

EFFECTS OF PLATEAU ZOKORS (*MYOSPALAX FONTANIERII*) ON PLANT COMMUNITY AND SOIL IN AN ALPINE MEADOW

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Effects of plateau zokors (*Myospalax fontanierii*) on seasonal above- and belowground plant biomass, plant species diversity, and soil moisture and organic matter were examined at an alpine meadow site in Qinghai Province, People's Republic of China. Above- and belowground biomass increased significantly in areas where zokors were removed or burrow systems were abandoned for 5 years compared with areas that zokors had occupied for >10 years. Biomass of monocotyledons was reduced greatly, but biomass of nonpalatable dicotyledons increased significantly, in occupied areas. Diversity of dicotyledons, monocotyledons, and total plants in unoccupied areas was significantly greater than in occupied or abandoned areas. Vegetation cover and height in occupied areas were significantly less than in unoccupied and abandoned areas. No consistent effect by zokors on soil moisture and organic matter was observed.

Key words: *Myospalax fontanierii*, plant biomass, plant species diversity, plateau zokor, soil moisture, soil organic matter

Small burrowing mammals alter a variety of vegetation and soil characteristics, including species composition, above- and belowground biomass, soil exchange capacity, water-holding capacity, organic matter, and inorganic nutrient levels (Chew 1978; Grant 1974; Huntly and Inouye 1988; Inouye et al. 1987; Laundré 1998; Reichman and Seabloom 2002). Subterranean herbivorous rodents forage on plants underground or pull them down from below, consuming roots or entire plants. Meanwhile, they continuously excavate underground tunnels and deposit soil aboveground (Gettinger 1984; Reichman and Smith 1985). These activities may have negative or positive effects on vegetation and physical and chemical properties of soil, especially when coupled with high densities of herbivores in steppe, prairie, and meadow habitats (Anderson

and MacMahon 1981; Reichman et al. 1982; Tilman 1983; Williams et al. 1986).

Plateau zokors, *Myospalax fontanierii*, are highly specialized subterranean herbivores broadly distributed in farm, prairie, alpine prairie, and meadow habitats in Qinghai-Tibet plateau, People's Republic of China (Zhang et al. 1999). They exhibit several ecological characteristics that could influence plant communities, soil moisture, organic carbon, or soil nutrients. Unlike aboveground herbivores, plateau zokors spend their entire lives in underground burrow systems. The distribution and population density of plateau zokors, the only subterranean rodent species in Qinghai-Tibet plateau, are limited by elevation, vegetation, precipitation, and anthropogenic disturbance (Zhang et al. 1999). Because plateau zokors traditionally have been viewed as pests and competitors with cattle for rangeland resources, eradication programs

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to reduce the populations have been carried out by local governments and farmers every year. However, zokors still occur on approximately 3.8×10^6 ha (nearly 11.4% of total available grassland), at average densities of 5–20 animals/ha in the grassland of Qinghai Province (Zhang et al. 1999).

After many years of occupation, plateau zokors have created large, distinct areas within the grassland matrix by burrowing and mound building, where ecosystem processes may proceed at rates different from those outside unoccupied areas. However, the current status of zokors as a farming and agricultural pest in Qinghai-Tibet and their natural role as agents of vegetation disturbance have not been well documented (Wang and Fan 1987; Zhang et al. 1998).

The goal of this research was to assess the impact of burrow activity by plateau zokors on seasonal plant biomass, species diversity, soil moisture, and organic matter of alpine meadows in the region of Qinghai-Tibet plateau after occupation for different lengths of time. Specific objectives were to determine the effect of digging and grazing activities of plateau zokors on plant biomass, community structure, and soil characteristics and to assess the effect of areas created by plateau zokors on ecosystem processes in alpine meadows. We hypothesized that long-term occupation by plateau zokors reduced both above- and below-ground plant biomass, soil moisture, and organic matter. These effects may lead to further alterations of nutrient cycling and trophic dynamics in this alpine meadow ecosystem.

MATERIALS AND METHODS

This study was conducted from 1989 to 1998 at the Haibei Alpine Meadow Ecosystem Research Station, the Chinese Academy of Sciences, Menyuan County, approximately 155 km N of Xining, the capital of Qinghai Province, People's Republic of China (37°29'–37°45'N, 101°12'–101°33'E; elevation: 3,200–3,300 m). Climate is typical for alpine continental areas with no summer but with cold and warm sea-

sons. Annual mean temperature is -2°C (range from 27.5°C in July to -35.0°C in January), and annual mean precipitation is 530 mm, 55% of which occurs between June and August (Xia 1988). The habitat is an extensive grassland of alpine meadow and shrubs. Dominant monocotyledons in the meadow include *Kobresia humilis*, *Stipa aliena*, *Elymus nutans*, *K. pygmaea*, *Poa*, and *Carex*. Major nonpalatable dicotyledons include *Potentilla anserina*, *Ajania tenuifolia*, *Leontopodium nanum*, *Potentilla nivea*, *Potentilla bifurca*, *Elsholtzia calycocarpa*, *Morina chinensis*, *Anaphalis lactea*, and *Pedicularis kansuensis* (Yang 1982; Zhang and Jeffrey 1996). *Saussurea katochaete*, *Aster flaccidus*, *Taraxacum mongolicum*, *Glaux maritima*, *Gentiana straminea*, *Gueldenstaedtia diversifolia*, *Trigonella ruthenica*, and *Gentiana farreri* are the chief palatable dicotyledons. *Dasiphora fruticosa* is the principal shrub in this region (Cinotta et al. 1992; Zhang and Jeffrey 1996; Zhang and Zhou 1992; Zhang et al. 1994). Average density of the plateau zokor here is 15 animals/ha (range from 10 to 25/ha).

Study sites were located in broad valley bottoms of the alpine meadow, approximately 2 km N of the research station. Eighteen 0.25-ha circular study sites were selected in May 1989. While investigating population densities of the plateau zokor in October of each year, we mapped the distinct areas within the grassland matrix and mounds created by these animals. Plateau pikas (*Ochotona curzoniae*) and marmots (*Marmota himalayana*) in this region were eliminated by the local government using poison baits in March and April 1989, and only a few kansu pikas (*O. cansa*) and root voles (*Microtus oeconomus*) have immigrated since that time (Zhang et al. 1998). Plateau zokors were removed from 9 sites in 1992 and 1993. The distinct areas within the grassland matrix left by zokors in these sites were investigated and mapped.

Three treatments were established for analysis in 1998. Nine circular study sites were occupied continuously by plateau zokors over a 10-year period during which new mounds always were present. In each circular site, the large, distinct areas ($>100\text{ m}^2$) created by plateau zokors within the grassland matrix, in which new mounds could be found every year, were selected. Total area in these 9 circular sites was approximately 0.7 ha. Nine circular study sites in which plateau

zokors were removed in 1992 or 1993 constituted abandoned areas. In each of these circular study sites, the large, distinct areas ($>100\text{ m}^2$) created within the grassland matrix by plateau zokors before 1989 but abandoned when the zokors were removed or the habitat was abandoned, with no subsequent reoccupation and disturbance of other small mammals, were selected. Total area in these 9 circular sites was nearly 0.5 ha. Unoccupied area (approximately 1.5 ha) without mounds or tunnels in the 18 circular study sites also was sampled.

Aboveground biomass was estimated monthly from 24 May to 26 September 1998 by clipping 5 sampling quadrats (50 by 50 cm) that were chosen randomly within each treatment. Vegetation was clipped, sorted, dried at 60°C for 48 h, and weighed. For evaluation of seasonal biomass dynamics, plant material was separated and categorized as monocotyledons, palatable dicotyledons, and nonpalatable dicotyledons. Plants were sampled in August when many monocotyledon species could be clearly distinguished. Twenty sampling quadrats (25 by 25 cm) in each treatment were selected randomly. Plant species diversity, vegetation cover, and plant height were measured in each quadrat using the method introduced by Chapman (1976). Ninety-eight percent of total belowground biomass was distributed in the top 30 cm of soil, and foraging and burrowing activity of plateau zokors was chiefly at depths of 3–20 cm in alpine meadow (Yang 1982; Zhang 1999). Belowground biomass (g) was estimated monthly from May to October using 5 randomly selected sampling cuboids (25-cm length by 25-cm width by 30-cm depth) in each treatment. These were separated into segments 0–10 cm, 11–20 cm, and >20 cm below the substrate, and the roots were picked carefully from each layer, washed, dried at 60°C for 48 h, and weighed. Soil samples were taken in each treatment during August 1998. Nine cores were taken at depths of 0–5 cm, 6–10 cm, 11–15 cm, 16–20 cm, and 21–30 cm at random locations in each treatment area. Prew weighed sample rings (aluminum cylinders 5.0 cm in diameter and 3.5 cm tall) were pushed into the soil paralleling the surface, removed, weighed, and dried at 60°C for 48 h. These cylinders were weighed again to determine percentage of soil moisture (Berg et al. 1997; Spencer et al. 1985). Dried soil samples were crushed and passed through a 1.0-mm sieve to remove

roots visible in the sieved samples. Total organic matter (percentage of soil composition) was determined by ashing (Schulte 1988). The Shannon–Wiener index, $H' = -\sum P_i(\ln P_i)$ (Pielou 1966), was used to calculate species diversity for total plant species, monocots, and dicots. Statistical analyses consisted of analysis of variance (ANOVA) accomplished with SPSS (Nie et al. 1975). Normality of data was tested with g_1 and g_2 statistics. One-way ANOVA was used to detect differences in vegetation cover, plant height, and diversity. Percentage data were not transformed because they statistically met the assumption of normality. Two-way ANOVA was used to analyze differences in above- and belowground, monocot and dicot biomass among treatments and months, and soil moisture and organic matter among treatments and layers. Differences between groups were tested by Tukey post hoc tests (Sokal and Rohlf 1981). Analyses were conducted on log-transformed data using $x + 1.0$ for the above- and belowground, monocot and dicot biomass, soil moisture, and organic matter (Sokal and Rohlf 1981). The criterion for statistical significance was $P < 0.05$. Results are expressed as mean \pm SE.

RESULTS

Forty-two plant species were found in unoccupied areas and 24 in both continuously occupied and abandoned areas (Table 1). Vegetational diversity indices varied significantly among the 3 treatments ($F = 43.67$, $d.f. = 2, 57$, $P < 0.001$). Diversity in unoccupied areas was higher than in continuously occupied ($P < 0.001$) and abandoned areas ($P < 0.001$). Occupied areas exhibited significantly higher vegetation diversity than abandoned areas ($P < 0.01$). Similarly, both monocotyledon ($F = 38.28$, $d.f. = 2, 57$, $P < 0.001$) and dicotyledon ($F = 19.69$, $d.f. = 2, 57$, $P < 0.001$) diversity was significantly different among the 3 treatments. Monocotyledon diversity in unoccupied areas was significantly higher than in occupied ($P < 0.001$) or abandoned areas ($P < 0.01$). Diversity of monocotyledons did not differ between occupied and abandoned areas ($P = 0.122$). Diversity of dicotyledons was greater in unoccupied areas than in occupied ($P < 0.01$) and abandoned

TABLE 1.—Number of plant species sampled, diversity of plant species (H'), cover and height of vegetation in August 1998 in the 3 treatments: occupied by plateau zokors for >10 years, abandoned for 5 years, and unoccupied in alpine meadows. Significant differences among treatments are indicated by different superscripts. Diversity, cover, and height are given as mean \pm SE.

Vegetation characteristics	Treatment		
	Occupied	Abandoned	Unoccupied
Number of species			
Monocotyledon	3	5	10
Dicotyledon	21	19	32
Total vegetation	24	24	42
Species diversity (H')			
Monocotyledon	0.606 \pm 0.156 ^b	1.029 \pm 0.125 ^b	1.824 \pm 0.081 ^a
Dicotyledon	2.357 \pm 0.033 ^c	1.931 \pm 0.076 ^b	2.701 \pm 0.049 ^a
Total vegetation	2.520 \pm 0.037 ^c	2.280 \pm 0.052 ^b	2.892 \pm 0.034 ^a
Cover (%)	19.2 \pm 2.4 ^c	47.1 \pm 4.8 ^b	81.2 \pm 3.5 ^a
Height (cm)	9.7 \pm 1.4 (n = 20)	23.8 \pm 3.2 (n = 20)	42.2 \pm 3.4 (n = 20)

areas ($P < 0.001$). Dicotyledon diversity was greater in occupied than in abandoned areas ($P = 0.01$). Vegetation cover ($F = 70.00$, $d.f. = 2, 57$, $P < 0.001$) and height ($F = 33.90$, $d.f. = 2, 57$, $P < 0.001$) differed significantly among the 3 treatments. Vegetation cover in occupied areas was significantly less than in unoccupied ($P < 0.001$) and abandoned areas ($P < 0.001$). Vegetation cover in unoccupied areas also was significantly greater than in abandoned areas ($P < 0.001$). Unoccupied areas were characterized by significantly greater vegetation height than occupied ($P < 0.001$) or abandoned areas ($P < 0.001$). Vegetation height in abandoned areas was significantly greater than in occupied areas ($P < 0.001$).

The interaction of treatment and months for total aboveground biomass (Fig. 1a) was significant ($F = 6.33$, $d.f. = 8, 8$, $P < 0.01$). Nevertheless, patterns were consistent, and differences were significant among the 3 treatments ($F = 102.82$, $d.f. = 2, 8$, $P < 0.001$) and among months ($F = 62.44$, $d.f. = 4, 8$, $P < 0.001$). Treatment effects by months were significant (May: $F = 22.18$, $d.f. = 2, 12$, $P < 0.01$; June: $F = 76.58$, $d.f. = 2, 12$, $P < 0.01$; July: $F = 87.98$, $d.f. = 2, 12$, $P < 0.01$; August: $F = 46.53$, $d.f. = 2, 12$, $P < 0.01$; September: $F = 22.20$,

$d.f. = 2, 12$, $P < 0.01$). Greatest peak total aboveground biomass (413.6 g/m²) was found in unoccupied areas and least peak (170.2 g/m²) in continuously occupied areas. Unoccupied areas exhibited significantly more total aboveground biomass than did occupied ($P < 0.001$) or abandoned areas ($P < 0.001$). Total aboveground biomass in abandoned areas was significantly greater than in occupied areas ($P < 0.001$).

The interaction of treatment and month for biomass of monocotyledons (Fig. 1b) was significant ($F = 9.57$, $d.f. = 8, 8$, $P < 0.01$). Nevertheless, patterns were consistent, and differences were significant among the 3 treatments ($F = 303.83$, $d.f. = 2, 8$, $P < 0.001$) and among months ($F = 32.57$, $d.f. = 4, 8$, $P < 0.001$). Treatment effects by months were significant (May: $F = 72.27$, $d.f. = 2, 12$, $P < 0.01$; June: $F = 13.86$, $d.f. = 2, 12$, $P < 0.01$; July: $F = 59.69$, $d.f. = 2, 12$, $P < 0.01$; August: $F = 118.38$, $d.f. = 2, 12$, $P < 0.01$; September: $F = 46.17$, $d.f. = 2, 12$, $P < 0.01$). Biomass of monocotyledons in unoccupied areas was significantly higher than in occupied areas ($P < 0.001$). Biomass of monocotyledons in abandoned areas was greater than in occupied areas ($P < 0.001$) but lower than in unoccupied areas ($P < 0.001$).

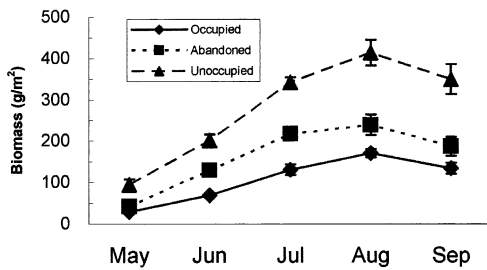
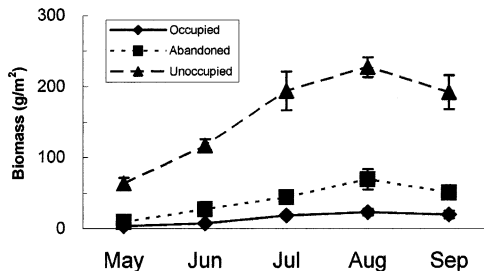
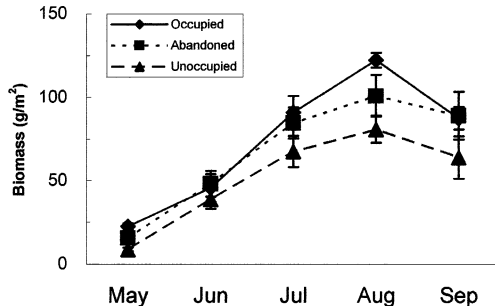
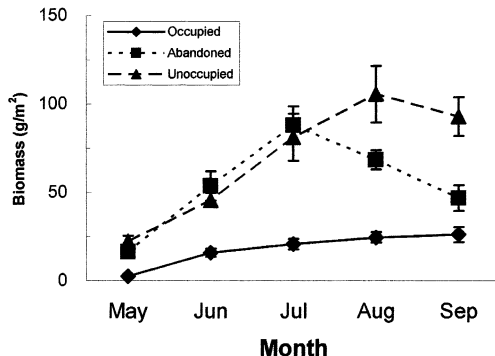
a. Total above-ground biomass**b. Monocotyledon biomass****c. Nonpalatable dicot biomass****d. Palatable dicot biomass**

FIG. 1.—Intraseasonal variation in plant biomass for a) all aboveground plants, b) monocotyledons, c) nonpalatable dicots, and d) palatable dicots on areas occupied by plateau zokors for >10 years, abandoned for 5 years, and unoccupied in alpine meadow during 1998. Symbols represent mean, error bars represent SE.

Biomass of nonpalatable dicots (Fig. 1c) differed significantly among treatments ($F = 11.76$, $d.f. = 2, 8$, $P < 0.01$) and among months ($F = 64.44$, $d.f. = 4, 8$, $P < 0.001$). The interaction between treatment and months was not significant ($F = 1.10$, $d.f. = 8, 8$, $P > 0.05$). Biomass of nonpalatable dicots was greater in occupied ($P < 0.001$) and abandoned ($P < 0.01$) areas than in unoccupied areas. No significant difference was found in biomass of nonpalatable dicots between abandoned and occupied areas ($P = 0.501$).

The interaction between treatment and months for biomass of palatable dicots (Fig. 1d) was significant ($F = 4.09$, $d.f. = 8, 8$, $P < 0.05$), and differences were not consistent among treatments and months.

Belowground biomass (Table 2) differed significantly among treatments ($F = 197.25$, $d.f. = 2, 10$, $P < 0.001$) and among months ($F = 7.45$, $d.f. = 5, 10$, $P < 0.01$). No interaction existed between treatment and months ($F = 1.86$, $d.f. = 10, 10$, $P > 0.05$). Belowground biomass in occupied areas was reduced significantly by approximately 80% compared with unoccupied areas ($P < 0.001$). Belowground biomass in abandoned areas was significantly greater than in occupied areas ($P < 0.001$).

The interaction of treatment and depth for soil moisture (Table 3) was significant ($F = 8.84$, $d.f. = 8, 8$, $P < 0.01$), and differences were not consistent among treatments and soil depths. The interaction between treatment and soil depth for soil organic matter (Table 3) was significant ($F = 8.21$, $d.f. = 8, 8$, $P < 0.01$), and differences were not consistent among treatments and soil depths.

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table dicots on areas occupied by plateau zokors for >10 years, abandoned for 5 years, and unoccupied in alpine meadow during 1998. Symbols represent mean, error bars represent SE.

TABLE 2.—Total belowground biomass (g/m²) of plants in the 3 treatments: occupied by plateau zokors for >10 years, abandoned for 5 years, and unoccupied in alpine meadow during 1998. Sample size is 5 for each treatment.

Month	Biomass ($\bar{X} \pm SE$) by treatment		
	Occupied	Abandoned	Unoccupied
May	278.9 \pm 10.4	1,021.2 \pm 16.1	1,666.6 \pm 13.4
June	261.5 \pm 7.0	1,111.9 \pm 15.8	1,586.3 \pm 12.8
July	228.5 \pm 6.8	968.6 \pm 15.3	1,472.3 \pm 16.5
August	363.2 \pm 13.1	1,229.6 \pm 16.4	1,960.1 \pm 17.3
September	426.2 \pm 13.2	1,369.8 \pm 16.3	2,297.5 \pm 12.8
October	489.1 \pm 13.2	1,546.6 \pm 19.4	2,450.3 \pm 16.3

DISCUSSION

Diversity of both monocots and dicots, vegetation cover, and vegetation height decreased in alpine meadows continuously inhabited by zokors. Meadows abandoned for 5 years had values intermediate to those for unoccupied and occupied areas. Aboveground biomass in occupied areas was reduced by approximately 59% and belowground biomass by about 80%, compared with unoccupied areas.

In addition, long-term effects of plateau zokors resulted in reduced soil moisture and organic matter. These results supported our prediction that long-term burrowing activities of plateau zokors reduced vegetation in alpine meadow.

Unlike aboveground herbivores, plateau zokors may affect plant community composition in 2 basic ways: excavating tunnel systems and foraging underground or depositing soil on the surface during spring and fall. Areas with pocket gophers had

lower production of forage, with increased biomass of plants avoided by pocket gophers and decreased biomass of preferred plants (Foster and Stubbendieck 1980; Laycock and Richardson 1975; Spencer et al. 1985). Although subterranean rodents, such as pocket gophers (*Geomys attwateri*) and plateau zokors, are typical generalist herbivores (Wang et al. 2000; Williams and Cameron 1986a), they exhibit some dietary preferences. The difference in biomass among the treatments in our study was caused by the greater biomass of nonpalatable dicots in occupied areas, perhaps due to the preference of plateau zokors for specific plants in alpine meadow.

When pocket gophers were excluded from a Texas coastal prairie, a decrease in bare ground and concomitant increase in cover, frequency, and biomass of certain plant species, particularly little bluestem grass, ensued (Williams and Cameron 1986b). Our results suggest that after pla-

TABLE 3.—Soil characteristics in soil layers at 5 depths under 3 treatments: occupied by plateau zokors for >10 years, abandoned for 5 years, and unoccupied in alpine meadow during August 1998. Sample size is 9 for each treatment.

Soil layer (cm)	Moisture (%) by treatment ($\bar{X} \pm SE$)			Organic matter (%) by treatment ($\bar{X} \pm SE$)		
	Occupied	Abandoned	Unoccupied	Occupied	Abandoned	Unoccupied
0–5	24.2 \pm 0.4	27.0 \pm 0.4	30.4 \pm 0.3	13.5 \pm 0.1	13.2 \pm 0.8	17.9 \pm 0.6
6–10	23.7 \pm 0.3	26.3 \pm 0.7	28.4 \pm 0.9	13.5 \pm 0.2	15.1 \pm 0.6	15.6 \pm 0.6
11–15	23.0 \pm 0.3	25.4 \pm 0.3	25.2 \pm 0.8	12.9 \pm 0.1	14.6 \pm 0.1	14.5 \pm 0.3
16–20	22.1 \pm 0.3	25.0 \pm 0.0	24.5 \pm 0.6	12.9 \pm 0.2	14.5 \pm 0.5	13.5 \pm 0.2
>20	22.1 \pm 0.3	23.6 \pm 0.2	21.5 \pm 0.1	12.3 \pm 0.5	13.2 \pm 0.1	11.5 \pm 0.6

teau zokors have been absent for >5 years, cover and height of plants and biomass of monocotyledons increased. However, the significant difference in these aspects between abandoned and unoccupied areas indicates that the rate of recovery in the areas of alpine meadow disturbed by plateau zokors is slow.

Deposition of considerable amounts of soil on the surface also could affect species composition, abundance, and biomass of plants. In alpine meadow during spring and fall, plateau zokors deposit large numbers of mounds that cover vegetation (Wang and Fan 1987). Mean survival of plants buried by these mounds was very low and strongly influenced plant growth and productivity (Grant et al. 1980; Tilman 1987; Williams et al. 1986; Zhang et al. 1998). Overall, dicots, especially nonpalatable species such as *A. tenuifolia*, *L. nanum*, and *Potentilla nivea*, survived burial much better than other forbs (Zhang 1999). Eventually, this could result in nonpalatable dicot species becoming dominant in abundance and biomass even though total aboveground biomass was greatly reduced.

Plateau zokors deposited at least 1,024 kg year⁻¹ individual⁻¹ of soil (Wang and Fan 1987). Mounds deposited on the surface by plateau zokors caused an increase in bare ground and altered soil texture and water-holding characteristics (Wang and Fan 1987; Wang et al. 2000; Zhang 2000). The same result was caused by pocket gophers at Cedar Creek, Minnesota (Huntly and Inouye 1988). Although we found no consistent effects by zokors on soil moisture or soil organic matter, such effects, if realized, ultimately alter plant growth and influence vegetational succession.

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