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THE EFFECTS OF POCKET GOPHERS ON SURVIVORSHIP, GROWTH, AND REPRODUCTION OF LARGE BEARDTONGUE

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Abstract. A three-year study examined how pocket gophers affect patterns of survivorship, growth, and reproduction of large beardtongue (*Penstemon grandiflorus*, Scrophulariaceae). With their mound-building and tunneling behavior, pocket gophers create areas with sparse vegetation. Plants growing naturally in areas with pocket gopher disturbances exhibited higher rates of mortality, but surviving plants grew faster and reproduced sooner than other plants. In an experiment in which beardtongue was transplanted into two gopher-proof pens, one with and one without other vegetation, plants growing in the pen with bare soil exhibited higher rates of survivorship, growth, and reproduction, compared to the plants in the naturally vegetated pen. A root-removal experiment designed to simulate gopher herbivory showed that root loss of a kind normally experienced by beardtongue resulted in higher rates of mortality. However, reproduction in surviving plants was not affected by root removal. The data show that although pocket gophers reduce the survivorship of individual plants, their presence actually helps perpetuate large beardtongue in the landscape.

INTRODUCTION

In the North American prairie and adjacent oak savanna habitats, pocket gophers were important agents of disturbance prior to European settlement (Mielke 1977). Through their earth moving activities, pocket gophers and other fossorial animals modify the prairie and savanna landscape in several ways, including the creation of soil mounds, feeding tunnels, and underground food caches. These features have been found to influence the survivorship, recruitment, growth, reproduction, and biomass of the surrounding vegetation (Platt 1975, Tilman 1983, Hobbs and Mooney 1985, Reichman and Smith 1985, Reichman 1988). Feeding principally on herbaceous plants (Behrend and Tester 1988), pocket gophers can also affect the vegetation through their herbivory. The purpose of this study was to determine the extent to which pocket gophers affect survivorship, growth, and reproduction of large beardtongue (*Penstemon grandiflorus* Nutt., Scrophulariaceae) through their herbivory and mound building.

MATERIALS AND METHODS

The Study Area and Plant

The study area comprises approximately 25 ha of oak woodland and savanna located at Cedar Creek Natural History Area, East Bethel, Minnesota. Cedar Creek is situated on a 2,200 sq km sand plain formed 12,000 to 13,000 years ago by glacial outwash at the end of the Wisconsin glaciation. Large beardtongue is a perennial forb which grows in well-drained, usually sandy, habitats, principally in the eastern portion of the Great Plains (Great Plains Flora Association 1986). First-year beardtongue plants usually consist of a single leafy rosette. The size, and sometimes the number, of rosettes increases with age, and a flowering stem, or stems, can be produced during the second or subsequent years. 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.

Tagging and Monitoring of Plants

In 1986, 28 flowering stems located in openings in the woodland were randomly selected, and each was used as the center of a circular plot (4 m diam). These 28 stems and all beardtongue in the plots were tagged, for a total of 941 plants. In order to increase the number of flowering plants included in the study, additional flowering plants throughout the study area were tagged in 1986 (107) and 1987 (1,098) and marked with stakes to facilitate subsequent relocation.

In summer 1987 and 1988, previously tagged plants were located. If the plant was present, its growth form (stem or rosette) was recorded. For rosette plants, the number of rosettes for each plant was also recorded, and the maximum diameter of each rosette was measured. For stem plants, the number of stems for each plant was recorded, and the height of each stem was measured. For some of the comparisons, rosette plants 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). Stem plants were similarly divided into three size classes based on total stem height of all stems (Small Stems: less than 48.0 cm: Medium Stems: 48.0-59.9 cm: Large Stems: 60 cm or greater). The size intervals used for both rosette and stem plants were selected to produce size categories with approximately equal numbers of plants in 1986.

Measuring Effects of Surrounding Vegetation on Survivorship, Growth, and Reproduction

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 my study, gophers are the primary cause of bare soil, although thatch ants, which produce soil rings around their mounds, are minor contributors. In order to determine if rates of beardtongue are different for plants growing where gophers are active, the percent cover of 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 groups of approximately equal size for comparison. Plants with bare-ground cover estimates equaling or exceeding 20% were defined to be growing in sparsely vegetated areas. Plants with bare-ground cover estimates less than 20% were defined to be growing in densely vegetated areas.

To test the effect of surrounding vegetation on survivorship, growth, and reproduction in the absence of gophers, a separate experiment was begun in July 1989. One hundred twenty beardtongue 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 2 m apart, and both were 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. In June 1990, the plants were remeasured, and the reproductive status of all surviving plants was recorded.

Measuring Effects of Root Loss on Survivorship, Growth, and Reproduction

Previous laboratory observations of captive gophers showed that although pocket gophers readily eat the fleshy beardtongue roots, they generally avoid the woody caudex, stem, and leaves (unpublished data). To simulate root herbivory in the field and to measure the effect of root loss on plant survivorship, growth, and reproduction, a root-pruning experiment was conducted in August 1988. In this experiment, 45 plants were carefully excavated and assigned to one of three treatments: no root removal, 25% root removal, and 75% root removal. The roots of plants assigned to one of the two root removal classes were pinched off at the caudex until an estimated 25%, or 75% of the root mass had been removed. All plants were transplanted immediately following root removal. An identical experiment was conducted in June 1989.

In summer 1989 (June for the first experiment, July for the second), the number of surviving plants in each treatment was recorded for both experiments. The proportion of surviving transplants which had flowered was also recorded for each of the three treatments. In addition, the fruiting stems were collected for later analysis of reproductive output. The total volume of the pods produced by a plant was used as a measure of pod volume. Pod volume was estimated by first measuring the area of a pod and then using the formula of a cone to convert the area into a volume estimate. Area was measured from overhead with the pod lying on its side and using image analysis software (Olympus Corporation) and a Zeos 286 computer with a video camera attachment. Pod volume was highly correlated with seed production, (r=.88, p<.001, n=11).

RESULTS

Survivorship

Effects of plant size.

Mortality rates in rosette plants, non-reproductive individuals,decreased with increasing size of the rosette (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<.001), using Log-Likelihood Ratio Test for Contingency Tables, (Zar 1974).

Effects of vegetation cover.

Overall, plants growing in sparse vegetation, as determined by the point frame method, sustained significantly higher rates of mortality (25.3%, n=648) than did plants growing in densely vegetated areas (12.5%, n=945; G=41.78, p<.0001). There was a significant positive correlation between the percent coverage of bare ground in the 28 plots established in 1986 and the mortality rate of the plants in those plots during the subsequent year, r=.50 (Spearman), p<.02. There was also a significant positive correlation between bare ground coverage and density of beardtongue in the 28 plots, r=.42, p<.05.

In the experimentally devegetated, gopher-proof pen, survivorship of transplanted beardtongue (91.8%) was significantly greater than in the naturally vegetated control gopher-proof pen (68.8%), G=18.08, p<.001.

Effects of mound building by gophers.

During this study, 66 plants were determined to have been 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=1,662 for rosette plants versus 0.2%, n=1,358 for stem plants, G=53.816, p<.001). Overall, buried and killed rosettes were smaller in diameter than other rosettes (13.68 ± 1.40 cm, n=63 for buried

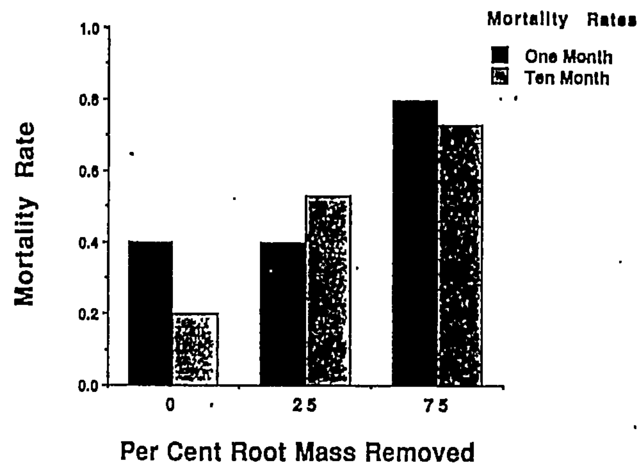

Figure 1. Mortality rates for beardtongue plants in which 0%, 25%, or 75% of the root mass had been experimentally removed. Shown are the results for two separate experiments, one in which survivorship was recorded 10 months following root removal, and one in which it was recorded 1 month following root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

versus 19.59 ± .36 n=1,599 for nonburied, t=3.27, p<.002; SE provided, data log transformed before analysis). The annual probability of being buried and killed for small and medium rosettes was 7.6%.

Effects of root removal.

Removal of root tissue significantly reduced survivorship of beardtongue (Figure 1). This was true both ten months following root removal (G=9.26, p<.01; first experiment) and one month following root removal (G=6.79, p<.05; second experiment). There was no transplant effect with respect to survivorship (mortality rate of transplanted controls: 30%, n=30; mortality rate of comparably sized nontransplanted plants: 17.3%, n=243, G=1.88, p>.10).

Reproduction

Effects of plant size.

The probability of flowering increased with plant size (small rosette: 1.3%, n=151; medium rosette: 5.6%, n=198; large rosette: 30.4%, n=250; extra-large rosette: 79.3%, n=222; stem plants: 62.9%, n=491). Similarly, the total height of flowering stem(s) produced by a rosette plant increased with rosette size (r=.287, p<.001, n= 551). The number of flowering nodes on a stem was significantly correlated with the height of the stem (r=.803, p<.001, n=1,020). Thus, large plants were more likely to flower and to produce larger inflorescences than were small plants.

Effects of vegetation cover.

The rate of reproduction in plants growing naturally in sparsely vegetated areas (39.6%, n=492) did not differ significantly from that of plants growing in densely vegetated areas (42.8%, n=817; G=1.17, p>.25). The relative proportions of large, medium, and small flowering stems in densely vegetated areas (n=350) also did not differ from those in sparsely vegetated areas (n=139; G=1.66, p>.10).

Plants transplanted into the experimentally devegetated, gopher-proof pen reproduced at a significantly higher rate than did plants in the vegetated control pen (devegetated pen: 69.7%, n=109; control pen: 31.7%, n=82; G=26.2, p<.001; percentages based on surviving plants).

Effects of root removal.

The transplanting procedure did not affect the probability of reproducing in beardtongue (control transplants: 58.3%, n=12; comparably sized nontransplanted plants: 47.2%, n=197; G=0.204, p>.50). Because of the low rate of survivorship in root-pruned plants, the two pruning treatments were grouped for the analyses of reproduction. Root pruning did not affect the rate of flowering in the surviving transplants (root-pruned plants: 81.8%, n=11; control plants: 58.3%, n=12; G=0.599, p>.25). Root pruning also did not affect the plant reproductive output as measured by total volume of pods produced (root-pruned plants: 1,305.7 + 272.2 mm^3, SE, n=9; control plants: 1,297.1 ± 350.9 mm^3, n = 7; t=.015, p>.50).

Growth

Effects of vegetation cover.

The likelihood that a plant would increase in size class was significantly greater among plants growing in sparsely vegetated areas than among those growing in densely vegetated areas (X2 = 7.77, p<.005). Plants transplanted into the experimentally devegetated, gopher-proof pen were significantly more likely to increase in size class than plants in the vegetated control pen (devegetated pen: 94.5%, n=109; control pen: 64.6%, n=82; G=26.7, p<.001, percentages based on surviving plants).

Effects of root removal.

Because most of the plants which survived the root removal treatment flowered the following year, and because the production of a stem is considered an increase in size class, the conclusion regarding the effect of root removal on growth is identical to that for reproduction: no effect. Too few surviving plants remained rosettes to permit a separate analysis of the effect of root removal on growth of plants which did not reproduce.

DISCUSSION

Herbaceous plants of grasslands and savannas regularly experience a variety of disturbances, including soil excavation by fossorial animals and herbivory both above and below ground (Mielke 1977, Behrend and Tester 1988, Gibson 1989, Contreras and Gutierrez 1991). Through their differential effects on survivorship, growth, and reproduction of individual plants of different species, these disturbances can influence the community composition of the vegetation (Platt 1975). The results reported in this paper show that pocket gophers can significantly increase mortality in one forb species, large beardtongue, through their mound-building activities and possibly through their underground herbivory. At the same time, however, plants which are growing where gophers are active grow faster and reproduce sooner. In addition, the density data presented, along with other preliminary data on recruitment (unpublished), indicate that recruitment is higher in gopher areas than in areas where gophers are not active and where there is little bare soil.

Thus, although pocket gophers reduce survivorship of beardtongue plants in affected areas, they appear to help perpetuate large beardtongue in the larger landscape. In addition, the gophers can be viewed as altering their environment in a way which enhances the growth, reproduction, and recruitment of a food plant.

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