



Promoting the Science of Ecology

---

Vegetation Trends in Tallgrass Prairie from Bison and Cattle Grazing

Author(s): E. Gene Towne, David C. Hartnett, Robert C. Cochran

Reviewed work(s):

Source: *Ecological Applications*, Vol. 15, No. 5 (Oct., 2005), pp. 1550-1559

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/4543462>

Accessed: 06/04/2012 19:37

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



*Ecological Society of America* is collaborating with JSTOR to digitize, preserve and extend access to *Ecological Applications*.

<http://www.jstor.org>

## VEGETATION TRENDS IN TALLGRASS PRAIRIE FROM BISON AND CATTLE GRAZING

E. GENE TOWNE,<sup>1,3</sup> DAVID C. HARTNETT,<sup>1</sup> AND ROBERT C. COCHRAN<sup>2</sup>

<sup>1</sup>Division of Biology, Kansas State University, Manhattan, Kansas 66506 USA

<sup>2</sup>Department of Animal Sciences and Industry, Kansas State University, Manhattan, Kansas 66506 USA

**Abstract.** Comparisons between how bison and cattle grazing affect the plant community are understood poorly because of confounding differences in how the herbivores are typically managed. This 10-year study compared vegetation changes in Kansas (USA) tallgrass prairie that was burned and grazed season-long at a moderate stocking rate by either bison or cattle. We held management practices constant between the herbivores and equalized grazing pressure by matching animals so that the total body mass in all pastures was similar each year. Trends in species cover and diversity indices in the bison and cattle pastures were compared with ungrazed prairie that also was burned annually. We found that little bluestem (*Schizachyrium scoparium*) cover decreased over time in bison pastures, and big bluestem (*Andropogon gerardii*) cover increased over time in cattle pastures. Grazing by either herbivore increased the canopy cover of annual forbs, perennial forbs, and cool-season graminoids, but both annual and perennial forb cover increased at a greater rate in bison pastures than in cattle pastures. Missouri goldenrod (*Solidago missouriensis*) and heath aster (*Symphotrichum ericoides*) were primarily responsible for the increased forb cover in grazed pastures. Species richness at both small (10 m<sup>2</sup>) and large (200 m<sup>2</sup>) spatial scales increased at a greater rate in bison pastures than in cattle pastures, but richness did not change through time in ungrazed prairie. The number of annual forb species was significantly higher in bison pastures than in pastures grazed by cattle. Residual graminoid biomass at the end of the grazing season was lower in bison pastures than in cattle pastures, whereas forb residuum increased over time at a greater rate in pastures grazed by bison than in pastures grazed by cattle. Although bison and cattle differentially altered some vegetation components, the plant communities in bison and cattle pastures were 85% similar after 10 years of grazing. We conclude that most measurable differences between bison-grazed and cattle-grazed pastures in tallgrass prairie are relatively minor, and differences in how the herbivores are typically managed may play a larger role in their impact on prairie vegetation than differences between the species.

**Key words:** bison *cf.* cattle; grazing effects; herbivory; Konza Prairie (Kansas, USA); plant community; species richness; temporal heterogeneity.

### INTRODUCTION

Herbivores are a major influence in shaping the composition, structure, and dynamics of grassland vegetation (Hobbs 1996, Fuhlendorf and Engle 2001). Tallgrass prairie evolved under grazing pressure from numerous ungulate species, but bison (*Bison bison*) likely played a keystone role in its development (Knapp et al. 1999). Following the demise of free-ranging bison herds, cattle (*Bos taurus*) have been the dominant herbivore on Kansas grasslands for more than 150 years. Although bison and cattle are similar physiologically, the response patterns of prairie vegetation to their grazing may be different.

Various aspects of foraging ecology have been compared between bison and cattle (Peden et al. 1974, Plumb and Dodd 1993, Stuetter and Hidinger 1999, Van

Vuren 2001), but reports of vegetation changes from their grazing are anecdotal. Comparisons of temporal changes in prairie vegetation in response to bison and cattle grazing are confounded by differences in how each herbivore species is normally managed. Most cattle grazing systems in tallgrass prairie entail the use of young animals that graze only during the May–September growing season on prairie that is annually burned. For operations that elect to keep reproductive herds on pasture year-round, providing protein and energy supplements is a standard, and usually necessary, management practice. Supplementation, however, can influence animal behavior and alter grazing distribution patterns (Krysl and Hess 1993). In contrast to cattle, bison traditionally remain on pasture year-round with minimal management and may not receive dietary supplementation except when managed in conventional production operations. Comparisons between bison and cattle also are confounded because average body masses for all age and sex categories are lower in bison

Manuscript received 30 December 2004; revised 4 February 2005; accepted 8 February 2005. Corresponding Editor: D. S. Schimel.

<sup>3</sup> E-mail: egtowne@ksu.edu

than those typically found in cattle (Towne 1999). Consequently, intake and grazing intensity may be much greater for cattle than for bison even if animal density is the same.

The objectives of this study were to compare the effects of monospecific grazing by bison and cattle on long-term patterns of change in plant species composition and diversity in tallgrass prairie. Addressing this issue is important because replacement of native with introduced ungulates has been one of the most significant changes in North American grasslands in recent history. To achieve similar grazing pressure and hold management practices constant, we equalized total body mass between herbivores and limited grazing to the vegetation growing season. Specific items of interest in this study included trends of individual plant species in response to bison and cattle grazing compared with ungrazed prairie, temporal changes in species richness and diversity, and patterns of above-ground biomass at the end of the grazing season.

#### STUDY SITE AND METHODS

The study (1995–2004) was conducted on Konza Prairie Biological Station, a 3487-ha tallgrass prairie located in the Flint Hills of northeastern Kansas, USA (39°05' N, 96°35' W). Mean annual precipitation is 811 mm, with ~75% falling during the April through September growing season. Rainfall during the growing season was below average in six years of this study, whereas annual precipitation was below the long-term average in five years. Vegetation in the area is dominated by perennial warm-season grasses, primarily big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and indiangrass (*Sorghastrum nutans*), although interstitial forb species constitute more than 75% of the species richness (Towne 2002). Botanical nomenclature follows Kartesz (1999).

In 1994 we constructed eight pastures in an area that had been burned and grazed by cattle at a light stocking rate during the two previous growing seasons. In the preceding 20 years, the area had been ungrazed by large ungulates and burned on average every two years. Each pasture was 4.9 ha plus a 0.2-ha corner section that was cross-fenced to exclude grazing. Upland prairie dominates the area, although minor amounts of lowland and hillside topographic sites occur in each pasture. Soils on the upland sites are relatively shallow, cherty, silty clay loams overlying limestone and shale layers (Udic Argiustolls, Florence series). Focal attractants (e.g., shade trees, ponds, and cages) were absent, except for a water tank that was located near each pasture gate. All pastures were burned annually in April.

To compare vegetation trends in the bison and cattle pastures with ungrazed prairie, we selected the upland sites of two nearby watersheds (average size = 25 ha) for sampling. Both watersheds had not been grazed by livestock for more than 20 years, and had been burned on average every three years until they were converted

to an annual burn regime in 1994. An unburned, ungrazed treatment was not incorporated into the experimental design since that is not a standard management practice for Flint Hills (Kansas, USA) rangeland.

#### *Grazing management*

Four pastures were assigned randomly for bison grazing and the remaining four pastures were designated for cattle grazing. Each pasture kept the same herbivore grazing treatment throughout the study. Because bison have a slower growth rate than beef cattle, 2-yr-old bison bulls were required to equalize the mass of yearling cattle steers (12 to 14 months of age). Using 2-yr-old bulls to characterize bison grazing is appropriate since their diet and foraging behavior is similar to all other age and sex classes except calves and elderly bulls (Coppedge and Shaw 1998, Post et al. 2001). The bison were obtained from the Konza Prairie herd that graze year-long with minimal management in a 988-ha enclosure (Towne 1999), whereas the cattle were Angus × Hereford steers selected from the Kansas State University Department of Animal Science herd. Over the course of the study, individual masses at the start of the grazing season averaged 253 kg for the bison and 258 kg for the cattle. The annual stocking rate was 1.7 ha/animal unit (au), which is slightly heavier than the 2.1 ha/au that is considered standard for moderate season-long steer grazing in Flint Hills rangeland.

At the beginning of the grazing season (~1 May), all animals were weighed following an overnight fast and sorted into four groups of bison and four groups of cattle. Each group consisted of four animals selected so that their total mass was similar across groups and species within a given year. Total animal mass at the start of the grazing season averaged 993 kg (annual range of 827–1085 kg) in each bison pasture and 1011 kg (annual range of 821–1063 kg) in each cattle pasture. After initial release, the animals were allowed to graze in their designated pastures without interference until their removal in early October.

#### *Vegetation sampling*

Beginning in 1995 we sampled vegetation in 20 permanently marked 10-m<sup>2</sup> circular plots that were evenly spaced along four randomly located 50-m-long transects on the upland sites in all eight pastures and the two ungrazed watersheds. The transects were distributed throughout the pasture to maximize spatial heterogeneity, but were not located within 30 m of the water tank. Every year in June and August, the canopy cover of vascular plants in each plot was visually estimated using a modified Daubenmire cover scale (Bailey and Poulton 1968). Cover of individual species was determined by converting each Daubenmire scale value to the midpoint of the cover range and then averaging across the 20 plots in each pasture. To detect changes in diminutive and low-density species, frequency of

occurrence (the proportion of plots where an individual species occurred) also was calculated. Species diversity was measured using two indices at two different spatial scales. First, we calculated alpha diversity for each 10-m<sup>2</sup> plot using the Shannon index ( $H' = -\sum p_i \times \ln p_i$ , where  $p_i$  = the relative cover of each species). We also calculated diversity at the 200-m<sup>2</sup> spatial scale with Shannon's index on the average percentage cover of all species across the 20 plots in each pasture. Species richness at the small spatial scale was the average number of species detected in each plot, and species richness at the large scale was the cumulative number of plant species in the 20 plots. The floristic similarity between bison vs. cattle pastures, and grazed vs. ungrazed prairie was estimated using Sorensen's qualitative similarity index (Magurran 1988).

At the end of the grazing season, after the animals were removed, residual biomass in each pasture was measured by clipping all vegetation in 20 × 50 cm quadrats placed at 3-m intervals along a randomly selected line adjacent to each plant composition transect (60 clipped plots per pasture). Vegetation in the quadrats was clipped at ground level, separated into graminoid, forb, and woody components, oven-dried at 60° C, and weighed. The coefficient of variation (CV) of clipped biomass for all plots in each pasture was calculated as an indication of spatial variability in grazing patterns. To compare the amount of residual biomass in grazed pastures with annual aboveground net primary productivity for the area, we clipped five quadrats in each of the eight pasture sections that were protected from grazing ( $n = 40$  plots).

#### Data analysis

Canopy cover of species with >2% mean cover in any year or treatment, and cover of species within similar taxonomic and life-form groups (e.g., legumes, sedges, warm-season grasses, cool-season grasses, annual forbs, annual grasses, perennial forbs, and woody species) were arcsine square-root transformed before analysis. We analyzed the data using a repeated-measures mixed model, with grazing treatment and year as fixed effects and pasture as a random effect. A significant treatment × year interaction in the repeated-measures analysis indicates that the regression slopes differed among grazing treatments, and that differential changes occurred over time. Temporal trends in vegetation were analyzed with a regression model using the annual deviation from the mean year value as a covariate. We then used orthogonal contrasts to compare which treatments had different slopes.

Species richness, Shannon's diversity, frequency of occurrence, and residual biomass were analyzed with the same models used for canopy cover. Frequency percentages were transformed to the arcsine of the square-root before analysis. We used SAS procedures (SAS Institute 1999) to analyze all data, with 0.05 as the probability level to establish statistical significance.

## RESULTS

### Warm-season grasses

Temporal trends in the cover of perennial warm-season grasses increased in the absence of grazing but did not significantly change through time in either bison or cattle pastures (Table 1). Response patterns of the individual species, however, varied among treatments. Big bluestem cover increased ( $P < 0.0001$ ) in cattle pastures and in ungrazed prairie, but did not significantly change through time in bison pastures (Fig. 1a). In contrast, little bluestem cover declined ( $P < 0.05$ ) in bison pastures, but remained stable in pastures grazed by cattle and in ungrazed prairie (Fig. 1b). Switchgrass (*Panicum virgatum*) cover increased in the absence of grazing, declined in pastures grazed by cattle, and remained unchanged through time in bison pastures (Table 1). Other differential cover responses to grazing treatment included tall dropseed (*Sporobolus compositus*), which declined ( $P < 0.01$ ) in ungrazed prairie, and side-oats grama (*Bouteloua curtipendula*), which increased ( $P < 0.05$ ) in response to grazing by either bison or cattle (Table 1). Trends in indiagrass cover remained stable through time in all treatments (Table 1).

### Cool-season graminoids

The cover of perennial cool-season grasses (predominantly Scribner's panicum [*Dichanthelium oligosanthos*] and prairie Junegrass [*Koeleria macrantha*]) increased ( $P < 0.01$ ) with similar slopes in both bison and cattle pastures, but declined through time in the absence of grazing (Fig. 1c). Kentucky bluegrass (*Poa pratensis*) cover did not change significantly through time in either grazed or ungrazed prairie (Table 1). Canopy cover of sedges (primarily *Carex inops* and *Carex meadii*) also increased ( $P < 0.01$ ) with similar patterns in both bison and cattle pastures, and declined through time in ungrazed prairie (Table 1).

### Perennial forbs

Perennial forb cover increased ( $P < 0.0001$ ) in response to grazing, but the temporal changes were greater in bison pastures than in cattle pastures (Fig. 1d). Two species, Missouri goldenrod (*Solidago missouriensis*) and heath aster (*Symphotrichum ericoides*), were primarily responsible for the increased forb cover in grazed pastures. Missouri goldenrod cover increased at a significantly greater rate over time in bison pastures than in cattle pastures (Fig. 1e), but heath aster followed similar temporal increases in response to either bison or cattle grazing (Table 1). Western ironweed (*Vernonia baldwinii*) also increased in both bison and cattle pastures, and aromatic aster (*Symphotrichum oblongifolium*) increased in bison pastures, but the magnitude of their changes through time were relatively small (Table 1). Pitcher's sage (*Salvia azurea*) cover increased with similar slopes in all three treat-

TABLE 1. Comparison of percent cover for various dominant and subdominant species between the first and last year of the study in bison pastures, cattle pastures, and ungrazed tallgrass prairie.

Species	Percent cover, 1995			Percent cover, 2004†		
	Bison	Cattle	Ungrazed	Bison	Cattle	Ungrazed
<b>Graminoids</b>						
<i>Andropogon gerardii</i>	37.5	33.5	28.6	37.3	49.8+	60.8+
<i>Bouteloua curtipendula</i>	1.8	0.9	5.3	2.8+	1.7+	3.6
<i>Dichanthelium oligosanthes</i>	3.2	3.1	4.5	3.9+	5.7+	0.4-
<i>Koeleria macrantha</i>	0.2	0.4	0.8	5.9+	3.9+	0.1-
<i>Panicum virgatum</i>	0.6	2.2	2.6	0.3	0.5-	6.7+
<i>Poa pratensis</i>	3.7	2.7	0.5	0.2	0.2	0
<i>Schizachyrium scoparium</i>	27.1	17.5	13.4	14.6-	17.7	22.8
<i>Sorghastrum nutans</i>	9.8	13.6	18.8	10.9	11.2	24.9
<i>Sporobolus compositus</i>	0.7	2.2	4.1	0.6	1.2	0.7-
Warm-season grasses	79.5	72.6	76.8	68.5	86.3	122.7+
Cool-season grasses	7.7	7.6	9.4	11.2+	10.7+	0.6-
Sedges	9.3	7.8	3.3	11.6+	14.1+	1.4-
<b>Forb and woody species</b>						
<i>Ambrosia psilostachya</i>	4.8	4.0	2.4	28.7	31.9	16.0
<i>Amorpha canescens</i>	2.4	6.3	5.2	3.5	9.9+	5.0
<i>Salvia azurea</i>	0.9	1.7	6.5	3.9+	7.8+	10.3+
<i>Solidago missouriensis</i>	0.4	0.4	3.1	16.6+	2.4+	0.6
<i>Symphyotrichum ericoides</i>	1.3	1.4	5.6	19.4+	20.4+	1.1-
<i>Symphyotrichum oblongifolium</i>	0.4	0.3	3.7	3.1+	1.3	2.7
<i>Vernonia baldwinii</i>	0.5	0.4	0.5	0.9+	0.7+	0.3
Perennial forbs	20.8	22.4	38.0	94.0+	81.2+	39.9
Herbaceous legumes	4.7	6.8	5.5	4.9	7.5	2.7
Annual forbs	2.2	1.6	0.8	9.7+	4.4+	0.5

† For values in 2004, a positive sign indicates a significant temporal increase in the regression slope, whereas a negative sign indicates that the trend decreased ( $P < 0.05$ ) over time.

ments, and was the only forb species that significantly increased in ungrazed prairie (Table 1). Western ragweed (*Ambrosia psilostachya*), a dominant forb in tallgrass prairie, followed similar temporal fluctuations in both grazed and ungrazed treatments (Table 1). Cover of herbaceous legume species did not differ among treatments and remained stable through time (Table 1).

*Annuals*

The cover of annual forbs increased at a greater rate in pastures grazed by bison than in pastures grazed by cattle, and did not change through time in ungrazed prairie (Fig. 1f). Average cover of annual grasses (primarily Japanese brome [*Bromus japonicus*] and six-weeks fescue [*Vulpia octoflora*]) was higher ( $P < 0.01$ ) in bison pastures than in pastures grazed by cattle, but their cover never exceeded 0.5% in any year. Annual grasses were absent in ungrazed prairie.

*Woody species*

Leadplant (*Amorpha canescens*) cover increased ( $P < 0.0001$ ) in response to cattle grazing, but did not change through time in either bison pastures or ungrazed prairie (Table 1). The cover of all other shrub species (primarily rough-leaf dogwood [*Cornus drummondii*] and Arkansas rose [*Rosa arkansana*]) averaged  $<0.5\%$  and did not differ among treatments.

*Diversity indices*

During the study, 139 plant species were encountered in bison pastures, 128 species found in cattle pastures, and 89 species found in ungrazed prairie. There were 35 perennial, 32 annual, and 6 biennial species that occurred in the grazed pastures but did not appear in ungrazed prairie. In comparison, seven perennial forb species were present in the ungrazed watersheds but never were detected in either the bison or cattle pastures. After 10 years of grazing, the similarity index between bison and cattle pastures was 85%, whereas bison pastures and ungrazed prairie were 62% similar, and cattle pastures and ungrazed prairie were 67% similar.

Species richness at small (10 m<sup>2</sup>) spatial scales increased ( $P < 0.0001$ ) in response to grazing, although the rate of increase was greater in bison pastures than in pastures grazed by cattle (Fig. 2a). In contrast, richness did not change through time in ungrazed prairie. At larger (200 m<sup>2</sup>) spatial scales, species richness in all treatments exhibited similar temporal patterns as richness at the small scale (Fig. 2b). After 10 years of grazing, species richness was 37% higher in bison pastures and 29% higher in cattle pastures than in ungrazed prairie. Higher species richness in bison pastures than in cattle pastures primarily was due to an increase in the number of annual forbs. In ungrazed prairie, the average number of annual forb, annual grass, perennial forb, warm-season grass, cool-season grass, and sedge

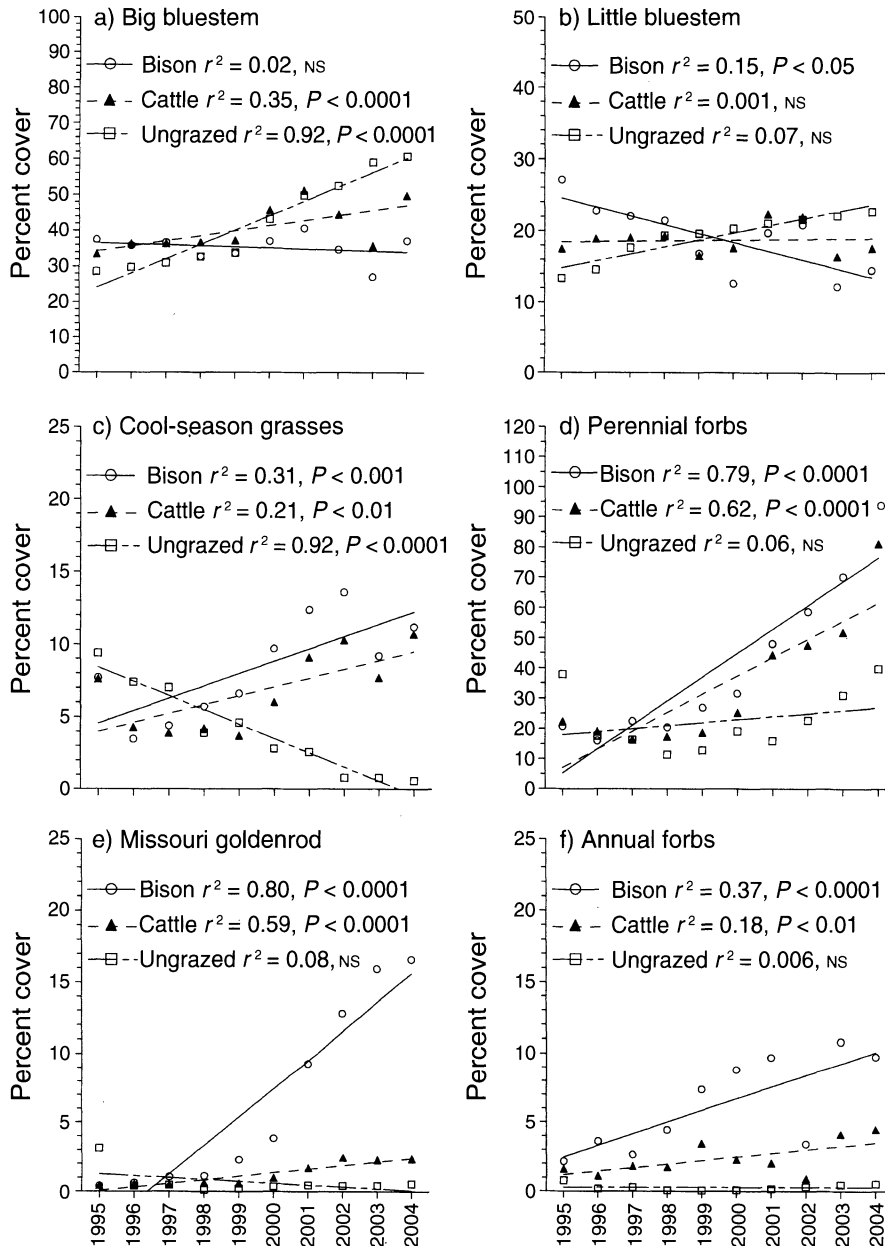


FIG. 1. Temporal trends in canopy cover from bison and cattle grazing compared with ungrazed tallgrass prairie at Konza Prairie Biological Station, Kansas, USA, for six species or life-form groups.

species all were lower ( $P < 0.05$ ) than in pastures grazed by either bison or cattle (Table 2). Exotic species averaged 3.6% of the floristic richness in bison pastures, 3.4% in cattle pastures, and 2.0% in ungrazed prairie.

Trends in the Shannon diversity index increased ( $P < 0.0001$ ) in response to either bison or cattle grazing at both the 10-m<sup>2</sup> (Fig. 2c) and the 200-m<sup>2</sup> spatial level (Fig. 2d), with the largest temporal changes occurring in bison pastures. In ungrazed prairie, diversity at the plot level exhibited a weak but significant decline, whereas diversity at the pasture scale did not change over time.

#### Frequency of occurrence

After 10 years of grazing, the frequency of 22 perennial species increased ( $P < 0.05$ ) in bison pastures, whereas the frequency of 23 species significantly increased in cattle pastures (Table 3). Prairie dropseed (*Sporobolus heterolepis*) frequency declined in bison pastures, and the frequency of Kentucky bluegrass and blue wild-indigo (*Baptisia australis*) declined in both bison and cattle pastures. In ungrazed prairie, seven perennial species increased and six species declined in frequency.

The frequency of occurrence of annual forbs fluctuated dynamically among years, but average frequen-

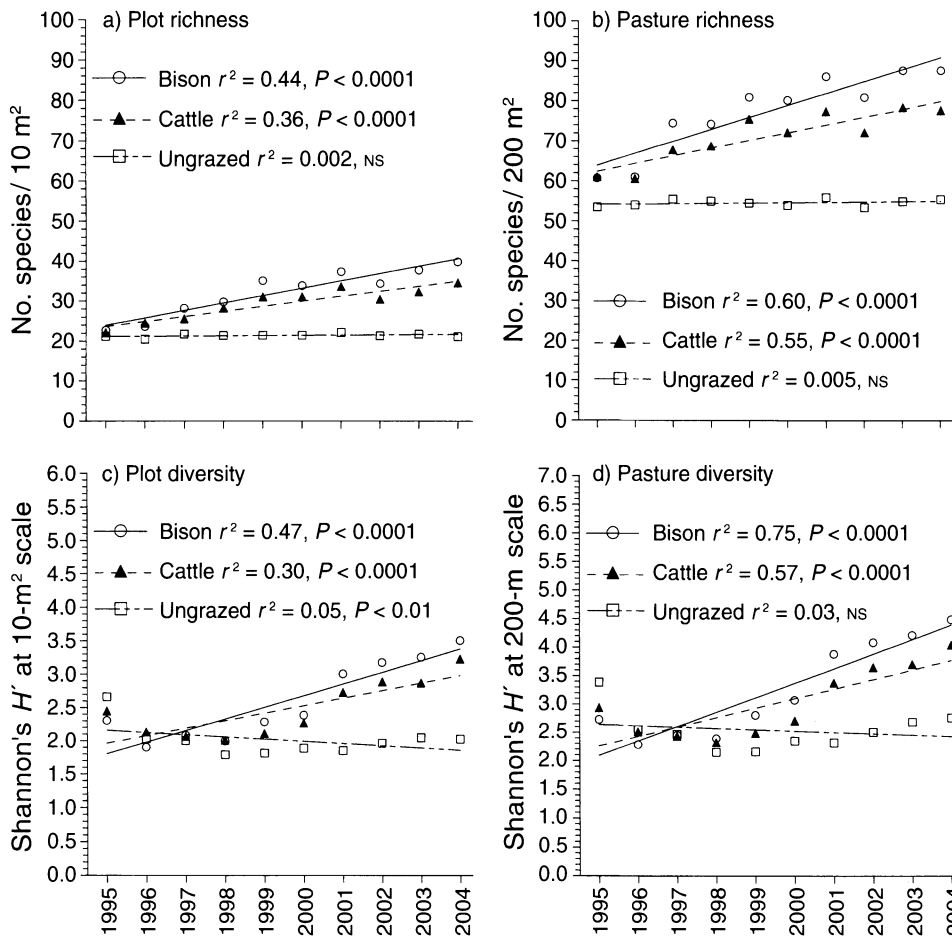


FIG. 2. Temporal trends in plant species diversity indices at different spatial scales (10-m<sup>2</sup> plots vs. 200-m<sup>2</sup> pastures) in response to bison and cattle grazing compared with ungrazed tallgrass prairie: (a, b) species richness; (c, d) the Shannon diversity index,  $H'$ .

cies of daisy fleabane (*Erigeron strigosus*) and grooved flax (*Linum sulcatum*) did not differ between bison and cattle pastures, whereas average frequencies of spotted mat-spurge (*Chamaesyce maculata*) and common pepperweed (*Lepidium densiflorum*) were higher ( $P < 0.001$ ) in bison pastures than in pastures grazed by cattle (data not shown). The frequencies of all annual forb species were significantly lower in ungrazed prairie than in either bison or cattle pastures.

*Residual biomass*

Temporal trends in residual graminoid biomass followed similar patterns in both bison and cattle pastures, with slopes that did not differ from 0 (Fig. 3a). Over the 10-year period, however, the average amount of residual graminoid biomass at the end of the grazing season was lower ( $P < 0.01$ ) in pastures grazed by bison ( $170 \pm 2 \text{ g/m}^2$  [mean  $\pm$  SE]) than in pastures grazed by cattle ( $202 \pm 2 \text{ g/m}^2$ ). On average, bison removed 54% of the annual net graminoid production, compared with 46% graminoid removal by cattle. Both removal rates, however, are within the projected goal of 50% removal with moderate stocking. Temporal

trends in residual forb biomass increased over time with similar slopes in both bison and cattle pastures, but the patterns of change did not differ from 0 in ungrazed prairie (Fig. 3b). Although a highly significant ( $P < 0.0001$ ) year  $\times$  treatment interaction indicated inconsistent patterns, average forb residuum was usually higher in bison and cattle pastures than in ungrazed prairie. Woody biomass averaged  $<4 \text{ g/m}^2$  and did not differ among treatments or change through time.

The CV for residual grass biomass was different ( $P < 0.001$ ) among all three treatments, with highest variability in bison pastures and lowest variability in ungrazed prairie (Table 4). The variability of residual forb biomass also fluctuated from year to year, but the average CV was similar between bison and cattle pastures and was lowest ( $P < 0.01$ ) in ungrazed prairie (Table 4).

DISCUSSION

Preferential grazing by ungulates is a major factor inducing shifts in rangeland plant communities (Weaver and Darland 1948, Herbel and Anderson 1959). Although bison and cattle have a high degree of similarity

TABLE 2. Average number of species in different life-form and taxonomic groups in bison pastures, cattle pastures, and ungrazed tallgrass prairie in the first and last year of the study.

Group	No. species, 1995			No. species, 2004		
	Bison	Cattle	Ungrazed	Bison	Cattle	Ungrazed
Warm-season grasses	9.8	9.5	9.0	14.0 <sup>a</sup>	11.5 <sup>b</sup>	9.5 <sup>bc</sup>
Cool-season grasses	4.3	5.3	4.5	6.0 <sup>a</sup>	6.3 <sup>a</sup>	2.5 <sup>b</sup>
Sedges	4.3	4.3	4.0	5.5 <sup>a</sup>	6.0 <sup>a</sup>	4.0 <sup>b</sup>
Perennial forbs	30.8	31.3	30.5	38.5 <sup>a</sup>	37.0 <sup>a</sup>	32.0 <sup>b</sup>
Annual forbs	7.5	6.5	3.5	15.5 <sup>a</sup>	11.0 <sup>a</sup>	4.5 <sup>b</sup>
Annual grasses	0.3	0	0.5	3.3 <sup>a</sup>	2.3 <sup>a</sup>	0 <sup>b</sup>
Biennial forbs	2.0	1.3	1.0	2.0 <sup>a</sup>	1.5 <sup>ab</sup>	0.5 <sup>b</sup>
Woody species	2.0	2.3	2.0	2.5	2.3	2.5
Legume species	8.0	9.5	9.0	10.0	9.8	9.0
Total richness	60.8	61.0	53.5	87.8 <sup>a</sup>	77.8 <sup>b</sup>	55.5 <sup>c</sup>

Note: Within each year, means in the same row that have the same superscript lowercase letter are not significantly different at  $P < 0.05$ .

TABLE 3. Percentage frequency of the dominant species and those subdominant perennial species that changed ( $P < 0.05$ ) between the first and last year of the study in bison pastures, cattle pastures, and ungrazed tallgrass prairie.

Species	Frequency (%), 1995			Frequency (%), 2004†		
	Bison	Cattle	Ungrazed	Bison	Cattle	Ungrazed
<b>Graminoids</b>						
<i>Andropogon gerardii</i>	100	100	100	100	100	100
<i>Bouteloua curtipendula</i>	97.5	86.3	97.5	100	92.5	100
<i>Bouteloua gracilis</i>	3.8	2.5	7.5	22.5+	21.3+	22.5+
<i>Dichanthelium acuminatum</i>	11.3	16.3	7.5	42.5+	35.0+	2.5
<i>Dichanthelium oligosanthos</i>	100	100	97.5	100	100	87.5-
<i>Eragrostis spectabilis</i>	63.8	73.8	32.5	86.3+	93.8+	62.5+
<i>Koeleria macrantha</i>	27.5	28.8	42.5	100+	96.3+	22.5-
<i>Panicum virgatum</i>	23.8	53.8	37.5	20.0	50.0	47.5
<i>Poa pratensis</i>	52.5	53.8	55.0	26.3-	18.8-	0-
<i>Schizachyrium scoparium</i>	96.3	98.8	87.5	100+	98.8	95.0+
<i>Sorghastrum nutans</i>	98.8	100	100	100	100	100
<i>Sporobolus compositus</i>	63.8	75.0	72.5	87.5+	97.5+	75.0
<i>Sporobolus heterolepis</i>	21.3	25.0	30.0	10.0-	27.5	35.0
<b>Forb and woody species</b>						
<i>Achillea millefolium</i>	32.5	11.3	42.5	60.0+	30.0+	12.5-
<i>Ambrosia psilostachya</i>	100	100	65.0	100	100	77.5+
<i>Amorpha canescens</i>	48.8	73.8	57.5	60.0+	80.0+	60.0
<i>Antennaria neglecta</i>	47.5	18.8	7.5	72.5+	50.0+	7.5
<i>Artemisia ludoviciana</i>	32.5	21.3	40.0	38.8	25.0	5.0-
<i>Asclepias verticillata</i>	16.3	25.0	15.0	12.5	25.0	30.0+
<i>Baptisia australis</i>	27.5	26.3	0	3.8-	6.3-	30.0+
<i>Brickellia eupatorioides</i>	35.0	37.5	82.5	48.8+	53.8+	40.0-
<i>Dalea candida</i>	42.5	38.8	12.5	67.5+	67.5+	25.0+
<i>Dalea purpurea</i>	66.3	68.8	55.0	92.5+	87.5+	65.0
<i>Lespedeza capitata</i>	13.8	27.5	10.0	36.3+	47.5+	20.0
<i>Mimosa nuttallii</i>	1.3	1.3	30.0	1.3	7.5+	30.0
<i>Oxalis stricta</i>	40.0	31.3	17.5	88.8+	76.3+	0
<i>Psoralidium tenuiflorum</i>	35.0	40.0	7.5	55.0+	47.5+	7.5
<i>Ratibida columnifera</i>	10.0	23.8	0	70.0+	71.3+	2.5
<i>Ruellia humilis</i>	92.5	96.3	57.5	95.0	100+	62.5
<i>Salvia azurea</i>	45.0	53.8	80.0	57.5+	66.3+	77.5
<i>Sisyrinchium campestre</i>	25.0	10.0	15.0	68.8+	82.5+	15.0
<i>Solidago missouriensis</i>	61.3	53.8	35.0	98.8+	73.8+	25.0
<i>Symphyotrichum ericoides</i>	87.5	88.8	82.5	100+	100+	80.0
<i>Symphyotrichum oblongifolium</i>	26.3	28.8	85.0	37.5+	40.0+	77.5
<i>Vernonia baldwinii</i>	40.0	45.0	30.0	66.3+	65.0+	40.0

Note: Frequency is based on occurrence in 10-m<sup>2</sup> plots;  $n = 80$  plots for bison and cattle, and  $n = 40$  plots for ungrazed prairie.

† For values in 2004, a positive sign indicates that the frequency of occurrence was significantly higher than in 1995, whereas a negative sign indicates that frequency was significantly lower than initial levels.



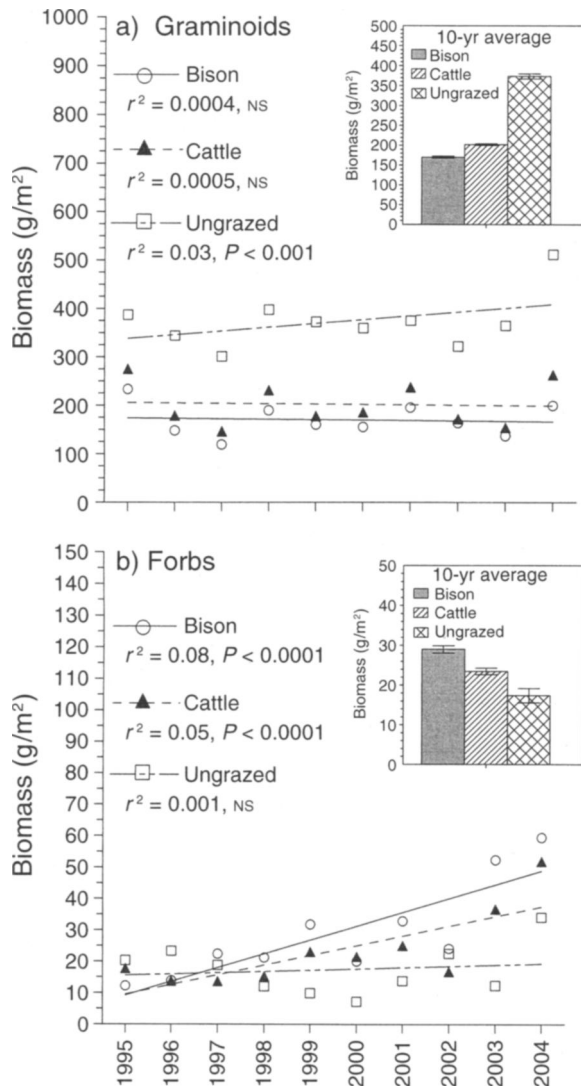


FIG. 3. Changes through time in (a) residual graminoid and (b) residual forb biomass in response to bison and cattle grazing compared with ungrazed tallgrass prairie. The inset in each panel represents the 10-year mean ( $\pm$ SE).

in modifying the composition and diversity of tallgrass prairie, differences in foraging behavior and physical impacts between the herbivores caused divergent trends over time in some plant species. The most conspicuous difference between bison and cattle pastures was the proliferation of Missouri goldenrod and annual forbs in response to bison grazing.

Repeated grazing on the warm-season perennial grasses reduces their competitive dominance and enables subordinate and unpalatable species to increase (Hartnett et al. 1996, Howe 1999). In this study, perennial forbs that responded to grazing by bison and cattle through competitive release included Missouri goldenrod, heath aster, and ironweed. Although western ragweed putatively increases in response to grazing

(Gillen et al. 1991), fluctuations in cover followed similar patterns in both grazed and ungrazed prairie without directional change, suggesting that its abundance may be driven by interannual precipitation patterns, or some other climate variable.

Canopy cover of herbaceous legumes did not change through time in any treatment, whereas leadplant, a woody legume often considered palatable to herbivores (Hickman and Hartnett 2002), increased in cattle pastures. Abundance of some legume species are reduced due to white-tailed deer (*Odocoileus virginianus*) browsing (Ritchie and Tilman 1995), but consumption of legumes by bison and cattle is apparently minor in seasonally grazed tallgrass prairie. Indeed, the frequency of occurrence of many legume species increased in response to ungulate grazing. The frequency of blue wild-indigo, however, declined significantly in both bison and cattle pastures while increasing in ungrazed prairie. But because blue wild-indigo is unpalatable and rarely consumed by ungulates (Gates 1930), grazing may have created conditions favorable for increased insect herbivory (Evans et al. 1989).

Ungulate grazing created a mosaic of patches with different degrees of utilization, which increased species richness compared to ungrazed prairie. Defoliation of the dominant grasses allows short-stature plants to more effectively compete for light (Fahnestock and Knapp 1994). Thus, the frequency of many low-growing perennials (e.g., western yarrow [*Achillea millefolium*] and field pussytoes [*Antennaria neglecta*]) increased significantly in both bison and cattle pastures. In addition, supine annual species (e.g., spotted mat-sperge and prostrate knotweed [*Polygonum aviculare*]) were common in bison-grazing lawns, infrequent in cattle pastures, and absent in ungrazed prairie. Wallowing by bison also created unique disturbance sites that contributed to increased species richness. Bison wallows provide a suitable microhabitat for many ephemeral annuals and early-successional plants (Pol-

TABLE 4. Coefficients of variation (CV) for residual grass and forb biomass in bison pastures, cattle pastures, and ungrazed tallgrass prairie.

Year	Grass			Forbs		
	Bison	Cattle	Ungrazed	Bison	Cattle	Ungrazed
1995	49 <sup>a</sup>	42 <sup>a</sup>	22 <sup>b</sup>	134	131	124
1996	65 <sup>a</sup>	40 <sup>b</sup>	22 <sup>c</sup>	164 <sup>a</sup>	106 <sup>b</sup>	100 <sup>b</sup>
1997	61 <sup>a</sup>	35 <sup>b</sup>	22 <sup>b</sup>	145 <sup>a</sup>	140 <sup>a</sup>	97 <sup>b</sup>
1998	67 <sup>a</sup>	38 <sup>b</sup>	26 <sup>b</sup>	134 <sup>a</sup>	119 <sup>a</sup>	83 <sup>b</sup>
1999	84 <sup>a</sup>	51 <sup>b</sup>	35 <sup>c</sup>	172 <sup>b</sup>	226 <sup>a</sup>	121 <sup>c</sup>
2000	74 <sup>a</sup>	46 <sup>b</sup>	30 <sup>c</sup>	131	168	148
2001	68 <sup>a</sup>	38 <sup>b</sup>	21 <sup>c</sup>	114	101	120
2002	65 <sup>a</sup>	36 <sup>b</sup>	27 <sup>b</sup>	126	100	111
2003	87 <sup>a</sup>	42 <sup>b</sup>	24 <sup>c</sup>	109	116	113
2004	66 <sup>a</sup>	36 <sup>b</sup>	28 <sup>b</sup>	113	120	98
Average	69 <sup>a</sup>	40 <sup>b</sup>	26 <sup>c</sup>	134 <sup>a</sup>	133 <sup>a</sup>	112 <sup>b</sup>

Note: Within each biomass component, row means that have the same superscript lowercase letter are not significantly different at  $P < 0.05$ .

ley and Collins 1984), and the mesic conditions in wetlands allowed establishment of species that otherwise seldom occur on upland prairie (e.g., inland rush [*Juncus interior*] and Carolina foxtail [*Alopecurus carolinianus*]).

Increasing species richness and habitat heterogeneity with ungulate grazing is undesirable if the invasion or spread of nonnative species is accelerated. Although the average number of exotic species occurring annually in bison and cattle pastures ( $n = 2.8$  and  $2.4$  species, respectively) was higher than in ungrazed prairie ( $n = 1.1$  species), all of the exotics were non-invasive (i.e., not capable of displacing native species), and except for the ubiquitous Kentucky bluegrass, none attained  $>1\%$  mean cover in any year. Most of the exotic species ( $n = 9$ ) were annuals or biennials and occurred in disturbed or heavily grazed patches that had not burned, suggesting that the absence of fire, rather than grazing per se, was the preponderant factor influencing their occurrence. Thus, moderate grazing provided niches for some ephemeral fire-sensitive exotic species, but it did not enhance invasion at the expense of native species. This response pattern, however, would have been different if aggressive, fire-tolerant exotic species such as sericea lespedeza (*Lespedeza cuneata*) or Caucasian bluestem (*Bothriochloa bladhii*) had been present in the pastures.

Differences in grazing distribution between bison and cattle influenced burn patterns and the subsequent effect fire has on some species. Higher variability of residual grass in bison pastures ( $CV = 69$ ) than in cattle pastures ( $CV = 40$ ) indicated that bison grazing was more spatially heterogeneous than cattle grazing. That was because bison established large grazing lawns that were heavily utilized while other areas were grazed lightly. In contrast, cattle created smaller grazed patches that were more uniformly distributed throughout the pasture. Thus, cattle pastures had a larger fuel load than bison pastures and burned more completely. This provided a positive feedback for species that respond favorably to fire, but created a more hostile environment for fire-sensitive species. The grazing lawns in bison pastures lacked sufficient fuel to carry a fire, creating an extensive mosaic of burned and unburned areas. Annual forbs, annual grasses, and cool-season graminoids are particularly intolerant of recurring fire (Towne and Kemp 2003) and were the primary beneficiaries of heterogeneous burn patterns in grazed pastures. Thus, depending upon the herbivore, grazing created protective niches of varying sizes that reduced the extent and intensity of fire and buffered the response patterns of many species to annual burning.

Historically, overstocking by domestic livestock has been a common occurrence, and cattle often are characterized as destructive agents responsible for destabilizing some grassland ecosystems (Fleischer 1994), whereas bison are frequently portrayed as intrinsically beneficial (Wuerthner 1998). However, we found that

plant communities in bison-grazed and cattle-grazed pastures were relatively similar through time, suggesting that differences in how the herbivores are typically managed may play a larger role in their impact on prairie vegetation than differences between the species. Arguably, confining bison in small pastures prevents their natural patterns of movement, and presumably could exacerbate defoliation patterns. Grazing lawns were prominent features in the bison pastures and the closely cropped grasses resembled overgrazed prairie. The creation of grazing lawns, however, is typical of many ungulate species (McNaughton 1984, 1986), and even under light stocking rates, bison create localized grazing lawns (Vinton et al. 1993, Coppedge and Shaw 1998). Thus, vegetation dynamics in small pastures are a microcosm of patterns that occur in larger areas. At a regional scale, however, vegetation changes between the herbivores may become more disparate because cattle movements are regulated by distance from water and shade, whereas bison are less constrained and roam more widely (Peden et al. 1974, Plumb and Dodd 1993, Wuerthner 1998, Van Vuren 2001).

### Conclusions

Compared to cattle grazing at similar densities, bison grazing increased plant species richness and spatial heterogeneity, but dramatically increased the cover of Missouri goldenrod and annual forbs. The increased forb cover combined with lower grass cover in bison pastures created a distinctive contrast to cattle pastures, despite a high degree of similarity in the vegetation. Plant community differences between bison-grazed and cattle-grazed pastures, however, were not as large as those differences between grazed and ungrazed prairie. Moderate stocking with either bison or cattle increased spatial heterogeneity and promoted biodiversity of tallgrass prairie.

### ACKNOWLEDGMENTS

The logistics of coordinating and implementing this project would not have been possible without the astute input of Konza Prairie site manager Tom Van Slyke, foremen Jim Larkins and Dennis Mossman, and Department of Animal Science herdsman Gary Ritter and Wayne Adolf. Appreciation also is extended to Amanda Kuhl and the LTER clipping crews for the biomass collections, to Ken Kemp for statistical consulting, and to the numerous personnel who helped with fence building, roundup, and watering the animals. Konza Prairie Biological Station is a preserve of The Nature Conservancy managed by the Division of Biology at Kansas State University. Support for this project was provided by a USDA grant, Konza Prairie Biological Station, and the Long-Term Ecological Research program.

### LITERATURE CITED

- Bailey, A. W., and C. E. Poulton. 1968. Plant communities and environmental interrelationships in a portion of the Tillamook Burn, northwestern Oregon. *Ecology* **49**:1–13.
- Coppedge, B. R., and J. H. Shaw. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. *Journal of Range Management* **51**:258–264.

- Evans, E. W., C. C. Smith, and R. P. Gendron. 1989. Timing of reproduction in a prairie legume: seasonal impacts of insects consuming flowers and seeds. *Oecologia* **78**:220–230.
- Fahnestock, J. T., and A. K. Knapp. 1994. Plant responses to selective grazing by bison: interactions between light, herbivory, and water stress. *Vegetatio* **115**:123–131.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* **8**:629–644.
- Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* **51**:625–632.
- Gates, F. C. 1930. Principal poisonous plants in Kansas. Agricultural Experiment Station Technical Bulletin 25. Kansas State University, Manhattan, Kansas, USA.
- Gillen, R. L., F. T. McCollum, M. E. Hodges, J. E. Brummer, and K. W. Tate. 1991. Plant community responses to short duration grazing in tallgrass prairie. *Journal of Range Management* **44**:124–128.
- Hartnett, D. C., K. R. Hickman, and L. E. Fischer-Walter. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Journal of Range Management* **49**:413–420.
- Herbel, C. H., and K. L. Anderson. 1959. Response of true prairie vegetation on major Flint Hills range sites to grazing treatment. *Ecological Monographs* **29**:171–186.
- Hickman, K. R., and D. C. Hartnett. 2002. Effects of grazing intensity on growth, reproduction, and abundance of three palatable forbs in Kansas tallgrass prairie. *Plant Ecology* **159**:23–33.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* **60**:695–713.
- Howe, H. F. 1999. Dominance, diversity, and grazing in tallgrass restoration. *Ecological Restoration* **17**:59–66.
- Kartesz, J. T. 1999. A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland. First Edition. In J. T. Kartesz and C. A. Meacham, editors. Synthesis of the North American flora. Version 1.0. [on CD.] North Carolina Botanical Garden, Chapel Hill, North Carolina, USA.
- Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. *BioScience* **49**:39–50.
- Krysl, L. J., and B. W. Hess. 1993. Influence of supplementation on behavior of grazing cattle. *Journal of Animal Science* **71**:2546–2555.
- Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, USA.
- McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist* **124**:863–886.
- McNaughton, S. J. 1986. Grazing lawns: on domesticated and wild grazers. *American Naturalist* **128**:937–939.
- Peden, D. G., G. M. Van Dyne, R. W. Rice, and R. M. Hansen. 1974. The trophic ecology of *Bison bison* L. on shortgrass plains. *Journal of Applied Ecology* **11**:489–497.
- Plumb, G. E., and J. L. Dodd. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. *Ecological Applications* **3**:631–643.
- Polley, H. W., and S. L. Collins. 1984. Relationships of vegetation and environment in buffalo wallows. *American Midland Naturalist* **112**:178–186.
- Post, D. M., T. S. Armbrust, E. A. Horne, and J. R. Goheen. 2001. Sexual segregation results in differences in content and quality of bison (*Bos bison*) diets. *Journal of Mammalogy* **82**:407–413.
- Ritchie, M. E., and D. Tilman. 1995. Responses of legumes to herbivores and nutrients during succession on a nitrogen-poor soil. *Ecology* **76**:2648–2655.
- SAS Institute. 1999. SAS system for windows. Version 8.01. SAS Institute, Cary, North Carolina, USA.
- Steuter, A. A., and L. Hidingier. 1999. Comparative ecology of bison and cattle on mixed-grass prairie. *Great Plains Research* **9**:329–342.
- Towne, E. G. 1999. Bison performance and productivity on tallgrass prairie. *Southwestern Naturalist* **44**:361–366.
- Towne, E. G. 2002. Vascular plants of Konza Prairie Biological Station: an annotated checklist of species in a Kansas tallgrass prairie. *Sida* **20**:269–294.
- Towne, E. G., and K. E. Kemp. 2003. Vegetation dynamics from annually burning tallgrass prairie in different seasons. *Journal of Range Management* **56**:185–192.
- Van Vuren, D. H. 2001. Spatial relations of American bison (*Bison bison*) and domestic cattle in a montane environment. *Animal Biodiversity and Conservation* **24**:117–124.
- Vinton, M. A., D. C. Hartnett, E. J. Finck, and J. M. Briggs. 1993. Interactive effects of fire, bison, (*Bison bison*) grazing, and plant community composition in tallgrass prairie. *American Midland Naturalist* **129**:10–18.
- Weaver, J. E., and R. W. Darland. 1948. Changes in vegetation and production of forage resulting from grazing lowland prairie. *Ecology* **29**:1–29.
- Wuerthner, G. 1998. Are cows just domestic bison? Behavioral and habitat use differences between cattle and bison. Pages 374–383 in L. R. Irby and J. E. Knight, editors. International symposium on bison ecology and management in North America. Montana State University, Bozeman, Montana, USA.