The Influence of Crowding and Pocket Gopher Disturbance on Growth and Reproduction of a Biennial, *Tragopogon dubius*

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Abstract. Comparisons between the effects of plant density and pocket gopher (*Geomys bursarius*) disturbance (burrows and mounds) on the growth and reproductive output of a biennial, *Tragopogon dubius*, revealed that the former has a greater influence than the latter. Simulated burrow treatments in areas of high vegetation density differentially affected plant mortality, whereas burrows in low-density areas did not. Conversely, total plant biomass and measures of reproductive output differed significantly in areas of low plant density but showed no differences in high-density areas. Occupied natural burrows yielded higher plant biomasses than vacant natural burrows, and both produced higher biomasses than adjacent controls. No effects of mounds on the growth and reproductive output of *T. dubius* were evident.

Key words: burrows, fossorial herbivore, *Geomys bursarius*, mounds, oldfield vegetation, Pocket gopher, *Tragopogon dubius*

Introduction

Most individual plants are subjected to the dual influences of competition and herbivory. Adjacent individuals may compete for sunlight, water, nutrients, and mutualists, and virtually all plants are fed upon at some point in their life cycle. Investigations of such interactions are complicated and difficult and so have tended to concentrate on one aspect or the other. Further complications exist because some herbivores have both direct (e.g., consumption) and indirect (physical disturbance) effects on plants, and very little is known about the relative influence of these factors.

This study was undertaken to concurrently analyze the effects of a subterranean mammalian herbivore the plains pocket gopher (*Geomys bursarius*) and plant density on the growth and reproduction of *Tragopogon dubius*, a biennial plant species. The study followed an earlier investigation of the effects of these factors on an annual species, *Berteroa incana* (Reichman, 1988). *Tragopogon dubius* is common in old fields, where it often is subject to the influences of high densities of other early-successional plant species. In addition, it can be subject to the direct (consumption; Williams and Cameron, 1986; Behrend and Tester, 1988) and indirect (physical disturbance via burrows and mounds; Andersen 1987, 1988; Gibson 1989; Reichman and Smith 1985; Reichman 1988; Reichman et al. 1993) effects of pocket gophers, effects that can significantly alter plant density and community structure (Huntly and Inouye 1988; Huntly, 1991). *Tragopogon dubius* is a favored dietary item for pocket gophers (Behrend and Tester, 1988), and studies have revealed the effects of simulated gopher herbivory of this species (Reichman and Smith 1991).

This study was designed to determine the joint impacts of the presence of potentially competing vegetation and pocket gopher activity (mounds and burrows) on *T. dubius*. Analyses were made of the impact of simulated pocket gopher burrows, in the presence and absence of additional vegetation, on the growth and reproduction of *T. dubius*. Simulated burrows were constructed to provide more effective control over burrow variables, and treatments included open ("vacant") burrows and burrows refilled with soil to mimic backfilling behavior by pocket gophers. The effects of natural occupied and vacant burrows and mounds, also were analyzed by comparing their influence on *T. dubius* to paired controls in old-field vegetation directly adjacent to the pocket gopher disturbances.

Methods

The experimental arrangement is that of Reichman (1988). Two sets of experiments, termed Pen experiments and Field experiments, were conducted in Field 44 at Cedar Creek Natural History Area 45 km north of Minneapolis, MN. Pen experiments involved simulated burrows within gopher exclosures whereas Field experiments were outside the pens and employed naturally occurring pocket gopher mounds and vacant and occupied burrows.

Pen Experiments

The pens were 14 m in diameter, extended 1.6 m above the ground and into the ground, and had complete wire bottoms, thereby totally excluding pocket gophers. Two pens contained background old-field vegetation (32.2 and 38.6 stems/0.1m^2; these densities are similar to those in the surrounding fields) and were termed "vegetated" pens. Two other pens (termed "devegetated") were sprayed with Roundup at the initiation of the experiment in May, effectively denuding the surface.

Fourteen replicates of each of four treatments and 14 controls with no treatment were established in the vegetated and devegetated pens. The four treatments initially imposed were:

- Vacant - simulated burrows with no further manipulation (simulating vacant burrows)
- Occupied - simulated burrows from which emerging roots were to be trimmed (simulating occupied burrows from which pocket gophers trimmed the roots)
- Top - burrows refilled with soil from the upper 10 cm of soil (simulating backfilling with the most nutrient-rich of the locally nutrient-deficient soils; Inouye et al., 1987)
- Deep - burrows refilled with soil from a depth > 60 cm (soil especially nutrient-deficient; Inouye, et al., 1987)

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In the two latter treatments, the soil was packed to a density equivalent to that measured for gopher burrows at Cedar Creek (Reichman, 1988). No substantial root growth occurred in the Trimmed treatment, so it was combined with the Vacant treatment to yield three treatments (Vacant, Top, Deep) and one control, each having 14 replicates, except for the Vacant treatment with 28.

Simulated burrows were constructed by driving an 8-cm-diameter PVC pipe horizontally 1 m through the ground at a depth of 12.5 cm. and extracting the soil plug. This diameter and depth are similar to those of burrows found in Field 44 (Reichman, 1988). The simulated burrows radiated from a central pit like spokes from a hub, and each pen (two vegetated and two devegetated) contained two pits. Treatments were assigned randomly to spokes within vegetated and devegetated pens. Plugs were inserted in the open end of the simulated burrows to reduce moisture loss.

Four individual *Tragopogon dubius* rosettes were transplanted evenly and directly over each spoke after burrow construction in July and served as repeated measures for each treatment (for statistical analysis, the values for the four repeated measures/replicate were averaged). The transplanted rosettes had germinated in small pots that spring and were statistically indistinguishable in size at the time of transplantation (10-15 cm tall; ANOVA for size differences between treatments - $F = 0.06$, $df = 3{,}279$, $P > 0.75$). A 10-cm swath was cut over treatment sites in vegetated pens to facilitate initial success during transplantation. These manipulations yielded an arrangement of 14 replicates of two treatments (Top and Deep) and the controls plus 28 replicates of the Vacant treatment (after combining the Vacant and Occupied treatments), each with four repeated measures (transplanted *T dubius*), for a total of 280 individual plants.

Field Experiments

Similar *T. dubius* rosettes were transplanted onto fresh (< 2 weeks old) mounds and over vacant and occupied burrows (as determined by whether an excavated opening was plugged within 24 hrs). Burrows were located by probing the soil, a difficult technique in the loose sandy soil of Cedar Creek. Therefore, when the plants were harvested the soil below was excavated to confirm the presence of a burrow and whether it was vacant or occupied (again, based on whether the opening went unplugged for 24 hrs).

Fifty-three mounds and 50 locations over both vacant and occupied burrows received transplants. Controls also were established 25 cm from each experimental transplant. Subsequent mortality from an extreme drought over the 2 years of the investigation substantially reduced survivorship, in some cases yielding sample sizes too small to promote confidence in statistical results (see results).

Analysis

Entire plants were harvested from all experimental units in August, slightly over 2 years after they were planted. The number remaining alive for each experimental unit was recorded. Root crown diameter, plant height (both of which are accurate indicators of reproductive output for T. dubius; Gross 1981, 1984; Gross and Werner 1982), and the total number of capitula also were recorded. Specimens were oven dried at 60 C. for 72 hours. Subsequently, the masses of the root and stem tissue were recorded separately and summed to yield total biomass of the plant.

Model II regression analyses (using the Bartlett three-group method) were applied to relate plant height, number of capitula, stem biomass, and root biomass to total biomass. Calculations were made by treatment and for values combined for all replicates. Replicated goodness of fit test (G-statistic) was used to compare mortality (number of repeated measures/replicate alive) in the Pen experiments.

Two-way ANOVA was used to compare the effects of treatment and vegetation density on plant growth and reproduction in the Pen experiments (variances for the variables were homogeneous). Where significant treatment effects were detected, a Tukey-Kramer a posteriori separation procedure was applied to determine which treatments differed significantly from each other (Sokal and Rohlf, 1981). No significant differences in total plant biomass occurred between the two vegetated pens or between the two devegetated pens ($F = 2.02$, $df = 1{,}29$, $P > 0.05$ and $F = 0.78$, $df = 1{,}64$, $P > 0.05$ respectively). Therefore, the data for each set of two pens were combined for the analyses.

Mortality in the Field experiments was extremely high. Therefore, the controls for all treatments (mounds, vacant and occupied burrows) were combined and compared to each treatment with a Student's t-test.

It should be noted that the 14 or 28 replicates of each simulated burrow treatment were arrayed in only two pens each for vegetated and devegetated manipulations and that transplants in the field experiments were placed over just a few separate burrow systems. This could be considered a form of pseudoreplication (Hurlbert, 1984). The required effort, expense, and disturbance precluded constructing 140 separate gopher exclosures or finding 50 separate burrows systems. The results should be considered in light of this caveat.

Results

All of the measures of plant growth and reproduction were correlated significantly with total plant biomass and exhibited the same pattern of response, in both direction and magnitude, between controls and treatments (Table 1). Therefore, total plant biomass will be used as the primary measurement variable for comparisons between treatments.

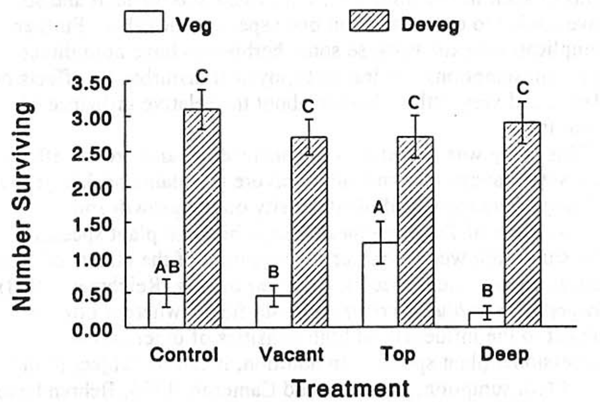

FIG. 1. Average number of plants alive (out of four initially transplanted) after 2 years for controls and treatments in vegetated and devegetated pens (vertical bars = S. E.'s). Bars sharing letters are statistically indistinguishable from each other. Sample size for each from left to right = 6, 14, 9, 25, 11, 13, 4, 13.

Pen Experiments

The number of individuals alive 2 years after transplantation was significantly lower in vegetated pens than in devegetated pens ($F = 255.4$, df = 1,139, $P < 0.0001$; Fig.1). Within vegetated pens, plants over the Top treatment survived in significantly greater numbers than plants over Vacant and Deep treatments; survival of the controls was intermediate and statistically indistinguishable from survival of the treatments (Fig. 2; $F = 5.38$, df = 3,29, $P < 0.01$). No significant differences occurred in survival between treatments within devegetated pens (Fig. 1).

The average plant biomass was significantly greater in devegetated than in vegetated pens ($F = 12.68$, df = 1, 94, $P < 0.001$; Fig. 1). Within devegetated pens, control plants were significantly smaller than those in the three treatments ($F = 2.86$, df = 3, 94, $P < 0.05$; Fig. 2; stem and root biomass, root crown diameter, and plant height showed statistically similar patterns), but no significant differences occurred among controls and treatments within vegetated pens ($F = 0.92$, df = 3, 29, $P > 0.05$; Fig. 2).

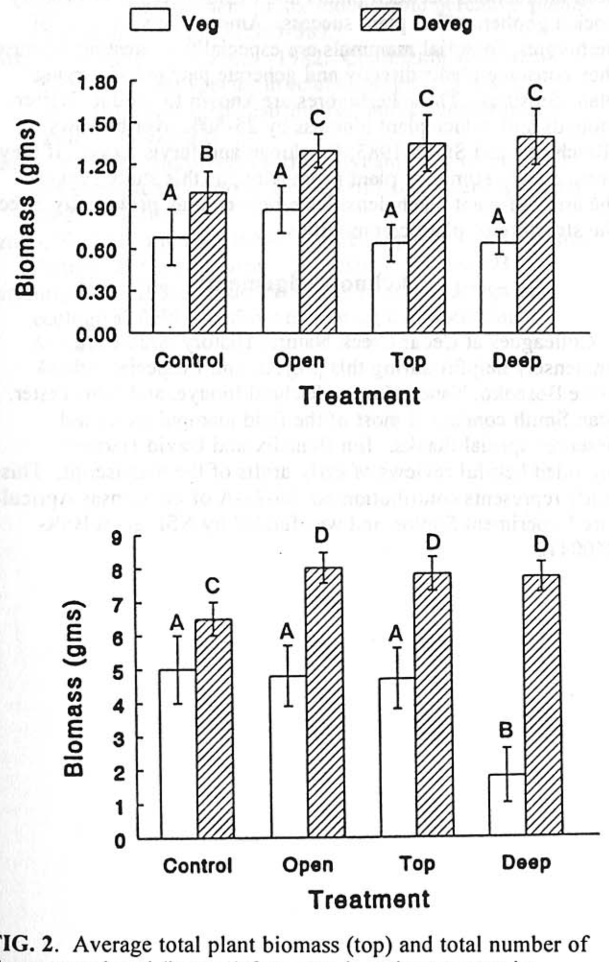

FIG. 2. Average total plant biomass (top) and total number of flowers produced (bottom) for controls and treatments in vegetated and devegetated pens (vertical bars = S. E.'s). Bars sharing letters within either graph are statistically indistinguishable from each other. See Fig. 1 for sample sizes.

A similar pattern was exhibited for the total number of flowering heads produced (Fig. 2). Significantly more were produced in the devegetated pens than the vegetated pens ($F = 11.22$, df = 1, 94, $P < 0.001$), and the controls in the devegetated pens produced significantly fewer flowers than plants in any of the treatments ($F = 2.99$, df = 3, 94, $P < 0.001$). Within the vegetated pens, plants over burrows refilled with top soil produced fewer flowering heads ($F = 3.68$, df = 3, 94, $P < 0.001$) than plants in other treatments (unlike values for total biomass, where no differences were exhibited within the vegetated pens).

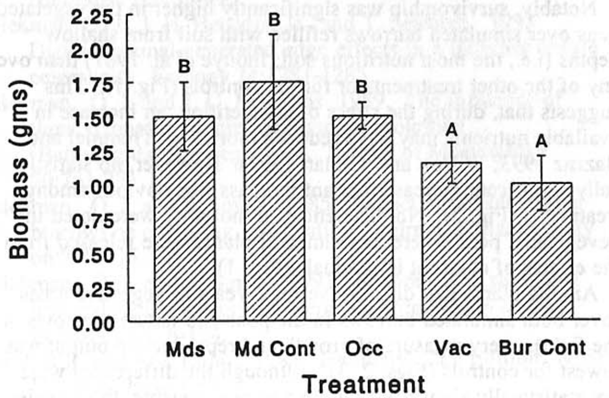

FIG. 3. Total biomass of plants on mounds and adjacent controls and over occupied and vacant burrows and their controls (vertical bars = S. E.'s). Bars sharing letters are statistically indistinguishable from each other.

Field Experiments

Total biomass of individual *T. dubius* plants on mounds and adjacent controls did not differ significantly (Fig. 3). However, significant differences occurred among plants growing over occupied burrows, those over vacant burrows, and control plants, with those on occupied burrows exhibiting the highest biomass response ($F = 5.41$, df = 1, 38, $P < 0.01$; Fig. 3). These differences are in spite of very small sample sizes, which resulted from high mortality during the experiments. Mortality did not differ between plants on mounds and their controls or between plants on the occupied and vacant burrows and their controls However, many more plants over burrows, whether occupied or vacant, and their controls died than did compared to plants on the mounds or their controls.

Table 1. Product moment correlations between total plant biomass and other variables measured in the study. Df = 94, all $P < 0.001$

Variable	r
Stem Biomass	0.982
Root Biomass	0.873
Root Crown Diameter	0.785
Heigh	0.637
Total Number of Flowers	0.693

Discussion

Under certain circumstances, the simulated and natural pocket gopher disturbances analyzed in this study did affect experimental plants. Furthermore, Reichman and Smith (1991) showed that *T. dubius* was affected significantly more by herbivory simulating pocket gopher foraging than by aboveground herbivory. However, as with an earlier investigation of an annual species (Reichman and Smith 1985), the survival, growth, and reproduction of individuals was affected more by the presence of nearby plants than by specific gopher generated disturbances (Figs. 1, 2, 3).

Notably, survivorship was significantly higher in the vegetated pens over simulated burrows refilled with soil from shallow depths (i.e., the most nutritious soil; Inouye et al. 1987) than over any of the other treatments or for the controls (Fig. 1). This suggests that, during the stress of competition, an increase in available nutrients may have reduced mortality (Tremmel and Bazzaz 1993; Wilson and Tilman 1993). However, no statistically significant increase in plant biomass was obvious among treatments (Fig. 2). No differences in mortality were noted in devegetated pens where experimental plants were released from the effects of adjacent individuals (Fig. 1).

Among plants that did survive for 2 years in vegetated areas (over both simulated burrows in the pens and natural burrows in the field), every measure of growth and reproductive output was lowest for controls (Figs. 2, 3). Although the differences were not statistically significant within any one measure, this consistent pattern suggests that controls tended to have particularly low values for all aspects of growth and reproduction. This pattern is the opposite of what was found in a similar experiment using an annual species (*Berteroa incana*; Reichman 1988), where control plants tended to be the largest.

The disparity between the annual and biennial species may be related to several characteristics of these growth forms. Initially, the annual species may not have had enough time to recover from the trauma of transplantation and respond to the treatments before flowering. The biennial species could overcome the transplantation trauma in the first year and respond to the imposed gopher disturbances in the following year when it flowered. Additional factors associated with growth form (upright for the annual and low for the first year biennial) and root structure probably contributed to the differences exhibited by the two types of plants.

Total plant biomass in the devegetated pens was significantly lower for control plants than for any of the treatments (Fig. 2). A comparison of the patterns of mortality and total biomass between vegetated and devegetated pens reveals an example of the relationship between pocket gopher disturbances and the influences of plant density in this particular system. Differences in mortality between treatments occurred under regimes of high plant densities, whereas no differences occurred in areas relieved of potential competition. Conversely, differences in biomass occurred only in devegetated areas. Thus, the effects of gopher disturbances on mortality were manifested under high plant density (i.e., competition) for the reasons discussed above. Pocket gopher effects on biomass occurred only at low competitor densities, perhaps because only under these circumstances would any burrow effect be directed primarily at the experimental plants and not diluted by numerous adjacent neighbors.

The biennial species did not show any statistically significant response to mounds. Because mounds are more ephemeral than burrows (especially in the sandy soils of Cedar Creek), any potential effects of mounds may have been ameliorated by the second year as the mounds eroded.

Reichman and Smith (1985) found that plant biomass was significantly greater directly adjacent to burrows than in random samples taken from the surrounding field. This was interpreted as an ability by foraging pocket gophers to locate areas of highest resource concentration. Results from the current experiments suggest the alternative explanation, i.e., that gophers actually might increase productivity by generating disturbances via their burrowing activities. In the current study, not only was plant biomass greater over all of the burrows treatments than for controls, but the highest values were recorded over occupied burrows, suggesting that ongoing activity stimulates plants even more than the past construction of a burrow. Other authors have noted that disturbances can break up soil aggregates and increase the surface area available for nitrification processes (Jenny 1930). This may partly explain why Grant et al. (1980) found a net increase in plant production where gophers occurred, even though the animals ate vegetation and killed it with their mounds. Furthermore, Reichman et al. (1993) found that the influence of pocket gopher burrows and mounds extends up to 0.5m from the disturbance.

Many of the sample sizes in these experiments were quite small (because of the extreme drought in central Minnesota during the 2-year investigation), perhaps obscuring treatment effects or skewing results. Nevertheless, the results suggest that both interactions between plants and disturbances generated by pocket gophers affect plant success. Among the vast array of herbivores, fossorial mammals are especially interesting because they consume plants directly and generate patches of varying plant densities. These herbivores are known to produce barren mounds and reduce plant biomass by 25-50% over burrows (Reichman and Smith 1985; Reichman and Jarvis 1989). If they concurrently stimulate plant production, as this study suggests, the array of plant patch densities produced may profoundly affect the structure of plant communities.

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