

REPORT

The ghost of granivory past

H.F. Howe and J.S. Brown

Department of Biological
Sciences (MIC 066), University of
Illinois at Chicago, 845 W.
Taylor Street, Chicago, Illinois
60607, U.S.A.
E-mail: hfhowe@uic.edu

Abstract

We report a 36-month echo of vole (*Microtus pennsylvanicus*) seed-selection in the composition of synthetic forb communities in Wisconsin. An initial study showed direct suppression of an exceptionally large-seeded (seed > 15 mg) species (*Silphium integrifolium*, Asteraceae) by seed-size predation by rodents during the winter, resulting in indirect release of small-seeded (seed \leq 1.5 mg) species. Twelve months after planting, plant diversities (Simpson's D) were 33% higher in plots exposed to winter seed selection by rodents. Thirty-six months after planting, *Silphium integrifolium* had almost equalized densities in rodent access ($20.8 \pm 4.1 \text{ m}^{-2}$) and exclusion ($29.0 \pm 5.2 \text{ m}^{-2}$) plots, but still suppressed both large-seeded ($\geq 3.5 \text{ mg}$) and small-seeded ($\leq 1.5 \text{ mg}$) species ($F_{1,16} = 11.84$ and $F_{1,16} = 10.42$, $P \leq 0.005$, respectively). A multivariate analysis of covariance (MANCOVA) distinguished effects of *Silphium integrifolium* (Wilk's lambda $P = 0.029$) from echoes of earlier winter granivory (Wilk's lambda $P = 0.014$). Thirty months after rodent exclusion, diversity (D) remained 27% higher in plots once opened to winter granivory (adjusted mean $4.70 \pm 0.37 \text{ SE}$) as compared with closed plots (3.70 ± 0.26 ; $F_{1,16} = 5.12$, $P < 0.05$). Echoes of earlier granivory remained after rodent-induced imbalances in the abundances of the competitive driver of this system, *Silphium integrifolium*, all but disappeared.

Keywords

Granivory, *Microtus*, plant community, prairie, seed-size selection, *Silphium*, vole.

Ecology Letters (2001) 4: 371–378

INTRODUCTION

Mammals may either increase or decrease the diversity of plant communities (Huntly 1991). Ungulates often increase diversity by grazing or browsing dominant plant species, thereby releasing subdominants (Belsky 1986; Howe 1999a; Knapp *et al.* 1999), or by combining suppression of dominants with creation of habitat heterogeneity through trampling, wallows and redistributing available nitrogen in waste (Collins 1987; Hobbs *et al.* 1991; Hobbs 1996; Proulx & Mazumder 1998). Much smaller rodents such as voles (*Microtus*) are more selective in food choice, and are therefore expected and have been found to reduce plant diversity in early forest succession (Ostfeld & Canham 1993; Ostfeld *et al.* 1997) and in early prairie succession (Howe & Brown 1999). Although initial vole effects in these experiments were clearly due to herbivory rather than granivory, subsequent granivory could easily dampen or amplify these effects.

In a departure from this pattern of small-mammal reduction of plant diversity, we reported that vole (*Microtus pennsylvanicus* [Ord] Rhoades, Microtinae) access increased

diversity of synthetic tallgrass prairie vegetation in Wisconsin, U.S.A., through suppression of an otherwise aggressive dominant forb, *Silphium integrifolium* Michx. (Asteraceae) (Howe & Brown 2000). Unlike other experiments of this kind, rodents were allowed access for only a limited time: the effect was recorded the first season following an October planting, after which rodents but not birds had been allowed access for 6 months. In that first season, *Silphium integrifolium* strongly suppressed small-seeded species, which as a group had seeds too small (≤ 0.1 – 1.5 mg) to be of interest to mammalian granivores. Where voles depleted *Silphium integrifolium* seeds ($> 15 \text{ mg}$) on the soil surface, small-seeded species responded with higher densities, contributing to 33% higher overall community diversity.

Here we revisit the experiment at its termination 36 months after planting, and 30 months after gates were closed to rodents. We ask two questions: (1) Is there statistical evidence that effects detected shortly after planting in immature vegetation persist in mature vegetation the third season after planting? Persistent effects would be echoes of rodent foraging from October 1997 to April 1998,

in vegetation that had since been protected from voles; (2) To what degree do effects persist after the competitive driver in the system, the aggressive forb *Silphium integrifolium*, shows no residual influence of rodent granivory? The original effects, massive depletion of seeds of this species on the soil surface and correspondingly low densities of otherwise highly competitive seedlings where rodents had access, were beyond statistical dispute. But a square metre that harbours 80 *Silphium integrifolium* seedlings 15 cm high cannot harbour 80 robust adults 2 m high. The question remains, what residual effects exist in other vegetation after intraspecific competition equalizes densities of this plant in the two treatments?

METHODS

The experiment was planted as a surface "frost seeding" (following Rock 1981) on sandy loam from 17 to 19 October 1997 near Viola, Vernon County, Wisconsin (details are in Howe & Brown 2000; also Howe 1995, 1999b). Eighteen 1.2 m high 2 × 2 m exclosures of hardware cloth, with edges sunken 0.6 m into the earth surface, were established on plowed ground 4 m parallel to the edge of a secondary *Acer/Quercus/Carya* forest at the edge of a 2-ha grassland restoration experiment planted in 1990 (plant nomenclature follows Mohlenbrock 1986). Two metre wide aisles between exclosures were planted with *Poa pratensis* in June 1996 to provide cover to encourage vole access by the time prairie species were planted (Batzli & Cole 1979; Lindroth & Batzli 1984). Bird netting precluded access by seed-eating birds from planting time in October 1997 until May 1998, by which time surviving seeds on the surface had germinated.

Eight tallgrass legumes (Fabaceae and Mimosaceae) and eight members of the sunflower family (Asteraceae) were planted in a broadcast-seeding in densities of 100 seeds m⁻². Large-seeded species (> 3.5 mg per seed) that persisted to the end of the experiment included *Desmodium glutinosum* (seed 32.1 mg), *Echinacea pallida* (5.4 mg), *Echinacea purpurea*

(4.1 mg), *Heliopsis belianthoides* (3.5 mg), *Lupinus perennis* (23.2 mg) and *Silphium integrifolium* (15.2 mg). *Cassia marilandica* (23.1 mg) and *Desmanthus illinoensis* (5.3 mg) germinated but disappeared quickly. Small-seeded species (most ≤ 1.5 mg seed⁻¹) that persisted in at least some plots included *Achillea lanulosa* (0.1 mg), *Aster laevis* (0.2 mg), *Astragalus canadensis* (1.7 mg), *Ratibida pinnata* (0.6 mg) and *Solidago rigida* (0.7 mg). *Dalea candida* (1.4 mg) never appeared, and *D. purpureum* (1.5 mg) and *Lespedeza virginica* (2.8 mg) disappeared quickly.

Eight 5 × 5 cm rodent gates were cut in six randomly selected plots on 19 October 1997 and permanently closed 24 April 1998 ("winter access" for seed predation). Gates were cut in six more plots on 20 May 1998 and closed on 4 November 1998 ("summer access" for herbivory). Six remaining plots remained closed ("no access"). Rodents were sampled until 1998 as reported by Howe & Brown (2000), until exclosures were permanently closed. Exclosures closed in May 1998 had little vegetation, and clearly did not contain rodents. Exclosures closed in November 1998 held semimature vegetation that could have hidden rodents. Two Sherman live traps baited with sunflower seeds and millet were left in them for 10 days in October 1998 and yielded no animals; seed baits left on the ground remained untouched. Live traps were placed in all exclosures in the summer and fall of 1999 and the summer of 2000 for 4 days; no animals were caught and no evidence of rodent activity (runways, cut vegetation, droppings) was seen in the exclosures, although ample evidence of this kind was apparent in vegetation around exclosures.

Individual plants were counted in a centred 1 m² plot in early fall (September or early October) from 1998 through 2000, with timing determined by maturity of late species (primarily *Aster laevis*). Here we compare vegetation recorded in 1998 after one season of growth with those in 2000 after three seasons of growth. Summary statistics (e.g. Table 1) are given for 1999, but full discussion is deferred to save space.

Year	Large-seeded (m ⁻²)		Small-seeded (m ⁻²)	
	Winter access	Closed	Winter access	Closed
1998	132.3 ± 9.8	167.8 ± 11.2	114.8 ± 6.7	78.0 ± 4.7
1999	99.5 ± 16.5	129.2 ± 15.3	121.2 ± 7.5	80.7 ± 5.0
2000	45.2 ± 3.7	44.3 ± 4.0	48.5 ± 5.0	33.3 ± 6.4

Table 1 Number of individuals m⁻² of large- and small-seeded prairie dicots in plots exposed to granivory by small rodents from October 1997 to April 1998 ($N = 6$), or closed ($N = 12$). Shown are means and standard errors of the mean¹

¹A multivariate ANOVA showed significant changes in numbers of large-seeded plants between years ($F_{1,33} = 149.65$, $P < 0.0001$) and suggestive evidence of effects of early rodent access ($F_{1,33} = 3.22$, $P = 0.08$). Changes in the numbers of individuals of small-seeded species showed clear year ($F_{1,33} = 70.89$, $P < 0.0001$) and early rodent access ($F_{1,33} = 15.82$, $P < 0.0001$) effects.

Plant diversity was assessed by species richness, defined as the number of experimental species in each m^2 , and Simpson's D :

$$D = 1 / \sum p_i^2$$

where p is the frequency of species i among all individuals of a given sample (1 m^2 per enclosure).

Results from the first growing season were reported for three treatment levels: closed, open during the winter of 1997–98, and open during the summer of 1998 (Howe & Brown 2000). Because no hint of an herbivore or other rodent effect for plots open during the summer of 1998 occurred in any of the three seasons (Howe & Brown 2000 and unpublished), here we pool those data with data from closed plots.

Interactions among variables used in ANCOVAs and MANCOVAs were tested for nonlinearities that would call results into question. None were found.

RESULTS

Density

Lingering effects of rodent granivory occurred against a decline in the total number of plants present as vegetation matured (Table 1). The number of experimental plants of all species declined from $246.3 \pm 9.0 \text{ SE m}^{-2}$ in October 1998 to $83.0 \pm 4.5 \text{ m}^{-2}$ in 2000, with an obvious effect of year since planting ($F_{1,33} = 261.55$, $P < < 0.0001$), but none of animal access ($F_{1,33} = 0.66$, $P > 0.4$). At first there were more individuals of large-seeded species ($156.0 \pm 9.0 \text{ m}^{-2}$ – $44.6 \pm 2.9 \text{ m}^{-2}$) and fewer individuals of small-seeded species ($90.3 \pm 5.60 \text{ m}^{-2}$ – $38.4 \pm 4.8 \text{ m}^{-2}$). A multivariate ANOVA discerned residual effects of early rodent access

during the winter for small-seeded species (Table 1). By the autumn of the year 2000, densities of large-seeded species were similar in enclosure and access treatments, although composition showed residual effects of seed predation 30 months earlier (below).

The competitive driver in this system, *Silphium integrifolium*, declined from 79.1 ± 3.1 seedlings m^{-2} in plots protected from rodents in October 1998 to $29.0 \pm 5.2 \text{ m}^{-2}$ in October 2000, and from $32.5 \pm 3.2 \text{ m}^{-2}$ in 1998 in plots exposed to earlier winter granivory to $20.8 \pm 4.1 \text{ m}^{-2}$ in 2000. Differences between treatments in 1998 were highly significant ($P < < 0.001$, Howe & Brown 2000); in 2000 they were not close (Table 2).

Role of *Silphium integrifolium*

At the end of the first growing season, *Silphium integrifolium* had suppressed small-seeded species, which were released where rodents had depleted *Silphium integrifolium* seeds (Howe & Brown 2000). *Silphium integrifolium* continued to suppress other vegetation; in 2000 a negative regression between the density of this species and densities of all other experimental species indicates such an effect, but the contrast between plots accessible to voles in the winter of 1997–98 and those not accessible remains the best clue to causation (Fig. 1). Evidence of suppression of *Silphium integrifolium* on small-seeded species detected in 1998 was repeated in 1999; by October 2000 the effect was general. A multivariate analysis of the effects of *Silphium integrifolium* density on the densities of other large-seeded and small-seeded experimental plants demonstrated a highly significant impact (for other large-seeded plants, $F_{1,16} = 11.84$, $P < 0.005$, for small-seeded plants, $F_{1,16} = 10.34$, $P = 0.005$).

Table 2 Plant densities m^{-2} of composites and legumes planted in a frost-seeding in October 1997 in $18.2 \times 2 \text{ m}$ enclosures that were still present in October 2000. Also shown are results of univariate ANOVAs for each species. Mean numbers m^{-2} are accompanied by standard errors for 6 plots in the winter access treatment and 12 in the no access level. Because 100 seeds m^{-2} of each species was planted, counts and their means are percentages of seeds represented by plants

Species binomial	Rodent access		$F_{1,16}$
	Winter access	No access	
<i>Achillea lanulosa</i>	0.8 ± 0.5	0.0 ± 0.0^1	5.031**
<i>Aster laevis</i>	11.0 ± 3.6	3.8 ± 2.2	3.221*
<i>Astragalus canadensis</i>	4.6 ± 3.0	9.4 ± 3.8	0.656
<i>Desmodium glutinosum</i>	0.5 ± 0.5	3.6 ± 1.4	2.449
<i>Echinacea pallida</i>	0.5 ± 0.2	0.2 ± 0.1	0.800
<i>Echinacea purpurea</i>	13.7 ± 2.3	5.8 ± 1.3	10.296***
<i>Heliopsis belianthoides</i>	7.7 ± 2.4	4.8 ± 1.4	1.192
<i>Lupinus perennis</i>	0.3 ± 0.2	0.2 ± 0.1	0.593
<i>Ratibida pinnata</i>	7.7 ± 1.7	3.0 ± 0.6	10.299***
<i>Silphium integrifolium</i>	20.8 ± 4.1	29.0 ± 5.2	1.045
<i>Solidago rigida</i>	24.3 ± 2.5	17.2 ± 2.2	4.023*

* $P \leq 0.1$, ** $P \leq 0.05$, *** $P \leq 0.005$.

¹Mean and SE $< 0.1 \text{ m}^{-2}$.

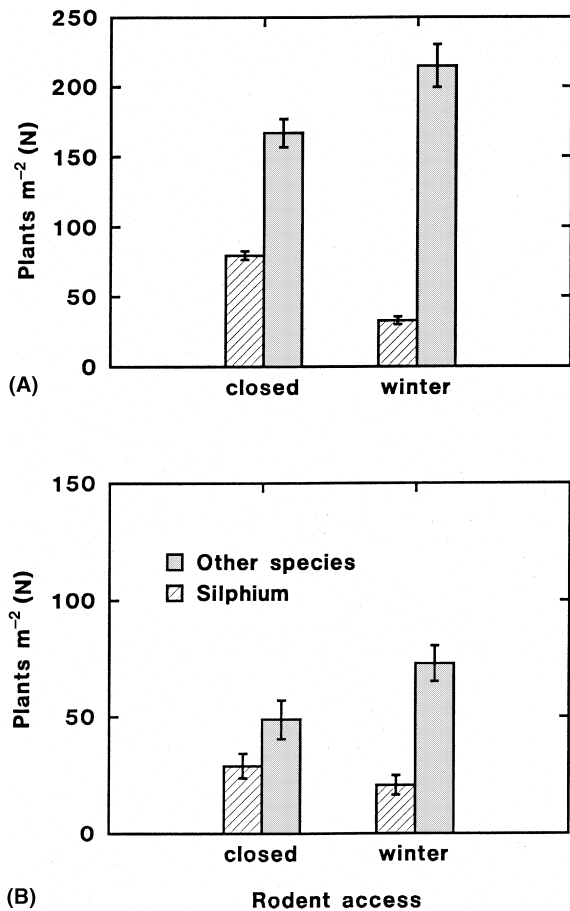


Figure 1 Densities of *Silphium integrifolium* and other experimental plants over two seasons. (A) The 1998 data reported in another form by Howe & Brown (2000); (B) the echo remained in the year 2000 at densities diminished by plant maturation and attrition. "Winter" means winter access to rodents in 1997–98; closed means that no mammal access was allowed. Means are accompanied by one standard error.

Species responses

Mean densities of experimental dicots that survived three seasons varied from $0.06 \text{ plants m}^{-2}$ for *Achillea lanulosa* to 29.0 m^{-2} for *Silphium integrifolium* in plots closed to rodents (Table 2). Overall, a repeated measures analysis of *Silphium integrifolium* densities over three seasons showed a strong effect of animal access shortly after planting ($F_{1,16} = 39.50$, $P < 0.001$), which appeared to have lasting effects on other species. In October 2000, densities of small-seeded *Achillea lanulosa* and *Ratibida pinnata* and large-seeded *Echinacea purpurea* were significantly ($P \leq 0.05$) higher in plots to which rodents had winter access from October 1997 to April 1998, and densities of small-seeded *Aster laevis* and *Solidago rigida* were suggestively ($P < 0.1$) higher. All small-seeded species that persisted showed higher numerical

means in winter-access plots, contributing to the general effect for the guild (Table 1). In addition, three large-seeded species (*Echinacea pallida*, *Heliopsis belianthoides* and *Lupinus perennis*) showed nonsignificant numerical increases in winter access plots, joining the significant effect for *Echinacea purpurea* to produce a general positive response of this guild to rodent access. Highly significant differences in *Silphium integrifolium* densities between plots with and without rodent access in 1998 almost disappeared by October 2000. In the general ANCOVA, two species (*Astragalus canadensis* and *Desmodium glutinosum*) showed nonsignificant higher densities in rodent-exclusion plots. Other species (*Dalea candida*) had never appeared, and four initially uncommon species (*Cassia marilandica*, *Dalea purpurea*, *Desmanthus illinoensis*, *Lespedeza virginica*) disappeared.

Rodent effects are partly confounded by competitive effects of *Silphium integrifolium*, as evidenced by at least the negative sign of the effect of this species on densities of all other vegetation (Table 3). A multivariate analysis of covariance (MANCOVA) distinguished effects of *Silphium integrifolium* (Wilk's lambda $P = 0.029$) from echoes of winter granivory 30–36 months earlier (Wilk's lambda $P = 0.014$). *Silphium integrifolium* significantly suppressed *Astragalus canadensis*, *Desmodium glutinosum* and *Heliopsis belianthoides*. Independent of that effect, residual suppression from rodent access was suggestive for *Astragalus canadensis* and significant for *Desmodium glutinosum*. Residual release from rodent access was suggestive for *Solidago rigida*, and significant for *Echinacea purpurea* and *Ratibida pinnata*. Despite the fact that significant differences in *Silphium integrifolium*

Table 3 Summary of effects from a multivariate analysis of covariance (MANCOVA) distinguishing the effects of rodent access in the winter of 1997–98 from continuing effects of suppression by *Silphium integrifolium*. The rodent effect shows the difference in plant density (m^{-2}) between winter exclusion and vole inclusion (two decreased with vole inclusion, three increased). The *Silphium integrifolium* effect is the slope of the relationship (always negative) between the density of this species and the aggregate density of other species

Species binomial	Effect		Model R ²
	Rodent	<i>Silphium integrifolium</i>	
<i>Aster laevis</i>	3.054	-0.140	0.231
<i>Astragalus canadensis</i>	-4.533**	-0.528****	0.537
<i>Desmodium glutinosum</i>	-2.078**	-0.131**	0.379
<i>Echinacea purpurea</i>	3.599***	-0.088	0.441
<i>Heliopsis belianthoides</i>	0.462	-0.234****	0.551
<i>Ratibida pinnata</i>	2.283***	-0.012	0.394
<i>Solidago rigida</i>	3.376*	-0.051	0.211

* $P \leq 0.1$, ** $P \leq 0.05$, *** $P \leq 0.01$, **** $P \leq 0.001$.

had disappeared (Table 2), increases or decreases in other perennials remained.

Richness and diversity

The number of species m^{-2} declined from the first growing season in 1998 (11.8 ± 0.2 se m^{-2}) to the end of the growing season and experiment in October 2000 (7.2 ± 0.4 m^{-2} ; $F_{1,33} = 106.91$, $P < 0.001$), with no influence of animal access ($F_{1,33} = 0.27$, $P > 0.61$). Over all 18 plots, there were as many large- as small-seeded species, and both declined in parallel (6.1 ± 0.2 – 3.7 ± 0.3 m^{-2} and 5.8 ± 0.1 – 3.4 ± 0.2 m^{-2} , $F_{1,33} = 42.00$ and $F_{1,33} = 127.66$, $P < 0.001$, respectively). Again there was no influence of rodent access on species number m^{-2} (for both $F_{1,33} < 2.50$, $P > 0.1$), only an effect on the identities of species present in each treatment (Table 2). Simpson's diversity (D), a surrogate for community structure that is sensitive to both the number of species and to the evenness of distribution, was influenced by rodent granivory. Over both years an ANOVA demonstrated a clear decline in D over time ($F_{1,33} = 38.14$, $P < 0.001$), with an apparent effect of animal access in the winter of 1997–98 ($F_{1,33} = 20.28$, $P < 0.001$). In the 1998 growing season directly after planting, a D of 5.63 ± 0.18 in plots closed to rodents the previous winter increased 33% to 7.50 ± 0.32 in plots exposed to rodent granivory.

By October 2000, it was important to distinguish effects of rodent access during the winter of 1997–98 from ongoing and perhaps intensifying *Silphium integrifolium* suppression (Fig. 2). An analysis of covariance (ANCOVA) on the year 2000 data showed a strong suppression of *Silphium integrifolium* on Simpson's D (-0.068 , $F_{1,15} = 24.271$, $P < 0.001$). Also remaining was an effect of early granivory independent of *Silphium integrifolium* ($F_{1,15} = 4.898$, $P < 0.05$; overall $R^2 = 0.711$). Adjusted least squares means of D attributable to the rodent effect are 3.70 ± 0.26 for closed plots and 4.70 ± 0.37 for plots open to rodents in the winter of 1997–98, still 27% higher after 30 months without rodent access, independent of contemporary *Silphium integrifolium* effects.

DISCUSSION

Climatic variables are the best predictors of the general form of plant communities (Holdridge 1947), but vertebrate herbivores often mold the species composition and to some degree the structure of those communities (Huntly 1991). For instance, climate may ordain grassland or savanna vegetation in the Serengeti, but the number, movements and foraging habits of ungulates strongly influence plant productivity, dominance and diversity (McNaughton 1984, 1985; Belsky 1992). Similarly, climate favours hardwood

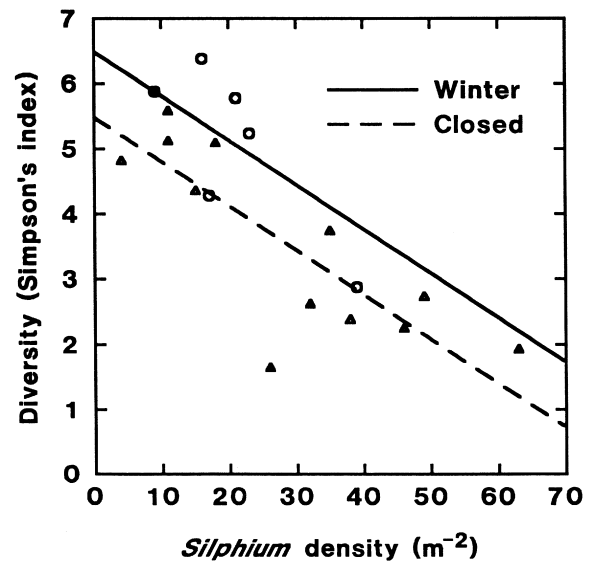


Figure 2 Simpson's diversity (D) of plots exposed to rodent granivory in the winter of 1997–98, or closed to rodent access, as a function of *Silphium integrifolium* density in the autumn of 2000. Shown are the regressions of the ANCOVA model under the assumption of homogeneity of slopes. The intercept of the regression is higher for plots open during the first winter after planting (6.488) than those that remained closed (5.482) but slopes are similar (-0.068 ; interaction test for slope heterogeneity, $P > 0.36$), indicating a persistent impact of early exposure to seed-size selection ($R^2 = 0.711$). Circles are diversities for plots that were open to winter seed predation 30 months earlier; triangles are diversities of plots that were not.

forests in eastern North America, but deer or voles determine which tree species survive early succession to be represented in mature forests (De Steven 1991; Ostfeld *et al.* 1997). Accumulated foraging decisions by large and small vertebrates often mold those communities that climate allows.

Vertebrate herbivores may increase or decrease plant diversity, depending on what and how much they eat, and what else they do. Most research to date is on effects of ungulate herbivores, which usually increase plant diversity at low to moderate grazing intensities by selectively suppressing dominant plants, thereby allowing subdominants to flourish (Belsky 1986, 1987; Collins 1987; Collins *et al.* 1998; Howe 1999a; Knapp *et al.* 1999). A common mechanism is that when aggressive dominant species are repressed or eliminated, once competitively saturated communities become unsaturated, leaving resources and room for subdominant competitors (Cornell & Lawton 1992). The other general mechanism for increasing plant diversity is structural disturbance, wherein ungulates create habitat heterogeneity through spatially selective foraging (Seft *et al.* 1987; Proulx & Mazumder 1998), wallows and trampling

(Collins 1987; Belsky 1992), and depletion or concentration of nitrogenous waste in urine and faeces (Hobbs 1996; Frank *et al.* 1997). By one mechanism or another, light to moderate habitat use by ungulates and other large mammals tends to increase plant diversity.

Ubiquitous but less obvious small vertebrates may also play fundamental roles. Some, such as gophers (*Geomys*) or other digging mammals create structural heterogeneity by physically altering soil exposure and properties (Platt 1975; Huntly & Inouye 1987). Voles (*Microtus*) alter the course of secondary succession in eastern North America by selectively killing the seedlings of otherwise common hardwood trees, eliminating some species outright and reducing others by 20–80% (Ostfeld & Canham 1993; Ostfeld *et al.* 1997), while differential seed depletion by heteromyid rodents may change shrub to grassland deserts (Brown & Heske 1990). In herbaceous plant communities, vole herbivory on nitrogen-fixing legumes may potentially affect community structure by altering nutrient dynamics (Sirotnak & Huntly 2000). Voles that selectively suppress subdominant vegetation skew the competitive structure of communities, enhancing the fortunes of dominant species and through direct and indirect effects reducing plant community diversity (Howe & Brown 1999). Unlike impacts of free-ranging grazing ungulates, which always favour some feeding areas and leave others untouched, and are in any case now absent from most natural or seminatural habitats in eastern and central North America, small rodents are ubiquitous. Rodents vary in abundance in space and time, but it is difficult to imagine of a habitat of any extent without them.

Strong influences of rodent granivory are well recognized in deserts (Brown & Heske 1990), but the primary influence of rodents on more mesic plant communities is thought to be reduction of diversity from selective herbivory (Batzli & Pitelka 1970; Batzli 1985; Reader 1991, 1992; Hulme 1996; Ostfeld *et al.* 1997; Howe & Brown 1999; Sirotnak & Huntly 2000). In the present experiment, postseeding granivory by meadow voles (*Microtus pennsylvanicus*) alters species composition of emerging plant communities (Howe & Brown 2000). It is instructive that here rodent granivory so depresses seedling emergence of an otherwise dominant forb (*Silphium integrifolium*) that forbs with less preferred seeds are favoured, thereby raising the diversity (Simpson's *D*) of plots used by voles. Increased plant diversity from ungulate use is to be expected, but this is apparently a novel rodent effect.

Rodent granivory is potentially relevant to natural communities because seed attrition constantly occurs, reducing the potential template of seeds and therefore seedlings available for emergence (Schupp & Fuentes 1995; Harms *et al.* 2000). In native tallgrass vegetation in North America, effects of selective seed attrition are likely to be evident after fire or grazing reduces the cover of dominant

vegetation and litter, thereby permitting episodes of seedling recruitment (Knapp & Seastedt 1986; Glenn-Lewin *et al.* 1990; Howe 1995, 1999a, b). Recruitment from seed is rare without disturbance in tallgrass prairies (Glenn-Lewin *et al.* 1990), and therefore the opportunity to witness effects of selective foraging that results in differential and spatially heterogeneous seed attrition is unlikely in the absence of disturbance.

The present study indicates that echoes of seed-size selection linger years beyond the event. The multispecies assemblage of seedlings in a community offers a potential template for everything that follows, much as the seed bank in a forest or prairie is an earlier potential template for the seedling assemblage (Howe & Westley 1997; Howe & Miriti 2000). In this experiment some species initially favoured by suppression of the aggressive dominant *Silphium integrifolium* remained more common where voles had access than where they did not, while others showed a delayed positive or negative response to much earlier rodent access. Six months after gates were closed, *Aster laevis*, *Astragalus canadensis*, *Ratibida pinnata* and *Solidago rigida* were more common where rodents had once had access, whereas *Desmodium glutinosum* and *Silphium integrifolium* were less common (Howe & Brown 2000). Thirty months after gates were closed, *A. laevis*, *R. pinnata* and *S. rigida* still were more common where voles once had access, as was the aggregate guild of species with seeds too small to be of interest to rodents. *Achillea lanulosa* persisted only where voles had once reduced *Silphium integrifolium*. In a delayed response, large-seeded *Echinacea purpurea* had become a major beneficiary of earlier *Silphium integrifolium* suppression (Table 2). This is a long-term response of a vigorous plant to earlier granivory affecting a competitor, which parallels a similar response by this species to continuing exposure to vole granivory and herbivory in an ongoing Illinois experiment (Howe & Brown, unpublished).

An intriguing insight is that these echoes of earlier granivory probably could not have been recognized if the first census of plants had been three seasons into the study, or in a remnant patch. Connell (1980) has explored the notion of the "ghost of competition past", reflected by existing plant associations shaped by much earlier competitive partitioning of resources. Here we find the "ghost of granivory past", reflected by community-wide responses to conditions that later disappeared. Before germination we counted dramatic differences in seeds remaining on the ground in plots open to or closed to rodents, and we later documented correspondingly stark differences in densities of *Silphium integrifolium* seedlings (Howe & Brown 2000). Clear differences in *Silphium integrifolium* densities in turn helped demonstrate significant direct suppression of other species by this plant, and therefore helped identify significant indirect response by other species to rodent removal of *Silphium*

integrifolium seeds. By the third season of maturation, all such differences in *Silphium integrifolium* densities disappeared. We suggest that a square metre can only hold 20–30 adults of this species, and many did. Yet where voles had thinned *Silphium integrifolium*, templates of residual subdominant populations remained nearly as different in vole-accessible as compared with vole-inaccessible plots as after the first season. The ecological echo persists, but its history would have been lost without experimental documentation when communities were established.

The ghost of granivory past may reflect either of two causes, which cannot be resolved with this experiment. The ghost could reflect different time lags in response of *Silphium integrifolium* as compared with other vegetation in the short term (e.g. three to several years), or to more permanent structural changes in these communities of long-lived plants. These amount to transitory or long-term priority effects by whatever long-lived perennials manage to establish. Either short- or long-term priority effects in natural grasslands could be affected by the natural dynamism of rodent densities, resulting in dynamic templates of seeds and seedlings surviving to recruit into mature vegetation.

It is fair to question why persistent effects of rodent granivory exist in our experimental communities, but not in native communities. Voles are known to prefer anthropogenic pasture or forage communities to native vegetation with higher fibre content (Lindroth & Batzli 1984), and strong experimental rejection of vole effects in native tallgrass vegetation (Gibson *et al.* 1990) makes it clear that what we find in synthetic native assemblages planted at equal densities is not obvious in remnant prairies of tough, small-seeded grasses and forbs.

Our interpretation is that native tallgrass prairie is what rodents, and at times other herbivores, fail to eat (Howe & Brown 2000). Over time random processes winnow some species and favour others, leaving biological communities with something like a log-normal species abundance distribution, with some species common and most infrequent or rare (Preston 1948, 1962; MacArthur & Wilson 1967; Magurran 1988). We do not doubt these random processes (Maina & Howe 2000), but suggest that they may be confounded by deterministic phenomena that are simply difficult to detect or distinguish in the absence of controlled manipulations. One such phenomenon is selective suppression of subdominant forbs by voles, which concomitantly favours less palatable grasses and forbs – reflecting a ghost of herbivory past that is best discovered by planting native vegetation in unusual densities (Howe & Brown 1999). Here we find comparable but increased plant diversity due to indirect effects of size-selective granivory. In effect, random processes are left to generate characteristic species-abundance distributions from that subset of the potential tallgrass community that is unpalatable as shoots, unappeal-

ing as seeds, or rare enough to escape rodents in space or time.

ACKNOWLEDGEMENTS

We are grateful to N. Cordeiro, C. Martinez-Garza, E. O'Brien and V. Turner-Erfort for help in early stages of the project, to G. Nessler for assistance throughout this project, and to the National Science Foundation of the U.S.A. for major financial support.

REFERENCES

- Batzli, G.O. (1985). Nutrition. In: *Biology of the New World Microtus* (ed. Tamarin, R.H.), pp. 779–811. American Society of Mammalogists, Shippensburg, Pennsylvania.
- Batzli, G.O. & Cole, F.R. (1979). Nutritional ecology of microtine rodents: digestibility of forage. *J. Mammal*, 60, 740–750.
- Batzli, G.O. & Pitelka, F.A. (1970). Influence of meadow mouse populations on California grassland. *Ecology*, 51, 1027–1039.
- Belsky, A.J. (1986). Does herbivory benefit plants? A review of the evidence. *Am. Naturalist*, 127, 870–892.
- Belsky, A.J. (1987). The effects of grazing: confounding the ecosystem, community, and organism scales. *Am. Naturalist*, 129, 777–783.
- Belsky, A.J. (1992). Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *J. Vegetation Sci.*, 3, 187–200.
- Brown, J.H. & Heske, E.J. (1990). Control of a desert-grassland transition by a keystone rodent guild. *Science*, 250, 1705–1707.
- Collins, S.L. (1987). Interaction of disturbances in tallgrass prairie: a field experiment. *Ecology*, 68, 1243–1250.
- Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. (1998). Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, 80, 745–747.
- Connell, J.H. (1980). Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, 35, 131–138.
- Cornell, H.V. & Lawton, J. (1992). Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *J. Anim. Ecol.*, 61, 1–12.
- De Steven, D. (1991). Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. *Ecology*, 72, 1076–1088.
- Frank, D.A., Inouye, R.S., Huntly, N., Minshall, G.W. & Anderson, J.E. (1994). The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. *Biogeochemistry*, 26, 163–188.
- Frank, D. & Zhang, Y. (1997). Ammonia volatilization from a seasonally and spatially variable grazed grassland: Yellowstone National Park. *Biogeochemistry*, 36, 189–203.
- Gibson, D.J., Freeman, C.C. & Hulbert, L.C. (1990). Effects of small mammal and invertebrate herbivory on plant species richness and abundance in tallgrass prairie. *Oecologia*, 84, 169–175.
- Glenn-Lewin D.C., Johnson, L.A., Jurik, T., Akey, A., Loeschke, M. & Rosburg, T. (1990). Fire in Central North American grasslands: Vegetative reproduction, seed germination, and seedling establishment. In: *Fire in North American Tall Grass*

- Prairies* (eds S.L. Collins and L.L. Wallace). University of Oklahoma Press, Norman, pp. 28–45.
- Harms, K.E., Wright, S.J., Calderon, O., Hernandez, A. & Herre, E.A. (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, 404, 493–495.
- Hobbs, N.T. (1996). Modification of ecosystems by ungulates. *J. Wildlife Manage*, 60, 695–713.
- Hobbs, N.T., Schimel, D.S., Owensby, C.E. & Ojima, D.S. (1991). Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology*, 72, 1374–1382.
- Holdridge, L.R. (1947). Determination of world plant formations from simple climatic data. *Science*, 105, 367–368.
- Howe, H.F. (1995). Succession and fire season in experimental prairie plantings. *Ecology*, 76, 1917–1925.
- Howe, H.F. (1999a). Dominance, diversity and grazing in tallgrass restoration. *Ecol. Restoration (North Am.)*, 17, 59–66.
- Howe, H.F. (1999b). Response of *Zizia aurea* to seasonal fire and mowing. *Am. Midland Naturalist*, 141, 373–380.
- Howe, H.F. (2000). Grass response to seasonal burns in experimental plantings. *J. Range Manage.*, 53, 437–441.
- Howe, H.F. & Brown, J.S. (1999). Effects of birds and rodents on synthetic tallgrass communities. *Ecology*, 80, 1776–1781.
- Howe, H.F. & Brown, J.S. (2000). Early consequences of rodent granivory on synthetic dicot communities. *Ecol. Applications*, 10, 917–924.
- Howe, H.F. & Miriti, M.N. (2000). No question: seed dispersal matters. *Trends Ecol. Evol.*, 15, 434–436.
- Howe, H.F. & Westley, L.C. (1997). Ecology of pollination and seed dispersal. In: *Plant Ecology*, 2nd edn (M. Crawley, ed.), pp. 262–281. Blackwell Scientific, London.
- Hulme, P.E. (1996). Herbivory, plant regeneration and species coexistence. *J. Ecol.*, 84, 609–616.
- Huntly, N. & Inouye, R. (1988). Pocket gophers in ecosystems: patterns and mechanisms. *Bioscience*, 38, 786–793.
- Huntly, N. (1991). Herbivores and the dynamics of communities and ecosystems. *Annu. Rev. Ecol. Syst.*, 22, 477–503.
- Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C. & Towne, E.G. (1999). The keystone role of bison in North American tallgrass prairie. *Bioscience*, 49, 39–50.
- Knapp, A.K. & Seastedt, T.R. (1986). Detritus accumulation limits productivity of tallgrass prairie. *Bioscience*, 36, 662–668.
- Lindroth, R.L. & Batzli, G.O. (1984). Food habits of the meadow vole (*Microtus pennsylvanicus*) in bluegrass and prairie habitats. *J. Mammal*, 65, 600–606.
- MacArthur, R. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Magurran, A.E. (1988). *Ecological Diversity and its Measurement*. Princeton University Press, Princeton.
- Maina, G. & Howe, H.F. (2000). Inherent rarity in community restoration. *Conservation Biol.*, 14, 1335–1340.
- McNaughton, S.J. (1984). Grazing lawns: animals in herds, plant form, and coevolution. *Am. Naturalist*, 124, 863–886.
- McNaughton, S.J. (1985). Ecology of a grazing ecosystem, the Serengeti. *Ecol. Monographs*, 53, 291–330.
- Mohlenbrock, R.H. (1986). *Guide to the Vascular Flora of Illinois*. Southern Illinois University Press, Carbondale, Illinois, USA.
- Ostfeld, R.S. & Canham, C.D. (1993). Effects of meadow vole population density on tree seedling survival in old fields. *Ecology*, 74, 1792–1801.
- Ostfeld, R.S., Manson, R.H. & Canham, C.D. (1997). Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology*, 78, 1531–1542.
- Platt, W.J. (1975). The colonization and formation of equilibrium plant species associations on badger disturbances in a tallgrass prairie. *Ecological Monographs*, 45, 285–305.
- Preston, F. (1948). The commonness and rarity of species. *Ecology*, 29, 254–283.
- Preston, F. (1962). The canonical distribution of commonness and rarity: part I. *Ecology*, 43, 185–215.
- Proulx, M. & Mazumder, A. (1998). Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient rich ecosystems. *Ecology*, 79, 2581–2592.
- Reader, R.J. (1991). Control of seedling emergence by ground cover: a potential mechanism involving seed predation. *Can. J. Bot.*, 69, 2084–2087.
- Reader, R.J. (1992). Herbivory as a confounding factor in an experiment measuring competition among plants. *Ecology*, 73, 373–376.
- Rock, H. (1981). *Prairie Propagation Handbook*, 6th edn, Wehr Nature Center, Milwaukee, Wisconsin.
- Schupp, E.W. & Fuentes, M. (1995). Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience*, 2, 267–275.
- Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. (1987). Large herbivore foraging and ecological hierarchies. *Bioscience*, 37, 790–799.
- Sirotnak, J.M. & Huntly, N.J. (2000). Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology*, 81, 78–87.

BIOSKETCH

H.F. Howe employs experimental restoration ecology to explore fire and animal effects on synthetic tallgrass assemblages. He also studies effects of tropical forest fragmentation on frugivore abundance and tree recruitment.

Editor, S. Milton

Manuscript received 13 February 2001

First decision made 26 March 2001

Manuscript accepted 24 April 2001