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Pocket Gophers in Ecosystems: Patterns and Mechanisms

Pocket gophers profoundly affect microtopography, soils, plants, and other animals

Nancy Huntly and Richard Inouye

Pocket gophers, despite their relatively small size, are an important element controlling ecosystem structure and development. Mielke (1977, p. 171) argues that "... Geomyidae provide a dynamic force to direct the biogeochemical attributes of the North American Prairie lands. ... [T]he activities of fossorial rodents may provide an explanation for the genesis of North American Prairie soils," and Grinnell (1923, p. 148) asserts that "... our native plant life, on hill and mountainside, in canyon and mountain meadow, would soon begin to depreciate, were the gopher population completely destroyed."

Effects on the productivity, heterogeneity, and trophic structure of ecosystems, occurring on various temporal and spatial scales, have been described for pocket gophers. Gophers influence the physical environment, altering patterns and rates of soil development and nutrient availability, microtopography, and the consequent abiotic environment. They affect the demography and abundance of plant species, changing vegetational patterning and diversity. They affect the behavior and abundance of other herbivores, from grasshoppers and ground squirrels to large grazers.

In this article, we review the reported effects of pocket gophers on ecosystems and discuss their probable underlying mechanisms. Like other herbivores, gophers interact with their environment, both physical and biotic, by diverse pathways, only one of which is direct herbivory. In our studies of pocket gophers, we ask how the biotic processes of herbivory and competition interact in the context of the entire ecosystem to produce the observed patterns of diversity, productivity, and species composition. In suggesting mechanisms for the observed patterns we draw heavily on our ongoing studies of pocket gophers in old-field ecosystems at Cedar Creek Natural History Area, Minnesota.

The activities of pocket gophers cascade through the trophic web

Pocket gopher biology

Pocket gophers (Figure 1) are members of the rodent family Geomyidae. Their common name derives from the external, fur-lined cheek pouches possessed by all geomyids. These pouches are used to transport plant material to and from food caches. Pocket gophers are active year-round, and caches provide stores for getting through times when fresh vegetation is not readily available.

All pocket gophers are fossorial herbivores. They do much of their feeding from belowground, using systems of tunnels that they actively excavate and maintain. In constructing tunnels, pocket gophers move soil to the ground surface and deposit it in piles called mounds (Figure 2). In areas with seasonal snow cover, gophers also tunnel through the snow to obtain plants to eat. Some of these tunnels are filled with soil from underground tunnels, resulting in long, cylindrical earthcores. Tunneling often is extensive, and these mounds and earthcores may cover as much as 25–30% of the ground surface (Hobbs and Mooney 1985, Hooven 1971, Turner et al. 1973).

Tunnel systems are costly to build and maintain. Vleck (1979) estimated the energy cost of burrowing to be from 360 to 3400 times that of aboveground travel. Pocket gophers' feeding selectivity may reflect constraints imposed by these high energetic costs (Andersen and MacMahon 1981, Vleck 1979). Because of their high energetic demands, and because they are active year-round, gophers may have large effects as consumers, despite their relatively small size (the approximately 30 species range from approximately 60 to 900 g in mass). Energy flow through pocket gopher populations has been estimated to be 2200 $MJ \cdot ha^{-1} \cdot yr^{-1}$ in chaparral (Gettinger 1984) and at least 1100 $MJ \cdot ha^{-1} \cdot yr^{-1}$ in montane meadow (Anderson and MacMahon 1981). These values far exceed that reported for other small mammals and are comparable to those reported for

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some large grazers.

Pocket gophers have broad diets, consuming both roots and shoots of annual and perennial grasses, forbs, and (occasionally) woody plants (Andersen 1987a, Andersen and MacMahon 1981, Bandoli 1981, Behrend and Tester 1988, Hooven 1971, Zinnel 1988). Although they depend on tunnels for access to plants, they forage some aboveground, near burrow openings.[1]

Even though their diets are broad, pocket gophers forage selectively. They prefer areas of high soil nitrogen (Hobbs et al. 1988, Inouye et al. 1987b) and high primary productivity (Inouye et al. 1987c, Reichman and Smith 1985, Tilman 1983; Figure 3) and show preferences among plant species. Most studies indicate that forbs are preferred over grasses and that succulent belowground storage organs are consumed preferentially (Bandoli 1981, Behrend and Tester 1988, Turner et al. 1973, Williams and Cameron 1986).

The effects reported for gophers are likely to occur in arid and grassland habitats throughout the world. Pocket gophers inhabit almost half of North America (Mielke 1977), including most grasslands and arid scrublands of the western half of the continent, from sea level to alpine areas. Other fossorial herbivores, in the rodent families Cricetidae, Spalacidae, Rhizomyidae, Octodontidae, Ctenomyidae, and Bathyergidae, occur in savanna, grassland, and arid scrub habitats in South America, Asia, Africa, and Europe (Andersen 1987a, Nevo 1979). These animals are morphologically and behaviorally similar to pocket gophers. Densities of pocket gophers and other fossorial herbivores often are locally high, ranging to more than 200 per ha and frequently are 50–100 per ha (Nevo 1979). Pocket gophers are agricultural pests; many states offer bounties for pocket gophers because of the damage they cause to crops.

Because of their fossorial life-style, their behavior, and their population structure, pocket gophers influence ecosytems in diverse ways (Figure 4). Their tunneling activity, consumption and wastage of plants, and production of excrement all have direct and indirect, long-term and short-term effects on other ecosystem components. Individuals differentially use vegetation patches and plant species; populations tend to be spatially clumped (Nevo 1979); and individuals are aggressively territorial (Nevo 1979). Thus the effects both of individual pocket gophers and of gopher populations are spatially variable on a variety of scales. This heterogeneity in their influences is undoubtedly important to the widely reported tendency of pocket gophers to increase plant diversity (Hobbs et al. 1988, Inouye et al. 1987b, Spencer et al. 1985, Tilman 1983).

Figure 1. The plains pocket gopher, *Geomys bursarius*, is abundant at Cedar Creek.

Gophers as soil engineers

The most obvious effects of pocket gophers are due to the mounds and earthcores that they produce while enlarging and maintaining their tunnel systems. No studies have accu-

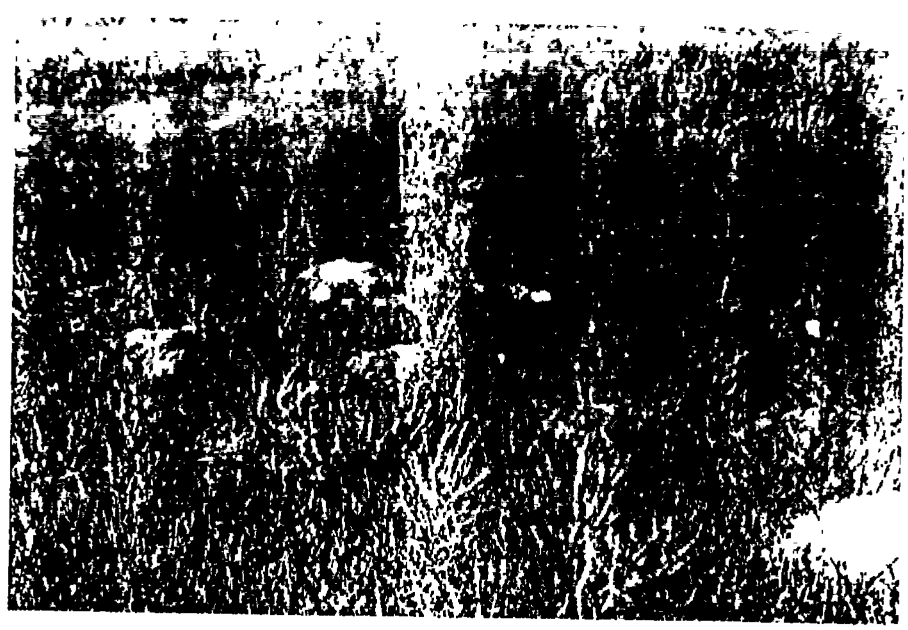

Figure 2. Gopher mounds dot the landscape in this 11-year-old field. The vegetation of gopher mounds differs in biomass and species composition from that in adjacent undisturbed areas.

[1] N. Huntly, 1988, unpublished observations.

rately measured all long-term soil-moving by free-living gophers, but existing estimates of soil moved to aboveground range from 1 to 8.5 $kg \cdot m^{-2} \cdot yr^{-1}$(Andersen 1987b). Grinnell (1923) offers the conservative estimate that pocket gophers deposit at least 8000 T/yr at the soil surface in Yosemite National Park.

The flora of gopher mounds typically differs from the surrounding vegetation (Hobbs et al. 1988, Hobbs and Mooney 1985, Inouye et al. 1987b, McDonough 1974, Williams et al. 1986) and changes as gopher mounds age (Foster and Stubbendieck 1980, McDonough 1974). Frequently, forbs or annuals are more abundant on mounds (Hobbs et al. 1988, Inouye et al. 1987b, Spencer et al. 1985, Tilman 1983, Williams et al. 1986). Mounds have been assumed to affect plant community diversity and species composition simply by providing space for colonization by so-called fugitive species, plants that are competitively eliminated over time by other plants (e.g., Hobbs et al. 1988, Hobbs and Hobbs 1987, McDonough 1974). By creating a mosaic of patches of varying successional age, gopher mounds could increase diversity and allow different kinds of plants to coexist. However, this interpretation has not been tested rigorously (cf. Hobbs and Hobbs 1987).

The competitive relations of plants can involve both demographic differences, such as colonization ability (Shmida and Ellner 1985), and differences in resource requirements (Tilman 1982, 1988). Many studies show that pocket gopher mounds differ in physical and chemical properties from undisturbed soil; gopher mounds may function as patches of differing resources for plants, rather than simply as colonization sites.

Gopher mound soil frequently differs in texture and water-holding characteristics from surrounding undisturbed soil (Andersen 1987a,b; Grant et al. 1980); and levels of various soil nutrients, including nitrogen, phosphorus, and potassium, may be significantly higher (Andersen and MacMahon 1985, Grant and McBrayer 1981, Koide et al. 1987) or lower (Inouye et al. 1987b, Koide et al. 1987, McDonough 1974, Spencer et al. 1985) in gopher mounds than in undisturbed soil. The potential importance of these nutrient differences has not been fully appreciated. We have found that both time since abandonment from agriculture (field age) and soil nitrogen content are significant predictors of plant absolute and relative abundance during old-field succession at Cedar Creek (Inouye et al. 1987c, Tilman 1988). This observation suggests significant roles for both demographic differences (particularly dispersal ability and maximal growth rate) and resource competitive differences in determining plant species' distributions.

Our work at Cedar Creek clearly demonstrates that nitrogen, the soil nutrient most limiting to primary productivity and to the growth rates of many plant species, is affected by gophers' activities. The effects of gophers on soil nutrients result from the way that gophers forage and from the vertical distribution of nutrients in the soil. At Cedar Creek, nitrogen content of soils drops rapidly with increasing depth (Inouye et al. 1987b,c). In excavating foraging tunnels, gophers deposit mounds of nitrogen-poor subsurface soil on the ground surface. Thus, soil nitrogen is redistributed, creating patches of surface soil with lower than average nitrogen content (Figure 5).

The changes that pocket gophers cause in the vertical and horizontal distribution of soil nitrogen and in plant biomass affect the resources available to plants in several ways (Figure 6). First, the average level of nitrogen is changed. The long-term effect of gopher mounds at Cedar Creek is a net lowering of nitrogen content of surface soils. However, over the short term, nitrogen availability on and near mounds will be higher per unit plant biomass, because mounds are initially unvegetated. Second, the spatial pattern of soil nitrogen is changed: soil nitrogen becomes more heterogeneous. Third, the relationship between soil nitrogen and light, another resource that limits plant growth, is altered.

The change in relative availabilities of soil nitrogen and light is particularly important to plant diversity at Cedar Creek; the uncoupling of the availability of limiting soil resources and light is probably a general mechanism by which gophers increase the diversity of plant communities. In undisturbed vegetation, more soil nitrogen results in more plant growth and thus in higher plant biomass; therefore, light penetration through the plant canopy is reduced. As a result, the availability of light to subcanopy plants is inversely related to the availability of nitrogen. Gophers tend to uncouple these two resources by creating patches of bare or less densely vegetated ground.

In the presence of gophers, light availability is more variable and, on average, higher; nitrogen availability is more variable and, on average, higher; and the negative correlation between the availabilities of nitrogen and light that exists in undisturbed vegetation is loosened (Figure 6). These changes produce a far greater range of resource conditions for plants. Therefore, a higher diversity of plants should coexist, if plants differ in their relative competitive abilities for nitrogen and light. Work at Cedar Creek has shown that the dominant plant species do in fact differ in their nitrogen and light need

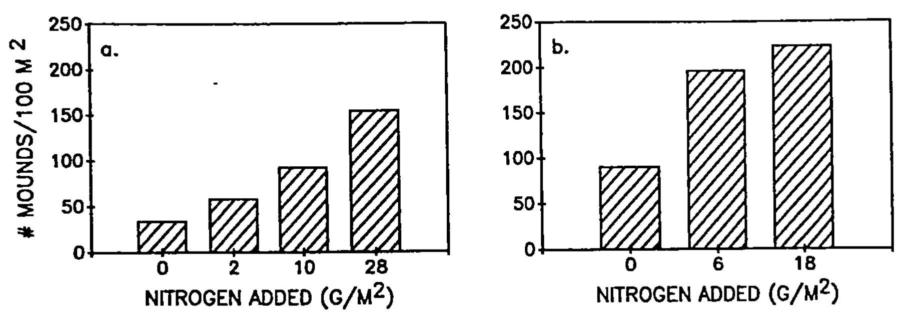

Figure 3. Gophers at Cedar Creek forage selectively in areas of higher-than-average productivity. The graph shows number of gopher mounds produced over the course of three years on (a) 4 × 4 m plots and (b) 20 × 50 m plots that were fertilized with various levels of nitrogen. The 20 × 50 m plots were located in a field in which background soil nitrogen levels were higher.

Scale		
1 week, 1 m^2	1 year, 100 m^2	50 years
increased light penetration	increased resource heterogeneity	altered soil fertility
altered soil resources	increased topographic heterogeneity	altered rate of succession
decreased plant biomass	increased plant species richness	altered path of succession
increased available resources	increased variability in plant biomass	altered topography
new colonization sites	more microhabitats for consumers	

Figure 4. Pocket gophers affect ecosystem processes over a variety of spatial and temporal scales.

and that dominance and species composition change with changes in nitrogen and light availability (Tilman 1987, 1988). Variation among plants in nitrogen and light requirements is common (Chabot and Mooney 1985, Tilman 1982, 1988).

The changes that gophers cause in plants' resources affect plant biomass and species composition. In Cedar Creek old-fields, the abundance of annual forbs (e.g., pepper-grass, *Lepidium densiflorum*; bindweed, *Polygonum convolvulus*; hoary alyssum, *Berteroa incana*) was higher and that of perennial prairie grasses (e.g., big bluestem, *Andropogon gerardi*; little bluestem, *Schizachyrium scoparium*) was lower near or on gopher mounds than elsewhere in the same fields. Over all fields, plant diversity (species richness) was significantly greater on or near gopher mounds; the average increase in species per 1 × 0.5–meter plot ranged from 4.7% to 47.8%. Eight of 16 fields more than 20 years in age had significant increases of at least 30% in per-plot diversity (Inouye et al. 1987b). The spatial patterning of soil nitrogen that results from gopher foraging may contribute to larger scale vegetational diversity; plot-to-plot similarity in species composition decreases with field age, as cumulative gopher activity increases (Inouye et al. 1987c).

Experiments at Cedar Creek verify that gophers cause these changes in plant species composition and diversity. Fertilized plots from which gophers were excluded showed lower and more variable plant biomass than did similar plots available to gophers. Where gophers were present, light penetration was higher and more variable, the relationship between soil nitrogen and light levels was more variable, and plant diversity was, on average, higher (Inouye et al. 1987b).

Plant species composition also differed between the two sets of plots in agreement with the patterns seen in old-fields: abundance and proportional abundance of annual plants and forbs were greater where gophers were present. In unfertilized plots, relative abundances of annuals and forbs were 8.5 times and 7.7 times greater where gophers were present. Annual plants and forbs were totally absent from plots receiving the highest levels of nitrogen fertilization when gophers were excluded; they were maintained at 5% and 18% of total plant biomass, respectively, in the plots accessible to gophers. In these experimental plots, variation in total soil nitrogen increased with cumulative gopher-mound production, whereas mean total nitrogen decreased.

Because plant species typical of early stages in succession tend to have both faster growth rates at low nitrogen and higher dispersal rates than do later successional plants (Tilman 1988), the activities of pocket gophers decrease the rate of plant succession at Cedar Creek. Andersen and MacMahon (1985) report that pocket gophers on Mount St. Helens increase the nutrient content of surface soils and increase the rate of succession. At both sites, plant diversity is increased by gophers. The differences in effects on soil quality between these two studies derive from differences in the vertical distribution of soil nutrients. On Mount St. Helens, nutrient content of the soil was lowest nearest the surface, because of deposition of volcanic tephra. Similar long-term increases in surface soil nutrients may occur in other areas where surface nutrients are exhausted by plant growth or leaching.

In addition to effects on species composition and diversity, gophers may also influence local and system-wide primary productivity. Grant et al. (1980) found gopher mounds to result in a net increase of approximately 5.5% in overall primary production in shortgrass prairie. In their study, the area around mounds had significantly increased production

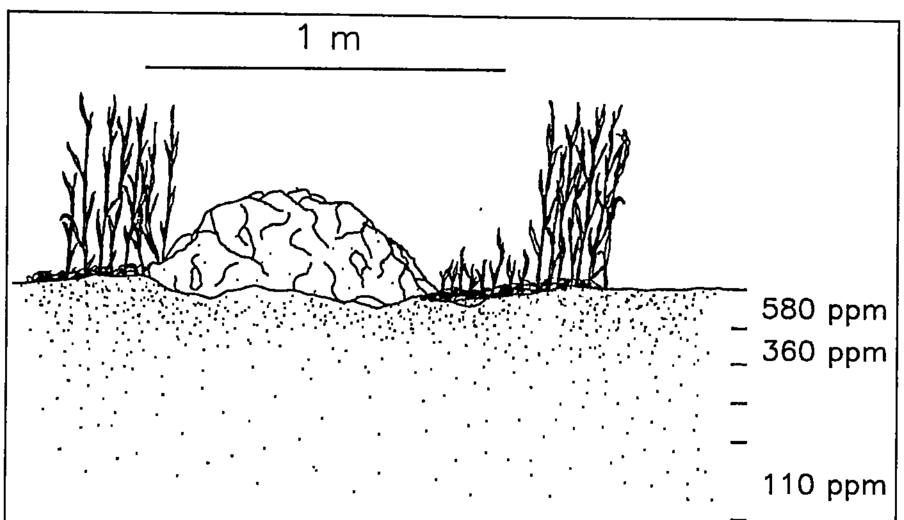

Figure 5. Soil total nitrogen content (ppm, at right, for 10-centimeter intervals) decreases with depth at Cedar Creek. Consequently, gopher mounds have lower total nitrogen, on average, than surrounding undisturbed soil. Over short time intervals, however, the amount of nitrogen that is mineralized and remains in the soil available to plants may be greater near or on mounds because of the lower plant biomass. Areas grazed by gophers (e.g., at right of mound) also have lower plant biomass and thus may have more available nitrogen over the short term.

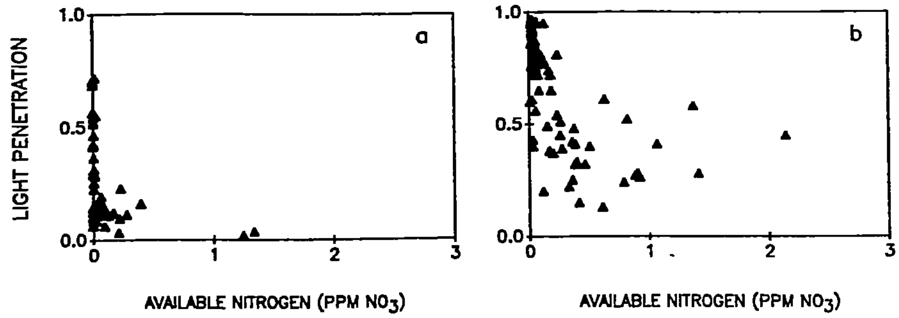

Figure 6. The correlation of light penetration (proportion of sunlight penetrating to the soil surface) with soil available nitrogen (2 M KCl-extractable NO_3) for (a) areas from which gophers have been excluded and (b) areas open to gophers at Cedar Creek. The range of combinations of these two plant resources is far greater when gophers are present.

that more than offset the local bare area of the mounds. This short-term (within one growing season) enhanced productivity did not involve colonization. Water was eliminated as a cause of the local increased productivity; nutrients were not measured but are a likely cause. Spencer et al. (1985) also report enhanced productivity around mounds.

Not all of the soil excavated by burrowing gophers is moved to the ground surface. Some is packed into old tunnels, filling them. The limited data on backfilling indicate that it may be ecologically significant. Andersen (1987b) found that 41%–87% of excavated soil was deposited as backfill; this backfill ranged to 30 l/da. Effects of backfilling on plants remain unknown, but backfilled soil has been found to differ in bulk density (Andersen 1987b) and in nutrient content[2] from undisturbed soil.

In addition to moving and mixing soils, pocket gophers affect soil development in more subtle ways. Uneaten food caches and excrement concentrated in den areas can create patches of high nutrient availability. Sampling the soil profile above dens and food caches, Zinnel (1988) found that total nitrogen in the top 60 cm of soil was significantly higher in the vicinity of dens and caches. In these areas, root biomass was higher and roots penetrated more deeply into the soil.

The influence of such localization of waste on patterns of nutrient distribution can be large. The meadow vole (*Microtus pennsylvanicus*) also deposits feces in discrete "latrines." Voles at Cedar Creek foraged preferentially and left greater numbers of feces on plots where fertilization with a sodium salt caused elevated plant tissue sodium levels. Consequently, plants that grew on those plots had tissue nitrogen levels comparable to those of plants that had been fertilized with 5 g nitrogen/m^2 (Inouye et al. 1987a).

Gophers also have longer-term effects on soil development. Many midwestern and western North American grasslands are characterized by the presence of mima mounds. These roughly circular soil lenses are up to approximately 2 m high, 25–50 m in diameter, and 50 to more than 100/ha in density (Cox and Gakahu 1986); they cause an undulating topography. These mounds are most likely created through the long-term accumulation of soils moved by fossorial mammals, especially pocket gophers (Cox and Gakahu 1986, Mielke 1977, Scheffer 1958). Areas of mima-like topography on other continents also appear to be caused by fossorial rodents (Cox and Gakahu 1987, Cox et al. 1987, Cox and Roig 1986).

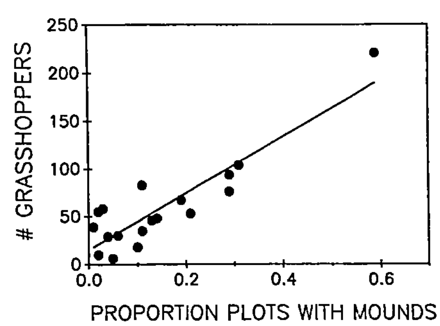

Figure 7. The abundance of grasshoppers (number swept from 160-meter transect) in Cedar Creek old-fields is correlated with the abundance of gopher mounds (proportion 1.0- × 0.5-meter plots with mounds).

Mima mounds differ ecologically from intermound areas in many ways. Mound soils are deeper and more fertile (Cox and Gakahu 1985, Cox and Zedler 1986, Mielke 1977). Vegetation differs in species composition, and primary productivity is higher (Cox and Zedler 1986, Mielke 1977, Ross et al. 1968). Mima mounds also may be foci of activity for other animals, including small mammals and large grazers (Cox and Gakahu 1985, Ross et al. 1968).

Gophers may influence soil fertility over the long term in areas where mima mounds do not form. Laycock and Richardson (1975) report that the control portion of a 31-year gopher removal experiment in Colorado had significantly higher levels of several soil nutrients than did the area from which gophers were removed. Other investigators also suggest that the longer-term activities of gophers result in increased rates of soil development and higher soil fertility (Grinnell 1923, Hole 1981, Mielke 1977).

Gophers as consumers of plants

Pocket gophers significantly alter vegetational abundance and composition directly by consuming plants. Effects of direct consumption are difficult to measure independent of other effects. However, direct demographic effects of gopher feeding have been estimated for some trees at Cedar Creek.[3] This study shows that gophers play a major role in the slow invasion of abandoned fields by red oaks (*Quercus rubra*) and white pines (*Pinus strobus*). Oaks and pines grow slowly in the sandy, nitrogen-poor Cedar Creek soils, and their growth is further decreased by browsing by white-tailed deer (*Oedocoileus virginiana*). As many as one percent of young (less than 2 m in height) pines and oaks at the margins of old-fields are killed each year by pocket gophers

[2] O. J. Reichman, 1985, personal communication. Kansas State University, Manhattan.

[3] R. Inouye and T. Allison, 1988, personal communication. Idaho State University, Pocatello, and Ohio State University, Marion.

Figure 8. Melanopline grasshoppers (here, *Melanoplus femurrubrum*) are often seen sunning (as above) or ovipositing on gopher mounds.

that graze off their roots. This is a minimum estimate of gopher effect, because only trees that are killed, remain in place, and show obvious gopher grazing are counted. Although one percent per year at first seems to be a small amount of mortality, trees grow slowly and remain within the size classes vulnerable to gophers for approximately 30 years. Thus, more than 25% of young trees may be killed by gophers. Gopher grazing of roots may contribute to the slow observed growth rates of these trees, but this effect has not been quantified.

As consumers of plants, pocket gophers indirectly affect plant nutrient levels. Gophers concentrate their foraging in patches of locally high productivity, and consumption of aboveground parts lowers standing plant biomass. Where lower plant biomass is present, available soil nitrogen levels remain higher than when biomass is at equilibrium with soil nitrogen (Tilman 1988). Lower standing biomass also results in higher and more variable levels of light penetration through the canopy. Thus, gophers can change the absolute and relative availabilities of soil resources and light without producing mounds; reducing plant biomass by grazing plants can have the same effect (Figure 5).

Many studies indicate that the soil-moving activities of gophers increase the abundance of plants that gophers prefer to eat. Annuals, short-lived perennials, and forbs tend to be more abundant where gophers are active (Hobbs et al. 1988, Inouye et al. 1987b, Laycock and Richardson 1975, Tilman 1983, Turner et al. 1973, Williams et al. 1986). At Cedar Creek, early successional plants are preferred by pocket gophers (Behrend and Tester in press, Tilman 1983), gophers are more abundant in younger fields (Huntly and Inouye 1987, Inouye et al. 1987b), and gophers' activities slow succession (Inouye et al. 1987b, Tilman 1983). These facts raise the interesting possibility that the overall effects of gophers, under at least some conditions, may result in gophers effectively farming their preferred resources. Although many data support this hypothesis, it has not been directly tested.

Gopher effects on other animals

Gophers also might be expected to affect the abundance and activities of other animals. The large changes they cause in the physical environment and vegetation could affect other herbivore populations; gophers are also a food resource for carnivores.

Our studies at Cedar Creek indicate that pocket gophers do significantly affect other herbivores. Most strikingly, it appears that the abundance of grasshoppers in Cedar Creek old-fields is increased by gophers (Figures 6 and 7). In five years of studying grasshoppers at Cedar Creek, we have found gopher mound density to be a strong predictor of grasshopper density. No other factor that we measured (including mean and variance of plant biomass, cover, diversity, and nitrogen content and the mean and variance of soil nitrogen) was as well correlated with grasshopper abundance.

Experiments verify that gophers benefit grasshoppers at Cedar Creek and suggest a mechanism for this counterintuitive result. Grasshoppers become more abundant immediately following nitrogen fertilizaton, but they subsequently decrease in abundance if gophers are absent. When gophers are present, grasshopper numbers remain high.[4] This surprising net positive effect of one major herbivore group on another appears to be mediated by changes that gophers cause in the physical environment. The tunneling and mound-building of gophers produces a heterogeneous mosaic of physical conditions and vegetation that is beneficial to grasshoppers, especially *Melanoplus spp.*, the dominant group at Cedar Creek (Figure 8). Most grasshoppers, including the melanoplines, oviposit in open soil, where the survival probability of eggs and nymphs is greatest (Dempster 1963). Most egg pods of melanoplines at Cedar Creek were located in experimental plots receiving high nitrogen addition; within high-nitrogen plots, eggs were found primarily in gopher mounds (Goldburg 1986). Thus, gopher mounds appear to increase the successful recruitment of grasshoppers and result in higher densities than might otherwise occur.

Additionally, the small-scale mosaic of bare areas, low-density vegetation, and high-density vegetation that occurs where gophers are active allows grasshoppers to exploit vegetation more efficiently. As poikilotherms, nymphal and adult grasshoppers are sensitive to cold or wet weather. Survival and growth depend both on warm, dry conditions and on a rich food supply (Dempster 1963). These conditions are met in the heterogeneous vegetation produced by gophers. Grasshoppers appear to be the most significant invertebrate her-

[4]N. Huntly and R. Inouye, 1988, unpublished manuscript.

bivore in early- and mid-successional Cedar Creek old-fields and several melanoplines are major pests of crops and rangelands (Capinera and Sechrist 1982). The interaction of grasshoppers with pocket gophers may have significant consequences for both natural and agricultural ecosystems.

Other experiments at Cedar Creek suggest strong links between gophers and groups of herbivores other than grasshoppers. The foraging activity (measured by mound production) of gophers increased greatly when belowground or aboveground feeding invertebrates were chemically removed from small plots.[5] This result suggests competitive interactions between herbivore groups, interactions that probably are mediated through changes in the plants available as food. The quick increase in foraging activity of gophers probably reflects a response to a local increase in plant biomass, as has been found elsewhere when invertebrates were removed from an old-field (Shure 1971).

Pocket gophers may influence the behavior and abundance of other vertebrates. Abandoned gopher burrows are used by amphibians, reptiles, and other mammals (Vaughan 1961). Pocket gophers form a substantial portion of the diet of various birds (Franklin 1988), mammals (Fichter et al. 1955), and snakes (Hisaw and Gloyd 1926). Franklin's (1988) and Fichter et al.'s (1955) data suggest that pocket gophers and other small mammals are important to the population density and breeding success of owls and coyotes.

Conclusions

Pocket gophers have large effects on soil fertility. Because of this, gophers change the resource environment of plants and have major indirect effects on plant communities. Gophers increase spatial variation in the availability of soil nitrogen. The relationships between total soil nitrogen and available soil nitrogen and between soil nitrogen and available light are looser when gophers are present. These effects cause development of a plant community that is more diverse and that differs in species composition from what would otherwise occur.

Gophers also have direct effects on plant populations. Their above- and belowground consumption is selective and favors ungrazed plants over those that are preferentially consumed.

The changes that gophers cause in the physical environment and in vegetation affect the herbivore food web, and gophers and other small herbivores provide the major food source of many carnivores. Thus, the activities of pocket gophers cascade through the entire trophic web, in a way similar to that demonstrated by Carpenter and Kitchell (page 764 this issue) for fish in lake ecosystems.

[5]N. Huntly and R. Inouye, 1988, unpublished manuscript.

Acknowledgments

This work was supported by the National Science Foundation (BSR 8114302 and BSR 8612104) under the Long Term Ecological Research program and by grants from the University Research Committee and the Faculty Research Committee of Idaho State University. We thank David Grigal, John Tester, and David Tilman, our collaborators in the Cedar Creek studies, and several reviewers whose suggestions improved this manuscript.

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