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The role of small-scale disturbances in structuring the  
plant community of native and reconstructed prairies

by

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A dissertation submitted to the graduate faculty  
in partial fulfillment of the requirements for the degree of  
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## ABSTRACT

Understanding the link between pattern and process is an important goal in ecology, and much research has focused on how small-scale disturbances act to produce spatial patterns in plant communities. In this research, I investigated the role of small-scale disturbances in structuring the plant communities of native and reconstructed prairies, with an explicit emphasis placed on understanding how spatial and temporal patterns in disturbance production affect seedling recruitment.

Two studies investigated the spatial and demographic relationships between gopher mound production and four plant species in a native prairie. The spatial distributions of three species were positively related to the pattern of mound production, while the spatial distribution of one perennial grass species was unrelated. Seedling survivorship of all species was generally greater when growing directly on mounds than off mounds. Survivorship by seedlings growing on mounds was unrelated to the rate of neighborhood mound production, while survivorship by seedlings growing off mounds was negatively related. These studies provided evidence that mounds serve as sites for seedling recruitment into grasslands. Because mound production is spatially and temporally autocorrelated, these small-scale disturbances directly contribute to the formation of spatial patterns in native prairie plant communities.

Two additional studies were conducted as part of a large, landscape-level experiment to explicitly investigate how the spatial and temporal patterns in the production of small-scale disturbances affect seedling recruitment into reconstructed prairie. Seeds of forb species were planted on and off small-scale soil disturbances constructed to mimic gopher mounds. As predicted, seedling recruitment was greater on mounds than off mounds. However, there was no evidence that seedling recruitment was affected by the spatial or temporal patterns of mound production. In addition, there was some evidence that selective herbivory by small mammalian herbivores reduced the diversity of recruited seedlings, but herbivory pressure was

approximately equal on and off mounds. The vegetation structure of the reconstructed prairies was different from that of native prairies, making it difficult to draw conclusions about the effects of disturbance production patterns on seedling recruitment into native prairies. Nevertheless, the studies provided important insights as to the similarities and differences in function of small-scale soil disturbances in native and reconstructed prairies.

## CHAPTER 1. GENERAL INTRODUCTION

### Introduction

The impact of disturbance on plant community structure and diversity has been an important topic in plant ecology for many years (*e.g.*, Cooper 1926, Watt 1947, Pickett and White 1985). The current predominant theory suggests that maximum species diversity occurs under conditions of intermediate disturbance rate and intensity (Grime 1973, Connell 1978, Huston 1979), with disturbance rate defined as the mean number of disturbance events per unit time, and disturbance intensity defined as the biomass damage inflicted by each disturbance event (Pickett and White 1985). However, recent studies suggest that other aspects of the disturbance regime may be more important than rate and intensity for maintaining plant community structure and species diversity in a number of ecological systems. Collins and Barber (1985) and Collins (1987) reported that the interaction between different types of natural disturbances was most important for maintaining community structure and diversity in tallgrass prairie, while Moloney and Levin (1996) showed that the spatio-temporal architecture of a disturbance regime may be as important as rate and intensity in determining plant community structure and diversity. To date, however, few studies of natural disturbance have included an explicit consideration of the spatio-temporal architecture of the disturbance regime or have experimentally examined the importance of spatio-temporal disturbance architecture in regulating plant community structure and diversity. This void provided the motivation for this dissertation research.

### Pocket gopher mounds

The soil disturbances produced by subterranean mammals are an ideal model system for studying how plant communities are impacted by the spatio-temporal architecture of a small-scale disturbance regime. Subterranean rodents are found on every major continent except

Australia (Lacey et al. 2000), and many of these animals produce small-scale soil disturbances in distinctive spatial and temporal patterns. In addition, a significant body of research, at least in North America, has focused on the role of these disturbances in structuring plant communities. However, little of the research linking small-scale disturbance production and plant community structure has been conducted with an explicit consideration of the spatio-temporal architecture of the disturbance regime (exceptions include Hobbs and Mooney 1985, Thomson et al. 1996).

The plains pocket gopher (*Geomys bursarius*) is a subterranean rodent found commonly throughout the eastern Great Plains of North America, including the tallgrass prairie remnants of Iowa (Zimmerman 1999). Pocket gophers live and forage in underground burrows, periodically expel soil onto the surface, and create a mosaic of soil disturbances across the grassland landscape. Gopher mounds can cover as much as 5% to 20% of a field surface (Grant et al. 1980, Reichman et al. 1982, Spencer et al. 1985, Klein 1997), although the production of mounds is quite patchy. Klaas et al. (2000) found that the production of mounds on an Iowa prairie was highly clustered at spatial scales of less than 20 m, with the locations of mound clusters remaining relatively static over years.

Mound-building activity physically alters the environment. Long-term gopher activity increased microtopographic variation and relative soil height in one study (Inouye et al. 1997). The soil of gopher mounds is lower in nutrients, particularly phosphorus, nitrogen, and potassium, than undisturbed soil (Spencer et al. 1985, Inouye et al. 1987, Zinnel and Tester 1990), because mounds are created by gophers pushing nutrient-poor subsurface soil to the ground surface. In this way, gopher activity actually increases the spatial heterogeneity of nutrients in surface soil (Inouye et al. 1987). The percentage of bare ground increases in areas with gopher mound-building activity (Foster and Stubbendieck 1980, Grant and McBrayer 1981), and plant biomass directly over gopher mounds and burrows is lower than in undisturbed areas (Reichman and Smith 1985, Reichman et al. 1993). However, it was

recently reported that pocket gopher tunnels had only a minor effect on the plant community in Texas coastal prairie (Rezsutek and Cameron 2000). The bare ground of gopher mounds provides important space for seedling recruitment in the thick matrix of perennial grasses and forbs in tallgrass prairie (Gross and Werner 1982, Belsky 1986, Goldberg 1987, Goldberg and Gross 1988, Reader and Buck 1991), and more seedlings are found on mounds than off mounds (Martinsen et al. 1990).

The physical changes caused by gopher mound production also have an influence on plant community composition. Gopher mounds reportedly slow the rate of succession in old fields by continuously re-starting succession on new mounds (Tilman 1983, Inouye et al. 1987). After the eruption of Mound St. Helens, gopher mounds were important for facilitating succession in the extremely disturbed environment (Andersen and MacMahon 1985). Under less extreme conditions, annual plant species have been found in higher abundance in areas with gopher mounds than in areas without mounds (Laycock and Richardson 1975, Schaal and Leverich 1982, Inouye et al. 1987). Perennial grasses reportedly decrease in the presence of mounds, while forbs increase (Williams and Cameron 1986, Martinsen et al. 1990). Many researchers report that plant species diversity increases in areas with pocket gopher activity (Tilman 1983, Inouye et al. 1987, Huntly and Inouye 1988, Huntly and Reichman 1994), but the relationship between diversity and mound production seems to be dependent upon the scale at which it is measured. At a small scale (*i.e.*, the size of a single mound), it has been reported that species richness and diversity remain unchanged over time by disturbance (Williams et al. 1986) or are reduced on mounds (Umbanhowar 1992, Wolfe-Bellin and Moloney *in review*). At a larger scale (*i.e.*, the size of a whole prairie remnant), however, it has been reported that species richness and diversity are higher in areas of high gopher activity than in areas without gopher mounds (Tilman 1983, Inouye et al. 1987, Huntly and Inouye 1988, Huntly and Reichman 1994).

The relationship between gopher mound production and the demography of individual plant species has also been studied in a few species. *Berteroa incana*, a weedy annual, and *Tragopogon dubius*, a weedy biennial, both grew larger and reproduced more prolifically when growing on gopher mounds and burrows than in undisturbed areas (Reichman 1988, 1996). *Penstemon grandiflorus*, a perennial forb, also grew faster and reproduced earlier when growing on gopher mounds than off mounds (Davis 1990, Davis et al. 1995). In addition, Davis et al. (1991a, 1991b) investigated the combined effects of fire and mound production on *P. grandiflorus* and concluded that the species ultimately depends on both mound production and fire for its long-term persistence.

Gopher mound production also affects the faunal communities of grasslands. Grasshopper abundance was positively related to mound production in one study (Huntly and Inouye 1988). In another study, the abundance of arthropods was higher in mounds and burrows, causing grasshopper mice, insectivorous small mammals, to forage on mounds more often than expected if foraging were random (Stapp 1997). In addition, Whittaker et al. (1991) reported that the abundance of adult male meadow voles was positively related to mound production in an old field, and that meadow voles seemed to travel preferentially across bare mounds. However, in a more recent study, Klaas et al. (1998) reported a negative trend in meadow vole abundance in areas of high mound production. The meadow vole is an important seedling herbivore in grasslands (Howe and Brown 1999), and the influence of mound production on the distribution of herbivores is potentially an indirect mechanism by which pocket gophers could affect plant communities. If herbivores avoid mounds, then plant species selectively grazed by those herbivores may be protected from herbivory on mounds and in areas of high mound production. On the other hand, if herbivores are attracted to areas of high mound density, then those same plant species may be at greater risk of herbivory when growing on mounds or near clusters of mounds. To date, however, no studies have

investigated whether the indirect effects of mound clustering, through changes in herbivore behavior, contribute to the influence of mound production on plant community structure.

### **Tallgrass prairie ecosystem**

The tallgrass prairie of central North America is an ecosystem of high plant species diversity. This diversity is maintained through a combination of climate and natural disturbances at large and small scales (Axelrod 1985). Historically, natural large-scale disturbances included fire and the grazing of bison herds. While bison grazing is nearly non-existent today, fire is commonly used as a management tool on prairie remnants. Fires usually occur at 3- to 5-year intervals in managed systems and affect tracts of land at relatively broad spatial scales. Fires remove aboveground vegetation and dead plant litter, reduce the cover and encroachment of woody vegetation, increase the productivity and reproduction of  $C_4$  grasses, and provide open space for seedling recruitment (Weaver and Rowland 1952, Knapp and Seastedt 1986, Hulbert 1987, Knapp et al. 1998). Overall, plant species richness is greatest at intermediate fire frequencies. Species richness decreases at one extreme under annual spring burn regimes because of the increased dominance of  $C_4$  grasses (Collins and Steinauer 1998), and also toward the other extreme with the complete absence of fire because of the accumulation of detritus (Knapp and Seastedt 1986).

Small-scale disturbances are also important for maintaining high plant species diversity and the characteristic plant community structure of tallgrass prairie. Historically, natural small-scale disturbances included badger diggings, ant mounds, pocket gopher mounds, and other disturbances created by small animals. In some ways, these small disturbances affected the plant community in a manner similar to the effects of large-scale disturbances. Small disturbances effectively removed aboveground vegetation and dead plant litter, providing space for seedling recruitment (Gross and Werner 1982, Belsky 1986, Goldberg 1987, Goldberg and Gross 1988) and influencing the environment in many of the ways discussed earlier.

Tallgrass prairie covered vast expanses of central North America in the early 1800's, but today less than one-tenth of one percent of the original area remains in some states and provinces of the eastern Great Plains (Samson and Knopf 1994). The fragmentation of the prairie landscape has caused a decline in species richness and diversity in the tallgrass plant community (Noss 1987, Wilcove 1987, Leach and Givnish 1996). It has been suggested that species richness has declined in prairie remnants because species richness is strongly recruitment limited (Tilman 1997) and seed dispersal between distant prairie remnants is rare. Leach and Givnish (1996) attributed the decline in species richness on small prairie remnants in southern Wisconsin to the suppression of fire, an important large-scale disturbance. Fragmentation of the prairie landscape has greatly reduced the occurrence of large-scale disturbances. Grazing by herds of large herbivores is less common on small prairie remnants, and fires occur only on carefully managed remnants. Small-scale disturbances, however, have not been impacted as greatly by fragmentation and are still abundant on prairie remnants. Thus, it is important to understand the role of small-scale disturbances, alone and in combination with large-scale disturbances, in regulating plant species diversity and community structure in tallgrass prairie.

### **Prairie restoration**

Concern over the loss of native prairie has led to prairie restoration efforts within the past century. The first attempt at prairie restoration was begun by Aldo Leopold at the University of Wisconsin Arboretum in the 1930's (Jordan et al. 1987). Eventually this early attempt was deemed a failure (Jordan et al. 1987), but it did lead to additional restoration work at the University of Wisconsin Arboretum in the 1950's by J. T. Curtis. Curtis used the restoration process begun by Leopold to study the importance of fire in prairie ecology (Curtis and Partch 1948). This second attempt at prairie restoration was more successful, resulting in what is today called the Curtis Prairie (Cottam and Wilson 1966). In recent decades, prairie



restoration has become more widespread, and handbooks of detailed restoration instructions are now available (*e.g.*, Thompson 1992, Shirley 1994, Packard and Mutel 1997).

Restoration provides an opportunity to gain ecological knowledge about an ecosystem. In fact, Leopold's failed attempt at prairie restoration provided an opportunity for others to study the importance of fire in prairie ecology (Jordan et al. 1987). Some authors have even gone so far as to call restoration an "acid test for ecology" (Bradshaw 1987) and the "ultimate test of ecological theory" (Ewel 1987). Indeed, the process of restoration does provide a framework in which basic ecological questions can be addressed, thus facilitating the accumulation of basic ecological knowledge as well as information that can be applied to the restoration process. Two of the four studies reported in this dissertation were conducted on restored prairie, using the process of restoration as a framework for testing predictions about how the spatio-temporal architecture of a small-scale disturbance regime functions to maintain and increase plant species diversity in prairies.

According to Packard and Mutel (1997), the Society for Ecological Restoration defines *restoration* to include all of the following: natural area management, *reconstruction* (*i.e.*, planting native seed on plowed ground), and *rehabilitation* (*i.e.*, improving a degraded site). I have used the term restoration in the same general sense so far, but hereafter I will use the more technical term reconstruction to describe sites where native prairie seed has been planted on plowed ground.

## **Research questions**

This research consists of four studies. The first study investigated the effects of gopher mounds and fire on the spatial distribution and demography of a short-lived legume in a native tallgrass prairie. The specific goals in the study were to (1) characterize the relationship between the pattern of gopher mound production and the legume; (2) quantify the demographic response of the legume to conditions on and off gopher mounds; and (3) investigate among-

year differences in the demographic response to conditions on and off mounds, in which the most striking difference between years was the occurrence or absence of fire.

In the second study, I investigated how the spatial distribution and demography of four plant species, representing a range of life history strategies and palatabilities to mammalian herbivores, were directly and indirectly influenced by the spatial pattern of natural gopher mound production on a native tallgrass prairie. In this study, I characterized the relationship between the spatial distribution of each species' adult population and the long-term production of gopher mounds. I then conducted a two-year study to determine whether the spatial relationships between the plants and mounds were caused by (1) the direct demographic response of plants to growth immediately on mounds or off mounds, as well as (2) a more indirect demographic response of plants to growth in areas of different neighborhood mound production rates. I predicted that the direct demographic response of plants to mounds would be caused by two factors, reduced competition with neighboring plants on mounds and reduced risk of herbivory by small mammalian herbivores on mounds. I predicted that the indirect demographic response of plants to mound production rate would be caused primarily by a further reduction in risk of herbivory in areas of high mound production, since small mammals are thought to avoid these areas.

Study three investigated whether the spatial and temporal patterns in the production of small-scale soil disturbances in prairie influence seedling recruitment and thus plant species diversity and community structure. This study took a more experimental approach than the first two, because it was conducted on reconstructed prairie and involved the construction of artificial, small-scale soil disturbances designed to mimic gopher mounds. Thus, restoration was used as a framework in this study to address basic ecological questions about the function of small-scale soil disturbances and the patterns in which they are created for maintaining and increasing plant species diversity in prairies. An additional goal of the study was to investigate

how small-scale soil disturbances could be used to increase species diversity in reconstructed prairies, which frequently exhibit low plant species diversity.

Study four was conducted in the same experimental framework as study three. It was conducted to investigate specifically (1) how the selective foraging of mammalian herbivores regulates the recruitment of seedlings in reconstructed prairie, (2) whether seedlings growing on mounds are safer from mammalian herbivores than are seedlings growing off mounds, and (3) how the effects of mammalian herbivory on seedling recruitment are modified by the spatial architecture of the disturbance regime.

### **Dissertation organization**

This dissertation is organized as six chapters. The first chapter consists of a general introduction and review of the background literature. Chapters 2-5 are papers prepared for publication. Chapter 2 has been published in the *Canadian Journal of Botany*, and authorization for copyright transfer has been granted by the publisher. Chapter 3 will be submitted to *Ecology*, Chapter 4 will be submitted to *Ecological Applications*, and Chapter 5 will be submitted to *Oecologia*. Finally, the sixth chapter consists of a general conclusion of the research results.

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## **CHAPTER 2. THE EFFECT OF GOPHER MOUNDS AND FIRE ON THE SPATIAL DISTRIBUTION AND DEMOGRAPHY OF A SHORT-LIVED LEGUME IN TALLGRASS PRAIRIE**

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### **Abstract**

Many studies have reported that gopher mounds can increase species diversity and spatial heterogeneity of plant communities, but few studies have experimentally linked these small-scale disturbances to spatial heterogeneity in the distribution of individual plant populations. In this study, we directly tested for a spatial relationship between the pattern of gopher mound production and the distribution of a short-lived legume, *Medicago lupulina*, across a tallgrass prairie remnant. In addition, we conducted a 3-year study examining the demographic response of *M. lupulina* to mound and off-mound planting treatments, during which a spring fire occurred one year. We found that the spatial distribution of *M. lupulina* was positively correlated with the distribution of mounds. Germination was significantly greater off mounds in all years, while survivorship and fecundity were significantly greater on mounds in the two years without fire. During the fire year, survivorship was significantly greater off mounds and fecundity was approximately equal on and off mounds. We conclude that the positive spatial relationship between *M. lupulina* and mounds is caused by the direct dependence of *M. lupulina* on mounds for survivorship in most years. Gopher mounds provide microsites where plant competition and risk of herbivory are reduced. Overall, gopher mounds can directly produce spatial heterogeneity in the plant community, but the strength of this effect may be significantly modified in some years, particularly those in which a spring fire occurs.

## Introduction

The impact of disturbance on plant community structure and diversity has been an important topic in the plant ecology literature for many years (e.g., Cooper 1926, Watt 1947, Levin and Paine 1974, Connell 1978, Pickett and White 1985, see citations in Sousa 1984). The predominant theory suggests that maximum species diversity occurs under conditions of intermediate disturbance rate and intensity (Grime 1973, Connell 1978, Huston 1979), with disturbance rate being defined as the mean number of disturbance events per unit time, and disturbance intensity being defined as the biomass damage inflicted by each disturbance event (Pickett and White 1985). However, recent studies suggest that other aspects of the disturbance regime may be more important than rate and intensity for maintaining plant community structure and species diversity in a number of ecological systems. Collins and Barber (1985) and Collins (1987) reported that the interaction between different types of natural disturbances was most important for maintaining community structure and diversity in tallgrass prairie, while Moloney and Levin (1996) showed that the spatial and temporal architecture of a disturbance regime may be as important as rate and intensity in determining plant community structure and diversity. Even so, few studies have directly examined the relationship between the spatial and temporal architecture of a disturbance regime and the distribution of plant species within the plant community (Moloney and Levin 1996).

We investigated the spatial and temporal effects of pocket gopher mound production and fire on the distribution and demography of *Medicago lupulina* L. (black medic, Fabaceae), a short-lived plant species, in a tallgrass prairie plant community. We chose *M. lupulina* as a model species primarily because it is short-lived and would show a more rapid demographic response (and perhaps a more clear cut spatial response) to treatment effects than would a more long-lived species. Fire was included as a factor in the study because our study site was burned in the second year of the three-year demography experiment, but it serves as an interesting contrast to the gopher mound treatments because gopher mound

production and fire represent two distinct, yet important, types of disturbance with respect to their spatio-temporal architecture in tallgrass prairie systems.

Gopher mounds, which at our study site are produced by the burrowing activity of the plains pocket gopher (*Geomys bursarius*), are repeatedly constructed within a single growing season in clusters ranging over spatial scales of one to twenty meters (Klaas et al. 2000). Pocket gophers tunnel underground in search of roots from preferred plant species (Andersen 1988, Behrend and Tester 1988) and periodically expel soil onto the surface (Adams 1966, Hobbs and Mooney 1991, Moloney 1993, Klaas et al. 2000). Previous research has shown that gopher mounds provide bare ground suitable for seedling recruitment (Gross and Werner 1982, Belsky 1986, Goldberg 1987, Goldberg and Gross 1988, Peart 1989, Martinsen et al. 1990). Annual plant species are found in greater abundance in areas with gopher activity (Laycock and Richardson 1975, Schaal and Leverich 1982, Inouye et al. 1987), and plant species diversity and spatial heterogeneity increase with gopher mound-building activity (Tilman 1983, Hobbs and Mooney 1985, Inouye et al. 1987, Huntly and Inouye 1988, Huntly and Reichman 1994).

In contrast to the localized effects of gopher mound production, fires commonly occur at 3- to 5-year intervals in managed systems and affect tracts of land at relatively broad spatial scales (e.g., see Leach and Givnish 1996). Fires today are often used as management tools on grassland remnants to remove aboveground vegetation and dead plant litter, reduce the cover and encroachment of woody vegetation, increase the productivity and flowering of C<sub>4</sub> grasses, and provide open space for seedling recruitment (Weaver and Rowland 1952, Knapp and Seastedt 1986, Hulbert 1987, Knapp et al. 1998). Overall, plant species richness is greatest at intermediate fire frequencies, with richness decreasing at one extreme under annual spring burn regimes, due to the increased dominance of C<sub>4</sub> grasses (Collins and Steinauer 1998), and toward the other extreme with the complete absence of fire, due to the accumulation of detritus (Knapp and Seastedt 1986). It is unclear how the effects of fire

might affect the impact of gopher disturbances on prairie plant species, but some clues might be obtained by examining the effects of these kinds of disturbances on demographic processes.

The direct relationship between the production of gopher mounds and the demography of individual plant species has been examined in some studies. Reichman (1988, 1996) found that *Berteroa incana*, a weedy annual, and *Tragopogon dubius*, a weedy biennial, grew larger and produced more seeds when growing on gopher mounds and burrows than in undisturbed areas. Davis (1990) and Davis et al. (1995) found the same result with a perennial forb, *Penstemon grandiflorus*, which grew faster and reproduced earlier in the bare soil of gopher mounds than in undisturbed areas. In addition, Davis et al. (1991a, 1991b) investigated the combined effects of fire and mound production, concluding that *P. grandiflorus* ultimately depends on both mound production and fire for the bare space required for its long-term persistence.

Similar to the studies described above, we investigated the demographic response of *M. lupulina* to growth on and off gopher mounds, with and without the effects of a spring burn prior to the growing season. However, we expanded the scope of our study to include a consideration of the relationship between the spatial distribution of mound production and the demography and spatial distribution of *M. lupulina*, since this may be of critical importance in determining the ultimate success of *M. lupulina*, as well as a number of other species, in the prairie plant community (cf., Leach and Givnish 1996, Moloney and Levin 1996). Our ultimate goal is to understand the role of gopher mound disturbance in structuring plant communities.

The specific goals in this study were to (1) characterize the relationship between the pattern of gopher mound production and the distribution of *M. lupulina* within a tallgrass prairie, and (2) quantify the demographic response of *M. lupulina* to conditions on and off gopher mounds. The demographic experiment was repeated for three years, with a spring

burn occurring during the second year of the study, allowing us to (3) investigate among-year differences in the demographic response of *M. lupulina* to conditions on and off gopher mounds, in which the most striking difference between years was the occurrence or absence of fire. While we attribute most of the measured among-year differences in *M. lupulina* demography to the fire, we cannot eliminate other possible among-year differences, such as weather conditions. We predicted that the distribution of *M. lupulina* would be positively related to the immediate and long-term patterns of gopher mound production, and that germination rate, seedling survivorship to adulthood, and reproduction would be greater when *M. lupulina* grew on mounds as compared to off mounds. In the year of the fire, however, the large-scale disturbance was predicted to override the demographic benefits provided by small-scale mound disturbances, neutralize the positive impact of mounds on demography, and cause no difference in germination rate, seedling survivorship, and reproduction on and off mounds. Both mounds and fire provide bare soil for seedling establishment, and space for growth of newly emerging seedlings has been acknowledged as the primary requirement for successful establishment of annuals (Ross and Harper 1972). Thus, we predicted greater success at each demographic stage for *M. lupulina* when growing on mounds compared to off, except for the year when fire provided bare space for seedling establishment across the entire landscape. In addition, similar demographic results have been found in earlier studies of individual plant species growing on gopher mounds (Reichman 1988, 1996; Davis 1990; Davis et al. 1991a, 1991b, 1995).

## Methods

### Study organism

*Medicago lupulina* is a legume native to west Asia that is now naturalized throughout North America (Turkington and Cavers 1979). It commonly occurs in tallgrass prairies, where it grows as an annual or short-lived perennial (Turkington and Cavers 1979). Previous

studies have reported that *M. lupulina* is more abundant on soil disturbances than in undisturbed vegetation (Reader and Buck 1991), that *M. lupulina* density increases with decreasing vegetation density (Pavone and Reader 1985a), and that *M. lupulina* seedling emergence and seedling density increase with decreasing vegetation density (Hogenbirk and Reader 1989, Reader 1991, Reader and Beisner 1991). These factors make it a suitable candidate for examining the response of disturbance-sensitive species to the impact of gopher mound and fire disturbance regimes in tallgrass prairie ecosystems.

### Study site

The study was conducted in northwest Iowa at Anderson Prairie State Preserve (Emmet County T100N R34W), an 80-hectare remnant of tallgrass prairie managed by the Iowa Department of Natural Resources. Anderson Prairie is located within the prairie pothole region of the tallgrass prairie ecosystem found across north-central North America. The tallgrass prairie ecosystem is extremely fragmented, with as little as one-tenth of one percent of it remaining in some states and provinces of the eastern Great Plains (Samson and Knopf 1994). Much of the remaining tallgrass prairie is scattered as small remnants of less than 100 hectares, with the history and current management of each remnant being unique. Anderson Prairie was grazed by cattle until the mid-1970s, but has never been plowed. At the time of this study, the prairie was managed with controlled fires set every three to five years in the early spring. Vegetation on the site is representative of typical tallgrass prairie remnants and consists of approximately 150 plant species. The native grasses *Andropogon gerardii* Vitman and *Sorghastrum nutans* (L.) Nash are abundant and dominant. In addition, *Bromus inermis* L. and *Trifolium pratense* L., two exotic plant species, were planted on the site when it was grazed, and are abundant today. The plant community also naturally contains *M. lupulina*. The animal community on the site consists of small mammals and grassland birds typical of those found on prairie remnants, including the plains pocket gopher (*Geomys bursarius*).

In April 1994, a permanent 0.64-hectare plot was established at the study site (Klaas et al. 1998, 2000). The plot consisted of 64 10 m x 10 m cells arranged in a square with no buffers between cells. The plot was characterized by a moderate elevational gradient, with the southwest corner approximately 6 m higher in elevation than the northeast corner (Fig. 1). The soils across most of the plot consist of the Nicollet and Clarion soil series (L. Burras, *personal communication*), indicating a long history of mesic prairie vegetation, while the northeast corner contains the Webster soil series (L. Burras, *personal communication*), indicative of wet-meadow vegetation.

### **Survey of *Medicago lupulina* and gopher mound distributions**

In July 1995, we surveyed for the presence of *M. lupulina* in each cell. Gopher mounds were mapped in a series of surveys during 1994–1998. The locations of all fresh mounds were recorded at one-week intervals throughout the 1994, 1995 (Klaas et al. 2000), and 1996 growing seasons, and at three- to four-week intervals during the 1997 and 1998 growing seasons. We summed the total number of mounds produced within each cell during the 1994 growing season alone, and for the period 1994–1998. Mounds produced during 1994 were directly available to *M. lupulina* as bare soil during the year it was surveyed, and should be very closely related to the distribution of *M. lupulina* if it is completely dependent upon the existence of bare sites for successful establishment and growth. Mound production tallied over 1994–1998, on the other hand, was used to estimate the long-term probability of disturbances occurring at different locations within the site, since the location of gopher activity across landscapes remains relatively constant over years (Klaas et al. 2000). We expected to find a positive relationship between the distribution of *M. lupulina* and the 5-year pattern of disturbances if the clustered nature of gopher mound production has an indirect, landscape-level effect on the demography of *M. lupulina*, which could occur through changes in herbivore behavior caused by the presence of disturbance (e.g., Klaas et al. 1998).

Logistic regressions were performed using SAS (version 6.12, SAS Institute Inc.) to determine whether the presence of *M. lupulina* within each cell was related to mound number. Each cell was treated as an independent experimental unit. In addition, we included the average relative elevation (range 0 - 6 m) of each cell as a covariate to control for the effects of other environmental factors on the distribution of *M. lupulina*, since the 6 m elevational gradient is clearly associated with a strong environmental gradient at the study site.

We performed two sets of logistic regressions. In the first, we examined the relationship between the distribution of *M. lupulina* in 1995 and the distribution of mounds produced in 1994. Specifically, we included the following three variables in the model and tested for the significance of each in predicting *M. lupulina* presence: (1) mound production in 1994, (2) elevation, and (3) an interaction term for 1994 mound production x elevation. In the second logistic regression, we tested the relationship between the distribution of *M. lupulina* in 1995 and the distribution of long-term mound production, using the following variables: (1) mound production from 1994 through 1998, (2) elevation, and (3) an interaction term for 1994-1998 mound production x elevation. For each set of regressions, the best-fit model was determined with the Schwartz Criterion (SC). The SC indicates the fit of the model as each independent variable is added, adjusting for the number of explanatory variables and the number of observations included. The lowest SC value indicates the best-fit model.

### **Demographic experiments**

In addition to the surveys, we conducted an experimental study to determine the demographic response of *M. lupulina* when planted on and off mounds during three growing seasons. In two years, 1996 and 1998, the study plot had not been burned for at least 12 months before we began the experiment. In 1997, the plot and surrounding prairie had been



burned in a spring fire approximately 1.5 months before we planted. In all three years, *M. lupulina* was planted in late May or early June on and off gopher mounds in a paired-treatment experimental design. Each year, we planted seeds on 20 gopher mounds chosen at random from a pool of all mounds produced during the spring or fall prior to planting (on-mound treatment), with the constraint that on-mound treatments be separated by a minimum of 3 m. Each on-mound location was paired with an off-mound location 1.5 m west of the mound (off-mound treatment). On-mound treatments were bare of litter and other vegetation at the time of planting. Off-mound treatments, however, were covered by varying amounts of standing vegetation and litter, with the amount closely related to fire treatment. In the years without fire, off-mound standing vegetation was tall and dense, with plant litter  $3.8 \pm 0.7$  (Mean  $\pm$  1 SE) cm deep in 1996 and  $3.0 \pm 0.2$  cm deep in 1998. In the year of the fire, standing vegetation was only a few centimeters tall at the time we planted, and off-mound litter was  $0.7 \pm 0.1$  cm deep.

Each experimental unit (hereafter referred to as a grid) consisted of 49 *M. lupulina* seeds planted in a 7 x 7 array. Seeds were spaced at 5 cm intervals and planted 1 cm deep. Planting depth and spacing were chosen because they produced maximum germination during greenhouse planting trials. The location of each seed was marked with a small plastic stake for ease in relocating seedlings. Seeds were obtained from a commercial seed source in Pennsylvania.

The grids were planted during the following time intervals: 1 - 6 June 1996; 1 - 3 June 1997; and 16 - 19 May 1998. Germination was recorded on 13 June 1996, 27 June 1997, and 1 June 1998. In 1996, the experiment was continued for only one growing season (because the site was burned in spring 1997), with survivorship recorded five times between 27 June and 29 September 1996. The 1997 and 1998 experiments were continued for two growing seasons. In the 1997 experiment, survivorship was recorded 18 July 1997, 23 August 1997, and 23 July 1998. In the 1998 experiment, survivorship was recorded five

times between 18 June and 17 October 1998, and four times between 30 May and 7 September 1999.

Germination for each grid was calculated as the proportion of the original 49 seeds that germinated during the first growing season. Survivorship was calculated for each grid at each survey throughout the growing season, and is reported as the percentage of plants surviving of those that germinated. Once the plants began flowering, we recorded the number of racemes produced per plant and removed the racemes to prevent the dispersal of non-local seed on the study site. At the end of each study, plants were collected and dried at 65°C for a minimum of 7 days. Total biomass (above- and below-ground) of each plant was measured in 1996, while only above-ground biomass was measured in 1997 and 1998.

Pairwise, two-tailed t-tests were used to test for significant differences within years between the on- and off-mound germination rates and for differences between on- and off-mound plant biomass at the end of each experiment. Survivorship on and off mounds at each survey was also analyzed with pairwise, two-tailed t-tests, but we corrected for repeated comparisons within experiments using the Bonferroni method (in 1996,  $\alpha = 0.05/5 = 0.01$ ; in 1997,  $\alpha = 0.05/3 = 0.017$ ; in 1998,  $\alpha = 0.05/9 = 0.006$ ).

## Results

### Survey of *Medicago lupulina* and gopher mound distributions

*M. lupulina* was present during the 1995 floristic survey in 36 of the 64 cells, all located in the two-thirds of the plot with relatively high elevation ( $> 1.5$  m; Fig. 1). In 1994, 383 gopher mounds were produced in the plot, primarily in cells with relative elevation  $> 1$  m (Fig. 1). The two cells with greatest mound production in 1994 each contained 32 mounds, while 21 cells contained no mounds. Over the 1994 through 1998 growing seasons, 3012 gopher mounds were produced, with high mound production across most of the plot except for the east edge, where relative elevation was fairly low (Fig. 1).

The logistic regression models that most accurately predicted the distribution of *M. lupulina* contained two independent variables—mound production and elevation (Table 1). The explanatory power of the models decreased when mound production and elevation were entered singly, and when the mound x elevation interaction term was included (Table 1). In the model based on 1994 mound production, regression coefficients were positive for both mound production and elevation, indicating that the probability of finding *M. lupulina* increases with elevation and amount of disturbance (Table 2A). In fact, an examination of the odds ratios for the model including only 1994 mound data shows that the probability of finding *M. lupulina* in a cell increased by a factor of 1.3 for each additional mound in the cell and by a factor of 2.9 for a 1 m increase in relative elevation (Table 2A). For the logistic regression model based on 1994-1998 mound production, mound production and elevation were again positively related to *M. lupulina* presence (Table 2B), although the relationship between 1994-1998 mound production and the presence of *M. lupulina* was weaker than for 1994 mound production (Table 2). If we compare the odds ratios for the two models, we find that the odds ratio for elevation in the 1994-1998 mound model is slightly higher than in the 1994 mound model (3.4 vs. 2.9) and that the odds ratio for mounds is much lower (1.03 vs. 1.32; Table 2). However, the decrease in the mound odds ratio reflects the change in the number of mounds included in the model (3012 mounds for 1994-1998 vs. 383 for 1994 alone), not a change in the underlying relationship; i.e., one mound in the 1994-1998 model is the equivalent of 0.127 mounds in 1994 and  $1.32^{0.127} \approx 1.03$  (cf., Table 2).

### Demographic experiments

*M. lupulina* seedling germination was significantly greater in the off-mound treatments than in the on-mound treatments for all three years (Fig. 2). Survivorship, however, differed between mound treatments for years with fire and without fire (Fig. 3). In 1996 and 1998, both years without fire, survivorship was greater in the on-mound treatment

than off-mound treatment throughout the first growing season (Fig. 3), although this result was only significant for the last two surveys in the 1996 experiment (79-day survey: paired  $t = 3.70$ ,  $P = 0.002$ ; 108-day survey: paired  $t = 3.24$ ,  $P = 0.004$ ;  $\alpha$ -criterion = 0.01). In 1998, survivorship was greater on mounds throughout the first growing season (Fig. 3), but the difference was not statistically significant when the Bonferroni-corrected  $\alpha$ -value criterion was used. Plants from the 1998 experiment were also surveyed throughout the 1999 growing season. They exhibited low survivorship during the second year and, as in the first year, survivorship was greater on mounds than off, but with no statistical significance. On 30 May 1999, survivorship was  $6.75 \pm 2.03\%$  on mounds and  $3.80 \pm 1.43\%$  off mounds. By 7 September 1999, survivorship was  $2.22 \pm 1.09\%$  on mounds and  $1.30 \pm 0.56\%$  off mounds.

For the 1997 experiment, the year with a spring burn, survivorship was significantly greater off mounds than on mounds for both surveys conducted during the first growing season (21-day survey: paired  $t = -6.48$ ,  $P = 0.0001$ ; 57-day survey: paired  $t = -4.28$ ,  $P = 0.0004$ ;  $\alpha$ -criterion = 0.017; Fig. 3). This was opposite the trend for the two experiments in years with no fire. In the second growing season, survivorship for the 1997 plants was very low and not significantly different between mound treatments, although still slightly greater off mounds ( $2.78 \pm 1.37\%$ ) than on mounds ( $0.59 \pm 0.43\%$ ).

In 1996, a no-fire year, plant biomass at the end of the first growing season was significantly greater (paired  $t = 3.49$ ,  $P = 0.003$ ) for plants in the on-mound treatment ( $0.056 \pm 0.014$  g) than off-mound treatment ( $0.008 \pm 0.001$  g). For the 1997 fire-year experiment, survivorship was very low by the end of the experiment in 1998 and no significant difference between plant biomass in the on- and off-mound treatments was detected. Average individual plant biomass on mounds was  $0.042 \pm 0.007$  g, and off mounds was  $0.037 \pm 0.024$  g. In the 1998 experiment, a no-fire year, plants were collected at the end of the second growing season and survivorship was again very low. We could detect no significant difference in

plant biomass between the on- and off-mound treatments. Individual plant biomass was  $0.183 \pm 0.064$  g on mounds, and  $0.095 \pm 0.035$  g off mounds.

Reproduction occurred only on mounds during the first growing season in the two no-fire years (1996 and 1998; Table 3). During the second growing season of the 1998 experiment (second season data were not collected in the 1996 experiment), reproduction occurred both on and off mounds, with slightly greater reproduction in the on-mound treatment than off-mound (Table 3). In the 1997 fire-year experiment, no reproduction occurred on or off mounds during the first growing season, and reproduction was low both on and off mounds during the second season (Table 3).

### Discussion

Much evidence linking gopher mound production and plant community composition has been reported in the plant ecology literature (e.g., McDonough 1974, Spencer et al. 1985, Williams et al. 1986, Inouye et al. 1987, Peart 1989, Hobbs and Mooney 1991). Only a small body of work, however, has directly linked the presence of gopher mounds to the life history success of individual plant species (exceptions include Hobbs and Mooney 1985; Reichman 1988, 1996; Davis 1990; Martinsen et al. 1990; Davis et al. 1995), and few previous studies have considered the spatial context of the relationship (exceptions include Hobbs and Mooney 1985, Thomson et al. 1996). In addition, we know of only two sets of demographic studies that have examined the potential for a significant interaction effect between broad-scale disturbance and the more localized effects of gopher mound production on the demography and distribution of a plant species (Rice 1987; Davis et al. 1991*a*, 1991*b*). With this project, we explored these issues using a number of approaches incorporating *M. lupulina* as a model plant system. Our results suggest that the spatial context of the disturbance regime and the interaction between mound production and broad-scale disturbance, of which fire is an example, are critical for understanding the demography and

spatial distribution of *M. lupulina* and, by extension, may be important in understanding the distribution of other prairie plant species.

### **Spatial relationship to disturbance**

We found a general correlation between the distribution of *M. lupulina* and the presence of gopher mounds using a logistic regression approach. Of particular interest is the fact that the relationship was independent of the effects of the dominant environmental gradient occurring at the site, at least as represented by the lack of an interaction effect with elevation in the regression model. This strongly suggests that *M. lupulina* is dependent upon small-scale disturbances for its demographic success at Anderson Prairie and that it has a greater probability of occurring in areas with higher rates of disturbance. We can infer that this relationship occurs because of the demographic response to disturbance by *M. lupulina*, and we examined this more directly through the field experiments included in this study.

Elevation was also a significant predictor of the distribution of *M. lupulina*, with *M. lupulina* more likely to be found at higher elevations within the study site. The prairie pothole region, within which Anderson Prairie is located, is generally characterized by little elevational relief, and, as a consequence, a slight elevational difference can cause important soil moisture differences. At our research site, cells at lower elevations contained soils and vegetation associated with wet-meadows. It is likely that both pocket gophers and *M. lupulina* are excluded from these sites. Over the 5 years of this study, only a few mounds were produced in these locations and only during very dry weather. Fossorial mammals cannot burrow in wet soils, and growth of *M. lupulina* may also be prevented by high moisture, increased light competition with tall vegetation growing in wet soils, or some other environmental factor correlated with elevation.

### Demographic response to disturbance

Prior to this study, we hypothesized that *M. lupulina* germination rate, seedling survivorship to adulthood, and reproduction would be greater on mounds, while in years with fire, all three would show no differences on and off mounds. However, we found that germination was significantly greater off mounds in all years, independent of any among-year differences. Although the germination result was unexpected, it can be explained by the conditions under which the seeds were planted. Seeds in the off-mound treatment were planted in soil under  $3.4 \pm 0.2$  cm (Mean  $\pm$  1 SE) of litter in the two years without fire and under  $0.7 \pm 0.1$  cm of litter in the year with fire, while seeds in the on-mound treatment were always planted in bare soil. The environment under the litter was probably more humid, providing better conditions for germination and seedling emergence than the bare, dry soil on mounds (cf., Pavone and Reader (1985b), who found greater germination by *M. lupulina* in moss-covered sites with high microsite humidity as compared to dry sites without moss).

In contrast to the germination pattern, we found greater survivorship on mounds versus off mounds in years without fire, as expected. This can be attributed to the following two factors: (1) less competition for light on mounds, and (2) reduced herbivory by small mammals on mounds. The plants in the off-mound treatments produced less biomass than those in the on-mound treatments, and sometimes appeared etiolated due to growth under low light conditions. This is consistent with Ross and Harper's (1972) conclusions that space and light are the critical factors early in the life of a seedling for survival and growth (see also Moloney 1990). Other studies have also reported that *M. lupulina* exhibits greater survivorship on bare soil and in uncrowded areas with little shading (Turkington and Cavers 1979, Pavone and Reader 1985a, Hogenbirk and Reader 1989). Additionally, greater survivorship on mounds could be caused by reduced herbivory on mounds. Klaas et al. (1998) found that meadow voles, the most abundant herbivorous small mammal at our study site, tend to avoid gopher mounds, which should result in lower rates of herbivory for

seedlings growing on mounds versus off mounds. In addition, Reader (1992*a*, 1992*b*) found that greater seedling survivorship in areas of sparse vegetation was caused primarily by reduced herbivory rather than lack of plant competition.

Although seedlings growing on mounds exhibit higher rates of survivorship than those off mounds in most years, they could face an increased risk of mortality due to the production of fresh mounds. Gopher mound production is spatially autocorrelated (Klaas et al. 2000), so the chance of a mound being reburied is greater than that of an undisturbed site. In this experiment, we found that on-mound treatment grids were reburied 5 times as often as off-mound treatment grids (from 1996 through 1998, 10 on-mound grids and 2 off-mound grids were at least partially buried). The mortality of 39 *M. lupulina* plants growing on mounds was directly caused by the production of a new mound, while the mortality of 17 off-mound plants was caused by new mound production. The increased risk of mortality due to reburial on mounds, however, must be outweighed by the benefits of reduced competition and reduced risk of herbivory, since survivorship on mounds in years without fire was generally greater than that off mounds.

Interestingly, survivorship was significantly greater off mounds in the year of the fire, rather than simply remaining equal to the on-mound treatments, as initially predicted. While the difference in survivorship results among years could be due to differences in weather or another factor with year-to-year variability, it seems most likely that the spring fire played an important role. We attribute the greater survivorship off mounds in 1997 to an interaction among a variety of factors, including differences in water availability and risk of reburial on and off mounds in years with and without fire, coupled with diminished differences in competition and herbivory on and off mounds in the year of a fire. The soil of gopher mounds is more friable and has a greater water infiltration rate than intermound soil (Grant et al. 1980, Grant and McBrayer 1981), leaving the surface soil on mounds drier than that of intermound areas. In fact, soil samples collected on mounds in 1997 contained less soil



moisture than off-mound soil. In years without fire, tall surrounding vegetation partially shades mounds, preventing excessive water evaporation from the mound surface, but in the year of a fire, soil moisture is reduced across the whole prairie (Knapp et al. 1998) and no tall vegetation surrounds mounds to prevent rapid evaporation of surface soil moisture. In addition, as noted earlier, the risk of mortality due to reburial is greater on mounds than off. Finally, the conditions that normally make mounds better sites for seedling survivorship are no longer factors in the year of a spring fire. There is no litter layer in intermound spaces, and vegetation is shorter, providing similar conditions on and off mounds. Also, meadow voles avoid prairies during the first growing season after a fire (Vacanti and Geluso 1985), reducing the differences between on- and off-mound rates of herbivory. All these factors may contribute to the observed pattern of greater survivorship off mounds in the year of a fire.

Populations of short-lived species persist only if germination, seedling establishment, vegetative growth, and reproduction occur in every generation. Three of these life cycle stages—germination, seedling establishment, and vegetative growth—occurred both on and off mounds, but one stage—reproduction—was strikingly greater on mounds than off mounds in years without fire. In these years, only plants growing on mounds reproduced during the first growing season. This first season is critical for survival of short-lived species, and previous research has shown that *M. lupulina* plants which do not flower during the first season rarely flower during a second season (Turkington and Cavers 1979). Interestingly, in this study, *M. lupulina* that survived into the second season flowered both on and off mounds. Total reproductive output was greater for the plants on mounds, however, because survivorship on mounds was greater and a greater proportion of the surviving on-mound plants flowered. In the year of the spring fire, fecundity was quite low overall, with reproduction only occurring during the second growing season, and then occurring at approximately the same rate on and off mounds. Overall, fecundity was the highest when the

site had not been burned, with reproduction during the first growing season occurring only in the years without fire, and then only in plants growing on mounds.

## Conclusions

In this study, we found that *M. lupulina* was closely distributed in space with gopher mounds, and that this spatial affinity likely stems from the life history success of *M. lupulina* when growing on mounds in most years. The occurrence of a spring fire, however, appears to negate the benefit of growing on mounds. In most years, *M. lupulina* is reproductively most successful on mounds, but its seeds are too heavy for wind-dispersal and simply drop near the parent plant (Pavone and Reader 1982). The gopher mounds upon which individual plants reproduce and drop their seeds tend to be spatially and temporally autocorrelated (Klaas et al. 2000), so bare mounds required for the successful growth of progeny are generally available in sites near the adults. From these results, we predict that, in prairies that are infrequently burned or otherwise disturbed at a broad-scale, the spatial distribution of *M. lupulina* should remain closely tied to that of gopher mound production. If fire or other broad-scale disturbance were to occur frequently, however, it is possible that the relationship between the distribution of *M. lupulina* and mounds would break down, and *M. lupulina* could be distributed more widely across the site.

Through relationships between small-scale disturbances and individual plant species, like the one studied here, disturbances generated at small spatial scales can have large-scale impacts on grassland plant communities by providing the opportunity for more species to coexist within the same plant community. From this study, we have direct evidence of a short-lived forb utilizing gopher mounds for the successful completion of its life cycle, and of a resulting spatial affinity between the distribution of the forb species and small-scale disturbances. We also have evidence that the demographic effects of gopher mounds can significantly differ between years, with these differences likely attributable to interactions

with broad-scale disturbances, such as fire. Other relationships between mounds and annual plant species, and even between mounds and other plant functional groups, certainly must exist. The combined effects of these relationships should result in mounds maintaining, and even increasing, plant species diversity and spatial heterogeneity across prairie remnants. The fact that gopher mounds can increase species diversity and spatial heterogeneity in prairie remnants has been noted previously (Tilman 1983, Inouye et al. 1987, Huntly and Inouye 1988, Gibson 1989, Martinsen et al. 1990, Huntly and Reichman 1994), but in this project we demonstrated the direct impact of gopher mounds on a short-lived plant species, and the interactive effect of fire. Gopher mounds and other small-scale disturbances are important in plant communities dominated by long-lived perennials, because mounds provide space for the maintenance of short-lived species that could not otherwise compete with the dominant long-lived perennial vegetation.

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**Table 1.** Criterion for selecting the best-fit logistic regression model out of all possible parameter combinations, calculated for each mound production data set.

Independent variables included	Mound production data sets	
	1994 mounds	1994-1998 mounds
Mounds	70.2	87.2
Elevation	65.1	65.1
Mounds, Elevation	56.7	64.0
Mounds, Elevation, Mounds*Elevation	60.4	68.1

**Note:** Values are the Schwartz Criterion (SC). The lowest SC indicates the best-fit model for each set of logistic regressions.

**Table 2.** Results of best-fit logistic regression models for predicting *Medicago lupulina* presence within a 10 m x 10 m cell, using mound production and elevation as independent variables.

Parameter	Parameter estimate	SE	P	Odds ratio
A) 1994 mound production data set				
$\beta_0$	-4.0389	1.0634	0.0001	
$\beta_1$	0.2790	0.1076	0.0095	1.322
$\beta_2$	1.0712	0.3136	0.0006	2.919
B) 1994-1998 mound production data set				
$\beta_0$	-4.6578	1.2391	0.0002	
$\beta_1$	0.0307	0.0145	0.0335	1.031
$\beta_2$	1.2394	0.3094	0.0001	3.453

**Note:** Regression:  $P_{MI} = (\exp(\beta_0 + \beta_1(\text{mnd}) + \beta_2(\text{elev}))) / (1 + \exp(\beta_0 + \beta_1(\text{mnd}) + \beta_2(\text{elev})))$   
 where  $P_{MI}$  = the probability of *M. lupulina* presence in a cell, mnd = number of mounds produced per cell in 1994 or 1994-1998, and elev = elevation in meters.

**Table 3.** *Medicago lupulina* reproduction in each growing season of the 1996, 1997, and 1998 demography experiments.

Year	No. flowering plants / total no. plants		Racemes (Mean $\pm$ 1 SE)	
	On mounds	Off mounds	On mounds	Off mounds
1996 experiment (No fire)				
1st growing season	28 / 297	0 / 221	4.8 $\pm$ 0.8	0
2nd growing season	—	—	—	—
1997 experiment (Fire)				
1st growing season	0 / 33	0 / 160	0	0
2nd growing season	1 / 3	2 / 13	—	—
1998 experiment (No fire)				
1st growing season	7 / 62	0 / 46	3.3 $\pm$ 0.5	0
2nd growing season	12 / 17	8 / 15	17.7 $\pm$ 4.6	19.6 $\pm$ 6.2

**Note:** Values are the number of flowering plants of the total number of surviving plants at the end of the growing season, and the mean number of racemes produced per flowering plant. Data were not collected in the second growing season of the 1996 experiment, because the site was burned in spring 1997.

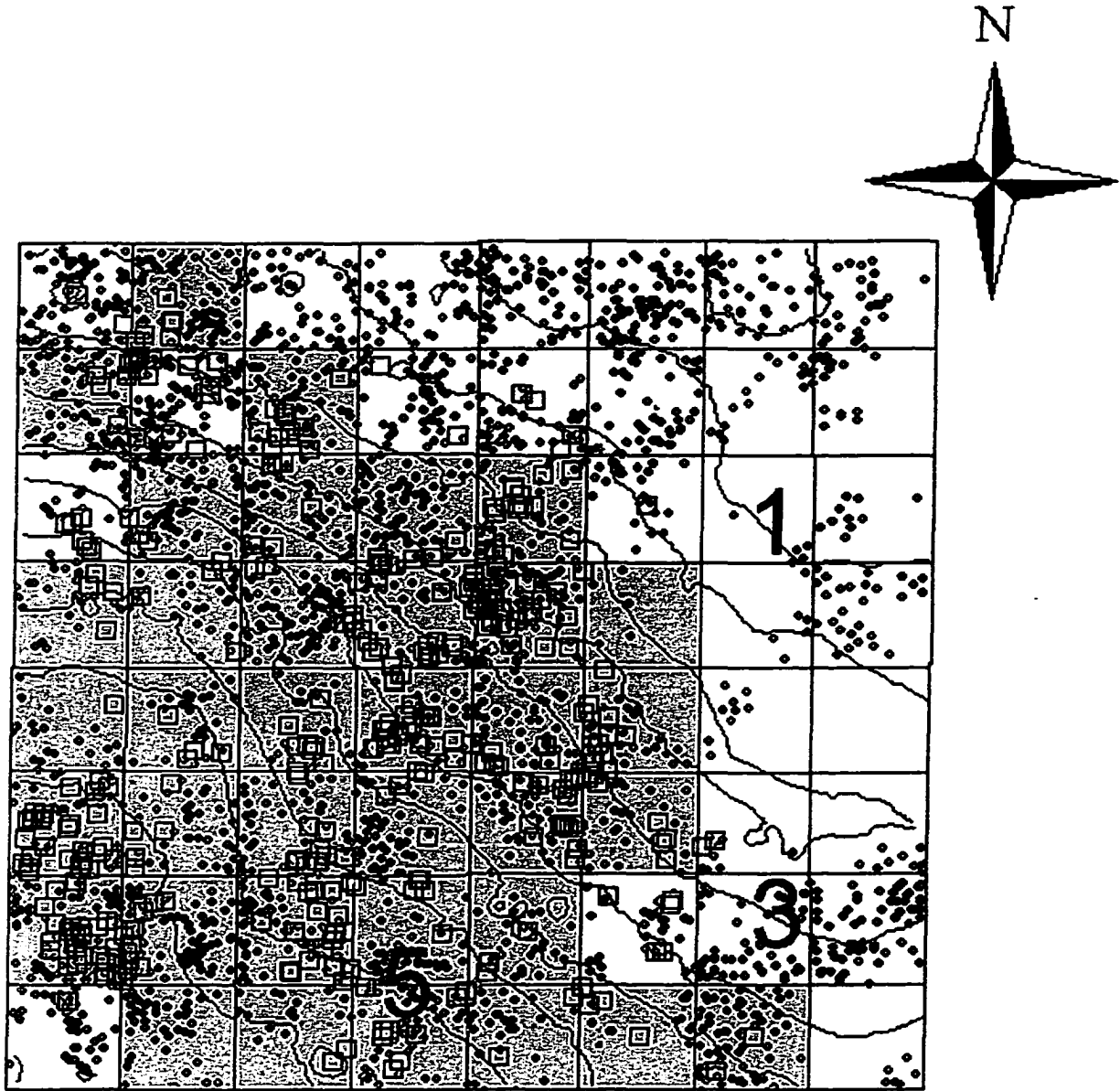
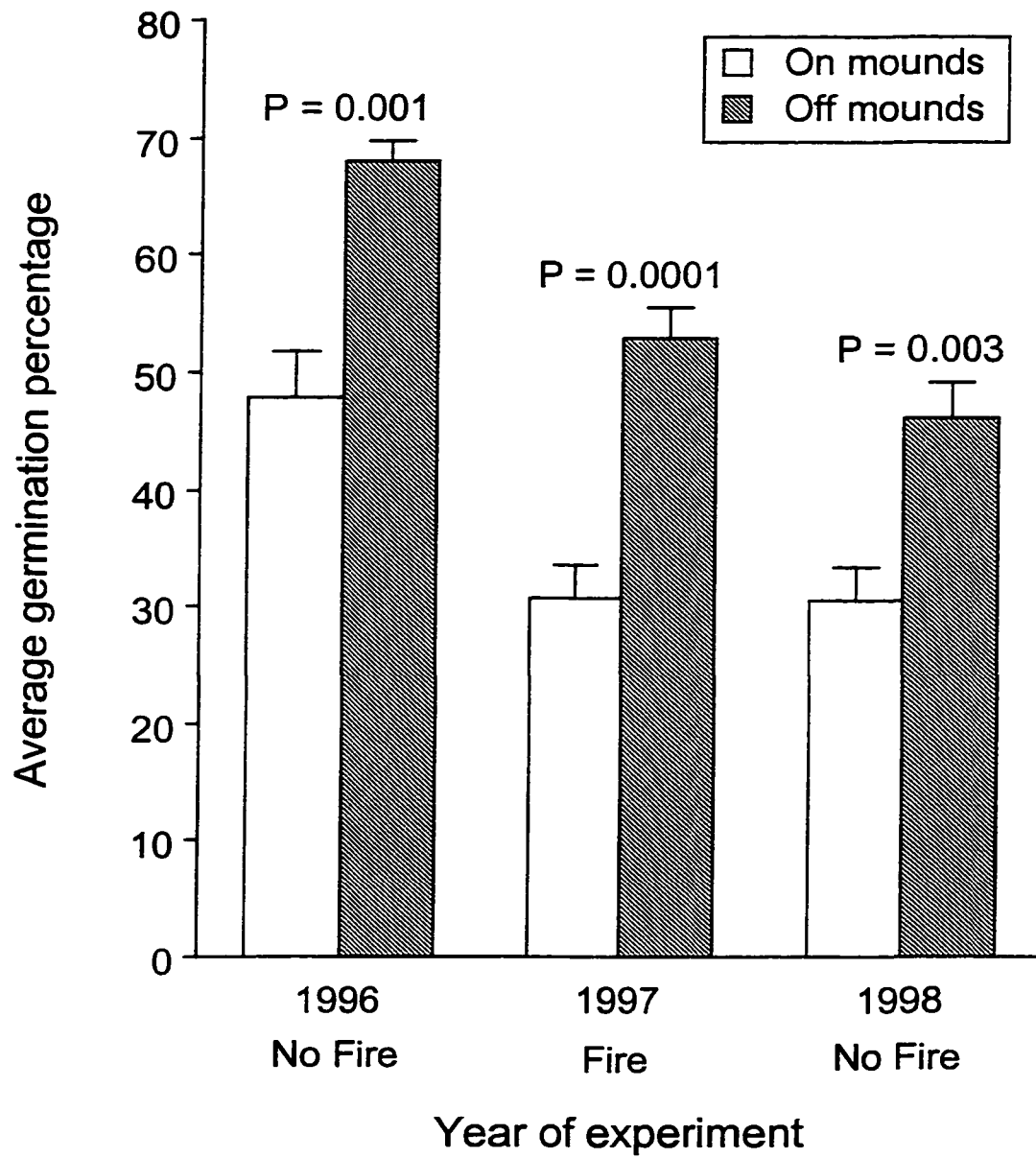
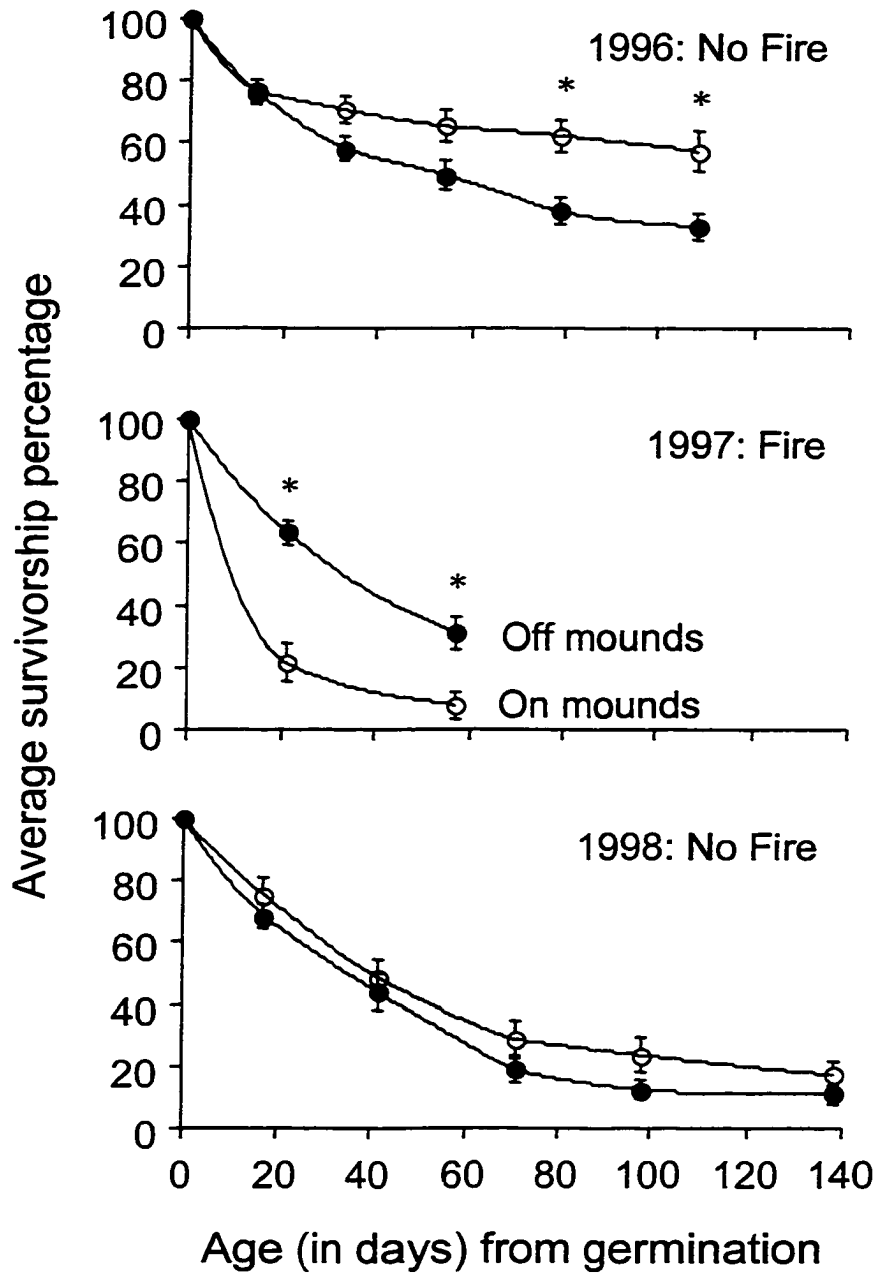


Fig. 1. Distribution of *Medicago lupulina* and gopher mound production across the study site. The presence of *M. lupulina* in each cell during 1995 is shown in gray. Gopher mounds produced during 1994 are shown as open squares. Gopher mounds produced from 1995 through 1998 are shown as gray points. Contour lines are elevation of the site at 0.5-m intervals, with relative elevation labeled at 1, 3, and 5 m. Grid lines on the map are at 10-m intervals.



**Fig. 2.** *Medicago lupulina* seedling germination in on- and off-mound planting treatments during the 1996, 1997, and 1998 demography experiments. Error bars are + 1 SE.



**Fig. 3.** *Medicago lupulina* survivorship on and off mounds during the first growing season in 1996, 1997, and 1998. Age zero indicates the first survey when germination was recorded (13 June 1996, 27 June 1997, and 1 June 1998). Open circles are on mounds, closed circles are off mounds. Error bars are  $\pm 1$  SE. Asterisks denote significantly different survivorship between on- and off-mound treatments per survey, using the Bonferroni-adjusted  $\alpha$ -values for the criteria.

### **CHAPTER 3. SMALL-SCALE DISTURBANCE PATTERNS AND DEMOGRAPHY OF PRAIRIE PLANT SPECIES**

A paper to be submitted to Ecology

Kelly S. Wolfe-Bellin and Kirk A. Moloney

#### **Abstract**

Understanding the link between pattern and process is an important goal in ecology, and recent studies have focused on how small-scale disturbances act to produce spatial patterns in plant communities. In this study, we investigated how the spatial pattern of gopher mound production affects the distribution and demography of four prairie plant species that represent a range of life history strategies and palatabilities to mammalian herbivores. First, we determined the relationship between the spatial distribution of each plant species' adult population in a prairie remnant and the spatial pattern of long-term mound production. We then conducted a two-year study examining the demographic response of each plant species to mound and off-mound planting treatments located in areas with different rates of mound production. The study was designed to determine whether the spatial relationships between plants and mounds are caused by (1) the direct demographic response of plants to growth immediately on mounds or off mounds, as well as (2) the indirect demographic response of plants when growing in areas of different neighborhood mound production rate, which may be driven by the behavioral response of mammalian herbivores to different patterns of small-scale disturbance. We found that the spatial distributions of three forb species' adult populations were positively cross-correlated with mound production at spatial scales of 20-30 m. Seedling survivorship, in general, was greater directly on mounds than off mounds for all species. Regarding the indirect effect of mound spatial patterns, survivorship by on-mound seedlings was uncorrelated with rates of local mound production, while survivorship by off-mound seedlings was negatively correlated with local mound production. Our results provide evidence that gopher mound

production can cause spatial patterns in grassland plant communities and that the process is largely driven by differences in survivorship among seedlings growing directly on and off mounds. An indirect effect of neighborhood mound production did not additionally contribute to the positive spatial relationships between mounds and plant species. In fact, the results indicate that high rates of mound production may have a negative effect on survivorship of seedlings growing in intermound spaces.

### **Introduction**

Understanding the relationship between pattern and process in plant communities has been an important goal in the field of plant ecology for many years (Watt 1947, Greig-Smith 1979), and it continues to be a topic that motivates modern ecological research (*e.g.*, Levin 1992, Lobo et al. 1998, Klausmeier 1999). Research on grasslands has revealed the importance of disturbances, at large and small spatial scales, in producing spatial heterogeneity in vegetation (Collins and Glenn 1995, Steinauer and Collins 1996). Large-scale disturbances on grasslands historically included fire or grazing by large herds of ungulates (Axelrod 1985). Small-scale disturbances historically were created by the burrowing and mound-building activity of fossorial rodents, and these rodents continue to be common on grassland remnants today (Benedict et al. 1996). Investigation of the role of fossorial rodents in producing grassland plant community structure is particularly interesting since fossorial rodents are so common and because they produce small soil disturbances in distinctive spatial patterns (Reichman et al. 1982, Klaas et al. 2000). In fact, a significant body of research has focused on the role of fossorial rodents in structuring grassland plant communities (*e.g.*, McDonough 1974, Platt 1975, Spencer et al. 1985, Williams et al. 1986, Inouye et al. 1987, Peart 1989, Hobbs and Mooney 1991). However, much of it has been conducted with a non-spatial approach, providing only general insights as to the impact of rodent burrowing and mound production on plant community diversity and the relative abundance of various plant functional



groups (but see Hobbs and Mooney 1985, Thomson et al. 1996). In this study, we investigated whether the spatial patterns in the plant community of a tallgrass prairie remnant are related to the spatial patterns of pocket gopher mound production. In addition, we investigated how the following two mechanisms contribute to the relationship: (1) the demographic response of plants to growth directly on mounds or off mounds, which we considered the direct response to mounds, and (2) the demographic response of plants when growing in areas of different neighborhood mound production rates, which we considered the indirect response to mound patterns.

The plains pocket gopher (*Geomys bursarius*) is a fossorial rodent found commonly throughout the eastern Great Plains of North America (Zimmerman 1999). Pocket gophers burrow underground, periodically expel soil onto the surface, and create a mosaic of soil disturbances that can cover as much as 20% of a grassland area (Grant et al. 1980, Reichman et al. 1982, Spencer et al. 1985). However, the production of mounds within an area is patchy. For example, Klaas et al. (2000) documented that the production of mounds on an Iowa prairie was spatially autocorrelated at scales of less than 20 m, with the locations of mound clusters remaining relatively static over years.

Mounds can directly affect the plant community by providing microhabitats of bare ground where seedling recruitment can occur (Gross and Werner 1982, Belsky 1986, Goldberg 1987, Goldberg and Gross 1988, Peart 1989, Martinsen et al. 1990) and where the soil environment is lower in phosphorus, nitrogen, and potassium than in undisturbed soil (Spencer et al. 1985, Inouye et al. 1987, Zinnel and Tester 1990). In addition, mounds provide space where both above- and belowground competition for resources are reduced (Huntly and Inouye 1988). In some species, the survivorship, growth, and reproduction of individual plants are greater when plants grow directly on mounds than off mounds (Reichman 1988, Davis 1990, Davis et al. 1995, Wolfe-Bellin and Moloney 2000). The production of mounds has been linked to increases in the abundance of annual species in plant communities (Laycock

and Richardson 1975, Schaal and Leverich 1982, Inouye et al. 1987) and to increases in species diversity and spatial heterogeneity (Tilman 1983, Hobbs and Mooney 1985, Inouye et al. 1987, Huntly and Inouye 1988, Huntly and Reichman 1994).

The influence of mound production on the faunal community of grasslands is a potential indirect mechanism by which pocket gophers could also influence the plant community. If herbivores avoid mounds, then plant species selectively grazed by those herbivores may be protected from herbivory when growing on mounds and in areas of high mound production. On the other hand, if herbivores are attracted to areas of high mound density, then those same plant species may be at greater risk of herbivory when growing on mounds or near clusters of mounds. Field studies examining the relationship between herbivores and gopher mounds, however, provide conflicting information about the herbivore response to mounds. Huntly and Inouye (1988) reported that grasshopper abundance was positively related to mound production. Whittaker et al. (1991) reported that the abundance of adult male meadow voles also was positively related to mound production, and that meadow voles seemed to preferentially travel across bare mounds. However, Klaas et al. (1998) found a negative relationship between meadow vole abundance and mound production on a prairie remnant in Iowa. Thus, it is unclear whether plants growing on mounds and in areas of high mound production face an increased or reduced risk of herbivory as compared to plants growing in undisturbed areas.

In this study, we examined the relationships between the spatial distributions of four plant species' adult populations in a prairie remnant and the spatial pattern of long-term mound production. The plant species represented a range of life history strategies and palatabilities to small mammalian herbivores. We also investigated the demographic response of each plant species to mound and off-mound planting treatments located in areas with different rates of mound production, to differentiate the relative contribution of direct and indirect mound effects in producing plant community spatial patterns. We predicted that any indirect effects of mound

spatial patterns would primarily be caused by the behavioral response of mammalian herbivores to small-scale disturbances. Although the direct demographic response of individual plant species to growth on and off gopher mounds has been reported in earlier studies (*e.g.*, Reichman 1988, Davis 1990, Davis et al. 1995), none of these studies included an explicit consideration of neighborhood mound production and how it indirectly influenced plant survivorship. In fact, few studies of gopher mound effects on plant communities have directly considered the spatial or temporal structure of the mound production regime (but see Moloney and Levin 1996). Thus, we explicitly studied the influence of spatial patterns of mound production on distribution patterns of adult plant populations and seedling survivorship.

We tested three general hypotheses. First, we hypothesized that the spatial distribution of adult populations of more palatable species would be positively correlated with the spatial distribution of long-term mound production, reflecting a strong positive relationship between seedling survivorship and rate of mound production. In contrast, adult populations of less palatable species were predicted to show no correlation with the spatial distribution of mound production, reflecting a weak relationship between seedling survivorship and rate of mound production.

Second, we hypothesized that seedling survivorship over time would be affected by whether seedlings were located directly on or off gopher mounds. We predicted that survivorship would be greater for all species on mounds as compared to off mounds, assuming that mounds serve as microsites where plant competition and risk of herbivory are reduced. In addition, the magnitude of the mound effect was predicted to be greater for palatable species than for unpalatable species, if this effect is partially driven by herbivory.

Third, we hypothesized that seedling survivorship would be correlated with the local rate of mound production. If small mammalian herbivores respond to mound production, either positively (*sensu* Whittaker et al. 1991) or negatively (*sensu* Klaas et al. 1998), then the local density of mound production could indirectly affect survivorship of nearby seedlings. Klaas et

al. (1998) found that the abundance of meadow voles was negatively related to mound production at our study site, and meadow voles are an important herbivore that can strongly affect seedling survivorship in grasslands (Howe and Brown 1999). Thus, we predicted that seedling survivorship both on and off mounds would be positively related to the degree of local mound production in the vicinity of each plant. Again, the magnitude of this effect was predicted to be greater for palatable species and less so for unpalatable species.

## Methods

### Study site

The study was conducted in northwest Iowa at Anderson Prairie State Preserve (Emmet County T100N R34W), an 80-ha remnant of tallgrass prairie managed by the Iowa Department of Natural Resources. Anderson Prairie was grazed by domestic cattle until the mid-1970's, but has never been plowed. Current management of the prairie at the time of the study included controlled fires every 3-5 years in the early spring. The most recent fire before the study was in April 1997. Vegetation on the site was representative of tallgrass prairie remnants and consisted of approximately 150 plant species. The native grasses *Andropogon gerardii* Vitman and *Sorghastrum nutans* (L.) Nash were abundant across most of the prairie. In addition, *Bromus inermis* L. and *Trifolium pratense* L., two exotic plant species, were planted on the site when it was grazed and were still abundant at the time of the study. The animal community on the site included the plains pocket gopher (*Geomys bursarius*) and meadow vole (*Microtus pennsylvanicus*).

In July 1996, a permanent 1.00-ha plot was established at the study site. The plot consisted of 100 10-m x 10-m cells arranged in a square with no buffers between cells (Fig. 1). The 1.00-ha plot was created by expanding a smaller 0.64-ha plot of 64 10-m x 10-m cells arranged in a square that had originally been established in April 1994 (Klaas et al. 1998, 2000). The smaller plot was enlarged by adding to it an additional row of 10-m x 10-m cells

around each edge. The 1.00-ha study plot was characterized by a moderate elevational gradient, with the southwest corner approximately 6 m higher in elevation than the northeast corner (Fig. 1). The soils across most of the plot consisted of the Nicollet and Clarion soil series (USDA-NRCS 1997 Soil Survey of Emmet County, Iowa), indicating a long history of mesic prairie vegetation. The northeast corner of the plot contained the Webster soil series (USDA-NRCS 1997 Soil Survey of Emmet County, Iowa), indicative of wet-meadow vegetation.

### Study species

Four plant species exhibiting different life-history strategies and palatabilities to small mammalian herbivores were used in the study (Table 1). The species included *Medicago lupulina* L., *Dalea purpurea* Vent., *Amorpha canescens* Pursh, and *Andropogon gerardii* Vitman (hereafter species will be listed by genus).

*Medicago* is a legume native to west Asia that is now naturalized throughout North America. It commonly grows as an annual or short-lived perennial in the region of our study (Turkington and Cavers 1979), and its abundance on some sites is reportedly greater on disturbed soil than in undisturbed vegetation (Reader and Buck 1991). In another study of *Medicago*, we found that the spatial distribution of this species was positively related to the distribution of gopher mounds and that survivorship and fecundity of *Medicago* were significantly greater on mounds than off mounds in years without a spring fire (Wolfe-Bellin and Moloney 2000). In addition, a study of seedling palatability revealed that *Medicago* and *Dalea* seedlings were more palatable to meadow voles (*Microtus pennsylvanicus*) than were *Amorpha* seedlings (Nickel et al. in prep.). From these factors, we predicted that *Medicago* would be most sensitive, of the four species in our study, to the gopher mound production regime. Because it is the smallest-statured and shortest-lived species in the study, *Medicago* is likely to be the most dependent on the reduced competition provided by gopher mounds for seedling survival and maintenance of its population. In addition, since it is a palatable species,

it is likely to show a strong response when protected from herbivory on mounds (assuming that mounds provide sites safe from small mammalian herbivores, *cf.* Klaas et al. 1998).

Both *Dalea* and *Amorpha* are long-lived perennial legumes native to the North American Great Plains that commonly grow in prairie remnants. Because these species are perennials, they were predicted to be less dependent on mounds for seedling survivorship and population maintenance than the shorter-lived *Medicago*. *Dalea* seedlings are more palatable to meadow voles than are *Amorpha* seedlings (Nickel et al. in prep), and *Amorpha* abundance showed no response to the presence or absence of mammalian herbivory in an old-field mammal exclosure experiment (Ritchie and Tilman 1985). Because of the differences in *Dalea* and *Amorpha* susceptibility to mammalian herbivory, we predicted that *Dalea* would be second to *Medicago* in sensitivity to gopher mound production, while *Amorpha* would be the least sensitive legume in our study to the mound production regime.

*Andropogon* is a native, long-lived perennial grass found throughout the tallgrass prairie region of the North American Great Plains; it is often the predominant species in tallgrass prairies (Runkel and Roosa 1989). *Andropogon* is the most abundant plant species across our study site, and we used its response to mounds and mound production rate as a pseudo-control against which the other species' responses were measured. We predicted that the sensitivity of *Andropogon* to mound production would be low. As an adult, it is generally avoided as a food source by meadow voles (Thompson 1965, Lindroth and Batzli 1984), and we assumed that its seedlings might also be relatively unpalatable. In addition, as a long-lived perennial grass, *Andropogon* probably is not dependent upon small disturbances for seedling survival and long-term population maintenance.

## **Field methods**

### **Surveys of plant population and gopher mound distributions**

To compare how the adult distributions of each plant species varied with the distribution of long-term mound production across the site, we used distribution data for each plant species collected during surveys in 1995 and 1997, and mound production data collected during a series of surveys from 1994 through 1997. The mound and plant species distribution data sets were all collected from the interior 80-m x 80-m sub-plot of the study plot (Fig. 1). The distribution of long-term mound production was determined from maps of mound locations compiled during gopher mound surveys conducted throughout the growing seasons of 1994, 1995 (Klaas et al. 2000), 1996, and 1997. For *Medicago*, the number of plants in a 0.5-m x 0.5-m quadrat located at the center of each 10-m x 10-m cell was counted on 24 July 1997. For *Dalea* and *Amorpha*, the number of plants growing in the southeast 5-m x 5-m corner of each 10-m x 10-m cell was also counted on 24 July 1997. For *Andropogon*, we used measures of plant cover within a 0.6-m x 0.6-m quadrat located on the west edge of each 10-m x 10-m cell from vegetation surveys conducted 27 June - 14 July 1995. In each case, the adult plant data for all four species were collected in quadrats in which the centers were separated by a minimum distance of 10 m and a maximum distance of 70 m.

### **Plant demography experiments**

We began the demography experiments in May 1998 by planting the four species in 20 randomized, complete blocks across the entire 100-m x 100-m study plot, with the on- and off-mound treatments applied in a pairwise fashion to each species within blocks. Twenty blocks of four mounds each were chosen at random from a pool of all mounds produced during the 1997 growing season or prior to planting in spring 1998. Mounds within blocks were located within 10 m of each other, and blocks were scattered across the plot in areas with different levels of surrounding local gopher mound-building activity (Fig. 1). Each of the four species

was planted on a separate mound chosen at random from within each block. Each on-mound location was paired with an off-mound location placed approximately 1.5 m west of the mound. The study site had been burned in a spring fire approximately 13 months before the time of planting. On-mound treatments were bare of standing vegetation and litter, but the off-mound treatments were covered with standing vegetation and plant litter  $2.78 \pm 0.10$  cm (Mean  $\pm 1$  SE;  $n = 80$ ) deep.

Each experimental unit (hereafter referred to as a grid) consisted of 49 seeds of one species planted in a 7 x 7 array. Seeds were spaced at 5-cm intervals and planted at a depth of 1 cm. The location of each seed was marked with a small plastic stake for ease in relocating seedlings. *Medicago* seeds were obtained from a commercial seed source in Pennsylvania, while the *Dalea*, *Amorpha*, and *Andropogon* seeds were purchased from commercial native seed producers in Iowa.

The blocks of grids were planted in random order from 16 May through 19 May 1998. Germination was recorded on 1 and 2 June 1998. Survivorship of seedlings was recorded four times during the 1998 growing season and four times during the 1999 growing season on the following dates (with the approximate number of days since germination noted in parentheses): 18-19 June 1998 (18 days), 13-14 July 1998 (42), 11-12 August 1998 (72), 7-8 September 1998 (99), 30 May 1999 (364), 28-29 June 1999 (393), 31 July-1 August 1999 (426), and 7-8 September 1999 (464). Germination for each grid was calculated as the percentage of the original 49 seeds that germinated during the first growing season. Survivorship was calculated for each grid at each survey and is reported as the percentage of plants surviving of those that germinated.

During each survey, the source of mortality for each dead plant was recorded as one of the following: herbivory, disturbance, or other. Herbivory included mortality due to mammal or insect herbivory; disturbance included mortality from mounds collapsing or burial by fresh gopher mounds; and the third category included plants that dried out, died during winter, or



could not be found. Most plants effectively disappeared after death and could not be located, so the greatest proportion of mortality was assigned to the third category.

On 8-9 October 1999, after two growing seasons, aboveground biomass of the remaining plants was collected and dried, at 65°C for 8 days, to constant mass. For the measurements, plants from each grid were pooled into one biomass sample, so we measured total biomass for each grid and calculated the average biomass per plant per grid. Values reported here are average aboveground biomass per plant per grid.

We recorded gopher mound production on the study plot in a series of surveys during the 1998 and 1999 growing seasons, to provide a measure of local mound production in the neighborhood surrounding each planting block. The locations of all individual fresh mounds produced across the plot were recorded on 4 May 1998, 15 May 1998, 2 June 1998, 19 June 1998, 14 July 1998, 12 August 1998, 18 October 1998, 30 May 1999, 29 June 1999, 1 August 1999, 8 September 1999, and 9 October 1999. Most of the mound surveys were conducted on the same dates as surveys for plant survivorship.

## **Data analyses**

### **Distribution of plant populations and gopher mound production**

Relationships between the spatial distribution of each plant species and long-term mound production across the study plot were analyzed in a series of spatial autocorrelation and cross-correlation analyses. First, we determined the rate of mound production per m<sup>2</sup> per year in a neighborhood of approximately 2.5-m radius around the center of each vegetation survey quadrat, using the neighborhood radius identified for the seedling survivorship response to mound production (see *Results—Seedling survivorship response to local rate of mound production*). For *Medicago* and *Andropogon*, we calculated the rate of mound production from the number of mounds produced during 1994–1997 within 2.5 m of each quadrat. For *Dalea* and *Amorpha*, we calculated mound production rate from the number of mounds produced

during 1994-1997 within each 5-m x 5-m quadrat in which the two plant species had been counted. We then conducted spatial autocorrelation analyses separately for each species and for mounds, to determine the scale over which significant spatial autocorrelation occurred within the adult distributions of each species and the distribution of long-term mound production. Finally, we conducted the following two sets of spatial cross-correlation analyses for each species: (1) species abundance or cover versus neighborhood mound production rate, and (2) species abundance or cover versus relative elevation. The cross-correlation analyses provided insight as to the spatial scale over which significant spatial cross-correlation occurred between species, mounds, and elevation. We calculated 95% confidence intervals for both the auto- and cross-correlations at each lag distance, using the following formula:

$$\frac{-1}{n} \pm \frac{2}{\sqrt{n}}$$

where  $n$  is the number of data pairs at each lag distance. In both the autocorrelation and cross-correlation analyses, we used a minimum lag distance interval of 10 m and a maximum lag distance interval of 40 m. Quadrat centers were separated by a distance of 10 m, dictating the minimum lag distance interval. In addition, only half the total distance measured in any direction over the plot may legitimately be represented in a correlogram (Rossi et al. 1992). Since the maximum distance between quadrat centers was 70 m, we plotted a maximum lag distance interval of 40 m, and only interpreted the results for a maximum lag distance of 30 m.

### **Plant demographic response to mound treatment**

All statistical analyses were conducted separately for each species. The germination and biomass results reported here for *Medicago* were also included in an earlier study (Wolfe-Bellin and Moloney 2000), but all other *Medicago* results in this paper are from new analyses or previously unpublished data. Pairwise, two-tailed  $t$ -tests were used to test for significant differences within species between on- and off-mound germination rates.

Mound treatment differences in survivorship over time were assessed within species by comparing the slopes of linear regression models of survivorship versus time for the two mound treatments. In these analyses, linear regressions of survivorship versus days since germination were first calculated separately per block for each species in each treatment and also for years 1 and 2 of the study. Survivorship values used in the linear regressions were transformed by calculating  $\log_e (\text{percent survivorship} + 1)$ . For the year-1 regressions, we fit no-intercept linear models to the data, because survivorship at day zero (day of germination) was included in the analyses, and was always 100%. The year-2 data were fit with standard linear regressions in which the intercept was allowed to vary, because survivorship at the beginning of year 2 was not standardized. Grids with no surviving plants at the beginning of year 2 were removed from the year-2 analyses, leaving fewer than 20 grids in each analysis. Mean slope and intercept values were then calculated from the separate linear regressions conducted for each year within each mound treatment. Survivorship decreased over time for all species in all treatments, so all slope values were negative. Thus, the mound treatment effect on survivorship over time was analyzed by comparing absolute slope values. Year-2 intercept values were not compared statistically because they were difficult to interpret biologically. Wilcoxon sign tests were used to test whether mean slope values were significantly different from zero, and Wilcoxon rank-sum tests were used to test whether mean slope values were significantly different between mound treatments for each species within each year.

Mound treatment effects on individual plant biomass at the end of the second growing season were tested using Wilcoxon rank-sum tests. Mound treatment grids were not paired for this analysis, because many grids did not contain surviving plants after two growing seasons. *T*-tests, linear regressions, and Wilcoxon tests were all conducted in SAS version 8.1 (SAS 2000).

### **Seedling survivorship response to neighborhood mound production rate**

To determine how the local rate of mound production affected seedling survivorship of each species when growing on and off mounds, we investigated the relationship between seedling survivorship on 12 August 1998 (72 days after germination) and local mound production in the neighborhood of each grid during 1998. The date of 12 August 1998 was chosen because it was late enough in the growing season that some seedling mortality had occurred, but not so late that survivorship was extremely low. In addition, the most complete mound production data set was available for mounds produced during 1998 through 12 August. Mounds in this analysis were produced during the 1998 growing season and were mapped during surveys conducted between 4 May and 12 August 1998. For this analysis, we first identified the local spatial scale over which mound production most strongly affected seedling survivorship, using a method briefly described here and described in more detail in Klaas et al. (1998). We then analyzed the data at that spatial scale for trends in the relationship between mound production and seedling survivorship.

The appropriate local spatial scale for subsequent survivorship analyses was identified by counting the number of mounds produced within 11 different distances of each on-mound grid (1-m; and 2.5-m to 25.0-m in 2.5-m increments). The distances represent radii of successively larger circles around each grid. When a circle fell partially outside the study plot, the following edge correction was performed on the mound count to adjust for missing data:

$$C_{ec} = \left(\frac{1}{b}\right)C$$

where  $C_{ec}$  was the edge-corrected count,  $b$  was the proportion of the circle contained in the study plot, and  $C$  was the uncorrected mound count (Klaas et al. 1998).

We conducted 88 correlations, examining the relationship between survivorship percentage within a grid on 12 August 1998 and number of mounds produced within a given radius of the on-mound grid. Correlations were calculated for each of the four species in the two separate mound treatments at the 11 radii. The Pearson correlation coefficients for each

species in each mound treatment were plotted against the range of radii to determine the radius with the highest descriptive power. This radius was considered the “neighborhood” around each grid (Klaas et al. 1998) and was used in subsequent comparisons of seedling survivorship and mound disturbance.

Using mound counts at this neighborhood distance, we conducted logistic regressions to examine more closely the relationship between survivorship on 12 August 1998 and mound production in the neighborhood of each grid. A logistic regression approach was used since survivorship of each seedling within a grid was a bivariate event, with a plant either alive or dead at the time of the survey. Separate logistic regressions were performed for each mound treatment and for each species. Standard errors and significance tests were corrected for overdispersion. We included the following two independent variables in the logistic regression models and tested for the significance of each in predicting the survivorship of seedlings on 12 August 1998: (1) mound counts at the designated radius, and (2) relative elevation of each grid within the study plot. Elevation was included because it is associated with a strong environmental gradient across the study site (Moloney and Wolfe-Bellin, unpublished analysis). Correlations and logistic regressions were conducted in SAS version 8.1 (SAS 2000).

## Results

### Distribution of plant populations and gopher mound production

The distribution of gopher mounds produced during 1994–1997 showed significant spatial autocorrelation at a lag distance of 10 m (Fig. 2). The distributions of *Medicago*, *Dalea*, and *Amorpha* also exhibited significant spatial autocorrelation at the 10-m scale, while *Andropogon* showed no significant autocorrelation at any of the spatial scales measured (Fig. 2). In the cross-correlation analyses, *Medicago*, *Dalea*, and *Amorpha* each showed significant correlation with elevation at spatial scales of 0–30 m, and significant correlation with long-term

mound production at spatial scales of 20 and 30 m (Fig. 3). *Andropogon* exhibited no significant correlation with elevation or mound production at any spatial scale (Fig. 3). The production of mounds was also significantly correlated with elevation at scales of 0–30 m (Wolfe-Bellin and Moloney, unpublished analysis), indicating that elevation may cause the significant cross-correlation between plant abundance and mound production found at 20 and 30 m for *Medicago*, *Dalea*, and *Amorpha*. To correct for the effect of elevation on these species, we fit separate linear regressions to the abundance of each species versus elevation, and used the residuals in cross-correlation analyses with mound production. This correction did not change our results; each of the three species was still positively correlated with mound production at 20 and 30 m.

### **Plant demographic response to mound treatment**

*Medicago* germination was significantly greater off mounds than on mounds (Fig. 4; Wolfe-Bellin and Moloney 2000). However, there was no statistical evidence of a significant mound treatment effect for *Dalea*, *Amorpha*, or *Andropogon* (Fig. 4). In general, germination rate was greatest for *Dalea*, intermediate for *Medicago* and *Andropogon*, and lowest for *Amorpha* (Fig. 4).

Survivorship of the seedlings that germinated was generally greater over time on mounds than off mounds for all species (Fig. 5), although the statistical significance of the treatment effect varied among species and growing seasons (Table 2). During the first growing season, the survivorship of all four species in both treatments decreased significantly over time, as indicated by the significantly negative slope values for all species in both treatments (Table 2). The survivorship of *Dalea* and *Andropogon* during the first growing season was significantly greater on mounds than off mounds (Table 2; Fig. 5). The survivorship of *Medicago* and *Amorpha* during the first growing season was slightly higher on mounds than

off mounds (Fig. 5), but the differences between mound treatment slopes were not statistically significant (Table 2).

In the second growing season, *Medicago*, *Dalea*, and *Amorpha* survivorship decreased less rapidly in both mound treatments than during the first season, while the decrease in *Andropogon* survivorship remained relatively constant between growing seasons (Table 2). The survivorship of *Dalea* and *Andropogon* continued to be significantly greater on mounds than off mounds during the second growing season, while there was no evidence of a significant mound treatment effect on *Medicago* or *Amorpha* survivorship (Table 2). In fact, *Medicago* survivorship in year 2 was slightly greater off mounds than on mounds, while neither the on- nor the off-mound survivorship slope value for *Amorpha* was significantly different from zero (Table 2). Survivorship of both *Medicago* and *Amorpha* was fairly low at the end of the first growing season (Fig. 5), leaving few surviving plants for survivorship measurements in the second season.

Disturbance, including collapsed soil and burial by fresh mounds, was a larger identifiable source of plant mortality throughout the study than was herbivory, and both caused a greater percentage of the mortality in the on-mound than off-mound treatments (Fig. 6). These data are included for a general comparison between mound treatments, but were not analyzed statistically for mound-treatment differences. The source of plant mortality could be identified for less than 20% of all plants, causing analyses to be heavily weighted by unknown mortality.

Biomass of the individual plants surviving at the end of two growing seasons was generally greater in the on-mound than off-mound treatment (Fig. 7). The mound treatment effect was statistically significant for *Dalea* and *Andropogon*, but not for *Medicago* or *Amorpha* (Fig. 7). Survivorship of all species was low at the end of the second growing season, leaving few grids with plants available for collection and causing difficulty in detecting a mound treatment effect.

### Seedling survivorship response to neighborhood mound production rate

The relationship between seedling survivorship on 12 August 1998 and mound number was strongly negative in the off-mound treatment for all four species at the 11 neighborhood radii and was weak in the on-mound treatment for all species (Fig. 8). The Pearson correlation coefficients were significantly different from zero ( $p \leq 0.05$ ) in the off-mound treatments for *Medicago* at all search radii between 2.5- and 25.0-m, for *Dalea* at the 12.5-m search radius, and for *Amorpha* at the 2.5-m and 5.0-m search radii. The Pearson correlation coefficients were not significantly different from zero in the off-mound treatment for *Andropogon* at any radii, nor for the on-mound treatments of any species at any radii. In the off-mound regressions for the four species, it appears that a threshold of descriptive power was reached at the 2.5-m search radius, with descriptive power generally remaining constant or becoming weaker at larger search distances. Thus, a neighborhood radius of 2.5-m was used in subsequent analyses of seedling survivorship.

The logistic regression models that most accurately predicted seedling survivorship on 12 August 1998 contained only one independent variable: mound count within the 2.5-m neighborhood around each on-mound grid. Relative elevation of each grid was never a significant source of variation in seedling survivorship, and was not included in the final models. The relationship between seedling survivorship and neighborhood mound count was negative for all species in both treatments, except for the *Amorpha* on-mound treatment (Table 3). However, there was no evidence of a significant neighborhood mound count effect on seedling survivorship for any of the species in the on-mound treatment (Table 3). In the off-mound treatment, the relationship between survivorship and neighborhood mound count was significant for *Medicago* and *Dalea*, but not for *Amorpha* or *Andropogon* (Table 3). The direction and strength of the relationship for each species easily can be interpreted by considering the odds ratio of the probability of seedling survivorship versus the probability of seedling death as each additional mound was produced within the neighborhood (Table 3). In



the on-mound treatments, the odds of seedling survivorship changed little with each additional mound produced within the 2.5 m neighborhood (odds ratio close to 1), while in the off-mound treatments, the odds of seedling survivorship decreased with each additional neighborhood mound (odds ratio less than 1). For each species, the number of mounds produced within the 2.5-m neighborhood during the first part of 1998 ranged from zero to a maximum that varied as follows (values in parentheses are the maximum number of mounds produced per m<sup>2</sup> and the percentage of ground covered by mounds if we assume that mounds are circular, have a diameter of 0.5 m, and do not overlap): *Medicago*: 14 mounds (0.7 mounds/m<sup>2</sup>, 14%); *Dalea*: 8 mounds (0.4 mounds/m<sup>2</sup>, 8%); *Amorpha*: 16 mounds (0.8 mounds/m<sup>2</sup>, 16%); and *Andropogon*: 14 mounds (0.7 mounds/m<sup>2</sup>, 14%).

## Discussion

### Distribution of plant populations and gopher mound production

The distributions of all three forb species, regardless of life history strategy or relative seedling palatability, were positively related to the production of gopher mounds. The distributions of *Medicago*, *Dalea*, and *Amorpha* showed significant positive spatial autocorrelation at the same 10-m scale as the distribution of long-term mound production. In addition, all three species showed significant positive cross-correlation with the distribution of mound production at larger spatial scales of 20–30 m. These results are consistent with those in an earlier study of the spatial relationship between *Medicago* distribution and both short- and long-term mound production (Wolfe-Bellin and Moloney 2000). The lack of any spatial structure in the distribution of *Andropogon* probably can be attributed to the fact that it was abundant across the entire study plot. The three forb species were distributed in a spatially heterogeneous manner across the landscape, with the distribution of each species positively related to the broad-scale pattern of mound production over time.

### **Plant demographic response to mound treatment**

We found that pocket gopher mounds influence the seedling survivorship of four plant species representing a range of life history strategies and palatabilities to small mammals. In general, the survivorship of all four species was greater on mounds, regardless of life history strategy or relative seedling palatability, although the strength of the statistical relationship varied among species. These results confirm that gopher mounds provide safe sites for seedling establishment (Gross and Werner 1982, Belsky 1986, Goldberg 1987, Goldberg and Gross 1988, Peart 1989, Martinsen et al. 1990), but do not support the prediction that plants with shorter life spans or greater palatabilities to small mammals are more dependent on mounds for survivorship. Interestingly, seedling germination was either unaffected by mound treatment or was actually greater off mounds. The germination result likely reflects the fact that the environment off mounds under plant litter is more humid than the bare soil environment on mounds. Another study of *Medicago lupulina* germination found that germination was greater in moss-covered sites with high microsite humidity than in dry sites without moss (Pavone and Reader 1985). Despite the mound treatment effects on germination, however, both survivorship and biomass of all species were generally greater on mounds than off, indicating that the conditions on mounds are better for plant growth than the conditions off mounds.

The positive mound treatment effect on plant growth could be attributed to two factors: (1) reduced competition for light or root space with neighboring vegetation when plants grow on mounds, and (2) reduced herbivory by small mammals on mounds. The survivorship results probably reflect both these factors, while the differences in plant biomass on and off mounds are likely an indication that the competitive environment on mounds is more conducive to plant growth. If reduced herbivory on mounds plays a significant role in the mound effect, then the magnitude of the mound treatment effect on survivorship should be greater for more palatable plant species. In fact, we found that the relative palatability of seedlings was not reflected in our results. *Dalea*, a relatively palatable species, and *Andropogon*, a relatively

unpalatable species, showed the strongest positive survivorship response to the on-mound treatment, while *Medicago*, the most palatable species, and *Amorpha*, a relatively unpalatable species, showed weaker survivorship responses to mounds. Of course, our index of relative palatability was based on laboratory trials of seedling preference (Nickel et al. in prep), and the relative palatabilities of seedlings in the lab may not be reflected in vole food preferences in a diverse natural prairie. Thus, the importance of herbivory in driving the mound treatment effect on seedling survivorship is unclear. We actually identified herbivory as the source of plant mortality more frequently on mounds than off mounds for *Medicago*, *Amorpha*, and *Andropogon*. However, the herbivory measured in this analysis was only that which was easily identified during field surveys. Stems that had been bitten by rodents or insects were easier to find in the on-mound than off-mound treatments, so the identification of herbivory may have been artificially low off mounds.

Although we found greater survivorship of all four species on mounds than off mounds, plants growing on mounds could face increased risk of mortality due to the production of fresh mounds or the shifting of loose soil on mounds. The risk of mound reburial potentially could be very high, given that mound production is spatially autocorrelated (Klaas et al. 2000). In fact, when we identified the sources of plant mortality throughout the entire study, we found that a greater proportion of mortality was caused by disturbance in the on-mound than off-mound treatment. However, the increased risk of disturbance mortality on mounds must be outweighed by the benefits of both reduced competition and reduced risk of herbivory on mounds, since survivorship was generally greater on mounds than off mounds for all species.

### **Seedling survivorship response to neighborhood mound production rate**

In the analysis of seedling survivorship at different rates of local mound production, we first identified the most appropriate spatial scale for the subsequent analyses of neighborhood

mound production rate, rather than imposing an arbitrary scale on the relationship (Levin 1992). The 2.5-m neighborhood radius we identified was considerably smaller than the 10-m radius identified by Klaas et al. (1998), using the same method, in which they found that meadow vole abundance was negatively associated with mound production. It seems plausible, however, that sessile plants should respond to a smaller neighborhood than do mobile small mammals.

As predicted, seedling survivorship was correlated with local mound production at the 2.5-m neighborhood scale. However, only survivorship in the off-mound treatment showed a response to neighborhood mound production, and the direction of the relationship was the opposite of that predicted. Survivorship was negatively related to the level of neighborhood mound production. Although the relationship was in the opposite direction from that predicted, the magnitude of the response was strongest for the two relatively palatable species, *Medicago* and *Dalea*, and weaker for the two relatively less palatable species, *Amorpha* and *Andropogon*.

One obvious explanation for the negative relationship between off-mound plant survivorship and neighborhood mound production rate is that plants growing in areas of high disturbance rate are at greater risk of being buried during the production of fresh mounds. However, a close examination of our data revealed that those seedlings in off-mound grids killed by mound burial were actually located in areas of relatively low neighborhood mound production. In addition, less than 5% of the individuals of any species in the off-mound treatment were killed by disturbance before 12 August 1998, the date when the survey data used in this analysis were collected. Finally, the maximum ground coverage by mounds throughout the first part of 1998 within any of the 2.5-m neighborhoods was 16%, which indicates a relatively low probability of seedling mortality due to burial by a mound.

The role of small mammalian herbivory in the negative relationship between off-mound plant survivorship and neighborhood mound production is not clear. However, the fact that we found a relationship for the two most palatable species, *Medicago* and *Dalea*, and not for the

two less palatable species provides some support that herbivory plays a role in this relationship. We suggest three scenarios by which the effects of herbivory may have contributed to our results. In the first, small mammalian herbivores might avoid foraging for seedlings directly on mounds where predation risk is high, thus contributing to our observation that seedling survivorship was greater on mounds than off mounds. At the same time, however, these herbivores may be attracted to areas of high mound production where young, possibly more palatable plants are growing on old mounds, thus contributing to the negative relationship between off-mound seedling survivorship and mound production rate. In this case, the abundance of meadow voles should be positively related to mound production, as was reported by Whittaker et al. (1991). In the second scenario, small mammals may preferentially forage on mounds and in areas of high mound production (as suggested by the results of Whittaker et al. 1991), which would explain the negative relationship between off-mound seedling survivorship and mound production rate. However, despite the increased herbivory pressure on mounds, the conditions of reduced plant competition on mounds may be far better for survivorship than the conditions off mounds. This would explain why on-mound seedling survivorship was greater than that off mounds, and was not affected by rate of neighborhood mound production. Third, it is possible that small mammalian herbivores avoid mounds and high mound production areas (as suggested by the results of Klaas et al. 2000), but the relationship between off-mound plant survivorship and mound production rate did not reflect this because small mammal populations could have been low in the year of our study. It is well-documented that small mammal populations can fluctuate widely within and between years (Krebs 1966, Gaines and Rose 1976, Getz et al. 1987), so it is possible that small mammalian herbivory did not directly contribute to the relationship we measured. In this case, possibly both seedling survivorship off mounds and rates of neighborhood mound production were related to other factors unmeasured in this study. Possibly the long-term activity of gopher burrowing in certain areas has changed the soil or some other aspect of the environment to

cause reduced survivorship of these forbs. Or, maybe pocket gophers preferentially burrow in certain areas because of some other factor, and this same factor causes reduced survivorship of these forb species.

Regardless of what causes this relationship, we have evidence that the survivorship of two relatively palatable forbs growing off gopher mounds is negatively related to the rate of neighborhood mound production. The lack of any response for seedlings growing on mounds is curious, but is likely due to the fact that conditions on mounds are generally better than those off mounds for plant survivorship, so seedlings on mounds are buffered from the effects of neighborhood disturbance. Off mounds, however, conditions are worse and seedlings may be more prone to the indirect influence of neighborhood mound production, whether it is due to the behavioral response of herbivores or other unmeasured factors.

## Conclusions

This study provides evidence that the spatial pattern of gopher mound production contributes directly to the spatial patterns in grassland plant communities. Earlier studies have provided evidence linking gopher mound production and plant community composition (*e.g.*, McDonough 1974, Spencer et al. 1985, Williams et al. 1986, Inouye et al. 1987, Peart 1989, Hobbs and Mooney 1991), but only a few studies have directly linked the presence of gopher mounds to the survivorship of individual plants (*e.g.*, Hobbs and Mooney 1985, Reichman 1988, 1996, Davis 1990, Davis et al. 1995), and even fewer have considered the spatial context of the relationship (*e.g.*, Hobbs and Mooney 1985, Thomson et al. 1996). We found a positive spatial relationship between the distributions of gopher mounds and the populations of plant species with a variety of life history strategies and palatabilities. In general, survivorship of seedlings was greater when growing directly on mounds than off, although the strength of the statistical evidence varied among species. However, when we looked at the indirect effect of neighborhood mound production on seedling survivorship, there was no relationship for

seedlings growing on mounds, and the relationship was actually negative for seedlings of some species growing off mounds. This leads us to conclude that gopher mound production can cause spatial pattern in grassland plant communities because seedlings survive better when growing directly on mounds than off mounds. Positive relationships between mound production and plant community spatial patterns develop over time because mound production tends to be spatially and temporally autocorrelated (Klaas et al. 2000). Since the indirect effects of local disturbance rate on seedling survivorship are either weak or negative, we conclude that indirect effects of local disturbance rate do not additionally contribute to the development of positive relationships between mound production and plant community spatial patterns.

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**Table 1.** Plant species included in the study.

Species	Family	Life-history strategy	Relative seedling palatability <sup>a</sup>
<i>Medicago lupulina</i> L.	Fabaceae	Short-lived forb	Palatable
<i>Dalea purpurea</i> Vent.	Fabaceae	Perennial forb	Palatable
<i>Amorpha canescens</i> Pursh	Fabaceae	Perennial forb	Unpalatable
<i>Andropogon gerardii</i> Vitman	Poaceae	Perennial grass	Unpalatable

<sup>a</sup> Relative palatability of *Medicago*, *Dalea*, and *Amorpha* to meadow voles was determined in laboratory feeding trials. *Andropogon* seedling palatability was untested.

**Table 2.** Summary statistics for linear regressions of  $\log_e$  (percent survivorship + 1) versus days since germination.

Species	Growing season	Mean slope (1 SE)		$S^c$	$p^c$
		On mound <sup>a</sup>	Off mound <sup>a</sup>		
<i>Medicago</i>	Year 1	-0.023 (0.004)***	-0.027 (0.003)***	455.0	0.23
	Year 2 <sup>b</sup>	-0.016 (0.004)*	-0.011 (0.004)	74.5	0.34
<i>Dalea</i>	Year 1	-0.015 (0.003)***	-0.036 (0.003)***	549.0	< 0.01
	Year 2 <sup>b</sup>	-0.010 (0.003)***	-0.016 (0.002)*	53.0	0.05
<i>Amorpha</i>	Year 1	-0.029 (0.006)***	-0.036 (0.005)***	341.5	0.40
	Year 2 <sup>b</sup>	-0.006 (0.006)	-0.027 (0.010)	15.5	0.18
<i>Andropogon</i>	Year 1	-0.008 (0.002)***	-0.010 (0.001)***	452.0	0.04
	Year 2 <sup>b</sup>	-0.004 (0.001)***	-0.011 (0.002)***	428.5	0.01

**Note:** A separate linear regression of plant survivorship versus time was calculated for each experimental unit (grid). We then calculated the mean ( $\pm$  1 SE) slope value of the regressions conducted for each species per mound treatment per year.

<sup>a</sup> Mean slope values were tested for significant differences from zero using Wilcoxon rank sign tests: \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ .

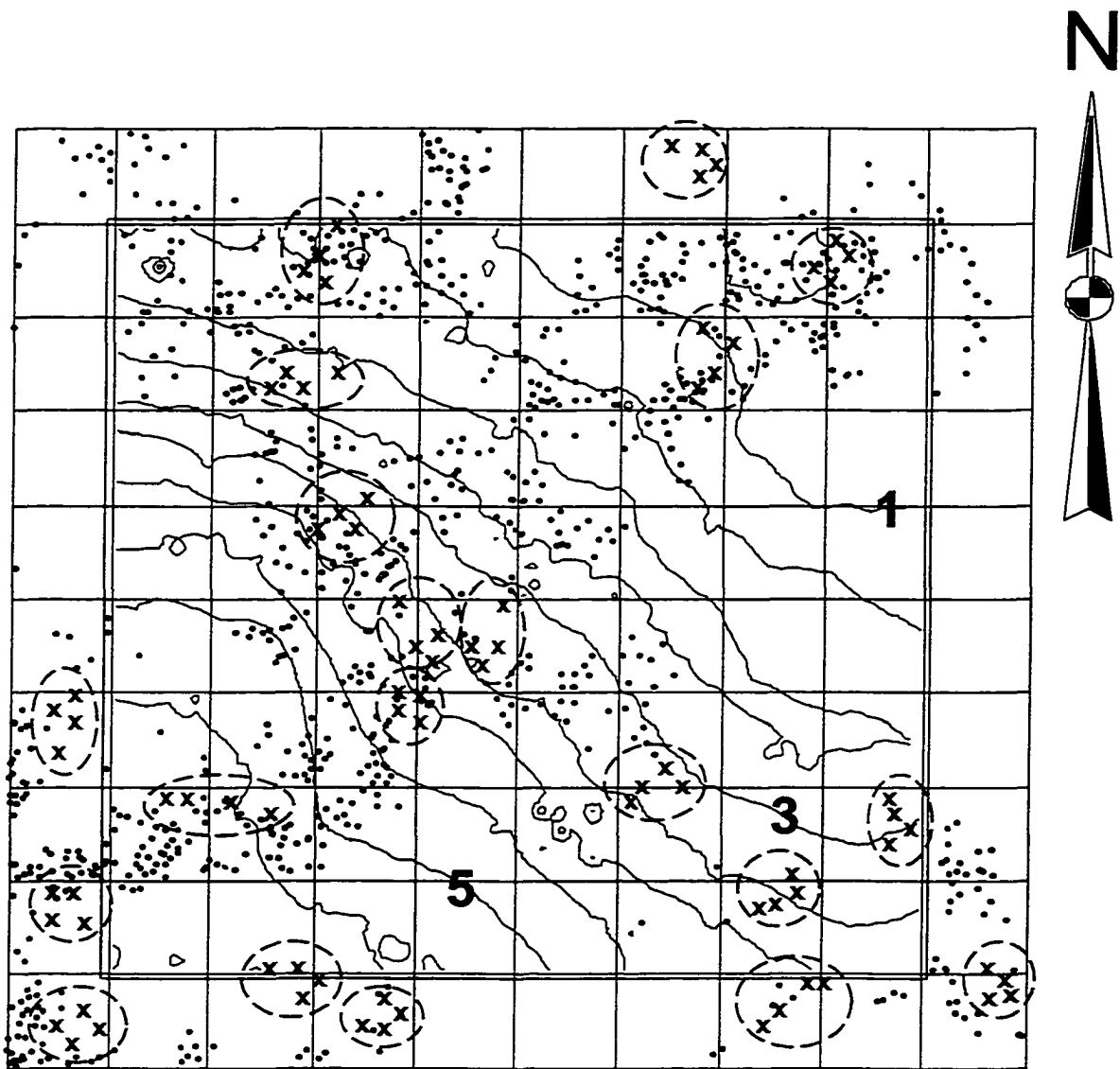
<sup>b</sup> Number of grids included in each year-2 slope calculation: *Medicago* on and off: 9; *Dalea* on: 15; *Dalea* off: 7; *Amorpha* on: 6; *Amorpha* off: 4; *Andropogon* on: 18; *Andropogon* off: 19.

<sup>c</sup> Values are from Wilcoxon rank-sum tests for mound treatment effects.

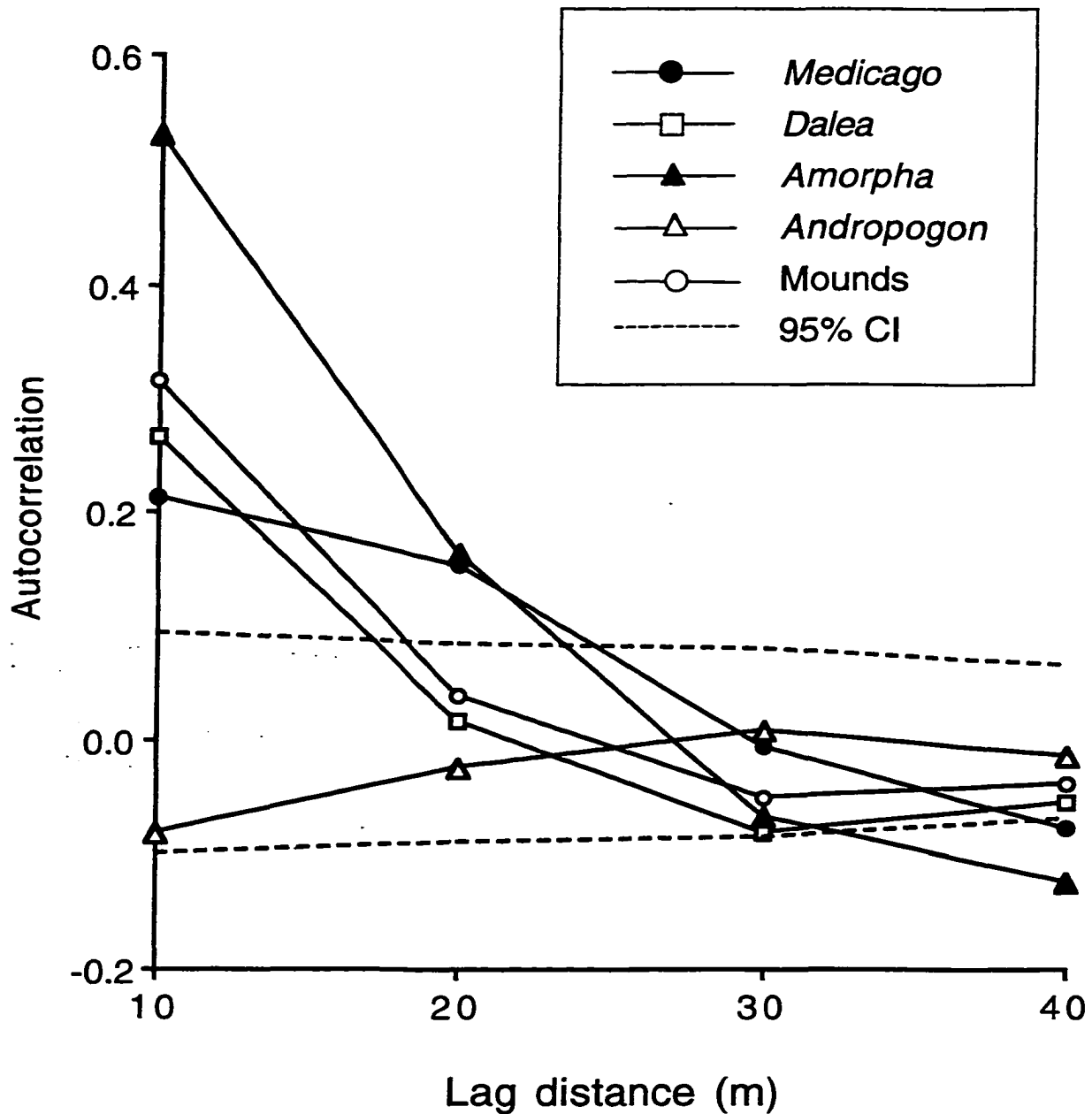
**Table 3.** Results of logistic regression models predicting the survivorship of each species on 12 August 1998, using mound production within a 2.5-m neighborhood around each on-mound grid as the independent variable.

Mound treatment	Species	Parameter	Parameter estimate	SE	<i>p</i>	Odds ratio
On	<i>Medicago</i>	$\beta_0$	-0.3757	0.4484	0.40	0.97
		$\beta_1$	-0.0334	0.0680	0.62	
	<i>Dalea</i>	$\beta_0$	-0.2268	0.4847	0.64	0.99
		$\beta_1$	-0.0139	0.1058	0.90	
	<i>Amorpha</i>	$\beta_0$	-0.5671	0.4217	0.18	1.01
		$\beta_1$	0.0143	0.0590	0.81	
	<i>Andropogon</i>	$\beta_0$	0.5377	0.3244	0.10	0.92
		$\beta_1$	-0.0807	0.0657	0.22	
Off	<i>Medicago</i>	$\beta_0$	-0.7337	0.2450	< 0.01	0.82
		$\beta_1$	-0.1954	0.0602	< 0.01	
	<i>Dalea</i>	$\beta_0$	-1.3791	0.3789	< 0.01	0.80
		$\beta_1$	-0.2224	0.1059	0.04	
	<i>Amorpha</i>	$\beta_0$	-0.9739	0.4416	0.03	0.82
		$\beta_1$	-0.1939	0.1268	0.13	
	<i>Andropogon</i>	$\beta_0$	0.0924	0.2048	0.65	0.96
		$\beta_1$	-0.0446	0.0412	0.28	

**Note:** Regression:  $P_{surv} = [\exp^{(\beta_0 + \beta_1(mndprod))}] / [1 + \exp^{(\beta_0 + \beta_1(mndprod))}]$ , where  $P_{surv}$  is the probability of a seedling surviving until 12 August 1998, and  $mndprod$  is the number of mounds produced during 1998 through 12 August within a 2.5-m radius of each on-mound grid.

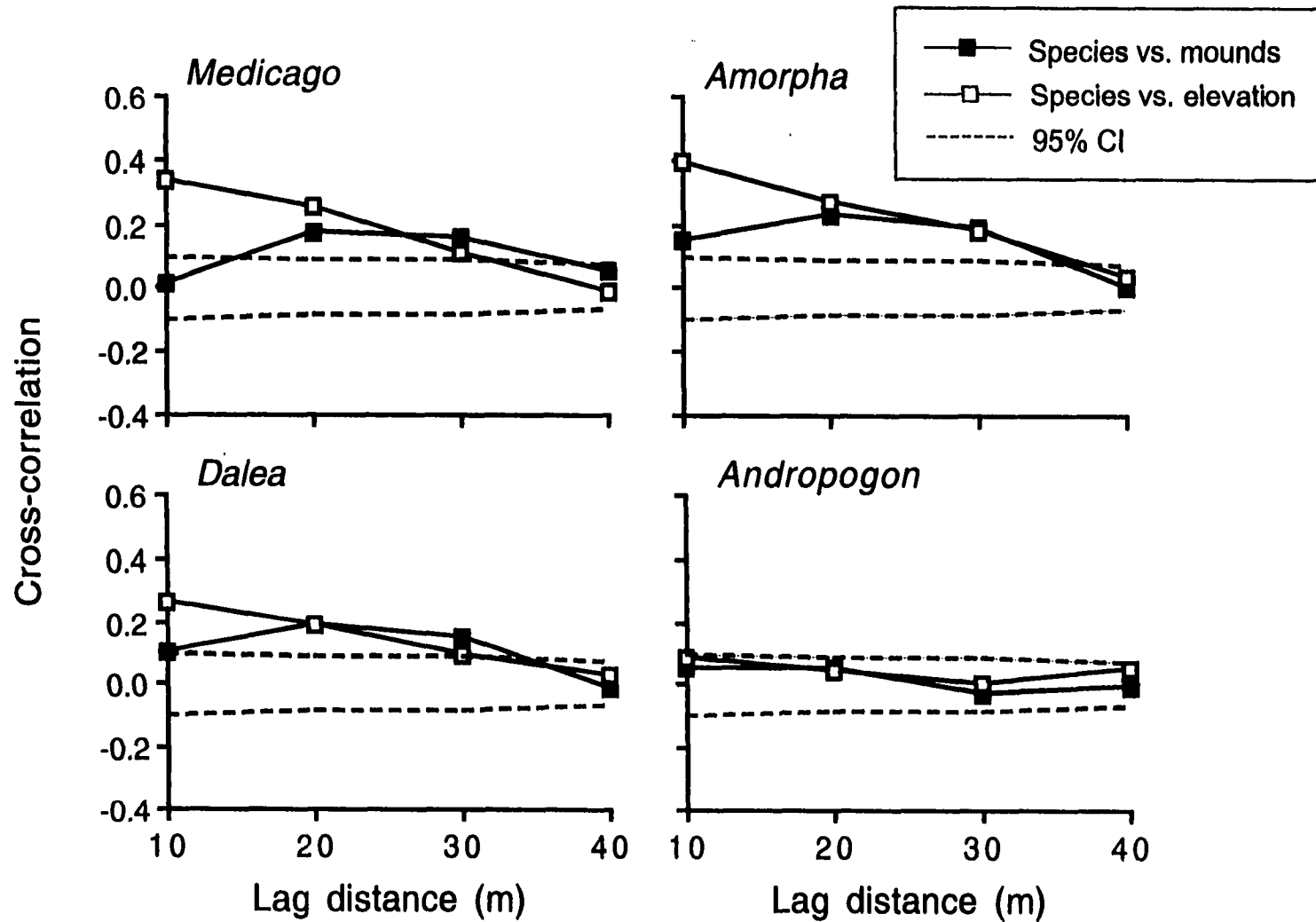


**Fig. 1.** Map of 1.00-ha study plot. Contour lines are elevation of the site at 0.5-m intervals, with relative elevation labeled at 1, 3, and 5 m. Grid lines on the map are at 10-m intervals. Double lines outline the 80-m x 80-m sub-plot within which we measured distributions of each plant species and long-term mound production. The location of each on-mound grid used for the demography experiments is denoted with an x, and each block of four on-mound grids is circled with a dashed line. Gopher mounds produced during the 1998 growing season through 12 August 1998 are shown as black points.

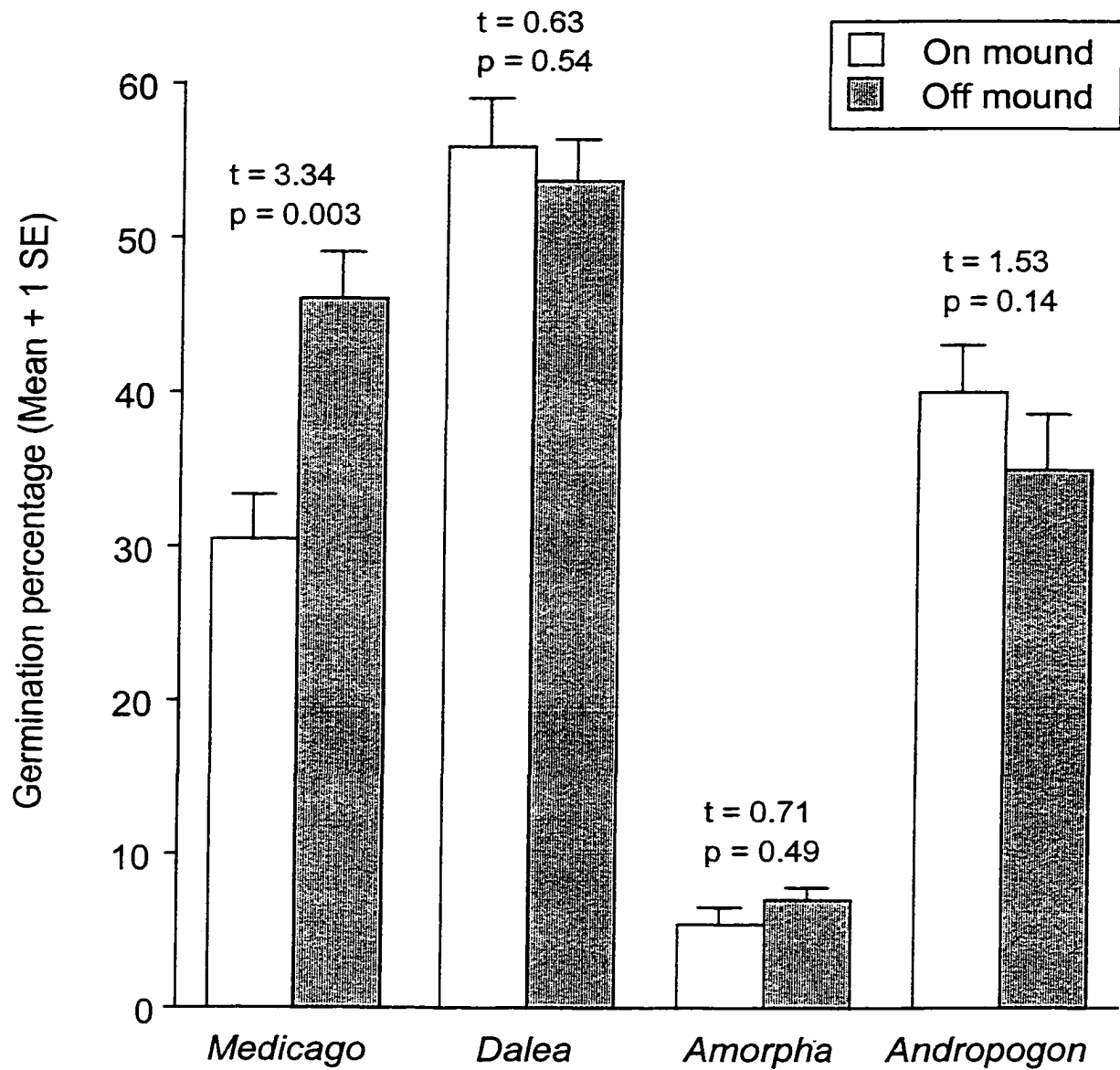


**Fig. 2.** Spatial autocorrelations calculated separately for the distributions of adults of each plant species and the distribution of gopher mounds produced 1994-1997 across the interior 80-m x 80-m of the study plot. Sample locations were separated by a minimum lag distance of 10 m. The maximum lag distance for which accurate autocorrelation values could be calculated was 35 m, half the maximum distance separating sample locations.

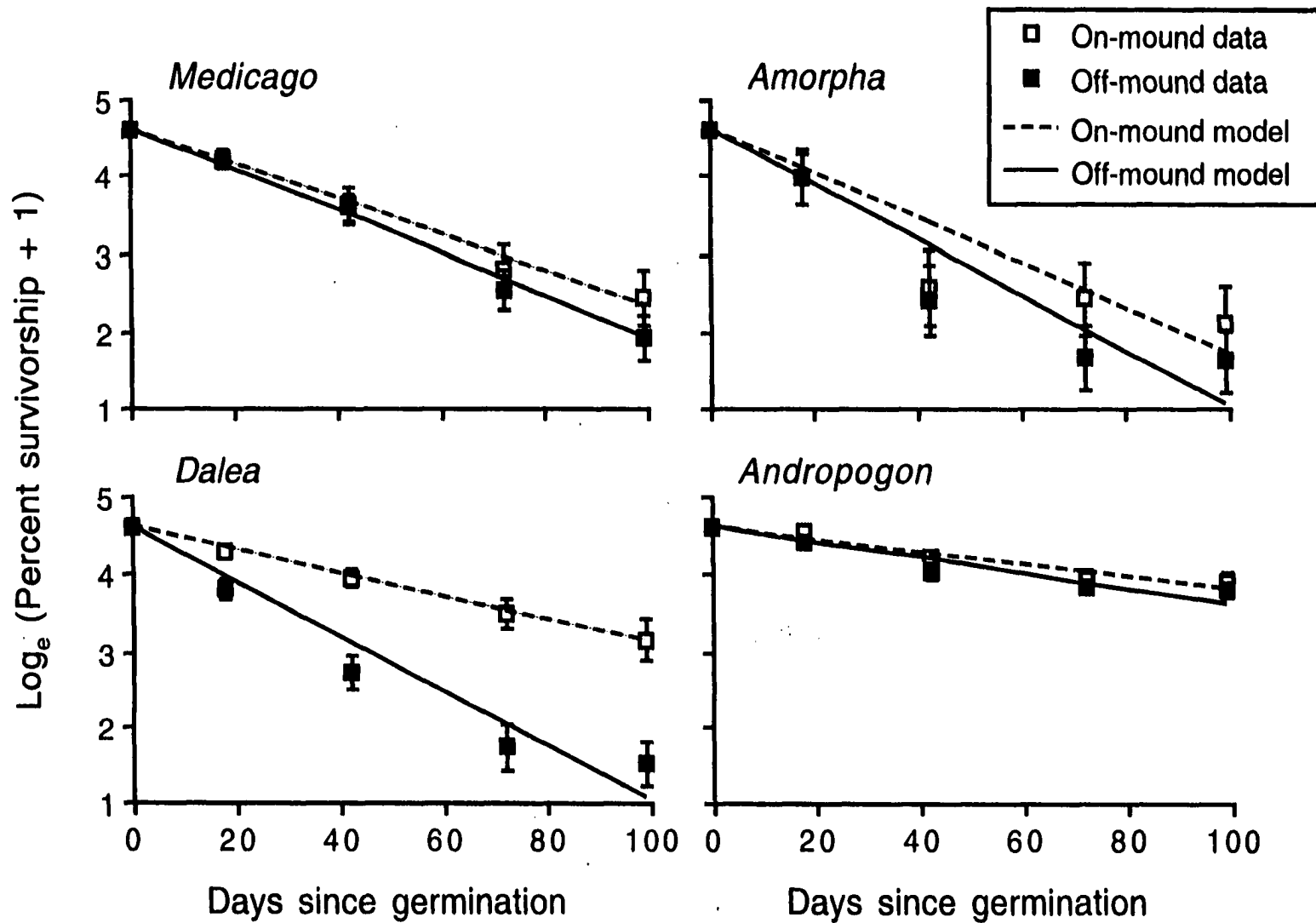




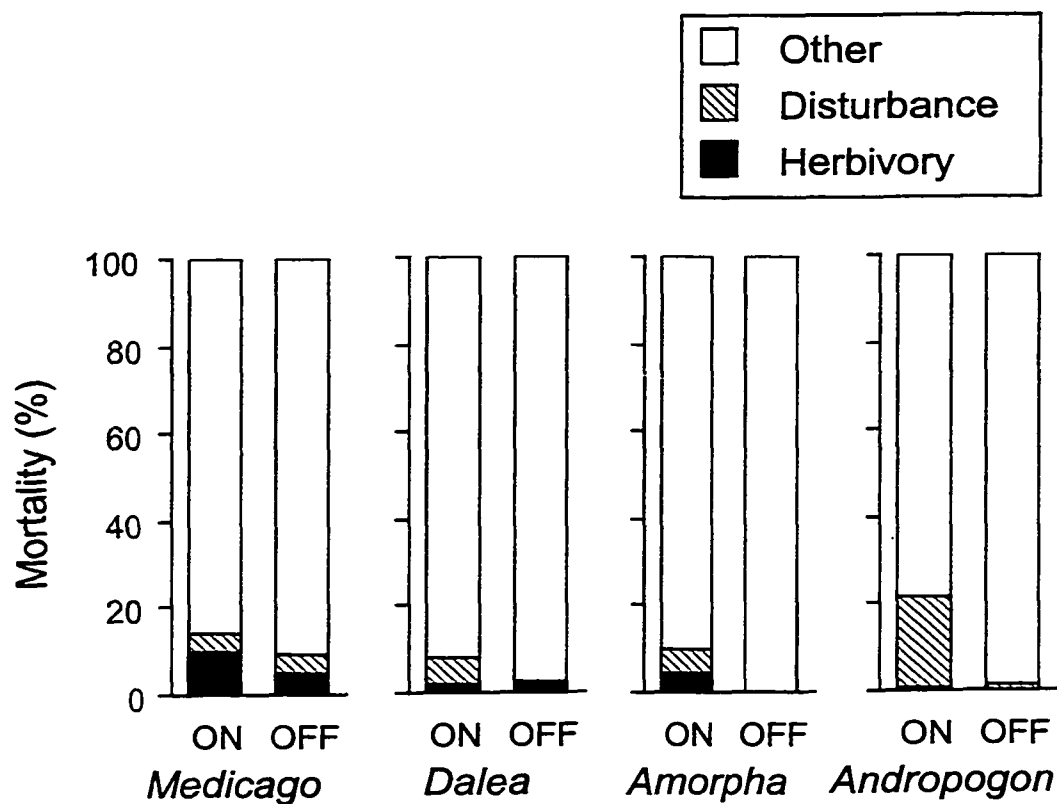
**Fig. 3.** Spatial cross-correlations calculated separately for the adult distribution of each plant species versus (1) the distribution of gopher mounds produced 1994-1997, and (2) relative elevation of the sample locations within the study plot. The correlation calculations were constrained as described in Fig. 2.



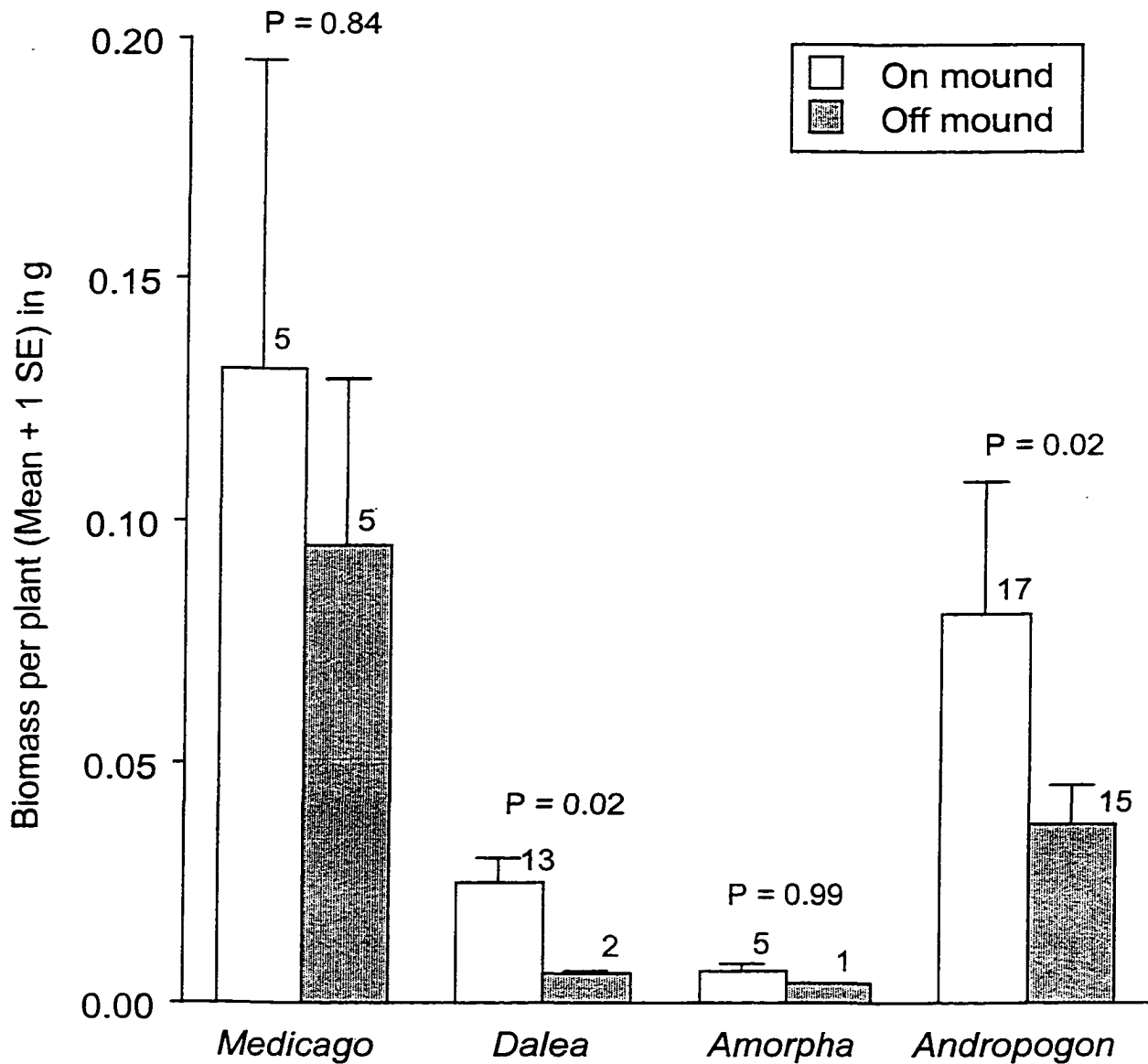
**Fig. 4.** Seedling germination for each species in on- and off-mound treatments. White bars are on mound, shaded bars are off mound. Error bars are + 1 SE. Values above the paired bars are results of pairwise, two-tailed *t*-tests of mound treatment effect.



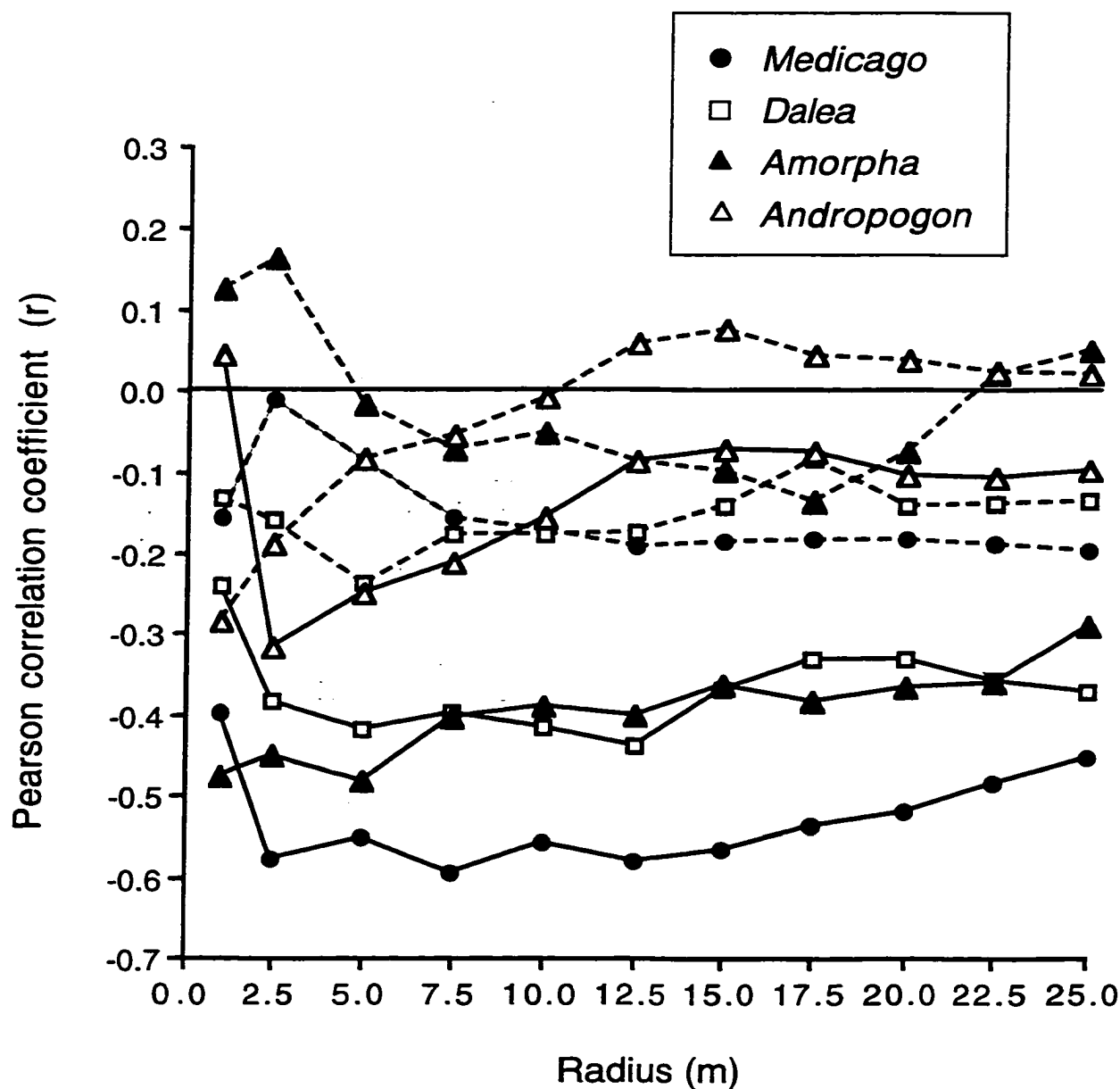
**Fig. 5.** Log-transformed survivorship for each species-plotted against days since germination in the first year of growth. Age zero is 1 June 1998, when germination was recorded. Squares are mean survivorship ( $\pm 1$  SE), as calculated from the field data collected at each survey date. Lines are the composite linear regression models of each species in each treatment, from the parameters listed in Table 2. Open squares and dashed lines are on-mound treatment, closed squares and solid lines are off-mound treatment.



**Fig. 6.** Sources of plant mortality throughout the two growing seasons. Bars represent all plants that died within each mound treatment and species, partitioned by the percentage of deaths attributed to each of three sources. See text for descriptions of each mortality source category.



**Fig. 7.** Individual plant biomass for each species in on- and off-mound treatments at the end of two growing seasons. Error bars are + 1 SE. Values immediately above each bar are the number of grids included in the analysis for each treatment. These values are less than 20 because many grids did not contain surviving plants after two growing seasons. Values above the paired bars are *p*-values from Wilcoxon rank-sum tests of mound treatment effect.



**Fig. 8.** Comparison of Pearson correlation coefficients for each of the 11 neighborhood radii in eight sets of regressions of seedling survivorship versus mound production. Seedling survivorship used in the regressions was recorded on 12 August 1998, and mound production was the number of mounds produced in the neighborhood of each experimental unit as recorded from 4 May through 12 August 1998. Dashed lines are on-mound treatments, solid lines are off-mound treatments.

**CHAPTER 4. DO SPATIAL AND TEMPORAL PATTERNS IN THE  
PRODUCTION OF SMALL-SCALE SOIL DISTURBANCES  
INFLUENCE SEEDLING RECRUITMENT  
IN RECONSTRUCTED PRAIRIE?**

A paper to be submitted to Ecological Applications

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**Abstract**

Research has long been conducted to investigate how small-scale soil disturbances affect prairie plant communities, but much of it has not explicitly considered the spatial and temporal structure of the disturbance regime. Thus, our understanding of the function of small-scale soil disturbances in structuring plant communities is incomplete. Small-scale soil disturbances likely provide habitat for seedling recruitment into prairies in the following three ways: aboveground competition is reduced, belowground competition is reduced, and sites safe from small mammalian herbivores are created. As spatial and temporal autocorrelation in the production of soil disturbances increase, we predict that the reduction in aboveground competition and protection from herbivory also increase, thus causing small-scale soil disturbances to affect plant communities in a more complex manner than is currently appreciated. In this study, we explicitly tested whether spatial and temporal patterns in the production of small-scale soil disturbances influence seedling recruitment and, thus, plant species diversity and community structure in prairie.

We conducted an experiment on reconstructed tallgrass prairie that had been planted approximately 6 years earlier. We sowed the seed of seven forb species in planting sites arranged in a factorial combination of (1) three spatial patterns of increasing spatial autocorrelation and (2) two temporal patterns where sites in one year were either spatially autocorrelated with, or located at random with respect to, site locations in the previous year. At half of the planting sites, we constructed small-scale soil disturbances designed to mimic

gopher mounds. At periodic intervals for two years we measured seedling recruitment in the planting sites. We predicted that each species would demonstrate a unique response to the planting pattern treatments and mound treatments, but that seedling recruitment and subsequent species diversity would be greater where soil disturbances were constructed than in undisturbed areas. In addition, both seedling recruitment and species diversity were predicted to increase with the degree of spatial and temporal autocorrelation in the production of disturbances.

We found that seedling recruitment was greater for all the species in the mound treatments than in the no-mound treatments, but we found no evidence that the spatial or temporal patterns in the production of mounds had an effect on seedling recruitment. We attributed the lack of any pattern effects on seedling recruitment to crucial differences in the function of small-scale soil disturbances in reconstructed tallgrass prairie and native tallgrass prairie. From this experiment, we have strong evidence that small-scale soil disturbances are important for seedling recruitment into prairie, but we hesitate to draw any conclusions about the importance of spatial and temporal patterns of disturbance on seedling recruitment in prairies. Nevertheless, this study did provide important insight as to the function of small-scale soil disturbances in reconstructed tallgrass prairie versus native tallgrass prairie, and we offer some suggestions for incorporating the plant community structure and function of native prairies into prairie reconstructions.

### **Introduction**

Plant species diversity is often low in tallgrass prairie reconstructions (Packard 1994, Kindscher and Tieszen 1998). To address this problem, we should consider whether the processes that maintain and increase plant species diversity in natural prairies may be used to increase species diversity in reconstructed prairies. The small-scale soil disturbance regime created through the burrowing activity of fossorial animals is one such process and could serve



as a useful tool for improving species diversity in prairie reconstructions. The animals that produce small-scale soil disturbances have been called ecosystem engineers, defined as organisms that modulate the availability of resources to other species, thereby maintaining or creating habitat for those species (Jones et al. 1994, 1997). Pocket gophers can be considered engineers in prairie ecosystems because they create a mosaic of small-scale soil disturbances across the landscape, which serve as sites where seedling recruitment can occur (*e.g.*, Gross and Werner 1982, Belsky 1986, Goldberg 1987, Goldberg and Gross 1988, Martinsen et al. 1990, Reader and Buck 1991, Wolfe-Bellin and Moloney 2000). Much research has been conducted on the general impact of gopher mound production on prairie plant communities. For example, the production of mounds has been linked to the abundance of annual species (Laycock and Richardson 1975, Schaal and Leverich 1982, Inouye et al. 1987) and to overall plant species diversity (Tilman 1983, Inouye et al. 1987, Huntly and Reichman 1994). However, most of this research has not considered how the spatial and temporal structure of the mound production regime influences seedling recruitment and, thus, influences plant species diversity and community structure in prairies (community structure being defined as the composition of species in the community and the distributions of those species; see Collins and Glenn 1995). But, without an explicit understanding of how spatial and temporal patterns in mound production affect seedling recruitment, our knowledge of how pocket gophers function as ecosystem engineers is incomplete (Moloney and Levin 1996). Thus, in this study we asked the questions: (1) do spatial and temporal patterns in the production of small-scale soil disturbances influence seedling recruitment in prairies, and (2) can these principles be applied to increase plant species diversity in reconstructed prairies?

Gopher mounds can cover as much as 20% of a grassland area (Grant et al. 1980, Reichman et al. 1982, Spencer et al. 1985), but the production of mounds occurs in distinctive patterns, due to the territorial behavior of gophers (Reichman et al. 1982). In one tallgrass prairie in Iowa, Klaas et al. (2000) documented that mounds were produced in clusters, with

mound production spatially autocorrelated at scales of less than 20 m. In addition, the production of mounds was spatially autocorrelated over time, with the locations of mound clusters remaining relatively static over years (Klaas et al. 2000).

Gopher mounds may directly provide habitat for seedling recruitment into grasslands in three ways: (1) biomass of aboveground vegetation is reduced or removed on mounds (Grant et al. 1980, Grant and McBrayer 1981, Reichman et al. 1993), making light more available (Umbanhowar 1992), and providing an environment where aboveground plant competition is reduced; (2) roots of neighboring vegetation are removed in mound soil (Grant and McBrayer 1981), providing space where belowground plant competition is reduced; and (3) openings in the adult vegetation canopy are created, providing sites that may be avoided by seedling herbivores. Rodent herbivory can have an important negative impact on seedling abundance, diversity, and biomass in grasslands (Hulme 1996, Edwards and Crawley 1999, Howe and Brown 1999), so if small mammals avoid mounds, then mounds may provide important safe sites for seedling survival. Field studies on the behavioral response of small mammalian herbivores to mounds report confounding results, however. Klaas et al. (1998) reported a negative relationship between meadow vole abundance and mound production on a prairie remnant in Iowa, while Whittaker et al. (1991) reported that the abundance of adult male meadow voles was positively related to mound production in a Minnesota prairie. In addition, Whittaker et al. (1991) reported that meadow voles seemed to preferentially travel across bare mounds. Although the response of small mammals to mounds may be complex, or may vary under different environmental conditions, we based our predictions in this study on the premise that small mammalian herbivores avoid the bare space created by mounds where the risk of predation may be high.

Regarding the mound effect on seedling recruitment, we predicted that both reduced aboveground competition and increased protection from small mammal herbivory will be enhanced by spatial and temporal autocorrelation in mound production. When mounds are

produced in clusters, cover of adult vegetation is reduced, more light is available, and aboveground competition is further reduced. In addition, whereas small mammal herbivores may occasionally venture onto single mounds, they should particularly avoid large clusters of mounds.

We tested whether the spatial and temporal patterns of mound production were reflected in seedling recruitment, by planting the seed of seven forb species onto sites arranged in patterns of varying spatial and temporal autocorrelation. Small-scale soil disturbances designed to mimic gopher mounds were constructed at half the sites. We conducted this experiment in a location where there were no pocket gophers or other animals producing natural soil disturbances. In this way, we could manipulate the environment to mimic the soil engineering effects of gophers in their absence (Jones et al. 1997). We constructed mounds over three areas, each approximately 0.30 ha in size, in order to mimic the impact of gopher mounds at a landscape-scale. Because we predicted that small mammalian herbivores play an important role in the functioning of soil disturbances in prairies, we manipulated the landscape at a scale large enough to influence the behavior of small mammals. We also conducted this experiment on sites where tallgrass prairie had been reconstructed (planted as seed on plowed land) approximately 6 years earlier. Our reasons for working in reconstructed prairie were threefold. (1) Plant community structure was simple and species diversity low, so we predicted that any changes in the plant community caused by our mound production regime would be relatively easy to measure. (2) Restoration can serve as a framework in which to test our ecological knowledge and has even been called an "acid test" of our ecological understanding (Bradshaw 1987). Thus, we decided to test our predictions about spatial and temporal patterns of disturbance in a restoration context. (3) We hoped that our ideas about the importance of disturbance patterns in regulating seedling recruitment could be applied to increase plant species diversity in reconstructed prairies.

We predicted that the seven species would exhibit different responses to both the soil disturbances and the pattern arrangements, depending on the aboveground growth pattern and rooting strategy of each, but in general the abundance of each species and species diversity were predicted to be greater on the soil disturbances than in the undisturbed areas. In addition, we predicted that the abundance of each species and species diversity would increase as the spatial patterns became more clustered and in the sites that were spatially autocorrelated over time versus those that were not.

## **Methods**

### **Study site**

The study was conducted at the Neal Smith National Wildlife Refuge (NSNWR), a 3500-ha refuge located in south-central Iowa near Prairie City (41° 36' N, 93° 25' W; Fig. 1). The refuge was created in 1991 when the United States Fish and Wildlife Service purchased a large tract of land that was being used primarily for rowcrop agriculture (Drobney 1994). The land originally was covered primarily with tallgrass prairie before conversion to agriculture in the late 1800s, and the primary goal at the NSNWR is to restore tallgrass prairie vegetation across most of the refuge (Drobney 1994). To achieve this goal, different sub-sections of the refuge have been planted with native tallgrass prairie seed each year since 1992. At the time of the study, planted sites were managed with annual, controlled fires set in early April each year. In addition, seeds of the dominant grass species were harvested with combines during October of each year.

### **Study species**

Seven forb species endemic to tallgrass prairies were used in the study. All the species are commonly found on native prairies, but were not abundant in the NSNWR prairie reconstructions, thus providing our motivation for attempting to get them established. The

species included *Amorpha canescens* Pursh, *Coreopsis palmata* Nutt., *Dalea purpurea* Vent., *Echinacea pallida* (Nutt.) Nutt., *Heuchera richardsonii* R. Br., *Liatris aspera* Michx., and *Viola pedatifida* G. Don (hereafter species will be labeled by genus). All seven species are naturally found in mesic to dry-mesic tallgrass prairies, the types of prairie being reconstructed at the NSNWR study sites. The species are from four plant families, and produce a range in seed sizes (Table 1).

As adults, the species represent a range in aboveground growth patterns and rooting strategies. All the species are perennials, but *Amorpha* is notably long-lived while *Coreopsis* is short-lived. All the species flower in mid to late summer in the region of the NSNWR, except *Viola*, which flowers in early summer. All the species also remain herbaceous as adults, except *Amorpha*, which becomes a woody shrub. *Amorpha* and *Coreopsis* are rhizomatous, and *Coreopsis* maintains a shallow root system. *Dalea*, *Echinacea*, and *Viola* grow from taproots. *Heuchera* forms a basal rosette of leaves, and grows from a branched caudex. *Liatris* stems grow erect, and arise from a corm.

The seven species have high conservation value and have been assigned coefficients of conservatism between 6 and 10 (on a scale of 0 being low conservatism and 10 being high conservatism; Table 1; see Ladd's 1997 list of conservatism coefficients in Illinois). Conservatism is a subjective ranking that indicates the degree to which a given species is representative of a high-quality prairie remnant in which vegetation structure, composition, and function are intact (Masters 1997). Thus, the species are all highly desirable in reconstructed prairie, and none of them were abundant at the NSNWR at the time of the study. In fact, the species were chosen in consultation with the staff at the NSNWR, who were interested in establishing populations of each species at the refuge.

## Experimental design

The experiment was conducted at two different sites within the NSNWR (Fig. 1). One site, hereafter labeled the low-diversity site, was located on a hilltop that had been planted with prairie seed in 1993. The site exhibited very low plant species diversity, with fewer than 10 plant species growing in abundance across the site. Two grass species, *Schizachyrium scoparium* (Michx.) Nash (little bluestem) and *Andropogon gerardii* Vitman (big bluestem), dominated vegetation at the site. The second site, labeled the high-diversity site, was located on a hillside that had been planted with prairie seed in 1995. Vegetation on the site was more diverse than the first site, with approximately 20 plant species growing abundantly. The vegetation was also taller and more dense than on the first site. The high-diversity site was dominated by two grasses, *Sorghastrum nutans* (L.) Nash (indian grass) and *A. gerardii*, and the forb *Chamaecrista fasciculata* (Michx.) Greene (partridge pea). The low diversity site was located at planting site 17, as designated in the NSNWR records, and the high diversity site was located at planting site 32 (Fig. 1).

Three permanent blocks were established in June 1998 at the NSNWR. Two blocks, labeled A and B, were located on the low-diversity site (Fig. 1). One block, labeled C, was located on the high-diversity site (Fig. 1). Each block was 52-m x 62-m in size and consisted of six 24-m x 18-m plots arranged in a 2 x 3 array with 4 m buffers between plots (Fig. 2). Six planting pattern treatments were applied within a block, one to each of the six plots. The six patterns consisted of a 3 x 2 factorial combination of three spatial and two temporal patterns of potential planting site locations. Each potential planting site was approximately a 0.20 m<sup>2</sup> circular area (the approximate size of a natural gopher mound). The three spatial patterns included arrangements of the potential planting sites as singles (labeled 1), clusters of four (labeled 4), and clusters of 16 (labeled 16). For the two temporal patterns, locations of potential planting sites in one year were either (1) spatially autocorrelated with planting sites in the previous year (labeled C, for correlated), or (2) located at random with respect to planting

sites in the previous year (labeled U, for uncorrelated). The spatial and temporal planting patterns combined for a total of six pattern treatments, which were labeled as: singles-correlated (1C), singles-uncorrelated (1U), clusters of four-correlated (4C), clusters of four-uncorrelated (4U), clusters of 16-correlated (16C), and clusters of 16-uncorrelated (16U; Fig. 2). The x-y coordinates of each individual potential planting site were assigned with a computer algorithm, and sites were each labeled in the field with a wire pin flag.

The spatial and temporal patterns were designed to test whether the degree of clustering seen in the natural production of gopher mounds is reflected in seedling recruitment. The spatial patterns included one treatment where planting sites were hyperdispersed across the landscape with no spatial autocorrelation between sites (1), and two treatments where sites were spatially autocorrelated at two different levels (4 and 16). The most spatially autocorrelated arrangement of sites was based on the degree of spatial autocorrelation found in the production of gopher mounds in native prairies (Klaas et al. 2000). We used the range in spatial autocorrelation patterns as a control to test whether the degree of clustering in mound production is reflected in seedling recruitment. Likewise, the temporal pattern treatments were based on the same principle. Natural mound production tends to be autocorrelated over years (Klaas et al. 2000), and we mimicked this in the autocorrelated temporal pattern treatment. To test whether temporal autocorrelation is important to seedling recruitment, we included the uncorrelated temporal pattern treatment as a comparison.

Each plot was further split in half, and one of two mound treatments was assigned at random to each half-plot (Fig. 2). In one half-plot, we constructed a soil disturbance at each potential planting site. The soil disturbances were designed to mimic natural gopher mounds, and hereafter will be referred to as “mounds.” Mounds were constructed by pouring 10 L of topsoil onto the field surface, which produced a circular mound of soil approximately 0.5 m in diameter (0.20 m<sup>2</sup> in area). Mounds were centered around pin flags marking the potential planting sites. Topsoil was purchased from a commercial nursery in central Iowa. This

treatment was labeled the mound treatment. In the second half of each plot, we did not construct soil disturbances at the potential planting sites. This treatment was labeled the no-mound treatment.

Each half-plot was further divided into six 6-m x 6-m quadrats arranged in a 2 x 3 array with no buffers between quadrats (Fig. 2). Sixteen potential planting sites were located in each quadrat. The arrangement of sites within a quadrat was determined by the spatial and temporal planting pattern treatment assigned to the plot within which a quadrat was located (Fig. 2). While the clustering of the planting sites varied between plots, the density of the sites remained constant at 0.44 sites/m<sup>2</sup>. In the quadrats to which the mound treatment was applied, approximately 9% of the ground surface was covered by mounds per year, which reflected a fairly typical rate of natural gopher mound production in native prairie (Klaas et al. 2000; chapter 3).

Within each half-plot, four quadrats chosen at random received a seed treatment, and the remaining two quadrats were left as unseeded controls (Fig. 2). In the seed treatment, seeds of the seven study species were planted on each of the 16 potential planting sites per quadrat. Before planting, approximately 50 seeds of each species were measured by volume and poured into envelopes. Although we tried to measure 50 seeds of each species, the number of seeds measured per species varied, primarily due to variation in how "clean" the seed was from bracts and other extra flower parts. We attempted to quantify the variability in seed number within species by randomly selecting 10 to 15 envelopes and counting the number of seeds per species in each envelope. We then calculated the average ( $\pm$  1 SD) number of seeds per species in each envelope (Table 1). For planting, one envelope containing all seven species was poured onto the center of each planting site. Seeds were gently scattered by hand in a circular area within a 15-cm radius of each planting site pin flag, and worked into the soil with a hand trowel. Seeds used in the plantings were fresh, having been harvested from local native prairies



in the autumn months immediately preceding our planting dates. Seeds were purchased from commercial native prairie nurseries in central and southern Iowa.

We planted seeds in two years, which hereafter will be identified as the 1998 and 1999 experimental years. The locations of potential planting sites were marked with wire pin flags in June 1998 and June 1999. Mounds were then constructed later during the 1998 and 1999 growing seasons (see Table 2 for dates). Seeds were planted in December 1998 on 1998 planting sites, and seeds were planted in December 1999-January 2000 on 1999 planting sites (see Table 2 for dates of planting). Thus, each planting site was seeded only once, unless locations in the 1999 experimental year happened to overlap with locations from the 1998 experimental year. By the end of the experiment, each quadrat contained one set of 16 planting sites from 1998 and one set from 1999.

## **Data collection**

### **Vegetation censuses**

The vegetation growing in a sub-set of the planting sites was surveyed periodically throughout the 1999 and 2000 growing seasons (see Table 2 for survey dates). Sites from the 1998 experimental year were surveyed five times during the 1999 growing season and twice during the 2000 growing season. Sites from the 1999 experimental year were surveyed twice during the 2000 growing season (Table 2).

For the surveys, we randomly selected three planting sites from each experimental year within each quadrat and surveyed those same sites during each survey. We surveyed the vegetation growing at each planting site by centering a circular sample frame around the pin flag marking the center of each planting site. The sample frame was 30 cm in diameter, which covered the area in which seed was planted at each site and was slightly smaller than the average constructed mound. In each sample frame, we identified all seedlings and counted the number of seedlings of each species. We distinguished seedlings of the seven planted species,

which hereafter will be labeled experimental species, from seedlings of other species, which hereafter will be labeled volunteer seedlings. We also identified each adult species and estimated the percentage of the sample frame it covered.

We combined data from the three sampled planting sites in each experimental year surveyed within each quadrat. For the experimental species as a group, we calculated the total abundance, species richness, and species diversity (using the Shannon-Weiner  $H'$  diversity index; Peet 1974) of seedlings per quadrat. We also calculated the total abundance of seedlings of each experimental species per quadrat. For the volunteer seedlings as a group, we calculated the total abundance and species richness per quadrat. In addition, we calculated the average percent cover and species richness of adult plants per site within each quadrat.

During the 1999 growing season, we noticed that the mound pattern treatments appeared to be positively affecting the growth of grasses in the immediate vicinity of the artificial mounds. To ascertain whether the mound treatments were affecting grass growth, we measured maximum grass height in each of the treatments on 7 and 8 July 1999. For the measurements, we placed a 0.6-m x 0.6-m sample frame around two randomly chosen 1998 planting sites used in the vegetation surveys within each quadrat and measured the height of the tallest grass plant in each sample frame.

### **Environmental variables**

To provide a measure of the light environment at planting sites in different pattern and mound treatments, we measured light reaching the soil surface in blocks A and C on 22 June 2000 and in block B on 29 June 2000. Within each plot, we took light measurements in two mound, no-seed quadrats and one randomly chosen no-mound, no-seed quadrat. In the mound quadrats, we measured light on one 1998 mound and one 1999 mound. In the no-mound quadrats, we measured light on one 1998 and one 1999 planting site. The planting sites used for the light measurements were chosen at random from those used in the vegetation surveys.

Thus, we measured light reaching the soil surface on two 1999 mounds, two 1998 mounds, and two no-mound sites per plot. We used two quantum sensors (400-700 nm) for each measurement. One sensor was placed approximately 2 cm above the soil surface to measure the photon flux of light penetrating the vegetation canopy. The second sensor was mounted on a tripod raised above the canopy to measure the photon flux of incident light. Data were expressed as the fraction of incident light penetrating the vegetation canopy. Readings for each sensor were taken automatically every 0.3 s for 3 s and averaged to one value. At each site, three readings were taken, and the average was used in subsequent data analyses. All measurements were taken within 2 hours of solar noon.

Soil moisture and other measures were also compared across all treatments. In one no-mound, no-seed quadrat chosen at random from each plot, we collected soil on 31 August 1999 from a 1998 mound, a 1999 mound, and an off-mound site. All sites within each quadrat were chosen at random. We measured soil moisture percentage in all samples, while the other soil measures were conducted only for soil samples from 1999 mounds and no-mound sites in the uncorrelated pattern plots. The other soil measures included total C (%), total N (%), available P, available K, pH, texture, and color. Soil moisture was determined by measuring the soil wet mass soon after the sample was collected and soil dry mass after nine days of drying at 65°C. Total C and N were measured by combustion (Nelson and Sommers 1996), available P by the Bray-1 method, and available K with the  $\text{NH}_4\text{OAc}$  method (Brown 1998). Texture was assessed by particle size analysis, and color was measured with a chromameter.

### **Statistical analysis**

Vegetation survey data were analyzed separately for each experimental year and for each survey. Here we report the results from two surveys of the 1998 plantings, one conducted during the first year of plant growth on 8-14 July 1999 and one conducted during the second year on 8 August-6 September 2000 (Table 2). We also report the results from one survey of

the 1999 plantings, conducted on 8 August-6 September 2000 during the first year of plant growth for those plantings (Table 2). Only the results from the surveys conducted near the end of each growing season are reported here because we were interested in assessing treatment effects on seedlings that had become established. The mid-July 1999 results are reported for the first-year survey of the 1998 sites, however, because this was the last survey during the 1999 growing season before mound sites were disturbed by new mounds. New mounds were constructed during 15 July-4 August 1999 (Table 2), so some of the sites surveyed during the last vegetation survey on 16-26 August 1999 were partially buried by the new mounds.

Using the quadrat-level vegetation data, we first examined the no-seed control quadrat treatments and found that seedlings of the experimental species were never found in the no-seed controls. Thus, all subsequent analyses of the vegetation survey data were conducted using only quadrats that received the seed treatment.

All data, including the vegetation survey data, light data, and soil data, were then treated by calculating the average values per half-plot. Vegetation data were analyzed with a mixed, split-plot ANOVA and with a mixed, split-plot ANCOVA. In the ANCOVA, we used average adult species richness as the covariate. We hypothesized that adult species richness might covary with seedling recruitment in either of the following ways: (1) we predicted a negative relationship if species richness was an inverse indicator of available niche space, and sites with high species richness were resistant to invasion (*e.g.*, Tilman 1997, Symstad 2000); or (2) we predicted a positive relationship if adult species richness was an indicator of the environmental suitability of an area for seedling survivorship, and sites with high species richness were less resistant to invasion (*e.g.*, Palmer and Maurer 1997, Smith and Knapp 1999, Levine 2000). However, we found that adult species richness never explained a significant portion of the variance in seedling survivorship. Thus, we only report results of the ANOVA analyses conducted without the adult species richness covariate. Since we report the results from two vegetation surveys of the 1998 experiment, we corrected for the repeated

comparisons within the 1998 experiment using the Bonferroni method ( $\alpha = 0.05/2 = 0.025$ ). Light and soil moisture data were analyzed with a mixed, split-plot ANOVA. For the other soil measures, we tested for differences between the 1999 mound and no-mound treatments with *t*-tests. In these tests, nearly all of the variables had unequal variances between the mound and no-mound soil, so we performed *t*-tests for unequal variances using the Satterthwaite correction. All analyses were conducted in SAS version 8.1 (SAS 2000).

## Results

### Treatment effects on experimental species

For all of the individual experimental species in all surveys, more plants were growing on mounds than in the no-mound sites for all of the planting treatments, and this mound treatment effect was significant in most cases (Figs. 3 and 4). However, there was never a significant spatial or temporal pattern treatment effect on any of the species (all *P*-values > 0.05). Of the experimental species, *Echinacea* was the most abundant in all three surveys, followed in order by *Viola*, *Dalea*, *Amorpha*, and *Liatris* (Figs. 3 and 4). *Coreopsis* and *Heuchera* were always rare (Figs. 3 and 4). In fact, *Coreopsis* was never identified during the 1999 survey (Fig. 3), possibly because it did not germinate or we did not recognize the seedlings. *Heuchera* and *Liatris* exhibited the greatest survivorship from the first year to the second in the 1998 experiment, with 83% of the *Heuchera* plants and 61% of the *Liatris* surviving. However, the number of *Heuchera* plants in both years was very low. *Viola* and *Echinacea* exhibited an intermediate level of second-year survivorship, with 39% and 29% survivorship, respectively. Survivorship of *Amorpha* and *Dalea* was the lowest, with 16% and 9% surviving to the end of the second season.

In all three vegetation surveys, abundance, species richness, and species diversity of the experimental species seedlings were greater in the mound treatments than in the no-mound treatments (Figs. 5, 6, and 7). The statistical evidence for this mound effect is somewhat weak

for the 2000 survey of the 1998 sites (Table 4), but is strong for both the 1999 survey of the 1998 sites (Table 3) and the 2000 survey of the 1999 sites (Table 5). We found little evidence that abundance, species richness, or species diversity of the experimental species were affected by the spatial or temporal pattern treatments (Table 3, 4, and 5). However, there was a significant block effect on the three measures of the experimental species in the two surveys conducted in 2000 (Tables 4 and 5). On the 1998 sites surveyed in 2000, all three measures were greater in blocks A and B than in block C, with  $13 \pm 1$  (Mean  $\pm 1$  SE) seedlings occurring on sites in both blocks A and B, and  $3 \pm 1$  seedlings in block C. Species richness was  $2.5 \pm 0.2$  on sites in both blocks A and B, and  $1.5 \pm 0.2$  in block C, and species diversity was  $0.57 \pm 0.06$  and  $0.56 \pm 0.06$  in blocks A and B, respectively, and  $0.37 \pm 0.06$  in block C. The trends for the 1999 sites surveyed in 2000 were similar.

There was also a large difference between experimental years in abundance of seedlings, species richness, and species diversity. All three measures were greater in the first year of the 1998 experiment than the first of year of the 1999 experiment (cf. Figs. 5 and 7). In fact, all three measures were generally greater during the second year of the 1998 experiment than in the first year of the 1999 experiment (cf. Figs. 6 and 7), and these surveys were conducted during the same time-period. These differences could have been due to between-year variability in the environmental conditions when the seeds were planted or at the time of germination, or in quality of seed.

The proportion of the 1998 plants that survived from the 1999 survey to the 2000 survey was fairly similar between mound treatments. In the mound treatment, 52% of the seedlings survived to the second year, while 58% of the seedlings survived in the no-mound treatment. Species richness and diversity in the mound treatment the second year were 63% and 54% of the levels in the first year, respectively, while in the no-mound treatment, they were 61% and 46%.

### **Treatment effects on seedlings of volunteer species**

The abundance of volunteer seedlings was greater in the no-mound sites than on mounds, while volunteer seedling species richness was greater on mounds than in the no-mound sites, in the two first-year surveys (Tables 3 and 5, Figs. 5 and 7). In the second-year survey of the 1998 sites, there was no evidence of a mound treatment effect on recruitment of volunteer seedlings (Table 4, Fig. 6). There also was no evidence of spatial or temporal pattern treatment effects on the number or richness of volunteer seedlings in any of the surveys (Tables 3, 4, and 5). There was a significant block effect on species richness in the first-year survey of the 1998 sites (Table 3), with  $2.3 \pm 0.4$  species in block A,  $4.2 \pm 0.4$  in block B, and  $4.7 \pm 0.4$  in block C. The block effect was also significant in the abundance of volunteer seedlings in the first-year survey of the 1999 sites (Table 5), with  $10.8 \pm 1.0$  seedlings in block A,  $10.8 \pm 1.0$  in block B, and only  $5.1 \pm 1.0$  in block C.

### **Treatment effects on adult vegetation**

In all three surveys, we found that the percentage of each planting site covered by adult vegetation did not vary with respect to the mound, spatial pattern, or temporal pattern treatments (Tables 3, 4, and 5, Figs. 5, 6, and 7). However, when we looked at all the vegetation surveys conducted throughout the study, in addition to the surveys discussed so far, we found that cover of adult vegetation did differ significantly in the mound and no-mound treatments (Fig. 8). Cover was greater in the no-mound sites than the mound sites in the other four surveys conducted during 1999 (Fig. 8). We think that the mound treatment reduced adult vegetation cover on planting sites early in the 1999 growing season before the dominant  $C_4$  grasses had grown to full height. In addition, the mound treatment had the same effect on vegetation cover in the 16-26 August 1999 survey, which we attributed to the bare space created when new mounds were constructed on 15 July - 4 August 1999. In the surveys conducted during 2000, we found that cover by adult vegetation was not significantly affected

by the mound treatment for both the second year of the 1998 experiment (results not shown) and the first year of the 1999 experiment (Fig. 8). In addition, we found no evidence of spatial or temporal pattern treatment effects on adult vegetation cover in any of the nine vegetation surveys. In the three vegetation surveys discussed in detail earlier, we found a significant block effect on adult vegetation cover (Tables 3, 4, and 5). As might be expected due to the differences in dominant vegetation on the three sites, adult vegetation cover was higher in block C than in blocks A and B. For example, in the 1998 planting sites surveyed 8 August - 6 September 2000, adult vegetation covered  $74.2 \pm 2.1\%$  of each site in block A,  $82.6 \pm 2.1\%$  in block B, and  $98.4 \pm 2.1\%$  in block C.

On the days when light measurements were taken, the incident light ranged from 1893 to  $2248 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ . The fraction of incident light penetrating the vegetation canopy was unaffected by the mound, spatial pattern, or temporal pattern treatments (Table 6, Fig. 9). However, we did find a significant mound x spatial pattern interaction, but in contrast with our predictions, the data did not indicate that incident light in the mound treatments increased as spatial autocorrelation increased (Fig. 9). We also found a significant block effect, with 42% incident light reaching the soil surface in block A, 33% in block B, and 25% in block C.

We found that maximum grass height was significantly greater in the mound treatments ( $94.6 \pm 1.3$  cm) than no-mound treatments ( $85.2 \pm 1.3$  cm;  $F = 46.9$ ,  $df = 1,15$ ,  $P < 0.0001$ ). We found no evidence that grass height was affected by spatial pattern treatment, there was no mound x spatial pattern interaction, and the temporal pattern treatments had not been applied when the measurements were taken. In addition, we found a significant block effect on maximum grass height ( $F = 74.89$ ,  $df = 2,13$ ,  $P < 0.0001$ ), with much taller grass in block C than in blocks A or B. However, this simply reflected the taller dominant grass species in block C than in blocks A and B.



### **Relationship between treatments and soil measurements**

Soil moisture was significantly affected by mound treatment ( $F = 24.33$ ,  $df = 2,24$ ,  $P < 0.0001$ ). We measured  $24.2 \pm 0.9\%$  soil moisture in 1999 mounds,  $18.3 \pm 0.9\%$  moisture in 1998 mounds, and  $15.0 \pm 0.9\%$  moisture in soil collected from the no-mound sites. There were no significant spatial or temporal treatment effects on soil moisture.

For the other measures related to soil fertility, total C, total N, available P, and pH were significantly greater in the mound soil than no-mound treatment soil (Table 7). In addition, the mound soil was significantly darker than the no-mound treatment soil (Table 7). In the texture analysis, mound soil contained significantly more sand and less clay than the no-mound treatment soil (Table 7).

## **Discussion**

### **Experimental plant species**

In the three vegetation surveys, *Echinacea* was always the most abundant of the seven experimental species, followed in order by *Viola*, *Dalea*, *Amorpha*, *Liatris*, *Heuchera*, and *Coreopsis*. This rank order in seedling abundance does not reflect the rank order in numbers of seeds planted in either experimental year (Table 1). Thus, we can exclude seed number as the cause of these among-species differences in seedling abundance, but there are a number of other possible causes. Some of these differences among species could include variation in the percentage of viable seeds, variation in the environmental conditions required for germination, or variation in the success of different growth forms under the conditions at the study sites. Interestingly, the three most abundant species produce taproots, although we have no evidence to determine whether this is cause or coincidence. We found that the rank order in seedling abundance was approximately the same in both the mound and no-mound treatments for all three surveys. Thus, the mound treatments did not differentially affect some species more than others, even though the species varied in aboveground growth patterns and rooting strategies

(see *Methods—Study species*). In fact, all the species responded to the mound treatments in a similar fashion, with greater seedling abundance in the mound treatment than no-mound treatment.

### **Treatment effects**

We consistently found a difference between the mound and no-mound treatments for almost every dependent variable measured. In the experimental species, individual species seedling abundance, total seedling abundance, species richness, and species diversity were greater in the mound treatment than the no-mound treatment. For seedlings of the volunteer species, we found in one survey that seedling abundance was greater in the no-mound treatment than the mound treatment, while species richness of the seedlings was greater in the mound treatment than no-mound treatment in another survey. We attributed the greater abundance of seedlings in the no-mound treatments to seedlings of *Taraxacum officinale* Weber (common dandelion) growing abundantly at the study sites. In the mound treatments, mounds probably buried the *Taraxacum* seeds and seedlings, whereas *Taraxacum* seedlings were very abundant where mounds were not constructed. The greater volunteer seedling richness in the mound treatments could have been a by-product of the soil used to construct the mounds. The mound soil may have contained a seed bank with species novel to the NSNWR sites, causing greater species richness in the volunteer species growing in the mound treatments than in the no-mound treatments.

In terms of variables predicted to be directly affected by the mound treatments, adult vegetation cover was reduced in the mound treatment compared to the no-mound treatment early in the 1998 growing season, indicating that more light should have been reaching the seedlings on mounds. However, the mound treatment effect on vegetation cover disappeared later in 1998 and in 1999. Interestingly, we found that grass growth was more vigorous in the immediate vicinity of mounds than in the no-mound treatment, a phenomenon that has been

reported in earlier studies (Grant et al. 1980, Reichman et al. 1993). Possibly because of the increased growth of grasses near mounds, we found no mound treatment effect on light penetrating the vegetation canopy when measurements were taken in June 1999, even though we had predicted that more light should reach the soil surface in the mound treatments than no-mound treatments.

The soil analyses showed that the soil used to create our experimental mounds contained more carbon, nitrogen, and phosphorus, and was darker, than the topsoil at the NSNWR, indicating that the mounds in this study may have been more fertile than the no-mound treatment soil. This is in contrast to the soil in natural gopher mounds, which is usually lower in nitrogen, phosphorus, and potassium than undisturbed soil (McDonough 1974, Grant and McBrayer 1981, Spencer et al. 1985, Inouye et al. 1987). However, soil from the no-mound treatment was also lower in pH and contained more clay than the mound soil, indicating that cation exchange capacity may have been higher, and nutrients more accessible to plants, in the topsoil at the NSNWR. While the trends in fertility between the mound and off-mound soil were unclear, we did find that the mound soil contained more moisture than the no-mound treatment soil, which likely had a positive influence on seedling survivorship. In addition, we observed that the mound soil was more friable than the off-mound soil, which probably also had a positive influence on seedling survivorship. The friable nature of mound soil has also been reported for natural gopher mounds (McDonough 1974).

We also found a fairly consistent block effect on most of the variables measured. This block effect was expected and is the reason we set up the experiment in a block design. We reported the block effects here, however, to highlight some of the differences between the high- and low-diversity sites where this experiment was conducted. The vegetation was much taller and denser in the high-diversity site where block C was located than in the low-diversity site where blocks A and B were located. These differences were reflected in the following trends: adult vegetation cover was greater in block C than blocks A and B, and light reaching

the soil surface was reduced in block C compared to blocks A and B. These effects, in turn, probably affected seedling recruitment of both the experimental species and volunteer species. Seedling abundance, species richness, and species diversity of the experimental species were all lower in block C than in blocks A and B. In addition, the abundance of volunteer seedlings was lower in block C than in blocks A and B. However, volunteer seedling species richness was greater in block C than the other blocks, which probably reflected the higher diversity of adult vegetation on block C.

In contrast to the strong mound treatment effects, we consistently found no effect of the spatial or temporal pattern treatments on any dependent variable measured, including recruitment of experimental and volunteers seedlings, adult vegetation cover, and light reaching the soil surface. We were surprised by this result, since we had hypothesized that disturbance patterns would affect all the measured variables. This lack of any pattern treatment effect could be due to a variety of factors. One factor could be low statistical power in our experiment with which to detect an effect of the main pattern treatments. This is a common limitation in a split-plot experimental design, where there is high replication for the split-plot treatment, in this case the mound treatments, and low replication for the main treatment, in this case the pattern treatments (Cochran and Cox 1957). In addition, with only three blocks, the statistical replication in this experiment was low from the start. However, we made the decision to apply the pattern and mound treatments at a labor-intensive landscape-level spatial scale, resulting in a trade-off with low statistical replication.

Besides the statistical issues with the experimental design, it is possible that we did not measure any pattern treatment effects because increasing spatial and temporal autocorrelation in the arrangement of planting sites truly has no effect on seedling recruitment or diversity in any grassland systems, whether the systems are native or reconstructed. While this could be true, we do not believe that the results of this experiment provide adequate evidence to either support or refute this conclusion. Many of the factors predicted to vary directly due to mound

construction, including adult vegetation cover and light reaching the soil surface, showed little response to the mound and no-mound treatments in this experiment. These are precisely the variables that differ between natural mounds and off-mound sites in native prairies (Grant et al. 1980, Grant and McBrayer 1981, Reichman 1993) and were the variables that we predicted would cause the pattern effects on seedling recruitment and diversity in this experiment. In addition, we measured significant effects of natural mound spatial autocorrelation on vegetation in native grasslands in an earlier study (chapter 3). However, there was a critical distinction between the study done on native prairie with natural gopher mounds as reported in chapter 3 and the experiment reported here. In the native prairie, we found that seedling survivorship was affected by mound spatial patterns, but that the effect occurred only for seedlings growing *off* mounds in the vicinity of mounds, and that the effect was negative. Seedling survivorship decreased as neighborhood mound production increased. Seedlings growing *on* mounds actually showed no response to the level of neighborhood mound production. In the experimental study reported here, we only planted seeds directly on mounds and in off-mound sites that were spatially separated from mounds by approximately a few meters. It is possible that seedlings growing off mounds in the immediate vicinity of the mounds would have showed a response to the spatial or temporal pattern treatments.

It seems more likely, however, that we did not find the predicted pattern treatment effects in reconstructed prairies because our predictions were based on work in native prairies, and there are crucial differences between the reconstructed prairie at our study sites and native tallgrass prairies. In this experiment, the strong mound treatment effects that we measured could have been due to any of the following: root-free space in mound soil where belowground competition was lower than in neighboring off-mound sites; greater water-holding capacity of the mound soil compared to the off-mound soil; or a fertilization effect of the mound soil compared to the off-mound soil. In contrast, the effect of natural gopher mounds on seedling survivorship in native prairies also may be caused by root-free space where belowground

competition is reduced, but two different factors also play a role. Increased light striking natural mounds allows aboveground competition to be lower than in off-mound sites, and reduced vegetation cover on natural mounds causes mounds to be safe sites from small mammalian herbivory. We predicted that increasing mound spatial and temporal autocorrelation in this experiment would multiply the light and mammalian herbivory safe-site effects, thus positively affecting seedling survivorship and providing a mechanism for increasing forb species diversity in reconstructed prairies. However, we found little evidence that the mound or pattern treatments affected light or adult vegetation cover at our reconstructed prairie sites. In addition, populations of small mammalian herbivores at our sites were low in the years of the study (chapter 5). Thus, we attributed the disparity between our predictions and our results to differences in vegetation structure and mound function between the reconstructed prairie at our study sites and native tallgrass prairies.

### **Crucial differences between reconstructed and native tallgrass prairie**

The vegetation on both study sites at the NSNWR was dominated by three species of  $C_4$  grasses, big bluestem, little bluestem, and indian grass. This is fairly common in tallgrass prairie reconstructions, where plant species diversity often is low and a few perennial  $C_4$  grasses dominate the vegetation (Packard 1994, Kindscher and Tieszen 1998). The seed of these grass species is more readily available and is less expensive than the seed of many forb species, so these species tend to be most abundant in seed mixes planted in tallgrass prairie reconstruction projects. In addition, big bluestem and indian grass become established quickly and grow aggressively, allowing them to quickly become dominant in prairie plantings (Betz 1984, Packard 1994). These grass species often grow as bunchgrasses, so a large amount of bare ground was available between the individual grass genets at our study sites. This seems like a good situation for the establishment of additional species' seedlings, but in fact these grasses are extremely tall and are able to outcompete most seedlings for available light. In

addition, most available root space is filled by grass roots, so the dominant grasses outcompete seedlings for water. So, once these dominant grasses are established, it is very difficult to introduce additional plant species. This problem actually provided some of the motivation behind our research, and we found that our constructed mounds provided space where belowground competition was reduced and seedling establishment occurred. However, in contrast to our predictions based on the vegetation structure of native prairies, the spatial and temporal patterns of mound production did not have any effect in the reconstructed prairie system. This was probably because the main factors predicted to cause mound pattern effects are light and vegetation cover, and both of these were not factors at our sites where  $C_4$  bunchgrasses dominated the vegetation.

Another critical difference between the reconstructed prairies in this study and natural prairies is that our reconstructed sites were burned each spring. Native prairies under typical management are usually burned only every three to five years (Schramm 1990). Annual burning is a common practice in most reconstructed prairies for approximately the first decade after planting and is done to promote growth of the native  $C_4$  grasses, allowing them to outcompete weedy vegetation (Schramm 1990). Because  $C_4$  grass productivity increases under an annual spring burn regime (Towne and Owensby 1984, Knapp et al. 1998), this practice also contributes to the continued dominance of the  $C_4$  grasses. So, while the practice of annual burning prevents the establishment of weedy species, it also contributes to the difficulty in establishing populations of additional native plant species.

In addition to the effects of annual burning on the productivity of the dominant grasses, there is also no accumulation of standing dead biomass or detritus from one year to the next. At our study sites, this contributed to the large amount of bare ground between individual grass genets. Because of this bare space, the mounds in our study had little effect on light availability or cover of adult vegetation. In addition, this bare ground probably leads to low populations of small mammalian herbivores. Previous studies have reported that vole populations are low on

prairies for at least one growing season following a spring fire (Vacanti and Geluso 1985, Clark and Kaufman 1990). Low vole populations might keep seedlings safer from herbivory across the entire site, but this is another indication of how reconstructed prairies are not functioning like native prairies. In addition, low populations of herbivores likely contributed to the lack of a disturbance pattern treatment effect in this study.

## Conclusion

We conducted this experiment to measure the effects of varying spatial and temporal patterns of mound production on seedling recruitment and species diversity in grasslands and to determine whether the insights gained could be applied to increase forb species diversity in tallgrass prairie reconstruction efforts. We have strong evidence from the study that mounds in reconstructed prairies provide space for the successful establishment of a variety of forb species, and we attribute this to the root-free space provided by mounds where belowground competition was reduced. However, we found no evidence that the spatial or temporal patterns of mound production are an important consideration when using mounds as planting sites. We are reluctant, however, to conclude that patterns of soil disturbances have no effect on seedling survivorship in any grasslands. Instead, we attribute this result in our study to important differences in vegetation structure and function between recently reconstructed and native prairies. Reconstructed prairies are typically low in plant species diversity and are dominated by highly productive  $C_4$  grasses. In addition, these sites are typically burned annually, contributing to the dominance of the  $C_4$  grasses and a lack of litter or other ground cover. This also contributes to low populations of small mammalian herbivores on reconstructed prairies. Thus, mounds do not have the same impact on reconstructed prairies as they have on native prairies, where they provide conditions of greater light availability and greater safety from herbivory than can be found off-mounds. Since mounds function differently in reconstructed and native prairies, we conclude that the effects of mound spatial and temporal patterns also



might be different in reconstructed and native prairies. In this reconstructed system, we found no evidence that disturbance patterns affect seedling recruitment and subsequent plant species diversity, but it seems likely that these same patterns should affect seedling recruitment in fully-functioning native prairies.

For reconstructed prairies to function more like native prairies, we suggest that  $C_4$  grass seeds should comprise a smaller proportion of the original seed mixes. In addition, more species of native forbs and native, rhizomatous  $C_3$  grasses or sedges should be included in the original seed planted on sites. These should fill in the space between the bunchgrasses, which would serve dual purposes: (1) the vegetation structure of reconstructed sites would more strongly reflect that seen on native prairies, and (2) it may be more difficult for weedy species to become established, thus eliminating the need to burn so frequently in the first years after planting. Both of these factors should help to reduce the dominance of  $C_4$  grasses on reconstructed prairie sites, which should allow the reconstructed prairies to function more like native prairies. Over time, we predict that spatial and temporal patterns of disturbance will then affect seedling establishment in these reconstructions, eventually leading to formation of the more complex vegetation structure typically found in native tallgrass prairies.

Although this study did not answer all the questions we asked, it was useful for providing insight as to the function of small-scale soil disturbances in natural and reconstructed tallgrass prairie. In addition, it provided insight regarding the crucial differences between how native prairies and reconstructed prairies function. In this way, the process of restoration has proven to be an "acid test" of our ecological knowledge (Bradshaw 1987), and has broadened our understanding of the role of small-scale disturbances in maintaining plant species diversity and community structure in native tallgrass prairie ecosystems.

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**Table 1.** Plant species used in the experiment. Values listed under the number of seeds planted are the mean number of seeds planted per site in 1998 and 1999, with 1 SD listed in parentheses.

Species	Family	Coefficient of conservatism <sup>a</sup>	Seed size (g) <sup>b</sup>	Number of seeds planted	
				1998 <sup>c</sup>	1999 <sup>d</sup>
<i>Amorpha canescens</i> Pursh	Fabaceae	8	0.002	42.8 (4.0)	52.0 (5.2)
<i>Coreopsis palmata</i> Nutt.	Asteraceae	6	0.003	54.6 (11.6)	43.3 (9.2)
<i>Dalea purpurea</i> Vent.	Fabaceae	9	0.002	39.8 (7.0)	48.3 (5.5)
<i>Echinacea pallida</i> (Nutt.) Nutt.	Asteraceae	7	0.006	61.8 (9.8)	51.7 (5.5)
<i>Heuchera richardsonii</i> R. Br.	Saxifragaceae	7	0.00004	50.9 (4.6)	54.6 (4.4)
<i>Liatris aspera</i> Michx.	Asteraceae	7	0.002	59.4 (7.2)	51.1 (8.8)
<i>Viola pedatifida</i> G. Don	Violaceae	10	0.001	50.8 (5.1)	52.5 (7.3)

<sup>a</sup> Coefficients were assigned for species in Illinois; see Ladd 1997.

<sup>b</sup> Values were estimated from commercial nursery seed catalogs.

<sup>c</sup> Seeds planted December 1998.

<sup>d</sup> Seeds planted December 1999-January 2000.

**Table 2.** Dates of events during the experiment.

Experiment year	Mounds constructed	Seed planted	Vegetation surveys
1998	9 July - 4 Sept. 1998	7 - 10 Dec. 1998	19 - 28 May 1999 7 - 11 June 1999 22 - 25 June 1999 8 - 14 July 1999 <sup>a</sup> 16 - 26 Aug. 1999 23 June - 3 July 2000 8 Aug. - 6 Sept. 2000 <sup>a</sup>
1999	15 July - 4 Aug. 1999	8 Dec. 1999 - 8 Jan. 2000	23 June - 3 July 2000 8 Aug. - 6 Sept. 2000 <sup>a</sup>

<sup>a</sup> Surveys for which vegetation survey results are reported.

**Table 3.** Results of mixed ANOVA examining the main spatial pattern treatment effect and split-plot mound treatment effect on experimental species, volunteer seedlings, and adult vegetation cover. Vegetation data were collected on 1998 sites in a survey conducted during the first year of plant growth, on 8-14 July 1999.

A. Experimental species							
Source of variation	df	Total seedling abundance		Species richness		Species diversity	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Block	2, 13	2.87	0.09	2.42	0.13	11.72	0.001
Spatial pattern	2, 13	0.67	0.53	0.27	0.77	0.19	0.83
Mound	1, 15	58.25	< 0.0001	35.32	< 0.0001	24.63	0.0002
Mound x Spatial	2, 15	0.02	0.98	0.44	0.65	0.66	0.53

B. Other species							
Source of variation	df	Volunteer seedling abundance		Volunteer seedling species richness		Adult veg % cover	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Block	2, 13	0.04	0.97	9.67	0.003	32.63	< 0.0001
Spatial	2, 13	0.11	0.90	0.94	0.41	0.97	0.40
Mound	1, 15	5.31	0.04	10.78	0.005	0.68	0.42
Mound x Spatial	2, 15	0.06	0.94	0.21	0.81	0.30	0.74

**Note:**  $\alpha$ -criterion =  $0.05 / 2 = 0.025$



**Table 4.** Results of mixed ANOVA examining the main spatial and temporal pattern treatment effects, and split-plot mound treatment effect, on experimental species, volunteer seedlings, and adult vegetation cover. Vegetation data were collected on 1998 sites during a survey conducted during the second year of plant growth, on 8 August-6 September 2000.

A. Experimental species							
Source of variation	df	Total seedling abundance		Species richness		Species diversity	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Block	2, 10	19.09	0.0004	8.41	0.007	4.01	0.05
Spatial pattern	2, 10	0.83	0.46	0.05	0.95	0.15	0.86
Temporal pattern	1, 10	0.01	0.91	2.10	0.18	3.17	0.11
Mound	1, 12	22.88	0.004	11.16	0.006	7.11	0.02
Mound x Spatial	2, 12	0.04	0.96	0.60	0.56	1.16	0.35
Mound x Temporal	1, 12	0.27	0.61	2.90	0.11	5.43	0.04

B. Other species							
Source of variation	df	Volunteer seedling abundance		Volunteer seedling species richness		Adult veg % cover	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Block	2, 10	5.94	0.02	3.84	0.06	35.32	< 0.0001
Spatial pattern	2, 10	0.33	0.72	1.04	0.39	2.01	0.18
Temporal pattern	1, 10	0.21	0.66	0.63	0.45	0.17	0.69
Mound	1, 12	0.65	0.44	0.26	0.62	0.32	0.58
Mound x Spatial	2, 12	0.32	0.73	4.79	0.03	0.05	0.96
Mound x Temporal	1, 12	0.06	0.82	0.26	0.62	1.58	0.23

**Note:**  $\alpha$ -criterion =  $0.05 / 2 = 0.025$

**Table 5.** Results of mixed ANOVA examining the main spatial and temporal pattern treatment effects, and split-plot mound treatment effect, on experimental species, volunteer seedlings, and adult vegetation cover. Vegetation data were collected on 1999 sites in a survey conducted during the first year of plant growth, on 8 August-6 September 2000.

A. Experimental species							
Source of variation	df	Total seedling abundance		Species richness		Species diversity	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Block	2, 10	11.14	0.003	10.20	0.004	8.67	0.007
Spatial pattern	2, 10	0.12	0.88	0.75	0.50	0.91	0.43
Temporal pattern	1, 10	0.20	0.67	0.25	0.63	1.10	0.32
Mound	1, 12	14.56	0.003	27.57	0.0002	40.43	< 0.0001
Mound x Spatial	2, 12	0.14	0.87	0.13	0.88	0.70	0.52
Mound x Temporal	1, 12	0.11	0.74	0.00	1.00	0.07	0.79

B. Other species							
Source of variation	df	Volunteer seedling abundance		Volunteer seedling species richness		Adult veg % cover	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Block	2, 10	11.61	0.003	0.53	0.61	43.29	< 0.0001
Spatial pattern	2, 10	1.47	0.28	0.05	0.95	1.08	0.38
Temporal pattern	1, 10	0.03	0.87	0.46	0.51	1.32	0.28
Mound	1, 12	5.48	0.04	11.27	0.006	0.01	0.94
Mound x Spatial	2, 12	4.15	0.04	7.62	0.007	0.59	0.57
Mound x Temporal	1, 12	0.10	0.75	0.19	0.67	2.91	0.11

**Table 6.** Results of mixed ANOVA examining the main spatial and temporal pattern treatment effects, and split-plot mound treatment effect, on the fraction of incident light penetrating the vegetation canopy.

Source of variation	df	<i>F</i>	<i>P</i>
Block	2, 10	5.32	0.03
Spatial pattern	2, 10	3.28	0.08
Temporal pattern	1, 10	0.77	0.40
Mound <sup>a</sup>	2, 24	0.93	0.41
Mound x Spatial	4, 24	2.89	0.04
Mound x Temporal	2, 24	0.20	0.82

<sup>a</sup> In this analysis, mound treatment included three groups, 1998 mounds, 1999 mounds, and no-mounds.

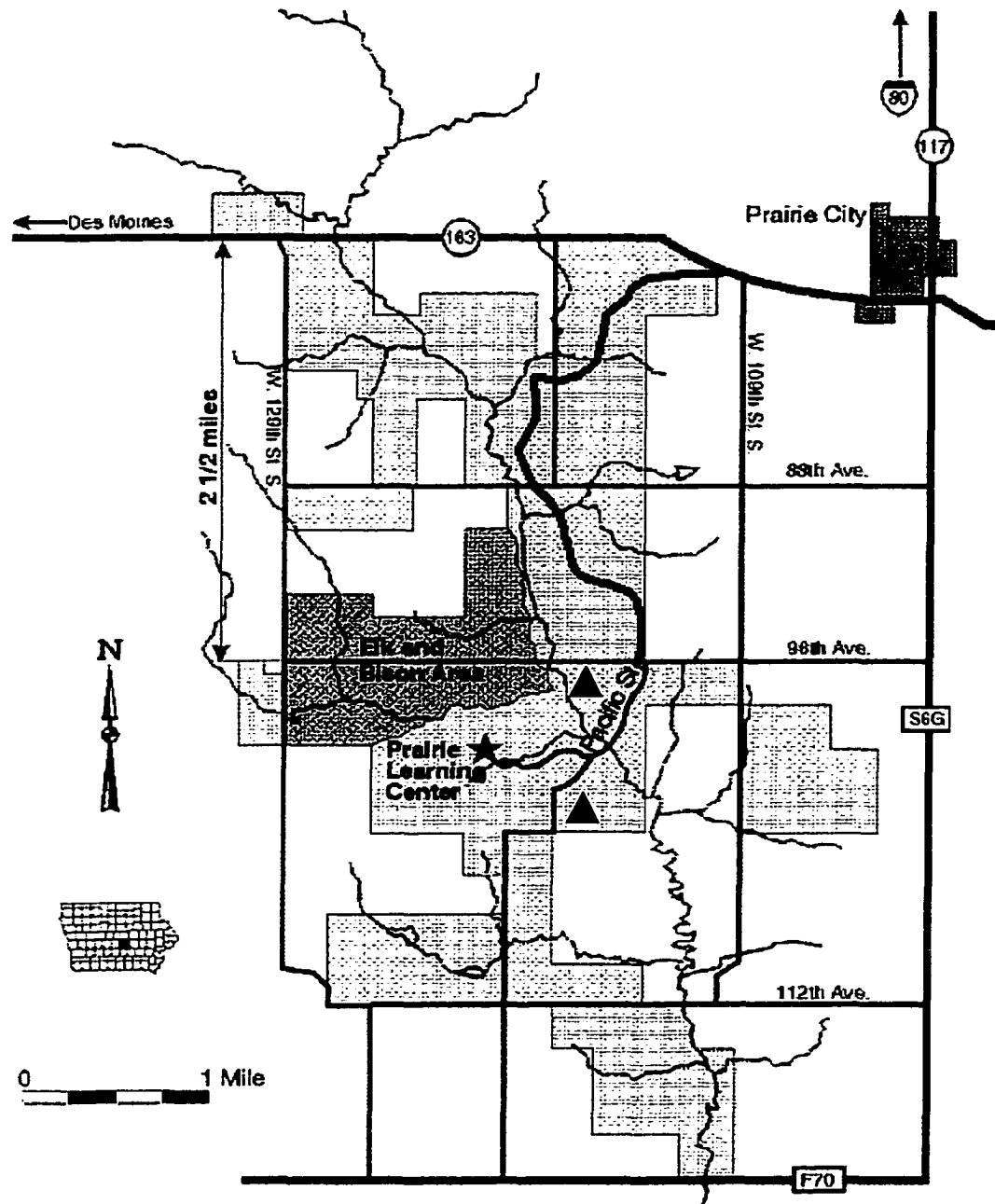
**Table 7.** Results of soil analyses from 1999 mounds and no-mound treatment soil samples.

Variable	1999 mound soil	No-mound topsoil	<i>t</i>	df	<i>P</i>
Total C (%)	7.78 (0.76)	2.17 (0.07)	7.39	8.13	< 0.0001
Total N (%)	0.51 (0.06)	0.18 (0.01)	5.56	8.07	0.0005
P (ppm)	41 (5)	24 (2)	3.11	9.73	0.01
K (ppm)	172 (37)	206 (5)	0.91	8.33	0.39
pH	7.6 (0.1)	6.8 (0.1)	8.03	12.40	< 0.0001
Particle size					
Sand (%)	21.9 (2.7)	2.8 (0.1)	7.14	8.03	< 0.0001
Silt (%)	62.0 (3.0)	69.1 (0.6)	2.35	6.57	0.05
Clay (%)	18.3 (1.5)	28.0 (0.6)	5.89	8.06	0.0004
Color					
Dry soil hue <sup>a</sup>	red-purple to purple	red			
Dry soil value <sup>b</sup>	3.96 (0.06)	4.44 (0.04)	6.69	13.10	< 0.0001
Moist soil hue <sup>a</sup>	red-purple to purple	red-purple			
Moist soil value <sup>b</sup>	2.84 (0.04)	3.26 (0.08)	4.41	12.30	0.0008

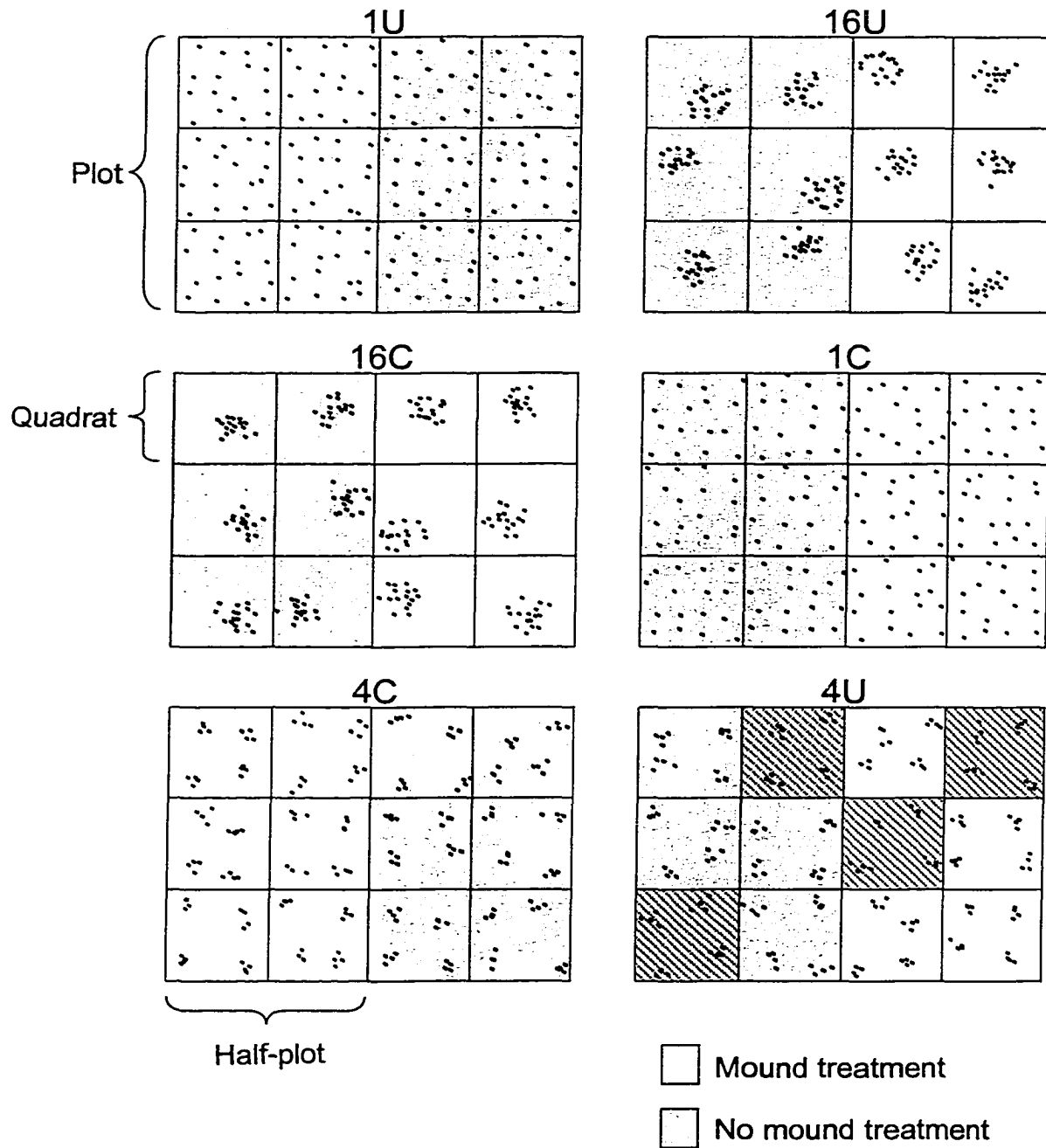
**Note:** Test results are from *t*-tests for unequal variances using the Satterthwaite correction.

<sup>a</sup> Hue refers to the dominant spectral color of the soil. Dry 1999 mound soil ranged from a hue of 1.3RP to 9.6P, while dry no-mound topsoil ranged from 2.1R to 10.0R. Moist 1999 mound soil ranged from 0.9RP to 9.0P, and moist no-mound topsoil ranged from 0.1RP to 9.5RP.

<sup>b</sup> Value is the darkness of the soil color, on a scale from 2 (dark) to 8 (light).



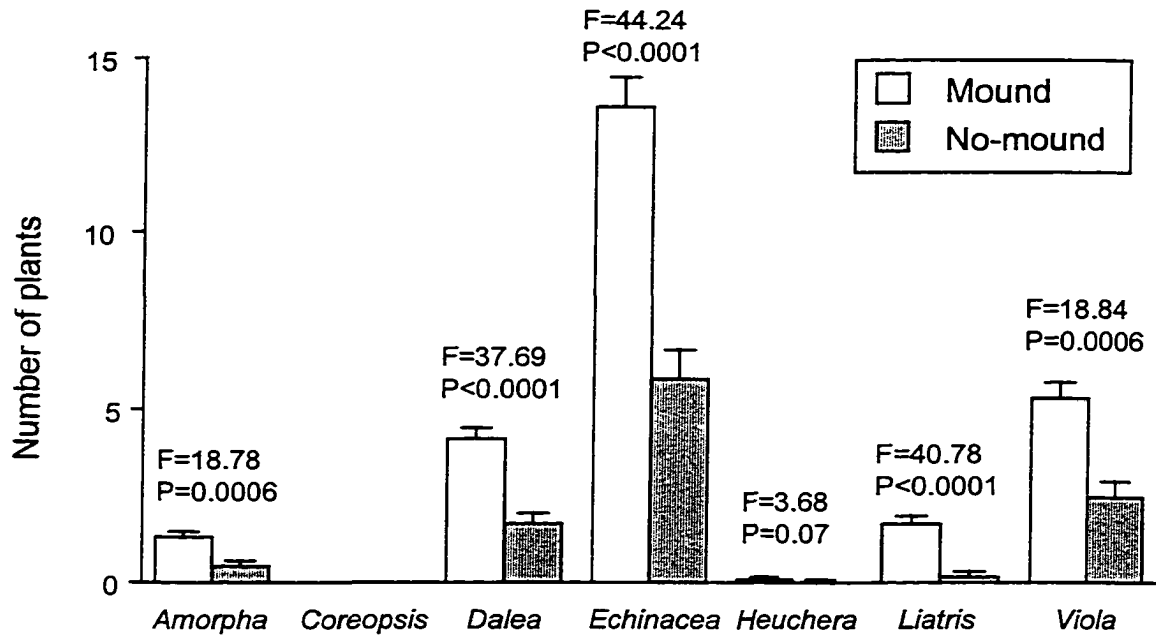
**Fig. 1.** General location and map of the Neal Smith National Wildlife Refuge (NSNWR). The extent of the NSNWR is shaded in light gray. The approximate locations of the study sites are labeled with black triangles. The low-diversity site (identified as site 17 in the NSNWR records) is the southern site, and the high-diversity site (identified as site 32 in the NSNWR records) is the northern site. Blocks A and B were located at the low-diversity site, and block C was at the high-diversity site.



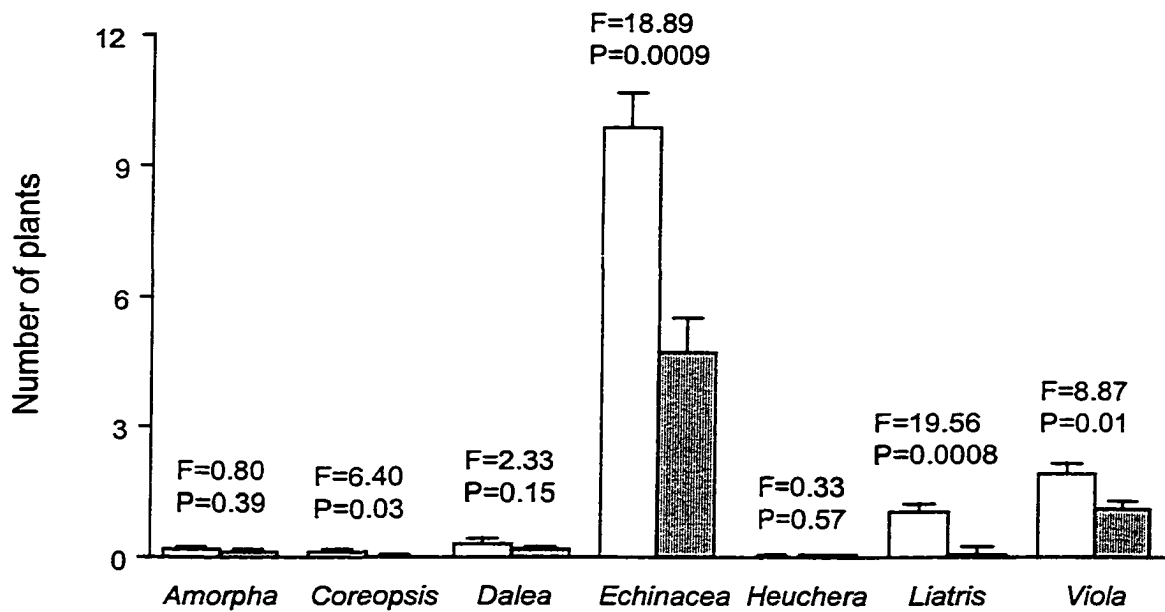
**Fig. 2.** Schematic diagram of block A, which is also representative of the general layout of blocks B and C. Gray points are locations of potential planting sites in 1998. In each half-plot, two quadrats received no seed treatment. For simplicity, these are indicated in plot 4U only (as hatched squares). See *Methods—Experimental design* for further description of block layout and treatments.

**Fig. 3.** Mean number of each experimental species found on 1998 sites surveyed during (A) the first year of plant growth, 8-14 July 1999, and (B) the second year of plant growth, 8 August-9 September 2000. Note that *Coreopsis* was not identified during the 1999 survey. Error bars are + 1 SE. The mound treatment results from a mixed ANOVA conducted separately for each species are listed.

### A) 1998 experiment: Survey 8-14 July 1999

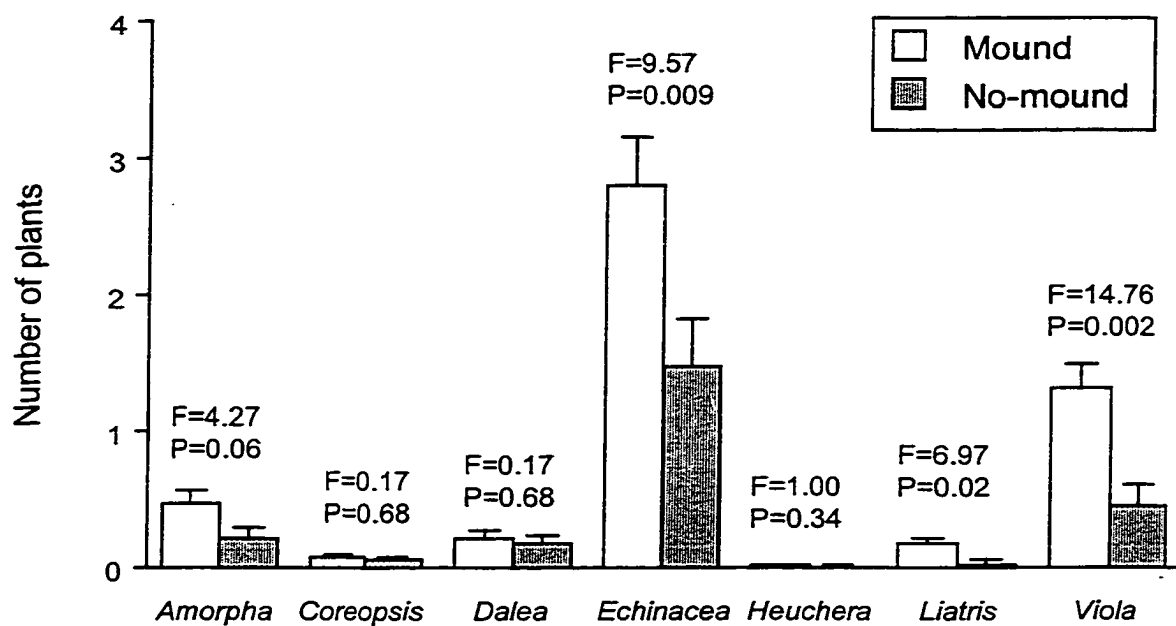


### B) 1998 experiment: Survey 8 Aug.-9 Sept. 2000



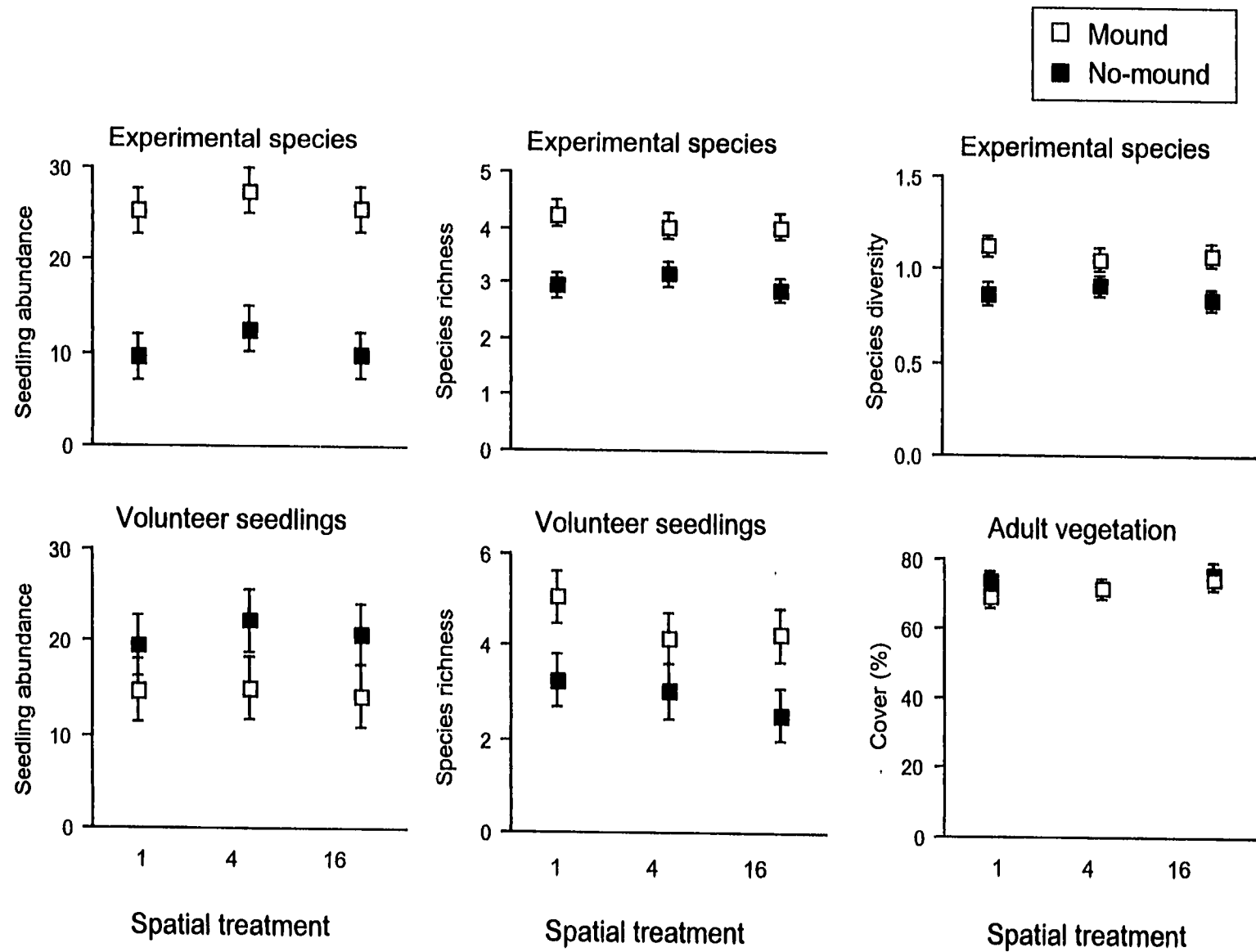


**1999 experiment: Survey 8 Aug. - 9 Sept. 2000**

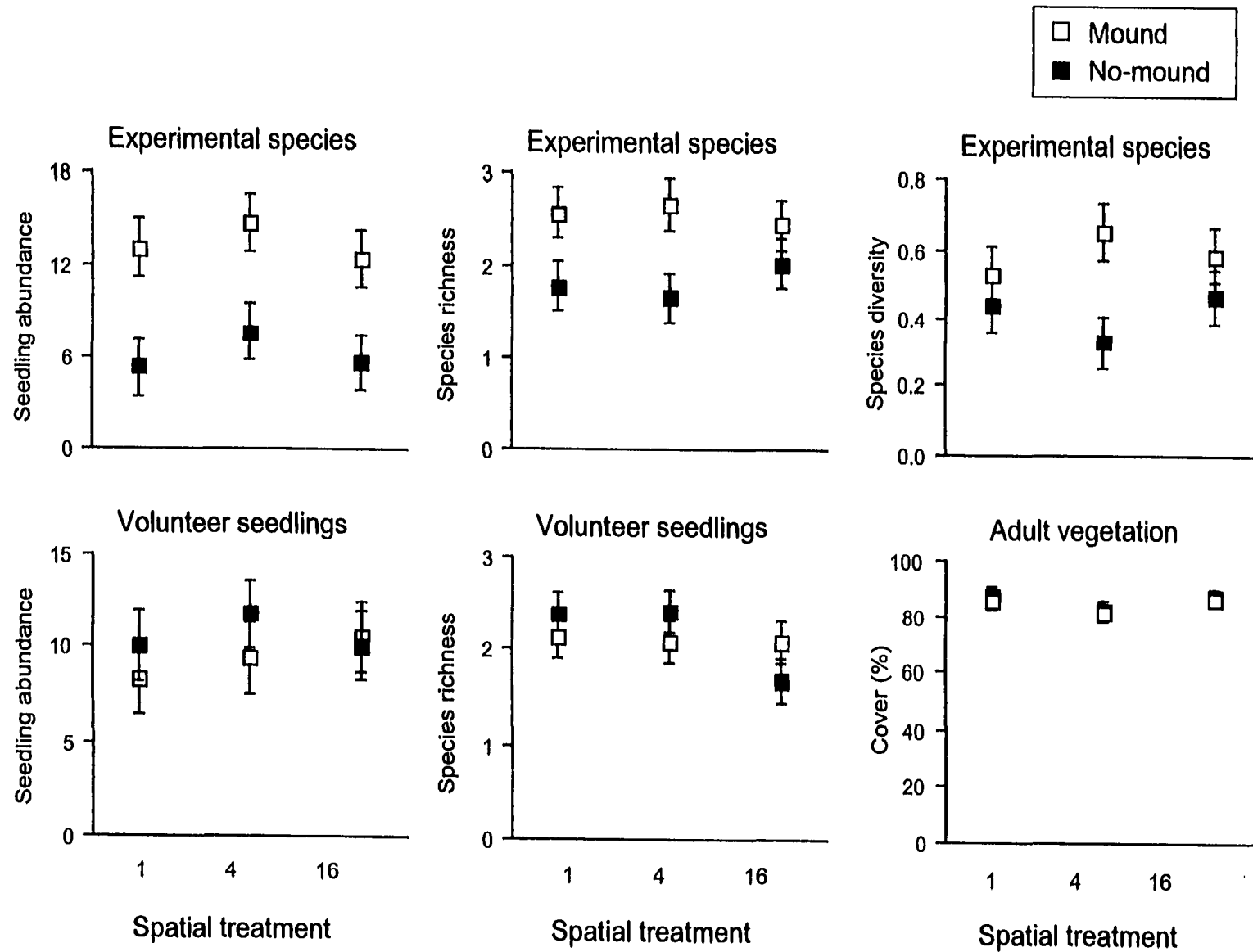


**Fig. 4.** Mean number of each experimental species found on 1999 sites surveyed during the first year of plant growth, 8 August-6 September 2000. Error bars are + 1 SE. The mound treatment results from a mixed ANOVA conducted separately for each species are listed.

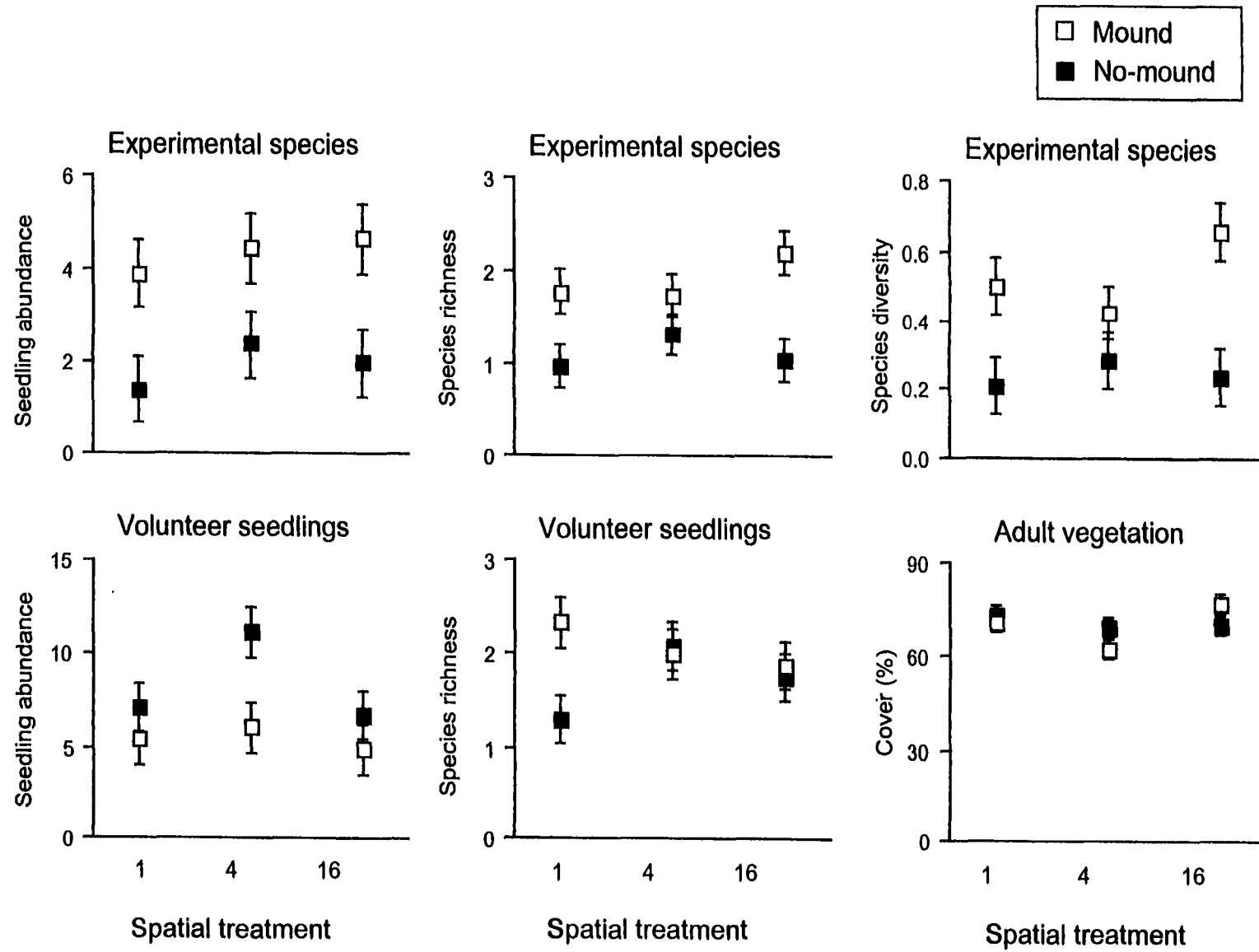
**Fig. 5.** Vegetation data collected on 1998 sites in a survey conducted during the first year of plant growth, 8-14 July 1999. The main spatial pattern treatment and split-plot mound treatment effects are shown. Values are means and error bars are  $\pm 1$  SE.



**Fig. 6.** Vegetation data collected on 1998 sites in a survey conducted during the second year of plant growth, 8 August-9 September 2000. The main spatial pattern treatment and split-plot mound treatment effects are shown. Values are means and error bars are  $\pm 1$  SE.

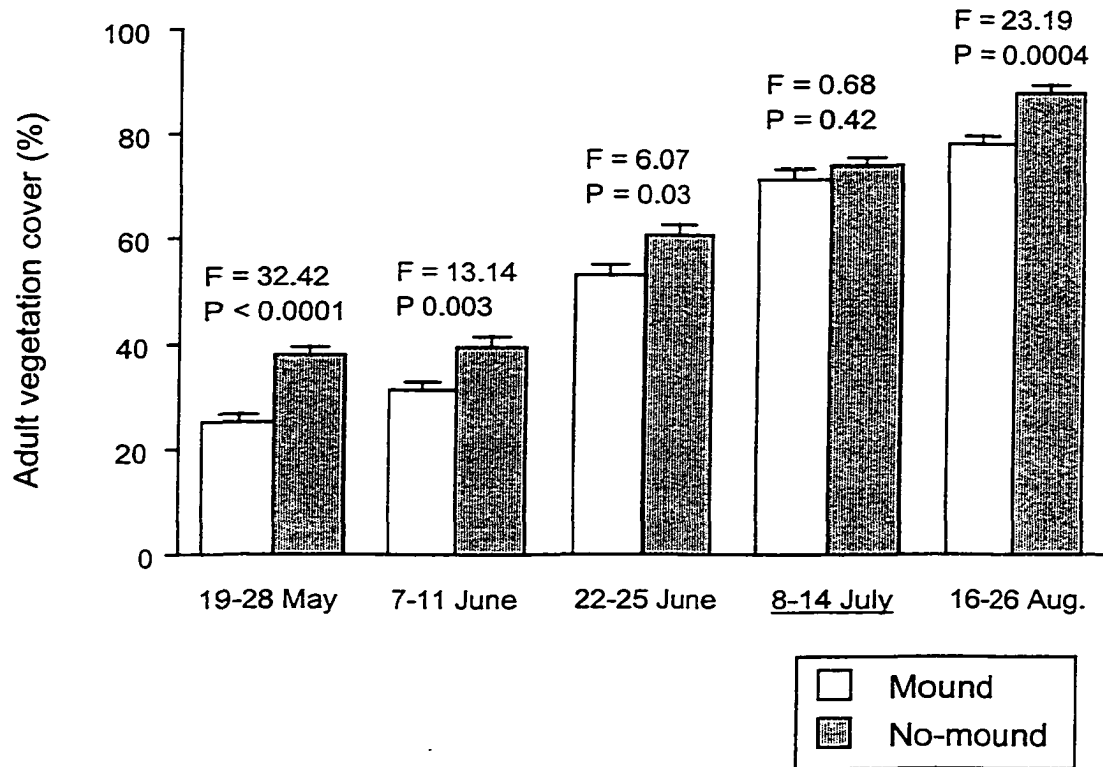
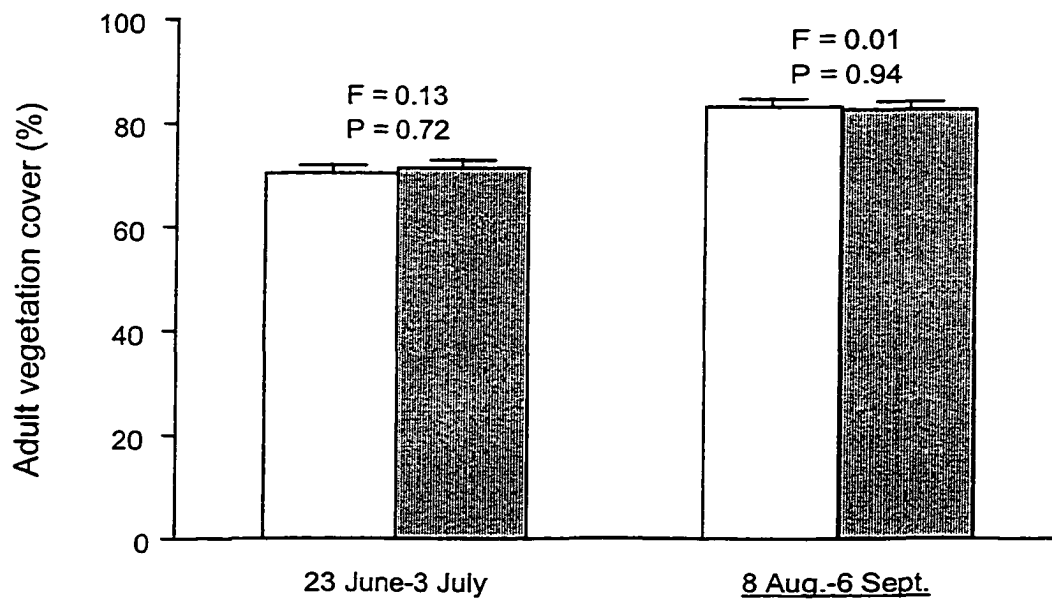


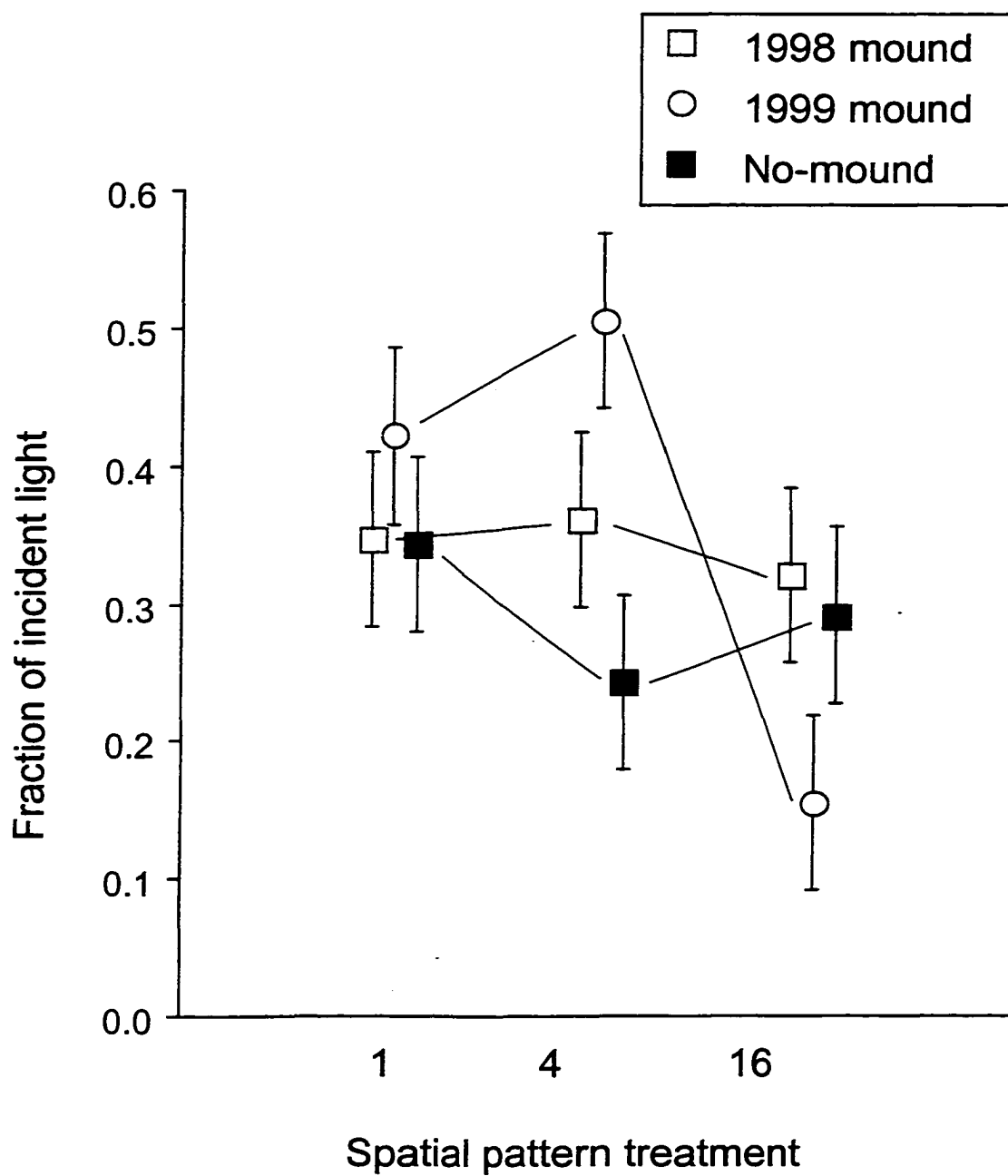
**Fig. 7.** Vegetation data collected on 1999 sites in a survey conducted during the first year of plant growth, 8 August-9 September 2000. The main spatial pattern treatment and split-plot mound treatment effects are shown. Values are means and error bars are  $\pm 1$  SE.



**Fig. 8.** Mean adult vegetation cover measured on the (A)1998 and (B)1999 sites in all surveys conducted during the first year of growth for each. Only the mound treatment effects are shown. Error bars are + 1 SE. The mound treatment results from a mixed ANOVA conducted separately for each survey are listed. Surveys used for analyses of other vegetation variables are underlined.



**A) 1998 experiment: 1999 surveys****B) 1999 experiment: 2000 surveys**



**Fig. 9.** Fraction of incident light penetrating the vegetation canopy. The main spatial pattern treatments and split-plot mound treatments are shown. Mound treatments included 1998 mounds, 1999 mounds, and no-mound sites. Values are means and error bars are  $\pm 1$  SE.

## **CHAPTER 5. INTERACTIVE EFFECTS OF MAMMALIAN HERBIVORY AND SMALL-SCALE SOIL DISTURBANCES ON SEEDLING RECRUITMENT IN RECONSTRUCTED PRAIRIE**

A paper to be submitted to *Oecologia*

Kelly S. Wolfe-Bellin and Kirk A. Moloney

### **Abstract**

Small-scale soil disturbances, such as gopher mounds, provide sites where seedling recruitment occurs in grasslands. One way in which small-scale disturbances may function as sites for seedling recruitment is by protecting seedlings from herbivory. In this study, we investigated whether protection from herbivory contributes to the successful recruitment of seedlings on small-scale disturbances, and whether this herbivory protection might additionally be affected by spatial autocorrelation in the disturbance production regime. We conducted a landscape-level experiment on reconstructed prairie to address these questions. We sowed the seed of seven forb species in planting sites to which the following three types of treatments were applied: (1) sites were arranged in two spatial patterns, representing extremes in spatial autocorrelation, (2) small-scale soil disturbances designed to mimic gopher mounds were constructed at half the sites, with the other sites left as no-mound controls, and (3) exclosures protecting seedlings from mammals of different size classes were constructed around the sites. After one growing season, we measured seedling recruitment of the seven forb species. In addition, we conducted a census of the small mammal populations at the study site. We found some evidence that selective foraging by small mammals reduced diversity of recruited seedlings, but seedling abundance was not affected by herbivory. In addition, herbivory pressure was only weakly affected by the mound treatments and was unaffected by the spatial pattern treatments. We found these results surprising, but attribute them to the low populations of small mammalian herbivores and to the unique vegetation structure at our reconstructed

prairie sites, both of which may have prevented the soil disturbances from functioning as they would in native prairies. Thus, we conclude that small-scale soil disturbances did not provide seedlings with much protection from mammalian herbivory, nor did the spatial autocorrelation of the disturbance production regime interact with mammalian herbivory to influence seedling recruitment, on this *reconstructed prairie*. However, we caution against inferring from these results that mounds do not function as seedling safe sites in *native prairies*. Instead, we suggest that this type of experiment be repeated at a site where the vegetation structure is more typical of native prairie ecosystems.

### Introduction

Small-scale soil disturbances, such as pocket gopher mounds, serve as sites where seedling recruitment into grasslands can occur (*e.g.*, Gross and Werner 1982, Belsky 1986, Goldberg 1987, Goldberg and Gross 1988, Martinsen et al. 1990, Reader and Buck 1991, Wolfe-Bellin and Moloney 2000). These disturbances may directly provide habitat for seedling recruitment in three ways: (1) more light is available on mounds than in intermound areas (Grant et al. 1980, Grant and McBrayer 1981, Umbanhowar 1992, Reichman et al. 1993), thereby reducing aboveground plant competition on mounds; (2) roots of neighboring vegetation are absent from mound soil (Grant and McBrayer 1981), thereby reducing belowground plant competition; and (3) openings in the adult vegetation canopy are created by mounds, providing sites that may be avoided by small mammalian herbivores.

It is well established that mammalian herbivory can have an important impact on seedling abundance, diversity, and biomass in grasslands (Hulme 1994, 1996a, 1996b, Edwards and Crawley 1999, Howe and Brown 1999), and that herbivory may influence plant survivorship as strongly as competition under different grassland canopy conditions (Reader 1992). However, the effect of mammalian herbivory on survivorship of seedlings growing on small-scale soil disturbances has not been well studied. Voles, important mammalian seedling

herbivores in grasslands, are subject to avian predation and prefer habitats with substantial ground cover (Reich 1981). Thus, it seems likely that they should avoid small-scale soil disturbances where they may be at risk of predation. However, field studies investigating the behavioral response of voles to gopher mounds report confounding results. In one study on an Iowa prairie remnant, meadow vole abundance was negatively related to mound production (Klaas et al. 1998). However, in another study on a Minnesota tallgrass prairie, meadow vole abundance was positively related to mound production, and meadow voles were reported to preferentially travel across bare mounds (Whittaker et al. 1991). Field studies specifically examining herbivory pressure under different soil disturbance conditions have also found confounding results. Klaas et al. (1998) found some evidence to suggest that meadow vole herbivory of forb seedlings was lower on gopher mounds than in intermound areas. However, another study found that herbivory of forb seedlings by California voles was greater on mounds than in intermound areas (Rice 1987). Thus, the relationship between small mammalian herbivores and small-scale soil disturbances is unclear and warrants further research.

The production of pocket gopher mounds in grasslands has been linked to increases in the abundance of annual plant species (Laycock and Richardson 1975, Schaal and Leverich 1982, Inouye et al. 1987) and to increases in overall plant species diversity (Tilman 1983, Inouye et al. 1987, Huntly and Reichman 1994). These community-level effects are largely attributed to seedling recruitment on mounds (*e.g.*, Martinsen et al. 1990, Reader and Buck 1991). Gopher mounds can cover as much as 20% of a grassland area (Grant et al. 1980, Reichman et al. 1982, Spencer et al. 1985), but the production of mounds occurs in distinctive patterns, due to the territorial behavior of gophers (Reichman et al. 1982). In fact, one study in an Iowa tallgrass prairie found that mound production was spatially autocorrelated at scales of less than 20 m and that locations of mound clusters remained relatively static over years (Klaas et al. 2000). The autocorrelated nature of the mound production regime may be an important

consideration in understanding how mounds provide seedlings with sites safe from herbivores. For example, small mammalian herbivores may occasionally forage for seedlings on single mounds, but they may completely avoid areas where mound production is extremely clustered. This could contribute to differences in seedling recruitment on mounds produced in different spatial patterns. In this study, we investigated whether protection from herbivory contributes to the recruitment of seedlings on small-scale soil disturbances and how this protection is affected by the spatial autocorrelation with which small-scale disturbances are produced.

Specifically, the study addressed how selective foraging by mammalian herbivores regulates seedling recruitment into prairies, and how the herbivory effect is modified by the presence of small-scale soil disturbances and the spatial architecture in which the disturbances are produced. The study was conducted in reconstructed prairie, as part of an established experiment investigating how spatial and temporal architecture in the production of small-scale soil disturbances influences seedling recruitment (see chapter 4). The study reported here consisted of three parts. The first part was a preliminary study to ascertain whether mammalian herbivory significantly affected seedling survivorship at the study site. The second part was an experiment in which seed planting sites were protected from herbivory by mammals of various sizes. The planting sites were located on and off small-scale soil disturbances and were arranged in two different spatial patterns. One pattern exhibited spatial autocorrelation typical in the natural production of gopher mounds, and the other pattern exhibited no spatial autocorrelation. The third part of the study consisted of censuses of small mammal populations at the study sites.

## **Methods**

### **Study site**

The study was conducted at the Neal Smith National Wildlife Refuge (NSNWR), a 3500-ha refuge of reconstructed tallgrass prairie located in south-central Iowa near Prairie City

(41° 36' N, 93° 25' W). The refuge was created in 1991 when the United States Fish and Wildlife Service purchased a large tract of land that was being used primarily for rowcrop agriculture (Drobney 1994). The land originally was covered primarily with tallgrass prairie before conversion to agriculture in the late 1800s, and the primary goal at the NSNWR is to restore tallgrass prairie vegetation across most of the refuge (Drobney 1994). To achieve this goal, sub-sections of the refuge have been planted with native tallgrass prairie seed each year since 1992. At the time of the study, planted sites were managed with annual, controlled fires set in early April. In addition, seeds of the dominant grass species were harvested with combines during October of each year. Mammalian herbivores at the NSNWR included meadow voles (*Microtus pennsylvanicus*), Eastern cottontail rabbits (*Sylvilagus floridanus*), and white-tailed deer (*Odocoileus virginianus*).

### Study species

We used seven forb species representing a range of seedling palatabilities to meadow voles, common seedling herbivores in grasslands. The species included *Amorpha canescens* Pursh, *Coreopsis palmata* Nutt., *Dalea purpurea* Vent., *Echinacea pallida* (Nutt.) Nutt., *Heuchera richardsonii* R. Br., *Liatris aspera* Michx., and *Viola pedatifida* G. Don (hereafter species will be labeled by genus). *Coreopsis*, *Dalea*, *Echinacea*, and *Liatris* seedlings are relatively palatable, while *Amorpha*, *Heuchera*, and *Viola* seedlings are relatively unpalatable to meadow voles (Table 1; relative palatabilities were determined in laboratory trials by Nickel et al. in prep). By using plant species with a range of seedling palatabilities, we hoped to determine whether herbivory affects seedling recruitment of all species or only species with palatable seedlings.

All seven species are endemic to tallgrass prairies and are naturally found in mesic to dry-mesic prairies, the types of prairie being reconstructed at the NSNWR study sites. The species are perennials from four plant families, representing a range of seed sizes,

aboveground growth patterns and rooting strategies (see chapter 4 for a more complete description of each species). All the species are commonly found on native prairies, but were not abundant in the NSNWR prairie reconstructions at the time of the study, which provided some motivation for our attempt to get them established.

### Experimental design

The study was conducted at two sites within the NSNWR (Fig. 1). One site, hereafter labeled the low-diversity site, was located on a hilltop that had been planted with prairie seed in 1993. The site exhibited very low plant species diversity, with fewer than 10 plant species growing in abundance across the site. Two grass species, *Schizachyrium scoparium* (Michx.) Nash (little bluestem) and *Andropogon gerardii* Vitman (big bluestem), dominated vegetation at the site. The second site, labeled the high-diversity site, was located on a hillside that had been planted with prairie seed in 1995. Vegetation on the site was more diverse on than the first site, with approximately 20 plant species growing abundantly. The vegetation was also taller and more dense than on the first site. The high-diversity site was dominated by two grasses, *Sorghastrum nutans* (L.) Nash (indian grass) and *A. gerardii*, and the forb *Chamaecrista fasciculata* (Michx.) Greene (partridge pea). The low diversity site was located at planting site 17, as designated in the NSNWR records, and the high diversity site was located at planting site 32 (Fig. 1).

Three permanent blocks were established in June 1998 at the NSNWR. Two blocks, labeled A and B, were located on the low-diversity site. One block, labeled C, was located on the high-diversity site. Each block was 52-m x 62-m in size and consisted of six 24-m x 18-m plots arranged in a 2 x 3 array with 4 m buffers between plots (Fig. 2). Three planting pattern treatments were applied within a block, with two plots per block receiving each treatment. The pattern treatments consisted of three spatial patterns of potential planting site locations. Each potential planting site was approximately a 0.20 m<sup>2</sup> circular area (the approximate size of a



natural gopher mound). The spatial patterns included arrangements of the potential planting sites as singles, clusters of four, and clusters of 16 (Fig. 2). The x-y coordinates of each individual potential planting site were assigned with a computer algorithm, and sites were each labeled in the field with a wire pin flag.

The spatial patterns were designed to test whether the degree of clustering seen in the natural production of gopher mounds has an influence on seedling herbivory and recruitment. The spatial patterns included one treatment where planting sites were hyperdispersed across the landscape with no spatial autocorrelation between sites (singles), and two treatments where sites were spatially autocorrelated at two different levels (clusters of 4 and 16). The most spatially autocorrelated arrangement of sites (clusters of 16) was based on the degree of spatial autocorrelation found in the production of gopher mounds in native prairies (Klaas et al. 2000). We used the range in spatial autocorrelation patterns as a control to test whether the degree of clustering in mound production is reflected in seedling herbivory and recruitment.

Each plot was further split in half, and one of two mound treatments was assigned at random to each half-plot (Fig. 2). In one half-plot, we constructed a soil disturbance at each potential planting site. The soil disturbances were designed to mimic natural gopher mounds, and hereafter will be referred to as “mounds”. Mounds were constructed by pouring 10 L of topsoil onto the field surface, which produced a circular mound of soil approximately 0.5 m in diameter (0.20 m<sup>2</sup> in area). Soil disturbances were centered around pin flags marking the potential planting sites. Topsoil was purchased from a commercial nursery in central Iowa. This treatment was labeled the mound treatment. In the second half of each plot, we did not construct soil disturbances at the potential planting sites. This treatment was labeled the no-mound treatment.

Each half-plot was further divided into six 6-m x 6-m quadrats arranged in a 2 x 3 array with no buffers between quadrats (Fig. 2). Sixteen potential planting sites were located in each quadrat. The arrangement of sites within a quadrat was determined by the spatial pattern

treatment assigned to the plot within which a quadrat was located (Fig. 2). While the clustering of the planting sites varied between plots, the density of the sites remained constant at 0.44 sites/m<sup>2</sup>. In the quadrats to which the mound treatment was applied, approximately 9% of the ground surface was covered by mounds per year, which reflected a fairly typical rate of natural gopher mound production in native prairie (Klaas et al. 2000; chapter 3).

Within each half-plot, four quadrats chosen at random received a seed treatment, and the remaining two quadrats were left as unseeded controls (Fig. 2). In the seed treatment, seeds of the seven study species were planted on each of the 16 potential planting sites per quadrat. Before planting, approximately 50 seeds of each species were measured by volume and poured into envelopes. Species were measured separately, and then mixed together in the envelopes. For planting, one envelope containing all seven species was poured onto the center of each planting site. Seeds were then gently scattered by hand in a circular area within a 15-cm radius of each planting site pin flag, and worked into the soil with a hand trowel. Seeds used in the plantings were fresh, having been harvested from local native prairies in months immediately preceding our planting dates. Seeds were purchased from commercial native prairie nurseries in central and southern Iowa.

We conducted seed plantings in two years, which hereafter will be identified as the 1998 and 1999 experimental years. The locations of potential planting sites were marked with wire pin flags in June 1998 and June 1999. Mounds were constructed during July and August 1998, and July 1999. Seeds were planted in December 1998 on 1998 planting sites, and seeds were planted in December 1999-January 2000 on 1999 planting sites. Thus, each planting site was seeded only once, unless locations in the 1999 experimental year happened to overlap with locations from the 1998 experimental year. By the end of the experiment, each quadrat contained one set of 16 planting sites from 1998 and one set from 1999.

### **Preliminary seedling herbivory study**

During 1999, we conducted a preliminary pilot study to test whether herbivory was a factor in regulating seedling recruitment within our experimental design. We planted seedlings of *Baptisia australis* (L.) R. Br. (Fabaceae, blue false indigo) on and off mounds in each of the pattern treatment plots. *Baptisia* was used because it is relatively palatable to meadow voles (Nickel et al. in prep) and its seedlings are large enough for easy identification of herbivory. In addition, it is native to tallgrass prairies, but did not grow naturally at the study sites.

*Baptisia* seedlings were planted in the following three planting treatments within each plot: (1) directly on a fresh 1999 mound (hereafter labeled "on-mound"); (2) in an off-mound site located approximately 1 m from the mound site (labeled "near-mound"), and (3) in an off-mound site located in a no-mound treatment quadrat, and at least 6 m from the mound site (labeled "far-mound"). Mound and no-mound quadrats were chosen at random from the four quadrats per half-plot to which seed treatments were assigned, with the stipulation that the mound and no-mound quadrats could not be immediately adjacent to one another. Mound and no-mound planting sites were chosen at random from the sixteen 1999 sites per quadrat. Each planting site (considered an experimental unit) contained a 3 x 3 array of *Baptisia* seedlings planted within an area of approximately 10-cm x 10-cm. Seedlings were germinated in peat pellets in the greenhouse and were planted in the field by placing the peat pellets approximately 2 cm into the ground. Seedlings were planted 25 August 1999, when they were approximately nine days old and displayed at least one true leaf. On 9 September 1999, 15 days after planting, we recorded the number of seedlings at each planting site exhibiting signs of mammalian herbivory. Seedlings that were missing entirely, or for which only a clipped stem remained, were considered eaten by mammals. After recording herbivory, we removed all surviving seedlings from the study sites.

We calculated the proportion of seedlings at each planting site that had been eaten. Because of the small number of seedlings per planting site, zeroes in the data were given the

value of  $1/4 \cdot n$ , and ones (100% herbivory) were given the value of  $(n - 1/4) \cdot n$  (where  $n = 9$ , the number of seedlings per planting site), as recommended by Snedecor and Cochran (1980). Values were arcsin square-root transformed to normalize the data (Snedecor and Cochran 1980). Statistical tests for treatment effects were conducted using transformed values, and values reported here were back-transformed. Data were analyzed with a mixed, split-plot ANOVA conducted in SAS version 8.1 (SAS 2000). We predicted that seedlings in the far-mound sites would experience the most herbivory and seedlings in the on-mound sites would experience the least.

### **Herbivory effects on experimental species**

The preliminary *Baptisia* herbivory study indicated that mammalian herbivory was an important source of seedling mortality (see *Results—Preliminary seedling herbivory study*). Thus, we investigated the importance of herbivory in regulating seedling recruitment of the seven original species in our study (See *Methods—Study species*). In addition, the direction of the mound treatment effect on *Baptisia* was the opposite of that predicted (see *Results—Preliminary seedling herbivory study*), prompting us to investigate whether mammalian herbivores of different sizes respond to the presence of small-scale soil disturbances differently.

To quantify how mammalian herbivory affected seedling recruitment of the experimental species, we constructed exclosures around a sub-set of the 1999 planting sites. Exclosures were constructed in three quadrats within each half-plot of all plots to which the singles or clusters of 16 spatial pattern treatments had been applied. The three quadrats in each half-plot were chosen at random from the four quadrats that received seed treatments. Thus, we investigated the role of herbivory in regulating seedling recruitment in the following treatments: two of the three spatial pattern treatments (singles and clusters of 16), and the mound and no-mound treatments.

Three types of exclosures were constructed per quadrat. The exclosures were designed to exclude mammals of different size classes. Exclosures were all constructed of 1.3-cm mesh galvanized steel hardware cloth and were 30 cm in height x 40 cm in diameter. The three types of exclosures differed as follows: (1) complete exclosures were designed to exclude all mammals; (2) exclosures with five 5-cm x 7.5-cm openings, spaced at even intervals around the base, were designed to allow access by rodents, but to exclude rabbits and larger mammals; and (3) exclosures with three 16-cm x 18-cm openings at the base were designed to allow access by rodents and rabbits, but to exclude larger herbivores. The exclosure treatments were labeled as follows: complete exclosures (CE), small-door exclosures (SDE), and large-door exclosures (LDE).

Exclosures were placed over the 1999 planting sites during the period 14-22 May 2000. Seeds had been planted on these sites 8 December 1999 - 8 January 2000. In the mound treatments, mounds had been constructed during the interval 15 July - 4 August 1999. Within quadrats in the single spatial pattern treatments, the first planting site to receive an exclosure was chosen at random from the 16 total 1999 sites. Then the two planting sites closest to the first were used for the second and third exclosures. In the clusters of 16 spatial pattern treatments, we chose three planting sites at random of the 16 total per quadrat, with the stipulation that the sites be spaced far enough apart to prevent the exclosures from abutting. In this way, the physical clustering of the exclosures was held approximately constant between the spatial pattern treatments. Within quadrats, the three types of exclosures were assigned at random to the three selected planting sites. Exclosures were centered around the pin flag marking the center of each planting site. Exclosures were anchored to the ground with U-shaped wire pins looped around the base and sunk into the ground approximately 8 cm.

The vegetation growing in the exclosure treatments was surveyed 6-12 September 2000. During the surveys, we centered a circular sample frame, 30 cm in diameter, around the pin flag marking the center of each planting site. In each sample frame, we identified and

counted the seedlings of the seven planted species (hereafter labeled the “experimental species”).

We also collected aboveground biomass of the experimental species seedlings that survived to the end of the experiment, since an earlier study of rodent herbivory in reconstructed prairie found that herbivory had a stronger effect on forb biomass than on plant abundance (Howe and Brown 1999). Plants were collected 12-14 September 2000. Seedlings within each planting site were separated by species and dried to constant weight at 70°C for 21 days. For each planting site, we calculated the total biomass, and the average biomass per plant, for each species.

To analyze the seedling abundance and biomass data, we first calculated summary values for each half-plot. We calculated the total abundance, species richness, and species diversity (using the Shannon-Weiner  $H'$  diversity index, Peet 1974) for seedlings of the experimental species in each half-plot. We also calculated the total seedling abundance for the palatable and unpalatable experimental species as groups and for each individual experimental species. With the biomass data, we calculated the total biomass, and average biomass per plant (regardless of species identification), per half-plot. We also calculated the total biomass, and average biomass per plant, for each of the individual experimental species. The vegetation survey and biomass data were all analyzed with a mixed, split-plot ANOVA conducted in SAS version 8.1 (SAS 2000). In the ANOVA, the spatial pattern treatments were considered a main plot treatment, while the mound treatments were a split-plot treatment, and the exclosure treatments were a further split-plot treatment. Data from the vegetation surveys were all balanced. The biomass data were unbalanced, however, due to exclosure treatments within some half-plots that contained no experimental seedlings surviving to the end of the experiment.

In the analyses, we first tested for the effects of planting site spatial pattern. Evidence from previous studies of seedling recruitment at the study sites (chapter 4) indicated that the

spatial pattern treatments had little effect on seedling recruitment, so we were most interested in testing for a significant spatial pattern x enclosure interaction, or a significant spatial pattern x mound x enclosure interaction. These interactions would indicate that herbivores exhibit contrasting responses to different small-scale disturbance patterns and that this behavioral response is reflected in seedling recruitment. Second, we tested for the effects of the mound treatments. Previously, we had found that seedling recruitment was higher on mounds than off mounds (chapter 4), and we expected to find that same result again. In this experiment, we were largely interested in mound x enclosure interactions, which would indicate that protection from herbivory is an important factor causing greater seedling recruitment on mounds than off mounds. Specifically, we predicted that seedling recruitment would be similar in mound sites under all enclosure treatments and that seedling recruitment in no-mound sites would increase as enclosures provided protection from more types of animals. Third, we tested for the effects of the enclosure treatments on seedling recruitment. With the doors of different sizes, we hoped to identify which herbivore size class most strongly influenced seedling recruitment at the site. In addition, as already mentioned, any significant interactions with the other treatments might indicate that herbivores in different size classes exhibited different responses to mound sites as compared to no-mound sites, or to the spatial patterns in which mounds were produced.

### **Small mammal censuses**

To estimate small mammal populations at the study sites, we live-trapped rodents for five consecutive days on 16-20 August 1999 and 14-18 August 2000. We placed Sherman live traps in two quadrats of each half-plot. The two quadrats were chosen at random from the four seed-treatment quadrats per half-plot, with the stipulation that the quadrats could not be immediately adjacent to one another. Two Sherman live traps were placed in the center of each quadrat. Traps were opened each evening at ca. 1700 h and baited with a small handful of dry

oats. We checked traps the next morning beginning at ca. 700 h. Captured animals were identified, weighed, sexed, ear-tagged, and released. For each quadrat, we tallied the number of captures per species.

To analyze the data, we calculated the total captures of each species per half-plot per year. We also calculated the total number of small mammals captured per half-plot per year. We analyzed the data with a mixed, split-plot ANOVA in SAS version 8.1 (SAS 2000) to determine whether small mammal captures differed by year and were affected by the spatial pattern and mound treatments.

## Results

### Preliminary seedling herbivory study

Mammalian herbivory killed 36% of the *Baptisia* seedlings, and 74% of the planting sites contained at least one eaten seedling. The proportion of seedlings eaten per planting site differed significantly among planting site locations (Table 2). The greatest proportion of seedlings was eaten in the on-mound sites ( $57.41 \pm 7.95\%$ ; Mean  $\pm$  1 SE), an intermediate proportion was eaten in the near-mound sites ( $32.10 \pm 7.95\%$ ), and the smallest proportion was eaten in the far-mound sites ( $19.75 \pm 7.95\%$ ). We found no evidence of a spatial pattern treatment effect on the proportion of seedlings eaten by mammals (Table 2).

### Herbivory effects on experimental species

In the surveys of experimental seedlings, we found no evidence of a spatial pattern treatment effect on total seedling abundance, species richness, or species diversity (Table 3), but each was greater in the mound treatment than the no-mound treatment (Table 3, Fig. 3). For the enclosure treatments, there was no evidence of an enclosure treatment effect on the abundance of experimental species seedlings, but there was an enclosure treatment effect on experimental species richness and diversity (Table 3). Species richness and diversity were



greatest in the complete-exclosure treatment and lower in both the small- and large-door exclosure treatments (Fig. 3). There was no statistical evidence of an interaction between the mound and exclosure treatments for any of the experimental species variables (Table 3), but an interaction was suggested by the trends in species richness and diversity (Fig. 3). The changes in both richness and diversity between the complete exclosures and small-door exclosures were greater in the no-mound treatment than in the mound treatment (Fig. 3).

When we examined the seedling abundance of the palatable and unpalatable experimental species as groups, we again found no evidence of a spatial pattern treatment effect (Table 4). However, seedling abundance of both groups was greater in the mound treatment than no-mound treatment (Table 4, Fig. 4). For the palatable species in the mound treatment, there was a trend that seedling abundance remained relatively constant across the exclosure treatments (Fig. 4). In contrast, in the no-mound treatment, palatable species seedling abundance decreased as exclosure door size increased (Fig. 4). However, there was no statistical evidence of an exclosure treatment effect or of an exclosure x mound treatment interaction for the palatable species (Table 4). For the unpalatable species, there was statistical evidence of both an exclosure treatment effect and an exclosure x mound treatment interaction (Table 4). Unpalatable species seedling abundance in the mound treatment decreased as exclosure door size increased and remained relatively constant across the exclosure treatments in the no-mound treatment (Fig. 4).

When we examined the seedling abundance for each of the individual experimental species, we found that *Echinacea* was the most abundant species in all mound and exclosure treatments (with  $1.78 \pm 0.31$  seedlings per half-plot), followed in order by *Viola* ( $0.63 \pm 0.13$ ), *Amorpha* ( $0.47 \pm 0.13$ ), *Liatris* ( $0.14 \pm 0.05$ ), *Dalea* ( $0.07 \pm 0.04$ ), and *Coreopsis* ( $0.07 \pm 0.04$ ; Fig. 5). *Heuchera* was never found in any of the exclosure treatment sites. All six of the species were found in the complete exclosure treatment, while *Coreopsis* and *Dalea* were absent from many of the door exclosure treatments (Fig. 5). Seedlings of both these

species are relatively palatable, and selective foraging on these species may have caused the reduction in species richness and diversity between the complete exclosures and the door exclosures. We found no evidence of a spatial pattern treatment effect on seedling abundance for any of the species, but there was a significant mound treatment effect on seedling abundance of *Amorpha* ( $F = 6.80$ ,  $df = 1,10$ ,  $P = 0.03$ ), *Echinacea* ( $F = 11.86$ ,  $df = 1,10$ ,  $P = 0.006$ ), and *Viola* ( $F = 6.33$ ,  $df = 1,10$ ,  $P = 0.03$ ). In all cases, there were more seedlings in the mound treatments than the no-mound treatments (Fig. 5). There was a significant exclosure treatment effect only on the abundance of *Amorpha* ( $F = 3.30$ ,  $df = 2,40$ ,  $P = 0.05$ ), with the greatest seedling abundance in the complete exclosures, the least in the small-door exclosures, and an intermediate level in the large-door exclosures. This exclosure treatment effect was interesting, since *Amorpha* seedlings are relatively unpalatable. In fact, the response of *Amorpha* to the exclosure treatments seemed to be the cause of the significant response of the unpalatable species as a group to the exclosure treatments.

In the biomass results, we found that total plant biomass was unaffected by the spatial pattern treatments, but was greater in the mound treatment than no-mound treatment (Table 5). There was no evidence of an exclosure treatment effect on biomass nor of an interaction between mound treatment and exclosure treatment (Table 5). For the individual species, an ANOVA could only be conducted for *Echinacea*. For the other species, there were too few planting sites with surviving seedlings to test for treatment effects on total biomass. In *Echinacea*, total biomass was significantly greater in the mound treatment than the no-mound treatment ( $F = 22.60$ ,  $df = 1,5$ ,  $P = 0.005$ ), but there was no evidence of an exclosure treatment effect ( $F = 1.88$ ,  $df = 2, 11$ ,  $P = 0.20$ ) or of a mound  $\times$  exclosure treatment interaction ( $F = 2.73$ ,  $df = 2,11$ ,  $P = 0.11$ ). When we analyzed the data for average biomass per plant, we found the same results. Average plant biomass (calculated over all species) and average biomass of *Echinacea* were greater in the mound treatment than the no-mound

treatment. In addition, there was no evidence of either exclosure treatment effects or mound x exclosure treatment interactions.

### **Small mammal censuses**

We captured four small mammal species in both years, including deer mice (*Peromyscus maniculatus*), meadow voles (*Microtus pennsylvanicus*), Western harvest mice (*Reithrodontomys megalotis*), and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*). In addition, we captured one common house mouse (*Mus musculus*) in 2000. We captured more total small mammals per half-plot in 2000 than in 1999 (Fig. 6), and the between-year difference was statistically significant (Table 6). The number of Western harvest mouse and thirteen-lined ground squirrel captures remained relatively constant between years (Fig. 6). However, the deer mouse captures increased from 1999 to 2000 ( $F = 34.10$ ,  $df = 1,50$ ,  $P < 0.0001$ ), and the meadow vole captures decreased from 1999 to 2000 ( $F = 12.54$ ,  $df = 1,50$ ,  $P = 0.0009$ ; Fig. 6). When we looked at how the small mammals as a group responded to the disturbance treatments, we found no evidence of a spatial pattern or mound treatment effect, or of a spatial pattern x mound treatment interaction (Table 6). We also found the same results when we looked at each of the species individually (all  $P$ -values  $> 0.05$ ). For some of the individual species, there was a significant difference in captures among blocks. Meadow voles and Western harvest mice were captured more frequently in block C than in blocks A and B, and thirteen-lined ground squirrels were captured only in blocks A and B.

## **Discussion**

### **Preliminary seedling herbivory study**

In the preliminary study of *Baptisia* herbivory, conducted in 1999, we found that a relatively large proportion of seedlings was eaten after only 15 days in the field, leading us to conclude that mammalian herbivory must play an important role in the recruitment of seedlings

at our study sites. Interestingly, we found that the rate of herbivory was greatest when seedlings were planted directly on mounds, intermediate for seedlings growing near mounds, and lowest for seedlings growing far from mounds. This was the opposite of what we predicted based on the idea that small mammals should avoid bare ground (cf. Klaas et al. 1998). So we speculated that larger mammals, such as rabbits or deer, might be important seedling herbivores at our sites, and that these animals may respond to small-scale disturbances differently than do small mammals. Thus, to investigate the importance of herbivory by different size classes of mammals in regulating seedling recruitment into reconstructed prairie, we constructed exclosures with different door sizes around a sub-set of the 1999 planting sites at the NSNWR study sites.

### **Herbivory effects on experimental species**

The exclosure experiment, conducted during the 2000 growing season, was designed to test for three main treatment effects on seedling recruitment: spatial pattern, mound, and exclosure. We found that seedling recruitment and biomass were not affected by the spatial pattern treatments, but we did find a strong mound treatment effect. As predicted, seedling abundance, species richness, and species diversity of the experimental species were greater in the mound sites than no-mound sites. In addition, palatable species, unpalatable species, and many of the individual experimental species were more abundant in the mound sites than no-mound sites. We also found that total, and average individual, plant biomass were greater in the mound treatment than in the no-mound treatment.

In the exclosure treatments, we found some evidence that the type of exclosure affected experimental species richness and diversity. Species richness and diversity were greatest in the complete exclosure treatment and decreased in both the small-door and large-door exclosures, indicating that any herbivory effects in the exclosure experiment were probably due to small mammals such as meadow voles. In addition, the species richness and diversity response to the

exclosure treatments differed somewhat between the mound and no-mound treatments, with seedling numbers in the mound treatments remaining relatively constant across the exclosure treatments and seedling numbers in the no-mound treatments decreasing as exclosure door size increased. Although there was no statistical evidence of mound x exclosure treatment interactions for species richness and diversity, the data trends indicate that herbivory pressure may have been greater in the no-mound treatments than in the mound treatments. Also, seedling abundance of the palatable species showed a similar response, with seedling numbers in the mound treatments remaining relatively constant across the exclosure treatments, while seedling numbers in the no-mound treatments decreased as exclosure door size increased. Again, there was no statistical evidence of a mound x exclosure treatment interaction for palatable species seedling abundance, but the trend could indicate that small mammalian herbivory had a stronger negative effect on palatable seedling abundance in the no-mound treatment than mound treatment. We found no statistical evidence of any exclosure treatment effects on biomass of the experimental species as a group or on biomass of individual species.

The fact that herbivory decreased species richness and diversity, but did not affect total seedling abundance or biomass, could be an indication that meadow voles were selectively feeding on some species and avoiding others. When we examined the individual species, it appeared that selective foraging on *Coreopsis* and *Dalea*, both relatively palatable species, might explain the reduction in species richness and diversity in the exclosures with doors. However, in general, there were too few seedlings of any of the species to statistically compare treatment responses among species.

In conclusion, some trends in the data indicated that selective foraging of palatable species by small mammals might have been slightly stronger off mounds than on mounds, but we found no statistical evidence of any interactions between the exclosure, mound, or spatial pattern treatments for most measures of the experimental species as a group and as individuals. Thus, although there is some evidence to indicate that seedling herbivory occurred at our sites,

herbivory contributed weakly to differences between seedling recruitment in the mound and no-mound treatments and was unaffected by the spatial autocorrelation of the mound production regime.

### **Small mammal censuses**

If small mammals were the most important herbivores at our study sites, as the exclosure results suggest, then it is not surprising that the herbivory signal was low during the 2000 growing season. Although total rodent captures were significantly greater in 2000, when the exclosure experiment was conducted, than in 1999, when the preliminary seedling herbivory study was conducted, meadow vole captures were lower in 2000 than in 1999. Of the four small mammal species captured both years at the study sites, meadow voles were the only herbivores (Wilson and Ruff 1999). Vole populations are known to fluctuate greatly within and between years (Gaines and Rose 1976, Getz et al. 1987), so it is possible that the vole population was larger at other times during the 2000 growing season and we happened to trap while the population was low. On the other hand, it is also well-documented that vole populations will remain low on prairies in the summer immediately following a spring fire (Vacanti and Geluso 1985, Clark and Kaufman 1990), and our sites were burned during the spring in both 1999 and 2000. Thus, it seems reasonable to assume that the meadow vole population was low at our study sites throughout the entire 2000 growing season, when we conducted the exclosure experiment.

In addition, when we analyzed the small-mammal capture data for spatial pattern and mound treatment effects, we found no evidence that total small mammal captures or captures of individual species were affected by the spatial pattern or mound treatments, nor were there any significant spatial pattern x mound interactions. Thus, it appears that small mammals at our sites did not adjust their behavior in response to the presence of small-scale disturbances or to the spatial patterns in which they were arranged.

## Conclusion

We conducted this study to test how selective foraging by mammalian herbivores may regulate seedling recruitment in a reconstructed prairie, and how small-scale soil disturbances and the spatial architecture of the small-scale disturbance regime may modify this effect. We found some evidence that selective foraging by small mammals reduced the diversity of recruited seedlings, but we did not find evidence that overall seedling abundance was affected by herbivory. In addition, we found only weak evidence that herbivory pressure differed between the mound and no-mound treatments and no evidence that herbivory pressure differed between the two spatial patterns of mound production. Seedling abundances of palatable and unpalatable species were affected by mound and exclosure treatments differently, but seedling recruitment of the individual species was too low to differentiate which species were most affected by herbivory. Thus, under the conditions at our reconstructed prairie sites in the year of this study, we conclude that herbivory contributed weakly to the reduction in seedling recruitment found in no-mound sites. However, we are hesitant to conclude that herbivory always contributes little to differential seedling survivorship on and off mounds in native prairies, because the conditions at our sites were unique to reconstructed prairies.

Our study sites were low in plant species diversity, were dominated by highly productive  $C_4$  bunchgrasses, and were burned each spring. These factors all contributed to vegetation structure at our sites that was vastly different from that found on native prairies. At our sites, bunchgrasses were spaced almost regularly across the ground, with patches of bare ground between grass genets. This bare ground influenced our results in two ways. First, the population of meadow voles, the most important herbivores at our sites, was low. Second, the mounds in our study were surrounded by bare ground, thus presenting to small mammals no contrast in predation risk between the mound and no-mound sites. Thus, we conclude that the small-scale disturbances we created in reconstructed prairie did not function as mounds do in native prairies, primarily because reconstructed prairies do not function like native prairies. We

suggest that the original seed mixes for prairie reconstructions need to contain a greater diversity of forbs, sedges, and  $C_3$  grasses to fill in the space between the dominant  $C_4$  bunchgrasses. This should serve two purposes: (1) the vegetation structure will more closely resemble that of native prairies, and (2) it may be difficult for weedy species to become established, thus eliminating the need to burn each spring in the first years after planting (Schramm 1990).

Although the results of this study were not strong, we still predict that small mammalian herbivores contribute significantly to the differences in seedling survivorship between mound and off-mound sites, and that disturbance regime spatial architecture may influence the relationship. However, interactions between small mammal herbivory and small-scale soil disturbances will only have a strong effect on seedling recruitment in grasslands that exhibit vegetation structure similar to that found on native prairies.

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**Table 1.** Plant species used in the experiment.

Species	Family	Seedling palatability to meadow voles <sup>a</sup>	
		Relative palatability	Relative rank <sup>b</sup>
<i>Amorpha canescens</i> Pursh	Fabaceae	Unpalatable	5
<i>Coreopsis palmata</i> Nutt.	Asteraceae	Palatable	2
<i>Dalea purpurea</i> Vent.	Fabaceae	Palatable	3
<i>Echinacea pallida</i> (Nutt.) Nutt.	Asteraceae	Palatable	4
<i>Heuchera richardsonii</i> R. Br.	Saxifragaceae	Unpalatable	7
<i>Liatris aspera</i> Michx.	Asteraceae	Palatable	1
<i>Viola pedatifida</i> G. Don	Violaceae	Unpalatable	6

<sup>a</sup> Palatabilities were determined by Nickel et al. (in prep) in laboratory feeding trials with meadow voles.

<sup>b</sup> In the relative rank, 1 is the most palatable species, 7 is the least palatable species.

**Table 2.** Results of mixed ANOVA examining the spatial pattern and planting site effects on the proportion of *Baptisia* seedlings eaten by mammals in the preliminary herbivory study.

Source of variation	df	<i>F</i>	<i>P</i>
Spatial pattern	2, 13	0.53	0.60
Planting site <sup>a</sup>	2, 30	11.23	0.0002
Planting site x Spatial	4, 30	0.93	0.46

<sup>a</sup> Planting site treatments included on-mound, near-mound, and far-mound. See *Methods—Preliminary seedling herbivory study* for a more complete description of the planting site treatments.

**Table 3.** Results of mixed ANOVA on vegetation survey data examining the spatial pattern, mound, and exclosure treatment effects on the experimental species.

Source of variation	df	Total seedling abundance		Species richness		Species diversity	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Spatial pattern <sup>a</sup>	1, 8	0.63	0.45	0.16	0.70	0.09	0.77
Mound	1, 10	11.01	0.008	11.22	0.007	3.27	0.10
Mound x Spatial	1, 10	1.39	0.27	1.86	0.20	0.95	0.35
Exclosure <sup>b</sup>	2, 40	1.74	0.19	5.08	0.01	3.59	0.04
Exclosure x Spatial	2, 40	0.87	0.43	1.03	0.37	1.25	0.30
Exclosure x Mound	2, 40	0.00	0.99	1.67	0.20	1.57	0.22
Exclosure x Mound x Spatial	2, 40	4.32	0.02	1.27	0.29	0.51	0.60

<sup>a</sup> Spatial pattern treatments included (1) the single arrangement of planting sites, and (2) the clusters of 16 arrangement of planting sites.

<sup>b</sup> Exclosure treatments included (1) complete exclosures, (2) small-door exclosures, and (3) large-door exclosures.

**Table 4.** Results of mixed ANOVA on vegetation survey data examining the spatial pattern, mound, and exclosure treatment effects on seedling abundance of the experimental species, separated by relative palatability.

Source of variation	df	Palatable species		Unpalatable species	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Spatial pattern <sup>a</sup>	1, 8	0.09	0.77	1.60	0.24
Mound	1, 10	10.17	0.01	8.74	0.01
Mound x Spatial	1, 10	0.78	0.40	1.93	0.20
Exclosure <sup>b</sup>	2, 40	0.11	0.89	4.75	0.01
Exclosure x Spatial	2, 40	0.50	0.61	0.62	0.54
Exclosure x Mound	2, 40	1.35	0.27	3.52	0.04
Exclosure x Mound x Spatial	2, 40	2.14	0.13	2.80	0.07

**Note:** Palatable species included *Coreopsis*, *Dalea*, *Echinacea*, and *Liatris*. Unpalatable species included *Amorpha* and *Viola*. *Heuchera* was also considered an unpalatable species, but it was never found in any of the exclosure treatment sites.

<sup>a</sup> Spatial pattern treatments included (1) the single arrangement of planting sites, and (2) the clusters of 16 arrangement of planting sites.

<sup>b</sup> Exclosure treatments included (1) complete exclosures, (2) small-door exclosures, and (3) large-door exclosures.

**Table 5.** Results of mixed ANOVA examining the spatial pattern, mound, and enclosure treatment effects on total biomass of the experimental species. Data were unbalanced for these analyses, because some treatments contained no surviving seedlings.

Source of variation	df	<i>F</i>	<i>P</i>
Spatial pattern <sup>a</sup>	1, 5	0.23	0.65
Mound	1, 5	13.81	0.01
Mound x Spatial pattern	1, 5	1.30	0.31
Exclosure <sup>b</sup>	2, 17	1.18	0.33
Exclosure x Spatial pattern	2, 17	0.06	0.95
Exclosure x Mound	2, 17	1.33	0.29
Exclosure x Mound x Spatial pattern	2, 17	0.37	0.70

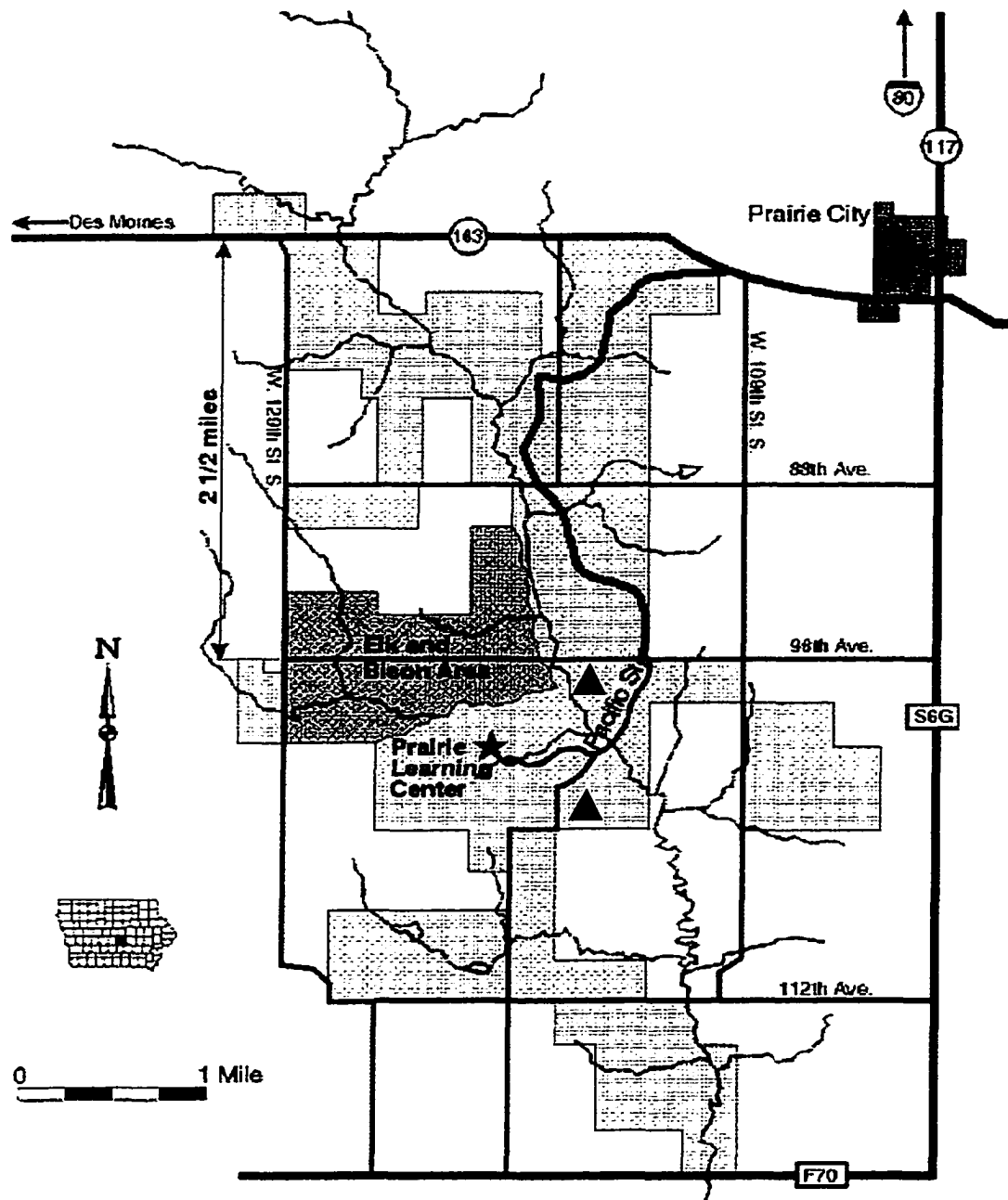
<sup>a</sup> Spatial pattern treatments included (1) the single arrangement of planting sites, and (2) the clusters of 16 arrangement of planting sites.

<sup>b</sup> Exclosure treatments included (1) complete exclosures, (2) small-door exclosures, and (3) large-door exclosures.

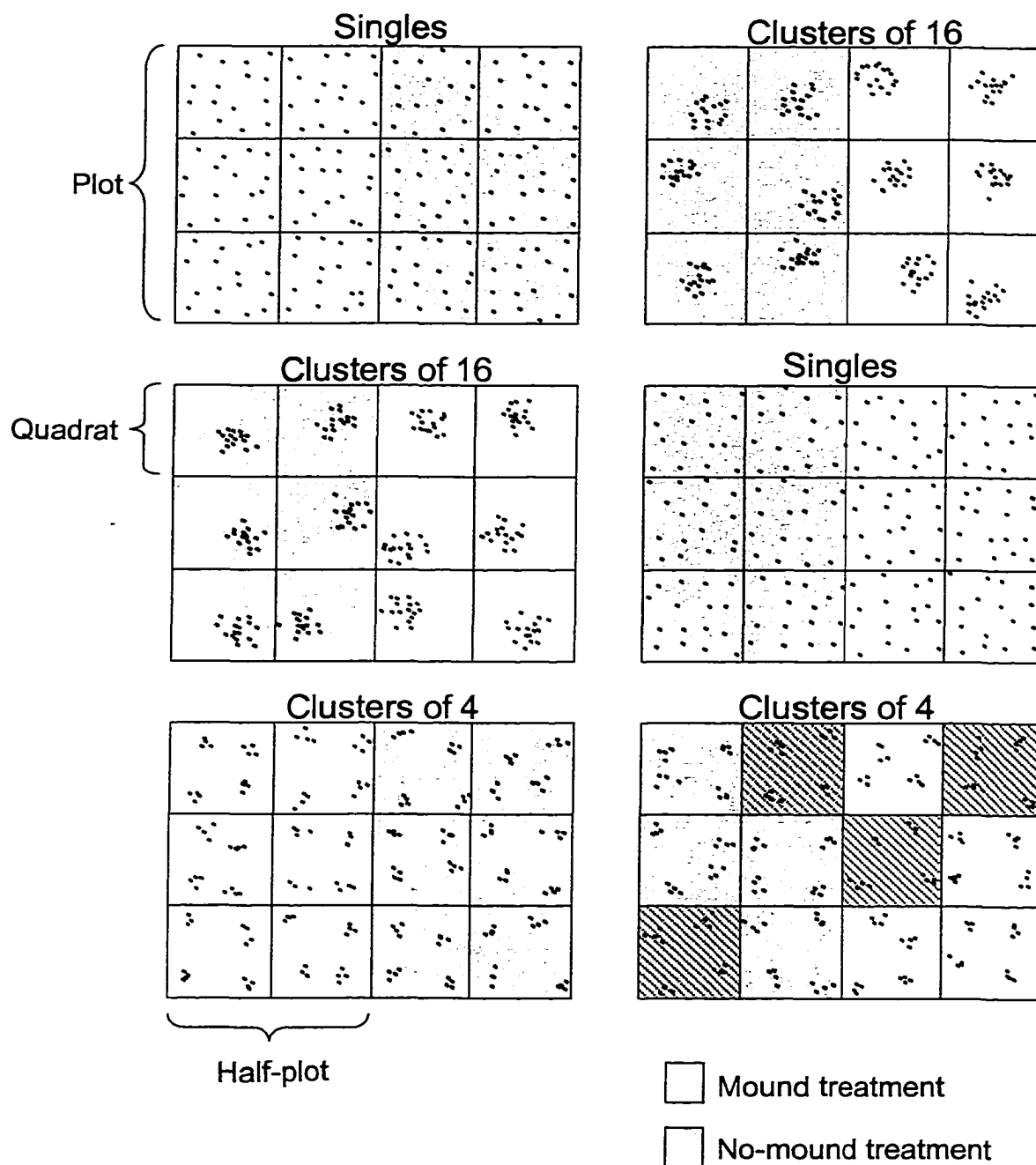


**Table 6.** Results of mixed ANOVA examining the year, spatial pattern, and mound treatment effects on the total small mammal captures in 1999 and 2000.

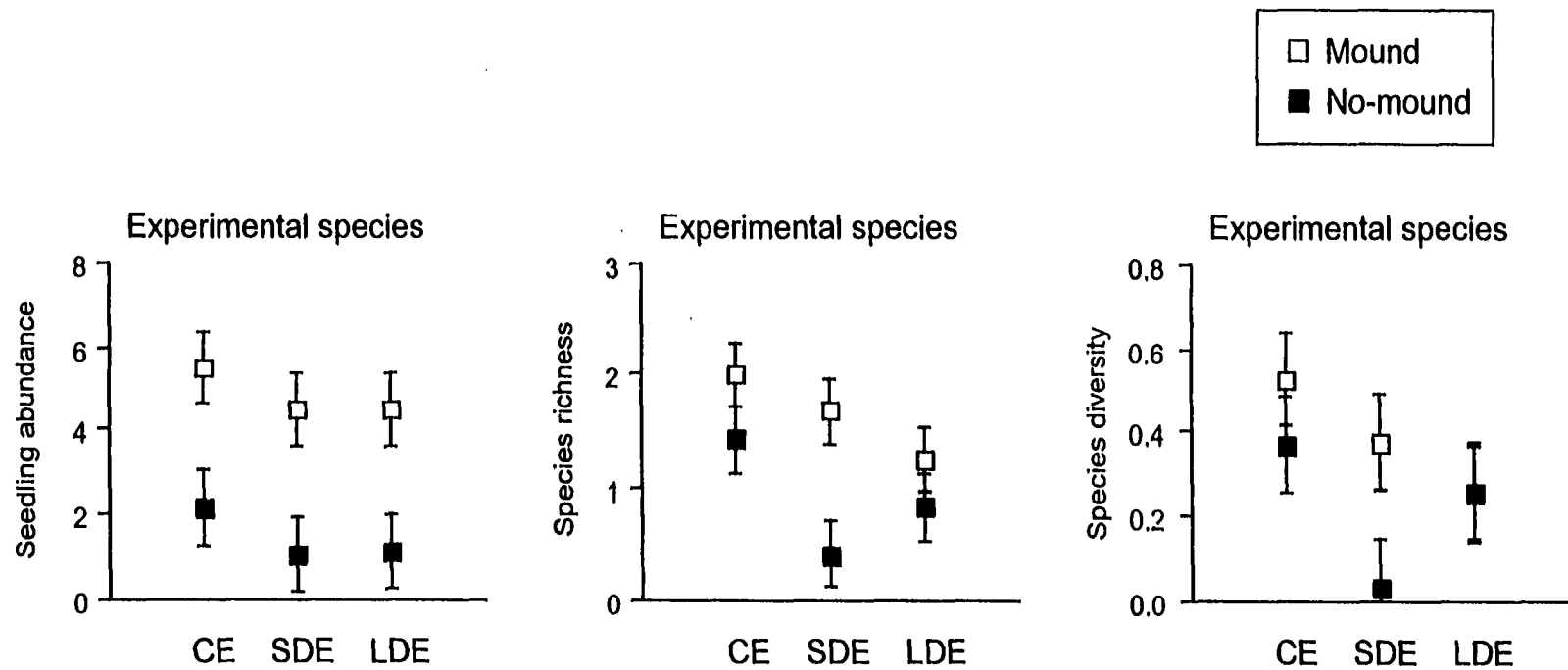
Source of variation	df	<i>F</i>	<i>P</i>
Year	1, 50	27.69	< 0.0001
Block	2, 13	2.09	0.16
Spatial pattern	2, 13	2.06	0.17
Mound	1, 50	1.56	0.22
Mound x Spatial pattern	2, 50	0.08	0.92



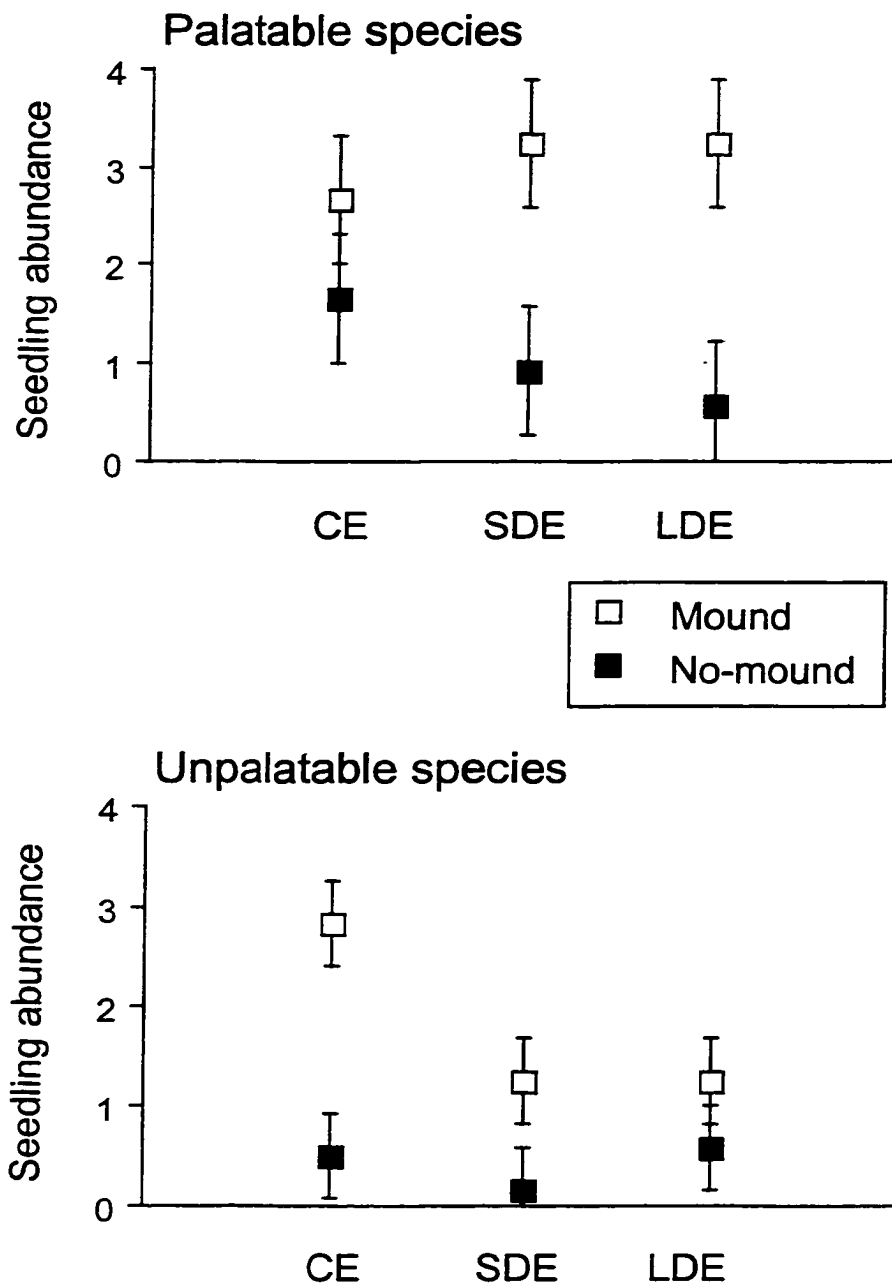
**Fig. 1.** General location and map of the Neal Smith National Wildlife Refuge (NSNWR). The extent of the NSNWR is shaded in light gray. The approximate locations of the study sites are labeled with black triangles. The low-diversity site (identified as site 17 in the NSNWR records) is the southern site, and the high-diversity site (identified as site 32 in the NSNWR records) is the northern site. Blocks A and B were located at the low-diversity site, and block C was at the high-diversity site.



**Fig. 2.** Schematic diagram of block A, which is also representative of the general layout of blocks B and C. Gray points are locations of potential planting sites in 1998. In each half-plot, two quadrats received no seed treatment. For simplicity, these are indicated in one of the clusters of 4 plots (as hatched squares). See *Methods—Experimental design* for further description of block layout and treatments.

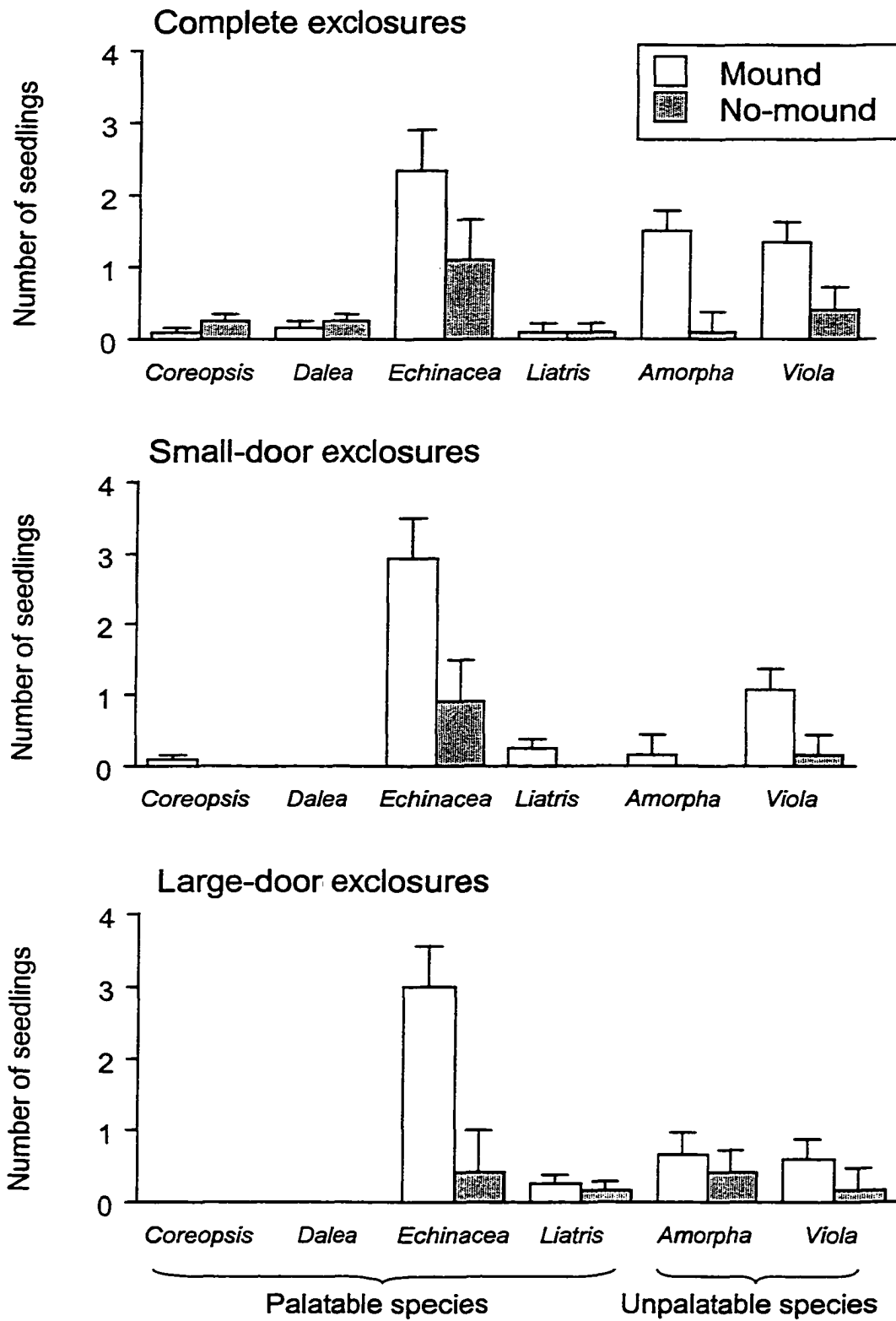


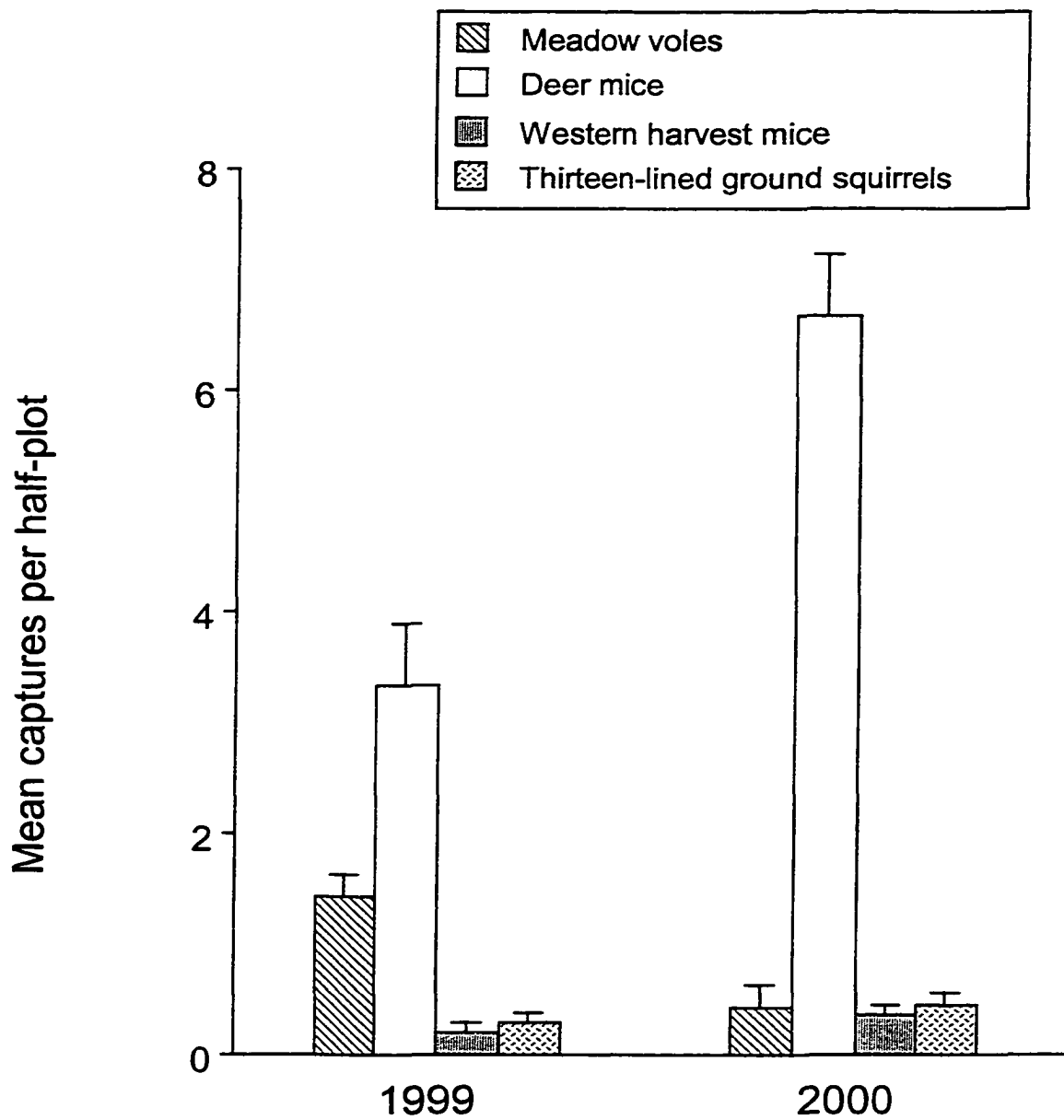
**Fig. 3.** Vegetation data for the experimental species, collected during surveys conducted 6-12 September 2000. The mound treatment and exclosure treatment effects are shown. Exclosure treatments are abbreviated as follows: complete exclosures (CE), small-door exclosures (SDE), and large-door exclosures (LDE). Values are means per half-plot, and error bars are  $\pm 1$  SE.



**Fig. 4.** Abundance of the experimental species, separated by seedling relative palatability. Data were collected during surveys conducted 6-12 September 2000. Palatable species included *Coreopsis*, *Dalea*, *Echinacea*, and *Liatris*. Unpalatable species included *Amorpha* and *Viola*. *Heuchera* was also considered an unpalatable species, but it was never found in any of the exclosure treatment sites. The mound and exclosure treatment effects are shown. Exclosure treatments are abbreviated as follows: complete exclosures (CE), small-door exclosures (SDE), and large-door exclosures (LDE). Values are means per half-plot, and error bars are  $\pm 1$  SE.

**Fig. 5.** Abundance of individual experimental species within the mound and no-mound treatments for each type of exclosure treatment. Species are separated by seedling relative palatability. *Heuchera* is not listed because it was never found during the vegetation surveys. Values are means per half-plot, and error bars are + 1 SE.





**Fig. 6.** Number of small mammal captures during five consecutive days of live-trapping on 16-20 August 1999 and 14-18 August 2000. Columns are mean number of captures per half-plot, and error bars are + 1 SE.



## CHAPTER 6. GENERAL CONCLUSIONS

This dissertation research demonstrated that small-scale soil disturbances serve as sites where seedling recruitment occurs in grasslands. While this has been shown previously (*e.g.*, Goldberg and Gross 1988, Martinsen et al. 1990, Reader and Buck 1991), the research presented here provided new insight as to how the spatio-temporal architecture of the small-scale disturbance regime affects seedling recruitment and, thus, influences plant community structure and diversity. In addition, this research provided insights as to how small-scale disturbances function as sites for seedling recruitment in natural prairies and reconstructed prairies.

In the first study, I found that a short-lived forb species utilized mounds for the successful completion of its life cycle, at least in years without a spring fire, which likely contributed to a positive spatial relationship between the distribution of the forb and the production of gopher mounds in a native prairie. Thus, this study provided evidence that the production of gopher mounds may contribute to the formation of spatial patterns in prairie plant communities.

In the second study, I found that the spatial distributions of three forb species, a short-lived palatable forb, a long-lived palatable forb, and a short-lived unpalatable forb, were all positively related to the distribution of gopher mound production in a native prairie. In contrast, I found no spatial relationship between the distribution of a long-lived perennial grass and mound production. In an experiment investigating the demographic response of each of the species when growing directly on mounds versus off mounds, and also when growing in areas of different neighborhood mound production rates, I found that survivorship of all four species generally was greater on mounds than off mounds. In addition, survivorship by on-mound seedlings was uncorrelated with rates of neighborhood mound production, while survivorship by off-mound seedlings was negatively correlated with local mound production. This indicated

that the conditions on mounds are generally better for seedling survivorship than are conditions off mounds, and seedlings growing on mounds may be buffered from any positive or negative effects of neighborhood disturbance rate. However, since the conditions off mounds are worse for seedling survivorship, seedlings growing off mounds may be susceptible to indirect, negative effects of neighborhood mound production, which could be caused by herbivores or other unmeasured factors. In general, this study provided evidence that the spatial distribution of mound production is positively related to the spatial distributions of a variety of plant species, and that the relationship is largely driven by the survivorship differences among seedlings growing directly on mounds versus off mounds. An indirect effect of neighborhood mound production did not additionally contribute to the positive spatial relationships between mounds and plant species, although an indirect effect was predicted. In fact, my results indicate that high rates of neighborhood mound production may actually have a negative effect on survivorship of seedlings growing in intermound spaces.

In the third and fourth studies, I conducted a large, landscape-level experiment to investigate explicitly whether the spatio-temporal architecture of the small-scale disturbance regime affects seedling recruitment and plant species diversity in grasslands. The experiment was conducted on reconstructed prairie and involved planting forb seeds on and off small-scale soil disturbances constructed to mimic gopher mounds.

In the third study, I predicted that seedling recruitment would be greater on mounds than off mounds, and that seedling recruitment should increase with increasing spatial and temporal autocorrelation in the mound production regime. I found conclusive evidence that seedling recruitment was greater on mounds than off mounds, but no evidence that seedling recruitment was affected by the spatial or temporal patterns of mound production. Although these results indicate that disturbance regime spatio-temporal architecture had no effect on seedling recruitment in reconstructed prairie, I am reluctant to conclude that spatio-temporal architecture is unimportant in understanding how small-scale disturbances affect seedling

recruitment into native prairies. The vegetation structure at the reconstructed prairie sites was vastly different from that found on native prairies, causing small-scale disturbances in the reconstructed prairie to function differently than they do in native prairies. Even though this study did not provide conclusive evidence regarding the effects of spatio-temporal disturbance architecture on seedling recruitment, it did provide important insight as to the differences in function of small-scale soil disturbances in reconstructed prairies versus native prairies.

The fourth study was conducted within the same experimental framework as the third study, but I specifically investigated how mammalian herbivory and the small-scale disturbance regime interacted to affect seedling recruitment. I predicted that protection from herbivory would contribute to the recruitment of seedlings on mounds and that this protection would be affected by the spatial autocorrelation with which small-scale disturbances were produced. I found some evidence that selective herbivory of palatable species by small mammals reduced the diversity of recruited seedlings, but herbivory pressure was approximately equal on and off mounds and under different spatial patterns of mound production. Thus, I concluded that the small-scale soil disturbances in this reconstructed prairie provided seedlings with weak protection from mammalian herbivory. However, I am hesitant to conclude from this study that mounds in native prairies do not serve as safe sites from small mammalian herbivory, since the reconstructed prairie vegetation structure was so different from that found on native prairies. Instead, this study provided more evidence of how small-scale soil disturbances function differently in reconstructed prairies than they do in native prairies.

Reconstructed prairies are typically low in plant species diversity and are dominated by highly productive  $C_4$  bunchgrasses. In addition, reconstructed prairies are typically burned annually, contributing to the dominance of  $C_4$  grasses, a lack of litter or other ground cover, and low populations of small mammalian herbivores. In contrast, native prairies are much higher in plant species diversity, contain a mix of bunchgrasses, rhizomatous grasses, and forbs, and are burned every few years. Thus, small-scale soil disturbances function as sites for

seedling recruitment for different reasons in reconstructed prairies and native prairies. In native prairies, mounds provide sites where above- and belowground competition with other plants are reduced and where seedlings might be protected from herbivory by small mammals. In reconstructed prairies, however, aboveground competition and protection from herbivory are nearly equal on small-scale disturbances and in intermound areas. Thus, mounds in reconstructed prairies function as sites for seedling recruitment mainly because of the reduced belowground competition in mound soil.

Since the results of the third and fourth studies were not applicable to native prairies, I suggest that a similar experiment investigating the effects of small-scale disturbance spatial and temporal patterns be conducted in a grassland system where the vegetation structure and small mammal community are more typical of those found in native prairies. Under these conditions, a more conclusive test of the importance of disturbance spatio-temporal architecture on seedling recruitment, including an investigation of the interactive effects of seedling herbivores, could be conducted.

This dissertation research demonstrated that small-scale soil disturbances are important sites of seedling recruitment in both native and reconstructed prairies, but for different reasons. In native prairies, mounds serve as sites where above- and belowground competition are reduced and where seedlings might be protected from herbivory by small mammals. Because the natural production of gopher mounds is spatially and temporally autocorrelated, the small-scale disturbance regime contributes to the formation of plant community spatial patterns. The production of gopher mounds seems to directly and indirectly influence seedling survivorship, suggesting that the role of gopher mounds in structuring native prairie plant communities may be more complex than is currently appreciated. In contrast, small-scale soil disturbances in reconstructed prairies serve as sites for seedling recruitment because belowground competition with neighboring plant roots is reduced. The mounds at my reconstructed prairie sites did not provide sites where aboveground plant competition was much reduced or where seedlings were

much protected from small mammalian herbivores. Thus, small-scale soil disturbances in reconstructed prairies provide sites where seedling recruitment can occur, but the spatio-temporal architecture of the disturbance regime has no additional, indirect effect on seedling survivorship. I suggest that efforts be made to improve the initial seed planting mixes on reconstructed prairies, so that they function more like native prairies. In addition, further research should be conducted on native prairies to investigate explicitly the effects of the spatio-temporal architecture of small-scale disturbance regimes on seedling recruitment and plant community structure.

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