EFFECTS OF POCKET GOPHERS (*GEOMYS BURSARIUS*) ON MICROTOPOGRAPHIC VARIATION

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Mounds of soil created by pocket gophers during the process of construction of burrows represent small-scale variation in topography and resources that may influence vegetation by creating a broader range of microsites for germination and growth. We mapped gopher mounds and measured microtopographic variation on 4 by 4-m plots that had been fertilized annually with four levels of nitrogen addition for 11 years. Fertilized plots had more mounds and greater topographic variation than unfertilized plots, and greater mean height of soil than unfertilized plots and adjacent unfertilized aisles. These changes in microtopography and height of soil, caused by the cumulative effects of locally greater activity by pocket gophers over more than a decade, illustrate one way in which burrowing animals can affect heterogeneity in soils.

Key words: *Geomys bursarius,* pocket gopher, gopher mound, microtopography, Cedar Creek

At a biogeographic scale, topographic variation (e.g., mountains and valleys) has significant effects on composition of species of plants (Whittaker, 1975). However, topographic variation also occurs at much smaller scales. Mima mounds are an example of topographic variation at a mesoscale. Mima mounds are believed to have been formed gradually by centuries of movement of soil by pocket gophers (Cox and Scheffer, 1991). The lateral translocation of soil by gophers results in mounds composed of soil and small stones. These formations, commonly reaching heights of 2 m and diameters of 20 m, often support a vegetation that is markedly different from that found in intermound areas (Cox and Scheffer, 1991).

Individual mounds produced by pocket gophers represent an even smaller scale of topographic variation. Mounds constructed by pocket gophers at Cedar Creek Natural History Area, for example, average ca. 0.6 m in diameter and 0.16 m in height. These soil mounds are produced and persist over much shorter periods of time than mountains or mima mounds, days to months rather than centuries to millenia, but these relatively short-lived structures can have long-term effects that are the result of changes in chemistry, texture, and heterogeneity of soil (Huntly and Inouye, 1988). Inouye et al. (1987*a*) found greater variability in total nitrogen in soil in areas with more gopher mounds. Greater variability of a primary limiting nutrient, such as nitrogen, may allow for coexistence of more species of plants than in a more homogeneous environment, due to the wider range of possible resource-use strategies (Tilman, 1982). Mounds constructed by pocket gophers can change bulk density of soil (Anderson, 1987), availability of germination sites (Hobbs and Mooney, 1985), and growth rates of plants (Huenneke et al., 1990). Mounds, thus, represent sudden, small-scale, changes in microtopography, akin to the larger-scale and longer-term phenomenon of mima mounding.

This study examined the effects of nitrogen addition on production of mounds and subsequent topographic variation through an 11-year fertilization experiment. The focus of the study was to determine if addition of nitrogen could have long-term effects on topographic variation due to differences in production of mounds between areas with varying levels of productivity.

MATERIALS AND METHODS

This study was conducted at the Cedar Creek Natural History Area (Cedar Creek) in eastcentral Minnesota 50 km N of Minneapolis. Cedar Creek is ca. 2,200 ha of active and abandoned agricultural fields, wetlands, fire-maintained oak savanna, and closed canopy forest. Located on the Anoka Sand Plain, Cedar Creek has minimal topographic variation and sandy nitrogen-poor soils (Grigal et al., 1974; Inouye et al., 1987*b*), making nitrogen the primary limiting nutrient for many plants (Tilman, 1984).

The plains pocket gopher, *Geomys bursarius*, is a fossorial herbivore that is common in agricultural fields, abandoned agricultural fields (old fields), and savannas at Cedar Creek. Pocket gophers build extensive underground burrow systems and deposit much of the soil that they excavate on the surface of the ground in discrete mounds.

In 1983, two grids of 4 by 4-m plots were established in an old-field (Cedar Creek 89) that was last cultivated in 1975. Each grid consisted of 64 plots in an 8-by-8 array; plots were separated by 1-m aisles. One grid, experiment 8, was undisturbed, and the second grid, experiment 9, was located on an area that was disturbed by disking before the grid was established. The disturbed area included a 10-m wide buffer on each side of the grid. Nitrogen treatments, applied as NH_4NO_3, consisted of annual additions of 0, 2, 9.5, or 27.2 g m^{-2} $year^{-1}$ (treatments 1, 2, 3, and 4, respectively). Plots receiving nitrogen were fertilized twice annually from 1983 through 1994 with one-half of the fertilizer added in late April or early May and one-half in June. In addition to nitrogen, fertilized plots received the same mix of other nutrients, which included Mg, P, K, and trace minerals, added to ensure that nitrogen remained the primary limiting nutrient.

From 1983 to 1985, mounds on the grids were counted periodically and mapped from late April through September. In 1992, censusing of mounds began in early July and ended in early September. Individual mounds were counted only once; maps were used to identify mounds that had been counted in earlier censuses. Mounds on the edge of plots were counted as being on the plot if >50% of the mound was on the plot. In June 1994, all mounds on the grids were mapped and classified as old (plants growing on or through the mound) or new (recently produced and uncompacted mounds, or flattened or compacted mounds with no plants growing on or through the mound).

Microtopography was measured on eight randomly chosen replicates of each treatment on each grid in July 1992. A rectangular frame, 3 by 1 m, was leveled over one side of a plot with the 3-m length of the frame parallel to the edge of the plot. A pole, ca. 3.5 m long, was placed horizontally on the frame parallel to and 25 cm in from the edge of the plot. Distance to the ground was measured at 25-cm intervals along the pole with the first and last measurements taken 50 cm from the sides of the plot. Similar measurements were taken with the horizontal pole 50, 75, and 100 cm from the edge of the plot. This resulted in 52 measurements of relative height in a 4 by 13 grid at 25-cm intervals. Microtopographic variation was quantified by calculating the standard deviation of the measured heights. Absolute height of the horizontal pole from the ground was not the same on all plots, but this did not affect the standard deviation of heights within each plot.

Height of plots relative to adjacent aisles was measured in 1993. A transit was used to measure height of soil at four locations on each plot (0.87 m toward the center of the plot diagonally from each of the four corners) and at the center of the aisle in two locations on each of two opposite sides of each plot (1 m and 3 m from the front of the plot). Average values were calculated for the four heights on each plot and for the four aisle heights adjacent to each plot. Height of plots was calculated as the difference between these two average heights. Because fertilizing and sampling these plots entailed walking in the aisles, average height of all plots was greater than zero. This did not, however, influence differences that might have existed among treatments, which were randomly assigned to the plots in each grid.

Data from the two grids were combined for these analyses. A Kruskal Wallis one-way analysis of variance was used to test for differences in number of mounds and in standard deviations of height of soil among treatments. One-way analysis of variance (ANOVA) was used to test for differences in average height of plot among treatments.

RESULTS

The cumulative number of mounds censused per plot over all censuses increased significantly with increasing level of addition of nitrogen ($P < 0.001$, $H = 23.287$, *d.f.* = 3,124; Fig. 1a). Microtopography differed significantly across treatments ($P = 0.005$, $H = 4.785$, *d.f.* = 3,58), with treatment 3 having the greatest standard deviation of measurements of height (Fig. 1b). Mean height of soil on plots, relative to height of aisle, was significantly different among nitrogen treatments ($P = 0.039$, $F = 2.956$, *d.f.* = 3,60), primarily due to the high mean height on treatment 4 (Fig. 1c). There was a significant positive relationship between number of mounds and topographic variation ($P = 0.017$, $R^2 = 0.091$, $y = 0.105x + 2.398$).

DISCUSSION

Mima mounds are, perhaps, the most dramatic illustration of the impact that pocket gophers can have on topographic variation, and subsequent differences in composition of species of plant between mounds and intermound areas (Cox and Scheffer, 1991). Although mima mounds are believed to have been formed over centuries, similar geomorphic processes of upward and lateral translocation of soil were evident at Cedar Creek after only 10 years. Fertilizing nitrogen-poor soils increased biomass of plants and indirectly increased the local activity of pocket gophers. A short-term consequence of increased activity of pocket gophers is an increase in diversity of plants and the heterogeneity of resources and germination sites of plants. Over a longer period of time, the continued deposition of mounds on fertilized plots significantly affected both microtopography and height of soil. These differences are particularly notable given the sandy soils and the rarity of stones of any

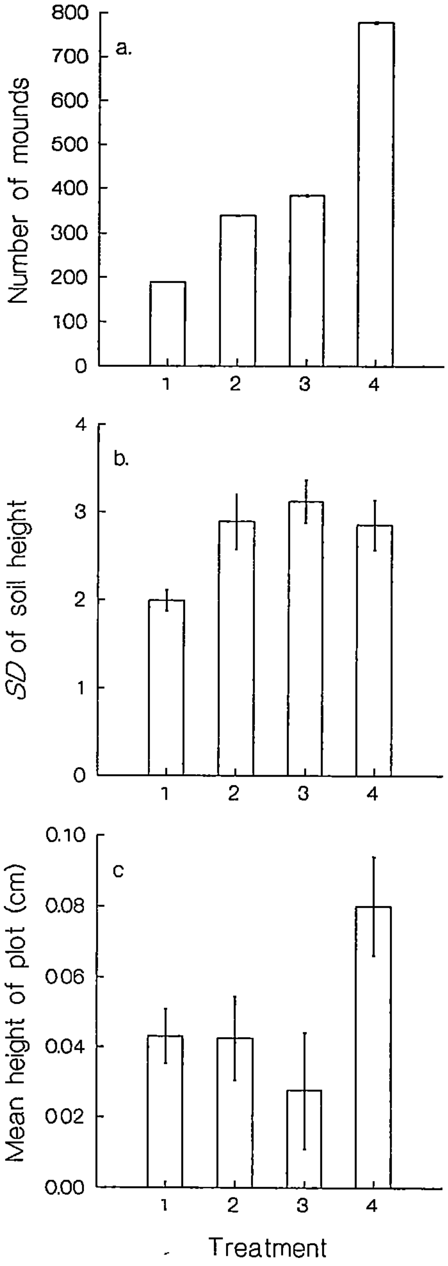

FIG. 1.—Mound and microtopography characteristics of 4 by 4-m plots: a, cumulative number of gopher mounds censused in 1983, 1984, 1985, and 1992:b, standard deviation of heights of soil measured in 1992:c, mean height of soil relative to adjacent aisles measured in 1993. Treatments 1, 2, 3, and 4 correspond to 0, 2, 9.5, and 27.2 g m^{-2} $year^{-1}$ of nitrogen addition. Error bars are ± 1 *SE*; *P*-values are from Kruskal-Wallis tests (a and b) or from ANOVA (c).

size at Cedar Creek, both of which probably make pocket gopher mounds more susceptible to erosion by wind and water than is the case at many other locations.

Responses of vegetation to fertilization also could have contributed to the measured differences in microtopographic variation. Because establishment of vegetation on mounds located on the high-nitrogen areas is more rapid than on low-nitrogen areas, mounds in those areas could be better protected from erosion by rain or wind.

Three processes may have contributed to differences in mean height of soil among the four treatments. First, the simple process of digging may decrease compaction of soil. Bare soils at Cedar Creek tend to be quickly compacted by rain, probably because of their high sand and low organic-matter content, suggesting that aeration of soils would not have a long-lasting effect on height of soil. Second, construction of short-lived, shallow, feeding tunnels, combined with the deposition of excavated soil on the surface of the same plot, could increase height of soil without altering the volume of soil on a plot. The total length of segments of burrows was greater under fertilized plots (Wasley, 1995), consistent with this mechanism. Finally, deposition of soil from adjacent areas may have contributed to greater height of soil by increasing the total volume of soil on a plot.

The topographic effects of pocket gophers that we report here are from an experimental system in which we created small patches with greater productivity, and which consequently were heavily used by pocket gophers for an extended period of time. We believe that similar processes also are operating in unmanipulated old-fields. Repeated censuses of pocket gopher mounds in 18 old-fields at Cedar Creek has shown that, at the scale of 10 by 12.5-m plots, densities of pocket gopher mounds were highly correlated between years (R. S. Inouye and N. Huntly, in litt.). Those areas, which consistently have higher densities of mounds are likely to develop greater microtopographic heterogeneity, together with an increased range of conditions likely to influence growth and diversity of plants. These changes in microtopography, together with effects of pocket gophers on productivity, the distribution and abundance of species of plants, and nutrient cycling (Andersen and MacMahon, 1985; Hobbs and Mooney, 1985; Huntly and Reichman, 1994; Inouye et al., 1987*a*; 1994; Mielke, 1977) illustrate the important influence that pocket gophers can have on ecosystems in which they occur.

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