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Combined Effects of Fire, Mound-building by Pocket Gophers, Root Loss and Plant Size on Growth and Reproduction in Penstemon grandiflorus

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ABSTRACT.—A 3-yr study examined how plant size and disturbances by fire and pocket gophers affected patterns of growth and reproduction in 2124 *Penstemon grandiflorus* plants. A late spring burn significantly reduced the probability of reproducing and the probability of increasing in size class both during the year of the burn and during the following year. Mound-building and tunneling behavior of pocket gophers create areas with sparse vegetation. Plants growing naturally in areas with these pocket gopher disturbances showed no change in the probability of reproducing, but did exhibit a significantly higher probability of increasing in size class, and therefore of reproducing sooner. Plants transplanted into an experimentally devegetated pen from which gophers were excluded exhibited greater rates of subsequent growth and reproduction than plants transplanted into a reference pen (naturally vegetated, gophers also excluded). A root removal experiment, designed to simulate gopher herbivory of roots, showed that root loss did not result in a decrease in rate of flowering or pod production in surviving plants. There was no evidence of a fire × vegetation cover interaction on *Penstemon* growth and reproduction. However, the effects of fire and gophers on growth and reproduction are mediated by plant size, with small plants being those most effected.

INTRODUCTION

By killing individual organisms and altering the availability of various resources, disturbances often play an important role in ecological systems (Odum *et al.*, 1979; Bazzaz, 1983). Knowledge of how individuals and populations of different species respond to disturbance is necessary to increase understanding of ecological systems at the community level (Brokow, 1985; Denslow, 1985). In addition, this knowledge is often important in conservation efforts (Pickett and Thompson, 1978). However, the study of the role of disturbance in natural communities is complicated by three factors. First, many organisms regularly experience more than one type of disturbance and these can interact with one another (Loucks *et al.*, 1985; Young, 1985; Collins, 1987; Gibson, 1989). Second, a single agent of disturbance, such as fire, can produce many different physical and biological effects (Daubenmire, 1968; Old, 1969). Third, the interpretation of disturbance is affected by the level of ecological organization considered and the scale and criteria used to measure the effects (Allen and Starr, 1982). Thus, to fully understand the role of disturbance in the ecology of individual species, comprehensive studies addressing all three of these issues need to be undertaken.

In the North American prairie and adjacent oak savanna habitats, both fire and pocket gophers were important agents of disturbance prior to European settlement (Daubenmire, 1968; Mielke, 1977; Grimm, 1984; Axelrod, 1985). Observations of grassland and savanna areas which experienced a reduction in the frequency of burning following settlement (Gleason, 1913), along with long-term experimental studies on the effects of fire in savanna habitats (Tester, 1989), have shown that regular burning helps to maintain populations of prairie plants in these communities by preventing encroachment of woody vegetation. At the same time, fire can be detrimental, even lethal, to individual prairie plants in these habitats, particularly when it occurs during the growing season (Vogl, 1974; Davis *et al.*, 1991).

Pocket gophers and other fossorial animals modify the prairie and savanna landscape in several ways through their earth-moving activities, 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; Davis *et al.*, 1991). Pocket gophers also affect the vegetation by herbivory (Behrend and Tester, 1988, Reichman, 1988).

Fire and pocket gophers are known to reduce survivorship of *Penstemon grandiflorus* (Scrophulariaceae) (Davis *et al.*, 1991). Specifically, some plants are buried and killed under soil mounds, some are likely killed as a result of belowground herbivory, and some are killed by fires that occur during the growing season. Reduction in survivorship is not the same as reduction in fitness, however. Disturbances which reduce survivorship may also reduce reproductive output among survivors, therefore reducing fitness even more. On the other hand, some plant species are capable of overcompensating following certain disturbances and significantly increase reproductive output (McNaughton, 1983; Paige and Whitham, 1987). It is possible that a disturbance that reduces survivorship may still produce an increase in the average fitness of plants if the reproductive output of survivors is sufficiently increased. Thus, a full understanding of the effects of fire and gophers on the fitness of individual *Penstemon* plants must take into account effects on growth and reproduction as well as survivorship. Only by knowing the effects of disturbance on the survivorship, growth and reproduction of individuals will be possible to understand the reasons for changes observed at the level of the population following these disturbances.

The purpose of this study was to determine the extent to which growth and reproduction of individual *Penstemon* plants are affected by three different disturbances: fire, mound-building by gophers and root loss. Since plant size is known to affect patterns of reproduction (Werner, 1975; Gross, 1981; Gross and Werner, 1983; Lacey, 1986), the relationship of plant size to growth and reproduction was studied as well.

STUDY AREA

The study area comprises approximately 25 ha of oak woodland and savanna located at Cedar Creek Natural History Area, East Bethel, Minn. Cedar Creek is situated on a 2200 km² sandplain formed 12,000–13,000 yr ago by glacial outwash at the end of the Wisconsin glaciation. It lies in a transition zone between the prairie to the W and the deciduous forest to the E. Aerial photographs dating back to 1938 indicate that, except for 1 ha which was abandoned more than 30 yr ago, the study area has never been cultivated. 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 herbacious community consisting mostly of native prairie grasses and forbs. Owing to the long absence of fire, parts of the study area are covered by a nearly closed canopy of oaks and a prominent layer of shrubs and understory trees (*Corylus american, Rhus glabra* and *Prunus virginiana*).

THE PLANT

Penstemon grandiflorus (Scrophulariaceae) is a perennial forb which grows in well-drained (usually sandy) habitats principally in the eastern portion of the Great Plains (Barkley, 1986). Herbarium specimens at the University of Minnesota indicate that the species has been collected mostly from prairie habitats in the W, from oak savanna habitats in the E-central part of the state, and from sandy bluffs of the Minnesota and Mississippi rivers. Young plants of *P. grandiflorus* usually consist of a single leafy rosette. The size, and sometimes the number, of rosettes increases with age and eventually a flowering stem, or stems, can be produced. Plants usually do not die after flowering. After flowering, plants may flower again the next year or may revert 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 (usually 1–2 cm beneath the soil surface) and which produces several succulent roots. The leafy flowering stalks grow up to 1.2 m tall and produce a raceme of large (4–5 cm) lilac-colored flowers which mature into subligneous capsules. No specialized seed-dispersal mechanism is evident. Seeds fall out of the open capsules during the autumn winter and subsequent spring as the dry stem falls over or leans askew. Longer distance dispersal may occur when seeds blow over the snow's surface in the winter. Mean densities of *Penstemon* in the three largest openings of the study area range from 1–3 plants per m^2. Local densities can exceed 10 plants per m^2.

MATERIALS AND METHODS

Tagging and monitoring of plants.—In 1986, 28 flowering stems located in openings in the woodland were arbitrarily 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. None of the 28 plots overlapped. In order to determine whether the size distribution of plants selected by this method could be considered a representative sample of the *Penstemon* growing in the study area, the size distribution of these plants was compared with the size distribution of randomly selected plants. The latter ($n = 111$) were obtained by establishing eight belt transects (20 cm wide) through each of the three largest openings in 1986. There was no difference between the size distributions in the 28 plots and in the belt transects ($G = 4.99$, $df = 4$, $P > 0.25$; size classes described below). Thus the plants in the 28 circular plots were considered to be representative of the plants growing in the study site. In order to increase the number of flowering plants included in the study, additional flowering plants were tagged in 1986 (107) and 1987 (1098) and marked with stakes to facilitate subsequent relocation. The flowering stems tagged in 1986 represented all the stems in the largest opening, and those tagged in 1987 represented all the flowering stems in the four largest openings.

In summer 1987 and 1988, previously tagged plants were located. 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 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.

Measuring the effects of surrounding vegetation on 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 order to determine if the growth and reproductive rates of *Penstemon* plants are affected by these patches of bare soil, the percent cover of bare soil within 20 cm of each plant was measured by using a point frame method (Bonham, 1989). The frame was positioned over the plant so that five pins were suspended over the ground at distances of 4, 8, 12, 16 and 20 cm from the plant in all 4 major compass directions. 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 for comparison. Approximately half the plants had bare ground cover estimates equalling or exceeding 20%, and these plants were defined to be growing in sparse vegetation. The remaining plants had bare ground cover estimates less than 20%, and these were defined to be growing in dense vegetation.

To test the effect of surrounding vegetation on growth and reproduction without the presence of gophers, a separate experiment was conducted in 1989. One hundred and twenty *Penstemon grandiflorus* plants 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. A small degree of transplant mortality occurred during the 1st wk and these plants were replaced with new plants. 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 remeasured and the reproductive status of all surviving plants was recorded.

Measuring effects of root loss on growth and reproduction.—Laboratory feeding trials have shown that *Geomys bursarius* feeds readily on *Penstemon grandiflorus* roots and leaves, with the fleshy roots being the plant part most often eaten (Davis *et al.*, 1991). To determine if gopher herbivory of *Penstemon* roots could affect plant growth and reproduction, a root-pruning experiment was conducted in August 1989. In this experiment, 45 plants were carefully excavated and 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 caudex until an estimated 25%, or 75%, had been removed. All plants were transplanted immediately following root removal and all were transplanted in the same field.

Several steps were taken to minimize the possible effects of plant size and microhabitat differences on subsequent growth and reproduction. The 45 plants selected for this experiment were rosette plants 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.

To minimize the stress of transplanting, all plants were watered immediately after being transplanted. They were also watered during the 2 days following transplanting. These measures eliminated any transplant effect on survivorship (Davis *et al.*, 1991). To test for a transplant effect on reproduction, flowering rates of control plants were compared with the flowering rates of comparably sized plants which had not been excavated.

In summer 1989, the proportion of surviving transplants which had flowered was 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 reproductive output. 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 Corp.) and a Zeos 286 computer with a video camera attachment. Pod volume was highly correlated with seed production, $r = 0.88$, $P < 0.001$, $n = 11$).

Prescribed burning.—Approximately 7 ha of the Cedar Creek study site were burned under controlled conditions on 6 May 1987 (temperature: 22 C; relative humidity: 30%; wind speed: 15 km/h). At Cedar Creek, *Penstemon grandiflorus* begins producing new growth by the end of April and reach their maximum size (rosette diameter or stem height) for the year by early June. Thus, plants were actively growing and had already produced substantial new growth, including both new rosettes and stems, when the area was burned.

Prior to European settlement, fires were common in the prairies and adjacent savannas during dry periods at almost any time of the year, but were probably especially common during the windy droughty periods of spring and autumn (Jackson, 1965). Spring 1987 was so dry in Minnesota that the Minnesota Department of Natural Resources had issued a fire ban over most of the state, including Cedar Creek. In fact the prescribed burn done in this study had been postponed several times due to the fire ban. Thus, it seems that the timing of the fire in this study likely corresponded to a natural time for fires in this environment.

Since the burn was not replicated, any subsequent differences in growth and reproduction between the burned and unburned sites could be due to unknown site differences (Hurlbert, 1984). Physical characteristics of the two sites were not measured; however, the size distributions of *Penstemon* plants in the burned ($n = 297$) and unburned ($n = 644$) areas were compared in 1986, the year prior to the burn. There was no difference in the two size distributions ($G = 0.329$, $P > 0.90$). Similarly there is no difference in the frequency of flowering in the two sites in the year prior to the burn (Burn = 5.4%, Unburn = 5.7%, $G = 0.005$, $P > 0.90$). Given that *Penstemon* was common in both areas prior to the burn and that the size distributions and rate of flowering were nearly identical in both areas, there is no reason to suspect the existence of some important site difference between the two immediately adjacent areas, although this possibility cannot be ruled out.

Data analysis.—Statistical analyses were conducted using the Statistical Analysis System (SAS). A linear categorical analysis (Grizzle *et al.*, 1969) was used to separate the individual and combined effects of plant size, burn history and vegetation cover on the probability of a plant reproducing and on the probability of increasing in size class. The CATMOD procedure of SAS was used for this purpose. Additional comparisons of were done using the log-likelihood ratio (G test), with the Yates correction applied for 2 × 2 tables.

Rosette diameter is commonly used as an index of size for plants with a rosette growth form and has been shown to be highly correlated with total dry mass (Werner, 1975; Gross, 1981). Most rosette plants in this study consisted of single rosettes. However, since approximately 25% of rosette plants consisted of more than one rosette, total rosette diameter (sum of diameters of all rosettes of a plant) was used as a measurement of size for rosette (nonreproductive) plants. For some of the comparisons, rosettes were grouped into one of four size classes, based on the measurement 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. Upper and lower limits of size classes were based on size distributions of more than 800 rosettes measured in 1986 and were chosen so that each size class contained approximately ¼ of the rosettes (actual percentages = 18%, 25%, 28%, 29%). Stems were divided into three size classes of approximately equal numbers, based on total stem height (sum of heights of all stems for the plant)—small stems: less than 48.0 cm; medium stems: 48.0–59.9 cm; large stems: greater than or equal to 60 cm.

Because *Penstemon* plants exhibit two completely different growth forms, stem and rosette, depending upon whether or not they are reproducing, it was not practical to use any actual measurement of size change to measure growth, even though these data were available. For example, using increase in rosette diameter as a measure of growth rate for rosettes would mean one would have to exclude plants which next year went on to flower. Thus, the probability of increasing in size class from one year to the next was used as an indication of growth. Since the natural growth of a plant is from rosette to stem, a change from a rosette growth form to a stem growth form was considered a move up in size class and a change from stem to rosette was considered a move down in size class.

RESULTS

REPRODUCTION

Effects of plant size.—The probability of flowering in the next year 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). Flowering plants (n = 491) exhibited a 62.9% likelihood of flowering during the following year. The total height of flowering stem(s) produced by a rosette plant increased with plant size (r = 0.287, P < 0.001, n = 551). The number of flowering nodes on a stem was significantly correlated with the height of the stem (r = 0.803, P < 0.001, n = 1020). Thus large plants were more likely to flower and to produce larger inflorescences than small plants.

Effects of fire.—During the 1st summer following the late spring burn in 1987, the percent of plants which flowered in the burned area (0.9%, n = 227) was significantly less than in the unburned area (17.1%, n = 568; $\chi^2 = 4.63$, P < 0.05). There was a nearly significant interaction between fire and size on reproduction ($\chi^2 = 8.56$, df = 4, P < 0.08) during year 1. This is due to the fact that small *Penstemon* plants seldom flower; thus while the last spring burn virtually eliminated flowering among large plants (which regularly flower), the flowering rate of small plants (very low to begin with) was not much affected. One year later, the rate of reproduction in the burned area (15.4%, n = 188) was still significantly less than in the unburned area (48.5%, n = 398; $\chi^2 = 10.85$, P < 0.01). Although plants in the burned area reproduced at a lower rate in the 2nd yr after the burn, the relative proportions of small, medium and tall stems did not differ in the burned (n = 29) and unburned (n = 193) areas (G = 0.665, P > 0.50).

Effects of vegetation cover.—The probability of flowering during the next year for plants growing naturally in sparse vegetation (39.6%, n = 492) did not differ significantly from that of plants growing in dense vegetation (42.8%, n = 817; G = 1.17, P > 0.25). 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 > 0.10). There was no interactive effect of fire and vegetation cover on *Penstemon* reproduction in either of the 2 yr following the fire (P > 0.50, for both fire × vegetation cover terms in the CATMOD analysis for each year). Similarly, there was no interactive effect of vegetative cover and plant size on *Penstemon* reproduction in either of the 2 yr following the fire (P > 0.40).

Plants transplanted into the experimentally devegetated gopher-proof pen were more likely to flower (69.7%, n = 109) than plants in the reference (vegetated) pen (31.7%, n = 82; G = 26.2, P < 0.001; percentages based on surviving plants). The increased probability of flowering in the devegetated pen was exhibited by both the large and extra large rosettes (devegetated pen: 86.0%, n = 57; reference pen: 46.2%, n = 52; G = 18.4, P < 0.001) and by the smaller 1st-yr rosettes (devegetated pen: 51.9%, n = 52; reference pen: 6.7%, n = 30; G = 17.3, P < 0.001). Not only were plants more likely to reproduce in the experimentally devegetated pen, but the reproductive output was larger as measured by the proportion of large, medium and small stems [devegetated pen: 52.6% (L), 11.8% (M), 35.5% (S), n = 76; reference pen: 19.2% (L), 19.2% (M), 61.5% (S), n = 26; G = 9.39, P < 0.005].

Effects of root removal.—The transplanting procedure did not affect the probability of reproducing in *Penstemon* [Reference transplants (no roots pruned): 58.3%, n = 12; non-transplanted and comparably sized plants: 47.2%, n = 197; G = 0.204, $P > 0.50$]. Due to the low rate of survivorship in root-pruned plants (19 of the 30 root-pruned plants died compared to only three of the 15 reference plants, Davis *et al.*, in press), 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, $P > 0.25$). Root pruning also did not affect the plant reproductive output (total volume of pods produced) (root-pruned plants: 1305.7 ± 272.2 mm^3, SE, n = 9; control plants: 1297.1 ± 350.9 mm^3, n = 7; t = 0.015, $P > 0.50$).

GROWTH

Effects of fire.—The probability that a plant would increase in size class was smaller for plants which experienced the late spring burn. This was true both in the growing season immediately following the fire ($\chi^2 = 16.80$, $P < 0.001$) and in the subsequent growing season ($\chi^2 = 15.99$, $P < 0.001$). In both years there was a significant fire × size interaction. During the 1st yr, this was due to small plants (small and medium rosettes) which exhibited a smaller probability of increasing in size class in the burned area (42.7%, n = 110) than small plants in the unburned area (60.8%, n = 240; $\chi^2 = 10.67$, $P < 0.0025$). The probability of increasing in size for larger plants (large and extra large rosettes) was not affected by fire during the 1st yr (burned area: 49.2%, n = 61; unburned area 39.5%, n = 124; $\chi^2 = 1.38$, $P > 0.20$). During the 2nd yr, the fire × size interaction was due to differences among the larger plants, which exhibited a smaller probability of increasing in size class in the burned area (30.3%, n = 122) compared to large plants in the unburned area (70.1%, n = 252; $\chi^2 = 48.9$, $P < 0.001$).

Effects of vegetation cover.—The likelihood that a plant would increase in size class was significantly greater among plants growing in sparse vegetation than among those growing in dense vegetation ($\chi^2 = 7.77$, $P < 0.005$). However, this difference was due primarily to small plants (small and medium rosettes) which exhibited a higher probability of increasing in size class in sparse vegetation areas (65.6%, n = 148) than in dense vegetation (48.2%, n = 191; $\chi^2 = 10.08$, $P < 0.005$). Large plants (large and extra large rosettes) in dense and sparse vegetated areas did not differ in their probabilities of increasing in size class (sparse: 59.7%, n = 201; dense: 57.6%, n = 271; $\chi^2 = 0.22$, $P > 0.50$). There was no interactive effect of fire and vegetation cover on *Penstemon* growth in either of the 2 yr following the fire ($P > 0.50$, for both fire × vegetation cover terms in the CATMOD analysis for each year).

Plants transplanted into the experimentally devegetated gopher proof pen were significantly more likely to increase in size class (94.5%, n = 109) than in plants in the reference (vegetated) pen (64.6%, n = 82; G = 26.7, $P < 0.001$). This difference was also true considering only plants which remained rosettes in 1990, *i.e.*, excluding those plants which reproduced (devegetated pen: 81.8% increased in size class, n = 33; reference pen: 48.2%, n = 56; G = 8.93, $P < 0.005$). The increased probability of increasing in size class in the devegetated pen was exhibited by both the large and extra large rosettes (devegetated pen: 100%, n = 57; control pen: 73.6%, n = 53; G = 14.88, $P < 0.001$) and by the smaller 1st-yr rosettes (devegetated pen: 88.5%, n = 52; control pen: 46.7%, n = 30; G = 14.37, $P < 0.001$).

Effects of root removal.—As reported above, most of the plants which survived the root removal treatment flowered the following year. Since the production of a stem is considered an increase in size class, the conclusion regarding the effect of root removal on growth is

TABLE 1.—Summary of the qualitative effects (—, 0, +) of three disturbances on the survivorship, growth, and reproduction of *Penstemon grandiflorus* plants. The plus signs in brackets [+] indicate that plants exhibited increases in growth and reproduction when transplanted into bare soil which had been experimentally produced (as opposed to having been produced by gophers). Survivorship effects are from Davis *et al.*, (1991)

	Fire	Root loss	Earth-moving by gophers
Survivorship	— (small plants) 0 (large plants)	— (especially large plants)	— (especially small plants)
Probability of reproducing among surviving plants	—	0	0, [+]
Reproductive output in flowering plants	0	0	0, [+]
Probability of increasing in size class among surviving plants	—	0	+, [+] (small plants) 0, [+] (large plants)

identical to that for reproduction: no effect. Only two of the 11 surviving root-pruned plants remained rosettes; thus it was not possible to do a separate analysis of the effect of root removal on growth of plants which did not reproduce.

DISCUSSION

In North American prairies and oak savannas, fire and pocket gophers are responsible for at least three different kinds of disturbances which potentially can affect the fitness of individual herbaceous plants. Fire during the growing season can burn aboveground biomass (Vogl, 1974); gophers can bury plants and/or surrounding vegetation through their mound-building activities (Davis *et al.*, 1991); and gophers can feed on plants (Behrend and Tester, 1988; Reichman, 1988). All three of these disturbances affect *Penstemon grandiflorus*, but in qualitatively different ways (Table 1).

Fire during the growing season and root removal result in tissue loss of individual plants. In this study, fire significantly reduced the rates of both growth and reproduction; however, root removal had no effect on either. This difference is likely due to the type of tissue lost in each case. Fires which occur during the growing season burn stems and leaves. Except for plants in the smallest size class, fire does not increase mortality rates (Davis *et al.*, 1991). Thus, following a burn, most plants draw on belowground energy reserves and produce new aboveground tissue. Reduction of energy reserves following the 1987 fire is the most likely explanation for the subsequent reduction in both growth and reproduction exhibited by *Penstemon*.

The root removal experiment only involved the removal of the fleshy roots; the woody caudex, the energy storage organ, was not affected. Thus, if a plant survived the loss of root tissue, it did not experience any appreciable reduction in stored energy. This may explain why surviving root-pruned plants did not exhibit any reduction in growth or reproduction. Other root-pruning studies found similar results, *i.e.*, no discernible effect on the functioning of surviving plants (Lovett Doust, 1980; Anderson, 1987).

The data showed that the reduction in growth and reproduction produced by fire persisted into the 2nd growing season following the burn. The reduction in growth and reproduction in *Penstemon* following fire clearly indicates that this species does not benefit from the loss of aboveground tissue (*e.g.*, through the overcompensation of reproductive output), as has been documented for *Ipomopsis aggregata* (Polemoniaceae), a species with a similar growth form—rosette young plants and stem mature plants (Paige and Whitman, 1987).

Individual *Penstemon* plants are often buried and killed under gopher mounds (Davis *et al.*, in press). This fact notwithstanding, this study showed that plants do experience some benefits from the earth-moving activities of gophers. Specifically, plants growing where gophers are active and where bare soil is abundant were found to grow faster than plants growing where gophers are absent and where other vegetation is more dense. Similar results (reduced survivorship but increased growth) were obtained at Cedar Creek for *Berteroa incana* plants growing on gopher mounds (Reichman, 1988).

When size is accounted for, the flowering rate of plants growing naturally where gophers are active is no different than for other plants. However, since the probability of flowering increases with increasing plant size, plants growing where gophers are active (and where bare ground is abundant) will reproduce sooner. This finding was confirmed by the higher reproductive rates of 2nd-yr plants growing in the devegetated gopher-exclusion pen and is consistent with other reports showing that dense surrounding vegetation reduces growth and delays flowering in herbaceous species (Holt, 1972; Werner, 1975; Gross and Werner, 1983).

It is important to note that separate bare ground measurements were made for each of the naturally growing plants in the study and that these measurements covered an area only 0.5 m^2 in size. It was not uncommon for plants only 1 or 2 m apart to differ greatly in the measurement of bare ground. Such differences can occur because the substrate is very heterogeneous where gophers are active. Patches of vegetation are intermingled with patches of bare ground associated with mounds and tunnels near the soil surface. The effect of the gophers is to produce a lattice of soil disturbances throughout the openings. The extent to which a plant is affected by gophers depends upon how close that plant is to a node (mound) or arc (tunnel) in the lattice.

Interactions between fire and pocket gophers and plant size.—The analysis of the naturally growing plants showed that the effects of fire and gophers on *Penstemon* growth and reproduction are mediated by the size of the plant: fire reduces the 1st-yr growth of small plants but not of large plants, and the presence of bare ground (and hence of gophers) increases the growth rates of small plants but not of large plants. In addition, small plants are more likely to be killed by a later spring burn than large plants, and also are more likely to be killed by being buried under a gopher mound (Davis *et al.*, 1991). Thus the aboveground effects produced by fire and gophers on individual plants are primarily the result of the effects on small plants. Large plants which possess larger caudices (Davis *et al.*, 1991), and thus greater belowground energy stores, are better able to absorb aboveground stresses produced by fire, gophers and surrounding vegetation than smaller plants.

Population-wide effects of fire and gophers.—Nonlethal injury has been proposed as a mechanism of population regulation in animals by reducing subsequent survival and reproduction (Harris, 1989). Since fire during the growing season reduces rates of both growth and reproduction in *Penstemon* for at least 2 yr subsequently, the population-wide reproductive output is significantly reduced. Although fire during the early growing season had little initial effect on the survivorship patterns of *P. grandiflorus* (Davis *et al.*, 1991), it is possible that the reduction in subsequent seed output throughout the population might effect future population size through a reduction in recruitment. However, due to the difficulty of assessing the importance of regular reproduction in a perennial plant (Andersen, 1989), this possibility cannot be evaluated at this point.

The effect of fire on individual plants is usually the nonlethal loss of tissue resulting in a reduction in growth and reproduction. On the other hand, plants which experience root loss or are buried under a gopher mound are either killed or they survive with no reduction in growth or reproduction, at least during the 1st yr following the encounter. In fact, the effect of the gopher's earth-moving activities is to increase the growth rates of surviving *Penstemon*. Plants not killed by being buried grow faster and reproduce sooner than plants growing where gophers are not active and the vegetation is dense. Since recruitment rates are also higher in areas with bare soil (Davis *et al.*, 1991), the gophers can be seen as altering their environment in a way which favors the growth, reproduction and recruitment of a food plant.

In conclusion, herbaceous plants of prairies and oak savannas regularly experience multiple disturbances, including fire, soil excavation by fossorial animals, and herbivory both above and below ground (Daubenmire, 1968; Mielke, 1977; Grimm, 1984; Behrend and Tester, 1988; Gibson, 1989). This and a companion study of the effects of these disturbances on *Penstemon grandiflorus* (Davis *et al.*, in press) show that these disturbances often result in tissue damage to individual plants. The data from these two studies show that the type of tissue damaged (root, stem or leaf) and the size of the plant are important in determining whether or not the disturbance reduced the fitness of the plant via decreased survivorship, growth or reproduction.

Even though both fire and gophers can reduce the fitness of individual plants, these are the same agents which produce the disturbances that maintain suitable habitat for *Penstemon*—the prairie openings with patches of bare soil (Davis *et al.*, 1991). These studies of *Penstemon* demonstrate why studies of the effects of disturbances on individual species need to examine the species at several levels of ecological organization (*e.g.*, individual and population) and to use several criteria (*e.g.*, survivorship, growth, reproduction and recruitment) in order to assess the full affect of the disturbances.

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