

## OBVIOUS AND CRYPTIC VOLE SUPPRESSION OF A PRAIRIE LEGUME IN EXPERIMENTAL RESTORATIONS

Barbara Zorn-Arnold, Joel S. Brown, and Henry F. Howe<sup>1</sup>

Department of Biological Sciences (Mail Code 066), University of Illinois at Chicago,  
845 West Taylor Street, Chicago, Illinois 60607, U.S.A.

Ecological conditions may amplify or diminish effects of herbivory. We use replicated prairie plantings established in 1997 to test for the effects of two components of ecological conditions, planting density (high or low density at a 10-fold difference) and planting season (spring or fall), on meadow vole (*Microtus pennsylvanicus*) herbivory of the prairie perennial *Desmanthus illinoensis* Michx. (Fabaceae). Over 3 yr, *Desmanthus* counts declined in plots planted at high density and in December compared with those planted at low density and in June. In 2000, obvious suppression of *Desmanthus* by voles was reduction of numbers: overall, *Desmanthus* was 58% less common in plots with vole access than in those without and was virtually eliminated where voles had access in December plantings. In June plantings, direct but cryptic suppression by voles reduced plant biomass (–51%), fecundity (–44%), and seed mass (–50%). In June plantings, *Desmanthus* adults produced nearly 3000 fewer seeds, each with half the mass, where voles had access compared with where they did not. *Desmanthus* abundance was much reduced in December plantings, where remaining individuals were smaller and had lower reproductive output than in June plantings, with vole herbivory accentuating seasonal effects. Our results offer insights into the reasons why populations of this legume are sparse in much of central North America and why restoration plantings of this plant sometimes fail.

*Keywords:* *Desmanthus*, herbivory, Illinois, *Microtus*, vole.

### Introduction

Vertebrate herbivory affects plants and plant communities in a variety of quite different ways (Huntly 1991). Herbivores may directly kill plants or reduce plant reproduction, with substantial consequences for population and community dynamics. By killing preferred hardwood tree seedlings, for instance, voles (*Microtus pennsylvanicus*) directly eliminate or suppress seedlings and saplings of some otherwise common species and indirectly alter the course of old-field tree succession by favoring some competitors at the expense of others (Ostfeld et al. 1997). Herbivore foraging also affects plant-plant interactions when direct effects are sublethal but indirect effects are determinative. Herbivory changes competitive outcomes in plants, suppressing those preferred by herbivores and, through indirect effects, releasing those that are not (Belsky 1987; Louda et al. 1990). Moreover, the variable nature of vertebrate foraging (e.g., Schoener 1971; Brown 1999) implies that effects of vertebrate herbivory on a given plant species differ substantially in space and time. Here, we use replicated plantings of tallgrass prairie species to evaluate the direct but sometimes subtle impact of vole herbivory, planting density, and planting season on life-history attributes and therefore reproductive fortunes of *Desmanthus illinoensis* Michx. (Fabaceae).

Direct and indirect processes shape ecological communities (Lawton 1999). Manipulated synthetic communities offer an

opportunity to distinguish effects of animal-plant from plant-plant interactions in ways that would be difficult to untangle in complex native floras (Jordan et al. 1987; Brown 1994; Howe 1994). For instance, experimental restoration can distinguish effects of vole herbivory on plant community composition (Howe and Brown 1999; Howe et al. 2002) and even separate echoes of past vole granivory from plant competition (Howe and Brown 2001). Controlled plantings of native species offer important insights into the influences of herbivores on plant interactions.

Experimental plantings can be used to test community effects on particular species and therefore offer insight into restoration practices that are likely to be effective. By itself, for instance, high planting density should decrease components of plant fitness, including vegetative growth (e.g., Salisbury 1942; Mack and Harper 1977; Inouye et al. 1980; Martinez-Garza et al. 2004), survival (Yoda et al. 1963; White 1985), and seed set (Harper 1977). Likewise, by itself, herbivory may reduce plant competitive ability (Schabel and Peart 1994; Nötzold et al. 1998), fecundity (Lee and Bazzaz 1980; Marquis 1984), or survival (Müller-Schärer 1991; Meiners and Handel 2000). Nitrogen-rich legumes may be particularly vulnerable to herbivory and consequently more difficult to maintain in grassland restorations.

Expectations of planting time are less straightforward. Through differences in germination or dormancy, planting time creates alternative compositions by promoting differences in seedling emergence and subsequent competitive outcomes (Ross and Harper 1972; Fowler 1984). In temperate regions, spring sowing results in an early establishment for some species but an additional season of waiting for other

<sup>1</sup> Author for correspondence; telephone 312-996-0666; fax 312-413-2435; e-mail hhowe@uic.edu.

species that require extended exposure of seeds to cold (cold stratification) or cool temperatures during germination, while autumn sowing favors those species that require frost and species that begin growing early in the next season (Keiffer and Ungar 2002). In restorations, late-season or frost seeding improves establishment of some native species but precludes or reduces the establishment of others (Jackson 1999). Our focal species, *D. illinoensis*, grows rapidly in early summer under uncompetitive conditions of an open field in association with other warm-season species.

Factors that affect plant life history will not be independent in nature; interactions among them could easily influence *Desmanthus* abundance and reproduction. Here, contingencies again suggest alternative outcomes (see Lawton 1999): plants experiencing both herbivory and competition may be weakened by either factor, with local conditions determining which has more influence on life history. Conversely, herbivores might consume competitors, leading to increases in reproduction of a target species (Inouye et al. 1980; see Lindroth 1989; Brown and Heske 1990; Louda et al. 1990; Mulder and Rues 1998; Howe and Brown 2001; Howe et al. 2002). Predictable contingencies in tallgrass restorations are that *Desmanthus* seedlings emerging with first spring growth of C<sub>3</sub> grasses are likely to face quite different competitive challenges than those emerging later with much slower C<sub>4</sub> grasses and late-blooming dicots. Through independent control of herbivore access, plant density, and species composition in the context of experimental restoration, animal-plant and plant-plant interactions can be teased apart, providing insight into subtle as well as obvious effects of herbivory on plant populations and ultimately restoration success.

Here, we ask how vole herbivory affects the life history of one important species, *D. illinoensis*, in replicated tallgrass communities. We test whether vole effects on *Desmanthus* abundance, size, and reproductive output vary with planting density and planting time. The leading principle is that life history is a malleable suite of traits that can be modified by environment. One working hypothesis is that voles directly reduce plant abundance, size, and reproductive success of this species; another is that initial growing conditions imposed by planting densities or planting seasons intensify vole effects differently, adding a suite of indirect effects that accentuate vole effects.

## Methods

### Study Species

*Desmanthus illinoensis* is a perennial mimosaceous legume up to 1.5 m tall with smooth, alternate, twice-pinnately compound leaves. Small white flowers cluster densely on short stalks from mid-June to August. Flat, crescent-shaped fruits remain on stems for several months; gravity-dispersed seeds drop from autumn through the following spring. Seeds germinate as soil warms, and seedlings continue to emerge throughout the season (Latting 1961). Of 18 species planted in 1997 (table 1 of Howe and Brown 1999), we selected *Desmanthus* as our focal species because of its use as a forage crop (Beran et al. 2000; Springer et al. 2001), its potential as a nitrogen fixer (Byun et al. 2004), and its initial prominence

in our synthetic assemblages planted at different densities and in different seasons.

### Experimental Design

The experiment consisted of 24 14 × 14-m small-mammal exclosures 1.23 m high with hardware cloth sunken 60 cm into the soil, arranged in a 4 × 6 grid on a back-hoed and disked hayfield at the Morton Arboretum, Lisle, Illinois (Howe and Brown 1999). Experimental treatments planted in June or December 1997 included 18 grasses and forbs sown at low density (35 seeds m<sup>-2</sup> per species) or high density (350 seeds m<sup>-2</sup> per species) in exclosures that either admitted or excluded voles. Birds, controlled initially, did not influence this species, so they are not discussed further. Each 14 × 14-m plot was divided into four 7 × 7-m subplots, of which two were randomly selected to admit and two to exclude voles. Exclusion subplots lacked gates and had aluminum flashing bent over the top as an outside overhang of 20 cm. Rodents were allowed access to half of the subplots with similar fences perforated by four ground-level 5 × 5-cm gates. For details of planting design, species planted, and selective herbivory on vegetation in the first season (1997), see a study by Howe and Brown (1999). The minimum number of voles (*Microtus pennsylvanicus*) per hectare at the site from live-trap censuses for May and October of 2000 was 155 and 35, respectively, following 2 yr of low abundance (Howe et al. 2002). No other vertebrate herbivores were observed.

### Plant Sampling

Biomass and reproductive sampling of this species in September 2000 was done in the context of estimates of abundance from October 1998 to 2000. *Desmanthus* plants were counted from five permanent square-meter sampling plots in each subplot, averaged by subplot, and used to estimate total abundance. *Desmanthus* plants were collected using five blind peg tosses in each of 96 7 × 7-m subplots. The plant closest to a landed peg was collected (table 1), excluding those in the five permanent square-meter sampling plots. If a peg landed in a permanent square-meter sampling plot, it was tossed again, and another plant was collected. Methods were designed to minimize bias and preserve the integrity of this ongoing experiment.

**Table 1**

**Number of *Desmanthus illinoensis* Plants Collected in 2000 for Analyses on Counts, Biomass, and Reproductive Measures**

Planting density	Voles	Plants collected	
		June plots	December plots
High	Present	35	5
High	Absent	49	30
Low	Present	35	10
Low	Absent	60	55

Note. Each cell represents samples out of 60 blind peg-toss collection attempts (five tosses per subplot for 12 subplots) outside of the five permanent square-meter plots. Samples of less than 60 per cell indicate that on some peg tosses, plants were not collected because they were within permanent sampling plots of other studies or had been collected for other random tosses or because there were no *Desmanthus* in the plot.

Response variables include aboveground vegetative biomass as a component of vigor and allocation percentage of biomass to reproduction, seed production, and mass per seed as components of fitness. We use a covariate of neighborhood biomass per subplot to factor out the effect of competition associated with plant crowding from competition that may be indirectly influenced by vole herbivory. *Desmanthus* biomass and reproductive output were assayed with (1) aboveground vegetation oven-dried to constant mass (hereafter "biomass"), (2) biomass percentage allocated to reproductive structures (fruit mass divided by the sum of aboveground biomass and fruit mass), (3) number of fruits per plant, (4) number of seeds per plant (fecundity), and (5) seed mass (total seed mass per fruit divided by number of seeds per fruit). Three fruits per plant were randomly collected; seeds were removed from capsules and counted by hand. Fecundity was calculated from seeds counted per fruit multiplied by the number of fruits per plant. Reproductive measures were averaged by plant and then by subplot.

Neighborhood biomass was determined by clipping vegetation in three randomly selected  $0.50 \times 0.50$ -m squares within each  $7 \times 7$ -m subplot after *Desmanthus* sampling. Belowground biomass was not sampled because extensive digging to expose diffuse root systems in hard clay soils would have compromised an ongoing experiment by eliminating the study species from some plots and disturbing surrounding vegetation in all plots. Samples of aboveground biomass were taken after the growing season to minimize effects on competitive relations among species.

### Statistical Analyses

We used repeated-measures MANOVA (Potvin 1993; von Ende 1993; Kleinbaum et al. 1998; Zar 1999; Tim 2002) to test for the effects of herbivory, planting density, planting season (grouping factors), and time (within factor) on *Desmanthus* counts from 1998 to 2000. To simplify the interpretation of treatment effects on *Desmanthus* counts, we also analyzed count data for the 2000 season separately from previous years with a Kruskal-Wallis ranked ANOVA (Zar 1999). This allowed an overview of ongoing treatment effects across time as well as close examination of effects on

*Desmanthus* abundance in a year of high vole numbers. We used data from the year 2000 to investigate the effect of planting density and vole herbivory on biomass and reproduction separated by planting season. December plantings held too few plants to use a statistical model that fully crossed planting density and vole treatments. Therefore, we first used a MANOVA (Scheiner 1993; Zar 1999) on data from December plantings to test for the effect of planting density on *Desmanthus* biomass and reproduction. Second, we used a MANCOVA on data from June plantings to test for the effects of planting density, vole herbivory, and surrounding biomass on *Desmanthus* biomass and reproductive output. An estimate of aboveground biomass of all plant species per subplot from the year 2000 served as the neighborhood biomass covariate for this analysis. Third, we used a MANOVA on data from treatments with low-density plantings without voles to test for the effect of planting season on *Desmanthus* biomass and reproduction.

For multivariate analyses, univariate tests were considered statistically significant if the associated Wilks's  $\lambda$  for experiment-wise error was significant at  $P \leq 0.05$ . Dependent variables were logarithmically transformed, with the exception of biomass percentage, which was arcsine-square root transformed. Transformations met the assumptions of normality and homoscedasticity. Analyses were conducted with Systat 10.

The experiment was designed to permit a split-plot analysis (which would have sharply reduced degrees of freedom) if field position effects were important, but they were not. Summary statistics due to vole herbivory or other factors given as reduction or increase percentage may be within treatments or pooled across treatments, as indicated.

## Results

### Abundance over Time

Planting density significantly affected *Desmanthus* counts ( $F_{1,89} = 52.32$ ,  $P < 0.0001$ ), suggesting sensitivity to plant crowding (table 2). Planting density interacted significantly with time (Wilks's  $\lambda = 0.651$ ,  $F_{2,88} = 23.624$ ,  $P < 0.0001$ ) in linear and nonlinear terms ( $F_{1,89} = 42.844$ ,  $P < 0.0001$ ;

**Table 2**

**Estimated Abundances for *Desmanthus illinoensis* Collected from Each Treatment (Planting Season, Planting Density, and Vole Presence or Absence)**

Planting time	Planting density	Voles	Plant count			Change 1998–2000 (%)
			1998	1999	2000	
June	High	Present	5.27 (12)	17.83 (10)	1.68 (7)	–68.0
June	High	Absent	5.14 (12)	6.70 (10)	5.00 (10)	–2.7
June	Low	Present	1.05 (12)	1.08 (12)	1.25 (10)	+19.0
June	Low	Absent	1.20 (12)	1.08 (12)	1.88 (12)	+56.6
December	High	Present	16.17 (12)	1.65 (9)	1.25 (6)	–92.3
December	High	Absent	12.7 (12)	1.60 (10)	1.85 (6)	–85.4
December	Low	Present	2.93 (12)	0.733 (9)	0.201 (4)	–93.1
December	Low	Absent	3.00 (12)	1.12 (11)	1.82 (11)	–39.3

Note. Each treatment contained 12 subplots. Plant counts represent means from five permanent square-meter stations per subplot. The number of subplots where plants were found is given in parentheses after plant counts.

$F_{1,89} = 6.764$ ,  $P < 0.05$ ). *Desmanthus* declined by 78% from 1998 to 2000 in high-density plots and by 37% in low-density plots (univariate  $F$ -test:  $F_{2,178} = 26.611$ ,  $P < 0.0001$ ). Planting season also interacted significantly with time (Wilks's  $\lambda = 0.672$ ,  $F_{2,88} = 21.506$ ,  $P < 0.0001$ ) in linear and nonlinear terms ( $F_{1,89} = 42.099$ ,  $P < 0.0001$ ;  $F_{1,89} = 26.418$ ,  $P < 0.0001$ ). Reflecting high establishment densities, *Desmanthus* in December plantings showed an 85% reduction in numbers by the year 2000, while lower establishment densities in June plots showed a 24% reduction in numbers from 1998 to 2000 (univariate  $F$ -test:  $F_{2,178} = 35.913$ ,  $P < 0.0001$ ). By the year 2000 (see table 2), densities were roughly 1–2 m<sup>-2</sup> in most circumstances. They were more than twice that value in high-density June plantings from which voles were excluded and were very sparse in December low-density plantings to which voles had access.

Planting season by density interacted with time (Wilks's  $\lambda = 0.788$ ,  $F_{2,88} = 11.811$ ,  $P < 0.001$ ) in linear and nonlinear terms ( $F_{1,89} = 17.245$ ,  $P < 0.0001$ ;  $F_{1,89} = 21.776$ ,  $P < 0.0001$ ) (see table 2). *Desmanthus* in high-density plots planted in June showed a 38% decline, whereas low-density plots planted in June showed a 39% increase from 1998 to 2000. In contrast, *Desmanthus* in December plantings declined in both density treatments; counts declined 89% in high-density plots and 66% in low-density plots from 1998 to 2000 (univariate  $F$ -test:  $F_{2,178} = 19.032$ ,  $P < 0.001$ ).

Kruskal-Wallis ANOVA revealed that in the year 2000, *Desmanthus* counts were 48% greater in high- than in low-density plots ( $F_{1,9} = 5.234$ ,  $P < 0.05$ ) and 58% lower in the presence than in the absence of voles ( $F_{1,9} = 17.366$ ,  $P < 0.01$ ) (table 2). *Desmanthus* in December plantings were 47% less common than their June counterparts ( $F_{1,9} = 3.532$ ,  $P < 0.05$ ).

### Biomass and Reproduction

Voies also affected *Desmanthus* biomass and reproductive performance. Elimination of *Desmanthus* from several December plots in the year 2000 made statistical tests on biomass and reproductive variables from December vole-accessible plots unreliable or infeasible (table 2). We used a MANCOVA to test for the effects of total surrounding plant biomass (covariate), planting density, and voies on *Desmanthus* biomass and reproduction in June plots. There were no significant main or interaction effects (surrounding biomass  $\times$  density and surrounding biomass  $\times$  vole) on any plant response variables, indicating that *Desmanthus* responded to neighbor crowding rather than neighbor size. This allowed us to factor out asymmetrical competition from herbivore effects on neighboring plants.

*Desmanthus* was affected by planting density in June plots (Wilks's  $\lambda = 0.555$ ,  $F_{6,25} = 3.345$ ,  $P < 0.05$ ). Biomass per *Desmanthus* plant was 55% greater in low- than in high-density plots ( $115.0 \pm 25.6$  and  $51.3 \pm 8.8$ , respectively) ( $F_{1,30} = 7.563$ ,  $P < 0.05$ ). Reproductive allocation, fruits per plant, seeds per plant, seeds per fruit, and mass per seed were not significantly affected by planting density.

Vole herbivory significantly affected *Desmanthus* in June plantings (Wilks's  $\lambda = 0.389$ ,  $F_{6,25} = 6.556$ ,  $P < 0.001$ ). Voies reduced biomass per individual by 51% and number of fruits per plant by 40% ( $F_{1,30} = 12.178$ ,  $P < 0.01$ ;  $F_{1,30} =$

$10.379$ ,  $P < 0.01$ ) (fig. 1a, 1b, respectively). In the absence of voies, *Desmanthus* in June plantings produced 44% more seeds per plant ( $F_{1,30} = 4.778$ ,  $P < 0.05$ ) with twice the weight per seed ( $F_{1,30} = 6.176$ ,  $P < 0.05$ ) compared to plants where voies had access (fig. 1c, 1d, respectively). Voies did not affect seeds per fruit.

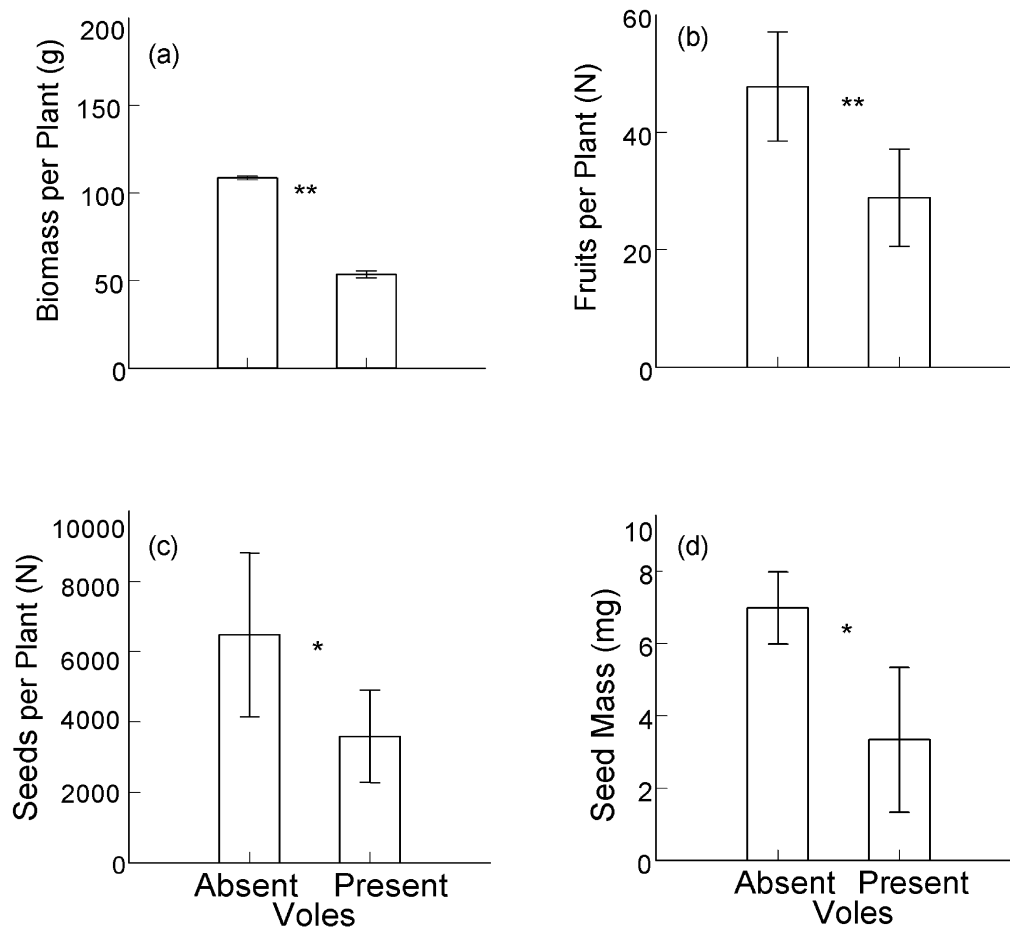
To assess effects imposed by sowing time on *Desmanthus* without complications of crowding or herbivory, we used a MANOVA with the effect of planting season restricted to low-density and vole-exclusion plots for the year 2000 (table 3). This test of planting season under the otherwise most favorable conditions in our design was significant (Wilks's  $\lambda = 0.163$ ,  $F_{6,14} = 12.024$ ,  $P < 0.001$ ). Biomass per plant was 78% greater for June relative to December plantings ( $F_{1,19} = 29.254$ ,  $P < 0.001$ ). Fruits and seeds per plant were 54% and 68% lower, respectively, in December than June plantings ( $F_{1,19} = 10.447$ ,  $P < 0.01$ ;  $F_{1,19} = 6.661$ ,  $P < 0.05$ ). Reproductive allocation was 38% higher in December than in June plantings ( $F_{1,19} = 7.985$ ,  $P < 0.05$ ), reflecting higher reproductive biomass per unit weight in smaller plants from December plantings. Planting season did not affect seeds per fruit or mass per seed.

### Discussion

Obvious and cryptic suppression of *Desmanthus illinoensis* by voies are direct effects that are indirectly influenced by ecological context. *Desmanthus* abundances declined with time as plants matured for all treatments, except June low-density plantings. In a year of high ambient vole abundance, voies all but eliminated the species in December plantings to which they had access, while in June plantings, vole access reduced only biomass and reproductive output. We hypothesize that *Desmanthus* withstands herbivory less well in a community context that increases preference of voies for its shoots and simultaneously favors its competitors.

The performance of *Desmanthus* in our experimental plantings offers clues to its sparse distribution in seminatural habitats in the Upper Midwest (see Latting 1961) as well as its disappearance in frost-seeding restorations (Jackson 1999). Despite far greater seedling emergence in our December than June plantings, fewer adults established, and abundance, plant size, and reproductive output were poorest in December plantings. These negative effects existed if voies were excluded but were strongly amplified by voies. By the end of the growing season in the year 2000, 3 yr after planting, voies and competition eliminated this species from some replicates and reduced *Desmanthus* to a trace component of communities planted with December frost seedings.

Density, herbivory, and planting season are each likely to influence fitness by altering plant size. Larger plants compete better (Berendse and Elberse 1990; see also Warren et al. 2002), conserve more water, use more resources, gain more carbon (Knapp and Fahnestock 1990), and are more likely to recover from insect damage in subsequent years (Marquis 1984; Horvitz and Schemske 2002) than smaller plants of the same species. We expected that high density, adverse competitive conditions in frost seedings, and vole herbivory would likewise affect *Desmanthus* size and fecundity. We did not expect major effects on seed size.



**Fig. 1** *Desmanthus illinoensis* biomass and reproductive response to vole access in June plantings. *a*, Biomass per plant; *b*, number of fruits per plant; *c*, number of seeds per plant; *d*, mass per seed. Means are  $\pm$ SE. One asterisk =  $P < 0.05$ , two asterisks =  $P < 0.01$ .

Reduced fecundity and inferior seeds affect fitness. All things being equal, reduced fecundity diminishes the opportunity for recruitment (Salisbury 1942). For instance, reduction in seed numbers of *Cirsium canescens* Nutt. (Asteraceae) by insect herbivores reduces density of progeny and restrains seedling recruitment (Louda and Potvin 1995). Seed size also influences recruitment. In general, larger plants have larger seeds (Harper 1977; Mack and Harper 1977; Sletvold 2002), and larger seeds have greater nutrient reserves (Salisbury

1942), have increased seedling emergence (Tripathi and Khan 1990), become larger seedlings (Salisbury 1942), grow more rapidly and produce more flowers (Stanton 1984), produce longer roots that confer greater drought tolerance (Wulff 1986), win intraspecific seedling competition more (Howe and Richter 1982), and increase adult longevity more (Silvertown 1981) compared to smaller seeds of the same species. Advantages of large seed size are particularly relevant in closed or crowded communities, such as prairies, where

**Table 3**  
Reproductive Allocation of *Desmanthus illinoensis* in the Year 2000 for Low-Density June and December Plantings Where Voles Did Not Have Access

Planting time	Individual biomass (g)	Biomass of reproductive structures (%)	Fruits per plant	Seeds per plant	Seeds per fruit	Seed mass (mg)
June	163.2 $\pm$ 42.9**	20.2 $\pm$ 3.7*	68.1 $\pm$ 16.3**	9902.0 $\pm$ 4490.3*	89.4 $\pm$ 19.6	7.9 $\pm$ 4.1
December	36.1 $\pm$ 5.8	32.7 $\pm$ 3.8	31.4 $\pm$ 5.4	3183.8 $\pm$ 822.4	77.8 $\pm$ 12.0	4.2 $\pm$ 0.4

Note. Analysis was performed on transformed data. Data given are mean  $\pm$  SE from vole-exclusion and low-density plantings. Degrees of freedom are 1 and 19.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

competition for light is intense (Rabinowitz 1978; Glenn-Lewin et al. 1990; see also Gross 1984). In comparisons among species, Rabinowitz and her colleagues (Rabinowitz and Rapp 1981; Rabinowitz et al. 1984) find that large-seeded grasses are more abundant than small-seeded grasses, despite dispersal advantages for small-seeded species. We hypothesize that voles compromise *Desmanthus* by simultaneously reducing seed number, seed size, and plant abundance.

Vole herbivory limited the reproductive potential of *Desmanthus* populations in both obvious and cryptic ways. Adult plant density and output in the year 2000 pooled across planting densities allowed calculation of seed rain, showing clearly how vole herbivory affected *Desmanthus* population prospects. In June plots, *Desmanthus* plant stands protected from voles produced 17,691 seeds  $m^{-2}$ , nearly three times the 5837 seeds  $m^{-2}$  in June plantings accessible to rodents. Comparable calculations for December plantings were 4133  $m^{-2}$  with voles excluded and 52 seeds  $m^{-2}$  with voles present. This amounts to a 99% reduction of seed density within the December plantings and more than a 99.95% reduction over the most favorable treatment in the experiment (June plots protected from voles). If each seed represents an opportunity for establishment and growth, recolonization by *Desmanthus* when voles are present involves thousands fewer opportunities per parent plant, and each opportunity is likely to have a diminished chance of germination and establishment as a consequence of drastically reduced seed size.

We hypothesize that competition from early germinators in December plantings may disadvantage this warm-season legume so that it succumbs easily to the burdens of herbivory. Early-season grasses *Elymus canadensis* L. and *Phalaris arundinacea* L. are favored in December plantings (see Howe et al. 2002), where *Desmanthus* abundance is lowest. *Desmanthus* growth is at a peak during July and August, when growth of cool-season grasses is low (DeHaan et al. 2003). The overall effect of voles is to accentuate disadvantages of some assemblages of competitors to *Desmanthus*, much as voles in quite different experimental communities accentuated advantages to otherwise dominant (e.g., *Rudbeckia subtomentosa* L.) species (Howe and Lane 2004). Our experiment provided some circumstances in which this legume survived vole herbivory, with partial and cryptic suppression of reproduction. Other refuge scenarios exist. Slow-growing *Betula pendula* L. seedlings in Finland (Pusenius et al. 2002) and *Desmanthus* individuals planted away from woodland edges in reconstructed tallgrass prairies in Iowa also escaped extreme vole herbivory pressure (Nickel et al. 2003). In highly disturbed moist pastures and old fields of the upper Midwest, where dominance by early  $C_3$  grasses and abundant microtine rodents is the norm, conditions may be unfavorable for *Desmanthus* largely because of vole herbivory on competitively weakened populations.

Habitats dominated by warm-season perennials suit *D. illinoensis* better. *Desmanthus illinoensis* prospers and even can become dominant when seeded with warm-season grasses, whether an exotic African grass (*Panicum coloratum* L.; Dovel et al. 1990) or native warm-season species (*Panicum virgatum* L. and *Sorghastrum nutans* L.; Posler et al. 1993). Our June plantings favor late-emerging  $C_4$  grasses that do not

limit *Desmanthus* growth as much as early-season grasses (see Howe et al. 2002). Alternative emergence scenarios probably affect *Desmanthus* abundance in natural habitats as well.

When planted with grass mixtures, nodulating legumes that fix nitrogen (N) can play important roles in livestock forage (Whitman 1980; Cook and Dolby 1981; Posler et al. 1993; Springer et al. 2001) as well as providing a source of N to soils that other plants can use (Harper 1977; Hoveland 1989). In high-density monocultures (72–157 plants  $m^{-2}$ ), *D. illinoensis* N fixation after the second year of growth can range from 60 to 142  $kg\ ha^{-1}\ N$  (Byun et al. 2004). Much lower field densities in our communities, even under the best conditions (three to five plants  $m^{-2}$  in June plantings with no vole access in 2000; see table 2) suggest that the community effect is not great. In the Chicago region, atmospheric deposition of  $NH_4^+$  and  $NO_3^-$  from industry and surrounding agriculture totaling 12–25  $kg\ ha^{-1}$  probably masks any effect (NADP station at Argonne National Laboratory from 1981–2004; <http://nadp.sws.uiuc.edu/sites/sitemap.asp?state=il>; see Lane and BassiriRad 2002). Nitrogen fixation may give associated species an advantage on low-N soils, but this is unlikely in N-rich soils or where atmospheric deposition is extensive.

Obvious and cryptic suppression of *D. illinoensis* by voles illustrates the power of experimental restoration as a scientific tool as well as the importance of contingent events. Absence of this species from a site might suggest that edaphic conditions or interactions with other plants precluded its presence, perhaps suggesting conditions falling outside the fundamental niche of the species or constrained by competitors to a limited realized niche elsewhere (e.g., Vandermeer 1972). Vigorous establishment of *Desmanthus* in all of our planting treatments but smaller adult size in communities established in December plantings indicates that competitive constraints are part of the story. The defining condition that determined presence or absence of the species in our experiment, however, is vole access to those communities planted in December. This obvious suppression of the species by voles would be anything but obvious in native communities in the absence of experimental manipulation, since the evidence (*Desmanthus* plants) would not exist. Likewise, in a natural world in which voles are ubiquitous and often common, cryptic suppression of *Desmanthus* reproduction from reduction in size, fecundity, and, most surprising, seed size would be invisible in the absence of experimentation. Without seeing how plants perform in a favorable community without voles, it is difficult or impossible to recognize the degree to which vole herbivory reduces components of fitness.

### Acknowledgments

We are grateful for comments on the manuscript from S. Balcomb, N. Cordeiro, P. Fine, C. Martinez-Garza, E. Hooper, N. Ingle, M. Jorge, G. Nunes-Iturri, E. O'Brien, S. Saha, A. T. Sullivan, and two anonymous reviewers. We thank C. Dunn and the staff at the Morton Arboretum for their support and students who helped maintain the experiment. We thank the National Science Foundation for financial support.

## Literature Cited

- Belsky AJ 1987 The effects of grazing: confounding the ecosystem, community, and organism scales. *Am Nat* 129:777–783.
- Beran DD, RA Masters, RE Gaussoin, F Rivas-Pantonia 2000 Establishment of big bluestem in Illinois bundleflower mixtures with imazapic and imazethapyr. *Agron J* 92:460–465.
- Berendse F, WTH Elberse 1990 Competition and nutrient availability in heathland and grassland ecosystems. Pages 93–115 in JB Grace, D Tilman, eds. *Perspectives on plant competition*. Academic Press, New York.
- Brown JH, EJ Heske 1990 Control of a desert-grassland transition by a keystone rodent guild. *Science* 250:1705–1707.
- Brown JS 1994 Restoration ecology: living with the Prime Directive. Pages 355–380 in ML Bowles, CJ Whelan, eds. *Restoration of endangered species: conceptual issues, planning, and implementation*. Cambridge University Press, Cambridge.
- 1999 Vigilance, patch use and habitat selection: foraging under predation risk. *Evol Ecol Res* 1:149–171.
- Byun J, CC Sheaffer, MP Russelle, NJ Ehlke, DL Wyse, PH Graham 2004 Dinitrogen fixation in Illinois bundleflower. *Crop Sci* 44:493–500.
- Cook SJ, GR Dolby 1981 Establishment of buffel grass, green banic, and siratro from seed broadcast onto a speargrass pasture in southern Queensland, Australia. *J Agr Res* 321:749–759.
- DeHaan LR, NJ Ehlke, CC Sheaffer, DL Wyse 2003 Evaluation of diversity among and within accessions of Illinois bundleflower. *Crop Sci* 43:1528–1537.
- Dovel RL, MA Hussey, EC Holt 1990 Establishment and survival of Illinois bundleflower interseeded into an stabled kleingrass pasture. *J Range Manag* 43:153–156.
- Fowler NL 1984 The role of germinating date, spatial arrangement, and neighborhood effects in competitive interactions in *Linum*. *J Ecol* 72:307–318.
- Glenn-Lewin DC, JL Johnson, T Jurik, A Akey, M Loeschke, T Rosburg 1990 Fire in central North American grasslands: vegetative reproduction, seed germination, and seedling establishment. Pages 28–45 in SL Collins, LL Wallace, eds. *Fire in North American tall grass prairie*. University of Oklahoma Press, Norman.
- Gross KL 1984 Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *J Ecol* 72:369–387.
- Harper JL 1977 *Population biology of plants*. Academic Press, New York.
- Horvitz CC, DW Schemske 2002 Effects of plant size, leaf herbivory, local competition and fruit production on survival, growth and future reproduction of a Neotropical herb. *J Ecol* 90:279–290.
- Hoveland CS 1989 Legume persistence under grazing in stressful environments in the United States. Pages 375–383 in GC Marten, ed. *Persistence of forage legumes*. American Society of Agronomy, Madison, WI.
- Howe HF 1994 Response of early and late-flowering plants to fire season in experimental prairies. *Ecol Appl* 4:121–131.
- Howe HF, JS Brown 1999 Effects of birds and rodents on synthetic tallgrass communities. *Ecology* 80:1776–1781.
- 2001 The ghost of granivory past. *Ecol Lett* 4:371–378.
- Howe HF, JS Brown, B Zorn-Arnold 2002 A rodent plague on prairie diversity. *Ecol Lett* 5:30–36.
- Howe HF, D Lane 2004 Vole-driven succession in experimental wet prairie restorations. *Ecol Appl* 14:1295–1305.
- Howe HF, WM Richter 1982 Effects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. *Oecologia* 53:347–351.
- Huntly N 1991 Herbivores and the dynamics of communities and ecosystems. *Annu Rev Ecol Syst* 22:477–503.
- Inouye RS, GS Byers, JH Brown 1980 Effects of predation and competition on survivorship, fecundity and community structure of desert annuals. *Ecology* 61:1344–1351.
- Jackson LL 1999 Establishing tallgrass prairie on grazed permanent pasture in the upper Midwest. *Restor Ecol* 7:127–138.
- Jordan WR III, ME Gilpin, JD Aber 1987 Restoration ecology: ecological restoration as a technique for basic research. Pages 3–22 in WR Jordan III, ME Gilpin, JD Aber, eds. *Restoration ecology: a synthetic approach to ecological research*. Cambridge University Press, Cambridge.
- Keiffer CH, IA Ungar 2002 Germination and establishment of halophytes on brine-affected soils. *J Appl Ecol* 39:402–415.
- Kleinbaum DG, LL Kuper, KE Muller, A Nizam 1998 *Applied regression analysis and other multivariate methods*. Duxbury, Pacific Grove, CA.
- Knapp AK, JT Fahnestock 1990 Influence of plant size on the carbon and water relations of *Cucurbita foetidissima* HBK. *Funct Ecol* 4:789–797.
- Lane DR, H BassiriRad 2002 Differential responses of tallgrass prairie species to nitrogen loading and varying ratios of  $\text{NO}_3^-$  to  $\text{NH}_4^+$ . *Funct Plant Biol* 29:1227–1235.
- Latting J 1961 The biology of *Desmanthus illinoensis*. *Ecology* 42:487–493.
- Lawton JH 1999 Are there general laws in ecology? *Oikos* 84:177–192.
- Lee TD, FA Bazzaz 1980 Effects of defoliation and competition on growth and reproduction in the annual plant *Abutilon theophrasti*. *J Ecol* 68:813–821.
- Lindroth RL 1989 Mammalian herbivore-plant interactions. Pages 163–206 in WG Abrahamson, ed. *Plant-animal interactions*. McGraw-Hill, New York.
- Louda SM, KH Keeler, RD Holt 1990 Herbivore influences on plant performances and competitive interactions. Pages 413–444 in JB Grace, D Tilman, eds. *Perspectives on plant competition*. Academic Press, New York.
- Louda SM, MA Potvin 1995 Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. *Ecology* 76:229–245.
- Mack RN, J Harper 1977 Interference in dune annuals: spatial pattern and neighborhood effects. *J Ecol* 65:345–363.
- Marquis RJ 1984 Leaf herbivores decrease fitness in a tropical plant. *Science* 226:537–539.
- Martinez-Garza C, S Saha, HF Howe, V Torres, JS Brown 2004 Size structure of tallgrass perennials. *Oecologia* 139:433–439.
- Meiners SJ, ST Handel 2000 Additive and nonadditive effects of herbivory and competition on the tree seedling mortality, growth, and allocation. *Am J Bot* 87:1821–1826.
- Mulder CPH, RW Ruess 1998 Effects of herbivory on arrowgrass: interactions between geese, neighboring plants, and abiotic factors. *Ecol Monogr* 68:275–293.
- Müller-Schärer H 1991 The impact of root herbivory as a function of plant density and competition: survival, growth and fecundity of *Centaurea maculosa* in field plots. *J Appl Ecol* 28:759–776.
- Nickel AM, BJ Danielson, KA Maloney 2003 Wooded habitat edges as refugia from microtine herbivory in tallgrass prairies. *Oikos* 100:525–553.
- Nötzold R, B Blossey, E Newton 1998 The influence of below ground herbivory and plant competition on growth and biomass allocation of purple loosestrife. *Oecologia* 113:82–93.
- Ostfeld RS, RH Manson, CD Canham 1997 Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78:1531–1542.
- Posler GL, AW Lenssen, GL Fine 1993 Forage yield, quality, compatibility, and persistence of warm-season grass legume mixtures. *Agron J* 85:554–560.

- Potvin C 1993 ANOVA: experiments in controlled environments. Pages 46–68 in SM Scheiner, J Gurevitch, eds. Design and analysis of ecological experiments. Chapman & Hall, New York.
- Pusenius J, K Prittinen, J Heimonen, K Koivunoro, M Rousi, H Roininen 2002 Choice of voles among genotypes of birch seedlings: its relationship with seedling quality and preference of insects. *Oecologia* 130:426–432.
- Rabinowitz D 1978 Abundance and diaspore weight in rare and common prairie grasses. *Oecologia* 37:213–219.
- Rabinowitz D, JK Rapp 1981 Dispersal abilities of seven sparse and common grasses from Missouri prairie. *Am J Bot* 68:616–624.
- Rabinowitz D, JK Rapp, PM Dixon 1984 Competitive abilities of sparse grass species: means of persistence or cause of abundance. *Ecology* 65:1144–1154.
- Ross MA, JL Harper 1972 Occupation of biological space during seedling establishment. *J Ecol* 60:77–88.
- Salisbury EJ 1942 The reproductive capacity of plants. Bell, London.
- Schabel AB, DR Peart 1994 Effects of competition, herbivory and substrate disturbance on growth and size structure in pin cherry (*Prunus pennsylvanica* L.) seedlings. *Oecologia* 98:150–158.
- Scheiner SM 1993 MANOVA: multiple response variables and multispecies interactions. Pages 94–112 in SM Scheiner, J Gurevitch, eds. Design and analysis of ecological experiments. Chapman & Hall, New York.
- Schoener T 1971 Theory of feeding strategies. *Annu Rev Ecol Syst* 2: 369–404.
- Silvertown SW 1981 Seed size, life span, and germination date as coadapted features of plant life history. *Am Nat* 108:409–506.
- Sletvold N 2002 Effects of plant size on reproductive output and offspring performance in the facultative biennial *Digitalis purpurea*. *J Ecol* 90:958–966.
- Springer TL, GE Aiken, RW McNew 2001 Combining ability of binary mixtures of native, warm season grasses and legumes. *Crop Sci* 41:818–823.
- Stanton ML 1984 Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* 65: 1105–1112.
- Timm NH 2002 Applied multivariate analysis. Springer, New York.
- Tripathi RS, MC Khan 1990 Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest. *Oikos* 57:289–296.
- Vandermeer JH 1972 Niche theory. *Annu Rev Ecol Syst* 3:107–132.
- von Ende CN 1993 Repeated-measures analysis: growth and other time dependent measures. Pages 113–137 in SM Scheiner, J Gurevitch, eds. Design and analysis of ecological experiments. Chapman & Hall, New York.
- Warren J, F Wilson, A Diaz 2002 Competitive relationships in a fertile grassland community: does size matter? *Oecologia* 132:125–130.
- White J 1985 The thinning rule and its application to mixtures of plant populations. Pages 291–309 in J White, ed. Studies on plant demography: a festschrift for John L. Harper. Academic Press, New York.
- Whitman PC 1980 Tropical pasture science. Oxford University Press, New York.
- Wulff RD 1986 Seed size variation in *Desmodium paniculatum*. II. Effects on seeding, growth and physiological performance. *J Ecol* 74:99–114.
- Yoda K, T Kira, H Ogawa, K Hozumi 1963 Self-thinning in overcrowded pure stands under cultivated and natural conditions. *J Biol Osaka City Univ* 14:107–129.
- Zar JH 1999 Biostatistical analysis. 4th ed. Prentice Hall, Upper Saddle River, NJ.