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Effects of Plains Pocket Gopher (Geomys bursarius) Disturbances on Tallgrass-prairie Plant Community Structure

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ABSTRACT.—Our objective was to evaluate the effects of soil disturbances created by the plains pocket gopher (*Geomys bursarius*) on the structure of a tallgrass-prairie plant community. We predicted that soil mounds and burrows would provide sites for the establishment of subordinate plant species, thereby increasing regional plant community richness in this ecosystem that is highly dominated by perennial C_4 tallgrasses. Our results, however, revealed that plant species richness and biomass were temporarily decreased or unaffected in areas disturbed by gophers. Moreover, the species found locally on mounds and burrows were a subset of the dominant plants present in the undisturbed plant community and graminoids were more frequent on disturbances than forbs. Our results indicate that perennial graminoids predominate in the rapid recovery of vegetation on pocket gopher mounds and burrows. This preempts the establishment of less frequent forbs and, contrary to our predictions, decreases plant community richness.

INTRODUCTION

North American pocket gophers (Geomyidae) are fossorial rodents recognized as important agents of soil alteration in grasslands (*e.g.,* Grinnell, 1923; Mielke, 1977; Andersen, 1987; Huntly and Reichman, 1994). They build extensive belowground foraging burrows and deposit tailings on the soil surface as mounds (Andersen, 1987; Reichman and Smith, 1990; Benedix, 1993). Recently, pocket gophers have been labeled ''ecosystem engineers'' because their physical activities modify, maintain or create habitats and alter resource availability for other organisms (*e.g.,* Huntly and Inouye, 1988; Moloney *et al.*, 1992; Jones *et al.*, 1994). Local plant responses to the burrow and mound disturbances created by pocket gophers are well documented in some ecosystems (*e.g.,* McDonough, 1974; Hobbs and Mooney, 1985; Spencer *et al.*, 1985; Huntly and Inouye, 1988; Martinsen *et al.*, 1990). Mounds are thought to influence plant species diversity by acting as seed catchments (Laycock, 1958; McDonough, 1974; Hobbs and Mooney, 1995) and providing space and resources for less competitive, colonizer species to become established (*e.g.,* Schaal and Leverich, 1982; Hobbs and Hobbs, 1987; Goldberg and Gross, 1988; Reader and Buck, 1991; Davis *et al.*, 1995). Mound disturbances can be primary sites of establishment for subdominant forbs and ruderal plants. Consequently, gopher mounds often undergo gap phase dynamics that differ from the surrounding plant community (Foster and Stubbendieck, 1980; Inouye *et al.*, 1987; Martinsen *et al.*, 1990; Stromberg and Griffin, 1996). By creating a mosaic of patches with various resource characteristics and successional ages, pocket gopher mounds frequently enhance resource heterogeneity and create distinctive spatial patterns in the plant community (*e.g.,* Hobbs and Mooney, 1985; Reichman *et al.*, 1993; Moloney and Levin, 1996). This heterogeneity likely is responsible for the increases in overall community richness at larger scales attributed to pocket gopher activity (*e.g.,* Tilman, 1983; Spencer *et al.*, 1985; Inouye *et al.*, 1987; Collins, 1989) despite plant species richness being

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increased (Andersen and MacMahon, 1985; Martinsen *et al.*, 1990; Reader and Buck, 1991), decreased (Gibson, 1989) or unaffected (Umbanhowar, 1995) directly on a mound.

Because burrows are less conspicuous and more difficult to experimentally manipulate than mounds, their impact on overlying vegetation has received considerably less attention. The most significant effects observed over burrows result from the consumption of belowground plant parts by gophers (Andersen, 1987; Reichman and Smith, 1990; Benedix, 1993), although the effect of the altered soil environment surrounding a burrow *per se* can influence plant responses even in the absence of herbivory (Reichman and Smith, 1985; Reichman, 1988; Reichman *et al.*, 1993). Plant biomass overlying abandoned burrows can remain lower than undisturbed areas for several years due to impeded root regrowth and lower nutrient and water availability (Reichman and Smith, 1985; Reichman, 1988). As a result, plants in areas adjacent to burrows can benefit from reduced competition and increased availability of resources (Reichman *et al.*, 1993).

We designed a study to examine the successional dynamics of mounds and burrows in an area recently abandoned by pocket gophers. We predicted: (1) In accordance with gap dynamics theory, soil mounds and burrows in the North American tallgrass prairie would disrupt the dominant C_4 grass canopy and create ''regeneration niches'' (*e.g.,* Platt, 1975; Grubb, 1977; Pickett, 1980; Denslow, 1985) for establishment of subdominant forbs and ruderal plant species, thereby promoting species coexistence and increasing overall community richness; (2) Species composition and plant productivity, particularly for forbs, would be more variable directly on mounds and burrows than in areas adjacent to disturbances or in nearby undisturbed prairie due to resource heterogeneity and microsuccessional turnover of species; (3) Areas adjacent to the mounds and burrows would significantly differ in productivity and composition as a result of ''competition-induced waves'' (Reichman *et al.*, 1993).

METHODS AND MATERIALS

Site description.—Our research was conducted at Konza Prairie Biological Station, a 3487 ha tallgrass-prairie preserve located in the Flint Hills region of northeastern Kansas (39°05′N, 96°35′W). Plant community composition and soil depth are important determinants of pocket gopher distribution on Konza Prairie (Benedix, 1993). In April 1993 we selected an upland site with deep soils and an active population of pocket gophers for this experiment. The microtopographical hummocks created by the presence of old mounds indicated that pocket gophers had been active in the area for many years. The site had been burned periodically before the start of the experiment and was burned annually in the spring for the duration of the study. Spring burning is the primary experimental treatment on Konza Prairie (Knapp *et al.*, 1998).

Due to heavy rains that inundated the Midwest in spring and early summer of 1993, it appeared that pocket gophers had either emigrated to drier land or drowned in their burrow systems, many of which contained standing water. Pocket gophers have been reported to drown in their underground tunnels (Reichman and Smith, 1990). Whatever their fate, pocket gopher activity decreased throughout 1993 and by spring 1994 no new mound-building activity was observed. The recent disappearance of pocket gophers from the site provided us with a novel opportunity to study successional changes that occurred on newly created mounds and burrows in the absence of concurrent herbivory and continually created disturbances.

Experimental design.—In April 1993, before the peak of pocket gopher mound-building activity, we established eight 4 m × 128 m belt transects in our 1.1 ha study area. We began monitoring pocket gopher activity on the site in May 1993. At that time new soil mounds

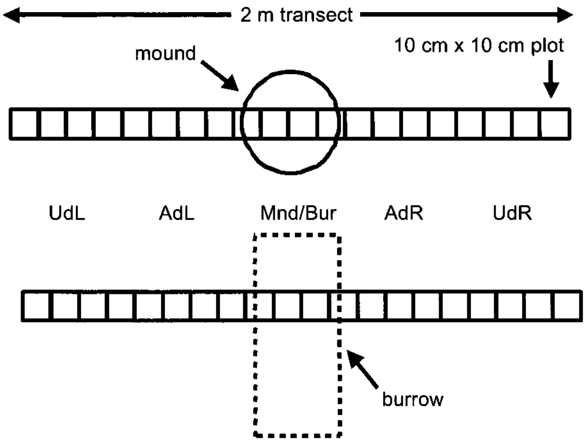

FIG. 1.—Diagram of 10 cm × 10 cm × 2 m sampling transects used to measure plant community composition, species richness and vegetation biomass across pocket gopher mounds and burrows. Transect sampling positions were derived by averaging five groups of four contiguous 10 cm × 10 cm plots. Transect sampling positions are: UdL = quadrats 1–4 in the undisturbed plant community; AdL = quadrats 5–8 adjacent to the disturbance; Mnd/Bur = quadrats 9–12 centered on the mound or burrow, respectively; AdR = quadrats 13–16 adjacent to the disturbance; and UdR = quadrats 17–20 in the undisturbed plant community

indicated a minimum of 14 active pocket gophers. We mapped new mounds biweekly and selected 39 mounds in these belt transects for studying plant species composition from August 1993 until August 1995. We selected another 30 new mounds that were not located in the belt transects for sampling vegetation biomass in September 1993. Mound diameters ranged from 20 cm to 40 cm in diameter and typically were 10 cm high.

We located burrow segments by probing the soil with a thin steel rod. Once a segment of burrow was located, a small hole was excavated and a plumber's sewer snake with several large lug nuts attached to the end was inserted into and advanced through the tunnel. We used a metal detector to follow the steel snake and mapped 1-m long burrow segments. We mapped 36 burrow segments in the belt transects by July 1993 to be used for studying plant species composition and another 20 segments not in the belt transects to be used for sampling vegetation biomass across burrows in September 1994.

Sampling methods.—We established permanent 2-m sampling transects (marked by wire flags) oriented north-south across the center of each mound and measured plant community composition by recording the presence of each species in each of 20 contiguous 0.01 m^2 plots (Fig. 1). Likewise, we established permanent 2-m transects centered perpendicular to each burrow and recorded the presence of each species in each of 20 contiguous 0.01 m^2 plots (Fig. 1).

Due to heavy storms and flooding at the study site, we did not begin sampling plant community composition across mounds and burrows until early August 1993. Plant community sampling in 1994 and 1995 was conducted in late May and again in mid-August to capture phenological shifts in species composition during the growing season. We do not believe that many species were missed in 1993 because the cold, cloudy and wet conditions early in the growing season slowed many species' growth. Proper species identification occasionally was difficult because of morphological similarities in vegetative characteristics.

Thus, some closely related taxa that could not be clearly and consistently identified were lumped (*e.g., Sporobolus* spp. and Cyperaceae, all sedge species in the genera *Carex* and *Cyperus*). Nomenclature follows the Great Plains Flora Association (1986).

We measured aboveground net primary production across mounds and burrows by clipping all aboveground vegetation in 20 contiguous 0.01 m^2 plots identical to those used for sampling plant species composition. No clipping occurred in plots used for sampling plant species composition until the completion of the experiment to avoid altering competitive relationships and influencing the successional dynamics on mounds and burrows. The mounds selected for harvesting plant biomass were clipped in September 1993, but the burrows selected were not clipped until September 1994. We did not clip these plots until the second season to provide us with a better indication of the effect of the burrow *per se* (*i.e.,* nutrient depletion or dessication) on productivity in the absence of root herbivory. In September 1995, after the final vegetation census, we clipped biomass samples on 21 of the original 39 mounds and 23 of the 36 original burrows. Only a subset of these samples were clipped because a mid-September frost killed many plants and prevented us from collecting biomass from all of the original transects. Biomass was always harvested after peak production, but before the onset of the major seasonal senescence. We separated graminoid and forb samples for each 0.01 m^2 plot and dried the tissue at 60 C for 72 h before weighing.

Data analysis and statistical procedures.—In order to increase the precision of our sampling estimates and reduce small-scale variability we combined the 20 contiguous 0.01 m^2 plots along each 2-m transect centered on mounds and burrows into five transect sampling positions: UdL = quadrats 1–4 in the undisturbed plant community; AdL = quadrats 5–8 adjacent to the disturbance; Mnd/Bur = quadrats 9–12 centered on the mound or burrow, respectively; AdR = quadrats 13–16 adjacent to the disturbance; and UdR = quadrats 17–20 in the undisturbed plant community (Fig. 1). Means were calculated for total-plant, graminoid and forb species richness and biomass by using four contiguous 0.01 m^2 plots from each transect sampling position. Replication was achieved by sampling across multiple, independent mounds and burrows. The five transect sampling positions were kept separate for all analyses (despite replication of Ad and Ud positions) in order to maintain a balanced experimental design for statistical analyses and better discern the presence of competition-induced waves. The data also were analyzed using individual 0.01 m^2 plots and pairs of 0.01 m^2 plots but are not reported here because considerable small-scale variability obscured plant responses to pocket gopher mounds and burrows.

Analysis of variance was used to determine if statistical differences occurred among transect sampling positions within sampling dates and pairwise comparisons of the transect sampling positions were calculated with Fisher's PLSD (StatView 5.0, SAS Institute, Cary, North Carolina). Statistically significant differences are reported at $\alpha < 0.05$ level unless otherwise stated.

RESULTS

Effects on plant community composition.—The most frequent plant species across mounds and burrows in August 1993 were the same among the various transect sampling positions (Table 1). The composition and relative frequencies of plant species remained the same in 1994 and 1995 (not shown). Plant species that recolonized mounds and burrows were a subset of the dominant species in the undisturbed plant community. Of the most frequent species in transect sampling positions across mounds and burrows, nine were graminoids and four were forbs (Table 1). The most frequent species at all transect sampling positions were the graminoids *Andropogon gerardii, Sorghastrum nutans* and individuals in the family Cyperaceae. No species was significantly positively or negatively affected by pocket gopher

TABLE 1.—Percent frequency of the thirteen most common plant species in five transect sampling positions across pocket gopher mounds and burrows in 1993. Different letters indicate a significant difference ($P < 0.05$) among transect sampling positions[1]

	Mounds					Burrows				
Plant species	UdL	AdL	Mnd	AdR	UdR	UdL	AdL	Bur	AdR	UdR
Graminoids										
Andropogon gerardii	82.7	82.1	73.1	76.3	78.8	68.8	78.5	72.2	68.1	72.9
Andropogon scoparius	9.0	15.4	5.1	8.3	10.9	17.4	13.9	13.2	12.5	13.2
Bouteloua curtipendula	4.5	5.8	7.1	6.4	6.4	2.8	2.1	4.2	4.2	2.8
Cyperaceae spp.	50.6	47.4	44.9	49.4	50.0	56.3	51.4	59.0	53.5	57.6
Dichanthelium oligosanthes	10.9ab	17.3a	6.4b	10.9ab	19.2a	9.7	7.6	7.6	6.3	16.0
Panicum virgatum	17.9	16.7	12.8	21.8	22.4	16.0	20.8	24.3	19.4	18.8
Poa pratensis	26.3	19.9	14.1	15.4	20.5	34.7	33.3	31.3	34.0	31.9
Sorghastrum nutans	54.5	56.4	43.6	51.9	55.1	65.3	54.9	60.4	55.6	53.5
Sporobolus spp.	3.8	3.8	1.3	4.5	3.8	9.0	8.3	4.9	10.4	6.9
Forbs										
Ambrosia psilostachya	7.1	5.1	3.2	5.1	5.8	5.6	10.4	6.3	11.1	5.6
Artemisia ludoviciana	12.2	5.8	7.1	5.1	5.8	12.5	14.6	11.8	17.4	13.2
Aster ericoides	15.4	17.3	7.7	15.4	14.1	22.9	21.5	22.2	18.8	26.4
Solidago missouriensis	13.5	9.0	7.1	7.1	3.2	8.3	9.0	10.4	8.3	4.9

[1] UdL = quadrats 1–4 in the undisturbed plant community; AdL = quadrats 5–8 adjacent to the disturbance; Mnd/Bur = quadrats 9–12 centered on the mound or burrow, respectively; AdR = quadrats 13–16 adjacent to the disturbance; and UdR = quadrats 17–20 in the undisturbed plant community (*see* Fig. 1)

mounds or burrows during the study. The only statistically significant differences in frequency of a particular species among transect sampling positions across mound disturbances was for *Dicanthelium oligosanthes* in August 1993 ($F_{4,190} = 2.54$; $P = 0.04$) and May 1995 ($F_{4,190} = 3.86$; $P = 0.005$). However, pairwise comparisons revealed that the frequency of *D. oligosanthes* was not significantly different on mounds than all other transect sampling positions (1993, Table 1; 1995, not shown). There were no significant differences in frequencies of any species among transect sampling positions across burrows in 1993 (Table 1) or during the 1994 and 1995 sampling dates (not shown).

Ambrosia artemisifolia had a frequency over 5% in some transect sampling positions across mounds and burrows during the 1994 and 1995 sampling dates, but was not significantly statistically affected by transect sampling positions. Occurrence of all other plant species was rare (defined as less than 5% frequency in all transect sampling positions and sampling dates). Rare species recorded included nine perennial grasses and 43 forbs, 8 of which were annuals. Two of these rare species, the perennial forbs *Cirsium undulatum* and *Lespedeza capitata,* were recorded only on mounds. Three rare species, the annual forbs *Hedeoma hispida* and *Plantago patagonica* and the perennial forb *Oxalis violacea,* were recorded only on burrows. However, the rarity of these species precluded any meaningful individual statistical comparisons of their frequencies and generalizations regarding their occurrence. None of the nonnative weeds commonly found on Konza Prairie (Freeman, 1998) were located on mounds or burrows.

Effects on plant species richness.—Total-plant and graminoid species richness were significantly lower on newly created mounds than adjacent to the mound or in the undisturbed plant community in 1993 (Fig. 2, Table 2). In May and August 1994 total-plant species richness also was significantly lower on mounds than adjacent to the mound or in the undisturbed plant community (Fig. 2, Table 2). In August 1994 graminoid richness was significantly lower on mounds than adjacent to the mound or in the undisturbed plant community (Fig. 2, Table 2). In May and August 1995 there were no overall statistically significant differences among transect sampling positions across mounds (Table 2). Forb richness across mounds was not significantly different at any transect sampling positions on any sampling date (Fig. 2, Table 2). There were no statistically significant effects of burrows on total-plant, graminoid or forb richness (Table 2).

Effects on plant productivity.—Mean graminoid, forb and total-plant biomasses were significantly lower on mounds than in transect sampling positions adjacent to the mound or in the undisturbed plant community during September 1993 (Fig. 3A, Table 3A). By contrast, variation of total-plant and graminoid biomass (as measured by the coefficients of variation) were significantly greater on mounds than in transect sampling positions adjacent to the mound or in the undisturbed plant community in 1993 (Fig. 3B, Table 3A). Coefficient of variation of forb biomass was not significantly affected by mounds during any sampling date (Fig. 3B, Table 3A). By 1995 there were no statistically significant differences among mounds and transect sampling positions adjacent to the mound or in the undisturbed plant community (Table 3A).

Mean total-plant, graminoid and forb biomasses in transects across burrows were not significantly affected by transect sampling position (Table 3B), but coefficient of variation of total-plant biomass was significantly higher on burrows than the transect sampling positions adjacent to the burrow or in the undisturbed plant community in September 1994 (Table 3B). In September 1995 there were no significant differences among the coefficients of variation for the five transect sampling positions across burrows (Table 3B).

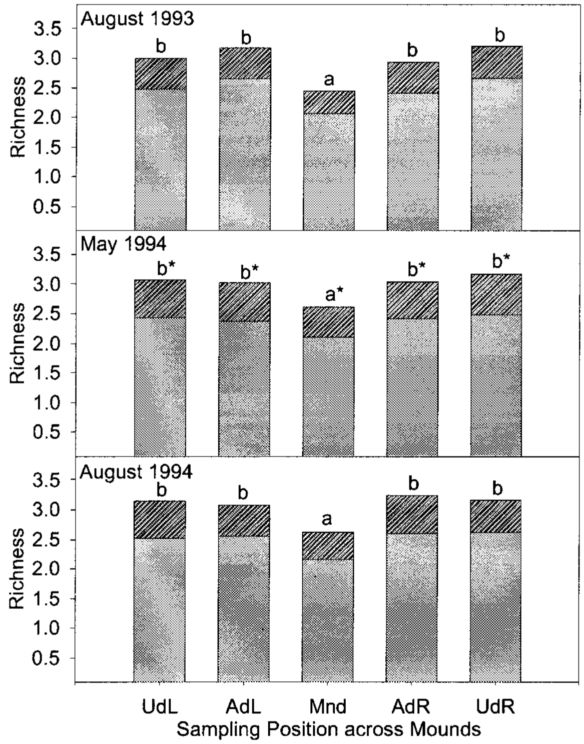

FIG. 2.—Mean richness (per 0.01 m^2) for graminoid (solid bars), forb (hatched bars) and total-plant (combined bar) species at five transect sampling positions across pocket gopher mounds (Fig. 1). Different letters on top of bars within a graph indicate a statistically significant difference at $P < 0.05$ for both total-plant and graminoid species richness (*$P < 0.1$ for graminoid species richness) among transect sampling positions. There were no significant differences between the sampling positions for forb species richness (*see* Table 2)

DISCUSSION

Our study demonstrated that plant species found on pocket gopher mounds and burrows in North American tallgrass prairie were a subset of the dominant species in the undisturbed plant community. Additionally, the richness and biomass of total-plant, graminoid and forb species either were temporarily decreased or unaffected by pocket gopher mounds and burrows. These findings are contrary to our prediction that frequency of the dominant plant species would decrease and provide opportunities for establishment of subdominant forbs and ruderals. Our prediction that plant production would be more variable directly on mounds and burrows than in areas adjacent to disturbances or in nearby undisturbed prairie was supported for total-plant and graminoid biomass on mounds and total-plant biomass on burrows. However, this variability was not due to a predicted microsuccessional turnover of species, but rather variation to amount of dominant plant species recolonizing mounds or burrows. This effect was no longer significant after 3 y. Unexpectedly, coefficient of variation in forb biomass was not significantly different on mounds or burrows at any time. These results show that in the absence of concurrent herbivory and continually created disturbances, pocket gopher mounds and burrows *per se* have only transient effects on

TABLE 2.—Analysis of variance for total-plant, graminoid and forb species richness at the five transect sampling positions across pocket gopher mounds and burrows

	Richness across mounds			Richness across burrows		
Date	Total-plant	Graminoid	Forb	Total-plant	Graminoid	Forb
August 1993	$F_{4,190}$ = 6.56****	$F_{4,190}$ = 5.02***	$F_{4,190}$ = 1.08 ns	$F_{4,175}$ = 0.07 ns	$F_{4,175}$ = 0.30 ns	$F_{4,175}$ = 0.37 ns
May 1994	$F_{4,190}$ = 3.07*	$F_{4,190}$ = 2.29 *o*	$F_{4,190}$ = 0.84 ns	$F_{4,175}$ = 0.67 ns	$F_{4,175}$ = 0.55 ns	$F_{4,175}$ = 1.77 ns
August 1994	$F_{4,190}$ = 3.53**	$F_{4,190}$ = 3.09*	$F_{4,190}$ = 1.11 ns	$F_{4,175}$ = 0.91 ns	$F_{4,175}$ = 0.36 ns	$F_{4,175}$ = 0.86 ns
May 1995	$F_{4,190}$ = 1.83 ns	$F_{4,190}$ = 1.94 ns	$F_{4,190}$ = 0.124 ns	$F_{4,175}$ = 0.40 ns	$F_{4,175}$ = 0.21 ns	$F_{4,175}$ = 0.67 ns
August 1995	$F_{4,190}$ = 1.24 ns	$F_{4,190}$ = 1.67 ns	$F_{4,190}$ = 0.72 ns	$F_{4,175}$ = 0.47 ns	$F_{4,175}$ = 0.64 ns	$F_{4,175}$ = 0.38 ns

ns = not significant; *o* = $P \leq 0.1$; * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; **** = $P \leq 0.0001$

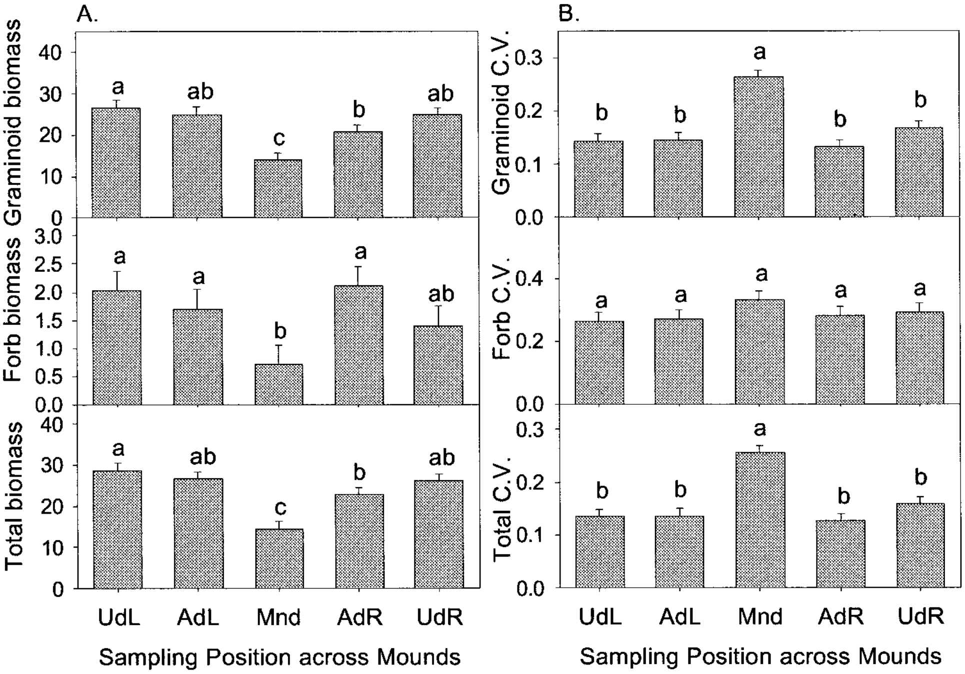

FIG. 3.—(A) Mean vegetation biomass (g/0.01m^2 ± 1 SE) and (B) coefficients of variation (CV ± 1 SE) of vegetation biomass for graminoid, forb and total-plant species at five transect sampling positions across pocket gopher mounds in September 1993. Different letters on top of bars within a graph indicates a statistically significant difference at $P < 0.05$

local richness and productivity of tallgrass prairie vegetation and do not increase regional community richness.

Pocket gopher mounds and burrows should influence plant community structure by providing space for less competitive, colonizer species to become established according to gap dynamics theory and the "regeneration niche" concept (*e.g.,* Platt, 1975; Grubb, 1977; Pickett, 1980; Denslow, 1985). In other ecosystems reduced competition and increased resource availability on soil disturbances allow species adapted to ephemeral, unpredictable environments, mostly forbs and annuals, to become established (Laycock, 1958; Schaal and Leverich, 1982; Goldberg and Gross, 1988; Martinsen *et al.*, 1990). This affects plant community structure by creating small patches containing species which typically are excluded from similar undisturbed communities (*e.g.,* Platt, 1975; Tilman, 1983; Spencer *et al.*, 1985; Huntly and Inouye, 1988). However, our results show that local plant species richness was decreased or unaffected on pocket gopher mounds and burrows and the species most frequently found on these disturbances were the dominant species in the undisturbed plant community. Mounds and burrows did not harbor a distinct guild of less frequent forbs and ruderal species as we predicted. Further, no nonnative weeds, commonly found in disturbed areas of Konza Prairie (Freeman, 1998), were found on mounds or burrows. Consequently, pocket gopher disturbances do not appear to promote higher species richness in this tallgrass prairie that is highly dominated by perennial C_4 tallgrasses. Although a few rare ruderal forbs were found only on mounds (*Cirsium undulatum* and *Lespedeza capitata*) or

TABLE 3.—Analysis of variance for total-plant, graminoid and forb vegetation biomass and coefficients of variation (CV) of vegetation biomass at the five transect sampling positions across (A) mounds and (B) burrows

A.

	Biomass across mounds			CV for biomass across mounds		
Date	Total-plant	Graminoid	Forb	Total-plant	Graminoid	Forb
1993	$F_{4,145}$ = 10.14****	$F_{4,145}$ = 8.84****	$F_{4,145}$ = 2.65*	$F_{4,145}$ = 16.49****	$F_{4,145}$ = 15.63****	$F_{4,145}$ = 0.91 ns
1995	$F_{4,100}$ = 0.84 ns	$F_{4,100}$ = 0.79 ns	$F_{4,100}$ = 0.13 ns	$F_{4,100}$ = 0.17 ns	$F_{4,100}$ = 0.68 ns	$F_{4,100}$ = 0.78 ns

B.

	Biomass across burrows			CV for biomass across burrows		
Date	Total-plant	Graminoid	Forb	Total-plant	Graminoid	Forb
1994	$F_{4,95}$ = 1.47 ns	$F_{4,95}$ = 1.18 ns	$F_{4,95}$ = 0.85 ns	$F_{4,95}$ = 2.62*	$F_{4,95}$ = 2.20 *o*	$F_{4,95}$ = 0.80 ns
1995	$F_{4,110}$ = 0.82 ns	$F_{4,110}$ = 0.79 ns	$F_{4,110}$ = 0.68 ns	$F_{4,110}$ = 0.52 ns	$F_{4,110}$ = 0.38 ns	$F_{4,110}$ = 1.06 ns

ns = not significant; *o* = $P \leq 0.1$; * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; **** = $P \leq 0.0001$

only over burrows (*Hedeoma hispida, Oxalis violacea* and *Plantago patagonica*) further studies are necessary to determine whether they require disturbances for establishment, especially as there were numerous other rare grasses and forbs, including some annuals, that were found with low frequencies in the undisturbed plant community but were not present on mounds and burrows. Local effects of pocket gopher mounds and burrows on species richness were statistically indistinguishable on mounds and burrows, adjacent to mounds and burrows and in the undisturbed plant community after two years.

Local effects of mounds and burrows on annual aboveground plant production also were temporary. Vegetation biomass was reduced and variability in biomass was increased on new mounds, but after three growing seasons there were no statistical differences among transect sampling positions on mounds and burrows, adjacent to mounds and burrows and in the undisturbed plant community after three years. A ''competition-induced biomass wave'' emanating away from mounds and burrows (sensu Reichman *et al.*, 1993) was not apparent in this study even when the 0.01 m^2 plots were analyzed separately or in pairs (not shown).

The only effect of burrows on biomass was a temporary increase in the coefficient of variation of total-plant biomass. Our expectations that even in the absence of herbivory, nutrient limitation and root dessication would affect plant recovery over abandoned burrow systems (Reichman and Smith, 1985; Reichman, 1988) were not supported. Species richness and plant biomass were not markedly affected by burrows. This indicates that, in the absence of repeated disturbance or herbivory, the plasticity of plant root systems and possibly the physiological integration of interconnected ramets equalizes plant responses over a locally heterogeneous soil environment (*e.g.,* Hartnett and Bazazz, 1985; Caraco and Kelly, 1991). The latter mechanism is likely because the large majority of dominant tallgrass-prairie grasses and forbs are rhizomatous. It also is possible that the impact of burrows on vegetation structure is expressed primarily belowground and these root disturbances are not pronounced enough to influence aboveground vegetation. Several studies examining above- and belowground herbivory suggest that plant responses to tissue consumption are asymmetric. Although aboveground defoliation frequently influences belowground root growth, root herbivory typically does not have the reverse effect (*e.g.,* Gange and Brown, 1989; Moran and Whitham, 1990; Denno *et al.*, 1995).

Two complementary explanations best describe the modest and transient effects of pocket gopher mounds and burrows on the local vegetation structure of tallgrass prairie and the absence of a suite of ruderal species establishing on these disturbances. Firstly, a lack of propagules from external source pools for the colonizer species may limit potential for less competitive species to become established on mounds and burrows. Restricted dispersal distances in undisturbed vegetation and complex life histories of many grassland species reduce the total number of species which can recolonize a disturbance at any given time (*e.g.,* Shmida and Ellner, 1984; Huston, 1994; Hurtt and Pacala, 1995; Tilman, 1997; Turnbull *et al.*, 2000). Secondly, clonal spread by neighboring plants can be the primary mechanism responsible for revegetation of disturbed areas in some grassland habitats (Collins, 1989; Gibson, 1989; Umbanhowar, 1995). Also, vegetative regrowth from roots and rhizomes of plants buried by soil mounds can rapidly refill space created by small disturbances, preventing less competitive species from becoming established (*e.g.,* Laycock, 1958; Foster and Stubbendieck, 1980; Goldberg and Gross, 1988; Gibson, 1989). Because the dominant grasses in this system, particularly *Andropogon gerardii* and *Sorghastrum nutans,* reproduce primarily by vegetative means, available space created by pocket gopher activity appears to be rapidly usurped by vegetative regrowth of C_4 tallgrasses. Fast rates of competitive displacement decrease coexistence of plant species, thus diminishing overall community richness (Tilman, 1988; Huston, 1994).

We expected pocket gopher mounds and burrows to have an early successional stage dominated by subdominant forbs and ruderal plant species; however, mounds and burrows did not undergo this transition. Rather, the most frequent plant species on mounds and burrows were a subset of the dominants found in the undisturbed plant community. Moreover, graminoid species were more frequent than forb species on mounds and burrows. This suggests a rapid filling-in of disturbances by vegetative reproduction of dominant tallgrasses and regrowth of vegetation buried by soil mounds rather than the microsuccession predicted by gap dynamics theory or the ''regeneration niche'' concept (Grubb, 1977; Pickett, 1980; Denslow, 1985) that has been documented for small-scale disturbances in other ecosystems (*e.g.,* Platt, 1975; Hobbs and Mooney, 1985; Spencer *et al.*, 1985; Goldberg and Gross, 1988; Huntly and Inouye, 1988; Kaczor and Hartnett, 1990). An interesting exception is the high percentage of Cyperaceae found on mounds and burrows. Although these species can reproduce vegetatively, they are also the most abundant plants in the soil seed bank of this tallgrass prairie (Rogers, 1998). Hence, they are not as recruitment limited as species dependent solely on seed rain for dispersal.

In a recent reexamination of effects of disturbances on community structure in other ecosystems, Mackey and Currie (2000, p. 483) stated that there was ''. . . little reason to believe that disturbance should play more than a subtle role in determining patterns of diversity in nature, contrary to most contemporary literature.'' Our results support this assertion by illustrating that the impact of mounds and burrows on tallgrass-prairie plant community structure is minimal in the absence of continued pocket gopher activity. The dynamic effects of burrow excavation and backfilling accompanied by regular surface mound deposition and the long-term effects of selective herbivory are likely to have a more profound influence on patterns of abiotic resources and plant community dynamics than temporary effects of a single disturbance event. Tallgrass prairie is an ecosystem with a long evolutionary history of large-scale disturbances, such as fire, drought and herbivory associated with large mammal grazing (Weaver, 1968; Axelrod, 1985; Collins and Wallace, 1990; Knapp *et al.*, 1998, 1999). The resilience of dominant tallgrass-prairie plant species to these disturbances limits coexistence with less competitive species, thus, limiting the overall effect of individual pocket gopher disturbances on plant community structure.

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