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Influence of grazing and fire frequency on small-scale plant community structure and resource variability in native tallgrass prairie

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In grasslands worldwide, grazing by ungulates and periodic fires are important forces affecting resource availability and plant community structure. It is not clear, however, whether changes in community structure are the direct effects of the disturbance (i.e. fire and grazing) or are mediated indirectly through changes in resource abundance and availability. In North American tallgrass prairies, fire and grazing often have disparate effects on plant resources and plant diversity, yet, little is known about the individual and interactive effects of fire and grazing on resource variability and how that variability relates to heterogeneity in plant community structure, particularly at small scales. We conducted a field study to determine the interactive effects of different long-term fire regimes (annual vs four-year fire frequency) and grazing by native ungulates (*Bos bison*) on small-scale plant community structure and resource variability (N and light) in native tallgrass prairie. Grazing enhanced light and nitrogen availability, but did not affect small-scale resource variability. In addition, grazing reduced the dominance of C_4 grasses which enhanced species richness, diversity and community heterogeneity. In contrast, annual fire increased community dominance and reduced species richness and diversity, particularly in the absence of grazing, but had no effect on community heterogeneity, resource availability and resource variability. Variability in the abundance of resources showed no relationship with community heterogeneity at the scale measured in this study, however we found a relationship between community dominance and heterogeneity. Therefore, we conclude that grazing generated small-scale community heterogeneity in this mesic grassland by directly affecting plant community dominance, rather than indirectly through changes in resource variability.

Patchiness in grassland communities 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 and temporal scales (Collins 1987, Wu and Loucks 1995, Collins and Smith 2006). Frequent fires and grazing by large ungulates are important processes affecting the biological diversity and heterogeneity of grassland vegetation (Collins 1992, Fuhlendorf and Smeins 1999). In North American tallgrass prairie, fire in the absence of grazers has a homogenizing effect on prairie plant communities (Collins 1992, Collins and Smith 2006) by uniformly removing aboveground biomass and litter, thereby favouring the dominance of a few species of warm-season grasses (Knapp et al. 1999), preventing establishment of woody plant species (Briggs et al. 2005), and reducing soil nitrogen (N) availability and heterogeneity (Blair 1997, Johnson and Matchett 2001). In contrast, activities of large herbivores, such as selective grazing, nutrient deposition (i.e. urine and dung patches) and soil disturbance (i.e. trampling and wallowing) enhance diversity, presumably by increasing heterogeneity in resource availability and altering species composition and community structure (Steinauer and Collins 1995, 2001, Augustine and Frank 2001).

Previous studies on the effects of fire and grazing on diversity and spatial heterogeneity of grassland plant communities focused on either the impact of fire (Collins 1992, 2000) or grazing (Steinauer and Collins 1995, 2001, Bakker et al. 2003, Frank 2005), with limited attention given to their combined effects (but see Fuhlendorf and Engle 2004, Archibald et al. 2005, Collins and Smith 2006), particularly with respect to concurrent assessment of changes in availability and heterogeneity of key resources and plant community structure. Previous studies showed that fire and grazing can interact at landscape scales through a series of positive and negative feedbacks, because fire influences grazing patterns (Vinton et al. 1993, Coppedge and Shaw 1998, Knapp et al. 1999) and grazing, in turn, modifies the effect of fire by altering the accumulation and distribution of fire fuels (i.e. litter). Such feedbacks create a

spatially and temporally variable mosaic of vegetation structure (Fuhlendorf and Engle 2001, 2004) and resource distribution (Hobbs et al. 1991).

Fire and grazing alter patch structure at a wide range of spatial scales (Fuhlendorf and Smeins 1999, Knapp et al. 1999, Collins and Smith 2006), and their impacts can feedback to affect processes acting at other scales (Steinauer and Collins 2001). Consequently, analysis at multiple spatial scales is necessary to describe and understand the patterns and processes underlying responses to fire and grazing (Fuhlendorf and Smeins 1996). Recently, Collins and Smith (2006) studied the interactive effects of grazing and fire frequency on plant community heterogeneity at 10-, 50- and 200-m^2 scales in tallgrass prairie. They found that individual effects of fire frequency and grazing were scale-independent, while their interactive effects changed with scale of measurement. At the 10-m^2 scale grazing increased spatial heterogeneity in annually burned sites but decreased heterogeneity in less frequently burned areas, while at the 50-m^2 scale grazing decreased heterogeneity in four-year burns only (Collins and Smith 2006). The potential mechanisms underlying these responses, such as changes in resource availability or heterogeneity, were not quantified. It is not clear whether changes in community heterogeneity reflect the direct effects of disturbance on community structure, or are mediated through disturbance-induced changes in the abundance and variability of key resources, such as nitrogen and light (Knapp and Seastedt 1986, Blair 1997, Johnson and Matchett 2001). In addition, the smallest scale of measurement in the study of Collins and Smith (2006) was large enough to potentially encompass high resource heterogeneity, along with the presence of smaller grazed and ungrazed patches (Steinauer and Collins 2001). Indeed, many of the specific effects of grazing occur on a smaller scale. For example, foraging decisions, urine and dung deposition and feeding stations may be important determinants of small-scale heterogeneity.

The objectives of our study were to assess the independent and interactive small-scale effects of fire frequency (annual vs four-year burning) and grazing by bison *Bos bison* on plant community structure (richness, diversity, evenness and dominance) and heterogeneity, and availability and variability of two key plant resources, soil nitrogen (N) and light in native tallgrass prairie. This approach allowed us to examine the relationship between small-scale resource availability or variability and plant community structure. We hypothesized 1) that grazing would increase small-scale spatial plant community heterogeneity and resource variability, while 2) annual burning would have a homogenizing effect on both small-scale plant community heterogeneity and variability in resources, and that 3) the interaction of grazing and fire-frequency would lead to the highest diversity and small-scale heterogeneity in areas that are grazed and burned once every four years. Finally, we expect that 4) increased resource variability would be correlated with increased plant community diversity and heterogeneity (Augustine and Frank 2001). To address these objectives, we quantified plant species composition and measured availability of N and light in small plots (12 0.25-m^2 plots in a grid within replicated 2×3 m sampling units) located within a long-term grazing and burning experiment in native tallgrass prairie.

Methods

Site description

The study was conducted at the Konza Prairie Biological Station (KPBS), a 3487-ha native tallgrass prairie and Long-Term Ecological Research (LTER) site located in the Flint Hills of northeastern Kansas, USA (39°05′N, 96°35′W). The vegetation is dominated by a matrix of C_4-grasses: *Andropogon gerardii, Andropogon scoparius, Sorghastrum nutans, Bouteloua curtipendula* and *Sporobolus asper* (nomenclature follows Great Plains Flora Associations 1986). Mean annual temperature is ~13°C and mean annual precipitation is 835 mm, with 70% occurring during the growing season from April to September.

Prior to the establishment of KPBS as a research site the area was grazed by cattle and burned frequently, as is typical in this region. Since 1972, replicated experimental watersheds have been burned in spring at frequencies ranging from annually to once every 20 years. Between 1987 and 1992 bison *Bos bison* were reintroduced on KPBS to evaluate the role of native, ungulate grazers in these grasslands. Current herd size is ~250 individuals which have access to a 989 ha area divided into ten watersheds, representing replicates of the following fire frequency treatments: burned at 1-, 2-, 4- and 20-year return intervals. The four-year fire return interval is replicated on four watersheds, while other fire return intervals are replicated on two watersheds each. The proportion of the total area burned in a given year varies, depending on the rotation of the prescribed fire treatments on the ten grazed watersheds. In 2004, a total of 42% of the area was burned. The majority (~870 ha) of the grazed area is native grassland, with an average annual aboveground net primary production (ANPP) of 417 g m^{-2} (Knapp et al. 1998b), while the remaining area is covered by riparian forest, roads and streams. Bison stocking rates are based on a targeted average annual aboveground biomass consumption of 25% of ANPP, although grazing rates vary temporally and spatially among and within watersheds as a function of burn history, time since last fire, topographic position, and other factors. Bison graze the area year-round and do not receive supplemental food.

Experimental design

Prior to reintroduction of bison in 1987, four permanent, fenced exclosures (each 5×5 m) were randomly located in upland grassland sites within the replicate one-year and two replicates of the four-year burned watersheds ($n = 4$ exclosures/watershed; $n = 16$ exclosures). These were established to assess the long-term effects of bison grazing on plant community structure and ecosystem processes. The annually and four-year burn fire regimes have been shown to have significantly different impacts on plant community composition and resource availability (Collins et al. 1995, Collins 2000, Johnson and Matchett 2001, Collins and Smith 2006).

In May 2004, we established within each exclosure, and in a representative area adjacent to each exclosure, 2×3 m sampling units. These paired grazed and ungrazed sampling

units were located 25 m apart, to avoid the possible impact of the exclosure on bison presence in the grazed unit. Each sampling unit was divided into a 3×4 grid of 12 0.25-m^2 plots (50×50 cm; $n = 384$ total), arranged in three rows of four adjacent plots, separated by 50 cm walkways. Plots inside the exclosures were located at least 1 m from the fence to avoid edge effects. Thus, four different treatments were examined: (1) annually burned and ungrazed, (2) annually burned and grazed, (3) burned every four years and ungrazed, and (4) burned every four years and grazed. Although Gibson et al. (1993) found no effects of small mammals on grassland community structure, to avoid any potential bias we omitted data from eighteen of the 0.25-m^2 plots with obvious rodent disturbances (i.e. visible soil disturbances) from our analyses.

One of the four-year burned watersheds was last burned in 2001 and the other in 2004; consequently the watersheds were in different phases of the fire cycle when data were collected. This may affect short-term variables, such as soil microclimate, light availability, soil N availability, and ANPP. In addition, green-up occurs earlier in the growing season following a spring fire due to removal of the litter layer, but maximum canopy density occurs in July (Turner and Knapp 1996) and maximum plant biomass is generally reached in late-July to early-August (Briggs and Knapp 2001). Post-fire effects on these variables after the first year are minimal as litter and standing plant biomass accumulates and light levels diminish at the soil surface (Knapp and Seastedt 1986). The major effects of burning on plant community structure and diversity reflect the cumulative effect of the long-term fire regime more so than individual fire events (Knapp et al. 1998a). In our study, the four-year burned watersheds were significantly different from each other for variability in light availability only ($p < 0.001$, $F_{1,3} = 12.89$; data not shown), while they did not differ for all other variables measured. This suggests that light variability reflected near-term drivers such as the removal of surface detritus by recent fire, whereas plant community structure represented the integrative effects of the longer-term fire regime. Thus, we felt comfortable treating the sampling units in both watersheds as replicates of the four-year burn treatments in subsequent analyses (below).

Measurements

In each of the 384 0.25-m^2 plots, plant species composition was measured in both mid-June and mid-August 2004 to capture peak cover values for both cool- and warm-season species. Percent cover of each species was estimated visually in 1% cover class intervals up to 5% and then 5% intervals thereafter. For each species, the maximum cover value from the combined spring and summer surveys was used in subsequent analyses.

Relative inorganic soil N availability was quantified using ca 60-day in situ incubations of ion exchange resin bags (Binkley and Matson 1983). Resin bags were constructed of nylon stockings, and contained 10 g of a 1:1 mixture of cation and anion exchange resins, preloaded with H^+ and Cl^-, respectively. One resin bag per 0.25-m^2 plot (total of 384 bags) was buried at a 10-cm depth on 14 June and retrieved on 13 August. To avoid soil disturbances in the plots, resin bags were buried at a fixed location (irrespective of vegetation type) on the border of each plot. 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 2M KCl and concentrations of NO_3^- and NH_4^+ were determined colorimetrically. Only NO_3^- values were used in statistical analyses because, like Baer et al. (2004) we found that resin-collected NO_3^- but not NH_4^+ was affected significantly by our treatments. We omitted 7 of 357 recovered resin bags from the analyses, because resin-collected NO_3^- values were more than 1000 times average, presumably as a result of recent urine and dung deposition in grazed plots or disturbance by small animals in ungrazed plots. However, results of analyses with and without these values were qualitatively similar.

Plot-level light availability was measured as percent light penetration to the soil surface, i.e. canopy transmittance, 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, set to measure across a 62.5 cm length, at the end of June, July and August, between 11:00 h and 15:00 h on clear days. Two diagonal ground level measurements per plot were averaged and one measurement was taken above the canopy. Here, we present data from August only, as this was the period of peak aboveground biomass.

Data analysis

Plant community structure in each plot was assessed using the following indices (Magurran 2003): species richness (S) was the total number of plant species per plot; Shannon's diversity index (H′) was calculated as $H' = -\Sigma p_i \ln(p_i)$ where p_i is the relative cover of species i. Evenness (E) was calculated as $E = \frac{H'}{\ln(S)}$; and Simpson's dominance index (D) was calculated as $D = \Sigma \frac{n_i(n_i - 1)}{N(N - 1)}$ where n_i is the cover of species i and N is the total cover.

Community heterogeneity in each 2×3 m sampling unit was calculated as the percentage dissimilarity (PD) in species composition among all possible comparisons of the 12 plots within a sampling unit: $PD = 1 - PS$ and $PS = 1 - 0.5\Sigma_{i=1}^{S}|p_a - p_b|$ where PS is the percent similarity, p_a is the proportional cover of species p in plot a, and p_b is the proportional cover of species p in plot b. Variability in resources was expressed as the percentage coefficient of variation (CV) per sampling unit.

The effects of the grazing and burning treatments on plant community composition and resource availability were tested using a mixed model ANOVA with the metrics of community structure and heterogeneity, resource availability, and the CVs for N and light availability as response variables. The paired grazed and ungrazed sampling units were blocked to control for smaller-scale variation (e.g. soils, aspect, etc.). Although four grazed/ungrazed sampling units (blocks) were nested within each of four watersheds and thus the fire treatments, the sampling units were considered independent experimental units. We believe this is justified based on 1) the size and heterogeneity of the

watersheds (ca 93 ha), 2) the heterogeneity of fire and grazing effects across the landscape, and 3) the distance between individual exclosures (ca 1 km). We believe that this distance is sufficient to achieve independence with respect to responses to burning and grazing, and is likely a more realistic approach than trying to impose fire and grazing treatments on smaller, replicated plots. This allowed us to treat grazing and fire treatments as fixed factors and block as a random nested factor. For these analyses data from the 12 small (0.25-m^2) plots within a sampling unit were averaged (except for PD and resource variability) and log-transformed when necessary to improve normality and homogeneity of variances.

We used multiple regression analysis to test whether plant community heterogeneity was related to changes in resource availability and variability or to changes in plant community structure. Previous studies have shown that dominance is a key factor affecting community structure in this tallgrass prairie ecosystem (Collins et al. 1998, Hartnett and Fay 1998). Therefore, we used the CV for plant community dominance, resource availability, resource variability as predictor variables and plant community heterogeneity (PD) as a response variable.

Statistical analyses were performed using SAS statistical software 8.0.

Results

Plant community responses

Significant interactions between fire frequency and grazing were found for diversity ($p = 0.043$, $F_{1,14} = 4.95$), evenness ($p = 0.002$, $F_{1,14} = 13.58$) and dominance ($p = 0.005$, $F_{1,14} = 11.35$), due to the significant impact of annual burning on the plant community in ungrazed areas only. Annually burned, ungrazed areas were dominated by one or a few abundant C_4 grass species, while grazing reduced the cover of dominant grasses and enhanced cover of forbs ($p = 0.013$, $F_{1,14} = 8.07$, data not shown). Consequently, dominance was highest in annually burned plots ($p = 0.011$, $F_{1,14} = 8.58$; Fig. 1D), which resulted in decreased diversity ($p = 0.013$, $F_{1,14} = 8.11$; Fig. 1B) and evenness ($p = 0.009$, $F_{1,14} = 9.17$; Fig. 1C) in these plots. Fire frequency had no effect on plant species richness ($p = 0.173$, $F_{1,14} = 2.06$; Fig. 1A). In contrast, grazing decreased dominance at the 0.25-m^2 plot scale ($p < 0.001$, $F_{1,14} = 131.68$; Fig. 1D) leading to higher species richness ($p < 0.001$, $F_{1,14} = 83.09$; Fig. 1A), diversity ($p < 0.001$, $F_{1,14} = 110.96$; Fig. 1B) and evenness ($p < 0.001$, $F_{1,14} = 96.17$; Fig. 1C).

Spatial heterogeneity in plant community composition, expressed as mean percentage dissimilarity (PD) among plots within a 2×3 m sampling unit, was not affected by fire frequency ($p = 0.843$, $F_{1,14} = 0.04$; Fig. 2) nor by a fire-grazing interaction ($p = 0.126$, $F_{1,14} = 2.64$). However, dissimilarity in plant community composition was higher in grazed compared to ungrazed sampling units ($p = 0.002$, $F_{1,14} = 14.91$).

Responses of key resources

Amounts of resin-collected soil NO_3^- were not affected by fire frequency ($p = 0.196$, $F_{1,14} = 1.85$) nor by a fire-grazing interaction ($p = 0.449$, $F_{1,14} = 0.61$), but grazing enhanced mean amounts of resin-collected NO_3^- ($p < 0.001$, $F_{1,14} = 33.34$; Fig. 3). Neither grazing ($p = 0.6584$, $F_{1,14} = 0.20$), nor fire frequency ($p = 0.3228$, $F_{1,14} = 1.05$), nor their interaction ($p = 0.4575$, $F_{1,14} = 0.58$) had a significant influence on NO_3^- variability (Fig. 3).

Mean light availability in August was highest in grazed areas ($p < 0.001$, $F_{1,14} = 112.14$; Fig. 3), but was not affected by fire frequency ($p = 0.837$, $F_{1,14} = 0.04$) or a

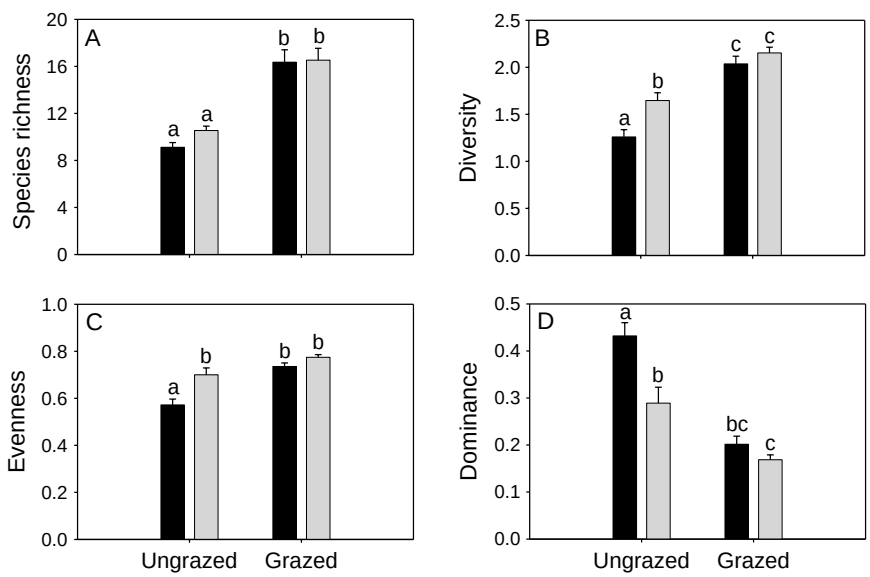

Fig. 1. The effects of grazing and burning regime on (A) species richness, (B) diversity (Shannon's index), (C) evenness and (D) dominance (Simpson's index). Black bars represent annually burned sites and grey bars represent sites burned once every four years. There were eight sampling units of 2×3 m per treatment ($n = 8$). Error bars are $+1$ SE of the means. Different letters above bars indicate significant differences at $p \leq 0.05$.

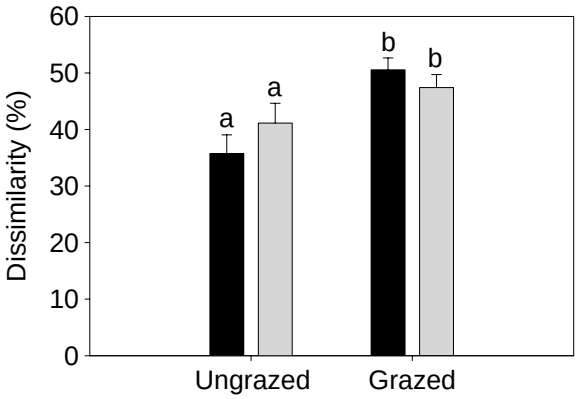

Fig. 2. Heterogeneity in plant community composition. Black bars are annually burned sites and grey bars are sites burned once every four years. There were eight sampling units of 2×3 m per treatment ($n = 8$). Error bars are $+1$ SE of the means. Different letters above bars indicate significant differences at $p \leq 0.005$.

fire-grazing interaction ($p = 0.909$, $F_{1,14} = 0.01$). Variability in light availability in August was neither affected by grazing ($p = 0.484$, $F_{1,14} = 0.52$), nor by fire frequency ($p = 0.671$, $F_{1,14} = 0.19$), nor by an interaction between grazing and fire treatment ($p = 0.109$, $F_{1,76} = 2.93$; Fig. 3).

Relationship between resource variability and plant community heterogeneity

In the multiple regression analysis, variation in dominance of plant species (CV of dominance) was positively related to plant community heterogeneity ($p < 0.001$, $F_{1,23} = 30.81$, $r^2_{model} = 0.75$); whereas neither mean NO_3^- and light availability nor variability in NO_3^- and light availability showed a significant relationship with community heterogeneity. Thus, community heterogeneity was found to increase with increasing variation in dominance only suggesting that fire- or grazing-induced changes in resource variability have little direct effect on plant community heterogeneity in this grassland, at least at the scales measured in this study.

Discussion

Our results show that grazing and annual burning had opposite effects on small-scale (0.25-m^2) plant community structure. In accordance with our hypothesis, grazing reduced dominance by a few species of grasses while it increased species richness, diversity, evenness and heterogeneity at the plant neighbourhood scale. In contrast, annual burning increased dominance thereby decreasing small-scale diversity and evenness, with the effect of annual burning stronger in ungrazed sites. However, neither species richness nor plant community heterogeneity was affected by fire frequency or a fire-grazing interaction. Grazing increased mean availability of both soil NO_3^- and light, but small-scale spatial variability of these resources was largely unaffected by fire frequency or a fire-grazing interaction. Moreover, the degree of plant community heterogeneity was not related to availability or spatial variability of resources, but was related only to small-scale variation in community dominance.

Plant community responses

The effects of grazing on small-scale plant community structure observed in this study are consistent with previous studies in a variety of grassland ecosystems and at a variety of scales (Bakker et al. 1983, 2003, Collins 1987, Berg et al. 1997, Collins et al. 1998, Bos et al. 2002, Frank 2005,

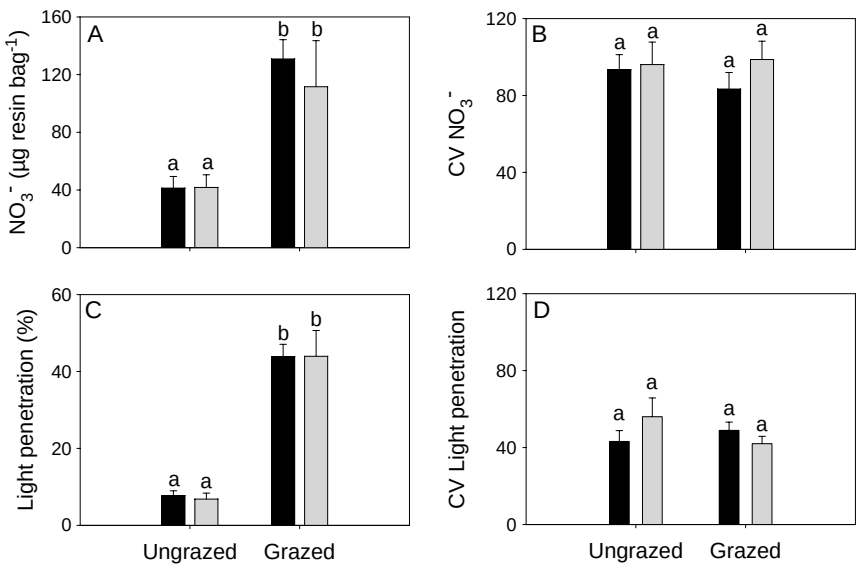

Fig. 3. The effects of grazing and burning regime on mean nitrate availability (A) light availability (C), and coefficients of variation (CV) for nitrate (B) and light penetration (D). Light availability is expressed as the percentage of full sunlight transmitted to the soil surface. For light availability and variability data for August (peak biomass) are shown. Black bars are annually burned sites and grey bars are sites burned once every four years. There were eight sampling units of 2×3 m per treatment ($n = 8$). Error bars are $+1$ SE of the means. Different letters above bars indicate significant differences at $p \leq 0.001$.

Collins and Smith 2006). Exclusion of grazers generally increases the dominance of a few species that can eliminate other species through competitive interactions (Knapp and Seastedt 1986, Belsky 1992, Fahnestock and Knapp 1993, Olff et al. 1997). In tallgrass prairies, bison preferentially graze dominant C_4 grasses (Fahnestock and Knapp 1993, Damhoureyeh and Hartnett 1997), which enhances forb abundance and increases species richness and diversity (Gibson and Hulbert 1987, Glenn and Collins 1990, Turner et al. 1995).

The small-scale effects of annual burning were opposite of those of grazing. Annual spring fires reduced diversity and increased the dominance of C_4 grasses, with the effect of burning being more pronounced in sites that were not grazed by bison. This concurs with larger-scale studies in tallgrass prairies showing that frequent burning increases the abundance of C_4 grasses and reduces the cover of forbs as well as overall species richness (Collins 1987, Gibson and Hulbert 1987) and that grazing can prevent the loss of diversity under frequent burning (Collins et al. 1998).

The development of plant community heterogeneity can either be enhanced or decreased by grazing depending on, for example, grazing intensity and scale of measurement (Bakker et al. 1983, Adler et al. 2001, Fuhlendorf and Engle 2001, 2004). Collins and Smith (2006) found that bison grazing in tallgrass prairies decreased heterogeneity at spatial scales larger than 10-m^2, which contradicted the prediction that heterogeneity would be enhanced at small spatial scales as a result of variable grazing intensity in space and time through selective foraging decisions (Adler et al. 2001). However, the smallest scale of measurement (10-m^2) in the study of Collins and Smith (2006) was larger than a typical feeding station and thus could include both grazed and ungrazed patches. It has been shown that large herbivores are able to specifically select for fine-scale food patches ($<$0.25-m^2), with altered forage quality and quantity (Steinauer and Collins 2001). Consequently, grazing could still enhance heterogeneity, but on much smaller scales than 10-m^2. Indeed, our results suggest that grazing by bison enhances heterogeneity (PD) in the plant community at a very small scale of measurement (0.25-m^2), which concurs with studies in other grasslands showing that grazing by large herbivores induces and maintains micropatterns in the vegetation (Bakker et al. 1983, Berg et al. 1997).

In contrast, neither fire frequency nor a fire-grazing interaction affected small-scale plant community heterogeneity. However, we hypothesized that fire-grazing interactions would lead to the greatest heterogeneity, because grazing is a selective process, whereas annual burning is non-selective and has been shown to homogenize community structure and ecosystem processes in tallgrass prairies (Hobbs et al. 1991, Blair 1997, Johnson and Matchett 2001, Collins and Smith 2006). Therefore, we expected the combination of grazing and four-year fire cycles to result in the greatest heterogeneity. Moreover, previous studies in tallgrass prairie found that larger-scale heterogeneity ($>$10-m^2 to hectares) was explained by interactions between burning and grazing regimes, even when comparing annual versus four-year burns which are both frequent fire cycles (Fuhlendorf and Engle 2004, Collins and Smith 2006). In contrast, we found no evidence for an interactive effect of fire and grazing on community heterogeneity at small scales. Therefore, we conclude that at the scale of measurement used in our study (0.25-m^2), the direct effects of a non-selective event such as burning were limited, while at larger scales the effects of fire frequency and interactions with grazers become apparent.

Responses of key resources

Both mean soil N availability and light levels were much higher in grazed compared to ungrazed sites, which is consistent with previous studies reporting enhanced resource levels with grazing in North American tallgrass prairie (Johnson and Matchett 2001, Bakker et al. 2003), and other temperate grasslands (Frank et al. 2000), as well as African savannas (Seagle et al. 1992, McNaughton et al. 1997). Herbivores can increase net N mineralization rates and levels of inorganic soil N (Seagle et al. 1992, Johnson and Matchett 2001) by consuming organic N in plant biomass and by returning labile forms of N to the soil (Ruess and McNaughton 1988). In contrast, fires generally decrease soil N availability and variability in grasslands (Hobbs et al. 1991, Ojima et al. 1994, Blair 1997, Johnson and Matchett 2001), although we did not find a significant difference between annually burned and four-year burned sites on resin-collected NO_3^- in this study. However, it is important to point out that reduced soil N availability with more frequent burning has been observed in ungrazed grasslands; other studies suggest that grazers can offset this effect (Johnson and Matchett 2001). Moreover, fire frequency had no effect on light levels in this study, although we expected reduced light levels in four-year burns as a result of litter accumulation (Knapp and Seastedt 1986). This may be because one of the four-year burned watersheds was burned in the year our study was carried out, while the other watershed was not. Fires are known to decrease the litter layer and hence enhance light availability. In the watershed burned in the year that this study was carried out no litter had accumulated, which may explain why light levels were not different from annually burned sites.

Small-scale spatial variability of resources was neither affected by the burning regime nor by the grazing treatment. In contrast, in Yellowstone National Park removal of grazers increased small-scale patchiness (10–200 cm) in soil N (Augustine and Frank 2001), while grazed sites showed an extremely fine-scale resource variability ($<$10 cm). However, it could be that our treatments did affect spatial patchiness of resources without affecting the coefficient of variation. Additional studies incorporating finer-scale sampling and the use of spatial statistics would be required to address this possibility. Also, according to Augustine and Frank (2001) resource heterogeneity may occur on a much smaller scale than used in our study. Finally, bison were expected to enhance resource variability through a patchy distribution of dung and urine, but this effect may be dependent on their density. Augustine and Frank (2001) estimated that with low elk densities in Yellowstone National Park (0.11–0.16 elk ha^{-1}) urine covered only 2.5% of the area, while in cattle-grazed pastures (3 cattle ha^{-1}) Afzal and Adams

(1992) estimated that 27% of the area was affected by urine. At KPBS bison stocking rates were relatively low ($\sim$0.25 bison ha^{-1}), and therefore it may be that the spatial extent of the effect of their urine on soil N variability was relatively small.

Relationship between resource variability and plant community heterogeneity

In our study we did not find a relationship between resource availability or variability and plant community heterogeneity, but community heterogeneity was related to variability in small-scale dominance by plant species, such as C_4 grasses. Thus, it seems likely that grazing directly affects community structure by altering patterns of dominance at small scales, where individual grazing patches or feeding stations may enhance heterogeneity. In contrast, previous studies suggested a link between fine-scale resource heterogeneity and plant species richness and diversity (Augustine and Frank 2001), and at larger spatial scales both resource and plant community heterogeneity increased with grazing (Bakker et al. 2003). It may be that there is a considerable amount of inherent heterogeneity in resource distribution at the small scale examined in the present study, which is neither explained by grazing nor by fire frequency, but which may fall within the tolerance levels of the dominant species (Baer et al. 2004). Conceivably, other resources such as soil P or water might also play a role in determining heterogeneity in the vegetation, although the relationship between grazing, heterogeneity in these resources and plant community structure will require further study.

In conclusion, although fire, grazing and fire-grazing interactions are often cited as important determinants of large-scale spatial patterns in grasslands, the relative importance of these factors at smaller-scales is not well understood. To our knowledge this is the first study to examine the long-term, cumulative effects of grazing, fire, and their interactions on small-scale resource availability and heterogeneity and small-scale plant community structure. We found that grazing was the primary determinant of fine-scale resource availability, species composition, and plant community heterogeneity in this tallgrass prairie. Grazing increased resource availability, as well as species richness, diversity and community heterogeneity. We did not find a relationship between small-scale variability or availability of resources and community heterogeneity, which suggests that at the plant neighbourhood scale, the main effect of grazing on community structure is mediated directly through the plant community via alterations in the degree of dominance by a few plant species rather than through changes in the abundance or variability of key resources. Thus, grazing appears to act directly on fine-scale plant community structure by reducing dominance rather than indirectly through changes in resource abundance and variability.

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