VEGETATIONAL GRADIENTS AND PROXIMITY TO WOODCHUCK (*MARMOTA MONAX*) BURROWS IN AN OLD FIELD

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Comparison of vegetation near and distant from 10 woodchuck (*Marmota monax*) burrows in a diverse field 6 years old revealed differences at both community and species levels. Total plant cover increased with distance from burrows. Species-richness was low near and distant from burrows and relatively high at intermediate distances, a result consistent with the intermediate disturbance hypothesis. Horsenettle (*Solanum carolinense*), Kentucky bluegrass (*Poa pratensis*), and fescue (*Festuca elatior*) increased, and orchardgrass (*Dactylis glomerata*) decreased with distance from burrows. While woodchucks strongly affect only a small fraction of the field (ca. 2%), they are important agents in creating a vegetational mosaic and in creating source areas for species of colonizing plants.

Key words: *Marmota monax,* burrows, disturbance, herbivory, plant communities, vegetation, woodchucks

Mammalian herbivores affect the growth, recruitment, and mortality of plants over gradients in time and space. A combination of herbivory (Bartholomew, 1970; Reichman and Jarvis, 1989) and physical disturbance of the soil or plants can create localized areas of impact embedded in a matrix of relatively undisturbed vegetation (e.g., Bradshaw and Goldberg, 1989; del Moral, 1984; Hobbs and Mooney, 1985; Koide et al., 1987). Such localized disturbances can increase diversity of plant species and contribute directly to the mosaic nature of vegetation (Huntly, 1991).

del Moral (1984) found that grazing and earth-moving by the Olympic marmot (*Marmota olympus*) reduced the abundance of common species of plants and increased diversity near but not distant from burrows. Merriam and Merriam (1965) found densities of grass and forbs and concentrations of soil nitrogen to decrease with distance from woodchuck burrows. Swihart (1991) suggested that shifts in the ratio of grass to forbs with distance from woodchuck burrows in hayfields was caused by two factors: differential consumption of plants and contrasting responses of forage and non-forage species to gradients in soil nitrogen.

Because of their relatively large size (2–5 kg), extensive burrow systems, and densities of ≤2.19 animals/ha, woodchucks (*Marmota monax*) have the potential of strongly affecting local vegetation (Swihart, 1991). Woodchucks spend more time foraging near burrows than farther away (Thompson, 1971); hence, their impacts on vegetation likely will be greatest near burrows. In fact, the standard method of quantifying effects of woodchucks has been to measure features of plants and soil at different distances from burrows assuming that their impact is inversely related to distance (Merriam and Merriam, 1965; Swihart, 1991; Thompson, 1971). A variety of methods have shown preferred plants to include dicots such as dandelion (*Taraxacum officinale*), common plantain (*Plantago major*), clover (*Trifolium* sp.—Swihart, 1990, 1991) and some grasses like *Poa* sp. (Grizzell, 1955; Hamilton, 1934; Twichell, 1939).

We report the effects that woodchucks have on the plant community of old field in

Virginia. While many studies have examined succession in old fields, few have examined the influence of mammalian herbivores as agents of vegetational change (Bowers, 1993). Other studies have examined effects of woodchucks at the level of plant communities, but they have focused on later rather than earlier seral stages or on agricultural settings that are essentially monocultures or are highly managed (Merriam and Merriam, 1965; Swihart, 1991). It is possible that effects of woodchucks on human-managed systems (orchards, pastures, and crop fields) or on older successional seres may differ from that of a dynamic early successional, unmanaged field. For example, Inouye et al. (1987) found pocket gopher mounds in older successional fields to support plant associations that differed from the field as a whole, but vegetation on and away from mounds in younger successional seres was not different. Armesto and Pickett (1985) provided a mechanistic explanation for such results; early in succession, turnover in species is rapid and may quickly erase any effect of disturbance. Later in succession, however, turnover of species is slower, inhibitory effects of dominant plants on the rest of the community are more pronounced, and the potential for large disturbance effects are enhanced.

MATERIALS AND METHODS

We were interested in measuring an overall effect that subsumed herbivory, nutrient addition, and physical disturbance (Huntly, 1991) rather than identifying the exact pathway(s) by which woodchucks affected vegetation. The null hypothesis, that vegetation and soil parameters would not differ along a gradient of increasing distance from burrows, was used to test the notion that woodchucks have greater effects near and weaker effects at some distance from burrows (Merriam and Merriam, 1965; Swihart, 1991; Thompson, 1971).

Our study was conducted in July 1991 in a 20-ha old field at the Blandy Experimental Farm, Clarke Co., Virginia. The field had been grazed by cattle with yearly mowings from the mid-1960s to 1986. In 1991, the field had not been under agricultural management for the past 5 years and was comprised of a diverse mix of early successional herbs and colonizing woody plants (Bowers, 1993).

We mapped all woodchuck burrows in the field. From the set of total burrows ($n = 43$), we randomly selected 10 for study with the constraint that each burrow be ≥ 10 m from its nearest neighbor. For each of the 10 burrows, we established transects in the four cardinal directions along which 0.25-m² (50- by 50-cm) quadrats were systematically placed at 0, 1, 2, 4, 8, and 16 m from main burrow entrances. Coverage by plant species within each quadrat was determined by visual comparison with reference disks of known percentages. Identification and taxonomy of plants follows Strausbaugh and Core (1970). We also collected soil cores (0.25 1; from the top 10-cm layer) at 0, 1, 2, 4, 8, and 16 m distance along one randomly selected transect at each burrow. Soil samples were weighed immediately after collection and dried at 32°C for 72 h. An estimate of percent soil moisture (dry : wet weight, g) was then calculated.

Repeated-measures analysis of variance (RMA) was used to test the hypothesis that plant cover was homogeneous over the six distance categories. Each burrow was considered as a subject; plant cover, averaged over transects for each distance, was the repeated-measures factor.

We used repeated-measures ANOVA to examine cover of individual plants, total coverage of plants, and species richness (the number of species of plants). While we restricted our analyses of species to the 10 most abundant plants, we included all species in analyses of total coverage of plants and species richness. All variables were normalized by arcsine transformation prior to analysis.

We also used trend analysis (Day and Quinn, 1989; Keppel, 1982) to examine relationships between the independent variable (distance) and the dependent variables (species cover, total cover, soil moisture, species richness). Trend analysis uses sums of squares to describe trends in terms of linear, quadratic, or cubic functions and is useful as a post hoc test to examine how abundance varies with distance in cases where earlier repeated-measures ANOVA were significant ($P \leq 0.05$).

Soil moisture also was analyzed according to the repeated-measures ANOVA. Associations

TABLE 1.—*The 10 most abundant species of plants in the field, their life-growth forms (h = herbaceous, w = woody, g = grass; p = perennial, b = biennial), and their mean percent cover (±1 SE) at distances of 0, 1, 2, 4, 8, and 16 m from burrows.*

Species[a]	Life-growth[a] form	Distance from burrows (m)					
		0	1	2	4	8	16
Allium vineale	hp	0.7	0.6	0.2	0.4	1.3	0.6
		(0.5)	(0.5)	(0.2)	(0.2)	(0.6)	(0.5)
Arctium minus	hb	12.0	4.7	1.6	0.0	0.3	0.0
		(8.5)	(2.9)	(1.4)	(0.0)	(0.3)	(0.0)
Carduus acanthoides	hb	9.5	10.1	7.6	4.7	4.5	4.5
		(3.1)	(2.5)	(21.0)	(2.1)	(13.0)	(2.0)
Celastrus scandens	wp	9.2	5.8	7.6	13.3	14.4	12.4
		(9.0)	(4.2)	(3.0)	(5.1)	(5.7)	(4.0)
Dactylis glomerata	gp	7.0	10.4	13.4	3.2	5.1	1.7
		(2.3)	(3.4)	(3.9)	(1.7)	(2.4)	(0.7)
Festuca elatior	gp	6.8	17.4	25.9	31.3	25.3	38.5
		(4.9)	(4.5)	(6.9)	(5.7)	(7.0)	(6.9)
Poa pratensis	gp	0.5	7.7	11.6	20.7	31.7	20.3
		(0.5)	(3.6)	(4.0)	(6.5)	(4.7)	(5.1)
Solanum carolinense	hp	0.0	2.3	2.5	3.8	4.3	3.0
		(0.0)	(0.8)	(0.8)	(0.7)	(0.9)	(0.9)
Solidago canadensis	hp	0.0	0.5	1.4	2.4	1.3	2.9
		(0.0)	(0.5)	(1.3)	(2.3)	(0.7)	(2.5)
Toxicodendron radicans	wp	0.0	0.1	1.7	3.3	1.7	1.3
		(0.0)	(0.1)	(1.1)	(2.0)	(1.5)	(1.3)

[a] Taxonomy and life-growth from Strausbaugh and Core (1970).

between total species cover (arcsine transformed) and soil moisture were tested using ANOVA.

We explicitly tested the ANOVA assumptions of multivariate normality, homoscedasticity, and random and independent sampling. Multivariate normality was met by adjusting the degrees of freedom according to Huynh and Feldt (1976).

RESULTS

We sampled vegetation and measured soil moisture for 23% (10 of 43) of the burrows in the field. The 10 most abundant species of plants (Table 1) accounted for ca. 87% of the total plant coverage. A total of 33 species of plants were censused.

Repeated-measures ANOVA showed that the abundance of four of the 10 common species of plants varied with distance from burrows (Table 1). *Solanum carolinense* and *Poa pratensis* were rare near burrows, relatively abundant at intermediate distances, and decreased in abundance with distance from burrows ($F = 9.35$; $d.f. = 5,45$; $P < 0.05$; and $F = 13.83$; $d.f. = 5,45$; $P < 0.01$, respectively). By trend analysis, *S. carolinense* and *P. pratensis* increased linearly with distance from burrows ($F = 11.9$; $d.f. = 1,45$; $P < 0.01$; and $F = 15.6$; $d.f. = 1,45$; $P < 0.05$, respectively). *Dactylis glomerata* was most abundant near burrows and decreased quadratically with distance ($F = 3.2$; $d.f. = 5,45$; $P < 0.05$; and $F = 16.0$; $d.f. = 1,45$; $P < 0.05$; repeated-measures ANOVA and trend analysis, respectively). *Festuca elatior* occurred at mean abundances of ca. 7% near burrows and increased 540% in a cubic-linear fashion to a high of 38% at 16-m distances ($F = 5.9$; $d.f. = 5,45$; $P < 0.01$; and $F = 27.4$; $d.f. = 1,45$; $P < 0.01$). There also was a trend for *Arctium minus* to decrease with distance from burrows ($F = 2.21$; $d.f. = 5,45$; $0.05 < P < 0.10$).

Total cover by plants was relatively low near burrows, and increased 167% to an asymptote of ca. 81% 4 m from burrow en-
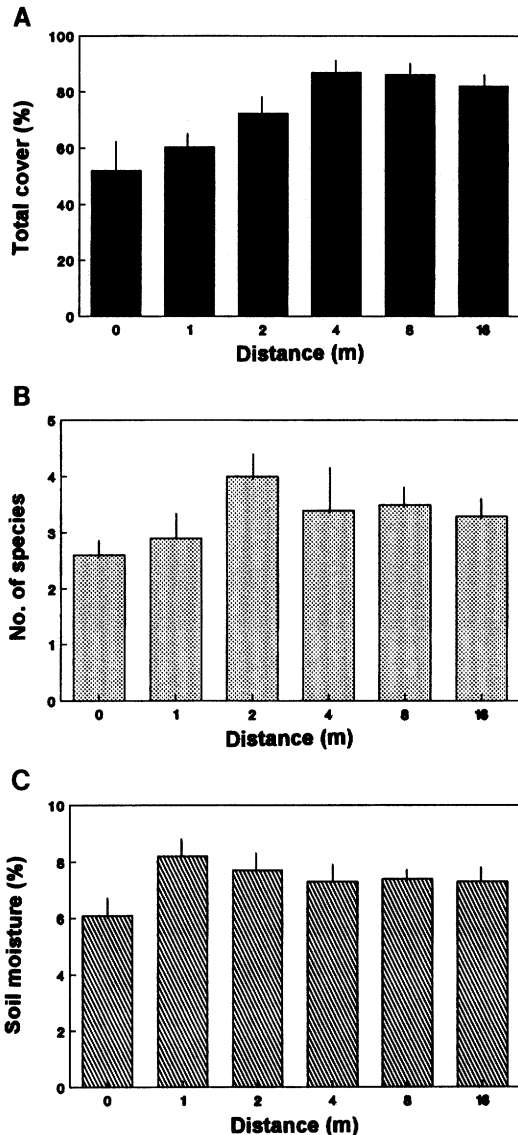
A

B

C

FIG. 1.—Variation in A) total percent plant cover, B) species (plants) richness, and C) percent soil moisture with distance from woodchuck burrows. Standard errors also are given.

trances (F = 6.3; $d.f.$ = 4,40; P < 0.01; a significant cubic trend, F = 8.6; $d.f.$ = 1,45; P < 0.05; Fig. 1). Number or richness of plant species was highest at intermediate distances (2 m from burrows) and lower near and at some distance from burrows (F = 2.38; $d.f.$ = 5,45; P < 0.05; Fig. 1). Soil moisture showed no significant effect with

distance (F = 1.81; $d.f.$ = 5,45; P > 0.05; Fig. 1). Further, regression analysis showed that only 0.9% of the variation in total cover by plants could be explained by soil moisture (F = 0.51; $d.f.$ = 1,58; P > 0.05). Calculations a posteriori for the repeated-measures ANOVA showed that power to detect distance effects was ca. 50% (with a type I error of 0.05 and a size of effect of 0.40—Cohen, 1991).

DISCUSSION

Woodchucks have the potential of affecting the plant community at several spatial scales. Because woodchucks spend more time near burrows and forage outwards, they create a localized disturbance gradient over which herbivory, nutrient enrichment, and physical disturbance of both soil and plants vary. That richness of plant species was highest at intermediate distances and lower near and distant from burrows is consistent with the intermediate-disturbance hypothesis (Connell, 1975). More specifically, this hypothesis predicts that both high and low frequencies of disturbance may create situations of low diversity of species, while more intermediate disturbance regimes may promote high diversity of species.

Bowers (1993) and Zeevalking and Fresco (1977) also found diversity of plant species to peak under intermediate levels of mammalian herbivory. Our interpretation of the results is that activity of woodchucks near burrows reduced the degree to which competitively dominant plants suppressed other less aggressive plants in the field. Specifically, species of plants that Bowers (1993) found to be frequently grazed reached highest levels of abundance at some distance from burrows; in several instances, these were tall and fast-growing, clonal, and highly competitive plants (*Poa, Festuca*). Close to burrows, however, species of plants tended to be mostly unpalatable, early successional, early colonizing annual and biennial species (*Arctium, Carduus*). At distances of less than ca. 4 m,

there appeared to be a shift from plants that were good competitors to plants that were good colonizers. Species (*Dactylis, Solanum*) that reached highest abundance at intermediate distances appear to be relatively unpalatable, relatively resistant to disturbance, but also may have lower colonizing ability than those closer to burrows. The diverse plant associations at intermediate distances appear to include a representative mix of species with different abilities, palatabilities, and life histories.

A number of other studies have documented similar distance-related patterns around burrows. For example, Inouye et al. (1987) suggested that the abundance and composition of plants near gopher burrows was influenced by selective grazing. Merriam and Merriam (1965) found alfalfa stems to increase 289% with distance from woodchuck burrows (1.28–3.71/m²). Swihart (1991) found that diversity of plant species was higher near burrows and lower at some distance in one hayfield, but peaked at 5 m distances in another. Nore generally, Armesto and Pickett (1985) found that general disturbances increased the diversity of plants in an old field.

By suppressing competitively superior plants close to burrows, woodchucks create opportunities for ruderal plants. These are the annual and biennial, early successional species that disperse well, reproduce vigorously, and generally are adapted to live in disturbed habitats (Grubb, 1977). Many ruderal species also have the ability of responding in dramatic fashion to the elevated nutrient levels at burrows (Inouye et al., 1987). Seed production of these short-lived species under reduced competition from dominants and elevated nutrient levels should be particularly high near burrows. Reichman and Smith (1985) suggested that increased vegetative growth around gopher mounds was due to competitive release of plants that were suppressed at some distance. Thompson (1971) found plant productivity and soil phosphorous were higher near than away from excavated burrows,

and Swihart (1991) found that crude protein of *Dactylis* was higher near burrows than 15-m distant.

By creating localized disturbances, woodchucks probably influence the larger-scale patterns of vegetation. Subsequent live trapping in 1992 showed that the density of woodchucks in the study field (ca. 1 animal/ha) approached the mid-range of densities collectively reported by Ferron and Ouellet (1988), Grizzell (1955), Swihart (1992), and Thompson (1971). The results presented here suggest that the strongest effects of woodchucks are limited to areas within a 4-m radius of burrows, a result comparable to the estimate of a 5-m radius by Swihart (1991) for two hayfields. On one hand, disturbance by woodchucks seems inconsequential when compared to the total area of the field. Specifically, we estimate that ca. 2% of the field is directly and strongly impacted by woodchucks—assuming four burrows/ha and an effect radius of 4 m. However, these small areas of disturbance, with high levels of nutrients and low levels of competition, represent important sites for seed production of ruderal plant species (Grubb, 1977). Considering that the availability of propagules can influence patterns of vegetation (Marks and Mohler, 1985) and sites near burrows might function as source habitats (Pulliam, 1988) for seed production of early successional species, it is likely that the overall dynamics and diversity of plants in a field may vary depending on whether woodchucks are present or absent (Swihart, 1991).

The unique plant communities and certain life history traits of plants associated with mammalian burrow systems have been recognized in other studies (Platt, 1975). Comparable studies examining effects of woodchucks on overall patterns of vegetation have been limited because they have focused on homogeneous, planted fields (Merriam and Merriam, 1965) or highly managed landscapes (Swihart, 1991). The present study suggests that woodchucks create a disturbance gradient that may con-

tribute to overall diversity of plant species in more natural systems both in space and over time.

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