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# Pocket gophers (*Geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east central Minnesota

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**Summary.** Pocket gophers (*Geomys bursarius:* Geomyidae Rodentia) are shown to affect soil resources and thus, indirectly, vegetation. Gophers reduce average soil nitrogen near the surface and increase point-to-point heterogeneity of soil nitrogen by moving nitrogen-poor subsurface soil to the soil surface. Data from 22 old fields at Cedar Creek Natural History Area, Minnesota, USA show correlations of soil nitrogen, vegetation, and gopher mounds that are consistent with this indirect mechanism by which gophers affect local species composition and old field succession.

**Key words:** *Geomys* – Soil nitrogen – Gopher mounds – Succession

Herbivores can influence vegetation in many different ways, both directly and indirectly. Selective feeding can affect plant populations directly by reducing growth and survival of preferred plant species. It may also indirectly benefit other, less preferred, species by reducing the rate at which preferred species deplete resources. These have been the most commonly discussed mechanisms by which herbivores influence their prey.

Herbivores may also affect plant communities by affecting the availability of resources that limit plants. This may occur in terrestrial plant communities where herbivores can alter soil structure or chemistry (e.g. Chew 1974, 1978; MacMahon 1981), and may be important in aquatic systems as well (Lehman 1980; Sterner 1986). Changing soil structure may change soil moisture retention or aeration, which in turn may influence rates of mineralization or decomposition. Herbivores also can change soil nutrient levels by depositing urine or feces, thereby creating locally high concentrations of nutrients (Woodmansee 1978). Herbivores, especially subterranean mammals, can also influence both soil structure and chemistry by moving soil.

In this paper we present data showing effects of a fossorial herbivore, the pocket gopher (*Geomys bursarius:* Geomyidae Rodentia), on both the average concentration and the heterogeneity of soil nitrogen, a limiting soil resource in old fields in east central Minnesota. Field manipulations demonstrate that gophers discriminate among patches of vegetation resulting from varying soil nitrogen availability and that gophers, in turn, significantly influence soil nitrogen availability and heterogeneity. We also report patterns of association of vegetation, soil nitrogen, and gopher mounds in 22 old fields ranging in age from 1 to 56 years since cultivation. These data are consistent with the patterns of gopher preference and feedback observed in our experiments. Our data suggest that gophers influence the rate of succession in these nitrogen-limited old fields and that the influence of gophers may change with field age.

## Methods

Cedar Creek Natural History Area is located on the Anoka County Sand Plain about 45 km north of Minneapolis, Minnesota, USA. The 2200 km$^2$ sand plain was formed 12–13000 years ago by glacial outwash at the end of the Wisconsin glaciation. Soils at Cedar Creek are primarily outwash sediments of well-sorted fine (Sartell and Zimmerman series) and medium (Nymore series) sands (Grigal et al. 1974), which are poor in nitrogen (Tilman 1983, 1984).

Pocket gophers (*Geomys bursarius*) at Cedar Creek are active year round. They are fossorial mammals that feed primarily by burrowing underground. In the process of burrowing, gophers move subsurface soil to the surface, thereby creating mounds that vary in size from less than 30 cm to more than 100 cm in diameter. Mounds appear throughout the year, but production peaks in late summer to fall.

### *Experimental plots*

In 1982 a grid of 4×4 m plots was established in a 15 year old field (Field A, #29 in Table 1) to study the response of vegetation to a gradient of nitrogen availability. The grid included 6 replicates of each of 8 levels of nitrogen addition (added as ammonium nitrate) ranging from 0 to 27 g/m$^2$/yr N; these 48 plots also received a complete mix of other soil nutrients (P, K, Ca, Mg, S, and trace metals; see Tilman 1987, for amounts). In addition, there were 6 plots that received no nutrients. The grid was fenced with 0.63 cm mesh hardware cloth from 84 cm below ground to 60 cm above ground and with poultry netting 180 cm high to exclude gophers and other mammalian herbivores.

In 1983 we established two additional grids of 4×4 m plots which were not fenced. The first unfenced grid was adjacent to the fenced grid in Field A. Treatments in this grid included 3 of the points along the nitrogen gradient in the fenced grid (treatments E, G, and I; Table 2), with 16 replicates of each treatment. For vegetation analyses

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Table 1. Field and gopher mound data for 22 old fields surveyed in 1983

| Field no. | Last cultivated | Prop. of quadrats with mound | Species richness | |
|---|---|---|---|---|
| | | | Mound present | Mound absent |
| 72 | 1927 | 0.02 | 12.0 | 9.5 |
| 69[a] | 1934 | 0.13 | 13.3 | 11.8 |
| 32 | 1941 | 0.05 | 11.0 * | 8.5 |
| 35 | 1941 | 0.02 | 4.0 | 7.3 |
| 45 | 1943 | 0.31 | 12.6 * | 9.5 |
| 5 | 1947 | 0.14 | 7.1 * | 5.2 |
| 27 | 1947 | 0.13 | 12.8 | 11.3 |
| 76 | 1952 | 0.10 | 8.2 | 7.6 |
| 77 | 1952 | 0.11 | 14.3 * | 10.9 |
| 70 | 1955 | 0.11 | 11.8 | 10.8 |
| 21 | 1957 | 0.03 | 9.3 * | 7.1 |
| 22[a,b] | 1957 | 0.01 | 9.0 | 10.3 |
| 26 | 1957 | 0.06 | 10.7 | 9.5 |
| 47 | 1959 | 0.04 | 12.0 * | 7.7 |
| 44 | 1961 | 0.21 | 10.9 * | 6.7 |
| 53 | 1961 | 0.29 | 7.9 * | 6.7 |
| 24 | 1968 | 0.29 | 9.9 | 10.1 |
| 29[a,b] | 1968 | 0.53 | 11.3 | 11.7 |
| 4 | 1971 | 0.59 | 5.0 | 5.2 |
| 40 | 1972 | 0.01 | 9.0 | 8.6 |
| 39 | 1975 | 0.19 | 11.2 | 11.5 |
| 41 | 1982 | [c] | [c] | [c] |

[a] Fields in which quadrats were layed out along the edge of unmanipulated control plots rather than on permanent transects

[b] $N=150$

[c] Presence/absence of mounds was not noted for these quadrats

* $P<0.05$

Table 2. Mean (std. dev.) number of gopher mounds produced on the unfenced grids in fields A (October 1983 to October 1985) and E (June 1983 to September 1985)

| | Treatment | Added nitrogen (g/m$^2$/yr of N) | Gopher mounds |
|---|---|---|---|
| Field A: | I | 0 | 0.2 (0.4) |
| | E | 5.6 | 1.3 (2.3) |
| | G | 17.5 | 7.3 (7.7) |
| Field E: | A | 0 | 5.4 (6.1) |
| | E | 5.6 | 9.3 (6.4) |
| | F | 9.8 | 14.8 (13.4) |
| | H | 28.0 | 24.8 (20.5) |

we excluded 4 replicates of each treatment that were sampled repeatedly for estimates of above- and below-ground biomass. The second unfenced grid was located in an 8-year old field (Field E, #39 in Table 1). This grid included 16 replicates of each of four treatments (A, C, F, H; Table 2). Plots in all three grids were fertilized twice annually, in mid May and again in early June (see Tilman, in press, for further details).

Vegetation on all plots was characterized using dry weight per species for strips 10 cm by 300 cm clipped at ground level. Light penetration, calculated as the proportion of light above vegetation reaching ground level, was measured using a 1.0 m long, integrating, cosine-corrected quantum sensor (Li-cor, Inc.). Light measurements were taken within two hours of solar noon on clear days, typically within one week of when plots were clipped. To estimate gopher activity we mapped gopher mounds on the unfenced grids every 2–4 weeks during the summer.

In September 1985 we took four 10 cm deep soil samples from every plot in the unfenced grids in Fields A and E and from treatments E, G, and I in the fenced grid in Field A. One sample was located in each corner of a plot, one meter in from each side. These samples were dried, seived, and analyzed colorimetrically for total nitrogen following a persulfate digestion (Tilman 1984).

### *Successional patterns*

In 1983 we sampled vegetation and soils in 22 old fields ranging in age since abandonment from 1 to 56 years (Table 1; Inouye et al. 1987). In 19 of the fields we established 4 parallel transects 40 m long spaced 25 m apart. On each transect we sampled 25 quadrats, 1 m × 1/2 m, spaced 1 1/2 m apart, for a total of 100 quadrats in each field. In the other 3 fields transects were located in unmanipulated control plots that were part of a separate experimental study. While the spacing between these transects was different, quadrat size and spacing between quadrats on each transect were the same. On each quadrat we estimated percent cover of bare ground, of litter, and of vegetation by species (for details of vegetation sampling see Inouye et al. 1987).

Total soil nitrogen was measured from a single 10 cm deep core in the center of each quadrat. Soil cores at the ends of each transect were 60 cm deep. These cores were subdivided into 0–10, 10–20, 20–40, and 40–60 cm depth ranges. Soil samples were dried, seived, and analyzed for total nitrogen.

We estimated gopher activity in all but one field (#41) by recording whether a mound was present in each 1 × 1/2 m quadrat.

We grouped plant species according to life history, growth form, and historical origin. Nonvascular plants included mosses and lichens. Introduced species are those not believed to have been found in the area prior to settlement by Europeans. Native species are those thought to have been present, but not considered to be prairie species, and true prairie species are those associated with prairie vegetation that extended into central Minnesota. These groupings were used to simplify analyses and to determine general patterns. Statistical analyses were done using SPSS version 7.9 on the University of Minnesota mainframe computer and using Statgraphics version 1.2 on an IBM PC-XT.

## Results

### *Experimental plots*

Gopher mounds on the unfenced grids were most common on plots that received the highest level of nitrogen addition (Field A: $X^2=162$, $P<0.001$; Field E: Anova $F=6.6$, $P<0.001$) (Table 2); gophers discriminated among 4 × 4 m patches which varied in productivity and may have varied in resource quality (e.g. plant nitrogen content).

**Table 3.** Partial correlation coefficients (holding 3 other variables constant) for plots in field E. Added nitrogen is weight of ammonium nitrate (g/m$^2$/yr)

| | Std. dev. nitrogen | Added nitrogen | No. mounds |
|---|---|---|---|
| Average soil nitrogen | 0.51** | 0.44** | −0.21$^a$ |
| Std. dev. nitrogen | | −0.19$^b$ | 0.39** |
| Added nitrogen | | | 0.49** |

** $P<0.01$; $^a$ $P=0.10$; $^b$ $P<0.15$

We used the standard deviation of the four soil samples taken in each plot (SD) as a measure of the variability in soil nitrogen within individual plots. To test whether heterogeneity in soil nitrogen increased with increasing gopher activity we correlated this measure with the number of mounds produced on each plot in the two unfenced grids between the time the plots were established and September 1985. In Field A, for all unfenced plots together there was a non-significant positive correlation between variability in soil nitrogen and number of mounds (SD = 1.9*MOUNDS + 71.0, $r=0.25$, $P=0.09$, $N=48$). With one outlier deleted, this correlation was highly significant (SD = 1.5*MOUNDS + 65.8, $r=65.8$, $P=0.003$, $N=47$). In Field E, there was a highly significant positive correlation between variability in nitrogen and number of mounds (SD = 0.9*MOUNDS + 46.4, $r=0.40$, $P=0.001$, $N=64$).

Table 3 gives partial correlation coefficients (holding all other listed variables constant) for mean and standard deviation of total nitrogen (for the 4 samples in each plot), amount of added nitrogen, and number of gopher mounds for the 64 plots in Field E. Standard deviation of nitrogen was significantly correlated with number of mounds and with average nitrogen. Average soil nitrogen was marginally negatively correlated with number of gopher mounds, and standard deviation of soil nitrogen tended to decrease with the amount of added nitrogen (Table 3).

In the rest of this section we compare the fenced and unfenced grids in field A only. These two adjacent grids provide a comparison of the response of vegetation to fertilization in the presence and absence of gophers.

On both grids plant biomass increased with added nitrogen, while light penetration and species diversity decreased with added nitrogen (Fig. 1). Average biomass was lower, while average light penetration and species richness were higher on the unfenced grid. On treatment G (17.5 g/m$^2$/yr N), light penetration was significantly more variable on the unfenced grid than on the fenced grid ($F=8.21$, $p<0.025$). Total biomass and species richness for treatment G were marginally more variable on the unfenced grid (biomass: $F=3.57$, $P<0.10$; species richness: $F=3.23$, $P<0.12$).

Differences in species composition on the fenced and unfenced grids were similar to those on old-field quadrats with and without gopher mounds present (see below). Absolute and proportional abundance of annuals and forbs were both higher on high nitrogen plots on the unfenced grid than on high nitrogen plots on the fenced grid (Table 4).

On the unfenced grid in the 15-year old field proportional biomass of annual plants was significantly positively correlated with the number of gopher mounds produced on a plot between 5 October 1983 and 25 July 1985 (vegetation was sampled in July 1985). This relationship was strongest for treatment G (17.5 g/m$^2$/yr N) plots alone ($r=0.93$, $N=12$, $P<0.001$), weaker for treatments E (5.6 g/m$^2$/yr N) and G ($r=0.78$, $N=24$, $P<0.001$), and still weaker when control plots were included ($r=0.38$, $N=36$, $P=0.02$).

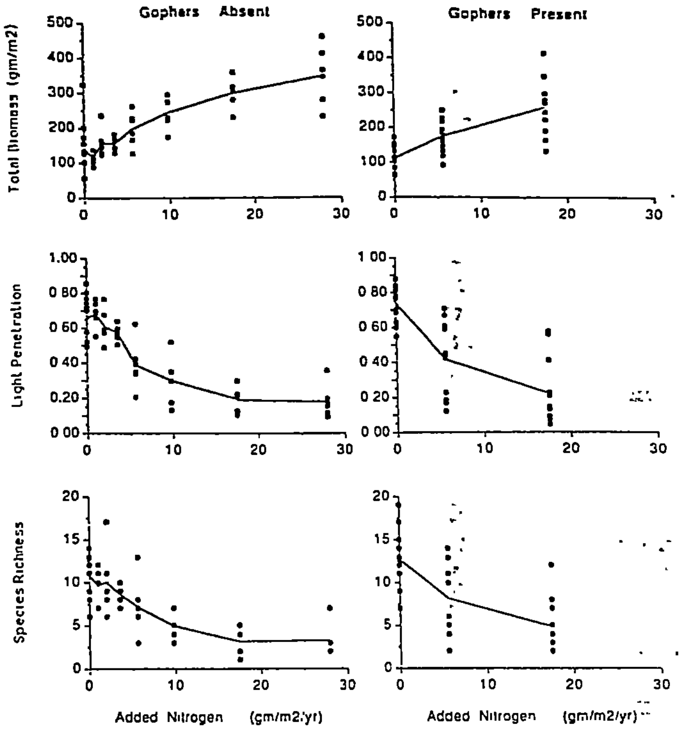

**Fig. 1.** Biomass, species richness, and light penetration as functions of added nitrogen (g/m$^2$/yr N) on fenced and unfenced grids

**Table 4.** Mean values (standard deviation) for proportional biomass of annuals and forbs for treatments I, E, and G on fenced and unfenced grids in Field A

| Treatment (g/m$^2$/yr N) | I (0) | E (5.6) | G (17.5) |
|---|---|---|---|
| Annual plants | | | |
| Fenced | 0.02<br>(0.01) | 0.02<br>(0.03) | 0.00<br>(0.00) |
| Unfenced | 0.17<br>(0.16) | 0.05<br>(0.09) | 0.05<br>(0.12) |
| Forbs | | | |
| Fenced | 0.03<br>(0.02) | 0.03<br>(0.04) | 0.00<br>(0.00) |
| Unfenced | 0.23<br>(0.18) | 0.10<br>(0.10) | 0.18<br>(0.21) |

### *Successional patterns*

Average total nitrogen in the top 10 cm of soil was significantly positively correlated with field age (NITROGEN = 6.8*AGE + 369, $r=0.67$, $P<0.001$, $n=22$). Each of the 22 values used in this regression represents a mean of either 100 or 150 individual samples. Figure 2 shows average values for the 60 cm cores at the ends of each transect ($n=8$). There were no significant correlations between total soil

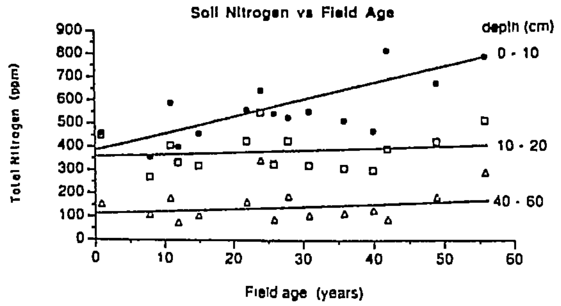

Fig. 2. Average total nitrogen in soil cores at 3 depths. These data are for cores at the ends of each transact: *each point* represents a mean of 8 samples in a field. Soil nitrogen was significantly correlated with field age only in the 0–10 cm depth range

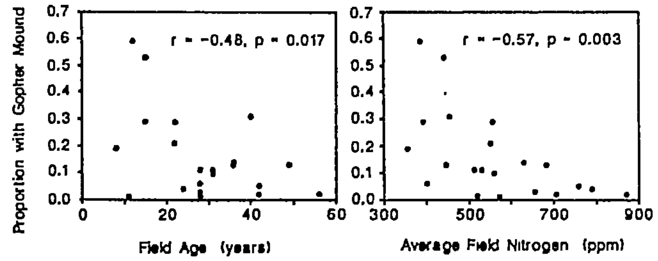

Fig. 3. Proportion of quadrats in each field on which a gopher mound was present plotted against field age and average field nitrogen (0–10 cm)

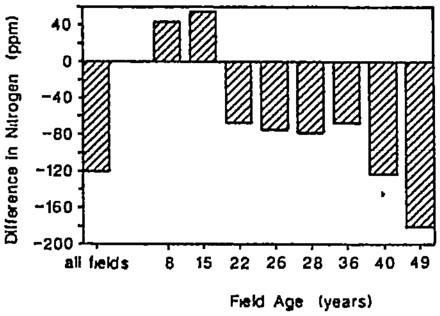

Fig. 4. The difference in average soil nitrogen between quadrats with and without mounds, for all fields together and separately for the 8 fields in which there were significant difference [difference = nitrogen(mounds present) − nitrogen(mounds absent)] For all fields combined, average soil nitrogen was lower on quadrats with mounds present. In the two youngest fields soil nitrogen was higher in quadrats with mounds present, in 6 older fields soil nitrogen was higher where mounds were absent

nitrogen and field age for any depth ranges below 10 cm, either separately or together. Average nitrogen decreased with depth in all fields.

Gopher mounds were present in 364 of the 2300 quadrats sampled. The proportion of quadrats in each field in which a mound was present was negatively correlated with field age and with average soil nitrogen at 0–10 cm depth (Table 1, Fig. 3). In the following analyses, soil nitrogen and vegetation for these 364 quadrats are compared with the same variables on the 1836 quadrats which lacked mounds.

For all fields together, average soil nitrogen (0–10 cm) was higher on quadrats without gopher mounds (mound present: $x = 457.4$, sd = 155.4; mound absent: $X = 577.8$, sd = 225.0) (Fig. 4). Similar comparison on a field by field basis showed 8 fields with significant differences on soil nitrogen on quadrats with versus without mounds. Of these, the 2 youngest fields had higher nitrogen values on quadrats with mounds present, and the 6 older fields had higher nitrogen values on quadrats with mounds absent (Fig. 4).

For all fields together, species richness (SR) was significantly higher on quadrats with mounds ($x = 9.87$, sd = 3.78) than on quadrats without mounds ($x = 9.03$, sd = 3.38). Within individual fields there were no significant differences in SR in 5 fields less than 20 years old (Table 1). In 8 of 16 fields more than 20 years old SR was significantly higher on quadrats with mounds present. In summary, there was no difference in SR on quadrats with or without mounds in younger fields, but SR was commonly higher where mounds were present in older fields.

Percent cover of a number of plant groups differed significantly on quadrats with and without gopher mounds (Table 5). For all fields together, cover of both nonvascular and vascular plants was higher where mounds were absent. Within fields, cover of nonvascular plants was significantly greater in the presence of mounds in 2 fields (#44 and #53), and significantly greater in the absence of mounds in 5 fields. Cover of vascular plants was significantly greater in the absence of mounds in 4 fields. In the second youngest field (#39), cover of vascular plants was significantly greater where mounds were present. Cover of all annual plants was greater where mounds were present for all fields together (Table 5), and within all seven individual fields for which there was a significant difference. Cover of annual forbs was greater where mounds were present, both for all fields together (Table 5) and within all 9 individual fields with significant differences. Perennial grasses and forbs were more abundant in the absence of mounds for all fields and within all individual fields for which there were significant differences. Sedges and woody species were rare in all fields, but for all fields cover of both groups was greater where mounds were absent (Table 5). Cover of sedges was greater in the absence of mounds within 4 individual fields. Cover of woody species was greater in the absence of mounds in 2 individual fields. Neither group was ever significantly more common in the presence of mounds. Not surprisingly, there was more bare ground on quadrats with mounds present than on quadrats without mounts, both for all quadrats (Table 5) and within 14 individual fields.

Introduced species was the only historical origin group that was more abundant in quadrats with mounds present. Both native and true prairie species were more common where mounds were absent (Table 5).

The plant groups in Table 5 that were more abundant on quadrats with mounds present decreased significantly in abundance with field age. All plant groups that were significantly more abundant on quadrats without mounds (e.g. perennials, true prairie species) increased in abundance with field age (Inouye et al. 1987).

There is an inherent weakness in the comparisons of plant abundance in old-field quadrats with and without mounds. Mounds were significantly more abundant in younger fields, and overall differences between the flora on and off mounds could reflect either a mound effect or a field age effect. We attempted to reduce the effect of field age on these comparisons in two ways. First, we made similar comparisons ($t$-tests) using data for individual fields.

Table 5. Average percent cover (std. dev.) of plant groups on quadrats with and without gopher mounds

| Group | Mound present ($N=364$) | Mound absent ($N=1836$) | $T$-test $P$ | Sign test | |
|---|---|---|---|---|---|
| | | | | Ratio | $P$ |
| Bare ground | 28.85<br>(19.85) | 8.41<br>(15.70) | 0.001 | 20:1 | 0.000 |
| Nonvascular | 6.38<br>(10.07) | 7.55<br>(14.85) | 0.064 | 8:13 | 0.383 |
| Vascular plants | 40.06<br>(13.44) | 46.36<br>(15.93) | 0.001 | 6:15 | 0.081 |
| Annuals | 14.75<br>(11.96) | 7.39<br>(9.58) | 0.001 | 18:3 | 0.002 |
| Perennials | 24.95<br>(15.22) | 38.44<br>(19.25) | 0.001 | 2:19 | 0.001 |
| Grasses | 21.52<br>(13.46) | 28.05<br>(15.04) | 0.001 | 3:18 | 0.002 |
| Annual grasses | 1.40<br>(3.45) | 1.51<br>(4.03) | 0.588 | 4:16 | 0.014 |
| Perennial grasses | 20.12<br>(13.38) | 26.52<br>(15.15) | 0.001 | 4:17 | 0.009 |
| Forbs | 17.67<br>(11.72) | 13.39<br>(11.26) | 0.001 | 16:5 | 0.029 |
| Annual forbs | 13.35<br>(11.05) | 5.88<br>(8.00) | 0.001 | 18:3 | 0.002 |
| Perennial forbs | 3.95<br>(6.73) | 7.02<br>(9.42) | 0.001 | 7:14 | 0.190 |
| Sedges | 0.68<br>(2.35) | 2.69<br>(6.02) | 0.001 | 5:15 | 0.044 |
| Woody species | 0.20<br>(0.89) | 2.20<br>(8.84) | 0.001 | 1:14 | 0.003 |
| Introduced species | 20.26<br>(13.50) | 9.92<br>(11.57) | 0.001 | 15:6 | 0.081 |
| Native species (not T.P.) | 6.78<br>(9.00) | 10.58<br>(13.47) | 0.001 | 6:15 | 0.081 |
| True prairie species | 10.75<br>(12.94) | 22.16<br>(19.53) | 0.001 | 3:18 | 0.002 |

Sign test ratios represent the number of individual fields in which cover was greater on quadrats where mounds were present vs the number of fields in which cover was greater where mounds were absent

Results of these tests were consistent with those using the entire data set, however many within-field comparisons were not significant, possibly because of reduced sample sizes. Second, we did sign tests (Sokal and Rohlf 1969, p 401) using the difference in average cover on quadrats with and without mounds for each field. The sign tests reflect correlations between gopher mounds and vegetation that are not influenced by between-field successional patterns in mound density.

Results of sign tests were consistent with $t$-tests using the entire data set (Table 5). With the exception of nonvascular plants all comparisons were significant, and the direction of the difference for nonvascular plants was consistent with that for the $t$-test. These results indicate that the correlational patterns between gopher mounds and plant species composition are not due simply to the negative correlation between mound density and field age.

## Discussion

Because nitrogen is the soil resource most often limiting primary production at Cedar Creek (Tilman 1983, 1984, 1987), changes in soil nitrogen caused by gophers could have significant influences on vegetation at Cedar Creek. Our data suggest that gophers, by creating mounds of subsurface soil on the ground surface, have two important affects on soil nitrogen, particularly in older, more nitrogen-rich fields. First, gophers reduce the average nitrogen concentration near the soil surface. Second, gophers increase the point-to-point variability in soil nitrogen.

The reduction in average soil nitrogen associated with gopher mounds is illustrated by the experimental data in Field E, where there was a slight negative correlation between soil nitrogen and number of gopher mounds (Table 3). The old field data lend more support to this hypothesis. For all 22 old fields together, and in 8 of 16 fields more than 20 years old, soil nitrogen was lower on quadrats where mounds were present than where mounds were absent (Table 5). The difference in soil N in the presence or absence of mounds was greater in older fields, where average soil nitrogen was higher (Figs. 2 and 4). It is in these fields that there is the greatest difference in soil N between surface soil and soil at depths greater than 10 cm, and that is where the dilution of nitrogen-rich surface soil should be most apparent.

The reduction in soil nitrogen that we found associated with gopher mounds is consistent with several other studies (e.g. Spencer et al. 1985; Reichman and Smith 1985), however it also has been reported that gophers may bring relatively nutrient rich soil to the surface or increase moisture retention, thereby enhancing productivity (e.g. Turner 1969; Grant et al. 1980; Laycock and Richardson 1975). Andersen and MacMahon (1985) reported that gophers facilitated succession following a volcanic eruption by modifying soil structure and by moving old soil to the top of a recently deposited layer of tephra. In addition to their effects on surface soils reported here, gophers may also increase subsurface soil nitrogen in very localized areas (e.g. in den sites) by abandoning food caches and by concentrating urine and feces (Zinnel pers. comm.).

The effect of gophers on variability of soil nitrogen is shown by the unfenced grids in Fields A and E, where variability in soil N within individual plots was positively correlated with gopher mound density (Table 3). The effect of individual gopher mounds on variability in soil nitrogen probably increases with field age and average field nitrogen, just as their effect on average nitrogen increased with field age. It is also likely that the relationship between variability in soil nitrogen and mound density is not strictly linear. At extremely high levels of disturbance we would predict that variability would eventually decrease, even in more nitrogen-rich fields, as soil became more uniformly mixed.

Both the reduction in average soil nitrogen and the increase in variability in soil nitrogen affect plant species composition and succession. It has been shown theoretically (Tilman 1982) and experimentally at Cedar Creek (Tilman 1984, 1987; Huntly and Inouye 1987) that soil resources can influence plant species composition and diversity. Soil nitrogen increases with time in old fields at Cedar Creek (Fig. 2), and there are significant correlations between soil nitrogen and the abundance of many plant groups and species (Inouye et al. 1987; Tilman 1987). By reducing surface soil nitrogen gophers influence species composition and probably slow the rate of succession in old fields.

Both the experimental data and the old field data indicate that gophers have a significant effect on species richness. For the experimental plots in Field A, variability in SR was greater where gophers were present than where they were excluded (Fig. 1). We found greater species richness associated with gopher mounds, particularly in older fields (Table 1). Increased SR in older fields resulted from an increase in species that were typically absent from older fields, but that were present in most quadrats in the youngest fields. Annuals and short-lived perennials are frequently unable to establish in the dense vegetation characteristic of older fields (Platt 1975; Gross and Werner 1982) and their persistence at Cedar Creek is probably dependent on the high-light environment of disturbances created by gophers. It is interesting that mounds are an important resource to these plant species even though bare ground contributed more than 10% cover for all quadrats in fields 30 years old (Inouye et al. 1987), and just under 10% cover on quadrats without mounds. The experimental plots for which Tilman (1983) reported a significant positive correlation between gopher activity and SR were located in Field E (#39 in Table 1). In our survey of old fields there was not a significant difference in SR on quadrats with or without gopher mounds in Field E (Table 1), but the greatest difference reported by Tilman (3–4 more species on plots that had been fertilized and then experienced the highest rate of gopher activity) is similar to that in our older fields (Table 1).

The effect of gophers on succession can be viewed in terms of the resource ratio hypothesis of succession (Tilman 1985). This hypothesis proposes that changes in species composition reflect tradeoffs between competition for soil resources (e.g. nitrogen) and light that occur during succession. On poor soils, biomass is lower and hence light availability is greater. Conversely, on rich soils total biomass is greater and light becomes more limiting. By creating openings in vegetation that are relatively low in nitrogen and high in light, gopher mounds recreate conditions more typical of the early stages of succession. This change in the ratio of soil nitrogen and light will be greatest in older, more nitrogen-rich fields. In younger fields the impact to individual mounds on soil nitrogen, light, and hence vegetation is likely to be less significant.

It is clear from the experimental data that gophers discriminate among local differences in productivity (Table 3). The old-field survey data suggest that gophers may also discriminate among naturally occuring patches that are relatively more productive. In the two young fields, soil N was greater where mounds were present (Fig. 4). Vascular plant cover was significantly greater in the presence of mounds in one of those fields ( #39). Those data may reflect a response of gophers to regions of higher soil nitrogen, and hence productivity (Reichman and Smith 1985). Such an effect might only be detectable in these younger fields where surface and subsurface soils were similar in nitrogen concentration (Fig. 2). In older fields, the greater difference in nitrogen concentration between surface and subsurface soils probably precludes detection of patch selection by gophers because of the dilution of surface soil by nitrogen-poor subsurface soil.

The effects on species composition of creating open patches in dense vegetation and of reducing soil nitrogen may be distinct. Reduction of above-ground biomass, by grazing for example, may temporarily increase light availability at the soil surface without directly changing the availability of soil resources. Reduction of plant biomass may also increase nitrogen availability to the remaining plants, however this effect is likely to be relatively short-lived. While these changes in resources may affect species composition over a growing season by increasing establishment and survival of 'understory' species (e.g. Armesto and Pickett 1985), the effects of this kind of disturbance are likely to disappear relatively quickly as the dominant species grow back. Where soil resources are changed, by gopher mounds, for example, the effect on species composition may be lasting. If soil nitrogen is reduced, total plant biomass would be lower even after plants have regrown, and the relative availability of nitrogen and light will have been changed.

The successional, between-field, pattern in gopher activity and the response of gophers to fertilized patches within fields seem somewhat contradictory. In the 22 old fields gopher activity decreased with increasing field age and with average field nitrogen (Fig. 3). On the experimental plots, and in two other old fields (25 and 49 years old) in which we have fertilized plots, mound production was positively correlated with added nitrogen (Table 3; Tilman 1983; Inouye and Huntly, unpublished work). Two hypotheses may explain this apparent contradiction.

First, there may be a decrease in gopher density as well as mound production in older fields. Although total plant biomass and cover (and hence food quantity) increased with field age (Inouye et al. 1987), it is possible that there are significant reductions in food quality associated with successional changes in the plant community. Alternatively, there may be changes in predation pressure with field age, although total plant cover, and probably protection from avian predators, increases with field age.

Second, our measure of gopher activity, mound density, may not provide an estimate of gopher population density that is independent of field age. The rate of mound production per gopher may be significantly lower in older fields due to increases in the food resources of gophers (root biomass and root production increase; McKane pers. comm.) or the existence of established burrow systems. Because our discussion hinges on the effects of gophers on soils due to mound production rather than on gopher density, the absence of a consistent relationship between mound density and gopher density would not change our conclusions. It would, however, explain why we observed fewer mounds in older, more nitrogen-rich fields.

If the rate of mound production decreases with field age then the relative importance of the different ways that gophers influence vegetation may also change with field age. With decreased mound production, changes in soil resources will be less frequent, and direct effects of feeding may become relatively more important. However, although the frequency of mound production was lower in older fields, the impact of individual mounds on average nitrogen, on heterogeneity in nitrogen, and hence on vegetation is greater in older more nitrogen-rich fields.

Because we are considering an effect of pocket gophers on a soil resource, and not a direct effect on vegetation, we see this as one of the many possible indirect interactions between consumers and producers. There are, of course, more direct ways that gophers can influence vegetation and succession in old-fields. Selective foraging could influence species composition and abundance directly. The effect of food choice on the rate or course of succession should vary with the quantity of food harvested and the degree to which there were preferences for early or late successional species. There may also be an increase in soil organic matter due to the decomposition of plants that are buried by gopher mounds. The absolute increase due to burial of plants is likely to be greater in older fields, which have greater vegetative cover, however it is not clear what the relative effect would be in young versus old fields because average soil organic matter is greater in older fields (Inouye et al. 1987).

In summary, our data suggest that gophers significantly slow succession in old fields at Cedar Creek by reducing the rate at which early successional species are displaced. Gophers increased heterogeneity in light availability and soil nitrogen, thereby creating favorable conditions for species characteristics of recently abandoned fields. In very young fields, where these species are already abundant, plant species diversity was not significantly higher where gopher mounds were present. In older fields and on our experimental plots, variability in soil nitrogen and abundance of early successional species were positively correlated with the presence of gopher mounds. Mound density declined with increasing field age, despite an increase in average soil nitrogen and total plant biomass.

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