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Comparison of the Effects of Crowding and Pocket Gopher Disturbance on Mortality, Growth and Seed Production of Berteroa incana

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ABSTRACT: This study examines the effects of plant competition and pocket gopher *(Geomys bursarius)* disturbances on the mortality, growth, biomass and seed production of *Berteroa incana*, a weedy old-field plant. Experimental plants were transplanted over simulated burrows, vacant natural burrows, active burrows and onto mounds cast during burrow excavations. The simulated burrows were excavated in pocket gopher exclosures which contained a natural old-field plant community, and in devegetated exclosures. The results reveal: (1) the presence of competing plants had a more significant effect on plant yield components of *B. incana* than pocket gopher disturbance; (2) any effects of pocket gopher disturbance on plant yield components were accentuated where the plants experienced increased competitive pressures, and (3) the most significant effect of pocket gophers on *B. incana* was mortality rather than changes in plant yield components. Plants growing on pocket gopher mounds had much higher mortality than adjacent controls, but those that survived grew larger and produced many more seeds than control plants off the mounds. The average seed mass, total number of seeds produced by a plant and the number of seeds per fruit were significantly correlated with total plant biomass.

INTRODUCTION

Competition among individual plants and physical disturbance of the environment influence the mortality, growth and reproduction of plants. Competition for resources such as light (Baker, 1972; Stanton, 1984), nutrients (Inouye *et al.*, 1987a; Tilman, 1983; Turitzin, 1981; Watson and Casper, 1984) and water (Roy and Mooney, 1982) have been shown to significantly reduce survival, biomass production and the number of seeds produced by plants.

Direct herbivory also affects plant biomass (Belsky, 1986; Dyer *et al.*, 1982; McNaughton, 1979; McNaughton *et al.*, 1983), plant fitness and community structure (Heithaus *et al.*, 1982; Louda, 1984; Marshall *et al.*, 1986; Rausher and Feeny, 1980), but the indirect physical impact of herbivores (and other organisms) on the environment may be even more important. Such impacts include soil compaction (Buechner and Dawkins, 1961; Lock, 1972) and localized site alterations which affect plant success (Cox, 1984; Inouye *et al.*, 1987b; Kalisz and Stone, 1984; Platt, 1975).

Competition among plants and depredations by herbivores interact in complex ways (Crawley, 1983). For example, Heithaus *et al.* (1982) found six factors associated with herbivory that affected plant yield components, three of which were also influenced by plant density. Similarly, Marshall *et al.* (1986) showed that water stress and nutrient limitation (which may simulate some types of competitive interactions) interacted with experimental defoliation to affect plant seed set. In addition, the response of two closely related plants in this latter investigation differed, further complicating the results.

Most studies of the effect of animals on plants have dealt with aboveground animals but all communities possess a diverse array of subterranean organisms, including nematodes, insect larvae and mammals which consume plant material and significantly affect soil characteristics. These herbivores are poorly known, presumably because of the difficulty in studying them in their dense opaque environment.

In this article I report the results of a study on the compound effects of competition between plants and physical alteration of the soil by a subterranean rodent, the plains pocket gopher (*Geomys bursarius*) on plant yield components of *Berteroa incana*. The plains pocket gopher belongs to a widespread family of rodents (Geomyidae) adapted to a fossorial existence. Studies of several genera of pocket gophers indicate that they spend most of their lives underground, where they make extensive burrows (Gettinger, 1984; Reichman *et al.*, 1982) while feeding on roots and whole plants pulled beneath the surface; they also occasionally forage on the surface near burrow openings (Howard and Childs, 1959). The burrow systems are dynamic, with new extensions being dug seasonally and old ones refilled and abandoned (Gettinger, 1984). Soil loosened during excavation is used to refill abandoned burrows or is deposited on the surface, forming conspicuous mounds. Burrows may underlie up to 7.5% of a field (Reichman, *et al.* 1982), while mounds can occupy another 5-25% of an area (Ellison, 1946; Grant *et al.*, 1980; McDonough, 1974). Some of the influences of pocket gophers on plants are known. For example, Reichman and Smith (1985) found that plant biomass directly over burrows is reduced by one third compared to adjacent, unaffected areas. Williams and Cameron (1986a,b) noted that the presence of pocket gophers did not alter plant diversity, but did decrease plant production. Tilman (1983) and Inouye *et al.* (1987b) found that pocket gopher activity increased plant diversity and slowed succession in old fields. Andersen and MacMahon (1981) and Andersen *et al.* (1980) discuss similar phenomena for alpine communities and Hobbs and Mooney (1985) analyze the influence of pocket gophers in serpentine soils. The indirect effects of pocket gopher mounds and soil disturbance have also been investigated in several areas (Ellison and Aldous, 1952; Hansen and Morris, 1968; Howard and Childs, 1959; Schaal and Leverich, 1982).

The main goal of this study was to compare the effects of pocket gopher disturbances (burrows and mounds) and crowding on the growth, mortality and reproductive success of an annual plant species. Naturally occurring and simulated burrows were incorporated into the study to allow controlled analyses of the effect of burrows on the target plant species. Empty burrows and burrows refilled with soil differing in nitrogen content provided a comparison of the impact of various types of burrow conditions on the target species. These burrow manipulations were conducted in areas characterized by natural old-field vegetation and areas devoid of vegetation to determine how pocket gopher disturbance and competition between individual plants interacted to affect plant yield components. The effects of active and abandoned burrows and mounds on plants were also analyzed.

METHODS

Two sets of experiments, termed the Pen Experiments and the Field Experiments, were conducted in Field 44 at Cedar Creek Natural History Area (CCNHA), 45 km N of Minneapolis. Soils at CCNHA are composed of fine and medium sands deposited by receding glaciers and are notable for their low nitrogen levels. Pocket gophers are most abundant in fields of intermediate age such as Field 44 (approximately 45 years old) where they have a significant impact on plants (Tilman, 1983, 1984). *Berteroa incana* was chosen as the target plant species because it is a common weedy plant and is a favored food for pocket gophers (Behrend, 1985). It is usually identified as an annual, although many of the individuals in an experiment at CCNHA involving potted plants flowered in their 2nd year (N. Huntly, pers. comm.).

Previous work at CCNHA revealed that nitrogen is the major limiting nutrient in the soils and that nitrogen concentration decreases with depth (Inouye *et al.*, 1987b). To determine if the soil used by pocket gophers for refilling burrows differed in nitrogen content and compaction from adjacent undisturbed soil, 45 paired samples were taken from plugs made by the pocket gophers to close open burrows and from adjacent burrow walls at a depth of 12.5 cm, the average depth of burrows in Field 44. Analyses for nitrogen content of soil samples were conducted using a colorimetric technique following a persulfate digestion (Tilman, 1984). Prior to taking each soil sample, a pocket soil penetrometer with a 3-cm face plate on the plunger was used to measure the compaction of soil in the plug and the adjacent burrow wall.

Pen experiments.—These experiments were located in four of six pens constructed to exclude pocket gophers in which simulated burrows (which could be manipulated more effectively than naturally occurring burrows) were excavated. The pens were 14-m in diameter, extended 1.6 m into the ground, and had a complete wire bottom. The pens were almost 20 years old so the disturbance caused by their installation had been overgrown with old-field vegetation. In two of the pens (termed "open"), vegetation was initially cleared by spraying with the herbicide Roundup and by periodically weeding out subsequent colonizers. These pens represented an extreme case of open ground, such as would be encountered on a pocket gopher mound. The other two pens (termed "vegetated") retained their background old-field vegetation (*see* Inouye *et al.*, 1987b). The pens had been used in previous experiments on pocket gopher foraging (Behrend, 1985) and as far as could be determined, had been treated identically. Plant density in the vegetated plots averaged 36.5 stems/ 0.1 m^2 and 28.1 g/m^2.

Two pits (2 m in diam and 40 cm deep), each with 18 designated "spokes" radiating out from the walls, were established in each of the four pens (*i.e*, 18 spokes/pit X 2 pits/ pen X 4 pens [two open and two vegetated] = 144 spokes). A control and four treatments were established along the axes of the "spokes." The controls had no excavation beneath them while the treatments were as follows:

—Open burrows
—Trimmed (open burrows from which any protruding roots would be trimmed)
—Top soil added (burrows refilled with relatively N-rich top soil)
—Deep soil added (burrows refilled with relatively N-poor soil collected from below 1 m).

The simulated burrows were excavated by driving a 1-m PVC pipe horizontally through the soil with a sledge hammer and removing the pipe and its associated soil plug. The resulting burrow was 8 cm in diam, a size characteristic of pocket gopher burrows at CCNHA, and was 12.5 cm below the surface, the average depth of burrows in Field 44. The mouths of the open burrow treatments were plugged with styrofoam cups and covered with soil to maintain the internal environments. The refilled burrows were filled with soil compacted to the degree exhibited by pocket gophers when they refill their own burrows (as indicated by the penetrometer measurements).

Each treatment was replicated along 14 spokes in the two vegetated pens and 14 spokes in the two open pens. Replicates were established randomly among the spokes. The 14 replicates each for the control and four original treatments required 70 simulated burrows (14 replicates X 5 treatments = 70 for both the open and vegetated pens), two less than were available, so one spoke in each pen was designated as a blank and received no treatment. During 2 months of plant growth, roots did not emerge into the trimmed treatment enough to be trimmed, so this treatment was excluded from the analyses.

Five individual specimens of *Berteroa incana* were transplanted along each spoke, serving as repeated measures for each replicate. The specimens were evenly spaced along the 1-m spokes, with the first and last individuals placed 15 cm from either end. All of the transplants came from within a 20 m X 20 m area less than 30 m from the pens. The plants, uniformly 10-12 cm in height, were extracted, with an associated soil plug, using a bulb-puller (7-cm diam and 10 cm deep). The plugs were placed into a shallow flat, soaked with water, and immediately transplanted into holes made by the bulb-puller over the spokes. A swath 10-cm wide was clipped over the spokes in the vegetated pens to minimize the initial effect of shading while the plants were recovering from transplantation.

It was predicted that plants would survive, grow and reproduce more successfully over the burrows refilled with the most nutritious top soil, less so over the controls, even less over the burrows filled with deep soil, and poorest over the open burrows.

Field experiments.—The second set of experiments had two components (involving burrows and mounds) that used transplants similar to those in the Pen Experiments.

Each planting over a burrow or on a mound was accompanied by a paired control transplanted less than 25 cm away.

The first component was the Burrow treatments which were designed to determine the effect of active and inactive burrows on the target species and the treatments were:

AB — burrows in which a pocket gopher was active

IB — burrows excavated by a pocket gopher but no longer inhabited

Active burrows systems were located by probing near fresh mounds (active burrow systems could not be excavated because pocket gophers rapidly seal off any portions of their burrows which are disturbed). Positions determined to be over active burrows were excavated when the plants were harvested at the end of the summer to verify their location over active burrows. Only those verified as being over active burrows (41 of 75 initial transplants) and their paired controls were included in the analyses of the AB treatment.

To construct the IB treatments, three pocket gophers were placed in each of the two unused pens and allowed to excavate burrows for 1 wk, after which the pocket gophers were removed. The vacant burrows were located by probing and 55 *Berteroa incana* specimens were transplanted over the vacated burrows. Gates were cut in the pens so all aboveground herbivores had access to the treatments (as with the treatments outside these pens), but the belowground wire continued to exclude surrounding pocket gophers. A 10-cm swath was cut along the AB and IB transplants and their controls to minimize the initial effect of shading.

The second component, the Mound treatments, was designed to compare the plant yield components of plants on mounds to adjacent controls and to compare the success of plants transplanted onto mounds with individuals occurring naturally on the mounds. The treatments were:

TM — mounds onto which *Berteroa* was transplanted

NM — mounds which had naturally occurring *Berteroa* growing on them

Fifty *Berteroa* specimens were transplanted onto fresh mounds (TM; the mounds were less than 1 mo old, as determined by comparison to mounds of known age). Usually two (three on one mound and one on several) plants were planted on each experimental mound. To determine the effect of transplantation on the plants, naturally occurring *B. incana* (NM) on the same mounds as the transplanted specimens were included in the analyses. All specimens (transplanted and naturally occurring) in the field experiments were 10-12 cm high. A 10-cm swath of vegetation was cleared around the TM controls to promote the initial establishment of the transplants.

Both the Pen and Field experiments were established between 15 May and 1 June 1985 when the *Berteroa* seedlings were a few weeks old. Entire plants were harvested over a 3-day period, starting on 30 July 1985, after most had completed flowering. The position (*e.g.*, first, second, etc. branch from the terminus) and length of the longest branch were recorded. The specimens were returned to the laboratory in labeled paper bags and oven-dried at 30 C for 72 h.

The parameters measured in the laboratory for each specimen were root dry weight, shoot dry weight, number of branches, number of fruits or fruit scars (remaining pedicle) on the longest branch, number of seeds in each of the five terminal mature fruits on the longest branch, and the total weight of up to 30 seeds from the five fruits. The phenological stage of one reproductive unit at the bottom, midpoint and top of the longest branch was determined on a scale of 0-5 (0 = no flowers, 1 = flower, 2 = green fruit, 3 = mature fruit, 4 = fruit, 5 = postdehiscent fruit. These categories do not necessarily represent equal ages for different plants). Combinations of the measured parameters were used to calculate total plant biomass (root biomass + shoot biomass), average biomass per seed (weight of seeds/number of seeds), average number of seeds per fruit, total number of fruits per plant (fruits/branch X number of branches), and total number (average number of seeds/fruit X total number of fruits) and weight (average weight/seed X total number of seeds) of seeds per plant. The calculations for total number of fruits and seeds was undoubtedly an overestimate, as they used data from the longest branch to extrapolate to the entire plant. The measured and calculated parameters are termed plant yield components.

Analyses. — Paired t-tests were calculated to analyze differences between nitrogen content of soil samples from pocket gopher burrows and differences in soil compaction within the burrow. No statistically significant differences were found between the four pits in the vegetated or the four in the open pens ($F = 0.83$ and 1.01, respectively, $df = 3,66$, $P < 0.05$) in the Pen Experiments. Thus, two-way ANOVAs were used to compare results incorporating the effects of burrow treatments and vegetated vs. open pens. Where significant differences were detected with these analyses, a Tukey-Kramer *a posteriori* procedure was applied to determine the location of the differences. Pearson correlation analysis revealed the relationships between various parameters on the experimental plants (all the data from the 14 replicates of the four treatments in the vegetated and open pens were combined yielding $N = 112$) and Spearman rank correlations were calculated for analyses of the relationship between assumed soil nitrogen content of the treatments in the pens and plant yield components.

In the Field Experiments, an RxC test for independence using a G-statistic was used to compare the percent mortality between various treatments and paired t-tests were calculated for comparisons between treatments and their paired controls.

Samples with heterogeneous variances were log-transformed before analysis. All procedures are from Sokal and Rohlf (1981); the analyses were done using Statpro (Penton Software).

RESULTS

Pen experiments. — There was significantly less nitrogen in the burrow plugs made by pocket gophers (293.9 ppm, SE = 17.2) than in the adjacent burrow wall (361.6 ppm, SE 16.2; $t = 5.53$, $df = 86$, $P < 0.001$). On a scale from 0-5, the mean soil compaction readings from the penetrometer were 2.61 (SE = 0.13) for the plugs and were significantly higher for the adjacent wall samples (4.14, SE = 0.09; $t = 10.48$, $df = 86$, $P < 0.0001$). Within the narrow range of burrow depth sampled (8-36 cm), there was no relationship between the depth of the wall sample and the nitrogen content of the sample ($r = -0.35$, $df = 20$, $P = 0.1$).

Height of the transplanted specimens did not differ significantly among the treatments within the pens at the time of transplantation ($F = 0.51$, $df = 9, 740$, $P > 0.75$). Thus, all treatments should have had equal chances at survival, growth and reproduction with regard to initial conditions. At the time of harvest, no detectable differences existed between the repeated measures along each spoke for any of the treatments (*i.e.*, there were no position effects along the simulated burrows; $F = 0.54$, $df = 4,508$, $P > 0.50$). Thus, the values for the five repeated measures were averaged and used as a single value for analyses of each of the 14 replicates of each treatment.

Mortality was very low within the pens, and virtually identical between treatments ($G = 1.61$, $df = 3$, $P > 0.5$; Table 1) and between the vegetated and open pens ($G = 1.11$, $df = 1$, $P > 0.50$; Table 1). Plants in the vegetated pens were significantly farther along in their development (slightly more than one stage; Tables 1 and 2) than those in the open pens for all treatments but no significant differences in phenology were detected between burrow treatments within the vegetated or within the open pens (Table 2). Only data for the middle position is presented in Table 1, but in all cases, comparisons of the top portions or the bottom portions between treatments yielded patterns identical to those exhibited by the middle portion, although in both the pen and field experiments the phenology of the top, middle and bottom portions of a branch were separated by about one stage of development with the top being the farthest along.

All parameters in Table 1 differ significantly between the vegetated and open pens with ANOVA F-values ranging from 3.98 to 245 ($df = 1,104$, all P between 0.01 and 0.0001; *see* Table 2 for an example using total biomass). For most parameters, the open

TABLE 1.—Mortality rate (%) and means and standard errors for several plant yield parameters in the vegetated and open pens. N = 14 for all treatments. Values for all variables are significantly different between the vegetated and open pens

	Mortality (%)	Phenol. (stage)	Total biomass (g)	Seed mass (mg)	# Seeds/ fruit	# Fruits/ branch	Total # of seeds	Total mass of seeds (mg)	Total # of fruits
Open									
Control	4.3	2.6(.1)	1.95(.30)	0.32(.02)	8.8(.30)	39.4(1.9)	2469.6(337)	719.8(89)	284.8(36.2)
Open	4.3	2.8(.1)	1.65(.25)	0.31(.02)	8.3(.27)	37.5(2.1)	2198.6(292)	649.9(101)	265.5(34.6)
Top soil	0.0	2.5(.1)	2.10(.24)	0.29(.02)	8.7(.24)	38.8(2.2)	2639.2(273)	730.8(88)	299.9(32.4)
Deep soil	4.3	2.6(.1)	1.67(.16)	0.28(.01)	8.1(.32)	36.4(2.1)	2383.4(140)	649.1(45)	261.4(14.3)
Vegetated									
Control	7.1	3.8(.1)	0.20(.01)	0.45(.02)	5.9(.19)	18.7(1.1)	115.6(18)	47.9(6.9)	22.4(1.9)
Open	4.3	3.7(.1)	0.17(.01)	0.41(.02)	6.0(.27)	17.6(0.7)	87.2(13)	32.1(4.1)	20.6(1.2)
Top soil	4.3	3.6(.1)	0.23(.02)	0.42(.02)	5.7(.17)	17.5(1.0)	116.4(23)	44.5(8.1)	25.8(2.9)
Deep soil	7.1	3.6(.2)	0.19(.01)	0.42(.02)	5.6(.12)	18.2(0.8)	96.6(16)	40.1(9.3)	23.9(2.4)

pens had the highest values. For example, plants in the open pens weighed over 10 times those in the vegetated plots, and produced almost 20 times as many seeds (Table 1). The average weight of seeds from plants in the vegetated pens were, however, over 40% higher than in the open pens (Table 1). As noted, the plants in the vegetated pens averaged about one stage farther along in phenological development than those in the open pens (Table 1).

While no statistically significant differences were detected among burrow treatments in the ANOVAs, there were significant rank correlations between the assumed nitrogen content of soil and values for total biomass and total number of seeds for both the vegetated and open pens ($r_s = 1.0$, $N = 4$, $P = 0.05$). Although nitrogen content was not actually determined for the soil in the simulated burrows, data from Inouye *et al.* [1987a] show a significant negative correlation between soil depth and nitrogen content. Therefore, for the rank correlation analysis it was assumed that the top soil contained the most nitrogen, the control somewhat less, and the deep soil even less; the open burrow, of course, had no nitrogen).

None of the 2-way ANOVAs for the parameters in Table 1 had significant interactive terms (Table 2).

Root biomass and stem biomass were highly correlated ($r = 0.92$, $df = 110$, $P < 0.001$). Total biomass was significantly correlated with several yield components, including seeds per fruit ($r = 0.73$), estimated total number of fruits per plant ($r = 0.94$), and estimated total number of seeds per plant ($r = 0.95$). Interestingly, the average weight per seed exhibited a significant negative relationship with total plant biomass ($r = -0.62$, $df = 110$, $P < 0.001$). Furthermore, the average weight per seed was negatively correlated with the total number of seeds per fruit ($r = -0.64$) and total number of seeds per plant ($r = -0.66$).

Field experiments. Burrow component.—Mortality was significantly higher over the active burrows (31.7%) than the paired controls (12.2%), the samples over (7.3%) inactive burrows, and samples adjacent to (9.1%) inactive burrows (Table 3; $G = 12.08$, $df = 3$, $P < 0.005$), suggesting that the actual presence of pocket gophers in the burrows significantly increased plant mortality. Furthermore, almost all of the plants scored as dead over active burrows were actually missing (suggesting they may have been consumed) while almost all of the dead plants over the other treatments were present as withered stems. Mortality was lower among the controls than on the mounds, but significantly so only for the naturally occurring plants (Table 3).

Mound component.—Paired comparisons of yield components between treatment and control plants on mounds revealed few differences. The average number of seeds per fruit among the transplants was significantly higher in the Controls than the Mound samples, but the reverse pattern was true for the total number of fruits per plant (Table

TABLE 2.—Summary of two-way analysis of variance on mean values of phenology and total biomass between vegetated and open pens and treatments within the pens

Source of variation	df	ss	ms	F'	P
Phenology:					
Pen	1	518.5	518.5	5.20	<0.025
Treatment	3	255.9	85.3	0.85	>0.50
Pen X Treatment	3	258.7	86.2	0.86	>0.50
Error	104	10375.0	99.8		
Total biomass:					
Pen	1	325.4	325.4	3.98	<0.05
Treatment	3	261.8	87.3	0.98	>0.50
Pen X Treatment	3	245.3	81.8	0.92	>0.50
Error	104	9188.2	88.3		

TABLE 3.—Mortality rate (%) and means and standard errors for several plant yield parameters from the Field Experiments. N = 41 for the AB treatment, 55 for IB, and 50 for TM and NM. Asterisks indicate where statistically significant differences ($P<0.05$) occurred between experimental and control pairs. Mortality was compared between all four members of the AB/IB treatments rather than just between experimental and controls of each (see text); mortality was significantly higher in the AB-Burrow samples than in the AB-Controls, IB-Burrows and IB-Controls. The TM values were significantly lower than the NM values for all variables except mortality, phenology, and seed mass

	Mortality (%)	Phenol. (stage)	Total biomass (g)	Seed mass (mg)	# Seeds/ fruit	# Fruits/ branch	Total # of seeds	Total mass of seeds (mg)	Total # of fruits
AB-Control	12.2	3.7(0.2)	0.36(.05)	0.27(.03)	6.8(.42)	15.7(1.4)	320.8(59)	15.7(1.4)	40.1(5.9)
AB-Burrow	31.7	3.8(0.2)	0.36(.05)	0.20(.03)	6.6(.50)	14.4(2.2)	391.5(93)	14.4(2.0)	38.8(7.3)
IB-Control	9.1	3.0(0.2)	0.30(.02)	0.29(.04)	7.7(.27)	19.5(1.4)	331.0(36)	19.5(1.4)	40.8(4.0)
IB-Burrow	7.2	3.5(0.2)	0.26(.02)	0.27(.02)	7.3(.36)	16.4(1.4)	338.1(68)	16.4(1.4)	38.4(5.2)
TM-Control	24.0	4.0(0.2)	0.19(.02)	0.33(.03)	7.4(.26)*	13.3(1.6)	212.5(32)	64.1(14.1)	17.1(2.6)*
TM-Mound	30.0	3.7(0.1)	0.26(.04)	0.34(.03)	6.5(.56)	17.5(1.4)	265.2(62)	73.1(15.7)	33.2(6.8)
NM-Control	12.0*	3.2(0.2)	1.75(.31)	0.29(.03)	7.9(.36)	24.2(2.4)*	904.1(134)*	230.0(32.0)	87.9(9.9)*
NM-Mound	32.0	3.0(.14)	2.64(.52)	0.33(.02)	8.5(.38)	35.1(2.8)	1076.1(129)	332.2(43.7)	121.8(13.3)

3). Because of these opposing patterns the total number of seeds produced did not differ between the two treatments. For the naturally occurring plants, the samples from the mounds had significantly longer branches ($t = 2.21$, $df = 64$, $P < 0.03$), more fruits per branch ($t = 2.93$, $df = 64$, $P < 0.04$), greater total number of fruits ($t = 1.97$, $df = 64$, $P < 0.05$), and more total seeds ($t = 1.92$, $df = 64$, $P < 0.05$) than the controls (Table 3).

The effect of transplanting plants is revealed in comparisons with the naturally occurring plants. In most cases, the values for both mounds and controls were significantly higher for the naturally occurring plants, in some cases several times higher (Table 3). Although the plants were transplanted early in their development, with a substantial plug of soil, the trauma they suffered is evident.

Discussion

Several important results characterized the effects of crowding and pocket gopher disturbance on the mortality, growth and seed production of the annual plant species in this study. First, as revealed by comparisons of the open and vegetated pens and the plants on and off mounds, competition with other plants had the most significant effect on yield components of *Berteroa incana*. There is no way to determine from the results of these experiments what important resources were the focus of competition, but previous work at CCNHA suggests that light, water and nitrogen are all important (Tilman, 1983). Other studies have shown that open areas on mounds have lower soil nitrogen and moisture than surrounding soil (Hobbs and Mooney, 1985; Inouye *et al.*, 1987a; Spencer *et al.*, 1985), so sunlight emerges as the most likely candidate as the important resource in short supply in the vegetated areas (Tilman, 1983). It should be noted that while the open pens share some traits with mounds (*e.g.*, low vegetation densities) other traits, such as soil nutrient content, probably differ between the two types of open areas.

Second, the presence of pocket gopher burrows, whether open or refilled with top or deep soil, active or inactive, had very little influence on yield components of *Berteroa incana*. It may be that such treatments do not affect the growth and reproduction of the plants, but it is also possible that the roots were not in the sphere of influence of the burrows long enough to suffer any measurable damage. The only case in which there was a detectable effect of the burrow treatments was in the vegetated pens where the plants had also experienced competition. While this pattern could be interpreted as a response to the interaction of competition and pocket gopher disturbance, there was no statistical indication of this (Table 2) interaction. While statistical differences between treatments in other circumstances were insignificant ($P \approx 0.1$), the values for total biomass and total number of seeds produced were rank-correlated with the assumed nitrogen content of the soil; burrows filled with top soil (containing the most nitrogen) support the greatest growth, with controls, deep soil and open burrows following behind. Even though the roots of *B. incana* penetrated only minimally into the various burrow treatments, the effect could be mediated through nitrogen diffusion from refilled burrows or by moisture stress engendered by the empty burrows. Although there was substantial variation in the data, the pattern suggests that the simulated burrow treatments may have had some effect on plant yield components.

The Field Experiments indicated that pocket gopher effects on annuals may be mediated through mortality rather than reduction in yield components. Mortality over active burrows in the field was significantly higher than in adjacent controls or over inactive burrows. Pocket gophers probably did not consume the roots of immature *Berteroa* plants (although mature plants were probably eaten), so early mortality of young plants may have been related to changes in soil moisture while the mortality of mature plants may have been caused by direct consumption. Furthermore, plants occurring naturally on mounds had higher mortality compared to controls off the mounds (although those that did survive were relatively successful at producing seeds).

While the plants in the vegetated pens were significantly smaller in every regard than those in the open pens, the smallest plants produced the largest seeds (r = −0.62). This could reflect the fact that plants in the more hospitable open pens continued to grow before setting seed (and thus possessed immature seeds when harvested), while those that were stressed in the vegetated pens were forced into a truncated growing season, producing fewer, but more mature, seeds at the time of harvest. The smaller plants in the vegetated pens did average about one stage farther along in their development than individuals in the open pens. The latter, however, averaged over 3.5 in their phenological stage, so they possessed mature fruits at the time of harvest. Baker (1972) and Stanton (1984) report that plants from shaded environments tend to produce larger seeds, and Cook (1979) discovered that plants on light regimes simulating relatively short (12L:12D) days produced larger seeds than those from longer-day (15L:9D) treatments. Although the relationship between seed size and seedling success is complex (Marshall *et al.*, 1986), under most circumstances larger seeds probably yield seedlings that are more successful than those from smaller seeds (Stanton, 1984), and the advantage may be even greater for plants faced with severe competition.

It is possible that pocket gopher mounds have a greater overall effect on plants than the burrows, at least as revealed by the current experimental design. Plants growing on the mounds (especially those occurring naturally on the mounds) were substantially larger and produced more seeds than their controls, but they also suffered a relatively high mortality. Furthermore, mounds provide important sites for seed germination (Platt, 1975; Schaal and Leverich, 1982). Thus, mounds are beneficial to weedy plants and also provide a good location for growth and reproduction if a seedling survives to maturity. Because mounds tend to be formed from deep soil, they may contain less nitrogen than adjacent samples from top soil (Hobbs and Mooney, 1985; Inouye *et al.*, 1987a; Tilman, 1983; Spencer *et al.*, 1985). Tilman (1983), however, ranked light ahead of nitrogen as a limiting factor in plant growth at CCNHA, suggesting that the openness of the mounds outweighs their relative nutrient deficiency as a factor in plant productivity.

Transplanted plants were significantly smaller and produced fewer seeds than plants occurring naturally. Although an attempt was made to minimize the effects of transplantation (and to keep them uniform over all treatments), the effects were significant over the short growing season of *Berteroa incana*. It is probable that the posttransplant trauma reduced any effects generated by the experimental treatments (compare the TM treatments and controls with their NM counterparts in Table 3).

It appears that the major influence on the success of *Berteroa incana* in an old field is the competitive environment in which it grows. While other factors could have been operating, it is reasonable to assume that light was the major factor limiting seedling growth in the experiments. Detrimental effects of pocket gophers were mortality of plants growing over active burrows, high mortality rates on mounds, and possibly lower success over abandoned burrows refilled with deep, less nutritious soil. Conversely, pocket gophers may enhance the success of annuals by providing mounds in crowded fields for germination and growth.

Tilman (1983) showed that at CCNHA plant production and succession toward a community dominated by perennial plants was promoted along an increasing nutrient gradient (primarily nitrogen). In this manner, perennials gradually exclude annuals from old fields, but pocket gopher activity produces patchiness in open space and soil nutrients, increasing species richness and diversity, and slowing succession toward fields dominated by perennials (Inouye *et al.*, 1987a,b; Tilman, 1983). The results reported herein indicate some of the ways in which the influences of competition and pocket gopher disturbance on individual plant species may generate the patterns seen at CCNHA.

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