

The effect of gopher mounds and fire on the spatial distribution and demography of a short-lived legume in tallgrass prairie

Kelly S. Wolfe-Bellin and Kirk A. Moloney

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* L., 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 2 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.

Key words: gopher mounds, fire, *Medicago lupulina*, disturbance, prairie, introduced species.

Résumé : Plusieurs études ont signalé que les buttes des géomys peuvent augmenter la diversité des espèces et l'hétérogénéité spatiale des communautés végétales, mais peu d'études ont relié expérimentalement ces perturbations à petite échelle, à l'hétérogénéité spatiale dans la distribution des populations végétales individuelles. Dans cette étude, les auteurs ont expérimenté directement l'existence d'une relation spatiale entre le patron de production des buttes par les géomys et la distribution d'une légumineuse à court cycle de vie, le *Medicago lupulina* L., dans un vestige de prairie à herbes hautes. De plus, pendant 3 ans, les auteurs ont examiné la réaction démographique du *M. lupulina* suite à des traitements d'implantation sur les buttes et hors des buttes, étude pendant laquelle un feu est survenu au cours d'une des années. Ils ont constaté que la distribution spatiale du *M. lupulina* est positivement corrélée avec la distribution des buttes. La germination est significativement plus forte en dehors des buttes, chacune des années, alors que la survie et la fécondité sont significativement plus élevées sur les buttes, au cours des 2 années sans feu. Au cours de l'année où le feu est survenu, la survie était significativement plus importante en dehors des buttes et la fécondité à peu près égale sur les buttes et en dehors des buttes. Les auteurs concluent que la relation spatiale positive entre le *M. lupulina* et les buttes est causée par la dépendance directe du *M. lupulina* sur les buttes, pour sa survie, la plupart des années. Les buttes des géomys fournissent des microsites où la compétition végétale et l'herbivorie sont réduites. En général, les buttes des géomys peuvent engendrer directement une hétérogénéité spatiale dans la communauté végétale, mais la force de cet effet peut être significativement modifiée certaines années, en particulier celles aux cours desquelles le feu intervient.

Mots clés : butte des géomys, feu, *Medicago lupulina*, perturbation, prairie, espèces introduites.

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 be-

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ing 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 examined directly 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 3-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 1–20 m (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 with 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 C₄ 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 because of the increased dominance of C₄ 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). 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 3 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 than 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 with 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; 43°26'N, 88°53'W), an 80-ha 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 ha, 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 3–5 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-ha plot was established at the study site (Klaas et al. 1998, 2000). The plot consisted of sixty-four 10 m × 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 1-week intervals throughout the 1994, 1995 (Klaas et al. 2000), and 1996 growing seasons, and at 3- to 4-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).

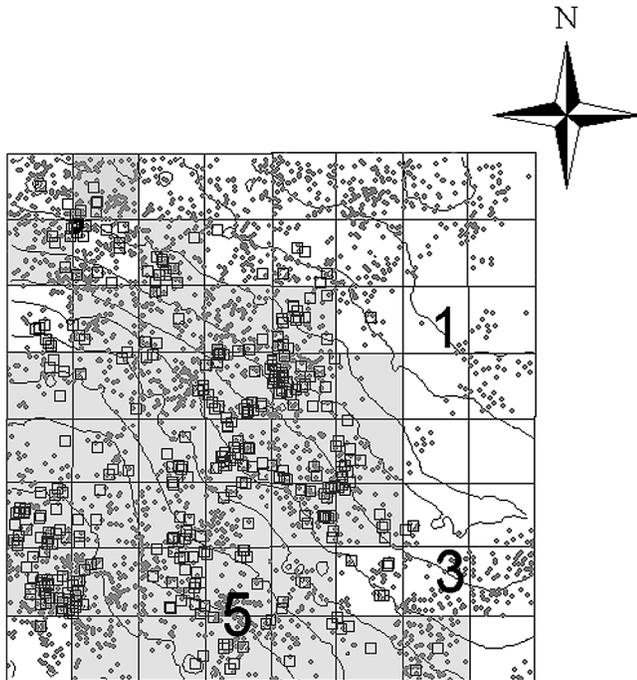
Logistic regressions were performed using SAS (version 6.12, SAS Institute Inc.) to determine whether the presence of *M. lupulina* within each cell was related to mound number. Each cell was treated as an independent experimental unit. In addition, we included the average relative elevation (range 0–6 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 × 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 × elevation. For each set of regressions, the best-fit model was determined with the Schwartz Criterion. The Schwartz Criterion 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 Schwartz Criterion 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 3 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

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.



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 ± 0.7 (mean ± 1 SE) cm deep in 1996 and 3.0 ± 0.2 cm deep in 1998. In the year of the fire, standing vegetation was only a few centimetres tall at the time we planted, and off-mound litter was 0.7 ± 0.1 cm deep.

Each experimental unit (hereafter referred to as a grid) consisted of 49 *M. lupulina* seeds planted in a 7×7 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 nonlocal 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 aboveground 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

Medicago 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 \times 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 2). 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 2). For the logistic regression model based on 1994–1998 mound production, mound production and elevation were again positively related to *M. lupulina* presence (Table 2), although the relationship between 1994–1998 mound production and the presence of *M. lupulina* was weaker than that 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 that 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

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 \times elevation	60.4	68.1

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

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

Medicago lupulina seedling germination was significantly greater in the off-mound treatments than in the on-mound treatments for all 3 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 in the 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 $t = 3.24$, $P = 0.004$; α -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 α -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 $t = -4.28$, $P = 0.0004$; α -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 ± 0.014 g) than off-mound treatment (0.008 ± 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 ± 0.007 g, and off mounds it was 0.037 ± 0.024 g.

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

Parameter	Parameter estimate	SE	P	Odds ratio
1994 mound production data set				
β_0	-4.0389	1.0634	0.0001	
β_1	0.2790	0.1076	0.0095	1.322
β_2	1.0712	0.3136	0.0006	2.919
1994–1998 mound production data set				
β_0	-4.6578	1.2391	0.0002	
β_1	0.0307	0.0145	0.0335	1.031
β_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} is the probability of *M. lupulina* presence in a cell, mnd is the number of mounds produced per cell in 1994 or 1994–1998, and elev is elevation in metres.

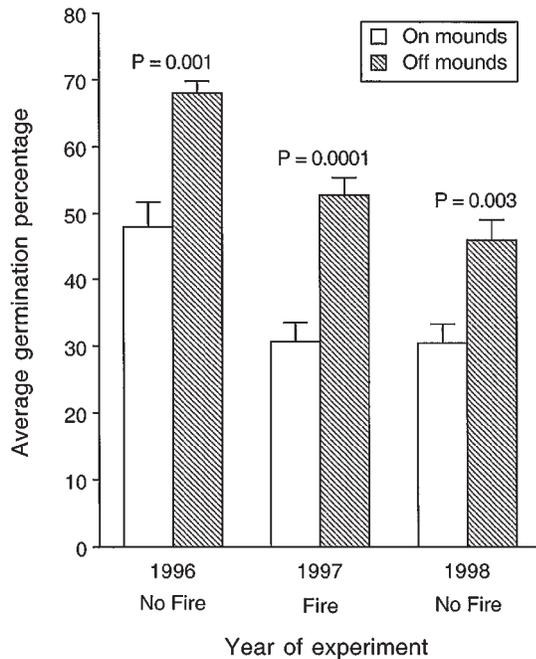
In the 1998 experiment, a no-fire year, plants were collected at the end of the second growing season and survivorship was again very low. We could detect no significant difference in plant biomass between the on- and off-mound treatments. Individual plant biomass was 0.183 ± 0.064 g on mounds and 0.095 ± 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. 1991a, 1991b). 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*.

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



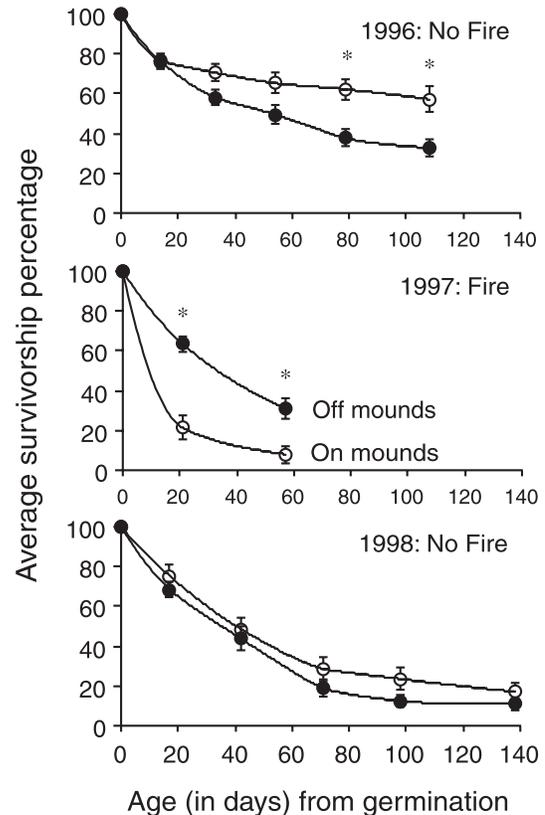
and, by extension, may be important in understanding the distribution of other prairie plant species.

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.

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 Bonferroni-adjusted α -values for the criteria.



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 ± 0.2 cm (mean \pm 1 SE) of litter in the 2 years without fire and under 0.7 ± 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 than in dry sites without moss).

In contrast with 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

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.

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 mammals 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 (1992a, 1992b) 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 because of 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 those collected off-mounds. 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 that 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 sec-

ond 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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