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Survivorship of penstemon grandiflorus in an oak woodland: combined effects of fire and pocket gophers

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Summary. The effects of fire and pocket gophers, *Geomys bursarius*, on the survivorship of *Penstemon grandiflorus* growing in an oak woodland in Minnesota were studied from 1986 to 1990. Plants growing in sparse vegetation experienced mortality rates twice that of plants growing in dense vegetation. This difference was due partly to pocket gophers whose earth moving activities reduce the density of vegetation and bury and kill individual *Penstemon* plants. Laboratory feeding trials showed that gophers readily eat *Penstemon*, particularly the fleshy roots. An experiment involving the removal of 25–75% of the root tissue in 90 plants showed that root loss significantly reduced survivorship, suggesting that gopher herbivory might also kill plants. When gophers were experimentally excluded, plants growing in sparse vegetation exhibited significantly lower mortality rates than those growing in dense vegetation. Plants in the smallest size class exhibited reduced survivorship following a late spring burn; however, overall patterns of survivorship of plants in burned areas did not differ markedly from those in the unburned areas. A longitudenal analysis of plants with different reproductive histories revealed no survivorship cost to reproduction. Mortality rates decreased with increasing plant size. Small plants were more likely to be killed by fire and by being buried under gopher mounds. Differences in underground energy reserves of small and large plants can account for most of the survivorship patterns observed in this study. The study shows that within openings of the oak woodland, fire and gophers reduce the survival of individual *Penstemon* plants. Nevertheless, since both gophers and fire also serve to perpetuate suitable habitat in the woodland, *Penstemon* is ultimately dependent on both for its long term persistence in the landscape.

Key words: *Penstemon grandiflorus* – *Geomys bursarius* – Fire – Disturbance

Fire and mound building animals affect organisms and ecosystems at several different levels of biological organization and spatiotemporal scales (Allen and Starr 1982; O'Neill et al. 1986; Huntly and Inouye 1988). At the scale of the landscape and at the level of the population or community, these forces can help maintain particular vegetation types (Platt 1975; Risser et al. 1981; Allen and Starr 1982; O'Neill et al. 1986; Huntly and Inouye 1988). However, at a much smaller scale and at the level of an individual plant, fire and mound building animals can be destructive forces (Ellison 1946; Moore and Reid 1951; Zedler et al. 1983; Reichman and Smith 1985; Reichman 1988).

Penstemon grandiflorus (Scrophulariaceae) is an herbaceous perennial found in sandy prairies in the Great Plains of North America (Barkeley 1986). At Cedar Creek Natural History Area in Bethel, MN, USA, it grows naturally in openings of the oak woodland and savanna habitats. It is known that open areas in the woody habitats at Cedar Creek are maintained by fire (Tester 1989) and it is suspected that pocket gophers slow the rate of tree invasion into openings through their herbivory (Huntly and Inouye 1988). Thus, at the level of the *Penstemon* population and in the context of the landscape at large, survivorship by *Penstemon* is enhanced by fire and gophers since both help to maintain the open habitat it requires. However, little is known regarding the effects of these two agents on the survivorship of individual plants. Since gophers are known to kill other plants through their herbivory and their mound building activities (Reichman 1988), and since fire is known to be lethal to plants under certain conditions, it is possible that these two agents may reduce the survivorship of individual plants even though they help to maintain the population as a whole. The purpose of this study was to determine to what extent fire and pocket gophers, singly and together, affect the survivorship of *P. grandiflorus* at the level of the individual plant.

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Methods

Study area and plant

The study area comprises 25 ha of oak woodland and savanna located at Cedar Creek Natural History Area, East Bethel, MN.

USA. Cedar Creek is situated on a 2200 km^2 sand plain formed 12,000 to 13,000 years ago by glacial outwash at the end of the Wisconsin glaciation. It lies in a transition zone between the prairie to the west and the deciduous forest to the east. Soils in the Cedar Creek oak savanna are excessively well drained and low in organic matter and total nitrogen (Grigal et al. 1974). Prior to the beginning of this study, the area had not been burned since 1955. Dominant trees in the study site are oaks (*Quercus macrocarpa*, and *Q. ellipsoidalis*). Openings are dominated by an herbaceous community consisting mostly of native prairie grasses and forbs. Patches of bare soil are common throughout the study area, particularly in the openings of the woodland where bare ground constitutes approximately 12% of the area. Most bare soil is produced by pocket gophers.

P. grandiflorus is a perennial forb which grows in well drained (usually sandy) habitats principally in the eastern portion of the Great Plains (Barkley 1986). Young plants of *P. grandiflorus* usually consist of a single leafy rosette. After flowering once, plants may flower again the next year or may revert back to a rosette growth form for a year or two before flowering again. The rosettes and flowering stems arise from a woody caudex which persists from year to year and produces several succulent roots.

Tagging and monitoring of plants

In 1986, 28 flowering stems located in openings in the woodland were randomly selected and each used as the center of a circular plot (4 m diam). These 28 stems and all *Penstemon* plants in the plots were tagged, for a total of 941 plants. In addition to being tagged, the location of each plant was recorded using a polar coordinate system. There was no difference between the size distributions of plants in the 28 plots and in 8 20 cm wide belt transects run through each of the 3 largest openings in 1986 ($G=4.99$, $df=4$, $p>0.25$). Thus the plants in the 28 circular plots were considered representative of the plants growing in the study site. Additional flowering plants were tagged in 1986 (107) and 1987 (1098) and marked with stakes to facilitate subsequent relocation.

In summer 1987 and 1988, previously tagged plants were located. If the plant was not present, it was presumed to have died and was recorded as such. If the plant was present, its growth form, rosette or stem (reproductive plant), was recorded. For rosette plants, the number of rosettes for each plant was recorded and the maximum diameter of each rosette was measured as an index of total dry mass (Werner 1975; Gross 1981). For some of the comparisons, rosettes were grouped into one of four size classes, based on the measurment of the total rosette diameter (Small Rosettes: less than 9.0 cm; Medium Rosettes: 9.0–13.9 cm; Large Rosettes: 14.0–20.9 cm; and Extra Large Rosettes: 21.0 cm or greater.

Measuring the effects of surrounding vegetation on survivorship

In environments inhabited by pocket gophers, the presence of bare soil in an area is a good indication of current or recent gopher activity (Foster and Stubbendieck 1980). In summers 1987 and 1988, percent cover by bare soil within 20 cm of each plant was measured by using a point frame method (Bonham 1989). The total number of pins (0–20) touching bare soil was recorded for each plant. Based on these measurements, plants were divided into two approximately equal sized groups for later analysis. Plants with bare ground cover estimates equalling or exceeding 20% (i.e., 4 or more pins touching bare soil), were defined to be growing in sparse vegetation. Plants with bare ground cover estimates less than 20%, were defined to be growing in dense vegetation. In addition, bare ground coverage for each of the 28 circular plots was measured in 1986 using a line-intercept method (4 lines, totalling 16 m, per plot).

To test the effect of surrounding vegetation on survivorship in the absence of gophers, one hundred and twenty *Penstemon* were transplanted into two previously existing gopher-proof pens (10 m diam) located in an old field at Cedar Creek (Lampe 1976). These pens were situated 2 m apart from one another and were both overgrown with old field vegetation. Analysis of soil cores from each pen showed that the soil in the two pens did not differ in percent total nitrogen or carbon. Two weeks prior to the experiment, all the vegetation in one of the pens was killed using an herbicide (*Roundup*). In each pen, the transplants consisted of 60 large or extra large rosettes excavated from a field at Cedar Creek and 60 smaller rosettes which had been germinated from seed in spring 1989. In both pens, the two size classes were planted alternately in a grid pattern. All plants were tagged and measured following transplanting in July 1989. Periodic subsequent weeding of the devegetated pen ensured that the *Penstemon* in this pen grew in very sparse vegetation. In June 1990, the plants were checked and their survivorship status recorded.

Measuring recruitment rates of penstemon in dense and sparse vegetation

Twenty plots (2 × 2 m) were set out in summer 1987, 10 each in dense and sparse vegetation. Densely vegetated plots contained less than 5% bare ground in the plot, while sparsely vegetated plots contained more than 5% bare ground in the plot (usually much more than 5%). All plants in the plots were tagged in summer 1987 and their positions recorded using a polar coordinate system. The plots were checked in summer 1988, at which time the number of new plants was recorded and all new plants were tagged. The plots were checked in the same manner again in summer 1989.

Test of palatability of P. grandiflorus to pocket gophers

In 1988, three pocket gophers were trapped in fields containing *P. grandiflorus*, placed into separate wire cages, and provided with known food plants for several days before being tested. Placed in a feeding apparatus similar to Behrend and Tester (1988), gophers were presented with two whole *P. grandiflorus* plants (a rosette plant and a reproductive plant) in order to determine whether or not they will eat this species and what parts of the plant they prefer. Plants were inserted through holes in a board so that the caudex and roots of a plant were suspended over the gopher's head. The holes were large enough for the gopher to gain access to the leaf and stem tissue if it wished. *Tragopogon dubius*, a known preferred food plant of *Geomys bursarius*, was also provided in the same manner in order to help assess the general hunger state of the animal. After three hours, the plants were collected and examined to determine what parts of the plant – caudex, fleshy roots, stem, leaves – were eaten. Eight feeding trials were conducted.

Measuring effects of root loss on survivorship

To measure the effect of root loss on plant survivorship we conducted a root pruning experiment. In August 1988, forty five *Penstemon* rosette plants were excavated, with care taken to extract the entire below ground tissue (caudex and roots). Upon excavation, the length and width of the caudex was measured using a hand held micrometer. A tape measure was used to measure the maximum horizontal spread of the roots. Plants were randomly assigned to one of three treatments: no root removal, 25% root removal (25% of the root mass removed), and 75% root removal. The roots of plants assigned to one of the two root removal classes were pinched off at the base until an estimated 25%, or 75%, had been removed. The plant was then immediately transplanted in the same field.

All plants were tagged and marked with a flag. In June 1989, 10 months following root removal, the plants were located and their status (alive or dead) recorded. An identical experiment, same sample size and procedures, was performed in June 1989. These plants were checked in July 1989, giving survivorship data one month following root removal.

The forty five plants selected for each experiment were selected in groups of three, such that the rosette diameter of each plant in a group differed from the other two by less than 2 cm. To reduce site effects, all three plants in a group were transplanted together, with approximately 75 cm separating each plant from the other two in the group. All plants were watered immediately after being transplanted. They were also watered during the two days following transplanting.

Prescribed burning

Approximately 7 ha of the Cedar Creek study site were burned under controlled conditions on May 6, 1987 (Temperature: 22° C, Relative Humidity: 30%, Wind Speed 15 km/h). At Cedar Creek, *P. grandiflorus* begins producing new growth by the end of April and reach maximum size (rosette diameter or stem height) for the year by early June. Thus, plants were growing and had already produced substantial new growth, including both new rosettes and stems, when the area was burned.

Physical characteristics of the two sites were not measured, however there was no difference in the size distributions of *Penstemon* plants in the burned ($n = 297$) and unburned ($n = 644$) areas in 1986, the year prior to the burn ($G = 0.329$, $p > 0.90$). Similarly, there was no difference in the frequency of flowering in the two areas in the year prior to the burn (Burned Area = 5.4%, Unburned Area = 5.7%; $G = 0.005$, $p > 0.90$). Thus, although we had only a single pseudoreplication burn plot (Hurlbert 1984), there is no reason to suspect the existence of some important site difference between the two adjacent areas.

Data analysis

In order to separate out the effects of size, burn status, and vegetation cover on survivorship, we used a linear categorical analysis (Grizzle et al. 1969). The CATMOD procedure of Statistical Analysis System (SAS) was used for this purpose. Additional comparisons of survivorship were done using the log-likelihood ratio (G test), with the Yates correction applied for 2 × 2 tables.

Results

Feeding trials

P. grandiflorus was eaten in seven of the eight feeding experiments. In the one experiment in which it was not eaten, the gopher did not feed on *T. dubius* either. The most common plant part eaten were the fleshy roots, eaten in six of the seven trials in which *Penstemon* was consumed. Leaf tissue was consumed in three trials, while

Table 1. 1986–87 and 1987–88 post-fire mortality rates for plants by size class, cover type, and fire history (late spring burn 1987)

Plant size	Veg. cover	1986–1987		1987–1988	
		Fire	*Nofire*	*Fire*	*Nofire*
Small rosette	Dense	42% (48)	19% (94)	38% (29)	65% (34)
	Sparse	42% (26)	39% (80)	67% (15)	57% (21)
		Mean = 42%	Mean = 28%	Mean = 48%	Mean = 62%
Medium rosette	Dense	6% (36)	21% (82)	15% (26)	10% (50)
	Sparse	21% (43)	34% (89)	33% (18)	31% (45)
		Mean = 14%	Mean = 27%	Mean = 23%	Mean = 20%
Large rosette	Dense	10% (40)	10% (78)	13% (31)	7% (78)
	Sparse	7% (27)	21% (72)	22% (27)	19% (67)
		Mean = 9%	Mean = 15%	Mean = 17%	Mean = 20%
Extra large rosette	Dense	0% (30)	3% (68)	4% (50)	4% (69)
	Sparse	14% (14)	23% (40)	10% (29)	6% (64)
		Mean = 5%	Mean = 10%	Mean = 6%	Mean = 5%
Flowering plant	Dense	0% (8)	19% (85)	0% (1)	7% (307)
	Sparse	25% (8)	33% (58)	0% (1)	15% (116)
		Mean = 13%	Mean = 24%	Mean = 0%	Mean = 9%

Categorical analyses

Source	1986–1987			Source	1987–1988		
	df	X^2	*P*		df	X^2	*P*
Intercept	1	134.22	0.0001	Intercept	1	79.51	0.0001
Size	4	38.30	0.0001	Size	4	78.94	0.0001
Fire	1	2.92	0.0877	Fire	1	1.67	0.1962
Size × Fire	4	12.56	0.0137	Size × Fire	4	2.83	0.5869
Cover	1	13.50	0.0002	Cover	1	5.23	0.0222
Size × Cover	4	5.31	0.2565	Size × Cover	4	1.59	0.8105
Fire × Cover	1	0.01	0.9163	Fire × Cover	1	0.02	0.8758
Size × Fire × Cover	4	4.00	0.4061	Size × Fire × Cover	4	3.36	0.4999

tissue from the woody caudex was eaten in only one of the trials.

Survivorship and plant attributes

Annual mortality rates in rosette plants (non-reproductive individuals) decreased with increasing plant size (small rosette: 36.2%, $n=229$; medium rosette: 24.8%, $n=266$; large rosette: 14.2%, $n=295$; extra large rosette: 7.6% $n=237$; $G=128.5$, $p \ll 0.0001$).

Overall, the annual mortality rate of reproductive individuals was greater than that of extra large rosettes, the rosette size most likely to flower (13.0%, $n=1065$ [reproductive plants] vs 8.3%, $n=411$ [extra large rosettes], $G=6.230$, $p<0.025$). However, considering only rosette plants that were in the two largest size classes in 1986, there was no difference in the 1988 survivorship between those plants which flowered in 1987 and those plants which remained rosettes during that year (16.8%, $n=155$ [remained rosette] vs 8.6%, $n=58$ [Flowered], $G=1.775$, $p>0,10$). There was no difference in the 1988 survivorship of plants which flowered both in 1986 and 1987 compared to plants which flowered in 1986 but did not flower in 1987 (11,8%, $n=17$ [Flowered both years] vs 9.4%, $n=32$ [Flowered in 1986, but not in 1987], $G=0.055$, $p>0.75$).

Survivorship, density, recruitment and vegetation cover

Plants growing in sparse vegetation sustained significantly higher rates of mortality than did plants growing in dense vegetation (Table 1). However, when gophers were excluded and the effect of vegetation cover on survivorship was studied directly (in the transplant experiments conducted in the gopher-proof pens), plants growing in dense vegetation experienced a higher rate of mortality (31.2%) than those growing in sparse vegetation (8.2%), $G=18.08$, $p<0.001$.

The percent bare ground in the 28 plots established in 1986 was positively correlated with the 1986 density of *Penstemon* plants in the plots ($r=0.42$, Spearman, $p<0.05$), and also with the mortality rate of the plants in those plots during the subsequent year, $r=0.50$, $p<0.02$.

Only nine new plants were recorded in the 20 recruitment study plots during the two ysear observation period (4 during the first year and 5 during the second year). All nine plants occurred in six of the ten sparsely vegetated plots.

Survivorship and mound building by pocket gophers

During this study, 66 plants were killed by being buried under the mounds made by pocket gophers, for an annual burying rate of 2.2%, $n=3020$. Rosette plants represented all but three of the buried and killed plants and were significantly more likely to be killed by burying than were stem plants (3.8%, $n=1662$ [rosette plants] vs 0.2%, $n=1358$ [stem plants], $G=53.816$, $p \ll 0.001$). Overall.

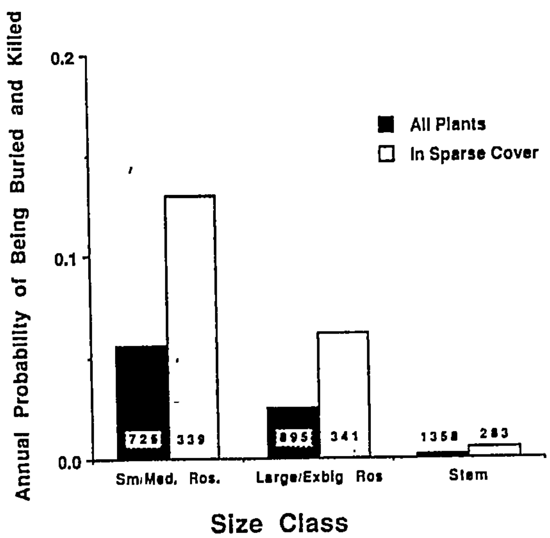

Fig. 1. Annual probability that a plant will be buried and killed for rosette plants of 2 size classes (small medium rosette plants and large/extrabig rosette plants) and for stem plants. Shown are results for all plants and then for only plants growing in sparsely vegetated areas, i.e., where pocket gophers are active

Table 2. Mortality rates of *Penstemon* growing in sparse vegetation, first including and then excluding plants that were buried and killed, compared to mortality rates of *Penstemon* growing in dense vegetation

Plant size	Dense cover	Sparse cover	*P*	Sparse cover excluding buried plants	*P*
Small and medium rosettes (Mortality rate in sparse areas due to being buried = 13.1%)	24.8% (399)	36.8% (337)	<0.001	27.1% (292)	>0.50
Large and extra big rosettes (Mortality rate in sparse areas due to being buried = 6.2%)	6.5% (444)	15.9% (340)	<0.001	10.3% (319)	=0.08
Stems (Mortality rate in sparse areas due to being buried = 0.5%)	9.2% (401)	20.8% (183)	<0.001	20.3% (182)	<0.001

buried and killed rosettes were smaller (total rosette diameter) than other rosettes (13.68+1.40 cm, $n=63$ [Buried] vs 19.59+0.36 $n=1599$ [Not Buried], $t=3.27$, $p<0.002$; SE provided, data log transformed before analysis). The annual probability of being buried and killed for small and medium rosette plants in sparse vegetation was 13.1% (Fig. 1).

The reduced survivorship exhibited by small and medium rosette plants in sparsely vegetation can be fully accounted for by the rates of burying for these two size classes (Table 2). However, the data for larger plants indicate that burying is not sufficient to account for all of the reduced survivorship observed in sparsely vegetated areas for these plants (Table 2).

Survivorship and root removal

Removal of root tissue significantly reduced survivorship of *Penstemon* both one month ($G=6.79$, $p<0.05$) and ten months ($G=9.26$, $p<0.01$) following root removal (Fig. 2). There was no transplant effect with respect to survivorship (mortality rate of transplanted control plants: 30%, $n=30$; mortality rate of comparably sized nontransplanted plants (17.3%, $n=243$, $G=1.88$, $p>0.10$).

Rosette diameter was very highly correlated ($p<0.0001$) with maximum spread of roots ($r=0.559$) and caudex volume ($r=0.565$; volume estimated by assuming a cylinder shape with length and diameter equal to the length and width of the caudex).

Survivorship and fire

Overall, plants which experienced the late spring (mid May 1987) burn did not exhibit different 1986–1987 or

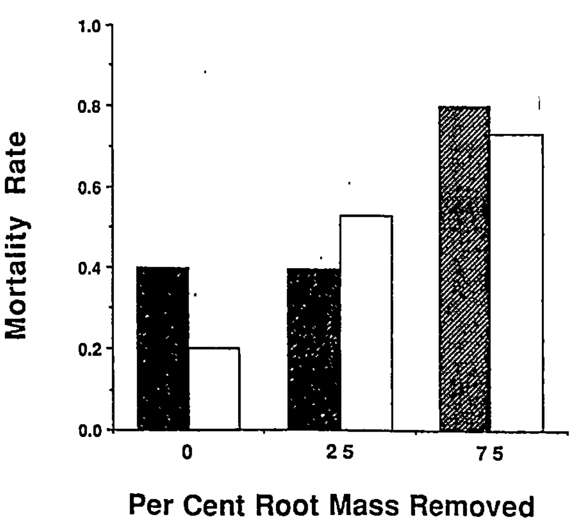

Fig. 2. Mortality rates for plants in which 0, 25% or 75% of the root mass had been experimentally removed. Shown are the results for two separate experiments, one in which survivorship was recorded 10 months (■) following root removal, and one in which it was recorded 1 month (□) following root removal. Sample size in both experiments was 45 (15 in each treatment)

1987–1988 mortality rates than did plants which did not experience a burn (Table 1). However, there was a fire × size interaction during the 1986–1987 period, and further analysis showed that plants which were small rosettes in 1986 sustained higher mortality rates after burning compared to small rosettes in the unburned compartment (41.9%, $n=74$ [burn area], 28,1%, $n=174$ [unburned area], $G=3.79$, $p=0.05$).

The probability of a plant being buried and killed was not affected by fire (3.1%, $n=225$ [burned area] vs 5.1%, $n=430$ [unburned area], $G=1.01$, $p>0.25$).

Discussion

One of the most consistent findings in this study was the increased rate of mortality of plants growing naturally in sparse vegetation. Most of the increased rate of mortality for small plants could be attributed to being buried under soil mounds produced by gophers. However, since large plants are seldom killed in this manner, their increased rate of mortality must be due to other causes. The significant increase in survivorship among plants growing in sparse vegetation when gophers were excluded indicates that gophers are in some other way also responsible for the increased mortality of the large plants. Gophers at Cedar Creek have been shown to cause mortality of other herbaceous plants through their herbivory (Reichman 1988). The feeding trials in our study showed that pocket gophers readily eat *Penstemon*, particularly the fleshy roots. This, along with the results of the root removal experiment and occassional observations of plants pulled down into burrows in the field (Davis, pers. obs.), suggests that gopher herbivory may be responsible for some of the increased mortality rates of plants growing where gophers are acitve. It should be noted that while the root pruning experiment showed that removal of root tissue alone can kill a plant, plant death caused by pocket gopher herbivory in the field might be due to the consumption of other plant parts.

The strong positive correlation between plant size and survivorship found in this study is consistent with previous studies of herbaceous plants (Werner 1975; Baskin and Baskin 1979; Gross 1981; Gross and Werner 1983). This study showed that being larger reduced the probability of mortality by both fire and burying. In both cases, the increased survivorship of large plants is likely due to the larger energy reserves possessed by these plants. Whether burned or buried a plant must use its below ground reserves to produce new tissue. Following the burn in this study, all plants except those in the smallest size class were able produce new above-ground tissue following the fire. In the case of burial, a plant may need to produce a new shoot up to 15 cm long in order to reach the top surface of a mound before new leaves can be produced (pers. obs.).

Our study provided no evidence of any interaction between fire and pocket gophers as far as *Penstemon* survivorship is concerned. Burying rates of *Penstemon* plants did not differ in burned and unburned areas, and neither of the interaction terms (fire × vegetation cover) in the two CATMOD analyses were statistically significant.

Little recruitment was observed during this study. What there was occurred in sparse vegetation in open areas. This, along with the density data, which showed that *Penstemon* is more abundant in sparse vegetation even though it experiences a higher mortality rate there, indicates that recruitment is most likely in open areas with patches of bare soil.

This along with a companion study (Davis et al. 1990) show that *P. grandiflorus* interacts with fire and pocket gophers in several ways. This study showed that plants growing where gophers are active experience significantly higher mortality rates; however, plants which survive in gopher areas grow faster and reproduce sooner than plants growing where gophers are not active (Davis et al. 1990). Fire can kill small plants, but in woodland and savanna areas *Penstemon* is ultimately dependent on fire for its continued persistence. Fire maintains the prairie openings; in turn these openings are inhabited by pocket gophers, which modify the soil and vegetation in a way which favors *Penstemon* recruitment.

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