

VOLE-DRIVEN SUCCESSION IN EXPERIMENTAL WET-PRAIRIE RESTORATIONS

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Abstract. A challenge of experimental restoration is to determine the reasons why restored communities develop as they do. Divergent successions in plantings of 16 tallgrass prairie species sown in equal densities in Wisconsin (USA) revealed strong effects of vole (*Microtus pennsylvanicus*) herbivory on vegetation initially protected for an establishment period of over 24 months, by which time all principal species were flowering and fruiting. Half of the plots were then subjected to 48 months of vole access. An otherwise common legume (*Desmodium canadense*) and grass (*Elymus virginicus*) were all but eliminated in 48 months of exposure: combined cover under protection was $43 \pm 6\%$, but plummeted to $<1\%$ cover when voles had access. Dicots not eaten by voles (*Pycnanthemum virginianum*, *Rudbeckia subtomentosa*) averaged $40 \pm 7\%$ cover where voles were excluded, but $68 \pm 8\%$ after 48 months of vole access. Repeated-measures analyses of variance revealed that net decreases (*D. canadense*, *E. virginicus*) or increases (*P. virginianum*, *R. subtomentosa*) in cover masked nonlinear effects reflecting vole-driven transient dynamics during divergent successional processes. Diversities diverged for three years after vole access; a dramatic convergence of diversities in the fourth year leaves grossly similar communities with similar numbers of species and similar levels of equity, but distinctly different species compositions. Vole-mediated effects on vegetation resemble those likely to occur in native prairies, without the catastrophic changes in cover and standing crop caused by rodents that occurred in some previous efforts of this research program.

Key words: biodiversity; ecology; experimental restoration; herbivory; *Microtus*; prairie; succession; vole; Wisconsin.

INTRODUCTION

A challenge in experimental restoration is to determine how mammalian herbivores shape grassland vegetation (Howe 1999a). Mammals increase or decrease diversity, lower standing crop, or leave both unchanged but alter species composition (Huntly 1991). Best understood are the effects of such large grazers as bison, cattle, and large antelope that preferentially eat dominant grasses and release subdominant competitors, with the net effect of increasing diversity (e.g., Belsky 1992, Proulx and Mazumder 1998, Knapp et al. 1999), and smaller ungulates that feed on young or subdominant foliage, potentially decreasing diversity (McNaughton 1985). In native prairie, herbivory interacting with fire increases diversity, lowers productivity, and may preclude long-term equilibria or increase their complexity and variety (Collins 1987, Milchunas and Laurenroth 1993, Proulx and Mazumder 1998). Massive impacts in grazing lawns near watering sites, on migration routes, and near wallows contrast with suitable forage that is untouched or lightly grazed by large ungulates (Senft et al. 1987, Bailey et al. 1996). Un-

gulate effects on vegetation are varied and potentially enormous, but localized in space and time.

Compared to ungulates, influences of smaller but ubiquitous mammalian herbivores are less appreciated, despite a venerable history of investigation (Pickworth Farrow 1917, Gill 1992, Hulme 1996). Selective herbivory of herbaceous vegetation by rabbits (Pickworth Farrow 1917) and voles (Batzli and Pitelka 1970), of seeds by kangaroo rats (Brown and Heske 1990), and of tree seedlings by voles (Ostfeld et al. 1997, Manson et al. 2001), alter species composition and diversity of English heath, desert grassland, coastal grassland, and hardwood forest, respectively. In central North America, Clay and Holah (1999) find that aversion by voles to a toxic fungus-infected grass (*Fescue arundinacea*) may result in over dominance of that species, resulting in low grassland diversity. In East Africa, Keesing (2000) finds that small mammalian herbivores and granivores (“cryptic consumers”) limit vegetation enough to limit ungulate populations, and vice versa. Ubiquitous effects of small mammals may be unnoticed from sheer familiarity; few places lack rabbits and rodents that have the potential to shape contemporary plant communities. Effects of small mammals may be substantial, and much more widespread than ungulates, especially in human-altered habitats where ungulates are rare.

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PLATE 1. Representative plots in August 2002. (Left) Plot to which voles had been admitted for 48 months, following 26 months of enclosure, characterized by a dense stand of perennial black-eyed Susan (*Rudbeckia subtomentosa*) and some taller rosinweed (*Silphium integrifolium*). (Right) Plot from which voles had been excluded since planting, 74 months earlier, characterized by rye grass (*Elymus virginicus*) and tick-trefoil (*Desmodium canadense*), with scattered black-eyed Susan and rosinweed. Aluminum flashing on the fence shows through vegetation in the background of each plot. Photo credit: H. F. Howe.

Restoration practiced as experimental science has been enlightening (Jordan et al. 1987, Howe 1999a). Manipulation of vole numbers on native prairie did not show much effect (Gibson et al. 1990), whereas experimental plantings of tallgrass species sown in more even distributions produced striking effects of vole herbivory. For instance, rodent seed predation on especially edible large seeds of normally uncommon *Silphium integrifolium* (rosinweed) in Wisconsin released subdominant plants and increased overall plant diversity, whereas exclusion of voles resulted in overwhelming dominance of this aggressive species (Howe and Brown 2000, 2001). The latter experiment, a different planting on higher ground at the same site as the present study, demonstrated heavy winter seed predation under snow by rodents, the effects of which lasted 30 mo after the animals were permanently excluded from the plots. In contrast, exclusion at planting in a large experiment in Illinois showed that birds reduced seedling emergence >20%, while voles had no effect on seeds or emerging seedlings on open ground, which they avoided (Howe and Brown 1999). When vegetation later provided sufficient cover (10–30 cm), voles selectively reduced dicot biomass nearly 60%. In a later year when vole densities nearly doubled, they reduced overall standing crop by as much, and reduced abundances of most species 16–95% (Howe et al. 2002). In the first case, preference for large rosinweed seeds and aggressive dominance of that species when seeds were not depleted by rodents resulted in suppression of other species. In the Illinois example, seedlings and juveniles of unusually abundant plants of high food value were decimated, resulting in an exaggerated community-wide effect. A question is whether such exaggerated effects are likely in mature vegetation that has passed the especially vulnerable seed and seedling stages.

The present study directly addresses the question of vulnerability to voles of large, reproductively mature plants in artificial plantings. We use a 6-yr enclosure experiment in Wisconsin to explore the effects of herbivorous meadow voles (*Microtus pennsylvanicus*) on adult flowering vegetation in replicated synthetic communities of perennial plants of wet tallgrass prairie. We ask whether ambient populations of these rodents: (1) alter species composition; (2) influence plant diversity; and (3) influence aggregate community characteristics (standing crop, cover, soil nitrogen, and the mix of grasses and forbs). While rodents are known to alter grassland communities by seed predation and herbivory of seedlings and juvenile plants, our question here is whether robust reproductively mature vegetation is susceptible to pervasive alteration by small herbivorous rodents.

METHODS

Site and preparation

We use techniques of experimental prairie restoration to investigate vole-influenced prairie succession. The experiment was in a 4-ha field next to a larger 1990 grassland planting on the floodplain of Elk Run Creek near Viola, in unglaciated Vernon County, Wisconsin, USA (43°33.312' N, 90°44.323' W; GPS within 5 m). Plots were located in sandy loam in wet mesic habitat that consistently floods in April and May, and occasionally is inundated after midsummer or autumn rains (see Plate 1).

In 1995, ground for the enclosure experiment was plowed and disced; eighteen 4 × 4 m plots were delineated in a 3 × 6 east-west grid, with each plot separated from others by a 3-m lane planted with Kentucky bluegrass (*Poa pratensis*). The north side of the grid

bordered a 4-ha wet-mesic prairie restoration (Howe 1999b), the south a former wet pasture of grasses (e.g., *Phalaris arundinacea*, *Poa palustris*), goldenrods (*Solidago* spp.), and asters (e.g., *Aster prenanthoides*, *A. simplex*). Elk Run Creek was 15 m east; a wet hollow was 15 m to the west.

Exclosures on the 4 × 4 m plots were erected in 1995. Around each plot, 0.6-m trenches were dug with a self-propelled trencher, and 1.2-m hardware cloth fences with 1-cm mesh were erected. Each hardware cloth fence was topped with a 40-cm sheet of aluminum flashing bent over the top to exclude climbing rodents. A 2-m poultry-netting fence was erected inside each exclosure to further exclude deer (*Odocoileus virginianus*). Vegetation next to fences was clipped to 0.5 m to prevent access by climbing rodents.

Sixteen tallgrass prairie species were planted on 15 June 1996 (authorities follow Mohlenbrock 1986). Species were chosen to include a mix of grasses and forbs that were known to grow on wet, seasonally flooded sites in the area. An attempt was made to exclude otherwise suitable species that aggressively clone when planted in open ground (i.e., in a restoration). The 16 perennials chosen included the grasses wild rye *Elymus virginicus* (Poaceae), American manna grass *Glyceria grandis*, and fowl manna grass *G. striata*, and forbs native yarrow *Achillea lanulosa* (Asteraceae), swamp milkweed *Asclepias incarnata* (Asclepiadaceae), senna *Cassia hebecarpa* (Caesalpiniaceae), tick trefoil *Desmodium canadense* (Fabaceae), shooting star *Dodecatheon meadia* (Primulaceae), purple coneflower *Echinacea purpurea* (Asteraceae), early sunflower *Helipopsis helianthoides* Sweet (Asteraceae), blue lobelia *Lobelia silphitica* (Lobeliaceae), beardstongue *Penstemon digitalis* (Scrophulariaceae), mountain mint *Pycnanthemum virginianum* (Labiatae), tall black-eyed Susan *Rudbeckia subtomentosa* (Asteraceae), rosinweed *Silphium integrifolium* (Asteraceae), and grass-leaved goldenrod *Solidago graminifolia* (Asteraceae).

Exclosures remained closed from June 1996 to August 1998, by which time vegetation was 0.5–2.1 m high. On 22 August 1998, two 5 × 5 cm gates were cut at ground level in each wall of nine exclosures arrayed in a regularly interspersed pattern on the grid. Gates excluded juvenile eastern cottontails (*Sylvilagus floridanus*), but admitted small rodents.

Because sowing density strongly influences species abundance at establishment (e.g., Howe 1994a, 1995), and high densities strongly favor large-seeded species (e.g., Howe and Brown 1999, Howe et al. 2002), all species in this experiment were sown at the same low densities (50 seeds/m² per species, or 800 total seeds/m², mixed with damp sand). Weeds were controlled by weekly clipping in May and June. Even distributions at planting allow animal treatments rather than planting densities to determine differences in species abundance distributions.

Sampling

Small rodents were censused with Sherman live traps (Sherman Traps, Tallahassee, Florida, USA) from 1998 through 2002; here we report results of mid-August censuses. One trap was placed outside the northeast corner of each of 18 exclosures (hereafter, “grid traps”), and one inside each (“exclosure traps”). An additional 18 traps were placed 5–6 m around the exclosure grid, spaced to coincide with neighboring exclosures (hereafter “field traps,” with six north, six south, three east, and three west of the exclosure grid). Overall trapping area for these 36 traps was 1500 m² (0.15 ha). Traps were baited with mixed cracked corn, millet, and sunflower seeds, and checked morning and evening for three days and three nights. Captured mammals were weighed, sexed, temporarily marked with individually unique fur clippings (readable for 2–3 mo), and released. The trap in each exclosure and inspection for runways and holes confirmed exclusion of voles from gateless exclosures, and confirmed rodent use of exclosures with gates.

Most species planted in June 1996 were evident by August 1998 within a 2 × 2 m square centered inside each exclosure. *Desmodium canadense* were counted before (22 August 1998) and shortly after gates were opened (12 October and 2 November 1998) as an index of initial rodent effect. On 21 August 1998, and annually in early September, vegetation cover for four sample subplots of 1 m² each per plot was mapped using a polyvinylchloride frame 1 m² in size. Dominant vegetation reaching the canopy was drawn to scale and later converted to area with a digital planimeter (e.g., Howe 1995). Aboveground standing crop was determined with four 50 × 50 cm clippings to ground level in early September of each year. Clippings were oven dried at 100°C and weighed to 0.1 g.

Cover is the preferred response variable because the method is not destructive. Cover reflects an estimate of the surface occupied in a space-limited system. Clipping removes some living tissue and either removes or augments litter, thereby creating one or more confounding effects (i.e., measurement changes the system being studied, sensu Heisenberg 1930). Cover provides the variable with sufficient sampling intensity to evaluate species responses. More limited samples of standing crop allow estimation of aboveground productivity.

Soil cores collected in the first week of September 1998–2001 were used to determine total and inorganic nitrogen in ug per g of soil. Four 2 × 10 cm cores were taken from each exclosure, pooled, and put on ice. Half of each sample was sieved (4 mm), root fragments >2 mm were picked out, and a 10-g subsample was extracted with 100 mL of 1 mol/L KCl for determination of total Kjeldahl nitrogen (hereafter, total N in ug/g of soil; Robertson et al. 1999). A 20-g subsample was used for gravimetric moisture content. Frozen KCl extract was saved for analysis of NO₃⁻ and NH₄⁺ on an

TABLE 1. Rodents trapped in the vicinity of exclosures in August from 1998 to 2002.

Species	Common name	Rodents (N)†				
		1998	1999	2000	2001	2002
<i>Microtus ochrogaster</i>	prairie vole	0	20	0	0	0
<i>Microtus pennsylvanicus</i>	meadow vole	327	108	200	149	182
<i>Peromyscus leucopus</i>	white-footed mouse	7	7	0	0	0
<i>Zapus hudsonius</i>	meadow jumping mouse	14	0	33	25	14

† Minimum number of rodents alive per hectare, calculated from rodents trapped in 1500 m² just outside, and within 6 m of the outside, of the plot grid.

Alpkem autoanalyzer (Alpkem, Wilsonville, Oregon, USA). Because midsummer available soil nitrogen is more variable than fall soil nitrogen (Lane 2002), we augmented the September collections with a July collection in 2002.

Analysis

Simpson's diversity index (D) was adapted as proportional diversity (D_{pr}):

$$D_{pr} = 1 / \sum p_i^2$$

where p is the proportion of a square meter occupied by species i among species in the square meter. This is not strictly diversity, which is calculated from counts (e.g., Howe et al. 2002), but serves as an index of heterogeneity. Analyses were on the mean of four measures of D_{pr} for each exclosure. Species richness was the number of species appearing in the four square meter samples of cover in each exclosure.

Statistical analyses were accomplished with Systat 10 (SPSS 2000); means are accompanied by one standard error. Proportions (e.g., area) and percentages are presented for clarity. Because some values were $\leq 5\%$ or $\geq 95\%$, the arcsine square root transformation was used for analyses of proportional data. The vole effect is reported on the basis of linear or polynomial regressions of the repeated-measures analysis. Repeated-measures ANOVA accommodates repeated sampling over time, distinguishes vole effects from initial planting or other historical effects, and indicates whether net effects in the last year reflect consistent or inconsistent vole-induced change. Wilk's lambda (λ) is the chosen indicator of multivariate robustness; individual univariate tests are not considered significant unless the accompanying multivariate λ is significant.

RESULTS

Rodent environment

Rodent censuses indicated that the overwhelming majority of foliage eating rodents in and near exclosures were meadow voles (*Microtus pennsylvanicus*), a mostly herbivorous rodent averaging 35 ± 2 g in August ($N = 15$ females and 15 males; Table 1). Plots of first catches of individuals showed that rodent sampling around exclosures was virtually complete within 72 h. For instance, in 1998 such a regression showed 18–22 *M. pennsylvanicus* alive in and among the ex-

closures (estimated from 95% confidence intervals at the x -axis). Perimeter traps in the fields a few meters away showed no relationship between number of first captures and hours since trapping began ($F_{1,4} = 0.06$, slope = 0.013, $R^2 = 0.02$, $P > 0.80$). For practical purposes, in 1998 and later, the pool of rodents in surrounding fields was infinite, though dominated by *M. pennsylvanicus*.

Exclosures and gates were effective. None of the traps set inside gateless exclosures captured mammals, nor did runways, holes, or clipped vegetation indicate their presence. By contrast, on the day gates were cut in 1998, sunflower seeds placed inside each gate at nine accessible exclosures at 1700 hours were cracked and chewed in all exclosures within 12 h. *Microtus pennsylvanicus* was caught regularly within accessible exclosures from 1998 through 2002; *Zapus hudsonius* and *Peromyscus leucopus* were occasionally caught inside rodent-accessible plots. The presence of agile climbers like *P. leucopus* was indicated by a comprehensive collection of seed heads (100%) from two large-seeded composites (*Heliopsis helianthoides* and *Silphium integrifolium*) in October and November 1999 in rodent-accessible plots, rodent harvest of 30% of such heads in the same plots in 2000, and $\sim 20\%$ in 2002. In 2001, $\sim 60\%$ of the heads of smaller seeded but much more abundant *Rudbeckia subtomentosa* were removed by rodents in the same accessible plots. Absence of such collections in gateless exclosures attests to the integrity of fences and flashing to mice, and indicates that birds were not responsible for harvest of seed heads.

Initial plant community

By August 1998, adult vegetation averaged 1.1 ± 0.1 m high, with most species common in plots later assigned to both vole-access treatments (under the 1998 column in Table 2). The only common weed was *P. pratensis* L. ($6.8 \pm 1.2\%$ cover), the cover species planted in the aisles. Some effects of vole access in August 1998 were immediate; *D. canadense* were rapidly clipped at the base and cut into sections, amounting to a 50% decline in stems over the first 8 wk after gates were opened ($F_{1,50} = 5.185$, $P < 0.05$).

Plant succession

Five years of data on cover indicated ongoing succession, independent of and influenced by voles (Table

TABLE 2. Canopy cover (percentage/m²) in late summer, for 1998–2001 (mean \pm 1 SE) for plants with and without voles.

Rodents present?†	Percent canopy cover/m ²					Vole \times cover effect‡ ($F_{4,64}$)
	1998	1999	2000	2001	2002	
<i>Desmodium canadensis</i>						
Yes	19.1 \pm 5.2	15.0 \pm 3.8	2.6 \pm 1.2	2.7 \pm 1.6	0.9 \pm 0.5	4.504**
No	19.0 \pm 5.8	27.8 \pm 7.7	19.9 \pm 3.0	17.3 \pm 2.9	30.7 \pm 6.9	
<i>Echinacea purpurea</i>						
Yes	8.2 \pm 1.8	4.1 \pm 1.3	0.4 \pm 0.2	0.8 \pm 0.6	0.8 \pm 0.7	1.285
No	6.0 \pm 1.5	0.9 \pm 0.5	0.3 \pm 0.2	0.3 \pm 0.2	0.1 \pm 0.1	
<i>Elymus virginicus</i>						
Yes	15.3 \pm 5.0	0.6 \pm 0.3	0.3 \pm 0.1	0.9 \pm 0.3	0.1 \pm 0.1	5.718***
No	13.4 \pm 5.4	21.0 \pm 7.3	27.6 \pm 9.3	13.7 \pm 4.7	6.3 \pm 1.6	
<i>Glyceria striata</i>						
Yes	0	0	0	1.6 \pm 0.7	0.1 \pm 0.1	NA
No	0	0	0	5.4 \pm 2.5	0.7 \pm 0.6	
<i>Heliopsis helianthoides</i>						
Yes	13.8 \pm 4.8	16.2 \pm 8.7	7.3 \pm 6.8	4.6 \pm 3.5	1.2 \pm 0.9	0.747
No	11.4 \pm 4.6	10.0 \pm 6.6	8.9 \pm 6.9	7.8 \pm 5.7	0.9 \pm 0.9	
<i>Lobelia silphitica</i>						
Yes	12.9 \pm 3.0	1.0 \pm 0.9	0	0	0	0.558
No	16.6 \pm 4.2	3.5 \pm 1.6	0.6 \pm 0.4	0.2 \pm 0.1	0	
<i>Pycnanthemum virginianum</i>						
Yes	4.0 \pm 0.8	6.9 \pm 1.8	14.8 \pm 3.3	7.8 \pm 1.8	11.0 \pm 3.1	2.281§
No	0.3 \pm 0.1	3.5 \pm 1.1	5.9 \pm 1.9	5.6 \pm 1.2	5.2 \pm 1.4	
<i>Rudbeckia subtomentosa</i>						
Yes	3.4 \pm 0.8	14.9 \pm 4.3	39.3 \pm 7.6	54.2 \pm 8.6	56.6 \pm 8.3	5.096***
No	3.1 \pm 0.9	10.1 \pm 2.8	19.9 \pm 4.5	28.1 \pm 5.2	35.2 \pm 6.3	
<i>Silphium integrifolium</i>						
Yes	7.8 \pm 1.0	30.8 \pm 5.4	19.4 \pm 5.1	15.7 \pm 5.0	16.8 \pm 6.0	1.240
No	7.8 \pm 1.7	15.1 \pm 2.8	8.4 \pm 2.7	7.2 \pm 2.4	6.3 \pm 1.6	
<i>Solidago graminifolia</i>						
Yes	0	1.7 \pm 0.6	4.6 \pm 1.1	5.6 \pm 1.5	4.9 \pm 2.0	0.979
No	0	0.6 \pm 0.3	1.1 \pm 0.5	2.4 \pm 1.4	1.6 \pm 0.8	

** $P \leq 0.01$; *** $P \leq 0.001$; § $P = 0.1$; NA means "not applicable."

† Vegetation was planted in rodent-proof enclosures in June 1996; voles were admitted to nine enclosures in August 1998, but voles continued to be excluded in nine others. Shown is the F statistic for the repeated-measures effect.

‡ Analyses are on arcsine square-root transformed data, as many values are $\leq 5\%$ or $\geq 95\%$ (Sokal and Rohlf 1981). Repeated-measures ANOVA for *S. graminifolia* were tests for 1999, 2000, and 2001, because the species did not reach the canopy in 1998; the analyses for *E. purpurea* and *L. silphitica* are for the 1998 to 1999 transition ($F_{1,16}$), because these species disappeared later. *Glyceria striata* only appeared in the canopy in 2001, and data were insufficient for analysis.

2, Plate 1). Striking negative vole effects were 60-fold and 30-fold disparities in cover of *E. virginicus* and *D. canadense* in vole-accessible plots as compared with vole-exclusion plots, respectively, despite similar cover before voles were admitted to half the plots. Both of these species showed patchy distributions that, in the absence of voles, excluded each other. In 1998, before voles could have had an effect, the correlation of *D. canadense* and *E. virginicus* cover was negative ($r = -0.64$, $P < 0.005$), with one but often not both present. This reduced the power of analysis for each species separately over all plots. Negative effects of voles for these two plants contrasted with increases in cover of the dominant *R. subtomentosa*, which doubled in the presence of voles, a widespread but incremental increase of *P. virginianum*, and an apparent four-fold but nonsignificant increase in cover of *S. graminifolia*

with vole access. *Echinacea purpurea* and *L. silphitica* emerged but were too rare to analyze; *S. integrifolium* did increase in vole-accessible plots one year after gates were opened, but then declined overall (cover \times vole interaction, Wilks' lambda = 0.444, $F_{4,13} = 4.065$, $P < 0.025$). One large, well-established forb, *H. helianthoides*, declined over time but did not respond to vole herbivory ($P > 0.35$).

Where species respond similarly to vole herbivory but do not often co-occur, analysis by individual species response may underestimate herbivore effects on susceptible or resistant plants. Analyses of pooled cover of the most frequently eaten species (*D. canadense* and *E. virginicus*) and the least frequently eaten species (*P. virginianum* and *R. subtomentosa*) illustrate the community-wide vole effect (Fig. 1). In four years of vulnerability to voles, an otherwise common legume

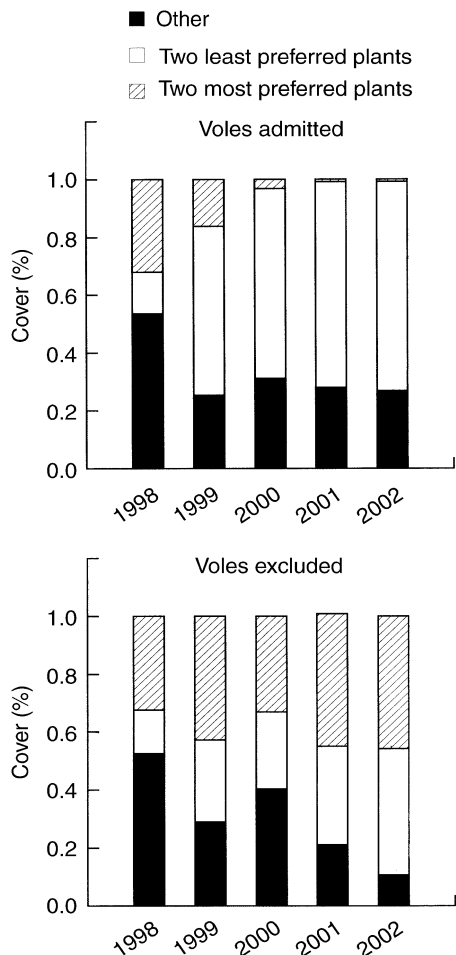


FIG. 1. Vole influence over five years on cover of the most preferred plants (*Desmodium canadense* and *Elymus virginicus*) and least preferred plants (*Pycnanthemum virginianum* and *Rudbeckia subtomentosa*) in exclosures to which voles had been admitted in 1998, 26 mo after planting, compared with those from which voles had been permanently excluded. Without voles, either *D. canadense* or *E. virginica* or both accounted for 17–40% of cover in individual exclosures after 48 mo of exposure; with voles, 0–4% of the cover could be attributed to these species. Parallel analysis of cover of either *P. virginianum* or *R. subtomentosa* or both showed lower values after 48 mo where voles were absent (9–70%) than where they were present. Voles accelerated an increase of less preferred species that was underway in their absence.

and a grass were all but eliminated by voles, while the advance of two vigorous competitors was accelerated by voles. The univariate F test on the pooled cover of *D. canadense* and *E. virginicus* is highly significant ($F_{4,64} = 13.496$, $P < 0.001$), reflecting powerful negative linear ($F_{1,16} = 24.620$) and nonlinear ($F_{1,16} = 7.226$ – 34.781 , $P < 0.025$ – $P < 0.001$) effects over four years, with a highly significant multivariate effect (Wilks' lambda = 0.245, $F_{4,13} = 10.035$, $P < 0.001$). The univariate F test on the pooled cover of *P. virginianum* and *R. subtomentosa* is also significant ($F_{4,64} = 5.447$, $P = 0.001$), reflecting positive linear ($F_{1,16} =$

10.886, $P = 0.005$) and nonlinear ($F_{1,16} = 9.803$, $P < 0.01$; Wilks' lambda = 0.197, $F_{4,13} = 13.285$, $P < 0.001$) effects over four years after voles were admitted.

The net effect of vole herbivory after 48 mo of exposure show that *D. canadense* and *E. virginicus* had less cover in vole-accessible plots ($F_{1,16} = 18.865$ and 5.914, $P < 0.001$ and $P < 0.05$, respectively), while *G. striata*, *R. subtomentosa*, and *S. integrifolium* individually were more common ($F_{1,16} = 3.096$, 4.253, and 2.864, $P \leq 0.1$). If the pooled cover of the most eaten and least eaten pairs are tested for that year to counter mutual exclusion, differences are obvious ($F_{1,16} = 42.494$ and 6.060, $P < 0.001$ and $P = 0.025$, respectively). Analyses on biomass of the pooled two most eaten and two least eaten plants roughly parallel cover, with less statistical resolution because of lower sampling efforts on standing crop. Voles accelerated an increase in *P. virginianum* and *R. subtomentosa* that otherwise occurred more gradually in their absence.

Several species occurred too infrequently to be individually analyzed for a vole effect. Some established in numbers early and then all but disappeared (*E. purpurea* and *L. silphitica*), with no detectable vole effect. Others did not appear in early samples, but later assumed some prominence, with a suggestion of vole suppression (*G. striata*), or release by vole presence (*S. graminifolia*). These might show more decisive effects with time. Within six years of planting, seven species appeared but were too scarce for species-specific analysis (<1% cover): *Achillea lanulosa*, *Asclepias incarnata*, *Cassia hebecarpa*, *Dodecatheon meadia*, *Glyceria grandis*, and *Penstemon digitalis*.

Heterogeneity and richness

Adaptation of Simpson's diversity index as an index of heterogeneity ("proportional diversity" or D_{pr}) indicates similar community structure in 1998 before voles were admitted to some plots, and then a 32%, 55%, and 54% drop in the index for vole-accessible plots vs. exclusion plots over the next three years, followed by a stabilization of both treatments at a 55% reduction in the fourth year (Fig. 2). Repeated-measures analyses indicates a vole effect ($F_{4,64} = 7.127$, $P < 0.001$), driven by a negative nonlinear term ($F_{1,16} = 21.169$, $P < 0.001$; Wilks' lambda = 0.374, $F_{4,13} = 5.434$, $P < 0.01$). The overall decline in D_{pr} from 5.7 in 1998 to 4.2 in 2001 is largely attributable to the vole effect in vole-accessible plots. D_{pr} was low in all plots in 2002. The convergence of D_{pr} in 2002 reflects two distinct communities of similar heterogeneity but different composition (Fig. 2, Table 2). Species number declined from 8.6 ± 0.2 m² in 1998 to 5.8 ± 0.4 m² in 2002 ($F_{4,64} = 8.698$, $P < 0.005$) without a significant vole effect ($F_{4,64} = 0.282$, $P > 0.5$). Species were lost in both treatments over time, but the vole effect was due to differences in species distribution, not number.

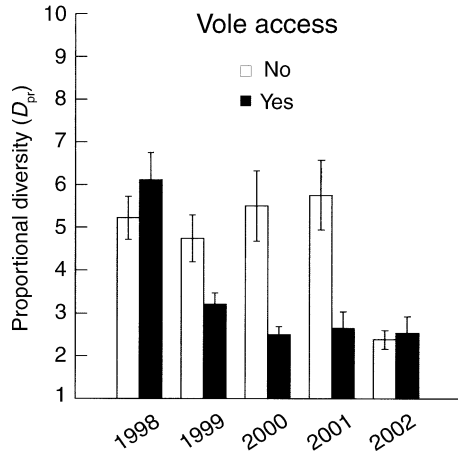


FIG. 2. Proportional diversity (D_{pr}) calculated from cover maps for plant assemblages protected from voles for 26 mo after planting and then exposed to voles for 48 mo. Error bars represent ± 1 SE.

Aggregate characteristics

Voies reduced overall cover of planted species, largely due to effects on grasses. Cover of planted species was 93–100% where voles were excluded, with most plots near 100%. Where voles had access, cover of planted species dropped from 100% in 1998 to 92%, 89%, 98%, and 93% in 1999, 2000, 2001, and 2002. This was a significant repeated-measures effect ($F_{4,64} = 5.159$, $P < 0.001$; Wilks' lambda = 0.422, $F_{4,13} = 4.451$, $P < 0.001$), with a significant nonlinear ($F_{1,16} = 11.335$, $P < 0.005$) term. Experimental dicots averaged between 80% and 93%, with no significant vole influence. Cover of experimental grasses started at 15% where voles later had access in 1998 and 13% where they did not, and increased to as high as 20% when protected from voles, but dropped to $<0.5\%$ where voles had access for 48 mo. Reduction in grass cover in response to vole access was a significant repeated-measures effect ($F_{4,64} = 2.752$, $P < 0.05$; Wilks' lambda = 0.470, $F_{4,13} = 3.665$, $P < 0.05$) resulting from diffuse linear and nonlinear effects.

Voies changed species composition without changing some aggregate community variables. Vegetation height averaged 1.5 ± 0.1 m in 2002, with no significant influence of voles ($P > 0.1$). Overall standing crop of experimental plants varied widely, from a high of 1240 ± 95 g/m² in 2000 to a low of 664 ± 56 g/m² in 2002, without a clear influence of vole access (vole by mass interactions, $F_{4,64} = 1.935$). Experimental dicots ranged from a high of 867 ± 121 g/m² in 2000 to a low of 595 ± 87 g/m² in 1998, with no clear vole effect. However, experimental grasses ranged from a high of 373 ± 115 g/m² in 2000 to 110 ± 36 g/m² in 2002, with a significant vole overall reduction of grasses (Wilks' lambda = 0.487, $F_{4,13} = 3.421$, $P < 0.05$).

We did not detect herbivore-induced reduction of soil N associated with elimination of legumes (*D. cana-*

dense) with repeated-measures ANOVA. Total N ($\mu\text{g N/g soil}$) for all plots was 2040 ± 147 in 1998, 1876 ± 164 in 1999, 2156 ± 159 in 2000, 2311 ± 148 in 2001, with no hint of vole influence (all statistics $P > 0.75$). Overall concentrations of NO_3^- of 4.1, 0.9, and 2.0 $\mu\text{g/g}$ for 1999, 2000, and 2001 showed no hint of a vole effect (all $P > 0.95$). Concentrations of NH_4^+ of 3.5, 2.1, and 3.1 $\mu\text{g/g}$ did suggest marginal influences of voles for some years ($P > 0.1$), but differences were inconsistent in sign. Total N in July 2002 was comparable to September values of previous years (2147 ± 146 $\mu\text{g/g}$), and was not different between vole access and exclusion plots ($t = 0.494$). When used with fall collections in a repeated-measures ANOVA, no interaction with vole presence was evident ($P = 0.75$). Summer available nitrogen ($\text{NO}_3^- + \text{NH}_4^+$; $\sim 1\%$ of total N) did not show a vole effect ($P > 0.50$). Ammonium was more evident in July than September (19.0 ± 0.8 $\mu\text{g/g}$), but neither it nor nitrate (3.8 ± 0.4 $\mu\text{g/g}$) differed with vole access ($P > 0.75$). The statistics do not suggest that more comprehensive fall sampling would show a vole effect on soil nitrogen, and the July sample is comparable to those in early fall. Soil water content of 21.1%, 28.0%, and 26.5% of soil volume in 1999, 2000, and 2001 did not reflect vole access ($P > 0.15$). Although a repeated-measures ANOVA did not show a significant parametric effect of vole presence on NO_3^- , values with voles present (not present) of 4.14 (4.06), 0.91 (0.82), 2.00 (1.93), and 4.02 (3.83) $\mu\text{g/g}$ were consistently higher with voles present. The probability of this occurring by chance is $0.5^4 = 0.06$, suggesting that vole presence increased available NO_3^- . A definitive test is not possible with the data at hand (see Piper 1995).

DISCUSSION

Climate and soil determine the structure of plant communities (Holdridge 1947), but the relative abundance of plant species within that structure is influenced by herbivores (Huntly 1991). These perspectives have wide recognition in general ecology, but have not yet received adequate recognition in grassland restoration (Bakker and Berendse 1999). Possibilities relevant here include rodent herbivory that: (1) shapes successional change through reduction or elimination of preferred forage species, release of competitors of preferred forage species, or changes nitrogen dynamics, and (2) alters community fate. A challenge in experimental restoration ecology is to understand that change without exaggerating it by methodological artifact. In the case of earlier experimental restorations in this research program (Howe and Brown 1999, 2000, 2001, Howe et al. 2002), rodent influence is far more dramatic than is obvious in native prairies with millennia of exposure to voles. Such effects could be artifacts of exposure of seeds and vulnerable seedlings to voles that would not occur with adult plants, or could reflect equitable planting distributions that present more ed-

ible plants to rodents than heavily skewed species abundance distributions common in nature. The present study demonstrates that vole herbivory can shape community composition without exaggerated effects on cover, standing crop, or nitrogen dynamics.

Shaping transient dynamics

Herbivore effects vary with conditions under which forage plants grow. Wet tallgrass sites have fewer species than dry or mesic sites (Peet et al. 1983), and prairie restorations have much lower richness and diversity than native remnants (Howe 1995, Galatowitsch and van der Valk 1996; also Bakker and Berendse 1999). Proulx and Mazumder (1998) point out that the impact of ungulate herbivory on vegetation differs in degree and sometimes in sign with soil nutrients and moisture. Wetter sites permit more rapid recovery of plants damaged by mammals than drier sites, dampen extreme reductions in species number, diversity, and standing crop, and blunt changes in nutrient and light availability that confound interpretation of herbivore effects. Transient dynamics (sensu Tilman 1997) inherent in succession pass more rapidly in resource-rich environments than in resource-poor environments (Huston 1994), a point relevant to this experiment. Because seedling establishment under dense tallgrass canopies is negligible (Glenn-Lewin et al. 1990), protection of vegetation in a wet mesic environment for two seasons makes it likely that initial (4–10 yr) effects of voles, once admitted, largely represent differential attrition of plants or subsequent growth responses by competitors that are already present, and minimizes effects of selective seed or seedling predation that might be evident after major disturbance, such as fire, mowing, or catastrophic browsing or grazing (e.g., Glenn-Lewin et al. 1990, Howe et al. 2002). Without opportunity for extensive population-level recruitment from seed, we test whether voles shape vegetation from selective herbivory of and compensatory response by existing plants.

Voiles did shape mature vegetation, but subtly. Herbivory by voiles along Elk Run did not sharply reduce standing crop, change species richness, reduce vegetation height, or expose bare ground that encouraged regeneration from seed, even when vole densities were up to three times higher than those that produced such effects in a more mesic planting (cf., Howe et al. 2002). After 48 mo of access, voiles altered plant community composition by direct effects of selective herbivory that reduced mean cover of tick trefoil (*Desmodium canadense*) from 31% to <1% and Virginia rye (*Elymus virginicus*) from 6% to 0.1%. Indirect effects included accentuated dominance of less preferred mountain mint (*Pycnanthemum virginianum*) from 5% to 11% and perennial black-eyed Susan (*Rudbeckia subtomentosa*) from 35% to 57%. Vole herbivory over four seasons virtually eliminated two otherwise common species and accelerated domination by two less pre-

ferred species. In contrast to a major experiment with vole access at planting on mesic soils (Howe et al. 2002), net effects on mature vegetation in wet-mesic soils along Elk Run were confined to composition and cover. Voiles did not produce differences in diversity, standing crop, or height that might confound successional dynamics.

Voiles also did not obviously alter nitrogen dynamics, a major effect of ungulate grazing (Hobbs 1996). Despite a 89% reduction in cover of the nodulating legume *Desmodium canadense* over four years, vole exposure did not reduce total or available soil N. A possibility is that in these heavily organic soils, unlike sand prairies studied by Knops et al. (2000) and others, legumes account for such a small proportion of the total nitrogen budget that selective herbivory on them makes little difference. The question remains open because the background level of N fixation by legumes in native tallgrass prairie soils is unknown (Blair et al. 1998). Available N in this system is such a small part of the total (1%), that short-term suppression of NO_3^- or NH_4^+ by voiles through suppression of legumes is unlikely.

Herbivory and community fate

Six years after planting and four years after admitting rodents to flowering and seeding vegetation along Elk Run, divergent succession is far from over. Linear and nonlinear terms in polynomial regressions from the repeated-measures analyses show that positive or negative net effects of voiles mask an array of complex species responses. *Desmodium canadense* drops out of the system where voiles have access, while *R. subtomentosa* increases steadily, without an obvious asymptote to date. Some affected species either decline at a slowing rate (*E. virginicus*), or show complicated behavior with a net increase (*P. virginianum*, *S. graminifolia*), but unclear trajectories. Other species (*Helianthus helianthoides*, *Silphium integrifolium*), as elsewhere (Howe et al. 2002 and Howe and Brown 2001, respectively), change markedly in cover but not in response to vole herbivory. One important insight is that voiles eliminated two otherwise common species (*D. canadense* and *E. virginicus*) while accelerating an increase in two other species (*R. subtomentosa* and *P. virginianum*) that was already in progress. A second interesting finding is that diversities converged, but community compositions did not.

While pervasive and continuing, vole effects on tallgrass vegetation are a challenge to predict. The particular species involved and the contingent nature of diet choice ensure that direct and indirect effects of vole herbivory will be dynamic. Three issues stand out.

First, much of the character of a community depends on attributes of “strong interactors” (Paine 1992, Huston 1997), and it therefore matters which species voiles eat or ignore. For instance, selective depletion of seeds of a dicot with large seeds, *Silphium integrifolium*, had a major effect on diversity in another experiment at

this site, but equally severe depletion of *Desmodium glutinosum* had negligible impact because the species was uncommon even when voles were excluded (Howe and Brown 2001: Table 3). Nearby restorations accessible to voles harbor vigorous stands of reed canary grass (*Phalaris arundinacea*) and big bluestem (*Andropogon gerardii*). In the Illinois experiment (Howe et al. 2002), voles reduce numbers of canary grass, but less than other species that are negatively affected by herbivory. In the neighboring restoration at the Wisconsin site referred to earlier, some big bluestem grass is cut and segmented in autumn, but is not obviously eaten by voles during the growing season (H. F. Howe, *personal observation*). An implication is that inclusion of either of these species would have maintained greater grass presence, illustrating the importance of particular species in outcomes of herbivory on low diversity systems. In general, where voles deplete a community dominant, like *Silphium*, they are likely to increase diversity, much as ungulates do. Where voles deplete subdominant species, they decrease diversity (e.g., Howe and Brown 1999). In the present study vole herbivory drove divergences in diversity for three years after admission to mature vegetation, but diversities converged at a low level in the fourth year, evidently from competitive dominance of different species in exclusion plots than in rodent-accessible plots. After 48 mo of exposure, communities accessible to voles differed in species composition, but not in diversity, from those that were not accessible to voles.

Second, contingent diet choice compounds the contingent nature of competitor response (Belsky 1987). Together they reduce the predictability of a given herbivore effect on a particular system. Food preference depends on the quality and availability of alternate foods (Schoener 1971, Brown 1999), offering the best general framework for understanding why catastrophic rodent herbivory occurs in some circumstances (e.g., Howe et al. 2002), is a shaping function in others (Batzli and Pitelka 1970, Howe and Brown 2000, 2001, this study), or has no obvious effect on vegetation (Gibson et al. 1990). As in similar experiments, synthetic communities along Elk Run are quickly dominated by plants that voles do not care to eat. These altered successional trajectories may result in replicated communities that resemble some native remnants on similar soils, or produce other alternative stable or unstable states.

Finally, variation in vole use of habitat is more likely from changes in densities within and between years, rather than variation in space. Free-ranging ungulates consistently ignore large areas of apparently useable habitat (e.g., Senft et al. 1987), while microtine rodents consistently occupy available habitat (Hamback et al. 1998; see Schweiger et al. 2000), but vary several fold in density within and between years (Taitt and Krebs 1985). A possible consequence is that vegetation may recover if vole densities remain low for a year or more,

as indicated by the absence of vole effects on most species in years of low vole abundance in the Illinois experiment in this research program (Howe et al. 2002, Martinez-Garza et al. 2003). In the present experiment, vole presence has remained much more consistent than in the Illinois experiment.

Implications for experimental restoration

Ecological restoration is often employed as an art as much as science, with the general method being trial and error in the attempt to reestablish a particular image of a community that existed before human disturbance (see Zedler 1996, Howe 1999a). As a science, experimental restoration uses insights from intact communities and explicit experimental designs to attempt to discover why restored communities do or do not differ from native remnants (Jordan et al. 1987, Howe 1994a, b). Exploration of small mammal effects on grassland communities is in an early trial and error phase (Howe 2002). The effort draws interest from observations that small mammals do have ungulate-level effects on African grassland (Keesing 2000), that a related vole alters many aspects of California grassland (Batzli and Pitelka 1970), that mice alter meadow composition in England (Hulme 1996), and that meadow voles in eastern North America both affect succession of early herbaceous old-field vegetation (Bowers 1993), and are capable of changing the direction of advanced old-field succession by selective elimination of seedlings of several tree species (Ostfeld et al. 1997). Such pervasive evidence of impacts of small mammals on such a wide variety of ecosystems, combined with evidence that voles sometimes have little effect (Gibson et al. 1990), indicate that experimental dissection of the influences of small mammal herbivory may illuminate much about the structure and composition of plant communities that cannot be explained by plant-plant interactions alone. One means of approaching this abundance of effects in native grassland is to use synthetic assemblages to test ideas that are not easily examined in native communities.

The present program of small-scale experimental restoration in Illinois and Wisconsin allows some issues to be tested that could not be evaluated in intact communities. For instance, the discovery that initial seed-size selection by rodents has at least a 30-mo legacy in community composition and diversity would be difficult to detect in native grassland, as would the discovery in the same experiment that vole herbivory can be negligible due to chance planting of nonpreferred species (Howe and Brown 2000, 2001). The plant species available to animals matter, and effects on seed banks create an important history of potential response to community change (see Huston 1997). Vole effects on larger plantings in Illinois show that especially edible tallgrass prairie species, when planted in high abundances, can be selectively culled in times of moderate vole abundance, recover quickly in years of vole

scarcity, and suffer ungulate-level decimation in times of high vole densities (Howe and Brown 1999, Howe et al. 2002). Edible species are scarce in native prairie, and therefore difficult to identify and study. Access to mature vegetation rather than large artificial cohorts of exposed seeds and seedlings dampens these massive effects on standing crop and aspect, as suggested by the present experiment. However, vole herbivory does alter plant community composition through differential culling and release of species, bringing experimental restoration a step closer to assessing the kinds of rodent influence likely in native remnants or larger restorations. Further precision, and tests of additional hypotheses, will be possible through simultaneous imposition of early and delayed rodent access, hierarchical exclusion of mammals by size (e.g., Bowers 1993), and manipulation of planting density, composition, and enclosure scale. Our prediction is that grassland restoration will not be well understood, or predictable, until the dynamics of small mammal impacts are far better understood than present knowledge permits.

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