Feedback Loops in Ecological Hierarchies Following Urine Deposition in Tallgrass Prairie

Ernest M. Steinauer; Scott L. Collins

Ecology, Vol. 82, No. 5. (May, 2001), pp. 1319-1329.

Stable URL:
http://links.jstor.org/sici?sici=0012-9658%28200105%2982%3A5%3C1319%3AFLIEHF%3E2.0.CO%3B2-3

Ecology is currently published by Ecological Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/esa.html.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

http://www.jstor.org
Fri Oct 12 16:01:23 2007

Ecology, 82(5), 2001, pp. 1319–1329

FEEDBACK LOOPS IN ECOLOGICAL HIERARCHIES FOLLOWING URINE DEPOSITION IN TALLGRASS PRAIRIE

ERNEST M. STEINAUER[1,3] AND SCOTT L. COLLINS[2]

[1]*Department of Botany and Microbiology, University of Oklahoma, Norman, Oklahoma 73019 USA*
[2]*Division of Biology, Kansas State University, Manhattan, Kansas 66506 USA and Department of Zoology, University of Maryland, College Park, Maryland 20742 USA*

Abstract. Although theory predicts that large-scale factors will constrain small-scale interactions, the potential for small-scale events to impact large-scale patch structure is less clear. We examined experimentally the effects of urine deposition, a highly localized event, on small- and large-scale vegetation structure and spatial variation in tallgrass prairie. The response by vegetation to urine deposition may be mediated by grazing. Thus, we also determined the probability of urine patches serving as foci for grazing events by bison. Likelihood of bison grazing was much higher on vs. off urine patches, and grazed areas initiated on urine patches expanded well beyond the area of urine deposition. Abundance of four common graminoid species, and of all graminoids combined, increased on urine patches in ungrazed prairie, while the abundance of *Andropogon gerardii* and total graminoids decreased on urine patches in grazed prairie. The abundance of *Aster ericoides,* and all forbs combined, increased on urine patches in ungrazed, but not in grazed, prairie. Species richness and Shannon-Weiner diversity increased on urine patches in ungrazed prairie but were not affected by urine treatment in grazed prairie. Total spatial variance of graminoids increased relative to controls in response to urine treatment, grazing, and the combination of these treatments. For forbs, total variance increased marginally compared to controls only in response to urine treatment in ungrazed prairie. In combination, urine patches plus grazing produced unique large-scale patch structure compared to urine patches in ungrazed prairie. The most important impact of urine patches on community structure resulted from preferential grazing of urine patches by bison, which increases both the size and severity of the grazed area. Urine patches are thus an example of a small-scale perturbation that generates larger-scale patch structure in tallgrass prairie.

Key words: bison grazing and patch dynamics; grazing; hierarchy theory; Konza Prairie Biological Station (Kansas, USA); patch structure; small perturbation affects large-scale structure; spatial structure in grassland vegetation; spatial variation; species diversity; tallgrass prairie, effects of urine and grazing; vegetation structure.

INTRODUCTION

Patch dynamics and community structure in many plant communities are affected by a variety of biotic and abiotic factors that occur at overlapping spatial and temporal scales (White 1979, Pickett and White 1985). Interactions among these forces result in a complex and hierarchical patch structure (Wu and Loucks 1995), which leads to patterns of spatial variation that are far more complicated than those derived from any single biotic or abiotic factor. Indeed, these interactions may produce emergent patch structure at scales that differ from any particular patch-generating phenomenon.

Patterns of spatial and temporal complexity in North American grassland vegetation have been well documented (Wells 1970, Anderson 1982, Collins and Barber 1985, Collins 1992, Joern and Keeler 1995, Knapp et al. 1998, Stohlgren et al. 1999, Collins 2000). This complexity is generated by multiple mechanisms (e.g., climate variation, fire, herbivory, and interspecific interactions [Barnes et al. 1983, Singh et al. 1983, Milchunas et al. 1988, Umbanhowar 1992, Milchunas and Lauenroth 1993, Knapp et al. 1998]), all of which operate at different and overlapping spatial and temporal scales. Complexity is enhanced not only because of differences in scale, but because some common mechanisms, such as fire, influence patch structure in a fundamentally different way than do other factors, such as grazing by large herbivores (Collins 1987, Hartnett et al. 1996, Collins et al. 1998). Thus, a combination of fire and grazing in grasslands creates a patch structure that is different from that generated by either mechanism alone. Understanding the complex response of tallgrass prairies to the interaction of patch-generating processes will provide valuable insights regarding the maintenance of species diversity in this once-extensive ecosystem (Samson and Knopf 1996).

Many types of patch-forming events in grasslands are highly localized spatially (<1.0 m^2), and their effects may interact with common large-scale processes,

Manuscript received 29 April 1999; revised 22 February 2000; accepted 10 April 2000; final version received 17 May 2000.

[3] Present address: Massachusetts Audubon Society, 153 Hummock Pond Road, Nantucket, Massachusetts 02554 USA. E-mail: esteinauer@massaudubon.org

such as fire and grazing (Collins and Barber 1985). Although hierarchy theory (O'Neill et al. 1986, Allen and Hoekstra 1992) predicts that large-scale factors may constrain small-scale dynamics (Allen and Starr 1982), there is increasing evidence that small-scale forces may affect larger scale, higher-level factors through interactions among lower-level components (Polis and Holt 1992).

The activities of large herbivores, such as bison (*Bos bison*), affect patch structure in grasslands at a variety of spatial scales (Knapp et al. 1999) and include impacts that may feed back up through hierarchical levels. Grazing by herds of bison, for example, affects grassland structure at large spatial scales, and the bison affect structure at smaller scales by creating wallows, trampling vegetation and compacting the soil (Wallace 1987), and redistributing nutrients via excretion (McNaughton 1983, Coffin and Lauenroth 1988, Day and Delting 1990, Steinauer and Collins 1995). When nutrients, particularly nitrogen, are added to herbaceous communities such as grasslands, productivity increases and diversity decreases (DiTommaso and Aarssen 1989, Tilman and Pacala 1993, Stevens and Carson 1999, Gough et al. 2000). Urine excretion, in particular, creates small patches (~0.25 m^2) with elevated N concentrations (Stillwell and Woodmansee 1981, Stillwell 1983), increased aboveground production (Steinauer and Collins 1995), and altered botanical composition (Norman and Green 1958, Day and Detling 1990, Steinauer and Collins 1995) compared to off-patch areas. Most other aspects of grazing reduce standing biomass while increasing diversity as predicted by the intermediate-disturbance hypothesis (Connell 1978, Armesto and Pickett 1985, Milchunas et al. 1988, Huston 1994).

Herbivores preferentially graze vegetation on urine patches because of increased plant production and leaf nitrogen concentration (Day and Detling 1990, Jaramillo and Detling 1992*b*). This evidence suggests that the localized impacts of excretion may create large-scale grazing lawns (McNaughton 1984), implying that a small-scale patch-forming event generates patch structure and vegetation change at a larger spatial scale. Although the independent effects of these factors have been frequently studied in many systems, the interactive effects of nutrient addition and disturbance are likely to produce complex patterns of species diversity in plant communities (Moen and Collins 1996, Collins et al. 1998, Gough and Grace 1998, Wilson 2000).

Earlier, we demonstrated experimentally that plant production was strongly affected by urine addition in ungrazed prairie (Steinauer and Collins 1995), yet the degree to which vegetation response to urine deposition is detectable against the considerable heterogeneity present in tallgrass prairie subjected to a complex disturbance regime remains unclear. In this paper, we address the following questions: (1) What are the effects of urine patches, bison grazing, and the combination of the two on overall plant community structure and diversity, and the abundance of common plant species and major functional groups in grazed and ungrazed tallgrass prairie? (2) What are the effects of urine patches, bison grazing, and the combination of the two on spatial patterns in grazed and ungrazed tallgrass prairie? (3) Do urine patches serve as foci for bison grazing? To address these questions we established four belt transects in both grazed and ungrazed tallgrass prairie and applied artificial bison urine at random locations along two of the transects in each grazing treatment. We measured differences in plant species composition, species diversity, and abundance of grasses and forbs among the transects, and tested for interactions among treatments. We also assessed whether bison preferentially graze on urine patches vs. off-patch areas.

METHODS

Study site

The study was conducted during 1992 in tallgrass prairie at Konza Prairie Biological Station (KPBS) in Riley and Geary counties, Kansas. KPBS is managed as a series of permanent, replicated burn units (watersheds) subjected to a variety of fire regimes, a subset of which are grazed by bison. Dominant plant species at KPBS are C_4 grasses: *Andropogon gerardii, A. scoparius, Sorghastrum nutans, Bouteloua curtipendula, Panicum virgatum,* and *Sporobolus asper* (nomenclature follows the Great Plains Floral Association [1986]), although a diverse array of other grasses and forbs also occurs throughout the region (Freeman 1998). The climate is continental. Mean annual temperature is 13°C and mean annual precipitation is 835 mm, 72% of which occurs from April to September. Study sites were on Tully soils, which are dark, fertile, cherty silt or silty clay loams derived from limestone bedrock (USDA 1975).

Data collection

We selected two study sites, one in a watershed grazed by bison, the other in an adjacent ungrazed watershed. Both sites are routinely burned in the spring of every fourth year, and both were burned in the spring of 1992. At each site we established four 42-m parallel transects, 5 m apart and oriented west to east, on nearly level areas lacking obvious vegetation gradients. We selected our transect length to be long enough to contain several urine patches and our plot size to be smaller than a urine patch but large enough to allow for sampling of eight transects in a reasonable time period. Transects were permanently marked at both ends and at 10.5-m intervals using aluminum pipe driven into the ground. We visually estimated canopy cover of all vascular plant species in 5% cover classes in 128 contiguous 32 × 32 cm plots along each transect in late May and again in late July 1992. Canopy cover values less than 5% were estimated in 1% classes. A 50-m tape was stretched along the transects during vegetation sampling to assure precise location of the plots. We then randomly selected two transects in each watershed for urine application. We thus had four treatments at the transect level with two transects each: ungrazed without urine ($-G-U$, controls), ungrazed with urine ($-G+U$), grazed without urine ($+G-U$), and grazed with urine ($+G+U$).

Two urine patch distributions were generated in which nine plots were randomly selected for urine application. Each distribution was used on one transect in each watershed. We applied urine evenly within a 0.28-m^2 circular frame centered on the selected plots immediately following vegetation sampling in May. The frame entirely covered one plot and approximately one third of the two adjoining plots. However, vegetation responded to urine treatment (evidenced by increased production and dark green color) in the majority of the two adjoining plots and we considered all three to be urine-treated for the purposes of data analysis. There was some overlap of plots receiving urine treatment in one of the distribution patterns because selected plots were either adjacent to each other or had only one plot between them. This resulted in 24 urine-treated plots on one transect in each watershed and 27 on the other for a total of 51 urine-treated plots in each watershed.

Data analysis

Probability of bison grazing.—The likelihood of bison grazing on urine-treated plots vs. that on non-treated plots on the two urine-treated transects in the grazed treatment was tested using χ^2 analysis. Individual plots were considered grazed if visual inspection during the July vegetation-sampling period revealed that >50% of the vegetation in the plot showed signs of bison grazing. The expected number of urine-treated and untreated plots that were grazed was calculated based on the proportion of all plots grazed along both transects.

Community structure.—We examined the effects of urine treatment and grazing on plant community composition, species diversity (richness, evenness, and Shannon-Weiner diversity [H']), canopy cover of common plant species, and cover of plant functional groups (graminoids and forbs) on a subsample of the plots. We used the 51 urine-treated plots on the urine-treated transects and the plots with corresponding locations on the non-urine-treated transects in both watersheds to create equal sample sizes for statistical comparisons.

We used multi-response permutation procedure (MRPP; Zimmerman et al. 1985, Biondini et al. 1988) to assess differences in community composition among transects using canopy cover data. MRPP is a bootstrapping technique that compares the mean ecological distance (Euclidian distance in this case) between members of predefined groups, in this case plots receiving specific treatments, against mean distance within groups created at random from the same data set. The P value is the percentage of distances within the groups created at random that is equal to or smaller than that of distances within the treatment groups. MRPP is appropriate for ecological data because it relaxes assumptions concerning normality of the data structure and it appears to be as robust as the traditional F test (Zimmerman et al. 1985). MRPP tests were carried out using PC-ORD version 2.0 (McCune and Mefford 1995).

Because we are interested in the interactive effects of urine deposition and grazing by bison on plant community structure, we used two-way ANOVA and Tukey's multiple range test (SAS 1992) to test for differences in (1) canopy cover of plant functional groups (total graminoid and total forb cover), (2) cover of the five most common graminoid and forb species, and (3) plant species richness, evenness, and H' among treatments. Pretreatment variability in these parameters among individual plots was high. Therefore, with the exception of plant functional group cover, we tested treatment effects on the percentage change in the above parameters from May to July rather than on actual abundance or diversity values using the following formula:

$$\frac{\text{July} - \text{May}}{\text{May}}.$$

Differences in plant functional group cover between grazing treatments in May prior to urine treatment were tested using a t test. The percentage cover values for total graminoid and total forb cover in May and in July were square-root, arcsine transformed prior to statistical analysis. The percentage change in cover data for individual plant species and in diversity data were not substantially different from that expected for a normal distribution, and the use of transformed data changed test results little. Therefore, we used nontransformed data for these parameters.

Spatial variation.—We examined patterns in the spatial distribution of total graminoid cover and total forb cover at scales ranging from 0.64 to 11.2 m (2–35 plots) with semivariance analysis using GS+ version 1.1 software (Gamma Designs 1990). Semivariance was calculated as

$$t(h) = \left(\frac{1}{2}N[h]\right)S(y_i - y_{i+h})^2$$

where $t(h)$ = semivariance at lag distance h, y_i = measured sample value (e.g., canopy cover) at plot i, y_{i+h} = measured sample value at plot $i + h$, and $N(h)$ = total number of sample couples for the interval h. If spatial dependence exists among sample units, then semivariance increases with distance until levelling off a more-or-less constant value, the "sill," where spatial dependence no longer exists. The sill then provides an estimate of *total* sample variance (v^2). The range is the

TABLE 1. Results of multi-response permutation procedure (MRPP) tests comparing species composition between grazing treatments within urine treatments, between urine treatments within grazing treatments, and across urine and grazing treatments in May and July (1992; at Konza Prairie Biological Station, Kansas, USA) using canopy cover data.

Site comparison†	Date	Intersite distance‡ Site 1	Intersite distance‡ Site 2	Test statistic§	P
Grazing within Urine					
−G−U vs. + G−U	May	12.99	11.60	−5.35	<0.001
	July	22.00	20.56	−3.51	<0.001
−G+U vs. + G+U	May	12.13	11.39	−5.79	<0.001
	July	34.16	25.53	−21.35	<0.001
Urine within Grazing					
−G−U vs. −G+U	May	12.99	12.13	−0.95	0.15
	July	22.00	34.16	−16.81	<0.001
+G−U vs. +G+U	May	11.60	11.39	−3.18	0.009
	July	20.56	25.53	−9.23	<0.001
Urine across Grazing					
−G−U vs. +G+U	May	12.99	11.39	−6.81	<0.001
	July	22.00	25.53	−17.92	<0.001
−G+U vs. +G−U	May	12.13	11.60	−6.59	<0.001
	July	34.16	20.56	−5.72	<0.001

† Site 1 vs. Site 2. Treatment codes: +G = grazed (by bison); −G = not grazed; +U = urine added; −U = no urine added.

‡ Intersite distance is the mean Euclidian distance within the species-by-samples data matrix for the grazing/urine treatments in the site-comparison column. Higher intersite distance values indicate greater variation in species composition among the samples within a treatment.

§ More negative test statistics indicate greater species-composition differences between treatments.

lag distance between samples at which the still is reached. Plots separated by distances less than the range exhibit spatial dependence while those separated by greater distances do not. The nugget variance represents sampling error or variance that occurs at spatial scales smaller than the plot size. The structural variance equals the sill minus the nugget and represents the spatial component of variance (Schlesinger et al. 1996).

Since $t(h)$ is a measure of variance, its value increases as y (in this case plant cover) increases. This has the effect of inflating $t(h)$ on transects with high mean abundance (e.g., during July) vs. those with low mean abundance (e.g., during May). Therefore we standardized abundance values for each transect at each sample date by dividing each individual cover value by the transect mean cover prior to semivariance analysis. Following this, data for each transect were z-transformed (Sokal and Rohlf 1981) to reduce skew and kurtosis. We calculated the nugget, structural, and total variance and the range for both graminoid and forb cover along each transect using a spherical model (Trangmar et al. 1985). Although other models (e.g., exponential or linear) occasionally had better fits to the data, especially for May data, we always used the spherical model to maintain consistency. In all such cases, r^2 values were only marginally less for the spherical compared to other models.

Because of considerable variability in nugget, total, structural, and range values among transects prior to urine application, we compared urine and grazing treatment effects on the percentage change in these parameters from May to July using analysis of variance and Tukey's multiple range test. Change for each parameter was calculated as (July − May)/May. Sample sizes for semivariance parameters were small ($n = 2$) and approximately normally distributed. Arcsine square-root transformation changed ANOVA results marginally. Therefore, we present statistical tests performed on non-transformed data.

RESULTS

Probability of grazing.—Urine-treated plots on the two urine-treated transects in the grazed areas were much more likely to be grazed by bison than were plots on the same transects to which urine was not applied ($\chi^2 = 29.27$, $P < 0.001$). Thirty-three of the 51 urine-treated plots (65%) and 40 of the 205 non-urine-treated plots (18%) were grazed by the July sample date. In addition, 23 of the 40 grazed non-urine-treated plots were in grazing patches containing urine-treated plots.

Community structure.—There were significant differences in plant community composition between grazed and ungrazed transects in both May and July (−G−U vs. +G−U and −G+U vs. +G+U, Table 1). However, the effects of grazing on community composition between sample dates varied between urine treatments. On transects without urine patches, composition became somewhat more similar between ungrazed and grazed areas (−G−U vs. +G−U, less negative MRPP [multi-response permutation procedure] test statistic in July compared to May, Table 1). In contrast, on transects with urine patches, compositional dissimilarity increased substantially between grazed and ungrazed areas (−G+U vs. +G+U, much more negative MRPP test statistic in July compared to May). The effects of urine treatment on community composition within grazing treatments were similar on ungrazed (−G−U vs. −G+U) and grazed (+G−U vs. +G+U) sites. In both cases, differences in community composition between urine-treated and untreated plots increased during the growing season, although the increase was considerably greater in the ungrazed watershed (Table 1). A strong interaction among treatment effects is shown in the urine across grazing analysis (Table 1). In this case compositional dissimilarity between control (−G−U) and urine plus grazing (+G+U) treatments increased dramatically from May to July.

There was considerable fine-scale variation in abundance patterns of both graminoids and forbs along the transects at both sample dates. In general, urine-treated plots on ungrazed transects often had the highest graminoid cover in July (Fig. 1). In contrast, graminoid cover on urine-treated plots on grazed transects tended to be lower than average in July. Urine patches were not strongly associated with either peaks or troughs in forb cover on grazed or ungrazed transects (data not shown). Instead, peaks in forb cover typically resulted from the random occurrence of large individual forbs or forb clones.

Total graminoid cover was significantly lower on the grazed compared to the ungrazed transects in May prior to urine application ($t = -5.25$, $P < 0.001$, Fig. 2), whereas forb cover was similar across all treatments at the start of the experiment ($t = 0.54$, $P = 0.588$, Fig. 2). By July, there was a significant grazing × urine-addition interaction for graminoids ($F = 80.23$, $P < 0.001$) but not for forbs ($F = 1.38$, $P = 0.247$). Total graminoid cover was lowest on the +G+U plots and highest on the −G+U plots (Fig. 2). Forb cover in July was significantly greater on the −G+U plots compared to other treatments (Fig. 2).

Individual graminoid species were more likely to be affected by urine and grazing treatments than were forbs (Table 2). There was a significant grazing × urine-addition interaction for three grasses (*Andropogon gerardii, A. scoparius,* and *Sorghastrum nutans*) and one forb (*Aster ericoides*). Change in cover of *A. gerardii,* the most abundant plant species on the Konza Prairie Biological Station (KPBS; Kansas, USA) was greatest on the −G+U plots and least on the +G+U plots. *A. scoparius, S. nutans, Carex brevior,* and *A. ericoides* all had a significantly greater increase on the −G+U plots compared to some of the other treatments (Table 2).

There was a significant grazing × urine-treatment interaction on percentage change in species richness ($F = 4.23$, $P = 0.039$), evenness ($F = 6.60$, $P = 0.011$), and Shannon diversity (H'; $F = 11.04$, $P = 0.001$). Richness increased on all treatments between May and July (Fig. 3). Urine treatment resulted in a significantly smaller increase in richness in ungrazed compared to grazed prairie. The change in richness on grazed plots was similar between urine treatments and intermediate between the changes on ungrazed plots. Evenness decreased on all treatments between May and July, es-

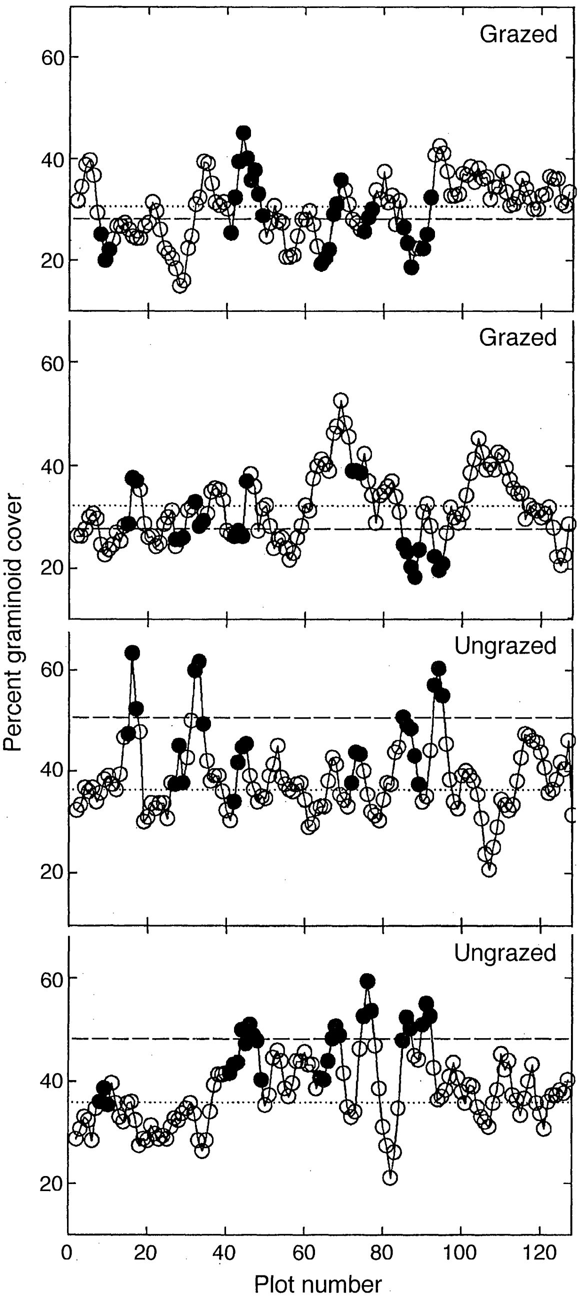

FIG. 1. Smoothed plots of graminoid cover along replicate transects in grazed and ungrazed prairie. Data were smoothed by calculating a running average of three adjacent plots. Urine-treated plots are indicated by solid circles. Mean graminoid cover on urine-treated plots is indicated by a dashed line, and mean graminoid cover on non-urine-treated plots is indicated by a dotted line.

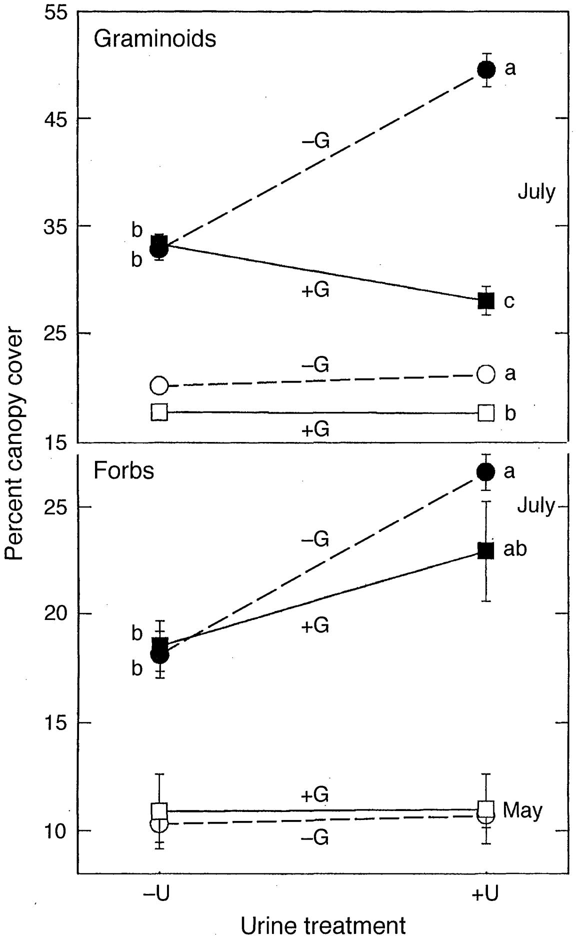

FIG. 2. Mean canopy cover of graminoids and forbs among urine and grazing treatments in May (open symbols) and July (solid symbols). Plots treated with urine (+U) are on the right side of the figure, and plots not treated with urine (−U) are on the left. Grazed plots (+G) are indicated by squares and solid lines; ungrazed plots (−G) are indicated by circles and dashed lines. Only a subset of the plots on each transect was tested ($n = 51$, see *Methods: Data analysis: Community structure*). Within functional groups and month, the data points with different lowercase letters are significantly different at $P < 0.05$ (ANOVA and Tukey's multiple range test) among grazing and urine treatment combinations. Error bars indicate ±1 SE.

pecially on −G+U plots (Fig. 3). The change in evenness was significantly less on +G+U plots compared to −G+U plots while non-urine-treated plots were intermediate. The change in H' was small but positive on all but −G+U plots where it decreased significantly compared to other treatments (Fig. 3).

Spatial variability.—All semivariograms calculated with functional-group abundance data in May had relatively large nugget to total variance ratios (overall mean: 0.70 in May), indicating considerable pretreatment variation in functional-group abundance at spatial scales smaller than our plot size. Changes in semivariance parameters on control (−G−U) transects for graminoids between May and July were small (nugget = −3.1%, structural = +10.5%, total = +1.2%), suggesting that patterns in graminoid abundance are seasonally stable in the absence of perturbation. Nugget, structural, and total variance of forbs decreased from May to July (−20.0%, −15.1%, and −18.4% respectively) on control transects, suggesting that patterns in forb abundance become more homogenous during the growing season.

Although there were sometimes large differences in mean percentage change of variance parameters among treatments between May and July, only the change in total variance for graminoids was significant (Fig. 4). Both grazing and urine treatment increased total variance for grasses compared to controls, though only the difference between −G−U and −G+U transects was significant. Patterns of change in total variance for forbs were similar to that for graminoids with the greatest difference also between the −G−U and −G+U transects (Fig. 4). However, despite the large mean changes in forb variance, differences among treatments were only marginally significant ($P = 0.066$).

There were no significant effects of either urine treatment or grazing on the range at which variation occurred for either graminoids or forbs.

DISCUSSION

Our results support the hypothesis that small-scale patch-forming processes can affect large-scale patterns in vegetation structure. Also, the results of our experiments demonstrate that different components of the disturbance regime interact to affect community structure. In particular, we found significant interaction effects of urine deposition and grazing on species richness, evenness, diversity, total cover of grasses, cover of several individual species, and on overall community composition (Tables 1 and 2, Figs. 2 and 3). The mechanism involved is the strong preference bison exhibit for grazing on urine patches, which likely results from the increase in vegetation abundance and/or nutrient concentration on urine patches (Jaramillo and Detling 1992*b*). Observations of urine patches in an earlier study at the Konza Prairie Biological Station (KPBS) indicated that insect herbivory was also greater on certain species, particularly *Panicum virgatum*, on vs. off urine patches (E. M. Steinauer, *personal observation*). Thus, urine patches provide a focal point for grazing by a variety of aboveground herbivores.

Not only were urine patches more likely to be grazed by bison, but so were adjacent areas. Our results suggest that urine patches provided initiation points for local bison-grazing events that resulted in grazed patches considerably larger than the urine patch. Since bison grazing influences fire frequency and intensity by altering patterns of fuel accumulation (Steuter et al. 1995), these impacts may be translated to even larger spatial scales. Fire, in turn, has a strong influence on site selection for grazing by bison (Vinton et al. 1993,

TABLE 2. Mean percentage change in canopy cover of the five most common graminoid and four most common forb species from May to July calculated as (July–May)/May.

Species	Grazing/urine treatment†						G×U interaction	
	−G−U	−G+U	+G−U	+G+U	*F*	*P*	*F*	*P*
Graminoids								
Andropogon gerardii	88.4^{B}	131.5^{A}	105.0^{AB}	33.1^{C}	14.61	<0.001	28.02	<0.001
A. scoparius	59.1^{B}	138.2^{A}	103.5^{B}	53.9^{B}	7.02	<0.001	12.11	<0.001
Bouteloua curtipendula	63.0	78.0	68.1	90.0	1.88	0.135	0.05	0.821
Carex brevior	62.7^{B}	120.4^{A}	71.7^{AB}	84.7^{AB}	3.42	0.019	2.90	0.090
Sorgastrum nutans	48.9^{B}	142.1^{A}	63.5^{B}	58.6^{B}	11.3	<0.001	14.71	<0.001
Forbs								
Ambrosia psilostachya	58.3	108.8	40.3	62.6	1.43	0.238	0.35	0.554
Amorpha canescens	381.0	154.6	80.5	114.3	2.07	0.114	2.75	0.103
Artemesia ludoviciana	51.8	35.4	82.4	60.8	1.12	0.343	0.00	0.985
Aster ericoides	71.7^{B}	199.5^{A}	95.3^{B}	79.7^{B}	17.84	<0.001	25.51	<0.001

Notes: Individual grazing/urine treatment combinations were tested with a one-way ANOVA while G×U interaction was tested with a two-way ANOVA (see *Methods: Data analysis: Community structure*). Only a subset of the plots on each transect was tested (see *Methods: Data analysis: Community structure*). Urine (U) and grazing (G) treatments are as in Table 1.

† Within a row, means followed by different capital letters are significantly different at the $P < 0.05$ level (Tukey's multiple range tests).

Steuter et al. 1995) and vegetation response to urine addition (Steinauer and Collins 1995). Though the present study examined only plant species and community dynamics, ecosystem processes such as production and nutrient cycling are also known to be affected by urine application (Jaramillo and Detling 1992*a*), grazing (Turner et al. 1993), and fire (Knapp and Seastedt 1986).

Results of this and other studies suggest that control in ecological hierarchies does not proceed solely from higher to lower levels (Senft et al. 1987, Wu and Loucks 1995). Instead, feedback from lower to higher levels appears to occur via interactions among components of the different levels (e.g., urine patches affect bison grazing patterns). In this study, feedback loops did not skip hierarchical levels. Urine patches affected bison grazing (one level), and other studies (Vinton et al. 1993, Steuter et al. 1995) have shown that bison grazing affects fire frequency and intensity (one level), but in our several years of studying urine patches at KPBS, we found nothing to indicate that urine patches have any direct impact on fire (two levels).

Interactions between urine treatment and grazing produce four general patch types in grazed grassland: ungrazed areas with low N availability, ungrazed with high N patches, grazed areas with low N availability, and grazed patches formed around local nutrient hot spots. Though the occurrence of urine patches in "ungrazed" prairie seems unlikely, grazing is not a uniform process across the landscape (Senft et al. 1987, Briggs et al. 1998). Thus, some urine patches in grazed areas remain ungrazed by bison. Therefore, urine deposition and grazing produce a complex combination of patch types that increases overall heterogeneity in tallgrass prairie.

This study supports our earlier findings (Steinauer and Collins 1995) that urine patches have considerable impact on small-scale vegetation structure and diversity in ungrazed tallgrass prairie. Urine patches were visible in the ungrazed prairie as roughly circular areas with increased plant abundance and a deep-green color and they appeared as distinct peaks in plots of graminoid abundance for the ungrazed prairie. This is consistent with our earlier studies in which graminoid abundance nearly doubled on vs. off urine patches in ungrazed prairie (Steinauer and Collins 1995). While average forb abundance was greater on urine-treated compared to untreated transects in ungrazed prairie, peaks in forb abundance typically were not associated with urine patches but instead reflected the occurrence of a large individual forb or forb clone. This contrasts with our previous study in which forb abundance in tallgrass prairie was not affected by urine treatment in the year of application. However, these earlier studies occurred on hilltop locations with relatively shallow soil or in a year with a late-season drought. Therefore, low soil moisture may have inhibited forb response to urine treatment in our earlier studies (Briggs and Knapp 1995).

As in our previous studies, species richness and Shannon-Weiner diversity were reduced following urine treatment in ungrazed prairie (Fig. 3). This may result from increased size and competitive abilities of C_4 grasses on urine patches followed by reduction in light penetration to lower strata (Collins et al. 1998, Stevens and Carson 1999, Gross et al. 2000). The loss of diversity following urine treatment was not evident on grazed transects likely because bison reduced the cover of the C_4 grasses. These results parallel the interaction between fire and bison grazing on species diversity in tallgrass prairie. Repeated spring burning in areas without large herbivores increases the relative cover of C_4 grasses while reducing forb abundance and species diversity (Collins et al. 1995). However, large

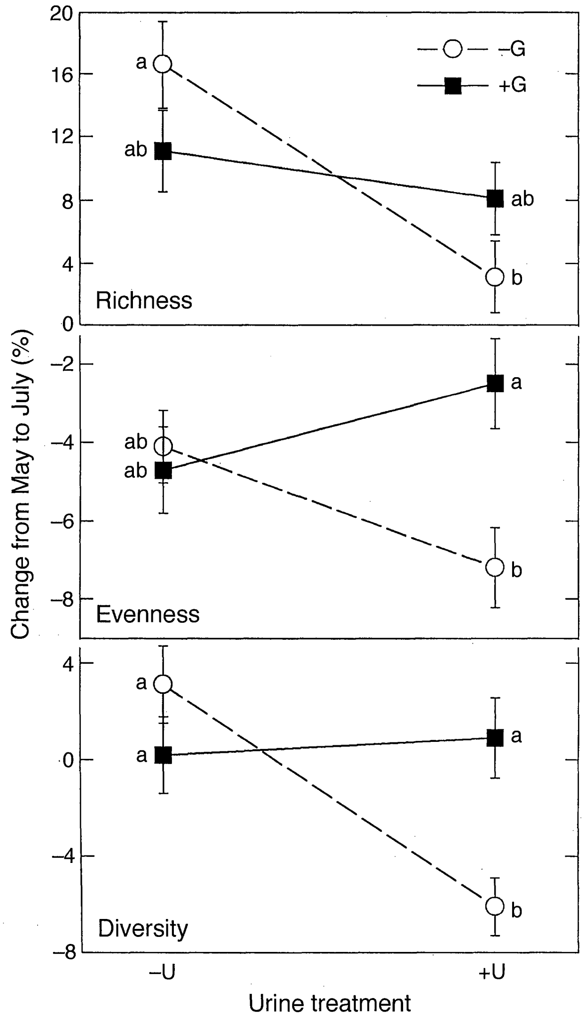

FIG. 3. Urine treatment and grazing effects on the percentage change in species richness, evenness, and Shannon-Weiner diversity (H'), from May to July, calculated as (July−May)/May. Symbols are as in Fig. 2. Within each panel, data points with different lowercase letters are significantly different at $P < 0.05$(ANOVA and Tukey's multiple range test) among grazing and urine-treatment combinations. Error bars indicate ±1 SE.

herbivores, by reducing the abundance of graminoids, reverse the negative impacts of burning on forb abundance and species diversity (Collins et al. 1998).

We found significant differences in community structure among urine and grazing treatments as well as substantial changes in structure between sample dates (Table 1). Our analytical approach, multi-response permutation procedures (MRPP), is sensitive to differences in relative species-abundance patterns as well as changes in species composition. In our case, the relatively large differences in graminoid abundance account for much of the differences among treatments. Although species richness was different among treatments as well, these changes resulted primarily from fluctuations among a suite of relatively uncommon forb species (Steinauer and Collins 1995). Uncommon species with low abundance tend to have little impact on MRPP or other multivariate analysis techniques.

Total (sill) variance of graminoid cover changed very little between May and July on the control (−G−U) transects, indicating the short-term stability of the perennial graminoid component in the absence of perturbation (Fig. 4). Total variance of graminoids increased in response to urine treatment, grazing, or both compared to controls. Total variance of forbs decreased on control transects between May and July but increased to some degree on the urine-treated and grazed transects, though differences were only marginally significant ($P = 0.066$). Grazing tended to moderate seasonal changes in total forb variance for both urine treatments (4.3% for +G−U, vs. −18.4% for −G−U, and 32.3% for +G+U vs. 70.3% for −G+U). This reflects

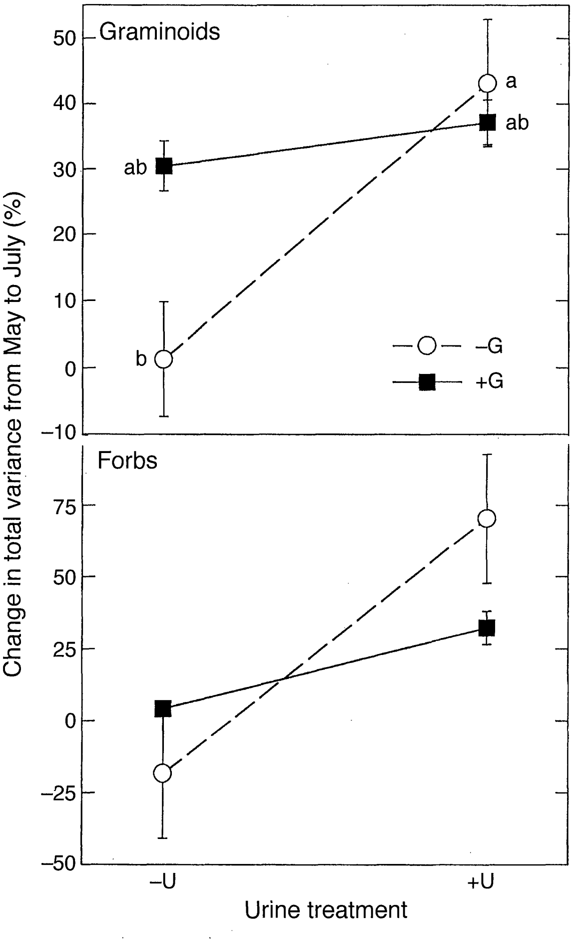

FIG. 4. Mean percentage change ($n = 2$) in total (sill) variance for graminoid and forb cover from May to July, calculated as (July−May)/May. Data were relativized by dividing by mean abundance per transect, then z-transformed prior to semivariance analysis. Symbols and lines are as in Fig. 2. Within each panel, data points with different lowercase letters are significantly different at $P < 0.05$ (ANOVA and Tukey's multiple range test) among grazing and urine treatment combinations. Error bars indicate ± 1SE.

the well-documented competitive interactions between forbs and graminoids in grasslands (Tilman 1984, 1987, Gibson 1988*a*, *b*, Vinton et al. 1993, Turner and Knapp 1996), where increases in graminoid cover during the growing season may suppress forb growth. Grazing reduces graminoid cover in a patchy manner and increases local forb abundance through release from competition (Vinton and Hartnett 1992, Collins et al. 1998).

Nugget variance accounted for a relatively large portion of the total (sill) variance of functional-group abundance along all transects on both sample dates. This indicates that much of the variation in functional-group abundance patterns along our experimental transects occurred at spatial scales smaller than our plot size (32 × 32 cm). Bartha et al. (1995), for example, found that peaks in spatial heterogeneity for individual species and functional groups at KPBS occurred at spatial scales ranging from 10 to 20 cm.

We were surprised to find no significant change in the range component of semivariance since both urine-treated and grazed patches were larger than the plot size. However, we applied urine to random locations along the transects. Similarly, grazed patches varied widely in size and also occurred at random locations along the transects. Also, while urine treatment clearly produced peaks of plant abundance in ungrazed prairie, the effect was more complicated in grazed prairie. In both cases, but especially in grazed prairie, at least some of the variation in affected areas was within the range of variation found in untreated prairie (Fig. 1). Thus, treatment effects did not clearly translate to an increase in the range component of semivariance. Despite the preponderance of small-scale pattern, results from our experiment demonstrate that patch structure in grassland vegetation also occurs at larger scales, and the scale of that structure varies in response to interactions among large- and small-scale processes.

In summary, urine patches are an important component in maintaining heterogeneity in tallgrass prairie. Urine patches had the immediate effect of creating small patches with increased nutrient availability and high cover of graminoids. As cover of graminoids increased, total species richness and diversity decreased on these patches. In our study and others (Day and Detling 1990, Jaramillo and Detling 1992*b*), urine patches were strongly preferred as grazing sites by large herbivores (McNaughton 1986, Senft et al. 1987, McNaughton et al. 1997, Frank et al. 1998). Grazing of urine patches reduced graminoid cover and moderated the negative impacts of urine treatment on plant diversity. In addition, grazing initiated on a urine patch often spread considerably beyond the urine patch boundary, increasing the spatial scale of vegetation patterns. Bison grazing, in turn, influenced fire frequency and intensity by altering patterns of fuel accumulation (Steuter et al. 1995). Thus, urine patches are an example of a small-scale impact that can be transmitted up ecological hierarchies through interaction with other disturbances to impact processes operating at larger spatial scales.

ACKNOWLEDGMENTS

We thank Al Steuter, Linda Wallace, Tony Joern, and two anonymous reviewers for critical review of the manuscript. Brian Maurer generously provided many helpful suggestions on the spatial-autocorrelation analyses. Financial supported was provided to E. M. Steinauer by The Nature Conservancy and by the University of Oklahoma Graduate Student Senate. Logistical support was provided by Konza Prairie Biological Station, and the Konza Prairie LTER Program.

LITERATURE CITED

Allen, T. H. F., and T. W. Hoekstra. 1992. Towards a unified ecology. Columbia University Press, New York, New York, USA.

Allen, T. F. H., and T. B Starr. 1982. Hierarchy: perspective for ecological complexity. University of Chicago Press, Chicago, Illinois, USA.

Anderson, R. C. 1982. An evolutionary model summarizing the roles of fire, climate and grazing animals in the origin and maintenance of grasslands: an end paper. Pages 297–308 *in* J. R. Estes, R. J. Tyrl, and J. N. Brunken, editors. Grasses and grasslands: systematics and ecology. University of Oklahoma Press, Norman, Oklahoma, USA.

Armesto, J. J., and S. T. A. Pickett. 1985. Experiments on disturbance in old-field plant communities: impact on species richness and abundance. Ecology **66**:230–240.

Barnes, P. W., L. L. Tieszen, and D. J. Ode. 1983. Distribution, production, and diversity of C_3 and C_4-dominated communities in a mixed prairie. Canadian Journal of Botany **61**:741–751.

Bartha, S., S. L. Collins, S. M. Glenn, and M. Kertész. 1995. Fine-scale spatial organization of tallgrass prairie vegetation along a topographic gradient. Folia Geobotanica and Phytotaxinomica **30**:169–184.

Biondini, M. E., P. W. Mielke, and K. J. Berry. 1988. Data-dependent permutation techniques for the analysis of ecological data. Vegetatio **75**:161–168.

Briggs, J. M., and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position and fire as determinants of aboveground biomass. American Journal of Botany **82**: 1024–1030.

Briggs, J. M., M. D. Nellis, C. L. Turner, G. M. Henebry, and H. Su. 1998. Landscape perspective of patterns and processes in tallgrass prairie. Pages 265–282 *in* A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, Oxford, UK.

Coffin, D., and W. K. Lauenroth. 1988. Effects of disturbance size and frequency on a shortgrass plant community. Ecology **69**:1609–1617.

Collins, S. L. 1987. Interaction of disturbances in a tallgrass prairie: a field experiment. Ecology **68**:1243–1250.

Collins, S. L. 1992. Fire frequency and community heterogeneity in tallgrass prairie vegetation. Ecology **73**:2001–2006.

Collins, S. L. 2000. Disturbance frequency and community stability in native tallgrass prairie. American Naturalist **155**:311–325.

Collins, S. L., and S. C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. Vegetatio **64**:87–94.

Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. Ecology **76**:486–492.

Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science **280**:745–747.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science **199**:1302–1310.

Day, T. A., and J. K. Detling. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. Ecology **71**:180–188.

DiTommaso, A., and L. W. Aarssen. 1989. Resource manipulation in natural vegetation: a review. Vegetatio **84**:9–29.

Frank, D. A., S. J. McNaughton, and B. F. Tracy. 1998. The ecology of the earth's grazing ecosystems. BioScience **48**: 513–521.

Freeman, C. C. 1998. The flora of Konza Prairie: a historical review and contemporary patterns. Pages 69–80 *in* A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, Oxford, UK.

Gamma Designs. 1990. Geostatistics for agronomic and biological sciences, version 1.1. Gamma Designs, Plainwell, Michigan, USA.

Gibson, D. J. 1988*a*. The relationship of sheep grazing and soil heterogeneity to plant spatial patterns in dune grassland. Journal of Ecology **76**:233–252.

Gibson, D. J. 1988*b*. The maintenance of plant and soil heterogeneity in dune grassland. Journal of Ecology **76**:497–508.

Gough, L., and J. B. Grace. 1998. Herbivore effects on plant species density at varying productivity levels. Ecology **79**: 1586–1594.

Gough, L., C. W. Osenberg, K. L. Gross, and S. L. Collins. 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. Oikos **89**: 428–439.

Great Plains Floral Association. 1986. Flora of the Great Plains. University of Kansas Press, Lawrence, Kansas, USA.

Gross, K. L., M. R. Willig, L. Gough, R. Inouye, and S. B. Cox. 2000. Patterns of species diversity and productivity at different spatial scales in herbaceous plant communities. Oikos **89**:417–427.

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.

Huston, M. A. 1994. Biological diversity. Cambridge University Press, Cambridge, UK.

Jaramillo, V. J., and J. K. Detling. 1992*a*. Small-scale grazing in a semi-arid North American grassland. I. Tillering, N uptake, and retranslocation in simulated urine patches. Journal of Applied Ecology **29**:1–8.

Jaramillo, V. J., and J. K. Detling. 1992*b*. Small-scale grazing in a semi-arid North American grassland. II. Cattle grazing of simulated urine patches. Journal of Applied Ecology **29**: 9–13.

Joern, A., and K. H. Keeler, editors. 1995. The changing prairie. Oxford University Press, Oxford, UK.

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.

Knapp, A. K., J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. 1998. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, Oxford, UK.

Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. BioScience **36**:662–669.

McCune, B., and M. J. Mefford. 1995. PC-ORD, version 2.0. Oregon State University, Corvallis, Oregon, USA.

McNaughton, S. J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. Ecological Monographs **53**: 291–320.

McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form and coevolution. American Naturalist **124**:863–886.

McNaughton, S. J. 1986. On plants and herbivores. American Naturalist **128**:765–770.

McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1997. Promotion of the cycle of diet-enhancing nutrients by African grazers. Science **278**:1798–1800.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs **63**:327–366.

Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist **132**:87–106.

Moen, J., and S. L. Collins 1996. Trophic interactions and plant species richness along a productivity gradient. Oikos **76**:603–607.

Norman, M. J. T., and J. O. Green. 1958. The local influence of cattle dung and urine upon the yield and botanical composition of permanent pasture. Journal of the British Grassland Society **13**:39–45.

O'Neill, R., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey, USA.

Pickett, S. T. A., and P. S. White, editors. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology & Evolution **7**:151–154.

Samson, F. B., and J. J. Knopf, editors. 1996. Prairie conservation: preserving North America's most endangered ecosystem. Island Press, Corvelo, California, USA.

SAS Institute. 1992. SAS, version 6.08. SAS Institute, Cary, North Carolina, USA.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology **77**:364–374.

Senft, R. L., M. B. Coughenour, D. W. Baily, R. L. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. BioScience **37**:789–799.

Singh, J. S., W. K. Lauenroth, R. K. Heitschmidt, and J. L. Dodd. 1983. Structural and functional attributes of the vegetation of northern mixed prairie of North America. Botanical Review **49**:117–149.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition. W. H. Freeman & Company, San Francisco, California, USA.

Steinauer, E. M., and S. L. Collins. 1995. Effects of urine deposition on small-scale patch structure in prairie vegetation. Ecology **76**:1195–1205.

Steuter, A. A., E. M. Steinauer, G. L. Hill, P. A. Bowers, and L. L. Tieszen. 1995. Distribution and diet of bison and pocket gophers in a sandhills prairie. Ecological Applications **5**:756–766.

Stevens, M. H. H., and W. P. Carson. 1999. Plant density determines species richness along an experimental fertility gradient. Ecology **80**:455–465.

Stillwell, M. A. 1983. Effects of bovine urinary nitrogen on the nitrogen cycle of a shortgrass prairie. Dissertation. Colorado State University, Fort Collins, Colorado, USA.

Stillwell, M. A., and R. G. Woodmansee. 1981. Chemical transformation of urea-nitrogen and movement of nitrogen in shortgrass prairie soil. Soil Science Society of America Journal **45**:893–898.

Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications **9**:45–64.

Tilman, G. D. 1984. Plant dominance along an experimental nutrient gradient. Ecology **65**:1445–1453.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along an experimental nitrogen gradient. Ecological Monographs **57**:189–214.

Tilman, D., and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13–25 *in* R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities. University of Chicago Press, Chicago, Illinois, USA.

Trangmar, B. B., R. S. Yost, and G. Uehara. 1985. Application of geostatistics to spatial studies of soil properties. Advances in Agronomy **38**:45–95.

Turner, C. L., and A. K. Knapp. 1996. Response of a C_4 grass and three C_3 forbs to variation in nitrogen and light in tallgrass prairie. Ecology **77**:1738–1749.

Turner, C. L., T. R. Seastedt, and M. L. Dyer. 1993. Maximization of aboveground grassland production: the role of defoliation frequency, intensity, and history. Ecological Applications **3**:175–186.

Umbanhowar, C. E. 1992. Abundance, vegetation and environment of four patch-types in a northern mixed prairie. Canadian Journal of Botany **70**:277–284.

USDA [United States Department of Agriculture]. 1975. Soil survey of Riley County, Kansas. United States Department of Agriculture, Washington, D. C., USA.

Vinton, M. A., and D. C. Hartnett. 1992. Effects of bison grazing on *Andropogon gerardii* and *Panicum virgatum* in burned and unburned tallgrass prairie. Oecologia **90**:374–382.

Vinton, M. A., D. C. Hartnett, E. J. Finke, 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.

Wallace, L. L. 1987. Effects of clipping and soil compaction on growth, morphology, and mycorrhizal colonization of *Schizachyrium scoparium,* a C_4 bunch grass. Oecologia **72**: 423–428.

Wells, P. V. 1970. Postglacial vegetational history of the Great Plains. Science **167**:1574–1582.

White, P. S. 1979. Pattern, process and natural disturbance in vegetation. Botanical Review **45**:229–299.

Wilson, S. D. 2000. Heterogeneity, diversity, and scale in plant communities. Pages 53–69 *in* M. Hutchings, E. A. John, and A. J. Stewart, editors. Ecological consequences of habitat heterogeneity. Blackwell Science, Oxford, UK.

Wu, J., and O. L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Quarterly Review of Biology **70**:439–466.

Zimmerman, G. M., H. Goetz, and P. W. Mielke, Jr. 1985. Use of an improved statistical method for group comparisons to study the effects of prairie fire. Ecology **66**:606–611.