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Concurrent Effects of Fire Regime, Grazing and Bison Wallowing on Tallgrass Prairie Vegetation

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ABSTRACT.—We examined the effects of fire regime and bison activity on the plant communities of active bison wallows and the surrounding grazing lawns at Konza Prairie Biological Station in northeastern Kansas, USA. In both mid-June and late July the grazed sites had higher species richness and more vegetation cover than the wallow edges regardless of fire regime. The percent cover of most dominant perennial species was significantly higher on grazing lawns than in wallows. Annual species and exotic species had significantly higher cover in wallows than in grazing lawns and in annually burned sites compared to those burned at a 4-y interval. Overall, treatment effects on community structure and individual species abundance were stronger in the June. However, in July there was significantly more bare ground wallows around sites burned at a 4-y interval, suggesting increased wallowing activity at these sites. This finding suggests a strong effect of fire regime on seasonal bison activity, which further indicates the importance of multiple interacting disturbances for generating local- and landscape-level vegetation patterns in tall grass prairie.

INTRODUCTION

North American grasslands were created and historically maintained by disturbance regimes that influenced spatial and temporal community dynamics through differentially affecting the abundance of individual plant species (Collins, 1987, 2000; Gibson, 1988, 1989; Vinton *et al.*, 1993; Suding, 2001). Fire and the activities of large grazers, particularly bison (*Bos bison*), were the two most important disturbances that shaped and maintained the plant communities of tallgrass prairie, which was once the predominant ecosystem throughout much of central North America (Hartnett *et al.*, 1997; Collins and Steinauer, 1998; Knapp *et al.*, 1999). However, due to the eradication of bison from nearly all of their former range and the suppression of fire on most remaining prairies, we have only limited knowledge regarding the effects and interactions of these disturbances (Hartnett *et al.*, 1996; Collins and Steinauer, 1998). Therefore, investigating the concurrent effects of fire and bison activity on existing tallgrass prairie is critical for understanding vegetation dynamics of native grasslands, for directing management of existing prairie preserves and for informing prairie restoration efforts.

In tallgrass prairie, frequent spring fires generally promote the growth of warm-season grasses and prevent the encroachment of woody species (Collins, 1987; Gibson, 1988). Fire mediates plant competition and, consequently, intermediate fire frequencies produce higher species richness than either annual burning, which strongly favors the dominant warm season grasses, or long fire intervals that allow competitive exclusion of some fire-adapted

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species (Gibson and Hulbert, 1987; Collins, 2000; Suding, 2001). Bison grazing at moderate intensity also increases diversity by releasing the subdominant grasses and forbs from the competitive effects of the dominant prairie grasses (Hartnett *et al.*, 1996; but *see* Vinton *et al.*, 1993). Grasslands have coevolved with large grazers and periodic grazing actually enhances the growth of many forage plant species, thus attracting more grazers to the area (McNaughton, 1984).

In addition to the direct effects of fire and grazing, there are several important interactions between fire and bison behavior (Knapp *et al.*, 1999). Bison respond strongly to the increased production of palatable grasses after fire and are known to track post-fire growth across the landscape (Vinton *et al.*, 1993; Briggs and Knapp, 1995; Coppedge and Shaw, 1998). Nonrandom grazing and wallowing by bison may alter fuel loads within patches of prairie, thereby altering local fire behavior and intensity as well as overall spatial patterns (Knapp *et al.*, 1999). The interaction of fire and grazing also affects plant community composition (Hartnett *et al.*, 1996) and belowground processes such as root growth and nutrient cycling (Johnson and Matchett, 2001).

Bison also influence prairie vegetation by wallowing. Wallowing behavior, which peaks during the late summer and early fall, creates large shallow depressions scraped bare of vegetation from repeated mud- or dust bathing (Coppedge and Shaw, 2000; McMillan *et al.*, 2000). These soil disturbances have several localized effects on plant communities, including destroying plants that formerly occupied the wallow site, providing varied microhabitats for future colonization and indirectly affecting the surrounding vegetation by altering the local species pool and seed rain (Gibson, 1989; Hartnett *et al.*, 1997; Rogers and Hartnett, 2001). Because the physical impressions of wallows may persist for years, bison wallowing may also have significant long-term ecological impacts (Polley and Collins, 1984; Gibson, 1989). The intensity of wallowing activity varies temporally and spatially, and, as such, bison wallows undergo a number of successional trajectories (Collins and Uno, 1983; Polley and Collins, 1984; Knapp *et al.*, 1999). Most wallows at Konza Prairie hold water briefly in the spring but soon dry, thus providing suitable habitat for colonization by early successional and ruderal plant species (Gerlanc and Kaufman, 2003). However, when bison wallowing activity increases in mid- to late summer, most vegetation in the wallow interior is destroyed, leaving distinct edges that comprise both typical prairie species and early successional species facilitated by soil disturbance (Collins and Uno, 1983; McMillan *et al.*, 2000).

The effects of fire and grazing on tallgrass prairie are well-documented. Several studies have examined the vegetation of bison wallows, but the relationships among these three disturbances has received little attention (Collins, 1987; Vinton *et al.*, 1993; Collins and Steinauer, 1998). Studying the concurrence of local disturbances (*i.e.*, concentrated grazing and wallowing) and landscape-level disturbances (*i.e.*, fire) is necessary for understanding the diverse effects that fire and bison have on the vegetation dynamics of tallgrass prairie. Furthermore, such research will have important implications for prairies in which fire and bison are used as management tools. Our objective was to assess the bison-mediated effects of fire regime on the vegetation of bison wallows and the immediately surrounding grazed prairie at two times during the growing season. We were particularly interested in community responses and the relative abundance of three focal groups of plants—dominant perennial species, annual species and exotic species—at the edges of active wallows and in adjacent grazing lawns. These groups are important components of the Konza Prairie flora and therefore changes in their relative abundance may be particularly indicative of disturbance effects on community structure and vegetation dynamics.

METHODS

Study site.—We conducted this study in the summer of 2001 at Konza Prairie Biological Station, a 3487 ha tallgrass prairie in the Flint Hills of northeastern Kansas (39°05′N, 96°35′W). Grassland vegetation at the site comprises approximately 230 species and is dominated by characteristic tallgrass prairie species, particularly the warm-season grasses *Andropogon gerardii*, *Schizachyrium scoparium* and *Sorghastrum nutans* (Towne, 2002). Subdominant species include several warm- and cool-season graminoids and forbs; there are relatively few exotic species at the site (Freeman, 1998). Konza Prairie is divided into watersheds (mean size = 65 ha) subjected to prescribed fire at intervals from 1 to 20 y. Our sites were located within adjacent watersheds of 120 and 135 ha burned at 1- and 4-y intervals, respectively. Both watersheds were burned in spring 2001 to control for the effects of time since fire. It should be noted, however, that many of the results from the 4-y fire regime are likely due to the previous spring fire and therefore might not be a consequence of that fire interval.

Bison were introduced to Konza Prairie in 1987 after nearly 100 y of absence from the region. Currently, more than 200 animals occupy a 1012 ha enclosure that encompasses 10 watersheds representing replicated spring fire regimes of 1-, 2-, 4- and 20-y burn intervals. Bison wallow and graze throughout the enclosure, but summer wallowing is concentrated on relatively flat grazing "lawns" (sensu McNaughton, 1984) primarily located on mid-level terraces and uplands (Coppedge and Shaw, 2000; McMillan *et al.*, 2000). Even within this relatively small enclosure, bison preferentially graze, and presumably wallow, in more recently burned areas due to the increased production and palatability of grasses in the post-fire growing season (Vinton *et al.*, 1993; Briggs and Knapp, 1995). The bison wallows we studied were roughly elliptical, 2 to 5 m along the long axis and were shallow but distinct from the surrounding vegetation. By mid-June all of the wallows included in this study were dry, bare of vegetation and showed evidence of recent dust bathing by bison. When we describe wallow vegetation we refer to the vegetation present on the distinct outer edges of active wallows rather than the bare wallow interiors.

Plant community sampling.—To assess plant community responses to fire regime and bison activity, we sampled wallow edge vegetation and the surrounding grazed areas in mid-June and again in late July. We examined the vegetation of one site of each habitat type from six grazing lawns in each of the two watersheds, producing a sample size of six wallows paired with six grazed areas from each fire regime. We chose grazing lawns haphazardly. We identified focal wallows randomly within each grazing lawn from those of medium size with a clearly defined edge. We were unable to truly replicate fire regimes, as is the case for many studies of fire effects (Van Mantgem *et al.*, 2001). However, because our study was observational rather than manipulative (Heffner *et al.*, 1996) and the time since fire was important to control, we believe that it is appropriate to use spatially distinct grazing lawns as experimental units for our analyses.

We placed belt transects running north-south and east-west through each wallow and recorded plant species present in four 0.2 m^2 quadrats located at the wallow edge and four 0.2 m^2 quadrats located 5 m into the surrounding grazing lawn. The grazed prairie quadrats were at least 5 m of any other wallows and all sites were at least 20 m from roads or fences. The percent cover of plant species rooted within each quadrat was estimated using the Daubenmire (1959) method modified with the addition of a category for species covering 0 to 1% of the area. We also recorded the percent cover of bare ground and used changes in bare ground cover between the two sampling period as a surrogate for directly measuring the intensity of bison wallowing and grazing. We averaged the midpoint cover values

TABLE 1.—Community parameters of all wallows and grazed sites and comparisons between fire regimes within habitat types for the June sampling period. Because all analyses were non-parametric, treatment medians are shown. Differences between wallows and grazed areas were analyzed with Wilcoxon signed-rank tests and differences between burn regimes within habitats types were analyzed with Mann-Whitney U tests. Significant differences are marked for treatments in which the parameters were greater (*, significant at $\alpha < 0.05$; **, significant at $\alpha < 0.01$)

	Habitat type		Wallow edge		Grazed prairie	
Variable	Wallow edge	Grazed prairie	1-year	4-year	1-year	4-year
Richness	20.0	30.0**	25.0**	19.0	32.0	29.0
Diversity (H')	2.53	2.84*	2.65	2.45	2.89	2.80
Evenness (J)	0.83	0.83	0.85	0.83	0.84	0.81
Vegetation percent cover	67.19	110.01**	87.32**	58.38	115.13	106.94
Percent annuals	22.07**	18.09	27.89	19.35	25.10**	10.10
Percent exotics	15.59**	6.79	17.31	15.04	8.71*	5.23

(0.5, 3.0, 15.0, 37.5, 62.5, 85.0 and 97.5%) of the four quadrats at each wallow and prairie sample to more accurately assess species abundance at the site level. Plant nomenclature follows Kartesz (1999) and designation of plant biological attributes follows Kartesz (1999), Freeman (1998) and Towne (2002).

Data analysis.—For each site, we calculated species richness, Shannon's diversity index (H') and Pielou's evenness index (J). Additionally, we calculated the total vegetation cover as well as the percent of the species pool comprising exotic and annual species at each site. Due to the non-normal distribution of our data, we analyzed these aggregate measures of community structure as well as the abundance of individual plant species between fire treatments within each habitat type with Mann-Whitney U-tests. Because wallow and grazed prairie sites were spatially paired and, therefore, not independent, we used Wilcoxon signed-rank tests to analyze differences in community characteristics and species abundance between wallow edges and grazing lawns. We also used Wilcoxon signed-rank tests to assess the temporal changes in plant communities because we sampled from the same quadrats in June and July. For all analyses of focal species, we included only those that occurred in at least three sites due to the inability of our statistical methods to determine the significance of treatment effects for species with fewer than three non-zero cover values. We conducted Spearman rank correlations (two-tailed significance) to examine relationships among site variables. We used SPSS 11.0 for all analyses (SPSS, Inc., 2002).

RESULTS

In the June sampling period, 87 species were present at the sites, 21 of which appeared at only one site and 9 of which appeared at only two sites. Vegetation differed significantly between wallows and grazing lawns and between fire regimes within habitats by a number of community characteristics (Table 1). In both fire regimes, the species richness, diversity and total percent vegetation cover were significantly higher at grazed prairie sites than at wallow edges. Alternatively, the percent of species that were exotic or annual was higher in wallow sites. Within both habitat types, the median values for species richness, diversity, evenness, percent vegetation cover, percent exotic species and percent annual species were all higher in annually burned sites than in those burned at a 4-y interval (Table 1).

Focal species (dominant perennials, exotics and annuals) varied widely in their response to fire regime and habitat type but we did identify some differences among treatments within groups. Most dominant perennial prairie species (7 of 11) had significantly higher

TABLE 2.—Median percent cover of dominant prairie species in the June sampling period. The species shown here were those present at more than 8 of the 24 sites with a median percent cover $>1\%$ for at least one habitat type. Note that only data for native perennial species are presented here. Differences between wallows and grazed areas were analyzed with Wilcoxon signed-rank tests and differences between fire regimes within habitat types were analyzed with Mann-Whitney U tests. Significant differences are marked for treatments in which species are more abundant (*, significant at $\alpha < 0.05$; **, significant at $\alpha < 0.01$)

	Habitat type		Wallow edge		Grazed prairie	
Species	Wallow edge	Grazed prairie	1-year	4-year	1-year	4-year
Ambrosia psilostachya	0.75	1.25	2.51**	0.25	1.69**	0.82
Andropogon gerardii	5.69	20.63**	4.57	9.0	23.44	19.13
Bouteloua curtipendula	0	3.75	4.5*	0	2.32	3.75
Carex inops	0.32	1.32**	0.57	0.82	3.82	4.94
Carex meadii	0.75	4.63*	1.63	1.44	4.08	4.10
Dicanthelium oligosanthes	0.82	5.07**	0.75	1.13	2.07	6.0
Salvia azurea	0	1.88	0	0	1.88	1.88
Schizachyrium scoparium	0.75	7.88**	0.75	0.44	9.19	7.85
Sorghastrum nutans	1.88	16.07**	0.75	4.94	10.69	18.51
Sporobolus compositus	2.38	4.5*	0.38	4.13	4.5	3.75
Symphyotrichum ericoides	1.63	6.88	3.51	1.57	5.01	8.38

Bromus japonicus and *Poa pratensis*, both exotic species, were also dominant according to the criterion above; *see* Table 4

TABLE 3.—Median percent cover of native annual species in the June sampling period. Differences between wallows and grazed areas were analyzed with Wilcoxon signed-rank tests and differences between fire regimes within habitat types were analyzed with Mann-Whitney U tests. Significant differences are marked for treatments in which species are more abundant (*, significant at $\alpha < 0.05$; **, significant at $\alpha < 0.01$). Analyses that could not be conducted due to insufficient sample sizes were excluded

	Habitat type		Wallow edge		Grazed prairie	
Species	Wallow edge	Grazed prairie	1-year	4-year	1-year	4-year
Chamaesyce serpens	0	0.19	0.07	0	0.25**	0.13
Erigeron strigosus	0	0.07*	—	—	0.19	0
Hedeoma hispida	0.13	0.07	0.57	0	0.13*	0
Hordeum pusillum	0.75**	0	11.63*	0.13	0.13*	0
Linum sulcatum	0	0	—	—	—	—
Plantago rhodosperma	0.13	0.13	0.13	0.13	0.13	0.07
Silene antirrhina	0	0.13	—	—	0.13	—
Spermolepis inermis	0	0.13*	—	—	0.44	0
Vulpia octoflora	0	0	—	—	—	—

The exotic species *Bromus japonicus*, *Lepidium densiflorum*, *Medicago lupulina* and *Polygonum aviculare* are also annual; *see* Table 4. Other native annual species observed in too few sites for analysis were the following: *Alopecurus carolinianus*, *Ambrosia artemesiifolia*, *Chaerophyllum procumbens*, *Chamaesyce glyptosperma*, *Euphorbia marginata*, *Lomatium foeniculum* and *Triodanis leptocarpa*

TABLE 4.—Median percent cover of exotic species in the June sampling period. Differences between wallows and grazed areas were analyzed with Wilcoxon signed-rank tests and differences between fire regimes within habitat types were analyzed with Mann-Whitney U tests. Significant differences are marked for treatments in which species are more abundant (*, significant at $\alpha < 0.05$; **, significant at $\alpha < 0.01$). Analyses without sufficient sample sizes were excluded

	Habitat type		Wallow edge		Grazed prairie	
Species	Wallow edge	Grazed prairie	1-year	4-year	1-year	4-year
Bromus inermis	0	0	0.38	0	0.07	0
Bromus japonicus	3.38	0	1.13	7.5	0	0
Lepidium densiflorum	0.94**	0.13	1.94	0.94	0.63*	0.07
Poa pratensis	10.5*	4.63	12.38	10.5	5	2.32
Polygonum aviculare	0	0	1.19**	0	—	—

Medicago lupulina was also present but did not occur in enough sites for analysis

percent cover in the grazing lawn sites than at the wallow edges (Table 2). There were also significant effects of habitat and fire regime on the total percent of annuals in the species pool at the site level (Table 1). Several individual annual species were significantly more abundant at sites burned every year, and no annual species had higher median percent cover in the sites with 4-y fire intervals (Table 3). Indeed, although the percent cover of annual species was higher overall in wallows than in prairie sites, sites burned annually had a significantly higher percent of annual species than those burned every 4 y regardless of habitat type (Kruskal-Wallis test, $\chi^2 = 11.61$, $P = 0.001$).

Six exotic species were present at the study sites and composed a large percent of the total vegetation cover in some quadrats. Two of the six, *Lepidium densiflorum* and *Poa pratensis,* had significantly higher percent cover at wallow edges than corresponding grazed prairie, and no species had higher cover in grazed prairie than wallows (Table 4). At wallow sites, *P. pratensis,* a naturalized grass now among the more common C_3 graminoids at Konza, had the highest percent cover of all species and *Bromus japonicus,* a more recent invader from Asia, was also among the most abundant species found in this study. *Poa pratensis* was also one of the most common species in the grazing lawn quadrats. In both wallow and prairie sites most exotic species had higher median percent cover in the annual fire regime. Across both fire regimes, the percent of annual and exotic species present in wallows was significantly correlated with their presence in the corresponding grazed sites (Fig. 1). However, all wallows included in this study supported a higher percent of exotic species than their spatially paired grazed sites and 10 of 12 wallows supported a higher percent of annual species than their corresponding grazed sites. This pattern is largely explained by the significant correlation between percent of exotic species and cover of bare ground across all sites (Spearman rank correlation, $r_s = 0.62$, $P = 0.001$).

Plant community structure underwent significant temporal change due both to normal seasonal effects (*e.g.*, decreased cover of cool-season forbs and increased cover of C_4 grasses) and to differences in bison activity over the growing season. Fewer species were present aboveground in July than in June (80 compared to 87), and the values for most community parameters were lower in the second sampling period regardless of site type (Table 5). Overall, none of the focal species analyzed for the June sample increased significantly in percent cover from June to July. Eleven of 27 focal species decreased significantly between the two sampling periods. The two most abundant species, *Andropogon gerardii* and *Sorghastrum nutans,* were among those that decreased significantly in cover when all site types are considered (Wilcoxon signed-rank test, $Z = -2.35$, $P = 0.019$; $Z = -2.99$, $P = 0.003$,

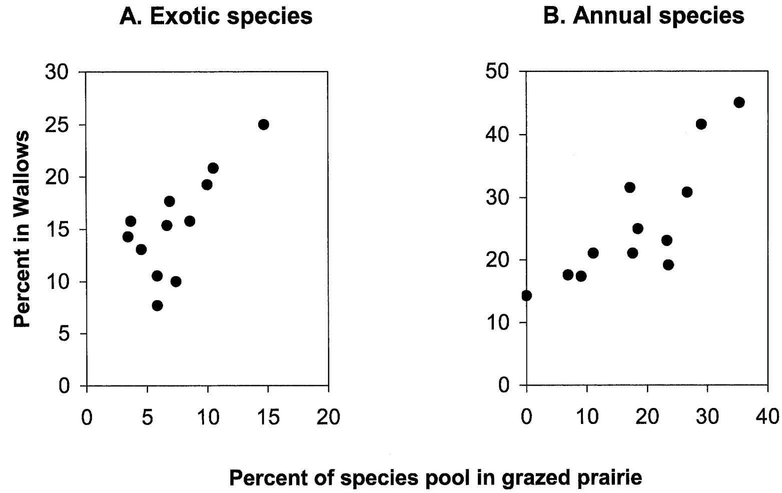

FIG. 1.—Scatterplots showing A. the percent of exotic species and B. the percent of annual species in spatially paired grazed areas and wallows in June. Both the percent of exotic species and the percent of annual species were significantly correlated between spatially paired wallow and grazed sites (Spearman rank correlation, $r_S = 0.64$, $P = 0.026$; $r_s = 0.80$, $P = 0.002$, respectively)

respectively). Although the pair-wise comparisons of percent cover for individual species could not indicate compositional changes in plant communities from June to July, the significant decrease in community evenness (Pielou's J) between sampling periods suggested that as species disappeared and the growing season progressed, sites became more strongly dominated by a smaller number of species.

The most dramatic temporal change was the increased percent cover of bare ground June to July. This change was presumably due to increased bison wallowing, increased grazing and trampling in the grazed sites and decreased cover of cool-season species in all sites. The wallow edges in the 4-y fire regime experienced the greatest increase in bare ground, suggesting that they were being enlarged, whereas the increases in the 1-y fire regime wallows and in the grazed sites were relatively small and not statistically significant (Fig. 2). Qualitative observations suggested that by late July bison spent much more time in the

TABLE 5.—Temporal changes in community parameters from mid-June to late July. All analyses were done with Wilcoxon signed-rank tests and the direction of change between the two sampling periods is noted: positive, negative or 0 for no significant change (*, significant at $\alpha < 0.05$; **, significant at $\alpha < 0.01$)

	Habitat type		Wallow edge		Grazed prairie	
Variable	Wallow edge	Grazed prairie	1-year	4-year	1-year	4-year
Richness	neg.**	neg.**	0	neg.*	neg.*	neg.*
Diversity (H′)	neg.**	neg.**	neg.*	neg.*	neg.*	neg.*
Evenness (J)	neg.**	neg.**	neg.*	neg.*	neg.*	neg.*
Vegetation percent cover	neg.**	neg.**	neg.*	neg.*	0	neg.*
Percent annuals	neg.*	0	0	neg.*	0	0
Percent exotics	0	0	0	neg.*	neg.*	0

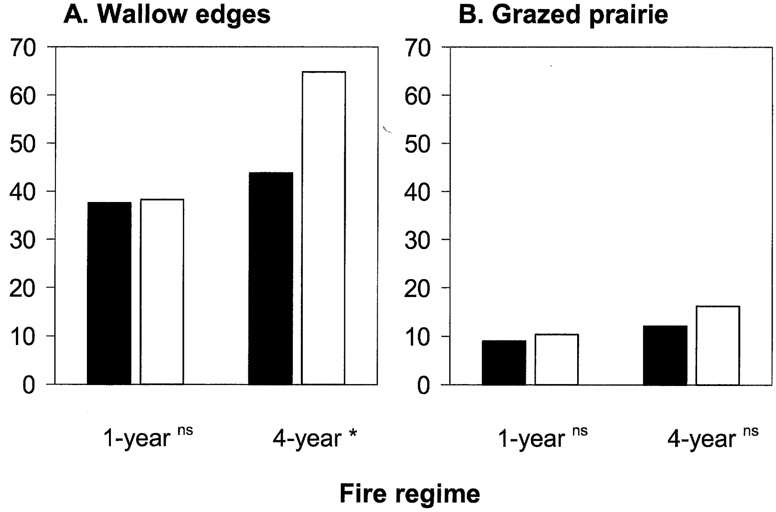

FIG. 2.—Temporal changes in percent cover of bare ground at A. wallow sites and B. grazed sites in both fire regimes. Although median cover increased in all site types from June to July, only wallows in the 4-y fire regime changed significantly, as indicated with an asterisk (Wilcoxon signed-rank test, Z = –2.06, P = 0.039)

watershed burned at 4-y intervals and, therefore, it seems likely that the increased wallowing activity was a direct consequence of the increased allocation of time spent in this watershed.

DISCUSSION

In this study we found several community and individual species responses that were contrary to findings in otherwise similar studies that examined only one type of disturbance. For example, the percent of both annual and exotic species was higher in the grazed sites subjected to annual burning than in those with a 4-y fire interval, whereas in ungrazed prairie annual burning decreases the prevalence of such species (Smith and Knapp, 1999). In ungrazed tallgrass prairie the cover of dominant warm-season grasses increases as the growing season progresses, particularly following a spring fire in an infrequently burned area (Vinton *et al.*, 1993; Blair, 1997; Suding, 2001). However, in this study the percent cover of the two most dominant species, *Andropogon gerardii* and *Sorghastrum nutans*, as well as many other species, significantly decreased between mid-June and late July, likely due to increased grazing and wallowing as the summer progressed. Additionally, whereas studies examining fire effects that have been conducted in ungrazed prairies and on relic bison wallows have shown that plant diversity is highest at an intermediate fire frequency (Collins and Uno, 1983; Gibson and Hulbert, 1987; Hartnett *et al.*, 1996; Collins 2000), we found higher species diversity and percent vegetation cover in annually burned wallows than those burned at a 4-y fire interval (Table 1). These results suggest that the plant community effects produced by bison responses to fire timing and frequency differ from those produced by fire alone.

Many studies have shown positive relationships between the degree and frequency of disturbance and the abundance and spread of exotic plant species (Vitousek, 1990; Mack *et al.*, 2000; Harrison *et al.*, 2001). The grassland flora of Konza Prairie comprises relatively few exotic species, and only a small percentage of these are considered to be highly invasive

(Freeman, 1998; Smith and Knapp, 1999; Towne, 2002). Therefore, it is not surprising that even severely disturbed areas, such as grazing lawns and bison wallows, supported a small number of exotic plants. However, in agreement with other findings from Konza (Hartnett *et al.*, 1996; Smith and Knapp, 1999, 2001; Towne, 2002), the exotic species that we did find were most abundant at species-poor sites subjected to frequent disturbance. In our study, the amount of bare ground (which we interpreted as an indication of the intensity of bison activity) was significantly correlated with the percent of exotic species at the site level. Additionally, the percent of exotic species in paired wallow and prairie sites were also strongly correlated (Fig. 1). It was not possible to determine whether the wallows facilitated the spread of these species into the surrounding grazing lawn or if the wallows simply provided suitable habitat for species already present in the area. Regardless, wallowing clearly increased the local abundance of species that prefer ruderal habitats, which in turn would alter the seed rain and likely further the spread of such species given appropriate conditions. From these results and those of other studies on invasive plants, we suggest that in prairies with larger pools of well-dispersed exotic plant species, bison wallows in burned prairie may be ideal colonization sites for exotic or native invasive species (Gibson, 1989; Tilman, 1997; Harrison *et al.*, 2001). Given the difficulty of controlling highly competitive exotic plants, the potential role of bison as invasion facilitators should be considered before introducing them to an enclosed area (Mack *et al.*, 2000).

The effects of fire regime, bison wallowing and grazing activity on vegetation structure and community composition, differed between our two sampling periods. McMillan *et al.* (2000) found that summer wallowing activity peaked in late June to early July and that the period before mid-June had much lower wallowing intensity than the period between mid-June and late July. Therefore, in this study the June sample primarily evaluated the effects of bison activity in past years, the previous spring's fire and moderate wallowing, whereas the July sample evaluated the effects of more intense wallowing and grazing. Although we did not directly measure bison activity, we suggest that by late July, grazing and wallowing intensity were much higher at the sites located in the 4-y fire regime. Long-term studies at Konza Prairie have shown that nutrient availability and plant productivity are greater after fire in infrequently burned sites than in annually burned sites (Vinton *et al.*, 1993; Briggs and Knapp, 1995; Blair, 1997). Selective grazing and wallowing in the 4-y fire regime sites as a result of this post-fire pulse in productivity was likely responsible for the enlargement of wallows in this watershed (Fig. 2). Although we only examined the plant communities of wallows and grazing lawns in 2001, the difference in bison activity between fire regimes during this summer will certainly affect future vegetation dynamics of the sites.

Bison wallows were once among the most widespread soil disturbances in central North American grasslands. Their vegetation often differed strikingly from that of the surrounding prairie (Collins and Uno, 1983; Polley and Collins, 1984; Hartnett *et al.*, 1997; Knapp *et al.*, 1999). As demonstrated in this study, individual bison wallows may shift between periods of intense use and nonuse depending largely on the fire regime of the surrounding landscape, thereby creating a fire-regulated mosaic of active, recently active and long inactive wallows. In corroboration with previous studies, we also found that fire, grazing and wallowing in tallgrass prairie may affect community composition differently when they co-occur in relatively small areas compared to when one of them is the sole disturbance (Hartnett *et al.*, 1996; Collins and Steinauer, 1998). Although we were unable to quantify the statistical interaction of these disturbances in this study, our results demonstrate that their effects are not simply cumulative. As a result, at Konza Prairie the concurrence of fire, grazing and wallowing have created highly heterogeneous habitats and, therefore, highly diverse plant assemblages, at local and landscape scales.

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LITERATURE CITED

BLAIR, J. M. 1997. Fire, N availability and plant response in grasslands: a test of the transient maxima hypothesis. *Ecology,* **78**:2539–2368.

BRIGGS, J. M. AND A. K. KNAPP. 1995. Interannual variability in primary productivity in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *Am. J. Bot.,* **82**:1024–1030.

COLLINS, S. L. 1987. Interaction of disturbance in tallgrass prairie: a field experiment. *Ecology,* **68**:1243–1250.

———. 1992. Fire frequency and community heterogeneity in tallgrass prairie vegetation. *Ecology,* **73**:2001–2006.

———. 2000. Disturbance frequency and community stability in native tallgrass prairie. *Am. Nat.,* **155**:311–325.

——— AND E. M. STEINAUER. 1998. Disturbance, diversity and species interactions in tallgrass prairie, p. 140–156. *In:* A. K. Knapp, J. M. Briggs, D. C. Hartnett and S. L. Collins (eds.). Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, N.Y. 386 p.

——— AND G. E. UNO. 1983. The effect of early spring burning on vegetation in buffalo wallows. *Bull. Torrey Bot. Club,* **110**:474–481.

COPPEDGE, B. R. AND J. H. SHAW. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. *J. Range Manage.,* **51**:258–264.

———. 2000. American bison Bison bison wallowing behavior and wallow formation on tallgrass prairie. *Acta Theriol.,* **45**:103–110.

DAUBENMIRE, R. F. 1959. Canopy coverage method of vegetation analysis. *Northwest Sci.,* **33**:43–64.

FREEMAN, C. C. 1998. The flora of konza prairie: a historical review and contemporary patterns, p. 69–80. *In:* A. K. Knapp, J. M. Briggs, D. C. Hartnett and S. L. Collins (eds.). Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, N.Y. 386 p.

GERLANC, N. M. AND G. A. KAUFMAN. 2003. Use of bison wallows by anurans on Konza Prairie. *Am. Midl. Nat.,* **150**:158–168.

GIBSON, D. J. 1988. Regeneration and fluctuations of tallgrass prairie vegetation in response to burning frequency. *Bull. Torrey Bot. Club,* **115**:1–12.

———. 1989. Effects of animal disturbance on tallgrass prairie vegetation. *Am. Midl. Nat.,* **121**:144–154.

——— AND L. C. HULBERT. 1987. Effects of fire, topography and year-to year climatic variation on species composition in tallgrass prairie. *Vegetatio,* **72**:175–185.

HARRISON, S., K. RICE AND J. MARON. 2001. Habitat patchiness promotes invasions by alien grasses on serpentine soil. *Biol. Conserv.,* **100**:45–53.

HARTNETT, D. C., K. R. HICKMAN AND L. E. FISCHER WALTER. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *J. Range Manage.,* **49**:413–420.

——— A. A. STEUTER AND K. R. HICKMAN. 1997. Comparative ecology of native and introduced ungulates, p. 72–105. *In:* F. L. Knopf and F. B. Sampson (eds.). Ecology and conservation of Great Plains vertebrates. Springer-Verlag, N.Y. 320 p.

HEFFNER, R. A., M. J. BUTLER, IV AND C. K. REILLY. 1996. Pseudoreplication revisited. *Ecology,* **77**:2558–2562.

JOHNSON, L. C. AND J. R. MATCHETT. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. *Ecology,* **82**:3377–3389.

KARTESZ, J. T. 1999. A synonymized checklist of and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland. *In:* J. T. Kartesz and C. A. Meacham (eds.). Synthesis of the North American flora, Version 1.0. North Carolina Botanical Garden, Chapel Hill, N.C.

KNAPP, A. K., J. M. BLAIR, J. M. BRIGGS, S. L. COLLINS, D. C. HARTNETT, L. C. JOHNSON AND E. G. TOWNE. 1999. The keystone role of bison in North American tallgrass prairie. *BioScience,* **49**:39–50.

MACK, R. N., D. SIMBERLOFF, W. M. LONSDALE, H. EVANS, M. CLOUT AND F. A. BAZZAZ. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.,* **10**:689–710.

MCMILLAN, B. R., M. R. COTTAM AND D. W. KAUFMAN. 2000. Wallowing behavior of American bison (Bos bison) in tallgrass prairie: an examination of alternative explanations. *Am. Midl. Nat.,* **144**: 159–167.

MCNAUGHTON, S. J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *Am. Nat.,* **124**:863–886.

POLLEY, H. W. AND S. L. COLLINS. 1984. Relationships of vegetation and environment in buffalo wallows. *Am. Midl. Nat.,* **112**:178–186.

ROGERS, W. E. AND D. C. HARTNETT. 2001. Temporal vegetation dynamics and recolonization mechanisms on different-sized soil disturbances in tallgrass prairie. *Am. J. Bot.,* **88**:1634–1642.

SMITH, M. D. AND A. K. KNAPP. 1999. Exotic plant species in a C_4-dominated grassland: invisibility, disturbance, and community structure. *Oecologia,* **120**:605–612.

———. 2001. Size of the local species pool determines invisibility of a C_4-dominated grassland. *Oikos,* **92**:55–61.

SPSS, INC. 2002. SPSS for Windows, Release 11.0. SPSS Inc., Chicago, Ill.

SUDING, K. N. 2001. The effect of spring burning on competitive ranking of prairie species. *J. Veg. Sci.,* **12**:849–856.

TILMAN, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology,* **78**:81–92.

TOWNE, E. G. 2002. Vascular plants of Konza Prairie Biological Station: an annotated checklist of species in a Kansas tallgrass prairie. *Sida,* **20**:269–294.

VAN MANTGEM, P., M. SCHWARTZ AND M. KEIFER. 2001. Monitoring fire effects for managed burns and wildfires: coming to terms with pseudoreplication. *Nat. Areas J.,* **21**:266–273.

VINTON, M. A., D. C. HARTNETT, E. J. FINCK AND J. M. BRIGGS. 1993. Interactive effects of fire, bison (Bison bison) grazing and plant community composition in tallgrass prairie. *Am. Midl. Nat.,* **129**:10–18.

VITOUSEK, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosytem studies. *Oikos,* **57**:7–13.

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