



Vegetation responses to different spatial patterns of soil disturbance in burned and unburned tallgrass prairie

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Abstract

Pocket gopher (Geomyidae) disturbances are created in spatially predictable patterns. This may influence resource heterogeneity and affect grassland vegetation in a unique manner. We attempt to determine the extent to which density and spatial pattern of soil disturbances influence tallgrass prairie plant community structure and determine how these disturbances interact with fire. To investigate the effects of explicit disturbance patterns we created simulated pocket gopher burrows and mounds in various spatial patterns. Simulated burrows were drilled into the soil at different densities in replicated plots of burned and unburned prairie. Separate plots of simulated mounds were created in burned and unburned prairie at low, medium, or high mound densities in clumped, uniform, or random spatial dispersions. In both burned and unburned plots, increased burrow density decreased graminoid biomass and increased forb biomass. Total-plant and graminoid biomass were higher in burned than unburned plots while forb biomass was higher in unburned plots. Total-plant species richness was not significantly affected by burrow density or burning treatments, but graminoid species richness increased in unburned plots and forb species richness increased in burned plots. Plant species richness was temporarily reduced directly on mound disturbances compared to undisturbed prairie. Over time and at larger sampling scales, the interaction of fire and mound disturbance patterns significantly affected total-plant and graminoid species richness. The principal effect in burned and unburned prairie was decreased total-plant and graminoid species richness with increased mound disturbance intensity. Although species richness at small patch scales was not increased by any intensity of disturbance and species composition was not altered by the establishment of a unique guild of disturbance colonizing plants, our study revealed that interactions between soil disturbances and fire alter the plant community dominance structure of North American tallgrass prairie primarily via changes to graminoids. Moreover, these effects become increasingly pronounced over time and at larger spatial sampling scales.

Introduction

A major goal of ecological research is to identify patterns of plant community structure and attempt to elucidate the mechanisms responsible for generating those patterns. Due to behavioral constraints stemming from territoriality, optimal foraging, and predator avoidance, pocket gophers (Geomyidae) generate spatially non-random soil disturbances in many systems (e.g., Reichman et al. (1982); Huntly and Inouye

(1988); Benedix (1993); Moloney and Levin (1996)). These animal-generated disturbance patterns may alter patterns of resource availability and ultimately affect patterns of plant community structure.

Pocket gopher mounds tend to exhibit a clumped spatial dispersion (Andersen 1987; Moloney et al. 1992; Klaas et al. 2000). Additionally, the spacing within and between individual burrow systems has been shown to be uniform for all sizes and both sexes of gopher within a population (Reichman et al. 1982),

despite varying among populations because of different soil characteristics and food densities (Reichman et al. 1982; Andersen 1987; Benedix 1993). As a result, burrows and mounds create an explicit mosaic of patches with various resource characteristics and successional ages, thereby enhancing heterogeneity and possibly creating distinctive spatial patterns in the plant community (Hobbs and Mooney 1985; Reichman and Smith 1985; Moloney et al. 1992; Inouye et al. 1997). Increased spatial heterogeneity of resources and increased germination sites for subordinate plant species are likely responsible for commonly observed increases in overall plant community diversity associated with pocket gopher activity (Tilman 1983; Spencer et al. 1985; Inouye et al. 1987; Collins 1989; Stromberg and Griffin 1996). Consequently, different spatial patterns of disturbance are likely to influence heterogeneity in different ways and lead to unique plant community responses at a variety of spatial scales.

We attempt to determine the extent to which the density and spatial pattern of small soil disturbances influence tallgrass prairie vegetation. We hypothesized that, similar to other ecosystems where pocket gophers are present, soil mound and burrow disturbances would disrupt the dominant C_4 grass canopy and create opportunities for the establishment of subordinate plant species, thereby promoting coexistence and increasing overall community diversity. We also predicted that the characteristic patterns of pocket gopher burrows and mounds would alter resources differently than other patterns of disturbance and have a distinct effect on plant community structure.

An additional aspect of our study was to examine how plant community structure responds to the interaction of soil disturbances and fire across multiple sampling scales. The effects of fire on small-scale patch dynamics are poorly understood at present, yet may be potentially important in influencing the heterogeneity necessary for maintaining plant species diversity (Collins and Gibson 1990; Hartnett and Fay 1998). Because fire promotes the growth of the dominant C_4 grasses (e.g., Gibson and Hulbert (1987); Knapp et al. (1998)), we predicted that annual burning would lessen the effects of soil disturbances on subordinate plant species. In this paper, we assess the role small-scale disturbances play in the maintenance of plant diversity in the North American tallgrass prairie and the manner in which they interact with fire to affect plant community structure across a variety of temporal and spatial sampling scales.

Methods

Study site

This research was conducted between July 1994 and September 1997 at the Konza Prairie Biological Station in northeastern Kansas, USA (39°05' N, 96°35' W). The experiment was performed on a deep soil bench in a watershed that is edaphically and floristically similar to areas where pocket gophers are found, but the absence of soil hummocks from old mounds indicated that no gophers had been present in the area for many years (pers. obs.). Soil depth and plant community composition are important determinants of pocket gopher distribution at Konza Prairie, however, emigration constraints appear to prohibit their occupying all suitable sites. The area has been periodically burned over the past 20 years as part of a prescribed burning plan.

Experimental design for simulated burrows

During summer 1994, when natural populations of pocket gophers were active at Konza Prairie, trenches were excavated with a backhoe and different densities of simulated burrows (1.5 m long, 10 cm diameter) were drilled horizontally from the side-wall of the trench into randomly assigned plots. Simulated burrows were drilled 20 cm below the soil surface into 2.5 m plots in the previously undisturbed, adjacent prairie. Burrows were created at densities of one, three (characteristic), and seven per 2.5 m. Characteristic burrow densities and diameters were determined from a nearby, active population of pocket gophers at Konza Prairie (Rogers 1998). Control plots with no burrows drilled were also established. All plots were burned at the outset of the experiment in 1994. In 1995–1997 randomly assigned unburned and annually, late-spring burned treatments were maintained. All burrow densities were randomly assigned to replicated plots within burned and unburned plots (4 replications per burn*burrow treatment). Every year following spring burning, a sharpened PVC pipe was used to ream the simulated burrows and remove root regrowth.

Plant species composition data were collected by denoting the presence of species along permanent 2.5 m sampling transects divided into twenty-five 0.01 m² quadrats within each plot. These transects overlaid and were oriented perpendicularly to simulated burrows and were approximately 1.2 m away from

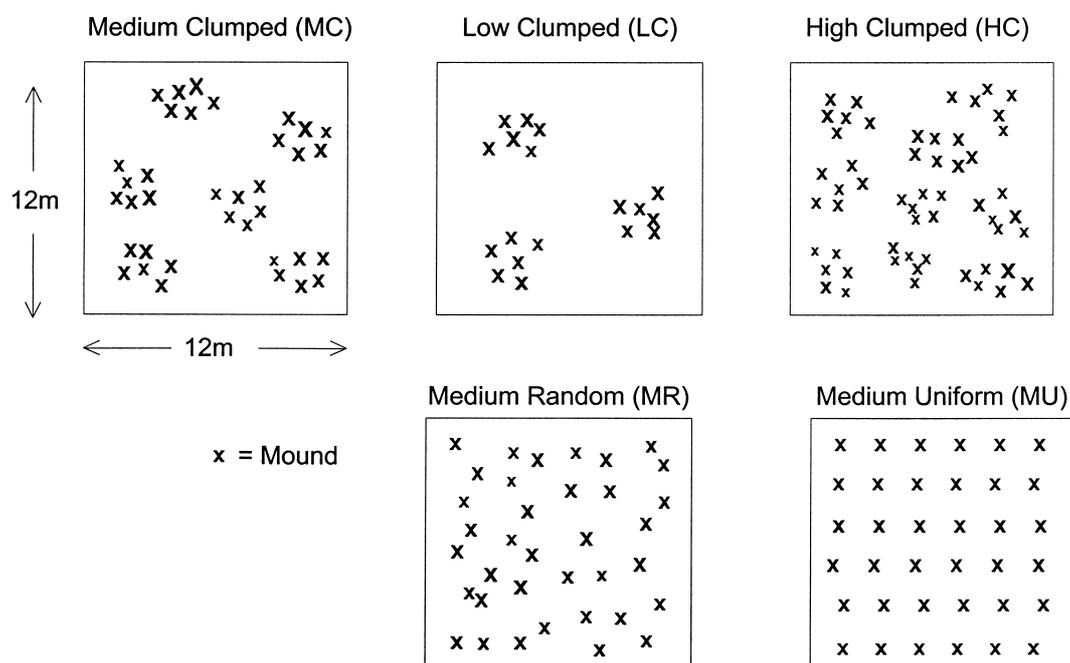


Figure 1. Schematic diagram of simulated mound plots (mound density/dispersion pattern). Characteristic mound density and dispersion (MC) are designated as medium (36 mounds) and clumped (aggregate spacing) respectively in a 12 m \times 12 m plot. This pattern was varied by decreasing (18 mounds) and increasing (54 mounds) mound density to give the low/clumped (LC) and high/clumped (HC) treatments respectively. The characteristic dispersion pattern was also varied by keeping density constant and altering the spatial pattern of mounds. A medium density of mounds (36 mounds) were randomly (MR) and uniformly (MU) dispersed within plots. All mound disturbance patterns were randomly assigned to replicated burned and unburned plots.

the excavated trenches. Only annually burned plots were sampled in August 1994 because all plots were burned in spring 1994 and burrows were not constructed until summer 1994. Vegetation sampling in 1995 and 1996 took place in early June and again in mid-August to account for different seasonal phenologies and to insure adequate sampling of all species present.

Aboveground net primary production (ANPP) was estimated in September 1997 by clipping all vegetation to ground-level in the permanent 0.01 m² quadrats along each 2.5 m transect. Clipping occurred after peak biomass production, but before the onset of senescence. Only biomass from the current growing season was sampled, including senesced vegetation from the current year. Litter that had accumulated over multiple years in unburned plots was not collected. Graminoid and forb biomass from each quadrat was separated, dried at 60 °C for approximately 72 h and weighed.

Experimental design for simulated mounds

Twenty 12 m \times 12 m plots containing artificially created soil disturbances (approximately 20 cm diameter, 10 cm height each) were established nearby using tailings from the simulated burrow excavations. Simulated mounds were created at either low, medium (characteristic) or high relative densities and arranged in either clumped (characteristic), uniform, or random dispersions in each plot (Figure 1). Patterns of mound dispersion are naturally clumped and the characteristic density was determined from the average density of mounds found in an active population of pocket gophers at Konza Prairie (Rogers 1998). Each disturbance pattern was replicated in both burned and unburned plots. All plots were burned in spring 1994 prior to initiation of the experiment and fire treatments for replicated unburned and annually, spring burned plots were maintained during subsequent years of the experiment.

Plant species composition was sampled twice each growing season by recording the presence of species in permanent 0.01 m² quadrats along a 2 m transect

centered on a mound. Five mounds in each plot were selected as replicates for study. Again, only a sub-set were sampled in August 1994. Vegetation sampling in 1995 and 1996 took place in early June and mid-August to obtain adequate estimates of all species and capture phenological differences.

Data analysis and statistical procedures

Plant species richness (total number of species present per unit area) and functional group richness (number of graminoid or forb species present per unit area) were calculated using early June and mid-August species composition data as repeated measures to provide yearly assessments of vegetation structure. Richness in 1994 was calculated from species composition data collected in August only. Because considerable phenological variability occurred among years, each year of data were analyzed separately.

Data for 2 m transects across mounds were grouped into three sampling positions: undisturbed vegetation (Und, two outermost 0.01 m² quadrats per transect), adjacent to mound (Adj, two 0.01 m² quadrats per transect), and directly on mound (Mnd, two 0.01 m² quadrats per transect). Presence-absence data were collected and a richness value in each quadrat was obtained, however, transects, rather than individual quadrats, were considered replicates for statistical purposes. Species richness in the two Mnd quadrats centered directly on each mound were also used to test for differences among the mound disturbance patterns (see Figure 1).

In an attempt to discern whether the effects of particular mound patterns were manifest at a larger spatial scale, species richness was also compared among the various mound disturbance patterns at 0.2 m² (combining all twenty 0.01 m² quadrats in each 2 m sampling transect). The statistical comparisons of interest for this study were those that occurred among treatments within a particular sampling scale and sampling period. In other words, we only compared results with data from the same sampling scales. Data were analyzed using analysis of variance (repeated measures for 1995 and 1996) and multiple regression in StatView 5.0 (SAS Institute, 1998).

Techniques for ordination and classification of multi-variate species composition data were used to determine whether particular disturbance and fire treatments differed in species composition (Jongman et al. 1995). These analyses were conducted using Two-way Indicator Species Analysis (TWINSPAN)

and Detrended Correspondence Analysis (DCA) (Hill 1994).

Results

Plant community response to simulated burrows

Total-plant species richness was not significantly affected by any burrow density or fire treatments in 1994 ($F_{3,12} = 1.102, p = 0.386$), 1995 (Table 1A), or 1996 (Table 1B). However, in both 1995 and 1996 graminoid species richness was significantly higher in unburned plots, while forb species richness was higher in burned plots (Table 1). Surprisingly, burrow density did not significantly affect graminoid or forb species richness (Table 1). Likewise, ordination procedures did not reveal any strong species compositional differences among the various simulated burrow densities in burned or unburned plots and, thus, are not presented here (see Rogers (1998)).

Total-plant biomass was greater in burned plots than unburned plots ($F_{1,24} = 60.5, p < 0.0001$), but there were no significant differences in total-plant biomass among burrow density treatments ($F_{3,24} = 1.4, p = 0.26$). Graminoid biomass was significantly greater in burned than unburned plots (Table 2A, Figure 2A) while forb biomass was significantly greater in unburned than burned plots (Table 2B, Figure 2B). Graminoid biomass significantly decreased with increasing burrow density (Table 2A, Figure 2A) while forb biomass significantly increased with increasing burrow density (Table 2B, Figure 2B).

Plant community response to simulated mounds

In 1994, total-plant species richness in burned and unburned plots was significantly lower on mounds than either adjacent to the mound or in undisturbed prairie (Table 3A). This effect weakened, but remained significant in 1995 (Table 3B). By 1996, the sampling positions across mounds in burned and unburned plots were not statistically different from each other (Table 3C). Likewise, graminoid and forb richness were significantly lower on mounds in 1994 (Table 3A) and 1995 (Table 3B), but statistically indistinguishable from sampling positions adjacent to the mound and in undisturbed prairie in 1996 (Table 3C). Unfortunately, we were unable to collect biomass across simulated mounds, however, during this study biomass was concurrently collected across nearby

Table 1. Mean (± 1 SE) total-plant, graminoid, and forb species richness (0.01 m^{-2}) along simulated burrow transects in burned and unburned plots in (A) 1995 and (B) 1996 and results of repeated measures analysis of variance. Variables are: Fire = burn manipulation (burned or unburned) and Bu = burrow density (Time = June and August sampling periods, not shown). Burrow densities are 0, 1, 3, or 7 burrows per 2.5 m transect.

Richness	Burned				Unburned				Anova		
	0 bu (n = 8)	1 bu (n = 8)	3 bu (n = 8)	7 bu (n = 8)	0 bu (n = 8)	1 bu (n = 8)	3 bu (n = 8)	7 bu (n = 8)	Fire	Bu	Fire \times Bu
(A) 1995											
Total	3.18 \pm 0.28	3.38 \pm 0.20	3.29 \pm 0.33	3.45 \pm 0.11	3.57 \pm 0.11	3.53 \pm 0.15	3.60 \pm 0.19	3.36 \pm 0.13	ns	ns	ns
Graminoid	1.98 \pm 0.14	2.36 \pm 0.17	1.99 \pm 0.12	2.21 \pm 0.04	2.57 \pm 0.15	2.73 \pm 0.06	2.76 \pm 0.16	2.51 \pm 0.05	***	ns	ns
Forb	1.21 \pm 0.16	1.02 \pm 0.09	1.31 \pm 0.23	1.24 \pm 0.11	1.00 \pm 0.08	0.80 \pm 0.13	0.84 \pm 0.09	0.85 \pm 0.10	*	ns	ns
(B) 1996											
Total	2.93 \pm 0.20	3.33 \pm 0.26	3.10 \pm 0.33	3.52 \pm 0.32	3.84 \pm 0.15	3.72 \pm 0.20	3.29 \pm 0.16	3.56 \pm 0.16	<i>o</i>	ns	ns
Graminoid	2.04 \pm 0.15	2.51 \pm 0.16	2.01 \pm 0.10	2.32 \pm 0.15	2.96 \pm 0.15	2.97 \pm 0.07	2.76 \pm 0.14	2.88 \pm 0.18	***	ns	ns
Forb	0.90 \pm 0.10	0.82 \pm 0.12	1.09 \pm 0.27	1.20 \pm 0.18	0.88 \pm 0.12	0.76 \pm 0.13	0.54 \pm 0.05	0.69 \pm 0.10	*	ns	ns

ns: not significant; *o*: $0.05 < p < 0.1$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

naturally created pocket gopher mounds. Total-plant, graminoid and forb biomass were temporarily decreased on mounds, but were statistically indistinguishable from undisturbed vegetation after three years (Rogers et al. 2001).

Different vegetation patterns emerged by examining species richness among various mound disturbance patterns (Figure 1). In 1994, there were no significant differences in total-plant or graminoid species richness among disturbance patterns at the local mound (0.01 m^2 , Table 4A) or sampling transect (0.2 m^2 , Table 4B) scales. There was a significant interaction between burning and disturbance pattern for forb species richness in 1994 at the local mound scale (0.01 m^2 , Table 4A), however, all of the plots had been recently burned and six of the ten treatments had zero forbs present on mounds in the first growing season. Few significant differences occurred between fire and mound disturbance patterns for total-plant, graminoid, and forb species richness at the local mound scale (0.01 m^2) in 1995 and 1996 (Table 4A).

Highly statistically significant effects for total-plant species richness were found in 1995 and 1996 at the sampling transect scale (0.2 m^2 , Table 4B, Figure 3A, B). Total-plant species richness was markedly lower in the unburned, high density/clumped disper-

sion (HC) treatments in 1995 and 1996 (Figure 3A, B). In 1996, total-plant species richness in the burned plots was highest in the low density/clumped dispersion (LC) treatments (Figure 3B). These responses were primarily influenced by changes in graminoid species richness (Table 4B, Figure 3C, D.). Forb species richness was not significantly affected by mound disturbance pattern or fire (Table 4B, (Figure 3E, F)). Woody species were included in the total-plant species richness analysis despite contributing less than 1% to all plots. Again, ordination procedures did not reveal any species compositional differences among the various simulated mound disturbance patterns in burned or unburned plots and are not presented here (see Rogers (1998)).

Discussion

Our study revealed that, although simulated pocket gopher mounds and burrows did not increase overall plant species richness or alter community composition as we predicted, interactions between soil disturbances and fire significantly altered the dominance structure of this North American tallgrass prairie. Interestingly, our results suggest that spatial and tempo-

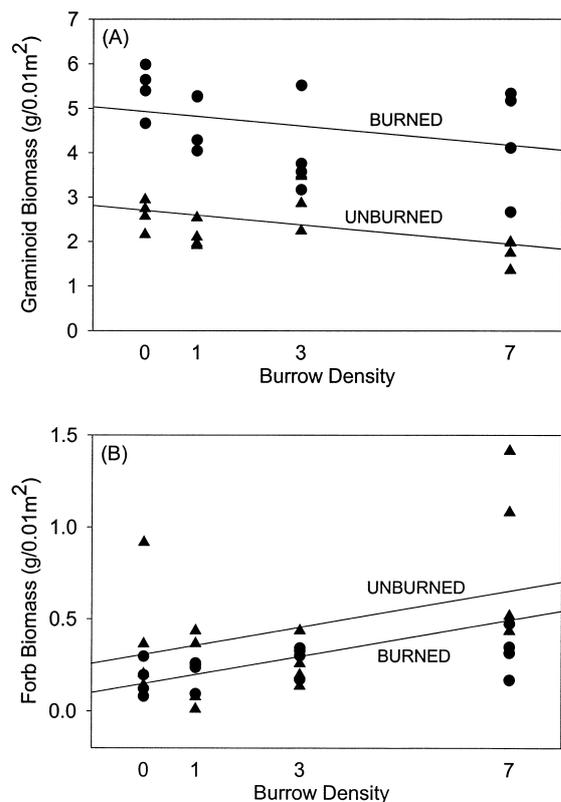


Figure 2. Effects of simulated burrow density on mean graminoid biomass ($\text{g}/0.01\text{m}^2$) in (A) burned and (B) unburned plots and mean forb biomass ($\text{g}/0.01\text{m}^2$) in (C) burned and (D) unburned plots. Simulated burrow disturbance treatments are 0, 1, 3, and 7 burrows ($n = 4$ each burn treatment) per 2.5 m sampling transect. Vegetation in each plot was clipped in twenty-five 0.01 m^2 contiguous quadrats along each simulated burrow disturbance transect. Circles represent biomass data in burned plots, triangles represent biomass data in unburned plots, and lines represent least-squares regressions (see Table 2 for statistics).

ral variation in richness caused by gopher activity is primarily driven by graminoids. This fire*gopher disturbance effect on community structure is in sharp contrast to vegetation responses to fire*ungulate grazer interactions where the major effects are associated with changes in forbs (Collins et al. 1998; Hartnett and Fay 1998; Knapp et al. 1999). Moreover, these effects became more pronounced with time at larger sampling scales, thereby indicating small-scale soil disturbances influence plant community structure in ways that have been previously unappreciated.

Simulated burrow effects on community structure

The lack of an effect of simulated burrow densities on species richness was surprising. There were no

significant effects of different burrow densities or fire on total-plant species richness, however, fire had a significant effect on functional group richness. In both 1995 and 1996, forb species richness was higher in annually burned plots while graminoid species richness was higher in unburned plots. Other researchers have found decreased forb species richness in spring burned areas because fire favors the dominant C_4 grasses (Knapp and Seastedt 1986; Gibson and Hulbert 1987; Collins and Gibson 1990).

Total-plant biomass along simulated burrow transects was predictably greater in burned than unburned plots (Knapp and Seastedt 1986; Knapp et al. 1998), but total-plant biomass appeared to be unaffected by simulated burrow density. Separately examining the contributions of graminoid and forb species to total-plant biomass showed graminoid biomass was lower in unburned than burned plots. Moreover, graminoid biomass in both burned and unburned plots decreased with increased burrow density. Forb responses were opposite. Forb biomass was higher in unburned than burned plots and forb biomass increased with burrow density in both burned and unburned plots. The magnitude of this effect appeared greater in unburned than burned plots suggesting that strong competitive effects of C_4 grasses in frequently burned prairie constrained forb responses to burrow disturbances (Gibson and Hulbert 1987; Hartnett and Fay 1998). In unburned prairie, where grasses are less competitively dominant, colonization opportunities for establishment of additional forbs are still limited, explaining low richness values and lack of compositional shifts, but pre-existing forbs are capable of more fully exploiting altered resource conditions created by burrows. Because increased biomass is often an indirect assessment of increased fecundity and plant fitness in grassland forbs (Hartnett 1990; Bazzaz 1996), these subtle responses to burrow disturbances may have long-term effects on the maintenance and regulation of grassland community structure.

It is interesting to note that while graminoid biomass was higher in burned compared to unburned plots, graminoid species richness was lower in burned compared to unburned plots. Conversely, forb biomass was lower on burned plots compared to unburned plots, while forb species richness was higher on burned plots compared to unburned plots. Whether this pattern denotes a trade-off between functional group richness and biomass is unclear and merits further investigation (e.g. Korner (1994); Smith et al. (1997)).

Table 2. Multiple regression analysis for effects of fire (burned or unburned) and simulated burrow density (0, 1, 3 or 7 burrows/2.5 m²) on (A) graminoid and (B) forb biomass.

Variable	Coefficient	1 SE	Std. Coeff.	t-value	P-value
(A) Graminoid ^a					
Intercept	2.687	0.237	2.687	11.335	<0.0001
Fire	2.235	0.271	0.817	8.237	<0.0001
Burrow density	-0.111	0.051	-0.218	-2.203	0.0357
(B) Forb ^b					
Intercept	0.302	0.078	0.302	3.858	0.0006
Fire	-0.188	0.090	-0.323	-2.095	0.0450
Burrow density	0.049	0.017	0.455	2.953	0.0062

ANCOVAs were not significant for the interaction of fire and burrow density (graminoid mass: $F_{1,28} = 0.159$; forb mass: $F_{1,28} = 2.99$) but main effects were significant. ^a $F_{2,31} = 36.35$, $r^2 = 0.715$, and $p < 0.0001$. ^b $F_{2,31} = 6.56$, $r^2 = 0.311$, and $p = 0.0045$.

Table 3. Mean (± 1 SE) total-plant, graminoid and forb species richness (0.01 m⁻²) at different transect sampling positions across simulated mounds in (A) 1994, (B) 1995, and (C) 1996 and results of analysis of variance (repeated measures for 1995 and 1996). Variables are: Fire = burn manipulation (burned or unburned); Pos = transect sampling positions (Und, undisturbed; Adj, adjacent to mound; Mnd, directly on mound); and Time = June and August sampling periods in 1995 and 1996 (not shown).

Richness	Burned			Unburned			Anova		
	Und (n = 18)	Adj (n = 18)	Mnd (n = 18)	Und (n = 18)	Adj (n = 18)	Mnd (n = 18)	Fire	Pos	Fire \times Pos
(A) 1994									
Total	3.78 \pm 0.30	3.53 \pm 0.27	0.33 \pm 0.11	3.67 \pm 0.22	3.58 \pm 0.21	0.33 \pm 0.13	ns	****	ns
Graminoid	2.56 \pm 0.24	2.50 \pm 0.20	0.28 \pm 0.09	2.58 \pm 0.15	2.53 \pm 0.16	0.25 \pm 0.10	ns	****	ns
Forb	1.22 \pm 0.16	1.03 \pm 0.20	0.06 \pm 0.04	1.08 \pm 0.12	1.06 \pm 0.13	0.08 \pm 0.05	ns	****	ns
(B) 1995									
Total	3.35 \pm 0.12	3.60 \pm 0.12	3.08 \pm 0.12	3.53 \pm 0.13	3.52 \pm 0.12	2.98 \pm 0.12	ns	***	ns
Graminoid	2.31 \pm 0.09	2.45 \pm 0.09	2.15 \pm 0.08	2.35 \pm 0.09	2.34 \pm 0.08	2.09 \pm 0.10	ns	*	ns
Forb	1.04 \pm 0.07	1.15 \pm 0.08	0.94 \pm 0.07	1.18 \pm 0.07	1.18 \pm 0.07	0.89 \pm 0.07	ns	**	ns
(C) 1996									
Total	3.25 \pm 0.11	3.35 \pm 0.11	3.21 \pm 0.11	3.19 \pm 0.10	3.08 \pm 0.10	3.20 \pm 0.11	ns	ns	ns
Graminoid	2.23 \pm 0.09	2.43 \pm 0.10	2.33 \pm 0.08	2.38 \pm 0.08	2.34 \pm 0.08	2.30 \pm 0.09	ns	ns	ns
Forb	1.02 \pm 0.06	0.91 \pm 0.07	0.89 \pm 0.07	0.81 \pm 0.06	0.75 \pm 0.06	0.91 \pm 0.07	<i>o</i>	ns	ns

ns: not significant; *o*: 0.05 < $p < 0.1$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; ****: $p < 0.0001$

Simulated mound effects on community structure

Interactions between simulated mounds and fire also generated interesting effects on vegetation structure. Total-plant species richness was locally (0.01 m²) reduced on mounds compared to undisturbed vegetation, however, this transient effect was no longer apparent after two years. Also, there were no striking effects of mound density/dispersion pattern on richness at this local patch scale until the third year of study. This response was driven by a markedly lower total-plant species richness in the unburned high density/clumped mound treatment (HC) and was more pronounced at a larger sampling scale (0.2 m²).

Significant effects of mound density/dispersion patterns became strongly manifest over time at the sampling transect scale (0.2 m²) which included both the area over the soil mound and nearby vegetation. In 1995 and 1996 there were highly significant effects of burning and mound disturbance patterns on total-plant species and graminoid species richness. Most notable was the reduced total-plant and graminoid species richness on more highly disturbed plots. The principal effect in burned plots was decreased total-plant and graminoid species richness in all treatments but the lowest disturbance intensity (LC), whereas in unburned plots total-plant and graminoid species richness was markedly reduced only in the high disturbance intensity treatment (HC).

Table 4. Results of analysis of variance (repeated measures in 1995 and 1996) for total-plant, graminoid, and forb species richness in various mound disturbance patterns at (A) the local mound scale, 0.01 m² and (B) the sampling transect scale, 0.2 m² (see Figure 3). Variables are: Fire = burn manipulation (burned or unburned) and Ptn = mound disturbance pattern (see Figure 1) (Time not shown).

Richness	1994			1995			1996		
(A)	Fire	Ptn	Fire x Ptn	Fire	Ptn	Fire x Ptn	Fire	Ptn	Fire x Ptn
Total	F _{1,26} =0.01ns	F _{4,26} =0.61ns	F _{4,26} =1.4ns	F _{1,90} =0.28ns	F _{4,90} =1.1ns	F _{4,90} =2.0ns	F _{1,90} =0.01ns	F _{4,90} =3.0*	F _{4,90} =0.82ns
Graminoid	F _{1,26} =0.12ns	F _{4,26} =0.89ns	F _{4,26} =1.1ns	F _{1,90} =0.13ns	F _{4,90} =0.83ns	F _{4,90} =2.0ns	F _{1,90} =0.12ns	F _{4,90} =1.5ns	F _{4,90} =0.94ns
Forb	F _{1,26} =0.36ns	F _{4,26} =1.2ns	F _{4,26} =2.8*	F _{1,90} =0.3ns	F _{4,90} =1.8ns	F _{4,90} =2.1o	F _{1,90} =0.1ns	F _{4,90} =2.2o	F _{4,90} =0.61ns
(B)	Fire	Ptn	Fire x Ptn	Fire	Ptn	Fire x Ptn	Fire	Ptn	Fire x Ptn
Total	F _{1,26} =0.64ns	F _{4,26} =1.8ns	F _{4,26} =1.3ns	F _{1,90} =5.8*	F _{4,90} =4.2**	F _{4,90} =5.2***	F _{1,90} =0.03ns	F _{4,90} =5.7***	F _{4,90} =5.5***
Graminoid	F _{1,26} =0.32ns	F _{4,26} =0.54ns	F _{4,26} =1.2ns	F _{1,90} =2.9o	F _{4,90} =4.2**	F _{4,90} =4.9**	F _{1,90} =0.39ns	F _{4,90} =3.8**	F _{4,90} =4.0**
Forb	F _{1,26} =3.1o	F _{4,26} =1.5ns	F _{4,26} =1.4 ns	F _{1,90} =2.4ns	F _{4,90} =1.7ns	F _{4,90} =2.1o	F _{1,90} =0.29ns	F _{4,90} =2.0o	F _{4,90} =1.6ns

ns: not significant; o: 0.05 < p < 0.1; *: p < 0.05; **: p < 0.01; ***: p < 0.001

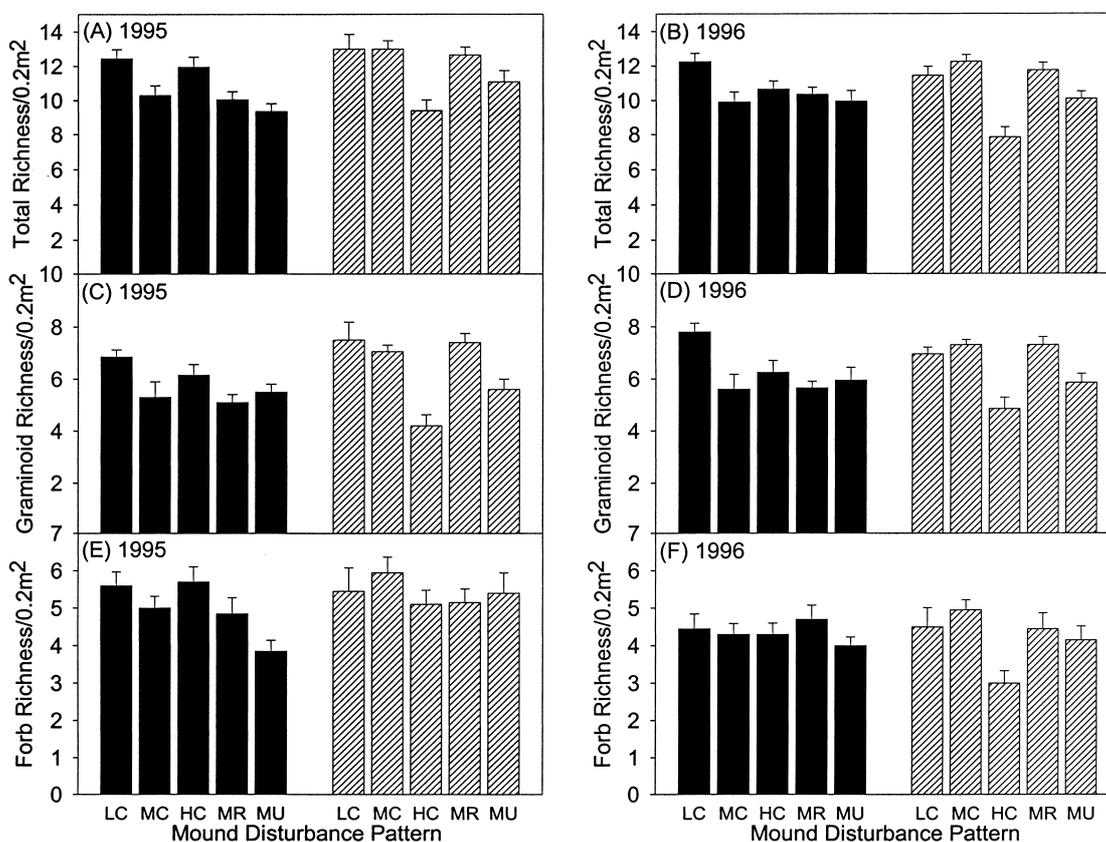


Figure 3. Total-plant species richness in (A) 1995 (n = 200) and (B) 1996 (n = 200), graminoid species richness in (C) 1995 (n = 200) and (D) 1996 (n = 200), and forb species richness in (E) 1995 (n = 200) and (F) 1996 (n = 200) at the transect sampling scale (0.2 m⁻²) in burned (solid bars) and unburned (hatched bars) plots with different simulated mound disturbance patterns (see (Table 4B) for statistics). Mound density/dispersion patterns are: low/clumped (LC); medium/clumped (MC); high/clumped (HC); medium/random (MR); and medium/uni-form (MU) respectively.

Decreased richness directly on mound disturbances occurred immediately and weakened with time, while differences among mound density/dispersion

patterns were manifest with time and became more pronounced at larger spatial sampling scales. In general, these results suggest that spatial patterns of dis-

turbance per se may not influence patterns of community structure to the same extent as the magnitude of a disturbance. In fact, disturbance intensity seemed to be the primary factor influencing vegetation in both simulated burrow and simulated mound experiments. For both studies, the most profound effects on plant community structure occurred between experimental treatments with the highest and lowest disturbance intensities. Surprisingly, no level of disturbance intensity positively affected plant species richness.

Consequences for tallgrass prairie plant diversity

Theory predicts that species composition on mound disturbances will be different from surrounding vegetation (e.g., Grubb (1977); Platt and Weis (1977); Chesson (1986); Petraitis et al. (1989)), regardless whether diversity directly on a disturbance is higher (Martinsen et al. 1990; Reader and Buck 1991), lower (Gibson 1989), or unaffected (Umbanhowar 1995) compared to the undisturbed plant community. Consequently, richness and diversity have frequently been observed to be higher at larger sampling scales that incorporate both disturbed patches and undisturbed vegetation (e.g. Platt (1975); Tilman (1983); Spencer et al. (1985); Inouye et al. (1987); Hobbs et al. (1988); Collins (1989)). Our data do not support these observations. In fact, increased mound disturbance intensity (HC) generated lower richness at larger sampling scales. No plant species were significantly restricted to disturbances nor was species composition significantly altered by burrows and mounds during this study. Thus, it does not appear that, at least in the absence of continued disturbance and concurrent herbivory, pocket gopher disturbances generate enough environmental heterogeneity in this ecosystem to provide invasion and establishment opportunities for subordinate plant species (cf. badgers in Platt (1975)). Other observations from our study further support this hypothesis. For example, burrow densities increased forb biomass but not forb richness suggesting burrows alter resource availability in ways that enhances existing forbs growth, but they do not generate colonization opportunities for additional species.

Comparisons with large-scale disturbances

Our study supports observations that small disturbances like pocket gopher mounds and burrows, while less important to the maintenance and regulation of grassland plant diversity, have subtle and potentially

influential effects on vegetation dynamics (Inouye et al. 1987; Collins 1989; Gibson 1989). Tallgrass prairie plant community structure and vegetation physiognomy have an evolutionary history of strong interactions with large-scale disturbances, such as fire and large mammal grazing, which has led to adaptations allowing competitive dominants (C_4 tallgrasses) to rapidly recover from disturbance events (Weaver 1968; Stebbins 1981; Axelrod 1985; Collins and Gibson 1990). The C_4 tallgrasses positively respond to fire in a variety of ways (Knapp and Seastedt 1986; Gibson and Hulbert 1987; Knapp et al. 1998). Frequent fires reduce plant diversity in tallgrass prairie by decreasing forb abundances, while ungulate grazers tend to reverse this effect (Collins et al. 1998; Hartnett and Fay 1998; Knapp et al. 1999). An unexpected result of our study was that graminoids showed greater variation in species richness in response to simulated pocket gopher disturbances than forbs, the opposite of vegetation responses to fire or large ungulate grazing (e.g., Collins et al. (1998); Hartnett and Fay (1998); Knapp et al. (1999)). Altered resource conditions created by mounds and burrows appear to be readily exploited by the dominant graminoids, likely via increased vegetative propagation. This limits community coexistence with less competitive species and reduces the overall effect of individual pocket gopher disturbances on plant diversity. Whereas grazing creates establishment opportunities and a competitive release for forb species by decreasing the dominance of C_4 tallgrasses, pocket gopher disturbances have a stronger effect on the frequency of subdominant graminoids. Since small soil disturbances are rapidly recolonized by expansion of nearby existing species (e.g. Parish and Turkington (1990); Umbanhowar (1995); Rogers et al. (2001)), pocket gopher mounds and burrows do not provide opportunities for establishment of subdominant species in tallgrass prairie. Consequently, the overall effect is a decrease in plant community diversity as gopher disturbance intensity increases.

Interactions between soil disturbances and fire

Our study has also revealed interesting interactions between soil disturbances and fire at larger spatial and temporal sampling scales. Interactions among disturbances can have profound effects on the manner in which plant communities respond to particular disturbances (Collins 1989; Wu and Loucks 1995; Chesson and Huntly 1997). Our results show that the in-

fluence of small soil disturbances on vegetation patterns was decreased in the presence of frequent fire. Again, this was likely due to the competitive superiority of C₄ grasses in annually burned areas. Fire increases vegetative propagation of these grasses which increases the rate of succession on soil disturbances (Gibson 1989; Collins 1989). In this manner, these findings support those of others where localized changes in community structure on a single, small disturbance are temporary and it is only through the continual process of disturbance that community alterations persist and intensify (e.g., Rapp and Rabinowitz (1985); Hobbs and Hobbs (1987); Goldberg and Gross (1988); Carson and Pickett (1990); Parish and Turkington (1990); Reader and Buck (1991)). Nevertheless, our findings do indicate that high intensities of pocket gopher disturbances can alter community structure in both burned and unburned prairie in ways that may be of increased importance over time and at larger spatial scales. The effect of these disturbance patterns on plant community structure is likely further amplified in the presence of continued gopher activity and selective herbivory.

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