

# Reversal of fortune: plant suppression and recovery after vole herbivory

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**Abstract** It is not clear how plant species preferred as forage by rodents persist in prairie vegetation. To test permanence of suppression of wet-mesic prairie vegetation by vole (*Microtus pennsylvanicus*) herbivory in synthetic experimental communities, access treatments were reversed after 9 years of vole exclusion or access. Between 1996 and 2004, rye grass *Elymus virginicus* (Poaceae) and tick-trefoil *Desmodium canadense* (Fabaceae) achieved mean cover of up to 30 and 25%, respectively, in plots where voles were excluded, but disappeared from plots where voles had access. To determine whether these species remained vulnerable to vole herbivory as established adults, and to determine whether the species could recover if vole herbivory were removed, access treatments were reversed at the end of the 2004 growing season and monitored through 2007. Repeated measures ANOVA demonstrated dramatic vole suppression of established *E. virginicus*, but not *D. canadense*, indicating continuing vulnerability of the grass but not of the adult legume. Release from vole herbivory resulted in re-growth of rye, but not tick-trefoil, which was apparently suppressed by established vegetation. Two additional common planted species did not respond to treatment reversal, nor did 11 much less common planted species that comprised a minor portion of the vegetation. Dominant perennial black-eyed Susan *Rudbeckia subtomentosa* (Asteraceae) did not change in plant numbers by year or treatment, but expanded or contracted in stems per plant

and cover as *E. virginicus* was suppressed or released by vole herbivory or its absence. Results indicate that preferred food plants may persist through capacity to quickly recover during periods of relative vole scarcity, or reach a refuge in maturity.

**Keywords** Experimental restoration · *Microtus* · Plant–animal interactions · Prairie vegetation

## Introduction

Mammalian herbivores frequently alter the species composition of plant communities upon which they feed (Huntly 1991; Pacala and Crawley 1992; Olf and Ritchie 1998). Bison in North American grasslands and large ungulates in African savannas suppress dominant vegetation, often increasing plant diversity by releasing subdominants (see McNaughton 1985; Collins 1987; Belsky 1992; Knapp et al. 1999). Much smaller rodents also have dramatic effects on plant community composition (Brown and Heske 1990; Edwards and Crawley 1999; Keesing 2000). Voles, for instance, may alter forest succession by eliminating seedlings of some tree species more than others (Ostfeld et al. 1997; Manson et al. 2001), may change competitive interactions between herbaceous species (e.g., Batzli and Pitelka 1970; Olofsson et al. 2002, 2004, 2005; Hambäck et al. 2004), and may alter genetic composition of plant populations (Prittinen et al. 2006). Adaptation of techniques used in experimental restoration (Jordan et al. 1987) is enlightening because herbaceous grasses and forbs that rarely if ever achieve dominance in nature do so in plantings when protected from voles, sometimes reaching 80% cover in individual plots (Howe and Lane 2004). The implication is that top-down effects of rodent herbivory

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collectively shape the species composition of herbaceous plant assemblages (Howe and Brown 1999; Howe et al. 2006; Olofsson et al. 2004, 2005; del-Val and Crawley 2005). It is even possible that voles, like much larger herbivores, maintain alternative stable states of vegetation composition (Dublin et al. 1990). In tallgrass and oldfield habitats where voles are potentially common, it is at least likely that their presence or absence bound alternative states of plant community composition.

Of direct interest here is recovery of suppressed vegetation when voles are not common. A question is whether voles actually eliminate preferred food species or temporarily suppress them, allowing rapid re-emergence when rodent numbers fluctuate two- to tenfold within and between seasons (Taitt and Krebs 1985). Treatment reversal in this vole enclosure experiment offers insight into the question of whether contemporary North American tallgrass prairies actually are “what voles choose not to eat” (Howe et al. 2002), or simply appear to be what voles choose not to eat, with suppressed food species persistent but largely invisible.

Earlier studies found that the response of an experimental wet-mesic plant assemblage to vole herbivory depended on the responses of three key species to vole herbivory (Howe and Lane 2004). These included the direct reduction of rye (*Elymus virginicus*) and tick-trefoil (*Desmodium canadense*) from herbivory. With or without continuous vole access from 1998 to 2002, an aggressive forb (*Rudbeckia subtomentosa*) increased in abundance, with voles accelerating the process, leading to strong dominance in vole-accessible plots. Here I ask: (1) is vole herbivory capable of suppressing better established rye and tick-trefoil that have had several years to achieve substantial dominance; (2) are these species, following suppression by voles, capable of recovering quickly when rodents are excluded; (3) what is the effect of treatment reversal on competitive response of the aggressive dominant *R. subtomentosa*?

## Materials and methods

### Set-up and treatments

The experiment was in a 4-ha field that included a larger 1990 grassland planting on the floodplain of Elk Run Creek near Viola, in unglaciated Vernon County, Wisconsin (43°33.312'N, 90°44.323'W; GPS within 5 m). The experiment was established on seasonally flooded ground in 1995 (details in Howe and Lane 2004). A total of 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* L., Poaceae). Enclo-

tures 1.5-m high of 1-cm-mesh hardware cloth were erected on all plots in 1995. Each fence was sunken into 0.6-m trenches, and topped with a 40-cm sheet of aluminum flashing bent over the top to exclude climbing rodents. Vegetation next to fences was clipped to 0.5 m as needed to prevent access by climbing rodents.

A total of 16 tallgrass prairie species were planted on 15 June 1996 at a density of 50 seeds per species per square meter. Species chosen were known to grow on wet, seasonally flooded sites in the area. Of the 16 perennials planted, five including wild rye *Elymus virginicus* L. (Poaceae), tick trefoil *Desmodium canadense* (L.) D.C. (Fabaceae), mountain mint *Pycnanthemum virginianum* (L.) Dur. and B. D. Jacks. (Labiatae), tall black-eyed Susan *R. subtomentosa* Pursh. (Asteraceae), and rosinweed *Silphium integrifolium* Michx. (Asteraceae) reached at least 5% cover in several plots and were common enough to be potentially important in the last 6 years of the experiment. In total 11 other planted species, including American manna grass *Glyceria grandis* S. Wats., and fowl manna grass *Glyceria striata* (Lam.) Hitchc. (Poaceae), native yarrow *Achillea lanulosa* Nutt. (Asteraceae), swamp milkweed *Asclepias incarnata* L. (Asclepiadaceae), *Baptisia leucantha* T. and G. (Fabaceae), shooting star *Dodecatheon meadia* L. (Primulaceae), purple coneflower *Echinacea purpurea* (L.) Moench. (Asteraceae), early sunflower *Heliopsis helianthoides* (L.) Sweet (Asteraceae), blue lobelia *Lobelia silphitica* L. (Lobeliaceae), beardstongue *Penstemon digitalis* Nutt. (Scrophulariaceae), and grass-leaved goldenrod *Solidago graminifolia* (L.) Nutt. (Asteraceae) collectively accounted for <1 to almost 4% cover. Despite weeding, nine species that were not planted but invaded the enclosures (six native, three exotic) collectively averaged ~2% cover.

Enclosures remained closed from June 1996 to August 1998 to allow vegetation to establish up to full height of 2.1 m. On 22 August 1998, two 5 × 5-cm gates were cut at ground level in each wall of nine enclosures arrayed in a regularly interspersed pattern on the grid. Gates excluded eastern cottontails (*Sylvilagus floridanus*), but admitted small rodents. This pattern of admission and exclusion remained until 20 August 2004, when gates were closed and rodents removed from nine “access plots,” and similar gates were cut in the nine plots from which rodents had been previously excluded. Treatment reversal was maintained until the end of the experiment in August 2007.

Of the 18 enclosures erected, results from a balanced design of ten are reported here. Two enclosures were compromised by rodents burrowing under fences between 2002 and 2007, and are not used here. Six upstream enclosures were flattened by a major flood in August 2007 and were effectively destroyed. The others, protected from the force of the current but in standing water 5–20 cm deep for a week, could be sampled for plant cover, number and stems

in 2007 (standing water is annual in early summer and not unusual after August or September storms).

### Sampling and analysis

Small rodents were sampled in July and August with Sherman live traps from 1998 up to and including 2007; here I report results of August censuses except for 2007, when standing water precluded the August census. One trap was placed outside the north-eastern corner of each of 18 exclosures. An additional 18 traps were placed ~6 m around the exclosure grid, spaced to coincide with neighboring exclosures, with six north, six south, three east, and three west of the exclosure grid. Overall trapping area for these 36 traps was 1,500 m<sup>2</sup> (0.15 ha). Traps were baited with mixed cracked corn, millet, and sunflower seeds and checked morning and evening for 3 days and 3 nights. Captured mammals were weighed, sexed, temporarily marked with individually unique fur clipping (readable for 2–3 months), and released. Periodic trapping in each exclosure and inspection for runways confirmed exclusion of voles from gateless exclosures, and confirmed rodent use of gated exclosures. Species reported here and in Howe and Lane (2004) that were captured outside exclosures were also captured within accessible exclosures, in addition to an immature rat (*Rattus norvegicus*). For continuity, 2002 estimates are included here. Rodent numbers are estimates of the minimum number alive at the site during the trapping period.

Cover, plant counts, and number of stems are non-destructive response variables that indicate different responses to herbivory or competition from neighbors. Cover estimates the surface occupied in a space-limited system, reflecting canopy occupied that intercepts light. Number of individuals shows the long-term capacity for response to conditions, with increasing or decreasing numbers over time indicating population change. Number of stems reflects differences in plant size, as individual plants increase or decrease likelihood of occupying canopy and blocking light to competitors. Not all individuals or stems reached the canopy to be reflected by cover; cover more closely reflected success in blocking light to competitors.

Samples were taken with a 1-m<sup>2</sup> square PVC frame. Cover is easily assessed in these plots because few species reach the canopy in a square meter and rarely inter-digitate; I placed the frame over the vegetation and drew canopies to scale on a 10 × 10-cm grid. Individuals were counted as one or more stems emerging from a common base (often there were several stems per individual) within frames. These non-destructive measures provide the variables with sufficient sampling intensity to evaluate species responses. More limited destructive samples of total above-ground biomass (two 0.25 m<sup>2</sup> per 4 × 4 m exclosure per year)

showed no effect of vole herbivory on standing crop in the previous study (Howe and Lane 2004), an absence of response maintained in the present study. Standing crop will not be discussed further. Estimates of possible below-ground response to herbivory were precluded by the need to avoid disturbance. As with rodents, continuity is provided by use of 2002 data, allowing analysis of three seasons before and three after reversal of rodent treatments.

Statistics were accomplished with Systat 11; means are accompanied by one SE. Repeated measures ANOVA accommodates repeated sampling over time. The contrast of interest is how plots from which voles were excluded until the end of the 2004 growing season responded to admission of rodents, as compared with those to which voles had been admitted, and then were excluded. Results are corrected for the number of species tested. Cover, number of plants, and number of stems are treated as effectively independent (i.e., many plants do not reach the canopy; a plant may have one or many stems). Reported for each of three species are changes over time within a set of five exclosures receiving the same treatment, and interactions between treatments.

## Results

### Rodent environment

Rodents captured from 2002 to 2007 remained the same as in the earlier study (Table 1), except that no *Peromyscus* were captured 2002–2007. Clipped seed heads of *S. integrifolium* in late autumn indicated *Peromyscus* presence in accessible plots outside of the trapping period. By far the most important rodent herbivore remained the meadow vole (*Microtus pennsylvanicus*), with occasional prairie voles (*Microtus ochrogaster*). Vole numbers showed fluctuations of 1.5- to twofold from year to year in the 6 years reported here (Table 1), and only a threefold fluctuation over the full 10 years of this study (see Table 1 of Howe and Lane 2004). Possible effects of an unprecedented spike in numbers of jumping mice (*Zapus hudsonius*) in 2006 are unknown. These are seed-eaters, but hibernate through much of the autumn, winter and early spring when granivory would most plausibly affect the experimental vegetation (Jackson 1961). Important rodent herbivores remain meadow voles.

### Vegetation response

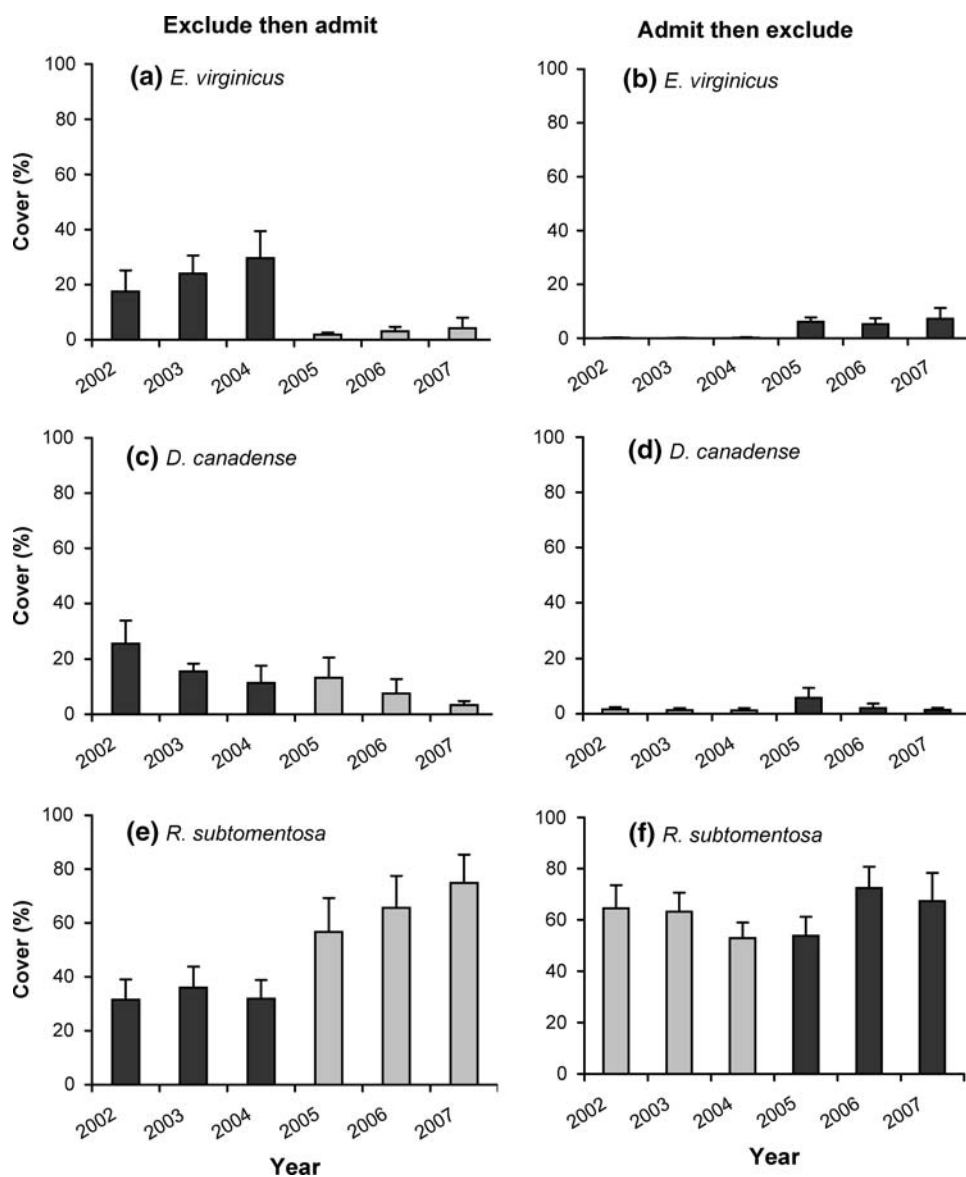
Of the 16 species planted, three showed responses to reversal in vole herbivory (Fig. 1, Table 2). *P. virginianum* and *S. integrifolium* changed to some degree from 2002 to 2007 (*P. virginianum* cover  $10.7 \pm 2.7$  to  $5.9 \pm 2.6\%$ , plants 1.0

**Table 1** Minimum number of rodents alive per hectare trapped in the vicinity of exclosures in growing seasons of 2002–2007<sup>a</sup>

Species	Common name	2002	2003	2004	2005	2006	2007
<i>Microtus ochrogaster</i>	Prairie vole	0	0	7	7	0	0
<i>Microtus pennsylvanicus</i>	Meadow vole	182	101	255	208	154	134
<i>Zapus hudsonius</i>	Meadow jumping mouse	14	0	13	54	80	13

<sup>a</sup> Calculated from rodents trapped in 1,500 m<sup>2</sup> beside exclosures to 6 m outside of the plot grid

**Fig. 1** Response in cover of three common species (*Elymus virginicus*, *Desmodium canadense* and *Rudbeckia subtomentosa*) to reversal of vole access treatments at the end of the 2004 growing season. **a, c, e** Plots from which voles were excluded from 2002 to August 2004, then allowed access until August 2007. **b, d, f** Plots to which voles were admitted from 2002 to August 2004, and then removed and excluded until August 2007. Dark bars indicate vole exclusion, shaded gray bars indicate vole access



$\pm 0.2$  to  $0.6 \pm 0.2$ , stems  $8.0 \pm 2.7$  to  $9.9 \pm 5.6$ ; *S. integrifolium* cover  $10.4 \pm 3.2$  to  $11.4 \pm 4.6\%$ , plants  $2.1 \pm 0.6$  to  $1.8 \pm 0.8$ , stems  $3.4 \pm 1.0$  to  $7.0 \pm 2.5$ ), but vole access had no detectable effect. In total 11 species were individually too scarce for analysis and collectively showed no consistent response to vole treatments.

*E. virginicus* and *D. canadense*, both species strongly suppressed by voles in the earlier years of the experiment, responded to different degrees to release from vole herbivory,

and to novel exposure to vole herbivory as fully established 9-year-old adults. The most dramatic effect was for *E. virginicus*, which was virtually absent where voles had access until late season 2004, increased to 5–7% cover after vole exclusion in 2004, and showed a substantial increase in number of plants detected. This species had reached over 30% cover and up to four clumps and  $\sim 25$  flowering stems m<sup>-2</sup> by the end of the 2004 season under vole exclusion, but was strongly suppressed when voles were admitted, although not to the

**Table 2** Plant and stem number by year; means  $\pm$  1 SE

Species	Vole treatment	2002	2003	2004	2005	2006	2007
<b>Plant number</b>							
<i>Elymus virginicus</i>	Exclude/admit <sup>a</sup>	1.4 $\pm$ 0.5	3.2 $\pm$ 1.0	4.0 $\pm$ 1.4 ***	1.1 $\pm$ 0.4	1.8 $\pm$ 0.5	0.8 $\pm$ 0.5*
	Admit/exclude <sup>b</sup>	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	0.2 $\pm$ 0.1	2.0 $\pm$ 0.6	2.2 $\pm$ 0.9	2.2 $\pm$ 0.7**
<i>Desmodium canadense</i>	Exclude/admit	2.6 $\pm$ 0.5	3.2 $\pm$ 0.6	1.8 $\pm$ 1.0 **	1.1 $\pm$ 0.5	1.0 $\pm$ 0.4	1.1 $\pm$ 0.5**
	Admit/exclude	0.2 $\pm$ 0.1	0.5 $\pm$ 0.3	0.3 $\pm$ 0.2	0.8 $\pm$ 0.5	0.6 $\pm$ 0.3	0.6 $\pm$ 0.4 NS
<i>Rudbeckia subtomentosa</i>	Exclude/admit	2.5 $\pm$ 0.6	3.5 $\pm$ 0.4	3.6 $\pm$ 0.6 NS	3.2 $\pm$ 0.3	2.7 $\pm$ 0.4	3.0 $\pm$ 0.1 NS
	Admit/exclude	3.2 $\pm$ 0.5	3.8 $\pm$ 0.5	4.7 $\pm$ 0.6	3.6 $\pm$ 0.4	3.4 $\pm$ 0.4	3.4 $\pm$ 0.3 NS
<b>Stem number</b>							
<i>E. virginicus</i>	Exclude/admit	22.8 $\pm$ 10.5	29.2 $\pm$ 8.5	26.7 $\pm$ 8.0 ***	2.1 $\pm$ 1.0	6.4 $\pm$ 2.7	2.8 $\pm$ 2.2**
	Admit/exclude	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	0.2 $\pm$ 0.1	7.6 $\pm$ 2.2	8.5 $\pm$ 3.6	13.7 $\pm$ 8.3 NS
<i>D. canadense</i>	Exclude/admit	5.6 $\pm$ 1.8	7.1 $\pm$ 1.7	2.8 $\pm$ 1.8 NS	4.8 $\pm$ 2.6	4.8 $\pm$ 3.3	2.8 $\pm$ 1.1 NS
	Admit/exclude	0.3 $\pm$ 0.1	0.8 $\pm$ 0.5	0.8 $\pm$ 0.5	3.0 $\pm$ 1.9	2.4 $\pm$ 1.9	0.8 $\pm$ 0.5 NS
<i>R. subtomentosa</i>	Exclude/admit	12.8 $\pm$ 4.3	24.8 $\pm$ 5.6	12.6 $\pm$ 2.7 NS	20.9 $\pm$ 5.0	26.2 $\pm$ 6.4	41.8 $\pm$ 0.2***
	Admit/exclude	26.2 $\pm$ 5.9	35.2 $\pm$ 9.2	19.4 $\pm$ 3.3	25.6 $\pm$ 5.6	33.6 $\pm$ 5.9	39.0 $\pm$ 11.0 NS

\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$  corrected for multiple species, NS not significant (repeated measures analysis). Rows reflect change over time within each set of five plots receiving the same treatments; asterisks between treatments within species indicate interactions of plant or stem number and changes in patterns of vole access

<sup>a</sup> Voles were excluded for growing seasons 2002–2004, and then admitted for 3 years

<sup>b</sup> Voles had access for growing seasons 2002–2004, and then were removed and thereafter excluded

degree they had been suppressed in plots accessible to voles from 1998 to 2004 (Fig. 1a, b). *E. virginicus* cover in the two sets of plots (vole access followed by vole exclusion versus vole exclusion followed by vole access) was clearly statistically different (cover by treatment interaction,  $P < 0.001$ ). The legume *D. canadense* did not respond to removal of vole suppression in 2004, but did decline in cover and number of plants after voles were admitted to plots from which they had been excluded since 1998 (Fig. 1c, d). The two sets of reversals differed for *D. canadense* (cover by treatment interaction,  $P < 0.01$ ), but the absence of an abrupt effect or obvious clipping of stems, as in *E. virginicus*, suggests that suppression of established adult *D. canadense* was due to suppression by competing vegetation, principally *R. subtomentosa*, rather than direct suppression by vole herbivory.

*R. subtomentosa*, an aggressive perennial that displaced most species where voles had access from 1998 up to and including 2002, responded quickly to reduction of *E. virginicus* after 2004 when voles were admitted to plots where they had been absent with an increase in cover (Fig. 1e). *R. subtomentosa* response to vole reduction of *E. virginicus* involved a sharp increase in number of stems, but not number of plants (Table 2). No consistent change in *R. subtomentosa*

occurred when voles were excluded from plots to which they had originally had access (Fig. 1f); the sharp expansion of cover when voles were admitted to original exclusion plots contrasted with apparent priority effects where voles had had access (cover by treatment interaction,  $P < 0.001$ ).

Two species were significant components of vegetation ( $\sim 10\%$  cover,  $\sim 1$ – $2$  plants  $m^{-2}$ ) but did not respond to treatments. The mint *P. virginianum* averaged  $9.4 \pm 3.4\%$  cover,  $1.4 \pm 0.9$  plants  $m^{-2}$ , and  $10.4 \pm 1.9$  stems  $m^{-2}$ , and rosinweed *S. integrifolium*  $10.6 \pm 1.9\%$  cover,  $2.0 \pm 0.5$  plants  $m^{-2}$ , and  $5.0 \pm 1.6$  stems  $m^{-2}$ , without consistent effects of vole presence or absence. A total of 11 other planted experimentals were not especially significant components of vegetation, collectively accounting for  $3.9 \pm 1.7\%$  cover,  $0.9 \pm 0.5$  plants  $m^{-2}$ , and  $1.4 \pm 0.9$  stems  $m^{-2}$ , with no collective response to treatment reversal.

Nine species that invaded the plots also reached the canopy. Six were native forbs (*Aster simplex* Willd., *Eupatorium perfoliatum* L., *E. purpureum* L., *Solidago altissima* L., all Asteraceae) or sedges (two *Carex* spp., Cyperaceae), and two were common non-native species (*Erigeron* spp., Asteraceae, an agronomic *Phalaris arundinacea* L. cultivar, Poaceae). Invaders collectively accounted for  $2.2 \pm$

1.9% cover, and did not respond to treatment reversal. However, the plots that started with vole access had fewer invasives (0.8–3.9% cover) than those from which voles were first excluded first and then admitted (1.8–10.6% cover; cover by initial treatment effect,  $P < 0.05$ ).

## Discussion

Interactions of plants with their vertebrate herbivores exemplify contingencies in ecological interactions (Lawton 1999). Diet selection depends on the needs of an animal, the inherent quality of the food, and what else there is to eat (Schoener 1971). Response to herbivory depends on tolerance or resilience of particular plant species (e.g., Belsky 1987), which in turn reflects nutrient availability or stress experienced by plants (Olofsson et al. 2002, 2007). These are contingent effects that are quite likely to lead to alternative compositional states in native communities (Beisner et al. 2003) or in restorations that start with different trajectories (Suding et al. 2004). Depending on initial physical environment and local vole preferences, a given planting design may well yield quite different plant assemblages.

Contingent foraging decisions may mean that relationships between voles and particular plant species differ in important ways under different conditions (see Bonsall et al. 2003). Vole populations at any given time reflect food distributions in habitats where the rodents have sufficient cover (Lin and Batzli 2001; see Howe and Brown 1999), but foods quite likely differ from place to place. In an enclosure experiment in Illinois, for instance, voles devastated plantings that presented the animals with much higher densities of palatable species than normally exist in nature (Howe et al. 2002, 2006), and strongly affected succession in early years of the present experiment in Wisconsin (Howe and Lane 2004). In another set of replicated plantings 200 m from the present experiment, voles strongly affected recruitment from seed but had no detectable effect on standing vegetation, evidently because surrounding vegetation was better to eat (Howe and Brown 2000). In Indiana, the difference between solid stands of Eurasian grasses and woody invasion depended on infection of the grasses with fungal symbionts that produced toxic alkaloids (Clay and Holah 1999; Clay et al. 2005). Where the grasses were inedible to voles and the potential invaders were not, well-defended grasses and rodents forestalled succession. These examples, and treatment reversal in this experiment, underscore what Huston (1997) noted in other grassland experiments of low-diversity systems: outcomes depend critically on which plants are involved and the conditions under which they compete for nutrients and space. The important addition here is the extent to which they are palatable to abundant vertebrate herbivores.

Voies eat grasses as well as woody and herbaceous dicots. The reasons behind food choice are complex and contingent, but voles generally avoid high levels of constitutive or induced silica (Massey et al. 2007a, b), other fiber, and protein-binding phenolics (Marquis and Batzli 1989). In the present study, the key species were rye grass (*E. virginicus*) and aggressive response by perennial black-eyed Susan (*R. subtomentosa*). Voies, which clearly suppressed both rye (*E. virginicus*) and tick-trefoil (*D. canadense*) in the earlier study (Howe and Lane 2004), quickly cut this well-established grass, but did not cut the well-established adult legume, where the species had been protected. *Rudbeckia* responded quickly and vegetatively to removal of *E. virginicus* by voies where the grass, in the absence of voies, had earlier achieved substantial dominance. After a year of expansion of canopy but no increase in number of plants, *R. subtomentosa* suppressed *D. canadense*. Other species planted in this experiment did not experience important direct or indirect effects from vole herbivory, or were too rare or variable from plot to plot for detection of effects.

Experimental restoration can be enlightening, if limitations of artificial communities are kept in perspective. Ecological restorations, especially on rich wet soils, are simpler, less diverse communities than native assemblages on similar soils (Galatowitsch and van der Valk 1996). This may occur because fewer species are planted than accumulate over time in native prairie, because early priority effects in abnormal successional sequences accentuate competitive suppression, or because early herbivory distorts initial species-abundance distributions (Howe and Brown 1999; Olofsson et al. 2005; Howe et al. 2006). It is also increasingly plausible that dominance relations among species may be skewed when potentially aggressive species are released from suppression by soil-borne pathogens (Beckstead and Parker 2003). Advantages of experimental restoration reflect this simplicity, with interactions among a few key dominant species that are more easily detected than interactions among sparse individuals in more diverse native prairies.

The present experiment offers insights into vole-mediated effects of herbivory that could not be detected from observation in native prairies. Reproductive parameters were not evaluated closely (e.g., Zorn-Arnold et al. 2006), but the simplicity of these wet-mesic plantings helped interpretation. The most startling discovery was that with voies excluded, *E. virginicus* could achieve substantial dominance (80% cover in some plots), far higher than normally occurs in nature (Howe and Lane 2004). Upon treatment reversal in 2004, mean cover fell from 30 to <2–4%. While recruitment from seed cannot be ruled out, the general suppression of seedling recruitment under a heavy canopy (Glenn-Lewin et al. 1990), the unlikelihood of a persistent seed bank of seeds preferred by voies for food, and the

difficulty of seeing suppressed *E. virginicus* that do not produce flowering stems or numerous tillers, makes it at least as likely that the species was present but not detected when voles were present. More easily sampled *D. canadense* was suppressed in cover and numbers by voles early in the experiment 2 years after planting, but when thoroughly established at 9 years after planting was less affected by vole herbivory than by aggressive competition from *R. subtomentosa*. Similar patterns of latency or refuge in maturity from vole herbivory may occur in other herbaceous communities where dense cover allows substantial vole populations to persist.

The winning tactic of the dominant species in this experiment, which was the overwhelming dominant under vole herbivory, was clear. *R. subtomentosa* changed in cover from year to year and treatment to treatment, becoming an overwhelming dominant, often a monoculture at canopy level, when *E. virginicus* was diminished by vole herbivory and as *R. subtomentosa* itself suppressed other potential competitors. The number of plants did not change within or between treatments; well-established individuals had few stems and little cover when suppressed by rye grass protected from voles, but quickly produced extra stems and occupied more space when an opportunity arose due to the novel suppression of grasses. It appears that priority effects of *R. subtomentosa*, abetted by this flexibility in stem production and canopy monopolization, minimized recovery of *D. canadense* when vole herbivory stopped.

Treatment reversal offers insight into issues regarding plant persistence and restoration prognoses left open by earlier studies. If, as argued in earlier reports, long histories of vole herbivory have culled preferred food plants from native prairies since modern *Microtus* appeared in this hemisphere ~500,000 years ago (Kurten and Anderson 1980; e.g., Howe and Brown 2001; Howe et al. 2002, 2006), the question remains how edible plants survive in the face of ubiquitous rodents. Voles fluctuate in numbers in response to food limitation, weather, or episodic predation in mid-latitudes, and cycle strongly at high latitudes (Taitt and Krebs 1985; Klemola et al. 2003). Plant recovery when the animals are at low densities is most likely if aggressive species can persist in vegetation with a latent capacity for rapid recovery, or if species vulnerable to vole herbivory early in life become less vulnerable as long-lived perennial adults through chemical defenses or increased toughness.

Both latent capacity and age refuges exist in this experiment. Latent response of an aggressive competitor occurs, as evidenced by *E. virginicus* recovery after voles were excluded. In contrast, *D. canadense* achieved a refuge in maturity, probably from increased stem diameter and toughness (see Marquis and Batzli 1989; Massey et al. 2007a, b; A. Sullivan, unpublished manuscript). A similar result occurred in a prior experiment in which seeds of *Sil-*

*phium integrifolium* were decimated by rodents, but the established plants were invulnerable (Howe and Brown 2001). In such cases one expects recruitment from seed only when rodents are scarce. In contrast, another legume in an Illinois experiment (*Desmanthus illinoensis* Michx.) was clearly vulnerable to herbivory at all stages for 3 years after planting (Zorn-Arnold et al. 2006), but not in later years, either as an established adult or small seedling (Howe et al. 2006). In that case either a cross-generational induction of defenses in shoots and seeds, or a change in diet of, or exposure to, principle herbivores, might account for the result. The mystery of why edible species persist in a world of potentially devastating rodent herbivores likely lies in contingencies of diet choice, variation in exposure to enemies, capacity to reproduce rapidly to take advantage of opportunity, or ability to assimilate resources for defenses in maturity.

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