PATTERNS AND PREDICTORS OF PLANT DIVERSITY AND COMPOSITIONAL CHANGE IN A RESTORED MICHIGAN TALLGRASS PRAIRIE

by

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ABSTRACT

Tallgrass prairies are one of the most threatened ecosystem types in Michigan and throughout North America. Dow Field is a small remnant prairie in the University of Michigan's Nichols Arboretum in Ann Arbor, Michigan, that is being actively restored after many years of fire suppression. Starting in 1991, the prairie was divided into 10 management zones that were burned on 1 or 3 year intervals in April or November, and vegetation in 60 $2m^2$ sample plots was monitored annually until 2007. In this study, I examined trends in the plant community over time, including diversity, species abundance, and community compositional change. I also explored the environmental and management factors that most influenced diversity and compositional change, and evaluated successional trajectory in the context of restoration goals.

Over time, native species richness increased slightly, but exotic species richness and dropped dramatically after several years of burning. *Andropogon gerardii* (big bluestem) was the most dominant species in the prairie and reduced diversity through competitive exclusion, but there were no clear patterns in how the different fire regimes affected diversity or the abundance of *A. gerardii*. Instead, soil depth and soil clay were found to be the most reliable predictors of diversity, likely because increased soil moisture led to higher *A. gerardii* productivity and competitive ability. Year-to-year change in community composition was found to be affected by time since fire and fluctuations in growing season temperature and rainfall. Examining successional trajectory showed that the restoration has been most successful at reducing exotic species and increasing species heterogeneity, but has largely failed to increase native species richness to the level of remnant prairies, likely because of high *A. gerardii* abundance and low availability of native propagules.

To Michelle, with love.

And to my father, Larry Heslinga, who brought me outside.

Acknowledgements: First, I wish to thank my advisor Bob Grese, who willingly shared his data, expertise, and good humor over the course of the project. Clearly, this project would have been nowhere without him, and it is unlikely that a prairie community would exist at Dow Field if it were not for his foresight twenty years ago. Bill Currie willingly jumped into the project midstream and provided valuable suggestions throughout. Thanks to Don Zak, Mark Hunter, MaryCarol Hunter, and Allison Krueger for advice and technical assistance with the soil analyses. Laura Klem at CSCAR helped greatly with statistical procedures in chapter 3. Thanks to Aunita Erskine for enthusiastically sharing her knowledge of local prairies, and to Jason Tallant from City of Ann Arbor Natural Areas Preservation and Paul Muelle from the Huron-Clinton Metroparks for providing information on the management history of local remnants. Thanks to T.J. Smith, who took GPS points of the sample plots, to Jeff Plakke, who let me tag along for prescribed burns, and to all the other good folks at Matthaei Botanical Gardens and Nichols Arboretum (MBGNA) who showed their interest and support along the way. This research was partially funded through the MBGNA-facilitated Nanette R. LaCross Award. Finally, thanks to my wife Michelle, who cut buckthorn, pulled garlic mustard, and sacrificed in many other ways for me over the last three years.

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Chapter 1: Background, Site Characteristics, and Data Collection

Prairie Conservation, Restoration, and Research

Once one of the most extensive ecosystem types in North America, the tallgrass prairie now remains in about 0.1% of its original range (Samson and Knopf 1994). Most prairies, because of their rich soils and absence of trees, have been lost to agriculture (Howe 1994). Others face less obvious but also serious problems such as overgrazing, fire suppression, invasive species, and landscape fragmentation (Simberloff and Gotelli 1983, Risser 1988, Howe 1994, Cully et al. 2003, Lett and Knapp 2003). The loss of prairie habitat since the time of European settlement has led to a sharp decline of prairie-dependent biodiversity. For example, grassland bird species have shown steeper and more consistent declines than any other group of North American species (Knopf 1994). The degradation of prairies also alters ecosystem functions such as erosion control, water filtration, and nutrient cycling (Raison 1979, Wedin and Tilman 1990, Seastedt 1995). In addition, the deep roots of many prairie plants store large amounts of carbon in the soil, an important ecosystem service in the context of global climate change (Seastedt and Knapp 1993, Contant et al. 2001, Derner et al. 2006). In order to preserve or expand remaining prairie ecosystems, it is critically important for ecologists, land managers, and restoration practitioners to have a firm knowledge of prairie ecology and to understand how management practices affect prairie ecosystems.

Michigan Prairies in Context

Unlike the Great Plains region, there were never large, continuous expanses of prairies in Michigan, but about 25,000 ha of the southern part of the state was covered with open grassland at the time of European settlement (Kost 2004). These prairies were the easternmost extension of the so-called prairie peninsula, a finger of the Great Plains prairie biome that extended into Southern Michigan, Northern Indiana, and Northwestern Ohio (Transeau 1935, Anderson 1982). Throughout this entire region, prairies were once part of a heterogeneous landscape that was an extensive patchwork of prairies, oak savannas, and open oak-hickory forests (Albert 1995).

Much of the remaining prairie flora in Southern Michigan and other parts of the eastern Midwest persists on marginal land such as railroad rights-of-way (Thompson 1975 , Kost 2004), historic cemeteries (Pleznac 1982), or areas otherwise unsuitable for agriculture or development. These small prairie remnants often have low ecological integrity due to fragmentation, fire suppression, and invasion by non-native or woody species (Leach and Givnish 1996, Chapman and Brewer 2008). According to the Michigan Natural Features Inventory, there are only about 195 ha (less than 1% of the original landcover) of upland prairie left in the state (Kost 2004), making tallgrass prairies one of the most threatened ecosystems in the area, in need of informed management and restoration.

Despite the importance and rarity of eastern prairies, there has been a surprising lack of published research on their ecology or management. Some studies from the region have focused on recreated or replanted prairies (Suding and Gross 2006, MacDonald et al. 2007); others have been merely descriptive (Gleason 1917, Thompson

1975, Anderson 1982). However, there are few if any studies that have focused on plant community dynamics in remnant prairies, especially within the context of restoration. In this thesis, I explore the plant community at a restored remnant Michigan prairie and the factors that influence its diversity, composition, and dynamics. Ultimately, by investigating the plant community of the prairie, I hope to progress our understanding of the ecology of small eastern prairies, both with respect to theoretical community ecology and applied restoration and management.

Study Site Description

Dow Field is an approximately 4 ha tallgrass prairie in the University of Michigan’s Nichols Arboretum, a 50 ha park and natural area in the city of Ann Arbor in Washtenaw County, MI (42°16’ N, 83°43’ W). The climate is humid continental with cold winters and hot summers. Over the course of the study (1991-2007), monthly means of daily maximum temperature ranged from 0° C in January to 29° C in July, and mean annual precipitation was 97.3 cm, about half of which fell during the growing season (May-Sept). Climate data were gathered from a weather station located at the University of Michigan North Campus, about 1 km away from the study site (Dennis Kahlbaum, University of Michigan, Department of Atmospheric, Oceanic, and Space Science, unpublished data). Dow Field is located on a flat glacial outwash terrace in the Huron River valley, and the soils are classified as Boyer loamy sand. A layer of coarse gravel lies beneath the sand at a depth of up to 1 m. The site is bordered by rolling glacial moraines that support an oak-hickory forest to the south and west, and the outwash terrace continues to the north and east to the river, which supports a planted conifer stand, an oak savanna remnant, a wet prairie remnant, and bands of dry-mesic prairie vegetation along a set of railroad tracks.

Management History

Prior to European settlement, there is evidence that the area along the Huron River in Washtenaw County was extensively burned by Native Americans for agriculture, hunting, or cultural purposes. A stone plow and fire-cracked rocks found adjacent to Dow Field indicate that the site was burned and possibly cultivated by Native Americans during this time although sustained cultivation is unlikely given the droughty soil conditions (Bob Grese, personal communication). The Michigan Central Railroad between Ann Arbor and Detroit was completed in 1839, and thereafter sparks from coal locomotives routinely maintained prairie vegetation along the Huron River (Sheldon 1967). Interestingly, the influential community ecologist Henry Gleason used these Huron River Valley railroad corridor prairies to inform his founding theories of plant associations, although we do not know if he studied Dow Field in particular (Gleason 1917). Until the 1940s, the land was owned by the utility company Detroit Edison. Little is known about how the land was used during this time, though some county records show a built structure and an orchard on part of the site in the late 1800s (Evarts and Stewart 1874). The land came under the management of the Nichols Arboretum in the 1940s, and was mowed as a rough lawn for 35-40 years. In the mid 1970s, the field was allowed to grow all year, but was mowed once each fall. Under the guidance of University of Michigan professor Bob Grese, who noticed the characteristic prairie species at the site, a plan was implemented in 1988 to mow some of the field and burn other sections in the fall or spring. Volunteers inventoried the plant community in Dow

Field along transects every 25 meters along a center line through the field in 1988 and 1989.

In 1990, a more structured plan was implemented to systematically restore and manage the prairie through reintroduction of prescribed fire. A series of 60 permanent sampling plots were established to monitor the progress of the restoration and plant community changes in each of the treatments. The prairie was divided into two sections based on the dominant grasses found in the 1988 and 1989 surveys; a small section at the north edge was dominated by *Schizachyrium scoparium* (little bluestem) (stratum 1), but the majority of the prairie was dominated by *Andropogon gerardii* (big bluestem) (stratum 2). Within each stratum, three major treatments were initiated in different sections of the prairie: triennial spring burns, annual spring burns, and annual fall burns. The triennial burns were staggered, starting in 1991, 1992, or 1993. In 2000, in part because of concerns over the negative response of arthropod populations to annual fires (Treemore-Spears 2000), the burn pattern was altered so that all annual burns were changed to 3 year burns. Also, the burn season of all the treatments was reversed so that spring-burned plots were burned in the fall and vice versa (Table 1.1, Fig 1.1). Since 1991, woody species that have invaded the prairie were removed periodically by cutting. There were no burns from fall 2006 to fall 2007 due to unforeseen restrictions to fire emergency vehicle access. Throughout the study, there was no intentional planting or seeding in the study area. Thus, the restoration was completely reliant on the existing seedbank and possibly some seed rain from nearby plantings and remnants of prairie vegetation.

Treatment Zone			**Burn Schedule**	
Stratum	*Substratum*	*Section*	*1991-1998*	*1999-2007*
2	1	1	Triennial spring, starting in 1993	Triennial fall, starting in 2002
2	1	2	Triennial spring, starting in 1991	Triennial fall, starting in 2000
2	1	3	Triennial spring, starting in 1992	Triennial fall, starting in 2001
2	2	1	Annual spring	Triennial fall, starting in 1999
2	2	2	Annual spring	Triennial fall, starting in 2000
2	3	1	Annual fall	Triennial spring, starting in 2000
2	3	2	Annual fall	Triennial spring, starting in 2000
1	1	-	Triennial spring, starting in 1992	Triennial fall, starting in 2001
1	2	-	Annual fall	Triennial spring, starting in 2001
1	3	-	Annual spring	Triennial fall, starting in 2002

Table 1.1. Treatment zones in Dow Field. Stratum 1 is dominated by *S. scoparium*; stratum 2 is dominated by *A. gerardii*.

Figure 1.1. Map of management zones and sampling plots in Dow Field. The treatment zone labels correspond to Stratum-Substratum-Section as described in Table 1.1.

Field Sampling

In 1990, 60 1m x 2m plots were arranged along transects down the approximate centerline of each treatment. There were 15 plots in each substratum in stratum 2, and 5 plots per substratum in stratum 1. Data were collected annually from 1991-2003, and in 2007. Data were gathered in early September, when grass height reached its maximum. In each plot, species were identified and assigned a percent cover at canopy height, such that total percent cover for each plot equaled 100%. Species with less than 5% cover were assigned 0%. As another measure of abundance, individuals of each species were counted, but for bunchgrasses, the number of genets was estimated instead of taking on the tedious task of counting individual stems. A series of 5 measurements of the height of the tallest grass was taken down the lengthwise centerline of the plot, and the mean height of *A. gerardii*, *S. scoparium*, and *Sorghastrum nutans* (Indian grass) were visually estimated.

To compare the diversity of Dow Field with reference sites, I surveyed 5 dry-mesic prairie remnant sites near Ann Arbor (Shanghai Prairie, Highland Cemetery, Swift Run Preserve, Barton Park, and Dexter-Huron Metropark) in August, 2008. At each site, I took stem counts and percent cover estimates from 5 randomly-placed 1 x 2 m sample plots. Shanghai Prairie and Highland Cemetery both have areas of wet prairie, but I surveyed only the upland portions. For direct comparison, I also surveyed Dow Field in the same manner as the other sites in 2008.

Soil Analysis

Soil depth was measured by professors Bob Grese and Gary Fowler in 1999 by inserting a 2.5 cm diameter metal soil corer in the center of each plot until the corer stopped at the hard gravel layer (see Nelson and Anderson 1982, also Tepley 2001). In early April, 2008, I used a 2.5 cm diameter soil corer to collect 3 soil samples along the centerline of each plot to a depth of 20 cm, including the organic (O) horizon where present (n = 3 samples x 60 plots = 180). The three samples from each plot were combined, roots and other particles greater than 2 mm were removed, and the combined samples were analyzed for texture and organic matter. I used the hydrometer method (Bouyoucos 1962) to determine percent of sand, silt, and clay (i.e., soil texture). Organic matter content was determined by wet combustion using the modified Walkley-Black method (Walkely and Black 1934), where organic carbon is oxidized by chromic acid and the spectral absorbance of the product is compared against a set of known standards.

General Approach

The main objective of this study is to examine the interrelated role of fire and site conditions in influencing vegetation patterns and dynamics in Dow Field. Because of the complex nature of community data and the wide variety of questions that range from theoretical to practical, the analyses were split into three chapters. The following lists the major questions addressed in each chapter.

Chapter 2

- What species were found in Dow Field, and how did they contribute to community composition?
- How did native and exotic species differ in their responses to management?
- How did diversity levels in Dow Field compare to nearby prairie remnants?

Chapter 3

- Which environmental and management factors most influenced diversity?

Chapter 4

- How did species composition change over time?
- What factors most influenced year-to-year compositional change?
- How did successional trajectory relate to restoration goals?

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Chapter 2: Long-Term Patterns of Plant Diversity in Dow Field

Introduction

Species identity, number, and abundance are the fundamental components of all ecological communities and can give indications of ecosystem structure and function. Biodiverse ecosystems can enhance ecosystem productivity (Tilman and Downing 1994), preserve nutrient cycles (Risser 1988), resist disturbances and invasion by exotic species (Tilman and Downing 1994, Kennedy 2002), provide wildlife habitat (Van Dyke et al. 2007), or serve recreational or aesthetic purposes (Munro 2006). The number of species in a given area (species richness) is the simplest index of diversity (Magurran 2004), can give a general indication ecosystem health (Woodward et al. 1999), and is the basis for many studies. Species richness can be measured across spatial scales (Whittaker 1960) or be partitioned by functional group (Howe 1994) or native status (Suding and Gross 2006) to give more information about the composition of a community.

In ecological restoration, diversity is particularly important because a common goal is to recreate plant communities similar to those found in historic records or remnant sites (Sluis 2002, Cipollini et al. 2005, Martin et al. 2005). Most restorations seek to increase species richness because the initial degraded state has few species in comparison with the reference ecosystem. Restored communities, however, often have lower diversity than the remnant they are trying to mimic even after several years of management (Kindscher and Tieszen 1998, Sluis 2002, Polley et al. 2005) and thus do not achieve a “complete restoration” (Howell and Jordan 1989). In prairie ecosystems, this may be a result of having relatively little information on how species composition and richness change over long time scales in response to restoration and management (Gibson and Hulbert 1987, Sluis 2002), and the patterns of diversity found in those studies may depend on the specific climate or site conditions where the study took place. Thus, describing changes in diversity over time is critical for our understanding of how specific communities function and for our ability to restore those systems.

My objective in this chapter is to describe the patterns of species diversity in Dow Field, a restored remnant prairie, in response to 16 years of restoration. I partitioned total species richness into native and exotic species richness, because I predicted that native and exotic species richness would have vastly different responses to repeated fire (Smith and Knapp 1999). I also compared levels of diversity in Dow Field to 5 nearby prairie remnants that have similar soil conditions and plant communities as Dow Field. This chapter ultimately defines the plant community in Dow Field in terms of species composition and richness, which then allows investigation into the factors that influence diversity (chapter 3) and species composition (chapter 4).

Methods

A description of the study site and data collection procedures can be found in chapter 1.

Species richness is the number of species in a given area (Magurran 2004). In this study, I used plot-level species richness (alpha richness), treatment-level species richness (the number of unique species occurring in all plots within a treatment), or prairie-level species richness (the number of unique species occurring in all plots combined, or gamma richness) for a given year, depending on the scale of interest (Whittaker 1960). I used average plot-level species richness to compare diversity between management zones in Dow Field, which allowed direct comparisons between treatments with different numbers of plots (Hurlbert 1971). Also, to account for the two components of diversity, richness and evenness, I calculated the Shannon diversity index ($H' = -\Sigma\, p_i \ln(p_i)$, where p_i is the proportion of individuals of a species to the number of individuals in the community) for each management zone in each year. I used the Shannon evenness index ($E = H'/\ln(S)$, where S is treatment-level species richness) to isolate the evenness component. Because H' was highly correlated with species richness ($r = .879$) and species richness is a more intuitive index of diversity, I primarily used species richness in the analysis.

All statistics were generated in SPSS 16.0.2 for Windows (SPSS, Inc. 2008). I performed linear correlations of year vs. richness to identify dominant increasing or decreasing trends in species richness, native species richness, or exotic species richness over time at the prairie level, the plot level averaged for the entire prairie, and the plot level averaged by management zone, or substratum (Wilson et al. 1996). I focused my analysis on stratum 2, which was dominated by *Andropogon gerardii* (big bluestem) and was much larger and had three times more sample plots than stratum 1.

A one-way ANOVA with Tukey's HSD multiple comparison test was used to identify significant differences in species richness between sites ($\alpha < 0.05$). No assumptions were seriously violated for any statistical test.

In addition to species richness, I calculated the average plot level percent cover of grasses, native grasses, forbs, and native forbs. Stem count differences between 1991 and 2007 were used to calculate the change in abundance of the top 5 most frequently occurring native and exotic species. I used stem counts because some species, particularly those with low biomass (e.g., *Panicum oligosanthes*, panic grass), were not abundant enough to be assigned a percent cover (see chapter 1).

Results

Prairie-Level Diversity and Species Occurrence

Seventy-three species were observed in Dow Field from 1991 to 2007, 50 (68%) of which were native, and 23 (32%) of which were exotic. Based on presence-absence data at the plot level, by far the most frequently occurring species in Dow Field during the study was *A. gerardii*, which occurred in 751 (89%) of the 840 sample units (SUs) (60 plots x 14 years = 840). In contrast, the second most frequently occurring C_4 grass, *Schizachyrium scoparium* (little bluestem), occurred in only 39% of SUs. *Solidago speciosa* (showy goldenrod) was the forb with the highest occurrence and the second most common species overall (62% of SUs). *Poa pratensis* (Kentucky bluegrass) (61% of SUs) was by far the most prevalent exotic species. Most species (62%) were uncommon, occurring in less than 5% of the sample units. Appendix 2.1 lists the species in order of occurrance based on plot-level presence-absence data.

There were 69 species observed in stratum 2 over the course of the study. *A. gerardii* was nearly ubiquitous, occurring in 613 (97%) of the 630 of the sample units (45 plots x 14 years = 630). Stratum 2 also had a high occurrence of *P. pratensis* (86% of SUs) and *S. speciosa* (56% of SUs).

S. scoparium was the most frequently occurring species in Stratum 1, found in 182 (87%) of the 210 sample units (15 plots x 14 years = 210). *S. speciosa* (79% of SUs), *Panicum oligosanthes* (panic grass) (70% of SUs), and *A. gerardii* (65% of SUs) were also very common. There were only 52 species observed in stratum 1 over the course of the study. The bulk of the difference in richness compared to stratum 2 is likely because stratum 1 had one-third the sample area of stratum 2.

There were 6 species observed in the 1988 and 1989 transect surveys that were not found in the study plots in subsequent years. These were *Juglans nigra* (black walnut), *Monarda fistulosa* (bee balm), *Asclepias tuberosa* (butterfly milkweed), *Veronicastrum virginicum* (Culver's root), *Vernonia missourica* (Missouri ironweed), and *Ratibida pinnata* (yellow coneflower). Since the transect surveys covered slightly different areas of the field than the study plots, their absence after 1990 could be due to the location of the transects, not local extinction. On the other hand, since most of these species except *J. nigra* are fairly common in adjacent areas that have been restored on an ad hoc basis over the same time period, it is rather surprising that they did not colonize any of the study plots.

Prairie-Level Changes in Species Richness over Time

From 1991 to 2007, the total number of species observed in all plots throughout the prairie fluctuated between 40 and 51 but did not have a significant increasing or decreasing trend over time (Fig. 2.1). However, richness did increase considerably from the transect surveys in 1988 and 1989, although there was not a perfect correspondence between transect and plot location and area. Native species richness did not show a significant trend over the 16 year period, but there was a steady increase from 1992 to 1997 followed by a period of oscillation between years. Exotic species richness declined over time from 16 species in 1991 to 11 species in 2007 ($p = 0.003$, $r^2 = 0.542$ for linear trend).

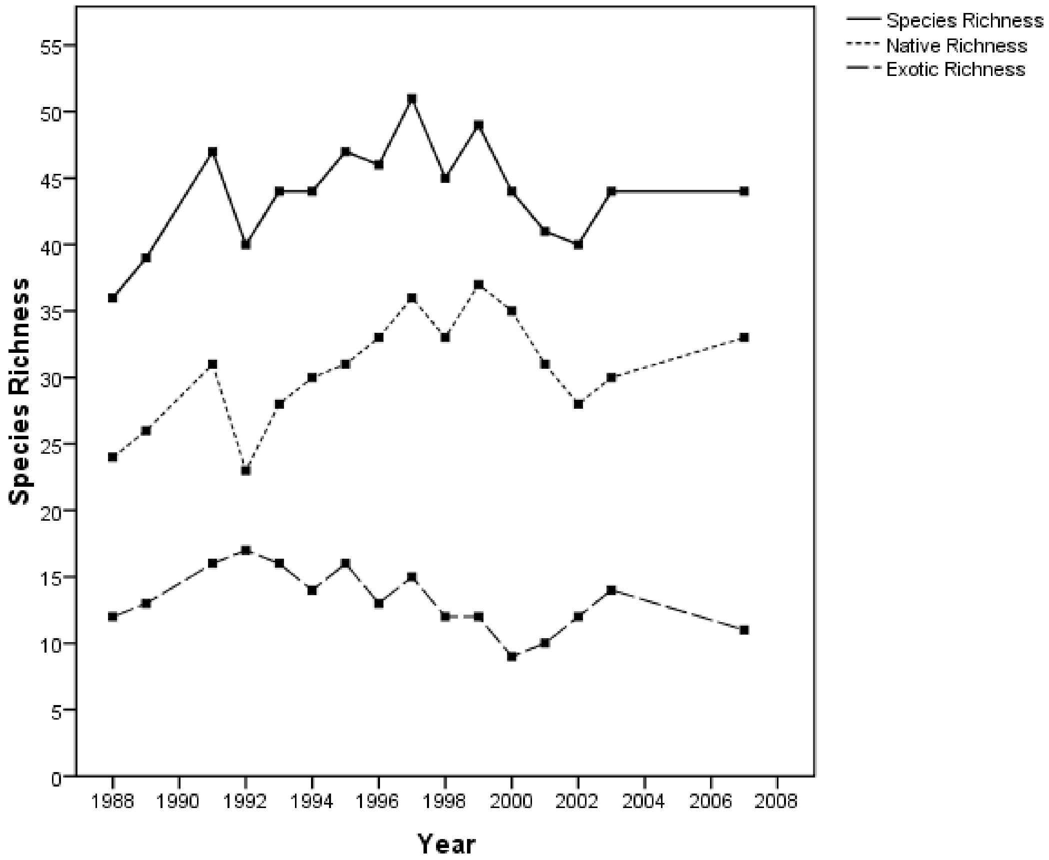


Figure 2.1. Prairie-level species richness, native species richness, and exotic species richness, including data from 1988 and 1989 transect surveys.

Over the 16 year period, mean plot-level species richness for all treatments combined ranged from 9.4 species per plot to 6.6, and showed a significant linear decline through time ($p = 0.024$, $r^2 = 0.360$ for linear trend, Fig 2.2). Species richness varied most in the first several years of restoration, and declined steadily from 1997 to 2002, after which there was a gain of about 1 species per plot by 2007. Meanwhile, average plot native species richness increased from 5.1 to 6.3 ($p = 0.011$, $r^2 = 0.428$ for linear trend), while exotic species richness declined from about 3.9 to about 1.3 ($p < 0.0005$, $r^2 = 0.764$ for linear trend), with the sharpest decline in the first several years after fire reintroduction (Fig. 2.2). Also, there was a highly significant increase in plot-level evenness (*E*) over time from 0.687 to about 0.829 ($p < 0.0005$, $r^2 = 0.706$ for linear trend).

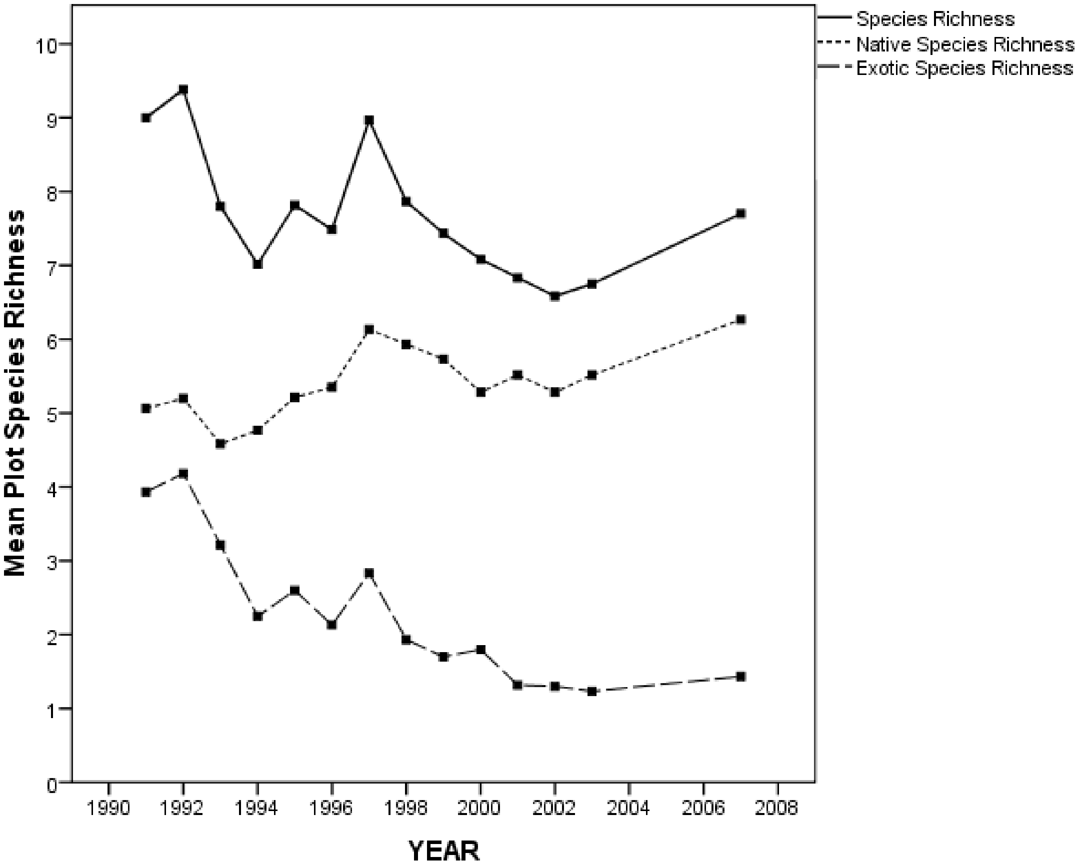


Figure 2.2. Average native, exotic, and total plot-level species richness for all plots in the prairie from 1991 to 2007.

Prairie-Level Trends in Abundance

From 1991 to 2000, there was a considerable increase in average plot level native grass percent cover, while total grass abundance did not change substantially due to the decrease in exotic grasses (Fig 2.3). From 2000 to 2007, grass and native grass percent cover were nearly equal and showed a slight decline over time. Average plot-level forb and native forb percent cover showed an approximately opposite trend; there was little movement in either from 1991 to 2000, but both increased by about 10 percent from 2000 to 2007.

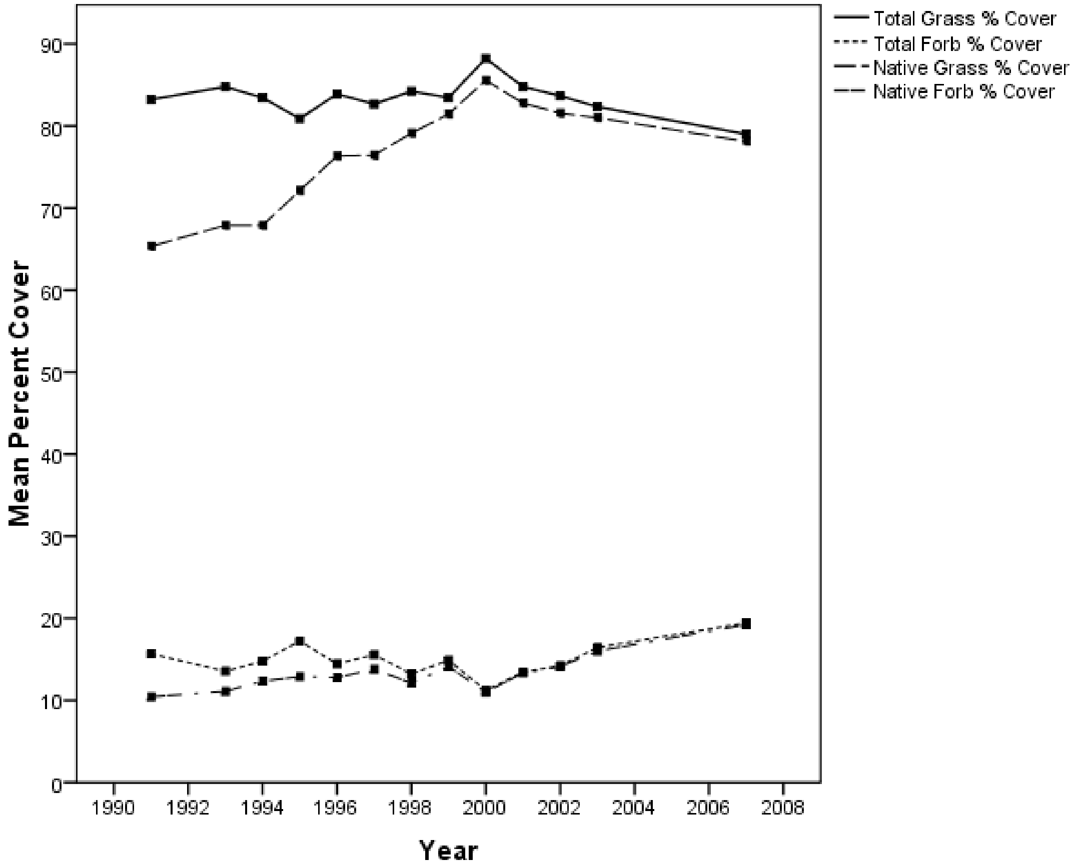


Figure 2.3. Average plot-level forb percent cover, grass percent cover, native forb percent cover, and native grass percent cover for the entire prairie from 1991 to 2007.

For individual species responses of the most frequently occurring species, *S. speciosa* increased the most (178%), while the native bunchgrasses had more modest increases (Tab 2.1). Two native species (a C_3 grass and a legume) declined in abundance over the 16 year period. Only one exotic species (*Hypericum perfolatum*, St. John's wort) showed increased abundance. Most notably, *P. pratensis* and *C. maculosa*, two problematic invasives in many prairies, decreased by 85% and 97%, respectively.

Native Species	Percent Change
Solidago speciosa	+ 178
Andropogon gerardii	+ 42
Schizachyrium scoparium	+ 4
Panicum oligosanthes	- 15
Desmodium canadense	- 57
Exotic Species	
Hypericum perforatum	+ 29
Rumex acetosella	- 13
Poa pratensis	- 85
Hieracum sp.	- 97
Centuarea maculosa	- 97

Table 2.1. Change in abundance of frequently occurring native and exotic species between 1991 and 2007.

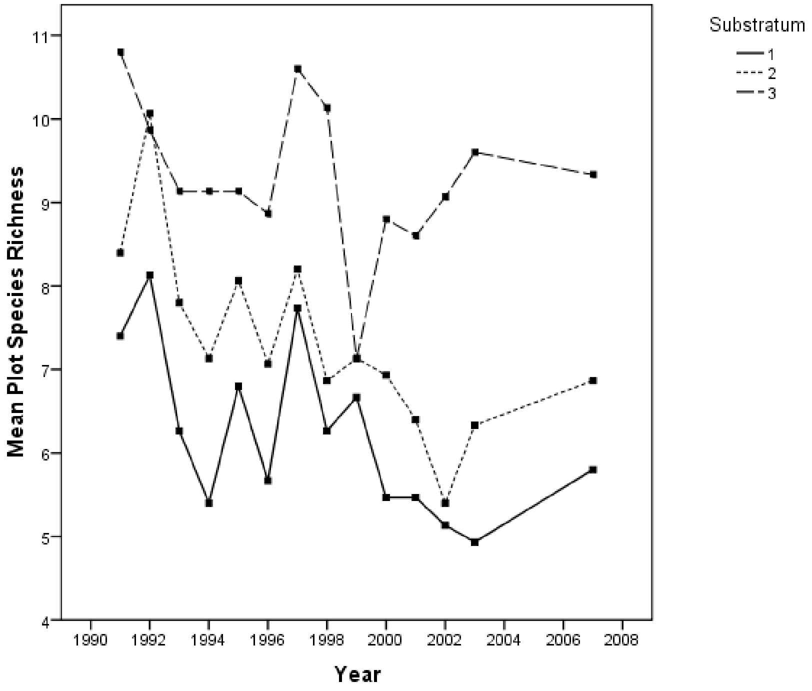
Diversity in Stratum 2

Stratum 2 is the large section of the prairie dominated by *A. gerardii* and has 3 substrata which were burned on different schedules (see chapter 1). Average plot-level species richness decreased over time in substrata 1 and 2, but not in substrata 3, which had wide fluctuations in species richness but consistently had the highest total species richness and native richness throughout the study (Fig 2.4a, Tab 2.2). Substratum 3 also underwent the greatest increase in native species richness, from 5.8 to 8.1 species per plot. In contrast, substratum 1 had the lowest species richness and native species richness, and neither substrata 1 nor 2 underwent a significant increase or decrease in native species richness over time (Fig 2.4a and 2.4b, Tab 2.2).

Exotic species richness declined throughout time but leveled out after 2000 or 2001 in all substrata, but the hyperbolic trend was most pronounced in substrata 2 and 3 (Fig 2.4 c). Because of this, I compared best-fit quadratic curves to the linear trend. Indeed, for all three substrata, a quadratic curve described the data better than a linear curve, although the difference was minimal for substratum 1 (substratum 1: r^2_{quad} =

0.616, $p = 0.001$; substratum 2: $r^2_{quad} = 0.913$, $p < 0.0005$; substratum 3: $r^2_{quad} = 0.853$, $p < 0.0005$). The greatest decrease in exotic species richness was in substratum 3, which dropped from 5.0 to 1.3 species per plot.

a.



b.

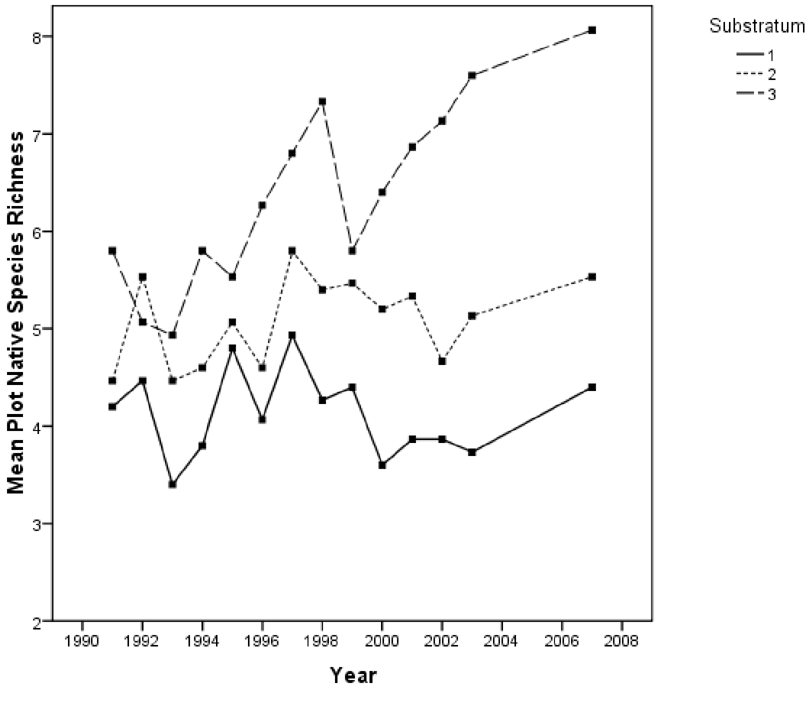
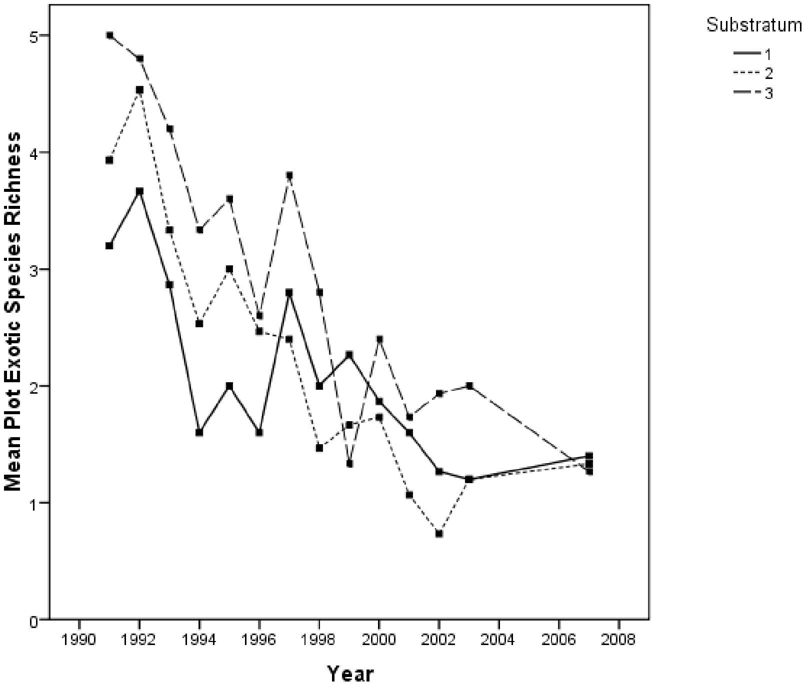


Figure 2.4. Average plot-level species richness (a), average plot-level native species richness (b), average plot-level exotic species richness over time for each substratum in stratum 2.

c.



d.

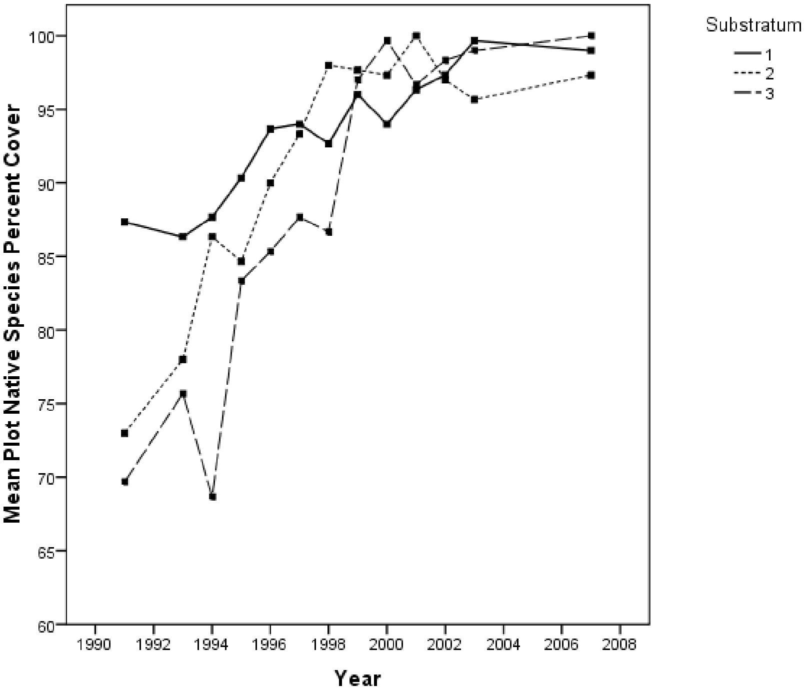


Figure 2.4. Average plot-level exotic species richness (c), and average plot-level native percent cover (d) over time for each substratum in stratum 2.

Stratum 2	**Substratum**	r^2
Species Richness	1	0.383*
	2	0.518**
	3	0.094
Native Richness	1	0.009
	2	0.154
	3	0.746**
Exotic Richness	1	0.559**
	2	0.797**
	3	0.789**

Table 2.2. Linear trends between averaged plot-level diversity measures and year for each substratum in stratum 2. * = significant at the 0.05 level; ** = significant at the 0.01 level.

Native species percent cover increased dramatically in all treatments over time ($p < 0.0005$ for linear trend in all substrata; Fig. 2.4d). By 2000, all of the treatments had between 95% and 100% native cover. However, most of the native cover in each treatment was contributed by *A. gerardii*. In substratum 1, which began with the highest native percent cover and had the highest *A. gerardii* percent cover throughout the study, 80% to 90% of native abundance was contributed by *A. gerardii*.

Diversity in Stratum 1

Average plot-level native species richness significantly increased over time in substrata 1 (3.8. to 7.2 species per plot) and 2 (5.0 to 7.8), whereas exotic species richness decreased in substrata 2 (2.8 to 1.0) and 3 (4.4 to 0.4; Tab 2.3). The decrease in exotic species richness in stratum 3, which was the most dramatic of the 3 substrata, is reflected in the significant decline in total species richness (13.0 to 6.6).

Substratum 3, which was burned annually in the spring until 1999 and then was burned every three years in the fall, had the highest species richness for the first half of the study and the highest native species richness for all but two years. Subtrata 1 and 2 had very similar changes in species richness and native species richness over time, even though substrata 2 began with annual fall burns, while substrata 1 only had triennial burns.

Stratum 1	**Substratum**	r^2
Species Richness	1	0.075
	2	0.038
	3	0.593**
Native Richness	1	0.396*
	2	0.558**
	3	0.162
Exotic Richness	1	0.057
	2	0.430*
	3	0.687**

Table 2.3. Linear trends between averaged plot-level diversity measures and year for each substratum in stratum 1. * = significant at the 0.05 level; ** = significant at the 0.01 level.

Comparison to Reference Prairies

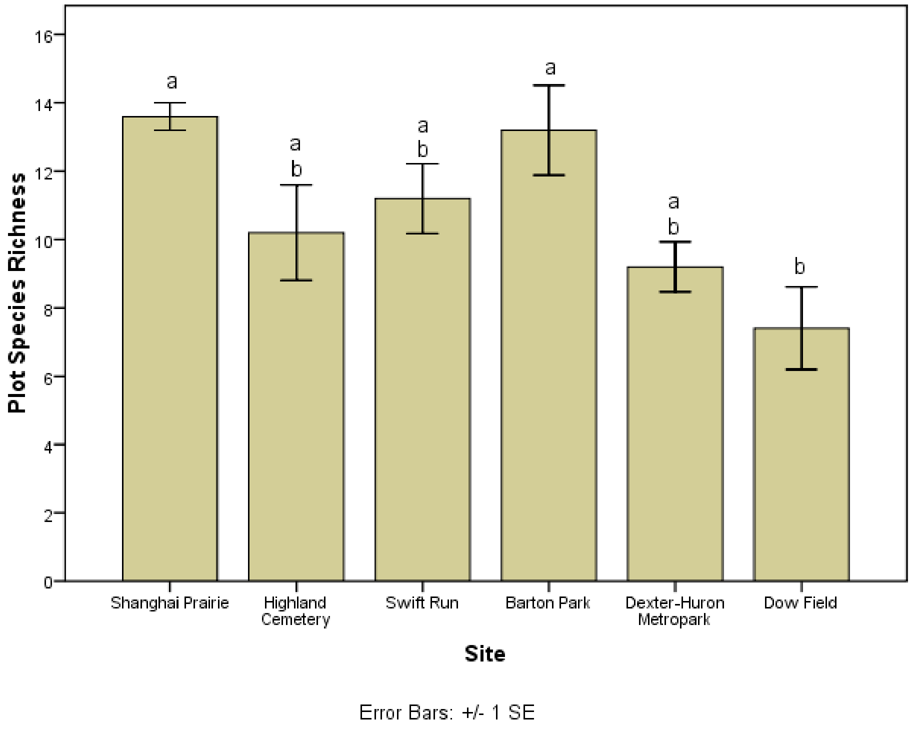


Figure 2.5. Average plot-level richness of Dow Field and 5 nearby prairie remnants in 2008. Bars with the same letters are not significantly different ($\alpha = 0.05$).

Site	**Species Richness**	**% Native Species**	***H'***
Shanghai	30	86.7	2.95
Highland	28	89.3	2.68
Swift Run	24	95.8	2.68
Barton	32	65.6	2.77
Dexter-Huron	20	90.0	2.65
Dow	19	78.9	2.57

Table 2.4. Prarie-level diversity of Dow Field and 5 nearby prairie remnants in 2008.

Appendix 2.2 lists the species found in each of the sites. Dow field had the lowest average plot species richness of all the sites surveyed ($F = 4.926$; $df = 5,24$; $p = 0.003$, Fig 2.5). At the site level, Dow Field also had the lowest species richness and Shannon index value (*H'*), and the second-lowest percentage of native species (*Tab 2.4*).

Discussion

Species Occurrence and Frequency

The plant community of Dow Field was characterized by a few dominant species, while nearly 60% of species observed over the course of the study occurred in less than 1% of the sample plots. This strongly right-skewed species frequency distribution is characteristic of many community types (McCune and Grace 2002) and has an approximately lognormal distribution (Limpert et al. 2001). *Andropogon gerardii* was at the top of the frequency distribution, which is often the case in remnant and restored tallgrass prairies throughout North America (Gibson and Hulbert 1987, Svejcar 1990). Species composition was similar to that of other prairies in the region, as Dow Field had 23 of 34 species (68%) listed by Chapman (1984) as occurring in more than half of the dry-mesic prairies in southern Michigan (Kost 2004).

Changes in Species Richness and Abundance

For all plots combined, both species richness and exotic species richness declined over time at the average plot level, and exotic richness declined at the prairie level. A drop in species richness frequently occurs in early stages of ecological succession, when many of the opportunistic species are replaced or outcompeted by mid-successional perennials, such as the matrix-forming C_4 grasses (Pickett 1982, Sluis 2002). In this case, the decline in populations of exotic species accounted for the bulk of the drop in species richness. In fact, only one native species (*Asclepias syriaca*, a weedy perennial) became extinct from the plots over the course of the study, whereas four weedy exotic species (*Plantago major, Taraxicum officinale, Setaria glauca,* and *Dactylis glomerata*) became locally extinct (see chapter 4).

The decreasing trend in exotic species richness was likely a direct result of repeated fire, which has successfully controlled fire-intolerant exotic species in many prairie restorations (e.g., Smith and Knapp 1999, Wilson and Partel 2003, Bruvig et al. 2007). Some of the exotic species found in Dow Field, particularly *P. pratensis* and *C. maculosa*, are aggressive and persistent in many prairies and can be very difficult to control or eradicate (Sheley et al. 1998, DiTamoso 2000, Cully et al. 2003). From the standpoint of restoration, the precipitous decline in both *P. pratensis* and *C. maculosa* over time in Dow Field was an unexpected, but encouraging result.

The decrease in *P. pratensis* following fire in Dow Field is consistent with other studies (Abrams 1988, Smith and Knapp 1999). As in this study, MacDonald et al. (2007) found that mid-spring burns reduced *C. maculosa* in a reconstructed Michigan prairie, but they also found that it was reduced in unburned plots, possibly because of competition from C_4 grasses. However, Emery and Gross (2005) found that annual or biennial April or October burns did not reduce the population of *C. maculosa* in another planted Michigan prairie. Instead, they found that mid-summer burning was the only treatment that reduced *C. maculosa*. In reality, the reduction of persistent exotics such as *C. maculosa* may be influenced by other factors in addition to fire timing or frequency, such as the severity of invasion, the potential for competitive pressure from warm-season prairie grasses, or abiotic site conditions.

The increase in the exotic *H. perforatum* over the course of the study was counter to my initial expectations, but other studies have found increased abundance and seed production in *H. perforatum* following fire (Tilsdale et al. 1959, Briese 1996). Although *H. perforatum* increased by nearly 30%, it resides in the understory and has low biomass, so its ability to compete with native prairie species may be insignificant.

For the management zones in stratum 2 and at the level of the entire prairie, the greatest drop in exotic species richness occurred from 1991 to 2000, after which exotic richness remained relatively stable or increased slightly. This hyperbolic trend is most pronounced in substrata 2 and 3, which were burned annually for the first 8 years of the study. Substratum 1, which had only triennial burns throughout the study, had the least and most linear decrease in exotic species richness of the three substrata. Thus, there is a correlation between annual burns and a decline in exotic species, a finding supported by other studies (e.g., Smith and Knapp 1999). The period of triennial burns after 1999 in substrata 2 and 3 and over the entire study period in substrata 1 may have allowed some exotics to persist by allowing two growing seasons for recovery between fires.

The leveling out of exotic richness after 2000 could also indicate that exotic species richness had reached a baseline level, and that no amount of annual burning would have resulted in complete eradication. The exotic species that remained after 8 to 10 years of restoration were apparently able to tolerate occasional fire, coexist with native prairie grasses and forbs, and possibly persist indefinitely at low levels in the community. Several studies have documented a decline in exotic species with repeated fire on short timescales or between communities burned at different frequencies (Pendergrass et al. 1998, Smith and Knapp 1999, MacDonald et al. 2007), but this is the first study to my knowledge to show long-term dynamics within the same plots in response to changes in management. Ultimately, the nonlinear trend in exotic species decline in Dow Field may be the combined result of reaching the baseline level of exotic species and the reduced fire frequency after 1999 in two of the substrata.

Average plot-level native species richness for the whole prairie increased steadily over time, but native richness did not show a significant linear trend at the prairie level. The lack of an increase in prairie-level native richness indicates that there were few new immigrants of native species to the prairie over the course of the study. Therefore, the gain in plot-level native richness was probably due to the increased distribution of certain species that were already present in the prairie. The increase in evenness was probably also due to the positive response of native populations to repeated fire, causing them to appear in more plots, and is consistent with the notion that evenness increases as succession progresses (Wilson et al. 1996). Indeed, plots with higher native species richness tended to have higher evenness as well ($r = 0.288$, $p < 0.0005$). Since only 12 native species newly colonized the prairie during the study, most of which established only small or transient populations (see chapter 4), the increase in plot-level richness over time is likely due in part to the arrival of a few immigrants, but mostly to the spread of fire-dependent species over time.

The trends in forb and grass percent cover over time are consistent with what others report in relation to fire frequency (Peet et al. 1975, Gibson and Hulbert 1987, Collins and Gibson 1990). Native grass cover increased with higher fire frequency from 1991 to 1999, while exotic grasses (mostly cool-season) decreased over the same time period. After fire frequency was reduced after 1999, grasses lost some dominance in favor of forbs. Three of the 5 most common native species in Dow Field increased in abundance (based on stem counts) from 1991 to 2007. The increase in *A. gerardii* and *S. scoparium*, both dominant C_4 grasses, is an almost axiomatic community response to repeated fire in prairies (Peet et al. 1975), and *S. speciosa* is also well adapted to fire (Towne and Owensby 1984). The native C_3 grass *P. oligosanthes* declined slightly over time, as is often reported for cool-season exotic grasses after fire (Cully et al. 2003). The over 50% drop in the legume *D. canadense* was initially unexpected, but some previous studies have reported declines over time because of its early-successional status (Betz et al. 1997) or because of selective herbivory by small mammals (Howe and Lane 2004).

In stratum 2, substratum 3 had the greatest native species richness and was the only management zone that increased in native richness over time. The differences in level and rate of increase in native species richness between the three substrata could be explained by different levels of competition from *A. gerardii*, the dominant grass. Potential colonizers may have been excluded from substratum 1, which had a very high abundance of *A. gerardii*, while there may have been more available resources (e.g., space, light, nutrients) in substratum 3 because *A. gerardii* abundance was much lower. Competition can greatly shape diversity trends and community structure (Tilman 1994), but other spatially heterogeneous factors can also influence diversity such as disturbance regime, soil conditions, nutrient availability, and productivity (Tilman 1994, Grace 1999, Polley et al. 2005); these will be explored in chapter 3.

Diversity in Stratum 1

In stratum 1, the small area of the prairie dominated by *S. scoparium*, the differences in fire frequency and season between the three substrata did not affect the plant community in expected ways. Substrata 1 and 2 had very similar trends with regard to species richness and native species richness despite differences in fire season and frequency. Substratum 3, which shared common fire season with substratum 1 and fire frequency with substratum 2, underwent erratic changes in species richness and native richness, although it maintained the highest of both over much of the 16 year period. The decline in exotic species richness in substrata 2 and 3 agreed most with my expectations, and was probably a result of higher fire frequency than in substratum 1 (Smith and Knapp 1999). Ultimately, the sample size (5 plots per substratum) may be too small to draw generalizations from stratum 1.

Comparison to Reference Prairies

Dow Field had lower diversity than any of the remnant sites. Restored sites often have lower species richness than remnant sites, usually because the seed mix used establish the prairie did not reflect the diversity of remnant sites (Kindscher and Tieszen 1998, Allison 2002, Sluis 2002). Polley et al. (2005) suggested that greater resource partitioning and fewer limitations on dispersal or recruitment lead to higher species diversity in remnant prairies. In the case of Dow Field, which is a restored remnant that was unseeded, the level of diversity was probably equally influenced by site history as it was by the post-1988 management. The period of mowing from the 1940s to 1980s filtered out species that were unable to survive repeated mowing or maintain a viable presence in the seedbank for more than 40 years. Thus, only the species that could tolerate these conditions emerged after the reintroduction of fire. Even though the remnants had several native species not found in Dow Field, dispersal from remnants probably did not significantly influence diversity. Indeed, only one of the 10 native immigrants to the sample plots over the course of the study are capable of long-distance wind dispersal (*Solidago rigida*), and it probably was present in or adjacent to Dow Field but did not colonize the plots until midway through restoration (see chapter 4).

Aside from site history, fire frequency may have influenced the differences in diversity between Dow Field and the remnant sites. Shanghai Prairie, Highland Cemetery, and Dexter-Huron Metropark have all been managed sporadically in the recent past on the order of 1 or 2 fires per decade whereas Dow Field was burned every 1 to 3 years. Although Swift Run and Barton Park were burned about as often as Dow Field, those remnants were augmented with seed at various times since the mid 1990s (Jason Tallant, City of Ann Arbor Natural Areas Preservation, pers. comm.). Frequent fire contributes to high productivity of matrix-forming grasses, which can then competitively exclude subdominant prairie forbs and reduce diversity (Collins 1990). Kucera and Koelling (1964) were among the first to suggest that diversity may be maximized in prairies by periodic but not annual fires (the intermediate disturbance hypothesis, or

IDH), and later studies have supported IDH for prairies as well (Gibson and Hulbert 1987, Peterson and Reich 2008).

Another reason for the comparatively low species richness in Dow Field could be that some of the remnants had higher environmental heterogeneity. High diversity is often associated with spatial variation in site conditions such as soil properties and topography (Grace et al. 2000). Dow Field had some spatial variation in soil characteristics, but the range of difference may not have been enough to appreciably influence species composition (see chapter 3). In contrast, Shanghai Prairie and Highland Cemetery had substantial changes in topography within the site that created gradients from wet to dry prairie vegetation. Even though the samples were taken only on the upland portions, within-site variation in topography may have allowed some wet-mesic species such as *Silphium terebinthinaceum* (prairie dock) and *Coreopsis tripteris* (tall coreopsis) to also colonize upland areas because of their close proximity. Ultimately, the comparatively low diversity at the plot and prairie scales in Dow Field is probably a combination of management history, site characteristics, and restoration based only on seedbank recovery. Moreover, the consistently low diversity over time justifies the restoration goal of increasing species diversity and demonstrates the need for continued restoration, which should include strategies to introduce additional native species to the prairie.

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Appendix 2.1. Species in Dow Field listed in order of frequency of occurrence in the sample plots based on presence-absence data from 1991 to 2007.

Rank	Species	Common Name	Frequency	Functional Group	Stratum 1	Stratum 2
1	*Andropogon gerardii*	Big bluestem	0.892	C4 graminoid	X	X
2	*Solidago speciosa*	Showy goldenrod	0.617	forb	X	X
3	*Poa pratensis*	Kentucky bluegrass *	0.611	C3 graminoid	X	X
4	*Panicum oligosanthes*	Panic grass	0.496	C3 graminoid	X	X
5	*Desmodium canadense*	Canada tick-trefoil	0.410	legume	X	X
6	*Schizachyrium scoparium*	Little bluestem	0.387	C4 graminoid	X	X
7	*Rumex acetosella*	Creeping sorrel *	0.348	forb	X	X
8	*Hypericum perforatum*	St. John's wort *	0.336	forb	X	X
9	*Solidago nemoralis*	Gray goldenrod	0.298	forb	X	X
10	*Sorghastrum nutans*	Indian grass	0.274	C4 graminoid	X	X
11	*Oxalis stricta*	Common wood sorrel	0.220	forb	X	X
12	*Potentilla simplex*	Common cinquefoil	0.213	forb	X	X
13	*Aster oolentangiensis*	Prairie aster	0.200	forb	X	X
14	*Aster laevis*	Smooth aster	0.192	forb	X	X
15	*Achillea millefolium*	Yarrow	0.183	forb	X	X
16	*Hieracium spp.*	Hawkweed *	0.180	forb	X	X
17	*Daucus carota*	Queen Anne's lace *	0.158	forb	X	X
18	*Centuarea maculosa*	Spotted knapweed *	0.149	forb	X	X
19	*Potentilla arguta*	Prairie cinquefoil	0.125	forb	X	X
20	*Phleum pratense*	Timothy *	0.112	C3 graminoid	X	X
21	*Antennaria parlinii*	Pussytoes	0.083	forb	X	X
22	*Erigeron annuus*	Daisy fleabane	0.082	forb	X	X
23	*Trifolium pratense*	Red clover *	0.080	legume		X
24	*Rudbeckia hirta*	Black-eyed susan	0.079	forb	X	X
25	*Digitaria cognata*	Fall witchgrass	0.076	C4 graminoid	X	X
26	*Eragrostis spectabilis*	Purple lovegrass	0.065	C4 graminoid	X	X
27	*Dactylis glomerata*	Orchard grass *	0.065	C3 graminoid	X	X
28	*Ascelpias syriaca*	Common milkweed	0.056	forb	X	X
29	*Rubus allegheniensis*	Blackberry	0.044	woody	X	X
30	*Elymus repens*	Quack grass *	0.044	C3 graminoid		X
31	*Rhamnus spp.*	Buckthorn *	0.043	woody	X	X
32	*Carex bicknellii*	Bicknell's sedge	0.040	C3 graminoid	X	X
33	*Cyperus lupulinus*	Sedge	0.038	C3 graminoid	X	X
34	*Solidago rigida*	Stiff goldenrod	0.036	forb	X	X
35	*Aster ericoides*	Heath aster	0.032	forb		X
36	*Plantago lanceolata*	English plantain *	0.032	forb	X	X
37	*Malus spp.*	Crab apple	0.031	woody	X	X
38	*Setaria pumila*	Yellow foxtail *	0.029	C4 graminoid	X	X
39	*Symphyotrichum pilosus*	White aster	0.027	forb	X	X
40	*Vitis spp.*	Wild grape	0.026	woody	X	X
41	*Euphorbia corollata*	Flowering spurge	0.024	forb	X	
42	*Melilotus alba*	White clover *	0.024	legume		X
43	*Plantago major*	Common plantain *	0.021	forb	X	X
44	*Apocynum androsaemifolium*	Dogbane	0.018	forb	X	X

Rank	Species	Common Name	Frequency	Functional Group	Stratum 1	Stratum 2
45	*Cornus foemina*	Gray dogwood	0.017	woody		X
46	*Rosa spp.*	Rose	0.017	woody	X	X
47	*Solanum nigrum*	Nightshade	0.017	forb		X
48	*Rubus spp.*	Raspberry	0.014	woody	X	X
49	*Toxicodendron radicans*	Poison ivy	0.013	woody		X
50	*Antennaria neglecta*	Cat's foot	0.013	forb	X	X
51	*Linaria vulgaris*	Butter and Eggs *	0.011	forb	X	
52	*Fraxinus pennsylvanica*	Red ash	0.008	woody		X
53	*Carex cephalophora*	Sedge	0.008	C3 graminoid		X
54	*Morus alba*	White mulberry *	0.007	woody		X
55	*Verbascum thapsus*	Mullien *	0.007	forb		X
56	*Quercus rubra*	Red oak	0.006	woody	X	X
57	*Carex pensylvanica*	Pensylvania sedge	0.006	C3 graminoid	X	X
58	*Physalis virginiana*	Ground cherry	0.006	forb	X	X
59	*Vicia americana*	American vetch	0.006	legume	X	X
60	*Taraxicum officinale*	Dandelion *	0.006	forb		X
61	*Quercus velutina*	Black oak	0.005	woody	X	
62	*Oenothera biennis*	Evening primrose	0.005	forb		X
63	*Cirsium arvense*	Canada thistle *	0.005	forb		X
64	*Prunus serotina*	Black cherry	0.004	woody	X	X
65	*Cerastium arvense*	Mouse-eared chickweed *	0.004	forb	X	X
66	*Dianthus armeria*	Deptford pink *	0.004	forb		X
67	*Abrosia artemisiifolia*	Common ragweed	0.002	forb		X
68	*Botrychium dissectum*	Grape fern	0.002	forb		X
69	*Acer ginnala*	Trident maple *	0.002	woody		X
70	*Carya spp.*	Hickory	0.001	woody		X
71	*Solidago canadensis*	Canada goldenrod	0.001	forb		X
72	*Conyza canadensis*	Horseweed	0.001	forb		X
73	*Lespedeza capitata*	Prairie bush clover	0.001	legume	X	

* Exotic species

Appendix 2.2. Species found in nearby prairie remnants surveyed in 2008. S = Shanghai Prairie, H = Highland Cemetery, SR = Swift Run Preserve, B = Barton Park, DH = Dexter-Huron Metropark, and D = Dow Field.

Species	**S**	**H**	**SR**	**B**	**DH**	**D**
Achillea millefolium			X	X	X	X
*Ailanthus altissima**		X				
Andropogon gerardii	X	X	X	X	X	X
Anemone virginiana				X		
Apocynum androsaemifolium			X			
Asclepias syriaca						X
Asclepias tuberosa	X	X			X	
Asclepias verticillata	X					
Aster ericoides	X	X	X			
Aster laevis	X	X	X			X
Aster novae-angliae	X					X
Aster oolentagiensis	X	X	X	X	X	X
Carex bicknellii						X
Carex pennsylvanica	X	X	X		X	X
Carex sp.	X			X		
Carex stricta		X				
*Centuarea maculosa**				X		X
Comandra umbellata	X					
Coreopsis tripteris		X				
Cornus foemina	X	X	X		X	X
Corylus americana		X		X		
Cratageous sp.			X	X	X	
*Daucus carota**				X		
Desmodium canadense					X	X
*Dianthus armeria**				X		
Elymus canadensis		X				
Equisetum hyemale	X	X			X	
Erigeron annuus				X		
Euphorbia corollata	X	X		X	X	
Euthamia graminifolia			X			
Fragaria virginiana	X		X	X		
Helianthus divericatus		X				
*Hieracium spp.**	X			X		
*Hypericum perfolatum**				X		
Juncus sp.				X		
Juncus tenuis			X			
Juniperus communis	X					
Liatris aspera	X	X				
*Linearia vulgaris**				X		
Lithospermum canescens		X				
Lobelia spicata	X					
*Lonicera tatarica**			X	X		
*Melilotus alba**	X				X	
Monarda fistulosa			X	X		
Panicum oligosanthes	X			X	X	X

Species	**S**	**H**	**SR**	**B**	**DH**	**D**
Penstamon digitalis			X			
Penstamon hirsutus				X		
Phlox pilosa	X					
*Plantago lanceolata**				X		
*Poa pratensis**	X			X	X	X
Potentilla arguta				X		
Prunus serotina			X	X		
Pteridium aquilinum				X		
Pycanthemum virginanum			X			
Quercus muehlenbergii		X				
Quercus velutina		X				
Ratibida pinnata		X				
*Rhamnus cathartica**		X				
*Rhamnus frangula**	X	X				X
Rosa carolina		X		X	X	
Rubus strigosis		X	X	X	X	X
Rudbeckia hirta	X					
*Rumex acetosella**				X		
Salix sp.		X				
Schizachyrium scoparium	X	X			X	X
Silphium terebinthinatum	X		X			
Solidago canadensis			X			
Solidago juncea	X					X
Solidago nemoralis			X	X	X	X
Solidago rigida	X			X		X
Solidago speciosa				X	X	X
Sorghastrum nutans	X				X	
Spirea alba			X			
*Trifolium repens**				X		
Vitis riparia		X	X			
Zizia aurea			X			

* exotic species

Chapter 3: Predictors of Plant Diversity in Dow Field

Introduction

The environmental factors that determine plant diversity in communities is a major question in ecology (e.g., Grime 1973, Tilman and Pacala 1993). Many past and recent studies have examined the ecological factors or processes that influence diversity in grasslands including succession (Tilman 1988, Howe 1995), disturbance (Collins et al. 1995, Suding 1999, Collins 2000), productivity (Zimmerman and Kucera 1977, Gough et al. 1994, Tilman et al. 1996), nutrient availability (Raison 1979, Ojima et al. 1994), soil conditions (Nelson and Anderson 1983, Seastedt 1995), climate (Knapp 1984, Nippert et al. 2006), herbivory (Anderson et al. 2001, Howe and Lane 2004), competition (Grime 1973, Smith et al. 1999), and species pool (Rabinowitz 1980, Gough et al. 1994). In a comprehensive review, Grace (1999) identified at least 12 categories of environmental factors that influence plant diversity in herbaceous communities, which highlights the complexity of the question.

Identifying the determinants of diversity has practical applications for restoration, where the goal is often to recreate plant communities similar to remnants or historic conditions (Howe 1994). Dow Field has low species richness compared to nearby remnant prairies (see chapter 2), so increasing diversity was a major goal of restoration. It is important for managers of Dow Field and similar prairies in the region to understand how management actions and uncontrolled environmental conditions affect the plant community in order to achieve restoration goals. Therefore, the objective of this chapter is to identify the spatially heterogeneous site conditions that influenced species richness in Dow Field.

I evaluated several abiotic variables for their ability to predict plot-level species diversity in Dow Field. I evaluated the effect of fire frequency on species richness, because fire alters environmental conditions and favors certain species over others (Gibson and Hulbert 1987, Anderson 1990, Collins 1992, Wilson 2007). I analyzed physical soil properties (percent sand, percent silt, percent clay, and depth), which have been shown to influence plant communities by controlling soil moisture, nutrient retention, and root growth (Seastedt 1995). I also measured soil organic matter, which can indicate the level of soil fertility and thereby influence community composition (Kindscher and Tieszen 1998).

Because of its high abundance in Dow Field, I analyzed *Andropogon gerardii* (big bluestem) percent cover as an independent variable acting on species richness. Its competitive role in regulating species diversity has been discussed in many studies (e.g., Abrams and Hulbert 1987, Collins and Gibson 1990, Smith et al. 1999), and is due to its ability to acquire aboveground resources (light and space) and belowground resources (water and nutrients) efficiently across a range of conditions (Silletti et al. 2004, Polley et al. 2007). *Andropogon gerardii* generally increases in abundance with repeated fire (Peet et al. 1975, Gibson and Hulbert 1987, Svejcar 1990) and in response to certain soil conditions (Gibson and Hulbert 1987, Seastedt 1995, Turner and Knapp 1996). Therefore, I expected *A. gerardii* to play a mediating role in determining diversity:

factors such as fire and soil conditions may directly influence diversity, but they may also act indirectly by influencing the competitive ability of *A. gerardii* against other species.

Methods

Statistical Approach

A description of the study design and data collection is found in chapter 1. For this analysis, the statistical population was defined as the section of the prairie where *A. gerardii* was the dominant grass at the beginning of the study (stratum 2). Stratum 2 contains 45 plots, 15 in each of three main management zones (see chapter 1). In this case, the data for each plot was averaged across all years (n = 45 plot averages). Aggregating the time-series data reduces the detail of the dataset, but the advantage gained by reducing noise from autocorrelated year-to-year variability outweighs the loss of yearly specificity. In chapter 4, I include data from all years to explore community change over time.

I analyzed possible relationships between environmental variables and species richness using simple linear correlation in SPSS 16.0.1 (SPSS, Inc. 2008). Correlation is useful because the results are easy to interpret and can help identify dominant trends in the data. However, simple linear correlations do not take into account the effects of other variables, indirect effects, nonlinear relationships, or other confounding factors. A more robust method of analyzing community data is ordination, a statistical technique which combines all variables together in a single model. I then used the results of the ordination to inform a path analysis, a kind of structural equation model. The path analysis was used to propose a causal model that accounts for possible indirect effects of certain variables.

Ordination

To determine the distribution of the plots based on species composition and to identify environmental factors that relate to plot-level diversity, I used Nonmetric Multidimensional Scaling (NMS) ordination (Kruskal 1964). Ordination in general is a statistical technique for use with large, many-dimensional datasets that arranges elements (in this case, sample plots) along an axis or axes according to some criteria (in this case, species composition) so that similar elements are near each other and dissimilar elements are far apart (McCune and Grace 2002). NMS ordination is an iterative technique that ordinates on the basis of ranked distances between sample units, foregoes the requirement of data normality, and avoids some other problems of using other ordination methods on community data (McCune 1997, McCune and Grace 2002). The NMS procedure uses "stress" as a measure of distance between plots in the original many-dimensional space and plots in a reduced-dimensional space. The selection of the final ordination is based on optimizing the tradeoff between low stress (good model fit) and low dimensionality (ease of interpretation). In NMS, the axes of the resulting ordination are unitless and their order is arbitrary. Axes can be assigned meaning by comparing the strength and direction of correlation vectors to the axes (McCune and Grace 2002). I used PC-ORD 5.10 (McCune and Mefford 2006) to perform the ordination.

Two matrices were created to conduct the ordination, one containing average stem counts for species in each of the 45 plots over the study period, and the other containing environmental variables, averaged over time where appropriate, for each of the plots. Rare species were retained in the species matrix despite contributing to noise in the ordination because the question of interest involved species richness. Outlier analysis was performed in PC-ORD, and plot 31 was identified as an extreme outlier, likely because of very high stem counts for *Atennaria parlinii* (smooth pussytoes), a forb that occurred in few other plots. Because of this, I omitted plot 31 from the ordination and path analysis.

The ordination was run using Sorenson distance and 250 runs each of real data and randomized data. Assessing the change in stress as a function of dimension revealed that a 3-dimensional ordination was the best solution. The starting seed of the lowest stress ordination was then used to perform a 3-dimensional ordination with 1 run of real data to obtain the final solution. The final ordination was rotated so that the relationship between axis 1 and species richness, the variable of greatest interest, was maximized to simplify interpretation.

Path analysis

Path analysis is a statistical modeling technique where a causal model is proposed based on outside knowledge of the system, and then non-significant pathways are removed. I used the variables that had the strongest relationships to the data according to the ordination (*A. gerardii* abundance [stem counts], fire frequency, soil depth, and soil clay) as independent (exogenous) variables to explain spatial differences in species richness in Dow Field. Direct pathways from fire frequency and soil characteristics to species richness were not included in the *a priori* model because evidence from the bivariate correlations and ordination suggested that *A. gerardii* abundance was by far the major control of diversity; thus direct effects were probably weak (Grime 1973, Smith et al. 1999, Mancera et al. 2005). Model analysis was conducted in AMOS 16.0 (Arbuckle 2007).

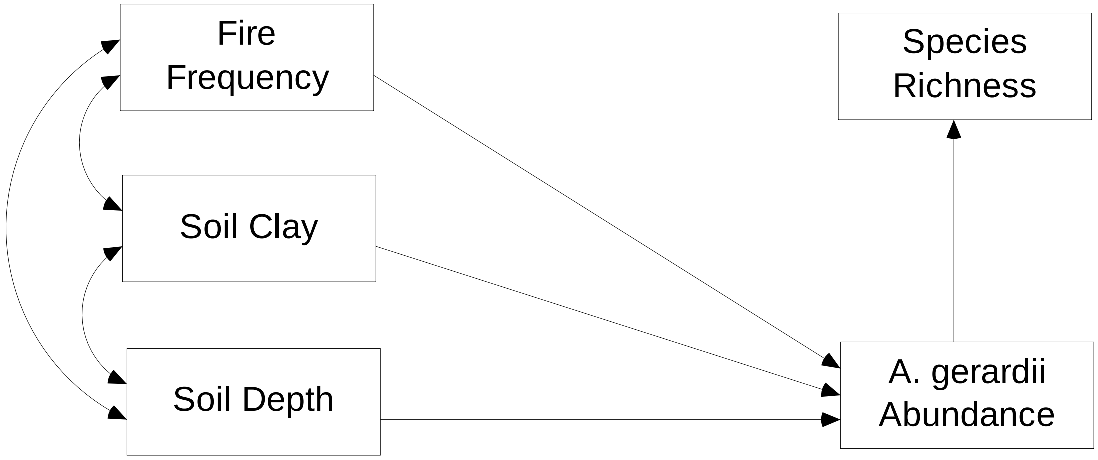


Figure 3.1. Proposed path model, which accounts for all indirect effects of fire frequency, soil depth, and soil clay on species richness in Dow Field mediated by *A. gerardii* abundance. Straight lines are hypothesized causal links and curved lines are autocorrelations between variables.

Because of the relatively low sample size, I tested the statistical significance of the indirect effects (i.e., the pathways where *A. gerardii* is a mediator) using the bootstrapping procedure in AMOS 16.0 (Arbuckle 2007). The bootstrap approximation was obtained by using two-sided percentile-based confidence intervals (Preacher and Hayes 2004).

Interpolation maps were created using the kriging feature in ArcGIS 9.2 to show the spatial characterization of variables that were included in the path analysis.

Results

There were 69 species observed in the 45 plots over the course of the study, and species richness averaged over time for each plot ranged from 3.0 to 12.8. Bivariate correlations revealed several significant linear relationships between species richness and several measured environmental and community variables (Table 3.1). The strongest of these correlations by far was *A. gerardii* abundance, which had a strong negative linear relationship to species richness and native species richness. A simple linear regression showed that species richness declined by about 1.0 for every 42% increase in *A. gerardii* percent cover ($r^2 = 0.542$, $p < 0.0005$). Interestingly, the correlation coefficients of *A. gerardii* and species richness with respect to other environmental variables had nearly equal magnitude but opposite sign in every case. Fire frequency, soil depth, and percent clay showed weaker but statistically significant linear relationships with species richness. There was no significant relationship between species richness and soil sand, silt, or organic matter.

		Species Richness	Native Richness	Exotic Richness	*A. gerardii* % Cover	Grass Height	Fire Frequency	Soil Depth	% Sand	% Silt	% Clay	% Organic Matter
Species Richness	*r*	1.000										
Native Richness	*r*	.889**	1.000									
Exotic Richness	*r*	.606**	.175	1.000								
A. gerardii % Cover	*r*	-.736**	-.698**	-.366*	1.000							
Grass Height	*r*	-.727**	-.674**	-.387**	.872**	1.000						
Fire Frequency	*r*	.440**	.395**	.250	-.487**	-.437**	1.000					
Soil Depth	*r*	-.427**	-.385**	-.249	.345*	.330*	-.387**	1.000				
% Sand	*r*	.156	.132	.107	-.108	-.224	-.207	.423**	1.000			
% Silt	*r*	-.050	-.022	-.072	.021	.098	.243	-.462**	-.975**	1.000		
% Clay	*r*	-.425**	-.424**	-.179	.338*	.534**	.025	-.158	-.725**	.553**	1.000	
% Organic Matter	*r*	.215	.108	.270	-.211	-.169	.437**	-.493**	-.503**	.529**	.244	1.000

** Correlation is significant at $\alpha = 0.01$.

* Correlation is significant at $\alpha = 0.05$.

Table 3.1. Bivariate correlations between environmental and community variables in Dow Field.

The stress of the NMS ordination dropped by 6.3 points between 2- and 3-dimensional ordinations, but only by 2.9 points when a fourth dimension was added. Therefore, I concluded that a 3-dimensional ordination was the optimal solution for the data. The stress of the final ordination was 11.270, indicating a good fit with the data (McCune and Grace 2002). Axes 1, 2, and 3 accounted for 35.7%, 33.1%, and 20.8% of the observed distances in the original 69-dimensional space, respectively (total of 85.5%).

The strongest correlations were with axis 1, which indicates that there were strong relationships between species richness (which was rotated to maximize its relationship to axis 1) and several environmental variables (Fig 3.1). The results of the ordination were not substantially different than the results of the simple linear correlations: fire frequency was positively correlated with axis 1, while soil percent clay, soil depth, and *A. gerardii* percent cover had a negative correlation with axis 1 (Table 3.2). Also, both native and exotic species richness were strongly positively correlated with axis 1, and thus with total species richness. Soil percent sand, percent silt, and percent organic matter had $r^2 < 0.10$, and were not considered to be significant predictors of community diversity.

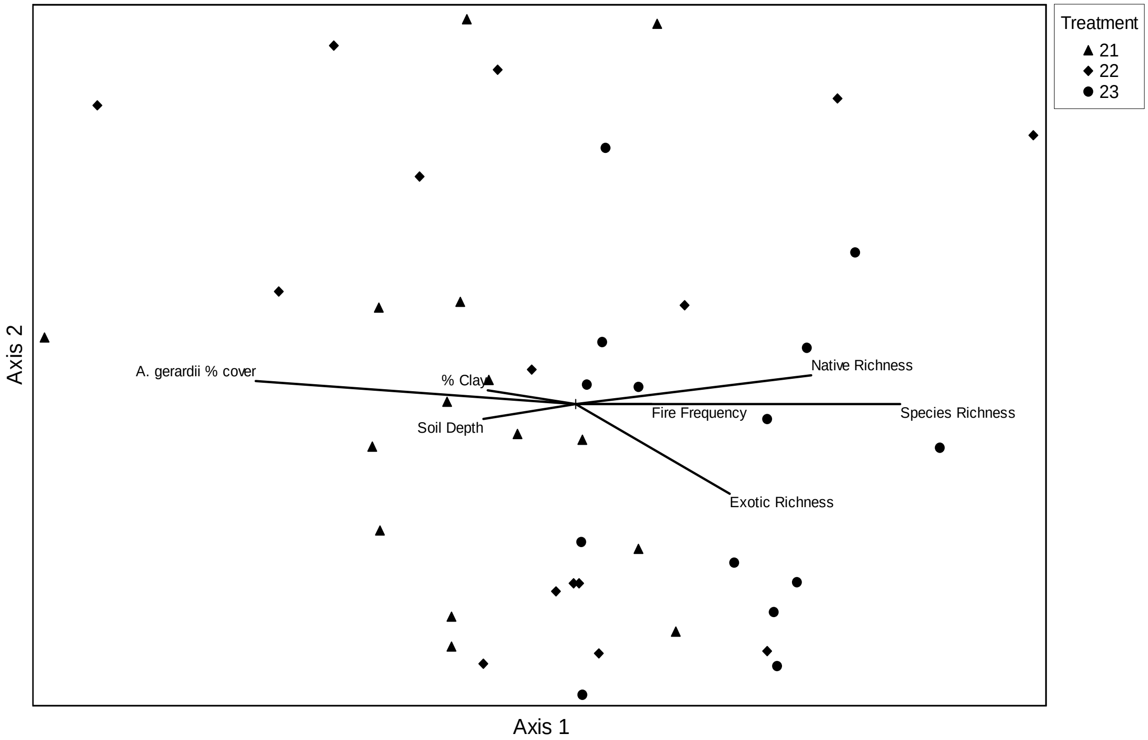


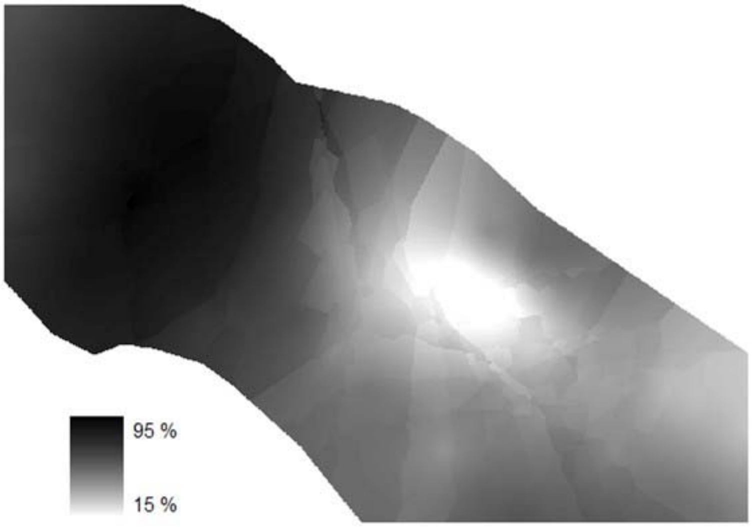
Figure 3.2. Nonmetric multidimensional scaling (NMS) ordination based on the 69 species that occurred in 44 plots in stratum 2. Points are sample units averaged over time, and the distance between points is proportional to the dissimilarity in species composition. The 3-dimensional ordination is plotted against axes 1 and 2, which together explain 68.8% of the variability in the data. In NMS, the order of the axes is arbitrary. All correlation vectors have $r^2 > 0.10$, and lengths of the vectors indicate the strengths of the correlations.

Variable	***Direction***	***r^2***
Species Richness	+	0.656
Native Richness	+	0.476
Exotic Richness	+	0.311
Fire Frequency	+	0.153
Soil Clay	-	0.178
Soil Depth	-	0.186
A. gerardii % cover	-	0.646

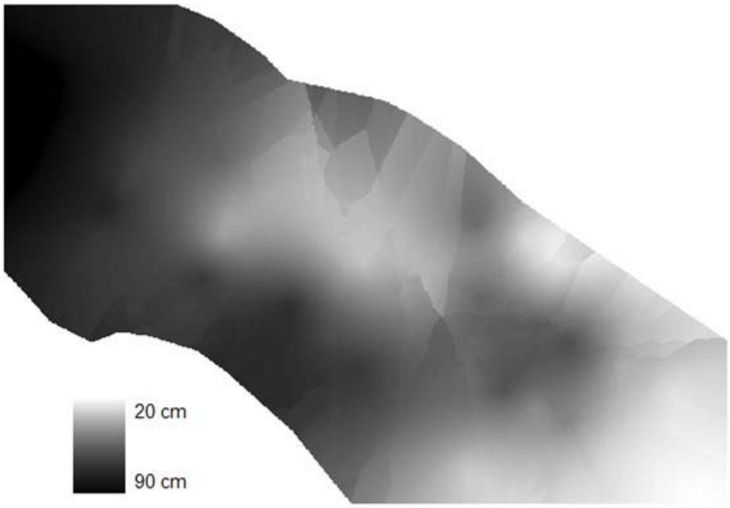
Table 3.2. Correlations between axis 1 and environmental variables with $r^2 > 0.10$ in descending order of correlation direction and strength.

In general, plots in substratum 1 were scored low on ordination axis 1, which means that the average community composition was characterized by high *A. gerardii* abundance and low species richness. Also, substratum 1 had deeper soils with higher clay content. In contrast, plots in substratum 3 scored high on axis 1 and had low *A. gerardii* abundance, high species richness and native richness, and shallower soils with lower clay content. Substratum 2 was a heterogeneous mixture of these characteristics, likely because it was split in two sections that spanned the length of the prairie. Figure 3.2 shows interpolations of actual site conditions, which confirm the arrangement of the plots in ordination space.

a.



b.



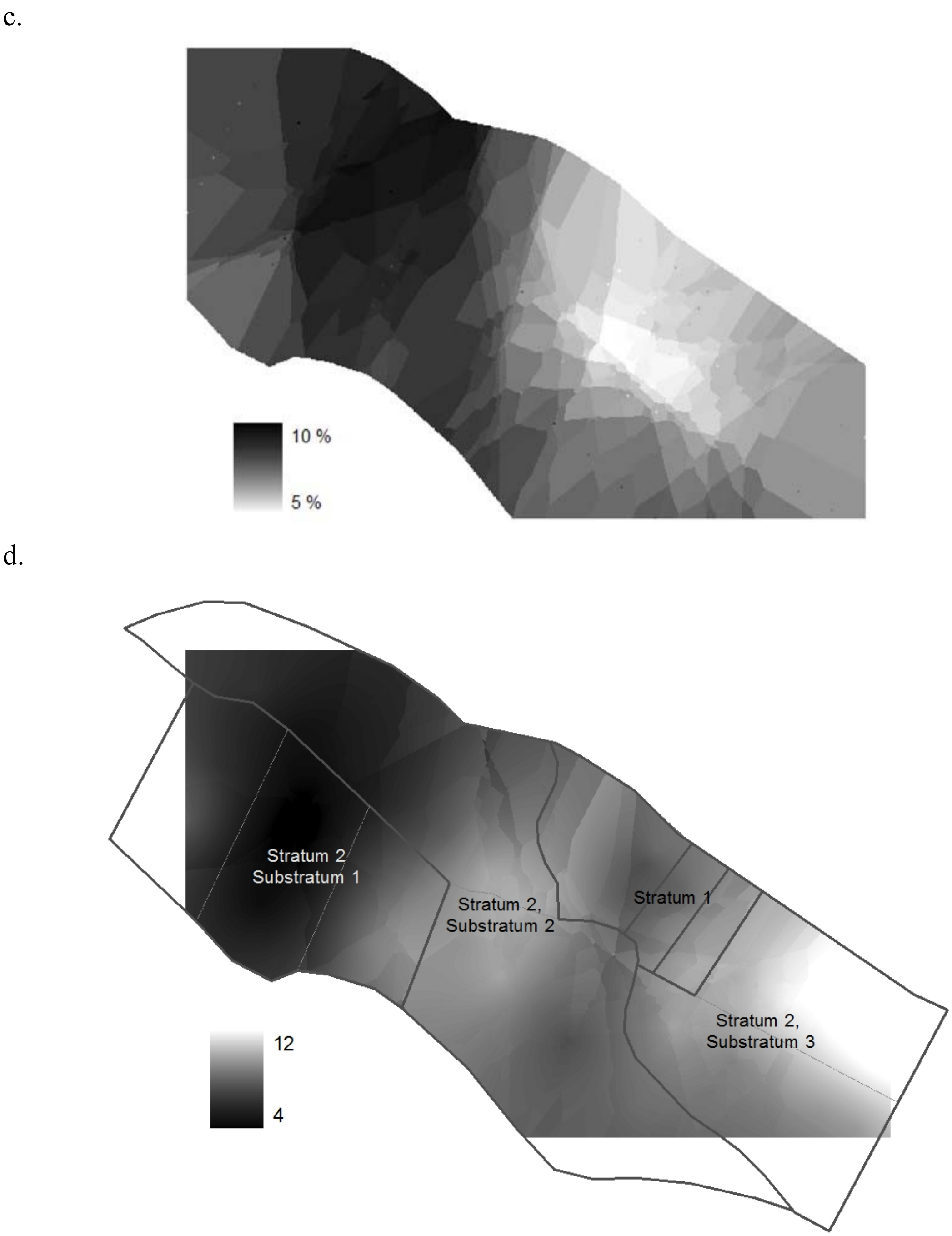


Figure 3.3. GIS interpolations of site characteristics relating to species richness based on results of Nonmetric Multidimensional Scaling ordination. *Andropogon gerardii* percent cover (a); soil depth (b); soil percent clay (c); species richness (d). The interpolations show the entire prairie, but stratum 1 was not included in this chapter’s analyses.

Path Analysis

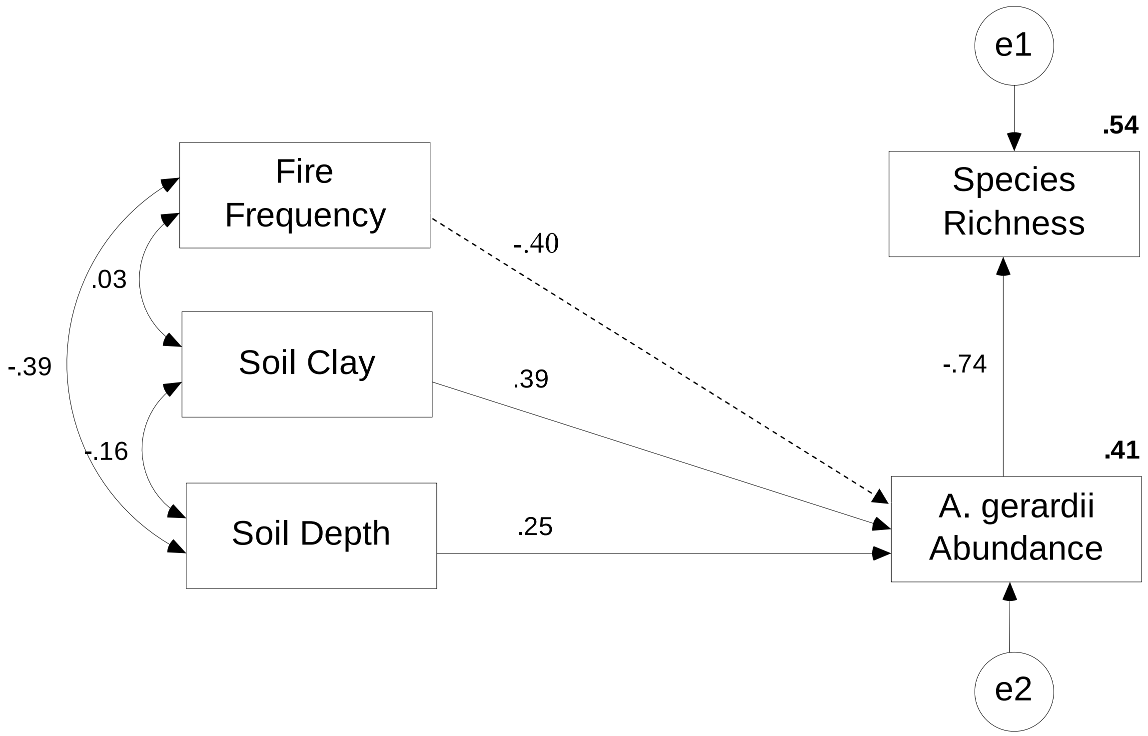


Figure 3.4. Conceptual model of factors controlling diversity in Dow Field. Standardized path coefficients are shown for significant pathways, and r^2 values are given in bold for the dependent variables. The dashed line between fire frequency and *Andropogon gerardii* abundance represents a questionable result (see discussion). The model accounts for 41% of the variability in *A. gerardii* abundance and 54% of the variability in species richness.

All paths in the model were significant ($p < 0.05$), and the final model accounted for 41% of the variability in *A. gerardii* abundance and 54% of the variability in species richness. However, the model fell outside of the range usually considered statistically valid (Comparative Fit Index (CFI) = 0.870, Root Mean Square Error of Approximation (RMSEA) = 0.013), probably due to low sample size (Laura Klem, University of Michigan Center for Statistical Consultation and Research, personal communication). Despite the low sample size and dubious statistical nature of the final model, the bootstrapping test for statistically significant indirect effects showed that all three indirect pathways were significant at the $\alpha = 0.05$ level ($p = 0.002$ for fire frequency → *A.*

gerardii → species richness, $p = 0.015$ for soil % clay → *A. gerardii* → species richness, and $p = 0.018$ for soil depth → *A. gerardii* → species richness). Thus, the model is still conceptually useful for envisioning the effects of soil characteristics and competition on species richness.

Discussion

The level of species richness was significantly correlated with *A. gerardii* abundance, fire frequency, soil depth, and soil clay content, as was shown by the bivariate correlations and the ordination results. By far the strongest relationship in the data was the negative relationship between *A. gerardii* abundance and species richness. This relationship seems to supersede those between species richness and other variables, as evidenced by the equal magnitude but opposite direction of correlations of *A. gerardii* and species richness with respect to all other variables, even those with nonsignificant correlations.

Andropogon gerardii, a matrix-forming C_4 grass, is an integral part of nearly all remnant and restored tallgrass prairie communities throughout North America. It contributes greatly to the physical structure of prairies and regulates ecosystem processes such as the cycling of water and nutrients. The success of *A. gerardii* as a dominant species in prairies is owed largely to its ability to intercept light and uptake nitrogen and water efficiently across a broad range of conditions (Gibson and Hulbert 1987, Wedin and Tilman 1990).

The strong negative correlation between *A. gerardii* and species richness indicates that *A. gerardii* displaced many of the subdominant prairie forbs in Dow Field by competitive exclusion, a finding supported by many other studies (e.g., Abrams and

Hulbert 1987, Collins and Gibson 1990, Collins 1992, Smith et al. 1999). Dominant species in a variety of ecosystem types have been shown to induce interspecific competition on neighboring individuals, thereby decreasing overall community diversity (Goldberg and Barton 1992). This is often shown experimentally by reducing the abundance of the dominant species and observing resulting changes in species diversity (e.g., Smith et al. 1999, Silletti et al. 2004). Although there were no explicit experimental manipulations of *A. gerardii* abundance in Dow Field, there was considerable spatial variation in *A. gerardii* abundance (and thus species richness) that was directly related to changes in soil characteristics.

One of the significant predictors of species richness was depth of soil to the gravel layer, an effect that was likely mediated by *A. gerardii* abundance. Shallow soils (< 0.50 m) tended to have a lower abundance of *A. gerardii*, and thus reduced competitive pressure on other species. The inability for *A. gerardii* to dominate on shallow soils is likely due in part to the physical barrier of the gravel layer restricting belowground growth of deep-rooted species. Rooting depth of *A. gerardii* can exceed 2 m (Weaver 1958), whereas other potentially dominant C_4 grasses such as *Schizachyrium scoparium* (little bluestem) have more intermediate rooting depth (Weaver 1958, Craine et al. 2002). Indeed, *S. scoparium* was the dominant grass in shallower soils throughout Dow Field. Some deep-rooting prairie forbs (e.g., *Solidago rigida*, *Silphium terebinthinatum*, *Lespedeza capitata*) might also have been excluded from areas of shallow soil, but any direct effect of shallow soil on overall diversity was probably trivial.

Shallow soil depth also likely contributed to lower soil moisture retention because the water would percolate quickly through the underlying layer of coarse gravel.

Moreover, Tepley (2002) found that there was a much greater percentage of coarse gravel underneath the shallow soils than under the deeper soils in Dow Field. Deeper soils also tended to have more clay content than shallow soils, which were sandier, amplifying the variability in water holding capacity. *A. gerardii* can be competitive in a range of soil conditions, including soils with high soil moisture such as wet prairies and sedge meadows (Bowles et al. 1996, Copeland et al. 2002), whereas *S. scoparium* is generally restricted to mesic or dry-mesic sites (Anderson et al. 1984). With less aboveground biomass than *A. gerardii*, *S. scoparium* may have allowed other species to coexist because of lower light interception.

Soil clay was another predictor of *A. gerardii* abundance and thus species richness. In the generally sandy and droughty soils of Dow Field, small differences in clay content (which ranged from 5 to 10%) may influence soil moisture enough to considerably impact the plant community. Many studies have found that community productivity is limited by water availability, especially in frequently-burned prairies (Anderson 1982, Abrams et al. 1986, Briggs and Knapp 1995, Knapp and Smith 2001). These studies are consistent with the findings in Dow Field that average maximum stem height of *A. gerardii* in the plots (an approximation of biomass) was positively correlated with soil depth ($p = 0.027$), clay content ($p < 0.005$), and annual rainfall ($p < 0.005$). Some studies have found an increase in ecosystem productivity is related to an increase in diversity (Tilman and Downing 1994), but that relationship can be reversed when a highly competitive species becomes dominant (Silletti et al. 2004). Higher clay content in soils also generally increases cation exchange capacity, a measure of nutrient availability (Seastedt 1995). In soils with higher clay content, *A. gerardii* may be able to capitalize on increased water and nutrient availability more efficiently that other species (Piper 1995, Herbert et al. 2004), possibly because of traits such as superior root structure (Craine et al. 2002) or mycorrhizal associations (Smith et al. 1999) that are lacking in subdominant species. The result is increased aboveground *A. gerardii* biomass, which leads to competitive exclusion of other species by means of superior light interception (Risser 1988, Herbert et al. 2004, Collins and Steinauer 1998).

The correlations between fire frequency, *A. gerardii* abundance, and species richness were unexpected given our knowledge how plant communities respond to disturbance. Most studies conclude that diversity in prairies is more or less consistent with the intermediate disturbance hypothesis (IDH), which states that diversity is maximized when disturbance is neither very frequent nor very infrequent (Grime 1973, Connell 1978, Peterson and Reich 2008). The historical fire frequency in North American prairies is often thought to be 3 to 5 years (Wright and Bailey 1982). Prairies that undergo very frequent fire (e.g., annual burning) often have low diversity compared to those burned at lower intervals or not at all (Gibson and Hulbert 1987, Collins and Gibson 1990). By removing aboveground biomass, fire alters nitrogen, moisture, and light availability so that the competitive ability of C_4 grasses is increased, which then leads to exclusion of subdominant species and a reduction in overall diversity (Knapp and Seastedt 1986, Svejcar 1990, Briggs et al. 1994, Blair 1997).

The relationship observed in Dow Field contradicts the IDH. Fire frequency in the prairie ranged from 5 to 11 fires over the 16 year period, and species richness was highest in frequently burned management zones and lowest in infrequently burned areas. However, this “effect” is likely an artifact of the placement of the management zones.

Stratum 2, substratum 1 (burned triennially throughout the study) was coincidentally located in the area of highest initial *A. gerardii* abundance which created a correlation between low fire frequency and high *A. gerardii* abundance. Additionally, fire frequency had no effect on the rate of *A. gerardii* increase in the treatments. Any true effects of fire on *A. gerardii* or diversity were likely obscured by the nature of the study (i.e., observational, not experimental) and the lack of replication of the treatments. However, the results demonstrate that lower fire frequency alone was not enough to overcome the opposing effects of soil characteristics (which were not known at the time of the layout of the management zones) to limit coexistence between *A. gerardii* and subdominant species.

Conclusion

The specific differences in fire regime between management zones did not influence the spatial distribution of *A. gerardii* or species richness in predictable ways, although the frequent fire in general was probably central to increasing the abundance of *A. gerardii* and decreasing diversity over time. Rather, variability in soil properties that increased soil moisture seemed to determine the spatial differences in species richness across Dow Field by increasing the competitive ability of *A. gerardii*.

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Chapter 4: Plant Community Compositional Change in Dow Field

Introduction

The change in communities over time, in terms of both species composition and abundance, is a central theme in ecology (Ives et al. 1999). Change in plant communities is driven primarily by disturbance, which alters abiotic conditions and the competitive abilities of species in the community (Tilman 1982, Pickett et al. 1987). In ecosystems such as prairies that depend on a high frequency of disturbance, plant communities can shift in response to individual disturbance events as well as to changes in multi-year trends in the disturbance regime (Collins and Gibson 1990, Howe 1995). The high incidence of severe disturbance in prairies and the potential for rapid shifts in composition make prairies ideal systems in which to study compositional change, as evidenced by the large body of research on succession in grasslands (eg. Gibson and Hulbert 1987, Collins 1992, Howe 1995, Tilman et al. 1996, Polley et al. 2007).

The degree to which disturbances affect compositional change in prairies can depend on the timescale of interest. For example, year-to-year compositional change in grasslands has been shown to be influenced by time since fire and anomalous weather (Gibson and Hulbert 1987, Nippert et al. 2006, Wilson 2007, Anderson 2008), whereas changes on longer timescales can be affected by interactions between historic fire regime, abiotic site conditions, and species interactions (Abrams and Knapp 1986, Gibson and Hulbert 1987, Collins 2000). Changes in species composition or abundance between pairs of consecutive years may merely represent fluctuations around a loose equilibrium (DeAngelis et al. 1985). Together, the cumulative effects of repeated disturbance can in part determine successional direction over time (DeAngelis and Waterhouse 1987). Alteration of the disturbance regime of a community is central to ecological restoration, where the goal is often to alter the successional trajectory of the ecosystem to reach a more desirable state (SER 2004, Prach and Hobbs 2008). The outcome of many restoration projects, therefore, depends on the practitioner's understanding of change in the ecosystem as well as their ability to predict how the community may change in the future. Assessing successional change can be an effective way to evaluate restoration progress and inform adaptive management decisions (Masters 1997, Pastorok et al. 1997, Korb et al. 2003).

To that end, I evaluated changes in species composition in Dow Field for year-to-year change as well as cumulative sucessional trajectory over the entire study period. I also related compositional change to environmental factors in order to determine the factors that most influenced compositional change and evaluate restoration progress. I hypothesized that compositional change between pairs of consecutive years would be greatest when growing season temperature and precipitation differed the most from previous years, and when time since fire was minimized. I also predicted that the successional trajectory of treatments over the 16 years of the study would converge on communities characterized by increased native diversity and abundance, and a high abundance of *A. gerardii*.

Methods

Site description, study design, and methods for data collection are given in chapter 1.

Trends in prairie-level species composition

I used presence-absence species data from the entire prairie to investigate year-to-year changes in species composition in Dow Field. To identify species that colonized or were extirpated from the prairie during the study, I identified species that were not present in 1991 or later, but had a presence in all subsequent years after their appearance (immigrations), and species that consistently occurred but were not found in any years after their disappearance (local extinctions).

To quantify the magnitude of species turnover in the whole prairie between pairs of consecutive years, I used the Sorensen dissimilarity index based on species presence only (i.e., neglecting any measures of abundance). The Sorensen index is given by the equation $C_s = 1 - 2w/(A+B)$, where w is the number of species shared between communities a and b, and A and B are the species richness of each community (Magurran 2004). Thus, values close to zero indicate similar community composition, whereas values near one indicate many different species between years. When multiplied by 100, these values indicate the percentage of species turnover in the community (McCune and Grace 2002).

Treatment-level compositional change

For this finer-scale analysis, I combined plot-level stem count data to obtain treatment-level averages of community composition (for stratum 2, n = 7 treatments x 14 years = 98). I did the same for other community characteristics such as species richness and percent cover of certain species groups for use in correlation overlays. As in other chapters, I defined the population as the plant community in stratum 2, the large section of the prairie dominated by *Andropogon gerardii* (big bluestem).

I used nonmetric multidimensional scaling (NMS) ordination (Kruskal 1964, Mather 1976), a procedure described in detail in chapter 3, to characterize plant community change at the treatment level. The ordination was done using PC-ORD 5.10 (McCune and Mefford 2006) using untransformed data because common transformations that can improve assumptions of normality (square root and arcsine square root) resulted in higher final stress in the ordination. Species that occurred in less than 5% of the plots were removed to reduce statistical noise, leaving 51 out of 69 species for ordination. The ordination was performed using Sorenson distance and 250 runs each of real data and randomized data. Assessing the change in stress as a function of dimension revealed that a three-dimensional ordination was the best solution. The starting seed of the lowest stress ordination was then used to perform a three-dimensional ordination with 1 run of real data to obtain the final solution. I used successional vectors to connect points from consecutive years within each treatment, where the length of the vectors corresponds to the magnitude of compositional change between consecutive years. I then used simple linear regression to compare vector length with environmental variables to determine the factors that contribute to compositional change (Anderson 2008).

To elucidate the overall successional trajectory over the 16 years of the study, I performed another NMS ordination, this time using only the 1991 and 2007 data points for each treatment. By using only the first and last data points, I was able to obtain a model of cumulative successional magnitude and direction for the entire study (Kahmen and Poschlod 2004). The ordination was obtained following the same procedure as above, and resulted in a two-dimensional solution. Measured community characteristics relevant to restoration (e.g., species richness, evenness, native and exotic richness and abundance) were then overlaid to show relationships with the movement of the treatments through time. To better visualize succession, the ordination was rotated to maximize the relationship between time and axis 1.

Successional progress in terms of community characteristics (species richness, evenness, etc.) was evaluated by comparing the directional similarity between successional vectors and correlation vectors in relation to the ordination axes. For example, if successional trajectory in a treatment was positively correlated with both ordination axes, then correlation vectors of community characteristics that were also positively correlated with both axes (or negatively correlated with both) were considered good descriptors of how the community changed over time. Community changes could still be described by correlation vectors that related to successional direction in only one of the two dimensions, but they had lower descriptive power.

As a comparison to the ordination results, simple linear regression using all years of data was used to calculate trends in community characteristics over time (Wilson et al. 1996).

Results

Ten native species and two exotic species newly colonized the prairie during the study (Table 4.1). Most of the colonizers first appeared in the first several years of the study, presumably in response to the reintroduction of fire and the resulting changes in resource availability. Five species became locally extinct from the plots during the study, only one of which was native (*Asclepias syriaca*, common milkweed). There were also a few species that were observed sporadically throughout the study, but did not occur with enough consistency to be considered either immigrations or extinctions.

Immigrations	*Extinctions*
Potentilla arguta (1992)	*Plantago major** (1997)
Antennaria neglecta (1993)	*Taraxicum officionale** (1999)
Cornus foemina (1994)	*Setaria glauca** (2000)
Euphorbia corollata (1995)	*Dactylis glomerata** (2001)
Quercus velutina (1996)	*Asclepias syriaca* (2002)
Carex bicknellii (1996)	
Carex pensylvanica (1996)	
Solidago rigida (1996)	
Carex cephalophora (1997)	
Botrychium dissectum (1997)	
*Linaria vulgaris** (1999)	
*Cirsium arvense** (2002)	

* exotic species

Table 4.1. Prairie-level immigrations and extinctions. The year indicates time of appearance or disappearance.

At the prairie level, the Sorensen dissimilarity index between pairs of consecutive years ranged from 0.119 (11.9% turnover) to 0.253 (25.3% turnover) ($\mu = 0.173$, $\sigma = 0.04$). The greatest year-to-year changes in species composition corresponded with the major alterations of the management regime (Fig 4.1). Dissimilarity was about twice as high in 1989 and 1991 when the initial burning regime was being established than it was at its lowest point. There was also a substantial increase in dissimilarity in 2000 and 2001 when all annually-burned treatments were switched to triennial fires and burn season was changed in each treatment. By about three years after a change in the disturbance regime, the rate of compositional change stabilized at a relatively low level, between 12% and 18% turnover between consecutive years. Although this procedure is helpful to identify trends in compositional change between paired years, it does not account for cumulative community change or successional direction.

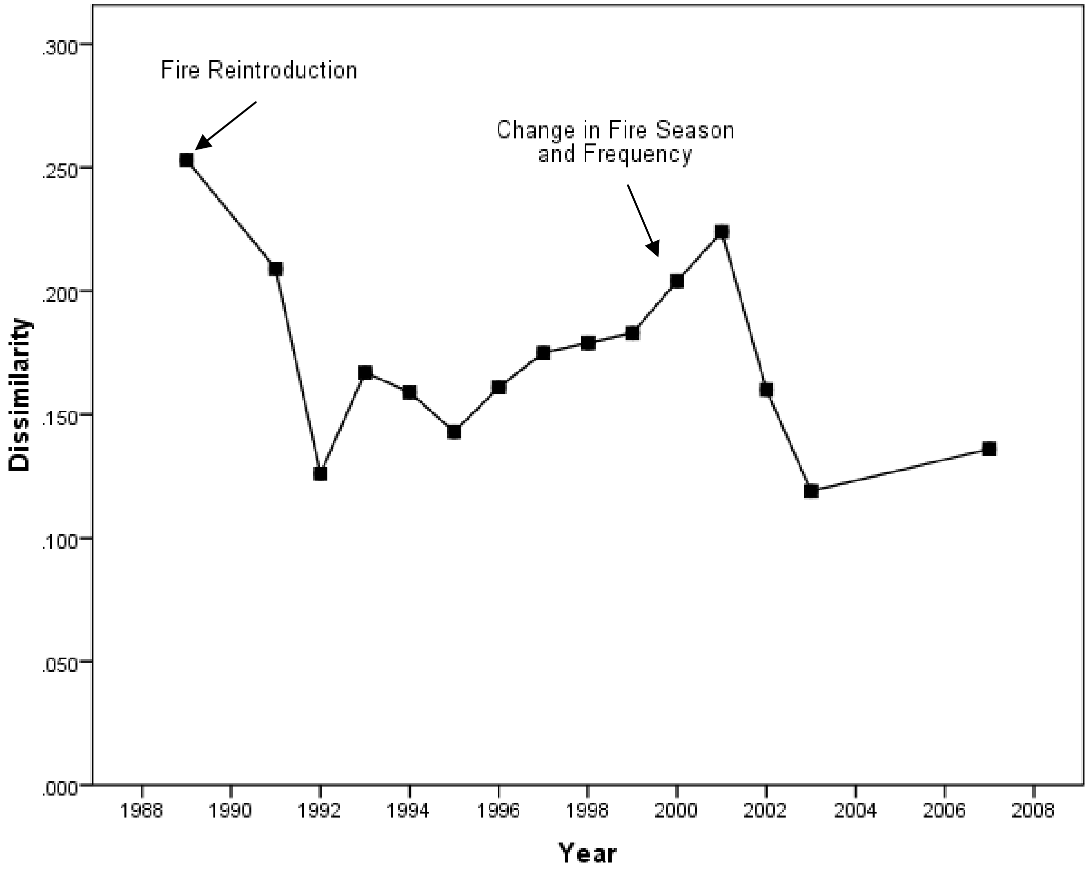


Figure 4.1. Prairie-level community dissimilarity in Dow Field over the course of the study, based on species presence-absence data.

For the analysis of treatment-level compositional change in Stratum 2, the stress of the NMS ordination dropped by 6.2 points between two- and three-dimensional ordinations, but only by 3.7 points when a fourth dimension was added. Therefore, I concluded that a three-dimensional NMS ordination was the optimal solution for the data. The stress of the final ordination was 12.80, indicating a relatively good fit to the data (Fig. 4.2). Axes 1, 2, and 3 accounted for 21.9%, 19.9%, and 48.7% of the observed distances in the original 51-dimensional space, respectively (total of 90.6%).

The successional vectors connecting the re-sampled treatments indicate a considerable amount of change between years. Vector length, which indicates the magnitude of compositional change, varied from 0.130 (13.0% turnover) to 0.558 (55.8% turnover) between years ($\mu = 0.305$, $\sigma = 0.10$).

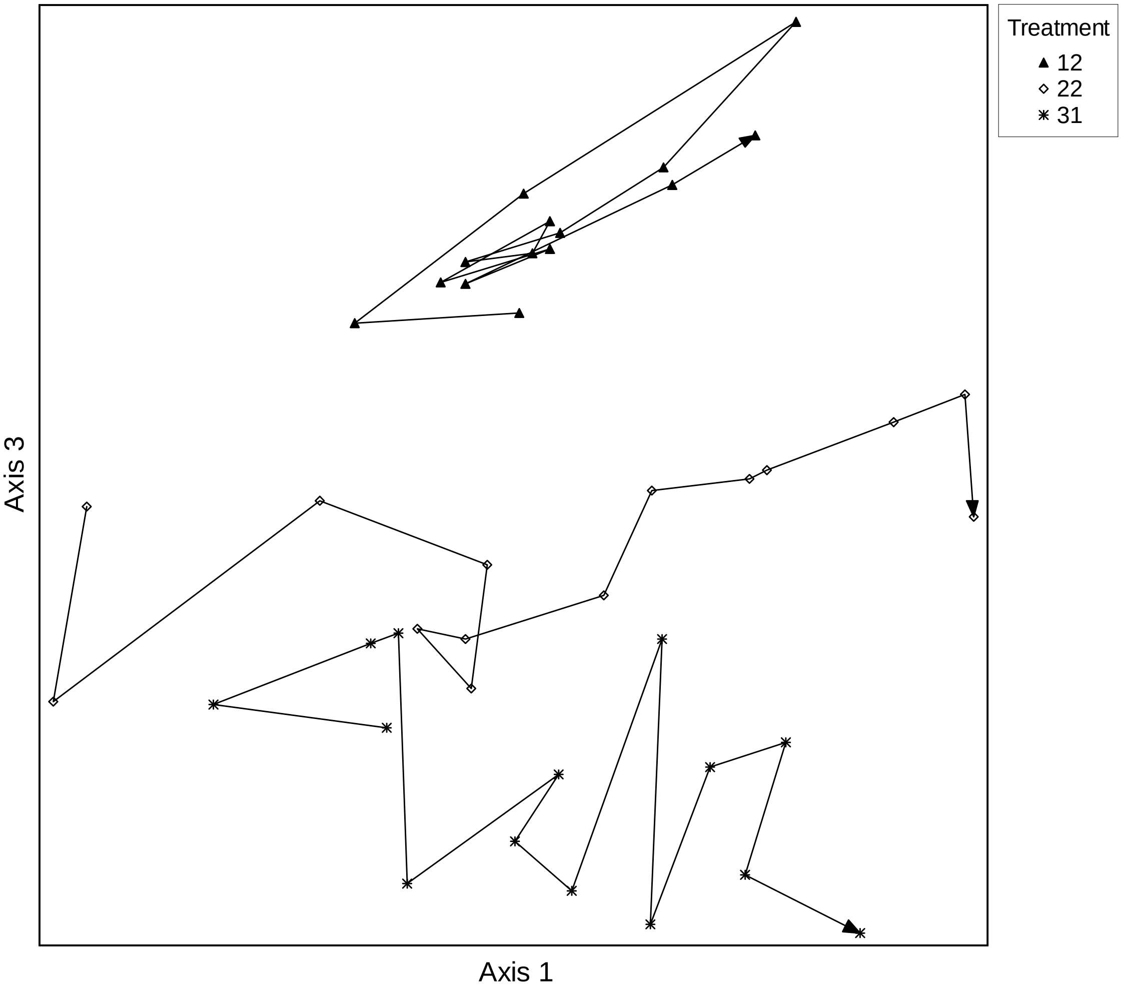
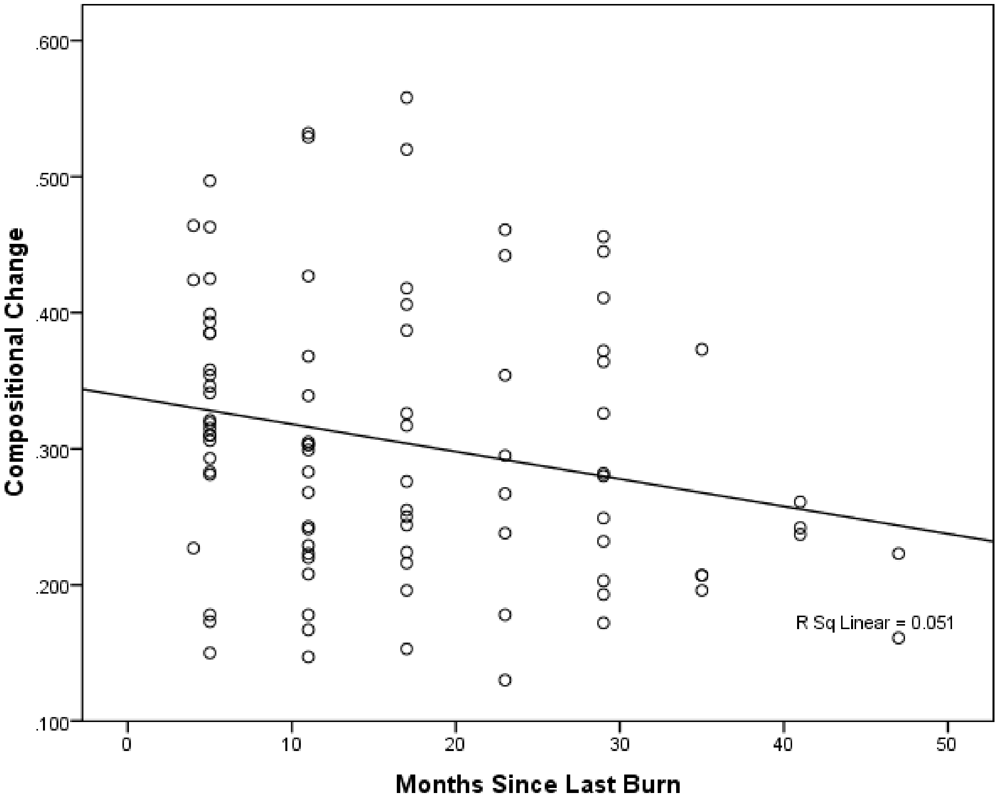
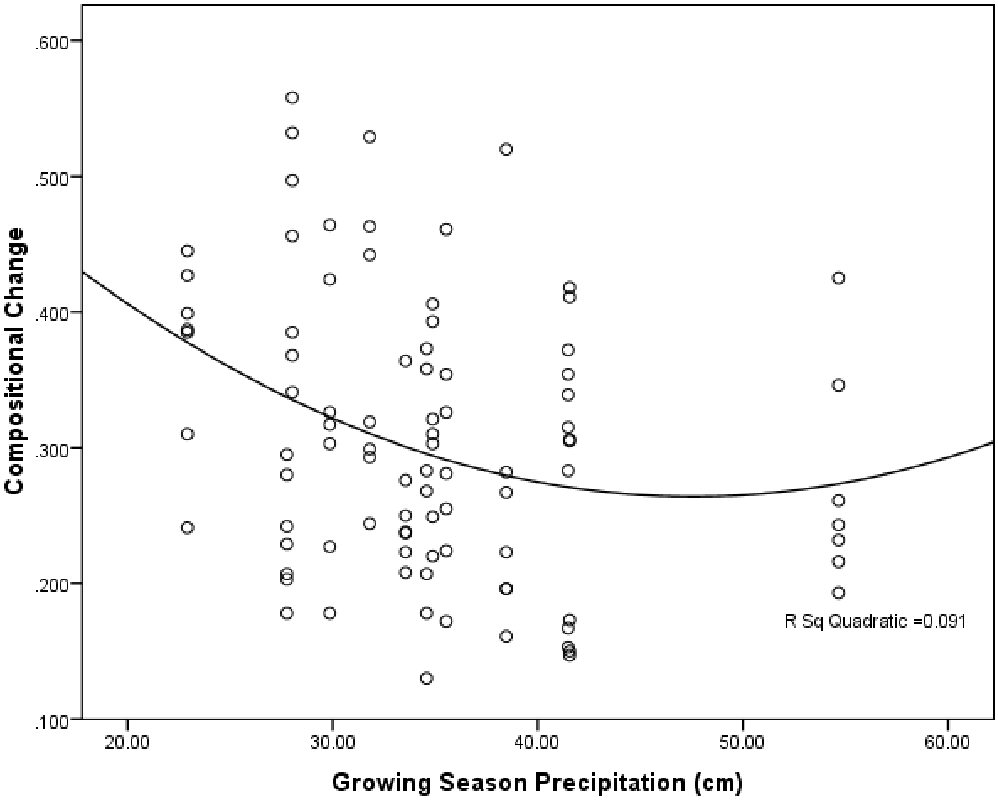


Figure 4.2. Three-dimensional nonmetric multidimensional scaling (NMS) ordination based on the 51 most common species in Stratum 2 plotted on axes 1 and 3, which together account for 70.6% of the variability in the data. Points are the average composition of all sample units within a treatment in a given year, and the distance between points is proportional to the dissimilarity in species composition. For clarity, only 3 representative treatments are shown: 212 (lowest average plot-level species richness, highest average plot-level *A. gerardii* abundance), 231 (highest average plot-level species richness, lowest average plot-level *A. gerardii* abundance), and 222 (median average plot-level species richness and *A. gerardii* abundance).

Linear correlations between vector length and environmental factors revealed that compositional change was linearly related with time (in months) since last burn (r = -

0.225, *p* = 0.032), growing season precipitation (*r* = -0.256, *p* = 0.014), and change in average maximum July and August temperature between consecutive years (*r* = 0.285, *p* = 0.006) (Fig. 4.2). Since compositional change seemed to increase the more precipitation deviated from average, a quadratic line was fit to better explain the data (r_{quad} = 0.302). However, I found only a weak, nonsignificant positive linear relationship between compositional change and magnitude of year-to-year change in precipitation. Also, change in average maximum temperature had no apparent effect on compositional change until the year-to-year temperature change exceeded 3 °C. The substantial variation in species composition among treatments likely contributed to the weakness of the correlation coefficients.





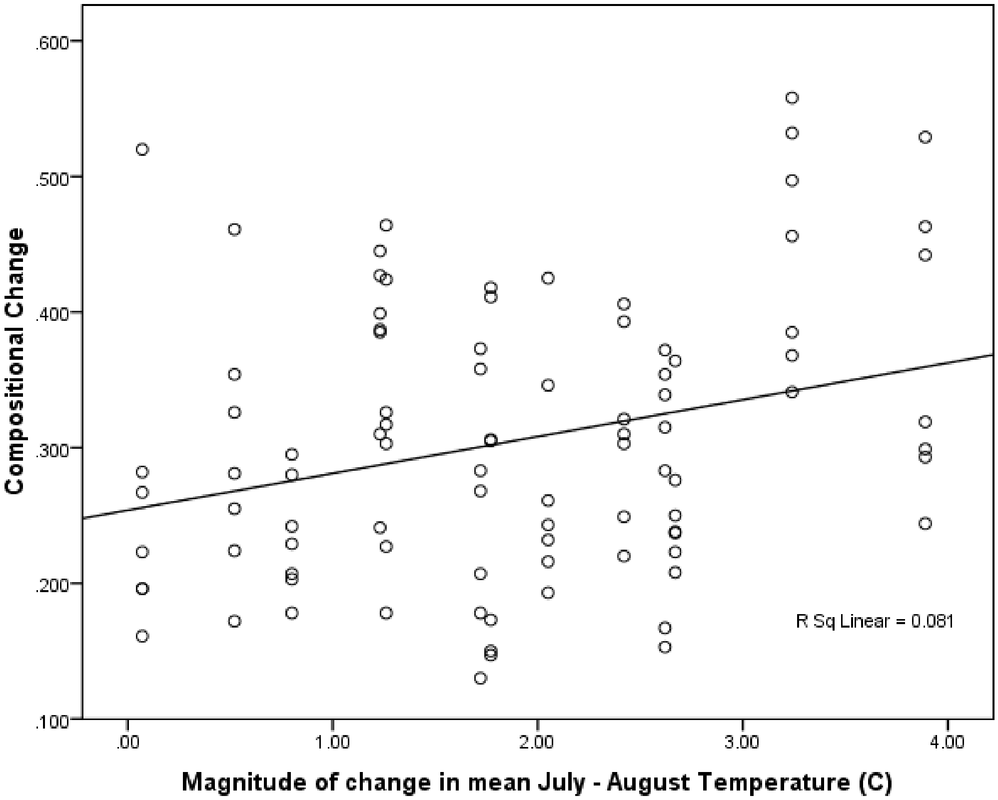


Figure 4.3. Relationships of environmental factors to compositional change in stratum 2.

Successional Trajectory

The stress of the NMS ordination of the 1991 and 2007 data points dropped by 15.7 points between one- and two-dimensional ordinations, but only by 2.8 points between two and three dimensions. Therefore, I concluded that a two-dimensional ordination was the best solution for the data. The stress of the final ordination was 7.69, indicating a very good fit to the data (Fig. 4.4). Axes 1 and 2 accounted for 62.3% and 29.1% of the observed distances in the original space, respectively (total of 91.4%).

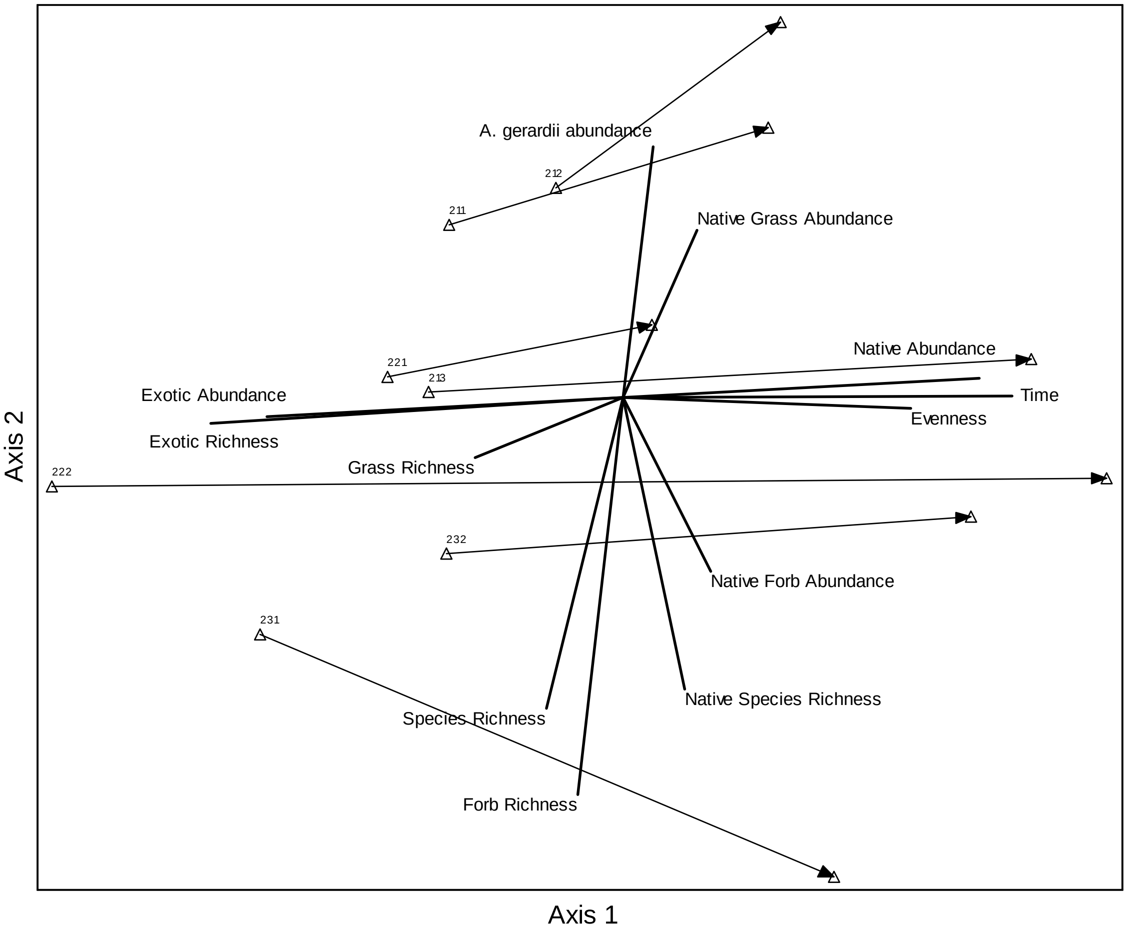


Figure 4.4. Two-dimensional NMS ordination showing the direction of compositional change for each treatment from the beginning (1991) to the end (2007) of the study. The distance between points is proportional to the dissimilarity in species composition. Correlation coefficients of community characteristics are represented by the correlation vectors. Total correlation strength is indicated by vector length; $r^2 > .200$ for all vectors.

Variable	**Axis 1**	**Axis 2**
Time	0.858	0.051
Species Richness	-0.380	-0.767
Evenness (E)	0.739	-0.140
Native Richness	0.343	-0.744
Exotic Richness	-0.884	-0.224
Grass Richness	-0.529	-0.339
Forb Richness	-0.293	-0.869
Native Abundance	0.822	0.187
Exotic Abundance	-0.822	-0.187
Native Grass Abundance	0.375	0.316
Native Forb Abundance	0.407	0.330
A. gerardii Abundance	0.242	0.689

Table 4.2. Pearson correlation coefficient (*r*) values between environmental variables and ordination axes.

The correlation vectors reveal two strong gradients in community characteristics that correspond to the ordination axes and thus to the successional trajectory of the treatments. First, all treatments underwent an increase in evenness (Shannon's evenness index, $E = H' / \ln(S)$) and native species abundance, and a drop in exotic species richness and abundance. This gradient was closely related with the time component and axis 1. The second gradient, more aligned with axis 2, showed that plots with higher *A. gerardii* abundance had lower species richness, which describes a great deal of the spatial differences between plots (see chapter 3). *Andropogon gerardii* abundance, as well as the successional direction of all treatments except for 231, was positively related to both ordination axes. This indicates, with the one possible exception, that all treatments increased in *A. gerardii* abundance and decreased in species richness over the course of restoration. However, the directional similarity between treatment succession and the *A. gerardii* vs. species richness gradient (axis 2) was weak compared to the time, evenness, and native abundance vs. exotic richness and abundance gradient (axis 1).

The ordination results show minor gains in native species richness and native forb abundance with respect to axis 1. Any gains in native richness were apparently too minor to outweigh the loss of exotic species enough to significantly increase total species richness in any of the treatments. Also, most of the increase in native species abundance was likely due to the simultaneous decrease in exotic abundance and the increase in *A. gerardii* abundance.

The magnitude of total compositional change from 1991 to 2007 ranged from 0.402 (40.2% turnover) in treatment 221 to 0.872 (87.2% turnover) in treatment 222 ($\mu = 0.586$, $\sigma = 0.16$) (Table 4.3). The three treatments in substratum 1 (lower fire frequency), underwent less compositional change than treatments in substrata 2 and 3 (higher fire frequency) ($\mu = 0.548$ and $\mu = 0.615$, respectively), but there was not a significant linear relationship between total compositional change and fire frequency. There was also no significant linear relationship between compositional change and species richness or *A. gerardii* abundance.

Treatment	***Sorensen Distance***
211	0.511
212	0.434
213	0.699
221	0.402
222	0.872
231	0.580
232	0.604

Table 4.3. Treatment community dissimilarity from 1991 to 2007.

The linear regression trends of community characteristics over time largely support the results of the NMS ordination (Appendix 4.1). The differences between the ordination and regression results can be explained by the simplifying nature of the ordination procedure.

Discussion

Species Immigration and Extinction

Species immigration and extinction is a basic component of ecological succession in all plant communities, and is heavily influenced by disturbance (MacArthur and Wilson 1967, Pickett et al. 1987, Glenn and Collins 1992). The pulse of immigration in the first several years of the study is likely a consequence of substantial changes in environmental conditions and resource availability following the reintroduction of fire (Tilman 1982, Collins and Gibson 1990). Most of these species were likely constituents of the seedbank and were able to reestablish after conditions became more favorable for germination and growth (Rabinowitz 1981, Glass 1989), or existed at low levels as vegetative propagules while the field was maintained as a rough lawn for about 40 years (Abrams 1988). Another possibility for colonization is wind dispersal from nearby prairie remnants or plantings. However, only two of the 12 immigrant species (17%) have seeds capable of long-distance wind dispersal: *Solidago rigida* (stiff goldenrod) and the exotic *Cirsium arvense* (Canada thistle). Four species, including a regionally uncommon prairie sedge (*Carex bicknellii*, Bicknell's sedge), first appeared in 1996, which was an extreme drought year. Altered moisture conditions and reduced aboveground biomass of the dominant grasses in 1996 could have allowed subdominant species such as *C. bicknellii* and *Carex pensylvanica* (Pennsylvania sedge) to become established from previously dormant propagules.

The lower number of extinctions compared to immigrations was probably related to low overall diversity and few occurrences of rare or conservative species in Dow Field (Glenn and Collins 1992). *Asclepias syriaca*, which that readily colonizes oldfields and highly disturbed ground, likely disappeared as a result of increasing abundance of later-successional perennials over time (Pickett 1982). Two exotic forbs and two exotic grasses were extirpated during the course of the study, and although all of those are at least somewhat fire-intolerant, it took nearly a decade of prescribed fire to reduce their population beyond occurrence in the plots. Future monitoring may find more extinctions of exotic species as some populations continue to decline, but it is likely that some exotic species will persist at a baseline level and be unaffected by continued management. For example, Wilson and Partel (2003) found that no management strategy (combinations of clipping and herbicide) was able to eliminate *Agropyron cristatum* (crested wheatgrass) from a Kansas prairie. Emery and Gross (2005) were able to reduce *Centuarea maculosa* (spotted knapweed) from a Michigan prairie through growing season burns, but the population persisted at low levels even after management. In Dow Field, *C. maculosa* and *Poa pratensis* (Kentucky bluegrass) may be two exotic species that persist indefinitely, although percent cover of these species have dropped 4-fold and 6-fold since the beginning of the study, respectively. As in most restoration projects, the complete eradication of invasive species is not a realistic goal in Dow Field and may conflict with other management goals (Wilson and Partel 2003, Gillespie and Allen 2004, Brudvig et al. 2007).

Prairie-Level Compositional Change

It is almost axiomatic that prairie community composition and structure is greatly influenced by the frequency and timing of fire (e.g., Gibson and Hulbert 1987, Collins and Gibson 1990, Howe 1995, Peterson and Reich 2008). Repeated fire can have a stabilizing effect by maintaining a prairie community of relatively similar composition over time, but species composition and relative abundances can oscillate around a loose equilibrium (Curtis 1959, DeAngelis et al. 1985, Collins 2000). However, changes to the disturbance regime can cause changes in species composition and successional trajectory (DeAngelis and Waterhouse 1987).

In Dow Field, the two periods of greatest prairie-level plant compositional change coincided with changes in the disturbance regime. The first of these was at the beginning of the study, after fire was reintroduced to the site after more than 40 years. The reintroduction of fire to prairie remnants can cause drastic shifts in vegetation characterized by increased abundance of native prairie grasses (Peet et al. 1975, Collins and Gibson 1990, Briggs et al. 1994) and a drop in overall forb and woody plant abundance (Gibson and Hulbert 1987, Collins and Gibson 1990, Henderson 1990). These changes also occurred in Dow Field (see chapter 2) except for a drop in woody plant abundance which had previously been minimized by frequent mowing. The second period of high year-to-year change occurred immediately after the management in substrata 2 and 3 changed from annual to triennial burns. Previous studies have found that fire frequencies of 3 to 5 years cause a lower abundance of grasses, higher forb abundance, and higher overall diversity compared to annual burned sites (Collins and Gibson 1990, Collins et al. 1995 Peterson and Reich 2008). In Dow Field, decreasing the fire frequency to 3 year intervals affected the plant community less dramatically compared to the changes after the initial fire reintroduction. Indeed, there was a slight decrease in grass percent cover and a gain in forb cover after 2000, but the change was minor compared to the substantial increase in native grass abundance in the first several years of the study. It is possible that first 9 years of annual fires set the plant community on a successional trajectory that did not change appreciably as a result of the modified fire regime (see *Successional Trajectory* below). It is important to note that this site-level analysis identifies short-term periods of major change in species composition, but it does not account for cumulative change or direction over time.

Determinants of Annual Compositional Change

Compositional change decreased with time since fire, presumably because fire immediately alters the availability of resources such as light, space, water, and nutrients, and the variation in availability of these resources typically decreases with time after fire (Ojima et al. 1990; Briggs et al. 1994). The magnitude of compositional change was also negatively related to total growing season precipitation, which indicates that the greatest changes occurred in drought years. Species composition in prairies has been found to vary along spatial (Nelson and Anderson 1983, Gibson and Hulbert 1987, Grace et al. 2000) and temporal (Abrams et al. 1986, Henderson 1990, Tilman and El Haddi 1992) gradients in soil moisture and precipitation, although Alder and Levine (2007) reported no changes in composition with temporal variation in rainfall in a Kansas prairie. The response of community structure to water availability stems from the role of water as a limiting resource in many prairies, especially those with coarse soils as in Dow Field (Anderson 1982, Knapp et al. 1993, Seastedt 1995).

Tilman (1987) suggested that prairies may be nitrogen-limited in wet years and water-limited in drought years. Therefore, depending on the amount of rainfall in a given year, one would expect to find altered competitive relationships among species that would lead to changes in community structure. Higher temperatures reduce water availability by increasing the rate of surface evaporation and photosynthetic rate in plants

(Knapp et al. 1993). Climactic factors also interact with fire to jointly influence compositional change (Gibson and Hulbert 1987, Anderson 2008). The unshaded, dark colored soil surface following fire leads to higher soil temperatures, which increases the rate of evaporation, reduces soil moisture, and promotes early germination of dominant prairie grasses (Knapp and Seastedt 1986, Svejcar 1990).

The statistically significant linear relationship between temperature change and compositional change could be due to the disproportionate influence of the two years that had large (> 3 C) changes in average maximum temperature from previous years. Nonetheless, the compositional changes resulting from temperature and rainfall differences between consecutive years raise questions about the stability of species composition in prairie communities in the context of global climate change. The increased temperatures and precipitation extremes predicted by climate models (eg. Field et al. 2007) may have unpredictable consequences for succession in prairies (Nippert et al. 2006).

Interestingly, there was no significant relationship between treatment diversity and compositional change. This is at odds with the hypothesis that diverse communities should be more stable, popularized by Elton (1958) and later adopted by other ecologists (eg. Tilman and Downing 1994, see Cottingham et al. 2001). In fact, there was a weak, nonsignificant relationship between diversity and compositional change that suggests that the lowest diversity treatments were the most compositionally stable. Most likely, diversity was reduced by competitive pressure from *A. gerardii*, which stabilized community composition by preventing the coexistence of other species (Collins and Gibson 1990, Smith et al. 2004, Polley et al. 2007).

Successional Trajectory

In general, the direction of compositional change over the study period was remarkably similar among most treatments, regardless of differences in fire frequency or other spatially variable site conditions. One explanation for this is that composition had relatively little opportunity to change relative to other treatments because of the lack of diversity of available propagules and high competitive pressure from *A. gerardii* across the site from the outset of the restoration. This is consistent with the initial floristic composition model of succession, which states that the majority of species are present at the beginning of succession (Egler 1954; Collins et al. 1995). Indeed, there were only 15 species that newly colonized the sample plots over the study period. Therefore, the observed changes in composition resulted largely from different population responses of certain species to fire. This is especially true in restorations that begin with a high abundance of exotic species as in Dow Field, as repeated fire tends to reduce exotic grasses and forbs in favor of fire-dependent native species (Peet et al. 1975; Towne & Owensby 1984; Gibson & Hulbert 1987; Henderson 1990; MacDonald et al. 2007).

The relative positions of the treatments along the *A. gerardii* vs. species richness (axis 2) gradient in 1991 did not change by 2007, indicating that there was no apparent difference in how fire frequency influenced dominance or richness. The treatments with lower fire frequencies (substratum 1) had higher *A. gerardii* abundance throughout time than substrata 2 and 3, but this was likely a coincidence of starting the triennial burns in the area of the prairie heavily dominated by *A. gerardii* (see chapter 3). The lack of difference in how fire regimes affected the community is consistent with Gibson and Hulbert (1987), who found that *A. gerardii* abundance did not differ between areas burned every 1 and 4 years in a Kansas prairie, although abundance was lower in completely unburned areas. According to Wright and Bailey (1982), historical fire frequency in most North American prairies was 3 to 5 years. If their estimate is accurate, between-treatment differences in community composition may only be affected by a wider range of fire frequencies than was tested in this study.

Despite the similarities in relative position and successional direction of the treatments, there was some divergence in community composition by 2007 compared to 1991. The two treatments that differed most in direction from the other treatments were initially at the high and low extremes of axis 2, which was highly correlated with *A. gerardii* abundance and species richness. Treatment 212, which had high *A. gerardii* abundance and very low species richness at the outset, shifted towards even higher *A. gerardii* abundance and lower species richness. Conversely, the treatment with lowest initial *A. gerardii* abundance (231) was largely resistant to increases in *A. gerardii* and was able to maintain relatively high diversity.

In contrast, Baer et al. (2005) found that plant community composition converged over 3 years in a prairie restoration where soil depth and nitrogen were altered to increase heterogeneity. They attributed the convergence to the dominance of *Panicum virgatum* (switchgrass), which was successful across a range of soil conditions. Although *A. gerardii* has been shown to be competitive across a wide gradient of environmental conditions and was dominant throughout the restoration, there was substantial variation in *A. gerardii* across the prairie that was related to soil conditions. There may be a critical level of *A. gerardii* abundance after which the community becomes increasingly dominated by *A. gerardii*, species richness declines, and other restoration tools besides fire must be used in order to deflect successional direction towards a more diverse community. Dominant species have been hypothesized to alter community structure and successional direction by competing against neighboring individuals, although few studies have actually tracked community response to varying levels of dominance over time (Tilman 1987, Goldberg & Barton 1992; Callaway & Walker 1997). Most field studies that have shown the effects of a dominant species on successional development have focused on invasive exotic species. For instance, Titus and Tsuyuzaki (2003) found that development of an early-successional montane forest was deflected to a new community type as the dominance of a non-native tree species increased. Because of its central importance to the physical structure of tallgrass prairies, the dominance *A. gerardii* may influence compositional change differently than would exotic species, and this has unique implications for prairie management. Also, this study was limited to one site, so attributing the divergence in successional trajectory to the variation in *A. gerardii* abundance should be viewed with caution.

It is possible that composition in the treatment where *A. gerardii* abundance increased will eventually converge if frequent burning is continued, and that the slight divergence in composition seen in the first 16 years of restoration is an intermediate point in succession. *Andropogon gerardii* may increasingly dominate community structure even in areas at the margins of its preferred habitat if there continues to be a lack of native competitors to fill vacant resource niches (Tilman 1982, Sher et al. 2000).

Restoration Progress

Ecological restoration is largely the process of altering the successional trajectory of a degraded ecosystem (SER 2004). I overlaid correlation vectors of community characteristics on the NMS ordination of cumulative successional trajectory to evaluate restoration progress in Dow Field. The correlation vectors that were most parallel to the successional vectors connecting the 1991 and 2007 treatment-level data best described successional changes. The ordination output showed that changes in community characteristics have been both positive and negative with respect to restoration goals in Dow Field over the first 16 years of fire reintroduction.

One positive outcome of the restoration derived from the ordination of cumulative successional trajectory is that exotic species richness and abundance dropped in all treatments. The decrease in fire-intolerant exotic species was likely a direct result of frequent fires (Smith and Knapp 1999, Cully et al. 2003, Suding and Gross 2006). Total species richness declined somewhat as well, especially in the management zones that began with high *A. gerardii* abundance and low species richness. However, the drop in species richness was probably most influenced by the strong decline in exotic species over time.

Native species richness had a positive but weak relationship with successional trajectory. Thus, it was unable to overcome the loss of exotic species in order to increase total species richness. The lack of a substantial increase in native diversity since 1991 likely indicates that the diversity of the pre-restoration seedbank reached the limit of its expression in the aboveground community, probably within the first several years after fire reintroduction (Abrams 1988, Glass 1989). Successful immigration from nearby prairie remnants and plantings was limited, likely because the few seeds of subdominant species that may have reached the site from other areas had little chance of competing with *A. gerardii*.

The correlation vector for species evenness, an important component of diversity, was strongly aligned with successional vectors for all treatments. This is contrary to our expectations given the simultaneous increase in *A. gerardii* dominance in most treatments (Collins 1992, Smith et al. 1999). However, successional trajectory in management zones with high *A. gerardii* abundance tended to be slightly less aligned with increasing evenness and more aligned with increasing *A. gerardii* than other treatments. This is supported by the bivariate regressions, which show that although evenness was higher in 2007 than in 1991 in every treatment, the most significant linear trends were in treatments 222 and 232 which had relatively low abundance of *A. gerardii*.

All management zones except for 231 increased with respect to axis 2, which was highly correlated with *A. gerardii* abundance. The dominance of *A. gerardii* and its strongly competitive relationships with other native grass and forb species is a point of concern for future restoration efforts. Diversity likely will not increase until management practices are adopted that reduce *A. gerardii* dominance (Howe 1994). Prescribed fire at lower intervals (5-10 years) often reduces the dominance of C_4 grasses and can increase diversity to a point, but also can lead to invasion by fire-intolerant exotic and woody species (Collins et al. 1995, Peterson and Reich 2008). In Dow Field, high fire frequency likely contributed to *A. gerardii* dominance, but it was also adept at reducing the populations of many aggressive exotics such as *P. pratensis* (a 6-fold decrease) and *C. maculosa* (a 4-fold decrease) to background components of the community.

In general, because diversity was heavily influenced by the available propagules at the beginning of restoration, it is unlikely that altering the fire regime alone will cause a substantial decrease in *A. gerardii* abundance or an increase in native diversity. Other methods to reduce *A. gerardii*, such as conducting growing season burns (Howe 1995), herbicide applications (Wilson and Partel 2003), or fungicide application to reduce mychorrhizal associations with dominant grasses (Smith et al. 1999), may be more effective ways to reduce competitive pressure on subdominant species. Because the seedbank has reached its full potential and the possibility of immigration is low, seeds or plugs of native species may have to be introduced to in the reduced-*A. gerardii* environment to increase diversity to the level of high-quality prairie remnants in the region.

Conclusion

After more than 16 years of prescribed fire in Dow Field, perhaps the greatest progress made towards restoration goals was the reduction of exotic species richness and abundance. Native species richness did not increase appreciably, probably due to the combined effects of a limited species pool and high competitive pressure from *A. gerardii*, the dominant grass. Fire frequency influenced the magnitude of annual compositional change along with climate variability. Although differences in fire frequency had no affect on successional direction between treatments, fire in general was almost certainly a major driver behind the decrease in exotic species, the increase in *A. gerardii* abundance, and changes in other community attributes over time.

The divergence in community composition over time suggests that there may be a critical level of *A. gerardii* abundance after which restoration trajectory is deflected to an increasingly low-diversity community. For restoration projects that seek to increase species richness, the abundance of dominant competitors may have to be addressed prior to attempts to increase species diversity such as seeding or planting.

NMS ordination and restoration progress

Using NMS ordination, I created an encompassing picture of community succession that showed simultaneously that certain attributes of the plant community in Dow Field shifted in ways that were congruous with restoration goals while others did not. This is an advantage over conventional statistics, most of which are able to focus only on one or a few variables at a time. In complex ecological systems that vary over time and space, it is often difficult to conceptualize the relationships between variables, especially if the results of univariate statistics seem to conflict. Visualizing the system as a whole can reveal unexpected trends that may otherwise be obscured. For example, it would have been nearly impossible to predict the divergent successional pathways with respect to the *A. gerardii* and species richness gradient using conventional procedures.

On the other hand, ordination seeks out the strongest patterns in the data, which comes at the price of specificity. This makes it difficult to quantify elements on the ordination output with respect to actual community characteristics. Statements such as "evenness increased" or "exotic species abundance decreased" may not provide enough detail in cases where restoration success is evaluated by reaching quantitative benchmarks (Zedler 2007). The reduced dimensionality of the ordination, which is critical for interpretation, can also lead to apparent conflicts between multivariate and bivariate results. For instance, treatment 231 actually decreased in species richness and increased in *A. gerardii* abundance, but the ordination shows the trajectory in 231 as negatively aligned with *A. gerardii* abundance and positively with species richness. It is worth reiterating that because NMS ordination uses a reduced-dimensional model to describe changes in a many-dimensional ecosystem, the axes explain variation in aggregate species composition, not the absolute level of any one species or community characteristic.

As McCune and Grace (2002) have emphasized, ordination is primarily an exploratory device that can quickly highlight the strongest patterns in a dataset. Conventional analytical methods can then be used to expand on patterns made apparent by the ordination, potentially saving time by focusing the analysis on the most interesting trends. Ultimately, the combination of NMS ordination with conventional statistical methods is perhaps a more powerful way to assess restoration projects than either univariate or multivariate procedures alone.

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Appendix 4.1. Plant community changes in Dow Field between 1991 and 2007. The regression coefficient (*β*) is the rate of increase or decrease with year. * = regression is significant at α = 0.05, ** = significant at α = 0.01.

Treatment		**1991**	**2007**	***β***
A1	Species Richness	8.4	6.4	-0.204*
	Evenness	0.746	0.798	0.001
	Native Richness	5.2	4.8	-0.037
	Exotic Richness	3.2	1.6	-0.167**
	Grass Richness	4.2	3.4	-0.054
	Forb Richness	3.4	2.0	-0.166**
	A. gerardii Abundance	51.0	82.0	2.359**
	Native Grass Abundance	62.0	89.0	2.177**
	Native Forb Abundance	5.0	6.0	0.028
	Native Abundance	70.0	98.0	2.233**
	Exotic Abundance	30.0	2.0	-0.224**
A2	Species Richness	4.6	3.0	-0.079
	Evenness	0.607	0.920	0.012
	Native Richness	2.4	1.4	-0.071*
	Exotic Richness	2.2	1.6	-0.008
	Grass Richness	2.6	2.2	0.017
	Forb Richness	2.0	0.6	-0.101
	A. gerardii Abundance	87.0	92.0	0.278
	Native Grass Abundance	94.0	98.0	0.164
	Native Forb Abundance	0.0	0.0	-0.022
	Native Abundance	94.0	99.0	0.179
	Exotic Abundance	6.0	1.0	-0.179
A3	Species Richness	9.2	8.0	-0.029
	Evenness	0.692	0.829	0.005
	Native Richness	5.0	7.0	0.104
	Exotic Richness	4.2	1.0	-0.133*
	Grass Richness	3.0	3.4	-0.015
	Forb Richness	5.6	4.0	-0.013
	A. gerardii Abundance	97.0	57.0	-2.244**
	Native Grass Abundance	97.0	57.0	-2.511**
	Native Forb Abundance	1.0	43.0	2.832**
	Native Abundance	98.0	100.0	0.327
	Exotic Abundance	2.0	0.0	-0.327
B1	Species Richness	8.4	7.6	-0.082
	Evenness	0.729	0.775	-0.002
	Native Richness	4.5	5.4	0.067
	Exotic Richness	3.9	2.3	-0.149**
	Grass Richness	4.3	2.8	-0.084*
	Forb Richness	3.8	4.4	0.000
	A. gerardii Abundance	62.5	74.4	1.010**
	Native Grass Abundance	66.9	84.4	1.249*
	Native Forb Abundance	10.0	8.8	-0.204

	Native Abundance	78.1	95.0	1.089**
	Exotic Abundance	21.9	5.0	-1.040**
B2	Species Richness	8.4	6.0	-0.191**
	Evenness	0.598	0.834	0.012**
	Native Richness	4.4	5.7	0.046
	Exotic Richness	4.0	0.3	-0.237**
	Grass Richness	3.3	2.6	-0.061**
	Forb Richness	5.0	3.3	-0.128*
	A. gerardii Abundance	35.0	63.6	2.723**
	Native Grass Abundance	48.6	85.7	2.330**
	Native Forb Abundance	18.6	14.3	-0.192
	Native Abundance	67.1	100.0	2.137**
	Exotic Abundance	32.9	0.0	-1.892**
C1	Species Richness	11.9	9.9	-0.084
	Evenness	0.691	0.771	0.005
	Native Richness	5.3	8.1	0.251**
	Exotic Richness	6.6	1.7	-0.335**
	Grass Richness	4.6	3.3	-0.073*
	Forb Richness	7.1	6.1	-0.022
	A. gerardii Abundance	37.1	42.1	0.445
	Native Grass Abundance	45.0	68.6	1.226*
	Native Forb Abundance	11.4	29.3	1.710**
	Native Abundance	58.6	100.0	3.032**
	Exotic Abundance	41.4	0.0	-0.302**
C2	Species Richness	9.9	8.9	-0.030
	Evenness	0.805	0.860	0.007*
	Native Richness	6.3	8.0	0.101*
	Exotic Richness	3.6	0.9	-0.131**
	Grass Richness	4.4	2.8	-0.103**
	Forb Richness	5.5	5.6	0.037
	A. gerardii Abundance	60.6	58.8	1.692*
	Native Grass Abundance	60.6	67.5	2.039**
	Native Forb Abundance	18.8	30.6	-0.483
	Native Abundance	79.4	100.0	1.643**
	Exotic Abundance	20.6	0.0	-1.609**

Chapter 5: Conclusion

Context and Objectives

Tallgrass prairies once covered much of central North American including southern Michigan, but are now one of the most threatened ecosystem types throughout the region (Chapman and Brewer 2008). Dow Field is a small remnant prairie in Ann Arbor, Michigan, that experienced fire suppression for much of the last century. By the late 1980s, the site had low native diversity and high abundance of invasive exotic species. In 1988, fire was reintroduced to the site with the purpose of restoring the native plant community.

This study explored plant community data that was collected annually from a series of plots throughout the prairie from 1991 to 2007. The three areas of investigation involved describing the differences in the plant community across time and in comparison to other prairie remnants (chapter 2), exploring the factors that contributed to diversity (chapter 3), and understanding successional change in the context of restoration (chapter 4).

Study Conclusions

Chapter 2

- Seventy-three species were found in Dow Field over the study period; the native grass *Andropogon gerardii* (big bluestem) had the highest abundance in terms of presence-absence frequency and percent cover

- After fire reintroduction, exotic species declined in richness and abundance while native species richness did not increase appreciably
- After nearly 20 years of restoration, species richness in Dow Field was about 70% that of other nearby prairie remnants

Chapter 3

- *Andropogon gerardii* reduced plot-level species richness, likely through its ability to acquire water, nutrients, and light efficiently
- Soil depth and clay, which enhance *A. gerardii* productivity by increasing soil moisture, were also significant predictors of diversity.
- Differences in fire season or frequency did not appear to affect diversity levels across Dow Field.

Chapter 4

- Growing season rainfall, average maximum summer temperature, and time since fire were the greatest influencers of year-to-year compositional change
- In general, most sections of the prairie moved towards communities characterized by higher evenness, lower exotic richness and abundance, higher native abundance, higher *A. gerardii* abundance, and lower species richness.
- Successional direction may be influenced by initial dominance of *A. gerardii*
- The lack of increase in native species richness likely resulted from past management as a lawn, limited dispersal from nearby remnants, and competitive pressure from *A. gerardii*

Study Limitations

Because this study was limited to one site, caution should be exercised when generalizing these conclusions to other prairies under different conditions. Additionally, there was only one of each of the burn treatments, and without replication it is difficult to draw conclusions with certainty especially with regard to how the fire regime influenced the plant community. A related problem was that the between-treatment soil and plant community heterogeneity at the beginning of restoration did not allow for truly experimental comparison, because the treatments did not start on equal footing. These issues became especially apparent in chapter 3 where the relationship between fire frequency and *A. gerardii* abundance was the opposite of what is reported in the literature. I ultimately concluded this to be an artifact of the initial species composition and treatment setup. Finally, changing the fire regime in 1999 limited the types of statistical analyses that could be conducted because of crossover effects.

However, one must keep in mind that the fire treatments and sample plots were initiated primarily to monitor the progress of restoration and not as a controlled experimental study. Few actual restoration projects begin with a homogeneous substrate or many treatment replications. Also, although the change in fire regime in 1999 limited the use of certain analyses, adaptive management is an important strategy in many restorations (Pastorok et al. 1997). Therefore, the untidy aspects of this study are examples of what ecologists or practitioners might expect when analyzing the progress of an actual restoration. The long-term nature of the study and the multivariate approaches to data analysis help to alleviate some of these methodological pitfalls. Also, most of the results are in general agreement with other theoretical or observational studies, which brings validity to the conclusions.

However, similar studies are needed to confirm the results observed in Dow Field. Additional research is particularly important for small prairies in the eastern Midwest because most of our knowledge of prairie ecology and management comes from a handful of large Great Plains sites that have different species composition, climate, soils, and herbivory pressure. Some key areas of investigation are:

- How diversity can be optimized and rare species conserved in the small, isolated remnants throughout southern Michigan and the eastern prairie region
- The role of *A. gerardii* dominance in determining diversity and successional trajectory
- How fire season and frequency influence diversity and species composition in eastern prairies, particularly at a broader ranges than tested in Dow Field (e.g. lower fire frequencies, growing season burns)
- The interacting effects of climate and fire in influencing short- and long-term compositional change

Management Recommendations

It is possible that the plant community in Dow Field will never completely reflect historic conditions regardless of what restoration steps are taken. However, the management strategy could be altered in an attempt to include a wider range of species and functional groups. This will likely require limiting the abundance of *A. gerardii* to reduce competitive pressure on subdominant species. Many studies have suggested strategies to achieve this. Howe (1994) recommended utilizing growing season burns to reduce *A. gerardii* and other C_4 grasses, thereby increasing diversity. Moreover, several studies have demonstrated that dormant season burns such as those used in Dow Field directly increase *A. gerardii* dominance (Peet et al. 1975, Biondini et al. 1989, Glen-Lewin et al. 1990, Howe 1994). Therefore, an altered fire regime that decreases the frequency of spring and fall burns and possibly utilizes growing season burns may help slow or reverse the trend in *A. gerardii* dominance. The direct application of herbicides (Wilson and Partel 2003) or using fungicides to reduce mycorrhizal relationships with *A. gerardii* roots (Smith et al. 1999) may also be viable management strategies to reduce *A. gerardii* in Dow Field.

Because of the small species pool and little evidence of species immigration from other sites, seeding and planting species with regional conservation value or limited dispersal capabilities will be necessary to fill vacant resource niches once *A. gerardii* is reduced (Howe 1994, Bruvig and Mabry 2008). Species that may be good candidates for introduction are those that were found in other remnants but not in Dow Field such as *Comandra umbellata* (bastard toadflax), *Liatris aspera* (rough blazing star), and *Lithospermum canescens* (hoary puccoon). This strategy is reminiscent of successional restoration, where late-successional or conservative species are seeded into an established matrix of grasses (Packard 1994, Betz 1997). However, because *A. gerardii* is highly competitive above- and belowground and native species richness peaked from 1998 to 1999 (see chapter 2), a more aggressive approach than Packard (1994) suggested must be taken to allow the new species to become established in a competitive environment.

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