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Planting densities and bird and rodent absence affect size distributions of four dicots in synthetic tallgrass communities

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Abstract Variability in the size distributions of populations is usually studied in monocultures or in mixed plantings of two species. Variability of size distributions of populations in more complex communities has been neglected. The effects of seeding density (35 or 350 seeds/species/m²) and presence of small vertebrates on the variability of size distributions were studied for a total of 1,920 individuals of 4 species in replicated synthetic communities of 18 species in northern Illinois. End-of season height and above-ground biomass were measured for prairie perennials *Dalea purpurea* (purple prairie clover), *Echinacea purpurea* (purple coneflower), *Desmanthus illinoensis* (Illinois bundleflower) and *Heliopsis helianthoides* (early sunflower). Variability in biomass distribution of the four target species was twice as great at low than at high densities when small vertebrates were excluded. Our results suggest that inter- and intraspecific competition may affect all individuals more under high-density conditions, thereby reducing the variability in their biomass distributions within this community. This result, a consequence of plant-plant interaction, is obscured when small birds or mammals are present, presumably because either or both add variance that overwhelms the pattern.

Keywords *Dalea* · *Desmanthus* · *Echinacea* · *Heliopsis* · Tallgrass prairie

Introduction

The size distribution of a population expresses the natural variation among individual plants: it often also reflects

fitness hierarchies because large plants are generally more fecund than smaller conspecifics (Salisbury 1942; Mack and Harper 1977). Studies of monocultures show that differences in seedling density change initial size distributions. In general, plants in high-density monocultures are smaller and more variable in their size distributions than conspecifics at low densities (Harper 1977). Populations growing in high-density monocultures experience interference among individuals earlier, with the result that some small individuals are suppressed while larger ones gain a disproportionate advantage (Weiner 1985). In mixed plantations of two species, variation may arise due to species-specific competitive abilities (Westoby 1984; Weiner 1985; Scheiner 1987; Schwinning and Weiner 1998). These results from studies of monocultures and mixes of two species leave open the question whether density similarly affects size distributions in more complex polycultures or natural communities. One could imagine circumstances in which heterospecifics have similar effects on the growth of a given plant as have conspecifics. Alternatively, heterospecific effects might be so varied as to differ substantially from those of conspecifics, thereby limiting the relevance of results from studies of monocultures.

An outcome consistent with results from studies in monocultures would be if plants in high-density polycultures had greater variance in size distribution than those in low-density polycultures because the competitive abilities of species were dissimilar. For instance, the size distributions of plants of large- and small-statured species together could be analogous to the large and small individuals of one species, resulting in higher community variance at high than low densities.

In theory, a quite different outcome is possible. If individuals or species affect each other in the same proportion, variation in size distributions may be lower at high than low densities (Koyama and Kira 1956; Westoby 1984; Weiner and Thomas 1986; Weiner 1990; Bonan 1991; Hutchings 1997). In effect, diffuse competition from many species would affect individuals of a target species similarly. In real communities, grazing could alter the

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interactions among species, and therefore affect size variability. For instance, herbivores may increase variation of size distributions in a community if some species are preferentially suppressed and others ignored, or decrease it by reducing the sizes of large individuals or eliminating small ones (Cottam 1986; Gange and Brown 1989; Weiner 1988, 1993). Interactions between planting densities and herbivores in polycultures could change the predictions that have been made for monocultures, depending on which species are preferred by herbivores and the competitive abilities of eaten or ignored species.

Here we report the variation in end-of season biomass and height distributions of four dicots growing in a tallgrass polyculture in northern Illinois designed to test effects of ambient populations of foliage-eating rodents (*Microtus pennsylvanicus*) on synthetic prairies (Howe and Brown 1999; Howe et al. 2002). We ask: (1) whether the variation of above-ground biomass and end-of season height are higher in high- than low-density plantings, as happens in monocultures; and (2) whether size distributions of species that differ in size (a surrogate for competitive ability) and preference to small rodents are affected in predictable ways. Species preferred by rodents are expected to have lower variability in size distribution than species not preferred by rodents if the individuals of the species with the largest or smallest plants are diminished in size or eliminated by rodents. Either rodent effect could decrease variability in size distribution. However, at low plant densities, variability in size distributions of species not preferred by rodents may increase due to compensatory growth as competing plants are suppressed by herbivory.

Materials and methods

This experiment was carried out in Ware Field at the Morton Arboretum, Lisle, northern Illinois, United States (Howe and Brown 1999). In November 1995, 24 plots of 14×14-m were delineated, backhoed (plowing did not break the sod), later disked, and prepared for 1997 planting. Twelve plots used for the analysis reported here were planted in December 1997; 18 species were sown in 6 plots at low density (35 seeds/species/m², overall density 630 seeds/m²) and 6 plots at high density (350 seeds/species/m², overall density 6,300 seeds/m²). Each of the 12 plots had trenches around them, and each plot was bisected in each axis by similar trenches. This resulted in four 7×7-m subplots nested within each of the twelve 14×14-m plots. Hardware cloth 1.23-m high fenced the subplots. Each subplot corresponded to a different animal effect: bird (presence/absence) and mammal (presence/absence), fully crossed within each plot. Birds were excluded from half of the 48 subplots with 1.8-cm Bird-X netting from planting until June 1998. Rodents were excluded with aluminum flashing bent over the fences 15 cm on the outside in half the subplots to prevent voles from climbing over; rodents were admitted with 4 5×5-cm gates at ground level in half the subplots. The key rodent at issue, the meadow vole (*Microtus pennsylvanicus*), is folivorous in the growing season and partially granivorous in the winter. Bird enclosure is included as a level of treatment because birds are a potential source of variation in plant growth, although their indirect effect is through granivory that influences emergence density rather than folivory (Howe and Brown 1999).

In addition to the 12 plots examined here, we also examined size distributions for the same species in plots planted in June 1997. Those plants were two seasons old by the time final samples were

taken, and showed no significant difference in variation of size measures. We attribute this to two possible factors. One is possible loss of individuals before they were marked in their second year (seedlings from the December planting were marked as they emerged, and therefore were a representative sample of known age). A second is that, by the end of the second season, these perennial plants had reached mature size, and showed less variation overall. These results are not considered further.

For our analysis of size distributions we chose four tallgrass dicots of different sizes that are differentially preferred by small voles. Three species were browsed by voles in 1997 [*Dalea purpurea* (Fabaceae), *Echinacea purpurea* (Asteraceae), *Desmanthus illinoensis* (Mimosaceae)], and one was unaffected by voles [*Heliopsis helianthoides* (Asteraceae)]; see Howe and Brown 1999; Martínez-Garza et al. 2003]. Mean number of individuals per m² in low and high density, respectively, in our synthetic communities for target and other abundant dicots in 1998 were *Echinacea purpurea* (7.88/m² and 38.58/m²), *Heliopsis helianthoides* (5.81/m² and 39.10/m²), *E. pallida* (5.97/m² and 24.51/m²), *Rudbeckia hirta* (3.92/m² and 15.01/m²), *Solidago rigida* (5.53/m² and 17.15/m²), *Desmanthus illinoensis* (2.97/m² and 14.14/m²), *Achillea lanulosa* (0.94/m² and 7.39/m²) and *Dalea purpurea* (0.53/m² and 3.18/m²). Grasses in 1998 included *Elymus canadensis* (6.74/m² and 24.30/m²), *Panicum virgatum* (0.26/m² and 0.26/m²), *Phalaris arundinacea* (0.83/m² and 1.93/m²), *Koeleria micrantha* (3.04/m² and 1.10/m²), and *Sorghastrum nutans* (0.00/m² and 0.01/m²; Howe et al. 2002). Ten randomly selected seedlings of each of the four focal species in each subplot were tagged [closest seedling of a species to 10 random points per subplot, with assignments of points independent for each species (40 assignments per subplot)] in May 1998 for a total sample of 1,920 plants.

We measured above-ground biomass and height to evaluate size distributions. End-of-season height was measured in 1998 for all survivors of the 1,920 plants originally marked at the beginning of the growing season (hereafter height). Above-ground biomass was determined by randomly collecting five of the ten selected individuals per species per subplot. These 960 plants were oven-dried to constant mass at 100°C, and weighed (hereafter biomass).

All analyses were performed with STATISTICA 5.1 (StatSoft 1998). Multivariate Analysis of Variance (MANOVA) was used to test the effects of species, planting density and presence of small vertebrates on biomass and height. The variation in the distribution of biomass and height was described using the coefficient of variation calculated as the standard deviation of size (biomass or height) multiplied by 100 and divided by mean size (CV = SD * 100/mean) and it was corrected for sample size (Sokal and Rohlf 1995). CV is highly correlated with other measures of size distribution (i.e. Ginni coefficient; Weiner and Thomas 1986). Differences in the CV of size for species, planting densities, and presence of small vertebrates were tested with Analysis of Variance (ANOVA). Biomass, height and survival percentage were log-transformed to satisfy ANOVA assumptions. Means are accompanied by their standard errors throughout.

Results and discussion

End-of-season biomass and height

There was a general suppression of size at high densities. A three way MANOVA with species, planting density and presence of small vertebrates as fixed factors, and biomass and height as dependent variables showed that species had different end of season biomasses and heights (Wilks' lambda 0.06, F =152.1, $P_{(6, 310)}=0.0001$), with planting density having large effects on these variables pooled across species (Wilks' lambda 0.75, F =25.5, $P_{(2, 310)}=0.0001$). Presence of small vertebrates did not affect size

Table 1 Univariate analysis of variance of end of season above-ground biomass and height of four dicots growing in synthetic tallgrass prairie communities of 18 species in northern Illinois in November 1998. Samples are based on means of ten plants for height and five plants for biomass of each species per plot, for six plots per treatment

Factor	F	df	P
Species			
Biomass	70.96	3, 155	0.00001
Height	164.51	3, 155	0.00001
Density			
Biomass	49.73	1, 155	0.00001
Height	16.24	1, 155	0.00001
Presence of vertebrates			
Biomass	1.34	3, 155	0.09
Height	2.17	3, 155	0.25
Species * Density			
Biomass	0.81	3, 155	0.02
Height	3.35	3, 155	0.49
Species * Presence of vertebrates			
Biomass	0.56	9, 155	0.82
Height	0.58	9, 155	0.81
Density * Presence of vertebrates			
Biomass	1.02	3, 155	0.38
Height	1.19	3, 155	0.31
Species * Density * Presence of vertebrates			
Biomass	1.07	9, 155	0.38
Height	0.72	9, 155	0.68

at the end of the season (Wilks' lambda 0.94, $F = 1.44$, $P_{(6, 310)} = 0.019$). Second degree interactions in the MANOVA were not significant. Univariate analyses of variance for biomass and height separately are shown in Table 1. Pooled across species, individual plants were significantly heavier (4.18 ± 0.70 g) and taller (0.37 ± 0.03 m) at low than at high densities (1.13 ± 0.40 g and 0.29 ± 0.02 m). Post-hoc Tukey tests revealed that all species showed significantly higher biomass in low-density plantings except *Dalea*, while only *Desmanthus* showed significantly greater height in low than high-density plantings (Table 2). The overall effect of a ten-fold difference in planting density was a dramatic reduction in biomass with increased density (-73% per plant), and a slight reduction in height (-22% per plant, driven largely by *Desmanthus*).

Plant density affects performance in monocultures and polycultures. The general case seems to be that species are stunted in various measures of size as density increases

(Harper 1977). However, where competition for light is critical, dense stands may promote allocation to growth in height rather than mass. For instance, in the woodland annual *Impatiens pallida*, crowded plants are taller than uncrowded plants (Weiner et al. 1990). Our four species in complex polycultures generally declined in biomass with increased planting density, as is the usual case in monocultures (Harper 1977). *Dalea* biomass and height were not affected by density, probably because it is the smallest species and it is already suppressed by the dominant species independent of density.

Coefficient of variation (CV) in size distributions

Of special interest is the variation in plant performance as a function of community seeding density. A three way ANOVA with species, planting density and presence of

Table 2 End-of-season above-ground biomass and height of four dicots growing at high and low densities in synthetic tallgrass prairie communities of 18 species in northern Illinois in November 1998. Samples are based on means of ten plants for height and five plants

for biomass of each species per plot, for 6 plots per treatment. Number of asterisks shows the probability of significant differences between high and low density treatment tested with the Post-hoc Tukey test

	Biomass (g \pm SE)		Height (m \pm SE)	
	High	Low	High	Low
<i>Dalea</i>	0.16 \pm 0.02	0.39 \pm 0.09	0.20 \pm 0.01	0.20 \pm 0.01
<i>Echinacea</i>	1.45 \pm 0.21	4.39 \pm 0.80*	0.12 \pm 0.01	0.14 \pm 0.01
<i>Desmanthus</i>	0.44 \pm 0.08	2.89 \pm 0.80***	0.29 \pm 0.03	0.43 \pm 0.03**
<i>Heliopsis</i>	2.40 \pm 0.33	8.41 \pm 1.95**	0.54 \pm 0.04	0.67 \pm 0.04

* $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$

Table 3 Univariate analysis of variance of the coefficients of variation (CV, %) of biomass and height of four dicots growing in synthetic tallgrass prairie communities of 18 species in northern Illinois in November 1998. CVs were corrected for sample size and calculated with a sample of ten plants for height and five plants for biomass of each species per plot, for six plots per treatment

Factor	F	df	P
Species			
CV of biomass	11.34	3, 154	0.00001
CV of height	9.48	3, 154	0.00001
Density			
CV of biomass	4.25	1, 154	0.04
CV of height	0.23	1, 154	0.63
Presence of vertebrates			
CV of biomass	3.03	3, 154	0.03
CV of height	2.63	3, 154	0.05
Species * Density			
CV of biomass	1.29	3, 154	0.27
CV of height	0.98	3, 154	0.40
Species * Presence of vertebrates			
CV of biomass	0.66	9, 154	0.74
CV of height	0.87	9, 154	0.54
Density * Presence of vertebrates			
CV of biomass	2.68	3, 154	0.04
CV of height	2.13	3, 154	0.09
Species * Density * Presence of vertebrates			
CV of biomass	0.91	9, 154	0.51
CV of height	1.33	9, 154	0.22

Table 4 Coefficients of variation (CV, %) of biomass and height of four dicots growing in synthetic tallgrass prairie communities of 18 species in northern Illinois in November 1998. CVs were corrected for sample size and calculated with a sample of ten plants for height and five plants for biomass of each species per plot, for six plots per treatment. *Different letters* show significant differences among species with post-hoc Tukey test at least at $P \leq 0.05$

	CV (%)	
	Biomass	Height
<i>Dalea</i>	50.59 a	41.42 a
<i>Echinacea</i>	80.43 bc	34.53 a
<i>Desmanthus</i>	96.26 b	51.24 b
<i>Heliopsis</i>	70.83 c	41.33 a

small vertebrates as fixed factors, and CV of biomass or CV of height as dependent variables, showed that the species had different CVs of biomass and height (Table 3). Post-hoc Tukey tests revealed that the four target species varied substantially in the CV of biomass but slightly in the CV of height (Table 4). Moreover, the CV of height is inconsistent with different levels of animal access, whereas the CV for biomass is much greater, and significantly greater for plots accessible to birds, rodents, or both than those from which all small vertebrates are excluded (Table 5). Against this background of overall variation in CV, variation in each measure with density in animal-free enclosures reflects effects on size and fitness hierarchies due to plant-plant interactions without confounding effects of vertebrate granivory or herbivory.

Table 5 Coefficients of variation (CV, %) of biomass and height of four dicots growing in synthetic tallgrass prairie communities of 18 species in northern Illinois under different treatments of vertebrate presence. CVs were corrected for sample size and calculated with a sample of ten plants for height and five plants for biomass of each species per plot, for six plots per treatment. *Different letters* show significant differences among treatments with post-hoc Tukey test at least at $P \leq 0.05$

Treatment	CV (%)	
	Biomass	Height
All small vertebrates admitted	81.7 a	46.6 a
Birds excluded	68.3 a	42.3 ab
Mammals excluded	83.8 a	37.4 b
All excluded	64.3 b	42.3 ab

Biomass

Variation in biomass distribution was greater in low-density than high-density plantings when small vertebrates were excluded, but indistinguishable when they had access. Pooled over all four target species, the CV of biomass was significantly higher at low than high densities only when small vertebrates were excluded (Table 6, Fig. 1). Individual species showed significantly different CVs of biomass (Table 4). The presence of small vertebrates did not affect the CV of biomass at the species level (interaction species * presence of small vertebrates, Table 3). Of interest is the pooled effect over all four species because it shows a community-level response.

Table 6 Coefficients of variation (*CV*, %) of biomass of four dicots growing in synthetic tallgrass prairie communities of 18 species in northern Illinois at two planting densities and under different treatments of small vertebrate presence. *CV*s were corrected for sample size and calculated with a sample of five plants of each species per plot, for six plots per treatment

Treatment	CV (%) biomass		<i>P</i> H vs L
	High	Low	
All small vertebrates admitted	84.9	78.5	0.99
Birds excluded	65.7	70.8	0.99
Mammals excluded	78.5	89.1	0.98
All excluded	46.1	82.5	0.02

Height

Variation in height of all four species pooled was not influenced by planting densities over animal access treatments. The *CV* of height of the four target species pooled was indistinguishable at different planting densities (low density: 42.68 ± 2.1 ; high density: 41.58 ± 1.52 ; Table 3), across all treatments of vertebrate access. Species differed in *CV*s of height (Table 3). Tukey tests revealed that *Desmanthus* showed the highest variation in height distribution irrespective of density (Table 4). The other three species were similar with lower variation.

Survival

Mortality of marked seedlings was low, with no evidence that voles killed large or small individuals. A three way ANOVA with species, planting density and presence of small vertebrates as fixed factors, and survival percentage as dependent variable showed that survival differed by species, with *Dalea* and *Desmanthus* showing significantly lower survival ($84 \pm 0.02\%$ and $90 \pm 0.01\%$, respectively) than *Echinaceae* and *Heliopsis* ($99 \pm 0.003\%$ and $99 \pm 0.002\%$ respectively; Table 7). Survival was significantly higher at low ($95 \pm 0.01\%$) than at high density plantings ($91 \pm 0.01\%$; Table 7). Second degree interactions in the ANOVA were not significant. Survival was indistinguish-

Table 7 Analysis of variance of survival percentage of four dicots growing in synthetic tallgrass prairie communities of 18 species in northern Illinois at two planting densities and under different treatments of small vertebrate presence. Survival was calculated with a sample of ten plants of each species per plot, for six plots per

Factor	F	<i>df</i>	<i>P</i>
Species	36.98	3, 154	0.00001
Density	8.14	1, 154	0.004
Presence of vertebrates	0.64	3, 154	0.65
Species * Density	1.49	3, 154	0.21
Species * Presence of vertebrates	0.89	9, 154	0.52
Density * Presence of vertebrates	1.29	3, 154	0.27
Species * Density * Presence of vertebrates	0.93	9, 154	0.49

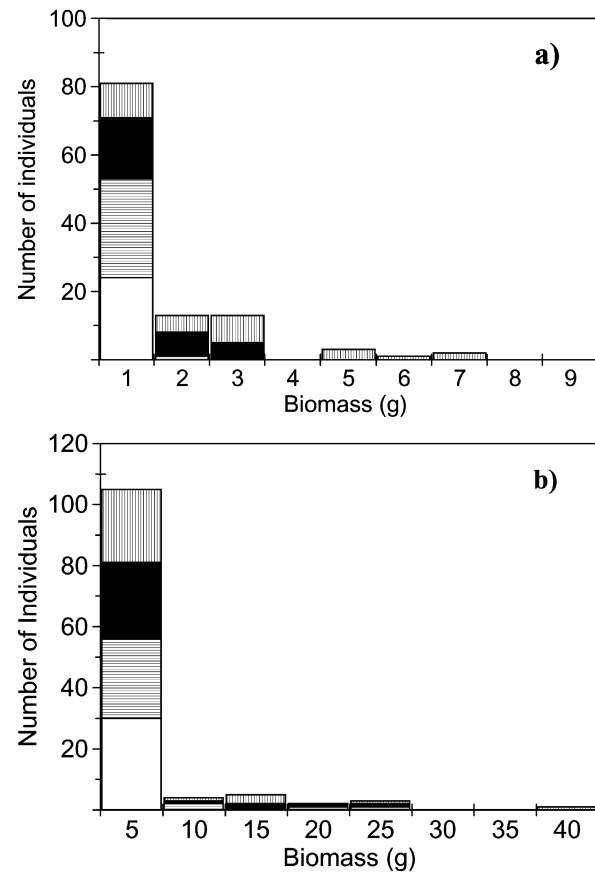


Fig. 1 Biomass distributions of *Dalea* (white), *Desmanthus* (horizontal lines), *Echinacea* (black), and *Heliopsis* (vertical lines) growing in synthetic tallgrass prairie communities of 18 species in northern Illinois when small vertebrates are excluded (a) in high density and (b) low density plantings. Note the difference in range of biomass for high compared to low density

able under different treatments of small vertebrate presence. In a previous study (Howe and Brown 1999), abundant voles browsed foliage, potentially changing competitive relationships, but did not kill the plants. In the 1998 season of low vole abundance and low plant mortality, there was no suggestion that large or small

treatment. The survival percentage for the species was calculated as the number of individuals originally marked surviving to the end of the growing season, divided by the number of individuals marked at the beginning of the growing season

individuals of these target plant species suffered disproportionate losses among the 1,920 marked plants.

Conclusions

Variability in size distributions results from variation in age and growth rates, and may be accentuated or suppressed by competition within and between species (Westoby 1984; Bonan 1991; Hutchings 1997) or by herbivory (Gange and Brown 1989). Variability in size distributions is rarely studied in multi-species communities (Keddy 1990), leading to the interesting question of when and how differences in densities affect plants in complex polycultures, as compared with monocultures in which variation in size and fecundity generally increase with density.

In our system, planting density affected measures of mean size as expected, but did not show greater variability in size with planting density. The overall variation in biomass of four target species was highest at low planting densities compared with high planting densities ten times higher. At high densities, interference among individuals and among species may have affected each species in the same proportion (Westoby 1984; Weiner 1985; Scheiner 1987; Schwinning and Weiner 1998). The mechanism cannot be tested directly with this experiment, but the evidence is as strong as exists to date. Our results are consistent with the assemblage-level thinning hypothesis (Stevens and Carson 1999), which holds that density alone may drive species richness through thinning events, similar to what happens in monocultures. Species in a community may have such broad niche breadths that inter- and intra-specific competition is similar for all of them. Therefore, in high planting densities, these equal interactions may decrease the variability in the size distributions of the component species of a community.

Animal activities might be expected to insert systemic bias or stochastic noise into the variability of size distributions, either from direct reduction of numbers or biomass (e.g. Howe and Brown 1999; Howe et al. 2002; Martínez-Garza et al. 2003), or indirect release of competitors least eaten by herbivores (Dirzo and Harper 1980; Howe and Brown 2000, 2001). High survival of our marked cohorts indicates that voles did not remove plants, but even when little indication of browsing was evident in this year of low vole abundance, rodents increased the variation in size distributions enough to obscure effects of plant-plant interactions. Birds have an indirect effect, removing up to 20% of the seeds of grasses and some forbs in high-density plantings, leaving the possibility open for release of less preferred dicots (Howe and Brown 1999). In our system this was a reflection of bird exclusion in the previous planting year, but the effect a year later was still sufficient to obscure effects of plant-plant interactions on size distributions.

Communities reflect the sum of population dynamics of different species, with or without strong interaction effects (e.g. Paine 1992; Stevens and Carson 1999). In our system

size variation in a multispecies community did not behave as in monocultures; size variation was least in high density plots. Moreover, this result was only evident in plots from which small vertebrates had been excluded, suggesting that they added variation that obscured the effects of plant-plant interaction acting alone.

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