

ENHANCEMENT OF DIVERSITY VIA DISTURBANCE AND SEED ADDITION IN TWO SAND
PRAIRIES DOMINATED BY DIFFERENT GRASSES

BY

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DISSERTATION

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy in Plant Biology
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2012

Urbana, Illinois

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ABSTRACT

Grassland diversity can be reduced by native and non-native dominant species, through heightened competition for resources and low colonization by non-dominant species. Traits of the dominant species may influence these interactions and also the extent to which the dominant is affected by disturbance. Disturbances that reduce dominant species may enhance community structure due to competitive release, but non-dominant species may require additional types of disturbance that create regeneration microsites, such as reduced litter and increased bare soil. In addition, community structure may be limited by seed availability, or a combination of microsite and seed limitation. Studies of these factors aid our basic ecological understanding of the maintenance of diversity in grasslands, but also are pertinent to restoration and management of grasslands. The goal of this research was to gain a better understanding of dominant and non-dominant species coexistence by examining 1) diversity of two communities dominated by contrasting dominant grasses, 2) responses of the communities to manipulative disturbances, and 3) responses to augmentation of microsite and seed availability.

First, I address the questions: Does community structure aboveground and in the seed bank differ between communities dominated by contrasting grasses? Do community dynamics in these communities differ over time? In a sand prairie in northwestern Illinois, USA, baseline community structure was compared in two communities dominated by either *Schizachyrium scoparium*, a native warm-season (C4) grass, or *Bromus inermis*, a non-native cool-season (C3) grass. Five years of vegetation surveys and a single-year seed bank sampling were conducted. A decline in % cover of non-dominant species with increasing % cover of dominant species suggests suppression of non-dominant species by both dominant grasses. However, greater diversity in the *Schizachyrium* than *Bromus* community and loss of species over time from the *Bromus* community suggests that negative effects on non-dominant species may be stronger in the *Bromus* community. In addition, differences in seed banks between the two communities

indicate possible differences in site history, another potential influence on aboveground community structure beyond the presence of different dominant species.

Second, this research asked: How does dominant species identity influence response to disturbance? What is the relative importance of dominant species reduction vs. independent stimulus of non-dominant species? How does frequency of disturbance influence response of dominant and non-dominant species? Separate disturbances were targeted to reduce the dominant grass (mowing) and create regeneration microsites at different frequencies (soil disturbance for a single or five years). Mowing reduced % cover of *Bromus* more than *Schizachyrium*, and displaced *Bromus*, but not *Schizachyrium*, as the dominant species. Species richness increased less by reduction of the dominant alone and more when combined with the greatest frequency of soil disturbance. However, microsites from soil disturbance were ephemeral, especially in the *Bromus* community. The extent of dominant species reduction depended on species identity and amount of tissue loss, which in turn determined whether or not non-dominant species abundance increased following disturbance. Newly disturbed microsites fostered colonization by non-dominant species in both communities. The results indicate the importance of species identity when pairing management techniques and dominant reduction. They also show that annual spring mowing is a tool managers may use for control of *Bromus*. In addition, the independent response of non-dominant community structure to disturbances that reduce competition from those that stimulate new colonization indicates the importance of multifaceted disturbances in restoration and maintenance of non-dominant species diversity in grasslands.

Third, this research asked: What is the relative importance of microsite vs. seed limitation in sand prairies dominated by different grasses? This question was addressed in both the *Schizachyrium* and *Bromus* communities in a factorial microsite (gap) and seed limitation (seed augmentation) experiment. In gap plots, species richness increased in the *Schizachyrium*, but not *Bromus* community. In seed addition plots, species richness did not

differ from controls in either community. In seed + gap plots combined, species richness was greatest and species composition diverged most from control plots in both communities. Low recruitment in gaps in the *Bromus* community may indicate inferior microsites and/or greater seed limitation in that community. In contrast, the low establishment of sown species in undisturbed vegetation showed that traits common to both dominant species, such as high production of biomass and dead vegetation, may make communities difficult to invade, regardless of dominant species identity. Finally, results for combined gap and seed addition plots indicate removal of multiple limitations is necessary to achieve the greatest change in community structure and species composition, independent of dominant species identity.

Key words: Bromus inermis, community structure, disturbance, dominant species, grassland diversity, microsite limitation, sand prairie, Schizachyrium scoparium, seed addition, seed bank, seed limitation, species identity

ACKNOWLEDGEMENTS

My advisor, Carol Augspurger, deserves many thanks -- she has been patient and supportive, always challenging me to be a stronger researcher and writer. Her advice continues to shape my writing and teaching. She, along with my initial advisor, Adrienne Edwards, helped channel my enthusiasm for prairie restoration and applied ecology into research. Before her departure to California, Adrienne was also integral to initial research design. Present and past committee members have provided valuable feedback on my research and writing, as well as thoughtful conversation: Ken Paige, John Taft, Brenda Molano-Flores, Carla Caceres, and Ken Robertson. Beth Morgan, Ed Dole, and my advisor were valued mentors for teaching at the college level. Field work was made more enjoyable by many graduate and undergraduate students, including Tiffany Bone, Chi Ho Chan, Ryan Fitzgerald, Dan Harvey, Cynthia Pancake, Gaelle Seyi, and Jason Zylka. I am grateful to Richard Lankau and German Bollero for their statistical advice. My graduate experience was made richer by fellow graduate students who provided mutual support and precious friendships: Jenny Duggan, Moni Berg-Binder, Cathy Bechtoldt, Carrie DeJaco, Nicole Davros, and Suzanne Beyeler. Brenda Molano-Flores and Mary Ann Feist offered their house as a sanctuary while I finished writing, and always accompanied by excellent conversations. Many thanks go to my colleagues at Luther College who encouraged me with carrots to complete my dissertation. Finally, my family has always been a solid source of support and entertainment. My parents were the initial source of my love of plants and the outdoors, through their interests and opportunities they provided for me.

Funding for research was provided by grants from the Illinois DNR Wildlife Preservation Fund, Illinois Native Plant Society, and University of Illinois (Philip W. Smith and Clark research awards and a Plant Biology summer fellowship). At the Lost Mound study site, Alan Anderson, Randy Nybøer, and Dan Wenny were always helpful and accommodating. Genesis Nursery (Tampico, IL) provided all seeds used in seed-addition experiments free of charge.

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CHAPTER 1: GENERAL INTRODUCTION

Maintenance of grassland diversity is influenced by multiple factors and processes including competition, availability of regeneration microsites, traits of the species pool, and/or site history. In communities that include competitive dominants, such as perennial grasslands, the coexistence of dominant and non-dominant species may be facilitated by disturbances that reduce dominant species, thereby providing reduced competition space and/or regeneration microsites for other species (Platt 1975, Tilman 1994, Collins et al. 1998). Herbivory by large ungulates, management techniques used to mimic herbivory, and removal of vegetation by digging animals may provide such disturbances. However, the response of a community to disturbance can be tempered by identity of dominant species through differences in phenology, structure, and native/non-native origin (Jackson et al. 2010). Even when competition has been reduced and suitable microsites are present, recruitment can be prohibited by the absence of seed from local sources, i.e., seed rain or seed bank. Seed addition can be used to test for seed limitation in specific communities by supplementing inadequate production of seeds and/or overcoming limited dispersal to microsites (Clark et al. 2007). Therefore, application of disturbances, coupled with seed addition, may be necessary to enhance community structure.

The overall objective of this research was to determine how disturbances affect plant community structure in grasslands, and how the species pool, including dominant grass identity and seed limitation, influences responses to disturbance. Experimental treatments were applied to reduce dominant grasses and native seed added to test for seed limitation. Response of community structure were compared in a formerly grazed sand prairie in two communities dominated by different perennial matrix grasses, one a native, warm-season grass and the other an introduced, cool-season grass. Results from this study inform basic ecological understanding of factors that influence community structure and can be applied to restoration for reduction of dominant grasses. This application is critical, as temperate grasslands are one of

the most critically threatened biomes (Hoekstra et al. 2005), and ecologically based knowledge of factors that enhance community structure, including disturbance, dominant grass identity and seed addition can be used to restore degraded grasslands.

Study System

The study site is located on dry-mesic sand prairie at the Lost Mound Unit of the Upper Mississippi River National Wildlife Refuge in JoDaviess County, Illinois (hereafter Lost Mound). This inland sand deposit was formed from glacial outwash deposited along the historic floodplain of the Mississippi River (Willman and Frye 1970). In 1917, the 810+ ha prairie site was commissioned as a U.S. Army base for munitions storage and was heavily grazed for the next 80 years with approximately 1,500 head of cattle yearly from May to October. When the base was closed and cattle were removed permanently from the site in 2000, the sand prairie that emerged was degraded, and included several dominant introduced invasive species.

Lost Mound is of particular conservation importance because it is one of the largest continuous prairies in Illinois, a state with less than 0.10% of its original native prairie remaining (IDNR 1994). Additionally, surveys of the site by H. A. Gleason (1910) provide a comparative historical reference to a time when only periodic and restricted grazing occurred on the site. Finally, the results from this research can be used for active management to enhance native community structure on the protected site.

This study focuses on two communities dominated by grasses with contrasting location of origin, phenology, and growth form: *Schizachyrium scoparium* (Michx.) Nash (little bluestem) (hereafter *Schizachyrium*), a native, warm-season (C4), bunch grass, or *Bromus inermis* Leyss. (smooth brome) (hereafter *Bromus*), a non-native, cool-season (C3), mat-forming grass. Non-dominant species in both communities were composed of native and introduced species, varied life histories and functional guilds. *Schizachyrium*, a common native grass in North American mixed-grass and dry prairies, dominates much of the dry-mesic sand prairie at Lost Mound. It

shows tolerance of moderate grazing (Anderson and Briske 1995) and low nitrogen levels (Fargione and Tilman 2005) that may allow it to outcompete non-dominant species. Native warm season grasses commonly dominate restored grasslands, and their reduction is a target of some restoration practices (Seabloom et al. 2003). In its native central Europe, *Bromus* is found as a non-dominant species in grasslands or patchily in disturbed areas (J. Taft, pers. comm.), but now has populations established worldwide with extensive acreage in North America (Ottinowski et al. 2007). *Bromus* commonly invades native prairies (Blankenspoor and Larson 1994, Vinton and Goergen 2006) and is present in several invasion foci at Lost Mound. Based on its documented history as an invader and association with decreased native diversity (Blankenspoor and Larson 1994), it is a logical target for reduction, and frequently the subject of control in restoration and management of native grasslands and restorations.

Overview

Chapter 1. Combined effects of dominant species identity and history of disturbance on grassland community structure and species composition

Our objective was to compare community structure and composition of non-dominant species between two communities based on the differences in identity of dominant species, i.e., *Schizachyrium* and *Bromus*, and recovery from a history of disturbance. The chapter used five years of vegetation surveys and a single-year seed bank sampling to address these objectives. Observations over time allowed assessment of community dynamics, including potential convergence within and/or divergence between the two communities. Assessments were based on a combination of standard measures of community structure, plant traits, similarity indices, and multivariate ordination. Comparisons of the non-dominant community structure and composition between these communities and over time allow detection of effects of differing dominant grass species and site history of disturbance.

Chapter 2. Facilitating grassland diversity through disturbance: Effects of dominant species identity, dominant reduction, and microsite creation on community structure

Chapter two builds on the information provided in Chapter one to assess how dominant grass identity and different modes of disturbance may interact, and the implications for maintenance of diversity interactions. Diversity in grasslands is promoted by mechanisms that mediate coexistence of dominant and non-dominant species. Disturbances (sensu Sousa 1984) may alter competitive balance through reduction of the dominant and subsequent competitive release of non-dominant species (Collins et al. 1998), but can be influenced by the identity of the dominant species (Jackson et al. 2010). Disturbances also can change resource availability, increasing opportunities for recruitment and colonization by non-dominant species (Martin and Wilsey 2006).

Over five years, this study applied mowing in the spring, with and without soil disturbance. Mowing targeted, but was not exclusive to, dominant species and tested for the effect of multiple years of biomass removal. Mowing disturbance was timed specifically to reduce *Bromus* via spring mowing, when its stored reserves have been mobilized to aboveground tissue (Willson and Stubbendieck 2000). We expected less reduction of *Schizachyrium*, given that disturbance was not at its maximum time of growth. We also predicted that the reduction of both dominant grasses would provide competitive release for non-dominant species.

Spring soil disturbances, applied for a single year or five consecutive years, created microsites with greater bare ground and lower litter and agitated the soil seed bank. Soil disturbances, applied at different frequencies, allowed assessment of an independent stimulus of non-dominant species that are frequently lost as grassland become degraded. Dominant species abundance and non-dominant community structure, including species richness, % cover, biomass, composition, and similarity, were assessed annually to detect temporal and cumulative effects of disturbance. Analysis of non-dominant species was conducted at multiple

levels: whole community, by plant traits, species composition, and association with the documented seed bank to allow detection of species groups and sources responding to disturbances. Soil seed bank data collected in Chapter one was used to detect recruitment from the seed bank into the vegetation.

Chapter 3. Microsite and seed limitation in two communities dominated by contrasting grasses

Chapter three investigates microsite and seed limitation from the perspective of influence by dominant grass identity. In both the *Schizachyrium* and *Bromus* community, we tested for microsite and seed limitation in a factorial experimental design: microsite creation (gap), seed addition (seed) and both (seed + gap). Microsite availability was assessed in two ways: First, microsites (=gap) were created by removing all live vegetation (above and belowground) and allowed to re-vegetate by potentially suppressed local vegetative and seed sources, including seed rain and seed bank. Second, seeds of 21 native species were added to intact vegetation (=seed) to compare the invasibility of the dominant grasses. Seed limitation was assessed via establishment of sown species in seed and seed + gap plots compared to control and gap plots, respectively. Seed addition served to compensate for both seed production and limited dispersal, as all sown species were present in the 810+ ha sand prairie that contained the two communities, but fewer than half were present in the experimental plots. Microsite quality was assessed by % cover of bare ground, dead vegetation, and dominant grass. To detect microsite and/or seed limitation, species richness, % cover, diversity, evenness, and composition of unsown and sown non-dominant species were compared across treatments and communities. Microsite and seed limitation of individual species and locally occurring species (not sown) with a seed bank were assessed by comparing frequencies of individual species.

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CHAPTER 2: COMBINED EFFECTS OF DOMINANT SPECIES IDENTITY AND HISTORY OF DISTURBANCE ON GRASSLAND COMMUNITY STRUCTURE AND SPECIES COMPOSITION

ABSTRACT

Communities dominated by different species and recovering from past disturbance, such as a legacy of past grazing, may differ in community structure, species composition, and short-term community dynamics. In particular, these communities may differ based on changes in abundance of dominant grasses, introduction of non-native dominant species, and negative impacts on non-dominant species. Five years of vegetation surveys and a single-year seed bank sampling were conducted in a sand prairie in northwestern Illinois, USA that was heavily grazed for 80 years, but recently released from grazing. Comparisons were made between two communities, dominated by either *Schizachyrium scoparium*, a native, warm-season (C4) grass, or *Bromus inermis*, a non-native, cool-season (C3) grass. Although % cover of the dominant species was greater for the native than non-native grass, species richness and diversity of non-dominant species were greater in the native than non-native grass community; % cover, evenness and frequency of non-dominant species were the same in the two communities. Percent cover of non-dominant species declined with increased % cover of dominant grass in both communities. Based on non-dominant species' location of origin, life history, and functional guild, communities differed for species richness, but generally not for % cover. Bray-Curtis indices showed greater within- than between-community similarity, but non-dominant species composition overlapped considerably between the two communities. Over time, the non-native grass community lost species at both site and plot levels and had turnover of species with the greatest importance, whereas the native grass community maintained or gained species and the most important species remained stable. In the seed bank, differences in seed

density, species richness, and composition indicated that present-day recruitment and regeneration-potential differed between the two communities. Differences in the seed bank also suggest that each community may have been influenced by additional aspects of site history beyond their commonly shared history on the site. Finally, a survey comparing present-day vegetation with a 1908 survey showed increased species richness (mostly native) in 2009, in addition to changes related to general succession and long-term grazing. Overall, this study found support for effects of both identity of dominant grasses and past history on non-dominant community structure, species composition, and community dynamics over time. Contrasting patterns of non-dominant species richness and abundance indicate that the combination of dominant grass identity and site history will continue to influence the progression of this site's recovery from long-term grazing.

Key words: Bromus inermis, grassland diversity, phenology, plant traits, sand prairie, seed bank, Schizachyrium scoparium, site history, species identity

INTRODUCTION

Plant community structure and composition are influenced by both species interactions, including competition between dominant and non-dominant species (Grime 1998, Harpole and Tilman 2006), and site history (MacDougall and Turkington 2005, Petermann et al. 2010). Dominant species, i.e., the most abundant species in a given community, may differ in traits and thus alter resource availability between otherwise similar environments (Wilson and Clark 2001, Seabloom et al. 2003). Site history includes disturbances that may select for disturbance-tolerant species (Wilson and Tilman 2002). The effects of contrasting dominant species and site history may be intertwined as replacement of one dominant species with another may have occurred as a result of species introduced during past disturbances. As a result of contrasting dominant species identity and site history, non-dominant community structure (i.e., species

richness, % cover, frequency, diversity, and evenness) may differ between communities, and when combined with yearly variation, may vary in distinct ways over time.

Dominant species with contrasting traits, including differences in phenology, physiology, and structure, may differ in resource uptake (Tilman and Wedin 1991), biomass production (Crawley et al. 1999, Bakker and Wilson 2001), and/or litter production (Vinton and Goergen 2006). These differences may select for non-dominant species that possess complementary traits to the dominant species (Fargione and Tilman 2005, Gilbert et al. 2009). Dominant species differ in their ability to inhibit new species establishment (Tracy et al. 2004, Emery and Gross 2007). For example, dominant grasses from different functional groups, i.e., C3 or C4 photosynthetic pathways, may differ in their effects on non-dominant species richness, % cover, diversity, and evenness (Miles and Knops 2009).

Changes in community structure in response to site history of disturbance may be separated into changes that occur during and after specific events (Milchunas et al. 1988, Olf and Ritchie 1998). Disturbances, including long-term heavy grazing, may eliminate or reduce the abundance of species that are disturbance-intolerant. Therefore, upon cessation of grazing, the species pool is restricted to disturbance-tolerant species, and this legacy may persist unless previously existing species re-enter the community through dispersal. In addition, recovery from disturbance may be complicated by the presence of species that were introduced during disturbance events (Corbin and D'Antonio 2004, Davies et al. 2009). In particular, invasion by non-native species is commonly associated with disturbances and altered disturbance regimes (Hobbs and Huenneke 1992). Legacies of site history may persist in current community structure and composition, and may also persist as a memory of past history in the seed bank (Korb et al. 2005).

Communities are dynamic, changing in response to availability of resources (Adler and Levine 2007), species interactions, and environmental change through time (Elmendorf and Harrison 2009). Patterns of community change during and after disturbance are likely to

fluctuate as new resources become available and others are removed, providing benefits to different species through time (Foster et al. 2004, Funk et al. 2008). Communities may continue to change even after measureable differences in resources have declined, potentially attributable to priority effects and species interactions (Milchunas and Lauenroth 1995, Coffin et al. 1996). Identity of dominant species may provide additional influence on community change through effects on community invasibility (Emery and Gross 2006) and loss of species through time. In particular, replacement of a native with a non-native dominant may alter species interactions, such that over time, non-dominant species composition converges among sites as influenced by the traits of the new dominant species, i.e., biotic homogenization (McKinney and Lockwood 1999, Olden et al. 2004). At the same time, this invaded community may diverge from the community that maintained the native dominant species, but potentially to different degrees.

This study was based in a human-altered perennial grassland that experienced long-term historical disturbance, and, by design, half of the study locations were previously invaded by a non-native species. The long-term, site-wide, grazing disturbance was followed by a short window of recovery. Specifically, we sampled sand prairie that was heavily grazed for approximately 80 years (grazing ceased 5 years prior to the start of this study). Study plots were dominated by either a native C4 grass, *Schizachyrium scoparium* or invaded by *Bromus inermis*, a non-native C3 grass. It was assumed that because grazers had even access across the site, background disturbance was similar between these communities, and that both communities were drawing from the same regional species pool.

This study allowed us to answer the question: How do two communities dominated by contrasting grasses, but both recovering from a history of disturbance, differ in community structure and composition of non-dominant species? Five years of vegetation surveys and a single-year seed bank sampling were completed. Observations over time allowed assessment of community dynamics, including potential convergence within and/or divergence between the

two communities. Assessments were based on a combination of standard measures of community structure, plant traits, similarity indices, and multivariate ordination. Comparisons of the non-dominant community structure and composition between these communities and over time allow detection of effects of differing dominant grass species and site history of disturbance.

METHODS

Study Site

The study site was a dry-mesic sand prairie at the Lost Mound Unit of the Upper Mississippi River National Wildlife Refuge (42° 13' N, 90° 20' W) in Jo Daviess County, Illinois U.S.A. The underlying soil material, derived from glacial outwash sand deposited along the historic floodplain of the Mississippi River (Willman and Frye 1970), is susceptible to wind erosion when vegetation cover is reduced (Gleason 1910; Curtis 1959) and has low organic content (Symstad 2004).

At Mount Carroll, Illinois, 50 km from the research site, spring and summer precipitation during the sampling period (2005–2009) ranged from drought (2005) to above average conditions (multiple years), compared to 30-year mean values (spring: 270 mm, summer: 334 mm) (Fig 1.1) (Illinois State Climatologist's office). Mean daily temperatures in the growing season were similar to the long-term average (15 °C, 1971-2000). Yearly number of days above 32.2 °C (90 °F) varied greatly among years (38, 15, 26, 3, and 5 days in 2005–2009, respectively), compared to the 30-year mean (15 days).

In 1917, the site was commissioned as a U.S. Army munitions storage base; infrastructure included parallel rows (at approximately 125-m intervals) of soil-covered bunkers and access roads. Vegetation and seed bank survey sites were located in areas between the rows that were undisturbed by ground-moving activities. The site was heavily grazed during its

80+ years as an Army base with approximately 1,500 head of cattle yearly from May to October. The base was closed in 2000 and cattle were removed permanently from the site. The approximately 2,000 ha of sand prairie that emerged was degraded and included several dominant non-native invasive species.

This study focuses on two communities dominated by either the native grass, *Schizachyrium scoparium* (Michx.) Nash (little bluestem), or the non-native grass, *Bromus inermis* Leyss. (smooth brome). *Schizachyrium scoparium* (hereafter *Schizachyrium*), a warm-season (C4), perennial grass with a bunch-grass growth form, dominates much of this sand prairie. *Bromus inermis* (hereafter *Bromus*), a cool-season (C3), perennial, non-native Eurasian grass with spreading rhizomes, commonly invades native prairies (Otfinowski and Kenkel 2008). Its invasion has been associated with decreased native diversity (Blankenspoor and Larson 1994). By 2005, *Bromus* was present in several invasion foci at the site; its presence was likely a combination of localized seeding and subsequent spread. Additional species in both communities included native and non-native species of varied life histories and functional guilds; none reached similar abundances as either dominant grass, and thus all other species in the communities are collectively referred to as non-dominant species. It was assumed that the vegetation of these two communities was similar historically.

Vegetation Surveys

Five transects, each 50-m long, were placed in each community, with all ten transects located within a 3 km radius; transects were separated by ≥ 125 m. Transect placement was aimed at maximizing the ecological and environmental variability among transects, while maintaining the dominance by the two focal grasses. Three criteria were used to select placement of transects. First, a visual estimate of dominance (approximately 50 percent) by either dominant grass was required. This visual estimate of cover was later quantified during field surveys. Second, transects were oriented to avoid the shrub, *Rhus aromatica*, and large

patches of crown-vetch, *Coronilla varia*, a non-native, nitrogen-fixing invasive species. Third, transects in the *Bromus* community were placed in what appear to be three separate invasion foci, interspersed within the larger *Schizachyrium* community. Two transects were placed in each of two of the *Bromus* foci, and a single transect in the third foci.

Vegetation surveys of species composition and percent cover were conducted in June and August, 2005–2009, along each 50-m transect. At 10-m intervals along each transect, a 2 x 4-m plot was marked on alternating sides of the transect, at a random distance of 1 - 9 m from the transect (5 plots per transect, 25 plots in each community). Within each 2 x 4-m plot, a permanent 1 x 0.5-m sampling plot was randomly placed along the centerline of the larger plot. The 2 x 4 m plots were not sampled but provided orientation for the location of the 1 x 0.5-m plot and were used as reference for a concurrently conducted study in adjacent areas. Percent cover was estimated by assigning a Daubenmire cover class (Daubenmire 1959) to each species present in each plot. Species frequently overlapped so that values for some plots exceeded 100 % cover. Nomenclature and species trait classification follow Gleason and Cronquist (1991). Plant traits included location of origin (native, non-native), life history (perennial; biennial and annual) and functional guild of perennial species (grass, forb, sedge, legume).

Data from June and August vegetation surveys were combined to create a list of species and values for species richness and % cover for each plot. The higher % cover value (i.e., June or August value) was used for species present during both surveys.

Seed Bank Survey

In April 2006, soil samples were collected from a 2 x 4 m plot adjacent to each vegetation plot. Sampling at this time allowed natural overwintering of the seed bank (i.e., cold treatment), but occurred prior to the full onset of spring germination. Twelve soil cores (2 cm diameter, 6 cm depth) spaced approximately 0.5 m apart were taken from each plot and

combined to create one sample for each plot (5 plots per transect: 25 plots in *Bromus*, 24 plots in *Schizachyrium* due to loss of a sample). The total volume of soil sampled from each plot was 226 cm³ (total soil volume sampled = 5,655 cm³ in each community).

Samples were processed by passing each sample through a sieve (4.75 mm² mesh) to remove root and bud material. Each processed sample was then spread <1 cm thick over a sterile soil mix (1 : 3 ratio of sand : growing mix composed primarily of sphagnum peat moss, plus perlite, lime, gypsum and a wetting agent) in a planting tray (20 x 20 x 3 cm depth) lined with fine mesh to reduce loss of soil. Planting trays were placed in a temperature-controlled (range: 15 - 30 °C) greenhouse at the University of Illinois at Urbana-Champaign. Trays were rotated regularly to diminish effects of placement within the greenhouse and sterile trays were placed on each bench to detect possible seed contamination. Artificial light (1000 watt metal halide) was used to supplement natural light during low light (below 900 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in daytime hours. To avoid loss of seedlings during drying-rewetting periods, an automatic mist system was used to supplement hand watering.

The species composition, richness, and density (i.e. number of individuals) of the germinable seed bank were determined by identifying and counting species of individual seedlings as they emerged between April and November, 2006. When necessary, individuals were transplanted and grown until species identity could be verified. Some individuals died prior to identification and were documented as 'un-identified'. Trays were observed daily during the first three months, four times weekly for the next two months, and two times weekly during the last month. To ensure equal germination opportunity for the entire soil sample, the top 1 cm of each tray was mixed in July after germination rates had fallen abruptly.

Comparisons to Historical Survey

A historical vegetation survey of the site in 1908, conducted by H. A. Gleason (1910) when only periodic and restricted grazing occurred on site, provides a comparative reference to

the site prior to heavy grazing. In 2009, a survey was conducted to compare present-day vegetation to Gleason's 1908 quantitative survey. An attempt was made to replicate Gleason's transect placement based on Gleason's 1908 photographs, but it was not possible to relocate his exact transect location. Specifically, Gleason sampled a community dominated by *Leptoloma cognatum*, but, although this species was present, it did not dominate any portion of the area in 2009. Gleason's survey was located in a drier prairie along the dry- and dry-mesic prairie continuum, compared to the *Schizachyrium* and *Bromus* communities that form the main part of this manuscript. Within the site selected, vegetation surveys conducted in June 2009 adhered to sampling regimes provided by Gleason (1910). Forty small plots (0.5 x 0.5 m) spaced at approximately 2-m intervals (2 paces) along an 80-m transect were surveyed in 1908 and 2009 to assess species composition, richness, and frequency within each plot.

Data Analysis

Descriptions of the vegetation and seed bank at the site level included summary measures of community structure and individual species composition compiled for each community. Also at the site level, importance values were calculated for each species; importance value (IV) = Relative % cover + Relative frequency. Statistical comparisons were made at the plot level, and used original, not relative, values of % cover of dominant grass and community structure of non-dominant species, including species richness, % cover, Shannon-Wiener diversity (H') and evenness ($E_{1/D}$ of Smith and Wilson 1996). Separate repeated measure ANOVAs were made for each variable using proc mixed (SAS) for mixed models. Plots, blocked within transects, were included as random effects. Community, year, and the community x year interaction were included as fixed effects. The best-fit model for covariance structure of each model was based on Akaike's Information Criteria, Corrected (AICC) (Littell et al. 2006). Frequency of species occurrence (i.e., number of plots in which a species occurred) consisted of count data; a repeated measure ANOVA was run in proc genmod (SAS) for

generalized linear models, using a negative binomial distribution and transect as a block effect. Percent cover of dominant grass was modeled as a covariate in all models of community structure. In the case of a significant overall model, post-hoc (using 'estimate' statement in proc mixed), protected univariate comparisons were made to detect significant differences between communities in a single year, and/or between years. All variables, except evenness, met assumptions of normality based on examination of residuals. Evenness was transformed using the natural log; untransformed values are presented in the text.

Plant traits were compared in two ways: 1) with a multi-year repeated measures model, and 2) in a single-year model (2006); 2006 had both vegetation and seed bank data and dominant grass cover did not differ significantly between communities. Perennial legumes were present in only one plot in 2006, and so this category was removed from analyses. The remaining trait categories were analyzed in separate ANOVAs to maintain assumptions of independence. The single year model was run in proc glm (SAS) with transect as a block effect. Results did not differ between the two approaches for species richness of any trait category and differed for only one category of % cover (annuals + biennials). In the multi-year model, % cover of annuals + biennials was significantly greater (approximately 1 % cover) in the *Schizachyrium* than *Bromus* community; this difference was not significant in the 2006 model. Given this small difference, the 2006 single-year model was deemed to be the appropriate representation for comparisons between the two communities, while using a smaller number of statistical tests. Comparisons between vegetation and seed bank were made separately because of differences in sampling methods, except for calculation of Jaccard's index of similarity, which uses species lists and not abundances (Mueller-Dombois and Ellenberg 1974).

To detect within- and between-community similarity for each year of vegetation data and single year of seed bank data, a Bray-Curtis index value was calculated for each pair-wise comparison of plots (Clarke and Gorley 2006). Prior to calculation of similarity values, % cover (density for seed bank) of each species within each plot was standardized by total % cover (or

density), and a single extreme outlier plot was removed from all years. Non-metric multi-dimensional scaling (NMDS) diagrams were constructed for each year using Bray-Curtis values. Analysis of similarity (ANOSIM), a non-parametric test, was used to compare Bray-Curtis values between communities in each year and seed banks. SIMPER analysis, a method of assigning % contribution of individual species to Bray-Curtis values, was used to further interpret dissimilarities between communities (Clarke and Gorley 2006). All ordinations and related analyses were conducted in PRIMER v6.

RESULTS

Vegetation

Site level descriptions

The community dominated by *Schizachyrium* maintained ≈ 50 species (48, 48, 52, 53, and 48 species in 2005–2009, respectively) (Appendices A.1-A.5). Non-dominant species were predominantly native, while eight non-native species represented 16–25 % of yearly total importance values. Perennial species dominated in number and importance of species in all years, while biennial and annual species contributed 12–18 species in any given year, albeit at low importance values. *Schizachyrium scoparium* had the greatest single-species importance value in each year. Among non-dominant species, Poaceae and Asteraceae comprised the greatest importance values in all years. Five species, all perennial grasses or forbs, maintained the greatest importance values through time, but their relative rank changed over time. Some species with lower importance values, especially short-lived species of all life histories, disappeared and reappeared during the five years. Four species (three non-native) were gained between 2005–2008 and then maintained, while one species did not reappear after 2005. Mean % cover of bare ground ranged from 1 - 5 % in 2005–2009. This community had 18 unique species not in the *Bromus* community.

The community dominated by *Bromus* maintained on average 37 species, and slowly lost species over time (41, 38, 35, 36, and 34 species in 2005–2009, respectively) (Appendices A.1-A.5). Non-dominant species were predominantly native, while eight non-native species represented 25–35 % of total importance values. Perennial species dominated in number and importance in all years, with biennial and annual species contributing only 2–7 species with low importance values. *Bromus inermis* had the greatest single-species importance value in each year. Among non-dominant species, Poaceae comprised the greatest importance value from 2005–2009; Cyperaceae was second from 2005–2007, and Asteraceae from 2008–2009, driven by the increase in one native perennial species, *Ambrosia psilostachya*. Only two non-dominant species, a native and non-native grass, remained consistently high in importance over time; while short-lived species disappeared and reappeared. Seven species present in 2005–2006 never reappeared, while one native annual and one non-native perennial forb were gained in 2006 and no other new species were documented by 2009. Mean % cover of bare ground ranged from 0.5–2 % over five years. Eight species, six native and two non-native perennial species, were unique to this community compared to the *Schizachyrium* community.

Plot level comparisons of vegetation between communities and over time

Dominant Grass

Mean percent cover of dominant grasses differed significantly between communities ($F = 6.92$, $df = 1$, $p < 0.05$) and over time ($F = 16.55$, $df = 4$, $p < 0.01$) (Fig. 1.2). The native grass, *Schizachyrium*, had significantly greater cover than the non-native grass, *Bromus*, in all years except 2006. A significant interaction term between community and year ($F = 5.95$, $df = 4$, $p < 0.01$) arose from greater inter-annual variation of % cover for *Bromus* than *Schizachyrium*.

Total mean % cover, i.e., dominant + non-dominant species, did not differ between communities ($F = 3.2$, $df = 1$, NS), nor was there any interaction of community with year ($F =$

0.98, $df = 4$, NS). Total % cover differed significantly over time ($F = 76.04$, $df = 4$, $p < 0.01$); the pattern generally reflected % cover of non-dominant species.

Non-Dominant Species

Mean species richness differed significantly between *Schizachyrium*- and *Bromus*-dominated grasslands and among years (Fig. 1.3 A, Table 1.1). Among years, species richness was 2–4 species greater per plot, on average, in the *Schizachyrium* than *Bromus* community. A significant interaction term between community and year represented the intermediate temporal peak of species richness in the *Schizachyrium* versus the intermediate depression and species loss in the *Bromus* community over time. Species richness co-varied significantly with % cover of the dominant grass.

Mean percent cover of non-dominant species did not differ between the two communities (Fig. 1.3 B, Table 1.1). However, total cover of non-dominant species decreased significantly (40%) in the first three years and then stabilized. Non-dominant perennial grass species, especially *Poa pratensis* and *Koeleria macrantha*, accounted for approximately 75 % of this reduction. In both communities, % cover of non-dominant species co-varied significantly with % cover of the dominant species.

Mean frequency of species occurrence (i.e., number of plots in which species occurred) did not differ between communities or over time (Fig. 1.3 C, Table 1.1). The number of common species (i.e. high frequency) was relatively stable over time. Number of moderately common species decreased in both communities, but frequency of rare species increased only in the *Schizachyrium* community over time.

Mean community diversity (H') was significantly greater in the *Schizachyrium* than *Bromus* community overall and in all years (Fig. 1.3 D, Table 1.1). A significant interaction between community and year appeared to be caused by a marginally significant reduction in diversity in only the *Schizachyrium* community in 2009.

Mean evenness did not differ between communities, nor was there any interaction of community with year (Fig. 1.3 E, Table 1.1). Evenness differed significantly over time and with % cover of the dominant grass. The significant increase from 2006–2007 corresponded with a reduction of % cover of non-dominant species, potentially related to the reduction of *P. pratensis* and *K. macrantha*.

Relationship between Dominant Grass and Non-dominant Community Structure

Percent cover of dominant grass was a significant predictor of species richness only in the *Schizachyrium* community (Fig. 1.4 A). The negative relationship was consistent among years 2005–2008, but was not significant in the *Schizachyrium* community in 2009. Percent cover of dominant grass was a significant predictor of % cover of non-dominant species in both communities (Fig. 1.4 B). The negative slope of this relationship was significant in all years (data not shown) and did not differ significantly between communities in any year except 2007 ($p < 0.01$). Regressions did not differ between years in either community, except between 2006–2007. The intercept for % cover of non-dominant species was lower in the *Bromus* (169) than *Schizachyrium* (183) community in 2006, a general trend that was amplified in 2005 and 2008–2009 (data not shown).

Plant Traits: Vegetation (2006)

Mean species richness differed between communities with regard to location of origin, life history, and perennial functional guild (Fig. 1.5 A-C, left side). Species richness was significantly greater in the *Schizachyrium* than *Bromus* community (Fig. 1.5 A). Species richness was greater for native than non-native species in both communities. However, native, but not non-native, species richness was significantly greater in the *Schizachyrium* than *Bromus* community. Species richness of perennial species exceeded biennial and annual species in both communities, and both life history categories were significantly greater in the

Schizachyrium community (Fig. 1.5 B). Perennial grass and forb species richness exceeded sedge species in both communities (Fig. 1.5 C). Species richness of only perennial forb species was significantly greater in the *Schizachyrium* than *Bromus* community.

Overall, the two communities showed quite similar mean % cover based on plant traits (Fig. 1.5 D-F). Percent cover was greater for native than non-native species in both communities (Fig. 1.5 D). Percent cover of native species did not differ significantly between the two communities, while non-native species were significantly greater in the *Bromus* community. Perennial species dominated both communities, with > 90 % of abundance (Fig. 1.5 E). Percent cover for both life history categories did not differ significantly between communities. Perennial functional guilds showed decreasing % cover from non-dominant grasses, forbs, and sedges in both communities (Fig. 1.5 F). Perennial forb species differed significantly and had nearly twice as much % cover in the *Schizachyrium* than *Bromus* community.

Seed Bank

Site level descriptions

Thirty-six species were identified from the 562 seedlings in the seed bank of the *Schizachyrium* community (Appendix B). Species were predominantly native (26), except nine non-native species comprising 20 % of total importance values (total excludes one species of unknown origin). Perennial, annual, and biennial species were represented in decreasing number (18, 12, and 5 species), but differing % of importance values (34, 51, and 15 %). Among perennial species, forb species were greatest in number, followed by grass, then sedge species. Six families shared the greatest importance values and were represented by single (e.g. Primulaceae, Campanulaceae) or multiple species (e.g., Asteraceae, represented by 7 species). Nine species present in this community's seed bank were absent from the *Bromus* seed bank.

Thirty-four species, 26 native and 8 non-native, were identified from the 1,304 seedlings in the seed bank of the *Bromus* community (Appendix B). Importance of non-native species exceeded that of natives by almost 2:1. Three non-native species, including perennial forbs, *Potentilla argentea* and *P. recta*, and the annual, *Arenaria serpyllifolia*, were among the four greatest importance values. Perennial, annual, and biennial species were represented in decreasing number (22, 9, and 3 species) and importance (65, 34, and 2 % of importance values). Perennial species decreased in number and importance from forb to grass and sedge species. Rosaceae (two *Potentilla* spp.) dominated importance values over Poaceae (eight spp.) and Caryophyllaceae (one species). Seven seed bank species represented in *Bromus* seed bank were absent from the *Schizachyrium* community.

Comparisons between Vegetation and Seed Bank

Species richness was lower in the seed bank than vegetation (2006) in the *Schizachyrium* community (Appendices A.2 and B.1). Fifty-four % (26 of 48 species) of the vegetation was represented in the seed bank, whereas 72 % (26 of 36) of the seed bank was represented in the vegetation. Species of greatest importance in the seed bank (predominantly native annual species) were of low importance, or not present, in the vegetation. The dominant grass, *Schizachyrium*, did not germinate from the seed bank.

Species richness was similar in the seed bank and vegetation of the *Bromus* community (Appendices A.2 and B). Sixty % (22 of 37 species) of the vegetation was represented in the seed bank, whereas 65 % (22 of 34) of the seed bank was represented in the vegetation. Perennial and annual species comprised the greatest importance in the seed bank and were of low or moderate importance, or not present, in the vegetation. Only one *Bromus* seedling germinated from the seed bank.

Plant Traits: Seed Bank

At the plot level, although mean species richness of the seed bank was similar between communities, native species dominated the *Schizachyrium* community, whereas mean number of native and non-native species were equal in the *Bromus* community (Fig. 1.5 A). Native species richness was significantly greater in the *Schizachyrium* than *Bromus* community, and non-native species richness was significantly greater in the *Bromus* community. Perennial species richness was significantly greater in the *Bromus* than *Schizachyrium* community, whereas biennial and annual species richness was significantly greater in the *Schizachyrium* community (Fig. 1.5 B). Perennial grass and forb species richness were significantly greater (> 1.5 times) in the *Bromus* than *Schizachyrium* community, and greatly exceeded sedge species richness in both communities (Fig. 1.5 C).

Mean density of seedlings from the seed bank was significantly greater (> double) in the *Bromus* than *Schizachyrium* community, largely because of significant differences in non-native species (Fig. 1.5 D-F). Seedling density was greater for perennial than biennial and annual species in the *Bromus*, but not *Schizachyrium* community (Fig. 1.5 E). Density of perennial species was significantly greater in the *Bromus* than *Schizachyrium* community. Density of perennial grass and forb species were significantly greater in the *Bromus* than *Schizachyrium* community (Fig. 1.5 F). Perennial legumes were absent and sedges had very low densities in both communities.

Species composition and abundance: Similarity *within* and *between* communities and over time

Within-community similarity

Among vegetation plots of the *Schizachyrium* community, within-community similarity of species composition and abundance decreased over time, as indicated by NMDS diagrams (Fig. 1.6 A-E) and mean Bray-Curtis similarity index values (Table 1.2). In the vegetation of the

Bromus community, within-community similarity varied among years, but was more similar in 2009 than in 2005. In the seed bank, similarity among plots was greater within the *Bromus* than *Schizachyrium* community (Fig. 1.6 F, Table 1.2). Within-community Bray-Curtis similarity values of the vegetation were similar when averaged from 2005–2009: 33.2 and 32, in the *Schizachyrium* and *Bromus* communities, respectively; whereas in the seed bank, within-community similarity values were greater for *Bromus* than *Schizachyrium*.

Between-community similarity

Between-community similarity values of the vegetation were smaller than within-community values (Table 1.2). Underlying species composition and abundance differed significantly between *Bromus* and *Schizachyrium* communities (Table 1.2, ANOSIM results). Although ANOSIM results confirm that similarity was less between than within communities, low global R values indicate that there was considerable overlap in species composition and abundance between the two communities. Global R values decreased over time, indicating an increase in similarity between the two communities, which is also reflected in the greater overlap of plots of the two communities in NMDS diagrams over time (Fig. 1.6 A-E). In the seed bank, species composition and abundance differed significantly between *Bromus* and *Schizachyrium* communities (Fig. 1.6 F, Table 1.2, ANOSIM results), and to a much greater extent than the vegetation (Global R = 0.511). In the vegetation and seed bank, the most abundant species in each community contributed the most, via contrasting abundances in each community, to low similarity between communities (Appendices A.1-A.5 and B.1, SIMPER results). The relative rank of species contributing to these low similarities in the vegetation changed from 2005–2009, but generally the species remained the same.

Similarity of species composition (Jaccard's index), using species lists at the whole community level, showed similarity between the vegetation and the seed bank was greater in the *Schizachyrium* (40) than *Bromus* (33) community.

Comparisons between 2009 and Gleason's 1908 vegetation survey

Total number of species was nearly twice as great in 2009 than 1908 (Table 1.3) because of greater numbers of native annual and perennial species. Number of non-native species, as well as perennial grass and sedge species, were greater in 2009 than 1908, whereas there was no change in number of forb or legume species. Mean species richness was greater in 2009 (9.03 ± 0.33 , mean per plot \pm SE) than 1908 (3.4 ± 0.33 SE).

A greater number of species was present at high frequencies in 2009, whereas a single species, *Leptoloma cognatum*, was the most frequent in the 1908 survey (Figure 1.7). Rank of frequencies dropped more sharply in 1908 than 2009, but number of rare species was similar between the surveys. Examination of the most frequent species (presence >25 % of plots in either 1908 or 2009) showed that species present in 1908 were also observed in 2009, albeit at different rank and frequency (Table 1.4). The most common grass in 1908, *Leptoloma cognatum*, was only moderately common in 2009. Other grasses common in 1908 were present at similar rank, but greater frequency in 2009 (*Panicum villosissimum* and *Schizachyrium scoparium*). Although total number of forb species was the same in 1908 and 2009, frequency of forb species, except *Ambrosia psilostachya*, was much lower in 2009.

DISCUSSION

Five years of vegetation surveys and a single-year seed bank sampling of these two communities dominated by contrasting grasses showed both differences and similarities in community structure and species composition. Furthermore, their changes over time highlighted underlying differences in community dynamics. Species richness of both the vegetation and seed bank was greater in the *Schizachyrium* than *Bromus* community, but their vegetation was similar in % cover, frequency, and evenness of non-dominant species. Seed bank densities were greater in the *Bromus* than *Schizachyrium* community. Similarity of species composition and abundance was greater within than between communities, but there was

considerable overlap of species composition between communities. Overall, these results indicate influences of both dominant species identity and site history in regulation of this previously disturbed grassland. The intertwined nature of these factors in these communities precludes identification of which factor was more important in determination of the species pool at the outset of this study. However, some results suggest potential ways these factors influenced these communities and may continue to do so in the future. Contrasting traits of the native and non-native dominant grasses appeared to alter conditions for coexistence and regeneration of non-dominant species in their respective communities. Their shared history of long-term grazing and environmental factors likely influenced common responses between the two communities. However, it appeared that site-wide history was not uniform, but unique aspects of site histories occurred in each community.

Site level: Vegetation

Species richness of native species in both communities was comparable to other sand prairie grasslands in the region, but both communities had greater species richness of non-native species by comparison (Ebinger et al. 2006, McNicoll and Augspurger 2010).

Theoretically, the communities studied developed from the same species pool of this 2,000 ha grassland. However, lower species richness, greater importance of non-native species, and fewer than half the number of unique species in the *Bromus*- than *Schizachyrium*-dominated community indicate that both species interactions at the plot level and aspects of site history unique to each community have been important in determining differences in community structure and species composition.

Community structure: Comparisons between communities

Dominant Grass

Greater mean % cover per plot of *Schizachyrium* than *Bromus* was a consequence of transect locations. However, given the direction of differences of corresponding community structure, contrasting traits of the dominant grasses should be considered in addition to their % cover. For example, lower % cover for *Bromus* may not have equated to lower competitive ability, as Gerry and Wilson (1995) found competition by *Bromus* to be stronger below than aboveground. In addition, differences between structural forms, i.e., bunch vs. rhizomatous growth, reflect different growth strategies for capturing light (Wilsey 2010) that may create differences in light available to other species. Other comparisons of warm- (C4) and cool-(C3) season grasses have shown differing belowground structure (Belnap and Phillips 2001), litter production (Vinton and Goergen 2006), and contrasting nutrient uptake and availability (Christian and Wilson 1999, Craine et al. 2002). Any, or all, of these trait differences may ultimately have cascading effects on the communities that they dominate.

Non-Dominant Species

Despite greater mean % cover per plot of the dominant native grass in the *Schizachyrium* community, species richness and diversity (H') were greater there, which is similar to other studies comparing native and non-native dominated communities (Levine et al. 2003). Trait differences of dominant grasses, as discussed above, may have contributed to this effect by facilitating coexistence of non-dominant species in the *Schizachyrium* community, or, alternatively, suppressing non-dominant species in the *Bromus* community. However, effects of dominant species, especially non-native invaders, can be difficult to separate from effects of site history (MacDougall and Turkington 2005). Long-term, heavy grazing can reduce species richness through selection against disturbance-intolerant species, even when grasslands evolved with grazers (Milchunas et al. 1988, Olf and Ritchie 1998). It is possible that localized

grazing in areas currently dominated by *Bromus* lowered species richness more than in the *Schizachyrium* community and exaggerated dispersal limitation in this grassland. Thus, 'recovery' of diversity of these post-grazing communities depends upon priority effects of the different dominant and non-dominant species present after removal of grazers, in addition to dispersal limitation of native species (Coffin et al. 1996, Tilman 1997, Seabloom et al. 2003, DiVittorio et al. 2007). Indeed, dispersal limitation may only be overcome through addition of seeds.

Mean % cover per plot of non-dominant species did not differ between communities, and, in part, may reflect non-dominant species' response to environmental conditions common to both communities. However, % cover of non-dominant species must be considered in conjunction with its significant covariation with % cover of dominant grass (Table 1.1) and overall lower % cover of *Bromus* (Fig. 1.2). This relationship is best illustrated by examining dominant and non-dominant species on an individual plot level in both communities.

Decreasing % cover of non-dominant species with increasing % cover of dominant grass (Fig. 1.4 B) indicates the potential of both grasses as superior competitors, as was found in other studies of these dominant species (Goldberg 1987, Wedin and Tilman 1993, Gerry and Wilson 1995, Fargione and Tilman 2005). In addition, similar slopes of this relationship between the two communities, but lower intercept of the *Bromus* community, shows that at a given % cover of both grasses, % cover of non-dominant species would be predicted to be lower in *Bromus* than *Schizachyrium*. These same effects were illustrated by similar mean % cover of non-dominant species (Fig. 1.3 B), despite lower mean % cover of *Bromus* (Fig. 1.2).

A negative relationship of species richness with % cover of dominant grass in the *Schizachyrium* community may result from reduced niche space when a single species has the most effect on diversity (Crawley et al. 1999, van Ruijven et al. 2003) (Fig 1.4 A). The absence of this relationship for the *Bromus* community suggests two potential mechanisms. First, *Bromus* may be capable of suppression so that only a subset of species are able to co-exist

with *Bromus*, as supported by the lower diversity when *Bromus* has invaded species-rich prairies (Boettcher and Bragg 1989). Second, differential history of disturbance may have reduced the species pool in the community presently dominated by *Bromus*; thus, even when *Bromus* was low in % cover, no additional species were available to recruit.

Plant Traits

Greater species richness in the *Schizachyrium* than *Bromus* community for most plant traits analyzed may reflect contrasting resource partitioning by the dominant grasses (Callaway et al. 2003, Harpole and Tilman 2006). Widespread dominance of perennial grasslands by warm-season grasses, such as *Schizachyrium*, may have selected for non-dominant species with complementary traits, including traits that result in different temporal resource use by dominant and non-dominant species (Fargione and Tilman 2005). Therefore, species from the regional species pool that can coexist with warm-season *Schizachyrium* may encounter greater competition from cool-season *Bromus*. For example, species that recruit and complete most of their life cycle by the middle of summer, including biennial and annual species, are likely to encounter increased competition from *Bromus* during key establishment and growth periods. In addition, these species encounter lower % cover of bare ground in the *Bromus* than *Schizachyrium* community. Indeed, some biennial and annual species, present in both the seed bank and vegetation of the *Schizachyrium* community, were present in the seed bank of the *Bromus* community, but absent from its vegetation. Perhaps *Bromus* inhibits establishment of some species present in the community, as found in other studies (Foster 1999, Dilleuth et al. 2009). However, this limited establishment in *Bromus* contrasts with a mesocosm study in which the addition of seeds resulted in greater recruitment in *Bromus* than *Schizachyrium* (Emery and Gross 2007).

Lower species richness of perennial forbs in *Bromus* than *Schizachyrium* may also be affected by similar barriers to establishment as biennial and annual species, given their greater

richness per plot in the seed bank of the *Bromus* community. However, absence of some perennial forb species from both the vegetation and seed bank of the *Bromus* community may also reflect effects of long-term cattle grazing regimes on perennial forbs (Leach et al. 1999, Fuhlendorf and Engle 2001).

Percent cover did not differ between communities for most plant traits analyzed. It is possible that once species are established, they are responsive to environmental factors shared in common between the two communities (Adler and Levine 2007) and/or are affected by complementary or antagonistic interactions with neighboring non-dominant species (Smith and Knapp 2003). Some differences between communities may have arisen from differences in non-dominant species composition. In addition, greater % cover of non-native species may have been the result of favorable conditions created by *Bromus* (Simberloff and VonHolle 1999), such as changes to the soil biota (Jordan et al. 2008). Mechanism(s) for lower % cover of perennial forb species were not readily apparent, but in a study in another *Bromus*-invaded grassland, Williams and Crone (2006) modeled the negative effects of *Bromus* on population growth of a native perennial forb.

Comparisons between Vegetation and Seed Bank

Comparisons of the vegetation and seed bank of both communities allow insight into current regeneration. The greater value of Jaccard's similarity index in the *Schizachyrium* than *Bromus* community and the greater proportion of seed bank species represented in the vegetation for the *Schizachyrium* ($\approx 75\%$) than *Bromus* (60 %) community indicate greater recruitment from the seed bank (and potential feedback) in the *Schizachyrium* community. As discussed above, opportunities for recruitment into the vegetation may be more limited in the *Bromus* community, thereby reducing the similarity between above and belowground components.

Seed banks also provide a memory of historical species composition (Rabinowitz 1981). Dominance of the *Bromus* seed bank by *Potentilla argentea*, *P. recta*, *Arenaria serpyllifolia*, and *Sporobolus cryptandrus*, all species associated with disturbed areas (or establish in areas with bare ground) (Thompson and Grime 1979, Endress et al. 2007, Leicht-Young et al. 2009, Nordbakken et al. 2010), may indicate their greater importance in the *Bromus* community historically. In contrast, in the *Schizachyrium* seed bank, three of these four species ranked only moderate in importance, indicating lower historical input. *Sporobolus cryptandrus*, high in importance in the seed banks of both communities, has abundant seed banks, even when not present at high levels in the vegetation (Abrams 1988, Fahnestock et al. 2003). These contrasts between the two communities support greater levels of historical disturbance in the *Bromus* than *Schizachyrium* community, similar to another study that found differences in the seed bank based on different historical disturbance regimes (Korb et al. 2005).

Seed Bank: Plant Traits

Contrasts in the plant traits of the seed banks of the two communities show differences in their regeneration potential. Species' presence in a seed bank indicates potential for establishment in the event of a future disturbance (Chesson and Warner 1981), although vegetation establishment after disturbance is determined by many factors. Overall, in both communities, more than half of the vegetation had a dormant component for regeneration, similar to other seed bank studies in grasslands (Hopfensperger 2007). Greater species richness and density of non-native species in the *Bromus* community's seed bank indicates its high potential as a source of non-native, but not native, species, similar to other degraded systems (Bekker et al. 1997). In contrast, the seed bank of the *Schizachyrium* community serves as a repository for more native species present in the vegetation. Whereas high importance values and species richness per plot of biennial and annual species in the *Schizachyrium* community coincides with other studies (Willms and Quinton 1995, Tracy and

Sanderson 2000), greater importance of perennial species in the *Bromus* community arises from greater seed densities of non-native perennial species.

Species composition and abundance: Similarity *within* and *between* communities

Bray-Curtis indices for the vegetation showed greater similarity within than between communities indicating that factors unifying species composition and abundance may be present within each community, including identity of the dominant grass (Grime 1998) or each community's unique history of disturbance (Grime 2006). The flip-side of factors that unify each community is that between-community similarity is lower. However, overlap in species composition between the two communities, as indicated by ANOSIM results, is a reminder that both communities are derived from the same species pool. Indeed, changes to species composition take time, as new species are added to a community only after they overcome dispersal limitation (Coffin et al. 1996) and are subjected to different ecological filters in each community (Ricklefs 1987). Greater within-community similarity of the *Bromus* community's seed bank reflected the presence of several non-native perennial species at high abundance and frequency, in contrast to the *Schizachyrium* seed bank. As discussed above, these non-native species may reflect a unique disturbance history of the *Bromus* community.

Community dynamics over time

Comparisons over time, especially the more prevalent differences between communities, highlight patterns of community dynamics within each community. Percent cover of the dominant grass *Schizachyrium* was more constant compared to the greater annual variation of *Bromus*. This pattern could be attributed to lower tolerance of drought in C3 than C4 grasses (Wilson 2007). At the site level, relative constancy over time of the five most important non-dominant species in the *Schizachyrium* community contrasted with the replacement over time of the five top-ranked non-dominant species in the *Bromus* community. These differences may

reflect the presence of open niches, and thus greater instability of the *Bromus* community and/or greater resistance to change in the *Schizachyrium* community (Sankaran and McNaughton 1999), although the authors acknowledge the complex nature of stability (McCann 2000, Hooper et al. 2005).

Perhaps the most striking difference between the two communities over time is the greater species loss from the *Bromus* community at both the site and plot level. For species to be maintained, they must be long-lived or successfully recruit into the existing vegetation. Species richness at the outset of this study may have been the result of unique aspects of site history, but declining species richness indicates the potential for competitive exclusion by *Bromus* over time. Exclusion of establishment of biennial and annual species from the seed bank was discussed above. Further evidence includes three perennial species, *Potentilla argentea*, *P. recta*, and *S. cryptandrus*, which were dominant in the *Bromus* seed bank, but decreased in abundance or were eliminated over time from the *Bromus* vegetation. In contrast, in the *Schizachyrium* vegetation, *P. recta* and *S. cryptandrus* maintained similar levels of importance over time. Although the non-dominant species discussed here are non-native or ruderal species, their competitive exclusion from the *Bromus*, but not *Schizachyrium*, community might foreshadow low recruitment for desirable species as well.

Bray-Curtis indices showed increased similarity in the final year of the study in the *Bromus* community. It is difficult to detect biotic homogenization with the current design and short-term nature of this study. However, the increased similarity in the *Bromus* community, i.e., increased clustering of *Bromus* within *Schizachyrium* plots over time on the NMDS diagrams, and the concurrent loss of species over time, parallels the conditions associated with biotic homogenization: 1) dominance by a single invasive species and 2) native species are lost concurrent with this invasion (Olden et al. 2004). Although many studies of homogenization have shown increased similarity as non-native species increase their range (McKinney and Lockwood 1999), the results of this local study show potential homogenization over time, in the

presence of a non-native, invasive species. In contrast to the *Bromus* community, the *Schizachyrium* community showed decreasing similarity among plots over time. The source of this pattern was not apparent.

The two communities shared common responses over time of % cover, frequency, and evenness of non-dominant species. These measures fluctuated in parallel between the two communities and suggest a common response to environmental variables, including recent release from grazing. Release from heavy grazing or other disturbances can produce significant changes, as vegetation responds to changes in resources over time (Milchunas and Lauenroth 1995, Wilsey and Polley 2003).

Comparisons between 2009 and Gleason's 1908 vegetation survey

Greater species richness, greater frequency of species occurrence, and differing species composition in 2009 than 1908, may have occurred through the general process of succession. Sand prairies accrue species as sandy soils are stabilized (Inouye et al. 1987, McClain and Ebinger 2008). In addition, *Leptoloma cognatum*, dominant in 1908, is a 'mid-successional' grass, whereas *Schizachyrium*, dominant in 2009, is a 'late-successional' species (Collins and Adams 1983). However, perennial forb species, common in prairie remnants (Bowles et al. 2003, Taft et al. 2006), were lower in rank in 2009 than 1908, which parallels species loss in grasslands grazed for long periods of time (Leach et al. 1999, Fuhlendorf and Engle 2001). These same perennial forb species were also largely absent from the *Schizachyrium* community sampled in the main part of this study.

Use of a single historical survey as a reference point must take into consideration the spatial heterogeneity of the habitat sampled. Gleason (1910) indicated that the *Leptoloma* community sampled was not the most abundant community type. Rather, he provided detailed descriptive accounts of the dominant community type on site, a community with four approximately equal dominant grasses (including both *Leptoloma* and *Schizachyrium*). Thus,

while historical baseline surveys are useful in monitoring the health and change of native habitats (Rooney et al. 2004), any single quantitative survey must take into account other sources of historical information, including descriptive accounts.

Conclusions

Overall, these results support the importance of both dominant species identity and site history of disturbance in determination of community structure and species composition in this sand prairie grassland. Additionally, studying community change over time, albeit only 5 years, helped to identify patterns that would not be observable in a single year or shorter time frame. Results from the vegetation and seed bank required a revision of our assumption of equal site-wide disturbance, made at the outset of the study, to include potential localized areas of higher disturbance that corresponded with areas of *Bromus* invasion. Studies investigating the traits of *Bromus inermis* as an invader have started to accumulate, but this study adds to the knowledge of its potential impacts on native prairie grassland community structure and composition (but see Williams and Crone 2006, Dilleuth et al. 2009). Characteristics of the *Bromus* community, including lower species richness and diversity, greater species loss and turnover of common non-dominant species, and a pattern towards biotic homogenization over time, suggest that this community is moving further away from the site's historical origin as native grassland. In the *Bromus* community, suppression of non-dominant species regeneration indicates changes to ecological processes and, in combination with a smaller native species pool, indicates potential barriers that will restrict recovery of this community in the future. In contrast, the *Schizachyrium* community supported greater diversity, was more stable through time, and potentially more resistant to change than the *Bromus* community. However, lower frequency of perennial forb species in comparison to a 1908 survey indicate that even though historical disturbance unique to this community may have been lower than the *Bromus* community, the *Schizachyrium* community may also endure legacies from the 80+ years this site was grazed. The contrasting

results between these communities provide further support that identity of species, especially of a dominant, is important to community diversity. Finally, this study indicates that both invasion of natural habitat by a non-native dominant species and site history of disturbance have cascading effects on non-dominant species. Continuing studies to identify the impacts of non-native, invasive species on native communities will contribute to identifying means to potentially ameliorate their effects.

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CHAPTER 3: FACILITATING GRASSLAND DIVERSITY THROUGH DISTURBANCE: EFFECTS OF DOMINANT SPECIES IDENTITY, DOMINANT REDUCTION, AND MICROSITE CREATION ON COMMUNITY STRUCTURE

ABSTRACT

Grassland diversity can be reduced by native and non-native dominants, through heightened competition for resources and low colonization by non-dominant species. Extent of dominant species reduction via disturbance may differ based on traits of dominant species. Non-dominant species may respond to this competitive release, but also may require additional types of disturbances that reduce litter and increase bare soil to increase their colonization. In a study in northwestern Illinois, we compared the response of dominant species and non-dominant community structure to disturbances applied over five years in two sand prairie grasslands: communities dominated by either *Schizachyrium scoparium*, a native warm-season grass, or *Bromus inermis*, a non-native cool-season grass. Separate disturbances were targeted to reduce dominant grass % cover and biomass (spring mowing) and to create microsites for non-dominant species colonization at different frequencies (soil disturbance for a single or five years). Mowing reduced % cover and biomass of both dominant species, but reduced *Bromus* more than *Schizachyrium* after two years of mowing, and displaced *Bromus* as the dominant but not *Schizachyrium*. Non-dominant species richness increased less by reduction of the dominant alone and more when combined with the greatest frequency of soil disturbance that brought colonization from the extant vegetation and seed bank. However, microsites were ephemeral, with bare ground being lost more quickly from the *Bromus* than *Schizachyrium* community. Percent cover of non-dominant species increased with mowing in the *Bromus*, but not *Schizachyrium* community, presumably because of the greater negative effect of spring disturbance during the active growth period of *Bromus*. Analysis of non-

dominant community structure based on plant traits (location of origin, life history, functional group, and seasonality) paralleled overall community measures of diversity, although soil disturbance particularly favored annual and biennial species. Percent cover of existing native perennial species showed the strongest response to reduction of *Bromus*. The extent of dominant species reduction depended on species identity and amount of tissue loss, which in turn determined whether or not the non-dominant community benefitted from reduced competition. In contrast, newly disturbed microsites fostered colonization in both communities, which was less dependent on dominant identity. The divergent responses of the two dominant grasses indicate the importance of species identity when pairing management techniques and dominant reduction. Our results also show that annual spring mowing is a tool managers may use for control of *Bromus*. In addition, the independent response of non-dominant community structure to disturbances that reduce competition from those that stimulate new colonization indicates the importance multifaceted disturbances in restoration and maintenance of non-dominant species diversity in grasslands.

Key words: Bromus inermis, disturbance, grassland diversity, phenology, plant traits, Schizachyrium scoparium, seed bank, species identity

INTRODUCTION

Diversity in grasslands is promoted by mechanisms that mediate coexistence of dominant and non-dominant species. Disturbances (sensu Sousa 1984) may alter competitive balance through reduction of the dominant and subsequent competitive release of non-dominant species (Collins et al. 1998). However, species identity can affect how the dominant species responds to disturbance (Jackson et al. 2010) and interacts with non-dominant species (Hillebrand et al. 2008). Disturbances also can change resource availability, increasing opportunities for recruitment and colonization by non-dominant species (Martin and Wilsey 2006). Land managers and restoration ecologists need an increased understanding of

disturbances (Wilson and Gerry 1995, Doll et al. 2011), including their unpredictable outcomes (Hobbs and Huenneke 1992, Davies et al. 2009, Firn et al. 2010). If an ultimate goal of grassland management is increased native diversity, disturbance mode and frequency must mimic our growing understanding of the maintenance of grassland diversity via reduced competition from the dominant and creation of disturbed microsites for the colonization of non-dominant species (Platt 1975, Tilman 1994).

Disturbance, such as large ungulate herbivory, can lower dominant grass abundance when stored resources of grazed grasses are decreased (Donkor et al. 2002, Wilson and Partel 2003) and/or selectively reduced in comparison to neighbors (Towne et al. 2005). Loss of photosynthetic tissue at a vulnerable life stage (e.g., phenologically timed disturbances) may maximize the negative effect of disturbance (Hester et al. 2004, Knight 2007, MacDougall and Turkington 2007). For example, a spring disturbance should lower the abundance of a cool-season dominant grass, as stored resources have been transferred to aboveground growth that can be lost with spring tissue removal (Wilson and Clark 2001). Repeated tissue loss may compound the negative effects on dominant grass abundance (Vinton and Hartnett 1992). However, reduced abundance may be short-lived if tissue loss is minimal and/or species compensate for the loss. Compensation and/or tolerance might be expected from species that have evolved with grazing (Milchunas et al. 1988, Olf and Ritchie 1998), including the native grass *Schizachyrium scoparium* (Brown and Stuth 1993, Anderson and Briske 1995), or have been used as forage grasses, including non-native *Bromus inermis* (Otfinowski 2007), the two dominant grasses in this study.

Dominant species influence communities through facilitative and/or competitive interactions, with the direction of the interaction influenced by relative abundance and species identity (Gilbert et al. 2009, Gomez 2009). Specific traits, such as phenology, rooting depth (Fargione and Tilman 2005), and production and quality of litter (Vinton and Goergen 2006) may determine whether or not a dominant species stabilizes, facilitates, or impedes change to

community structure. Increasing attention to species identity has led to greater understanding of how dominant species differ in their invasibility (Crawley et al. 1999, Emery and Gross 2006, Wilsey 2010) and influence community structure (Meiners et al. 2004, McCain 2010, McNicoll and Augspurger: Ch. 1). However, there is a need for further investigation of how species identity influences dominant species response to disturbance (D'Antonio et al. 2001, Gendron and Wilson 2007). Such knowledge would be beneficial for land managers who target dominant species for reduction, including non-native invasive species, so they can reduce unforeseen results when traits interact with specific disturbance regimes (Suding et al. 2004).

Non-dominant species also may respond directly to disturbances. Reduction of the dominant can reduce competition for light (Foster et al. 2002, McCain et al. 2010) and below-ground resources (Veen et al. 2008), resulting in increased establishment, species richness, growth rates, and abundance of non-dominant species. However, disturbances targeted at the dominant species can negatively impact non-dominant species through damage or selectivity during grazing (Damhoureyeh and Hartnett 1997, Hickman and Hartnett 2002), non-target effects of herbicides (Wilson and Partel 2003, Flory and Clay 2009), and increased mortality with annual fire regimes (Briggs and Knapp 2001). Indirect negative effects on non-dominant species include changes to litter accumulation after mowing or loss of complementary effects, e.g., moisture retention, provided by dominant species (Smith and Knapp 2004, Gilbert et al. 2009).

Non-dominant species may require modes of disturbance directed at their establishment and colonization (Jutila and Grace 2002, Clark et al. 2007), independent of disturbances that target reduction of dominant species. In grasslands, establishment of non-dominant species is commonly limited to gaps or other suitable regeneration sites (Platt 1975, Grubb 1977, Gibson et al. 1989). Disturbances that concurrently remove litter, expose bare ground, and disturb the soil surface create regeneration microsites. Microsites become limited in space and time if they are taken over quickly by new species colonization, re-growth of the dominant, or litter

accumulation (Denslow 1980, Rapp and Rabinowitz 1985, Goldberg and Gross 1988, Renne and Tracy 2007). Thus, frequent disturbances may be necessary to provide a continual supply of microsites. Disturbance may activate propagules dormant in the soil seed bank (Pakeman and Small 2005). Grassland seed banks contain a subset of the community that may be inhibited in the absence of regular disturbance (Rabinowitz 1981, Johnson and Anderson 1986). Thus, the non-dominant community may require modes of disturbance that reduce the dominant and concurrently stimulate the non-dominant community. Multiple modes of disturbances were likely common in the presence of 'natural' disturbances by large grazers (Gibson 1989, Knapp et al. 1999), and may be simulated to achieve similar results.

Traits of non-dominant species, including location of origin, life history, functional groups, and seasonality, may interact with disturbance (Diaz et al. 2007). These traits are important in terms of specific restoration and management objectives and are addressed sequentially below. Knowing whether native and non-native species with similar traits respond the same to disturbance (Daehler 2003) is necessary for managing for native diversity. Mimicking historical disturbances may be necessary for native species establishment. However, disturbance must be used with caution, because it may cause non-native invasive species to increase in abundance (Hobbs and Huenneke 1992, DiVittorio et al. 2007, Eschtruth and Battles 2009), or, alternatively, the control of one invasive species can be followed by invasion by another non-native (Seastedt et al. 2008, Firn et al. 2010). Life history traits of species may determine whether species are limited more by neighbors than by opportunities for recruitment. Thus, competitive release may directly benefit extant perennial species (Warner and Chesson 1985); whereas disturbances that increase microsites may favor species with high propagule availability, including annual, biennial, and seed bank species. Responses to disturbance may differ among specific perennial functional guilds, e.g., woody and perennial forb species loss increases with repeated fires (Collins et al. 1998, Briggs and Knapp 2001, Collins and Calabrese 2012). An additional trait that may influence whether disturbance is beneficial or

detrimental is phenology, especially for disturbance that is seasonally timed. Disturbance effects on early or late season species depends on whether species are directly impacted by disturbance (Reed et al. 2005, Simmons et al. 2007) or alternatively, benefit from competitive release from dominant species that occupy the same temporal niche.

In this study, we compared dominant grass and non-dominant species response to disturbances in two sand prairie communities dominated by either *Schizachyrium scoparium* (Michx.) Nash (little bluestem) (hereafter *Schizachyrium*), a native, warm-season (C4) caespitose grass, or *Bromus inermis* Leyss. (smooth brome) (hereafter *Bromus*), a non-native, cool-season (C3), mat-forming grass. Over five years, mowing occurred in the spring, with and without soil disturbance. Mowing targeted, but was not exclusive to, dominant species and tested for the effect of multiple years of biomass removal. Soil disturbances, applied for a single year or five consecutive years, created microsites with greater bare ground and lower litter and agitated the soil seed bank. Dominant species abundance and non-dominant community structure, including species richness, % cover, biomass, composition, and similarity, were assessed annually to detect temporal and cumulative effects of disturbance. Analysis of non-dominant species was conducted at multiple levels: whole community, by plant traits, species composition, and association with the documented seed bank to allow detection of species groups and sources responding to disturbances. A concurrent study of the soil seed bank (McNicol and Augspurger Ch. 1) allowed detection of recruitment from the seed bank into the vegetation. The study site is a native sand prairie that had been heavily grazed for decades prior to its release from grazing in 2000. Thus, the site is not pristine but contains a predominantly native non-dominant community, areas where *Schizachyrium* is the dominant, and other locations where *Bromus* has become the dominant (McNicol and Augspurger Ch. 1).

In North American grasslands, both grasses inhibit non-dominant species; *Schizachyrium* may be dominant in prairie restorations or become so with annual spring burning regimes and *Bromus* has a documented history as an invader, and an association with

decreased diversity in native grasslands (Blankenspoor and Larson 1994, Williams and Crone 2006, Dilleuth et al. 2009). As *Bromus* causes native species loss, it is a higher priority for managers to control; *Schizachyrium* would likely be targeted for reduction only in locations with an imbalance between dominant and non-dominant species. Therefore, mowing disturbance was timed specifically to reduce *Bromus* via spring mowing, when its stored reserves have been mobilized to aboveground tissue (Willson and Stubbendieck 2000). We expected less reduction of *Schizachyrium*, given that disturbance was not at its maximum time of growth. We also predicted that the reduction of both dominant grasses would provide competitive release for non-dominant species. Soil disturbances, applied at different frequencies, allowed assessment of an independent stimulus of non-dominant species that are frequently lost as grassland become degraded.

METHODS

The study was conducted from 2005-2009 at the Lost Mound Unit of the Upper Mississippi River National Wildlife Refuge (42° 13' N, 90° 20' W), a dry-mesic sand prairie in Jo Daviess County, Illinois U.S.A. Soils are classified as Sparta loamy sand, with 1 to 6 percent slopes and low organic material and nitrogen content (Soil Survey Staff NRCS-USDA 2012, Symstad 2004). Average temperatures from March – August during the study (2005-2009 (max/min °C): 23/8, 22/7, 23/10, 21/8, and 21/8) were similar to the long-term average (1971-2000 (max/min °C): 22/8). Number of days above 32.2 °C (90 °F) varied among years (38, 15, 26, 3, and 5 days in 2005–2009, respectively); the 30-year mean was 15 days. Total growing-season precipitation (2005 – 2009 in mm: 335, 681, 683, 770, and 898) was greater than the 30-year average (604 mm) in all years, except for the dry year of 2005. Weather data were collected 50 km from the research site at Mount Carroll, Illinois (Illinois State Climatologist's office).

The site was formerly (1917-2000) a U.S. Army munitions storage base. The potential for UXOs (unexploded ordinances) on site eliminated the use of fire as a mode of disturbance at the time when this study was initiated. Infrastructure constructed on-site included parallel rows (at approximately 125-m intervals) of soil-covered bunkers and access roads. Placement of survey sites between rows of infrastructure avoided areas previously disturbed by ground-moving activities. During those eight decades, the entire site was heavily grazed yearly from May to October with approximately 1,500 head of cattle. Grazing management kept vegetation at very low stature (K. Robertson, pers. comm.), but species tolerant to such grazing, including native grasses, dominated much of the 2,000 ha of sand prairie when cattle were removed in 2000. Non-native invasive species, introduced both deliberately and accidentally, were common by 2005. The current distribution of *Bromus* at the study site is likely a combination of localized seeding and subsequent spread.

Five 50-m transects were placed in each community, with all ten transects located within a 3 km radius; transects were separated by ≥ 125 m. Transect placement was aimed at maximizing variability among transects, while maintaining the dominance by either dominant grass. Three criteria were used to select placement of transects. First, a visual estimate of dominance ($\sim 50\%$) by either dominant grass was required. This visual estimate of cover was later quantified during field surveys. Second, transects were oriented to avoid the shrub, *Rhus aromatica*, and large patches of crown-vetch, *Coronilla varia*, a non-native, nitrogen-fixing invasive species. Third, transects in the *Bromus* community were placed in what appeared to be three separate invasion foci, interspersed within the larger *Schizachyrium* community. Two transects were placed in each of two *Bromus* foci, and a single transect in the third focus.

Experimental Design

In April 2005, experimental and control plots were initiated along each transect (Appendix C). At 10-m intervals along each transect, three 2 x 4-m plots were marked on

alternating sides, starting at a random distance of 1 - 3 m from the transect. An additional plot was added alongside the original plots to accommodate a new treatment (M D06) added in 2006. Plots were separated by 1-m and randomly assigned to one of five treatments: 1) an unmanipulated control (C) (15 replicates) or one of four disturbance regimes: 2) mow (M) (15 replicates), 3) mow and a single-year soil disturbance applied in 2005 (M D05) (15 replicates), 4) mow and a single-year soil disturbance applied in 2006 (M D06) (15 replicates), 5) and mow and five consecutive years of soil disturbance (M DAll) (10 replicates). M D06 was added in 2006 to test for effect of year on soil disturbance/vegetation removal following drought in 2005.

All disturbance plots were mowed annually, for five years (2005-09, four years for M D06) with a string-trimmer weed whip to approximately 7 cm and vegetation was left in place. Mowing took place just prior to inflorescence emergence of *Bromus* and removed much of the live aboveground biomass. *Schizachyrium* was beginning to produce leaves at this time; therefore mowing removed standing dead vegetation and the tops of green leaves. Reduction of non-dominant species by mowing was limited largely to the few early-season species that exceeded 7 cm in height at the time of mowing.

Soil disturbance was applied to expose portions of the seed bank and create microsites. Soil disturbance plots were raked, removing cut vegetation and disturbing the soil to a maximum depth of 5 cm, leaving a mosaic of intact vegetation and disturbed soil. Disturbances applied in this study are somewhat analogous to large herbivore grazing (MacDougall and Turkington 2007) that removes living plant biomass, litter, and creates surficial disturbance. Limitations apply to this comparison, including no nutrient input from herbivore excretions or selectivity for palatable non-dominant species (Hobbs 1996, Hickman and Hartnett 2002). These disturbances are a feasible management tool, as mowing allows for targeting the dominant species based on height at the time of application, and raking gave an independent stimulation to non-dominant species.

Vegetation Survey and Sampling

From 2005-2009, in both June and late July/early August, percent cover and species richness were obtained from a permanent 1 x 0.5-m sampling plot randomly placed along the centerline of each 2 x 4-m treatment plot. A Daubenmire (1959) cover class was assigned to all species, dead vegetation, and bare ground in each plot. Analysis uses the higher % cover value (i.e., June or August value) when present in both times. Total % cover exceeded 100 % in some plots with much overlapping canopy cover among species.

Response of species with contrasting traits to disturbance and dominant grass identity was evaluated based on species' 1) location of origin (native, non-native), 2) life history (perennial; biennial + annual), 3) functional guild of perennial species (grass, forb, sedge, legume), and 4) seasonality (early, late). Trait classification was based on Gleason and Cronquist (1991), and season of growth was determined from published flowering dates from a region 125 miles east of the study site (Swink and Wilhelm 1994). Species with a starting flowering date before June 15 were designated as early-season and after June 15 as late-season.

Aboveground biomass was collected in July 2009 from a second 1 x 0.5-m sampling plot in the treatment plot, placed randomly, but > 60 cm from the permanent sampling plot. Biomass was clipped to ground level and separated into live dominant grass, graminoid (non-dominant grasses and sedges), forb, and perennial legume species. Biomass was dried in a forced-air oven at (70 °C) for 2 days and weighed. Plots with a high biomass of the fleshy cactus *Opuntia macrorhiza* required an additional day of drying.

The seed bank of each community was sampled in 2006. Soil cores were collected adjacent to treatment plots and assessed based on seedling emergence in a greenhouse (see McNicoll and Augspurger (Ch. 1) for detailed methods and results).

Data Analysis

Temporal Change

Change from 2005-2009 was assessed to detect cumulative effects of disturbance treatments on species richness, % cover of the dominant grass, and % cover of non-dominant species. Within each community, repeated measures ANOVAs (R-ANOVA) used proc mixed (SAS 9.1) with transects (= experimental unit) as random effects and treatment, year, and treatment x year as fixed effects. Covariance structure for analyses was selected based on Akaike's Information Criteria, Corrected (AICC) (Littell et al. 2006). Data for 'M D06' did not exist for 2005, and so values were identified as missing values. Post-hoc tests (ANOVA) in each year were used to discern differences among treatments.

Initial Conditions

To detect pre-existing differences among plots, initial (2005) species richness and % cover of non-dominant species were compared among all treatments using separate ANOVAs for each of the four plant traits outlined above. No plant trait differed in species richness among treatments, and only % cover of non-native and non-dominant perennial grass species differed among treatments. Initial (2005) % cover values for these two plant traits were included as a covariate in the 2009 analysis. For % cover of non-native species, use of the covariate did not affect the significance of main effects. For % cover of non-dominant grass species, use of the covariate changed the results, making treatment significant. Initial conditions were not used as covariates for all other traits.

Analysis of final year of study: 2009

For general comparisons at the community level, descriptive summaries included species richness (2005, 2009), relative importance values for each species, and frequency of occurrence of species in the vegetation and seed bank. At the plot level, % cover and biomass

of dominant grasses, non-dominant species, and individual non-dominant species based on plant traits were analyzed in separate models (% cover, biomass, species richness, Shannon-Wiener diversity (H') and evenness ($E_{1/D}$ of Smith and Wilson 1996)). Separate ANOVA models for each variable were analyzed in proc mixed (SAS 9.1) with transects (= experimental unit) as random effects and treatment, community, and treatment x community as fixed effects. Covariance structure for analyses was selected based on Akaike's Information Criteria, Corrected (AICC) (Littell et al. 2006). Post-hoc tests, using the 'estimate' statement in proc mixed for paired comparisons, were run if effects of treatment or treatment x community interaction were significant ($p < 0.05$). Evenness and all biomass values were square-root transformed to reduce skewness of data; untransformed values are presented in the text. Perennial legumes are not represented in plant traits because their low frequency in both communities prohibited balanced analysis. Initial analysis for biomass of forb species was followed by a second analysis to reduce the large influence of presence of a native cactus, *Opuntia macrorhiza* that is patchily distributed. Presence of a single pad of *O. macrorhiza* greatly skewed biomass values. A secondary analysis was conducted on a sub-sample of plots to represent the results of non-cactus forbs.

Comparisons of similarity using species presence/absence among treatments and between the seed bank and vegetation were made first with Jaccard's index (Mueller-Dombois and Ellenberg 1974). Second, similarity was assessed using a Bray-Curtis index, using species composition and abundance. Pair-wise similarity of plots was assessed with analysis of similarity (ANOSIM) to compare treatments and communities and create a non-metric multi-dimensional scaling (NMDS) diagram using PRIMER v6 (Clarke and Gorley 2006). Detection of recruitment from the seed bank used count data (frequency) of individual species occurring in the vegetation that were documented as 'seed bank' species (or not) based on seed bank sampling conducted in both communities in 2006 (McNicoll and Augspurger Ch. 1). Count data were compared using Chi-square analysis.

RESULTS

Response of Dominant Grass

Mean % cover of *Schizachyrium*, the native grass, was reduced ~ 30 % by the initial disturbance, but despite subsequent disturbances did not decline further over time (R-ANOVA, Treatment: $F_{4, 303} = 6.80$, $p < 0.01$, Year: $F_{4, 303} = 1.32$, NS, and Treatment x Year: $F_{15, 303} = 0.79$, NS) (Fig. 2.1 A). In contrast, % cover of *Bromus* was reduced by disturbance, which accumulated over time to 60 % reduction (Treatment: $F_{4, 307} = 34.95$, $p < 0.01$, Year: $F_{4, 307} = 49.66$, $p < 0.01$, and Treatment x Year: $F_{15, 307} = 1.7$, $p = 0.05$) (Fig. 2.1 B). After five years, *Schizachyrium* maintained its dominance over time in all disturbance and control plots (Appendix D.1). *Bromus* was displaced as the most abundant species in all disturbance treatments compared to its continued dominance in control plots (Appendix D.2).

By the fifth year of the study (2009), the greater reduction of *Bromus* than *Schizachyrium* was reflected as significant interactions between disturbance and community for both mean % cover (Fig. 2.2 A) and mean biomass (Fig. 2.2 B) (Table 2.1). However, % cover of both dominant species was lower in 2009 control plots than any other year, which obscured initial reduced % cover of *Schizachyrium* by mowing (2005-2008) and diminished the difference among treatment and control plots in the *Bromus* community. Reduction in % cover of both dominant grasses in disturbance plots was a response to annual mowing in all disturbance types, not to frequency or particular year of soil disturbance (Fig. 2.2).

Response of Non-Dominant Species

Based on comparison of species richness at the community level in 2005 and 2009, both communities lost species from undisturbed vegetation controls, while the number of species was maintained or increased in disturbance plots (Table 2.2). By 2009, total number of species in disturbance treatments exceeded controls by 7 - 17 species. In 2009, the total number of

species was greater by 6 to 11 species in the *Schizachyrium* than *Bromus* community when comparing the same disturbance treatments (except mow only).

Differences in mean species richness between disturbance treatments and controls appeared the year following disturbance in both communities (Fig. 2.1 C-D). In the *Schizachyrium* community, repeated soil disturbance was necessary to maintain the number of species gained (R-ANOVA, Treatment: $F_{4, 303} = 14.80$, $p < 0.01$, Year: $F_{4, 303} = 7.53$, $p < 0.01$, and Treatment x Year: $F_{15, 303} = 1.57$, NS). In the *Bromus* community, subsequent years of mowing generally maintained species richness, in direct contrast to loss of species over time from *Bromus* control plots (R-ANOVA, Treatment: $F_{4, 307} = 11.18$, $p < 0.01$, Year: $F_{4, 307} = 1.07$, NS, and Treatment x Year: $F_{15, 307} = 1.56$, NS).

After five years, in both communities mean species richness was significantly increased in disturbance plots and differed among disturbance treatments (generally: mow + repeated soil disturbance > mow + single-year soil disturbance \geq mow only > control) (Fig. 2.3 A, Table 2.1). In plots receiving repeated soil disturbance, mean species richness per plot doubled relative to control plots in *Schizachyrium* to 16 species and nearly doubled in *Bromus* to 14 species; compared to only ~ three species per plot gain with mow only or a single-year soil disturbance with repeated mowing.

Mean % cover of non-dominant species in the *Schizachyrium* community varied among all treatments (control and disturbance) over time (R-ANOVA, Treatment: $F_{4, 303} = 2.94$, $p < 0.05$, Year: $F_{4, 303} = 26.03$, $p < 0.01$, and Treatment x Year: $F_{15, 303} = 0.51$, NS); although post-hoc tests in each year showed no significant difference among treatments (ANOVAs, 2005: $F_{3, 47} = 0.37$, 2006: $F_{4, 60} = 0.69$, 2007: $F_{4, 60} = 1.53$, 2008: $F_{4, 60} = 1.76$, 2009: $F_{4, 60} = 0.98$). In the *Bromus* community, mean % cover of non-dominant species differed significantly among disturbance and control plots and over time (R-ANOVA, Treatment: $F_{4, 307} = 10.86$, $p < 0.01$, Year: $F_{4, 307} = 9.61$, $p < 0.01$, and Treatment x Year: $F_{15, 307} = 1.56$, NS); post-hoc tests in each year showed significantly greater % cover of non-dominant species in disturbance than control

plots four years (2008) after initiating disturbances (ANOVAs, 2005: $F_{3,12} = 0.45$, NS, 2006: $F_{4,61} = 2.37$, NS, 2007: $F_{4,61} = 2.01$, NS, 2008: $F_{4,61} = 6.55$, $p < 0.01$, 2009: $F_{4,61} = 10.23$, $p < 0.01$) one year after *Bromus* was significantly reduced (2007).

By 2009, a significant interaction between disturbance and community reflected the greater mean % cover of non-dominant species in disturbance than control plots (~ 35 %) in the *Bromus* and no effect of disturbance in the *Schizachyrium* community (Fig. 2.3 B, Table 2.1). In the *Bromus* community, % cover of non-dominant species was similar among the four experimental disturbances, regardless of frequency or particular year of soil disturbance.

Mean species diversity (H') increased as frequency of soil disturbance increased and was greater overall in the *Schizachyrium* than *Bromus* community (Fig. 2.3 C, Table 2.1), largely reflecting the pattern of species richness. Mean evenness did not differ among treatments, but was greater in the *Schizachyrium* than *Bromus* community (Fig. 2.3 D, Table 2.1).

Mean % cover of dead vegetation was significantly reduced by disturbance and lower in the *Bromus* than *Schizachyrium* community (Fig. 2.3 E, Table 2.1). In both communities, mean % cover of bare ground was significantly greater in repeated soil disturbance than other modes of disturbance or control plots (Fig. 2.3 F, Table 2.1). Both dead vegetation and bare ground were closely related to the raking treatment: For a single year soil disturbance in the initial year of treatment (e.g., MD05), % cover was similar between communities for dead vegetation (~ 30 % cover) (2005: $F_{1,8} = 1.67$, NS) and bare ground (~ 20 % cover) (2005: $F_{1,8} = 1.26$, NS). In the year following raking (e.g., MD05), % cover of dead vegetation increased to similar levels in both communities (~ 45 % cover) (2005: $F_{1,8} = 0.35$, NS); but % cover of bare ground was greater in *Schizachyrium* than *Bromus* community (2006: $F_{1,28} = 5.21$, $p = 0.03$), as bare ground remained elevated (~ 5 %) in the *Schizachyrium* community for at least two years, but reverted to similar % cover as 'mow only' in the *Bromus* community.

Community structure based on plant traits: 2009

Most plant traits showed greater mean species richness with disturbance, which was generally greater with increased frequency of soil disturbance (Fig 2.4 – panels on left). In both communities, native, biennial + annual, and early season species had significantly greater species richness in disturbance compared to controls (Table 2.3). Species richness of non-native, perennial, and late season species were also significantly greater in disturbance than control treatments, but accounted for smaller gains in numbers of species in both communities. Species richness of perennial grass and sedge species did not differ among treatments in either community. Biennial + annual species richness in disturbance plots was generally 2 X greater in the *Schizachyrium* than *Bromus* community (i.e., significant interaction effect of treatment and community, Table 2.3), despite similar values in their control plots. Of the 22 annual and biennial species present in the *Schizachyrium* community, 20 were either absent from control plots and/or showed a positive relationship of frequency of occurrence with disturbance (Appendix D.1). A similar pattern was evident among the 16 annual and biennial species in the *Bromus* community (Appendix D.2).

In the *Bromus* community, eight of nine plant traits had significantly greater mean % cover with disturbance, but % cover varied inconsistently among modes of disturbance for each trait. In contrast, in the *Schizachyrium* community % cover of plant traits generally did not differ among treatments (Fig 2.4 – panels on right, Table 2.3). In the *Bromus* community, % cover of native, perennial (grasses and forbs) and early season species were significantly greater in the *Bromus* disturbance treatments than control plots and were greater than all *Schizachyrium* plots (main effects of treatment and community, or significant interaction between treatment and community, Table 2.3), by generally ~ 20 to 40 percent. For non-native species, response to disturbance contrasted between the two communities, with % cover significantly lower (- 10 %) in *Schizachyrium* and greater (+10 %) in *Bromus* compared to their respective control plots. Non-native species response to disturbance could not be attributed to a single species in either

community, but was related to reduction of *Poa pratensis*, a cool-season perennial grass, in disturbance treatments in the *Schizachyrium* community and increase of annual *Medicago lupulina* in disturbance treatments in the *Bromus* community. Sedge and late season species showed no effect of disturbance treatments, but % cover of late season species was significantly greater in the *Bromus* than *Schizachyrium* community.

Biomass: 2009

Mean biomass of non-dominant graminoids did not differ among treatments, but was significantly greater in the *Bromus* than *Schizachyrium* community (Fig. 2.5 A, Table 2.3). Mean biomass of forbs did not differ among treatments or between communities (Fig. 2.5 B, Table 2.3), but means and variances were influenced considerably by the presence of *Opuntia macrorhiza*. A sub-sample of low-cactus plots (10 of 15 plots) showed no difference among treatments, but significantly greater forb biomass in the *Bromus* than *Schizachyrium* community (Fig. 2.5 C, Table 2.3).

Species Composition and Similarity

Jaccard's similarity of species composition, which does not take abundance into account, showed that within each community mow-only plots were most similar to control plots (Table 2.4). ANOSIM analysis showed that composition and abundance of non-dominant species did not differ among modes of disturbance (Global R-value = 0.028, $p = 0.68$), but was significantly divergent between communities (Global R-value = 0.415, $p < 0.01$). Thus, after five years of mowing and different frequencies of soil disturbances, species composition and abundance could not be associated with specific treatment or control plots within or between communities. The NMDS diagram represents these results, as treatments are generally evenly scattered across, but communities are grouped on opposite sides of, the diagram (Fig. 2.4). Greater similarity of all plots within the *Bromus* community is indicated by the tighter spatial

clustering of the *Bromus* (Bray-Curtis similarity = 39) compared to the *Schizachyrium* (30) community.

Examination of several species provides insight into the NMDS diagram. In both communities and across all treatments, two species with the greatest abundance and frequency were the native perennial forb, *Ambrosia psilostachya* and *Poa pratensis* (Appendix D). However, their relative abundance and frequency were greater in the *Bromus* than *Schizachyrium* community, increasing Bray-Curtis similarity among plots within the *Bromus* community. Among the 49 species shared by the two communities, many of these species differed greatly in their relative importance between communities. For example, *Koeleria macrantha*, a native, cool-season perennial grass, was frequent and abundant in the *Schizachyrium* community, but less so in the *Bromus* community; whereas *Sporobolus clandestinus*, a native, warm-season grass was more common in the *Bromus* than *Schizachyrium* community, contributing to dissimilarity between communities. The *Schizachyrium* community included 21 unique species, most of which occurred in one or more of the disturbance modes (Appendix D.1). The 12 species unique to the *Bromus* community were also found primarily in disturbance plots (Appendix D.2).

Comparisons of the vegetation (2009) and seed bank (2006)

In both communities, species composition of the seed bank and vegetation were more similar in disturbance than control treatments (Table 2.4), reflecting the greater number of seed bank species present in the vegetation of plots with disturbance, and in particular soil disturbance (Table 2.5). There was a greater overall frequency of all species with increased disturbance, but proportionally, frequency of seed bank vs. non-seed bank species in the vegetation did not differ among treatments in either community (CHI-SQ, *Schizachyrium*: $X_4 = 6.26$, NS, *Bromus*: $X_4 = 2.42$, NS) (Table 2.5). Patterns of frequency were similar in both communities, despite a seed bank density 2.5 X greater in *Bromus* than *Schizachyrium* (Ch. 1).

Several seed bank species that recruited into the vegetation of disturbance plots were absent or rare in vegetation of control plots. In the *Schizachyrium* community, these species consisted primarily of native annuals and biennials (e.g., *Triodanis perfoliata*, *Artemisia campestris*, and *Oenothera rhombipetala*) and less commonly perennial species (relative frequency in Appendix D). In the *Bromus* community, recruitment from the seed bank in disturbance treatments was evident among all life histories (e.g., non-native annual, *Medicago lupulina*, native biennial, *Erigeron strigosus*, and native and non-native perennial forbs, *Verbena stricta* and *Potentilla recta*). Nevertheless, species that dominated the seed bank did not dominate vegetation in disturbance or control plots in either community; and not all species with a seed bank were stimulated by disturbance, including two species abundant in the seed bank, but absent from the vegetation (annuals *Androsace occidentalis* and *Mollugo verticillata*).

DISCUSSION

Facilitation of non-dominant species diversity in this study depended on identity of the dominant grass, which influenced its reduction by mowing and potential for competitive release of non-dominant species. Diversity of non-dominant species was also facilitated by creation of microsites via soil disturbance that increased non-dominant species colonization. High frequency, i.e., repeated applications, of both disturbances was necessary, especially to sustain the negative effect on *Bromus* abundance and to maintain the continued presence of suitable microsites.

Response of Dominant Grass

The two dominant grasses differed in their response to a spring disturbance, because of differences in phenology. Mowing affected cool-season *Bromus* near its peak of photosynthetic activity (Willson and Stubbendieck 2000), while warm-season *Schizachyrium* was only beginning its growing season. The relatively small reduction and lack of cumulative effect of

mowing on *Schizachyrium* may have been a result of small overall tissue loss. In addition, *Schizachyrium* had warm season growth to recuperate lost tissue and stored resources (NGuessan and Hartnett 2011). Other studies also have found little reduction of *Schizachyrium*, even with multiple mowings during a single season (Williams et al. 2007) or cattle grazing (Towne et al. 2005). Further evidence is suggested by the resilience of *Schizachyrium* at the study site, despite ~ 80 years of cattle grazing. In contrast, mowing removed a large proportion of *Bromus* tissue, presumably reducing its energy reserves. This depletion at a key growth period has been shown to reduce the abundance of *Bromus* (Biligetu and Coulman 2010) and other non-native cool season grasses (Wilson and Clark 2001). The necessity of multiple years of mowing to significantly reduce *Bromus* indicates its resilience to tissue loss. The use of *Bromus* as a forage grass must have been based in part on its ability to withstand grazing (Otfinowski 2007). In contrast to mowing, neither dominant grass was affected negatively by soil disturbance and associated removal of dead vegetation, indicating a stronger effect of living biomass loss than nutrient loss by removal of decaying vegetation.

This study provides little support for annual spring mowing to substantially reduce *Schizachyrium* from grasslands where it inhibits growth and establishment of native diversity (McCain et al. 2010). Mowing times that correspond with grazing by native ungulate herbivores during mid-summer peak of growth (Towne et al. 2005, Jackson et al. 2010) or following burning (Pfeiffer and Hartnett 1995) may be more effective at re-establishing the coexistence of non-dominant species with *Schizachyrium*. Spring mowing of *Bromus* can control this non-native dominant, as supported by Hendrickson and Lund (2010). However, our results also show that mowing must extend beyond a single (or two) years of disturbance. Mowing is an alternative to the use of herbicides which have varied results in *Bromus* control (Ambrose and Wilson 2003, Hendrickson and Lund 2010, Bahm et al. 2011) and can cause lasting negative effects on non-target plant and non-plant species. Fire, a necessary disturbance in grasslands, produces similar positive control of *Bromus* (Willson and Stubbendieck 2000), but annual burning can

increase warm-season grasses (Tix and Charvat 2005) while reducing non-dominant species diversity (Collins et al. 1998).

Response of Non-Dominant Species

Species richness and diversity (H') increased with disturbances in both communities, but benefitted more by creation of microsites than from reduced competition alone. Dominant grasses can directly compete with non-dominant species, but reversing these effects by reducing dominant abundance has varied results on community structure (Smith et al. 2004, Gilbert et al. 2009). In both communities, reduction of the dominant, i.e., 'mow only' plots, was associated with greater species richness, which supports earlier suggestions of competitive suppression of species richness by both dominant species in this system (McNicol and Augspurger Ch. 1). However, this effect was produced by offsetting species loss from controls over time, rather than increased species colonization with mowing alone (Fig. 2.1). Light availability likely increased after mowing, but new colonization may have been inhibited by high levels of dead vegetation in 'mow only' treatments in both communities (Foster and Gross 1997), and enhanced growth of existing non-dominant species in the *Bromus* community. Increased species richness at the community level in the *Bromus* community indicates at least a low level of colonization (Table 2.2), but not enough to be reflected at the plot level. Overall, reduced competitive effects from both dominant grasses maintained but did not greatly increase non-dominant species richness.

Soil disturbance, in combination with reduction of the dominant grass, increased colonization by non-dominant species in both communities. Removal of litter reduces physical barriers and increases light (Jutila and Grace 2002) and bare ground increases seed-soil contact. Such conditions are necessary for establishment from seed of many species (Gross and Werner 1982) and for vegetative spread (Rapp and Rabinowitz 1985, Bullock et al. 1995). Dominant grass identity also impacted the availability of microsites and their colonization. The

large pulse of species richness following a single soil disturbance in the *Schizachyrium* community may have been due to bare ground that remained for one to two years, providing small regeneration sites, as has been found in other studies (Fowler 1988, Pakeman and Small 2005). In contrast, in the *Bromus* community, a single soil disturbance functioned similarly to 'mow only'. Bare ground was rare the year following soil disturbance and colonization may have been inhibited by extant perennials that increased following *Bromus* reduction.

Repeated soil disturbance was necessary to increase and maintain elevated species richness in both communities, emphasizing the ephemeral nature of microsites (Hobbs et al. 2007). The rapid loss of open microsites is particularly relevant for species dependent on recurrent microsites (e.g., annuals and biennials) (Goldberg and Gross 1988). In addition, unless perennials, a species-rich group in grasslands, establish when microsites are created, species gains from disturbance will be limited. Furthermore, our results indicate that loss of microsites and associated loss of species occurs more quickly in *Bromus* than *Schizachyrium* dominated grasslands. The temporal nature of microsites was detected in this 5-year study, which would not have been evident in studies of shorter duration.

Percent cover of non-dominant species was unaffected by reduction of *Schizachyrium*, but increased in response to reduction of *Bromus*. In the *Schizachyrium* community, non-dominant species may have been constrained by the continued high abundance of the dominant and its ability to reduce available soil nitrogen (Tilman and Wedin 1991, Harpole and Tilman 2006). More severe disturbances, e.g., removal of the dominant by fossorial mammals, might create the competitive release necessary for coexistence with *Schizachyrium*, as seen in high quality remnant prairies (Platt 1975). In contrast, greater % cover of non-dominant species in the *Bromus* community was likely a response to competitive release both above and below ground, given the ability of *Bromus* to reduce light availability, compete for soil resources (Gerry and Wilson 1995), and alter soil properties (Jordan et al. 2008). Although studies report successful reduction of *Bromus* (Blankenspoor and Larson 1994, Willson and Stubbendieck

2002, and Salesman and Thomsen 2011), documented competitive release of the non-dominant community following mowing or fire control measures is rare.

Community structure based on plant traits: 2009

Disturbance effects on non-dominant species with contrasting plant traits generally paralleled overall community measures of diversity; i.e., species richness of most traits responded positively to disturbance in both communities, while % cover of most traits increased with disturbance in the *Bromus* but not *Schizachyrium* community. Within this overall positive response, disturbance was more selective for some traits, most noticeably in greater colonization by annual and biennial species in both communities, and the increased % cover of perennial species following reduction of *Bromus*.

Species with a broad range of traits benefit from increased microsites (Rapp and Rabinowitz 1985, Fowler 1988). However, establishment by species with particular traits is influenced by many factors, including presence of propagules (Seabloom et al. 2003), evolutionary history of traits and disturbance (Diaz et al. 2007), and suitability of microsites. Species richness of annual and biennial species, as well as native and early season species, showed a strong positive relationship to disturbance, especially frequent soil disturbance. These species may be more sensitive to germination cues related to levels of red light and microclimatic factors (Chambers and MacMahon 1994), and thus readily establish when litter is reduced and bare ground increased (Wilson and Tilman 2002, Dickson and Foster 2008). In addition, given their dependence on recurring recruitment, their requirements for colonization may be met by a broader range of microsite quality (Denslow 1980), as produced by raking, which created gaps, but left much of the extant vegetation intact. In comparison, lower colonization of disturbances by perennial species and perennial functional groups may indicate that their requirements for colonization were not met by these disturbances, reflect an inherently lower dependence on recurrent recruitment, or indicate seed limitation in this group (Foster and

Tilman 2003). In the *Bromus* community, where there was greater colonization of disturbances by perennial forb species, several of the species are considered 'fugitive' or early successional species (Tilman 1994) and thus may recruit in conditions similar to annual and biennial species.

Change in % cover following reduction of a dominant grass may arise from extant or newly colonized individuals, and specific trait responses can reflect the size and nature of the resources released. In the *Schizachyrium* community, the resources released by the reduction of the dominant grass, such as light and bare ground, appeared to be adequate for increased % cover of annual and biennial species. However, these resources were insufficient for increased % cover of other traits, despite their increased colonization of disturbance plots. A greater reduction of *Schizachyrium* might be necessary for % cover of species with other traits to increase. In contrast, the reduction of *Bromus* benefited most species, with % cover increasing most in native and perennial (grass and forb) species. Species with these traits comprised the greatest portion of non-dominant species at the outset of the disturbance, reflecting a direct competitive release. Established vegetation can exert strong priority effects, especially in perennial communities composed of long-lived individuals, potentially restricting a greater change for species with other traits. The greater response of early than late season species to disturbance indicates that, in part, early season species may have received a greater release from cool-season competition. The lack of differentiation in % cover of most groups of traits may also reflect lack of severity of the disturbance applied, as compared to fire or reduction of perennial species from grazing systems (Diaz et al. 2007). The overall results provide additional indication that mowing disturbances were successful in targeting the dominant species, with minimal negative effects on extant non-dominant species. It is unclear why biomass of traits did not reflect the results documented with % cover.

Native non-dominant species generally dominated the response to disturbance in species richness and % cover. Native species may have an advantage due to abundance in the local species pool (DiVittorio et al. 2007) and/or an inherent adaptation to disturbances,

including mechanical disruptions to the soil layer by wallowing, trampling, and scraping of the soil by large ungulates (Knapp et al. 1999). In this study, this response included many common native species with low diversity value (e.g., perennial ragweed, *Ambrosia psilostachya*), but several native fugitive species that were not documented in the seed bank (e.g., *Linum sulcatum*, *Arabis lyrata*) also benefited from soil disturbance. The low colonization of non-native species and reduced % cover in the *Schizachyrium* community was unexpected, especially given the abundance of non-native species in the seed bank, particularly in the *Bromus* community (McNicoll and Augspurger Ch. 1). It is unclear whether this low response from non-natives is based on the species present, aspects of the disturbances, or interactions between them (Firn et al. 2008).

Species Composition and Similarity

Species composition and abundance did not diverge among treatments or converge within a particular mode of disturbance, and remained more similar within than between communities. Theory predicts that disturbances should select for species with traits adapted to such conditions (Grime 1977), but initial conditions and site history influence the trajectory of community change after disturbance (Milchunas and Lauenroth 1995, Coffin et al. 1996). Continued dominance of *Schizachyrium*, increased % cover of extant species in the *Bromus* community, and localized site history differences that influenced the species pool (McNicoll and Augspurger Ch. 1) all contributed to the amount of convergence/divergence that was possible among communities and treatments. Disturbances of greater severity might create greater compositional change (Spasojevic et al. 2010), but would still be strongly influenced by local species pool and would not create certainty of convergence (Jutila and Grace 2002).

Comparisons of the vegetation and seed bank

Recruitment by species with a seed bank was augmented via disturbance in both communities, but not disproportionately compared to regeneration via seed rain or vegetative spread. Similarity of species composition between the vegetation and seed bank was increased by disturbance, because an increased number of seed bank species recruited with disturbances. Regeneration of grasslands after disturbance has been documented to be heavily dependent on vegetative growth (Abrams 1988, Benson and Hartnett 2006). The moderate stimulation of the seed bank contrasts with other more extreme disturbances that may deplete (Abrams 1988) or favor (Pakeman and Small 2005) recruitment from the seed bank. Although disturbance stimulated many seed bank species that were common, it also stimulated recruitment of desirable native seed bank species (e.g., *Oenothera rhombipetala*) that would otherwise be excluded from undisturbed vegetation. However, as noted by other studies (e.g., Bossuyt and Honnay 2008 and references therein), reliance on recruitment only from the seed bank would not be adequate for restoration of many species, particularly in the *Bromus* community.

In summary, this study has shown that, in grasslands in which dominant species reduce native diversity, disturbance will be most effective when it targets vulnerabilities of the dominant species present, especially if it diminishes stored resources based on phenology and is applied multiple years. Reduction of the dominant may be followed by emergence of a suppressed native community. However, our results emphasize that dominant reduction may be insufficient to restore diversity, unless competitive release is accompanied by soil disturbances that create microsites for non-dominant species colonization. This study demonstrated that such disturbances may need to be applied regularly to maintain a continual presence of microsites and allow recruitment of species from the seed bank and spread of extant species in the vegetation.

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CHAPTER 4: MICROSITE AND SEED LIMITATION IN TWO COMMUNITIES DOMINATED BY CONTRASTING GRASSES

ABSTRACT

The relative importance of microsite and/or seed limitation on grassland community structure can be influenced by community context on potential seed sources. To investigate how two dominant grasses affect these limitations, we conducted a factorial microsite and seed limitation experiment in a sand prairie grassland in northwestern Illinois, USA. In two communities, dominated by *Schizachyrium scoparium*, a native warm-season grass, or *Bromus inermis*, a non-native cool-season grass, three experimental manipulations were applied to 30 x 30 cm plots. New microsites (=gaps) were created by removing vegetation and roots, then replacing the soil (and seed bank) into the plot and allowing re-colonization via vegetative and local seed sources. Seeds of 21 native species were added to undisturbed vegetation plots (=seed) and to an additional set of gap plots (=seed + gap) to test for concurrent microsite and seed limitation. In gap plots, species richness increased in the *Schizachyrium*, but not *Bromus* community. Recruitment from the local species pool was derived from all life histories and seed sources (seed rain and seed bank). In seed addition plots, species richness did not differ from controls in either community. In seed + gap plots, species richness was greatest and species composition diverged most from control plots in both communities. Percent cover generally followed patterns of species richness. Individual sown species differed in being either microsite or seed limited, but the majority of sown species had their greatest frequency in seed + gap plots. Low recruitment in gaps in the *Bromus* community may indicate inferior microsites and/or greater seed limitation in that community. In contrast, the low establishment of sown species in undisturbed vegetation showed that traits common to both dominant species, such as high production of biomass and dead vegetation, may make communities difficult to invade, regardless of dominant species identity. Finally, results for combined gap and seed addition

plots indicate removal of multiple limitations is necessary to achieve the greatest change in community structure and species composition, independent of dominant species identity.

Key words: Bromus inermis, disturbance, grassland diversity, microsite limitation, Schizachyrium scoparium, seed addition, seed bank, seed limitation, species identity

INTRODUCTION

Recognition of microsite and/or seed limitations led to a debate as to which factor was more important in influencing species diversity (Eriksson and Ehrlén 1992, Turnbull et al. 2000). It is now recognized that both factors influence community structure and species composition, but their relative importance depends on the context, including successional stage (Gross and Werner 1982, Turnbull et al. 2000), diversity of the existing community (Martin and Wilsey 2006, Frances et al. 2010), and characteristics of the species considered to be limited (Turnbull et al. 1999). Differences among dominant species may provide additional context (Crawley et al. 1999), especially in terms of availability of microsites. In addition, traits of the dominant species that allow or exclude non-dominant species coexistence influence seed availability within a particular community.

Communities are considered microsite limited when establishment from seed is restricted by absence of suitable sites for recruitment. Limitations to recruitment include low seed-soil contact (i.e., absence of bare ground), presence of abundant litter, and low light or moisture levels ('regeneration niche', sensu Grubb 1977), but also complete use of resources by existing vegetation that limits community invasibility (Gross et al. 2005). Tests of the microsite limitation hypothesis have typically involved adding seed to a community, and if the seeds fail to establish, communities are considered microsite limited. An alternative method is to create microsites experimentally and compare the resulting community structure to undisturbed communities. An advantage of the first method includes relatively simple interpretation, but the

second test can assess suppression of existing seed sources in the community, including seed rain and seed bank.

In grassland communities, traits of dominant grasses may influence the availability and suitability of microsites for establishment. Litter production by dominant grasses and its quality can affect the rate at which it decomposes (Vinton and Goergen 2006), affecting nutrient cycling and litter persistence as a barrier to seedling establishment (Foster and Gross 1997, Jutila and Grace 2002). Structural traits of dominant grasses, such as differences in height and growth form (e.g., caespitose vs. mat growth form) affect the amount of light that reaches the soil surface (Wilsey 2010) and potential for recruitment between bunches or culms. Similarly, differences in phenology and photosynthetic pathway (C3/C4) and timing of greatest canopy closure can influence species establishment and growth. Dominant identity may also influence temporal aspects of microsite persistence, with microsites being lost quickly from communities with rapid growth rates of dominant species (Renne and Tracy 2007), leaving a short window of time for seed to establish prior to gap closure. However, microsites may be limited regardless of identity of the dominant species if any one or combination of these traits exists among different dominant species.

Despite the potential for dominant species to negatively influence the quality of microsites, many native grasslands have high diversity in the presence of dominant grasses, possibly through disturbances that create gaps in grassland sod (Gibson et al. 1989). Disturbances by fossorial animals and their predators provide microsites in which above and belowground vegetation is removed, creating gaps of various sizes characterized by bare soil and lack of litter (Platt 1975, Hobbs et al. 2007, Questad and Foster 2008). These small-scale, high-intensity disturbances provide competition-reduced space, in addition to altered levels of soil moisture and nutrients and reduced soil compaction (Questad and Foster 2007). Species that do not tolerate encroachment may be dependent on a constant supply of such microsites for recruitment across a landscape, including many annuals, biennials, and fugitive perennials,

i.e., short-lived perennial species. In addition, even species that coexist with dominant grasses through niche partitioning (Fargione and Tilman 2005) may need to overcome initial barriers to establishment prior to coexistence as neighbors. Thus, gaps in the vegetation have the potential to increase species richness and alter species composition, and increase overall community diversity from increased heterogeneity across the landscape.

Even when suitable microsites are present, recruitment can be prohibited by the absence of seed from local sources, i.e., seed rain or seed bank. Seed addition can be used to test for seed limitation in specific communities by supplementing inadequate production of seeds and/or overcoming limited dispersal to microsites (Clark et al. 2007). Adding seeds of multiple species can detect seed limitation at the community and population level: at the community level seed limitation restricts species richness and/or other measures of diversity, whereas at the population level reflects inadequate presence of seed of a particular species therefore limiting population size. Seed additions of multiple species allows for assessment across an array of microsite quality, given differences among species in their requirements for recruitment.

Seed limitation has been identified in some grasslands (Tilman 1997, Foster and Tilman 2003), but not others (Turnbull 2000, Wilsey and Polley 2003). Seed availability is likely highest in remnant grasslands with high diversity and abundant seed sources of various species (Wilsey and Polley 2003). In contrast, site history may result in seed limitation, such as intense grazing, that decreases the abundance and distribution of various species in the local pool and the ability of their seeds to reach open sites (Seabloom et al. 2003). Seed limitation also may be more likely to occur in communities dominated by competitive grasses that exclude coexistence. However, communities that retain dormant seeds, regardless of low abundance in the existing vegetation, should be less likely to exhibit seed limitation.

Many communities are limited by both microsite and seed availability (Myers and Harms 2009). Removal of one limitation, without removal of the other limitation, may result in little

overall change to community structure. However, when both regeneration sites and seed sources are present in abundance, it would be expected to have the greatest effect in altering community structure and species composition.

In two communities with different dominant grasses, we tested for microsite and seed limitation in a factorial experimental design: microsite creation (gap), seed addition (seed) and both (seed + gap). Microsite availability was assessed in two ways: First, microsites (=gap) were created by removing all live vegetation (above and belowground) and allowed to re-vegetate by potentially suppressed local vegetative and seed sources, including seed rain and seed bank. Second, seeds of 21 native species were added to intact vegetation (=seed) to compare the invasibility of the dominant grasses. Seed limitation was assessed via establishment of sown species in seed and seed + gap plots compared to control and gap plots, respectively. Seed addition served to compensate for both seed production and limited dispersal, as all sown species were present in the 810+ ha sand prairie that contained the two communities, but fewer than half were present in the experimental plots. Microsite quality was assessed by % cover of bare ground, dead vegetation, and dominant grass. To detect microsite and/or seed limitation, species richness, % cover, diversity, evenness, and composition of unsown and sown non-dominant species were compared across treatments and communities. Microsite and seed limitation of individual species and locally occurring species (not sown) with a seed bank were assessed by comparing frequencies of individual species.

Microsite and seed limitation manipulations were carried out in two communities dominated by grasses with contrasting location of origin, phenology, and growth form: *Schizachyrium scoparium* (Michx.) Nash (little bluestem) (hereafter *Schizachyrium*), a native, warm-season (C4), bunch grass, or *Bromus inermis* Leyss. (smooth brome) (hereafter *Bromus*), a non-native, cool-season (C3), mat-forming grass. We expected microsite limitation to be less in the *Bromus* community, given that *Bromus* appears to be more invasible in seed addition experiments, although both grasses have shown at least a minimal level of invasibility (Emery

and Gross 2007, Wilsey 2010). However, both grasses produce abundant biomass and litter and their invasibility increases following mowing or raking disturbances (Foster et al. 2009, Williams et al. 2007). Seed limitation of native perennial species was expected in both communities, as the communities occur in a larger site dominated by sand prairie that was moderately to heavily grazed for 80+ years. Differences in seed limitation between the two communities were difficult to predict, because, although aboveground species richness is generally greater in the *Schizachyrium* community, species richness of the seed banks of both communities was similar (McNicol and Augspurger Ch.1). Combined microsite and seed limitation was expected in both communities.

METHODS

The Lost Mound Unit of the Upper Mississippi Wildlife Refuge (42° 13' N, 90° 20' W) contains a sand prairie that was formerly a U.S. Army munitions storage base in Jo Daviess County, Illinois, U.S.A. Base infrastructure included soil-covered bunkers and associated access roads, constructed so that much of the native vegetation was intact. Native vegetation persisted under moderate to heavy grazing that occurred annually (May to October) for 80+ years (1917-2000), with no grazing for seven years prior to the start of this study. Non-native species are also present on site from a combination of intentional and accidental introduction.

During the study period, spring-summer (March to August) average temperatures (2007-2009, max/min °C: 23/10, 21/8, and 21/8) were similar to the 30-year average (1971-2000: 22/8); days above 32.2 °C (90 °F) varied among years (2007-2009, # of days: 26, 3, and 5) compared to the 30-year average (15 days). Spring-summer total precipitation (2007-2009, mm: 683, 770, and 898) was greater than the 30-year average (604 mm) (Mount Carroll weather station, ~ 50 km from study site, Illinois State Climatologist's office).

Transects were placed in dry-mesic sand prairie on soil classified as Sparta loamy sand, 1 to 6 percent slopes (Soil Survey Staff NRCS-USDA 2012), with low organic material and

nitrogen content (Symstad 2004). Transect locations were based on visual dominance (approximately 50 percent) of one of the two focal grasses, but selected to capture a broad environmental background. *Schizachyrium* is present across most of the site, and *Bromus* invasions are distributed within the larger *Schizachyrium* community, likely an artifact of intentional introduction and subsequent spread. Transects were situated to avoid the shrub, *Rhus aromatica*, and large patches of crown-vetch, *Coronilla varia*, a non-native, nitrogen-fixing invasive species. A total of ten transects were placed across the site, five within each community. Transects were separated by ≥ 125 m; all were within a 3 km radius. Three invasion foci were identified for the *Bromus* community; two transects were placed in each of two foci and a single transect in the third.

Experimental Design

In May 2007, on each 50-m transect, at 10-m intervals, a set of four plots was located on alternating sides of the transect at a random distance of one to three meters from the centerline of the transect. Within each set of plots, individual plots were separated by one meter from one another and randomly assigned to one of four treatments (= total of five plots per treatment per transect, a total of 25 plots per treatment (except 24 for gap plots in *Schizachyrium* community)). Effects of seed and microsite limitation were tested in 30 X 30 cm permanent plots receiving one of four treatments: gap only (G), seed addition to intact vegetation (S), seed + gap (S + G), and control (C). Plots receiving gap treatment (G, S + G) were excavated to a 15-cm depth, all live vegetative was biomass removed, and soil was replaced into the plot. This manipulation removed all roots and shoots of competing dominant and non-dominant species from the plot, but returned the soil and associated seed bank. Plots that were sown (S, S + G) received addition of seeds several weeks after gaps were created. Seeds were scattered evenly in plots on a calm day using a barrier on the outside edge to keep seeds within the plot. In seed only (S) plots, vegetation was moved from side to side to encourage settling of seeds

beyond the vegetative canopy. Seeds added to gap plots were tamped to ensure seed-soil contact, but were not buried.

Thirty seeds each of 21 species were added to seed addition plots for a total of 630 seeds per 900 cm² plot (= 7,000 seeds/m²) (Table 3.1). Seeds, along with a legume-inoculant, were added in late May 2007, and due to low recruitment observed in 2007, seeds and inoculant were added to the same plots again in mid April 2008. Selection of the 21 species for seed addition was based on membership in the local sand prairie species pool, availability from the supplier (Genesis Nursery, Tampico, IL), and baseline community structure. Life histories were not evenly represented (only one annual and one biennial species) in the seed mix due to seed availability. All functional guilds were represented, with some bias towards forbs and legumes. This bias was justified, as analysis on the site (2009) showed species richness of forbs to be 20 % lower than a survey conducted in 1910 (Gleason), with many forbs and legumes documented by Gleason absent from both communities (Gleason 1910). *Schizachyrium* seed was omitted from the mix for the *Schizachyrium* community, and was observed to establish from local seed rain at rates similar to the *Bromus* community. To assess general viability of the seeds added, seeds were subjected to germination tests in the greenhouse, and all had > 50 % germination success, with most species > 80 % success. In 2008, *Anemone cylindrica* was not available, and so was not added a second time. Seed germination tests detected a seed contaminant, *Chenopodium alba*, after seeds had been added to field plots. *Chamaechaerista fasciculata*, the only annual species sown, produced seeds in both communities to naturally recolonize after initial sowing in 2007 and 2008.

All sown species were present on the larger 810+ ha sand prairie site, but only eight species were in the *Schizachyrium*, and four in *Bromus* experimental plots (Table 3.1) prior to seed addition. Therefore, in the results, 'sown species' present in control or gap plots represent a baseline for these species in the community, i.e., they were present in the extant vegetation or recruited from the seed bank, and were not the result of sowing.

Vegetation surveys of each 30 x 30 cm permanent plot were conducted in June and late summer (late July/early August) from 2007-2009. All species were identified in each plot and assigned a % cover value based on nine evenly divided cover classes, with the center point of each cover class used for statistical analyses. Early and late summer data were combined for each plot, with the larger percent cover value used for those species present in both survey times. Percent cover of dead vegetation and bare ground were evaluated with the same methods. Thus, species richness, composition, and cover values represent maximum values across the growing season for each plot, which is important given the growing season differences (e.g., cool vs. warm season) among species. Species nomenclature was based on Gleason and Cronquist (1991). Given the low recruitment from seeded species in 2007, and the presence of individuals as seedlings but not yet established in 2008, only 2009 data is analyzed here to document individuals that had established (i.e., absence of cotyledons was used to determine establishment vs. seedling status). Values are a conservative estimate of successful recruitment.

Natural soil disturbances were evaluated in both communities to detect bare ground created by various mammals, including underground feeding and tunneling by small mammals and diggings created by coyotes or other large mammals in search of prey (Huntly and Reichman 1994). In 2009, in an area near each experimental transect, visual observations were made along a 100-m transect with a 6-m width. Visible soil disturbances were categorized as either large (> 50 cm diameter) or small (25 - 50 cm diameter).

Seed bank sampling was completed in 2006 in both communities in conjunction with a concurrent study. Methods and results for seed bank characterization are provided in McNicoll and Augspurger (Chapter 1).

Data Analysis

At the site level, general comparisons consisted of summaries of species richness (total, sown species), frequency (i.e., the number of plots in which species occurred) (sown species, seed bank, and all individual species), and total % cover (individual species). Statistical tests were not performed on frequency of sown or individual species, or observational counts of natural soil disturbances as they did not meet assumptions of applicable statistical tests, or the number of tests to be performed would increase statistical error rates. Count data of frequencies of species in the seed bank (vs. not) were compared using Chi-square analysis.

At the plot level, species richness, % cover (bare ground, dead vegetation, dominant grass, non-dominant species, and non-dominant species based on sowing and life history), Shannon-Wiener diversity (H') and evenness ($E_{1/D}$ of Smith and Wilson 1996) were compared across treatments and communities. Separate ANOVA models for each variable were analyzed in proc mixed (SAS 9.1) as a factorial design with transects (= experimental unit) as random effects and treatment, community, and treatment x community as fixed effects. Covariance structure for analyses was selected based on Akaike's Information Criteria, Corrected (AICC) (Littell et al. 2006). When effects of treatment or treatment x community interaction were significant ($p < 0.05$), post-hoc comparisons were made between treatments using the 'estimate' statement in proc mixed.

Species composition and abundance were assessed in a Bray-Curtis similarity matrix, after species % cover values were standardized to 100 % to account for differences in total % cover among treatments. Using PRIMER v6 (Clarke and Gorley 2006), Bray-Curtis pair-wise similarity of plots was assessed with analysis of similarity (ANOSIM) to compare treatments to control plots within a community, and to create a non-metric multi-dimensional scaling (NMDS) diagram for all treatments and communities.

Comparisons of individual sown species limitations were made using patterns of frequencies across treatments: species were considered microsite limited if they occurred at

greater frequency in gap than control plots, seed limited if greater in seed than control plots, and concurrently microsite and seed limited if greatest in seed + gap plots.

RESULTS

Microsite creation and dominant grass response

Two years after experimental disturbance that removed all live vegetation, including the dominant grass, experimentally created microsites were still present; i.e., gaps had significantly greater bare ground and reduced dead vegetation than control plots in both communities (Fig. 3.1 A and B, Table 3.2). Dominant grasses re-encroached on gaps over this same period; however, % cover of *Schizachyrium* was still significantly lower in gap than control plots; whereas % cover of *Bromus* in gaps had returned to pre-gap abundance (Fig. 3.1 C, Table 3.2). *Schizachyrium* recolonized gaps slowly from the edge, whereas *Bromus* growth came from underground rhizomes that emerged throughout the gap.

Animal disturbed soil gaps were present on all five *Schizachyrium* transects and three of five *Bromus* transects. Natural gaps were not common. Density of small diameter gaps (< 50 cm) was 0.17/100 m² in *Bromus* and 0.13/100 m² in *Schizachyrium*, and large diameter gaps (> 50 cm) was 0.07/100 m² in *Bromus* and 0.17/100 m² in the *Schizachyrium* community.

Site level responses to microsite creation and seed addition

At the site level, all treatments increased the total species richness beyond that of control plots in both communities (Table 3.3). Natural colonization of gaps from vegetative spread, seed rain and seed bank, added 17 species to the *Schizachyrium* community and six to the *Bromus* community. The addition of seeds, without gaps, increased species richness by eight and seven species in the *Schizachyrium* and *Bromus* community, respectively. The combination of seed + gap increased site level species richness by 21 species in *Schizachyrium*

and 17 species in the *Bromus* community. Sown species increased species richness of both communities similarly, but a greater number of the sown species existed naturally in the *Schizachyrium* than *Bromus* community, as seen from greater numbers in the control and gap plots.

Of the 21 species sown, 18 species established at least once in either community (Table 3.1). Approximately half of sown species colonized undisturbed vegetation in seed addition plots in both communities, but in many cases only by a single or few individuals. Overall colonization may not have reflected the rate of seed additions as evidence of seed predation was observed (e.g., small mammal scat next to seed casings), especially in seed + gap plots.

Community structure responses to microsite creation and seed addition

Species richness was significantly greater in gaps than control plots in the *Schizachyrium* community (nearly 2X), but remained similar to control plots in the *Bromus* community (Fig. 3.2 A, Table 3.2). In contrast, species richness remained similar between seed addition and control plots in both communities. In seed + gap plots, species richness was greater than all other treatments, an effect that was greater in the *Schizachyrium* than *Bromus* community. Percent cover and diversity (H') of non-dominant species were significantly greater in the gap and seed + gap than control plots in *Schizachyrium* community (Fig. 3.2 B and C, Table 3.2). However, H' was greater in seed addition than control plots in the *Schizachyrium* community, showing at least some change to community structure through seed addition. In the *Bromus* community, % cover of non-dominant species was similar among all treatments, and diversity (H') was significantly greater only in seed + gap plots (Fig. 3.2 B and C, Table 3.2). Evenness did not differ among treatments or between communities (Fig. 3.2 D, Table 3.2).

Assessment of community structure based on seed source and life history

Species richness and % cover of unsown species was significantly greater in gap and seed + gap than control plots in the *Schizachyrium* community, but remained similar to controls in the *Bromus* community (Fig. 3.3 A and B, Table 3.2). This emphasized that in gaps in the *Schizachyrium* community, colonization and growth replaced and surpassed species richness of control plots, but in gaps in the *Bromus* community only returned to original levels. When considering sown species, their presence in control and gap plots reflected natural occurrence, i.e., background levels, of these species in both communities. Sown species in both communities showed significantly greater species richness and % cover in seed and seed + gap plots than either control or gap plots (Fig. 3.3 C and D, Table 3.2). This directly reflected seed addition manipulations, which was enhanced most in seed + gap plots.

For perennial species, in the *Schizachyrium* community, species richness was significantly greater in gap than control or seed plots, with the greatest augmentation in seed + gap plots in both communities (Fig. 3.3 E, Table 3.2). Percent cover of perennial species was similar among all treatments and between communities (Fig. 3.3 F, Table 3.2). Perennial species were derived from the existing or sown (i.e., 19 of 21 sown species were perennial) species pool. Biennial and annual species showed significantly greater richness and % cover in gap and seed + gap than control or seed plots in the *Schizachyrium* community, whereas all gap and seed manipulation treatments were significantly greater than control plots in the *Bromus* community (Fig. 3.3 G-H, Table 3.2). Biennial + annual species were largely derived from the existing local species pool.

Microsite vs. seed limitation of individual species

Comparisons of frequency of sown species in each treatment in both communities allowed for comparisons of individual species' microsite and seed limitation (Table 3.1).

Panicum oligosanthos showed microsite, but not seed, limitation in both communities; it readily

recruited from seed in gaps (via local seed source) and seed + gap plots, but was uncommon in control and sown plots. Other sown species that also appeared to be inhibited by lack of microsites included *Tradescantia ohiensis* in the *Schizachyrium* community and *Verbena stricta* in the *Bromus* community. Seed limitation appeared to be the primary limitation for *Chamaechaerista fasciculata* and *Euphorbia corollata*, as they established when added as seed, regardless of existing vegetation. Most sown species reached their highest frequencies when seed was added to previously disturbed gaps (=seed + gap), i.e., species were both seed and microsite limited, (e.g., *Dalea purpurea*, *Echinacea pallida*, *Lespedeza capitata*, and *Tradescantia ohiensis* in both communities, and *Schizachyrium* in the *Bromus* community). Low recruitment and frequency of other species may reflect local sources of mortality (e.g., seed predation), and/or lack of suitable microsites.

Microsite limitation of unsown perennial species was indicated by rarity of new establishment observed in control plots (1 plot in each community). Creation of gaps appeared to overcome this limitation, as shown with frequency of unsown perennial species (11 species in *Schizachyrium* and eight species in *Bromus*) that established from seed in *Schizachyrium* (23 plots), but less so in *Bromus* (14 plots). The presence of microsites benefitted several perennial species with biodiversity value that established from seed, including *Lithospermum carolinense* (5 individuals) and *Panicum villosissimum* (11 individuals) in both communities and *Monarda punctata* (2 individuals) in the *Bromus* community.

Microsite limitation release for seed banks

In control plots, seed bank and non-seed bank species contribute to aboveground vegetation in similar frequencies and species richness between the two communities (e.g., 70 – 80 % of vegetation frequency is from species with a documented seed bank) (Table 3.4, Appendix E). Gaps increased nearly two-fold the frequency of seed bank species in both communities. However, in the *Bromus* community, frequency of colonization of gaps by non-

seed bank species was lower than expected (CHI-SQ, $X_4 = 10.29$, $p = 0.02$). Both communities had species in the seed bank that were not present in any treatment: 9 seed bank species in the *Schizachyrium* community and 8 in *Bromus*, which included species that were abundant and rare in the seed bank.

Species composition and abundance

Species composition and abundance diverged significantly between gap and control plots in the *Schizachyrium* community, but remained similar in the *Bromus* community (Table 3.5). Colonization of gaps in the *Bromus* community was dominated largely by species with vegetative and/or seed bank reproduction that were common in the adjacent vegetation and control plots (Appendix E); whereas colonization of gaps in the *Schizachyrium* community came from species common in the surrounding vegetation, but also from species that were otherwise rare across the landscape. Sowing seed alone was not sufficient to alter species composition and abundance from control plots in either community. However, in combination, seed + gap plots showed significant divergence of species composition and abundance from control plots in both communities. Plots with little compositional change of non-dominant species from control plots (i.e., gap plots in the *Bromus* community and seed addition plots in both communities) show the greatest overlap in the center of the NMDS diagram (Fig. 3.5). In contrast, seed + gap plots in both communities, and gap plots in the *Schizachyrium* community show greater dispersion across the diagram, i.e. greater dissimilarity among plots, reflecting varied recruitment of species not abundant in control plots and varied recruitment among the species added as seed.

DISCUSSION

Microsite creation and dominant grass response

Microsites were present two years after removal of above- and below-ground vegetation, showing increased bare ground and reduced dead vegetation, and were at similar amounts in both communities. The presence of bare ground and absence of litter are important for colonization by new species, especially for establishment from seed (Jutila and Grace 2002). Bare ground, where vegetation has recently been removed, may also indicate the presence of greater soil resources, including greater nitrogen and reduced soil compaction (Questad and Foster 2007), important to germination and establishment of new individuals.

However, re-encroachment of the empty gap differed greatly between the two dominant grasses with *Schizachyrium* present only at the edges of the plots, whereas *Bromus* colonized across the plot. The two dominant grasses have different growth rates and tiller elongation which accounts for their general difference in growth form, i.e., bunch grass form of *Schizachyrium* and mat formation of *Bromus*. Creation of microsites may have stimulated growth in *Bromus*, through root cutting, and/or release of nutrients (Otfinowski and Kenkel 2008). The difference in % cover of the dominant grass may translate into different uptake of soil resources within a gap, reducing the quality of the gap below ground and likely decreasing the amount of light to the surface. Thus, although the presence of bare ground has been shown to increase colonization microsites in disturbed *Bromus* communities (McNicoll and Augspurger Ch. 2), the quality of these microsites is also dependent on reduction of the dominant species. *Schizachyrium* may continue to encroach upon gaps, but this does not preclude coexistence with long-lived perennial species that establish during ideal microsite conditions (i.e., the first few years after microsite creation) (Fargione and Tilman 2005)

Microsite Limitation

Microsite limitation was evident in both communities, as species richness did not increase with the seed addition alone. This general lack of invasibility may arise from the % cover of existing vegetation (dominant and non-dominant species), the absence of bare ground and abundant dead vegetation. In general, high abundance of both dominant species has been shown to have negative effects on non-dominant species, which in part may be due to the loss of microsites. The lack of microsites (i.e., potential for establishment from seed) can have as strong negative effects on species richness as the loss of species arising from high competition (Juttila and Grace 2002, Yurkonis et al. 2005). Greater seeding rates might have led to greater colonization rates (Frances et al. 2010) and our results would have reflected studies that showed greater invasibility of these grasses (Emery and Gross 2007, Wilsey 2010).

In the *Schizachyrium* community, gaps increased species richness, % cover, and diversity of non-dominant species and altered the non-dominant species composition. Thus, the *Schizachyrium* community is constrained by lack of microsites for new recruitment, and when created, native propagules from the existing species pool readily colonize microsites. Suppression of non-dominant species by *Schizachyrium* may be due, in large part, to its use of belowground resources (Tilman and Wedin 1991, Harpole and Tilman 2006) and production of large amounts of biomass by warm season grasses that is slow to decompose (Vinton and Goergen 2006). Gaps were colonized by species common in the vegetation, reflecting their abundant local source pool, but also by biennial, annual, and fugitive perennial species, that likely recruited from dormant seed banks and/or seed rain (Pakeman and Small 2005). This increased diversity and divergence of species composition of gaps from undisturbed controls indicates that gaps created a refuge for species dependent on reduced competition. Such gaps and the microhabitats created have been proposed previously for maintaining diversity in grasslands (Platt 1975, Hobbs et al. 2007), as they increase the heterogeneity across the landscape.

In contrast, gaps in the *Bromus* community returned to similar levels of species richness, % cover, diversity, and similar species composition to control plots. The absence of changes in gaps in *Bromus* could be attributed to several reasons: 1) Despite some bare ground and reduced dead vegetation, suitable microsites were not created given the rapid re-colonization of gaps by *Bromus* (DiVittorio et al. 2007). Rapid re-colonization of gaps by *Bromus* and *Ambrosia psilostachya*, a native perennial forb with a seed bank and potential for vegetative spread, likely reduced light availability in gaps and created greater competition for nutrient uptake, reducing the favorability of the gaps for recruitment. However, given that sown species established in similar conditions in seed + gap treatments, it is unclear why species that occurred in the *Bromus* seed bank did not have greater establishment. 2) Absence of changes in gaps in the *Bromus* community could be due to limited seed sources. Compared to the *Schizachyrium* community, differences in the community level species pool likely contributed to poor dispersal of rare species into gaps. 3) Recruitment in gaps in the *Bromus* community may have been limited by secondary effects by *Bromus*. Recruitment may have been limited by alteration of soil biota by *Bromus* (Jordan et al. 2008) as its presence in the soil alone has effects on establishment.

Seed Limitation

In both communities, seed limitation existed for a few, but not most sown species. Instead, most sown species were both seed and microsite limited, requiring both seed addition and microsites to establish. In the *Schizachyrium* community, greater species richness in seed + gap than gap plots showed that colonization from local sources (vegetative and by seed) had not yet saturated microsites, and/or species added were complementary to the existing species pool (Gilbert et al. 2009, Gomez 2009). In particular, seed addition to gaps augmented the perennial species pool that accounts for much of the diversity in grasslands.

Eight decades of moderate to heavy grazing at the site likely contributed to the rarity and low diversity of many species across the landscape (Hickman and Hartnett 2002), and the high % cover of the dominant species. However, removal of grazing seven years prior to the start of this study reduced the presence of microsites, as seen in the gradual loss of species over time from control plots at this site (McNicoll and Augspurger Ch. 1 and 2) and low recruitment in other studies (Wilsey and Polley 2003). Existing soil disturbances are present in both communities, but may not be sufficient to provide enough suitable microsites. Thus, at this site, native diversity is restricted by both lack of appropriate disturbances and restricted seed pools of long-lived perennial species in both communities. The *Bromus* community is further restricted by seed limitation of fugitive and other native species present in greater abundance in the *Schizachyrium* vegetation and seed bank. Differences in their species pools and seed limitation is likely a combination of the characteristics of each dominant grasses' coexistence with non-dominant species and differing site histories that altered the species pool.

Conclusion

The effects of microsite creation and seed limitation are context dependent, depending on the rate at which microsites are re-colonized by dominant grasses and the presence of a local species pool. Disturbances have the potential to enhance landscape and community diversity in the presence of an abundant local species pool, as long as gaps remain open for a period of time. In native grass dominated communities, such disturbances may come from native fossorial animals, although addition of species dispersal limited across the landscape likely need to be added as seed. However, this study has demonstrated the importance of small vegetation-free gaps in native grasslands to maintain populations of fugitive species. In contrast, it is difficult to envision change to communities dominated by *Bromus*, from only the creation of small microsites or seed addition, without the reduction of *Bromus* from the community as a whole.

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CHAPTER 5: GENERAL CONCLUSIONS

Chapter 1. Overall, this study found support for effects of both identity of dominant grasses and past history on non-dominant community structure, species composition, and community dynamics over time. Contrasting patterns of non-dominant species regeneration and growth indicate that the combination of dominant grass identity and unique aspects of site history will continue to influence the progression of this site's recovery from long-term grazing.

Chapter 2. The extent of dominant species reduction depended on species identity and amount of tissue loss, which in turn determined whether or not the non-dominant community benefitted from reduced competition. In contrast, newly disturbed microsites fostered colonization in both communities, which was less dependent on dominant identity. The divergent responses of the two dominant grasses indicate the importance of species identity when pairing management techniques and dominant reduction. Our results also show that annual spring mowing is a tool managers may use for control of *Bromus*. In addition, the independent response of non-dominant community structure to disturbances that reduce competition from those that stimulate new colonization indicates the importance multifaceted disturbances in restoration and maintenance of non-dominant species diversity in grasslands.

Chapter 3. Low recruitment in gaps in the *Bromus* community may indicate inferior microsites and/or greater seed limitation in that community. In contrast, the low establishment of sown species in undisturbed vegetation showed that traits common to both dominant species, such as high production of biomass and dead vegetation, may make communities difficult to invade, regardless of dominant species identity. Finally, results for combined gap and seed addition plots indicate removal of multiple limitations is necessary to achieve the greatest change in community structure and species composition, independent of dominant species identity.

FIGURES AND TABLES

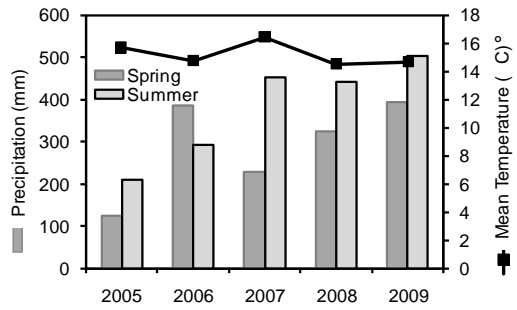


Figure 1.1. Total precipitation for spring (March-May) and summer (June-August) and mean daily temperatures for the growing-season (March-August) for 2005-2009 (Illinois State Climatologist's office).

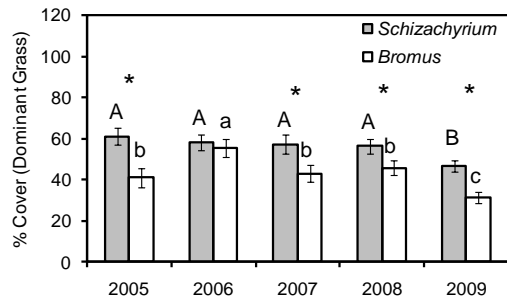


Figure 1.2. Percent cover (mean per plot \pm SE) of the dominant grass (*Schizachyrium scoparium* or *Bromus inermis*) in two communities over five years. * indicates a significant difference ($p < 0.05$) between communities in a particular year. Different letters of the same size of letters indicate significant differences ($p < 0.05$) among years within a given community.

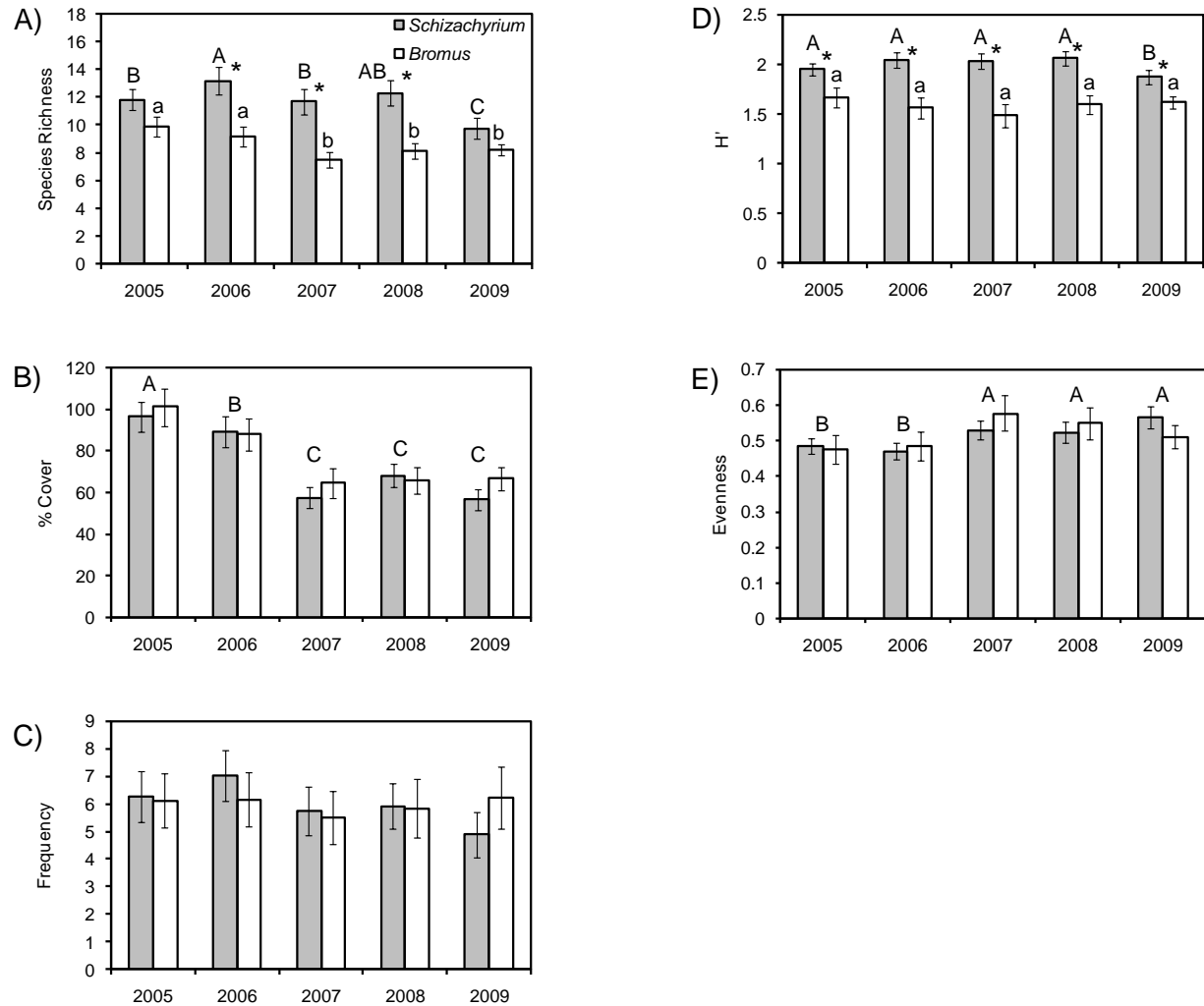


Figure 1.3. Community structure (species richness, % cover, frequency, diversity (H') and evenness) of non-dominant species in communities dominated by either *Schizachyrium scoparium* or *Bromus inermis* over five years. A, B, D, and E represent mean per plot \pm SE; C represents mean frequency of occurrence per species \pm SE. In A and D, * indicates a significant difference ($p < 0.05$) between communities in a particular year. Different letters of the same size letter indicate significant differences ($p < 0.05$) between years within a given community. In B, C and E, communities did not differ significantly; therefore, different letters represent significant differences ($p < 0.05$) between years, pooled between communities.

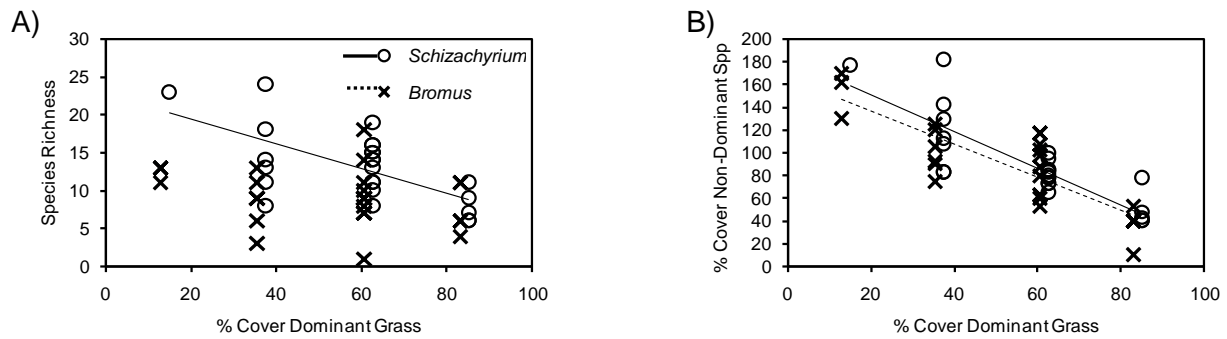


Figure 1.4. Species richness and % cover of non-dominant species as a function of % cover of dominant grass in 2006. Significant relationships in each community are indicated by presence of a regression line ($p < 0.01$) (A) *Schizachyrium*: $R^2 = 0.41$; (B) *Schizachyrium*: $R^2 = 0.69$, *Bromus*: $R^2 = 0.68$; comparison of slopes between communities: NS. Regressions were run in proc reg and slope comparisons were based on interactions in proc glm (SAS).

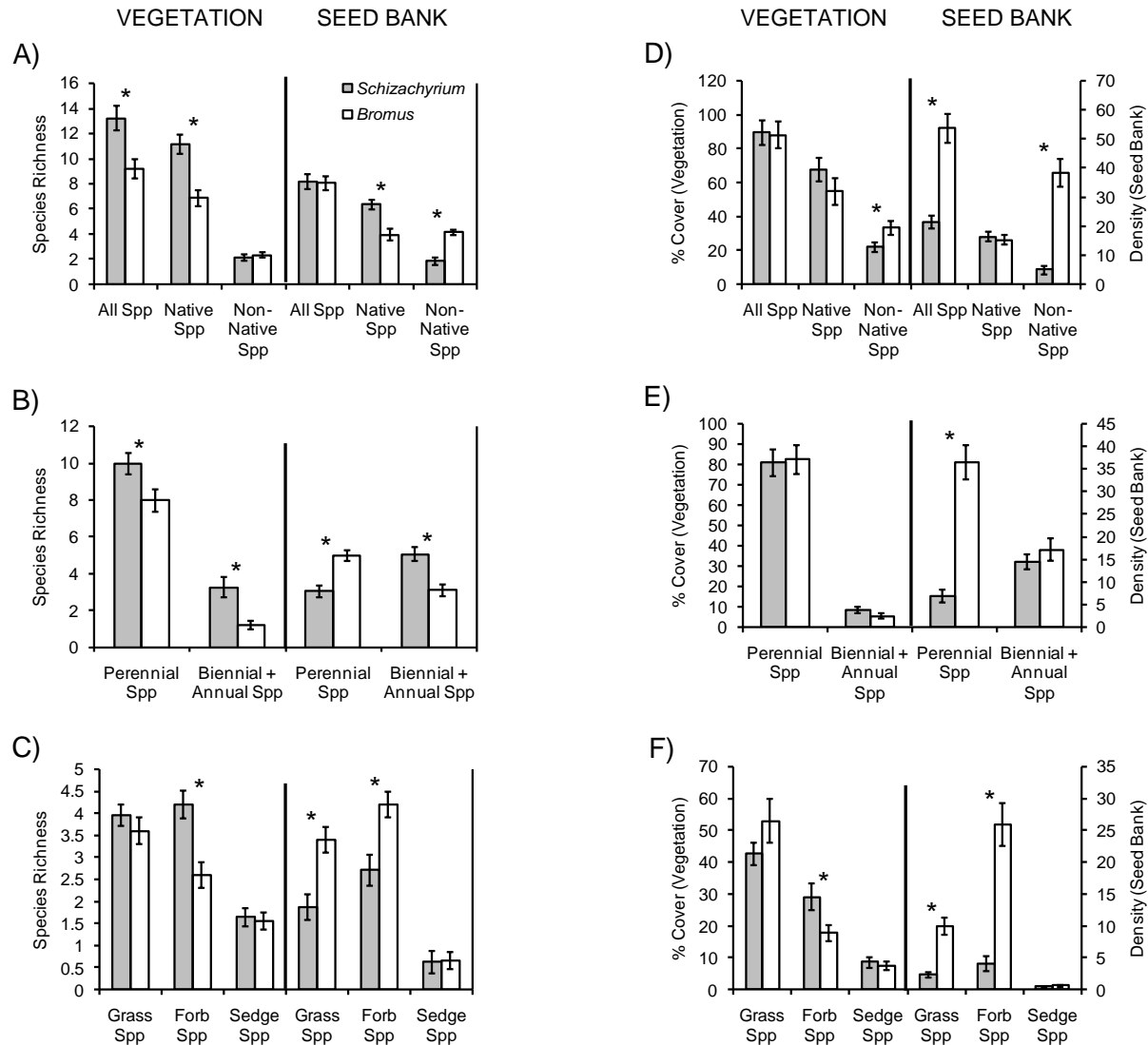


Figure 1.5. Community structure (mean per plot \pm SE) based on plant traits of non-dominant species in the vegetation and seed bank of two communities dominated by *Schizachyrium scoparium* or *Bromus inermis* in 2006. Species richness (A-C) and abundance (percent cover or density) (D-F) are shown for: all species combined and location of origin (A,D), life history (B,E), and functional guild of perennial species (C,F). Biennials and annuals were grouped together for analysis to improve normality of data; perennial legumes, present at low abundance, were dropped from statistical comparisons. Comparisons are limited to each paired set of bars (e.g. % cover of forb species between *Schizachyrium* and *Bromus* communities).

* above a category indicates a significant difference ($p < 0.05$) between communities (using a Bonferroni correction for multiple comparisons). Dominant grass cover was included as a covariate in vegetation analyses and was significant for all comparisons except % cover of non-native and sedge species and species richness of forb and sedge species. Interactions between community and % cover of dominant grass were significant for native, perennial, and perennial forb species richness.

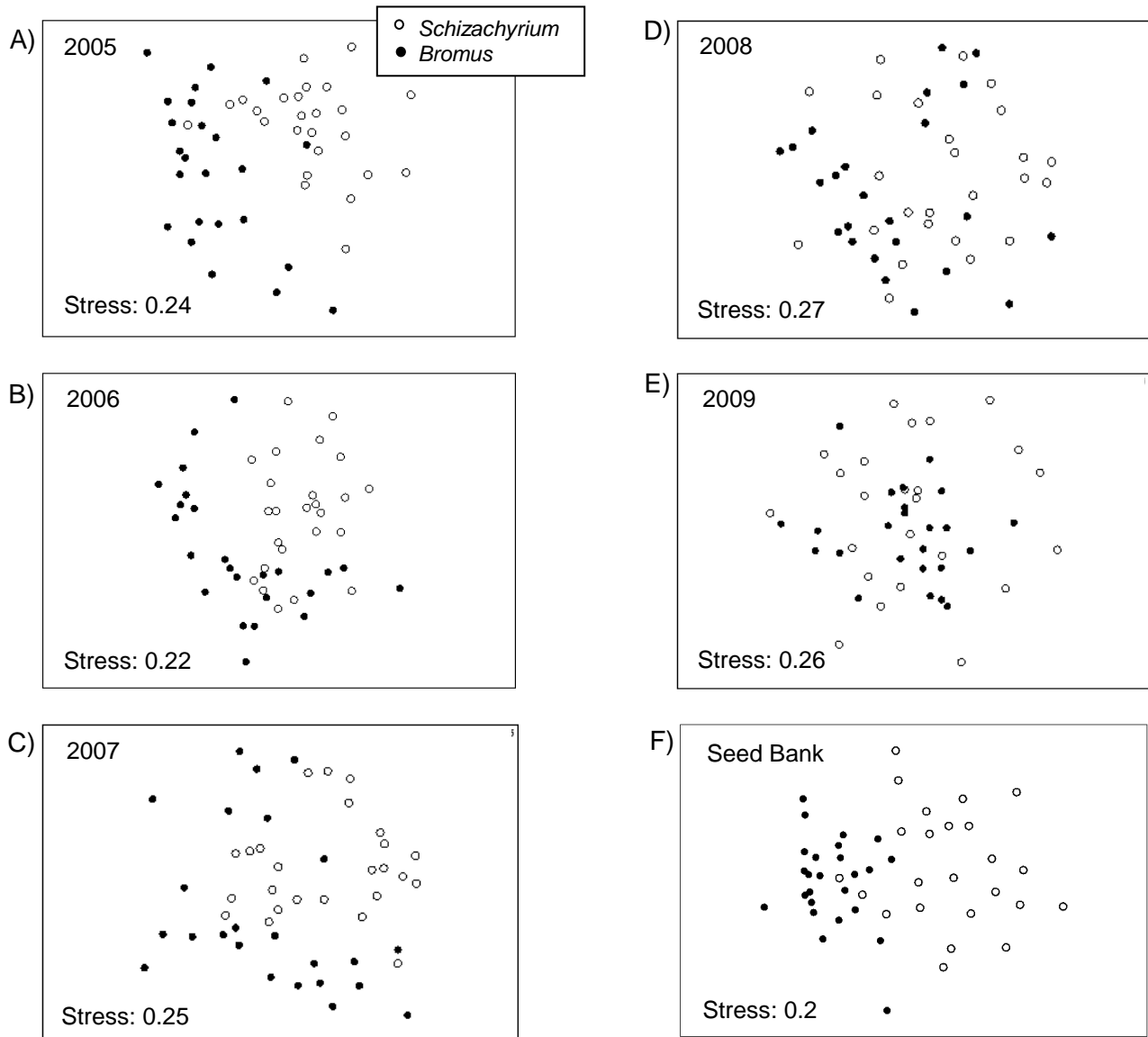


Figure 1.6. Non-dominant species similarity within and between *Bromus* and *Schizachyrium* communities visualized in non-metric multi-dimensional scaling (NMDS) diagrams. Each point represents an individual plot; its placement relative to other points is based on Bray-Curtis similarity indices calculated for the vegetation from 2005-09 (A-E) and the seed bank (F). There is no absolute scale for each diagram, but the rank order of similarity between plots is maintained within the diagram (i.e., plots grouped more closely together are more similar and vice-versa). Stress values on each NMDS diagram represent interpretability of relative placement of plots. As a general rule, lower stress values represent greater interpretability and values above 0.35 should not be interpreted (Clarke 1993).

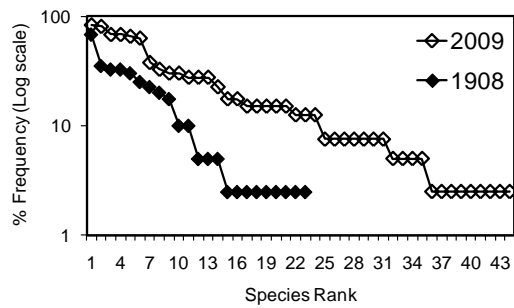


Figure 1.7. Percent frequency of species according to rank of species in 1908 (from Gleason 1910) and 2009. % frequency = # of plots in which a species occurred / 40 total plots x 100.

Table 1.1. Repeated measure ANOVAs comparing community structure of non-dominant species in communities dominated by either *Schizachyrium scoparium* or *Bromus inermis* over five years (2005-2009) and covariance with % cover of dominant grass. Significantly different responses are in bold. See Methods for descriptions of statistical tests.

		Species Richness		% Cover		Frequency		Diversity (H') (Shannon-Weiner)		Evenness (log ^e)	
Effect	df	F	P	F	P	F	P	F	P	F	P
Community	1	16.14	0.0002	1	0.3251	0.02	0.9869	16.3	0.0002	8.7	0.8924
Year	4	15.31	<.0001	64.4	<.0001	10.22	0.6594	2.3	0.0578	2.0	0.0002
Community x Year	4	5.69	0.0003	0.8	0.524	8.74	0.7781	3.6	0.0080	0.7	0.5049
% Cover of Dominant Grass	1	8.55	0.0038	62.3	<.0001	N/A	N/A	1.7	0.2257	0.5	0.0040

Table 1.2. Mean Bray-Curtis similarity values of species abundance and composition within and between *Bromus* and *Schizachyrium* communities for the vegetation (2005-2009) and seed bank (2006). Test statistics for non-parametric comparison between communities (ANOSIM): Global R represents the dissimilarity between communities (i.e., decreasing dissimilarity of vegetation over time). For reference purposes, a global R value of 0 indicates the same average within- and between-community similarity; as values approach 1, there is increasing similarity within, but not between communities (Clarke 1993). The p-value indicates the probability that there are no differences between the two communities (based on Bray-Curtis values).

Year	Bray-Curtis Similarity			ANOSIM (Between-Communities)	
	Within-Community		Between-Communities	Global R	P-value
	<i>Schizachyrium</i>	<i>Bromus</i>			
2005	37	32	27	0.338	< 0.01
2006	36	31	27	0.28	< 0.01
2007	32	27	24	0.224	< 0.01
2008	31	30	27	0.179	< 0.01
2009	30	40	31	0.165	< 0.01
Seed Bank	28	47	21	0.511	< 0.01

Table 1.3. Total number of species present in 1908 and 2009 surveys summed for categories of three plant traits.

Category:	Location Of Origin		Life History			Functional Guild (Perennials)				
	Native	Non	Peren	Bien	Ann	Grass	Forb	Sedge	Legume	Other
1908	23	0	19	2	2	7	10	1	1	0
2009	41	2	31	2	10	12	10	5	1	3

Table 1.4. Species reported in greater than 25 % of plots in either 1908 or 2009 surveys. All species were native perennials. Species were ranked according to decreasing frequency in a given survey year (1908 or 2009); identical frequencies were assigned the same rank; not all species from original surveys are listed. % frequency = # of plots in which a species occurred / 40 total plots x 100. **A. linariifolius* was absent from 2009 plots, but was present in the vicinity. *A. verticillata* was not listed in 1908.

Family	Species	Perennial Guild	Rank 1908	% Frequency 1908	Rank 2009	% Frequency 2009
Poaceae	<i>Leptoloma cognatum</i>	Grass	1	67.5	17	15
Poaceae	<i>Koeleria macrantha</i>	Grass	2	35	6	62.5
Poaceae	<i>Schizachyrium scoparium</i>	Grass	3	32.5	1	82.5
Poaceae	<i>Panicum villosissimum</i>	Grass	3	32.5	3	67.5
Asteraceae	<i>Aster</i>	Forb	5	30	*	*
Malvaceae	<i>Callirhoe triangulata</i>	Forb	6	25	36	2.5
Asteraceae	<i>Ambrosia psilostachya</i>	Forb	9	17.5	2	80
Selaginellaceae	<i>Selaginella rupestris</i>	Non-Flowering	15	2.5	3	67.5
Asclepiadaceae	<i>Asclepias verticillata</i>	Forb	*	*	5	65

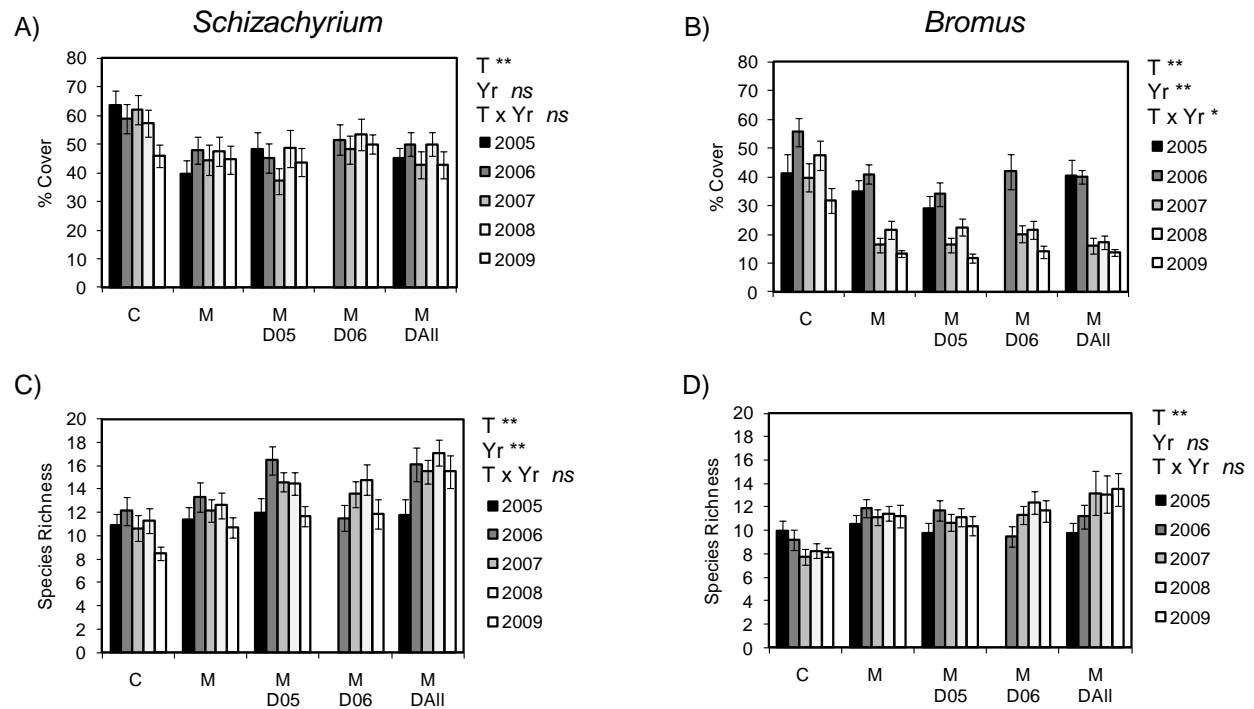


Figure 2.1. Percent cover (mean per plot \pm SE) of the dominant grass (*Schizachyrium scoparium* or *Bromus inermis*) and species richness (mean per plot \pm SE) in two communities with four different disturbance regimes over five years. Treatments are: control (C), 5 years of mowing only (M), 5 years of mowing with a single year of raking disturbance in 2005 (M D05), 4 years of mowing with raking disturbance in 2006 (M D06), and 5 years of mowing and raking 2005-2009 (M DAll). R-ANOVA results along the edge of each panel show statistical significance for main effects of treatment (T), year (Yr), and treatment x year interaction effects (T x Yr) at the $p < 0.01$ (**), $p < 0.05$ (*), and ns (not significant) level.

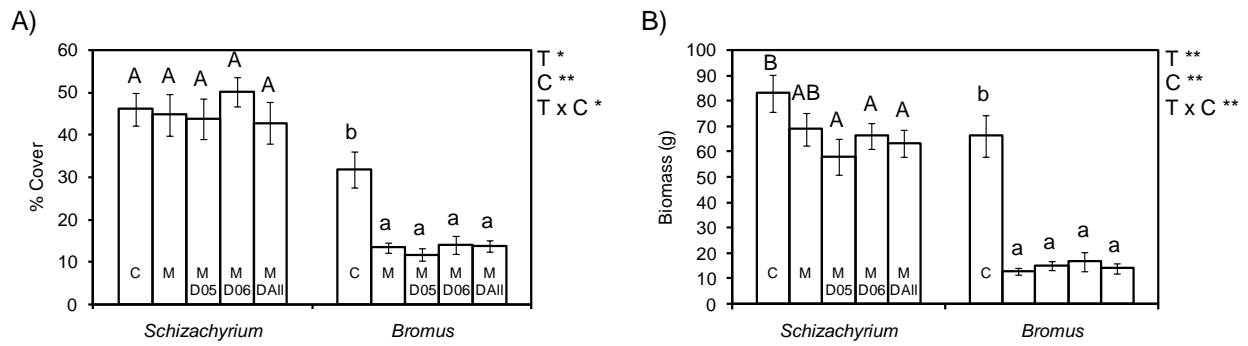


Figure 2.2. Percent cover and biomass (mean per plot \pm SE) of the dominant grass (*Schizachyrium scoparium* or *Bromus inermis*) in two communities in 2009 subjected to different disturbance treatments: control (C), 5 years of mowing only (M), 5 years of mowing with a single year of raking disturbance in 2005 (M D05), 4 years of mowing with raking disturbance in 2006 (M D06), and 5 years of mowing and raking 2005-2009 (M DAll). Treatment labels were omitted where size of bars did not allow, but treatments remain in same location as other labeled graphs. ANOVA summaries along the edge of each panel show statistical significance for main effects of treatment (T), community (C), and treatment x community interaction effects (T x C) at the $p < 0.01$ (**), $p < 0.05$ (*), and ns (not significant) level (detailed ANOVA results are in Table 2.2). Different letters of the same size of letters indicate significant differences ($p < 0.05$) among treatments within a given community (post-hoc).

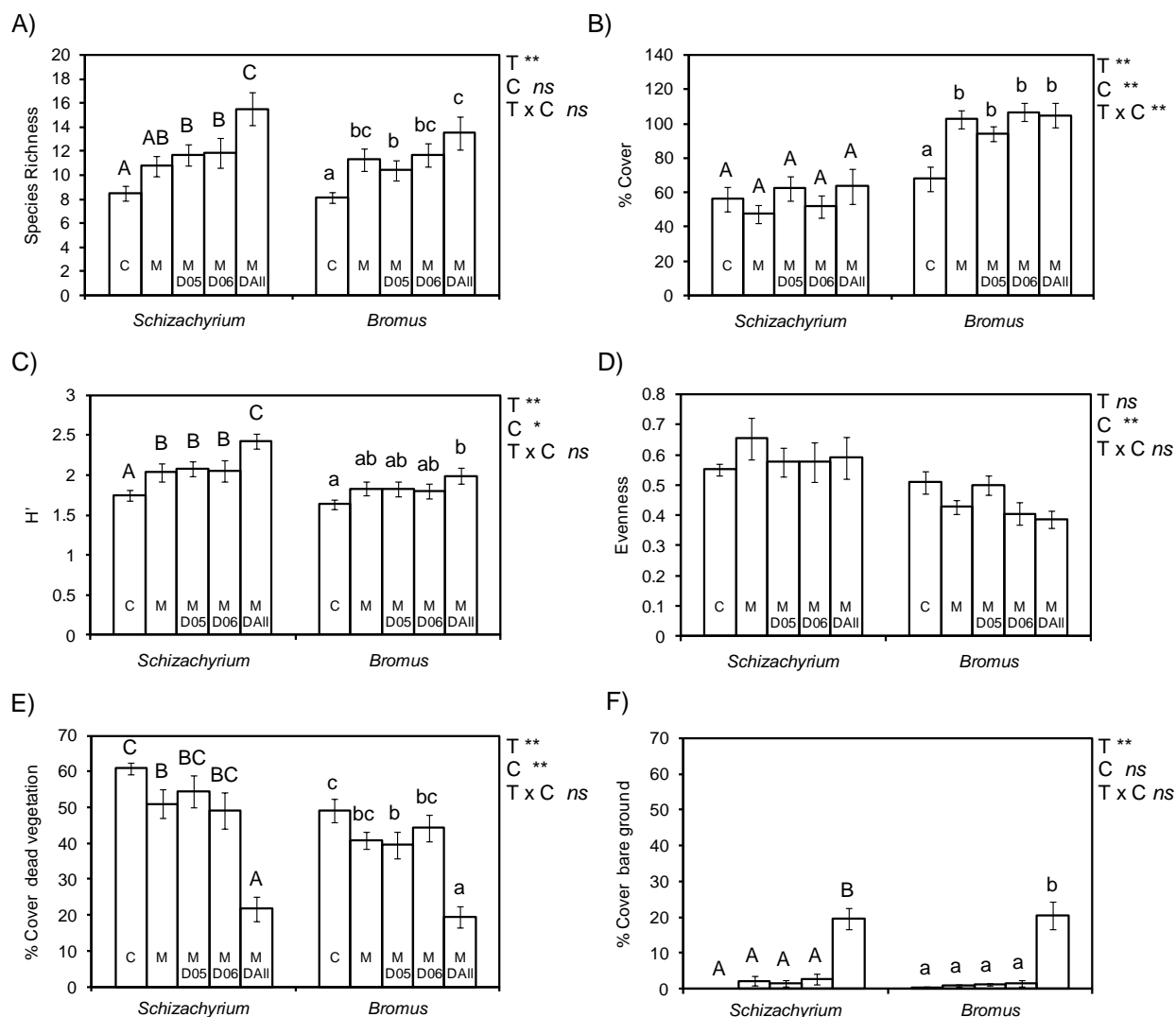


Figure 2.3. Community structure (species richness, % cover, diversity (H') and evenness) of non-dominant species, and % cover of dead vegetation and bare ground in 2009 in two communities with different disturbance regimes. Treatments, ANOVA summaries along the edge of each panel, and letters indicating significant differences among treatments are the same as in Fig. 2.2.

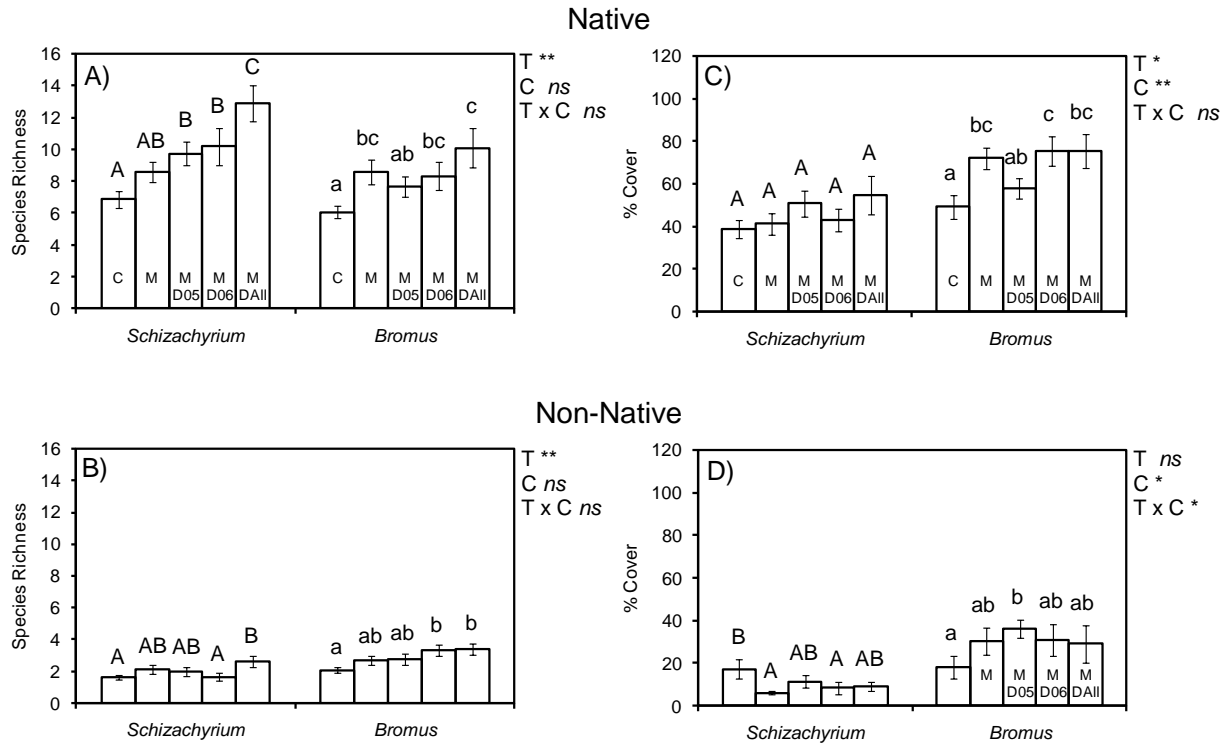


Figure 2.4. Community structure (mean per plot \pm SE) of non-dominant species according to plant traits in 2009 in two communities with different disturbance regimes. Treatments, ANOVA summaries along the edge of each panel, and letters indicating significant differences among treatments are the same as in Fig. 2.2.

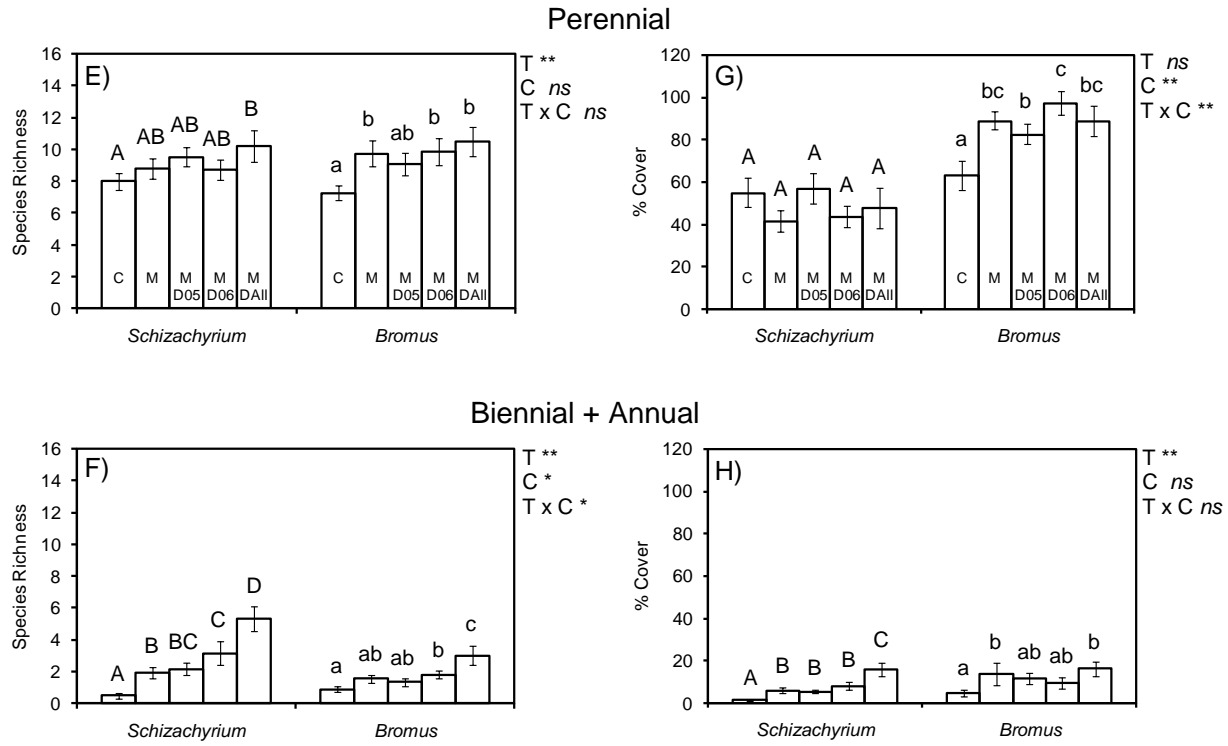
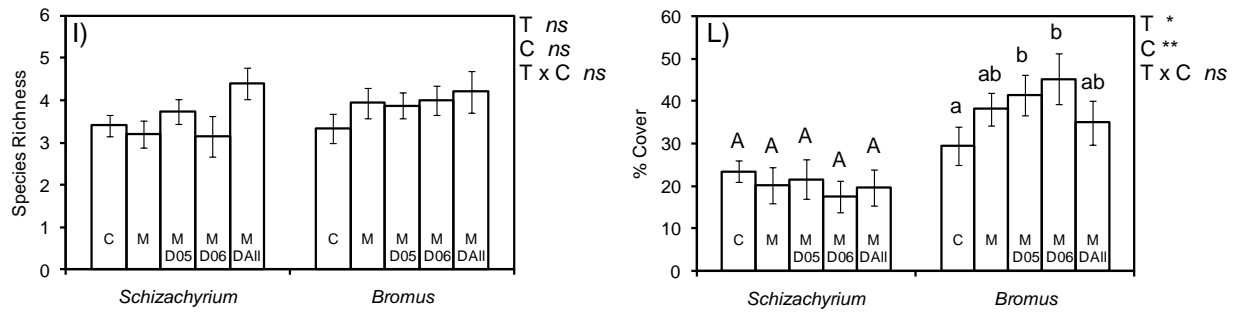
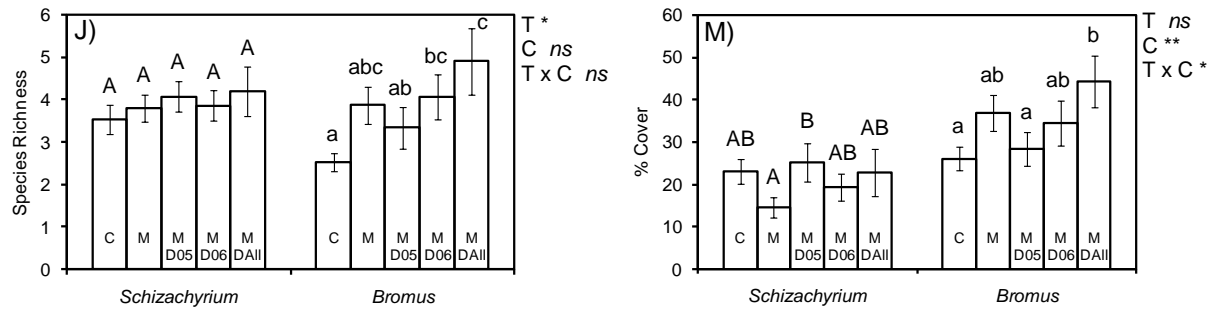


Figure 2.4 (cont.)

Perennial Grasses



Perennial Forbs



Perennial Sedges

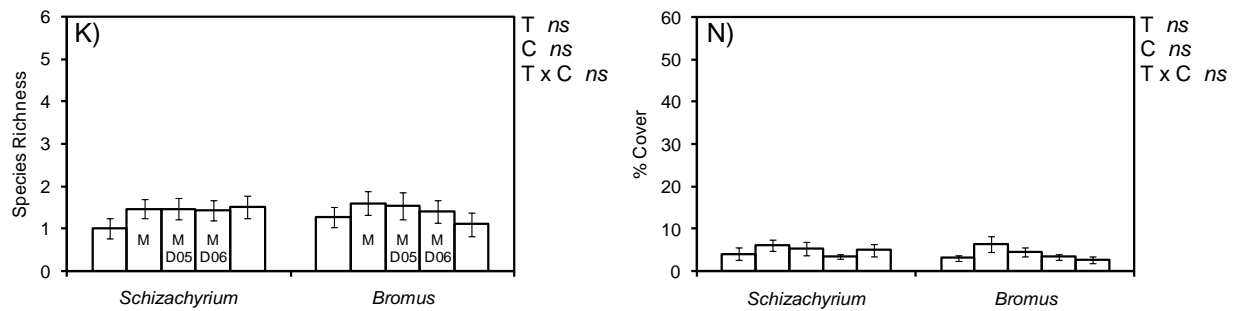


Figure 2.4 (cont.)

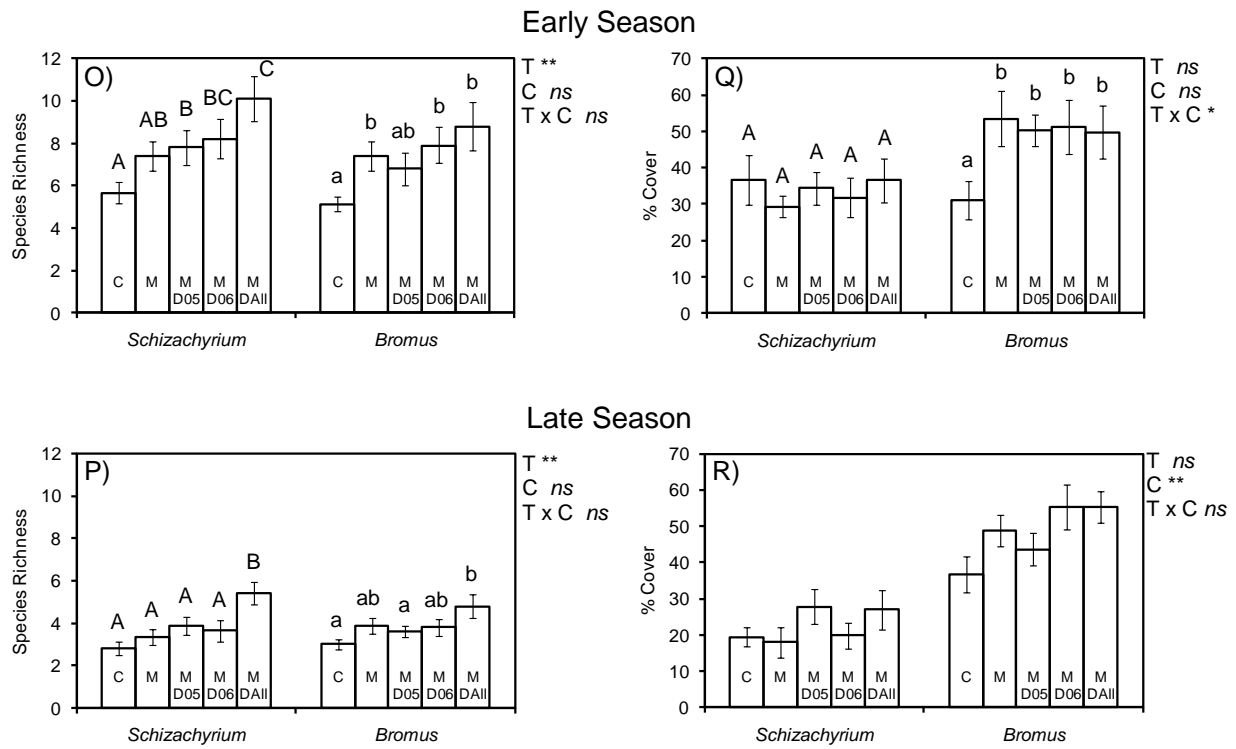


Figure 2.4 (cont.)

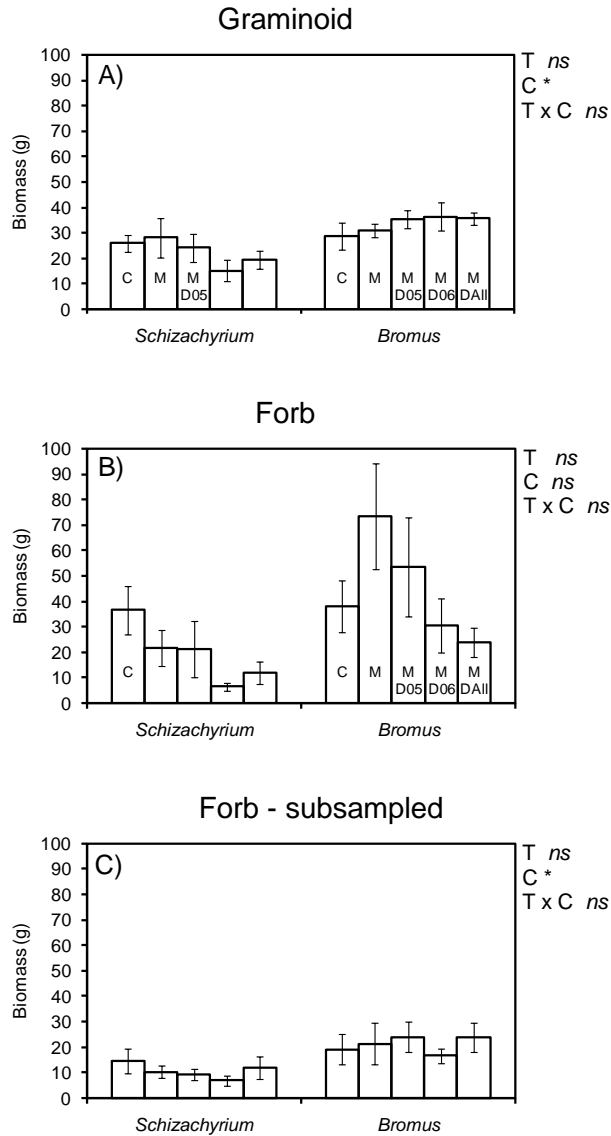


Figure 2.5. Biomass (mean per plot \pm SE) of non-dominant species in 2009 in two communities with different disturbance regimes. Treatments, ANOVA summaries along the edge of each panel, and letters indicating significant differences among treatments are the same as in Fig. 2.2.

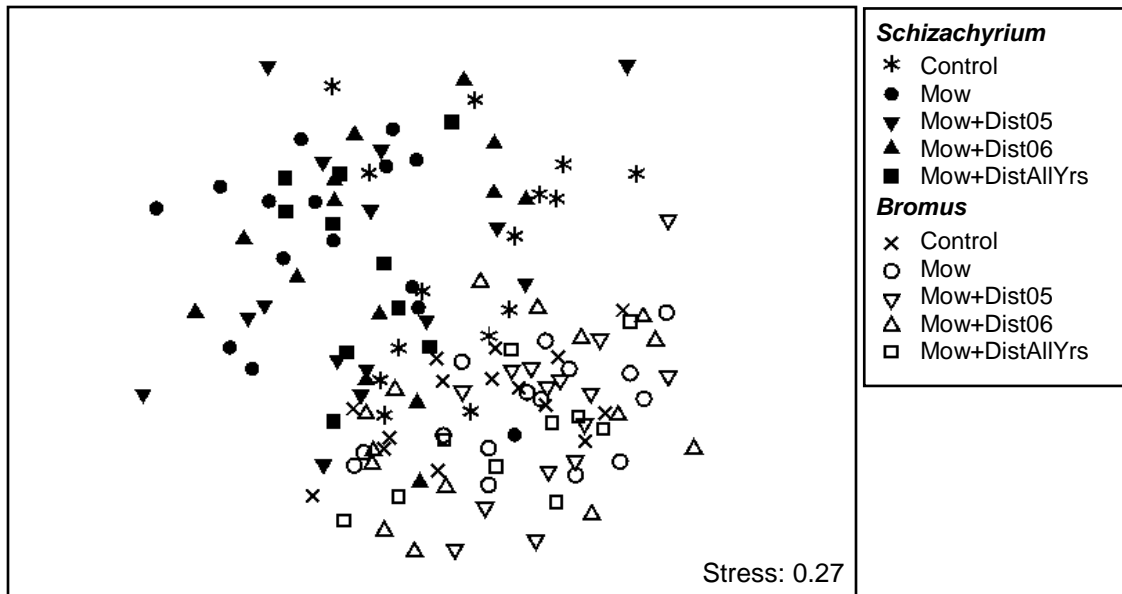


Figure 2.6. Non-metric multi-dimensional scaling (NMDS) diagram showing similarity of non-dominant species composition and abundance within and among treatments in the *Schizachyrium* and *Bromus* communities in 2009. A point represents an individual plot. Similarity is judged based on relative placement within diagram, with points closer together being more similar than those further apart. Stress value indicates the interpretability of relative placement of plots (with stress values closer to 0 as ideal and above 0.35 being unreliable) (Clarke 1993).

Table 2.1. ANOVA statistics (F) and significance (P) of the response of the dominant grass, either *Schizachyrium scoparium* or *Bromus inermis*, community structure of non-dominant species, dead vegetation, and bare ground to: experimental disturbances (treatment), dominant grass (community), and interaction effects (treatment x community) in the final year (2009) of the study. Statistically significant results ($p < 0.05$) are in bold.

	Treatment		Community		Treatment x Community	
	F	P	F	P	F	P
DOMINANT GRASS	(df* =4, 30)		(df = 1, 8)		(df = 4, 30)	
% Cover	3.67	0.0147	40.19	0.0002	3.08	0.0302
Biomass (sqrt)	20.38	<.0001	53.27	<.0001	7.17	0.0004
NON-DOMINANT SPECIES	(df = 4, 121)		(df = 1, 8)		(df = 4, 121)	
Species Richness	11.35	<.0001	0.39	0.5472	0.57	0.6851
% Cover	3.83	0.0058	29.72	0.0006	4.84	0.0012
Diversity (H')	7.40	<.0001	5.35	0.0489	0.75	0.5623
Evenness (sqrt) †	0.88	0.4849	12.04	0.0082	1.43	0.2469
DEAD VEGETATION	(df = 4, 120)		(df = 1, 8)		(df = 4, 120)	
% Cover	24.31	<.0001	11.72	0.0085	0.82	0.5138
BARE GROUND	(df = 4, 26)		(df = 1, 8)		(df = 4, 26)	
% Cover	37.01	<.0001	0.09	0.7780	0.16	0.9572

*Error degrees of freedom (df), calculated in SAS 9.0, varied among response variables based on covariance structure of random variables (Littell et al. 2002). Results are more conservative with this method (i.e., theoretically less Type 1 error), but did not change the overall significance of any variable.

†Error degrees of freedom for evenness: (df=4, 30; 1, 8; and 4, 30).

Table 2.2. Species richness at the community level in the first (2005) and last (2009) year of the study and the loss or gain in species richness (2009 – 2005) for four disturbance and control treatments in both focal communities. Treatments: control (C), 5 years of mowing only (M), 5 years of mowing with a single year of raking disturbance in 2005 (M D05), 4 years of mowing with a single year of raking disturbance in 2006 (M D06), and 5 years of mowing and raking 2005-2009 (M DAll). Number in parentheses = number of replicate plots.

	<i>Schizachyrium</i>					<i>Bromus</i>				
	C (15)	M (15)	M D05 (15)	M D06 (15)	M DAll (10)	C (15)	M (15)	M D05 (15)	M D06 (15)	M DAll (10)
2005	39	42	50	41	37	34	37	41	33	35
2009	34	41	51	50	50	29	43	40	44	44
Change over time	- 5	- 1	+ 1	+ 9	+13	- 5	+ 6	- 1	+11	+9

Table 2.3. ANOVA statistics (F) and significance (P) for comparisons of species richness, % cover, and biomass of non-dominant species in response to experimental disturbances (treatment), dominant vegetation identity (community), and interaction effects (treatment x community) in the final year (2009) of the study. Separation of species by plant traits is explained in Methods. Statistically significant results are in bold.

	Treatment (df)		Community		Community x Treatment	
	F	P	F	P	F	P
SPECIES RICHNESS	df^*		df^*		df^*	
Native	9.54	<0.0001	3.61	0.0931	0.98	0.4224
Non-native	4.49	0.0050	4.81	0.0593	1.70	0.1713
Perennial	4.26	0.0067	0.07	0.7962	0.87	0.4919
Biennial + Annual	19.34	<0.0001	5.28	0.0505	3.17	0.0163
Perennial Grass	1.93	0.1096	0.61	0.4562	1.01	0.4030
Perennial Forb	3.20	0.0247	0.08	0.7840	1.34	0.2741
Perennial Sedge	1.14	0.3419	0.00	0.9884	0.53	0.7117
Early Season	8.55	<0.0001	0.42	0.5336	0.26	0.9025
Late Season	7.13	0.0004	0.00	0.9931	0.59	0.6742
% COVER	$df = 4, 121$		$df = 1, 8$		$df = 4, 121$	
Native	3.31	0.0130	20.27	0.0018	2.09	0.0864
Non-native**	0.58	0.6758	5.43	0.0461	3.04	0.0200
Perennial	1.35	0.2552	35.31	0.0003	5.08	0.0008
Biennial + Annual	6.12	0.0002	1.45	0.2629	0.81	0.5228
Perennial Grass**	2.40	0.0534	18.30	0.0023	1.54	0.1948
Perennial Forb	1.20	0.3135	19.80	0.0019	2.78	0.0299
Perennial Sedge	2.33	0.0602	0.24	0.6395	0.33	0.8557
Early Season	1.06	0.3812	3.37	0.1034	2.42	0.0517
Late Season	2.27	0.0659	34.46	0.0003	2.04	0.0931
BIOMASS (sqrt)	df^*		df^*		df^*	
Graminoid	0.36	0.8349	6.34	0.0361	1.41	0.2509
Forb	2.57	0.0562	2.95	0.1237	1.03	0.4057
Forb - subsampled	0.58	0.6760	6.48	0.0350	0.33	0.8579

*Degrees of freedom (df) for species richness of native, biennial + annual, grass, sedge, and early: (df=4, 121; 1, 8; and 4, 121); non-native, perennial, and forb: (df=4, 34; 1, 8; and 4, 34); late (df=4, 30; 1, 8; and 4, 30); and for biomass of graminoid and forb: (df=4, 33; 1, 8; and 4, 33); forb – subsampled: (df=4, 84; 1, 8; and 4, 84). See footnote in Table 2.1 for explanation of error degrees of freedom.

**Initial conditions included as covariate. Non-native initial conditions: df 1, 128; $F=7.56$; $p = 0.0068$. Perennial grass initial conditions: df 1, 127; $F=33.17$; $p = 0.0001$.

Table 2.4. Jaccard's indices of similarity comparing species in disturbance treatments to control plots (vegetation); and seed bank to the vegetation in both communities. Treatments and abbreviations are the same as in Table 2.2.

	<i>Schizachyrium</i>					<i>Bromus</i>				
	C	M	M D05	M D06	M DAll	C	M	M D05	M D06	M DAll
Vegetation: Control to Disturbance treatment (2009)	--	64	53	56	59	--	61	61	56	53
Seed bank (2006) to Vegetation (2009)	30	38	40	39	46	31	34	47	41	44

Table 2.5. Comparison of frequency of non-dominant species in the vegetation, i.e., number of occurrences across all plots (2009), based on the species' documented (or not) in the seed bank in both communities. Number in () is the number of species accounting for frequency. For this table only, to account for differences in the number of replicates, frequency values for 'M D All' were calculated by multiplying the actual frequency by 1.5; the number of species remains unchanged.

	<i>Schizachyrium</i>					<i>Bromus</i>				
	C	M	M D05	M D06	M DAll	C	M	M D05	M D06	M DAll
Documented in seed bank	73 (17)	105 (22)	105 (24)	106 (25)	161 (28)	83 (14)	119 (18)	115 (23)	117 (23)	137 (22)
Not documented in seed bank	54 (17)	56 (19)	70 (27)	60 (25)	72 (22)	39 (15)	50 (25)	41 (17)	58 (21)	66 (22)

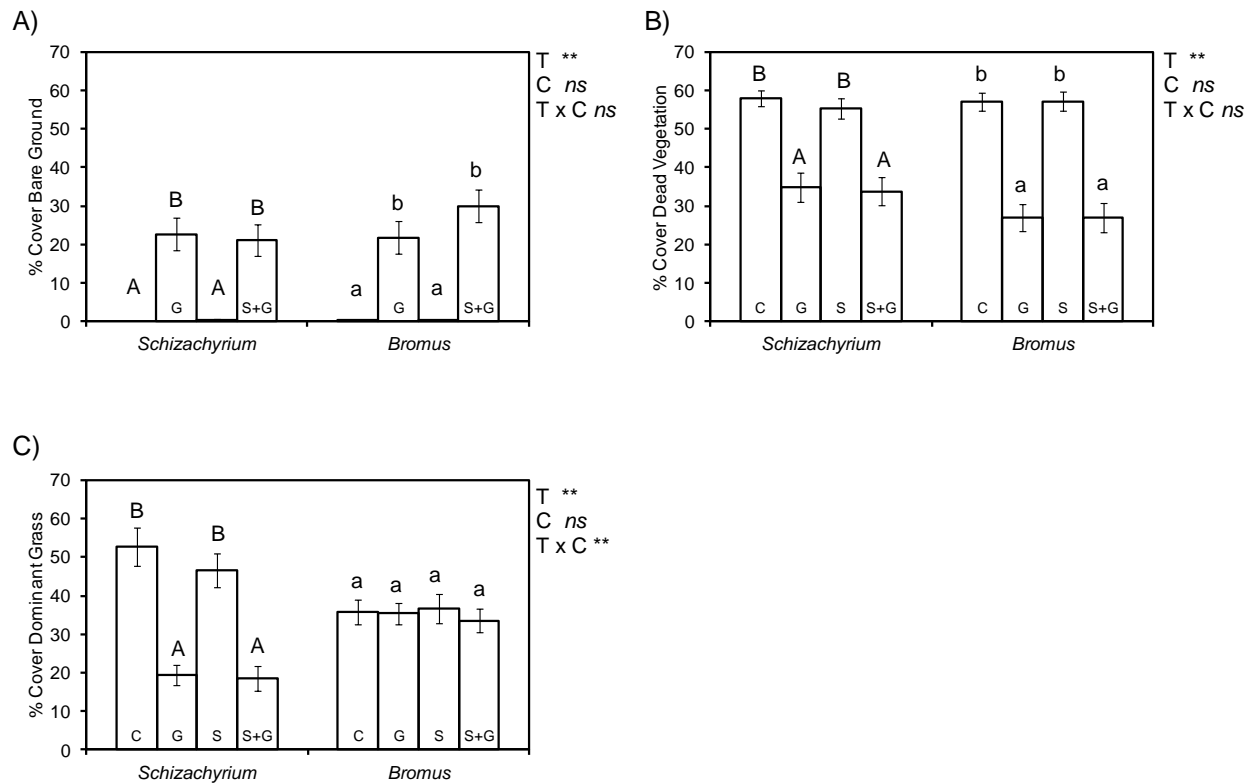


Figure 3.1. Percent cover (mean per plot \pm SE) of bare ground, dead vegetation, and the dominant grass (*Schizachyrium scoparium* or *Bromus inermis*) in four experimental treatments in each community in 2009. Treatments: control (C), above- and below-ground vegetation removed with bare soil replaced (G=Gap), seed addition to intact community with no disturbance (S=Seed), seed addition + gap disturbance (S + G = Seed + Gap). Treatment labels were omitted where size of bars did not allow, but treatments remain in same location as other labeled graphs. ANOVA results along the edge of each panel show statistical significance for main effects of treatment (T), community (C), and treatment x community interaction effects (T x C) at the $p < 0.01$ (**), $p < 0.05$ (*), and ns (not significant) level (Table 3.1). Different letters of the same size of letters indicate significant differences ($p < 0.05$) among treatments within a given community (post-hoc).

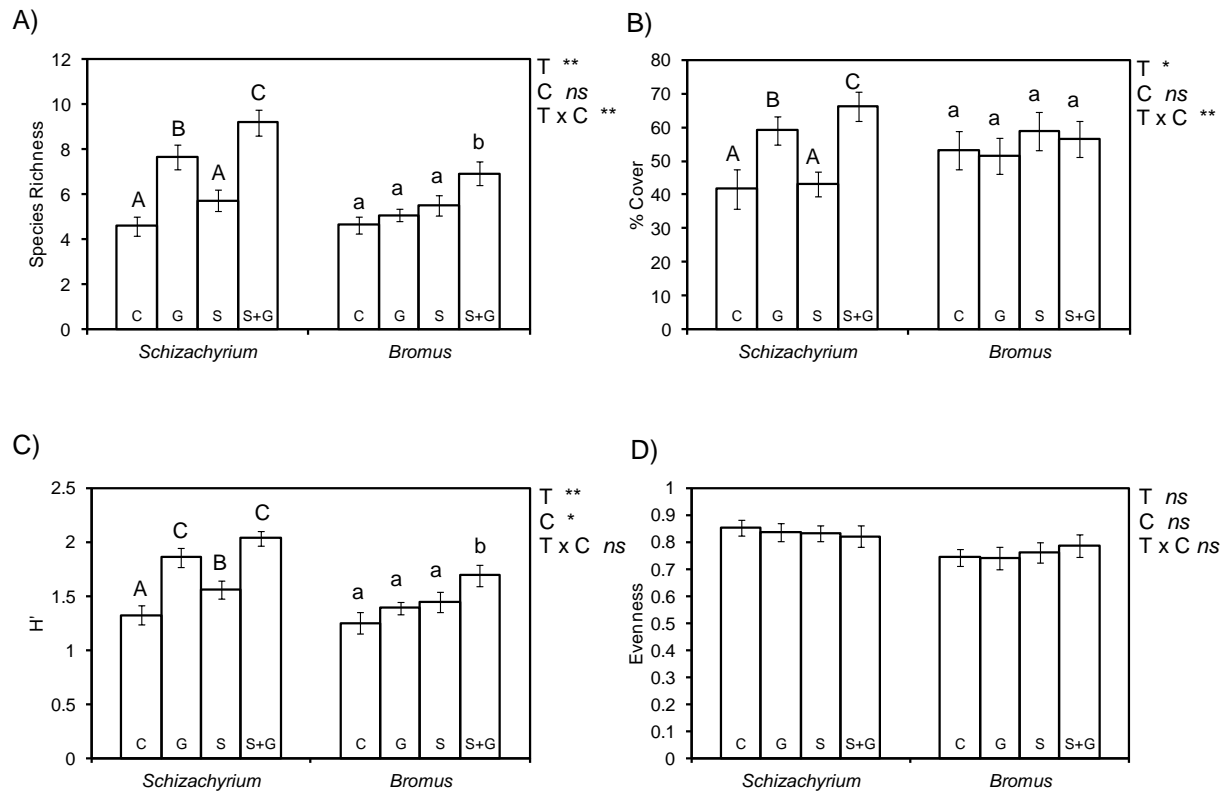


Figure 3.2. Community structure (species richness, % cover, diversity (H') and evenness) (mean per plot \pm SE) of non-dominant species, in seed-microsite limitation experimental treatments in both communities in 2009. See Figure 3.1 for treatments and statistical notations along and within each panel.

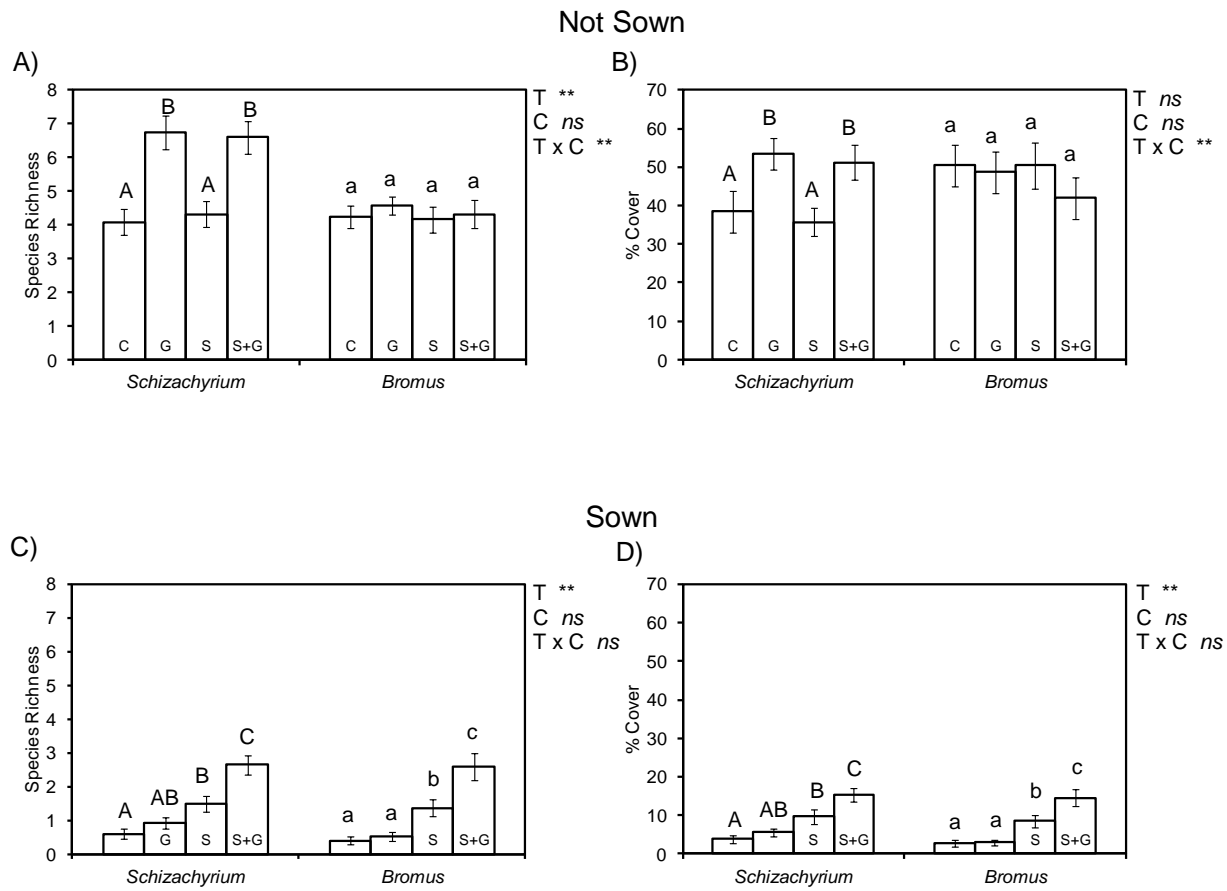


Figure 3.3. Species richness and % cover (mean per plot \pm SE) of non-dominant species, in seed-microsite limitation experimental treatments in both communities in 2009. Species 'not sown' are original to the community and 'sown' are species that are present in the local species pool, but were augmented with seed addition in seed-added plots (S, S + G). See Figure 3.1 for treatments and statistical notations along and within each panel.

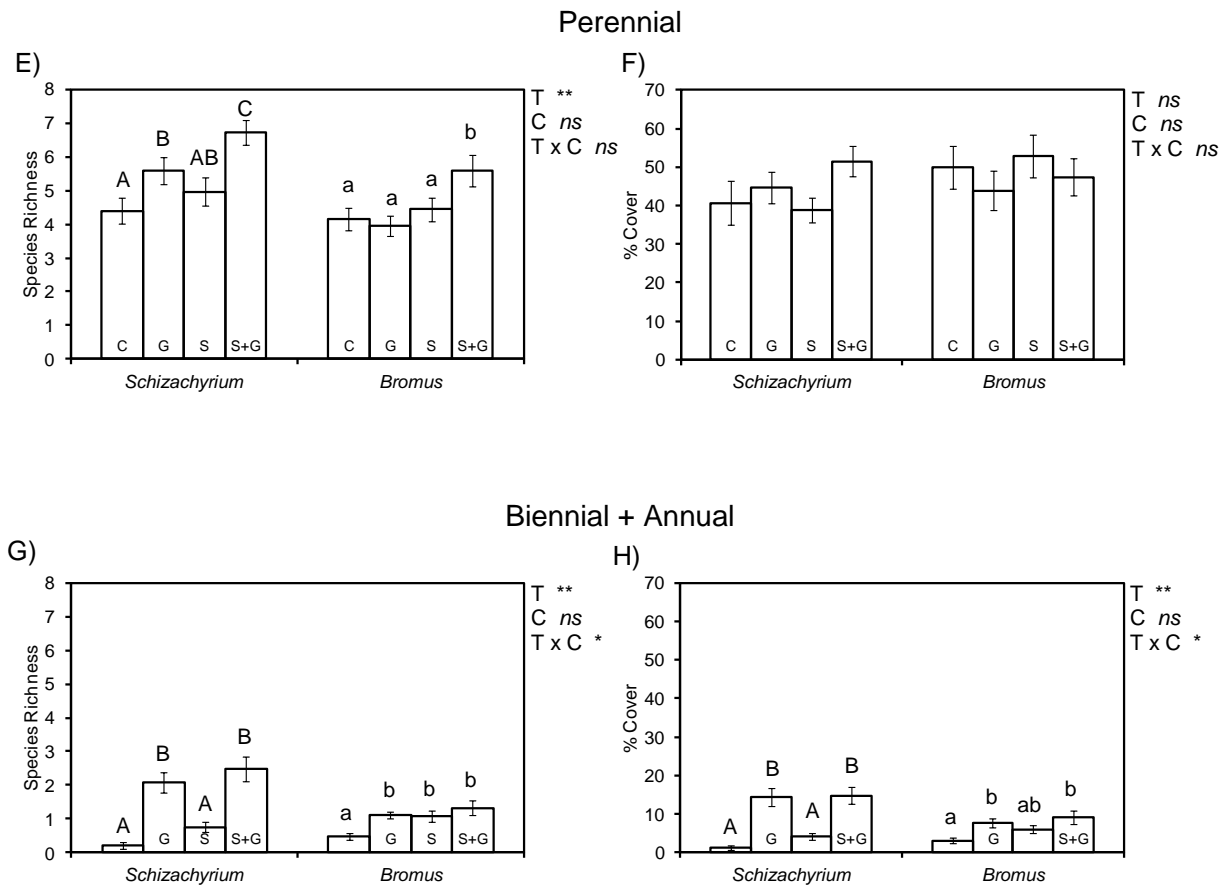


Figure 3.3 (cont.)

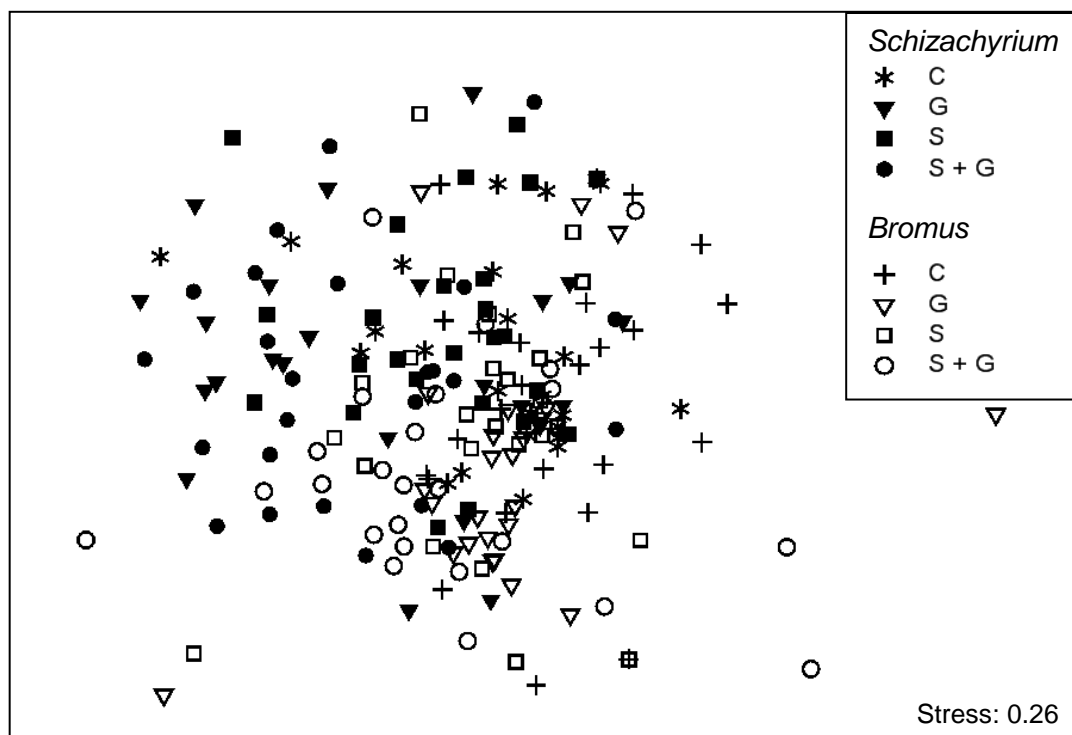


Figure 3.4. Non-metric multi-dimensional scaling (NMDS) diagram showing similarity of non-dominant species composition and abundance within and among seed-microsite limitation treatments in the *Schizachyrium* and *Bromus* communities in 2009. See Figure 3.1 for treatments abbreviations. A point represents an individual plot. Similarity is judged based on relative placement within diagram, with points closer together being more similar than those further apart. Stress value indicates the interpretability of relative placement of plots (with stress values closer to 0 as ideal and above 0.35 being unreliable) (Clarke 1993).

Table 3.1. Frequency of occurrence of 21 native species in 2009, sown in seed addition plots in 2007 and 2008. Treatments: control (C), above- and below-ground vegetation removed with bare soil replaced (G=Gap), seed addition to intact community with no disturbance (S=Seed), seed addition + gap disturbance (S + G = Seed + Gap). Species are classified according to family, life history (P = Perennial, B = Biennial, A = Annual) and guild (F = Forb, L = Legume, G = Grass, S = Sedge). Due to low recruitment observed after the initial seeding in 2007, the same species were added in 2008. *S. scoparium* was added only to *Bromus* plots. *A. cylindrica* was sown only in 2007, as seed was not available in 2008. All seed donated by Genesis Nursery, Tampico, IL.

Family	Species	Guild	Schizachyrium				Bromus			
			C	G	S	S + G	C	G	S	S + G
Fabaceae	<i>Amorpha canescens</i>	PL	0	0	0	1	0	0	0	2
Ranunculaceae	<i>Anemone cylindrica</i>	PF	0	0	1	3	0	0	0	1
Asteraceae	<i>Brickellia eupatoriodes</i>	PF	0	0	0	0	0	0	0	0
Cyperaceae	<i>Carex bicknellii</i>	PS	0	0	0	0	0	0	0	0
Cyperaceae	<i>Carex muhlenbergii</i>	PS	4	1	4	*	4	3	4	*
Caesalpiniaceae	<i>Chamaechrista fasciculata</i>	AL	0	0	12	14	0	0	12	10
Asteraceae	<i>Coreopsis palmata</i>	PF	0	0	0	0	0	0	0	1
Fabaceae	<i>Dalea purpurea</i>	PL	0	0	0	5	0	0	0	5
Asteraceae	<i>Echinacea pallida</i>	PF	0	0	2	10	0	0	1	11
Poaceae	<i>Elymus canadensis</i>	PG	0	0	0	0	0	0	0	0
Euphorbiaceae	<i>Euphorbia corollata</i>	PF	0	0	6	7	0	0	7	8
Poaceae	<i>Koeleria macrantha</i>	PG	7	5	8	5	2	1	1	2
Fabaceae	<i>Lespedeza capitata</i>	PL	0	1	2	4	0	0	4	5
Asteraceae	<i>Liatris aspera</i>	PF	1	0	0	0	0	0	0	1
Onagraceae	<i>Oenothera biennis</i>	BF	0	0	0	3	0	0	0	1
Poaceae	<i>Panicum oligosanthos</i>	PG	1	10	1	3	4	7	2	3
	<i>var. scribnerianum</i>									
Poaceae	<i>Schizachyrium scoparium</i>	PG	0	0	0	0	0	0	2	5
Asteraceae	<i>Solidago nemoralis</i>	PF	0	1	0	0	0	0	0	0
Asteraceae	<i>Solidago rigida</i>	PF	0	0	0	2	0	0	0	1
Commelinaceae	<i>Tradescantia ohimensis</i>	PF	1	3	1	7	0	0	1	9
Verbenaceae	<i>Verbena stricta</i>	PF	1	1	0	2	0	2	0	0

* *Carex* spp. established at low frequencies in Seed + Gap plots (*Schizachyrium*, 2, *Bromus*, 2) but given their young developmental stage could not be distinguished among seeded or other *Carex* species in the local species pool.

Sown species present in control or gap plots represent a baseline for these species in the community, i.e., they were present in the extant vegetation or recruited from the seed bank, and were not the result of sowing.

Table 3.2. ANOVA statistics (F) and significance (P) of bare ground, dead vegetation, dominant, and non-dominant species in seed-microsite limitation experiment (Treatment) in two communities (*Schizachyrium scoparium* or *Bromus inermis* community), and interaction effects (treatment x community) in the final year (2009) of the study. Statistically significant results ($p < 0.05$) are in bold.

	Treatment		Community		Treatment x Community	
	F	P	F	P	F	P
BARE GROUND	(df = 3, 183)		(df = 1, 8)		(df = 3, 183)	
% Cover	44.26	<.0001	0.41	0.5398	1.25	0.2925
DEAD VEGETATION	(df = 3, 24)		(df = 1, 8)		(df = 3, 24)	
% Cover	42.99	<.0001	0.82	0.3910	0.99	0.4145
DOMINANT GRASS	(df* = 3, 24)		(df = 1, 8)		(df = 3, 24)	
% Cover	13.42	<.0001	0.04	0.8404	10.77	0.0001
NON-DOMINANT SPECIES	(df = 3, 183)		(df = 1, 8)		(df = 3, 183)	
Species Richness	21.97	<.0001	3.84	0.0855	4.82	0.0030
% Cover	3.81	0.0111	0.07	0.7987	4.42	0.0050
Diversity (H')	16.70	<.0001	7.96	0.0223	2.56	0.0568
Evenness f	0.08	0.9715	1.44	0.2645	0.50	0.6853
NON-DOMINANT SPECIES: SUB GROUPS						
NOT SOWN	(df = 3, 24)		(df = 1, 8)		(df = 3, 24)	
Species Richness	9.06	0.0003	3.17	0.1129	6.14	0.0030
% Cover f	1.31	0.2717	0.11	0.7516	3.83	0.0109
SOWN	(df = 3, 191)		(df = 1, 191)		(df = 3, 191)	
Species Richness	33.93	<.0001	1.33	0.2504	0.22	0.8855
% Cover	26.52	<.0001	1.82	0.1792	0.18	0.9098
PERENNIAL	(df = 3, 183)		(df = 1, 8)		(df = 3, 183)	
Species Richness	10.09	<.0001	3.61	0.0938	1.42	0.2380
% Cover	0.54	0.6577	0.28	0.6122	1.99	0.1166
BIENNIAL + ANNUAL	(df = 3, 24)		(df = 1, 8)		(df = 3, 24)	
Species Richness	10.43	0.0001	1.73	0.2244	3.30	0.0375
% Cover	12.17	0.0001	1.23	0.3000	2.99	0.0509

*Error degrees of freedom (df), calculated in SAS 9.0, varied among response variables based on covariance structure of random variables (Littell et al. 2002). Results are more conservative with this method (i.e., theoretically less Type 1 error).

f Error degrees of freedom for evenness: (df=3, 23; 1, 8; and 3, 23) and for not-sown % cover (df=3, 183; 1, 8; and 3, 183).

Table 3.3. Site level species richness and sown species richness in four experimental treatments in both communities in 2009: control, above- and below-ground vegetation removed with soil replaced (Gap), seed addition to intact community with no disturbance (Seed), seed addition + gap disturbance (Seed + Gap).

	<i>Schizachyrium</i>				<i>Bromus</i>			
	Control	Gap	Seed	Seed + Gap	Control	Gap	Seed	Seed + Gap
Community Total	28	45	36	49	24	30	31	41
Sown Species only	6	7	9	13	3	4	9	15

Table 3.4. Frequency of non-dominant species in the vegetation (2009), based on species documented (or not) in the seed bank (2006, McNicoll and Augspurger Ch. 1) in each community. Treatments are control and Gap (above- and below-ground vegetation removed with soil replaced). Number in () is the number of species contributing to frequency.

	<i>Schizachyrium</i>		<i>Bromus</i>	
Frequency in vegetation:	Control	Gap	Control	Gap
Documented in seed bank	80 (14)	142 (26)	90 (13)	110 (20)
Not documented in seed bank	35 (14)	41 (19)	26 (11)	17 (10)

Table 3.5. Test statistics for non-parametric comparison between control and seed-microsite experimental treatments within each community (ANOSIM). Treatment descriptions as in Table 3.2. Global R represents dissimilarity of species composition and abundance between treatments. For reference purposes, a global R value of 0 indicates the same average within- and between-treatment similarity; as values approach 1, there is increasing similarity within, but not between treatment (Clarke 1993). The p-value (< 0.05) indicates the probability that there are significant differences between the two communities (based on Bray-Curtis values).

Pairwise Test	R-Value	p-value
<i>Schizachyrium</i>		
Control v. Gap	0.148	0.02
Control v. Seed Only	0.049	NS
Control v. Seed + Gap	0.285	0.01
<i>Bromus</i>		
Control v. Gap	0.079	NS
Control v. Seed Only	0.036	NS
Control v. Seed + Gap	0.136	0.01

APPENDIX A

Appendix A.1. Vegetation species composition and structure of *Schizachyrium* and *Bromus* communities at Lost Mound Sand Prairie in 2005.

Species were classified according to family, location of origin (N=native, I=introduced), life history (P=perennial, A=annual, B=biennial), and functional guild of only perennial species (F=forb, G=grass, S=sedge, L=legume). See footnote * for explanations of calculations of relative values.

Species are ordered by the Importance Value (IV) in the *Schizachyrium* community. The five highest IVs are underlined for both communities.

In each community, a numerical 'rank' was given to each species present according to decreasing IV (identical IVs in one community were assigned the same rank). *Panicum depauperatum* and *Cyperus filiculmis* may include individuals of congeners (*P. linearifolium* and *C. schweinitzii*), as they were difficult to distinguish in a vegetative state.

Family	Species	Origin: N, I			SCHIZACHYRIUM				BROMUS			
		Life History: P, B, A			Relative	Relative	Importance	Rank	Relative	Relative	Importance	Rank
		Guild: G, F, S, L			% Cover	(%)	Value		% Cover	(%)	Value	
Poaceae	<i>Schizachyrium scoparium</i>	N	P	G	38.8	7.8	<u>46.6</u>	1	0.4	0.4	0.8	34
Poaceae	<i>Koeleria macrantha</i> †	N	P	G	11.7	7.5	<u>19.2</u>	2	1.6	3.0	4.6	11
Poaceae	<i>Poa pratensis</i> †	I	P	G	10.9	7.8	<u>18.7</u>	3	20.1	9.3	<u>29.4</u>	2
Asclepiadaceae	<i>Asclepias verticillata</i>	N	P	F	4.0	7.5	<u>11.5</u>	4	3.4	6.7	10.0	7
Poaceae	<i>Sorghastrum nutans</i> †	N	P	G	5.5	3.4	<u>9.0</u>	5	5.7	2.2	7.9	9
Asteraceae	<i>Ambrosia psilostachya</i>	N	P	F	2.9	4.7	7.6	6	0.7	3.7	4.4	12
Cyperaceae	<i>Carex muhlenbergii</i>	N	P	S	2.5	4.4	6.9	7	2.0	7.0	9.1	8
Cyperaceae	<i>Cyperus filiculmis</i>	N	P	S	1.3	4.7	6.0	8	3.1	7.0	10.1	6
Poaceae	<i>Leptoloma cognatum</i>	N	P	G	1.3	3.4	4.8	9	1.7	3.3	5.0	10
Asteraceae	<i>Achillea millefolium</i>	N	P	F	1.3	3.4	4.8	9	1.0	3.3	4.3	13
Rosaceae	<i>Potentilla recta</i>	I	P	F	1.3	3.4	4.8	9	1.5	2.6	4.1	14
Solanaceae	<i>Physalis virginiana</i>	N	P	F	1.0	3.4	4.5	12	0.6	1.1	1.7	22
Polygalaceae	<i>Polygala polygama</i>	N	B		1.2	2.8	4.0	13	0.1	0.7	0.9	30
Poaceae	<i>Panicum oligosanthos</i> var. <i>scribnerianum</i>	N	P	G	0.8	2.5	3.3	14	0.6	3.0	3.5	16
Poaceae	<i>Sporobolus clandestinus</i> †	N	P	G	1.8	1.3	3.0	15	8.8	3.7	<u>12.5</u>	3
Asteraceae	<i>Erigeron strigosus</i>	N	B		0.8	2.2	3.0	15				
Cactaceae	<i>Opuntia macrorhiza</i>	N	P	F	1.0	1.9	2.9	17	1.5	2.6	4.1	14
Cyperaceae	<i>Carex tomsa</i>	N	P	S	0.4	2.2	2.6	18				
Poaceae	<i>Panicum depauperatum</i>	N	P	G	0.4	2.2	2.6	18				

Asteraceae	<i>Helianthus pauciflorus</i>	N	P	F	2.0	0.6	2.6	18				
Poaceae	<i>Poa compressa</i>	I	P	G	1.4	0.9	2.3	21	1.6	1.5	3.1	18
Caryophyllaceae	<i>Arenaria serpyllifolia</i>	I	A		0.4	1.9	2.3	21	0.4	1.9	2.2	20
Lamiaceae	<i>Hedeoma hispidum</i>	N	A		0.4	1.9	2.3	21	0.1	0.7	0.9	30
Poaceae	<i>Sporobolus cryptandrus</i>	N	P	G	0.6	1.6	2.2	24	3.9	6.3	<u>10.2</u>	5
Commelinaceae	<i>Tradescantia ohiensis</i>	N	P	F	1.1	0.9	2.1	25	0.1	0.4	0.4	36
Plantaginaceae	<i>Plantago patagonica</i>	I	A		0.3	1.6	1.9	26				
Campanulaceae	<i>Triodanis perfoliata</i>	N	A		0.3	1.6	1.9	26				
Cyperaceae	<i>Carex pensylvanica</i>	N	P	S	0.8	0.9	1.8	28				
Poaceae	<i>Panicum villosissimum</i>	N	P	G	0.3	1.3	1.5	29	0.7	1.9	2.6	19
Cyperaceae	<i>Carex brevior</i>	N	P	S	0.5	0.9	1.4	30	0.8	2.6	3.4	17
Asteraceae	<i>Artemisia campestris</i>	N	B		0.5	0.9	1.4	30				
Boraginaceae	<i>Lithospemum carolinense</i>	N	P	F	0.2	0.9	1.1	32	0.2	1.1	1.3	25
Selaginellaceae	<i>Selaginella rupestris</i>	N	P		0.2	0.9	1.1	32	0.5	0.7	1.2	27
Asteraceae	<i>Krigia virginica</i>	N	A		0.2	0.9	1.1	32				
Poaceae	<i>Bromus racemosus</i>	I	A		0.1	0.6	0.8	35	0.5	0.7	1.2	27
Brassicaceae	<i>Lepidium virginicum</i>	N	A		0.1	0.6	0.8	35	0.1	0.4	0.4	36
Scrophulariaceae	<i>Penstemon pallidus</i>	N	P	F	0.1	0.6	0.8	35				
Fabaceae	<i>Medicago lupulina</i>	I	A		0.4	0.3	0.7	38	5.1	5.6	<u>10.7</u>	4
Onagraceae	<i>Oenothera rhombipetala</i>	N	B		0.4	0.3	0.7	38				
Solanaceae	<i>Solanum carolinense</i>	N	P	F	0.1	0.3	0.4	40	0.2	1.1	1.3	25
Scrophulariaceae	<i>Veronica arvensis</i>	I	A		0.1	0.3	0.4	40	0.1	0.7	0.9	30
Oxalidaceae	<i>Oxalis dillenii</i>	N	P	F	0.1	0.3	0.4	40	0.1	0.4	0.4	36
Asteraceae	<i>Antennaria plantaginifolia</i>	N	P	F	0.1	0.3	0.4	40				
Asteraceae	<i>Brickellia eupatoriodes</i>	N	P	F	0.1	0.3	0.4	40				
Asteraceae	<i>Conyza canadensis</i>	N	A		0.1	0.3	0.4	40				
Euphorbiaceae	<i>Euphorbia corollata</i>	N	P	F	0.1	0.3	0.4	40				
Linaceae	<i>Linum sulcatum</i>	N	A		0.1	0.3	0.4	40				
Poaceae	<i>Panicum virgatum</i>	N	P	G	0.1	0.3	0.4	40				
Poaceae	<i>Bromus inermis</i>	I	P	G					28.9	9.3	<u>38.1</u>	1
Poaceae	<i>Paspalum setaceum</i>	N	P	G					0.3	1.5	1.8	21
Fabaceae	<i>Coronilla varia</i>	I	P	L					1.1	0.4	1.4	23
Polygonaceae	<i>Rumex acetosella</i>	I	P	F					1.1	0.4	1.4	23
Asteraceae	<i>Antennaria neglecta</i>	N	P	F					0.5	0.7	1.2	27
Rosaceae	<i>Potentilla argentea</i>	I	P	F					0.1	0.7	0.9	30
Poaceae	<i>Bouteloua hirsuta</i>	N	P	G					0.4	0.4	0.8	34
Cyperaceae	<i>Carex bicknellii</i>	N	P	S					0.1	0.4	0.4	36
Lamiaceae	<i>Monarda punctata</i>	N	P	F					0.1	0.4	0.4	36
Lamiaceae	<i>Verbena stricta</i>	N	P	F					0.1	0.4	0.4	36

* Relative % cover = $((Cvr_S / Cvr_{total}) \times 100)$; where Cvr_S = total % cover of single species, Cvr_{total} = total % cover of all species; Relative frequency =

$((\text{Freq}_S / \text{Freq}_{\text{total}}) \times 100)$; where Freq_S = number of plots (occurrences) where species is present, and $\text{Freq}_{\text{total}}$ = total of all occurrences of all species;

and Importance value (IV) = Relative % cover + Relative frequency. The sum of IVs of all species in the vegetation is 200.

† Non-dominant species with greater than 5 % contribution towards Bray-Curtis (B-C) dissimilarity (i.e., 100 - similarity) between *Schizachyrium* and *Bromus* communities (average B-C dissimilarity = 73): *P. pratensis* (14 %), *K. macrantha* (12), *S. nutans* (8), and *S. clandestinus* (7). % contribution based on SIMPER analysis (Clarke and Gorley 2006).

Appendix A.2. Vegetation species composition and structure of *Schizachyrium* and *Bromus* communities at Lost Mound Sand Prairie in 2006.

Refer to Appendix A.1. for explanation of table definitions and calculations.

		SCHIZACHYRIUM							BROMUS			
		Origin: N, I			Relative				Relative			
		Life History: P, B, A			Relative	Frequency	Importance		Relative	Frequency	Importance	
Family	Species	Guild: G, F, S, L			% Cover	(%)	Value	Rank	% Cover	(%)	Value	Rank
Poaceae	<i>Schizachyrium scoparium</i>	N	P	G	39.4	7.0	<u>46.4</u>	1	0.1	0.4	0.5	34
Poaceae	<i>Poa pratensis</i> †	I	P	G	10.3	7.0	<u>17.3</u>	2	15.8	9.9	<u>25.7</u>	2
Poaceae	<i>Koeleria macrantha</i> †	N	P	G	7.6	6.2	<u>13.8</u>	3	0.9	3.2	4.1	12
Asclepiadaceae	<i>Asclepias verticillata</i> †	N	P	F	4.3	6.8	<u>11.0</u>	4	5.7	7.1	<u>12.8</u>	3
Asteraceae	<i>Ambrosia psilostachya</i> †	N	P	F	5.5	5.1	<u>10.6</u>	5	1.0	4.0	5.0	11
Cyperaceae	<i>Cyperus filiculmis</i>	N	P	S	2.6	5.4	8.0	6	3.4	7.1	<u>10.5</u>	5
Poaceae	<i>Sorghastrum nutans</i> †	N	P	G	4.9	2.8	7.8	7	4.7	2.4	7.1	8
Asteraceae	<i>Achillea millefolium</i>	N	P	F	2.3	3.9	6.2	8	1.2	2.8	4.0	14
Cyperaceae	<i>Carex muhlenbergii</i>	N	P	S	2.2	3.4	5.5	9	0.8	4.7	5.6	9
Caryophyllaceae	<i>Silene antirrhina</i>	N	A		0.9	3.9	4.9	10	0.1	0.8	0.9	28
Solanaceae	<i>Physalis virginiana</i>	N	P	F	1.2	3.4	4.5	11	0.6	1.2	1.7	21
Rosaceae	<i>Potentilla recta</i>	I	P	F	1.7	2.8	4.5	12	0.3	2.0	2.3	20
Campanulaceae	<i>Triodanis perfoliata</i>	N	A		0.7	3.1	3.8	13				
Poaceae	<i>Leptoloma cognatum</i>	N	P	G	1.3	2.5	3.8	14	0.8	2.8	3.6	16
Asteraceae	<i>Erigeron strigosus</i>	N	B		0.6	2.5	3.1	15				
Cactaceae	<i>Opuntia macrorhiza</i>	N	P	F	0.9	2.3	3.1	16	2.0	3.2	5.1	10
Poaceae	<i>Panicum oligosanthos</i>	N	P	G	0.5	2.3	2.8	17	0.6	3.2	3.7	15
	var. <i>scribnerianum</i>											
Poaceae	<i>Sporobolus clandestinus</i> †	N	P	G	1.6	1.1	2.7	18	9.5	3.2	<u>12.7</u>	4
Asteraceae	<i>Helianthus pauciflorus</i>	N	P	F	2.1	0.6	2.7	19				
Poaceae	<i>Sporobolus cryptandrus</i>	N	P	G	0.5	2.0	2.4	20	2.9	6.7	9.6	6
Polygalaceae	<i>Polygala polygama</i>	N	B		0.5	2.0	2.4	20	0.1	0.8	0.9	28
Asteraceae	<i>Conyza canadensis</i>	N	A		0.5	2.0	2.4	20				
Poaceae	<i>Panicum depauperatum</i>	N	P	G	0.5	2.0	2.4	20				
Plantaginaceae	<i>Plantago patagonica</i>	I	A		0.5	2.0	2.4	20				
Poaceae	<i>Poa compressa</i>	I	P	G	1.4	0.6	2.0	25	0.8	0.8	1.6	24
Lamiaceae	<i>Hedeoma hispidum</i>	N	A		0.3	1.4	1.7	26				
Brassicaceae	<i>Lepidium virginicum</i>	N	A		0.3	1.4	1.7	26				
Caryophyllaceae	<i>Arenaria serpyllifolia</i>	I	A		0.3	1.1	1.4	28	0.4	2.4	2.8	17
Poaceae	<i>Panicum villosissimum</i>	N	P	G	0.3	1.1	1.4	28	0.7	2.0	2.7	19
Selaginellaceae	<i>Selaginella rupestris</i>	N	P		0.3	1.1	1.4	28	0.6	1.2	1.7	21
Boraginaceae	<i>Lithospermum carolinense</i>	N	P	F	0.3	1.1	1.4	28	0.2	1.2	1.4	25
Cyperaceae	<i>Carex tosa</i>	N	P	S	0.3	1.1	1.4	28				

Cyperaceae	<i>Carex pensylvanica</i>	N	P	S	0.5	0.8	1.4	33	0.1	0.4	0.5	34
Commelinaceae	<i>Tradescantia ohimensis</i>	N	P	F	0.5	0.8	1.4	33				
Fabaceae	<i>Medicago lupulina</i>	I	A		0.2	0.8	1.0	35	2.8	5.9	8.7	7
Cyperaceae	<i>Carex brevior</i>	N	P	S	0.2	0.8	1.0	35	0.9	3.2	4.1	12
Solanaceae	<i>Solanum carolinense</i>	N	P	F	0.2	0.8	1.0	35	0.6	1.2	1.7	21
Asteraceae	<i>Artemisia campestris</i>	N	B		0.2	0.8	1.0	35				
Onagraceae	<i>Oenothera rhombipetala</i>	N	B		0.2	0.8	1.0	35				
Oxalidaceae	<i>Oxalis dillenii</i>	N	P	F	0.1	0.6	0.7	40				
Polygonaceae	<i>Polygonum tenue</i>	N	A		0.1	0.6	0.7	40				
Polygonaceae	<i>Rumex acetosella</i>	I	P	F	0.4	0.3	0.7	42	0.4	0.4	0.8	33
Linaceae	<i>Linum sulcatum</i>	N	A		0.4	0.3	0.7	42				
Asteraceae	<i>Antennaria plantaginifolia</i>	N	P	F	0.1	0.3	0.3	44				
Asteraceae	<i>Brickellia eupatoriodes</i>	N	P	F	0.1	0.3	0.3	44				
Euphorbiaceae	<i>Euphorbia corollata</i>	N	P	F	0.1	0.3	0.3	44				
Poaceae	<i>Panicum virgatum</i>	N	P	G	0.1	0.3	0.3	44				
Scrophulariaceae	<i>Penstemon pallidus</i>	N	P	F	0.1	0.3	0.3	44				
Poaceae	<i>Bromus inermis</i>	I	P	G					38.6	9.9	<u>48.5</u>	1
Fabaceae	<i>Coronilla varia</i>	I	P	L					2.4	0.4	2.8	18
Euphorbiaceae	<i>Croton glandulosus</i>	N	A						0.2	1.2	1.4	25
Lamiaceae	<i>Monarda punctata</i>	N	P	F					0.2	1.2	1.4	25
Asteraceae	<i>Antennaria neglecta</i>	N	P	F					0.1	0.8	0.9	28
Poaceae	<i>Bromus racemosus</i>	I	A						0.1	0.8	0.9	28
Poaceae	<i>Paspalum setaceum</i>	N	P	G					0.1	0.8	0.9	28
Poaceae	<i>Bouteloua hirsuta</i>	N	P	G					0.1	0.4	0.5	34
Caryophyllaceae	<i>Saponaria officinalis</i>	I	P	F					0.1	0.4	0.5	34
Lamiaceae	<i>Verbena stricta</i>	N	P	F					0.1	0.4	0.5	34

† Non-dominant species with greater than 5 % contribution towards Bray-Curtis dissimilarity between *Schizachyrium* and *Bromus* communities (average B-C dissimilarity = 73): *P. pratensis* (15 %), *K. macrantha* (9), *S. clandestinus* (9), *S. nutans* (8), *A. verticillata* (6), and *A. psilostachya* (6).

Appendix A.3. Vegetation species composition and structure of *Schizachyrium* and *Bromus* communities at Lost Mound Sand Prairie in 2007.

Refer to Appendix A.1. for explanation of table definitions and calculations.

		SCHIZACHYRIUM							BROMUS			
		Origin: N, I			Relative				Relative			
		Life History: P, B, A			Relative	Frequency	Importance		Relative	Frequency	Importance	
Family	Species	Guild: G, F, S, L			% Cover	(%)	Value	Rank	% Cover	(%)	Value	Rank
Poaceae	<i>Schizachyrium scoparium</i>	N	P	G	49.8	7.9	<u>57.7</u>	1	0.2	0.9	1.1	25
Poaceae	<i>Poa pratensis</i> †	I	P	G	6.5	7.9	<u>14.4</u>	2	11.8	11.8	<u>23.6</u>	2
Poaceae	<i>Koeleria macrantha</i> †	N	P	G	6.5	6.3	<u>12.8</u>	3	0.5	2.4	2.8	14
Asclepiadaceae	<i>Asclepias verticillata</i>	N	P	F	2.9	7.2	<u>10.1</u>	4	3.3	7.5	<u>10.9</u>	4
Asteraceae	<i>Ambrosia psilostachya</i> †	N	P	F	3.7	5.7	<u>9.4</u>	5	3.9	5.7	9.6	7
Poaceae	<i>Sorghastrum nutans</i> †	N	P	G	5.4	2.8	8.2	6	8.0	2.8	<u>10.8</u>	5
Cyperaceae	<i>Cyperus filiculmis</i>	N	P	S	1.7	6.3	8.0	7	2.4	7.5	10.0	6
Asteraceae	<i>Achillea millefolium</i>	N	P	F	2.7	5.0	7.7	8	1.2	3.8	5.0	12
Solanaceae	<i>Physalis virginiana</i>	N	P	F	1.8	5.0	6.9	9	0.7	1.4	2.2	20
Cyperaceae	<i>Carex muhlenbergii</i>	N	P	S	1.7	3.1	4.9	10	0.8	4.2	5.1	11
Rosaceae	<i>Potentilla recta</i>	I	P	F	1.3	3.1	4.5	11	0.3	1.4	1.7	23
Poaceae	<i>Leptoloma cognatum</i>	N	P	G	1.1	2.5	3.6	12	0.4	1.9	2.3	19
Asteraceae	<i>Erigeron strigosus</i>	N	B		1.0	2.2	3.2	13				
Poaceae	<i>Panicum oligosanthos</i> var. <i>scribnerianum</i>	N	P	G	0.7	2.5	3.2	14	0.9	2.4	3.3	13
Poaceae	<i>Sporobolus clandestinus</i> †	N	P	G	1.7	1.3	2.9	15	11.0	3.8	<u>14.7</u>	3
Cactaceae	<i>Opuntia macrorhiza</i>	N	P	F	0.6	2.2	2.8	16	2.5	3.3	5.8	10
Asteraceae	<i>Conyza canadensis</i>	N	A		0.6	2.2	2.8	16				
Asteraceae	<i>Helianthus pauciflorus</i>	N	P	F	1.1	0.9	2.1	18				
Poaceae	<i>Sporobolus cryptandrus</i>	N	P	G	0.4	1.6	2.0	19	1.9	7.5	9.5	8
Cyperaceae	<i>Carex pensylvanica</i>	N	P	S	0.4	1.6	2.0	19	0.1	0.5	0.6	28
Brassicaceae	<i>Lepidium virginicum</i>	N	A		0.4	1.6	2.0	19				
Poaceae	<i>Panicum depauperatum</i>	N	P	G	0.4	1.6	2.0	19				
Poaceae	<i>Poa compressa</i>	I	P	G	1.0	0.6	1.7	23	0.6	0.9	1.6	24
Commelinaceae	<i>Tradescantia ohiensis</i>	N	P	F	0.7	0.9	1.6	24				
Poaceae	<i>Panicum villosissimum</i>	N	P	G	0.3	1.3	1.6	24	0.8	1.9	2.7	17
Boraginaceae	<i>Lithospermum carolinense</i>	N	P	F	0.3	1.3	1.6	24	0.2	0.9	1.1	25
Lamiaceae	<i>Hedeoma hispidum</i>	N	A		0.3	1.3	1.6	24				
Polygalaceae	<i>Polygala polygama</i>	N	B		0.3	1.3	1.6	24				
Cyperaceae	<i>Carex brevior</i>	N	P	S	0.3	0.9	1.2	29	0.5	2.4	2.8	14
Selaginellaceae	<i>Selaginella rupestris</i>	N	P		0.3	0.9	1.2	29	0.7	1.4	2.2	20
Solanaceae	<i>Solanum carolinense</i>	N	P	F	0.3	0.9	1.2	29	0.7	1.4	2.2	20
Onagraceae	<i>Oenothera rhombipetala</i>	N	B		0.3	0.9	1.2	29				
Polygonaceae	<i>Rumex acetosella</i>	I	P	F	0.5	0.3	0.8	33	0.1	0.5	0.6	28

Fabaceae	<i>Medicago lupulina</i>	I	A		0.2	0.6	0.8	34	2.5	3.8	6.3	9
Caryophyllaceae	<i>Arenaria serpyllifolia</i>	I	A		0.2	0.6	0.8	34				
Cyperaceae	<i>Carex tonsa</i>	N	P	S	0.2	0.6	0.8	34				
Asteraceae	<i>Krigia virginica</i>	N	A		0.2	0.6	0.8	34				
Oxalidaceae	<i>Oxalis dillenii</i>	N	P	F	0.2	0.6	0.8	34				
Scrophulariaceae	<i>Penstemon pallidus</i>	N	P	F	0.2	0.6	0.8	34				
Plantaginaceae	<i>Plantago patagonica</i>	I	A		0.2	0.6	0.8	34				
Fabaceae	<i>Strophostyles leiosperma</i>	N	A		0.2	0.6	0.8	34				
Campanulaceae	<i>Triodanis perfoliata</i>	N	A		0.2	0.6	0.8	34				
Asteraceae	<i>Antennaria plantaginifolia</i>	N	P	F	0.1	0.3	0.4	43				
Asteraceae	<i>Artemisia campestris</i>	N	B		0.1	0.3	0.4	43				
Asteraceae	<i>Brickellia eupatoriodes</i>	N	P	F	0.1	0.3	0.4	43				
Asteraceae	<i>Erigeron annuus</i>	N	B		0.1	0.3	0.4	43				
Euphorbiaceae	<i>Euphorbia corollata</i>	N	P	F	0.1	0.3	0.4	43				
Linaceae	<i>Linum sulcatum</i>	N	A		0.1	0.3	0.4	43				
Poaceae	<i>Panicum virgatum</i>	N	P	G	0.1	0.3	0.4	43				
Polygonaceae	<i>Polygonum tenue</i>	N	A		0.1	0.3	0.4	43				
Caryophyllaceae	<i>Silene antirrhina</i>	N	A		0.1	0.3	0.4	43				
Asteraceae	<i>Tragopogon dubius</i>	I	B		0.1	0.3	0.4	43				
Poaceae	<i>Bromus inermis</i>	I	P	G					39.9	11.8	<u>51.7</u>	1
Fabaceae	<i>Coronilla varia</i>	I	P	L					2.3	0.5	2.8	16
Lamiaceae	<i>Monarda punctata</i>	N	P	F					0.8	1.9	2.7	17
Poaceae	<i>Paspalum setaceum</i>	N	P	G					0.2	0.9	1.1	25
Asteraceae	<i>Antennaria neglecta</i>	N	P	F					0.1	0.5	0.6	28
Poaceae	<i>Bouteloua hirsuta</i>	N	P	G					0.1	0.5	0.6	28
Euphorbiaceae	<i>Croton glandulosus</i>	N	A						0.1	0.5	0.6	28
Poaceae	<i>Eragrostis spectabilis</i>	N	P	G					0.1	0.5	0.6	28
Caryophyllaceae	<i>Saponaria officinalis</i>	I	P	F					0.1	0.5	0.6	28
Lamiaceae	<i>Verbena stricta</i>	N	P	F					0.1	0.5	0.6	28

† Non-dominant species with greater than 5 % contribution towards Bray-Curtis dissimilarity between *Schizachyrium* and *Bromus* communities

(average B-C dissimilarity = 76): *P. pratensis* (12 %), *S. nutans* (11), *K. macrantha* (9), *S. clandestinus* (9), and *A. psilostachya* (6).

Appendix A.4. Vegetation species composition and structure of *Schizachyrium* and *Bromus* communities at Lost Mound Sand Prairie in 2008.

Refer to Appendix A.1. for explanation of table definitions and calculations.

Family	Species	SCHIZACHYRIUM				BROMUS			
		Origin: N, I				Relative			
		Life History: P, B, A				Frequency			
		Guild: G, F, S, L				Relative	Importance	Relative	Importance
						% Cover	Value	% Cover	Value
							Rank		
Poaceae	<i>Schizachyrium scoparium</i>	N	P	G		45.2	7.5	0.2	0.9
Poaceae	<i>Poa pratensis</i> †	I	P	G		6.8	7.5	7.6	10.9
Asteraceae	<i>Ambrosia psilostachya</i> †	N	P	F		6.3	7.2	10.0	10.0
Poaceae	<i>Koeleria macrantha</i> †	N	P	G		5.1	5.4	0.9	2.2
Asclepiadaceae	<i>Asclepias verticillata</i>	N	P	F		3.0	6.6	2.5	7.9
Poaceae	<i>Sorghastrum nutans</i> †	N	P	G		6.3	3.3	7.6	2.2
Asteraceae	<i>Achillea millefolium</i>	N	P	F		2.3	4.2	0.9	2.2
Cyperaceae	<i>Carex muhlenbergii</i>	N	P	S		2.2	3.9	0.9	4.4
Solanaceae	<i>Physalis virginiana</i>	N	P	F		1.5	4.2	0.8	1.7
Rosaceae	<i>Potentilla recta</i>	I	P	F		1.5	2.7	0.2	0.9
Cyperaceae	<i>Cyperus filiculmis</i>	N	P	S		0.9	3.3	1.5	5.2
Polygalaceae	<i>Polygala polygama</i>	N	B			0.9	3.3		
Poaceae	<i>Panicum oligosanthos</i>	N	P	G		0.8	3.0	1.0	2.6
	var. scribnerianum								
Campanulaceae	<i>Triodanis perfoliata</i>	N	A			0.7	2.7		
Cactaceae	<i>Opuntia macrorhiza</i>	N	P	F		1.0	2.1	2.5	3.5
Caryophyllaceae	<i>Silene antirrhina</i>	N	A			0.6	2.4		
Poaceae	<i>Sporobolus clandestinus</i> †	N	P	G		1.5	1.2	8.8	3.1
Asteraceae	<i>Erigeron strigosus</i>	N	B			1.2	1.5		
Asteraceae	<i>Helianthus pauciflorus</i>	N	P	F		1.2	1.5		
Asteraceae	<i>Conyza canadensis</i>	N	A			0.6	2.1	0.2	0.9
Poaceae	<i>Leptoloma cognatum</i>	N	P	G		0.8	1.5	0.4	2.2
Poaceae	<i>Poa compressa</i>	I	P	G		1.7	0.6	0.6	0.9
Poaceae	<i>Panicum depauperatum</i>	N	P	G		0.5	1.8		
Cyperaceae	<i>Carex brevior</i>	N	P	S		0.7	1.2	0.4	1.7
Poaceae	<i>Sporobolus cryptandrus</i>	N	P	G		0.4	1.5	1.3	6.6
Commelinaceae	<i>Tradescantia ohiensis</i>	N	P	F		0.6	0.9	0.1	0.4
Poaceae	<i>Panicum villosissimum</i>	N	P	G		0.3	1.2	0.8	1.7
Cyperaceae	<i>Carex pensylvanica</i>	N	P	S		0.3	1.2	0.2	0.9
Boraginaceae	<i>Lithospermum carolinense</i>	N	P	F		0.3	1.2	0.2	0.9
Brassicaceae	<i>Lepidium virginicum</i>	N	A			0.3	1.2		
Plantaginaceae	<i>Plantago patagonica</i>	I	A			0.3	1.2		
Polygonaceae	<i>Rumex acetosella</i>	I	P	F		1.2	0.3		
Fabaceae	<i>Medicago lupulina</i>	I	A			0.2	0.9	3.9	6.1

Caryophyllaceae	<i>Arenaria serpyllifolia</i>	I	A		0.2	0.9	1.1	33	0.1	0.4	0.5	30
Lamiaceae	<i>Hedeoma hispidum</i>	N	A		0.2	0.9	1.1	33				
Asteraceae	<i>Krigia virginica</i>	N	A		0.2	0.9	1.1	33				
Fabaceae	<i>Coronilla varia</i>	I	P	L	0.2	0.6	0.8	37	2.9	1.3	4.2	12
Solanaceae	<i>Solanum carolinense</i>	N	P	F	0.2	0.6	0.8	37	0.4	1.7	2.1	19
Selaginellaceae	<i>Selaginella rupestris</i>	N	P		0.2	0.6	0.8	37	0.7	1.3	2.0	22
Cyperaceae	<i>Carex tosa</i>	N	P	S	0.2	0.6	0.8	37				
Onagraceae	<i>Oenothera rhombipetala</i>	N	B		0.2	0.6	0.8	37				
Fabaceae	<i>Strophostyles leiosperma</i>	N	A		0.2	0.6	0.8	37				
Asteraceae	<i>Antennaria neglecta</i>	N	P	F	0.1	0.3	0.4	43	0.1	0.4	0.5	30
Poaceae	<i>Eragrostis spectabilis</i>	N	P	G	0.1	0.3	0.4	43	0.1	0.4	0.5	30
Oxalidaceae	<i>Oxalis dillenii</i>	N	P	F	0.1	0.3	0.4	43	0.1	0.4	0.5	30
Scrophulariaceae	<i>Penstemon pallidus</i>	N	P	F	0.1	0.3	0.4	43	0.1	0.4	0.5	30
Asteraceae	<i>Antennaria plantaginifolia</i>	N	P	F	0.1	0.3	0.4	43				
Asteraceae	<i>Brickellia eupatoriodes</i>	N	P	F	0.1	0.3	0.4	43				
Brassicaceae	<i>Draba reptans</i>	N	A		0.1	0.3	0.4	43				
Euphorbiaceae	<i>Euphorbia corollata</i>	N	P	F	0.1	0.3	0.4	43				
Linaceae	<i>Linum sulcatum</i>	N	A		0.1	0.3	0.4	43				
Poaceae	<i>Panicum virgatum</i>	N	P	G	0.1	0.3	0.4	43				
Asteraceae	<i>Tragopogon dubius</i>	I	B		0.1	0.3	0.4	43				
Poaceae	<i>Bromus inermis</i>	I	P	G					41.1	10.9	<u>52.0</u>	1
Euphorbiaceae	<i>Croton glandulosus</i>	N	A						0.4	1.7	2.1	19
Caryophyllaceae	<i>Saponaria officinalis</i>	I	P	F					0.5	0.4	1.0	29
Poaceae	<i>Bouteloua hirsuta</i>	N	P	G					0.1	0.4	0.5	30

† Non-dominant species with greater than 5 % contribution towards Bray-Curtis dissimilarity between *Schizachyrium* and *Bromus* communities

(average B-C dissimilarity = 74): *S. nutans* (12 %), *P. pratensis* (10), *A. psilostachya* (9), *S. clandestinus* (8), and *K. macrantha* (7).

Appendix A.5. Vegetation species composition and structure of *Schizachyrium* and *Bromus* communities at Lost Mound Sand Prairie in 2009.

Refer to Appendix A.1. for explanation of table definitions and calculations.

		Origin: N, I				SCHIZACHYRIUM				BROMUS			
		Life History: P, B, A				Relative	Frequency	Importance		Relative	Frequency	Importance	
Family	Species	Guild: G, F, S, L				% Cover	(%)	Value	Rank	% Cover	(%)	Value	Rank
Poaceae	<i>Schizachyrium scoparium</i>	N	P	G		45.6	9.4	<u>55.1</u>	1	0.6	0.4	1.0	27
Poaceae	<i>Poa pratensis</i> †	I	P	G		8.0	9.4	<u>17.4</u>	2	8.7	10.9	<u>19.5</u>	3
Asteraceae	<i>Ambrosia psilostachya</i> †	N	P	F		8.3	9.1	<u>17.4</u>	3	17.8	10.4	<u>28.3</u>	2
Poaceae	<i>Koeleria macrantha</i>	N	P	G		3.6	6.3	<u>9.9</u>	4	0.7	3.0	3.8	13
Asclepiadaceae	<i>Asclepias verticillata</i>	N	P	F		1.6	6.3	<u>7.9</u>	5	1.1	4.8	5.9	11
Poaceae	<i>Sorghastrum nutans</i> †	N	P	G		3.9	3.5	7.5	6	6.8	2.2	9.0	7
Cyperaceae	<i>Carex muhlenbergii</i>	N	P	S		2.6	4.3	7.0	7	1.0	4.3	5.4	12
Rosaceae	<i>Potentilla recta</i>	I	P	F		2.6	4.3	7.0	7	0.2	0.9	1.1	23
Asteraceae	<i>Achillea millefolium</i>	N	P	F		2.1	4.3	6.5	9	1.0	2.2	3.2	15
Fabaceae	<i>Coronilla varia</i> †	I	P	L		4.3	1.6	5.8	10	6.4	2.2	8.6	8
Solanaceae	<i>Physalis virginiana</i>	N	P	F		1.1	4.3	5.4	11	0.5	2.2	2.7	16
Cyperaceae	<i>Cyperus filiculmis</i>	N	P	S		1.3	3.1	4.5	12	1.7	7.4	9.1	6
Poaceae	<i>Sporobolus clandestinus</i> †	N	P	G		1.9	1.6	3.5	13	8.1	3.5	<u>11.6</u>	4
Asteraceae	<i>Helianthus pauciflorus</i>	N	P	F		1.5	2.0	3.5	14				
Poaceae	<i>Panicum oligosanthos</i> var. <i>scribnerianum</i>	N	P	G		0.7	2.8	3.5	15	0.5	2.2	2.7	16
Polygalaceae	<i>Polygala polygama</i>	N	B			0.7	2.8	3.5	15				
Commelinaceae	<i>Tradescantia ohiensis</i>	N	P	F		1.8	1.2	3.0	17	0.1	0.4	0.5	28
Cactaceae	<i>Opuntia macrorhiza</i>	N	P	F		1.0	2.0	3.0	18	3.4	3.5	6.8	10
Poaceae	<i>Leptoloma cognatum</i>	N	P	G		1.0	2.0	3.0	18	0.5	2.2	2.7	16
Boraginaceae	<i>Lithospermum carolinense</i>	N	P	F		0.5	2.0	2.5	20	0.2	0.9	1.1	23
Poaceae	<i>Panicum depauperatum</i>	N	P	G		0.4	1.6	2.0	21				
Poaceae	<i>Poa compressa</i>	I	P	G		0.7	0.8	1.5	22	0.7	0.9	1.6	22
Fabaceae	<i>Medicago lupulina</i>	I	A			0.3	1.2	1.5	23	3.3	7.4	<u>10.6</u>	5
Poaceae	<i>Sporobolus cryptandrus</i>	N	P	G		0.3	1.2	1.5	23	1.3	5.7	7.0	9
Cyperaceae	<i>Carex brevior</i>	N	P	S		0.3	1.2	1.5	23	0.4	1.7	2.1	20
Cyperaceae	<i>Carex pensylvanica</i>	N	P	S		0.3	1.2	1.5	23	0.2	0.9	1.1	23
Asteraceae	<i>Antennaria plantaginifolia</i>	N	P	F		0.6	0.4	1.0	27				
Poaceae	<i>Panicum villosissimum</i>	N	P	G		0.2	0.8	1.0	28	0.9	1.7	2.7	19
Caryophyllaceae	<i>Arenaria serpyllifolia</i>	I	A			0.2	0.8	1.0	28	0.1	0.4	0.5	28
Asteraceae	<i>Erigeron strigosus</i>	N	B			0.2	0.8	1.0	28				
Poaceae	<i>Panicum virgatum</i>	N	P	G		0.2	0.8	1.0	28				
Polygonaceae	<i>Rumex acetosella</i>	I	P	F		0.2	0.8	1.0	28				
Solanaceae	<i>Solanum carolinense</i>	N	P	F		0.1	0.4	0.5	33	0.6	2.6	3.2	14

Selaginellaceae	<i>Selaginella rupestris</i>	N	P		0.1	0.4	0.5	33	0.3	1.3	1.6	21
Euphorbiaceae	<i>Croton glandulosus</i>	N	A		0.1	0.4	0.5	33	0.2	0.9	1.1	23
Fabaceae	<i>Strophostyles leiosperma</i>	N	A		0.1	0.4	0.5	33	0.1	0.4	0.5	28
Asteraceae	<i>Brickellia eupatoriodes</i>	N	P	F	0.1	0.4	0.5	33				
Cyperaceae	<i>Carex tonsa</i>	N	P	S	0.1	0.4	0.5	33				
Poaceae	<i>Eragrostis spectabilis</i>	N	P	G	0.1	0.4	0.5	33				
Euphorbiaceae	<i>Euphorbia corollata</i>	N	P	F	0.1	0.4	0.5	33				
Asteraceae	<i>Krigia virginica</i>	N	A		0.1	0.4	0.5	33				
Linaceae	<i>Linum sulcatum</i>	N	A		0.1	0.4	0.5	33				
Oxalidaceae	<i>Oxalis dillenii</i>	N	P	F	0.1	0.4	0.5	33				
Scrophulariaceae	<i>Penstemon pallidus</i>	N	P	F	0.1	0.4	0.5	33				
Polygonaceae	<i>Polygonum tenue</i>	N	A		0.1	0.4	0.5	33				
Asteraceae	<i>Tragopogon dubius</i>	I	B		0.1	0.4	0.5	33				
Campanulaceae	<i>Triodanis perfoliata</i>	N	A		0.1	0.4	0.5	33				
Scrophulariaceae	<i>Veronica arvensis</i>	I	A		0.1	0.4	0.5	33				
Poaceae	<i>Bromus inermis</i>	I	P	G					32.0	10.9	<u>42.8</u>	1
Asteraceae	<i>Antennaria neglecta</i>	N	P	F					0.1	0.4	0.5	28
Poaceae	<i>Bouteloua hirsuta</i>	N	P	G					0.1	0.4	0.5	28
Caryophyllaceae	<i>Saponaria officinalis</i>	I	P	F					0.1	0.4	0.5	28
Poaceae	<i>Stipa spartea</i>	N	P	G					0.1	0.4	0.5	28

† Non-dominant species with greater than 5 % contribution towards Bray-Curtis dissimilarity between *Schizachyrium* and *Bromus* communities

(average B-C dissimilarity = 69): *A. psilostachya* (12 %), *P. pratensis* (11), *S. nutans* (10), *S. clandestinus* (8), and *C. varia* (6).

APPENDIX B

Appendix B. Germinable seed bank species composition and structure of *Schizachyrium* and *Bromus* communities at Lost Mound Sand Prairie in 2006. Species were classified according to family, location of origin (N=native, I=introduced), life history (P=perennial, A=annual, B=biennial), and functional guild of only perennial species (F=forb, G=grass, S=sedge, L=legume). Species are ordered by the Importance Value (IV) in the *Schizachyrium* community. The five highest IVs are underlined for both communities. Presence of a seed bank species in the vegetation is indicated by the vegetation IV of its respective community in 2006 (or * to indicate its presence in a year other than 2006). Empty cells represent species not observed in seed bank and/or vegetation.

		SCHIZACHYRIUM						BROMUS					
		Origin: N, I		Relative						Relative			
Family	Species	Life History: P, B, A		Relative	Freq-	Importance	IV	Relative	Freq-ucy	Importance	IV		
		Guild: G, F, S, L		Density	uency (%)	Value	Veg	Density	(%)	Value	Veg		
Primulaceae	<i>Androsace occidentalis</i>	N	A	15.3	9.3	<u>24.6</u>		7.2	6.0	<u>13.2</u>			
Campanulaceae	<i>Triodanis perfoliata</i>	N	A	12.6	9.8	<u>22.4</u>	3.8	1.2	4.5	5.7			
Poaceae	<i>Sporobolus cryptandrus</i>	N	P	8.0	8.2	<u>16.3</u>	2.4	15.0	12.1	<u>27.0</u>	9.6		
Caryophyllaceae	<i>Silene antirrhina</i>	N	A	6.2	6.2	<u>12.4</u>	4.9	0.5	2.5	3.0	0.9		
Asteraceae	<i>Conyza canadensis</i>	N	A	4.6	7.7	<u>12.4</u>	2.4	0.2	1.5	1.7	*		
Rosaceae	<i>Potentilla recta</i>	I	P	6.4	4.1	10.5	4.5	15.6	10.6	<u>26.1</u>	2.3		
	Un-identified monocot			9.8	0.5	10.3							
Rosaceae	<i>Potentilla argentea</i>	I	P	6.0	4.1	10.2		28.5	10.6	<u>39.1</u>	0.9		
Onagraceae	<i>Oenothera rhombipetala</i>	N	B	3.4	6.7	10.1	1.0	0.2	0.5	0.7			
Asteraceae	<i>Artemisia campestris</i>	N	B	6.9	2.1	9.0	1.0						
Molluginaceae	<i>Mollugo verticillata</i>	I	A	2.5	4.6	7.1		1.6	4.0	5.6			
Caryophyllaceae	<i>Arenaria serpyllifolia</i>	I	A	3.6	3.1	6.7	1.4	19.9	11.6	<u>31.4</u>	2.8		
Asteraceae	<i>Erigeron strigosus</i>	N	B	2.0	3.6	5.6	3.1	0.2	0.5	0.7			
Asteraceae	<i>Antennaria plantaginifolia</i>	N	P	1.2	3.1	4.3	0.3	0.1	0.5	0.6			
Brassicaceae	<i>Draba reptans</i>	N	A	1.2	3.1	4.3	*	0.1	0.5	0.6			
Cyperaceae	<i>Carex muhlenbergii</i>	N	P	1.1	2.1	3.1	5.5	0.6	2.5	3.1	5.6		
Brassicaceae	<i>Lepidium virginicum</i>	N	A	1.1	2.1	3.1	1.7	0.1	0.5	0.6	*		
Poaceae	<i>Poa pratensis</i>	I	P	0.9	2.1	3.0	17.3	3.4	8.5	11.9	25.7		
Oxalidaceae	<i>Oxalis dillenii</i>	N	P	0.7	2.1	2.8	0.7	1.5	4.5	6.0	*		
Cyperaceae	<i>Cyperus filiculmis</i>	N	P	0.7	2.1	2.8	8.0	0.2	0.5	0.7	10.5		
Asteraceae	<i>Ambrosia psilostachya</i>	N	P	0.5	1.5	2.1	10.6	0.1	0.5	0.6	5.0		
Asteraceae	<i>Achillea millefolium</i>	N	P	0.7	1.0	1.7	6.2	0.1	0.5	0.6	4.0		

Poaceae	<i>Eragrostis spectabilis</i>	N	P	G	0.5	1.0	1.6	*	0.2	1.0	1.2	*
Polygalaceae	<i>Polygala polygama</i>	N	B		0.5	1.0	1.6	2.4				0.9
Scrophulariaceae	<i>Verbascum thapsus</i>	I	B		0.4	1.0	1.4		0.5	1.5	2.0	
Poaceae	<i>Panicum villosissimum</i>	N	P	G	0.4	1.0	1.4	1.4	0.2	1.5	1.7	2.7
Asteraceae	<i>Krigia virginica</i>	N	A		0.4	1.0	1.4	*				
Polygonaceae	<i>Rumex acetosella</i>	I	P	F	0.4	1.0	1.4	0.7				0.8
Poaceae	<i>Vulpia octoflora</i>	N	A		0.4	1.0	1.4					
Caryophyllaceae	<i>Cerastium nutans</i>	N	A		0.5	0.5	1.0					
Lamiaceae	<i>Verbena stricta</i>	N	P	F	0.2	0.5	0.7		0.7	2.0	2.7	0.5
Asclepiadaceae	<i>Asclepias verticillata</i>	N	P	F	0.2	0.5	0.7	11.0	0.2	1.0	1.2	12.8
Cyperaceae	<i>Carex brevior</i>	N	P	S	0.2	0.5	0.7	1.0	0.2	1.0	1.2	4.1
Poaceae	<i>Panicum oligosanthes</i> var. <i>scribnerianum</i>	N	P	G	0.2	0.5	0.7	2.8	0.1	0.5	0.6	3.7
Plantaginaceae	<i>Plantago patagonica</i>	I	A		0.2	0.5	0.7	2.4				
Caryophyllaceae	<i>Saponaria officinalis</i>	I	P	F	0.2	0.5	0.7					0.5
Fabaceae	<i>Medicago lupulina</i>	I	A					1.0	1.2	4.5	5.7	8.7
Poaceae	<i>Leptoloma cognatum</i>	N	P	G				3.8	0.3	1.5	1.8	3.6
Cyperaceae	<i>Carex cephalophora</i>	N	P	S					0.2	0.5	0.7	
Asteraceae	<i>Aster cf. pilosus</i>	N	P	F					0.1	0.5	0.6	
Poaceae	<i>Bromus inermis</i>	I	P	G					0.1	0.5	0.6	48.5
Lamiaceae	<i>Lamiaceae sp.</i>	N	P	F					0.1	0.5	0.6	
Poaceae	<i>Paspalum setaceum</i>	N	P	G					0.1	0.5	0.6	0.9

Individual seedlings that died before they could be identified to species are grouped below.

Values in parentheses are absolute values and were not included in the calculation of relative values.

	Density	Frequency	Density	Frequency
Unidentified	(5)	(3)	(9)	(6)
Unidentified dicot (predominantly <i>Potentilla</i> sp.)	(21)	(9)	(10)	(9)
Unidentified monocot (predominantly Poaceae)	(8)	(5)	(2)	(2)
<i>Potentilla</i> sp. (species unidentified)	(5)	(4)	(39)	(13)

Relative density = $((\text{Den}_S / \text{Den}_{\text{total}}) \times 100)$; where Den_S = total number of germinated seedlings of single species, $\text{Den}_{\text{total}}$ = total number of all

seedlings of all species; Relative frequency = $((\text{Freq}_S / \text{Freq}_{\text{total}}) \times 100)$; where Freq_S = number of plots (occurrences) where species

is present, and $\text{Freq}_{\text{total}}$ = total of all occurrences of all species; and Importance value (IV) = Relative density + Relative frequency.

† Non-dominant species with greater than 5 % contribution towards Bray-Curtis dissimilarity between *Schizachyrium* and *Bromus* communities

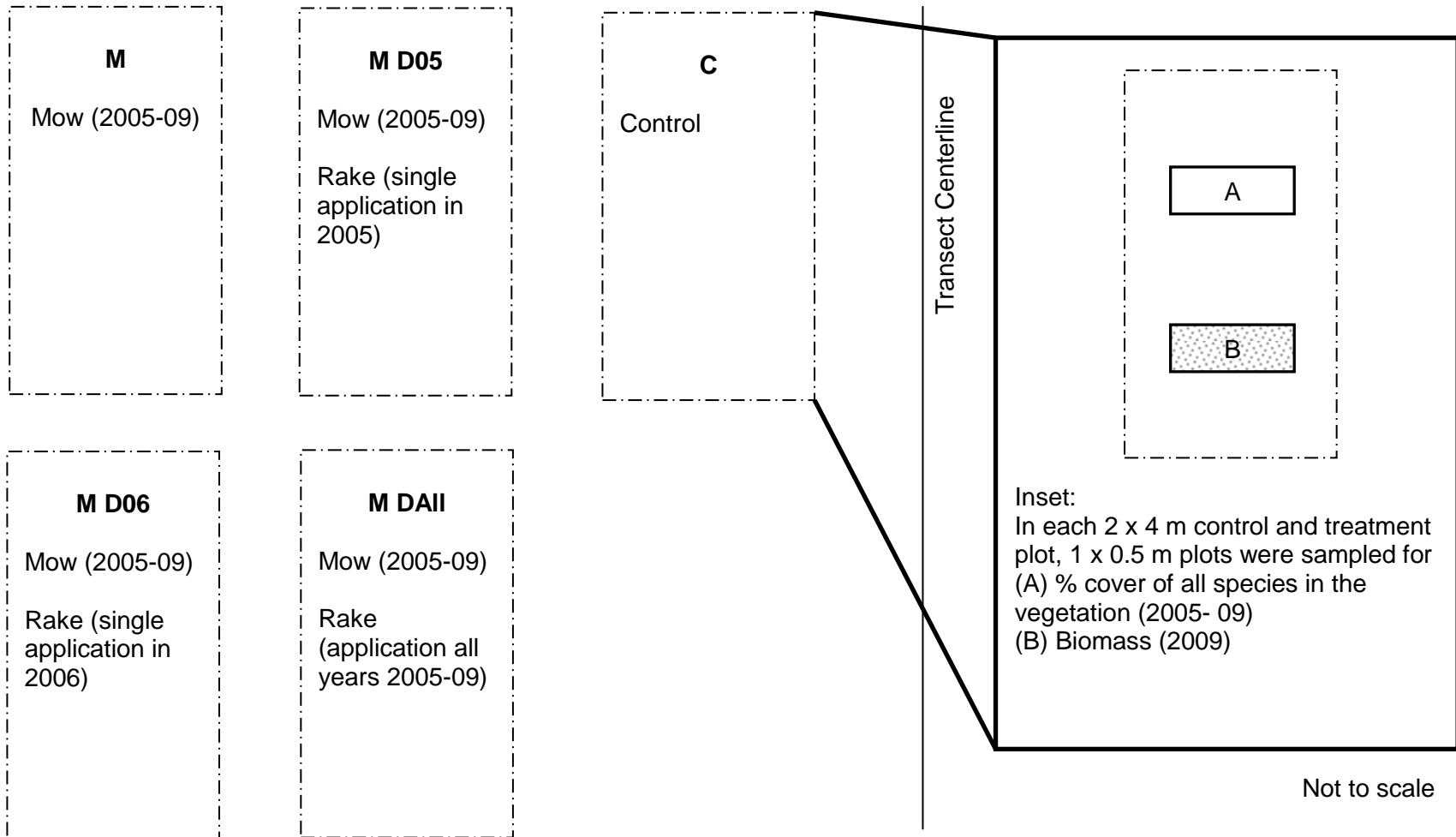
(average B-C dissimilarity = 79): *P. argentea* (15 %), *A. occidentalis* (11), *A. serpyllifolia* (11), *P. recta* (9), *S. cryptandrus* (9), *T. perfoliata* (9),

and *S. antirrhina* (5).

APPENDIX C

Appendix C. Example layout for a set of plots (repeated at 10-m intervals) on a 50-m transect:

- 2 x 4 m treatment plots (random assignment) separated by 1-m pathways
- Start point for each set of plots was located 1 – 3 m (random assignment) from transect
- Not all treatments were present in each set of plots (minimum of three per transect)
- After data collection, three plots of each treatment were selected randomly from each transect for inclusion in analysis.



APPENDIX D

Appendix D.1. Individual species in controls (C) and four disturbance treatments in the *Schizachyrium* community at Lost Mound, NWR, Illinois in 2009.

See footnote * for explanations of calculations of relative values. Disturbance treatments are control (C), 5 years of mowing only (M), 5 years of mowing with a single year of raking disturbance in 2005 (M D05), 4 years of mowing with raking disturbance in 2006 (M D06), and 5 years of mowing and raking 2005-2009 (M Dall). Classification of each species includes family, location of origin (N=native, I=introduced), life history (P=perennial, A=annual, B=biennial), functional guild of only perennial species (F=forb, G=grass, S=sedge, L=legume), and seasonality (E=early, L=late).

Species are ordered by the Importance Value (IV) in the control treatment. The five highest IVs are underlined for all treatments.

In each community, a numerical 'rank' was given to each species present according to decreasing IV (identical IVs in one community were assigned the same rank). All *Cyperus* were included as *Cyperus filiculmis*, but may include individuals of *C. schweinitzii*.

Family	Species	Origin	Life History	Guild	Seasonality	C				M				M D05				M D06				M Dall				Rank in Seed Bank (2006)
						Relative % Cover	Relative Frequency (%)	Importance Value	Rank	Relative % Cover	Relative Frequency (%)	Importance Value	Rank	Relative % Cover	Relative Frequency (%)	Importance Value	Rank	Relative % Cover	Relative Frequency (%)	Importance Value	Rank	Relative % Cover	Relative Frequency (%)	Importance Value	Rank	
Poaceae	<i>Schizachyrium scoparium</i>	N	P	G	L	45	11	<u>56</u>	1	49	9	<u>57</u>	1	41	8	<u>49</u>	1	49	8	<u>57</u>	1	40	6	<u>46</u>	1	
Poaceae	<i>Poa pratensis</i>	I	P	G	E	9	11	<u>20</u>	2	3	8	<u>11</u>	4	4	7	<u>11</u>	4	4	8	<u>12</u>	3	4	6	<u>10</u>	4	18
Asteraceae	<i>Ambrosia psilostachya</i>	N	P	F	L	8	10	<u>18</u>	3	5	7	<u>12</u>	3	7	6	<u>13</u>	2	6	7	<u>12</u>	2	7	6	<u>13</u>	2	21
Poaceae	<i>Koeleria macrantha</i>	N	P	G	E	4	8	<u>13</u>	4	7	6	<u>14</u>	2	4	6	<u>10</u>	5	5	4	<u>9</u>	4	5	5	<u>10</u>	3	
Poaceae	<i>Sorghastrum nutans</i>	N	P	G	L	4	4	<u>8</u>	5	5	4	9	6	8	4	<u>12</u>	3	2	2	5	10	4	4	7	6	
Cyperaceae	<i>Carex muhlenbergii</i>	N	P	S	E	3	5	8	6	1	3	4	12	3	4	7	7	2	5	7	7	2	5	7	7	16
Asclepiadaceae	<i>Asclepias verticillata</i>	N	P	F	L	1	6	7	7	3	8	<u>10</u>	5	3	6	8	6	3	6	<u>9</u>	5	2	5	7	7	31
Solanaceae	<i>Physalis virginiana</i>	N	P	F	E	1	6	7	7	1	3	4	14	1	2	3	20	1	2	3	18	1	2	3	23	

Asteraceae	<i>Achillea millefolium</i>	N	P	F	E	2	4	6	9	1	4	5	8	1	4	5	11	1	3	4	11	1	2	3	15	22
Rosaceae	<i>Potentilla recta</i>	I	P	F	E	2	3	5	10	1	3	4	14	2	3	4	13	1	2	2	22	2	2	5	9	6
Fabaceae	<i>Coronilla varia</i>	I	P	L	E	4	1	5	11	<1	1	1	25	3	1	4	15	3	1	4	13					
Cyperaceae	<i>Cyperus filiculmis</i>	N	P	S	E	1	4	4	12	1	4	5	8	1	5	6	8	1	4	5	9	1	2	3	15	19
Poaceae	<i>Leptoloma cognatum</i>	N	P	G	L	1	3	4	13	1	3	4	14	1	3	3	16	2	2	4	14	1	3	4	10	
Asteraceae	<i>Helianthus pauciflorus</i> †	N	P	F	L	2	2	4	14	<1	1	1	32	1	2	3	19	2	1	3	16	4	1	4	14	
Poaceae	<i>Panicum oligosanthos</i> <i>var. scribnerianum</i>	N	P	G	E	1	3	3	15	1	2	3	19	1	3	4	14	1	3	4	11	1	2	3	23	31
Cactaceae	<i>Opuntia macrorhiza</i>	N	P	F	E	1	2	3	16	4	3	6	7	2	3	5	10	4	3	7	6	2	1	3	19	
Commelinaceae	<i>Tradescantia ohiensis</i> †	N	P	F	E	2	1	3	17	<1	1	1	32				<1	1	1	35						
Polygalaceae	<i>Polygala polygama</i>	N	B		E	<1	2	3	18	1	4	5	8	1	4	5	9	1	4	6	8	1	2	3	15	23
Boraginaceae	<i>Lithospermum carolinense</i>	N	P	F	E	<1	2	3	18	<1	1	1	25	1	1	1	24	1	2	2	22	1	1	2	28	
Poaceae	<i>Poa compressa</i>	I	P	G	E	1	1	3	20	<1	1	1	32	<1	1	1	37					<1	1	1	38	
Cyperaceae	<i>Carex pensylvanica</i>	N	P	S	E	<1	1	2	21	2	2	4	13	<1	2	2	22	<1	1	1	35	2	1	3	19	
Poaceae	<i>Panicum cf. depauperatum</i>	N	P	G	E	<1	1	2	21	<1	1	1	25	1	3	3	16	<1	1	1	25	1	2	3	23	
Poaceae	<i>Panicum virgatum</i>	N	P	G	L	<1	1	2	21													<1	1	1	38	
Poaceae	<i>Sporobolus clandestinus</i>	N	P	G	L	1	1	2	24	4	1	5	11	1	1	1	24	2	1	3	16	2	1	3	19	
Asteraceae	<i>Antennaria plantaginifolia</i> †	N	P	F	E	1	1	2	24								1	1	2	24	<1	1	1	38	14	
Cyperaceae	<i>Carex tonsa</i>	N	P	S	E	<1	1	1	26	1	2	3	18	<1	1	1	37	<1	1	1	35	<1	1	1	38	
Campanulaceae	<i>Triodanis perfoliata</i>	N	A		E	<1	1	1	26	1	2	2	20	<1	2	2	22	1	2	3	18	1	3	4	10	2
Polygonaceae	<i>Rumex acetosella</i>	I	P	F	E	<1	1	1	26	<1	1	1	25	2	1	3	18					<1	1	2	29	25
Asteraceae	<i>Erigeron strigosus</i>	N	B		E	<1	1	1	26	<1	1	1	25	1	2	3	20	1	3	4	15	3	5	8	5	13
Fabaceae	<i>Medicago lupulina</i>	I	A		E	<1	1	1	26	<1	1	1	25	<1	1	1	30	<1	1	1	35	<1	1	2	29	
Poaceae	<i>Panicum villosissimum</i>	N	P	G	E	<1	1	1	26	<1	1	1	32	<1	1	1	30	<1	1	1	25	<1	1	1	38	25
Poaceae	<i>Sporobolus cryptandrus</i>	N	P	G	L	<1	1	1	26	<1	1	1	32	<1	1	1	37	<1	1	1	35	1	2	3	23	3
Polygonaceae	<i>Polygonum tenue</i>	N	A		L	<1	1	1	26					<1	1	1	37	<1	1	1	35	<1	1	2	29	
Poaceae	<i>Eragrostis spectabilis</i>	N	P	G	L	<1	1	1	26									<1	1	1	35	<1	1	1	38	23
Asteraceae	<i>Brickellia eupatoriodes</i> †	N	P	F	L	<1	1	1	26																	
Asteraceae	<i>Conyza canadensis</i>	N	A		L					1	3	4	14	<1	1	1	30	1	2	3	18	1	2	3	15	5
Selaginellaceae	<i>Selaginella rupestris</i>	N	P		E					1	2	2	20	1	1	1	24	<1	1	1	25					
Plantaginaceae	<i>Plantago patagonica</i> †	I	A		E					1	2	2	20	<1	1	1	30	<1	1	1	35	1	3	4	10	31
Cyperaceae	<i>Carex brevior</i>	N	P	S	E					1	2	2	20					<1	1	1	25					31
Asteraceae	<i>Artemisia campestris</i> †	N	B		L					1	1	2	24	<1	1	1	37	<1	1	1	35	2	1	3	19	10
Brassicaceae	<i>Lepidium virginicum</i>	N	A		E					<1	1	1	25	<1	1	1	37	<1	1	1	25	1	3	4	10	16
Lamiaceae	<i>Hedeoma hispidum</i> †	N	A		E					<1	1	1	32	<1	1	1	37	1	2	3	18	1	2	3	23	
Fabaceae	<i>Strophostyles leiosperma</i>	N	A		L					<1	1	1	32	<1	1	1	37	<1	1	1	25	<1	1	1	38	
Caryophyllaceae	<i>Arenaria serpyllifolia</i>	I	A		E					<1	1	1	32	<1	1	1	37					<1	1	2	29	12
Oxalidaceae	<i>Oxalis dillenii</i>	N	P	F	E					<1	1	1	32					<1	1	1	35	<1	1	1	38	19
Scrophulariaceae	<i>Veronica arvensis</i>	I	A		E					<1	1	1	32					<1	1	1	35					
Hypericaceae	<i>Hypericum perforatum</i>	I	P	F	E					<1	1	1	32													
Asteraceae	<i>Solidago nemoralis</i>	N	P	F	L									2	2	4	12	<1	1	1	35	<1	1	2	29	
Fabaceae	<i>Lespedeza capitata</i> †	N	P	L	L									1	1	1	24					<1	1	1	38	

Asteraceae	<i>Coreopsis palmata</i> †	N	P	F	L	1	1	1	24										
Solanaceae	<i>Physalis heterophylla</i> †	N	P	F	E	1	1	1	24										
Onagraceae	<i>Oenothera rhombipetala</i> †	N	B		L	<1	1	1	30	<1	1	1	25	<1	1	2	29	9	
Poaceae	<i>Bouteloua hirsuta</i>	N	P	G	L	<1	1	1	30										
Asteraceae	<i>Liatris aspera</i> †	N	P	F	L	<1	1	1	30										
Asteraceae	<i>Krigia virginica</i> †	N	A		E	<1	1	1	37	<1	1	1	25	<1	1	2	29	25	
Verbenaceae	<i>Verbena stricta</i>	N	P	F	E	<1	1	1	37					<1	1	1	38	31	
Brassicaceae	<i>Arabis lyrata</i>	N	B		E	<1	1	1	37					<1	1	1	38		
Asteraceae	<i>Antennaria neglecta</i>	N	P	F	E	<1	1	1	37										
Euphorbiaceae	<i>Euphorbia corollata</i> †	N	P	F	E	<1	1	1	37										
Cyperaceae	<i>Carex cephalophora</i>	N	P	S	E	<1	1	1	37										
Asteraceae	<i>Erigeron annuus</i> †	N	A		E	<1	1	1	37										
Caryophyllaceae	<i>Silene antirrhina</i>	N	A		E					<1	1	1	25	<1	1	2	29	4	
Asteraceae	<i>Gnaphalium obtusifolium</i> †	N	A		L					<1	1	1	25						
Linaceae	<i>Linum sulcatum</i> †	N	A		L					<1	1	1	35	<1	1	2	29		
Scrophulariaceae	<i>Penstemon pallidus</i>	N	P	F	E					<1	1	1	35	<1	1	1	38		
Poaceae	<i>Bromus racemosus</i> †	I	A		E					<1	1	1	35						
Solanaceae	<i>Solanum carolinense</i>	N	P	F	E					<1	1	1	35						
Iridaceae	<i>Sisyrinchium campestre</i> †	N	P	F	E					<1	1	1	35						
Brassicaceae	<i>Draba reptans</i> †	N	A		E									<1	1	1	38	14	
Asteraceae	<i>Hieracium longipilum</i> †	N	P	F	L									<1	1	1	38		

* Relative % cover = $((Cvr_S / Cvr_{total}) \times 100)$, where Cvr_S = total % cover of single species, Cvr_{total} = total % cover of all species; Relative frequency =

$((Freq_S / Freq_{total}) \times 100)$, where $Freq_S$ = number of plots (occurrences) where species is present, and $Freq_{total}$ = total of all occurrences of all species;

and Importance value (IV) = Relative % cover + Relative frequency. IVs presented are the values calculated prior to rounding of $Freq$ and Cvr .

† Non-dominant species unique to the *Schizachyrium* vegetation as compared to the *Bromus* community.

Appendix D.2. Individual species in controls (C) and four disturbance treatments in the *Bromus* community at Lost Mound Sand Prairie in 2009.

See footnote * for explanations of calculations of relative values. Disturbance treatments are control (C), 5 years of mowing only (M), 5 years of mowing with a single year of raking disturbance in 2005 (M D05), 4 years of mowing with raking disturbance in 2006 (M D06), and 5 years of mowing and raking 2005-2009 (M DAll). Classification of each species includes family, location of origin (N=native, I=introduced), life history (P=perennial, A=annual, B=biennial), functional guild of only perennial species (F=forb, G=grass, S=sedge, L=legume), and seasonality (E=early, L=late).

Species are ordered by the Importance Value (IV) in the control treatment. The five highest IVs are underlined for all treatments.

In each community, a numerical 'rank' was given to each species present according to decreasing IV (identical IVs in one community were assigned the same rank). All *Cyperus* were included as *Cyperus filiculmis*, but may include individuals of *C. schweinitzii*.

		C				M				M D05				M D06				M DAll				Rank in Seed Bank (2009)	
Family	Species	Origin	Life History	Guild	Seasonality	Relative % Cover	Relative Frequency (%)	Importance Value	Rank	Relative % Cover	Relative Frequency (%)	Importance Value	Rank	Relative % Cover	Relative Frequency (%)	Importance Value	Rank	Relative % Cover	Relative Frequency (%)	Importance Value	Rank		
Poaceae	<i>Bromus inermis</i>	I	P	G	E	32	11	<u>43</u>	1	12	8	<u>20</u>	2	11	9	<u>20</u>	3	12	8	<u>20</u>	2	2	25
Asteraceae	<i>Ambrosia psilostachya</i>	N	P	F	L	18	11	<u>29</u>	2	19	8	<u>28</u>	1	18	9	<u>27</u>	1	15	8	<u>23</u>	1	22	25
Poaceae	<i>Poa pratensis</i>	I	P	G	E	8	11	<u>19</u>	3	9	8	<u>18</u>	3	14	8	<u>22</u>	2	6	8	<u>13</u>	4	7	6
Poaceae	<i>Sorghastrum nutans</i>	N	P	G	L	10	3	<u>13</u>	4	6	2	8	8	3	1	4	15	11	3	<u>14</u>	3	5	9
Fabaceae	<i>Medicago lupulina</i>	I	A		E	4	7	<u>11</u>	5	10	7	<u>17</u>	4	10	7	<u>17</u>	4	6	6	12	6	9	9
Cactaceae	<i>Opuntia macrorhiza</i>	N	P	F	E	5	5	10	6	5	4	9	6	3	2	5	12	7	5	11	7	4	6
Cyperaceae	<i>Cyperus filiculmis</i>	N	P	S	E	2	8	10	7	1	5	6	12	1	5	7	9	1	4	5	12	1	21
Poaceae	<i>Sporobolus clandestinus</i>	N	P	G	L	4	4	8	8	4	3	6	10	2	2	5	14	9	3	11	8	4	8
Poaceae	<i>Sporobolus cryptandrus</i>	N	P	G	L	1	6	7	9	3	7	<u>10</u>	5	4	8	<u>12</u>	5	3	5	7	9	3	3
Cyperaceae	<i>Carex muhlenbergii</i>	N	P	S	E	1	4	5	10	3	4	7	9	2	5	7	8	1	4	5	14	1	11
Asclepiadaceae	<i>Asclepias verticillata</i>	N	P	F	L	1	4	5	10	1	4	6	13	1	4	5	11	2	4	6	11	3	18
Fabaceae	<i>Coronilla varia</i>	I	P	L	E	4	1	5	12	5	2	6	11	7	2	10	6	11	2	<u>13</u>	5	5	10
Poaceae	<i>Koeleria macrantha</i>	N	P	G	E	1	4	4	13	1	2	3	18	1	2	3	18	1	2	3	18	1	23

Poaceae	<i>Panicum oligosanthos</i> <i>var. scribnerianum</i>	N	P	G	E	1	3	4	14	<1	2	2	23	1	5	6	10	2	5	7	10	1	3	5	13	25
Poaceae	<i>Panicum villosissimum</i>	N	P	G	E	1	2	4	15	1	2	3	15	<1	1	1	26	<1	1	1	26	<1	1	1	31	16
Solanaceae	<i>Physalis virginiana</i>	N	P	F	E	1	2	3	16	<1	1	1	27	<1	1	1	26	<1	1	1	26	<1	1	1	31	
Poaceae	<i>Poa compressa</i>	I	P	G	E	1	1	3	17	<1	1	1	32	1	1	2	23	<1	1	1	26					
Poaceae	<i>Leptoloma cognatum</i>	N	P	G	L	<1	1	2	18	6	3	9	7	5	2	8	7	2	3	5	13	3	2	5	12	15
Asteraceae	<i>Achillea millefolium</i>	N	P	F	E	<1	1	2	18	1	4	6	13	<1	2	2	22	<1	2	2	21	1	2	3	23	25
Cyperaceae	<i>Carex brevior</i>	N	P	S	E	<1	1	2	18	1	2	3	18	1	3	4	16	<1	2	2	21	<1	1	2	25	18
Solanaceae	<i>Solanum carolinense</i>	N	P	F	E	<1	1	2	18	<1	1	1	27	<1	1	1	26	<1	2	2	21	<1	1	1	31	
Poaceae	<i>Schizachyrium scoparium</i>	N	P	G	L	1	1	2	22	1	1	1	26	2	1	3	20	3	1	4	16	4	1	6	11	
Rosaceae	<i>Potentilla recta</i>	I	P	F	E	<1	1	1	23	1	2	3	15	1	3	4	16	1	4	5	14	1	3	5	13	4
Selaginellaceae	<i>Selaginella rupestris</i>	N	P		E	<1	1	1	23	2	1	3	17	<1	1	1	32	1	1	2	20	<1	1	1	31	
Euphorbiaceae	<i>Croton glandulosus</i> †	N	A		L	<1	1	1	23	<1	1	1	27									<1	1	1	31	
Poaceae	<i>Bouteloua hirsuta</i>	N	P	G	L	<1	1	1	23	<1	1	1	32	1	1	2	23	1	1	1	25					
Boraginaceae	<i>Lithospermum carolinense</i>	N	P	F	E	<1	1	1	23	<1	1	1	32	<1	1	1	26					<1	1	1	31	
Fabaceae	<i>Strophostyles leiosperma</i>	N	A		L	<1	1	1	23	<1	1	1	32													
Caryophyllaceae	<i>Arenaria serpyllifolia</i>	I	A		E	<1	1	1	23					<1	1	1	32	<1	2	2	21	1	3	4	18	2
Caryophyllaceae	<i>Saponaria officinalis</i> †	I	P	F	L	<1	1	1	23									<1	1	1	26					
Asteraceae	<i>Heterotheca camporum</i> †	N	P	F	E					2	1	3	20	<1	1	1	32	<1	1	1	37					23
Cyperaceae	<i>Carex cephalophora</i>	N	P	S	E					1	1	2	21	<1	1	1	32									18
Poaceae	<i>Eragrostis spectabilis</i>	N	P	G	L					1	1	2	21													
Oxalidaceae	<i>Oxalis dillenii</i>	N	P	F	E					<1	2	2	23	1	2	3	19	1	2	3	19	1	3	4	18	7
Polygalaceae	<i>Polygala polygama</i>	N	B		E					<1	2	2	23	<1	1	1	32	<1	1	1	26	<1	1	2	25	
Polygonaceae	<i>Rumex acetosella</i>	I	P	F	E					<1	1	1	27	<1	1	1	32	2	1	3	17					
Brassicaceae	<i>Arabis lyrata</i>	N	B		E					<1	1	1	27					<1	1	1	37	<1	1	2	25	
Poaceae	<i>Paspalum setaceum</i> †	N	P	G	L					<1	1	1	32	3	2	5	13	<1	1	1	26	1	1	3	22	25
Brassicaceae	<i>Lepidium virginicum</i>	N	A		E					<1	1	1	32	<1	1	1	32	<1	1	1	26	<1	1	1	31	25
Cyperaceae	<i>Carex pensylvanica</i>	N	P	S	E					<1	1	1	32					<1	1	1	26					
Asteraceae	<i>Antennaria neglecta</i>	N	P	F	E					<1	1	1	32									3	1	4	17	
Hypericaceae	<i>Hypericum perforatum</i>	I	P	F	E					<1	1	1	32									<1	1	1	31	
Scrophulariaceae	<i>Penstemon pallidus</i>	N	P	F	E					<1	1	1	32									<1	1	1	31	
Asteraceae	unknown genus	N	P	F	L					<1	1	1	32													
Poaceae	<i>Panicum cf. depauperatum</i>	N	P	G	E					<1	1	1	32													
Asteraceae	<i>Tragopogon dubius</i> †	I	B		E					<1	1	1	32													
Rosaceae	<i>Potentilla argentea</i> †	I	P	F	E									1	1	2	21	<1	1	1	37	<1	1	2	25	1
Poaceae	<i>Panicum virgatum</i>	N	P	G	L									1	1	2	23									
Lamiaceae	<i>Verbena stricta</i>	N	P	F	E									<1	1	1	26	<1	1	1	26	1	3	5	13	13
Asteraceae	<i>Conyza canadensis</i>	N	A		L									<1	1	1	26	<1	1	1	26	<1	1	1	31	16
Caryophyllaceae	<i>Silene antirrhina</i>	N	A		E									<1	1	1	32	<1	1	1	26	<1	1	2	25	12
Asteraceae	<i>Erigeron strigosus</i>	N	B		E									<1	1	1	32	<1	1	1	37	<1	1	1	31	21
Scrophulariaceae	<i>Veronica arvensis</i>	I	A		E									<1	1	1	32	<1	1	1	37					
Asteraceae	<i>Solidago nemoralis</i>	N	P	F	L													<1	1	1	37	<1	1	2	25	

Cyperaceae	<i>Carex tonsa</i>	N	P	S	E	<1	1	1	37					
Brassicaceae	<i>Erysimum inconspicuum</i> †	N	P	F	E	<1	1	1	37					
Brassicaceae	<i>Lepidium campestre</i> †	I	B		E	<1	1	1	37					
Polygonaceae	<i>Polygonum tenue</i>	N	A		L					1	3	4	18	
Fabaceae	<i>Dalea purpurea</i> †	N	P	L	L					<1	1	1	31	
Poaceae	<i>Stipa spartea</i> †	N	P	G	E					<1	1	1	31	
Fabaceae	<i>Trifolium arvense</i> †	I	A		E					<1	1	1	31	
Campanulaceae	<i>Triodanis perfoliata</i>	N	A		E					<1	1	1	31	8

* Relative % cover = $((Cvr_S / Cvr_{total}) \times 100)$, where Cvr_S = total % cover of single species, Cvr_{total} = total % cover of all species; Relative frequency =

$((Freq_S / Freq_{total}) \times 100)$, where $Freq_S$ = number of plots (occurrences) where species is present, and $Freq_{total}$ = total of all occurrences of all species;

and Importance value (IV) = Relative % cover + Relative frequency. IVs presented are the values calculated prior to rounding of $Freq$ and Cvr .

† Non-dominant species unique to the *Bromus* vegetation as compared to the *Schizachyrium* community.

APPENDIX E

Appendix E. Individual species in microsite and seed limitation study in the *Schizachyrium* and *Bromus* communities at Lost Mound Sand Prairie in 2009. Treatments are control (C), gap (G), seed addition (S), and seed addition to gap (S + G). Frequency is the number of plots in which species were observed. Total % cover is a summed value across all plots in study. Classification of each species includes family, location of origin (N=native, I=introduced), life history (P=perennial, A=annual, B=biennial), and functional guild (F=forb, G=grass, S=sedge, L=legume, W=woody shrub). Species with a seed bank are indicated in bold (See McNicoll and Augspurger Ch. 1).

* indicates species sown as seed; their presence in C or G plots reflects the local species pool prior to seed addition. *S. scoparium* was added only to *Bromus* plots. All *Cyperus* were included as *Cyperus filiculmis*, but may include individuals of *C. schweinitzii*.

Family	Species	Guild	Frequency				Frequency				Total % cover				Total % cover			
			<i>Schizachyrium</i>				<i>Bromus</i>				<i>Schizachyrium</i>				<i>Bromus</i>			
			C	G	S	+ G	C	G	S	+ G	C	G	S	+ G	C	G	S	+ G
Asteraceae	<i>Achillea millefolium</i>	NPF	5	6	7	7	3	1	4	4	39	34	39	39	17	6	22	22
Asteraceae	<i>Ambrosia psilostachya</i>	NPF	20	19	19	21	21	20	22	22	190	229	151	218	284	501	312	279
Fabaceae	<i>Amorpha canescens</i> *	NPL				1				2				6				11
Primulaceae	<i>Androsace occidentalis</i>	NA								1								6
Ranunculaceae	<i>Anemone cylindrica</i> *	NPF			1	3				1			6	17				6
Asteraceae	<i>Antennaria neglecta</i>	NPF	1	2	1						6	11	6					
Brassicaceae	<i>Arabis lyrata</i>	NB				1				1				6				6
Caryophyllaceae	<i>Arenaria serpyllifolia</i>	IA		1		1	1	2		1		6		6	6	11		6
Asteraceae	<i>Artemisia campestris</i>	NB		1								6						
Asclepiadaceae	<i>Asclepias verticillata</i>	NPF	10	13	8	13	7	7	8	10	56	73	45	73	39	39	45	56
Poaceae	<i>Bromus inermis</i>	IPG					25	25	25	25					895	884	917	839
Cyperaceae	<i>Carex brevior</i>	NPS		2	1			2	1			11	6			11	6	
Cyperaceae	<i>Carex muhlenbergii</i> *	NPS	4	1	4		4	3	4		22	6	22		22	17	34	
Cyperaceae	<i>Carex pensylvanica</i>	NPS	3	3	3		1		1		17	17	17	17	6		6	
Cyperaceae	<i>Carex spp.</i>	NPS		1		2				1		6		11				6
Cyperaceae	<i>Carex tosa</i>	NPS	1	2	1	2					6	11	6	11				
Caryophyllaceae	<i>Cerastium sp</i>	NA				1								6				

Caesalpinaceae	<i>Chamaechrista fasciculata</i> *	NAL			12	14			12	10			67	90			67	56
Asteraceae	<i>Conyza canadensis</i>	NA		5	1	3						28	6	17				
Asteraceae	<i>Coreopsis palmata</i>	NPF								1								6
Fabaceae	<i>Coronilla varia</i>	IPL		1				3	1	2	2		6			150	72	111
Euphorbiaceae	<i>Croton glandulosus</i>	NA						1	1	3						6	6	17
Cyperaceae	<i>Cyperus filiculmis</i>	NPS	4	6	2	2		6	3	2	4	22	34	11	11	34	17	11
Fabaceae	<i>Dalea purpurea</i> *	NPL				5					5				28			28
Brassicaceae	<i>Draba reptans</i>	NA		2									11					
Asteraceae	<i>Echinacea pallida</i> *	NPF			2	10				1	11			11	56		6	62
Asteraceae	<i>Erigeron annuus</i>	NA		1		1							17		6			
Asteraceae	<i>Erigeron strigosus</i>	NB	1	3	1	2						6	17	6	11			
Euphorbiaceae	<i>Euphorbia corollata</i> *	NPF			6	7				7	8			34	39		39	45
Lamiaceae	<i>Hedeoma hispidum</i>	NA				1									6			
Asteraceae	<i>Helianthus pauciflorus</i>	NPF	5	5	4	4						106	50	22	78			
Poaceae	<i>Koeleria macrantha</i> *	NPG	7	5	8	5		2	1	1	2	50	28	78	28	22	6	6
Asteraceae	<i>Krigia virginica</i>	NA		3		2							17		11			
Brassicaceae	<i>Lepidium virginicum</i>	NA				3			1		1				17		6	6
Poaceae	<i>Leptoloma cognatum</i>	NPG	3	5	2	2		3	1		1	39	28	11	11	17	6	6
Fabaceae	<i>Lespedeza capitata</i> *	NPL		1	2	4				4	5		6	11	22			22
Asteraceae	<i>Liatris aspera</i> *	NPF	1								1	6						6
Linaceae	<i>Linum sulcatum</i>	NA		1									6					
Boraginaceae	<i>Lithospermum carolinense</i>	NPF	1	3	1	1					1	17	17	6	6			6
Fabaceae	<i>Medicago lupulina</i>	IAL		1		1		10	21	12	13		6		6	67	151	67
Fabaceae	<i>Melilotus sp.</i>	IBL									1							6
Molluginaceae	<i>Mollugo verticillata</i>	IA									1							6
Lamiaceae	<i>Monarda punctata</i>	NPF						1	1	1	1					6	6	6
Onagraceae	<i>Oenothera biennis</i> *	NB				3					1				17			6
Onagraceae	<i>Oenothera rhombipetala</i>	NB		6		3					1		56		17			6
Cactaceae	<i>Opuntia macrorhiza</i>	NPF	1	4		4		10	7	4	5	6	78		56	178	61	78
Oxalidaceae	<i>Oxalis dillenii</i>	NPF		3					5	1	3		17				28	6
Poaceae	<i>Panicum depauperatum</i>	NPG	1		1	1						6		6	6			
Poaceae	<i>Panicum oligosanthes</i> *	NPG	1	10	1	3		4	7	2	3	6	56	6	17	22	39	11
	var. scribnerianum																	
Poaceae	<i>Panicum villosissimum</i>	NPG		4		6		1	1	2	1		22		34	6	6	33
Poaceae	<i>Paspalum setaceum</i>	NPG							3	1	1						17	6
Solanaceae	<i>Physalis virginiana</i>	NPF	6	1	4	6		1	2	2		34	6	22	34	39	11	11
Plantaginaceae	<i>Plantago patagonica</i>	IA		2		4							11		22			
Poaceae	<i>Poa compressa</i>	IPG		1									6					
Poaceae	<i>Poa pratensis</i>	IPG	25	22	25	25		23	23	22	21	251	223	262	207	318	195	356
Polygalaceae	<i>Polygala polygama</i>	NB	3	10	2	11			1			17	89	11	73		6	
Polygonaceae	<i>Polygonum tenue</i>	NA		1									6					
Rosaceae	<i>Potentilla recta</i>	IPF	1	4	3	3		1	2	1		6	34	28	28	17	11	17

Anacardiaceae	<i>Rhus aromatica</i> var. <i>arenaria</i>	NW			2		1				11		6		
Polygonaceae	<i>Rumex acetosella</i>	IPF	1	1	1	1					6	6	6	6	
Poaceae	<i>Schizachyrium scoparium</i> *	NPG	25	22	25	23		2	5		1317	467	1161	462	22
Selaginellaceae	<i>Selaginella rupestris</i>	NP	3		1		2	1	2		17		6		11
Caryophyllaceae	<i>Silene antirrhina</i>	NA		3	1	3		2	1			17	6	17	11
Solanaceae	<i>Solanum carolinense</i>	NPF			1	1	2	1	1	1			6	6	6
Asteraceae	<i>Solidago nemoralis</i> *	NPF		1								6			
Asteraceae	<i>Solidago rigida</i> *	NPF				2			1				11		6
Poaceae	<i>Sorghastrum nutans</i>	NPG	2	3	9	9	1	1	1		56	17	106	128	6
Poaceae	<i>Sporobolus clandestinus</i>	NPG	2	1	2	2	2		3	3	45	6	22	11	11
Poaceae	<i>Sporobolus cryptandrus</i>	NPG					6	3	8	5					34
Fabaceae	<i>Strophostyles leiosperma</i>	NAL			1								6		
Commelinaceae	<i>Tradescantia ohimensis</i> *	NPF	1	3	1	7			1	9	6	17	6	39	6
Asteraceae	<i>Tragopogon dubius</i>	IB			1	1							6	6	
Campanulaceae	<i>Triodanis perfoliata</i>	NA	1	8		4					6	45		22	
Scrophulariaceae	<i>Verbascum thapsus</i>	IB							1						6
Verbenaceae	<i>Verbena stricta</i> *	NPF	1	1		2		2			6	17		11	11
Scrophulariaceae	<i>Veronica arvensis</i>	IA		2		3						11		17	