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An Experimental Study of the Effects of Shade, Conspecific Crowding, Pocket Gophers and Surrounding Vegetation on Survivorship, Growth and Reproduction in Penstemon grandiflorus

MARK A. DAVIS, BYRON RITCHIE, NORMAN GRAF AND KIM GREGG
Department of Biology, Macalester College, St. Paul, Minnesota 55105

ABSTRACT.—A variety of microhabitat changes occur as oak savannas are transformed into woodlands, including an increase in woody canopy shade and a decrease in patches of bare soil, the latter due to the decline of grassland dwelling and mound building animals such as badgers and pocket gophers. In an oak savanna and woodland in east central Minnesota, *Penstemon grandiflorus* (Scrophulariaceae) is associated with bare soil patches created by the northern plains pocket gopher, *Geomys bursarius,* and both species are confined mostly to openings in the woodland and savanna. The purpose of this study was to experimentally manipulate shade and bare soil in order to determine the relative effects of woody canopy shade and surrounding herbaceous vegetation on the survival, growth and reproduction of *Penstemon grandiflorus* in an experimental garden. During the three year experiment, unshaded plants growing in bare soil had the highest rates of survivorship, growth and reproduction, whereas shaded plants surrounded by herbaceous vegetation had the lowest respective rates. The results indicate a relatively high shade tolerance by *P. grandiflorus,* and thus the absence of this species from the closed canopy of the oak woodland must be due to factors other than shade. The absence of pocket gophers, *G. bursarius,* and hence bare soil, in woodlands is likely one of these factors.

INTRODUCTION

In east central Minnesota, remaining oak savannas, brushland and woodlands represent a dynamic transition zone between prairie and forest. Drought and frequent fires decrease tree cover in these habitats, whereas woody plants encroach into open areas in the absence of fire, transforming oak savannas into oak brushland and woodland (Cottam, 1949; Grimm, 1984; Abrams, 1992; Faber-Langendoen and Tester, 1993; Wovcha *et al.* 1995; Faber-Langendoen and Davis, *in press*). A variety of microhabitat changes occur as oak savannas are transformed into woodlands, including an increase in woody canopy shade and a decrease in patches of bare soil, the latter due to the decline of grassland dwelling and mound building animals such as pocket gophers.

In a previous study of *Penstemon grandiflorus* (Scrophulariaceae) growing in an oak savanna and woodland in central Minnesota, we found that plants grew faster and reproduced sooner when they grew in bare or partially bare soil patches produced by the northern plains pocket gopher (*Geomys bursarius*) (Davis *et al.,* 1991a). On a larger scale, both *P. grandiflorus* and *G. bursarius* are mostly confined to openings in the woodland and savanna and both are absent in closed canopy areas. Due to the nonexperimental approach of the 1991 study, it was impossible to determine to what extent shade tolerance or absence of bare soil contributed to the absence of *P. grandiflorus* in the woodland interior. The purpose of this study was to experimentally manipulate these two factors in order to determine the relative effects of canopy shade and bare soil on the survival, growth and reproduction of *P. grandiflorus.*

MATERIALS AND METHODS

The study area was located at Cedar Creek Natural History Area (45°25′N, 93°10′W), East Bethel, MN Cedar Creek is situated on a 2200 km^2 sandplain formed 12,000–13,000-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 well drained and low in inorganic matter and total nitrogen (Grigal *et al.,* 1974). This study was undertaken in one of the old fields at Cedar Creek.

Penstemon grandiflorus (Scrophulariaceae) is a perennial forb that 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, in Minnesota, the species grows in a variety of habitats, including sand prairies, oak savannas and bedrock bluff habitats along the Minnesota, Mississippi and St. Croix rivers. First year *P. grandiflorus* have a rosette growth form and usually consist of a single leafy rosette. The size, and sometimes the number, of rosettes increases with age, and eventually one or more flowering stems are produced. After flowering, plants may flower again the succeeding year or revert back to a rosette growth form for a year or two before flowering again (Davis *et al.,* 1991a). The rosettes and stems arise from a woody caudex 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) purple flowers in early June.

Experimental design.—We created an experimental garden to test the effects of surrounding herbaceous vegetation and shading by woody vegetation on *Penstemon* survivorship, growth and reproduction. In addition to these two factors, we examined the effects of gopher exclusion and crowding of seedlings. We included these latter two factors because *Penstemon* plants are commonly found growing within a few centimeters of one another and because a previous study (Davis *et al.,* 1991b) had shown that plants are occasionally buried under gopher mounds and that gophers may kill plants through underground herbivory.

We used a split-plot design. Ten large plots (13 × 17 m) were established in an old field at Cedar Creek, and five of the ten were randomly designated as gopher exclusion plots. A 1.2-m-deep trench was dug around the perimeter of these five plots and 1.5-m-high galvanized metal fencing (1.2 cm mesh) was placed in the trench, which was then filled in with the excavated soil.

Within each large plot, eight small plots (1 × 1 m) were established. Each small plot had a 1-m-wide buffer around it and plots were further separated by 1 m wide walkways. Thus, each small plot was 3 m away from adjacent plots. The three other factors were each implemented with two treatment levels (shade: shade/no shade; crowding: high/low; surrounding herbaceous vegetation: present [not weeded]/absent [weeded]) and were combined in a full factorial design (yielding 8 combinations). In late June 1990, first year *Penstemon* seedlings grown from seed by Prairie Restoration, Inc., Princeton, MN were transplanted into the plots. Nine seedlings were planted in each small plot in 3 rows of 3 plants each. In low crowding plots, 45 cm separated adjacent plants, while 5 cm separated adjacent plants in high crowding plots. In high crowding plots, the 9 plants were planted in the central area of the plot. Seedlings were watered every other day for the first 10 days following transplanting. A few seedlings died during this time and were replaced.

Shading by woody vegetation was simulated using commercial shade cloth with a shading effect of 80%. The 80% shade cloth was chosen because previous measurements of light intensity in the fully shaded areas of the oak woodland using a light meter indicated that the woody canopy reduced light levels about 80%. The shade cloth was attached to and draped over four iron reinforcement bars that were inserted into the ground at the four corners of the 1 m^2 plot. The shade cloth was positioned so that the top was approximately 75 cm above the ground. In order to allow air movement into the shaded plots, the side of the shade cloth facing north stopped 30 cm above the ground, and the sides of the shade cloth facing south, east and west stopped a few cm above the ground. Subsequent measurements of air temperatures taken under the shade revealed no difference compared to air temperatures taken in the shade of the adjacent woodland. The mesh screening easily allowed rain water to drip through. In early November of each year, the shade cloth was removed. It was replaced in early May, about the time the oaks leaf out at Cedar Creek.

Plots designated to be free of herbaceous vegetation were treated with Roundup herbicide in early June 1990, before planting the *Penstemon* plants. These plots were kept free of herbaceous vegetation throughout the experiment through periodic weeding.

A total of 12 measurements were made of the plants during the three years of the garden study. For each small plot, the number of surviving plants was recorded in late August of 1990, 1991 and 1992, and the number of reproducing plants was recorded during 1991 and 1992. Three additional measurements were made of first year plants: rosette diameter, number of leaves in the rosette and width of widest leaf (*e.g.*, Werner, 1975; Gross, 1981; Gross and Werner, 1983). The number and height of all flowering stems were recorded for reproducing second and third year plants. The number of flowering nodes is highly correlated with stem height (Davis *et al.*, 1991a). The number of surviving and reproducing plants and the means of the other variables were determined for each small plot and these data were used for subsequent statistical analysis. The data were log transformed before a split-plot full factorial analysis. Since the objective was to determine the effects of the various factors during each of the three years, a separate split-plot analysis was done for each year. Because the original split-plot analysis showed that gopher exclusion had no significant effect on any of the variables, and since none of the two-way, three-way, or four-way interactions involving gophers were significant, the gopher effect was deleted from the model and the data were reanalyzed using a randomized block design.

RESULTS

None of the three-way interactions was significant. Significant main effects or two-way interactions are summarized below and in Table 1.

1990 (1st year plants).—Weeding resulted in a 58% increase in the number of leaves produced by a plant and a 3% decrease in survivorship. High crowding also reduced growth, with plants in the high crowding plots producing 15% fewer leaves than plants in the low crowding plots. Rosette diameter and leaf width were both affected via interactions between weeding and shading and between weeding and crowding. Specifically, shading did not reduce either rosette diameter or leaf width in unweeded plants, but shading reduced rosette diameter by 13% and leaf width by 33% in weeded plants. High crowding did not reduce rosette diameter or leaf width in unweeded plants, but high crowding reduced rosette diameter by 13% and leaf width by 17% in weeded plants.

1991 (2nd year plants).—Weeding increased the number of stems produced per plant by 38% and mean stem height by 5%. Conversely, shading decreased the number of stems produced per plant by 31% and decreased mean stem height by 16%. Weeding interacted with shading to affect survivorship and number of reproducing plants. Specifically, there was high survivorship (82–89%) for all combinations except for plants growing in shaded and unweeded conditions (45%), and no plants growing in shaded and unweeded conditions reproduced during the second year. Weeding also interacted with crowding to affect the number of reproducing plants. In unweeded plots, the number of reproducing plants

TABLE 1.—Summary of significant ANOVA results, including means and standard deviations of the main effects (*0.05, **0.01, ***0.001). See text for details regarding the significant two way interactions. None of the three way interactions was significant. *NW* = Not Weeded; *W* = Weeded; *NS* = Not Shaded; *S* = Shaded; *HC* = High Crowding; *LC* = Low Crowding

Variable	Significant main effects or interactions
Survivorship '90	*NW* 8.875 ± 0.41 plants; *W* 8.60 ± 0.67 plants; F = 4.89*
Number of leaves '90	*NW* 6.93 ± 1.49 leaves; *W* 10.94 ± 2.88 leaves; F = 94.19***
	HC 8.22 ± 2.10 leaves; *LC* 9.65 ± 3.65 leaves; F = 7.93**
Leaf width '90	Weeding × Shading; F = 41.66***
	Weeding X Crowding; F = 9.23**
Rosette diameter '90	Weeding × Shading; F = 5.23*
	Weeding × Crowding; F = 4.93*
Survivorship '91	Weeding × Shading; F = 15.15**
Reproduction '91	Weeding × Shading; F = 11.41**
	Weeding × Crowding; F = 7.07**
Stem height '91	*NW* 36.63 ± 5.50 cm; *W* 38.54 ± 8.50 cm; F = 4.64*
	NS 40.65 ± 7.65 cm; *S* 34.12 ± 7.38 cm; F = 15.16***
No. stems/plant '91	*NW* 1.06 ± 0.14 stems; *W* 1.46 ± 0.52 stems; F = 25.98***
	NS 1.58 ± 0.58 stems; *S* 1.09 ± 0.24 stems; F = 39.44***
Survivorship '92	*NS* 7.10 ± 2.18 plants; *S* 3.60 ± 2.89 plants; F = 50.61***
	HC 4.70 ± 3.35 plants; *LC* 6.00 + 2.71 plants; F = 6.98*
Reproduction '92	*NW* 1.75 ± 2.38 plants; *W* 4.10 ± 3.23 plants; F = 23.48***
	NS 4.53 ± 3.17 plants; *S* 1.33 ± 1.91 plants; F = 43.54***
	HC 2.20 ± 2.83 plants; *LC* 3.65 ± 3.14 plants; F = 8.94**
Stem height '92	*NW* 44.07 ± 8.62 cm; *W* 49.13 ± 7.83 cm; F = 6.87*
No. stems/plant '92	*HC* 1.39 ± 0.35 stems; *LC* 2.55 ± 1.40 stems; F = 17.29***
	Weeding × Shading F = 5.69*

was very low (less than one individual on average) irrespective of plant crowding, whereas in weeded plots the low crowding treatment resulted in more than two additional reproducing individuals than in high crowding plots.

1992 (3rd year plants).—Weeding increased the number of reproducing plants in the 3rd year by 134% and the mean height of flowering stems by 11%. Shading reduced survivorship by 49% in year three and the number of reproducing plants in by 71%. High crowding reduced survivorship by 22%, the number of reproducing plants by 40%, and the number of flowering stems produced per plant by 33%. Weeding and shading interacted to affect the number of flowering stems produced per plant. Specifically, weeding had no effect under shaded conditions, but weeding increased the number of flowering stems produced per plant by 88% in unshaded conditions.

DISCUSSION

Effects of shade and surrounding herbaceous vegetation.—Previous experimental field studies have investigated the combined effects of shade and herbaceous competition on growth of tree seedlings (Shirley, 1945; Van Auken and Bush, 1991). These studies, along with a study of woody plant seedlings growing naturally (Wilson, 1991) showed that both shade and surrounding herbaceous vegetation can reduce seedling growth. This study showed similar results for *P. grandiflorus*, with both shade and surrounding herbaceous vegetation reducing survivorship, growth, and reproduction. Although rates of survivorship, growth and reproduction were reduced by shade, the data showed that *P. grandiflorus* is actually quite shade tolerant when surrounding herbaceous vegetation is removed. The pronounced suppressive effects of surrounding herbaceous vegetation are consistent with the findings of previous studies of *P. grandiflorus* plants growing naturally in the oak woodland (Davis *et al.,* 1991a, b) and for *Penstemon barbatas,* which was more likely to flower when growing in the bare soil produced by *G. bursarius* (Martinsen *et al.,* 1990).

We have not yet determined the precise mechanism by which growth and reproduction are reduced by surrounding herbaceous vegetation. In a study of *Schizacharium scoparium,* a C_4 prairie grass, Wilson and Tilman (1993) found that belowground competition with other herbaceous vegetation was more important than the aboveground competition for light in nitrogen poor soils. The fact that shade alone does not greatly reduce growth in *P. grandiflorus* indicates that the shade of surrounding herbaceous vegetation is probably not the primary mechanism reducing growth. *Penstemon grandiflorus,* which does grow in nitrogen poor soils, may, like *S. scoparium,* be a poor competitor for belowground resources. Another possibility is that the presence and buildup of litter may inhibit growth of the plants (Tilman and Wedin, 1991). This may be a particular problem for plants adapted to fire environments (Tilman and Wedin, 1991) and especially for plants with rosette growth forms (Weaver and Rowland, 1952), *e.g.,* young and nonreproducing *P. grandiflorus* plants.

Effects of pocket gophers and seedling density on Penstemon survivorship, growth, and reproduction.—Other studies have shown that pocket gophers can kill plants by burying them under soil mounds and by feeding on their roots (Martinsen *et al.,* 1990; Reichman and Smith, 1991). A previous study of plants growing naturally in at Cedar Creek indicated that this was true for *P. grandiflorus* as well (Davis *et al.,* 1991b). We had expected that gopher exclusion in the garden experiment would produce similar results. The absence of such an effect may be due to several factors. The rate and extent of new mound production in the field of the garden experiment may have been lower than that in some of the openings of the woodland, in which the previous studies were conducted. This possibility is supported by the fact that very few plants growing outside the exclosures were buried during the three year experiment.

Seedlings planted under high density conditions grew less during the first year. Davis *et al.,* (1991a) determined that the probability that a rosette plant would flower the subsequent year was strongly influenced by the size of the rosette. This was borne out again in this study as high density plants were less likely to reproduce the second year. The negative effects of high density continued into the third year of the study, with reduced survivorship as well as reduced reproductive effort in surviving plants.

Penstemon grandiflorus and its location in the oak savanna/woodland landscape.—That simulated woody canopy shade generally reduced survivorship, growth and reproduction in this species is not surprising, since its primary habitats are prairies and savannas (Barkley, 1986; Wovcha *et al.,* 1995). What did surprise us is how well *P. grandiflorus* grew in the shade when it did not have to contend with surrounding herbaceous vegetation. Although *Penstemon* clearly grows better in the sun, this study indicates that it is actually quite shade tolerant. The virtual absence of this species in the closed canopy areas of the study site thus must be due to factors other than shade of woody canopy. One possibility is the scarcity of bare soil in closed woodland areas due the abandonment of these areas by *G. bursarius.* The results from this study clearly showed that the combined effects of shade and surrounding herbaceous vegetation severely reduced survivorship, growth and reproduction of *P. grandiflorus.* Edaphic factors, which are known to differ under tree canopies in oak savannas (Ko and Reich, 1993), and root competition with trees (Skarpe, 1990 and Callaway *et al.,* 1991) are other factors that might confine *P. grandiflorus* to openings in the woodland despite its shade tolerance.

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