



Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie

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Disturbance; Fire; Grassland; Grazing; Plant community structure; Species diversity

Nomenclature

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Abstract

Questions: How do fire and grazing by bison affect the composition and structure of tallgrass prairie plant communities and their temporal stability? Are these responses modulated by topographic location?

Location: Konza Prairie Biological Station, Kansas, USA.

Methods: Plant community composition was monitored in permanent plots in native grassland sites receiving different long-term prescribed burning and bison grazing regimes across a topographic gradient (lowlands, slopes, uplands) following 20 yr of variable burning treatments and 13 yr of grazing by bison. A combination of multivariate analyses was used to determine how community structure, life forms and individual species responded to the accumulated effects of long-term fire and grazing by native bison in upland, slope and lowland soils.

Results: Species diversity was maximized in sites that were infrequently burned and grazed by bison with the strongest response on infrequently burned slope sites, while diversity was lowest on frequently burned ungrazed sites and on frequently burned slope sites. In general, grass cover was highest in infrequently burned ungrazed sites and lowest on frequently burned grazed sites, while forb richness was highest in infrequently burned and grazed sites. Community response to fire and grazing differed across the topographic gradient. In general, frequent burning favoured C₄ grasses, which reduced the abundance of C₃ forbs, especially in lowland sites. Responses of dominant grasses and forbs to fire and grazing varied depending on topographic position. Community stability was positively correlated with species richness.

Conclusions: Overall, we found that fire and grazing are the main determinants of plant community composition and structure in this grassland system, but that topography mediates these effects. A combination of bison grazing and periodic fire is necessary to maximize diversity and community stability across this native grassland landscape.

Introduction

Ecological communities change over space and time in response to the interaction of biotic and abiotic processes (Wu & Loucks 1995; White & Jentsch 2001; Smith et al. 2009). Biotic factors such as species interactions (e.g. competition, herbivory, predation), dispersal, colonization and biogeography influence community structure and composition, while abiotic forces that influence communities include spatial and temporal variation in environmental drivers (e.g. climate, soils, disturbance, N deposition; McNaughton 1983; Sousa 1984; Stevens

et al. 2004). The interactions between various biotic and abiotic processes are complex and dynamic over time, and in particular, initial patterns may not reflect long-term responses and dynamics to biotic or abiotic drivers. Therefore, long-term data and experimental manipulations are needed to assess how multiple drivers interact to affect plant community structure over the long term. Indeed, determining how interactions among biotic and abiotic processes affect communities remains a key ecological challenge as human activities continue to modify ecosystems globally. Understanding such interactions would increase our ability to predict the response of

plant communities to both natural and anthropogenic environmental change in the future.

In grasslands, plant communities are primarily influenced by a combination of biotic and abiotic factors including fire (Sauer 1950; Wright & Bailey 1982; Gibson 1988; Collins & Gibson 1990; Noy-Meir 1995; Bowman 1998; Collins & Steinauer 1998), grazing (Axelrod 1985; Milchunas et al. 1998; Vinton & Hartnett 1992; Vinton et al. 1993; Noy-Meir 1995; Cingolani et al. 2003), climate variability (Risser et al. 1981; Anderson 1982, 2008; Sousa 1984; Knapp 1985; Gibson & Hulbert 1987; Briggs & Knapp 1995; ; Hobbs et al. 2007) and soils/topography (Risser et al. 1981; McNaughton 1983; Abrams & Hulbert 1987; Gibson & Hulbert 1987; Coppedge et al. 1998; Cingolani et al. 2003). These factors interact over multiple spatio-temporal scales to influence community structure (Fuhlendorf & Engle 2001, 2004) primarily by affecting the availability of resources such as water, nitrogen and light (Jobbagy et al. 1996; Burke et al. 1998; Cingolani et al. 2003), which in turn affect the abundance and distribution of species, as well as interactions among species. Although the effects of these drivers have been studied extensively in many grasslands worldwide, their long-term interactive effects on plant community structure and dynamics, particularly in mesic tallgrass prairie, remain poorly documented.

In North American tallgrass prairie, fire and grazing by bison were the primary disturbances historically (Risser et al. 1981; Collins 1987), and their independent effects, in particular, on this system have been relatively well studied (Collins 1987, 1992; Gibson & Hulbert 1987; Collins et al. 1998; Towne et al. 2005). Together, fire and grazing are hypothesized to maximize diversity in tallgrass prairie ecosystems (Collins 1987; Collins et al. 1998), although most studies are short-term (less than 3 yr) or use data that may not include the cumulative impacts of these disturbances over the long term. However, understanding how combinations of key disturbances over the long term affect communities is essential to yield insights into how different species and life forms respond to extrinsic controlling factors (i.e. disturbances, climate, etc.) that also vary in time.

Not only have grasslands been a focal ecosystem for understanding the impacts of disturbance in ecological communities, they have also played a key role in quantifying temporal stability and for documenting how species diversity regulates community resistance and resilience to disturbance (Tilman 1999). In particular, research in grasslands has demonstrated a positive relationship between species richness and temporal stability (Hector et al. 1999; Tilman et al. 2006). However, most of these studies are based on data from small experimental plots. It is not clear how well these patterns hold at larger scales in native veg-

etation that is responding to long-term temporal variation in fire frequency, grazing pressure and interannual climate variability.

Tallgrass prairie generally consists of a few matrix-forming C_4 grasses and many interstitial forb species (Collins & Glenn 1991). The responses of a few common species to fire and/or grazing have been studied (Howe 1994; Pfeiffer & Hartnett 1995; Damhoureyeh & Hartnett 1997, 2002; Silletti & Knapp 2002), but most research has focused on community- (e.g., species diversity; Vinton et al. 1993; Hartnett et al. 1996; Collins et al. 1995; Spasojevic et al. 2010) and ecosystem-level responses (e.g. net primary production; Briggs & Knapp 1995; Fay et al. 2003) to disturbance. In general, frequent spring fire tends to increase above-ground production by a few dominant grass species, which results in lower species richness and diversity of forbs via competition for light (Hartnett et al. 1996). In the absence of grazing, accumulated grass biomass provides fuel for high frequency (annual) burning. Both bison and cattle preferentially graze on recently burned sites where grasses are abundant (Fuhlendorf & Engle 2001). Selective grazing of the dominant matrix grasses by bison (*Bos bison*) in burned areas results in a concomitant increase in forb cover, which increases species richness and diversity, but may lower fire frequency. Lower fire frequency makes the site less desirable for grazing by these grass specialists. These interactions are summarized in Fig. 1. Although these general trends are fairly well known, how they are mediated by edaphic properties (i.e. soil type or topographic position) and fire frequency is uncertain. For example, lowland prairie supports greater grass biomass and lower species diversity than upland prairie (Gibson & Hulbert 1987; Buis et al. 2009) and thus the response of lowland areas to variable fire and grazing may differ from that of upland sites that are

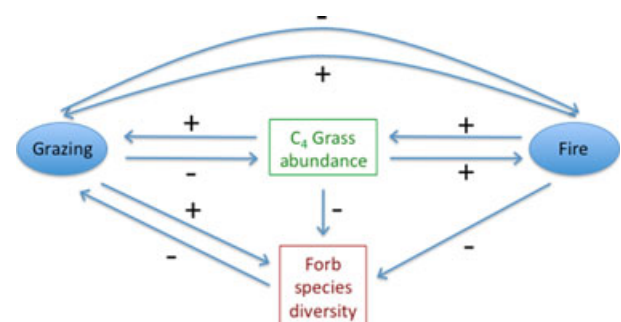


Fig. 1. Conceptual diagram showing the direct and indirect effects of fire and grazing on community structure in tallgrass prairie. The main impact of fire and grazing is on the abundance of C_4 grasses, which controls species diversity. Because C_4 grasses are most abundant on lowland soils, we hypothesize that these relations weaken from lowland to upland prairie.

more water- and nutrient-limited (Gibson & Hulbert 1987; Blair 1997).

Gibson & Hulbert (1987) used data from mesic grassland at the Konza Prairie Biological Station (KPBS) in northeastern Kansas, USA, to determine the interactive effects of fire, topography and year-to-year variation in climate on vegetation over the first 5 yr of an on-going, long-term, landscape-scale field experiment (1981–1985). These analyses occurred prior to the reintroduction of bison to this ecosystem. They found that time since last fire was the principal determinant of vegetation composition, and that cover of grasses decreased with time since fire, whereas cover of forbs and woody species increased with time since fire. Topography was the second most important gradient of variation; richness and diversity were higher on upland compared to lowland soils. Interactions between all three environmental drivers had differential effects on the abundance of individual species. However, as noted above, initial patterns and responses may not reflect long-term trends, and thus it is time to re-evaluate how fire, grazing and topography interact in this mesic grassland.

The purposes of our research were to re-examine and extend analyses of the long-term interactive effects of fire frequency and topography (soil type) on individual species, life forms and plant community structure following 20 yr of fire treatments coupled with 13 yr of grazing by bison in this native mesic grassland. Specifically we addressed the following hypotheses: (1) the impact of fire and grazing by bison on community structure differs in upland, slope and lowland sites; (2) C_4 grasses increase in response to fire and decrease in response to grazing whereas forbs do the opposite across all three topographic positions; (3) responses of dominant grass and forb species to fire and grazing vary across the topographic gradient; and (4) species richness increases community stability across all fire and grazing treatments. To test these hypotheses, we used data from an extensive sampling campaign in 1997 across 40 sites that differed in cumulative effects of different combinations of fire frequency (1, 2, 4, 20-yr burn frequencies), grazing (with or without bison) and topographic location (upland, slope, lowland). In addition, we used a temporal (1993–2000) data set of 32 sites varying in fire frequency, topographic position and grazing to determine the relationship between species diversity and temporal stability in a complex environmental context. All data were collected in a similar way to those in Gibson & Hulbert (1987). However, our data were collected after many more years of fire treatments and we now include sites currently grazed by bison, as well as sites located on slopes, in addition to upland and lowland soils.

Methods

Study sites

This study was conducted at the Konza Prairie Biological Station (KPBS), a 3487-ha native tallgrass prairie located in the Flint Hills of Kansas, USA. KPBS is a 36-km² topographically diverse area of native tallgrass prairie that has been divided along watershed boundaries into 64 fire management units, ranging in size from 12 to 136 ha. Replicate management units at KPBS have been experimentally subjected to 1, 2, 4 and 20-yr intervals of fire since 1972 (Knapp et al. 1998). In 1987 30 bison were introduced to a 1012-ha area of KPBS where they have free access to management units subjected to the above fire treatment intervals (these management units are referred to as 'grazed', while management units without bison are referred to as 'ungrazed'). Although only one portion of the landscape is grazed, the long-term nature of the treatments, along with the need to have bison freely select where they graze across topographic gradients and fire treatments, make this the optimal ecological design for fire-grazing research at this spatial scale.

Herd size was allowed to increase rapidly to 200 animals in order to maintain a grazing rate of ca. 25% removal of above-ground production each year (Towne 1999). By comparison, commercial cattle operations in the region generally graze about 50–60% of above ground production. The topographic variation at KPBS ranges from 320 to 444 m a.s.l., which allows the inclusion of three topographic positions (soil types) within each management unit – upland (Florence soil), slope and lowland (Tully soil) – in this study. Upland Florence soils are shallow, rocky, cherty silty clay loams, while lowland Tully soils are deeper, non-rocky silty clay loams. Slopes vary from shallow and rocky near the uplands to deeper and finer textured where they grade into lowland areas. Although lowlands are generally more productive than uplands, long-term observations at KPBS indicate that bison do not appear to prefer one topographic position to the other (B.L. Brock, J.M. Briggs and L.C. Johnson, unpublished data).

The vegetation at KPBS is predominantly native unplowed tallgrass prairie, with some woody vegetation in gallery forests along drainages (Knight et al. 1994) as well as in infrequently burned sites (Briggs et al. 2002). The grassland is dominated by a matrix of C_4 perennial grasses, including *Andropogon gerardii*, *Sorghastrum nutans*, *A. scoparius* and *Panicum virgatum*, although interstitial forb species comprise more than 75% of the species richness (Towne 2002). Common perennial forbs include *Aster* spp., *Kuhnia eupatorioides*, *Salvia azurea* and *Solidago* spp.

Vegetation sampling

We used two data sets for our analyses. The first (hereafter referred to as the 'spatial data set') was collected in 1997 from 40 upland, slope and lowland sites located among 16 management units subjected to 1, 2, 4 and 20-yr fire frequencies crossed with two grazing treatments (grazed or not grazed by bison) (Collins et al. 2002). In most cases, there are two replicate management units for each fire frequency per grazing treatment, resulting in 20 grazed and 20 ungrazed sites. The second (hereafter referred to as the 'temporal data set') includes long-term data from permanent plots that were collected over 8 yr (1993–2000) in upland, slope and lowland sites located among six management units subjected to 1, 4 and 20-yr fire frequencies crossed with two grazing treatments (grazed or not grazed by bison). The temporal data set contains 24 sites that are a subset of the spatial data set (See App. S1) that have been sampled annually from 1993 through 2000. Again, there are two replicates of each fire/grazing/soil type combination. We used the spatial data set to test for long-term community, life form and individual species responses to the cumulative impacts of fire frequency, grazing and topography. We used the temporal data set to assess changes in community composition over time, as well as community and life form temporal stability in relation to fire frequency, grazing and total richness.

Spatial and temporal data were collected using the same methods, following Gibson & Hulbert (1987). In each site, vegetation in permanent plots was sampled in the spring (May) and autumn (late Aug) of each year to capture within-season vegetation dynamics. The maximum cover value for each species was used in all analyses (May or Aug sample). Vegetation was sampled in five 10-m² circular quadrats equally spaced along each of four 50-m transects in each topographic position (upland, slope, lowland) for a total of 20 quadrats per topographic position (site). To sample the full variation on slopes, two transects were located near the upper crest and two near the foot, where soils grade into lowlands at each site. Cover of species in each quadrat was estimated using the Daubenmire scale (1 = 1%, 2 = 2–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–95%, 7 = 95–100%). Abundance of each species was determined by converting the Daubenmire scale to the midpoint of the cover range and then averaging by species across the 20 quadrats at a site (see Collins & Smith 2006).

Data analysis

In each of the following analyses, sites burned every 1–2 yr were considered as frequently burned while those burned every 4–20 yr were considered as infrequently burned

(Seastedt et al. 1991). Actual burn frequency (which took into account wild fires, etc.) is reported as the number of times burned since 1980, because some of the management units were not part of KPBS prior to that year.

Independent samples *t*-test and ANOVA were used on the spatial data to assess the effects of fire frequency, grazing and soil type on species richness and diversity (main effects averaged over other treatments). Species richness is the number of species found in the 20 quadrats at each fire/grazing/topographic position (site). Species diversity for each site was calculated using Shannon's index ($H' = -\sum(p_i \times \ln p_i)$), where p_i is the relative abundance of species i . Species diversity was regressed upon the number of times a site was burned (1980–1997) and over the percentage cover of *A. gerardii*. Multivariate analysis of variance (MANOVA) was used on the spatial data to determine whether there were any separate or interactive effects of fire, grazing and soil type on the cover and richness of different life forms, C₃ and C₄ species, and on overall species richness and diversity. These multivariate tests were followed up with univariate tests (between-subject tests, followed by the Bonferroni correction) in order to obtain estimated marginal means (App. S2 and S3). Percentage cover of different life forms and plants with different photosynthetic pathways were log₁₀-transformed and then regressed upon the number of times a site was burned (1980–1997). MANOVA was also used on the spatial data to evaluate how the abundance of common species responded to fire, grazing and soil type. Again, this multivariate test was followed by univariate tests (between-subject tests, followed by the Bonferroni correction) in order to obtain estimated marginal means (App. S4). Species included the four dominant grasses (*Andropogon gerardii*, *A. scoparium*, *Panicum virgatum* and *Sorghastrum nutans*), four common forbs (*Artemisia ludoviciana*, *Aster ericoides*, *Kuhnia eupatorioides* and *Salvia azurea*) and three woody species (*Amorpha canescens*, *Rosa arkansas* and *Symphoricarpos orbiculatus*). Finally, a permutational multivariate analysis of variance (PERMANOVA) using the Bray–Curtis similarity metric was used on the spatial data (1997) in order to assess differences in plant community composition resulting from the main effects (fire, grazing, soil type) and interactions between them. All statistical analyses were done with SPSS (SPSS 18.0 for Windows), except for the PERMANOVA on the spatial data, which was done using PRIMER plus PERMANOVA (Anderson 2001; McArdle & Anderson 2001).

Temporal data were used to evaluate the temporal stability of the plant community. Stability was measured as the ratio of mean abundance (percentage cover) to its temporal standard deviation (Tilman 1999). Larger values indicate greater temporal stability. We calculated the mean to variance ratio for C₃ forbs and for all species combined.

This value was regressed upon total species richness in order to determine how diversity influences community stability. We used MANOVA to determine how fire, grazing and soil type influence temporal stability of C_3 forbs, C_4 grasses and the entire plant community over time. This multivariate test was followed with univariate tests (between-subject tests, followed by the Bonferroni correction) in order to obtain estimated marginal means (App. S5). Only the upland and lowland soil types were included in analyses on temporal data because there was a lack of data from frequently burned sites on slope soils.

Detrended correspondence analysis (DCA; with rare species – those found in less than 10% of sites – removed and the remaining rare species down-weighted) was also used on the temporal data in order to assess differences in plant community composition of sites with different fire frequencies, grazing treatments and soil types, and to determine trajectories of change over time. Species and life form codes are given in App. S8. DCA of the temporal data was performed with PCORD (PCORD for Windows, Version 5.10).

Results

Main effects

Species richness and diversity were affected by fire frequency and grazing, but not by topography (Fig. 2; App. S2). Frequently burned sites (i.e. 1–2 yr return interval) had significantly lower species richness and diversity (Table 1) than sites with lower fire frequencies (i.e. 4–20 yr return interval) when averaged across soil types and grazing treatments (Fig. 2; App. S2). In the ungrazed sites there was a negative linear relationship between species diversity and the number of times a site was burned between 1980 and 1997, but there was no relationship in the grazed sites (Fig. 3). Grazing by bison significantly increased species richness and diversity when averaged over fire frequency and soil type (Fig. 2; App. S2). Species richness and diversity did not differ significantly between soil types when averaged across fire frequencies and grazing treatments (Fig. 2).

Life forms

Cover of C_3 plants, forbs and woody species was higher on infrequently burned sites, while cover of C_4 plants was higher on frequently burned sites (Table 1; App. S3). There was a positive linear relationship between the number of times a site was burned (1980–1997) and the cover of C_4 plants and a non-linear (inverse first-order polynomial) negative relationship between number of times a site was burned and the cover of C_3 plants (Fig. 4a). There was a non-linear (inverse first-order polynomial) negative rela-

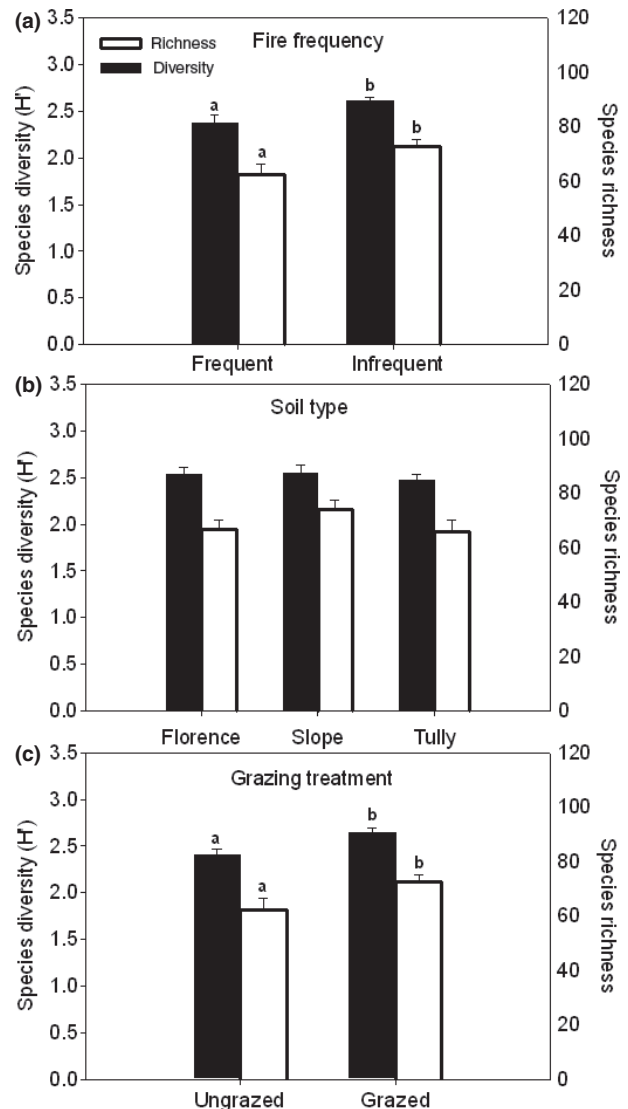


Fig. 2. Plant species richness and diversity ($H' = -\sum(p_i \times \ln p_i)$) in response to fire frequency (a), topography (soil type) (b) and bison grazing (c). Mean values ± 1 SE are presented. Bars with different letters (a, b) are significantly different ($P < 0.05$).

tionship between the number of times burned and forb cover, but there was no relationship between woody plant cover and fire frequency (Fig. 4b). Richness of C_3 plants, grasses, forbs, woody plants as well as overall richness and diversity were higher on infrequently burned sites (Table 1; App. S2). Cover of C_3 plants, C_4 plants and forbs was higher on lowland soils, while cover of woody species was greater on slopes (Table 1; App. S3). Richness of C_4 plants and grasses as well as overall diversity was highest on upland soils. C_4 richness was lowest on lowland soils, while grass richness and overall diversity were lowest on slope soils (Table 1; App. S2). C_4 and forb cover were greatest on ungrazed sites (Table 1; App. S3). Richness of

Table 1. Multivariate analysis of variance of the effects of fire frequency, soil type and grazing on percentage cover and species richness of plants with different photosynthetic pathways and different life forms. The fire column letters indicate the frequency at which a life form had the highest percentage cover or richness (F = frequent fire, I = infrequent fire), the soil column letters indicate the soil on which a life form had the highest cover or richness (P = upland, S = slope, L = lowland), and the grazing column indicates the grazing treatment under which a life form had the highest cover or richness (G = grazed, U = ungrazed). Significant interactive effects are shown in subsequent columns with significantly high (+) or low (–) values occurring in indicated treatment combinations. Superscript letters indicate level of statistical significance (a = $P < 0.001$, b = $P < 0.01$, c = $P < 0.05$).

Group	Fire	Soil	Grazing	F × S	G × S	F × G
Percent Cover						
C3	I ^a	L ^c				
C4	F ^a	L ^c	U ^b	+F × L, –I × S ^b		+F × U, –I × U ^a
Grasses						
Forbs	I ^a	L ^a	U ^b			+F × U, –F × G ^a
Woody spp.	I ^c	S ^c				
Richness						
C3	I ^a		G ^a	+I × S, –F × S ^c		
C4		P ^c	G ^a	+F × P, –F × S ^c		
Grasses	I ^c	P ^c	G ^c			
Forbs	I ^c		G ^a	+I × S, –F × S ^c	+G × L, –U × L ^c	
Woody spp.	I ^a		G ^b			+I × G, –F × U ^c
Overall Richness	I ^a		G ^a	+I × S, –F × S ^b	+G × P, –U × L ^c	
Diversity (H')	I ^a	P ^c	G ^a	+I × S, –F × S ^a		+I × G, –F × U ^b

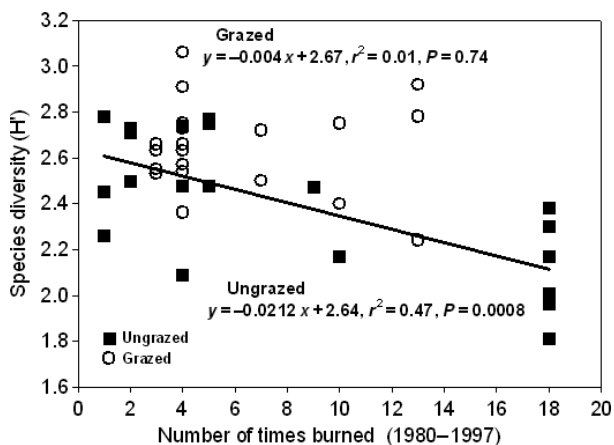


Fig. 3. Relationship between species diversity and the number of times a site was burned in grazed and ungrazed sites (1980–1997). Species diversity ($H' = -\sum(p_i \times \ln p_i)$) was calculated for 40 sites with different fire frequencies, grazing treatments and soil types.

all groups – C₃, C₄, grass, forb, woody – as well as overall richness and diversity, were significantly higher on grazed sites (Table 1; App. S2).

Fire and soil interacted such that cover of C₄ plants was greatest on frequently burned lowland sites (Table 1; App. S3). Richness of C₃ plants and forbs as well as overall richness and diversity were highest on infrequently burned slopes and lowest on frequently burned slopes. C₄ species richness was highest on frequently burned uplands. Fire and grazing interacted such that C₄ and grass cover were highest on frequently burned ungrazed sites, while woody richness, overall richness and overall diversity were all

lowest there (Table 1; App. S2). Grass cover was lowest on frequently burned grazed sites. Forb richness was highest on grazed lowland sites and lowest on ungrazed lowland sites, while overall richness was highest on grazed uplands and lowest on ungrazed lowlands.

Grass–forb interactions

Species diversity was negatively correlated with cover of *A. gerardii* in both frequently and infrequently burned sites (Fig. 5). The slopes of these relationships differed ($t = 6.99$, $df = 156$, $P < 0.0001$) indicating that *A. gerardii* had a stronger effect on richness in infrequently compared to frequently burned sites. Forb richness was positively correlated with overall richness ($P < 0.001$, $F = 3815.75$, $r^2 = 0.938$), indicating that forbs were the main group contributing to richness in this system.

Species responses

Cover of the dominant grass *Andropogon gerardii* as well as the three shrub species (*Amorpha canescens*, *Rosa arkansana*, *Symphoricarpos orbiculatus*) was unaffected by fire, grazing or soil type (Table 2; App. S4). Cover of *Sorghastrum nutans* was highest on frequently burned lowland sites. Cover of *Andropogon scoparius* was highest on frequently burned ungrazed sites. Finally, fire, grazing and soil interacted such that cover of *Panicum virgatum* was highest on frequently burned ungrazed lowlands.

Fire, grazing and soil type interactions also affected abundances of the dominant forbs (Table 2; App. S4).

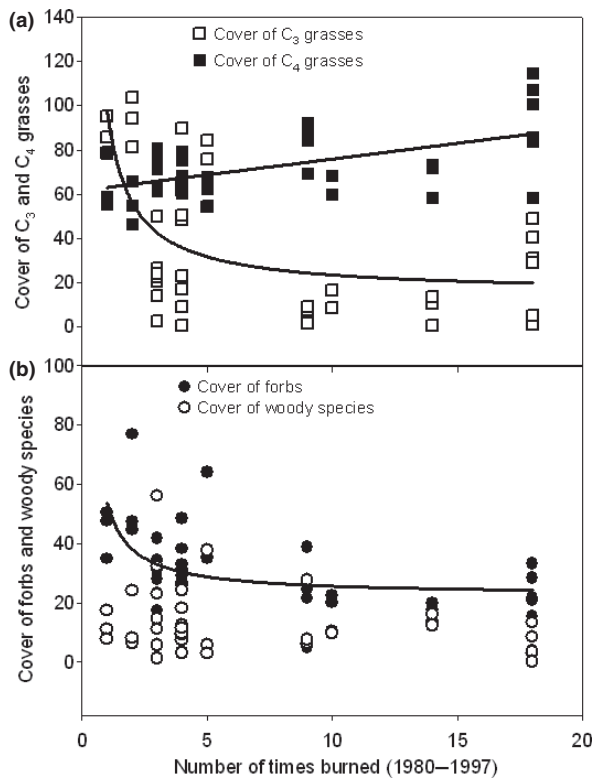


Fig. 4. Relationship between fire frequency and C₃ (non-linear inverse first-order polynomial) and C₄ (linear) plant cover (a) and fire frequency and percentage cover of forbs (non-linear inverse first-order polynomial) and woody species (b).

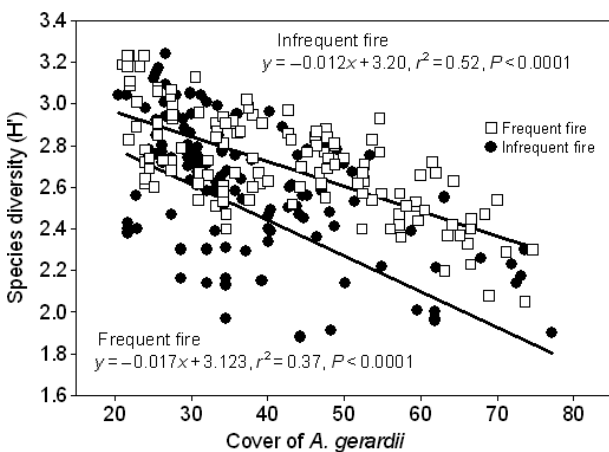


Fig. 5. Relationship between percentage cover of *Andropogon gerardii* and species diversity (H') for frequently and infrequently burned grassland based on data from 1993–2000. The slopes of the regressions are significantly different ($t = 6.99$ $df = 156$ $P < 0.0001$), indicating that cover of *A. gerardii* has a greater impact on diversity in infrequently burned grassland compared to frequently burned grassland.

Cover of *Artemisia ludoviciana* and *Aster ericoides* were greater in infrequently burned sites, while cover of *Salvia azurea* was highest on uplands. Cover of *Kuhnia eupatorio-*

ides was highest on infrequently burned slope sites and lowest on infrequently burned lowlands.

Community composition and stability

Community composition was significantly affected by the main effects of fire (PERMANOVA pseudo- $F = 4.83$, $df = 3$, $P = 0.001$), grazing (pseudo- $F = 3.14$, $df = 1$, $P = 0.011$) and topographic position (pseudo- $F = 4.60$, $df = 2$, $P = 0.001$). No significant interactions were found, although the fire times grazing interaction was nearly significant (pseudo- $F = 1.55$, $df = 3$, $P = 0.068$). *Andropogon gerardii* was the dominant species on all sites, and subordinate species, particularly forbs, drove the overall differences in community composition in response to fire, grazing and topographic position.

Detrended correspondence analysis (DCA) showed that species compositions of the grazed and ungrazed frequently burned sites differed (Fig. 6a, b). Overall, frequently burned sites also differed from infrequently burned sites in species composition, while the lowland sites (Tully soil) differed from the slope and upland (Florence soil) sites. The primary axis of variation (DCA axis 1), which accounted for 19.9% of the variation among sites, was related to fire frequency, with the frequently burned sites having low axis 1 values and the less frequently burned sites having high axis 1 values (Fig. 6a, b). DCA axis 2, which accounted for 13.8% of the variation, reflected the grazing treatment, with the grazed sites having higher DCA 2 values than the ungrazed sites. This corresponded to a strong differentiation in the ordination, with C₄ grasses to the lower left representing the dominant species in the frequently burned sites, versus woody species to the upper right that are abundant in unburned prairie, especially on slopes (Fig. 6c). Forbs and C₃ grasses, on the other hand are distributed throughout the ordination diagram. Thus C₄ grasses and shrubs characterize the endpoints along the fire frequency gradient.

Soil type did not affect the mean to variance ratio of any group, but frequent fire favoured cover stability of C₄ grasses (App. S6), while infrequent fire favoured stability of C₃ forbs. Stability of C₃ forbs and the total plant community increased with grazing. There was a positive linear relationship between overall species richness and plant community stability (cover stability) (Fig. 7a) and cover stability of C₃ forbs (Fig. 7b).

Discussion

The main effects of fire and grazing as seen in this study were mostly consistent with other fire–grazing studies in this and other mesic grasslands (Collins 1987; Gibson & Hulbert 1987; Collins et al. 1998; Knapp et al. 1999;

Table 2. Multivariate analysis of variance of the effects of fire frequency, soil type and grazing on relative cover values of common species. The fire column letters indicate the frequency at which a species had the highest cover (F = frequent fire, I = infrequent fire), the soil column letters indicate the soil on which a species had the highest (+) or lowest (–) cover (P = upland, S = slope, L = lowland), and the grazing column indicates the grazing treatment under which a species had the highest cover (G = grazed, U = ungrazed). Interactive effects are shown in subsequent columns, with high (+) and/or low (–) values occurring in indicated treatment combinations. Superscript letters indicate level of statistical significance (a = $P < 0.001$, b = $P < 0.01$, c = $P < 0.05$).

Species	Fire	Soil	Grazing	F × S	G × S	F × G	F × S × G
Grasses							
<i>Andropogon gerardii</i>							
<i>Andropogon scoparius</i>	F ^a		U ^c			+F × U ^c	
<i>Panicum virgatum</i>	F ^b	+L ^b	U ^b	+F × L ^b	+U × L, –G × P ^b	+F × U ^b	+F × L × U ^c
<i>Sorghastrum nutans</i>	F ^a	–S ^c		+F × L, F × S ^c			
Forbs							
<i>Artimisia ludoviciana</i>	I ^a						
<i>Aster ericoides</i>	I ^c						
<i>Kuhnia eupatorioides</i>		–L ^b		+I × S, –I × L ^c			
<i>Salvia azurea</i>		+P ^b					
Woody Species							
<i>Amorpha canescens</i>							
<i>Rosa arkansana</i>							
<i>Symphoricarpos orbiculatus</i>							

Towne et al. 2005; Burns et al. 2009). That is, high fire frequency (1–2 yr return interval) favoured the dominant grasses *A. scoparius*, *P. virgatum* and *S. nutans* and resulted in lower species richness within life forms (except C_4 plants), and overall richness and diversity. In mesic tallgrass prairie, frequent fire has been shown to reduce N availability as well as soil moisture (Risser & Parton 1982; Seastedt et al. 1991; Johnson & Matchett 2001; Shay et al. 2001). Dominant C_4 grasses may out-compete forbs through increased canopy shading and higher resistance to the direct effects of fire, as well as higher water- and N-use efficiencies (Seastedt et al. 1991). Therefore frequently burned sites have high grass cover and low forb cover.

In contrast to frequent fire, grazing by bison reduced the cover of *A. scoparius* and *P. virgatum*, and increased richness within all life forms, overall richness and diversity. This is due to preferential grazing of grasses by bison, which reduces above-ground biomass of dominant grasses and increases light availability for other species (Collins 1987; Hartnett & Fay 1998; Knapp & Seastedt 1998). Therefore, frequent fire and grazing have opposite effects on resource availability such that when combined, light and N availability increase and thus species richness increases (Collins et al. 1998). The separate and interactive effects of both of these environmental drivers on the plant community were apparent in the multivariate analyses of variance of the spatial data set, the DCA ordination (Fig. 6) and the diversity–fire frequency regression (Fig. 3). Specifically, the communities in ungrazed frequently burned sites were compositionally different from both grazed and ungrazed infrequently burned sites. Although there was a negative relationship between species diversity and the number of times a site was burned in ungrazed sites, this relationship

was largely driven by the extremely low diversity in the ungrazed annually burned sites. Therefore, there appears to be a threshold with annual spring burning such that certain species that can tolerate less frequent fires are unable to persist on annually burned sites. Diversity, on the other hand, was not affected by fire frequency in the grazed sites, which also supports the contention that grazing offsets the effects of fire (Collins et al. 1998; Fuhlendorf & Engle 2001).

Unlike previous studies (Abrams & Hulbert 1987; Gibson & Hulbert 1987), we found no main effect of soil type on richness or diversity when averaged across fire and grazing treatments; however, the relative cover of individual species and the composition of the plant communities did change across the landscape with respect to soil type. When fire and grazing were taken into account, variation in soil type significantly affected individual, life form and community level responses. This indicates that although fire and grazing are the main drivers of plant community composition and dynamics in tallgrass prairie, their effects are mediated to some degree by soil type.

The three topographic locations included in this study vary in percentage slope, soil texture, water-holding capacity and organic matter content (Ransom et al. 1998), and these factors likely interact with fire and grazing over time to affect vegetation composition and dynamics. For example, cover of woody species was much higher on slope (16.43%) soils than on lowland (5.96%) or upland (3.33%) soils. Some of these slopes are fairly steep, with areas of exposed soil and rock, reducing the probability that fire would carry across them completely, and possibly making them less desirable to bison as grazing sites. Lower fire frequency and reduced grazing intensity at these sites

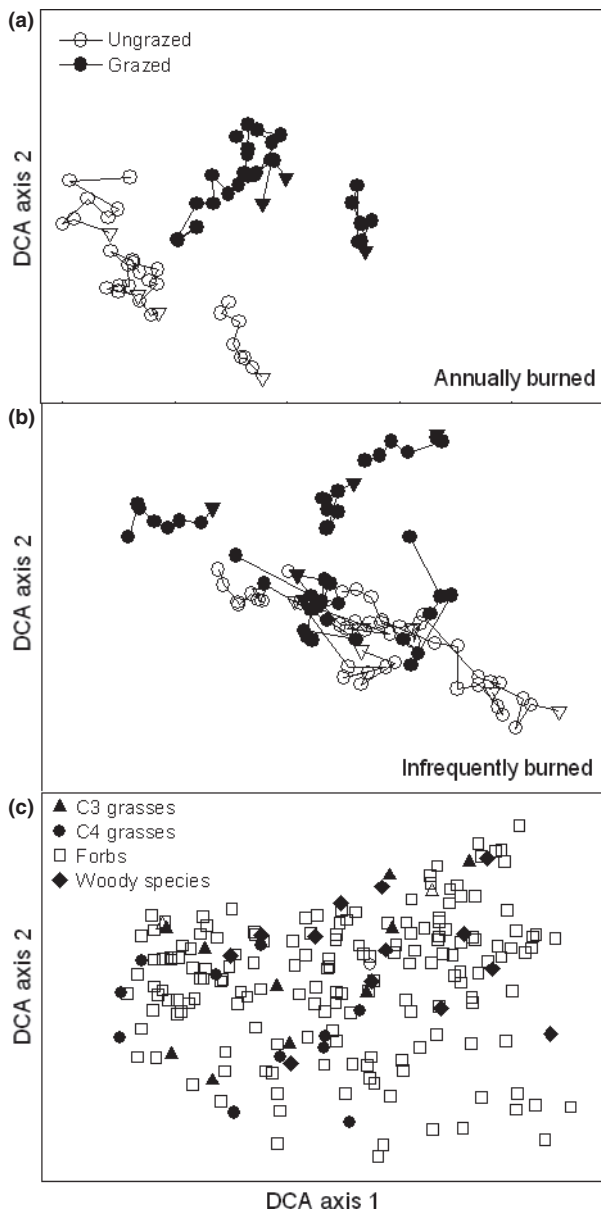


Fig. 6. Detrended correspondence analysis (DCA) ordination of sites over time (1993–2000). The site ordination is presented in two panels for clarity. Plot symbols represent one site in a given year, with those symbols from the same site connected by lines. Triangles represent sites in the last year of sampling (2000). (a) Frequently burned sites (every 1–2 yr), (b) infrequently burned sites (every 4–20 yr). (c) Corresponding species ordination. Species list and life form are given in App. G. Sites in the upper right are infrequently burned with high diversity of woody species. Sites in the lower left are frequently burned and dominated by C₄ grasses.

could promote the establishment and persistence of woody species, and result in an increase in woody cover over time (Briggs et al. 2002), as seen in our study.

Cover of C₃ plants, C₄ plants and forbs was greater on lowland sites (relative to slopes and uplands), and richness

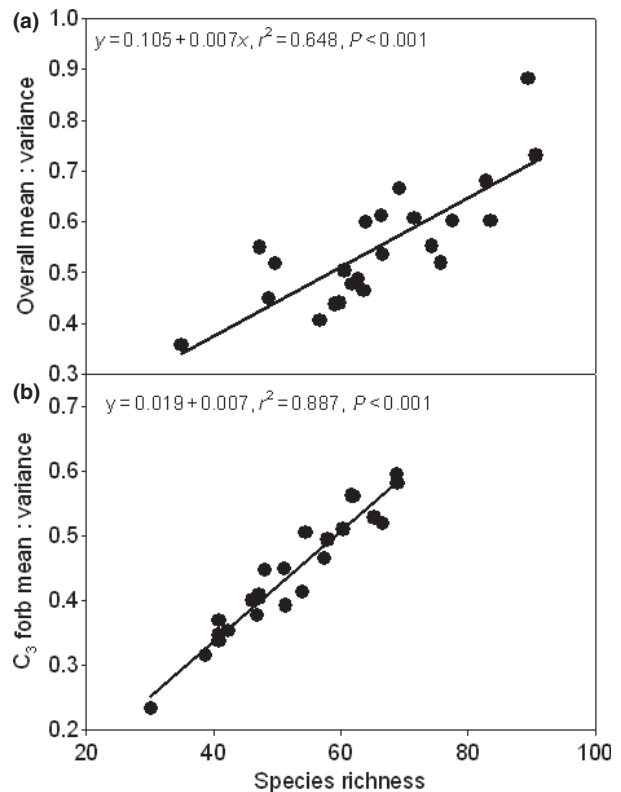


Fig. 7. Relationship between species richness and temporal cover stability of the plant community. (a) Total cover stability; (b) C₃ forb cover stability versus total richness.

of C₄ plants, grasses and overall diversity was greatest in uplands. A higher overall cover of vegetation on the lowland sites could be due to their deeper soils, which have greater water-holding capacity than slopes and upland soils (Knapp et al. 2002). Higher diversity on the upland sites could also be due to reduced dominance by a single species or group of species, leading to increased resource availability. Our results are mostly consistent with Gibson & Hulbert (1987), with the exception of forb cover, which they found to be highest on uplands. One reason for this difference could be that their study included data that were collected prior to the introduction of bison in 1987, and thus, the patterns that we found were likely the result of years of grazing.

Our data showed that both between and within life forms, individual species varied in their responses to fire, grazing and soil type over time. Thus the interaction between biotic and abiotic factors strongly influenced the distribution and abundance of dominant species in this tallgrass prairie. Abiotic factors, interspecific interactions, dispersal limitation and trophic structure strongly determine the local distribution and abundance of species in mesic grasslands (Lortie et al. 2004; Dickson & Foster 2008).

Species diversity, grazing and fire frequency are all reported to increase grassland community stability (Anderson & Brown 1986; Tilman 1999; Collins & Smith 2006). Their effects on functional groups and individual species are more variable, however. We found that the stability of C_3 forbs, C_4 grasses and the whole plant community was significantly affected by fire and grazing, but not soil type. Infrequent fire increased the cover stability of forbs, while frequent fire increased the cover stability of grasses, and grazing increased the cover stability of forbs and the overall community but did not affect cover stability of grasses. The positive relationship between species richness and stability indicates that diversity does affect the stability of C_3 forbs and the overall community, but not that of C_4 grasses. These findings provide support for the 'insurance hypothesis,' and are consistent with other studies (McNaughton 1993; Tilman & Downing 1994; Hobbs et al. 2007). Thus, because individual species and functional groups in this mesic grassland respond differently to environmental fluctuations, functional redundancy may maintain this mesic grassland in the face of environmental change (Yachi & Loreau 1999). That is, despite large fluctuations in the cover of certain individual species over time in response to disturbances such as fire and grazing, the overall community cover remained relatively stable. These findings indicate that management practices (e.g. grazing combined with infrequent fire) that aim to maximize C_3 forb and hence community-level richness will also enhance community stability (Fuhlendorf & Engle 2004).

Conclusions

We found that fire, grazing and soil type affected overall plant community composition, but surprisingly there were no significant interactions among these drivers at the community level. As a result, each landscape component contributes uniquely to landscape-scale diversity and dynamics. Species richness and community stability were maximized in this system with infrequent fire (every 4–20 yr) and bison grazing across a range of soil types in this grassland landscape. Unlike in previous studies, we found that richness did not differ along the topographic gradient. In addition, we found that richness on slope sites, which are abundant throughout the Flint Hills Region, was particularly responsive to fire frequency. We found that C_4 grasses appear to regulate community diversity in this ecosystem. Grass cover was negatively correlated with forb richness. However, grass cover is regulated by fire and grazing; fire increases and grazing reduces the collective abundance of these tall clonal C_4 species. Despite these general patterns, the abundance of dominant species increases or decreases in response to fire frequency and grazing, depending on topographic position. At the site

scale, we found diversity enhanced community and functional type stability, but grazing modulated this response. Overall, our study of the long-term effects of key natural disturbances demonstrates how richness, diversity and composition respond to grazing and variable fire frequency over the long term, and how these responses are modulated by topographic position.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Management units used in the spatial (1997) and temporal (1993–2000) data sets. U = ungrazed, N = native grazers (bison), numbers refer to fire frequency (every 1, 2, 4, or 20-yr), Letters refer to replicate management units (A,B, C, D, N, W), TU = Tully soils (lowlands), SL = slopes, and FL = Florence soils (level uplands).

Appendix S2. (a) Multivariate tests^c: effects of fire, grazing, and soil type on species richness of C₃ and C₄ plants. (b) Tests of between-subjects effects: effects of fire, grazing, and soil type on species richness of C₃ and C₄ plants. (c) Multivariate tests^c: effects of fire, grazing, and soil type on species richness of grasses, forbs, and woody plants. (d) Tests of between-subjects effects: effects of fire, grazing, and soil type on species richness of grasses, forbs, and woody plants. (e) Multivariate tests^c: effects of fire, grazing, and soil type on species richness and diversity (H'). (f) Tests of between-subjects effects: effects of fire, grazing, and soil type on species richness and diversity (H').

Appendix S3. (a) Multivariate tests^c: effects of fire frequency, grazing, and soil type on percent cover of C₃ and C₄ species. (b) Tests of between-subjects effects: effects of fire frequency, grazing, and soil type on percent cover of C₃ and C₄ species. (c) Multivariate tests^c: effects of fire frequency, grazing, and soil type on percent cover of grasses, forbs, and woody plants. (d) Tests of between-subjects effects: effects of fire frequency, grazing, and soil type on percent cover of grasses, forbs, and woody plants.

Appendix S4. (a) Multivariate tests^c: effects of fire frequency, grazing, and soil type on cover of individual species. (b) Tests of between-subjects effects: effects of fire

frequency, grazing, and soil type on cover of individual species.

Appendix S5. (a) Multivariate tests^b: effects of fire frequency, grazing, and soil type on temporal stability (mean:variance) of C₃ forbs, C₄ grasses, and all species combined. (b) Tests of between-subjects effects: effects of fire frequency, grazing, and soil type on temporal stability (mean:variance) of C₃ forbs, C₄ grasses, and all species combined.

Appendix S6. Map of the study area showing the grazed and ungrazed management units used in this study. The red line outlines the 1012 ha area where bison have free access to 10 management units burned at different fire frequencies. The yellow line outlines all the management units from which data were collected for this study. Some management units have multiple sites in them (e.g. upland, slope, lowland). Codes: N = grazed by bison; 1, 2, 4, 20 is the fire frequency. Small letters indicate replicates of fire frequency. Thus, N20b is replicate *b* management unit burned once every 20 yr and grazed by bison, whereas 004b is replicate *b* management unit burned once every 4 yr with no bison.

Appendix S7. Photograph of Konza Prairie showing the upland, slope and lowland 'sites' along the topographic gradient in a frequently burned grasslands. The yellow flowered forb in the foreground is *Solidago missouriensis*, the blue flowered forb is *Salvia azurea* and most of the grass culms are *Andropogon gerardii*.

Appendix S8. Species (and life form) used in the temporal ordination.

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