

Plant succession and gopher disturbance along an experimental gradient

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Summary. A field was disturbed via disking, divided into 36 plots, and fertilized with different ratios of N:Mg in 1980. High N:Mg supply ratios tended to favor the perennial grasses *Agrostis scabra* and *Agropyron repens* over annual plants. In 1981 the experimental field was invaded by a fossorial mammalian herbivore, the plains pocket gopher, *Geomys bursarius*. *Geomys bursarius* was significantly more active in plots dominated by *Agrostis scabra* and *Agropyron repens*. The gopher mounds it created were dominated by the annual grass *Setaria glauca* and the annual herb *Polygonum convolvulus*. Thus the direct effect of resource competition among these plants was counteracted by the indirect response of an herbivore to the treatments. Although nitrogen fertilization tended to increase the rate of successional replacement of annuals by perennials, the indirect response of gophers to nitrogen tended to slow the rate of succession. This suggests that herbivore responses to spatial variation in plant community composition and productivity may be an important determinant of the rate of succession and the species diversity of the community.

Introduction

Several recent papers have discussed the difference between the direct pairwise interactions between species which ecologists often study (competition, predation, mutualism, etc.), and the total effect that one species has on another in a natural community (Levine 1976; Holt 1977; Vandermeer 1980). The total effect of one species on another depends not only on the direct interactions between species but also on all the indirect effects propagated through other species and processes. For instance, the total effect of two species which are direct competitors may be functional mutualism when these species interact in a community with at least one other species present (Vandermeer 1980). This raises the possibility that direct interactions may be modified and even counteracted by indirect or propagated effects in natural communities. It thus has profound implications for field experimentation. A manipulation performed on a natural community will invariably have both direct effects and effects propagated through other species and processes. The observed response to the manipulation is the total response, which includes both direct and indirect effects. It seems likely that direct responses to a manipulation would dominate initially, but that indirect responses could become

increasingly important through time. In order to determine the mechanisms leading to the observed changes, it is necessary to distinguish these direct and indirect effects.

In 1980 I started a series of fertilization experiments on newly disturbed soil to determine what effects different supply rates of limiting soil nutrients might have on plant competition and succession. A fossorial mammal, *Geomys bursarius*, the plains pocket gopher, invaded this field during the second year of this experiment. At my study site female gophers weighed about 190 g and males about 250 g. Plains pocket gophers are completely herbivorous (Miller 1964), feeding on plant parts and whole plants both from tunnels dug just below the soil surface and at the surface near rounded mounds of bare soil (ca. 0.2 m² surface area, 10 cm height) created by tunnel excavation (Chase et al. 1982). The plains pocket gopher showed a significant dependence of its activity on the experimental treatments. In this paper I report the relationships among disturbance by gopher mounds, nutrient treatments, and the changes in the plant composition, dominance and species diversity of these experimental plots. These relationships suggest that herbivore-mediated indirect responses to changes in the supply rates of limiting nutrients may be an important determinant of the composition and diversity of early successional plant communities.

Methods

The study was conducted at Cedar Creek Natural History Area, located on a large glacial outwash sandplain 45 km north of Minneapolis, MN. The field used had been abandoned from agriculture since 1972. In 1980, a portion of this field was thoroughly disked, raked smooth, divided into 36 3 × 3 m plots, and each plot assigned to one of 6 treatments in a Latin squares design. The treatments consisted of 5 different ratios of nitrogen to magnesium fertilization, and a control which received no N or Mg. All plots received Ca, K and P at annual rates of 4, 15 and 10 g m⁻², with these nutrients supplied as reagent grade CaCO₃, commercial K₂O, and reagent grade H₃PO₄. The five treatments consisted of the following rates of N and Mg fertilization each year, applied in two equal amounts in early spring and early summer: Treatment A, 13.6 g N m⁻², 0.0 g Mg m⁻²; Treatment B, 10.2 g N m⁻², 0.9 g Mg m⁻²; Treatment C, 6.8 g N m⁻², 1.9 g Mg m⁻²; Treatment D, 3.4 g N m⁻², 2.9 g Mg m⁻²; Treatment E, 0.0 g N m⁻², 3.8 g Mg m⁻², with N supplied as commercial

NH_3NO_3 and Mg supplied as U.S.P. MgSO_4 . Treatment F was the control.

Vegetation was sampled by clipping plants at the soil surface and sorting to species. In 1980 and 1981 this was done manually with scissors, clipping all vegetation within $0.5 \text{ m} \times 3.0 \text{ m}$ quadrats in July 1980, within $0.5 \text{ m} \times 1.0 \text{ m}$ quadrats in September 1980 and within $0.33 \text{ m} \times 1.5 \text{ m}$ quadrats in July 1981. Gophers did not occur in the experimental plots in 1980. To avoid sampling variance which would have been caused by the inclusion of gopher mounds, the 1981 samples were collected immediately adjacent to the pre-determined sampling area if that area included a gopher mound. In 1982 samples were taken using a set of three rechargeable lawn edgers mounted in a "U". One of the lawn edgers cut along the soil surface and the other two cut vertically on each side of the horizontal edger. The clippers were guided along a 3 m long steel rod which was positioned beforehand by sliding it along the soil surface from one end of the area to be sampled. All vegetation in the resulting 10 cm wide swath was caught in a curved basket mounted directly behind the blades. Using this device, each plot was sampled in 1982 by clipping a strip 0.10 m wide by 3.0 m long. Such a long, narrow sampling quadrat averaged over much of the spatial heterogeneity within each plot which had resulted from the patchy pattern of gopher disturbance in 1981 and early 1982. The actual areas to be clipped were determined beforehand independent of any pattern of gopher disturbance within a plot. The slightly different methods used to sample vegetation in 1981 and 1982 allow analysis of the differences between gopher microhabitat choice and the effects of that choice on the vegetation.

Soil samples (15 cm cores) were collected for analyses of total nitrogen, extractable magnesium, and pH. Total

N was determined using an alkaline persulfate digestion to convert all N to NO_3 (Solorzano and Sharp 1980), followed by a 100X dilution and determination of NO_3 via cadmium reduction (Strickland and Parsons 1972). For Mg, soils were extracted for 0.5 h with 0.1 M NaCl (with pH adjusted to 2.5 with HCl) and Mg determined on an atomic absorption spectrophotometer. For pH, a slurry of equal volumes of soil and pH 7.0 distilled water were mixed and allowed to sit for 0.5 h before measurement.

Gopher response to treatments was estimated from the number of new gopher mounds occurring in each plot at three different times: July 1981, July 1982, and September 1982. These data were collected to determine possible patterns of gopher microhabitat choice and to serve as an index of gopher activity within individual plots. In July 1981 and July 1982 only mounds free of vegetation or with scattered annual plants were counted. Previous observations of revegetation of gopher mounds in this field indicated that such mounds should have been formed since snow melt of that year. Because gophers invaded the plots in spring of 1981, this method meant that all mounds were counted in July 1982, but that these same mounds were not counted again in July 1982. To prevent duplicate counts of mounds in September, 1982, only mounds with a rough soil surface that indicated that they had been made during the week since the last rain, or with a smooth surface, but completely free of vegetation, were counted. All these should have been formed after the July 1982 sampling.

Light attenuation by the vegetation was determined in July 1981 and August 1982 using a Lambda Instruments photosynthetically active cosine collector. For each plot, light intensity was measured above the plants and then at the soil surface, with these pairs of observations repeated 15 to 20 times. Proportional light penetration is expressed

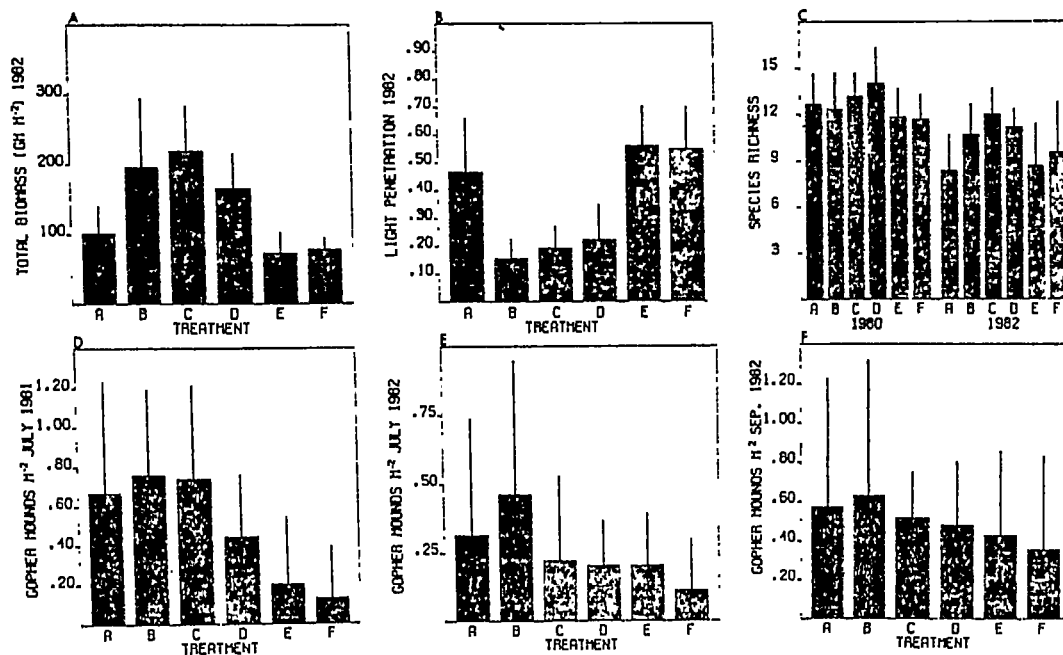


Fig. 1 A-F. The response of several variables to the imposed N:Mg fertilization gradient. The treatments ranged from Treatment A, which received high nitrogen but no magnesium to Treatment E, which received no nitrogen but high magnesium. Treatment F received neither nitrogen nor magnesium. Part A of this figure shows the response of total above-ground biomass to treatments. Part B shows light penetration to soil surface. Part C shows species richness in 1980 and 1982. Part D shows gopher activity in July 1981. Part E shows gopher activity in July 1982. Part F shows gopher activity in September 1982. The thin lines give the standard errors of the means

as the light intensity at the soil surface divided by the intensity above the vegetation.

In order to document patterns of gopher activity and plant colonization of gopher mounds in an unmanipulated area, in May 1980 a 0.1 hectare (31 × 31 m) plot was established on the natural vegetation approximately 30 m south of the disked experimental plot. At that time, all existing gopher mounds were flagged. As new mounds appeared, they were flagged and their surface area measured. On 23 June 1981, a survey of recent gopher mounds (those formed since August 1980) was performed to determine the abundance of all seedlings on the mounds. Mature plants at the edges of the mounds and the few mature plants at the center of a few mounds were not included.

Results

Gopher activity in natural vegetation

The two-year survey of gopher activity in the unmanipulated 0.1 hectare plot adjacent to the experimental plots revealed that the average gopher mound was 0.18 m² in surface area, with an average of 1,220 mounds h⁻¹ y⁻¹. This is comparable to disturbance of 2.2% of the soil surface per year by *Geomys bursarius*. The average density of seedlings on the mounds was 183 plants m⁻². Five species accounted for 99% of the plants on the new mounds in this 8 year-old field: *Polygonum convolvulus* (43%), *Agropyron repens* (26%), *Ambrosia artemisiifolia* (25%), *Carex* sp. (3%), and *Berteroa incana* (2%). Additionally, *Crepis tectorum*, *Chenopodium album*, *Vicia villosa*, *Lepidium densiflorum*, and *Lychnis alba* were observed on mounds.

Treatment effects for biomass, light, chemistry, gophers

Figure 1 shows the effect of fertilization treatments on above-ground plant biomass and light attenuation in 1982, on gopher disturbance rate in 1981 and 1982, and on species richness in 1980 and 1982. After the first year, plant biomass was highest in the treatments receiving intermediate levels of N and Mg, suggesting that both N and Mg were limiting along the experimental gradient. Light penetration was least in the treatments with the highest above-ground plant biomass. In general, gopher disturbance rates also tended to be higher in treatments A, B and C. ANOVA of the totals of all observed gopher disturbances on each plot showed a significant treatment effect ($F=2.91$, $P=0.04$) as well as a significant column effect ($F=4.36$, $P<0.001$). Approximately the following percent of the surface area of each plot was subject to gopher mound disturbance during 1981 and 1982, assuming a surface area of 0.18 m² per mound: Treatment A, 28%; Treatment B, 33%; Treatment C, 27%; Treatment D, 20%; Treatment E, 15%; Treatment F, 11%.

Treatment effects on plants

There were marked changes in the abundance of plant groups throughout this experiment. In the first season after disturbance, annual plants were 93% of the total biomass of all plots combined. This decreased to 21% the second year and increased to 51% the third year. ANOVA revealed that annual grasses and sedges (graminoids) did not show any significant response to treatments in 1980 or 1982, but

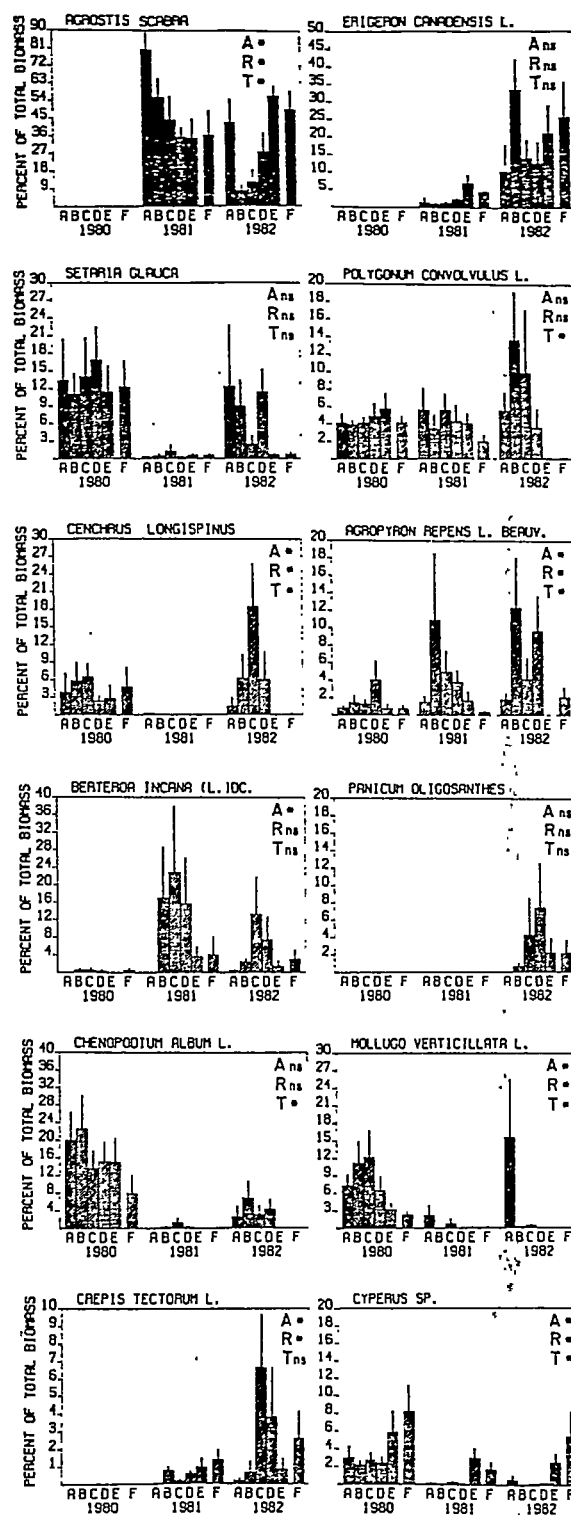


Fig. 2. The treatment responses of the 11 most abundant species in the experimental plots in 1982 and an additional species (*Cyperus* sp.) are shown for all 3 years of this experiment. The treatments ranged from Treatment A, which received high nitrogen but no magnesium to Treatment E, which received no nitrogen but high magnesium. Treatment F received neither nitrogen nor magnesium. The thin lines extending above the mean are the standard errors of the means. Species with significant ($P \leq 0.05$) responses of their relative abundance to treatments in 1982 are indicated by T*; those with insignificant responses ($P > 0.05$) by T ns. Species with significant trends in relative abundance are indicated by R*. Those with significant trends in absolute abundance are indicated by A*

Table 1. Non-parametric correlations among physical and biological variables of 1981. Plant data were analyzed as above-ground dry biomass. A two-tailed test of significance was used

1981	Mg	Light	CV Light	pH	Gopher	Biomass	Agros	Oeno	Bert	Arist	Poly	Agrop
Nitrogen	0.05	-0.31	0.11	0.14	0.45**	0.33*	0.15	-0.37*	0.51***	-0.57***	-0.15	0.46***
Magnesium		0.04	-0.13	0.34*	-0.01	0.16	-0.24	0.19	0.36*	-0.06	0.08	0.04
Light			-0.40*	0.35*	-0.72***	-0.83***	-0.76***	0.16	-0.26	0.46***	-0.50***	-0.65***
CV light				-0.47***	0.45**	0.31	0.36*	-0.11	-0.00	-0.33	0.35*	0.18
Soil pH					-0.14	-0.19	-0.33	-0.00	0.29	0.26	-0.44**	0.01
Gopher activity						0.68***	0.67***	-0.34*	0.37*	-0.58***	0.31	0.58***
Plant biomass							0.60***	0.06	0.43**	-0.46**	0.44**	0.61***
Agrostis								-0.18	-0.10	-0.41*	0.35*	0.52***
Oenothera									-0.29	0.26	0.37*	-0.06
Berteroa										-0.33*	-0.24	0.32
Aristida											-0.17	-0.34*
Polygonum												0.10
Agropyron												

* means $0.01 < P \leq 0.05$, ** means $0.005 < P \leq 0.01$, and *** means $P \leq 0.005$

did have a significant treatment effect in 1981. In 1981, annual graminoids were significantly more abundant in treatment E and F than in the other treatments. Annual herbs¹ did not have a significant treatment effect in any of the years. Perennial graminoids were rare in the first year. The second year, perennial graminoids had a significant treatment effect, with a pattern of decreasing dominance along the N:Mg gradient. In the third year, they also had a significant treatment effect, showing a "U-shaped" distribution along the gradient. Perennial herbs did not show a significant treatment effect in any year. They were rare the first and second year, and most abundant in treatments D and E the third year.

Figure 2 gives the treatment response of the 11 most abundant plant species of 1982 and another species showing a significant treatment effect in 1982. ANOVA of arc-sine-square-root transformed 1982 relative (proportional) abundance showed that 7 of these 12 species had significant treatment effects on their relative abundance (indicated by T* in Figure 2). An analysis for trends along the imposed gradient for treatments A to E in 1982 showed that there were significant linear or quadratic trends of treatment means for 6 of the 12 species based on relative abundance (indicated by R* in Figure 2) and for 7 of the 12 based on absolute abundance (indicated by A* in Figure 2). The plants are shown in order of their dominance, with *Cyperus* sp. added because of its significant treatment response.

Relationships among variables

Table 1 gives Spearman rank correlation coefficients among the major physical, chemical and biological variables for 1981, and indicates the level of statistical significance, using a two-tailed test. Table 2 provides comparable information for these variables in 1982. The plant species included in each table are presented in the order of their dominance for that year. All plant data for these tables were analyzed as absolute abundance, i.e., above-ground dry biomass of that species in a given plot. These nonparametric correlations show numerous statistically significant relationships among variables. In 1981, 4 of the 6 most abundant plant species were significantly correlated with total soil nitrogen,

4 with light availability at the soil surface, 5 with gopher activity, 2 with the coefficient of variation of light, 1 with pH and 1 with extractable soil Mg. In 1982, 4 of the 6 most abundant plant species had significant correlations with nitrogen, 5 with light availability, 2 with July 1982 gopher activity, 5 with the coefficient of variation of light, 1 with pH and none with Mg. Total biomass, which may be considered an index inversely related to the degree of nutrient limitation within a field (Tilman 1982), was significantly correlated with the abundance of 5 of the 6 most abundant plants in both 1981 and 1982.

Gopher-plant relationships

Figure 3 shows the dependence of gopher activity at all sampling dates on the above-ground dry plant biomass of each plot. There was a significant linear or quadratic dependence of gopher activity on total plant biomass for the July 1981 and the September 1982 samples, but not for the July 1982 samples.

Table 3 gives the relationships between gopher activity in 1981 and the relative abundances of annual and perennial grasses and herbs in both 1981 and 1982. Spearman rank correlation coefficients show a strong negative relationship between the relative abundance of annual grasses in the 36 plots in 1981 and the index of gopher activity in those plots in 1981. There is a strong positive relationship between the relative abundance of perennial grasses and gopher activity in 1981, and no significant relationships for either annual herbs or perennial herbs in 1981. In 1982, these correlations reversed. The relative abundance of annual grasses in plots in 1982 was significantly positively correlated with 1981 gopher activity and the relative abundance of perennial grasses in the plots was significantly negatively correlated with 1981 gopher activity.

Table 4 shows the dependence of the specific rate of weight change of the 6 most abundant plant species of 1982 on the index of gopher activity in 1981. The specific rate of change was calculated as $\ln(WT82/WT81)$ which equals $dWT/dt \cdot 1/WT$, where WT81 and WT82 are the above-ground dry biomasses of a species in a plot in 1981 and 1982, respectively. Table 4 also shows the dependence of the difference between the 1982 and the 1981 relative abundance of each species on 1981 gopher activity in each plot.

¹ More appropriately called forbs

Table 2. Non-parametric correlations among physical and biological variables measured in 1982. A two-tailed test was used

1982	Mg	Light	CV Light	pH	Gopher (7-82)	Gopher (9-82)	Biomass	Agros	Erig	Setar	Poly	Cenchr	Agrop
Nitrogen	-0.10	-0.43**	0.53***	0.08	0.42*	0.46**	0.47***	-0.06	0.55***	0.44**	-0.22	0.33*	0.62***
Magnesium		0.10	-0.12	0.44**	0.03	-0.01	-0.17	0.10	-0.10	-0.30	-0.16	0.04	-0.21
Light penetration			-0.81***	0.28	-0.14	-0.34*	-0.77***	0.35*	-0.17	-0.35*	-0.62***	-0.46***	-0.64***
CV light				-0.31	0.38*	0.38*	0.79***	-0.44**	0.10	0.43**	0.78***	0.39*	0.55***
Soil pH					0.06	-0.10	-0.33*	0.03	0.05	-0.22	-0.42*	-0.22	-0.17
Gopher activity (7-82)						0.14	0.22	-0.49***	0.14	0.32	0.44**	-0.25	0.19
Gopher activity (9-82)							0.36*	0.18	-0.25	0.22	0.26	0.00	0.29
Total biomass								-0.36*	0.31	0.59***	0.73***	0.37*	0.56***
Agrostis									-0.50***	-0.25	-0.55***	-0.03	-0.30
Erigeron										0.18	0.26	0.10	0.08
Setaria L.											0.55***	-0.18	0.19
Polygonum												0.19	0.40*
Cenchrus													0.12
Agropyron													

* means $0.01 < P \leq 0.05$, ** means $0.005 < P \leq 0.01$, and *** means $P \leq 0.005$

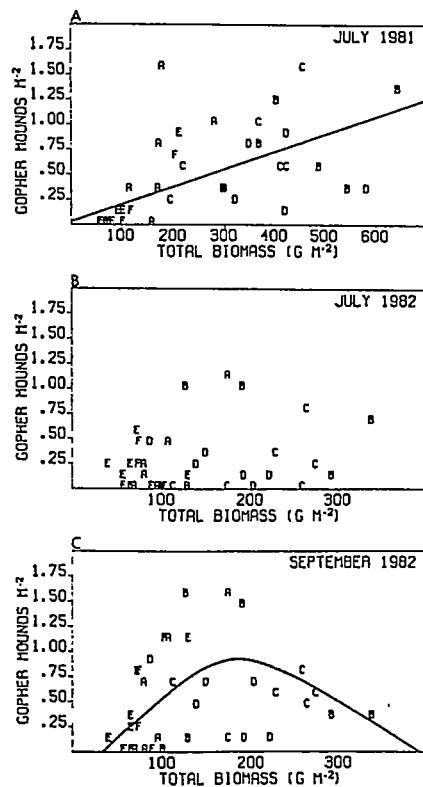


Fig. 3A-C. Gopher activity versus above-ground plant biomass (dry). A For July, 1981, linear regression gave $r = 0.54$ with 34 d.f., $P \leq 0.001$. Non-linear regression (quadratic) gave $r = 0.59$ with 33 d.f., $P \leq 0.001$. B For July, 1982, linear regression gave $r = 0.26$ with 34 d.f., $P = 0.125$. Non-linear regression (quadratic) gave $r = 0.27$ with 33 d.f., $P = 0.292$. C For September, 1982, linear regression gave $r = 0.17$ with 34 d.f., $P = 0.322$. Non-linear regression (quadratic) gave $r = 0.43$ with 33 d.f., $P = 0.037$

Both analyses use non-parametric Spearman rank correlation. Using either analysis, the perennial grass *Agrostis scabra* shows a highly significant negative dependence of its change in dominance on 1981 gopher activity. *Agropyron*

Table 3. Spearman rank correlation coefficients of 1981 gopher activity and the relative abundance of annual and perennial herbs and grasses. For all cases $n = 36$

Plant group	1981 Gopher activity	P
1981 Annual graminoids	-0.66***	$P < 0.001$
1981 Perennial graminoids	0.42**	$P = 0.006$
1981 Annual herbs	-0.13	$P = 0.44$
1981 Perennial herbs	0.35*	$P = 0.04$
1982 Annual graminoids	0.42**	$P = 0.01$
1982 Perennial graminoids	-0.52***	$P = 0.002$
1982 Annual herbs	0.26	$P = 0.125$
1982 Perennial herbs	0.43**	$P = 0.01$

repens, another perennial grass, also shows a negative dependence ($p = 0.06$). An annual grass, *Setaria glauca*, and an annual herb, *Polygonum convolvulus*, had positive dependences of their rate of change on 1981 gopher activity. The two remaining species did not have any significant dependence of their rate of change on 1981 gopher activity. Separate treatment-by-treatment analyses were made for the relative abundance difference data. These were in agreement with the analyses of the complete data set (Table 4) suggesting that the significant correlations of Table 4 are not hidden treatment effects.

Discussion

The results summarized in Figures 1 and 2 demonstrate that the imposed treatments – a gradient of N:Mg fertilization – had a major impact on most of the dominant plants and on several other physical and biological variables in the experimental plots. The patterns observed reflect the total effect on the treatments, and thus include both direct effects of the treatments on the plants and indirect effects of the treatments via other variables which changed in response to the treatments. If the number of significant correlations between a factor and the abundance of each of the 6 major plant species in 1981 and 1982 were used as an index of

Table 4. Dependence of the specific rate of weight change ($\ln(WT_{82}/WT_{81}) = dW/dt \cdot l/W$) and of change in the (relative) abundance of a species (R82–R81) on the index of gopher activity in 1981. All correlations are two-tailed Spearman rank correlations. Note that WT 81 and WT 82 are above-ground dry biomasses for a given species in 1981 and 1982, and R81 and R82 are the proportional abundances of a species in 1981 and 1982 based on above-ground dry biomass. The 6 most abundant plant species are shown; r is the correlation coefficient, n is the number of samples, and P is the probability of significant difference from no relationship. For $dW/dt \cdot l/W$, the number of samples is less than 36 because dW/dt could not be calculated for plots with either WT 81 or WT 82 equal to zero

Species	dW/dt l/w			R82–R81		
	r	n	P	r	n	P
Annual grasses						
<i>Cenchrus longispinus</i>	-0.03	6	$P=0.48$	0.10	36	$P=0.28$
<i>Setaria glauca</i>	0.30	25	$P=0.08$	0.29	36	$P=0.05$
Annual herbs						
<i>Erigeron canadensis</i>	-0.06	27	$P=0.38$	0.01	36	$P=0.47$
<i>Polygonum convolvulus</i>	0.28	28	$P=0.08$	0.32	36	$P=0.03$
Perennial grasses						
<i>Agropyron repens</i>	-0.42	16	$P=0.06$	-0.11	36	$P=0.27$
<i>Agrostis scabra</i>	-0.74	36	$P<0.001$	-0.69	36	$P<0.001$

the relative importance of that factor, the factors of Tables 1 and 2 would be ranked from most to least important as light (9), nitrogen (8), gophers (7), coefficient of variation of light (7), pH (2), and magnesium (1), where the parenthetical number is the total number of significant correlations. This suggests that an explanation of the observed patterns of plant dominance in 1982 must go beyond the direct responses of the plants to the imposed pattern of nitrogen and magnesium fertilization by considering possible indirect responses to the treatments. The two major indirect responses to the treatments seem to be vegetation interception of light and gopher activity. I must note, though, that the following attempt to evaluate the importance of indirect effects from this study is based on correlational analyses. Its main use is in the description of interrelationships and thus in the formation of hypotheses, but not in their testing. It is in that spirit that I offer the following discussion.

The patterns of species dominance along the imposed N:Mg gradient were more complex in 1982 than they were in 1981. In 1981 the 5 most abundant species had approximately Gaussian distributions along the imposed nutrient gradient (Figure 2). The separation of these species along the gradient suggests that they differ in their competitive abilities for N and Mg. The high nitrogen treatments were dominated by the perennial grasses *Agrostis scabra* and *Agropyron repens*, which are locally typical of later succession, while the low nitrogen treatments and controls were dominated by the annual grass *Aristida basiramea*, locally typical of very early succession. Thus, high rates of nitrogen supply increased the rate at which later successional species

became dominant. Because the 1980 and 1981 data were unaffected by gopher disturbance, a major indirect response to fertilization, and because it may have been too soon for light limitation at the soil surface to have influenced the growth of seedlings, the patterns of 1980 and 1981 are most likely indicative of direct effects of treatments on N and Mg competition among these plants.

Some of the major changes between 1981 and 1982 (Figure 2) were probably indirect responses to the treatments, possibly caused by the invasion of *Geomys bursarius* in 1981, by decreased light at the soil surface, or by changes in soil pH. Gopher effects on plants could result directly from gopher feeding, indirectly via the removal of competitors, and indirectly through the creation of gopher mounds. Because light limitation will affect seedlings and new shoots of establishing plants more than taller, established plants, it is likely that the light gradient of one year will have more of an impact on plant distributions the following years than the current year. Thus, the "U-shaped" light gradients of 1981 and 1982 are most likely to affect plant dominance patterns in 1982 and beyond. Soil pH is another potentially important variable. Although soil pH changed in response to NH_3NO_3 fertilization, the correlations of Tables 1 and 2 suggest that soil pH had a minor effect on the dominant plants. Even though the remainder of the discussion will focus on gopher-plant interactions, plant-light and plant-pH interactions are also likely important.

Tables 1 and 2 show strong negative correlations between gopher activity and average light availability at the soil surface. This probably resulted from the tendency for gopher activity to be greater in high biomass plots. Tables 1 and 2 also show highly significant positive correlations between gopher activity and the coefficient of variation of light within a plot in the same year. This caused soil N to be positively correlated with the coefficient of variation of light (Tables 1 and 2). This is a potentially major indirect response to treatments mediated through gophers. Gopher preference for higher productivity areas meant that gophers created microhabitats which were high in both nitrogen and light. These microhabitats – the gopher mounds – were dominated by annual plants (see, also, Weaver 1954; Platt 1975; Grime 1977; Platt and Weis 1977).

Gophers foraging activity may be influenced both by total plant biomass within each plot and by the plant composition of each plot. There were significantly positive correlations between total plant biomass and gopher activity in July 1981 and September 1982, but not in July 1982 (Tables 1 and 2). Increased gopher activity in high productivity areas is also suggested by the 10× greater rate of gopher disturbance in the fertilized plots compared to the adjacent unfertilized field. However, gopher activity was often maximal in plots of intermediate plant biomass (Figure 3), suggesting that gophers did not simply forage more heavily in microsites with more above-ground biomass, but chose plots using other criteria.

Gophers invaded the experimental plots in 1981 when the vegetation within plots was homogeneous. At the time of initial gopher invasion, the 36 experimental plots could be considered to be a microhabitat choice experiment for the gophers. Each plot contained a fairly uniform vegetation, but individual plots differed because of treatment and position. Thus, invading gophers experienced resource patches. Because the 1981 plant sampling was biased to avoid gopher mounds, the correlations between 1981 go-

pher activity and 1981 plant abundance (in Tables 1 and 3) should reflect gopher preference, not the response of plants to gopher activity. These data show a highly significant preference of gophers for plots dominated by perennial graminoids and an avoidance of plots dominated by annual graminoids. Because the long but narrow vegetation samples taken in 1982 included areas that had experienced gopher disturbance in 1981 and 1982, they should include information on vegetation response to gopher activity. The correlations between 1981 gopher activity and the abundances of plant groups in 1982 may thus reflect the effects of 1981 gopher activity on these plant groups. The switches from highly significant positive correlations to negative correlations, and vice versa, shown for annual and perennial graminoids in Table 3, dramatically illustrate the effects of gophers. These suggest that gophers feed preferentially on perennial graminoids, and that this activity favors annual graminoids and herbs. These groups may have increased simply because the superior competitors (perennial grasses) had been removed, or because gopher mounds were a particularly suitable habitat for their growth. Additionally, the difference between the 1982 and 1981 abundance of each of these plant groups is significantly positively correlated with 1981 gopher activity for annual graminoids (Pearson $r=0.54$, $n=36$) and is significantly negatively correlated with gopher activity for perennial graminoids (Pearson $r=-0.67$, $n=36$). Thus, on a plot-by-plot basis, gopher activity led to increased dominance of annual graminoids and to decreased dominance of perennial graminoids.

The effects of gopher activity may also be viewed on a species-by-species basis. The relationships between 1981 plant abundances and gopher activity (Table 1) suggest a strong preference of gophers for plots with relatively high biomasses of *Agrostis scabra*, *Berteroa incana*, and *Agropyron repens*, and an avoidance of plots with relatively high biomasses of *Oenothera biennis* and *Aristida basiramea*. The specific rate of weight change (dW/Wdt) or the change in relative abundance (1982 proportion - 1981 proportion) was negatively related to 1981 gopher activity for the perennial grasses *Agrostis* and *Agropyron* (Table 4). An annual grass, *Setaria glauca*, and an annual herb, *Polygonum convolvulus*, had their rate of change positively correlated with 1981 gopher activity.

These results suggest that gophers may have a feeding preference for *Agrostis* and *Agropyron*. A previous study of gopher stomach contents indicated that *Geomys bursarius* fed mainly on perennial grasses, especially *Agropyrons smithii*, *Stipa comata* and *Bouteloua gracilis* (Myers and Vaughan 1964). The increased abundance of the annuals *Setaria glauca* and *Polygonum convolvulus* with gopher activity, as reported here, suggests that these species are favored by either the decrease in perennial graminoids or by the increased availability of high light patches associated with gopher mounds. Both annuals are quickly replaced on nutrient-rich undisturbed plots by perennial plants, especially *Agrostis*, as shown by the 1980 and 1981 data of Figure 2. Table 2 shows that the strongest correlation for *Polygonum* is a highly positive correlation with the coefficient of variation of light. Observation of unmanipulated vegetation showed that *Polygonum* was the most common plant on gopher mounds. Within the experimental plots, *Polygonum* was clearly most abundant on recent mounds. Although *Setaria glauca* was rare on the unmanipulated field gopher mounds, it was abundant on new mounds in

the experimental plots in 1982, especially mounds in plots heavily fertilized with nitrogen (Table 2). These relationships imply that *Polygonum* and *Setaria* are light limited and increase on the high-light gopher mounds. Additionally, Table 2 suggests that *Setaria* is specialized on patches of high light which also have high soil nitrogen, while *Polygonum* is specialized on open sites with lower N. This is consistent with the higher abundance of *Polygonum* on gopher mounds in the nitrogen-poor field adjacent to the experimental plots.

All these analyses are potentially confounded by correlations among variables. To control for these, partial correlation analysis was performed for the relative abundance difference data in Table 4. These analyses determined the dependence of the change in relative abundance on 1981 gopher activity, controlling for either 1981 soil nitrogen or for both 1981 light penetration and 1981 total plant biomass. With both types of partial correlations, the increase in the relative abundance of *Setaria glauca* as gopher activity increased became more significant statistically. The highly significant negative correlation for *Agrostis scabra* remained. Thus, the relationships between gopher activity and the changes in the relative abundance of *Agrostis* and *Setaria* are not spurious correlations.

The rapid replacement of annuals by perennial graminoids in the plots receiving high to intermediate N:Mg ratios, which have the highest plant biomass and lowest light levels, suggests that seedlings of perennial graminoids may be superior competitors for light compared to seedlings of annual plants, since the perennials become more dominant as nutrients are increased and light at the soil surface is decreased (Tilman 1982). If natural biogeochemical processes tend to increase the level of soil nutrients, especially nitrogen, during succession (eg., Crocker and Major 1955; Olson 1958), this would suggest a successional replacement of annuals by perennials, as has often been reported. If gophers tend to forage preferentially on some of the dominant perennials, their foraging would retard this process, leading to local replacement cycles in which annuals were replaced by perennials because of soil development and plant competition for light, some of the perennials were eaten by gophers, the bare soil dominated by annuals, and those replaced by perennials, etc. Several previous studies have suggested that gophers retard succession in this manner (Weaver 1954; Foster and Stubbendieck 1980).

Microsite disturbance and succession have often been invoked as mechanisms allowing the coexistence of competing species (Paine 1966, 1969; Connell 1978; Huston 1979; Lubchenco 1978; Boorman and Fuller 1982). To test this hypothesis, Spearman rank correlations were obtained between 1981 gopher activity and the difference between the 1982 and 1981 species richness of each plot. These showed a highly significant positive dependence of the change in species richness on 1981 gopher activity ($r=0.47$, $n=36$, $P=0.003$). Linear regression of these data show that the plots experiencing the highest rate of gopher disturbance have, on average, between 3 and 4 more co-occurring species than those receiving the lowest rate of disturbance. The change in species richness is also highly positively correlated with the coefficient of spatial variation in light (Pearson $r=0.34$, $n=36$, $P=0.02$), suggesting that gopher disturbance may be indirectly allowing coexistence by increasing the spatial heterogeneity of light, which is a potentially limiting resource (Tilman 1982).

In total, the results of a three-year study of succession along an imposed N:Mg gradient suggest that there are strong effects of the imposed treatments on the species composition of the plant community. These effects have two components – a direct effect and an indirect effect propagated through other variables. The direct effect of resource competition among the major plant species seems to be displacement of annual plants by various species of perennial plants as nitrogen becomes increasingly available. However, the preference of plains pocket gophers for some of the dominant perennial species and the rapid growth of some annual species on gopher mounds tends to counteract the direct effects of the experimental manipulations, allowing the coexistence of more plant species in these plots. Because of effects propagated through an herbivore, soil nutrient supply rates have counteracting direct and indirect effects in this early successional community. If this proves to be a general phenomenon, the rate of change and species richness of early successional plant communities may be highly dependent on the local population densities of the dominant herbivores.

Acknowledgments. I thank members of the Youth Conservation Corps, the C.E.T.A. program, and summer field research assistants for their help. I thank Kathleen Zinnel for assistance with the computer data base, and John Tester, Nancy Huntly, Richard Inouye, Mark Stillwell and Kathleen Zinnel for their comments on this work. Kiezy Strauchon and Sue McEachern helped with the preparation of this manuscript. During the 1982 field season, this research was supported by National Science Foundation grant NSF-DEB 8114302.

References

- Boorman LA, Fuller RM (1982) Effects of added nutrients on dune swards grazed by rabbits. *J Ecol* 70:345–355
- Chase JD, Howard WE, Roseberry JT (1982) Pocket gophers. Geomyidae. In *Wild mammals of North America. Biology, management and economics*. Eds. Chapman JA, Feldhamer GA. The Johns Hopkins University Press, Baltimore. pp 239–255
- Connell J (1978) Diversity in tropical rainforests and coral reefs. *Science* 199:1302–1310
- Crocker RL, Major J (1955) Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *J Ecol* 43:427–448
- Foster M, Stubbendieck J (1980) Effects of plains pocket gophers (*Geomys bursarius*) on rangeland. *J Range Management* 33:74–78
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Amer Natur* 111:1169–1194
- Holt RD (1977) Predation, apparent competition and the structure of prey communities. *Theor Pop Biol* 12:197–229
- Huston M (1979) A general hypothesis of species diversity. *Amer Natur* 113:81–101
- Levine SH (1976) Competitive interactions in ecosystems. *Amer Natur* 110:903–910
- Lubchenco J (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Amer Natur* 112:23–39
- Miller RS (1964) Ecology and distribution of pocket gophers (Geomyidae) in Colorado. *Ecology* 45 (2):256–272
- Myers GT, Vaughan TA (1964) Food habits of the plain pocket gopher in eastern Colorado. *J Mammol* 45:588–598
- Olson JS (1958) Rates of succession and soil changes on southern Lake Michigan sand dunes. *Bot Gaz* 119:125–170
- Paine RT (1966) Food web complexity and species diversity. *Amer Natur* 100:65–75
- Paine RT (1969) A note on trophic complexity and community stability. *Amer Natur* 103:91–93
- Platt WJ (1975) The colonization and formation of equilibrium plant species associations on badger disturbance in a tall-grass prairie. *Ecol Monographs* 45:285–305
- Platt WJ, Weis IM (1977) Resource partitioning and competition within a guild of fugitive prairie plants. *Amer Natur* 111:479–513
- Solorzano L, Sharp J (1980) Determination of total dissolved nitrogen in natural waters. *Limnol and Oceanogr* 25:751–754
- Strickland JDH, Parsons TR (1972) A practical manual of seawater analysis. *Bull Fish Res Brd Can* # 167
- Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton, New Jersey
- Vandermeer JH (1980) Indirect mutualism: Variations on a theme by Stephen Levine. *Amer Natur* 116:441–448
- Weaver JE (1954) Stability, seasonal aspects, and other studies in prairie. In JE Weaver, *North American Prairie*. Johnsen, Lincoln, Nebraska, pp 118–148

Received May 10, 1983