IMPACT OF POCKET GOPHER BURROWS ON OVERLYING VEGETATION

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Abstract.—The impact of pocket gopher burrows on overlying vegetation was examined by analysis of plant samples taken from quadrats directly over active and vacant *Geomys bursarius* burrows, adjacent controls, and samples from the surrounding fields at sites in Kansas and Minnesota. The pocket gophers burrowed in that portion of the field which exhibited the greatest plant biomass. The biomass of plants (roots, stems, and both) directly over active burrows was, however, reduced by over one-third. The depletion was somewhat less over old, vacant burrows. The dominant forb species, with a tap root, was significantly more affected than the dominant grass, with a diffuse root system.

Pocket gophers (Geomyidae) exhibit several ecological characteristics which could influence the plant communities under which they live. As fossorial herbivores, they forage near burrow openings for vegetation or pull it down from below, consuming roots or entire plants (Howard and Childs, 1959; Miller, 1957). The impact of direct herbivory on both above- and below-ground vegetation should be significant, especially when coupled with high densities of herbivores (Andersen and MacMahon, 1981; Howard and Childs, 1959; Reichman et al., 1982) and elevated energy demands associated with the extreme costs of excavating burrows (Andersen, 1982; Andersen and MacMahon, 1981; Andersen et al., 1980; Vleck, 1979, 1981). In addition, physical alteration of the environment through construction of mounds and burrows influences plant communities (Platt, 1975; Tilman, 1982). Pocket gopher mounds may cover up to 8% of an area (Grant et al., 1980), where they bury existing vegetation (McDonough, 1974). The mounds can also serve as important germination sites (Platt, 1975; Schaal and Leverich, 1982), and alter the edaphic (Kalisz and Stone, 1984) and erosional characteristics of the soil (Ellison, 1946; Laycock and Richardson, 1975). Burrows can underlie 7.5% of an area inhabited by pocket gophers (Reichman et al., 1982) at one instant in time, and any effect could be considerably higher through time as new burrows are excavated (Gettinger, 1984).

Although some pocket gopher impacts have been documented, effects of the actual burrow cavities themselves are not known. The potential for negative impact directly over a burrow is substantial, either through the consumption or cutting of roots, or the production of an air space which would promote root desiccation. Conversely, when burrows are abandoned or filled in, the overlying vegetation could benefit from soil mixing and gradually return to a condition more characteristic of the surrounding unaffected field. The array of impacts, both detrimental and beneficial, should create a mosaic of successional microsites.

To analyze the impact of pocket gophers and their burrows on overlying vegetation, we measured plant biomass directly over pocket gopher burrows, in adjacent controls, and in random samples from the field surrounding the burrows at study sites in Minnesota and Kansas. Vegetation over burrows which had been vacant for one to three years (Tilman, 1983) was also analyzed at the Minnesota site. We hypothesized that pocket gophers would choose to burrow in that subset of the field which exhibited the greatest plant biomass, as this would maximize their food availability. Plant biomass in the uninhabited portion of the field should be somewhat lower, representing less appropriate burrowing areas. Plant biomass should be lower still over old pocket gopher burrows no longer in use, reflecting past depredations, and lowest directly over active burrows, where current impacts were occurring, even though these were in the midst of the area of highest plant biomass.

Methods

The Minnesota field work was carried out in August, 1983, at the Cedar Creek Natural History Area (CCNHA) in an old field approximately 45 km N Minneapolis using the burrows of the plains pocket

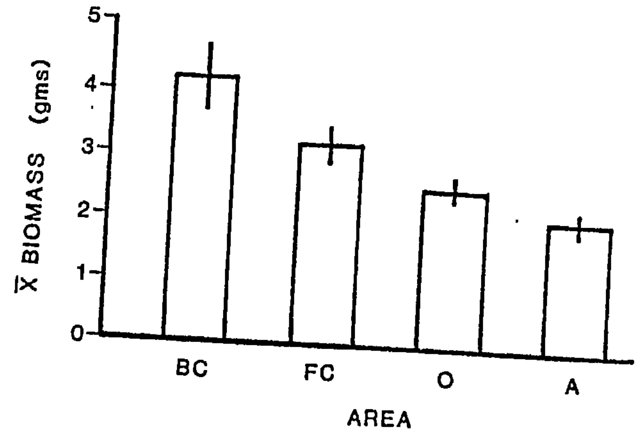

FIG. 1.—Histogram indicating the average plant biomasses in quadrats from four experimental areas at the CCNHA site. Vertical bars indicate standard errors. All four were statistically distinct from each other at the 0.05 probability level.

gopher, *Geomys bursarius*, the major herbivore in the area (Tilman, 1983). Although pocket gophers had been active over the entire northwestern corner of Field "E" (as designated in the current Long Term Ecological Research studies) in the past, only the northeastern portion of that corner was actively used at the time of the field work. Four subsets of the field were established for analysis, as follows:

1. Burrow Control (BC)—quadrats contiguous and perpendicular to active, new burrows.
2. Field Control (FC)—quadrats located over the entire field (located by tossing a wire rectangle over the shoulder; those that landed over new or old burrows were excluded).
3. Old (O)—directly over burrows that had not been active for 1–3 years, as determined by markers left from an earlier study (Tilman, 1983).
4. Active (A)—directly over burrows active at the time of the study.

The research at the Kansas site was carried out in August, 1984 on Hunters Island, 5 km S Manhattan, Kansas, using burrows of the same species of pocket gopher. This field site exhibited low diversity (five plant species were recorded) and was dominated by smooth brome (*Bromus inermis*). The quadrats sampled were similar to those at CCNHA except that vacant burrows could not be aged as at the CCNHA site, so no samples were taken over old burrows. In addition, the entire field was used by pocket gophers at the time of the study, so the FC samples tended to be near BC samples, unlike the CCNHA site where many of the FC quadrats were in parts of the field not recently used by pocket gophers.

All individual plants and their roots were extracted from 50 quadrats in each of the four areas at CCNHA. Seventy-five quadrats were sampled from each of the three areas on Hunters Island. The quadrats were 25 cm × 7 cm wide, a width characteristic of the pocket gopher burrows in both areas. The midline of each quadrat was centered over the midline of the underlying burrow for the O and A samples. Plants from each quadrat were sorted by species, dried at 40°C for 24 hours, and weighed after the roots had been cleaned of soil. The samples from CCNHA were weighed as complete plants while roots and stems of the plants from Hunters Island were weighed separately and the number of individual stems was recorded.

The total plant biomass, and the biomass of each of several of the most abundant (by biomass) plant species, were analyzed using one-way ANOVA. Roots and stems were analyzed separately, and combined, for the Hunters Island data. Because the data were not normally distributed, they were transformed using a Box-Cox transformation with a lambda value of 0.1, as determined by an iterative procedure (Sokal and Rohlf, 1981). If statistically significant differences were detected between the subsets of the field, a Tukey-Kramer procedure was employed to determine which subsets were statistically distinct (Sokal and Rohlf, 1981).

RESULTS

The CCNHA site.—There were statistically significant differences in total plant biomass between the four field subsets ($F = 6.41$, $d.f. = 3,187$, $P < 0.001$). As hypothesized, the biomass

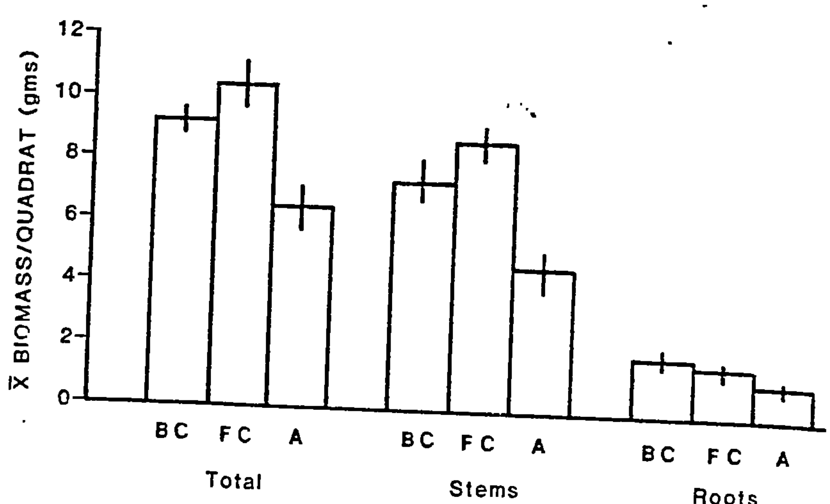

FIG. 2.—Histogram indicating the average plant biomasses for stems, roots, and both in quadrats from the three areas at the Hunters Island site. Vertical bars indicate standard errors In all cases the values for the quadrats over active pocket gopher burrows ("A") were statistically lower than the other two areas ($P < 0.05$), which were statistically indistinguishable from each other.

of vegetation was the highest in the BC quadrats (the subset of the field exhibiting the most pocket gopher activity but not directly over an active burrow), next highest in the FC quadrats, somewhat lower in the O quadrats (areas of past pocket gopher activity), and lowest in the A quadrats, the swath of current pocket gopher activity (Fig. 1). Each of the values was significantly different from all others at the 0.05 level (Fig. 1).

Sixteen species of plants were found in the quadrats, but only the four most abundant occurred in sufficient biomass to prompt statistical analyses. Patterns for individual plant species (*Agropyron rupens*, *Agrostis* sp., *Berteroa incana*, and *Crepsis tectorum*) were similar to those for total plant biomass, with BC quadrats usually possessing the highest biomass and A quadrats the lowest, but none of the individual plant species exhibited statistically significant differences between all of the areas, as occurred with values for total biomass. For example, biomass of *B. incana* showed significant treatment effects ($F = 4.52$, $d.f. = 3{,}168$, $P < 0.01$). Average biomass in the BC plot was 1.81 g, which was significantly greater ($P < 0.05$) than the values for FC (0.73 g), O (0.56 g), and A (0.48 g), none of which were statistically distinguishable from each other. The average biomass of those *B. incana* which were flowering was 1.06 g in the BC plots, significantly greater ($P < 0.05$) than the value for the N plots (0.67 g).

One might expect that a forb would suffer greater impact from a fossorial herbivore than a grass because of the differences in root configuration. Data from the CCNHA site revealed that the dominant forb in the field, *Berteroa incana*, was depleted more than the dominant grass species, *Agropyron rupens*, but the difference between them was marginally ($P < 0.06$) insignificant.

Hunters Island site.—The data for all five species combined indicate that biomass was significantly reduced in A quadrats for roots ($F = 5.37$, $d.f. = 2{,}221$, $P < 0.005$), stems ($F = 17.31$, $d.f. = 2{,}221$, $P < 0.001$), roots and stems combined ($F = 15.50$, $d.f. = 2.221$, $P < 0.001$), and number of individual stems ($F = 21.08$, $d.f. = 2{,}221$, $P < 0.001$) compared to the BC and FC quadrats, which were statistically indistinguishable from each other (Fig. 2).

Bromus inermis was the dominant plant species in the brome field, and it exhibited the same pattern as total biomass for all species, with the average biomass for the A quadrats being significantly lower than in the other two areas for roots, stems, both, and number of individual stems (Fig. 2). *Conyza canadensis* showed the same pattern, but *Sporobolus cryptandrus* and

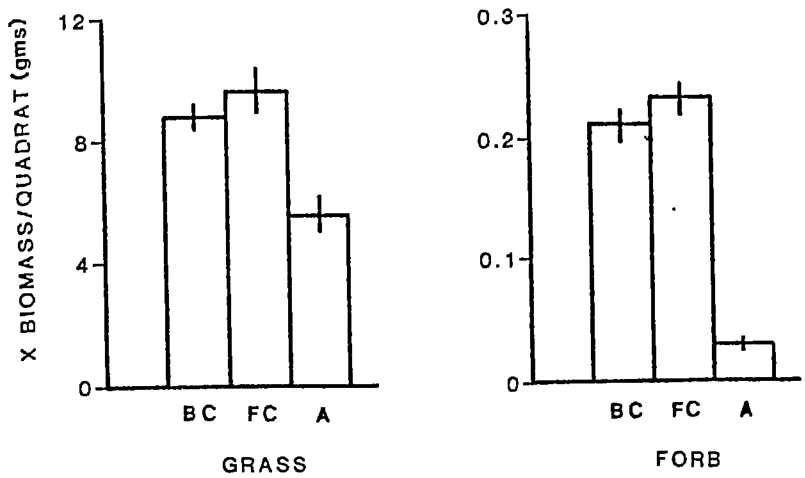

FIG. 3.—The average biomasses of the dominant grass (*Bromus inermis*) and the dominant forb (*Strophostyles helvola*) in the three areas at the Hunters Island site. Vertical bars indicate standard errors. The forb, with its tap root, suffered significantly greater depletion ($P < 0.01$) over active pocket gopher burrows than the grass, with its diffuse root system.

Ambrosia psilostachya occurred too infrequently to be analyzed. The roots of *Strophostyles helvola*, a forb, were significantly depleted over active burrows, compared to plants adjacent to the burrows and in the surrounding field. Biomass for the stems of *S. helvola* and biomass of its stems and roots combined were also reduced over active burrows, but the differences between these quadrats and the FC and BC quadrats were not statistically significant, perhaps due to the low occurrence of this species in the samples.

The biomass of the major grass species in the field (*Bromus inermis*) was reduced over burrows by less than 40% by pocket gopher activity whereas the major forb species (*Strophostyles helvola*) exhibited a significantly greater reduction of almost 90% ($F = 7.43$, $d.f. = 148$, $P < 0.01$; Fig. 3). In addition, the biomass of roots for the forb were significantly higher in the BC plots than in the FC plots, suggesting that the pocket gopher might have been seeking locally dense patches of the forb.

Discussion

Data from both study sites indicate that plant biomasses directly over pocket gopher burrows are reduced by one-third compared to adjacent control areas. The pattern could be explained in several ways. For example, it is possible, but highly unlikely, that pocket gophers chose that swath within the field that had the lowest plant biomass. It is possible that area BC, adjacent to the active burrows, exhibited the high biomass because of actual stimulation by the pocket gophers, perhaps through production of urine or feces, but it is unlikely that the effect would be spread evenly beside the swath of the burrow. Vegetation adjacent to the burrow could also be stimulated by altering local soil water relations, or by being freed from competition by the depletion of vegetation directly over the burrows.

The most plausible explanation for the pattern, evident in the data from the CCNHA site, is that the rodents chose that portion of the field which was generally most productive (BC had higher biomass than FC), and then significantly depleted the plant biomass to the lowest level recorded in the field directly over the burrows (A), a result which concurs with other studies at CCNHA (Tilman, 1983). In addition, biomass values were lower in the O areas than in the FC areas, suggesting that the impact persisted for up to several years. Data from the Hunters Island site were less revealing on this point, because there were no O quadrats, and because the pocket gophers foraged over the entire field and not in one subset that could be distinguished from the remainder of the field, as at the CCNHA site. The data from Hunters Island did, however, concur with data from CCNHA in relation to the impact on vegetation directly over active pocket gopher burrows.

This study appears to be the first to document the impact of pocket gophers on vegetation lying directly over burrow cavities, but experimental manipulations of pocket gophers, soil, and plants will be necessary to understand the actual mechanisms of the impacts. Although the impact is substantial (reducing plant biomass by one-third) and immediate, it would be difficult to detect from plant samples taken in a general area of pocket gopher activity rather than directly over the burrows. Even comparisons between experimental areas in which pocket gophers are present or absent might take decades to reveal any differences because significant impacts occurring directly over burrows would be moderated by the relatively small area over burrows at one instant in time, by the rate of new burrow construction, and by the tendency for vegetation over abandoned or refilled burrows to return to a condition more characteristic of the entire field.

Pocket gophers probably influence the dynamics and structure of plant communities through their effects on successional rates and microspatial distribution of germination and growth sites (Tilman, 1982, 1983). Specific impacts at any one time could become controlling factors, as, over many years, pocket gophers burrow through an area, each time exacting their toll and resetting the successional schedule or nudging the community in another direction.

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