlife habitat (Gilliam and Roberts 2003).

While fire-effects studies are common for a variety of forest communities, they often focus on arboreal effects. Furthermore, few focus on low intensity fire in eastern white pine forests. Studies of low intensity fire suggest direct effects on the understory, such as increases in cover and richness, last four years at most (Nuzzo et al. 1996; Neumann and Dickman 2001; Kemball et al. 2005). These studies support the general principle that understory response is roughly proportional to degree of fire intensity (Roberts 2004). In general, fire tends to result in increased species diversity, a short term increase in annuals and biennials, and increase in biomass or cover (Henderson and Statz 1995). We predicted that fire effects, indicated by changes in richness, diversity, dominance, average percent cover and species density, would begin to plateau or decline during the fourth or fifth growing seasons (grss) following the prescribed burns. The main questions of this study were:

(i) Are there significant changes in the understory persisting four and five grss after low intensity fire?

(ii) Are there significant understory differences between areas burned at low or moderate intensity?

(iii) How much effect does the sapling layer have on understory?

(iv) Are there significant changes in density or richness of the soil propagule bank four grss after low intensity fire?

METHODS

Study sites

The study sites were two stands approximately eight kilometers apart in a northern mesic eastern white pine dominated forest in southeastern Menominee Nation, in northeastern Wisconsin (44°56'N, 88°40' W)(Figure 1). Elevation is approximately 300 meters above sea level. Average growing season is approximately 133 days per year with an average summer temperature of 20° Celsius and an average winter temperature of -8° C. Average precipitation is approximately 81.76 cm (Mitchell 2004). Age of dominant white pines on both sites is approximately 150 years old (as of 2007). The soils of both stands consist of deep glacial deposits of loamy alluvium which are moderately well drained, not subject to erosion, and have a moderate nutrient level. The natural disturbance regime of the study sites is believed to have included large scale (greater than 405 ha) windthrow and a mixed fire regime. The mixed fire regime is thought to have included severe large-scale crown or surface fires on intervals of 200 to 300 years with low intensity fires on intervals of 20 to 40 years (Heinselman 1981, Abrams 2001).

Compartment 219 (Burns and 2 controls)

The burn site is nearly level to gently sloping (less than 6% slopes). Soils are fine sandy loams and some fine sands over sandy outwash overlying granitic Wolf River batholith. The taxonomic classification of the dominant soil series is sandy mixed, frigid Typic Haplorthods (Mitchell 2004). Although the site is dominated by eastern white pine, its Kotar habitat type is *Acer saccharum-Tsuga canadensis-Fagus grandifolia – Dryopteris spp.* according to Menominee Tribal Enterprises (Ron Waukau pers. comm. 6/06/08).

In 2001, basal area of the stand was 22 m^2/ha of white pine and 3.5 m^2/ha of hardwoods including sugar maple (*Acer saccharum* Marshall), red maple (*Acer rubrum* L.), northern red oak (*Quercus rubra* L.), American beech (*Fagus grandifolia* Ehrh.), bitternut hickory (*Carya cordiformis* (Wangenh.) K.Koch), and yellow birch (*Betula alleghaniensis* Britton) (Galbraith 2005). The subcanopy includes American elm (*Ulmus americana* L.), ironwood (*Ostrya virginiana* (Mill.) K.Koch.), and alternate leaved dogwood (*Cornus alternifolia* L.f.). The site has experienced two shelterwood cuts and an herbicide and mechanical treatment within the past 18 years as part of regular management by Menominee Tribal Enterprises (Table 6).

Compartment 344 (controls)

The remaining control units, which are located approximately eight km away from the burns, have slopes ranging from nearly level to 6 - 15%. Soil parent material is silty or loamy alluvium over sandy or loamy glacial till and is considered very bouldery. The taxonomic classification of the dominant soil series, Kennan silt loam, is coarse-loamy mixed, superactive, frigid Typic Glossudalfs (Mitchell 2004). A shelterwood cut to $11m^2$ basal area was completed in 1989 (Table 6). In 2001 basal area of white pine was 25.8 m^2/ha and hardwoods were $4.2m^2$/ha. The hardwood and sub-canopy components are very similar to Compartment 219.

In 2001 there were not significant differences in overstory composition, basal area, sapling density, understory composition or arboreal seedling density between this site and Compartment 219 (Galbraith 2005).

Compartment 221(uncut controls)

Because the units referred to as “controls” experienced overstory removals 18 years prior to sampling and could still be undergoing changes resulting from this disturbance (Cook et al. 2008), a secondary control site was added in summer 2007. This additional study site shares all of the above described characteristics of Compartment 219 and was in close proximity to that site (across the logging road forming the boundary of 219). Unlike the controls, this site has only experienced a sparse amount of single tree harvesting in the past to maintain stand health and vigor. Dying or diseased trees were removed when identified on occasional stand surveys but the most recent stand entry was at least ten years prior. The purpose of this site was to further refine the comparison between burns and controls and isolate treatment effects of the burn.

Table 6. Stand history of primary study sites.

Year	Compartment 344 - 4 controls	Compartment 219 - Burns and 2 controls		
~1862	Approximate year of stand establishment for both stands			
		1988	34.4 m^2 basal area/ha	
		Mar. 1989	Harvest to 60-70% crown closure(cc), 26.4 m^2 BA/ha	
1991	39 m^2 basal area/ha	Sep. 1989	M+H treatment: 3.5 liter glyphosate/ha and double pass Bracke scarifier	
Winter 1991	Harvest to 60-70% cc, 30 m^2 BA/ha, no site preparation	1993	Harvest to 50% cc, 23 m^2 BA/ha, no site prep	
			Burns	Controls
2002	30.6 m^2 BA/ha	2002	27.5 m^2 BA/ha	24.6 m^2 BA/ha
	No treatment	Apr. 2003	Low intensity prescribed burns	No treatment
Summer 2003	31 m^2 BA/ha	Summer 2003	26.3 m^2 BA/ha	24.6 m^2 BA/ha

Unit Layout and Treatments

Treatment units are 0.81 hectares (Galbraith 2005). Compartment 219 contained four burn units and two control units and compartment 344 contained four control units. In each unit a 15.2 by 15.2 meter grid of 16 permanent metal posts guided sampling. There was a 10.06 meter buffer between the boundary of the unit and the outer row of posts as well as a minimum 20-meter untreated buffer between units within compartments. In Compartment 221 posts were arranged 15.2 meters apart along three parallel transects that were 100 meters apart. There was at least a 20 meter buffer between the stand edge and first and last post on each transect. Following sampling, posts were grouped into “units” for analysis. Eight posts in closest proximity along the three transects were considered a unit.

Prescribed burn

Four units in Compartment 219 were burned with a relatively low intensity strip head fire with five to 10 meters between strips in April, 2003. Conditions during the burns were: nine days since last rain event, air temperature of 14 to 18°C, wind zero to 11.3 kph, and relative humidity 27 to 40 percent averaging 31 percent. There was high variability in fuel loads between units (Cook et al. 2008).

The fires burned only the surface of the forest floor and spread slowly. Average flame length was 0.78 meters (0.3 – 1.4) and flamefront intensity was 153 kWm^{-1}, which indicates a low intensity fire (Cook et al. 2008).

Heat sensitive paints that could detect a range of temperatures were applied to metal tags and placed at a range of heights (0.15, 0.30, 0.60, 0.91, and 1.22 meters above ground) on all 16 permanent posts. Each tag contained a small swath of paint representing each of the following temperatures: 79, 135, 204 and 288ºC; this range was selected based on the data for an oak woodland (Cole et al. 1992). Post-fire analysis of tags showed 66 percent of the post locations measured in the burns reached or exceeded 288°C at 0.15 meters above ground. At 1.22 meters above ground only 2 percent of the locations reached 288°C (Cook et al. 2008).

Field sampling

Burns and controls

Basal area, average diameter at breast height, and canopy tree status (living or dead), were recorded in 2001 and 2003 (Galbraith 2005).

Stems of sapling sized vegetation ($\geq$1.37 m tall but less than 20.3 cm dbh with a tree-like form, in the mid story or lower) were counted in 200 m^2 quadrats centered on eight of the 16 permanent posts in burns and four of the sixteen posts in controls.

Percent cover of herbaceous and woody vegetation (<1.37 m tall) was recorded in 16, one m^2 quadrats placed 1.5 m north and south of eight of the 16 posts during spring and summer of 2006 and 2007. Four burn units and six control units were sampled. Spring sampling dates were May 22 – June 22 and summer dates were August 6 - August 23.

Two soil propagule bank collections were taken at a random azimuth and distance (maximum five meters) from all 16 posts. Thirty two samples from each of three burns and three control units were collected during summer 2006 with a standard sized soil auger (7.5 cm wide and 21 cm deep) (Bigwood and Inouye 1988). Samples were placed in individual plastic bags and stored in a refrigerator until planting. Samples spent different amounts of time in the refrigerator but all were refrigerated for at least six weeks.

Understory sampling, using same method and locations, was completed in spring and summer 2002-04(Cook et al. 2008 and Galbraith 2005). The soil propagule bank had also been sampled at a similar intensity in summer 2001(Galbraith 2005).

Uncut controls

Basal area was sampled with a 10 factor prism in late July 2007. Understory vegetation was sampled in one square meter quadrats placed 1.5 m north and south of 37 posts along 3 transects. Saplings and propagule bank were not sampled.

Greenhouse

Soil propagule bank samples were homogenized in their individual containers and then spread over a mixture of sterilized potting soil and sand in individual growing trays. Trays were placed in a greenhouse at the University of Wisconsin Stevens Point which has varying levels of sunlight and temperatures during the year that are known to range from 12 to 31° C (Galbraith 2005). Trays received water as needed and were checked every four days for at least 90 days for emergent seedlings. Seedlings were counted and removed from the tray after identification.

Data Analysis

We calculated understory average percent cover and species richness at the unit level (richness) and quadrat level (species density). Average percent cover values were used to calculate the Shannon diversity index and dominance, the reciprocal of Simpson's index. Because dominance reflects the degree of difference between abundant species and less abundant species, as well as the number of abundant or common species, it can be a useful variable in addition to diversity (Peet 1975).

Multi Response Permutation Procedure (MRPP) in PC-ORD version 4.0 (McCune and Grace 2002) was used to test the above variables for significance between burn and control treatments in each year and season, as well as the uncut controls in summer 2007. This method was also used to test for differences in species density and average percent cover between low and moderately burned quadrats. Paired quadrats were categorized as low intensity if the sum of bottom two temperatures taken at the post during the burn were less than 845°C, and moderate intensity if the sum of the bottom two temperatures was greater than 845°C (Hobbs and Gimingham 1984). MRPP was also used to compare richness and density of soil propagule bank samples between burn and control units. MRPP is a non-parametric method of testing the hypothesis of no difference between two or more pre-existing groups. MRPP compares all possible permutations of data points in a selected space, calculates delta (or a weighted mean within group distance) and then tests the probability of groups having an equal delta if there were no difference between groups. For additional information on MRPP see Zimmerman et al. (1985) or McCune and Grace (2002).

Sorenson's index was used to compare species similarity of the understory in burn and control units four and five grss post treatment. It was also used to compare post burn propagule bank composition to post burn understory composition. Sorensons index, also called Bray-Curtis coefficient, is a proportion coefficient; it can be represented by the overlap between the area under two curves (McCune and Grace 2002). The index gives a percent dissimilarity; subtracting the result from one gives percent similarity which was used in our comparisons.

Indicator Species Analysis was used to determine significance of understory and propagule bank species indicating burn or control treatment. This method uses data on concentration of species abundance in a particular group (or treatment) and faithfulness of occurrence of a species in a particular group and results in an indicator value. The analysis is followed with a Monte Carlo test (n=1000) to test significance of indicator values.

Simple linear regression was used to test for significance of the relationship between density of saplings (in 200 m^2 plot) and understory cover and species density (average of paired quadrats within the 200m^2 plot (Figure 2)).

RESULTS

Pre-treatment

Sapling densities, although variable (Table 7), were not significantly greater in burns than controls pre-treatment (Table 8). In spring and summer 2002 there were not significant differences in understory richness, diversity, dominance, or percent cover between burn and control units (Cook et al. 2008). Species density was significantly greater in the control units in spring 2002 (p =.04) but not in summer (Table 9). The understory in the burns was on average 31% similar to the controls (Galbraith 2005). The soil propagule bank of burn and control units were also variable but overall had no significant differences in density or richness (Galbraith 2005).

Overstory vegetation

There was not an increase in mortality of overstory trees due to the prescribed burning treatment (Cook et al. 2008). Pre-treatment basal area of burns was 27.5 m^2/ha; 23.85 m^2 was white pine. Post treatment, basal area of burns was 26.31 m^2/ha; 23 m^2/ha of pine and 3.33 m^2/ha of hardwoods (Table 6).

Sapling layer

Although not significant, the burns had about 2,000 fewer saplings/ha than the controls in 2007. Average density almost doubled in the burns between 2001 and 2007 though (Table 7). This increase occurred following a large (64%) decrease in density between 2001 and 2004 (Cook 2005, Cook et al. 2008). Sapling density of control units increased more than four-fold the 2001 level by 2007 (p = 0.0033). The delayed but substantial response of the sapling layer in burns occurring within three to five grs after the burn was due in part to vigorous re-sprouting. A survey two grs following the burn treatment found 50% of the stems in the sapling layer had re-sprouted (Cook et al. 2008).

Table 7. Average sapling densities per hectare of burns and controls in 2002 and 2007. *2007 data reported with and without shrub species.*

	Avg. of all burns	Avg. of all controls
2002 (arboreal only)	1745 ± 410	1237 ± 664
2007 (all woody)	4817 ± 3510	7109 ± 1342
2007 (arboreal only)	3423 ± 2488	5440 ± 923

Table 8. *A*-(chance corrected within group agreement) and *p*-values for MRPP tests comparing sapling density between treatments and years. * significant at 95% confidence level. *2002 data are reported in Galbraith 2005.*

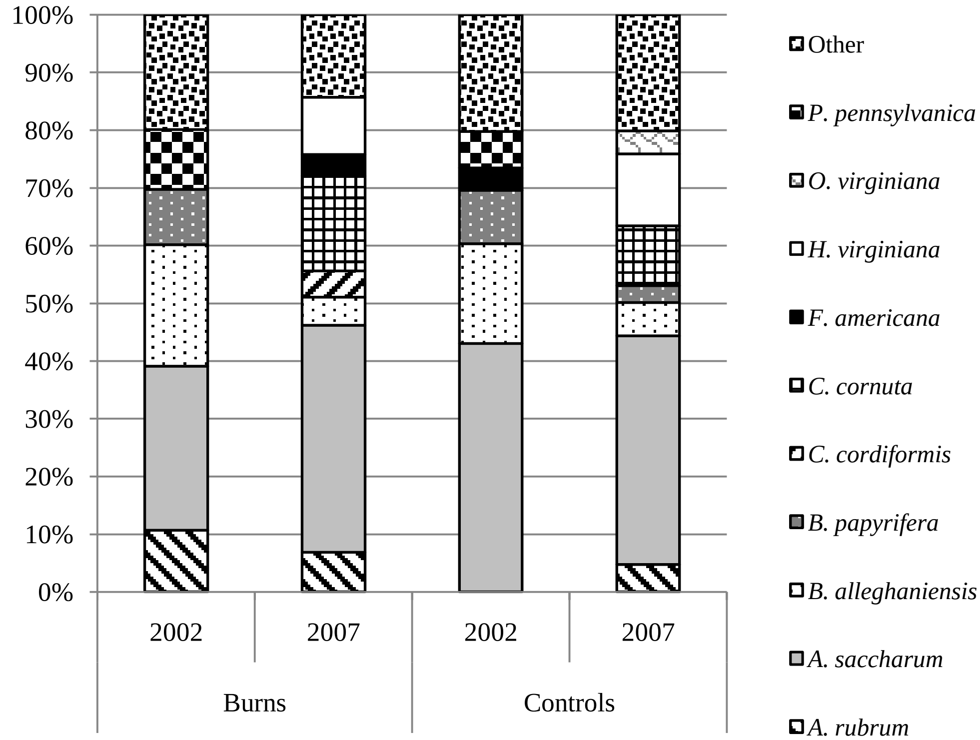
	A	**p-value**
2002 v 07		
Burns	0.0619	0.2012
Controls	0.6375	0.0033*
2002		
Burns vs. Controls	-0.00039	0.3946
2007		
Burns vs. Controls	0.1222	0.1391

Composition

The burns and controls had similar sapling layer composition (Figure 10). Sugar maple was the most abundant species in the sapling layer in burns and controls, increasing in both treatments between 2002 and 2007. Relative abundance of pin cherry, paper birch and yellow birch decreased in both burns and controls. Relative abundance of red maple saplings decreased in burns but increased in controls between 2002 and 2007. Absolute abundances also indicate burn effects on saplings. Yellow birch decreased in the burns but increased in controls. Bitternut hickory increased to almost 5% of saplings in burns. In controls ironwood became more abundant than pin cherry by 2007.

Quantitative comparison with pre-treatment data for the abundance of shrub species meeting the criteria of sapling was not possible; however it was noted that *Corylus*, *Hamamelis*, and *Sambucus* made up very little of the sapling layer in 2002. When these shrub species are included in the 2007 count, *Hamamelis* and *Corylus* are in the top five of all treatments. *Corylus cornuta* Marshall is the second most abundant species in the burns while *Hamamelis* takes this position in the controls (Figure 10, Appendix 1).

Figure 10. Relative abundance of saplings in burn and control units in 2002 and 2007.



Note: Only top five most abundant species are shown.

Understory

The understory of burns and controls had several important differences persisting five growing seasons following treatment.

Species density was significantly greater in controls pre-treatment (*A* = 0.285, *p* = 0.006, Table 9). Between 2002 and 2007, absolute values of richness, species density, diversity index, dominance and percent cover of burn units increased greatly compared to control units (Figure 11). Five grss post-treatment species density and diversity were significantly greater than controls in spring (*A* = 0.441, *p* = 0.003; *A*= 0.683, *p* = 0.001 respectively) and summer (*A* = 0.621, *p* = 0.002; *A* = 0.680, *p* = 0.002 respectively) (Table 9). Richness was nearly significantly greater in spring and summer 2007 as well, although it did not meet the threshold of significance (*A* = 0.277, *p* = 0.019; *A* = 0.302, *p* = 0.023) (Table 9).

The burn influenced the spring assemblage most dramatically. Four of the five variables, richness, species density, percent cover, and dominance, peaked in spring five grss post-burn. At this point richness had almost doubled (98% increase); species density had increased 139%, percent cover had increased by 12.7 times (a 1,172% increase), and dominance was 72% greater than pre-treatment. Diversity index peaked the spring of the second grs post-burns (Figure 11).

Values for the summer assemblage five grss post burns were beginning to stabilize. Richness and percent cover increased from grs four post burn, but much less than the increase in spring. From 2002, the overall increases from pre-treatment in richness and percent cover were 87% and 68% respectively. Species density, as well as dominance and diversity indices, decreased from summer 2006 to 2007.

Species density and percent cover of burn units were significantly greater than controls in spring five grss post-burns and in summer four and five grss post-burns (Table 4). Yet the only time richness was determined to be significantly greater than controls was before its peak (summer 2006). Diversity and dominance of understory were not significantly greater than controls at any time post-treatment (Table 9) although they were both consistently higher in 2006 and 2007 (Figure 11). Dominance in grs four and five post-burns exhibited an increase in spring and decrease in summer, almost mirroring a similar fluctuation in control units. Appendix 3 lists all understory species; Appendix 4 lists species specific to spring or summer.

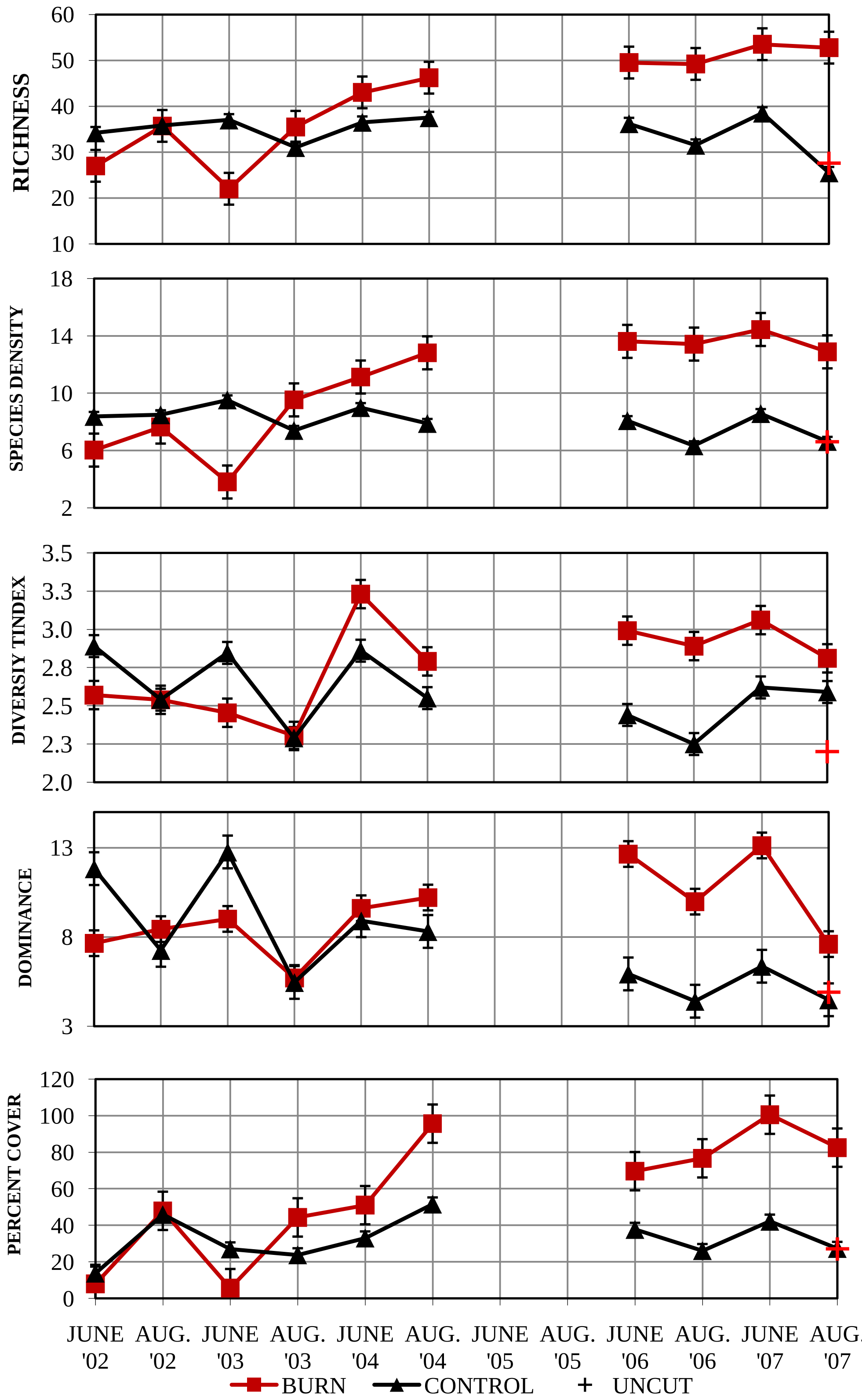
All of the above variables were significantly correlated except percent cover and dominance ($p \leq 0.05$) (Appendix 5).

Uncut controls were not significantly different than controls for any understory variable in summer 2007, the only time data were collected (Figure 11).

Table 9. *A*-(chance corrected within group agreement) and *p*-values for variables tested between burns and controls pre-treatment and four and five growing seasons following prescribed burns. * = significant at 95% confidence after Bonferroni correction; ° = significant at 95% confidence without Bonferroni correction. Significance was $p \leq 0.01$ after Bonferroni correction.

	Spring 2002		Summer 2002		Spring 2006		Summer 2006		Spring 2007		Summer 2007	
	A	*p*	*A*	*p*	*A*	*p*	*A*	*p*	*A*	*p*	*A*	*p*
Richness	0.287	0.013°	0.036	0.243	0.277	0.029°	0.453	0.006*	0.277	0.019°	0.302	0.023°
Species Density	0.285	0.285	0.285	0.006*	0.068	0.187	0.722	0.006*	0.441	0.003*	0.621	0.002*
Diversity	0.118	0.085	-0.015	0.485	0.141	0.055	0.169	0.052	0.089	0.111	0.035	0.318
Dominance	0.033	0.249	0.016	0.300	0.099	0.173	0.143	0.127	0.016°	0.379	-0.028	0.526
Percent Cover	0.142	0.048°	0.018	0.287	0.098	0.015°	0.258	0.006*	0.683	0.001*	0.680	0.002*

Figure 11. Richness, species density, diversity index, dominance, and percent cover of understory from 2002 to 2007. *2002-2004 data reported by Galbraith 2005 and Cook et al.2008.



Annual change

In burns, average annual change 02-06 compared to 06-07 was not significant for any variable in spring or summer except species density in summer (Table 10). In controls the annual change from 02-06 compared to 06-07 was not significant for any variable. The average annual change in richness and species density of burns in spring and summer 2002-2006 was significantly greater than in controls across the same period. Change in dominance in burns was also significantly greater than controls during spring 2002-06. Change in all five understory variables from 2006 to 2007 in burns was not significantly greater than in controls in spring or summer.

Table 10. *A*- (chance corrected within group agreement) and *p*-values for annual average change in variables from 02-06 compared to amount of change 06-07. * = significant at 95% confidence after Bonferroni correction; ° = significant at 95% confidence without Bonferroni correction. Significance level was $p \leq 0.008$ with Bonferoni correction.

	Burns 02-06 vs Burns 06-07		Controls 02-06 vs Controls 06-07		Burns 02-06 vs Controls 02-06		Burn 06-07 vs Controls 06-07	
SPRING								
	A	*p*	A	*p*	A	*p*	A	*p*
Richness	-0.017	0.511	0.591	0.284	0.646	0.005*	-0.11	0.789
Spp. density	0.115	0.098	-0.03	0.597	0.655	0.006*	-0.031	0.528
Diversity	0.268	0.048°	0.113	0.816	0.111	0.109	-0.080	0.730
Dominance	0.088	0.194	-0.064	0.639	0.507	0.007*	-0.129	0.902
Prcnt. Cover	0.015	0.387	0.329	0.017°	0.469	0.013°	0.055	0.227
SUMMER								
	Burns 02-06 vs Burns 06-07		Controls 02-06 vs Controls 06-07		Burns 02-06 vs Controls 02-06		Burn 06-07 vs Controls 06-07	
	A	*p*	A	*p*	A	*p*	A	*p*
Richness	0.125	0.131	-0.065	0.783	0.593	0.007*	0.196	0.0387
Spp. density	0.623	0.006*	0.092	0.233	0.694	0.006*	0.052	0.295
Diversity	0.268	0.049°	-0.113	0.816	0.111	0.109	-0.080	0.730
Dominance	0.014	0.376	-0.119	1.000	-0.038	0.516	0.031	0.328
Prnct. Cover	0.014	0.387	0.329	0.017	0.470	0.013°	0.054	0.227

Composition

Based on Sorenson's index, understory species composition of burns compared to controls in spring and summer 2006 and 2007 are not drastically different than in 2002 (Figure 12). The greatest similarity occurred in summer 2002, the summer before treatment. Compositional similarity of burns compared to controls continued to decline in grss four and five post treatment.

Indicator species analysis on spring and summer 2007 cover data showed 12 species among the spring assemblage and seven species among the summer were significant indicators of the burn treatment (Table 11). Although several species in the control units had high indicator values, only one was significant during one time period, *Osmorhiza claytonii* (Michx.) C.B.Clarke during summer 2006. Although non-significant according to the analysis, taxa with indicator values over 40 (on a scale of 1-100) in control units were: *Betula alleghaniensis*, *Dryopteris* spp., *Lycopodium obscurum* L., *Rubus pubescens* Raf., and *Trillium grandiflorum* (Michx.) Salisb. in spring 2006; *Actaea* spp, *Dryopteris* spp, and *Graminoid* spp, in summer 2006; *Dryopteris* spp, *Lycopodium dendroideum* Michx., *Huperzia lucidula* (Michx.) Trevis., *Smilax tamnoides* L., and *Trillium grandiflorum* in spring 2007 and *Tsuga canadensis* (L.) Carrière in summer 2007.

Figure 12. Average percent similarity of understory composition of burn units to control units pre-treatment (spring & summer 2002) and four and five growing seasons post-treatment. *Bars represent standard error. (Note: graph does not show values of 03-05).*

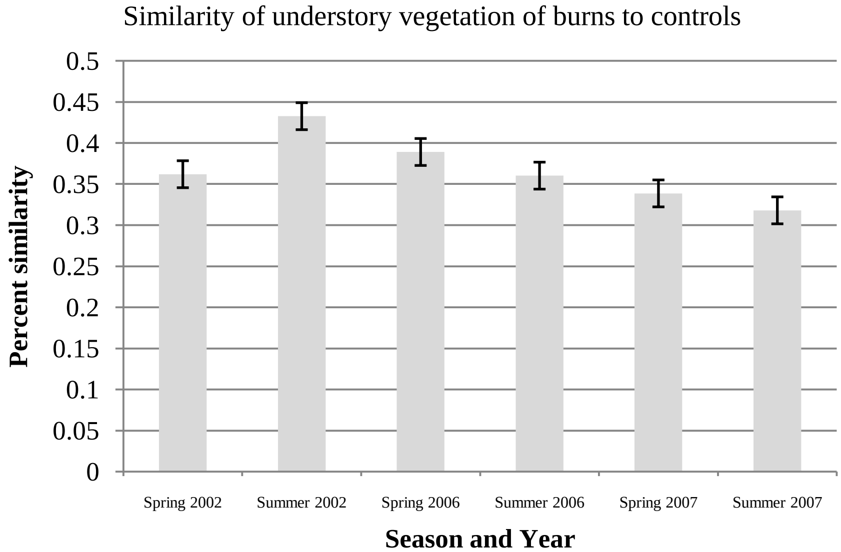


Table 11. Indicator values (IV) of understory species from comparison of burn and control units.

Species	Spring 06 IV	Spring 06 *p*	Spring 07 IV	Spring 07 *p*
Burns				
Aquilegia canadensis	-	-	75	0.017
Arisaema triphyllum	-	-	64.7	0.042
Aster macrophyllus	-	-	82.7	0.003
Athyrium filix-femina	75.8	0.02	71.3	0.015
Carex arctata	86.8	0.017	67.5	0.035
Carex deweyana	-	-	75.4	0.035
Carex pensylvanica	66.7	0.051	-	-
Galeopsis tetrahit	-	-	86.1	0.035
Galium triflorum	85.3	0.007	92.4	0.003
Linnaea borealis	-	-	66.7	0.04
Luzula acuminata	94.7	0.012	-	-
Mitella diphylla	-	-	69.4	0.025
Solidago spp.	65.2	0.046		
Streptopus lanceolatus	71.2	0.025	75.5	0.032
Taraxacum officinale	82.9	0.003	79.8	0.006
	Summer 06		**Summer 07**	
	IV	***p***	**IV**	***p***
Burns				
Aralia racemosa	91	0.024	93.3	0.001
Aster macrophyllus	81	0.023	81.2	0.004
Athyrium filix-femina	-	-	77.5	0.004
Dryopteris carthusiana	-	-	56.8	0.036
Galium triflorum	89	0.004	86.3	0.001
Mitella diphylla	90	0.018		
Solidago spp.			77.4	0.018
Taraxacum officinalis	70	0.038	-	-
Viola spp.	75	0.017	63.6	0.021
Controls				
Osmorhiza claytonii	87.1	0.029	-	-

Life forms

Five grss post treatment effects on life form distribution varied. Some life forms appeared to continue to respond to the treatment while others appeared to return to pre-treatment or converge with control treatment levels (Table 12, Figure 13).

Fern cover was not clearly affected by the burns. In burns, fern/clubmoss relative percent cover was less than 15% through grs five post-treatment while this life fomr made up over 20% of understory cover in summer each year (Figure 13). Average absolute percent cover of ferns/clubmosses was not very different between burns and controls (Table 12).

Relative cover of *Carex* and *Juncus* species increased due to the burn treatment. In burns cover increased to 17% in spring 2004 and was still between 4 to 5 % greater in burns than controls in 2007 (Figure 13).

Five grss following treatment relative cover of grasses was similar in burns and controls in spring and summer.

Burning caused annual forbs to increase. Five grss following burning annual forbs were still greater in burns although relative cover was low. Annual forbs made up less than 1% cover in both burns and controls pre-treatment. In summer 2003 in burns, annual forbs increased to 3%, then peaked at about 6% cover in spring and summer 2004 (Cook et al. 2008). While annual forbs were not a dominant component of understory, this was still at least a six fold increase in cover compared to pre-treatment.

The burns initially caused a great increase in relative cover of perennial forbs. By four and five grss following the treatment, relative cover of perennial forbs was similar to controls but average cover was still more than twice that of controls. Relative cover of perennial forbs also decreased annually from spring to summer in both controls and burns.

The treatment effect on shrubs was strong as well. Relative cover decreased the year of treatment but was similar to controls by five grss post treatment. Average absolute shrub cover was again about twice that of controls in grs five post treatment.

Arboreal seedlings were practically wiped out by the burn treatment initially (Figure 13). However, average absolute cover of tree seedlings was 50 and 100% greater in burns than controls in spring and summer five grss post treatment.

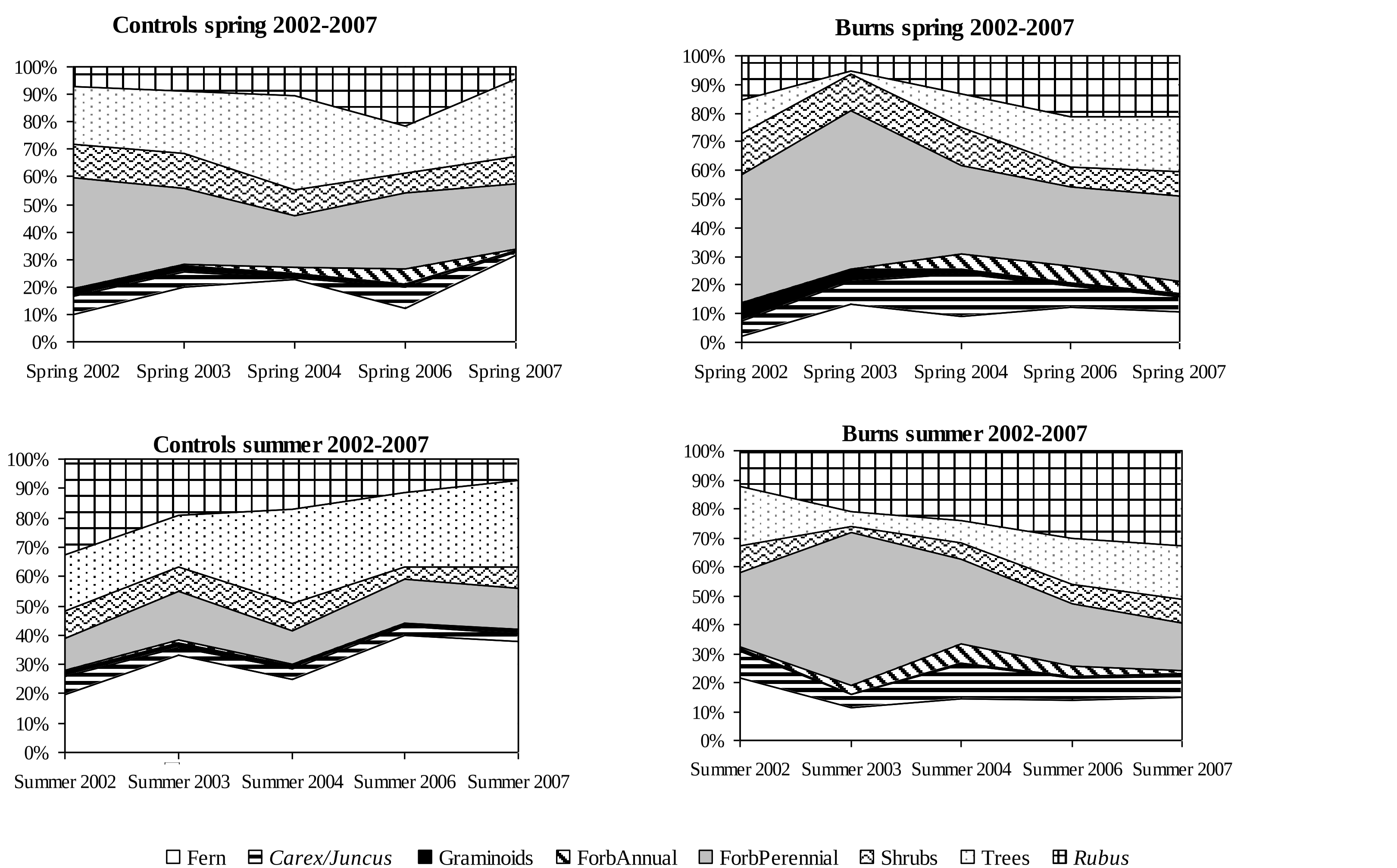
Relative cover of *Rubus* species contrasted between burns where it steadily increased and controls where it steadily decreased from 2002 to 2007.

In 2007, uncut controls had similar cover of ferns and clubmoss, grasses, annual forbs, and shrubs as controls. Uncut controls had less *Carex* than controls and no *Rubus* but greater cover of tree seedlings and perennial forbs than controls.

Table 12. Average percent cover by life form in burns and controls in spring and summer 2002, 2006 and 2007. *2002 data previously reported in Galbraith 2005.*

	Average Percent Cover (unit-level)								
	Ferns & clubmoss	Grasses	*Carex* & *Juncus*	*Rubus*	Forb-annual	Forb-perennial	Shrub	Tree	Total
					SPRING				
Burns n=4									
02 spring	0.164	0.47	0.429	1.24	0.03	3.57	1.15	0.89	7.9
06 spring	8.74	0.60	4.95	15.15	3.91	19.30	4.66	12.29	69.6
07 spring	12.86	0.54	6.27	27.11	3.30	26.49	9.25	16.90	102.7
Controls n=6									
02 spring	1.38	0.35	0.93	1.01	0.039	5.51	1.63	2.89	13.75
06 spring	10.38	0.17	0.41	3.6	0.194	7.37	2.61	12.68	37.5
07 spring	13.49	0.29	0.47	1.94	0.13	10.01	4.26	11.68	42.3
					SUMMER				
Burns n=4									
02 summer	10.23	0.54	4.47	5.86	0.143	12.42	4.32	9.90	47.9
06 summer	10.64	0.59	5.68	23.84	2.42	16.45	5.03	11.99	76.64
07 summer	12.54	0.45	5.52	29.84	1.23	15.09	7.25	17.49	89.41
Controls n=6									
02 summer	9.152	0.73	2.68	15.09	0.23	4.97	4.29	8.76	45.9
06 summer	10.42	0.22	0.75	2.94	0.12	3.89	1.06	6.71	26.11
07 summer	11.16	0.44	0.77	2.13	0.04	4.15	2.15	8.66	29.48
Uncut Controls n = 5									
07 summer	11.79	0.38	0.37	0	0.03	5.54	1.97	10.74	30.82

Figure 13. Relative cover by life form and season in burns and controls from 2002 to 2007. *2002-2004 data previously reported in Galbraith 2005 and Cook et al. 2008.*



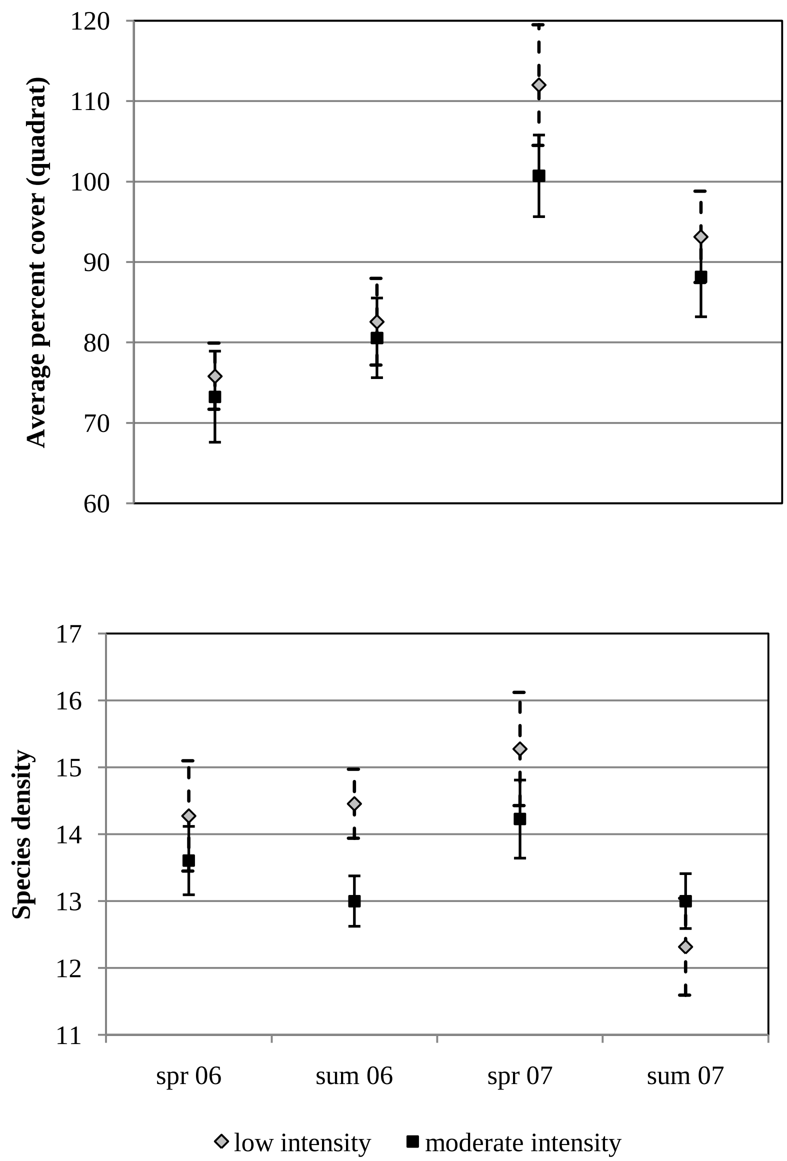
Intensity effect

In spring and summer 2006 and 2007 significant differences were not found in species density or percent cover between quadrats burned at low or moderate intensity (Table 13, Figure 14). The greatest difference in species density between low and moderate intensity quadrats was in summer 2006, but it was only a difference of just over one species. All other times had smaller differences in average species density. Average percent cover was very close between low and moderately burned quadrats. The largest difference occurred in spring 07 with a non-significant difference in cover of about 10%.

Table 13. *A*-(chance corrected within group agreement) and *p*-values from MRPP comparing species density and percent cover in low and moderately burned quadrats.

	A	*p*
Species density		
spring 06	- 0.0185	0.7437
summer 06	0.0506	0.0588
spring 07	- 0.0088	0.527
summer 07	0.0067	0.2785
Percent Cover		
spring 06	0.0027	0.326
summer 06	0.0128	0.2198
spring 07	- 0.031	0.1199
summer 07	- 0.013	0.582

Figure 14. Average percent cover and species densities of low and moderately burned quadrats of all burn units. Error bars indicate standard error.



Sapling layer effect

Five grss post-treatment density of the sapling layer had a small but significant impact on understory species density in the burn units during spring (r^2 =0.314, p = 0.0086), but not summer (r^2 =0.011, p = 0.858; Table 14). Average percent cover of the understory was significantly influenced by the sapling layer in summer (r^2 = 0.208, p = 0.0088), but not spring (r^2 = 0.1359, p = 0.038) five grss post treatment (Table 14).

Table 14. Results of regression tests on relationship of sapling layer density to understory species density and percent cover in spring and summer 2007(five grss post-treatment) on burn units.

	Slope	r^2	*p* value
Species density			
spring 2007	-0.0204	0.3137	0.00086
summer 2007	0.000896	0.0011	0.858
Percent cover			
spring 2007	0.1164	0.1359	0.038
summer 2007	0.1287	0.208	0.0088

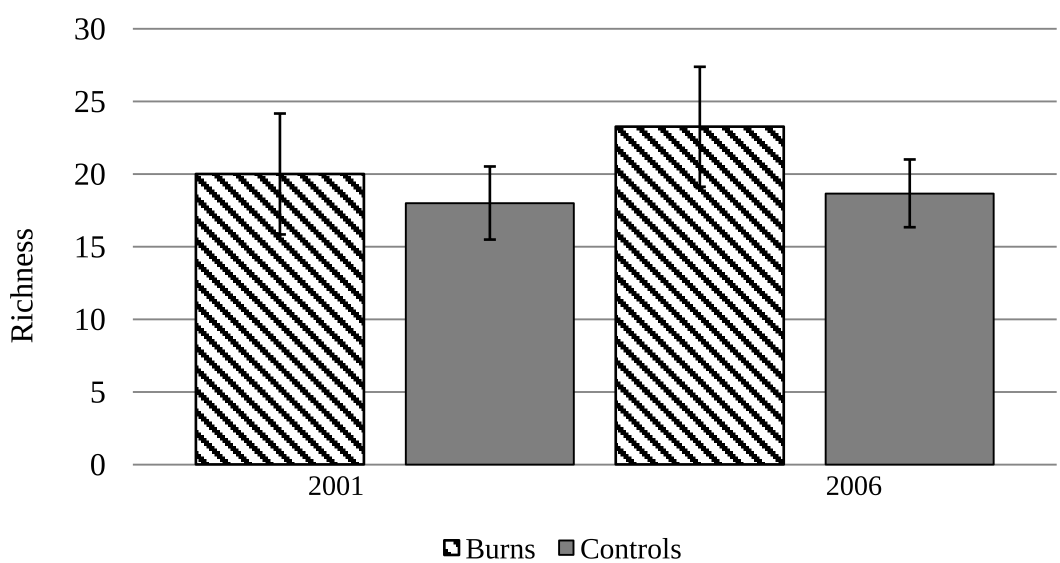
Note: significant *p* value was determined to be 0.025 after Bonferroni correction.

Soil Propagule Bank

Richness

From soil samples collected four grss post burn, 1039 individuals from 59 taxa emerged. Burn propagule bank samples contained 630 individuals and 42 taxa that germinated; 14 individuals (2%) were vegetative sprouts. Control propagule bank samples contained 409 individuals and 32 taxa that germinated; four individuals (~1%) were vegetative sprouts. Average propagule bank richness of burns in 2006 (23 taxa) was not significantly greater than pre-treatment (20 taxa, A = -0.117, p = 0.873; Figure 15), nor was it greater than controls in 2006 (A = -0.024, p = 0.537).

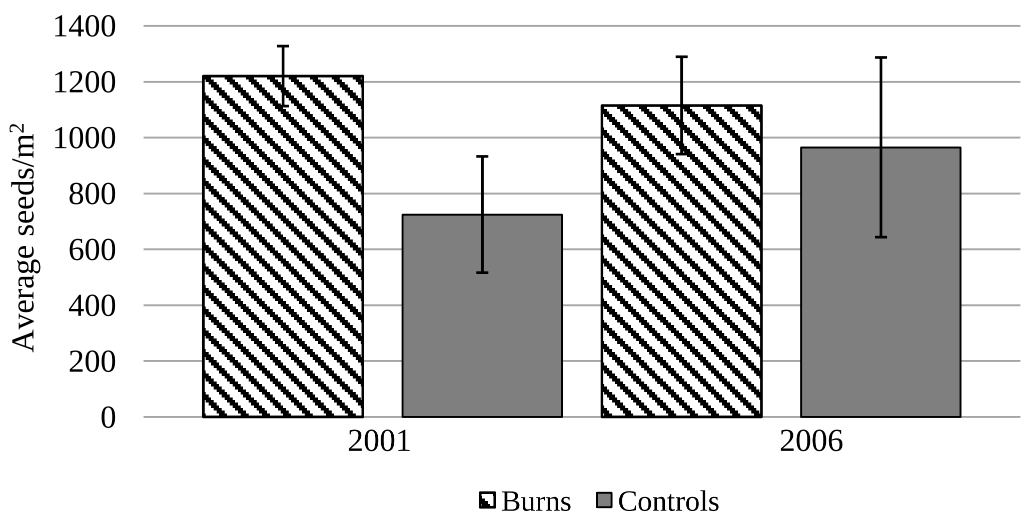
Figure 15. Average richness of soil propagule bank pre- and post- treatment in burn and control units. *Error bars indicate standard error. Pre-treatment values previously reported in Galbraith 2005.*



Density

Density (propagules/m^2) of the propagule bank in burn units four grss post burn (2006) was not significantly different than in 2002 (A = -0.065, p = 0.59). Density of propagule bank of control units was also not significantly different in 2006 than in 2002 (A= -0.094, p = 0.541). Burn unit propagule banks averaged 1115 seeds/m^2 while controls averaged 965 seeds/m^2 in 2006; this difference was not significant (A = -0.144, p =0.887; Figure 16).

Figure 16. Average seeds/m^2 in soil propagule bank of burns and controls in 2001 and 2006. Error bars indicate standard error. 2001 data previously reported in Galbraith (2005).



Composition

The soil propagule bank of burns was more similar (66%) to that of controls in 2006 than it was to understory of burn units (Appendix 7). The similarity of the propagule bank to the understory in burn units was 22% in spring 2002 and 26% in spring 2006 (Figure 17). In summer the propagule bank similarity to understory vegetation was almost the same in 2006 as it was in 2002 (33%).

An indicator species analysis comparing composition of burn and control propagule banks found no significant indicator species of either treatment. However, there were 15 species specific to burn propagule bank and four species specific to the control propagule banks (Table 15).

Figure 17. Average percent similarity of propagule bank to understory vegetation within treatments.

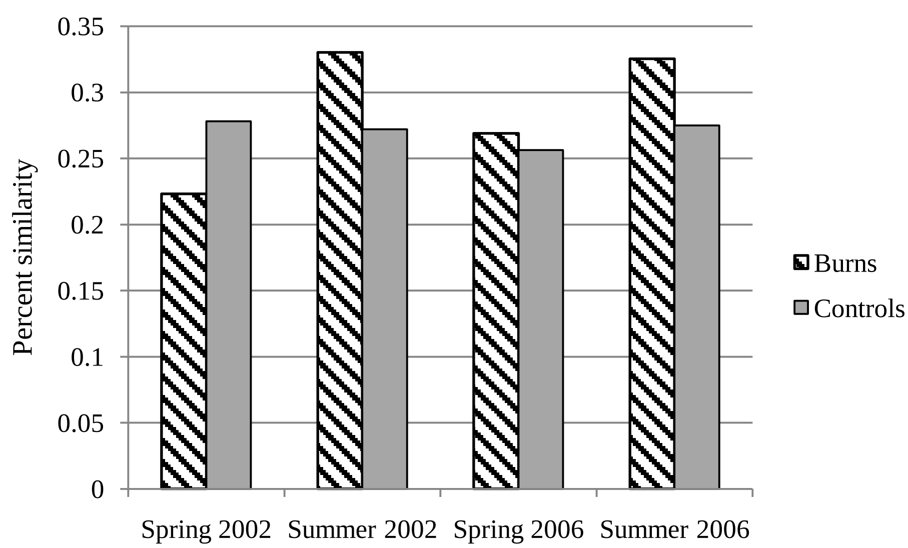


Table 15. Sprouts and seedlings emerging from soil propagule bank samples in 2006.

	Burns				Controls			
			Present in understory?				Present in understory?	
	Treatment Total	No./m²	Spr. 06	Sum. 06	Treatment Total	No./m²	Spr. 06	Sum. 06
Vegetative sprouts								
Aralia racemosa	4	7	x	x				
Aster macrophyllus	1	2	x	x				
Cryptotaenia canadensis	1	2						
Maianthemum canadense	5	9	x	x	1		x	x
Mitchella repens			x		1	2	x	x
Potentilla norvegica					2	4		
Viola spp	1	2	x	x				
Unknown dicot	2	4						
Total	14	26			4	6		
Seedlings								
Anemone quinquefolia	3	5	x	x	2	5	x	x
Antennaria spp.					11	26		
Aquilegia canadensis	1	2	x	x				
Aralia racemosa	5	9	x	x				
Aster macrophyllus	1	2	x	x				
Aster spp.	1	2						
Cardamine pensylvanica	1	2						
Carex spp.	42	74			17	40		x
Carex arctata	3	5	x	x				
Carex leptonervia	7	12	x	x	2	5	x	
Carex pedunculata	129	228	x	x	20	47	x	x
Carex pensylvanica	66	117			2	5		x
Chenopodium album	3	5						
Chenopodium simplex	9	16			16	38		
Conyza canadensis	4	7			3	7		
Corydalis sempervirens	3	5			1	2		
Dicentra spp.					56	132		
Diervilla lonicera	20	35	x	x	26	61	x	x
Erigeron annuus			x		2	5		
Fern spp.	11	19						
Galeopsis tetrahit	2	4	x	x	4	9	x	x
Galium triflorum	2	4	x	x	4	9	x	x
Grass spp.	5	9	x					x
Hydrophyllum virginianum	1	2	x					
Lactuca spp.	1	2	x	x				
Maiathemum canadensis	5	9	x	x	4	9	x	x
Osmorhiza claytonii	2	4	x	x				
Oxalis stricta	18	32	x	x	67	158		
Pilea pumila	3	5			1	2		
Poa alsodes	2	4	x		1	2		
Polygonum cilinode	45	80	x	x	16	38	x	x
Potentilla norvegica	9	16			21	50		
Rhus typhina	2	4	x	x				
Rubus alleghaniensis			x		3	7	x	x
Rubus idaeus	5	9	x	x			x	x
Rubus spp.	27	48		x	23	54		

Table 15. (continued)

	Burns				Controls			
			Present in understory?				Present in understory?	
	Treatment Total	No./m^2	Spr. 06	Sum. 06	Treatment Total	No./m^2	Spr. 06	Sum. 06
Sambucus pubens	27	48	x	x	33	78		x
Solanum nigrum	19	34			4	9		
Solidago spp.	1	2	x	x				
Stellaria aquatica	1	2			8	19		
Trientalis borealis			x		7	17		
Trillium spp.	2	4	x	x				
Viola spp.	37	65	x	x	16	38	x	x
Viola pallens	1	2						
Unknown graminoid	7	12			5	12		
Unknown dicot	91	161			31	73		
Total	616	1089			405	959		

DISCUSSION

Many results of this study are compatible with existing knowledge of low intensity fire effects. These included increase in sapling density and change in sapling composition; increase in measures of understory diversity and cover; annual change decreasing in fifth grs; changes in understory composition; distinction between response of spring and summer assemblages; and subtle changes in propagule bank density, richness and composition. Other results are stronger than expected. These included the degree of increase in sapling density; the degree of increase in diversity measures and cover, and the length of time they persisted; and continued divergence of understory similarity.

An increase in sapling layer density and re-sprouting five grss following prescribed burns is consistent with fire effects studies in northeastern Minnesota, central New York hardwoods, and dry Illinois barrens (Ahlgren and Ahlgren 1960, Ahlgren 1960, Swan 1970, Taft 2003). Although an increase in sapling density is common, the degree of increase in sapling density seems large, given the fire intensity. In burns saplings recovered to the point where density was not significantly different than controls, which increased by a factor of four during the study period. This increase occurred in a matter of three grss following a short term reduction the first two grss following the burns (Cook et al. 2008). The resulting sapling density in burns was 11 times greater than the 300 stems/ha four years following a prescribed burn in a Michigan pine forest (Neumann and Dickman 2001) and more than twice the 1088 stems/ha found seven grss after a spring burn in a mature red pine forest (Henning and Dickman 1996). However, our sapling densities were much less than that of a Minnesota forest three years following a prescribed burn (Buckman 1964). In addition to re-sprouting, reasons for increased sapling densities include recruitment of seedlings into the sapling class and possibly a stimulatory effect because of the season of burn. The spring burn may have made more nutrients available immediately when the growing season began (Schwemlein and Williams 2007). The concurrent and even greater increase in saplings in controls suggests the sapling layer in both treatments was being influenced by factors besides the burn treatment. The change in sapling composition in the burns illustrates effects of known differential sprouting capabilities among species following fire (Cook et al. 2008). Five grss following burns *Acer* spp., which comprised 85% of re-sprouts in 2004, were the dominant sapling species. Other species known to re-sprout following fire, such as *Corylus cornuta*, were abundant by five grss following the burn (Ahlgren 1966, Buckman 1962). Relative composition of species not considered re-sprouters (such as *Betula* spp and *Prunus pensylvanica*) declined in the sapling layer (Anderson 2004, Sullivan 1994). The sapling layers could still be responding to the opening of the overstory which occurred 10 years prior in burns and two controls and 12 years prior in the remaining controls.

As with saplings, increases in all understory variables except dominance (richness, species density, diversity, and percent cover) were expected, but the degree of increase and length of time they persisted were unanticipated. These variables are commonly known to increase after fire but usually plateau by the third or fourth year post burn (McGee et al. 1995, Nuzzo et al. 1996, Neumann and Dickmann 2001, Whelan 2005). All of our diversity measures except Shannon index did not peak until the fifth grs post-burn; richness, species density and cover especially had a greater degree of increase than other studies. A combination of increased light, soil moisture, nutrients, temperature, decreased competition, diversity of microclimates, differences in regeneration strategy, and the effect of multiple disturbances could explain these increases (Roberts and Gilliam 1995, Roberts 2004). Because of the low intensity, there was likely low or no volatilization of nutrients, except nitrogen; the nutrients made available by burning of plant biomass and litter were available to the understory immediately when the growing season began, and there was probably small losses of them due to runoff or erosion (Wein and MacLean 1983, Schwemlein and Williams 2007).

The delayed mortality of the sapling layer in the second grs post-burn could also be part of the reason for the extended response of these understory variables (Cook et al. 2008). Decreased competition, increased soil moisture and increased light would have been heightened as sapling densities dropped in 2004. This was the time period that annual forbs were most abundant. By five grss after the burns the sapling layer during spring and summer 2007 was found to have a small but positive effect on cover. The species dominating cover at this time were shade tolerant or able to flourish in sun or shade. *Aralia racemosa*, *Rubus alleghaniensis*, *Acer saccharaum*, and especially *Dryopteris* spp. would explain the increased cover in denser sapling areas. Furthermore, the decrease in species density in spring 2007 is likely due to greater cover by one or all of these species. The delayed mortality of the sapling layer influenced the postponement of succession in the understory. Increased resources caused an increase in annual forbs, followed by a gradual decline in annual forbs and increase in perennial forbs, trees and *Rubus*. While mortality of saplings created favorable conditions for annual forbs in the second grss post burns, the more dense areas of saplings created favorable conditions for the dominant perennial forbs in the fifth post-burn growing season.

Residual effects from the harvest 10 years prior, and harvest and mechanical and herbicide treatment 14 years prior are minor. Disturbances a decade or more apart are best assessed as separate events (Roberts 2004). The strong similarity of understory variables in controls and uncut controls confirms that the previous disturbances are not influencing the herbaceous layer directly.

The annual fluctuation of spring and summer assemblages is a well-known phenomenon (Small and MacCarthy 1992). Patterns of our understory variables across time indicated spring assemblages were more affected by the burns. This was not surprising. Burns were conducted in early spring, just before the growing season began so the spring assemblage was more diminished in the first grs post-burns than the summer assemblage and required additional recovery time (Cook et al. 2008).

The significant difference in average annual change of species density from summer 06-07 versus 02-06 indicated understory change was beginning to slow, something we had expected. Species density changed little in summer 06-07, contrasting significantly with the dynamics of 02-06. Yet this was the only variable showing this trend. The lack of significant differences in the average annual change of other variables in burns during 02-06 compared to 06-07 indicates the burns were still changing at the same rate as the previous four grss. This shows that effects of the burn were still strong during the fourth to fifth grs, something we had not expected. Again, some reasons for the amounts of change holding strong through the fifth grs are the direct effects of the burn, and indirect effects of the delayed sapling mortality.

The changes in life forms and indicator species of burn units were largely in line with known low intensity fire effects. Cover of ferns was not diminished by burning. Two fern species, *Athyrium filix-femina* (L.) Roth ex Mert. and *Dryopteris carthusiana* (Vill.) H.P. Fuchs were significantly associated with the burn treatment. Neumann and Dickman (2001) saw a non-significant increase in cover of *Dryopteris* species in areas once burned. Other studies have also noted an increase of *Dryopteris* following fire (Chapman and Crow 1981). The buds of these ferns were low enough in the duff or soil to be protected from the fire and were able to re-sprout (Walkup 1991, Whelan 1995). *Carex*/*Juncus* relative cover also increased in burns. Between spring 06 and 07 three species of *Carex* were important in the burns. Cover of *Carex/Juncus* stayed below 1% in the controls throughout the study period. There are conflicting records for response of *Carex pensylvanica* Lam., but it has been shown to increase 1-2 years following fire (Cope 1992). There is little information about the response of *Carex arctata* Boott and *C. deweyana* Schwein. to fire. But *Carex* species have been found to increase following fire in eastern North America (Buell and Cantlon 1953, Ahlgren 1960, Scheiner 1988) and in response to openings and temperature increase following disturbance (Brandel and Schutz 2005). The fact that two of these species were found in the propagule bank suggests that part of the *Carex* response was from seeds of carices in the propagule bank.

As with *Carex*, an increase in annual forbs often occurs post fire (Henderson and Statz 1995, Hutchinson et al. 2005). Most of the annual forbs that appeared following the burn likely colonized newly open ground created by consumption of plants and litter. Because the litter layer was not completely consumed (Cook et al. 2008) it is likely that most annuals were invader-type species rather than persisting in the soil seed bank, although some may have survived the fire in the lower litter layer. The additional sunlight available after the large amount of sapling mortality in the second grs probably enhanced conditions for these species. Annual forbs were on the decline by the fifth post burn grs due to competition from increasing perennial forbs, *Rubus*, and the recovering sapling layer.

Perennial forbs responded favorably because of the low temperature and short residence time of the burns. Since the fire was low intensity, it would not have affected the root systems of most of the perennial forbs that existed on the site pre-treatment. Even if perennial forbs were top killed they were likely able to re-sprout because their meristems were protected beneath the soil (Whelan 1995). Almost all of the species that were significant indicators of burns in spring and summer 06 and 07 were perennial forbs. The small number of indicator species in controls compared to burns found in this study was the opposite of what was found in a study of wildfire effects in Alberta (Lee 2004). In this study, most of the species found in controls could also be found in burns by the fifth grs post burns. However, because of the dense shade in controls and other factors, many of the species found in the burns were strongly associated with the burns and sparse or absent in controls. Likewise in summer there were fewer significant indicator species in burns. Several of the indicator species tended to decline in cover from spring to summer; this decline in cover would have influenced the measure of concentration and could have resulted in non-significant indicator values.

Tree seedlings are easily killed by a low intensity burn. Fire effects studies have noted that fire can improve the seedbed and thus regeneration (Heinselman 1981). While the fire did not result in bare mineral soil, the partial consumption of litter (Cook et al.

2008) likely improved the seedbed and contributed to the positive regeneration of tree seedlings by five grs post burns. Since the understory cover included all vegetation smaller than 1.4 m, some of our tree seedling cover may include tree seedlings that re-sprouted. Even so, these data show that following the burns, conditions were more favorable for germination and growth of tree seedlings. (See chapter 1 for additional data on tree seedlings).

An increase of *Rubus* is common after fire (Ahlgren 1960). Neumann and Dickman (2001) found cover of *Rubus* more than doubled five grss following low intensity fire in a southwest Michigan red and white pine plantation. The increase of *Rubus* was likely due to a combination of *Rubus* in the seed bank having favorable conditions, and re-sprouting of existing *Rubus* individuals. The decrease of *Rubus* in the controls probably occurred due to increased shading by the sapling layer (Tirmenstein 1991).

The similarity between burns and controls was somewhat unexpected. Although other variables suggested that the understory response slowed in the fifth grs post burn, similarity indices did not. Similarity of the understory of burns to controls continued to decrease steadily through summer 2007. The turnover in species in the fifth grs post burn was low enough that richness, diversity, and species density began to level, but great enough that the amount of similarity to controls continued to decline. While there is no measure of significance, the difference in similarity indices is an indication that the effect of the burns on species composition continues for at least five grss after burning and that the burn influenced divergence of understory species composition.

The lack of a clear difference between low and moderate intensity burned quadrats does not necessarily mean there was no intensity effect. However, the study design made detection of fine scale intensity effects more difficult. It is common for studies comparing intensity to consist of large blocks which are categorized into various levels of burning (Lee 2004, Wang and Kemball 2005). Although this study measured burn intensity during the fires at 16 locations per 0.81 hectare burn unit, effects on the understory were measured in quadrats 1.5 meters away from the posts where temperature was measured. Furthermore, the arrangement and amount of fuels was not uniform in the burn units due to the previous stand history. In a fire monitoring study, Cole et al (1992) found that fire temperatures can be highly variable even among similar vegetation types. While intensity may have had some significant effects, they likely occurred at a smaller scale than could be detected by our design.

Examination of the soil propagule bank showed non-significant differences in richness and density between burns and controls four grss after low intensity fire. Richness was non-significant despite five species of *Carex* being distinguished from soil propagule bank in 2006 but not in 2001.

Acknowledging that absence of a species in the propagule bank does not necessarily mean it was not present; the propagule bank of burns gained 18 and lost 15 species between 2001 and 2006. The opposite trend was true for controls which gained 4 species and lost 15 species. This contrast indicates continuing turnover in the propagule bank resulting from the burn treatment.

Similarity indices did not reflect large differences between propagule banks of burns and controls. The propagule bank of burn and controls were more similar to each other than either treatment's propagule bank was to its understory in each time period. It is common for propagule banks to have low similarity to the understory because of differential seed survival, and a lag between the time species produce seed or vegetative propagules and when those species are found in the seed bank (Archibold 1979, Leck et al. 1989, Schiffman and Johnson 1992, Leckie et al. 1999). One implication of low similarity of propagule banks to understory could be that the understory changed much more than the seed bank did in burns.

There were important differences in composition of the propagule bank. Indicator species analysis found no species significantly indicative of a particular treatment in the seed bank. However, if we assume that propagule bank of the control units is a good indicator of pre-treatment composition in burns, the burn treatment did affect the propagule bank composition. This is evident by the types of species found exclusively in either propagule bank. The burn propagule bank exclusively contained several species associated with disturbance, known to re-sprout following fire, or to invade from nearby such as *Aquilegia canadensis* L., *Aster macrophyllus* L., *Chenopodium album* L., *Lactuca* spp., and *Solidago* spp. (Stickney 1989, Neumann and Dickmann 2001, Wang and Kemball 2005). *Aquilegia canadensis, Aster macrophyllus* and *Lactuca* spp. likely invaded post-burn and had worked their way into the soil propagule bank by four grss after the burn. *Chenopodium album* and *Solidago* spp. were present in at least one burn unit pre-treatment (Galbraith 2005); these may have been able to persist since the the harvest ten years prior to the prescribed burns. Within days following wildfire Lee (2004) found fewer indicator species from the propagule bank than from the understory.

Conversely, there is sufficient rationale to explain why the four control-specific species were not found in the propagule bank of the burns. *Dicentra* spp., which was present in burns pre-treatment, could have been killed by conductive heat from the burn into the upper soil layer where its rhizomes are located. This could also have happened with *Mitchella repens* L. and *Potentilla norvegica* L., two other species with thin rhizomes found only in control propagule bank, the latter of which was present in burns pre-treatment (Galbraith 2005). Finally, *Antenaria* spp. is known as 'fire decreaser' so it is appropriate that it was not found in burns (Matthews 1993).

This study showed that low intensity prescribed fires in northern mesic white pine under shelterwood management initiated significant changes in the understory that persisted for at least five growing seasons. The sapling layer density rebounded above pre-treatment levels by five grss post-burn, a greater than expected response. The understory also exhibited a robust response to the burn with significant differences in richness, species density and cover between burns and controls persisting for four and five grss. The sapling layer had a small but significant influence in this response. We were unable to attribute any quadrat level differences in the understory to intensity effects. The scale at which intensity varied was fine due to distribution of fuels and size of the burn units. Burn intensity and post-burn effects were probably not measured at comparable scales either. Thus any changes in species density or cover due to intensity were not detected. By comparing our controls to uncut controls we are confident that the understory response was less impacted by this harvest than by the burn treatment. Our controls and uncut controls were very similar in all understory variables in summer 2007.

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DISCUSSION

Initial effect

Based on initial effects, the M+H treatment was more severe. Roberts' model of disturbance severity is a useful framework to compare the initial effects of the burn and M+H treatments. Degree of canopy cover removed, forest floor and soil disturbed and understory vegetation damaged are the main features of this model. Each of these was impacted to a greater degree in the M+H treatment (Roberts 2004).

The canopy did not experience additional mortality as a result of any of the treatments. However, that is not to say the canopy was not 'removed' in the context of the disturbance severity model. The sapling layer, even though small in diameter, can be considered part of the upper strata because its height was greater than 1.4 m. Vegetation of this size can exhibit some of the same effects as a canopy, such as shading, cooling, and above and below ground competition. In both treatments, the initial percentage of upper strata (sapling) removal was large but was greater in M+H treatments.

The M+H treatment disturbed much more of the soil and forest floor than the burn. Data presented in chapter one support this assertion. Burns did not have nearly the upper strata removal as M+Hs did. Any microclimate enhancement by the blackened soil surface in burns was likely cancelled out by the persistent upper strata, which experienced delayed mortality. The M+H treatment included a great deal of churning of the soil while the burn treatment did not even consume all of the litter layer for the most part (Cook 2005). Pre-treatment the amounts of coarse woody debris in treatment units were comparable (Cook 2005; Galbraith 2005). The treatments initially resulted in a decrease in coarse woody debris in three of the four burns and an increase in M+Hs (Cook 2005). More saplings died in M+H units, and they were either lying on the forest floor or at 45 degree or greater angle. Pits and mounds were not explicitly inventoried, but the burn treatment did not create any additional pit and mound topography. However, some small changes in microtopography were produced as a result of the mechanical treatment, which tended to knock saplings over and uproot some of them.

The M+H treatment removed more understory vegetation than the burns, partly because of the time of year that disturbance occurred. There was more vegetation on site in late September when the M+H treatment occurred than in April when the burn occured. However, even if both treatments occurred in the same month, the M+H treatment still probably would have removed more understory vegetation. The herbicide used was a non-selective type and likely killed more vegetation than the low intensity fire.

Four and five growing season effects

While indications of severity were evident immediately after the time of treatment, Roberts' model of disturbance severity is a useful framework in which to compare understory response five growing seasons following treatment.

Five grss after treatment, understory variables: richness, species density, diversity, and percent cover increased to a greater degree and persisted for longer than anticipated in burns (McGee et al. 1995, Nuzzo et al. 1996, Neumann and Dickmann 2001, Whelan 2005). In M+Hs these variables also increased compared to pre-treatment. These variables are commonly known to increase after fire but usually plateau by the third or fourth year post burn. In burns, the spring assemblage was also more affected by the treatment. Similarity of understory composition of burns and M+Hs to controls continued to decline in the fifth grss post-treatment while similarity of these two treatments to each other continued to increase. These effects can be partially attributed to the below features of the disturbance severity model.

First, the percent of upper strata removed; both treatments resulted in increased sapling density after five grss but to a greater degree in burns. By the fifth grss post-treatment sapling density had doubled in response to the prescribed burn treatment but had recovered to just above pre-treatment density in M+H units. While competition with the canopy remained constant, the large decrease in saplings contributed to less competition between the understory and upper strata in both burns and M+Hs, but to a greater degree in M+H units. This probably stimulated competition within the herbaceous layer since a shrub layer may lighten understory competition (Roberts 2004), and the M+Hs had a sparse sapling layer (including shrub species). Although difficult to definitively identify, the lower understory cover in M+Hs compared to burns suggests competition was greater there.

Another consideration in four and five grs effects is the forest floor environment, which differed between the prescribed burn and M+H treatment. The forest floor environment includes microclimate, coarse woody debris, pits and mounds, and mineral soil substrate.

Changes in microclimate, including heightened solar radiation, soil temperature, and soil moisture, were influenced by upper strata removal and were probably greater and longer lived in M+H units. The upper strata of M+H units took five grss to recover to just above pre-treatment density. In burns, microclimate changes were not in full effect until the second growing season due to delayed mortality of the sapling layer. This may partially explain the longer lasting than expected response by the understory in the burns. Arboreal seedling regeneration appears to have been influenced by microclimate created by upper strata removal.   Controls had the highest density of saplings in summer 2007, but the lowest seedling density. Concurrently the M+H units had the lowest sapling density and greatest seedling density.

Coarse woody debris is an important factor in the forest floor environment for water and nutrient retention as well as a substrate for understory plants. The volume and arrangement of debris in M+H units, discussed above, could have affected the response of the understory in the fourth and fifth grss due to shading or decreasing available space to grow. This may also partially account for the lower cover and other understory variables in M+Hs compared to burns.

The microtopography formed by pits and mounds can be important in herbaceous layer composition and response. M+H units had more microtopography than burns, which could be expected to affect richness even four and five grss later. However, this factor was not as strong as other effects of the burns as evidenced by the understory response.

Mineral soil substrate is another factor of the forest floor environment. The greater amount of mineral soil available immediately following the M+H treatment could have affected the course of understory response by favoring small seeded invader or colonizer type species. This does not appear to have been the case, although the greater amount of arboreal seedling regeneration in M+H units may be related to the amount of bare mineral soil. The burn treatments in general did not result in additional mineral soil substrate. There were some patches of ash where the litter layer was completely consumed, but these were few in number.

The above forest floor characteristics would seem to result in greater richness and cover in M+H units since they had stronger microclimate changes, more coarse woody debris, more microtopography, and more bare mineral soil. But nutrient availability is intertwined with these response factors. Both the burn and the M+H treatment likely resulted in increased nutrient availability compared to pre-treatment. However, even though the number of grss following treatment was the same, the M+H treatment occurred after the growing season. Nutrients made available by churning may have been leached from the soil following winter whereas the burns, which occurred as the growing season began, made nutrients immediately available to growing understory plants (Wein and MacLean 1983, Schwemlein and Williams 2007). Also, the initial decline in coarse woody debris immediately following the burns indicates consumption by the fire. The nutrients made available by consumption of some of the coarse woody debris likely account for the contrasting understory cover and richness four and five grss post-treatment in burns and M+Hs. Furthermore, the amount of coarse woody debris in our burn units was likely greater than other studies of low intensity fire effects, since the site had experienced a shelterwood cut twelve years prior to the burn treatment. This could account for the robust and longer lasting than expected response by the understory compared to the literature review. The season of burn and nutrient availability are the main factors in the difference in spring versus summer assemblage response in the burn units.

The degree of disturbance to understory vegetation is the third feature in Roberts' disturbance severity model. Damage to pre-existing plants was greater in the M+H treatment as discussed above.

Propagule availability was affected differently by the two treatments according to understory composition during the fifth post-treatment growing season. M+Hs experienced a large decrease in fern and clubmoss cover. Grasses were more abundant in burns, as were *Carex*/*Juncus*. *Rubus* cover was also greater in burns five grss post-treatment. Although annual forbs were on the decline, they were still much greater cover in burns than M+Hs in the fifth grss post-treatment. Perennial forbs were much more successful in burns compared to M+Hs. Shrub and tree species had greater cover in burns compared to M+Hs as well. The differences in life forms are due to the contrasting level of severity of these two disturbances. For instance although fern and clubmosses, perennial forbs, and shrubs and trees were top-killed, they were able to survive the burn treatment, while they experienced greater mortality from the M+H treatment. The top killing likely acted as a stimulatory effect, causing increased sprouting and growth while the more severe M+H treatment removed a greater portion of above-ground plant parts as well as dismantling roots, rhizomes, vegetative propagules, and deeply burying some seeds.

Soil propagule bank richness and density of burns and controls during the fifth grs post-treatment were comparable, indicating little influence on propagules by the burn treatment. However, comparison of species found exclusively in respective propagule banks indicated composition of burn propagule bank shifted to greater proportion of species associated with disturbance. Had I analyzed the soil propagule bank of M+H units this likely would have been the case but with fewer perennial forbs. These effects on propagule availability influence the continuing decline in similarity between burns and controls, as well as M+Hs and controls.

The M+H treatment was more severe based on Roberts' model of disturbance severity. The amount of sapling layer removed and disruption of the forest floor was greater in the M+H treatment, influencing the microclimate, microtopography, and the amount of coarse woody debris and mineral soil. Damage to pre-existing plants was greater in the M+H treatment, as was the disruption of propagule availability. All of these features indicated a more severe disturbance by the M+H treatment. The result was contrasting four and five year responses by the burns and M+H understories including increased understory richness, diversity, and cover in both treatments, but to a greater degree for a longer time period than expected in the burns. Reasons for this included greater understory competition in M+H units, delayed mortality of upper strata in burns leading to delayed microclimate changes, and greater nutrient availability in burn treatments due to season of burn and consumption of coarse woody debris. There were differences in life forms between the two treatments persisting by the fifth growing season as a result of the differences in severity. The burns ultimately seemed to have a stimulatory effect while M+H treatement resulted in greater mortality and longer recovery time. Similarity of both treatments' understories to the controls continued to decline in the fifth growing season as surviving plants continued to respond to the treatments. The initial effect on the propagule bank, while not dramatic in burns, was still evident in both treatments' understories due to surviving propagules and propagules dispersed following the treatmnents changing composition and abundance of species.

These results indicate the degree of change occuring from even fairly low intensity disturbances on a northern mesic forest understory. Qualitatively, effects of these disturbances need to be assessed according to management or restoration goals and carefully examined if applied to similar forest ecosystems.

APPENDICES

Appendix 1. Density of saplings by unit and averaged by treatment.

		Burns				
	Unit	1	2	3	4	Burns avg.
2001		2234.4	1884.0	1587.0	1275.0	1745.1
2007	(all woody)	1143.75	6306.25	8981.25	2837.5	4817.19
2007	arboreal only	925	3668.8	6750	2331.3	3423.0

		M+Hs			
	Unit	9	10	11	M+Hs avg.
2001		1394.0	900.0	1481.0	1250.00
2007	(all woody)	1950	2075	2000	2008.33
2007	arboreal only	1700	1512.0	825.0	1337.00

		Controls						
	Unit	5	6	12	13	14	16	Controls avg.
2001		1681.3	2350.0	643.8	975.0	1106.3	662.5	1236.5
2007	(all woody)	6025	7225	8962.5		6225		7109.375
2007	arboreal only	5987.5	6325.0	4250		5200.0		5440.0

Appendix 2. Density of saplings per hectare by species, averaged by treatment type in 2001/2002 and 2007. *2001/2002 data reported in Galbraith 2005 and Cook et al. 2008*.

	M+Hs		
2002		**2007**	
Acer saccharum	372.92	*Acer saccharum*	629.17
Acer rubrum	295.83	*Hamamelis virginiana*	483.33
Betula alleghaniensis	266.67	*Betula alleghaniensis*	220.83
Tsuga canadensis	85.42	*Corylus cornuta*	175.00
Quercus rubra	58.33	*Acer rubrum*	108.33
Betula papyrifera	37.50	*Fraxinus americana*	95.83
Ostrya virginiana	35.42	*Prunus virginiana*	95.83
Acer spicatum	33.33	*Quercus rubra*	37.50
Fraxinus americana	22.92	*Tsuga canadensis*	29.17
Fagus grandifolia	10.42	*Carya cordiformis*	16.67
Carpinus caroliniana	8.33	*Ostrya virginiana*	16.67
Abies balsamea	6.25	*Prunus serotina*	16.67
Tilia americana	6.25	*Acer spicatum*	12.50
Amelanchier spp.	2.08	*Betula papyrifera*	12.50
Populus grandidentata	2.08	*Populus tremuloides*	12.5
Prunus pensylvanica	2.08	*Prunus pensylvanica*	12.50
Prunus serotina	2.08	*Tilia americana*	12.50
Ulmus americana	2.08	*Abies balsamea*	4.17
	1250.00	*Fagus grandifolia*	4.167
		Sambucus canadensis	4.17
		Viburnum acerfolium	4.17
			2004.17
		w/out shrub spp.	**1337.5**

Appendix 2. continued

Burns			
2001		**2007**	
Acer saccharum	496.13	*Acer saccharum*	1896.88
Betula alleghaniensis	367.19	*Corylus cornuta*	793.75
Acer rubrum	186.72	*Hamamelis virginiana*	479.69
Prunus pensylvanica	181.25	*Betula alleghaniensis*	237.50
Betula papyrifera	167.19	*Carya cordiformis*	217.19
Tilia americana	80.47	*Fraxinus americana*	179.69
Fagus grandifolia	63.28	*Quercus rubra*	137.50
Fraxinus americana	63.28	*Prunus pennsylvanica*	132.81
Quercus rubra	54.69	*Acer rubrum*	329.69
Carya cordiformis	24.22	*Betula papyrifera*	92.19
Ulmus americana	17.19	*Sambucus spp.*	90.63
Ostrya virginiana	12.50	*Tilia americana*	79.69
Tsuga canadensis	10.94	*Fagus grandifolia*	46.88
Carpinus caroliniana	5.47	*Rhus hirta*	26.56
Populus grandidentata	5.47	*Prunus serotina*	20.31
Sorbus spp.	3.13	*Prunus virginiana*	15.63
Abies balsamea	2.34	*Populus grandidentata*	12.50
Populus tremuloides	1.56	*Ulmus americana*	9.38
Prunus serotina	1.56	*Ostrya virginiana*	6.25
Ulmus rubra	0.78	*Tsuga canadensis*	6.25
	1745.34	*Cornus alternifolia*	4.69
		Juglans cinerea	1.56
		Lonicera canadensis	1.56
		Ulmus rubra	1.56
		Viburnum acerfolium	1.56
			4821.88
		w/out shrub spp.	**3423.00**

Appendix 2. continued

Controls			
2001		**2007**	
Acer saccharum	532.29	*Acer saccharum*	2818.75
Betula alleghaniensis	213.54	*Hamamelis virginiana*	887.5
Betula papyrifera	114.58	*Corylus cornuta*	737.5
Prunus pensylvanica	78.13	*Betula alleghaniensis*	409.375
Fagus grandifolia	47.92	*Acer rubrum*	337.5
Tilia americana	41.67	*Ostrya virginiana*	281.25
Tsuga canadensis	40.63	*Betula papyrifera*	209.375
Acer rubrum	37.50	*Carpinus caroliniana*	190.625
Quercus rubra	32.29	*Quercus rubra*	184.375
Ostrya virginiana	22.92	*Tsuga canadensis*	175
Prunus serotina	16.67	*Tilia americana*	165.625
Carpinus caroliniana	15.63	*Prunus pensylvanica*	143.75
Fraxinus americana	15.63	*Fagus grandifolia*	131.25
Carya cordiformus	13.54	*Fraxinus americana*	118.75
Abies balsamea	6.25	*Prunus virginiana*	75
Populus grandidentata	3.13	*Carya cordiformis*	65.625
Acer spicatum	2.08	*Ulmus americana*	46.875
Ulmus rubra	2.08	*Abies balsamea*	28.125
	1236.46	*Cornus alternifolia*	28.125
		Prunus serotina	18.75
		Acer spicatum	12.5
		Viburnum acerifolium	12.5
		Pinus strobus	9.375
		Populus grandidentata	9.375
		Acer saccharinum	3.125
		Amelanchier	3.125
		Juglans cinerea	3.125
		Sambucus racemosa	3.125
		Ulmus rubra	3.125
			7112.5
		w/out shrub spp.	**5440.25**

Appendix 3. Species present in the understory of burns, M+Hs, controls, and/or uncut controls during 2006 and 2007

Abies balsamea (L.) Mill.
Acer rubrum L. var. rubrum
Acer saccharum Marshall
Acer spicatum Lam.
Actaea pachypoda Elliott
Actaea spp.
Adiantum pedatum L.
Anemone acutiloba (DC.) G.Lawson (formerly *Hepatica acutiloba*)
Anemone americana (DC.) H.Hara (formerly *Hepatica americana*)
Anemone quinquefolia L.
Aquilegia canadensis L.
Aralia nudicalis L.
Aralia racemosa L.
Arisaema triphyllum (L.) Schott
Aster macrophyllus L.
Aster spp.
Athyrium filix-femina (L.) Roth ex Mert.
Betula alleghaniensis Britton
Betula papyifera Marshall
Botrychium virginianum (L.) Sw.
Brachyelytrum erectum (Schreb. ex Spreng.) P.Beauv.
Cardamine parviflora Muhl. ex Willd.
Carex arctata Boott
Carex communis L.H.Bailey
Carex deweyana Schwein.
Carex intumescens Rudge
Carex leptonervia (Fernald) Fernald
Carex pedunculata Muhl. ex Willd.
Carex pensylvanica Lam.
Unknown Carex number six
Carex spp.
Carpinus caroliniana Walter
Carya cordiformis (Wangenh.) K.Koch
Caulophyllum thalictroides (L.) Michx
Cerastium fontanum Baumg.
Cirsium spp.
Circaea alpina L.
Clematis virginiana L.
Clintonia borealis (Aiton) Raf.
Coptis trifolia (L.) Salisb.
Cornus alternifolia L.f.
Cornus canadensis L.
Corylus cornuta Marshall

Appendix 3. continued

Dicentra cuccularia (L.) Bernh.
Dichanthelium depauperatum (Muhl.) Gould
Dichanthelium linearifolium (Scribn.) Gould
Diervilla lonicera Mill.
Dirca palustris L.
Dryopteris carthusiana (Vill.) H.P. Fuchs
Dryopteris intermedia (Muhl. ex Willd.) A.Gray
Elymus hystrix L.
Erigeron annuus (L.) Pers.
Eupatorium perfoliatum L.
Fagus grandifolia Ehrh.
Fragaria vesca L.
Fragaria virginiana Duchesne
Fraxinus americana L.
Galeopsis tetrahit L.
Galium aparine L.
Galium lanceolatum Torr.
Galium triflorum Michx.
Gaultheria procumbens L
Graminoid spp.
Gymnocarpium dryopteris (L.) Newman
Hamamelis virginiana L.
Huperzia lucidula (Michx.) Trevis. (formerly *Lycopodium lucidulum*)
Hydrophyllum virginianum L.
Ilex verticallata (L.) A. Gray
Unknown *Juncus* spp.
Lactuca canadensis W.Bartram ex Marshall
Lactuca spp.
Linnaea borealis L. subsp. americana (Forbes) Hultén ex R.T.Clausen
Lonicera canadensis L.
Lonicera hirsuta Eaton
Lycopodium annotinum L.
Lycopodium dendroideum Michx.
Lycopodium obscurum L.
Luzula acuminata Raf.
Maianthemum canadense Desf.
Maianthemum racemosum (L.) Link (formerly *Smilacina racemosa*)
Mitchella repens L.
Mitella diphylla L.
Mitella nuda L.
Oryzopsis asperifolia Michx.
Osmorhiza claytonii (Michx.) C.B.Clarke
Ostrya virginiana (Mill.) K.Koch
Oxalis stricta L.

Appendix 3. continued

Oxalis spp.
Panax quinquefolius L.
*Panax trifolius*L.
Pinus strobus L.
Plantago spp.
Poa alsodes A.Gray
Poa palustris L.
Polygala paucifolia Willd.
Polygonatum pubescens (Willd.) Pursh
Polygonum cilinode Michx.
Polygonum spp.
Populus grandidentata Michx.
Populus tremuloides Michx.
Prunus pensylvanica L.f.
Prunus serotina Ehrh.
Prunus virginiana L.
Prunella vulgaris L.
Pyrola elliptica Nutt.
Quercus rubra L.
Ranunculus abortivus L.
Ribes cynosbati L.
Ribes spp.
Rhus hirta (L.) Sudw.
Rubus allegheniensis Porter ex L.H.Bailey
Rubus hispidus L.
Rubus idaeus L.
Rubus pubescens Raf.
Rubus spp.
Sambucus canadensis L.
Sambucus racemosa L.
Schizachne purpurescens (Torr.) Swallen
Smilax tamnoides L.
Solidago flexicaulis L.
Solidago spp.
Sonchus oleraceus L.
Streptopus lanceolatus (Aiton) Reveal
Taraxacum officinale Weber
Thalictrum dioicum L.
Tilia americana L.
Trientalis borealis Raf.
Trillium grandiflorum (Michx.) Salisb.
Tsuga canadensis (L.) Carrière
Ulmus rubra Muhl.

Appendix 3. continued

Uvularia grandiflora Sm.
Uvularia sessilifolia L.
Viburnum acerifolium L.
Viola cucullata Aiton
Viola pubescens Aiton
Viola spp.

Appendix 4. Understory **s**pecies found exclusively in spring or summer (includes all treatments). *Not intended to indicate species life history characteristics; some occurrences are due to inconsistencies in identification.*

Spring only

Cerastium fontanum Baumg.
Dicentra cucullaria (L.) Bernh.
Elymus hystrix L.
Gaultheria procumbens L.
Lactuca canadensis L.
Lycopodium obscurum L.
Panax quinquefolius L.
Panax trifolius L.
Poa palustris L.
Populus grandidentata Michx.
Ranunculus abortivus L.
Smilax tamnoides L.
Viola cucullata Aiton
Viola pubescens Aiton

Summer only

Botrychium virginianum (L.) Sw.
Cornus canadensis L.
Dichanthelium depauperatum (Muhl.) Gould
Galium lanceolatum Torr.
Lycopodium annotinum L.
Polygala paucifolia Willd.
Prunella vulgaris L.
Ribes cynosbati L.
Rubus hispidus L.
Galium aparine L.
Sambucus canadensis L.
Uvularia grandiflora Sm.
Juncus spp.

Appendix 5. Output from Spearman's rank correlation between five understory variables.

		Percent Cover	Dominance	Species Density	Diversity	Richness
Percent Cover	Correlation Coefficient	1.000	.527	.809(**)	.682(*)	.715(*)
	Sig. (2-tailed)		.096	.003	.021	.013
Dominance	Correlation Coefficient	.527	1.000	.855(**)	.864(**)	.834(**)
	Sig. (2-tailed)	.096		.001	.001	.001
Species Density	Correlation Coefficient	.809(**)	.855(**)	1.000	.918(**)	.920(**)
	Sig. (2-tailed)	.003	.001		.000	.000
Diversity	Correlation Coefficient	.682(*)	.864(**)	.918(**)	1.000	.893(**)
	Sig. (2-tailed)	.021	.001		.000	.000
Richness	Correlation Coefficient	.715(*)	.834(**)	.920(**)	.893(**)	1.000
	Sig. (2-tailed)	.013	.001	.000	.000	

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

Appendix 6. Composition and density of arboreal seedlings spring and summer 2002 and 2007 by treatment. *2002 data previously reported in Galbraith 2005.*

	Burns			
	Spr. 2002	**Sum. 2002**	**Spr. 2007**	**Sum. 2007**
Acer rubrum	2656.25	5468.75	11250.00	7656.25
Acer saccharum	19062.50	29687.50	25781.25	10156.25
Betula alleghaniensis	156.25	625.00	312.50	0.00
Betula papyrifera	0.00	0.00	156.25	625.00
Carya cordiformis	0.00	0.00	0.00	156.25
Fagus grandifolia	0.00	156.25	468.75	781.25
Fraxinus americana	312.50	1562.50	2500.00	3750.00
Pinus strobus	156.25	937.50	312.50	625.00
Populus grandidentata	0.00	0.00	156.25	0.00
Prunus pensylvanica	468.75	781.25	2187.50	781.25
Prunus serotina	781.25	0.00	156.25	0.00
Quercus rubra	0.00	312.50	468.75	156.25
Tilia americana	0.00	156.25	156.25	937.50
Tsuga canadensis	0.00	156.25	312.50	0.00
Ulums rubra	0.00	156.25	1562.50	781.25
Total	**23594**	**40000**	**45781**	**26406**

Appendix 6. continued

	Mechanical and Herbicide			
	Spr. 2002	**Sum. 2002**	**Spr. 2007**	**Sum. 2007**
Abies balsamea	no data	416.67	0.00	0.00
Acer rubrum		2916.67	51875.00	46875.00
Acer saccharum		4375.00	10000.00	5208.33
Acer spicatum		5625.00	833.33	3750.00
Amelanchier spp.		833.33	0.00	0.00
Betula alleghaniensis		1041.67	8333.33	1250.00
Betula papyrifera		0.00	0.00	208.33
Carya caroliniana		208.33	0.00	0.00
Fagus grandifolia		208.33	0.00	0.00
Fraxinus americana		0.00	416.67	416.67
Ostrya virginiana		0.00	0.00	208.33
Pinus strobus		2500.00	208.33	416.67
Prunus pennsylvanica		0.00	208.33	625.00
Prunus virginiana		0.00	208.33	208.33
Quercus rubra		1250.00	1250.00	1458.33
Tsuga canadensis		625.00	1250.00	0.00
Total		**20000**	**74583**	**60625**

Appendix 6. continued

	Controls			
	Spr. 2002	**Sum. 2002**	**Spr. 2007**	**Sum. 2007**
Acer rubrum	33229.17	21250.00	18125.00	6093.75
Acer saccharum	17708.33	19166.67	20729.17	13437.50
Acer spicatum	416.67	0.00	208.33	0.00
Betula alleghaniensis	3750.00	416.67	2083.33	937.50
Betula papyrifera	0.00	0.00	104.17	0.00
Carpinus caroliniana	0.00	1145.83	104.17	0.00
Carya cordiformis	0.00	104.17	312.50	156.25
Fagus grandifolia	416.67	104.17	729.17	312.50
Fraxinus americana	104.17	833.33	729.17	1250.00
Ostrya virginiana	0.00	312.50	0.00	0.00
Pinus strobus	625.00	937.50	104.17	312.50
Prunus pennsylvanica	0.00	937.50	0.00	0.00
Prunus serotina	104.17	104.17	1875.00	0.00
Prunus virginiana	0.00	0.00	312.50	3125.00
Quercus rubra	312.50	104.17	0.00	1093.75
Tilia americana	208.33	833.33	0.00	468.75
Tsuga canadensis	416.67	729.17	0.00	0.00
Total	**57292**	**46979**	**45417**	**27188**

Appendix 7. Similarity matrix of burns soil propagule bank to controls soil propagule bank in 2006.

	Unit1	Unit2	Unit3	Unit4	Unit5	Unit13	Unit14
Unit1	0						
Unit2	0.606897	0					
Unit3	0.623932	0.648148	0				
Unit4	0.542484	0.454545	0.564706	0			
Unit5	0.575163	0.611111	0.5	0.582524	0		
Unit13	0.706349	0.777778	0.734266	0.703911	0.687151	0	
Unit14	0.549669	0.759336	0.751351	0.750973	0.712062	0.674877	0

Appendix 8. Average percent similarity of the understory between treatments pre-treatment and four and five growing seasons post-treatment. *2002 data previously reported in Galbraith 2005.*

	Spr. 2002	Sum. 2002	Spr. 2006	Sum. 2006	Spr. 2007	Sum. 2007
Burns vs M+H		0.3705	0.4541	0.4784	0.4690	0.5291
M+H vs Controls		0.5675	0.2824	0.2551	0.2560	0.2196
Burns vs Controls	0.3619	0.4325	0.3890	0.3602	0.3385	0.3179

Appendix 9. Taxa found exclusively in burn or control propagule bank in 2006 with regeneration strategy (invader, survivor, seed banker).

Species and treatment	**Regeneration strategy**
Burn propagule bank	
Aquilegia canadensis	survivor, invader
Aralia racemosa	No data
Aster macrophyllus	survivor, invader
Aster spp.	mostly invaders
Cardamine pensylvanica	No data
Carex arctata	No data
Chenopodium album	invader
Cryptotaenia canadensis	No data
Fern spp.	
Grass spp.	often invaders
Hydrophyllum virginianum	No data
Lactuca spp	Increased most in twice burned (Neumann)
Osmorhiza claytonii	survivor, invader
Rhus hirta	survivor
Solidago spp.	survivor, invader
Trillium spp.	Increased most in twice burned (Neumann)
Control propagule bank	
Antennaria spp.	invader, survivor
Dicentra spp.	No data
Mitchella repens	Decreases, rhizomes killed
Potentilla norvegica	Invader

Regeneration strategies based on Stickney 1989, Neumann and Dickman 2001, Wang and Kemball 2005.

Appendix 10. Photos of treatment units pre-treatment and four growing seasons post-treatment

A mechanical and herbicide unit immediately after treatment in fall 2002.
Photo courtesy Dr. James Cook.

Appendix 10. continued

A mechanical and herbicide unit four growing seasons post-treatment in summer 2006. Photo by Mary Bartkowiak.

Appendix 10. continued

A burn unit immediately after treatment in spring 2003. Photo courtesy Dr. James Cook.

Appendix 10. continued

A burn unit four growing seasons post-treatment in summer 2006. Photo by Mary Bartkowiak.

Appendix 10. continued

Control unit in summer 2006. Photo by Mary Bartkowiak

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