



Effects of Urine Deposition on Small-Scale Patch Structure in Prairie Vegetation

E. M. Steinauer, S. L. Collins

Ecology, Volume 76, Issue 4 (Jun., 1995), 1195-1205.

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.

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.

Ecology is published by The Ecological Society of America. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Ecology

©1995 The Ecological Society of America

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2001 JSTOR

EFFECTS OF URINE DEPOSITION ON SMALL-SCALE PATCH STRUCTURE IN PRAIRIE VEGETATION¹

E. M. STEINAUER AND S. L. COLLINS²

Department of Botany/Microbiology, University of Oklahoma, Norman, Oklahoma 73019 USA

Abstract. Large grazing mammals contribute to the species diversity of grasslands via direct and indirect effects of defoliation and urine deposition. We examined the influence of one and two applications of simulated bovine urine on vegetation structure on (1) tallgrass prairie burned either every 2 or 4 yr at Konza Prairie Research Natural Area (KPRNA), Kansas, and (2) unburned sandhills prairie at the Niobrara Valley Preserve, Nebraska. We also examined the influence of urine and the clipping of graminoids on an annually burned site at KPRNA.

Plant abundance in general increased on urine patches but the response appeared dependent on litter accumulation. C_4 grasses increased at the annual burn and Niobrara sites where litter levels were low. C_3 forbs increased at the 2- and 4-yr burn sites where litter levels were high. Urine treatment significantly affected community composition at all but the 2-yr burn site. Alpha-diversity decreased on urine patches at the annual and 4-yr burn sites but increased on urine patches at the Niobrara site. Beta-diversity increased on urine patches at the annual burn and Niobrara site but decreased on urine patches at the 4-yr burn site. The clipping of graminoids at the annual burn site reduced both α - and β -diversity and graminoid abundance while forb abundance was not affected.

Key words: α -diversity; β -diversity; clipping; nitrogen; sandhills prairie; simulated bovine urine; tallgrass prairie.

INTRODUCTION

Grassland vegetation is spatially and temporally variable (Weins 1976, Collins 1992, Glenn and Collins 1992, Seastedt and Knapp 1993). This variability or "patchiness" may result from several factors including immigration and extinction (Glenn and Collins 1992), competitive interactions (Tilman 1985), topography (Barns and Harrison 1982), climate (Gibson and Hulbert 1987, Tilman and El Haddi 1992), and disturbance (White 1979, Sousa 1984). More importantly these factors interact in a complex fashion to affect patch dynamics at multiple spatial and temporal scales (Collins and Uno 1983, Collins and Barber 1985, Collins 1987, Allen and Hoekstra 1992). Patchiness is important in providing a variety of habitat types for maintaining species diversity (Connell 1978, Huston 1979).

Large grazing animals contribute directly to patchiness in grasslands through defoliation, trampling (Wallace 1987), and excretion (McNaughton 1983). Urine deposition, for example, creates patches with elevated nitrogen (N) levels (Jaramillo and Detling 1992a), increased rates of nutrient cycling (Woodmansee 1978, Floate 1981) and altered species composition (Norman and Green 1958, Day and Detling 1990). In most studies of nutrient addition to grasslands, commercial fertilizer, typically ammonium nitrate, is broadcast on

large areas, often with repeated applications (e.g., Owensby et al. 1970, Tilman 1987) resulting in increased productivity, and in the abundance of C_3 grasses and forbs (Huffine and Elder 1960, Owensby et al. 1970). In contrast, urine patches are small (≈ 0.25 m²), and spatially and temporally stochastic. Approximately 75% of the N in urine is urea, which is rapidly transformed to ammonia in the soil (Stillwell and Woodmansee 1981). Nutrient inputs as urine patches may occur at spatial and temporal scales more in concordance with those that occurred historically in grazed North American grasslands (Mack and Thompson 1982, Milchunas et al. 1988). Indeed, Smith and Rice (1983) have shown that late successional grass species in tallgrass prairie utilize N applied in the form of urea more effectively than when applied as nitrate.

Ungulates preferentially graze vegetation on urine patches because of increased quantity and quality of nutrients compared to off-patch locations (Day and Detling 1990, Jaramillo and Detling 1992b). Grazing alters community composition by selective removal of certain species, which contributes to the increase in diversity on moderately grazed grasslands (Collins 1987). Bison diet, for example, typically includes $\approx 90\%$ graminoids (Krueger 1986, Plumb and Dodd 1993), while many forbs are avoided (Ward et al. 1991). Thus, urine patches provide initiation points for grazing events that further impact local species composition.

This study was undertaken to address the role of urine patches and grazing on small-scale patch structure and dynamics in tallgrass and sandhills prairies.

¹ Manuscript received 11 April 1994; revised 31 October 1994; accepted 2 November 1994.

² Present address: Ecological Studies Program, National Science Foundation, 4201 Wilson Boulevard, Arlington, Virginia 22230 USA.

Specifically, we examined the effects of urine treatment and the clipping of graminoids on (1) community composition, (2) α - and β -diversity, and (3) plant species and functional group abundance. Because plant growth is typically N limited in mesic North American grasslands (Tilman 1984, 1987, Seastedt et al. 1991), we predicted that production would increase on urine patches. Production and species richness are often inversely related (Grime 1973, Al-Mufti et al. 1977, Tilman 1993). Therefore, we predicted a decline in species richness and α -diversity on urine patches. Because species will likely respond differentially to urine treatment, and competitive interactions may be altered following N addition (Tilman 1985), we expected community composition to shift on urine patches. Because diversity is often increased by grazing (Collins 1987, Collins and Glenn 1988), we predicted that forb abundance, species richness, and diversity would increase on clipped plots and that the greatest increase in diversity would occur on fertilized and clipped plots.

MATERIALS AND METHODS

Study sites

The study was conducted during 1990 and 1991 in tallgrass prairie at Konza Prairie Research Natural Area (KPRNA) in Riley County, Kansas, and in sandhills prairie at the Niobrara Valley Preserve (NVP) in Brown County, Nebraska. Dominant plant species at both sites are C_4 grasses: *Andropogon gerardii*, *A. scoparius*, *Sorghastrum nutans*, *Bouteloua curtipendula*, *Panicum virgatum*, and *Sporobolus asper* at KPRNA and *A. hallii*, *A. scoparius*, *P. virgatum*, *Calamovilfa longifolia*, *B. hirsuta*, and *Sporobolus cryptandrus* at NVP. Nomenclature follows *Flora of the Great Plains* (Great Plains Floral Association 1986).

KPRNA is managed as a series of permanent, replicated burn units subjected to a variety of fire regimes. Fire was not a part of the management on our sites at NVP during this study. The climate is continental at both sites. Mean annual temperature is $\approx 13^\circ\text{C}$ at KPRNA and 8.8°C at NVP. Mean annual precipitation is 835 mm at KPRNA and 483 mm at NVP, 72 and 79% of which occurs from April to September at the two locations, respectively. April to September rainfall at KPRNA was 117 and 69% of the long-term average in 1990 and 1991, respectively, and 120 and 102% of average at NVP. Study sites at KPRNA were on Florence soils, which are dark, fertile, cherty silt or silty clay loams derived from limestone bedrock (USDA Soil Survey, Riley County, Kansas 1975). The study site at NVP was on Valentine soil which is deep, fine-grained eolian sand, low in nutrients and organic matter (USDA Soil Survey, Brown County, Nebraska 1993).

Experiment 1

Data collection and analysis.—Thirty 0.25-m² circular plots were located at each of three study sites in

TABLE 1. Chemical composition of simulated bovine urine.*

Compound	Amount (g/L)
Urea	13.648
MgCl ₂ ·6H ₂ O	0.750
MgSO ₄ ·7H ₂ O	0.725
CaCl ₂ ·2H ₂ O	0.091
KCl	7.015
KHCO ₃	6.830
NaCl	1.210

* From Stillwell 1978.

1990. Two sites were at KPRNA on ungrazed upland prairie; one site is burned every 2 yr (2-yr burn site) and the other is burned every 4 yr (4-yr burn site). Both sites were burned in 1989. One ungrazed upland site was located at NVP. Plots at the 2- and 4-yr burn sites were placed at 5-m intervals along parallel transects spaced 5 m apart. We used three 45-m transects at the 2-yr burn site and two 70-m transects at the 4-yr burn site. Because of considerable bare ground at NVP, the plots were scattered and constrained to contain at least 20% cover of *A. hallii*.

Ten plots at each site were systematically assigned to one of three urine treatments. In treatment 1, 2 L of simulated bovine urine (equivalent to 50.9 g N/m², Stillwell 1983 and Table 1) were applied in early June 1990 followed by 2 L of water (equivalent to 7.14 mm of precipitation) applied in mid-July. In treatment 2, 2 L of simulated urine were applied on both the above dates, and in controls, 2 L of water were applied on both dates. Treatments were applied evenly and slowly to the plot surface to prevent runoff. Canopy cover of vascular plant species rooted in each plot was visually estimated in 5% cover classes prior to urine application in June and July and in mid-August of 1990, and in late May, mid-July, and early September of 1991. Cover values under 5% were estimated in 1% classes.

We compared plant community response among treatment groups at each site using multi-response permutation procedures (MRPP, Zimmerman et al. 1985, Biondini et al. 1988) with canopy cover data. MRPP is a bootstrapping technique that compares the mean dissimilarity between members of predefined groups, in this case samples (plots) within treatments, against mean distances 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 are equal to or smaller than 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).

We used percent dissimilarity (PD), a measure of β -diversity, to assess compositional similarity of plots within each treatment group at each site. PD is defined as:

$$PD = 1 - PS$$

$$PS = 1 - 0.5 \sum_{i=1}^s |p_a - p_b|$$

where PS is percent similarity, p_a is the proportional cover of species p in quadrat a , p_b is the proportional cover of species p in quadrat b , and s is the total number of species (Whittaker 1975).

Alpha-diversity (richness [S = the number of plant species per plot], Shannon-Weiner diversity [$H' = -\sum p_i \ln p_i$ where p_i is the relative cover of species i , Greig-Smith 1983], and evenness [equitability = $H'/\ln(S)$, Pielou 1969]) was calculated as a measure of within-plot variability for each treatment group at each site. Because of considerable variation in α -diversity parameters among plots prior to treatment application, α -diversity values were standardized to reflect percentage change from pretreatment values on a plot-by-plot basis as follows:

$$\frac{\text{value at sample date} - \text{pretreatment value}}{\text{pretreatment value}},$$

prior to performing statistical tests.

Canopy cover values for species and functional group abundance were standardized in a similar manner as with α -diversity parameters, with the resulting values then arcsine-transformed to normalize data. Treatment effects on individual plant species and functional groups (C_3 graminoids, C_4 grasses, all grasses, all forbs, and all species), α -diversity, and PD were tested with t tests for the July 1990 data, and with ANOVAs for all subsequent sample dates. Data from treatment 1 and 2 plots for July 1990 at each site were combined prior to analysis, since at this time only one urine treatment had been applied to both sets of plots. Significance for all statistical tests throughout this paper is at the 0.05 % level unless otherwise indicated.

Experiment 2

Preliminary results from the 1st yr of data collection indicated that the number of plots per treatment was insufficient to test for treatment effects on individual species. Also, inconsistencies in species response to urine treatment at the 2-yr burn site appeared related to variation in soil depth among plots. In particular, the C_4 grasses tended to respond positively to urine treatment on relatively deep soils but negatively on shallow soils, likely because shallow soil sites became droughty early in the growing season. Because of these problems, a second, one-season experiment was initiated in 1991 at KPRNA on an annually burned low terrace with relatively deep Florence soil and lacking in obvious vegetation gradients. An annually burned site was selected for Experiment 2 because of the limited amount of space made available at KPRNA.

Data collection and analysis.—Urine treatments were the same as used in Experiment 1 but the number

TABLE 2. Multi-response permutation procedures (MRPP) test statistics comparing species composition among one and two urine treatments and controls within each study site for six sample dates (Experiment 1) using canopy cover data. More negative test statistics indicate greater differences among treatments.

Date	2-yr burn	4-yr burn	Niobrara
Jun 1990	0.789	-1.014	-0.620
Jul 1990	0.705	-2.119*	-0.937
Aug 1990	-0.634	-2.095*	-2.506*
May 1991	-0.119	-6.567**	-2.251*
Jul 1991	0.986	-8.306**	-3.097**
Sep 1991	1.307	-3.572**	-0.579

* $P \leq 0.05$, ** $P \leq 0.01$, $n = 10$ for all treatment and control plots.

of plots per treatment was increased to 50. Plots were arranged in a rectangular 5-m grid pattern to which treatments were randomly applied in mid-May and mid-July 1991. Canopy cover was visually estimated prior to urine applications in May and July and again in early September in the same cover classes as used in Experiment 1. Graminoid species were clipped to 5 cm in height to simulate grazing in 25 plots per treatment following canopy cover estimation and prior to the second urine treatment in July. All species were clipped to 5 cm in height in all plots following cover estimation in September. Clipped herbage was collected, air dried, sorted by species, oven dried for 24 h at 65°C, and weighed.

Treatment effects on community composition were tested with MRPP and PD using canopy cover data as in Experiment 1. Alpha-diversity was calculated with actual canopy cover data rather than relative values. Differences in functional group and individual species abundance were assessed using biomass for graminoids in July and for all species in September, but as canopy cover for forbs in July, because forbs were not clipped at the July sample date. Prior to statistical analysis of the July diversity and abundance data the values for treatment 1 and 2 plots were combined as in Experiment 1. Differences between urine treated and control plots were determined by t tests for July diversity and abundance data. Differences in diversity and abundance among urine treatments and between clipping treatments were compared using ANOVAs for September data.

RESULTS

Experiment 1

Community composition.—We found no significant differences in community composition (MRPP) among treatment groups at any site prior to urine application, or at the 2-yr burn site at any time following urine treatments (Table 2). There were significant treatment effects on composition in several subsequent sample periods at the 4-yr burn and Niobrara sites (Table 2). Differences peaked in July 1991 at both sites as indi-

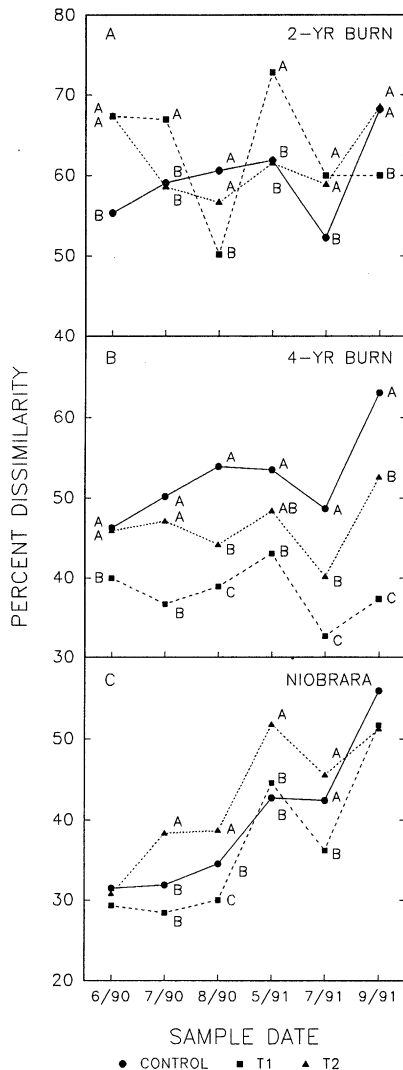


FIG. 1. Percent dissimilarity among plots within urine treatments at (A) the 2-yr burn, (B) the 4-yr burn, and (C) the Niobrara site (Experiment 1). Significant differences among treatments on the same date are indicated by different letters (t test for July 1990, ANOVA for all other dates, $P \leq 0.05$). T1 = one urine treatment ($n = 10$), T2 = two urine treatments ($n = 10$), Control ($n = 10$).

cated by the most negative MRPP test statistics (Table 2).

There were significant differences in percent dissimilarity (PD, β -diversity) among the three treatment groups prior to urine application at the 2- and 4-yr burn sites (Fig. 1a, b). PD varied widely in subsequent sample periods at the 2-yr burn site with no seasonal pattern or consistent relationship to urine treatment. Plots of PD values among treatments at the 4-yr burn site displayed similar patterns but diverged during the course of the study. PD values at this site were greatest on control followed by treatment 1, then treatment 2 plots. At the Niobrara site PD increased on all plots during

the course of the study (Fig. 1C) but was greatest on treatment 2 plots in all but the initial and final sample periods.

Alpha diversity was little affected by urine treatment at the 2-yr burn site. The only significant response to urine treatment was in August 1990 when Shannon-Weiner diversity was greater on treatment 1 plots relative to treatment 2 and control plots (Fig. 2a-c). Both richness and Shannon-Weiner diversity decreased with treatment at the 4-yr burn site (Fig. 2d-f), while evenness was not affected by treatment. Richness increased on treatment 2 plots at the Niobrara site, but significantly so in only two of five sample periods (Fig. 2g-i). Evenness decreased on treatment 2 plots at the Niobrara site but the only significant response was in May 1991. Shannon-Weiner diversity was not affected by treatment at the Niobrara site.

Functional group response.—We analyzed urine treatment effects on canopy cover for four plant functional groups: C_3 graminoids, C_4 graminoids, all graminoids, and all forbs. C_4 grasses averaged 82% of total graminoid cover, and thus their response to urine treatment closely paralleled that of total graminoid cover at all study sites. In addition, C_3 graminoid cover was not affected by urine treatment at any site or date. Therefore, we present results for total graminoid and total forb cover only.

Graminoid response to urine treatment varied among study sites. Graminoid cover was not affected by urine treatment at the 2-yr burn site at any sample date (Fig. 3a). Urine treatment reduced graminoid cover at the 4-yr burn site in both July and September 1991 (Fig. 3b). In contrast, graminoid cover increased with urine treatment at the Niobrara site on all post-treatment sample dates (Fig. 3c).

Forb cover increased with urine treatment at the 2-yr burn site in July and September 1991 (Fig. 3d), and at the 4-yr burn site in August 1990 and in all 1991 sample dates (Fig. 3e). Three common perennial forb species: *Aster ericoides*, *Ambrosia psilostachya*, and *Artemisia ludoviciana* accounted for most of the increase at the 4-yr burn site. There was no significant treatment effect on forb cover at the Niobrara site during the course of the study (Fig. 3f).

Experiment 2

Community composition.—There were no significant differences in community composition among plots assigned to treatment groups prior to the May treatment application (Table 3). Community composition was significantly affected by urine treatment at both the July and September sample dates. Because MRPP has no multiple comparison procedure analog, we performed two-way comparisons for September data using MRPP between all urine/clipping treatment combinations (15 total), as recommended by Zimmerman et al. (1985). All comparisons between clipped and unclipped treatments were significant regardless of urine treatment

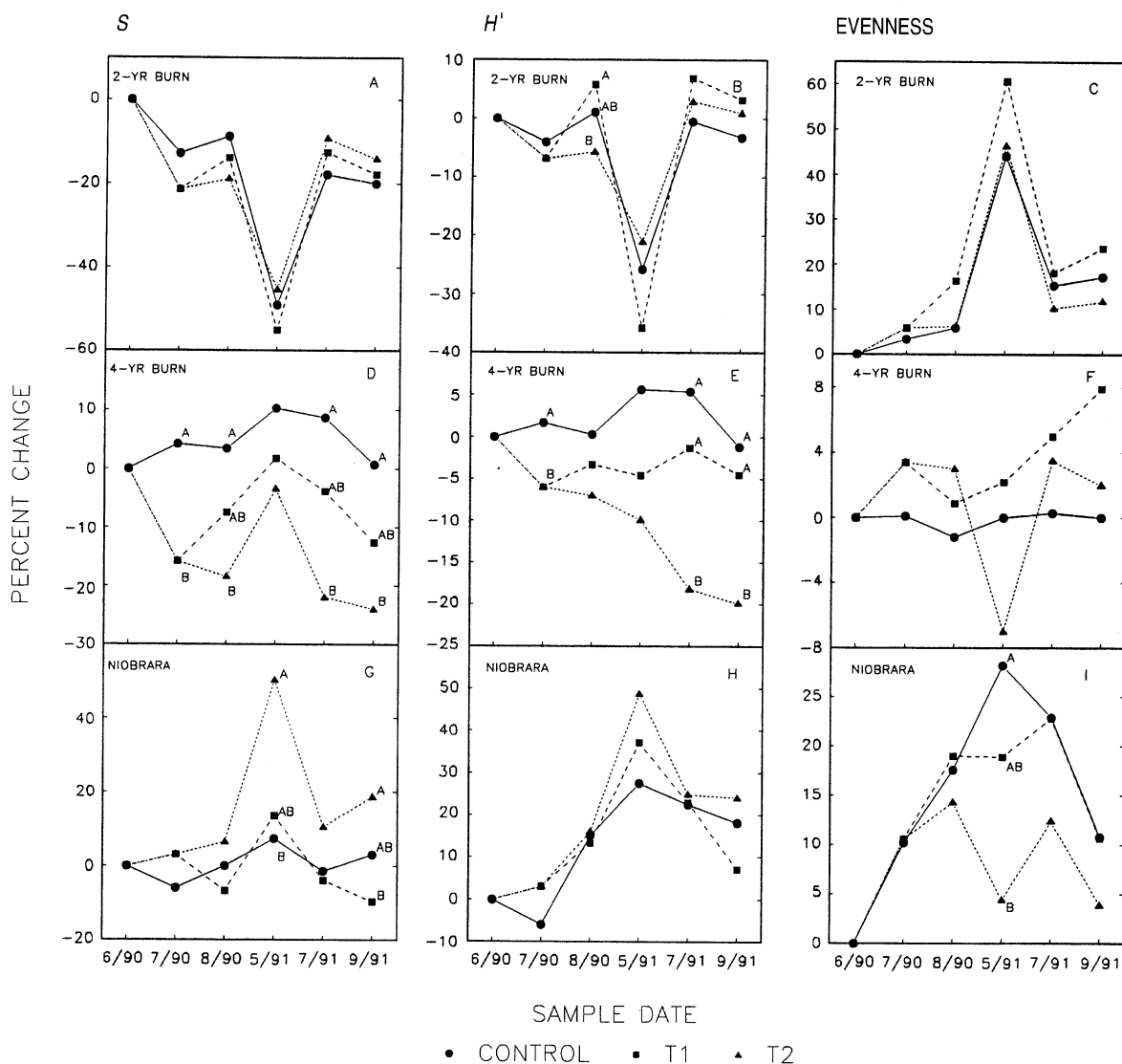


FIG. 2. Percent change in α -diversity (Species richness (S), Shannon-Weiner diversity (H'), and Evenness) from pretreatment values among treatments at the 2- and 4-yr burn and Niobrara sites (Experiment 1). Significant differences (t test for July 1990, ANOVA for all other dates, $P \leq 0.05$, $n = 10$ for each treatment and control group) among treatments on the same date are indicated by different letters. Treatments are as indicated in Fig. 1.

(Table 3), likely because of greatly reduced graminoid cover on clipped plots. Composition on both unclipped treatment 1 and 2 plots was significantly different from that on unclipped control plots, while only clipped treatment 2 plots were significantly different from clipped control plots (Table 3).

There were small but significant differences in percent dissimilarity (PD, β -diversity) among treatment groups in May prior to urine application (Fig. 4). PD decreased on all treatments between May and July, though, on average, the decrease was greater on urine-treated plots. PD increased between July and September for all clipped treatments. For both clipped and unclipped plots the greatest increase in PD between

July and September was on treatment 2 plots. For all urine treatments, PD was greater on clipped plots than on the corresponding unclipped plots, and significantly so for all but control plots.

Neither richness, evenness, nor Shannon-Weiner diversity were significantly different among plots assigned to treatment groups in May prior to urine application (Fig. 5). Both urine treatment and clipping reduced α -diversity. In July both Shannon-Weiner diversity and evenness but not richness were significantly lower on urine-treated than on control plots (Fig. 5b and c). In September all three parameters decreased significantly with both urine treatment and clipping. The species lost following urine treatment varied unpredictably among

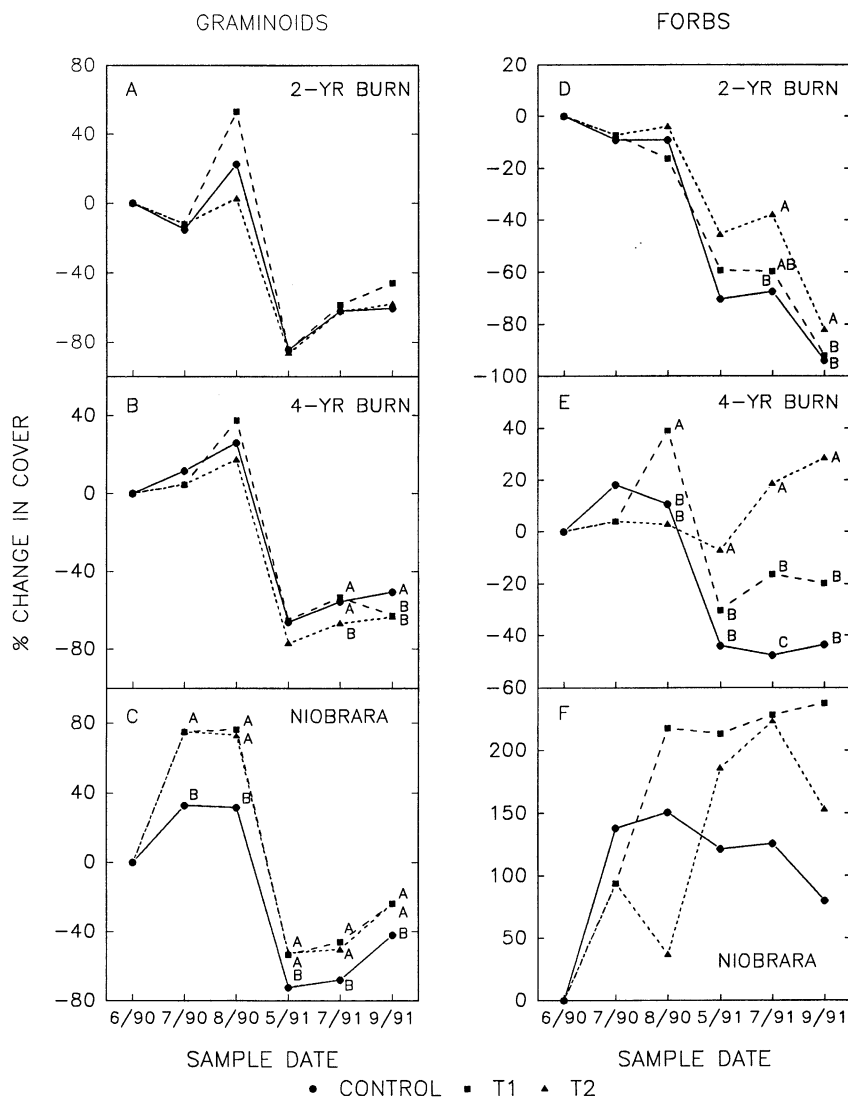


FIG. 3. Percent change in total graminoid and total forb cover from pretreatment values (Experiment 1). Significant differences among treatments on the same date are indicated by different letters (t test for July 1990, ANOVA for all other dates, $P \leq 0.05$, $n = 10$ for each treatment and control group). Treatments are as indicated in Fig. 1.

plots but were generally forbs with low initial abundance values on the plots from which they were lost. In contrast, species lost following clipping tended to be grass species with initially low abundance values.

Species and guild abundance.—There were no sig-

nificant differences in the percent cover of common graminoid or forb species or of all graminoid or forb species combined among plots assigned to the various treatment groups in May prior to treatment application (ANOVA, $P \leq 0.05$). Nine graminoid species occurred

TABLE 3. MRPP statistics of community composition for all two-way comparisons among urine/clipping treatment combinations in September using canopy cover data. More negative test statistics indicate greater differences among treatments.

	T1C	T2C	CCL	T1NCL	T2NCL
T2CL	-1.40				
CCL	-1.47	-3.18*			
T1NCL	-27.11*	-27.30*	-25.68*		
T2NCL	-22.20*	-22.89*	-21.29*	-1.48	
CNCL	-24.00*	-24.52*	-21.37*	-6.71*	-5.06*

* $P \leq 0.01$, $n = 25$ for each treatment in all comparisons. T1 = one urine treatment, T2 = two urine treatments, C = Controls, CL = Clipped, NCL = Not Clipped.

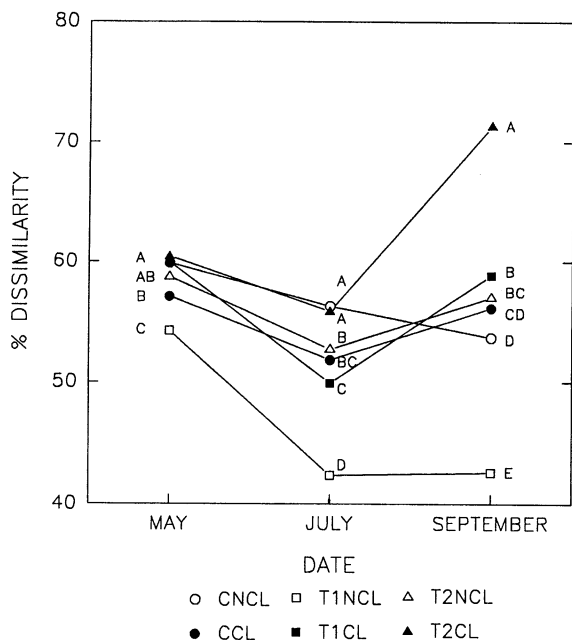


FIG. 4. Percent dissimilarity among plots within urine treatments at the annual burn site (Experiment 2). Significant differences among treatments on the same date are indicated by different letters (ANOVA, $P \leq 0.05$, $n = 300$ for each treatment). Treatments as in Table 3.

in a sufficient number of plots in July to test for treatment effects on biomass. Of these, *A. gerardii*, *B. curtipendula*, and *S. nutans*, as well as all graminoids combined, had significantly greater biomass on treated compared to control plots (Fig. 6). All except *S. nutans* had approximately double the biomass on treated compared to control plots. This trend continued on unclipped plots into September when *A. gerardii*, *B. curtipendula*, *Eragrostis spectabilis*, *S. nutans*, and all graminoids combined again had approximately double the biomass on treated compared to control plots (Fig. 7a). In contrast, on clipped plots, the biomass of *A. gerardii*, *B. curtipendula*, and *S. asper*, and all grass species combined was significantly greater on control and treatment 1 plots than on treatment 2 plots (Fig. 7b). Note that little growth of graminoids occurred on either clipped or unclipped plots between July and September (Fig. 7b and compare Figs. 6 and 7a).

Percent change in canopy cover was used to assess forb response to treatment in July as forbs were not clipped at that time, while biomass was used in September. There were no differences in total forb cover in July or total forb biomass in September among urine or clipping treatments (Fig. 8). Nine forb species occurred in enough plots to perform statistical tests but few responded to urine treatment. *Physalis pumila* had a marginal increase in cover on treated relative to control plots in July (mean increase in cover on treated plots = 80%, on control plots = 13%, $n = 13$, $P = 0.07$, t test). In September, *A. psilostachya* had signif-

icantly greater biomass on clipped treatment 2 plots than on either clipped treatment 1 or control plots, and *Aster oblongifolius* had significantly greater biomass on unclipped treatment 2 and control plots than on unclipped treatment 1 plots.

DISCUSSION

Urine treatment formed distinct patches on the prairie landscape recognizable at the community, guild, and individual species levels. Graminoid and total production increased in response to urine treatment at the annual burn and Niobrara sites, mostly as a result of

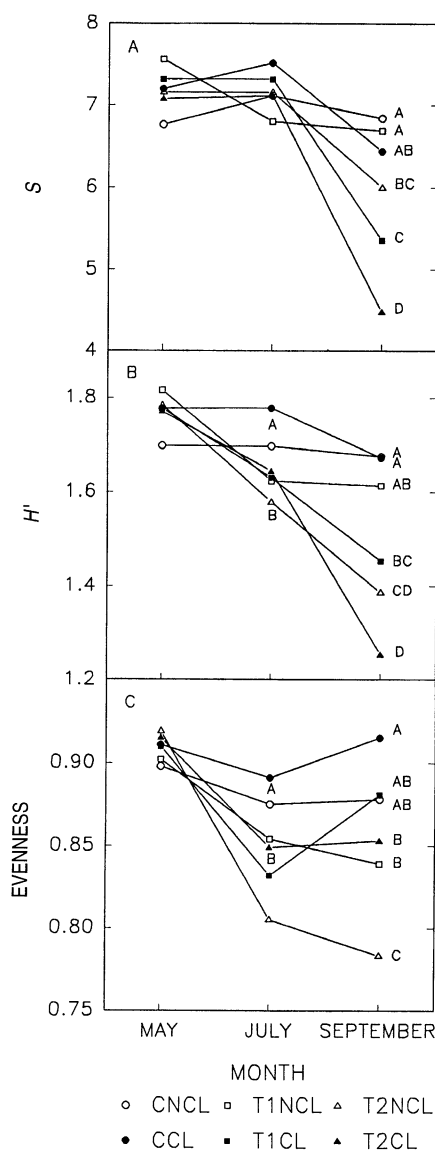


FIG. 5. Alpha-diversity at the annual burn site (Experiment 2). Significant differences among treatments on the same date are indicated by different letters (t test for July, ANOVA for September, $P \leq 0.05$, $n = 25$ for each treatment and control group). S = species richness, H' = Shannon-Weiner diversity. Treatments as in Table 3.

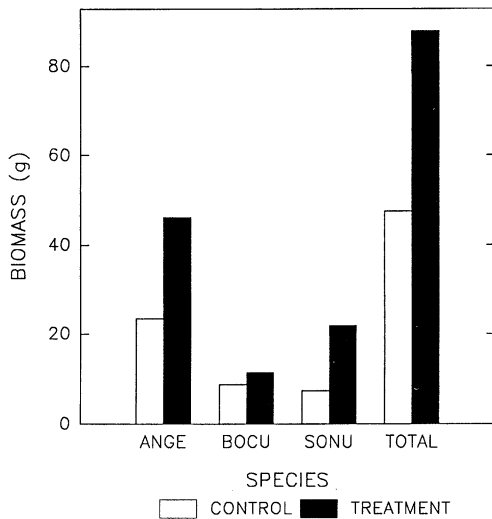


FIG. 6. Biomass of graminoid species with a significant (t test, $P \leq 0.05$) biomass response to urine treatment and total graminoid biomass on urine-treated and control plots at the annually burned site in July (Experiment 2). ANGE = *Andropogon gerardii* ($n = 50/25$ for treated and control plots, respectively), BOCU = *Bouteloua curtipendula* ($n = 44/24$), SONU = *Sorghastrum nutans* ($n = 36/10$), TOTAL = all graminoids combined ($n = 50/25$).

increased C_4 grass production. Forb production increased on urine-treated plots at the 2- and 4-yr burn sites, especially in the second season following application, which was a drier than average year. A few common perennial forb species accounted for the increase at the 4-yr burn site, while a wide variety of forbs increased at the 2-yr burn site. The variable responses of species and guilds to urine treatment among study sites appears linked in a complex manner to site environmental characteristics and disturbance history.

Our results contrast with those of most studies of small-scale disturbance in grassland communities (e.g., animal mounds [Platt 1975, Foster and Stubbendieck 1980, Gibson 1989] or harvester ant mounds [Coffin and Lauenroth 1990, Urbanhower 1992]). Such disturbances often result in a reduction or removal of established, competitive, plant species and replacement by successful colonizers (Platt 1975). Thus moderate levels of disturbance may increase species diversity by providing habitats for both late and early successional species (Connell 1978). In contrast, on urine patches, N levels are naturally increased but the vegetative structure is left initially intact. Thus vegetation dynamics on urine patches are likely driven by the ability to compete for N rather than colonizing ability. However, the focus of competition may shift if increases in biomass following N addition limit availability of other resources (e.g., light, water [Tilman 1985]). In this study, species characteristic of mature prairie (e.g., *A. gerardii*, *A. ericoides*) increased in abundance on urine patches. Late successional grasses, in particular, have

been shown to be strong competitors for N (Tilman and Wedin 1991).

Fertilization of grasslands often results in an increase in the abundance of C_3 relative to C_4 species (Owensby et al. 1970, Day and Detling 1990). In this study, C_3 and C_4 species response to urine treatment varied among sites and appears to be mediated by site disturbance history. The principal disturbance is fire at KPRNA and gopher mounds at NVP (Steuter et al., *in*

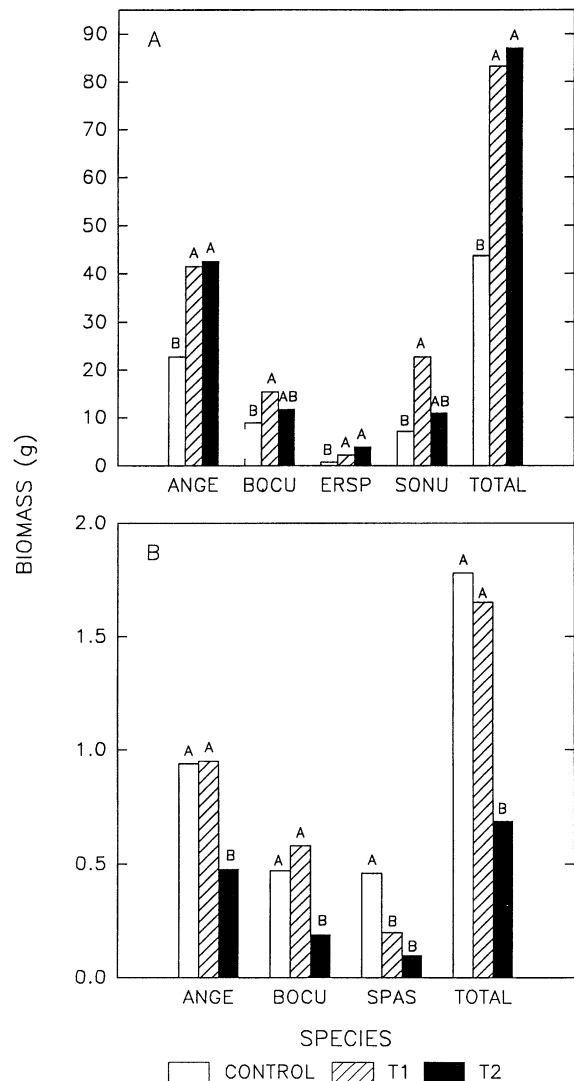


FIG. 7. Biomass of graminoid species with a significant (ANOVA, $P \leq 0.05$) biomass response to urine treatment and total graminoid biomass on unclipped (A) and clipped (B) urine-treated and control plots at the annually burned site in September (Experiment 2). Treatments as in Fig. 1. Species names as in Fig. 6 and ERSP = *Eragrostis spectabilis*, SPAS = *Sporobolus asper*. ANGE ($n = 25/25-24/23-25/25$ for unclipped/clipped treatment 1, treatment 2, and control plots, respectively), BOCU ($n = 25/22-24/21-24/23$), ERSP ($n = 4/NS-3/NS-5/NS$), SONU ($n = 17/9-15/8-17/6$), SPAS ($n = NS/11-NS/10-NS/16$), NS = non-significant response in treatment group.

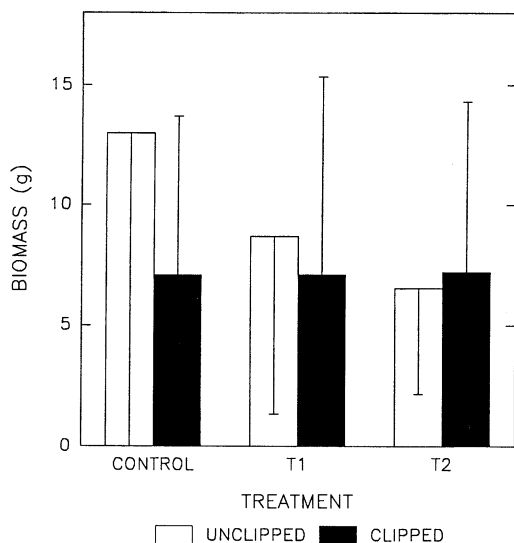


FIG. 8. Total forb biomass on clipped and unclipped urine-treated and control plots at the annually burned site in September (Experiment 2). Error bars = 1 SE, $n = 25$ for each treatment and control group. Treatments as in Fig. 1.

press), both of which reduce litter and standing vegetation. The resulting increase in light and temperatures at the soil surface (Hulbert 1969, Rice and Parenti 1978, Knapp 1984) favors C_4 grasses. Without disturbance, litter buildup increases shading and lowers soil temperatures, which favors C_3 species (Weaver and Roland 1952, Cristie and Detling 1982, Knapp and Seastedt 1986). Eventually production is predicted to become light-limited on undisturbed prairie and to increase little following nutrient addition (Knapp and Seastedt 1986). In this study, production of C_4 species increased on urine-treated plots at the annual burn site, which was the only site burned in the year of urine application and at the Niobrara site. However, C_3 production increased at the 4-yr burn site, especially in the 2nd yr following urine application, which was the 3rd yr since the site was last burned. Therefore, the results of this study suggest that N is a limiting nutrient on both burned and unburned prairie, but that the functional group which responds to N addition is determined by litter-mediated light and temperature regimes.

We predicted that species richness would be reduced on highly productive sites (e.g., urine patches) (Grime 1973, Huston 1979, Wilson and Shay 1990, Tilman and Olff 1991) because of increased competition for resources other than N (e.g., light). In accordance with our prediction, richness decreased on urine patches at the annual burn site where graminoid but not forb production increased, and at the 4-yr burn site where forb but not graminoid production increased. However, both production and richness increased on urine patches at the Niobrara site. Sparsely distributed vegetation at this site may have minimized competitive interactions among species despite increased production.

Urine treatment increased percent dissimilarity (PD, β -diversity) among plots at the annual burn and Niobrara sites, perhaps by enhancing initial differences caused by local species rarity (Glenn and Collins 1992). At the 4-yr burn site PD was relatively stable on urine-treated plots but increased during the course of the study on control plots. Urine treatment effects on plant diversity appear scale dependent (Glenn et al. 1992), since changes in α -diversity and β -diversity (PD) at a given study site were not necessarily uni-directional.

Moderate levels of grazing have been shown to increase diversity in tallgrass prairie (Collins 1987, Collins and Glenn 1988). In this study, a single July clipping of graminoids at the annual burn site reduced α -diversity but increased PD at the September sample period. However, our clipping treatment did not include other impacts of grazers, e.g., trampling (Wallace 1987) or wallowing (Collins and Uno 1983), which may increase diversity by providing establishment sites for ruderal species. The increase in PD in September on clipped plots may have resulted from the decrease in relative abundance of common C_4 grasses and an increase in the relative abundance of forb species, which varied substantially among plots. The increase in PD was greatest among clipped urine-treated plots, indicating that urine treatment compounded the effects of clipping on species composition. Below-normal precipitation during the interval between clipping and sampling may have contributed to low rates of species establishment and limited resprouting of clipped graminoids, especially on urine-treated plots, where salts in the urine may have increased water stress.

Simulated bovine urine increased the dominance of C_4 grass species, especially on recently burned sites which are preferentially grazed by ungulates, including bison (Shaw and Carter 1990, Vinton et al. 1993). The positive response of C_4 grasses on urine patches may provide a compensatory mechanism for the high levels of herbivory that these species incur on burned sites. However, urine patches are more likely to be grazed than off-patch areas (Norman and Green 1958, Day and Detling 1990, Jaramillo and Detling 1992b). In a companion study, we observed that simulated urine patches and the areas immediately surrounding them in a recently burned watershed at KPRNA experienced increased herbivory by bison (Steinauer 1994). We also noticed increased insect herbivory on urine-treated plots (Heidorn and Joern 1987; E. M. Steinauer, *personal observation*). The combination of urine treatment and grazing appears to impact vegetation to a greater extent than either acting alone.

Urine patches produce a high intensity but short duration nitrogen pulse in tallgrass and sandhills prairie, which results in increased abundance of late successional species: C_4 grasses in sites recently burned or with other canopy opening disturbances, or C_3 forbs in undisturbed sites. Though species diversity was reduced on areas directly impacted by urine, the unique

patches produced following urine treatment increased overall heterogeneity. In addition, the increased likelihood of grazing on urine patches and the areas surrounding them spreads the impact beyond the urine patch boundary and has more profound effects on small-scale patch dynamics in grasslands than do urine patches alone.

ACKNOWLEDGMENTS

We thank Tim Seastedt, Al Steuter, Linda Wallace, the Eco-lunch Group at the University of Oklahoma, and two anonymous reviewers for critical review of the manuscript, and the staffs of Konza Prairie Research Natural Area and the Niobrara Valley Preserve for use of their facilities and logistical support. Funding was provided to EMS by The Nature Conservancy and the Graduate Student Senate, University of Oklahoma. The Niobrara Valley Preserve is owned and managed by The Nature Conservancy. Konza Prairie is owned by The Nature Conservancy, managed by the Division of Biology at Kansas State University and is a Long Term Ecological Research Site (NSF grants DEB-8012166 and BSR-8514327).

LITERATURE CITED

- Allen, T. H. F., and T. W. Hoekstra. 1992. Towards a unified ecology. Columbia University Press, New York, New York, USA.
- Al-Mufti, M. M., C. L. Sydes, S. B. Furness, J. P. Grime, and S. R. Band. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *Journal of Ecology* **65**:759–791.
- Barns, P. W., and A. T. Harrison. 1982. Species distribution and community organization in a Nebraska Sandhills mixed prairie as influenced by plant/soil–water relationships. *Oecologia* **52**:192–201.
- Biondini, M. E., P. W. Mielke, and K. J. Berry. 1988. Data-dependant permutation techniques for the analysis of ecological data. *Vegetatio* **75**:161–168.
- Coffin, D. P., and W. K. Lauenroth. 1990. Vegetation associated with nest sites of western harvester ants (*Pogonomyrmex occidentalis* Cresson) in a semiarid grassland. *American Midland Naturalist* **123**:226–235.
- Collins, S. L. 1987. Interaction of disturbances in a tallgrass prairie: a field experiment. *Ecology* **68**:1243–1250.
- . 1992. Fire frequency and community heterogeneity in tallgrass prairie vegetation. *Ecology* **73**:2001–2006.
- Collins, S. L., and S. C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio* **64**:87–94.
- Collins, S. L., and S. M. Glenn. 1988. Disturbance and community structure in North American prairies. Pages 131–143 in H. J. During, M. J. A. Werger, and J. H. Willems, editors. Diversity and pattern in plant communities. SPB Academic, The Hague, The Netherlands.
- Collins, S. L., and G. E. Uno. 1983. The effects of early spring burning on vegetation in buffalo wallows. *Bulletin of the Torrey Botanical Club* **110**:474–481.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**:1302–1310.
- Cristie, E. K., and J. K. Detling. 1982. Analysis of interference between C₃ and C₄ grasses in relation to temperature and soil nitrogen supply. *Ecology* **63**:1277–1284.
- Day, T. A., and J. K. Detling. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology* **71**:180–188.
- Floate, M. J. S. 1981. Effects of grazing by large herbivores on nitrogen cycling in agricultural ecosystems. In F. E. Clark and T. Rosswall, editors. Terrestrial nitrogen cycles; processes, ecosystem strategies, and management impacts. *Ecological Bulletins-NFR* **33**:585–601.
- Foster, M. A., and J. Stubbendieck. 1980. Effects of the plains pocket gopher (*Geomys bursarius*) on rangeland. *Journal of Range Management* **33**:74–78.
- Gibson, D. J. 1989. Effects of animal disturbance on tallgrass prairie vegetation. *American Midland Naturalist* **121**:144–154.
- Gibson, D. J., and L. C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* **72**:175–185.
- Glenn, S. M., and S. L. Collins. 1992. Effects of scale and disturbance on rates of immigration and extinction of species in prairies. *Oikos* **63**:273–280.
- Glenn, S. M., S. L. Collins, and D. J. Gibson. 1992. Disturbances in tallgrass prairie: local and regional effects on community heterogeneity. *Landscape Ecology* **7**:243–251.
- Great Plains Floral Association. 1986. Flora of the Great Plains. University of Kansas Press, Lawrence, Kansas, USA.
- Greig-Smith, P. 1983. Quantitative plant ecology. Third edition. Blackwell Scientific, Oxford, UK.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* **242**:344–347.
- Heidorn, T. J., and A. Joern. 1987. Feeding preference and spatial distribution of grasshoppers (Acrididae) in response to nitrogen fertilization of *Calamovilfa longifolia*. *Functional Ecology* **1**:369–375.
- Huffine, W. W., and W. C. Elder. 1960. Effects of fertilization on native grass pastures in Oklahoma. *Journal of Range Management* **13**:34–36.
- Hulbert, L. C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology* **50**:874–877.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* **113**:81–101.
- Jaramillo, V. J., and J. K. Detling. 1992a. 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. 1992b. Small-scale grazing in a semi-arid North American grassland. II. Cattle grazing of simulated urine patches. *Journal of Applied Ecology* **29**:9–13.
- Knapp, A. K. 1984. Post-burn differences in solar radiation, leaf temperature and water stress influencing production in a lowland tallgrass prairie. *American Journal of Botany* **71**:220–227.
- Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience* **36**:662–669.
- Krueger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. *Ecology* **67**:760–770.
- Mack, R. N., and J. N. Thompson. 1982. Evolution in steppe with few large hooved mammals. *American Naturalist* **119**:757–773.
- McNaughton, S. J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecological Monographs* **53**:291–320.
- 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.
- Monk, C. D. 1967. Tree species diversity in the eastern deciduous forest with particular reference to north central Florida. *American Naturalist* **101**:173–187.
- 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.
- Owensby, C. E., R. M. Hyde, and K. L. Anderson. 1970.

- Effects of clipping and supplemental nitrogen and water on loamy upland bluestem range. *Journal of Range Management* **23**:341–346.
- Pielou, E. C. 1969. *An introduction to mathematical ecology*. John Wiley and Sons, New York, New York, USA.
- Platt, W. J. 1975. The colonization and formation of equilibrium plant associations on badger disturbances in tallgrass prairie. *Ecological Monographs* **45**:285–305.
- Plumb, G. E., and J. L. Dodd. 1993. Foraging ecology of bison and cattle on a northern mixed prairie: implications for natural area management. *Ecological Applications* **3**: 631–643.
- Rice, E. L., and R. L. Parenti. 1978. Decrease in production in undisturbed tallgrass prairie. *American Journal of Botany* **65**:1091–1097.
- Seastedt, T. R., J. M. Briggs, and D. J. Gibson. 1991. Controls of nitrogen limitation in tallgrass prairie. *Oecologia* **87**:72–79.
- Seastedt, T. R., and A. K. Knapp. 1993. Consequences of nonequilibrium resource availability across multiple time scales: the transient maxima hypothesis. *American Naturalist* **141**:621–633.
- Shaw, J. H., and T. S. Carter. 1990. Bison movements in relation to fire and seasonality. *Wildlife Society Bulletin* **18**:426–430.
- Smith, J. L., and E. L. Rice. 1983. Differences in nitrate reductase activity between species of different stages of old field succession. *Oecologia* **57**:43–48.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**: 353–391.
- Steinauer, E. M. 1994. Effects of urine deposition on small-scale patch structure and vegetative patterns in tallgrass and sandhills prairies. Dissertation. University of Oklahoma, Norman, Oklahoma, USA.
- 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**, in press.
- 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.
- Tilman, G. D. 1984. Plant dominance along an experimental nutrient gradient. *Ecology* **65**:1445–1453.
- . 1985. The resource-ratio hypothesis of plant succession. *American Naturalist* **125**:827–852.
- . 1987. Secondary succession and the pattern of plant dominance along an experimental nitrogen gradient. *Ecological Monographs* **57**:189–214.
- . 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* **74**:2179–2191.
- Tilman, D., and A. El Haddi. 1992. Drought and biodiversity in grasslands. *Oecologia* **89**:257–264.
- Tilman, D., and H. Olff. 1991. An experimental study of the effects of pH and nitrogen on grassland vegetation. *Acta Oecologia* **12**:427–441.
- Tilman, D., and D. Wedin. 1991. Dynamics of nitrogen competition between successional grasses. *Ecology* **72**:1038–1049.
- United States Department of Agriculture. 1975. Soil survey of Riley County, Kansas. United States Department of Agriculture, Washington, D.C., USA.
- . 1992. Soil survey of Brown County, Nebraska. United States Department of Agriculture, Washington, D.C., USA.
- Urbanhower, C. E. 1992. Abundance, vegetation, and environment of four patch types in a northern mixed prairie. *Canadian Journal of Botany* **70**:277–284.
- Vinton, M. A., D. C. Hartnett, E. J. Finck, and J. M. Briggs. 1993. Effects of fire regime and vegetation composition on bison (*Bison bison*) grazing patterns on tallgrass prairie. *American Midlands Naturalist* **129**:10–18.
- Wallace, L. L. 1987. Effects of clipping and soil compaction on growth, morphology, and mycorrhizal colonization of *Schizachyrium scoparium*, a C₄ bunch grass. *Oecologia* **72**: 423–428.
- Ward, L. E., R. Kazaier, and D. Hartnett. 1991. Forb species response to bison activity on Kansas tallgrass prairie. Supplement to the *American Journal of Botany* **78**:87–88.
- Weaver, J. E., and N. W. Roland. 1952. Effects of excessive natural mulch on development, yield, and structure of native grassland. *Botanical Gazette* **114**:1–19.
- Weins, J. A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* **7**:81–120.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* **45**:229–299.
- Whittaker, R. H. 1975. *Communities and ecosystems*. Second edition. Macmillan, New York, New York, USA.
- Wilson, S. D., and J. M. Shay. 1990. Competition, fire, and nutrients in a mixed-grass prairie. *Ecology* **71**:1959–1967.
- Woodmansee, R. G. 1978. Additions and losses of nitrogen in grassland ecosystems. *BioScience* **28**:448–453.
- 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.