

SMALL MAMMAL POPULATIONS OF AN OLD-FIELD CHRONOSEQUENCE: SUCCESSIONAL PATTERNS AND ASSOCIATIONS WITH VEGETATION

NANCY HUNTLY AND RICHARD S. INOUE

*Department of Ecology and Behavioral Biology, 318 Church St., S.E.,
University of Minnesota, Minneapolis, MN 55455*

Present address: Department of Biological Sciences, Idaho State University, Pocatello, ID 83209

ABSTRACT.—We sampled the small mammal fauna of 18 successional old-fields, aged 2–57 years since abandonment from agriculture, and examined patterns of diversity and abundance along successional and productivity gradients. Through time, vegetational standing crop, cover, litter, and plant species composition changed, but vegetational physiognomy did not; thus, we examined small mammal populations within a grassland chronosequence. Small mammal densities were low and were not strongly associated with successional time. Species richness and density, however, were strongly associated with vegetational standing crop and nitrogen content. *Peromyscus leucopus* densities were best correlated with variability in vegetation (*SD* vegetational biomass), whereas density of *Microtus pennsylvanicus* and *Sorex cinereus* were best correlated with vegetational nitrogen content. Overall, the data suggest that the diversity and abundance of small mammals were limited by nitrogen.

Populations of mammals change during vegetational succession and it has been suggested that changes in vegetational physiognomy are the major causes of changes in the assemblage of mammals (MacMahon, 1981). One might expect the abundance and species composition of small mammalian consumers to be influenced also by the availability of their resources, which changes through successional time. We examined the small mammal fauna of an old-field successional sequence on soils of low nitrogen content where there is a long period of change in vegetational species composition and productivity with correspondingly minor changes in vegetational physiognomy (Inouye et al., 1987b). We report patterns of change in the small mammal fauna during this 50+-year grassland chronosequence, and test for correlations of small mammal population density and diversity with vegetational abundance, nitrogen content, composition, and diversity.

METHODS

Study Site

The study was conducted at Cedar Creek Natural History Area (Cedar Creek) in east-central Minnesota, ca. 45 km N of Minneapolis. Cedar Creek is located on the Anoka County sand-plain, a 2,200 km² outwash deposited during the Wisconsin glaciation. Soils are sandy and contain little nitrogen; consequently, the process of secondary succession on abandoned farmland is slow. Vegetational changes during succession at Cedar Creek are reported in detail in Inouye et al. (1987b). Fields abandoned from agriculture are initially dominated by short-lived plants, including many introduced Eurasian species (e.g., *Berteroa incana*, *Crepis tectorum*, *Erigeron canadensis*, *E. strigosus*, *Aristida basiramea*). Through time, native perennial grasses and forbs characteristic of prairie (e.g., *Schizachyrium scoparium*, *Andropogon gerardi*, *Sorghastrum nutans*, and *Artemisia ludoviciana*, *Solidago rigida*, *S. graminifolia*) increase in abundance. Woody plants (e.g., *Rosa arkansana*, *Rubus* sp.) increase through time, but are small and uncommon more than 50 years after land has been abandoned. Previous studies of mammalian distributions along successional gradients have been on much richer soils (Beckwith, 1954; Hirth, 1959; Pearson, 1959) or in plantations (Atkeson and Johnson, 1979) where vegetation changed from grassland to woodland within ca. 15 years. In contrast, Cedar Creek has a long grassland chronosequence, in which productivity and species composition change markedly while vegetational physiognomy changes little.

Populations of small mammals and vegetational characteristics were measured in 18 old-fields that were abandoned between 1928 and 1982. Four parallel transects, 40-m long and 25-m apart, were located in each of 17 fields. In one field, Field 21, this spatial arrangement of transects was impossible, and one transect was perpendicular to the other three.

TABLE 1.—Number of captures of small mammals by species for 1984 and 1985.

Field	1984 Age	Microtus		Peromyscus		Sorex		Blarina		Zapus		Mus	
		'84	'85	'84	'85	'84	'85	'84	'85	'84	'85	'84	'85
41	2	0	0	3	5	0	0	0	0	0	0	1	0
39	9	0	0	3	2	0	0	0	0	0	0	0	0
40	12	0	0	0	0	0	4	0	0	0	0	0	0
4	13	1	0	5	6	0	1	0	0	0	1	0	0
24	16	0	0	3	6	0	2	0	0	0	0	0	0
44	23	1	1	0	0	1	4	0	0	0	0	0	0
53	23	0	0	0	1	0	1	0	0	0	0	0	0
47	25	0	1	0	0	0	1	0	0	0	0	0	0
21	27	8	0	0	2	13	7	1	1	0	3	0	0
26	27	6	0	0	5	0	0	1	0	0	0	0	0
70	29	0	0	0	1	0	0	0	0	0	0	0	0
76	32	0	2	5	7	2	2	0	0	0	1	0	0
77	32	0	2	0	4	0	5	0	0	0	0	0	0
5	37	1	0	2	0	2	0	0	0	0	1	0	0
27	37	1	1	0	0	3	3	0	0	0	0	0	0
45	41	0	1	0	1	1	1	0	0	0	0	0	0
32	43	0	4	0	0	1	2	0	0	0	0	0	0
72	57	1	0	1	4	1	2	1	0	0	0	0	0

Vegetation Sampling

Plant biomass and nitrogen content were estimated in 1984. In late July, the time of maximal standing crop, a 0.3-m by 2.0-m strip was clipped at ground surface at each of three points (10, 20, 30 m) along each transect. Samples were sorted to forbs, grasses, or litter, dried at 55°C, and weighed. Samples were then ground with a Wiley mill and analyzed for total tissue nitrogen content using a modified persulfate digestion (Tilman, 1983). Vegetational standing crop was calculated as the average biomass (g/m²) of grasses and forbs in each field. Vegetational nitrogen concentration (percent N by dry mass) was calculated as the average for all samples within a field, weighted by sample biomass. Vegetational nitrogen content (gN/m²) was calculated for each field as the average of the products of biomass and nitrogen concentration for each sample.

Small Mammal Sampling

We censused small mammal populations by trapping, using snap traps (48 × 100 mm Victor, Lititz Corp) baited with oatmeal and peanut butter. Each field was trapped for two periods of three consecutive nights each during late August and early September of 1984 and 1985 (six nights per field per year). Traps were located at 10-m intervals along the transects in each field, with one trap at 0, 10, 20, 30, and 40 m along each transect. Thus each field was trapped for 120 trap-nights each year over a 75-m by 40-m area (0.3 ha). The sum number of captures or species for the two years was used as the independent variable in analyses.

Gopher activity was measured as the number of mounds in six 20-m by 25-m areas formed by bisecting each transect and censusing mounds between it and the adjacent transect. In Field 21, where one transect was not parallel to the other three, two gopher mound counts were taken in areas of the same size, but centered on the offset transect. Average and standard deviation in mound density per 100 m² were calculated for each field from these mound counts.

We correlated total density, density by species, and species richness of small mammals with field age, field size, and several measures of vegetational quantity, quality, and variability. Because many of the independent variables were correlated, we used stepwise multiple regression as well as simple regression to identify the best predictors of mammalian abundance and diversity patterns. Both forward and backward stepwise regression procedures were used and, in all cases, gave the same results. Change in species composition of vegetation at Cedar Creek is sufficiently slow that correlation of vegetational measurements taken in 1984 with small mammal data taken in both 1984 and 1985 is warranted. Vegetational measurements taken in 1983 in these same fields were highly correlated with our 1984 data. Because Field 21 had transects in a slightly different configuration, and because it was near a field in which nitrogen fertilization experiments were done, we analyzed data both for all fields and omitting Field 21. In general, only analyses of *Microtus* abundance were significantly affected by inclusion or exclusion of Field 21.

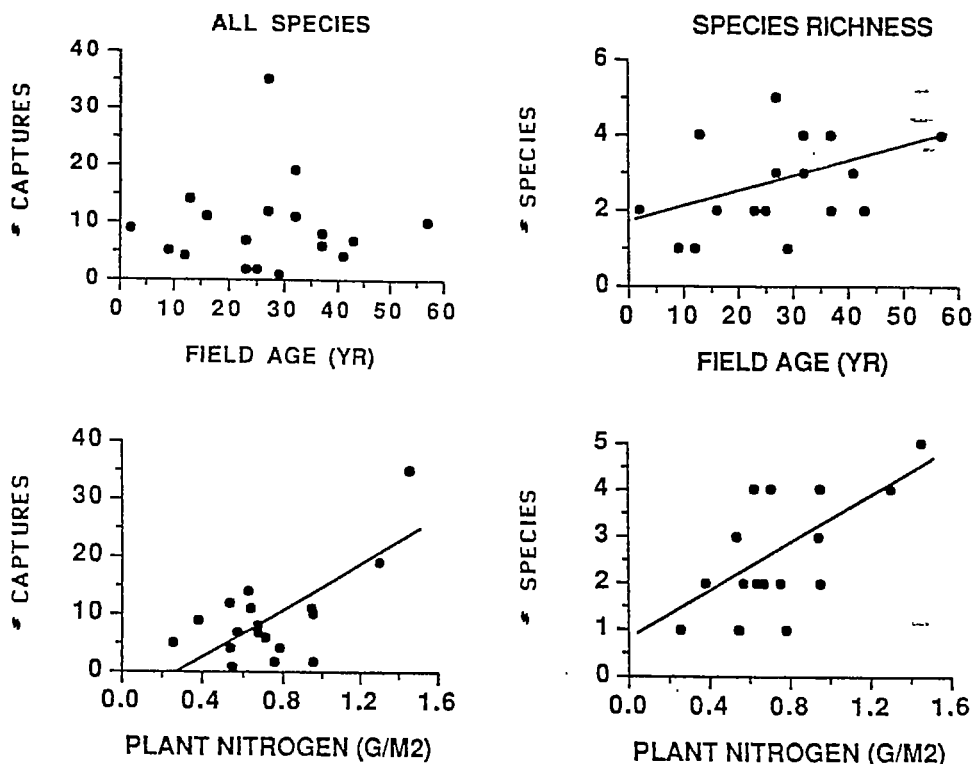


FIG. 1.—Total number of individuals and total number of species of small mammals captured for each field as functions of field age (years since abandonment from agriculture) and nitrogen content of vegetational standing crop (g/m^2).

RESULTS

Successional Patterns of the Vegetation

Previous sampling of percent cover by species along the transects in each field showed systematic changes in vegetational abundance and species composition with field age (Inouye et al., 1987b). Percent cover and species richness of vascular plants increased significantly with field age. Cover of annual plants decreased with field age, whereas cover of perennial grasses increased significantly. Average vegetational standing crop (VEG) ranged from 26.7 to 114.5 g/m^2 , and increased weakly with field age ($\text{VEG} = 47.78 + 0.68 \text{ age}$, $d.f. = 17$, $r = 0.38$, $P = 0.126$). Average nitrogen concentration varied from 0.68 to 1.23% for grasses and from 0.89 to 1.74% for forbs. For each group and for all vegetation, tissue nitrogen concentration was independent of field age (all $P > 0.8$). Vegetational nitrogen content (VEGN) also varied widely, from 0.53 to 1.45 g/m^2 , and tended to increase with field age ($\text{VEGN} = 0.54 + 0.007 \text{ age}$, $d.f. = 17$, $r = 0.34$, $P = 0.17$). Grass biomass increased weakly with field age ($y = 31.3 + 0.54 \text{ AGE}$, $r = 0.35$, $d.f. = 17$, $P = 0.15$), whereas forb biomass was independent of field age ($P > 0.5$). Litter biomass (LIT) tended to increase with field age ($\text{LIT} = 97.6 + 2.14 \text{ AGE}$, $d.f. = 17$, $r = 0.428$, $P = 0.076$).

Successional Patterns in Small Mammals

We caught individuals of six mammal species in our 18-field survey. In order of abundance, these were *Peromyscus leucopus*, *Sorex cinereus*, *Microtus pennsylvanicus*, *Zapus hudsonius*, *Blarina brevicauda*, and *Mus musculus* (Table 1). Total density was not linearly correlated with field age ($r = 0.020$, $d.f. = 17$, $P = 0.94$). Species richness (SR) increased weakly with field age ($\text{SR} = 1.6 + 0.04 \text{ age}$, $d.f. = 17$, $r = 0.405$, $P = 0.09$; Fig. 1). *Peromyscus leucopus* tended to

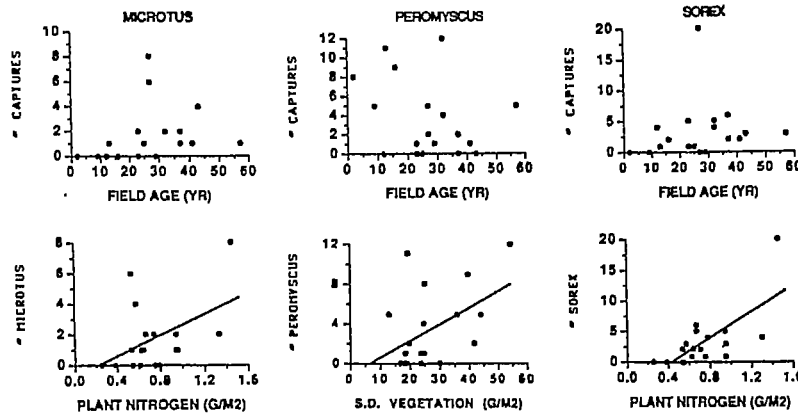


FIG. 2.—Total captures of *M. pennsylvanicus*, *S. cinereus*, and *P. leucopus* for each field as functions of field age (years since abandonment from agriculture) and the vegetational variable with which each was best correlated.

be found more often in younger fields; *Microtus* and *Sorex* were never found in fields less than 12 years old and were present in all fields greater than 30 years old. However, we found no significant linear or quadratic correlations of small mammal population densities with field age (Fig. 2; all $P > 0.2$). In contrast, both average (\bar{X}) gopher mound density and variability (SD) in mound density decreased significantly with field age ($\bar{X} = 20.9 - 0.4 \text{ AGE}$, $r = 0.54$, $d.f. = 17$, $P = 0.02$; $SD = 9.7 - 0.15 \text{ AGE}$, $r = -0.57$, $d.f. = 17$, $P = 0.01$; Fig. 3). The decrease in variability in mound density was not caused purely by the decrease in mound density, as coefficient of variation (CV) in mound density also decreased weakly with field age ($CV = 6.23 - 0.10$, $d.f. = 17$, $r = -0.42$, $P = 0.09$).

Associations of Small Mammals with Vegetation

Density and diversity of small mammals were significantly associated with vegetational variables which indexed resource levels. Total mammal density (N) was positively correlated with vegetational standing crop (VEG) ($N = -2.8 + 0.18 \text{ VEG}$, $r = 0.57$, $d.f. = 17$, $P = 0.01$) and with vegetational nitrogen content ($VEGN$) ($VEGN = -3.73 + 17.57 \text{ VEGN}$, $r = 0.67$, $d.f. = 17$, $P = 0.002$; Fig. 1). Species richness of small mammals also correlated positively with both standing crop and nitrogen content ($SR = 0.91 + 0.03 \text{ VEG}$, $r = 0.53$, $d.f. = 17$, $P = 0.02$; $SR = 0.72 + 2.56 \text{ VEGN}$, $r = 0.64$, $d.f. = 17$, $P = 0.004$).

Densities of several species also were correlated with vegetational standing biomass or nitrogen. *M. pennsylvanicus* density (Mp) increased with both variable ($Mp = -0.91 + 0.04 \text{ VEG}$, $r = 0.44$, $d.f. = 17$, $P = 0.07$; $Mp = -0.83 + 3.5 \text{ VEGN}$, $r = 0.46$, $d.f. = 17$, $P = 0.05$), but these correlations depended critically on inclusion of Field 21 (all $P > 0.6$ with Field 21 omitted). Because numerous studies report correlations of *Microtus* spp. density with plant cover (e.g., Birney et al., 1976; Eadie, 1953; Mossman, 1955; Tester and Marshall, 1961), we also correlated *M. pennsylvanicus* density with total vegetational percent cover, using data from a 1983 study in which cover was sampled along the same transects we used (Inouye et al., 1987b). There was no significant relationship between *Microtus* density and cover per se ($r = 0.26$, $d.f. = 17$, $P = 0.29$). *S. cinereus* density (Sc) was significantly positively correlated with both vegetational measures ($Sc = -3.4 + 0.1 \text{ VEG}$, $d.f. = 17$, $r = 0.54$, $P = 0.02$; $Sc = -4.9 + 11.0 \text{ VEGN}$, $d.f. = 17$, $r = 0.72$, $P < 0.001$). These two correlations were most significantly altered when Field 21 was omitted (both $P < 0.05$). Density of *P. leucopus* (Pl) was independent of both measures of plant productivity (both $P > 0.5$, $d.f. = 17$), but was significantly correlated with variability in vegetation (standard deviation in vegetational biomass, $SD\text{VEG}$) ($Pl = -1.03 + 0.17 \text{ SDVEG}$, $r = 0.49$, $d.f. = 17$, $P = 0.04$). Captures of the other 3 species were too infrequent for analysis.

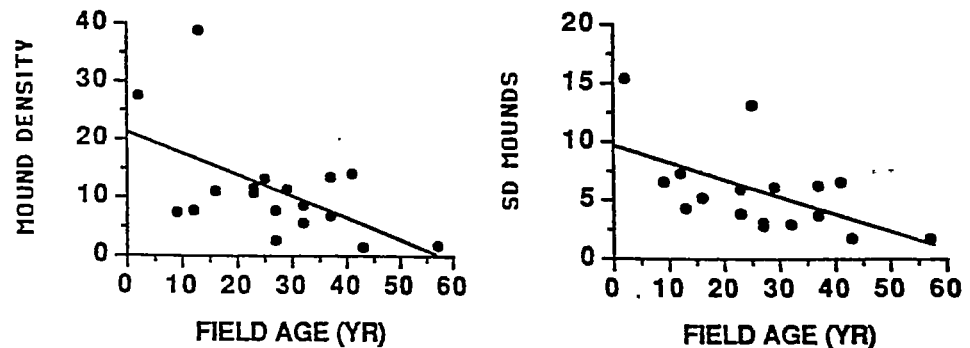


FIG. 3.—Mean pocket gopher mound density (number/100 m²) and standard deviation of the mean density as functions of field age (years since abandonment from agriculture).

Gopher mound density was marginally negatively correlated with vegetational biomass and nitrogen content ($\bar{X} = 21.6 - 0.16 \text{ VEG}$, $d.f. = 17$, $r = -0.43$, $P = 0.07$; $\bar{X} = 19.4 - 11.1 \text{ VEGN}$, $d.f. = 17$, $r = -0.37$, $P = 0.14$). Standard deviation of density also was only weakly related to vegetational measures ($SD = 8.7 - 0.05 \text{ VEG}$, $r = -0.32$, $d.f. = 17$, $P = 0.19$; $SD = 8.4 - 3.8 \text{ VEGN}$, $d.f. = 17$, $r = -0.31$, $P = 0.2$).

Because vegetational variables tended to be correlated, we used stepwise multiple regressions to determine which factors were best correlated with diversity and abundance of the mammalian fauna. We used measures of vegetational quantity (VEG), vegetational quality (VEGN), field size (hectares, HA), field age (AGE), and vegetational variability (SDVEG) in one set of tests with abundance of the 3 most common species, total abundance of small mammals, and species richness. Vegetational nitrogen proved to be an important predictor of all except *P. leucopus* (Table 2). Omitting Field 21 was critical only to *M. pennsylvanicus*, which was not significantly associated with any of the 5 variables when Field 21 was omitted ($P > 0.2$). Species richness and total density were about equally correlated with SDVEG and VEGN when Field 21 was omitted. For each, correlation was slightly greater for SDVEG (species richness: F -to-remove = 4.95 vs 4.68, $P = 0.04$ vs 0.05; total density: F -to-remove = 10.9 vs 3.01, $P = 0.005$ vs 0.01).

We also tested association of *Microtus* density with several other vegetational variables. The best correlation with *Microtus*, considering all data, was with forb biomass (FORB, g/m²) ($M_p = -0.7 + 0.12 \text{ FORB}$, $r = 0.74$, $d.f. = 17$, $P < 0.001$); this relationship did not depend critically on Field 21 ($P = 0.07$, omitting Field 21). *Microtus* density was also correlated with forb nitrogen content ($r = 0.58$, $d.f. = 17$, $P = 0.01$), but this correlation disappeared when Field 21 was omitted ($P > 0.7$). There was no significant correlation with grass biomass or nitrogen content or with the nitrogen concentration of any vegetational component (all $P > 0.3$). Stepwise regression using forb and grass biomass and nitrogen content showed only forb biomass to be correlated with *Microtus* density.

DISCUSSION

We found no strong associations between field age and total density, density of any species, or diversity of small mammals. Our data show similar qualitative patterns of occurrence in a successional sere to those reported previously in richer areas (Atkeson and Johnson, 1979; Beckwith 1954; Hirth 1959; Pearson, 1959), and do not depend critically on the establishment of woody vegetation. *Peromyscus leucopus* was most common in young fields, and *Microtus pennsylvanicus* and *Sorex cinereus* appeared beginning at about 20 years.

Both average density and variance in density of gopher mounds decreased significantly with field age, suggesting that either the population density or the behavior of pocket gophers changes systematically with field age. Several interpretations of the data are possible, and direct enumeration of gophers and determination of their foraging behavior are necessary to distinguish between these. Pocket gopher densities may in fact be lower in older fields. Alternatively,

TABLE 2.—Best predictors of small mammal density, diversity, and activity, based on stepwise multiple regression analyses, using 1984 age (AGE84), field size (HECTARES), average vegetational biomass (VEG), average vegetational nitrogen (VEGN), and standard deviation in vegetational biomass (SDVEG) as independent variables.

	Significant factors	Partial correlation coefficient	F-to-remove	Coefficient P	r ²	P
Species richness	VEGN	2.56	10.93	0.004	0.37	0.004
Total density	AREA	-0.83	5.06	0.04		
	VEGN	15.94	12.57	0.003	0.53	0.001
<i>Sorex</i>	VEG	-0.19	5.49	0.03		
	VEGN	25.56	14.84	0.002	0.60	0.001
<i>Microtus</i>	VEGN	3.46	4.40	0.05	0.17	0.05
<i>Peromyscus</i>	AGE	-0.15	6.18	0.03		
	SDVEG	0.22	10.33	0.006	0.39	0.09
Mound \bar{x}	AGE	-0.36	6.67	0.02	0.25	0.02
Mound SD	AGE	-0.15	10.36	0.006		
	HECTARES	0.44	5.92	0.028	0.45	0.004

individual gophers may simply produce fewer mounds in older fields, owing to higher available plant biomass, plant root biomass (R. McKane, personal communication) or the existence of established tunnel systems. The decrease in variance of mound density, i.e., the more even distribution of mounds in older fields, is particularly intriguing. Reichman et al. (1982) found that burrow length was higher in an area of lower plant biomass, but that burrow area and spacing between burrows were the same between sites. The decreased variance in mound density with field age may result from increasingly even exploitation of the food resources within individual gopher territories through time. This intriguing pattern has implications for the impact of gophers on plants (Inouye et al., 1987a) and warrants further investigation.

Our data support the suggestion of MacMahon (1981) that successional changes in vegetation cause successional changes in mammals, but also support the hypothesis that plant resources are important to the diversity, abundance, and species composition of the small mammal fauna. Both density and diversity of small mammals were correlated with measures of primary productivity, and were best correlated with vegetational nitrogen content, the amount of nitrogen present in standing live vegetation. This suggests that small mammal density and diversity are limited by resources, particularly by nitrogen (protein), which enters the food chain via primary production.

The data also suggest that resources, particularly nitrogen, are limiting to populations of voles (herbivores) and, indirectly, shrews (insectivores). This interpretation is supported by experimental nitrogen fertilizations in several fields at Cedar Creek. After beginning to fertilize vegetation in 3 fields with nitrogen, populations of both *Microtus* and *Sorex* increased significantly. Previous studies of *S. cinereus* in Minnesota have found no significant vegetational correlates of density (Iverson et al., 1967; Mierotto, 1967; Tester and Marshall, 1961). Perhaps vegetational abundance better reflects abundance of limiting invertebrate food resources for shrews in the low productivity environment of Cedar Creek (Inouye et al., 1987b) than in richer habitats.

We did not quantify the diet of *M. pennsylvanicus*, but our data suggest that forbs were limiting, in agreement with reports of Neal et al. (1973) and Meserve and Klatt (1985) that *M. pennsylvanicus* preferentially consume forbs. Although our data are in agreement with reports that *M. pennsylvanicus* and other microtines are associated with areas of high vegetational cover, they suggest a larger direct role of resources than often has been inferred. Our findings are in agreement with a strong association of *M. pennsylvanicus* with food resources, as reported by Batzli (1966), Cole and Batzli (1979), and Batzli et al. (1983) for other microtines. The best correlates of *Microtus* population density were vegetational nitrogen content or forb biomass, and these correlations were stronger than with biomass or cover of plants.

ACKNOWLEDGMENTS

This research was supported by NSF #8111403 to D. Tilman and J. Tester for Long-Term Ecological Research. We thank Cliff Maddox for plant tissue analysis, Robert Buck for statistical assistance, Elmer Birney for advice on distinguishing *Peromyscus leucopus* and *P. maniculatus bairdii* at Cedar Creek, and John Tester for comments on the manuscript.

LITERATURE CITED

- ATKESON, T. D., AND A. S. JOHNSON. 1979. Succession of small mammals on pine plantations in the Georgia piedmont. *Amer. Midland Nat.*, 101:385-392.
- BATZLI, G. O. 1968. Dispersion patterns of mice in California annual grassland. *J. Mamm.*, 49:239-250.
- BATZLI, G. O., F. A. PITELKA, AND G. N. CAMERON. 1983. Habitat use by lemmings near Barrow, Alaska. *Holarctic Ecol.*, 6:255-262.
- BECKWITH, S. L. 1954. Ecological succession on abandoned farmlands and its relationship to wildlife management. *Ecol. Monogr.* 24:349-376.
- BIRNEY, E. C., W. E. GRANT, AND D. D. BAIRD. 1976. Importance of cover to cycles of *Microtus* populations. *Ecology*, 57:1043-1053.
- COLE, F. C., AND G. O. BATZLI. 1979. Nutrition and population dynamics of the prairie vole, *Microtus ochrogaster*, in central Illinois. *J. Anim. Ecol.*, 48:455-470.
- EADIE, W. R. 1953. Responses of *Microtus* to vegetative cover. *J. Mamm.*, 34:263-264.
- HIRTH, H. F. 1959. Small mammals in old field succession. *Ecology*, 40:417-425.
- INOUE, R. S., N. J. HUNTLY, D. TILMAN, AND J. R. TESTER. 1987a. Pocket gophers (*Geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east-central Minnesota. *Oecologia*, 72:178-184.
- INOUE, R. S., N. J. HUNTLY, D. TILMAN, J. R. TESTER, M. STILLWELL, AND K. C. ZINNEL. 1987b. Old field succession on a Minnesota sand plain. *Ecology*, 68:12-26.
- IVERSON, S. L., R. W. SEABLOOM, AND J. M. HNATIUK. 1967. Small mammal distributions across the forest-prairie transition of Minnesota and North Dakota. *Amer. Midland Nat.*, 78:188-197.
- MACMAHON, J. A. 1981. Successional processes: comparisons among biomes with special reference to probable roles of and influences on animals. Pp. 277-304, in *Forest succession* (D. C. West, H. H. Shugart, and D. B. Botkin, eds.). Springer-Verlag, New York, 517 pp.
- MESERVE, P. L., AND B. J. KLATT. 1985. Evidence for noncycling populations and the importance of immigration in voles inhabiting an Illinois tallgrass prairie. *Amer. Midland Nat.*, 113:255-270.
- MIEROTTO, R. R. 1967. The distribution of small mammals across a prairie-forest ecotone. Unpubl. Ph.D. dissert., Univ. Minnesota, 81 pp.
- MOSSMAN, A. S. 1955. Light penetration in relation to small mammal abundance. *J. Mamm.*, 36:564-566.
- NEAL, B. R., D. A. PULKINEN, AND B. D. OWEN. 1973. A comparison of faecal and stomach contents analysis in the meadow vole (*Microtus pennsylvanicus*). *Canadian J. Zool.*, 51:715-721.
- PEARSON, P. G. 1959. Small mammals and oldfield succession on the piedmont of New Jersey. *Ecology*, 40:249-255.
- REICHMAN, O. J., T. G. WHITHAM, AND G. A. RUFFNER. 1982. Adaptive geometry of burrow spacing in two pocket gopher populations. *Ecology*, 63:687-695.
- TESTER, J. R., AND W. H. MARSHALL. 1961. A study of certain plant and animal interrelations on a native prairie in northwestern Minnesota. *Occasional Papers, Minnesota Mus. Nat. Hist.*, 8:1-51.
- TILMAN, D. 1983. Plant succession and gopher disturbance along an experimental gradient. *Oecologia*, 60:285-292.

Submitted 30 April 1986. Accepted 2 October 1986.