EFFECTS OF BISON AND CATTLE ON GROWTH, REPRODUCTION, AND ABUNDANCES OF FIVE TALLGRASS PRAIRIE FORBS

Said A. Damhoureyeh and David C. Hartnett

Division of Biology, Kansas State University, Manhattan, Kansas 66506

Forb populations were sampled on Kansas tallgrass prairie to examine the effects of native (bison) and domestic (cattle) ungulates on plant growth, reproduction, and species abundances. Five locally and regionally abundant native tallgrass prairie perennials, Baptisia bracteata, Oenothera speciosa, Vernonia baldwinii, Solidago missouriensis, and Salvia azurea, were selected for study. Replicate watershed-level treatments included three grazing regimes (ungrazed, grazed by cattle, and grazed by bison), and two spring fire frequencies (annually burned and burned at 4-yr intervals). The results show that forb responses to ungulates in tallgrass prairie are complex and vary significantly among plant species, ungulate species, fire regimes, and plant life history stages. Some forbs (e.g., B. bracteata, O. speciosa, and V. baldwinii) increased in growth and reproduction in grazed sites, indicating competitive release in response to selective grazing of the dominant warm-season matrix grasses. Forbs that reduced performance in grazed sites are likely negatively affected by disturbances generated by ungulate nongrazing activities, because none of the forbs studied were directly consumed by bison or cattle. Large grazers had no detectable effect on the frequency of plant damage by other herbivores or pathogens. Significant effects of grazers on patterns of flowering and seed production were not congruent with their effects on population densities, indicating that variation in sexual reproduction plays a minor role in regulating local population abundances. Furthermore, the native and domestic ungulates differ significantly in their effects on forb growth and reproduction.

Key words: bison; cattle; fire; forbs; grazing; tallgrass prairie.

Central North American grasslands evolved under grazing pressure from large ungulates such as bison, elk, deer, and pronghorn, and other vertebrate and invertebrate herbivores (Axelrod, 1985). Fire also influenced vegetation structure and dynamics, particularly in the tallgrass prairie region. Tallgrass prairie plant communities are dominated by grasses, but also include numerous herba.ceous and woody species, of which perennial forbs comprise the greatest number of species. Despite the stability of the dominant grass matrix, grassland vegetation is spatially and temporally variable (Collins, 1992), associated with stochastic dynamics of subdominant interstitial species, and variation in topography, weather, and disturbances (Steinauer and Collins, 1995).

The activities of large ungulates affect plants via both herbivory and disturbances associated with their nongrazing activities (McNaughton, 1979). Plant responses to herbivory vary based on the timing and frequency of defoliation, the type of herbivore, plant parts consumed, the intensity of competition, and resources available to the defoliated plant (Vinton and Hartnett, 1992). Grazing can stimulate short-term aboveground compensatory growth in tallgrass prairie grasses, but a decrease in growth rate can occur with grazing over longer time (Vinton and Hartnett, 1992). Large grazing animals contribute directly to patchiness in grasslands through defoliation, trampling, and excretion. Elevated nitrogen in areas were urine is deposited creates patchiness, increases rates of nutrient cycling, and changes plant species composition (Steinauer and Collins, 1995).

Both domestic (cattle) and native (bison) grazers are predominantly graminoid feeders, and they generally show high dietary overlap. Differences in foraging ecology between cattle and bison are due to differences in their morphology, social behavior, physiology, and environmental tolerance. Although both exhibit forage selectivity (i.e., use plant species and growth forms out of proportion to their availability), bison are less selective in foraging and show lower dietary niche breadth (number of available species/growth forms consumed) than cattle (Hartnett, Steuter, and Hickman, 1996). Cattle diets are characterized by lower percentage of graminoids and a higher browse/forb component relative to bison. In addition, behavioral differences between cattle and bison, such as wallowing by bison, also may result in unique patterns of environmental patchiness and plant responses.

Fire is also an important process in tallgrass prairie, and its role in vegetation and ecosystem dynamics has been well documented (Collins and Wallace, 1990). Heterogeneity and species diversity in tallgrass prairie are greatest on sites with less frequent fire. Frequent (e.g., annual) fire increases the growth, reproduction, and abundance of many grasses (Knapp, 1985), but generally decreases growth, reproduction, and relative abundance of forbs (Gibson and Hulbert, 1987). For example, Hartnett (1991) reported that the tallgrass prairie forb Ratibida columnifera (Asteraceae) had greater biomass production and higher fecundity in infrequently burned sites relative to annually burned sites. Fire regimes may also influence patterns of ungulate grazing and plant responses to grazing at several scales (Collins, 1987; Hobbs et al., 1991;
Vinton et al., 1993). Fire and plant competition are important in determining selection of patches, species, plants, or plant parts by grazers, and the responses of grasses following herbivory. In addition, variation in plant growth forms and size as a result of burning may influence grazing patterns and plant responses (Pfeiffer and Hartnett, 1995).

Forbs are recognized as important constituents of grassland vegetation. They are present as dominants or subdominants in most climax grasslands. In native Great Plains grasslands, the number of forb species outnumbers grasses by an order of magnitude. Distribution and abundance of forbs are largely responsible for the pattern of small- and mid-scale herbaceous diversity. Forbs are also more diagnostic of environmental conditions and disturbance patterns (Biondini, Steuter, and Grygiel, 1989). Because forb communities contribute significantly to biological diversity in tallgrass prairie and forbs provide a resource base for a diverse group of invertebrates, amphibians and reptiles, birds, and small mammals, their response to ungulate herbivores and to grazing management deserves additional attention.

Little research has been done on the effects of large grazers on the growth, reproduction, or other life-history traits of forb populations in tallgrass prairie, or the interacting effects of fire and grazing on forb populations. This study was initiated in 1992 to assess the effects of ungulate grazers (cattle and bison) on several tallgrass prairie forb species. The specific objectives were: (1) to examine the effects of grazers on different forb life-history components (growth, resource allocation, and fecundity), (2) to examine the variation in plant life-history responses to native (bison) vs. introduced (cattle) ungulate grazers, and (3) to assess the variation in plant responses to grazing associated with different fire frequencies (prairie burned annually and at 4-yr intervals). Forb responses to bison versus cattle are predicted to differ because the native ungulates include a smaller proportion of forbs in their diets, show greater patch selectivity, create greater environmental patchiness, and show greater selectivity for the dominant matrix grasses relative to cattle (Hartnett, Steuter and Hickman, 1996). Thus, we predict that the growth and reproduction of many forbs will be greater in tallgrass prairie grazed by bison than in sites grazed by cattle at similar intensities.

**MATERIALS AND METHODS**

**Study site**—Populations of five perennial forbs, Baptisia bracteata Muhl. ex Ell. var. glabrescens (Larisey) Isley, Oenothera speciosa Nutt., Vernonia baldwinii Torr., Solidago missouriensis Nutt., and Salvia azurea Lam., were sampled at the Konza Prairie Research Natural Area (KPRNA), a 34.87-km² native tallgrass prairie preserve located in north-central Kansas (39°05'N 96°35'W). The vegetation of KPRNA is typical of native tallgrass prairie and is dominated by a matrix of C₄ perennial grasses such as big bluestem (Andropogon gerardii), Indian grass (Sorghastrum nutans), little bluestem (Schizachyrium scoparium), switchgrass (Panicum virgatum), subdominant C₃ and C₄ grasses, and a diverse array of interstitial forbs, including composites, legumes, and numerous other taxa (Freeman and Hulbert, 1985). Average monthly temperature ranges from a January low of −2.7°C to a July high of 26.6°C, and average annual total precipitation is 835 mm. The forb populations were sampled and plants were harvested and measured in 1995, the fourth growing season after initiation of the grazing treatments on replicate watersheds. During 1995 monthly total precipitation showed a strong peak in May and little precipitation during the winter months. Total precipitation in 1995 was 989.2 mm, which is slightly greater than the annual average (18.5% above the 100-yr mean) and the seasonal distribution of precipitation was typical of most years.

**Species description**—The five species sampled are locally and regionally abundant in tallgrass prairie. These species were selected because they are abundant and widespread on Konza Prairie, maintaining significant populations on sites subjected to a variety of grazing and fire regimes. B. bracteata is a perennial legume that flowers early in the growing season (April–June) and it is characteristic of shallow-soil upland prairie on KPRNA. O. speciosa (Onagraceae) is a short rhizomatous perennial that flowers from May through June. It is characteristic of relatively open, shallow soils of tallgrass and mixed prairie. V. baldwinii is a rhizomatous perennial composite, forming tightly packed clumps of one to several stems. It flowers from July through October and it grows on all prairie types, open woods, and disturbed sites. S. missouriensis is a clonal perennial composite producing extensive, less densely packed clones covering one to several square metres. It flowers from July through October. S. azurea (Lamiaceae) is a perennial forb producing one to several stems, which flowers from June through October.

**Experimental design**—Replicate burning and grazing treatments on KPRNA are applied at the watershed level. KPRNA is divided into 60 watershed units (average size = 0.55 km²), each subjected to a specific combination of prescribed burn regime and grazing treatment. The effects of native and domestic ungulates on tallgrass prairie forb growth and reproduction were studied in populations randomly selected on replicate ungrazed watersheds, watersheds grazed by cattle, and watersheds grazed by bison, and two burn regimes (watersheds burned annually in spring and watersheds burned at ~4-yr intervals). The present study included 12 watersheds representing a factorial combination of three grazing treatments × two fire regimes × two replicates per treatment combination. Hereafter, these treatments will be referred to as cattle, bison, and ungrazed sites, and the different fire frequency treatments will be referred to as 1-yr and 4-yr sites. Cattle grazing is seasonal (May–October) each year, while bison grazing is year-long. However, the animal stocking densities are maintained such that the cumulative annual grazing intensity (amount of biomass removed per year) is the same for both grazing regimes. The cattle and bison grazing treatments used in this study were initiated in 1992 on replicate watershed units that had been previously ungrazed for at least 20 yr. The burning regimes were initiated on all watersheds in 1980. Thirty-six plants of each species were randomly selected in each site and harvested at the peak of flowering. One ramet per genet was randomly collected from each of 36 genets of S. missouriensis, while the entire genet was collected for the other clonal species, and for the single-stemmed O. speciosa.

Mean plant height, number of flowers (or capitula) per plant, and number of stems per plant were determined for each population. The reproductive parts (all reproductive organs and supporting structures from the base of the lowest capitulum or flower to the top of inflorescence) and vegetative structures were separated. Plants were dried at 75°C for 24–48 h, and vegetative and reproductive biomass were measured to the nearest 0.01 and 0.001 g, respectively.

A second sampling of each population was conducted at the time of seed maturity for each species. Thirty-six plants per species were located randomly within each watershed, and their inflorescences were collected. Total number of capsules or seed heads per plant, and total number of seeds per plant were measured. Number of dead seeds (obviously nonviable, infected by fungus, etc.) per plant was determined for B. bracteata, and number of capsules or seed heads per plant that were damaged by seed predators was measured for B. bracteata and V. baldwinii. Sexual reproductive effort (SRE) was calculated in two different ways, first as percentage of total shoot biomass in reproductive
structures (SRE1), then as number of flowers (flower heads) per gram plant biomass (SRE2). Biomass, height, fecundity, and reproductive effort were analyzed via two-way ANOVA. SRE1 data were arcsine transformed prior to analysis. Significant differences between means of treatment combinations were detected with Least Square Means (LSMEANS) (SAS, 1990), since no significant differences between the duplicate watersheds within treatments were found.

Data on the effects of ungulates on forb abundances (frequency and canopy cover) were obtained from other ongoing KPRNA studies (Hartnett, Hickman, and Fisher Walter, 1996; Hickman, 1996; and Konza Prairie Long Term Ecological Research (LTER) data set PVC02). Effects of bison on abundances (frequency and canopy cover) of forb species in the study site were obtained by measuring the canopy cover and frequency of each forb species in 30 replicate 10-m² plots in each site using a modified-Daubenmire cover-abundance scale. These data on species abundances in grazed and ungrazed tallgrass prairie are collected as part of the KPRNA NSF Long-term Ecological Research program. These data and detailed descriptions of methods are accessible via Worldwide Web site: http://climate.konza.ksu.edu/pvc02.html. Hickman (1996) assessed the effect of cattle on forb species abundances by measuring the frequency of each forb species in replicate grazed and ungrazed units using a point-intercept approach. Four replicate randomly located transects were established within each cattle and ungrazed site. One hundred random points were sampled along each transect and the closest rooted plant to each point was recorded. The frequency of each forb was calculated as the percentage of sample points at which it occurred. Although these two studies used slightly different sampling methods, they both incorporated similar measures of species abundance (frequency of occurrence) and both measured differences relative to ungrazed sites. In addition, these two studies involved nearby sites of nearly identical soils and vegetation, and both involved management regimes for livestock and bison characteristic of the tallgrass prairie region. Thus they allow a reasonable comparison of plant responses to bison and cattle under a typical tallgrass prairie management regime.

RESULTS

*B. bracteata*—*B. bracteata* plants in grazed sites showed significantly greater aboveground plant biomass than those of ungrazed sites (*F* = 22.59, *P* = 0.01), and bison grazing had a greater positive effect on plant biomass than did cattle (Fig. 1A). There were no significant differences in plant height or number of stems per plant among grazing treatments (Fig. 1B, C) although the patterns of differences among treatments in stem numbers were similar to patterns in plant biomass. In both burn regimes, plants in cattle sites produced significantly more biomass than those in ungrazed sites, whereas plants in bison 4-yr sites had the largest biomass of all treatment combinations (Fig. 1A).

Ungulates had no significant effects on sexual reproductive effort (SRE1, SRE2), or fecundity (number of flowers, number of capsules, and number of seeds per plant), but there was a trend of higher SRE and flower and fruit production in grazed relative to ungrazed sites (Fig. 1D–G). In general, although there were no statistically significant differences in reproductive traits among grazing treatments, there were consistent trends of lower numbers of capsules and seeds produced per plant in bison sites compared to cattle sites, and seed production was the lowest in bison sites (Fig. 1E, H). In the 4-yr sites, trends in flower production (ungrazed < cattle < bison) were opposite trends in mature capsule production and seed production (ungrazed > cattle > bison). Flower production tended to be higher in bison sites under the 4-yr burn regimes but higher in cattle sites under the annual burning regime. There was also a trend of increased percentage of damaged capsules and seeds per plant in sites with ungulates, but differences in damage rates were not statistically significant.

Overall total plant biomass and height of *B. bracteata* were significantly lower in the annually burned sites relative to 4-yr sites (*F* = 17.75, 40.61, *P* = 0.01, 0.003), whereas number of stems per plant was higher in 1-yr sites (*F* = 8.99, *P* = 0.04). There were no significant effects of fire frequency on sexual reproductive effort or fecundity measurements, although there was a consistent trend of lower SRE and fecundity in 4-yr sites relative to 1-yr sites.

*O. speciosa*—Plants in cattle sites were significantly larger in biomass (*P* < 0.05) and height (*P* = 0.05) than those of ungrazed sites (Fig. 2A, B). In contrast, bison resulted in reduced biomass (*P* = 0.07) and shoot height (*P* < 0.05) relative to ungrazed sites (Fig. 2A, B). SRE1, SRE2, and the production of flowers, fruits, and seeds were all consistently greater in cattle sites compared to ungrazed sites (Fig. 2C–G). Bison resulted in significant increase in SRE2 compared to ungrazed sites (*P* < 0.05) and cattle sites (*P* = 0.056) (Fig. 2E), but there were no significant differences between bison and ungrazed treatments for any other reproductive effort or fecundity variables.

There was no significant main effect of fire frequency on total plant biomass of *O. speciosa*, whereas plant height was consistently lower (*P* < 0.05) in annually burned watersheds relative to 4-yr watersheds (Fig. 2B). Fire frequency had no significant effect on sexual reproductive effort and a marginally significant effect on fecundity (*P* = 0.07), (Fig. 2G).

*V. baldwinii*—Shoot biomass of *V. baldwinii* was increased significantly by bison (Fig. 3A). Shoot biomass was almost doubled in 4-yr sites grazed by bison compared to ungrazed sites, whereas there were no significant differences in plant biomass between cattle and ungrazed sites (Fig. 3A). Similarly, trends in plant height and stem numbers suggest that bison had a greater positive effect on plant height and number of stems per plant than did cattle (Fig. 3B, C), although only mean stem numbers were significantly greater in bison compared to ungrazed sites (Fig. 3C). Effect of bison on plant biomass and number of stems were larger in 4-yr watersheds than in annually burned watersheds.

The presence of bison or cattle resulted in consistently greater SRE compared to ungrazed watersheds (mean SRE2 of all grazed plants was greater than ungrazed plants at the *P* = 0.07 level), but differences in SRE1 among watersheds were not statistically significant (Fig. 3D, E). Bison resulted in a significant increase in flowering in the 4-yr watersheds (Fig. 3G), and similar trends but no significant effects in the 1-yr sites. Fecundity (number of mature seed heads and seeds per plant) was also increased in the grazed watersheds, with effects of bison being greater than those of cattle (Fig. 3D, E).

ANOVA revealed a reduction in *V. baldwinii* plant height in annually burned watersheds compared to 4-yr sites (*P* = 0.08), however there was no significant main
Fig. 1. Growth and reproductive characters (mean ± 1 SE) of *B. bracteata* plants from tallgrass prairie sites. Total plant biomass = total aboveground biomass. SRE = sexual reproductive effort, SRE1 = % reproductive biomass, SRE2 = number of reproductive parts/total plant biomass. Open bars = populations in ungrazed sites. Cross-hatched bars = sites grazed by cattle. Slashed bars = sites grazed by bison. Similar lowercase letters above bars indicate no significant differences at the $P \leq 0.05$ level.
Fig. 2. Growth and reproductive characters (mean ± 1 SE) of *O. speciosa* plants from tallgrass prairie sites. Total plant biomass = total aboveground biomass. SRE = sexual reproductive effort, SRE1 = % reproductive biomass, SRE2 = number of reproductive parts/total plant biomass. Open bars = populations in ungrazed sites. Cross-hatched bars = sites grazed by cattle. Slashed bars = sites grazed by bison. Similar lowercase letters above bars indicate no significant differences at the *P* ≤ 0.05 level. Insufficient sample size precluded statistical analysis for data presented in D and F.
Fig. 3. Growth and reproductive characters (mean ± 1 SE) of *V. baldwinii* plants from tallgrass prairie sites. Total plant biomass = total aboveground biomass. SRE = sexual reproductive effort, SRE1 = % reproductive biomass, SRE2 = number of reproductive parts/total plant biomass. Open bars = populations in ungrazed sites. Cross-hatched bars = sites grazed by cattle. Slashed bars = sites grazed by bison. Similar lowercase letters above bars indicate no significant differences at the *P* ≤ 0.05 level.
effects of fire frequency on other growth or reproductive response variables. Percentage of flower heads aborted were generally high for V. baldwinii (21–42%) but there were no significant effect of fire or grazing treatments on abortion rates.

*S. missouriensis*—ANOVA revealed a significant effect of ungulates on plant height (cattle = bison < ungrazed, \( F = 5.42, P = 0.05 \)), but no significant effect on total plant biomass. In general bison resulted in a larger reduction in plant height than did cattle (Fig. 4B). Ungulates significantly increased SRE1 (\( F = 11.65, P = 0.008 \)), SRE2 (\( F = 6.11, P = 0.04 \)), fruit production (\( F = 43.81, P = 0.0003 \)), and seed production (\( F = 56.8, P = 0.0001 \)). Cattle resulted in greater sexual reproductive effort (SRE1, SRE2), and fecundity (flowers, fruits, and seeds production) relative to bison (Fig. 4C–G).

Annually burned sites showed significantly lower plant height (\( F = 15.79, P = 0.007 \)), and total plant biomass (\( F = 4.28, P = 0.08 \)) relative to 4-yr sites. In the 4-yr watersheds there was a trend of reduced total plant biomass and height in grazed relative to ungrazed sites (Fig. 4A, B), whereas effects of grazing on SRE and fecundity were generally greater in the annually burned sites (Fig. 4C–G).

*S. azurea*—ANOVA revealed a significant effect of ungulates on plant height (\( F = 14.33, P = 0.005 \)), while there were no significant effects on plant biomass or total number of stems per plant. In general, bison resulted in greater plant biomass and height, and lower number of stems per plant relative to plants in ungrazed sites, whereas cattle resulted in lower plant biomass, plant height, and number of stems per plant (Fig. 5A–C). Plants in bison sites were significantly larger in both biomass and height than plants in cattle sites (\( P < 0.05 \)). Bison resulted in consistently higher SRE1 (\( F = 5.62, P = 0.04 \)), SRE2 (\( F = 6.76, P = 0.03 \)), and the production of flowers (\( F = 19.34, P = 0.002 \)), fruits (\( F = 5.59, P = 0.04 \)), and seeds (\( F = 4.48, P = 0.06 \)) compared to plants in ungrazed sites (Fig. 5D–H). In 4-yr sites, bison resulted in significantly greater reproductive effort (SRE1) than did cattle.

Annually burned sites showed greater plant biomass (\( F = 4.00, P = 0.09 \)), and number of stems than 4-yr sites (\( F = 6.37, P = 0.05 \)). Although the effects of fire frequency on sexual reproductive effort and fecundity were not significant, in ungrazed sites there were trends of increased SRE and flower production in 4-yr sites relative to 1-yr sites. In sites grazed by cattle, the 4-yr burn cycle resulted in reduction in SRE2 and flower production relative to the annual burn cycle (Fig. 5D, E, G).

Data from other KPRNA studies (Hartnett, Hickman, and Fisher Walter, 1996; Hickman, 1996) showed significant effects of bison and cattle on the abundances of forb species. Abundance of *B. bracteata* and *S. azurea* decreased with cattle grazing, while there were increases in the abundance of *V. baldwinii* populations in cattle relative to ungrazed sites (Hickman, 1996). Cattle had no effects on the abundance of *S. missouriensis*. Populations of *B. bracteata*, *V. baldwinii*, and *S. azurea* showed decreased abundance in the bison sites, while *O. speciosa* and *S. missouriensis* population abundances were greater in grazed relative to ungrazed sites (LTER data-set PVC02, http://climate.konza.ksu.edu/pvc02.html). Populations of *O. speciosa*, *S. missouriensis*, and *S. azurea* showed lower abundance in annually burned watersheds than in 4-yr watersheds, while *B. bracteata*, and *V. baldwinii* showed greater abundance in 1-yr relative to 4-yr sites.

**DISCUSSION**

These results indicate that forb responses to ungulate grazers are complex and vary with forb species, ungulate species, fire regime, and plant life-history stage. For example, *B. bracteata* showed greater plant biomass and number of stems in grazed sites, while height was not affected. *O. speciosa* produced greater biomass and height in cattle sites, while bison had a negative effect. In *S. azurea*, above-ground biomass, height, and number of stems were reduced by the activities of cattle and showed small positive responses to bison. Biomass and number of stems of *V. baldwinii* were greater in sites with bison than ungrazed sites, whereas cattle did not affect these growth or morphological traits. *S. missouriensis* total biomass showed no significant response to ungulates, while height was reduced in watersheds with ungulate grazers. None of the forb species studied were directly consumed by bison or cattle except for some plants of *B. bracteata*.

Some forb species showed greater vegetative growth and/or reproduction in grazed than in ungrazed sites, indicating that they experienced a competitive release in response to grazing of the dominant competitive grasses. For example, *B. bracteata*, *O. speciosa*, and *V. baldwinii* all showed greater growth or fecundity in grazed sites, even though these species were not selected and directly consumed by bison or cattle. Grazing by bison increases light availability to ungrazed forbs (Fahnestock and Knapp, 1993), which may explain the potential benefits of selective grass herbivory on forb species. Removal of the grass canopy also results in warmer soil temperatures and increased soil moisture, which may stimulate earlier growth of subdominant ungrazed forbs in the spring (Fahnestock and Knapp, 1994). In tallgrass prairie, this competitive release of forbs in response to grazing is indicated by patterns of population abundances, e.g., reduced cover of matrix grasses in grazed sites is accompanied by increased survivorship and abundance of populations of subdominant species (Collins, 1987; Hartnett, Steuter, and Hickman, 1996). Because none of the forb species sampled in this study were directly consumed by bison or cattle, those that showed reduced growth in grazed sites were most likely negatively affected by the physical disturbance generated by the nongrazing activities of the animals.

Large ungulates can have different effects on different life-history stages, and SRE and fecundity measures showed complex responses also. For example, cattle increased SRE and fecundity in both *O. speciosa* and *S. missouriensis*, whereas bison had more positive effects on SRE and fecundity in *V. baldwinii* and *S. azurea*. Ungulates, in general, resulted in increased SRE and fecundity in *B. bracteata*, however opposite trends were evident in flowering compared to capsule and seed production. Cattle increased capsule and seed production in *B. bracteata*, while bison
Fig. 4. Growth and reproductive characters (mean ± 1 SE) of *S. missouriensis* plants from tallgrass prairie sites. Total plant biomass = total aboveground biomass. SRE = sexual reproductive effort, SRE1 = % reproductive biomass, SRE2 = number of reproductive parts/total plant biomass. Open bars = populations in ungrazed sites. Cross-hatched bars = sites grazed by cattle. Slashed bars = sites grazed by bison. Similar lowercase letters above bars indicate no significant differences at the *P* ≤ 0.05 level.
Fig. 5. Growth and reproductive characters (mean ± 1 SE) of S. azurea plants from tallgrass prairie sites. Total plant biomass = total above-ground biomass. SRE = sexual reproductive effort, SRE1 = % reproductive biomass, SRE2 = number of reproductive parts/total plant biomass. Open bars = populations in ungrazed sites. Cross-hatched bars = sites grazed by cattle. Slashed bars = sites grazed by bison. Similar lowercase letters above bars indicate no significant differences at the $P \leq 0.05$ level.
resulted in an increase in flower production and a decrease in capsule and seed production.

This variation in responses to native and domestic ungulate grazers may be a result of variation in the timing or intensity of physical impacts of the animals, the timing or intensity of defoliation of their primary grass competitors, variation in herbivory diet selectivity, variation among forb species in their phenotypic plasticity and responsiveness to the effects of herbivores, or other grazer-induced changes in their competitive neighborhood or abiotic environment.

Defoliation of a plant by one animal may alter the probability, intensity, and/or effects of other consumers, pathogens, or symbionts. Similarly, changes in the local environment caused by the grazing or nongrazing activities of large ungulates may also alter other plant consumer populations or plant susceptibility. However, no effects of large ungulate grazers on other biotic interactions such as insect and fungal damage were detected in this study. There were no significant differences in the amount of insect or pathogen damage to seeds or capsules between populations in grazed vs. ungrazed areas, suggesting that bison and cattle have little effects on other plant–consumer interactions.

Ungulate effects on abundance of the forb species studied here could not be predicted from their effects on plant reproduction (flower and seed production). In some cases, grazers resulted in significant effects on plant growth or reproduction, but no corresponding effect on population abundances. For all five species studied here, there was no relationship between seed production and abundances among populations of grazed and ungrazed sites (Spearman’s Rho varied considerably and was nonsignificant in all cases, [0.12 ≤ R ≤ 0.84]). The lack of parallel patterns of seed production and abundances of some forb populations among sites could be due to the fact that the abundance of many of these perennial forbs is more closely linked to patterns of vegetative reproduction and survivorship than to variation in flower and seed production. Vegetative reproduction is generally more important than sexual reproduction in influencing local population re-generation of perennials in tallgrass prairie vegetation (Hartnett and Keeler, 1995).

Frequent fire (annually burned sites) generally reduced the height of forbs and decreased their biomass, but increased number of stems per plant (changes in plant architecture and population structure toward smaller but more numerous shoots). In general, all of the studied species showed almost the same response to fire, except S. azurea, which showed an increase in plant total biomass under the annual fire treatment, and V. baldwinii in which aboveground plant biomass was not affected by the fire treatment. The effect of fire on SRE and fecundity was not significant for any species. In general, annual burning reduces species diversity and heterogeneity of grasses and forbs (Gibson and Hulbert, 1987; Collins, 1992). All the forbs in this study showed a decrease in abundance in annually burned sites except for V. baldwinii and B. bracteata.

This study was conducted in a year of slightly above-average precipitation, and the responses of plant populations to grazing treatments may be of much larger magnitude in a dry year where resource availability to plants is lower, and competition for water and other soil resources is greater. Thus, even larger competitive release responses among forbs may be predicted in grazed sites during a dry year. Alternatively, if grass–forb competition involves primarily aboveground competition for light, the lower grass canopy production in a dry year may result in a smaller competitive release response among forbs in grazed sites.

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