

Effects of fire and grazing on small-scale spatial heterogeneity in a tallgrass prairie



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Abstract

1. Grazing and fire are historically two important factors in the development and maintenance of many grassland systems. Most previous studies investigated their effects separately. We conducted a study to gain insight in the effects of fire, grazing and their interaction on small-scale (0.25 m^2) vegetation heterogeneity and distribution of resources. In four different treatments (1U = annually burned, ungrazed, 4U = 4-year burned, ungrazed, 1G = annually burned, grazed, 4G = 4-year burned, grazed) we measured plant species composition and resource availability.
2. Grazing had a positive effect on species richness, diversity and evenness, while it decreased the dominance of C_4 -grasses (e.g. *Andropogon gerardii*). Fire had an opposite effect, it reduced species richness, diversity and evenness and enhanced the cover of C_4 -grasses. The effect of fire was stronger in the absence of grazing.
3. Heterogeneity in the plant community was increased under grazing, whereas fire or a fire-grazing interaction had no significant effect on a small scale (0.25 m^2). The increased heterogeneity in grazed sites was strongly correlated with increased resource availability, and not with enhanced patchiness in resources distribution.
4. The availability of resources (light and N) was only affected by the grazing treatment. No spatial patterns in resource distribution were found in the present study.
5. We conclude that grazing is the most important factor on the small scale, determining the resource availability, vegetation composition and heterogeneity.

Introduction

Patchiness in grasslands is the result of a series of complex interacting biotic (e.g. grazing, soil disturbances by animals) and abiotic (e.g. topography, soil texture, fire, resource availability and heterogeneity) factors that act at different spatial scales (Collins 1987; Wu & Loucks 1995; Briggs *et al.* 1997). Consequentially, spatial heterogeneity is created, defined as the degree of dissimilarity from one point in a community to another (Collins 1990). Historically, frequent fires and grazing by large herds of bison (*Bos bison*) were important processes in North American tallgrass prairies, which contributed to the biological diversity and heterogeneity characteristic of these grasslands (Collins 1989; Collins 1992; Glenn *et al.* 1992; Fuhlendorf & Smeins 1999). Today, fire is commonly used as a management tool in tallgrass prairie, and grazing by cattle is a common land use form. Previous research on the effects of fire and grazing on diversity and spatial heterogeneity of plant communities focused on either the impact of fire (Collins 1989; Collins 1992) or grazing (Steinauer & Collins 1995; Nellis & Briggs 1997; Steinauer & Collins 2001; Bakker *et al.* 2003), but little attention has been paid to the interactions of both processes (Fuhlendorf & Engle 2004). However, there are indications that fire and grazing interact through a series of positive and negative feedbacks, thereby creating a shifting mosaic in vegetation patterns (Fuhlendorf & Engle 2001; Fuhlendorf & Engle 2004). For example, recently burned sites attract grazers (Vinton *et al.* 1993), which can reduce fuel loads for future fires, whereas ungrazed areas with a large accumulation of litter are more likely to burn. Thus, burning can alter the spatial effects of grazing and, in the long-term, the interactions of burning and grazing may cause a shifting mosaic of grazed and ungrazed patches in the landscape, whereas in the absence of fire a more stable mosaic may exist.

Fire and grazing alter patch structure at a variety of different spatial scales (Fuhlendorf & Smeins 1999; Knapp *et al.* 1999) and their impacts can feed back to affect processes that are acting at different scales (Steinauer & Collins 2001). Consequently, analysis of multiple scales is necessary to describe the spatial patterns and processes underlying responses to fire and grazing (Fuhlendorf & Smeins 1996). Grazing, for example, may have opposing effects on heterogeneity depending on the scale of observation. Fuhlendorf

& Smeins (1999) found that heavy grazing had a negative effect on spatial vegetation heterogeneity on a small scale (0.093 m²), whereas it enhanced heterogeneity on a large scale (1 km). For tallgrass prairies, data on the impact of the fire-grazing interaction on the small scale are still lacking.

The objective of the present study was to gain insight in the effects of fire frequency, grazing and their interaction on small-scale spatial heterogeneity in resource availability and plant species composition. The following questions were addressed:

- (1) How do levels of resource availability, species richness and diversity differ under different burning and grazing regimes?
- (2) Is small-scale heterogeneity of key resources (N and light) and plant communities affected by fire frequency, grazing, or an interaction of both?
- (3) Are there relationships between the vegetation patterns observed and the heterogeneity or availability of resources?

In order to answer these questions, we sampled availability and heterogeneity of two important plant resources (N and light) and documented plant species composition in small plots (12 0.25 m² plots, established in a grid within replicated 2 m x 3 m sampling units) with different grazing (grazed vs. ungrazed) and burning (annually vs. 4-year burn) regimes.

The hypothesis was that both grazing and infrequent fires, i.e. once every four years, would enhance N availability (Blair 1997; Johnson & Matchett 2001; Bakker *et al.* 2003), and increase plant species richness and diversity (Collins *et al.* 1998; Knapp *et al.* 1999). According to Hobbs *et al.* (1991) fire and grazing act together in a contingent manner to affect N budgets in the tallgrass prairie, because grazing modifies the effects of fire and the other way around. Light levels are thought to be reduced by infrequent fires due to litter accumulation, while grazing is expected to increase available light (Bakker *et al.* 2003), e.g. through consumption of biomass.

We expected that small-scale spatial heterogeneity would be affected, both independently and interactively, by fire frequency and grazing treatment. Regarding the main effects, fire has a homogenizing effect on the prairie landscape by uniformly removing

aboveground biomass and litter favoring dominance by a few species of warm-season grasses (Knapp *et al.* 1999) and reducing soil N availability and heterogeneity (Blair 1997). In contrast, herbivore activities, for example, grazing (i.e. selective removal of plants), nutrient deposition (i.e. urine and dung patches) and soil disturbances (i.e. wallowing) are more likely to create a heterogeneous pattern in resource availability and vegetation composition (Steinauer & Collins 1995; Hartnett *et al.* 1997; Steinauer & Collins 2001). Heterogeneity in resource availability and plant species composition may be enhanced when both fire and grazing act together, because grazing patches with different fuel loads cause patchy fires, and recently burned patches attract grazers (Vinton *et al.* 1993; Fuhlendorf & Engle 2001; Fuhlendorf & Engle 2004). Furthermore, spatial heterogeneity in resource distribution and vegetation composition are expected to increase with plant species richness and diversity, respectively (Whittaker & Levin 1977; Collins 1992; Tilman & Pacala 1993; Collins *et al.* 1998; Collins & Wein 1998). Consequently, we expected to find the highest heterogeneity in areas with high species richness and diversity, which usually are grazed (Collins *et al.* 1998; Knapp *et al.* 1999) and infrequently burned prairies (Knapp *et al.* 1998).

Materials and methods

Study site

The study was conducted at the Konza Prairie Biological Station, a 3,487-ha native tallgrass prairie and Long Term Ecological Research (LTER) site located in the Flint Hills of north-eastern Kansas, USA. The vegetation is dominated by a matrix of C₄-grasses: *Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, *Bouteloua curtipendula*, and *Sporobolus asper*. Konza Prairie is divided into a series of upland plateaus with mostly shallow soils, rocky slopes and lowlands with deeper soils. Mean annual temperature is about 13°C and mean annual precipitation is about 835 mm, with more than 70% of the rain falling from April to September. Since 1972, replicated experimental watersheds are burned in spring at frequencies ranging from annual burning to burning once every 20 years. Prior to the establishment of Konza Prairie as a research site the area was grazed by cattle and burned every 2-3 years on average. Between 1987 and 1992 bison (*Bos bison*) were reintroduced on Konza to evaluate the role of native, ungulate grazers in these grasslands. The herd was allowed to expand up to its current size of approximately 250 individuals and has unrestricted access to 989 ha of the landscape (Knapp *et al.* 1999). About 88% (870 ha) of this area is grazable, native tallgrass prairie, with an average annual net primary production (ANPP) of 417 g/m² (LTER data set). The remaining area is covered by forest, roads and streams. Bison stocking rates are based on an average annual aboveground biomass removal of 25% of the ANPP.

Data collection

In this study data were collected in 16 randomly located blocks, equally distributed over four large watersheds, two of which were annually burned and two of which were burned every four years. Each block consisted of two paired sampling units (6 m² each), one that was grazed by bison and one that had been ungrazed since bison re-introduction. Grazing was prevented by permanent, fenced exclosures of 5 m x 5 m, established in 1987 and 1992 prior to the re-introduction of bison. Consequently, four different treatments were created: (1) annually burned and ungrazed (1U), (2) annually burned and grazed (1G), (3)

burned every four years and ungrazed (4U) and (4) burned every four years and grazed (4G). Within a sampling block the grazed and ungrazed units were located 25 meters apart, so that the grazed unit was not affected by the possible impact of the enclosure on bison presence. Each sampling unit included 12 plots of 0.25 m², situated in three rows of four adjacent plots. Ungrazed plots were located at at least one meter from the fence of the enclosure to avoid edge effects.

In each of the 384 plots plant species composition, light availability, relative nitrogen availability and standing living biomass were measured. Plant species composition was sampled in spring (June) and summer (August) to include both cool- and warm-season species. Cover of each species was visually estimated as percent cover. For each plant species, the maximum cover value from the combined spring and summer surveys was used for further analyses. For each plot, species richness, diversity, evenness and dominance were calculated: (1) Species richness, S , the number of plant species, (2) Shannon's diversity index, $H' = -\sum p_i \ln p_i$, where p_i is the relative cover of species i , (3) Evenness, $E = H' / \ln(S)$ and (4) Simpson's dominance index, $D = \sum (n_i(n_i - 1)) / (N(N - 1))$, where n_i is the cover of species i and N is the total cover. Heterogeneity in each sampling unit was expressed as the percentage dissimilarity in species composition among all possible comparisons of the 12 plots within a unit. Percentage dissimilarity (PD) is defined as: $PS = 1 - PD$, where PS is percentage similarity. $PS = 1 - 0.5 \sum |p_a - p_b|$, where p_a is the proportional cover of species p in plot a , and p_b = the proportional cover of species p in plot b . Moreover, we calculated heterogeneity as the Euclidian distance (ED) among all possible comparisons of the 12 plots within a sampling unit. $ED = \sqrt{\sum (|c_a - c_b|)^2}$, where c_a is the actual cover of species c in plot a , and c_b is the actual cover of species c in plot b . Visible rodent disturbance, i.e. holes, occurred in 19 out of the 192 ungrazed plots (in 9 out of 16 enclosures). In these plots the vegetation composition was altered and therefore these plots were not included in analyses of plant species composition. There were no visible signs of rodent disturbance in the 192 grazed plots.

Relative inorganic soil nitrogen availability (NO_3^- and NH_4^+) was quantified using ion exchange resin bags. Resin bags were constructed of nylon stockings, and contained 10.0 gram of a 1:1 mixture of cation (Dowex HCR-W2) and anion (Dowex 1X8-50) exchange resins, preloaded with H^+ and Cl^- , respectively. Per plot, one resin bag was buried at a 10-

cm depth in mid-June and retrieved in mid-Aug. The bags were buried just outside the plot to minimize soil disturbances. The distribution of resin bags reflected the same spatial pattern as the distribution of plots. Harvested resin bags were kept in airtight plastic bags at 4°C until further processing. In the lab the resin bags were extracted with 100 ml 2 M KCl (2 hours, 300 rpm). Concentrations of nitrate and ammonium were determined colorimetrically using a Flow Solution autoanalyzer (Alpkem, Clackamas, Or.). Nitrate values were used for further analyses.

Light availability was measured as the light penetration to the soil surface (canopy transmittance). Canopy transmittance was calculated as the ratio of Photosynthetic Photon Flux Density (PPFD) at the soil surface divided by the PPFD above the canopy. Measurements were taken with a ceptometer (Decagon, AccuPAR LP-80) at the end of June, July and August, between 11.00 a.m. and 3.00 p.m. on a clear day. Per plot, two diagonal ground level measurements were taken and averaged (covering 62.5 cm each), and one measurement was taken above the canopy. Measurements were taken in different months to study the changes in light availability over time, which provides an indirect indication of changes in the amount biomass over the season.

Per plot, standing living biomass (gram/m^2) was estimated at the end of July, mid-August and the end of August, as a function of canopy height. Height was measured with a disk pasture meter (foam disk, diameter = 50 cm, weight = 447.1 gram). To quantify the relationship between settling height of the disk and the amount of standing living biomass, the disk was calibrated at 34 sampling sites randomly located in grazed, ungrazed, annually burned and 4-year burned watersheds. Per site, the biomass was clipped and sorted into dead organic material and living biomass. Sites were ranging in canopy height from 0-54.5 cm and in living biomass from 0-565.8 gram/m^2 . The best linear fit was found using untransformed living biomass data: $y = 9.3821x + 17.954$ ($r^2=0.87$, $P<0.001$, $F_{1,33}=220.51$, $n=34$).

Resource heterogeneity and heterogeneity in living biomass were expressed as the coefficient of variation per sampling unit.

Statistical analyses

The effects of grazing treatment (grazed vs. ungrazed) and burning treatment (annually vs. 4-year burned) were tested using a mixed model approach with species richness (S), diversity (H'), evenness (E), dominance (D), N availability, light availability, biomass, percent dissimilarity (PD), Euclidian distance (ED) and the coefficient of variation for N, light and biomass as respective response variables. For these analyses data of the 12 separate plots within a sampling unit were averaged to avoid pseudo-replication and log-transformed when necessary to improve normality and homogeneity of variances ($y=\log(x+1)$) (Zar 1999). The grazed and ungrazed sampling units within a block were considered as paired observations. In the analyses of light availability and biomass we used a repeated-statement to include the measurements from different months.

Statistical analyses were performed using the statistical packages SAS 1999 and SPSS 12.0.1 for windows.

Results

Plant community responses

The highest species richness was found under grazing ($P < 0.0001$, $F_{1,14} = 81.34$; Fig. 1A). Grazing also enhanced diversity ($P < 0.0001$, $F_{1,14} = 103.27$) and evenness ($P < 0.0001$, $F_{1,14} = 81.54$), while frequent fires had a negative effect on diversity ($P = 0.0128$, $F_{1,14} = 8.14$) and evenness ($P = 0.0089$, $F_{1,14} = 9.21$; Fig. 1B,C). An opposite pattern was found for dominance, which was lowest in grazed sites ($P < 0.0001$, $F_{1,14} = 117.54$) and highest under frequent burning ($P = 0.0118$, $F_{1,14} = 8.38$; Fig. 1D). Significant interactions between burning and grazing were found for diversity ($P = 0.0381$, $F_{1,14} = 5.24$), evenness ($P = 0.0026$, $F_{1,14} = 13.36$) and dominance ($P = 0.0050$, $F_{1,14} = 11.04$), showing that fires had a greater impact on plant communities in ungrazed areas.

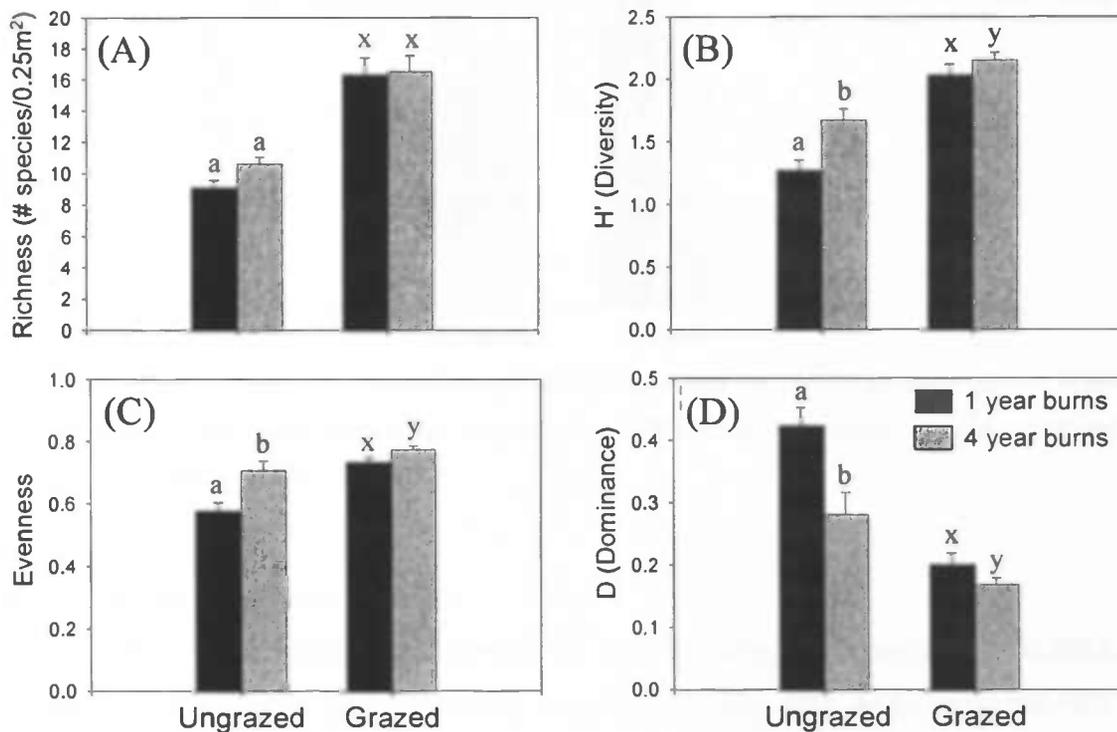


Fig. 1. Differences in species richness (A), diversity (B), evenness (C) and dominance (D) by grazing and per fire treatment. Error bars represent SEM. Different symbols represent significant differences at the level $P < 0.05$.

The ungrazed areas were dominated by a single species (*Andropogon gerardii*), whereas the cover of species in the grazed sites was more equally distributed among different species (Fig. 3). In ungrazed areas the most abundant species covered 75% and 52%, in annually and 4-year burned sites, respectively, while in grazed sites the most abundant species covered only 26% and 23% in annually and 4-year burned areas, respectively.

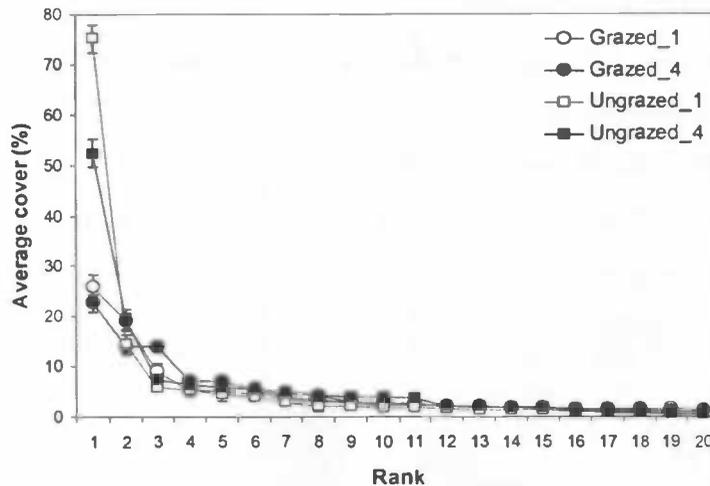


Fig. 3. The average cover of the 20 most abundant species per treatment. On the x-axis the species rank number. Error bars represent SEM.

In general, grazing strongly reduced the relative cover of C_4 grasses and enhanced the cover of forbs, although the C_4 -grass *Andropogon gerardii* was still the most dominant species in all treatments. *Ambrosia psilostachya* was the most abundant forb, in both grazed and ungrazed areas. Some forbs species were typically found in grazed sites and were lacking under ungrazed conditions, e.g. *Astragalus crassicaarpus* and *Ratibida columnifera*. Cover of *Carex brevior* was enhanced under grazing, whereas *Carex meadii* was more abundant in the absence of grazers. Some plant species were characteristic of 4-year burns, e.g. *Poa pratensis*, whereas others were more often recorded in annually burned sites, e.g. *Vernonia baldwinii* (Table 1, Appendix 1).

Plant community heterogeneity

Spatial heterogeneity in vegetation composition, expressed as the percentage dissimilarity among plots in a sampling unit, was only affected by the grazing treatment. The percentage dissimilarity was much higher in grazed areas (51% and 47% in 1- and 4-year

burns respectively) than in ungrazed areas (36% and 41% in 1- and 4-year burns respectively; $P=0.0013$, $F_{1,14}=16.18$; Fig. 2). Heterogeneity was not affected by the burning regime ($P=0.3365$, $F_{1,14}=0.99$) or by a fire-grazing interaction ($P=0.2256$, $F_{1,14}=1.61$; Fig. 2). Percentage dissimilarity was positively correlated with both species richness (Pearson's correlation coefficient $r=0.657$, $P<0.0001$) and diversity (Pearson's correlation coefficient $r=0.772$, $P<0.0001$).

For Euclidian distance, a heterogeneity measure that is not correlated with richness (Pearson's correlation coefficient $r=0.052$, $P=0.7794$) or diversity (Pearson's correlation coefficient $r=0.100$, $P=0.5862$), we did not find a significant effect of grazing ($P=0.6804$, $F_{1,14}=0.18$), fire ($P=0.4256$, $F_{1,14}=0.67$) or a fire-grazing interaction ($P=0.1478$, $F_{1,14}=2.35$) on vegetation patterns.

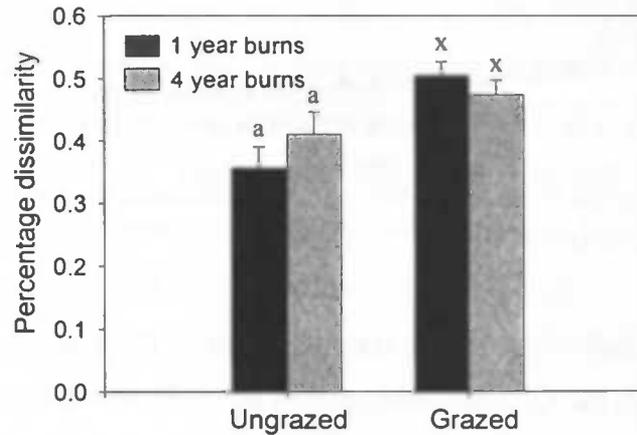


Fig. 2. Heterogeneity in vegetation composition per fire treatment and per grazing treatment, shown as the percentage dissimilarity among plots. Error bars represent SEM. Different symbols represent significant differences at the level $P<0.005$.

Effect of fire and grazing on resources

Grazing strongly enhanced mean levels of resin-collected soil nitrate ($P<0.0001$, $F_{1,14}=29.38$; Fig. 4A) and light ($P<0.0001$, $F_{1,74}=374.93$; Fig. 4B). Resin-collected NO_3^- values were extremely high in some grazed plots, presumably as a result of recent urine and dung deposition. Repeating the analyses without these extreme values still gave a similar result, with increased mean NO_3^- levels under grazing, indicating that the treatment response was not driven solely by extreme values. Mean light availability changed significantly over the study period ($p=0.0105$, $F_{2,74}=4.85$). In grazed areas light

levels at the soil surface first decreased and then increased again, indicating that accumulating aboveground biomass had been removed and that the canopy remained open as a result of herbivore activities, i.e. grazing and trampling. In ungrazed areas, light levels declined progressively over time from 15% of the total light penetration at ground level in June to 7% in August.

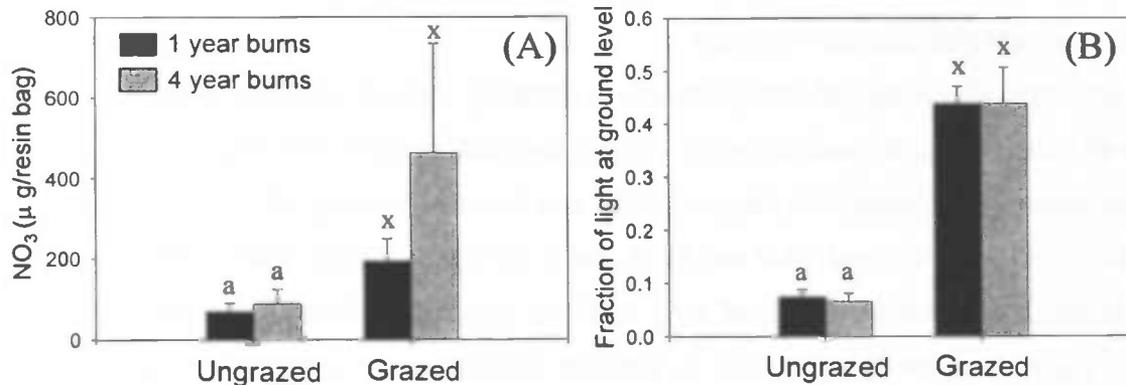


Fig. 4. (A) Effect of grazing and burning on nitrate availability. (B) Effect of grazing and burning on light availability. Only the light measurements of August (peak biomass) are shown in the graph. Error bars represent SEM. Different symbols represent significant differences at the level $P < 0.0001$.

Resource heterogeneity

Neither grazing ($P=0.8915$, $F_{1,14}=0.02$), nor fire ($P=0.5319$, $F_{1,14}=0.41$), nor an interaction of both ($P=0.4263$, $F_{1,14}=0.67$) had an effect on heterogeneity in NO_3^- levels.

With respect to heterogeneity in light levels, there was a significant negative effect of grazing ($P=0.0206$, $F_{1,76}=5.59$) and a significant interaction between grazing and fire treatment ($P=0.0017$, $F_{1,76}=10.58$). In annually burned sites, heterogeneity in light levels were slightly increased under grazing, whereas in 4-year burns heterogeneity in light levels were strongly reduced under grazing. Heterogeneity in light availability increased over time ($P=0.0043$, $F_{2,76}=5.87$).

Relationship between resource availability and vegetation heterogeneity

Simple regression analyses of the relationship between indices of community structure and resource availability showed that species richness ($P < 0.0001$, $F_{1,30}=21.80$, $r^2=0.42$), diversity ($P < 0.0001$, $F_{1,30}=26.45$, $r^2=0.47$) and vegetation heterogeneity, i.e. percentage dissimilarity ($P=0.0005$, $F_{1,30}=15.19$, $r^2=0.34$) were most strongly correlated with mean

light availability. Mean levels of available nitrate did not significantly correlate to species richness ($P=0.0697$, $F_{1,30}=3.54$, $r^2=0.11$), diversity ($P=0.0902$, $F_{1,30}=3.06$, $r^2=0.09$) or vegetation heterogeneity ($P=0.2248$, $F_{1,30}=1.54$, $r^2=0.05$). Neither heterogeneity in available light or nitrate, i.e. coefficients of variation, were related to species richness, diversity or vegetation heterogeneity.

Canopy height and biomass response

The average canopy height (and biomass) in annually burned, ungrazed areas in August was 40.9 cm (416 g/m^2) and in 4-year burned, ungrazed areas it was 38.2 cm (391 g/m^2). In the presence of grazers the canopy height was lower, averaging 16.2 cm (184 g/m^2) in annually burned sites and 14.7 cm (170 g/m^2) in 4-year burned sites. The amount of living biomass strongly decreased as a result of grazing ($P<0.0001$, $F_{1,74}=459.20$; Fig. 5A), while frequent burning had a positive effect on the standing living biomass ($P=0.0497$, $F_{1,74}=4.05$). There was no significant change in the amount of biomass over time ($P=0.2914$, $F_{2,74}=1.25$). That may be due to the fact that we started the biomass measurements late in the season (end of July), when the peak biomass was already almost reached. The heterogeneity in living biomass was much larger in grazed than in ungrazed sites ($P<0.0001$, $F_{1,76}=136.21$), but there was no effect of burning ($P=0.1295$, $F_{1,76}=2.35$) or a fire-grazing interaction ($P=0.3216$, $F_{1,76}=1.00$, Fig. 5B).

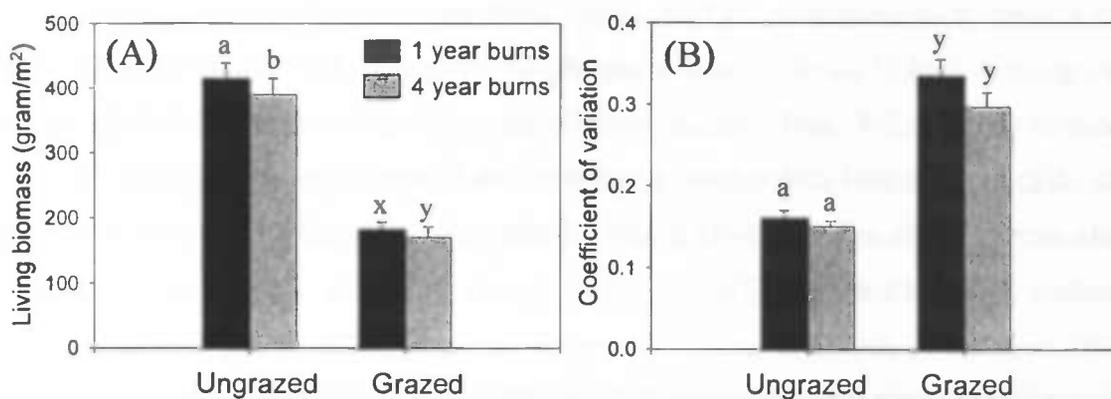


Fig. 5. (A) Living biomass per burning and grazing treatment. **(B)** Coefficient of variation for biomass per burning and grazing treatment. In the graph the data of August are shown, which is the peak biomass. Error bars represent SEM. Different symbols indicate significant differences at the level $P<0.05$.

The samples we used for calibration of the disk pasture meter provided an indication of the living/dead-ratio per treatment. This ratio was affected neither by the grazing ($P=0.935$, $F_{1,30}=0.01$) nor by the burning treatment ($P=0.080$, $F_{1,30}=3.29$). However, there was a trend towards a higher living/dead ratio in annually burned sites (5.39 ± 0.91), and a lower ratio in 4-year burned sites (3.65 ± 0.54), indicating that there was more dead organic material, i.e. litter, present in 4-year burned areas and thus, frequent burning reduced the litter layer.

Discussion

Plant community response

The results of this experiment have shown that grazing strongly affects small-scale heterogeneity in plant communities (i.e. percentage dissimilarity). In contrast there was no effect of the burning regime alone or of a fire-grazing interaction (Fig. 2). Moreover, grazing also had a very strong effect on species richness, diversity, dominance, evenness and the amount living aboveground biomass. The burning regime alone affected only the diversity, dominance and evenness of plant communities (Fig. 1, 5). Across all treatment combinations diversity was highest in 4-year burned and grazed sites (Fig. 1).

Effects of grazing regime

Grazing by bison increased species richness, diversity and evenness at the scale of small (0.25m²) plots. It had a negative effect on dominance and the amount of living biomass (Fig. 1, 5A). These results are consistent with earlier studies of grazing in a variety of grassland ecosystems (Bakker *et al.* 1984; Collins 1987; Berg *et al.* 1997; Knapp *et al.* 1999; Bos *et al.* 2002; Bakker *et al.* 2003). For example, livestock grazing on European salt marshes increases species richness, while in the absence of grazers abundant grasses dominate the vegetation (Berg *et al.* 1997; Olff *et al.* 1997; Bos *et al.* 2002). In an African tallgrass community the cover of tall species increases following protection from grazing (Belsky 1992). Thus, exclusion of grazers in grasslands generally leads to the dominance of a few species, that can eliminate other species through competitive interactions (Collins & Barber 1985; Knapp & Seastedt 1986; Fahnestock & Knapp 1993). The ungrazed tallgrass prairie is dominated by a small group of C₄-grasses, e.g. *Andropogon gerardii*, *Sorghastrum nutans*, *Schizachyrium scoparium* and *Panicum virgatum* (Knapp 1985; Briggs & Knapp 1995). Bison prefer and selectively remove these dominant grasses (Fahnestock & Knapp 1993; Damhoureyeh & Hartnett 1997), consequently enhancing the cover of forbs which is the most important contributor to richness and diversity (Gibson & Hulbert 1987; Glenn & Collins 1990; Turner *et al.* 1995).

Effects of fire frequency

The effects of a frequent burning regime (annual spring fires) were opposite from the effects of the grazing treatment. Annual spring fires decreased diversity and evenness, while the dominance of a few C₄ grasses was enhanced. The amount of living biomass slightly increased under annual burning, and the amount of litter was reduced, which is generally consistent with other studies that have demonstrated a stimulation of plant ANPP in burned tallgrass prairie (Briggs & Knapp 1995; Knapp *et al.* 1998). Frequent fires in tallgrass prairie favor C₄-grasses, which then come to dominate the vegetation, reducing the cover and richness of forbs and simultaneously decrease overall species richness, diversity and evenness (Collins & Barber 1985; Collins 1987; Gibson & Hulbert 1987). However, no burning at all may also cause a decline in richness and diversity, because in the absence of fire a thick litter layer develops (Knapp & Seastedt 1986), which limits the amount of light reaching the soil surface. Thus, intermediate burning frequencies may elicit the highest richness and diversity (Knapp *et al.* 1998), which is consistent with the result of our study. We showed that 4-year burns had a higher diversity and richness than annual burns, however the latter was not significantly altered (Fig. 1). Collins (1987) showed that the effect of fire and grazing is dependent on the plant species, i.e. some species increase with burning or grazing, whereas others decrease. For example, in our study, the grasses *Sorghastrum nutans* and *Schizachyrium scoparium* were more abundant in sites with a 4-year burning frequency, while *Andropogon gerardii* had a higher cover in annually burned areas.

Effects of the fire-grazing interaction

Burning had a greater impact on the vegetation in the absence of grazing compared to when grazers were present. The reduction in species richness and diversity in annually burned sites was much stronger in ungrazed than in grazed areas, indicating that grazing prevents the loss of diversity under conditions that would otherwise lead to a reduction in diversity (Collins *et al.* 1998). Moreover, grazing and frequent fires together enhanced the abundance of forbs, while frequent burning alone promoted dominance by C₄-grasses (Appendix 1, Table 1), which concurs with the study of Collins *et al.* (1998).

Plant community heterogeneity

Results of the present study, conducted at a small spatial scale (0.25 m²), suggested that heterogeneity in the plant community (percentage dissimilarity) was affected only by grazing, and not by fire or by a fire-grazing interaction (Fig. 2). This is in contrast to studies of larger-scale community responses that a significant interaction of fire and grazing on spatial heterogeneity in tallgrass prairie. For example, spatially discrete fires promote focal grazing (Vinton *et al.* 1993; Meers & Adams 2003; Fuhlendorf & Engle 2004) and ungrazed areas are more likely to burn due to higher fuel loads. Consequently, an interaction of fire and grazing increases large-scale (45 to 65 ha.) spatial and temporal patterns (Fuhlendorf & Engle 2004). Thus, on the large scale, the fire-grazing interaction might be the most important factor determining spatial heterogeneity in the plant community, whereas on a smaller scale grazing alone becomes a more important factor, while fire, a non-selective event, has less of an impact on vegetation patterns at this scale. In other grasslands types, e.g. a pasture (Bakker *et al.* 1984) and a sheep-grazed salt marsh (Berg *et al.* 1997), it was also found that micropatterns (<0.04m²) in the vegetation originate in areas under grazing, while no patterns develop in ungrazed sites.

When we expressed heterogeneity as Euclidian distance (ED), we did not find a significant effect of grazing, fire regime or a fire-grazing interaction on vegetation patterns. In contrast to the percentage dissimilarity, ED is not correlated with species richness and diversity. Thus, it seems that the changes in heterogeneity in plant communities observed in the present study were probably a function of changes in species richness and diversity under different fire and grazing regimes.

Despite the increased community heterogeneity, i.e. percentage dissimilarity, under grazing a large number of plant species is similar in grazed and ungrazed treatments. For example, *Andropogon gerardii* was the most dominant grass and *Vernonia baldwinii* was the most abundant forb in all treatments. Thus, only the abundance of these dominant species changed under grazing. Still, in grazed areas a lot more species were recorded (higher species richness), but these were mainly plants that occurred sporadically, i.e. covered a very small area (e.g. *Achillea millefolium*, *Antennaria neglecta*, *Astragalus crassicaarpus*, *Bouteloua hirsuta*, *Buhloe dactyloides*, *Linum sulcatum*, *Ratibida*

columnifera, Table 1, Appendix 1) and were not present in ungrazed sites at all, probably due to increased competition and reduced light availability.

Patch selection by herbivores

Grazing-induced patterns develop primarily when herbivores are selective. Patch selection and reselection by bison is affected by the abundance of C₄-grasses (Vinton *et al.* 1993), which are highly preferred as forage and compose the greatest part of a bison diet (Steuter *et al.* 1995). Moreover, forage quality and availability may influence patch selection and reselection of herbivores. It has been shown that plants in urine patches have a higher leaf-nitrogen content (Day & Detling 1990) and that bison preferentially graze in urine-treated plots (Steinauer & Collins 1995). Moreover, bison prefer recently burned patches, in which forage quality may be enhanced as a result of higher mineral N availability (Hobbs & Schimel 1984; Hobbs & Swift 1985). Bison tend to revisit previously grazed patches (Knapp *et al.* 1999), which may be due to increased food quality in these patches. Young growing shoots have a higher quality, i.e. nitrogen content, compared to matured plants (Ulyatt 1981; Crawley 1983). The removal of plant biomass, e.g. through grazing, causes a higher turnover of plant material and consequently increases the regrowth of fresh nutrient-rich tillers (Fox *et al.* 1998). Thus, initial patch selection may depend on initial forage quality, while revisitation of grazing patches may be due to increased forage quality after grazing, i.e. more young growing shoots and higher soil N availability (Johnson & Matchett 2001).

In the present study we did not measure the stability of grazing patches over time. However, Fuhlendorf & Engle (2004) showed that the fire-grazing interaction causes development of a shifting mosaic in the landscape on the large scale. Fire may make previously ungrazed patches more attractive to herbivores, thereby reversing grazing patterns, i.e. unattractive patches that are burned become attractive whereas previously preferred patches that are not recently burned are left ungrazed. Consequently, the mosaic of grazed and ungrazed sites is dynamic, depending mainly on the time since fire. In tallgrass prairies it has been shown that grazing patches are completely or partly abandoned and that new patches are reselected at high frequencies (Knapp *et al.* 1999). Established patches that are used intensively, become less attractive due to the increased

abundance of forbs and the reduced abundance of food plants and probably will be abandoned. When there is no fire acting on the landscape, the expectation is that grazing patches are more stable. Bakker *et al.* (1984) showed that grazing induced micro-patterns in a pasture were more or less stable, due to on the one hand the enhanced quality in previously grazed patches and on the other hand the accumulation of litter and reduced quality in patches that are left ungrazed. Thus, revisitation of previously grazed patches causes sharp boundaries between grazed and ungrazed vegetation.

Effect of fire and grazing on resources

Grazing had a strong positive effect on resource availability. Mean nitrate (NO_3^-) and light levels were much higher in grazed than in ungrazed areas, which is consistent with results of other studies (Seagle *et al.* 1992; McNaughton *et al.* 1997; Frank *et al.* 2000; Johnson & Matchett 2001; Bakker *et al.* 2003). Herbivores in grasslands are known to increase net nitrogen mineralization rates and the levels of available inorganic soil nitrogen (Seagle *et al.* 1992; Johnson & Matchett 2001). Grazers consume organic nitrogen in plant biomass and return labile forms of N (e.g. in dung and urine) to the soil (Ruess & McNaughton 1988). This process is much faster than mineralization of N in plant litter. Moreover, the movement of N from the aboveground pool to the belowground pool may act to conserve N that would otherwise be lost through burning (Hobbs *et al.* 1991).

Strikingly, the fire regime did not significantly alter NO_3^- availability, as indicated by resin-collected NO_3^- , whereas previous studies showed that frequent burning decreases soil N availability (Hobbs *et al.* 1991; Ojima *et al.* 1994; Blair 1997; Johnson & Matchett 2001). However, there was a non-significant trend towards lower NO_3^- levels in annually burned sites, compared to sites burned every four years (Fig. 4A).

I expected reduced light levels in 4-year burned areas, due to accumulated dead organic material (Knapp & Seastedt 1986). However, no effect of the burning regime on light availability was found. It might be that the time since last fire in the 4-year burns was not sufficient to encounter any effects, or that grazers reduced the accumulation of litter in some areas of the 4-year burned treatments. Differences between burning frequencies would be mainly caused by biomass accumulation, i.e. litter. Unfortunately we did not

obtain any accurate measure of the thickness of the litter layer, so we cannot conclude whether this factor is different or similar between burning treatments. However, our disk calibration samples suggest that there is more litter present in 4-year burns. For this study we used two watersheds with a 4-year fire frequency. Although these watersheds were not burned in the same year, we do not think that this affected our light measurements. Because the light availability did not significantly differ between watersheds ($P=0.236$, $F_{1,376}=1.42$).

Resource heterogeneity

Nitrate heterogeneity

We expected that grazing would enhance heterogeneity in NO_3^- availability through patchy deposition of for example urine and dung (Knapp *et al.* 1999; Bakker *et al.* 2003), yet, we did not find any significant differences in NO_3^- heterogeneity (measured as coefficient of variation) distribution between the treatments. Grazing may still positively influence the variation in N availability measured in other ways, which is indicated by the greater standard deviations in grazed sites (Fig. 4A, SEM are shown in this figure, but they give a good indication for SD because sample sizes are equal). The fact that we did not find differences in the coefficient of variation in N levels in this study may be due to the technique we used. In a natural situation, deposition of urine and dung patches would enhance nutrient levels temporarily, thereby creating a patchy distribution of N, which consequentially affects the vegetation patterns (Steinauer & Collins 1995). In the present study we obtained a measure of N availability that accumulated in resin bags throughout the study period, not taking into account the temporal variability. At a certain moment in time, patchiness might have existed, whereas integrated over the whole season this would be harder to detect. Moreover, we hypothesized that nitrogen availability in ungrazed plots would be low and homogeneously distributed, however, we found some extremely high N-values (NO_3^- -values over 2000 μg per resin bag, while the average ungrazed value was 80 μg NO_3^- per resin bag) and consequently more variation than expected in the ungrazed exclosures. The high values and variation inside the exclosures might be due to rodent disturbances (e.g. burrowing, deposition of urine and droppings). We found rodent

holes in 19 out of the 192 ungrazed plots (9 out of 16 exclosures), whereas the grazed plots had no holes at all. The disturbed plots were not the ones with the high N-values, but rodents might have had their disturbing effects on N throughout the whole exclosure.

Light heterogeneity

Strikingly, we did not find a positive effect of grazing on heterogeneity in light availability, as was found in earlier studies at Konza prairie (Bakker *et al.* 2003). The results of the present study indicated a reduction in light heterogeneity, especially in sites with a 4-year burning frequency. In contrast, the heterogeneity in biomass availability as a function of canopy height was strongly enhanced in grazed areas. We expected that light and canopy height measurements would show comparable results, because they are both indicators for available amount of biomass per plot. The differences we found may be due to the differences in measuring methods we used. Light availability was measured as the fraction of light at the ground level, thereby taking into account the litter layer that was present, whereas canopy height only included the amount of standing living biomass. High variation in the amount of litter (pers. obs.), might explain the different outcome of both measures.

Relationship between resource availability and vegetation heterogeneity

It was expected that compositional heterogeneity would be correlated to patterns in soil resources, i.e. N, and light availability (Collins 1992; Bakker *et al.* 2003). However we did not find this relationship in our study, perhaps due the methods we used to measure our resources. Future studies should, we have to obtain spatial measures of N availability over a shorter period of time and estimate the thickness of the litter layer in all plots. Although the distribution of resources may contribute to patchiness in the vegetation, it has been shown that light availability may be a stronger determinant for vegetation patterns than light heterogeneity (Bakker *et al.* 2003). Moreover, Baer *et al.* (2004) showed that mean levels of soil N are more important in prairie regeneration than N heterogeneity. However, Baer *et al.* (2004) suggested that satellite species which are the most important contributors to diversity, are in part maintained by heterogeneity in soil properties and vegetation patterns.

Conclusion

We conclude that on the small scale used in this study, grazing is the most important factor determining resource availability, species composition vegetation heterogeneity. Fire frequency or a fire-grazing interaction are less important at this scale, whereas on the large scale both factors determine the vegetation mosaic together (Fuhlendorf & Engle 2004). As we expected diversity was highest in grazed, 4-year burned sites. Species richness, diversity and vegetation heterogeneity were most strongly correlated to mean levels of light availability.

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Appendix 1

Table 1. In total 93 plant species were recorded in the plots. This table shows the average cover per plant species per treatment (n=96). U1=ungrazed, annually burned, U4=ungrazed, burned every 4 years, G1=grazed, annually burned, G4=grazed, burned every 4 years. Grey highlights represent the most dominant forb (*Ambrosia psilostachya*) and the most dominant grass (*Andropogon gerardii*).

	Ungrazed_1	Ungrazed_4	Grazed_1	Grazed_4
<i>Achillea millefolium</i>	0.00	0.00	0.59	0.42
<i>Agrostis hyemalis</i>	0.00	0.00	0.00	0.01
<i>Ambrosia psilostachya</i>	5.73	7.31	8.98	13.94
<i>Amorpha canescens</i>	5.22	3.93	4.38	2.35
<i>Andropogon gerardii</i>	75.17	52.35	25.81	22.66
<i>Antennaria neglecta</i>	0.00	0.01	0.06	1.27
<i>Aristida oligantha</i>	0.00	0.00	0.01	0.00
<i>Artemisia ludoviciana</i>	0.57	2.13	1.04	0.60
<i>Asclepias stenophylla</i>	0.01	0.00	0.00	0.00
<i>Asclepias tuberosa</i>	0.19	0.00	0.00	0.01
<i>Asclepias verticillata</i>	1.20	0.19	0.07	0.03
<i>Asclepias viridiflora</i>	0.00	0.01	0.00	0.00
<i>Asclepias viridis</i>	0.45	0.00	1.61	0.00
<i>Aster ericoides</i>	2.96	3.76	4.21	3.57
<i>Aster oblongifolius</i>	0.00	1.92	0.78	1.71
<i>Aster sericeus</i>	0.00	0.18	0.02	0.18
<i>Astragalus crassicaarpus</i>	0.00	0.00	1.23	0.17
<i>Baptisa australis</i>	0.00	0.00	0.00	0.52
<i>Bouteloua curtipendula</i>	4.38	4.92	8.99	14.10
<i>Bouteloua gracilis</i>	0.01	0.00	1.39	0.17
<i>Bouteloua hirsuta</i>	0.00	0.00	0.79	0.06
<i>Bromus japonicus</i>	0.00	0.00	2.94	0.13
<i>Buchloe dactyloides</i>	0.00	0.00	1.83	0.00
<i>Carex brevior</i>	0.17	0.07	1.81	0.25
<i>Carex heliophylla</i>	2.00	1.94	2.80	2.05
<i>Carex meadii</i>	3.94	4.14	0.85	2.93
<i>Cirsium undulatum</i>	0.04	0.08	0.44	0.18
<i>Conyza canadensis</i>	0.00	0.02	0.00	0.01

<i>Croton monathogynus</i>	0.00	0.00	0.00	0.03
<i>Cyperus lupulinus</i>	0.01	0.00	0.17	0.10
<i>Dalea candida</i>	1.08	0.00	0.13	0.05
<i>Dalea multiflora</i>	0.00	0.00	0.00	0.31
<i>Dalea purpurea</i>	0.34	0.00	0.21	0.07
<i>Delphinium carolinianum</i>	0.02	0.00	0.00	0.03
<i>Dichanthelium acuminatum</i>	0.00	0.21	0.04	0.07
<i>Dichanthelium oligosanthes</i>	1.56	5.91	5.29	5.34
<i>Echineacea angustifolia</i>	0.00	0.00	0.00	0.06
<i>Elymus canadensis</i>	0.00	0.00	0.18	0.09
<i>Eragrostis spectabilis</i>	0.06	0.00	1.52	0.26
<i>Erigeron strigosus</i>	0.02	0.06	1.08	1.00
<i>Euphorbia nutens</i>	0.21	0.15	0.25	0.18
<i>Hedeoma hispidum</i>	0.00	0.01	0.46	0.52
<i>Hymenopappus scabiosaeus</i>	0.46	0.00	0.06	0.23
<i>Koeleria pyramidata</i>	0.09	0.14	1.99	1.40
<i>Kuhnia eupatorioides</i>	0.53	0.45	0.41	0.18
<i>Lepidium densiflorum</i>	0.01	0.02	0.20	0.23
<i>Lespedeza capitata</i>	2.07	0.00	0.03	0.00
<i>Lespedeza stipulacea</i>	0.00	0.00	0.01	0.00
<i>Liatris punctata</i>	0.01	0.02	0.00	0.02
<i>Linum sulcatum</i>	0.04	0.00	0.80	0.58
<i>Lithospermum arvense</i>	0.00	0.00	0.06	0.08
<i>Medicago lupulina</i>	0.00	0.00	0.03	0.04
<i>Mirabilis linearis</i>	0.00	0.00	0.00	0.13
<i>Muhlenbergia cuspidata</i>	0.00	0.18	0.00	0.00
<i>Oxalis stricta</i>	0.12	0.12	0.88	0.97
<i>Panicum sp.</i>	0.00	0.00	0.05	0.00
<i>Panicum virgatum</i>	1.12	0.40	0.21	0.29
<i>Physalis pumila</i>	1.30	0.81	0.24	0.94
<i>Plantago patagonica</i>	0.02	0.00	1.58	0.33
<i>Plantago rhodosperma</i>	0.00	0.00	0.00	0.14
<i>Poa pratensis</i>	0.06	4.00	0.57	3.07
<i>Portulaca oleracea</i>	0.00	0.02	0.04	0.16
<i>Ratibida columnifera</i>	0.00	0.00	1.64	1.13
<i>Rosa arkensas</i>	0.34	0.80	0.45	0.21
<i>Ruellia humilis</i>	0.94	0.15	0.54	0.68

<i>Salvia azura</i>	1.85	2.11	1.50	2.22
<i>Schedonnardus paniculatus</i>	0.00	0.00	0.20	0.00
<i>Schizachyrium scoparium</i>	1.78	5.58	1.20	7.13
<i>Senecia plattensis</i>	0.00	0.00	0.02	0.05
<i>Setaria viridus</i>	0.00	0.00	0.14	0.02
<i>Shrankia nuttallii</i>	0.29	0.06	0.00	0.05
<i>Silene antirrhina</i>	0.00	0.00	0.07	0.14
<i>Sisyrinchium campestre</i>	0.36	0.00	0.03	0.04
<i>Solanum carolinense</i>	0.03	0.00	0.00	0.00
<i>Solanum rostratum</i>	0.00	0.00	0.00	0.00
<i>Solidago canadensis</i>	0.42	0.00	0.00	0.00
<i>Solidago missouriensis</i>	0.17	1.22	0.81	1.86
<i>Solidago rigida</i>	0.15	0.47	0.27	1.79
<i>Solidago speciosa</i>	0.00	0.00	0.00	0.26
<i>Sorghastrum nutans</i>	14.46	19.31	4.41	7.22
<i>Spermolepis inermis</i>	0.00	0.05	0.19	0.10
<i>Sporobolus asper</i>	0.37	6.31	5.08	2.47
<i>Sporobolus heterolepis</i>	0.00	0.59	0.00	0.00
<i>Symphoricarpos orbiculatus</i>	0.01	0.06	0.02	0.69
<i>Tragia betonicifolia</i>	0.00	0.00	0.39	0.00
<i>Tragia spec.</i>	0.00	0.00	0.00	0.11
<i>Triodanis leptocarpis</i>	0.00	0.00	0.07	0.04
<i>Triodanis perfoliata</i>	0.00	0.06	0.00	0.05
<i>Unid. 1 (no sample)</i>	0.00	0.02	0.06	0.23
<i>Unid. 2 (no sample)</i>	0.00	0.00	0.00	0.01
<i>Verbena stricta</i>	0.26	0.15	1.13	0.31
<i>Vernonia baldwinii</i>	1.26	0.27	2.70	0.89
<i>Viola pedatifida</i>	0.00	0.06	0.03	0.01
total # species/treatment	50.00	48.00	70.00	78.00