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## Does resource availability, resource heterogeneity or species turnover mediate changes in plant species richness in grazed grasslands?

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**Abstract** Grazing by large ungulates often increases plant species richness in grasslands of moderate to high productivity. In a mesic North American grassland with and without the presence of bison (*Bos bison*), a native ungulate grazer, three non-exclusive hypotheses for increased plant species richness in grazed grasslands were evaluated: (1) bison grazing enhances levels of resource (light and N) availability, enabling species that depend on higher resource availability to co-occur; (2) spatial heterogeneity in resource availability is enhanced by bison, enabling coexistence of a greater number of plant species; (3) increased species turnover (i.e. increased species colonization and establishment) in grazed grassland is associated with enhanced plant species richness. We measured availability and spatial heterogeneity in light, water and N, and calculated species turnover from long-term data in grazed and ungrazed sites in a North American tallgrass prairie. Both regression and path analyses were performed to evaluate the potential of the three hypothesized mechanisms to explain observed patterns of plant species richness under field conditions. Experimental grazing by bison increased plant species richness by 25% over an 8-year period. Neither heterogeneity nor absolute levels of soil water or available N were related to patterns of species richness in grazed and ungrazed sites. However, high spatial heterogeneity in

light and higher rates of species turnover were both strongly related to increases in plant species richness in grazed areas. This suggests that creation of a mosaic of patches with high and low biomass (the primary determinant of light availability in mesic grasslands) and promotion of a dynamic species pool are the most important mechanisms by which grazers affect species richness in high productivity grasslands.

**Keywords** Grazing · Species richness · Heterogeneity · Colonization · Tallgrass prairie

### Introduction

Grazing by large herbivores affects plant species richness in many terrestrial ecosystems, including temperate grasslands (Collins et al. 1998; Knapp et al. 1999). Recent reviews indicate that, at moderate to high plant productivity, the activities of grazers most often increase plant species richness (e.g. Olf and Ritchie 1998; Bakker 1998), while in ecosystems with lower productivity, grazing may decrease species richness (Milchunas et al. 1988, 1998; Proulx and Mazumder 1998). In the productive tallgrass prairie of North America, grazing by large ungulate herbivores, such as bison (*Bos bison*), generally increases plant species richness (Collins et al. 1998; Knapp et al. 1999). The potential mechanisms by which grazers may affect species richness are numerous (Olf and Ritchie 1998; Bakker 1998), but there have been few tests of these mechanisms in the field, and many studies of plant community responses to grazing have considered only one mechanism at a time (e.g. increased nutrient availability). In reality, the activities of grazers simultaneously affect multiple factors that may, independently or in combination, affect plant species richness. The objective of this study was to gain insight into the mechanisms underlying species richness responses to grazing by comparing, in a long-term grazing study under realistic field conditions, the relative importance of three factors which could alter plant species richness. Below we

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identify three hypotheses based on these factors and their potential relationship to grazer-mediated changes in plant species richness.

#### Resource availability hypothesis

Activities of grazers may result in greater availability of resources to plants. This hypothesis focuses on changes in mean levels of resource availability, as opposed to spatial patterns (see below). For example, consumption of biomass and trampling by grazers creates an environment with higher light availability than in ungrazed grassland. Reduced competition may lead to the coexistence of more species, especially those that are poor competitors for light (Grime 1979; Collins et al. 1998; Stevens and Carson 2002). Similarly, the activities of grazers can increase rates of net N mineralization and the availability of soil N (McNaughton et al. 1997; Knapp et al. 1999; Johnson and Matchett 2001), a nutrient that typically limits productivity in tallgrass prairie (Seastedt et al. 1991; Blair 1997). Thus, increased N availability may decrease the potential for competitive exclusion of plant species that are poor competitors for soil N.

#### Spatial heterogeneity hypothesis

The activities of grazers may lead to greater spatial heterogeneity in light and soil resources (i.e. water and N). Light, water and N are three key resources that have been linked to plant responses in tallgrass prairie (Seastedt and Knapp 1993; Knapp et al. 1999), in both the presence and absence of grazers. Herbivores can enhance heterogeneity of these plant resources by their grazing activities (i.e. patchy removal of aboveground biomass), nutrient redistribution (i.e. dung and urine deposition), and the creation of soil disturbances (i.e. wallows). Greater resource heterogeneity in the presence of grazers may allow for the coexistence of more species than does a homogeneous environment (Tilman and Pacala 1993; Collins and Glenn 1991; Collins and Wein 1998).

#### Local colonization and extinction hypothesis

The activities of grazers may increase rates of species turnover by creating patches suitable for colonization and seedling establishment, or by increasing the dispersal of plant species, while simultaneously eliminating some species in areas of local intensive grazing or disturbance. This could lead to higher local colonization and extinction rates in grazed areas than in ungrazed areas with a higher number of species that temporarily occur in local patches in grazed areas. This hypothesis is a metapopulation-based alternative to the above resource-based hypotheses. It focuses on the dynamics of species turnover to explain species richness responses to grazing (Olf and Ritchie 1998; Collins and Wein 1998).

In order to evaluate the relative importance of each hypothesis, we defined two criteria that would need to be satisfied for a specific hypothesis to be supported by the data. First, the phenomenon of interest (i.e. availability or heterogeneity of resources, or species turnover rate) must differ in grazed versus ungrazed sites. Second, the phenomenon should be positively correlated with plant species richness. To address these criteria, we quantified available soil N, soil water and light levels along permanent sampling transects in grazed and ungrazed tallgrass prairie, and used long-term plant species composition data to calculate species turnover rates along those same transects. Each of these factors was then related to observed differences in species richness.

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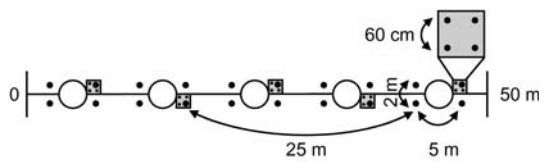
## Materials and methods

### Study site

We conducted this research at the Konza Prairie Biological Station, a 3,500-ha native tallgrass prairie ecological research site located in the Flint Hills of northeastern Kansas, United States. Konza Prairie is part of the USA network of Long-Term Ecological Research (LTER) sites (Callahan 1984). Soils at the site are cherty, silty clay loams on a bedrock of limestone. Topographic relief results in a conspicuous division of the landscape into a series of upland plateaus with mostly shallow soils, slopes with outcrops of limestone, and lowlands with deeper alluvial and colluvial soils (Oviatt 1998). Mean monthly temperatures range from  $-2^{\circ}\text{C}$  in January to  $27^{\circ}\text{C}$  in August, and rainfall averages 835 mm/year, with  $\sim 75\%$  falling during the growing season (April–October). The site is divided into replicated experimental watersheds which are burned in spring (10 April  $\pm 10$  days) at frequencies that range from annual burning to once every 20 years. Fire was an important factor in these grasslands historically, and frequent burning is a common management practice in this region (Knapp and Seastedt 1998). Introductions of bison (*Bos bison*) began in 1987 to evaluate the role of native, ungulate grazers in these grasslands and since 1992, approximately 220 animals have grazed a 949-ha portion of the site (Knapp and Seastedt 1998). For this study, we used only sites that had been burned annually since at least 1984, with and without the presence of bison.

### Sampling design

All plant, soil and light data were collected along 16 permanent sampling transects of 50 m length (Fig. 1), with four transects representing each of the four combinations of grazing treatment (grazed vs. ungrazed) and topographic position (upland vs. lowland). Four transects each were randomly located in upland and lowland topographic positions within replicate large watersheds (mean size of 69 ha each) assigned an annual spring burning treatment. These transects were designed for long-term sampling of plant community dynamics, and were established prior to the initiation of the grazing treatments. Since 1992, half of these transects have been subject to bison grazing, and half have remained ungrazed. Species composition data were collected annually in five 10-m<sup>2</sup> circular plots per transect, with sampling in both spring and fall to include both cool- and warm-season plant species. For this study, additional measurements of resource availability were done along these transects in a spatially explicit manner, centred on the permanent vegetation plots, so that resource availability and heterogeneity could be related to the existing long-term species composition data.



**Fig. 1.** Samples were collected along a longitudinal grid developed around permanent plant sampling transects. The *circles* represent permanent 10-m<sup>2</sup> plots, where species composition is surveyed every year. Each *dot* represents a sampling point. The *grey squares* are 1-m<sup>2</sup> plots, in which additional soil and vegetation samples were taken at 60-cm intervals

#### Resource availability

In 1998, we characterized levels and spatial patterns of resource availability in midsummer (a time of high leaf area and physiological activity). Measurements of resource availability (light, N and water) were taken at 560 sampling points; seven points on each of the five plots along each of the 16 transects, for a total of 140 samples per grazing treatment × topographic position combination. Extractable inorganic soil N (NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>) concentrations were used as an index of plant available N. Because of the high sample size required to detect spatial patterns, previous studies on soil N heterogeneity have used extractable inorganic N (Gross et al. 1995; Afzal and Adams 1992), total N (Collins and Wein 1998) or a phytometer approach (Miller et al. 1995). Concentrations of inorganic N are generally highly variable, and provide only a measure of available N pools at a single point in time. We collected soil samples in June when soils were moist, to correspond with a time when previous studies indicated peak net N mineralization rates and inorganic N concentrations (Turner et al. 1997; Blair 1997; Cui and Caldwell 1997). We assumed that these samples reflected spatial patterns in N availability, although absolute values must be interpreted with caution. Each sample consisted of two soil cores, 2 cm diameter × 10 cm deep. The samples were sealed in airtight bags, placed in a cooler in the field, and stored at 4°C until they could be processed (typically within 7 days). Field-moist subsamples (equivalent to approximately 10 g dry weight) were extracted with 2N KCl solution, and the filtered extract was analysed colorimetrically for NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N concentrations using an Alpkem FlowSolution auto analyser. Subsamples from the same soil cores used for N measurements were dried for 3 days at 60°C to determine gravimetric soil water content at the time of sampling.

Light penetration to the soil surface (canopy transmittance) was measured as the ratio of photosynthetic photon flux density (PPFD) at the soil level and above the canopy. Measurements were taken near the time of peak biomass (i.e. at the end of August), between 11:00 a.m. and 3:00 p.m., with a Sunfleck ceptometer (Decagon Devices). Each single measurement was a composite of five point measures. Canopy transmittance was calculated as the ratio of PPFD at the soil surface divided by PPFD above the canopy.

#### Resource heterogeneity

Mean absolute difference in values for water, light and N availability between pairs of sampling points, that are separated by a specific distance, was used as a measure of resource heterogeneity along transects. This is a geostatistical approach, in which the comparison of pairs of points at various distances (lags) yields information on spatial patterning, which can be summarized in a variogram (Robertson and Gross 1994; Turner et al. 1994). In theory, this approach yields an asymptotic model, in which the “sill” can be calculated as the level of heterogeneity, and the range as the distance at which sample points no longer show correlation. Mean absolute difference was calculated as:

$$d(h) = \frac{1}{N(h)} * \sum_{i=1}^N |z(x_i) - z(x_{i+h})| \quad (1)$$

In which  $d$  is the mean absolute difference and  $h$  is the lag-distance at which pairs of samples are compared.  $N(h)$  is the sample size for a particular lag-distance and  $z(x_i) - z(x_{i+h})$  is the difference in values of a specific pair of points. The absolute differences were used instead of the variance to avoid an overriding influence of extreme, but meaningful values, such as very high N values where recent urine patches were sampled. These calculations were done for each transect separately.

Many studies of heterogeneity use a square grid of sampling points to distinguish between semivariances in different directions (e.g. Isaaks and Shrivastava 1989). In our case, we wanted to link the resource data to long-term species composition data, so we modified the sampling design to fit the longitudinal transects (Fig. 1). With 20 regularly spaced samples, it was possible to calculate estimates for heterogeneity at various scales (2 m, 5 m, and 25 m) along the transects. To measure heterogeneity at a smaller scale, we added additional sampling points arranged in 60 cm × 60-cm squares to five of the regular sampling points along each transect (i.e. the grey squares in Fig. 1). These additional points were used only for analyses at the 60-cm scale. Each data point was used only once per lag-distance, to avoid unequal replication and prevent repeated use of only a subset of data points. As a result, ten pairs of points could be used for each lag-distance within a transect. Using ten data points per transect, or 40 data points per treatment, to estimate heterogeneity conformed to the sample size recommended by Rossi et al. (1992).

Because the mean absolute differences were not related to lag-distance for all the resources, i.e. the variograms were pure nugget models, with especially large noise at the smaller lag-distances, we were not able to calculate a sill. Instead, we use the differences between pairs of points at the largest possible distance within transects (i.e. the 25-m scale) as a measure for heterogeneity at the transect scale. The transect scale is also the largest scale at which plant species composition data were available.

Non-parametric Kruskal-Wallis ANOVAs were used to compare heterogeneity between treatments, because of deviations from assumptions of normality and homogeneity, as previously proposed by Afzal and Adams (1992). In addition to resource heterogeneity, percent difference in species composition between 30-m-spaced survey plots within a transect was calculated on the basis of presence or absence of species as a measure of vegetation heterogeneity.

#### Species turnover

Long-term data on species composition were used to calculate species turnover. A species turnover rate was calculated that included both colonization and extinction, and provided an index for the dynamics of species composition from one year to the next. Species turnover rate was calculated as:

$$\text{Species turnover rate}(t) = 1 - \frac{\text{Species in common}(t-1 \rightarrow t)}{\frac{TN(t-1) + TN(t)}{2}} \quad (2)$$

To calculate species turnover for an area in a specific year  $t$ , the number of species in that area present in both year  $t$  and year  $t-1$  was divided by the average total number of species ( $TN$ ) in that area and subtracted from 1. This yielded a value between 1 (all species are new) and 0 (species composition is identical in the 2 years).

## Statistical analyses

Analyses were conducted in three stages. First we tested whether grazing indeed led to higher species richness in our study area. Second we determined if the potential factors associated with each hypothesis were consistent with predicted effects of grazing, i.e. whether resource availability, heterogeneity and species turnover were higher in grazed than in ungrazed areas. Third, we investigated the relationships between the potential mechanisms underlying each hypothesis and observed differences in species richness.

The first two tests for effects of grazing treatment (grazed, ungrazed) and topography (upland, lowland) were accomplished as fixed factors in a two-way ANOVA, with species richness, species turnover, resource availability and resource heterogeneity as the respective response variables. Topography was included as a separate factor to test for potential interactions with grazing, and to reduce the amount of variation caused by differences in soil conditions between uplands and lowlands. However, no interactions between grazing treatment and topography occurred, so the effect of grazing treatment is presented and discussed without regard to topography.

The relative strength of each potential mechanism for explaining differences in species richness between grazed and ungrazed areas was assessed using both regression and path analysis. Simple regressions were calculated separately with each of the parameters related to resource availability, resource heterogeneity, and species turnover rate as explanatory variables, and using species richness values from the permanent transects as the response variable. In this context, regression analyses cannot demonstrate causation. However, it is a useful tool for comparing the mechanisms, since it is unlikely that factors strongly determining species richness would be unrelated to differences in species richness in the field. Multiple regression models were not employed because the factors were not independent, but path analysis was performed to provide a qualitative comparison of the relative strengths of correlations with species richness (Sokal and Rohlf 1995). The use of path analysis in this study was exploratory, because we did not have a predefined correlation structure between the variables (Petraitis et al. 1996). Correlations between pairs of explanatory variables were used in the path model when Pearson's correlation coefficients were significant and the correlation was biologically meaningful. Also the combination of long-term species composition data with estimates of heterogeneity did not provide a sufficient sample size to actually test the correlation structure (Grace and Pugsek 1998). Despite the number of correlations tested,  $\alpha$  was kept at 0.05 to reduce the chance of committing a type II error, since excluding a correlation that actually occurs would affect the path analysis negatively.

As the sample points within a transect were not independent and species richness and resource heterogeneity at the 25-m scale were properties of a transect, averages by transect were used as a single data point in the ANOVAs, regressions and path analyses. This reduced the sample size to 16 data points (4 transects  $\times$  4 sites).

In tests where percentages were involved, an arcsine-square root transformation was performed (Zar 1987). In some tests, a log-transformation was necessary to satisfy normality and homogeneity assumptions of parametric tests. Because soil N data deviated from normality even after transformation, a Kruskal-Wallis ANOVA was used in this case (Sokal and Rohlf 1995). All tests were performed with SPSS version 9.00.

## Results

### Plant community responses

Grazing had a clear positive effect on species richness in the permanent transects. Species richness in grazed areas increased by 25% over an 8-year period, while in ungrazed areas species richness declined slightly over the same

interval (ANOVA:  $F = 124.6$ ;  $df = 1, 12$ ;  $P < 0.001$ ; Fig. 2). Grazing also affected heterogeneity in plant communities. An analysis of plant composition data showed that percent difference between pairs of survey plots within transects at 30 m distance was much higher in grazed areas (52%) than in ungrazed areas (29%, ANOVA:  $df = 1, 28$ ;  $F = 6.4$ ;  $P = 0.017$ ).

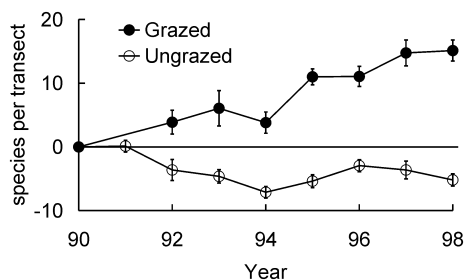
### Effect of grazing on resources and species turnover

Mean light levels were generally higher in grazed areas ( $F = 7.837$ ;  $df = 1, 12$ ;  $P = 0.016$ ), as were levels of inorganic N ( $F = 6.197$ ;  $df = 1, 12$ ;  $P = 0.028$ ; Fig. 3). No difference in mean soil water content was observed between grazed and ungrazed areas ( $F = 0.734$ ;  $df = 1, 12$ ;  $P = 0.408$ ). Resource heterogeneity was greater in grazed than in ungrazed areas for light ( $F = 40.6$ ;  $df = 1, 12$ ;  $P < 0.001$ ) and soil N ( $F = 5.4$ ;  $df = 1, 12$ ;  $P = 0.039$ ), but not for soil water content ( $F = 3.50$ ;  $df = 1, 12$ ;  $P = 0.086$ ). Plant species turnover rates were higher in the grazed treatments ( $F = 52.969$ ;  $df = 1, 28$ ;  $P < 0.001$ ).

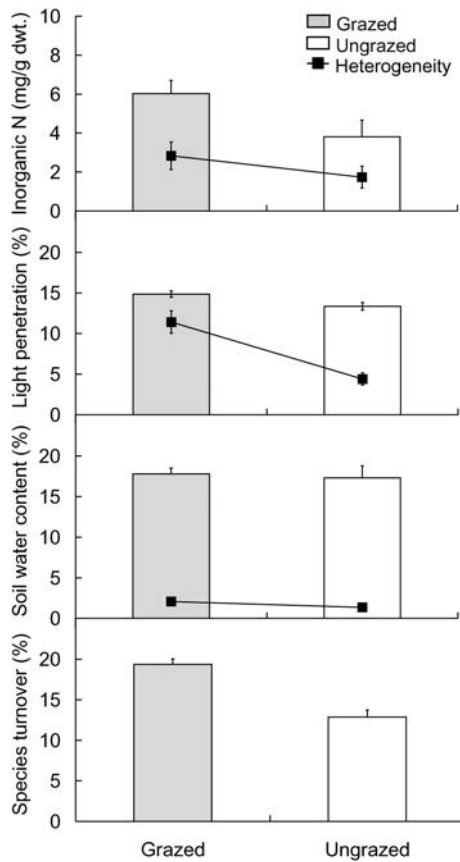
### Relating species richness to potential mechanisms

Simple regressions of species richness with resource levels in grazed and ungrazed prairie indicated that species richness was significantly related to soil N levels ( $t = 2.276$ ;  $df = 15$ ;  $P = 0.039$ ;  $R^2 = 0.27$ ), but there was a much stronger relationship of species richness to light penetration to the soil ( $t = 3.259$ ;  $df = 15$ ;  $P = 0.006$ ;  $R^2 = 0.43$ ). Regressions of species richness with resource heterogeneity revealed a very strong relation with heterogeneity in light ( $t = 4.259$ ;  $df = 15$ ;  $P = 0.001$ ;  $R^2 = 0.53$ ). In contrast, heterogeneity in soil water content ( $t = 1.642$ ;  $df = 15$ ;  $P = 0.123$ ) and inorganic N ( $t = 0.658$ ;  $df = 15$ ;  $P = 0.521$ ) were not significantly related to species richness. Species richness also showed a strong relationship to species turnover rates ( $t = 3.898$ ;  $df = 15$ ;  $P = 0.002$ ;  $R^2 = 0.48$ ) in the simple regression.

Heterogeneity in soil water and inorganic N had very low or negative correlations with species richness when assessed via path analyses (Fig. 4). In contrast, species



**Fig. 2.** Annual change in mean number of plant species per transect in grazed and ungrazed transects. Changes are reported relative to species richness in 1990 (mean of 35 species per transect). Error bars represent SEM. 90 1990, 92 1992, 94 1994, 96 1996, 98 1998

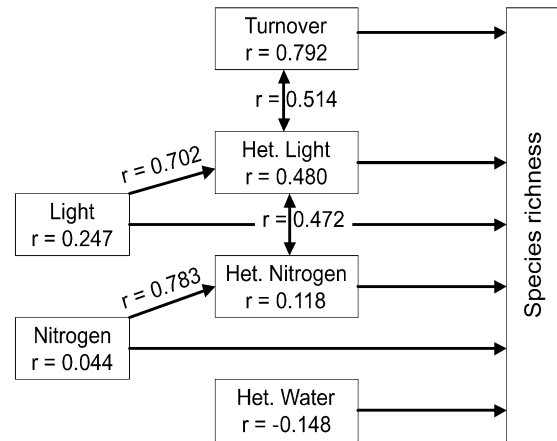


**Fig. 3.** Differences in resource availability, heterogeneity and species dynamics in grazed and ungrazed areas. Species dynamics is expressed as species turnover from 1997 to 1998. Heterogeneity is expressed as mean difference in resources levels between sampling points at a lag-distance of 25 m. Error bars represent SEM

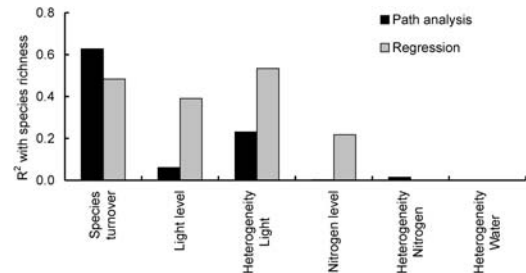
richness was strongly related to heterogeneity in light and species turnover. Mean levels of light and N showed a weaker relation with species richness. The path analysis indicated that mean light levels were strongly correlated with heterogeneity in light (Pearsons  $r=0.702$ ;  $df=15$ ;  $P=0.001$ ), in such a way that areas with a high light level also had the highest heterogeneity in light. Thus, results from the simple regressions and the path analysis were consistent, although the inclusion of interdependencies between the potential mechanisms affecting species richness in our model changed the relative importance of some mechanisms (Fig. 5). The most pronounced changes were in species turnover, which was more highly correlated with species richness when interdependencies were included. Levels of light and inorganic N had smaller correlations with species richness.

**Discussion**

Differences in species richness between grazed and ungrazed sites were evident after only a few years of grazing in this mesic grassland. The continuing positive trend indicates that species richness was still increasing in grazed areas. Although this research was confined to



**Fig. 4.** Diagrammatic representation of the path analysis of the importance of resource amount and heterogeneity (*Het.*) and species turnover as influences on species richness in a mesic grassland. All correlations of species richness with the potential mechanisms affecting this parameter are shown *within the boxes* and correlations between mechanisms are shown *across arrows*. Correlations are only included when significant and ecologically meaningful



**Fig. 5.** A comparison of coefficients of determination of all potential mechanisms affecting species richness from simple regressions with species richness and from the path analysis. Results from simple regressions are shown only when the slope deviated significantly from zero. Results from the path analysis are not shown when a negative correlation coefficient with species richness was found

annually burned watersheds, similar increases have been measured in watersheds with a lower fire frequency (Collins et al. 1998).

Our finding that inorganic N levels were higher in grazed than in ungrazed areas is consistent with other studies indicating enhanced N availability in the presence of grazers (McNaughton et al 1997, Frank et al. 2000). Although a one-time sampling of inorganic soil N is not a very robust measure of N availability throughout the year, when we compared our results with data from in situ N mineralization assays in the same area, the patterns were similar: soil N mineralization was greater in grazed sites (Johnson and Matchett 2001), supporting the trend in our data for greater N availability in grazed areas. The positive relationship between species richness and mean inorganic soil N concentrations suggests that higher N availability may play a role in enhancing species richness in these grasslands. However, in the path-analysis, the correlation coefficient for soil N availability and species richness was

negligible, at least at the temporal and spatial scales of this study.

Light levels and heterogeneity in light were strongly correlated, thus it is difficult to separate their role in determining species richness responses to grazing. Independent manipulations of mean light levels and heterogeneity have indicated that mean light availability, and not heterogeneity, governs species richness in successional field communities (Stevens and Carson 2002). Clearly, patches with short vegetation in grazed areas contribute to both high light levels and high heterogeneity in light. These patches can arise from either grazing or soil disturbance, such as trampling or wallowing by bison. The importance of light as a resource is underscored by the observation that grazing by large herbivores has the strongest positive effect on plant species richness in the most productive grasslands (Olf and Ritchie 1998), where competition for light would be greatest. In productive grasslands, patches with high light conditions would be expected to have a much greater effect than in unproductive grasslands, such as short-grass steppe where grazing does not increase species richness (Milchunas et al. 1998).

As heterogeneity in soil water content was not different between grazed and ungrazed sites, and both the simple regression and the path analysis produced a weak, and even negative, correlation between heterogeneity in soil water content and species richness, it is unlikely that heterogeneity in soil water content was an important mechanism affecting the response of species richness to grazing. A similar argument can be made against the potential importance of heterogeneity in inorganic soil N. Although heterogeneity in inorganic soil N was slightly greater in grazed areas than in ungrazed areas, heterogeneity in soil N concentration was not significantly related to plant species richness in our analyses, and the correlation with species richness in the path analysis was very low. In contrast, absolute levels and heterogeneity in light availability were much higher in grazed than in ungrazed areas and had a strong positive relationship with species richness. So, if resource heterogeneity is important in determining the species richness response to grazing in this grassland, our results suggest this is mainly heterogeneity in light.

The “pure nugget effect”, which prevented the modeling of variograms based on the resource data, indicates in ecological terms that for resource levels, pairs of data points at close proximity were not more alike than at larger distances. In other words, we found no evidence for spatial patterning in resource levels at the scales surveyed. It is still possible that spatial patterning occurs at smaller or larger scales than we covered in this study. For example, a high degree of heterogeneity in soil N at very small scales has been reported before (Jackson and Caldwell 1993; Gross et al. 1995). Afzal and Adams (1992) found that most heterogeneity in soil N occurred within 10 cm. A lack of spatial correlation of light levels is inconsistent with the results of Vinton et al. (1993), who reported that patches repeatedly grazed by bison were generally 5–10 m<sup>2</sup> in size.

The lack of correlation we observed between heterogeneity in soil N and species richness was surprising, but is consistent with the results of Steinauer and Collins (1995),

who detected only a minor effect of artificially created urine patches on plant species richness. These authors argued that the presence of a urine patch does not necessarily provide good conditions for new species to establish and, thus, only existing individuals profit from the N pulse. In contrast, patterns of heterogeneity in light due to biomass impacts by grazing and wallowing by bison are more persistent, because they occur repeatedly over longer periods of time (Vinton et al. 1993). Such a persistent spatial pattern in light may give species a better opportunity to colonize. Indeed, the increased likelihood of grazing around urine patches had more profound effects on small-scale patch dynamics than the urine patches alone (Steinauer and Collins 1995).

Bison generate disturbances in the vegetation (wallows, trails, etc.), and a number of plant species are associated with these non-grazing disturbances, with some dispersed via the fur and hooves of bison (Hartnett and Fay 1998). Comparisons of species turnover in grazed and ungrazed areas indicate that bison indeed enhanced species turnover in this grassland, and positive correlations between species turnover and richness suggest that species turnover contributes to higher species richness in grazed areas. Such a mechanism may be particularly important in this grassland in which there is a large species pool and turnover can be up to 30% per year (Collins and Glenn 1991).

Resource heterogeneity is not independent of, and may influence species turnover as well as heterogeneity in plant species composition, particularly if high resource patches are favourable for propagule transport, germination and establishment in grasslands (Collins and Glenn 1991). In a patchy environment, stochastic processes can play a more important role than in a uniform environment, with propagule transport, germination, establishment, and competitive outcomes within patches all influenced by stochastic elements. This is supported by our analysis of the spatial pattern in the plant species composition data, where we found greater differences between survey plots within a transect in grazed sites. Such a mosaic structure is often found in natural grasslands (e.g. Miller et al. 1995; Bakker et al. 1984). A heterogeneous environment also results in a broad range of conditions, which should benefit species with different sets of thresholds for certain resources. For example, plants with high light requirements and shade-tolerant plants can grow in close proximity when both high and low light conditions are available.

## Conclusions

An increase in plant species richness occurred after the introduction of grazers into tallgrass prairie, a result that is consistent with the effects of grazers in many mesic grasslands. While species richness patterns in grazed and ungrazed sites did not correlate with heterogeneity in soil water and inorganic N, a strong correlation to heterogeneity in light was found. This indicates that if resource heterogeneity is important in determining the species richness response to grazing in these grasslands, it is likely heterogeneity in light. When levels of soil N, water and

light were tested, mean light levels corresponded best to the observed species richness patterns, suggesting that open patches created by bison play an important role in plant community dynamics in these grasslands. A good correspondence of higher species turnover with species richness patterns also suggests a potential role of bison in local extinction and colonization events. A combination of these mechanisms, in which bison create patches of high light conditions where a higher colonization rate is achieved, due to a higher dispersal rate and to enhanced conditions for germination and establishment, is likely to determine the difference in plant species richness between grazed and ungrazed tallgrass prairie.

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