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Scott L. Collins

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INTERACTION OF DISTURBANCES IN TALLGRASS PRAIRIE: A FIELD EXPERIMENT¹

SCOTT L. COLLINS

Department of Botany and Microbiology, University of Oklahoma, Norman, Oklahoma 73019 USA

Abstract. A field study was conducted to address the roles of fire, cattle grazing, and the interaction of these two disturbances on plant species abundance and community structure in a tallgrass prairie. In 1985 and 1986, species composition was sampled in three replicates of the following grassland treatments: ungrazed + unburned (undisturbed), grazed + unburned, ungrazed + burned, and grazed + burned.

Cover of the matrix-forming species *Andropogon gerardii* was significantly greater, while cover of the nonmatrix species *Bromus tectorum* was significantly lower, on the burned treatments than on the unburned treatments. The number and cover of annuals were significantly higher on the grazed treatments than on the ungrazed treatments. Species richness increased with increasing disturbance intensity. Diversity, however, was lowest on the ungrazed + burned treatment and highest on the grazed + burned treatment. Burning significantly reduced species diversity on ungrazed treatments, and grazing significantly increased diversity on the burned treatment.

This study documented the dissimilar effects of different natural disturbances on grassland species, growth form characteristics, and community structure. In addition, the results emphasize the important role of interaction among disturbances on plant community structure in grasslands.

Key words: community structure; disturbance regime; diversity; fire; grazing; Oklahoma; tallgrass prairie.

INTRODUCTION

The role of natural disturbance has been well documented in many types of vegetation (White 1979, Sousa 1984a, Pickett and White 1985). Most community-level studies of disturbance focus on species richness and diversity (Sousa 1984a) often with reference to the intermediate disturbance hypothesis (IDH; Connell 1978) and its modifications (Miller 1982, Malanson 1984). IDH predicts that diversity will be maximized at intermediate levels of disturbance. Because the effects of disturbance on community structure may be complex, simple models such as IDH may not fully represent the interactive effects of several disturbances on different types of communities (e.g., Armesto and Pickett 1985, Collins and Barber 1985, Huston 1985).

Although many definitions of disturbance have been proposed (e.g., Grime 1979, Connell and Sousa 1983, Rykiel 1985), I prefer a definition independent of hierarchical scale and reference conditions: disturbance is a discrete event that alters the invariant structure of a system (S. Pickett et al., *personal observation*). Invariant structure is a hierarchical system of lower level units that persists because of its organization. For example, the invariant structure of grassland vegetation is composed of patches, each of which contains a different composition and abundance of species. A large-scale disturbance such as fire alters patch structure and

dynamics, which, when considered at the level of vegetation, alters the invariant structure of the grassland system.

A disturbance may be studied as a single event, or collectively, disturbances may be characterized by their frequency, intensity, and magnitude (Sousa 1984a, White and Pickett 1985). In addition, communities may be affected by several different types of disturbance. Together the different disturbances and their characteristics make up the disturbance regime of a community. Grasslands, for example, contain a complex disturbance regime that includes fire, grazing, and soil disturbance by animals, each of which differs in scale, frequency, and intensity. The effect of each type of disturbance on grassland vegetation is variable, and, more importantly, empirical evidence suggests that these disturbances interact to affect community structure (Collins and Uno 1983, Collins and Barber 1985). This evidence needs to be addressed under controlled field conditions.

The invariant structure of grassland communities includes matrix-forming species, which are superior competitors that consume the majority of resources, and nonmatrix species, which occupy areas between the matrix-forming dominants (Grubb 1986). In general, system structure (including richness and diversity) is controlled by the effects of matrix species on nonmatrix species. Specifically, the purposes of this research were to: (1) determine the effects of fire and grazing on cover and abundance of matrix and non-

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matrix species in tallgrass prairie, (2) determine how these disturbances affect community structure in this prairie, and (3) determine if these disturbances interact to affect plant community structure.

MATERIALS AND METHODS

Field methods

The study area is a 36.4 ha native tallgrass prairie located on the United States Department of Agriculture, Agriculture Research Service Livestock and Forage Research Station in El Reno, Canadian County, Oklahoma. For at least 15 yr prior to 1984, this prairie had been grazed by cattle only during the fall and winter, the area had not been burned, and it was never plowed. In 1984, the prairie was divided into two 18.2-ha sections. One section was burned in mid-April in 1984, 1985, and 1986. Six paired 0.1-ha exclosures were established along the dividing fence, three in the burned area and three in the unburned area. Fences and exclosures were constructed of two strands of electrified polywire. The remaining portions of each section were grazed each year by 13 cattle from mid-May until September. This provided a moderate to heavy stocking rate (≈ 1.4 ha per animal).

The experimental design provided four treatments of increasing disturbance intensity: (1) ungrazed + unburned ($-G-B$), (2) grazed + unburned ($+G-B$), (3) ungrazed + burned ($-G+B$), and (4) grazed + burned ($+G+B$). If one considers the amount of biomass destroyed as an operational measure of disturbance severity (Grime 1979), fire is a more severe disturbance than grazing, because with each event, more biomass is destroyed by fire than by grazing (see Collins and Barber 1985). The advantage of this experimental design is that the initial condition of all treatments was similar, so differences in composition and community structure of the treatments can thus be attributed to the addition or deletion of fire and/or grazing.

Vegetation in each exclosure was sampled with 15 randomly located 50×50 cm quadrats. To avoid edge effects, no vegetation sample was located within 2 m of a fence. Aerial cover of each species was visually estimated in 5% cover classes. The smallest cover value assigned to a species present in a quadrat was 1%. Species in the exclosure, but not sampled, were assigned a cover value of 0.1%. Vegetation in comparably sized areas outside each exclosure was similarly sampled. This provided three replicates of each treatment. Each treatment was sampled in mid-June 1985 and 1986. Sampling occurred in the late spring because (1) both warm- and cool-season species are present in the spring but not in the fall, thus providing a more complete sample of the vegetation; (2) soil moisture levels and growth of the matrix grasses at this site tend to decrease markedly around 1 July (T. Svejcar, *personal communication*); and (3) my own observations indicate that species richness at this site decreases throughout the growing season.

Clearly, the design used here imposed limitations on the extent of inferences from the data set (Hurlbert 1984, Brown and Waller 1986). The use of inferential statistics is valid within the confines of this design, and I recognize that my results cannot extend beyond comparisons within this tallgrass prairie. However, generalizations can be made by comparing results such as mine, from limited field experiments, with those from similar studies (Hawkins 1986).

Data analysis

Common taxa were categorized as either matrix or nonmatrix species, based on growth form and life history. The four most abundant matrix species were *Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Sporobolus asper* (nomenclature follows Gould [1975] for grasses and Waterfall [1972] for forbs). These potentially large perennial grasses form dense patches within this tallgrass prairie. Ten common grasses and forbs, six of which are annuals or monocarpic perennials, were identified as nonmatrix species. Together, the 14 matrix and nonmatrix species accounted for 80–95% of the plant cover on any one replicate (see Table 1). In addition, all species were categorized by growth form, as either (1) annual or monocarpic perennial, (2) polycarpic perennial, (3) grass and grasslike plant, or (4) forb.

Multivariate analysis of variance (MANOVA) was used to determine if there was an overall effect of burning, grazing, and burning \times grazing interaction for matrix and nonmatrix species groups. Data from each group for each year were treated separately. Data were cover values from 15 quadrats in each treatment replicate. To increase homogeneity of variances, all cover values were arcsine transformed prior to analysis (Sokal and Rohlf 1981).

Two-way analysis of variance (ANOVA) was used to determine if burning, grazing, or the interaction of burning and grazing significantly ($P < .05$) affected cover of each of the 14 matrix and nonmatrix species. Data were cover values for each species from quadrats in each treatment. Cover values were arcsine transformed prior to analysis. In addition, two-way ANOVA was used to determine if the combined cover values of the matrix and nonmatrix species differed significantly among treatments. If the interaction term was significant, the Tukey-Kramer unplanned comparisons test was used to determine the specific nature of the interactions (Sokal and Rohlf 1981).

Because most grasslands are patchy (Bakker et al. 1984), growth form variables were analyzed at the level of treatments rather than quadrats. Kruskal-Wallis one-way analysis of variance (KW-ANOVA) was used to determine if significant differences occurred in the number or cover of species in each category among the four disturbance treatments. To determine if fire alone had a significant effect, number and cover of species in each growth form category were compared on the

TABLE 1. Average cover values ($N = 45$ 0.25-m² quadrats) for common matrix-forming and nonmatrix species in four disturbance treatments in tallgrass prairie. -G = ungrazed, +G = grazed, -B = unburned, +B = burned.

Species	Year	Treatment				B	G	B × G
		−G − B	+G − B	−G + B	+G + B			
Matrix species								
<i>Andropogon gerardii</i>	1985	20.2	17.9	67.0	48.9			*
	1986	38.0	33.1	69.3	45.4			*
<i>Schizachyrium scoparium</i>	1985	4.1	4.0	3.9	3.9			
	1986	4.1	2.6	4.7	5.3			
<i>Sorghastrum nutans</i>	1985	4.4	9.9	8.2	9.8		*	
	1986	10.6	7.1	15.9	14.4	*		
<i>Sporobolus asper</i>	1985	12.9	14.7	5.3	6.1	*		
	1986	17.4	13.6	3.7	4.0	*		
Total matrix species	1985	41.6	46.5	84.3	68.8			*
	1986	70.1	56.4	93.6	69.0			*
Nonmatrix species								
<i>Achillea millefolium</i>	1985	0.7	2.3	0.5	1.8		*	
	1986	0.8	1.1	0.5	2.4		*	
<i>Ambrosia psilostachya</i>	1985	4.1	5.0	3.7	5.7			
	1986	3.3	4.2	4.9	6.7	*	*	
<i>Artemisia ludoviciana</i>	1985	4.6	3.0	1.0	1.1	*		
	1986	7.1	4.3	0.3	1.9			*
<i>Bromus tectorum</i>	1985	38.2	43.8	0.5	3.7	*		
	1986	16.0	22.1	0.2	2.9	*	*	
<i>Conyza canadensis</i>	1985	0.0	0.2	0.2	1.0			*
	1986	0.0	0.2	0.1	11.0			*
<i>Cyperus</i> sp.	1985	0.7	2.5	0.8	2.1		*	
	1986	0.9	1.2	0.8	0.6			
<i>Daucus carota</i>	1985	6.8	6.6	0.1	2.7			*
	1986	6.4	7.0	0.0	1.5	*		
<i>Dicanthelium oligosanthes</i>	1985	1.5	1.9	4.1	3.9	*		
	1986	2.0	2.1	4.5	6.5	*		
<i>Oxalis stricta</i>	1985	0.0	0.3	0.8	1.4	*	*	
	1986	0.1	0.4	0.4	0.7	*	*	
<i>Sonchus asper</i>	1985	1.5	0.9	0.5	0.6	*		
	1986	1.5	0.6	0.2	1.7			*
Total nonmatrix species	1985	58.1	66.4	11.9	24.0	*	*	
	1986	38.1	43.1	11.9	36.1			*

* $P < .05$, two-way ANOVA comparing burning effects (B), grazing effects (G), or the interaction of burning and grazing (B × G) on species cover.

grazed (-B+G vs. +B+G) and ungrazed (-B-G vs. +B-G) treatments with a Mann-Whitney U test. A similar procedure was used to test for a grazing effect on burned (+B-G vs. +B+G) and unburned (-B-G vs. -B+G) treatments.

Species diversity [$\exp(H')$] for each replicate was calculated as:

$$H' = -\sum p_i \ln p_i,$$

where p_i is the relative cover of species i . $\exp(H')$ is an index of the number of equally common species in a sample (Peet 1974). As recommended by Alatalo (1981) evenness (E) was calculated as:

$$E = (N_2 - 1)/(N_1 - 1),$$

where $N_2 = \exp(H')$ and $N_1 = 1/\sum p_i^2$. Richness (S) is the number of species present in each replicate. Statistical differences for diversity, evenness, and richness were determined with a KW-ANOVA, and differences using each index between either burned vs. unburned or grazed vs. ungrazed samples were assessed with a Mann-Whitney U test.

RESULTS

Species effects

For 1985 and 1986 data sets, MANOVA indicated that there was an overall burning ($F = 48.1$ and 25.0 , $P < .001$ for 1985 and 1986, respectively), grazing ($F = 3.9$ and 18.1 , $P < .005$), and a burning × grazing ($F = 5.1$ and 2.8 , $P < .03$) interaction effect within the matrix species group. During both years, *Andropogon gerardii* was the most abundant matrix-forming species in this tallgrass prairie (Table 1). This grass occurred in nearly every quadrat. Cover of *A. gerardii* was greatest on the burned, ungrazed treatment and lowest on the grazed, unburned treatment. Based on two-way ANOVA, the interaction effect of these disturbances significantly affected cover of *A. gerardii*. Burning and grazing effects on other matrix species were less pronounced (Table 1). Cover of *Sporobolus asper* was significantly lower on the burned treatments in 1985 and 1986. The response of *Sorghastrum nutans* was variable. In 1985, cover of *S. nutans* was significantly higher on the grazed treatments. In 1986, only the burning effect was significant. *Schizachyrium scoparium* showed

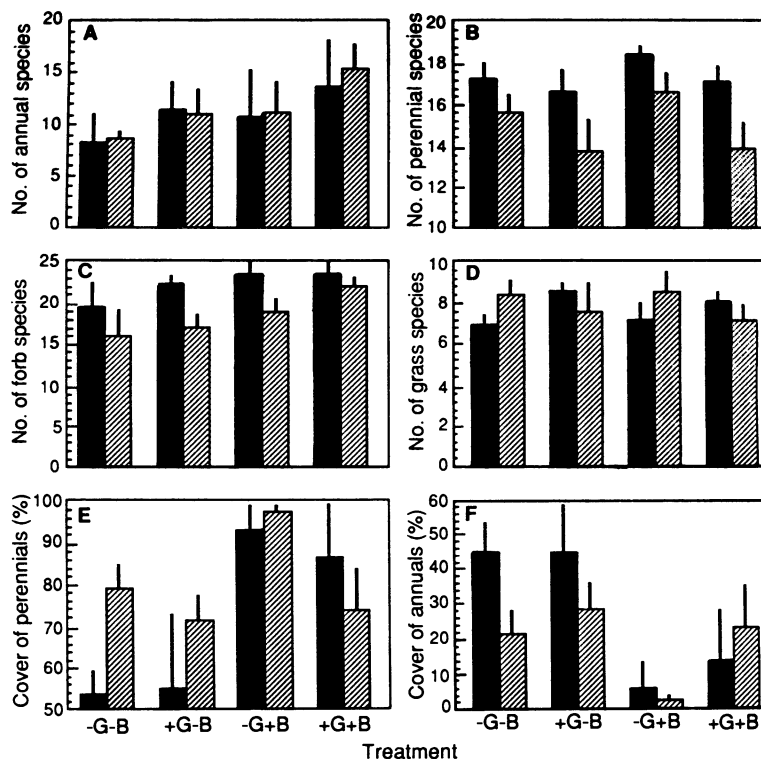


FIG. 1. Average number and cover ($N = 3$) of grass, forb, annual, and perennial species in four disturbance treatments in tallgrass prairie. +G = grazed, -G = ungrazed, +B = burned, -B = unburned. Solid bars, 1985; hatched bars, 1986. Error bars = 1 SD.

little response to either treatment. During both years, the interaction of burning and grazing affected total cover of the matrix grasses. A Tukey-Kramer unplanned comparisons test indicated that in 1985 burning significantly increased cover of matrix species on ungrazed treatments. None of the individual row or column comparisons was significant for matrix cover in 1986.

MANOVA indicated that there was an overall burning ($F = 30.4$ and 42.0 , $P < .001$ for 1985 and 1986, respectively), grazing ($F = 9.4$ and 5.0 , $P < .001$), and burning \times grazing ($F = 4.2$ and 3.4 , $P < .001$) interaction effect within the nonmatrix species group in 1985 and 1986. Based on two-way ANOVA, individual nonmatrix species exhibited at least one treatment response during at least one sample year (Table 1). In both years, the most common nonmatrix species was the annual grass *Bromus tectorum*. In 1985 and 1986, cover of *B. tectorum* was significantly lower on the burned treatments. In 1986, the grazing effect was also significant, reflecting increased cover of this annual on the grazed treatments. Only *Achillea millefolium* and *Cyperus* sp. showed no significant response to burning. Both of these taxa were significantly more abundant on grazed treatments. In general, burning produced significant effects on cover of the other nonmatrix species, and these effects were mostly consistent between years. Cover of *Ambrosia psilostachya*, *Conyza*

canadensis, *Dicanthelium oligosanthes*, and *Oxalis stricta* was significantly higher on the burned treatments. In contrast, *Artemisia ludoviciana*, *Daucus carota*, and *Sonchus asper* were significantly more abundant on the unburned treatments. In addition, cover of *A. psilostachya*, *C. canadensis*, and *O. stricta* was significantly more abundant on the grazed treatments.

Although the effects of disturbance were variable among the individual nonmatrix species, collectively, they showed a response opposite that of the matrix species. In both years, total cover of the nonmatrix species was significantly negatively correlated with total cover of matrix species (Spearman rank correlation, $r_s = -0.95$ and -0.83 , $P < .001$ for 1985 and 1986, respectively). In 1985, nonmatrix species were significantly more abundant on unburned and grazed treatments. The interactive effect of the disturbances was significant only during 1986.

Life form

Grazing and burning had significant effects on growth form characteristics of the species in the different treatments. Many trends were consistent between years. For example, the number of annuals and forbs increased with increasing disturbance intensity (Fig. 1A, C). On the burned and unburned grasslands, fewer perennial species occurred on the grazed treatments (Fig. 1B).

TABLE 2. Average values ($N = 3$) of diversity, evenness, and richness for plant species in four disturbance treatments in tallgrass prairie. +G = grazed, -G = ungrazed, +B = burned, -B = unburned.

Variable	Year	Treatment				B	G	A
		-G-B	+G-B	-G+B	+G+B			
Diversity	1985	7.7	8.6	4.7	9.1			
	1986	8.3	8.3	5.1	9.0			
Evenness	1985	0.57	0.56	0.43	0.44	*		
	1986	0.61	0.61	0.46	0.51	*		*
Richness	1985	26.7	30.7	31.1	32.7			
	1986	24.3	24.7	27.7	29.0	*		

* $P < .05$ (Kruskal-Wallis one-way ANOVA) for all (A) treatments, or (Mann-Whitney U test) for grazed vs. ungrazed (G) and burned vs. unburned (B) treatments.

Cover of perennials was greatest and cover of annuals was lowest on the burned, ungrazed treatment (Fig. 1E, F).

In 1985, cover of annuals was significantly different among the four treatments (KW-ANOVA, $H = 8.44$, $P = .04$); however, this primarily reflected the lower cover of annuals on the burned treatments (Mann-Whitney U test, $Z = 1.96$, $P = .02$). On the unburned treatments, the number of grass species in 1985 was significantly increased by grazing ($Z = 1.53$, $P = .05$; Fig. 1D). In addition, burning significantly increased cover of perennials and decreased cover of annuals in both the grazed and ungrazed comparisons.

In 1986, cover of perennials was significantly different among all treatments ($H = 8.13$, $P = .04$). In this year, grazing significantly reduced ($Z = 1.53$, $P = .05$) the number of perennial species and increased ($Z = 1.75$, $P = .03$) the number of forb species on the burned grassland. Grazing also significantly reduced cover of perennials ($Z = 1.96$, $P = .02$) and increased cover of annuals ($Z = 1.96$, $P = .02$) on the burned grassland. Burning significantly increased cover of perennials ($Z = 1.96$, $P = .02$) and reduced cover of annuals ($Z = 1.96$, $P = .02$) on the ungrazed grassland. Burning significantly increased the number of annual species on the grazed ($Z = 1.75$, $P = .03$) and ungrazed ($Z = 1.53$, $P = .05$) treatments. In addition, grazing significantly increased ($Z = 1.53$, $P = .05$) the number of annuals on the unburned grassland.

Community structure

During both years, species richness increased with increasing disturbance intensity (Table 2). In 1986, burning significantly increased richness on the grazed treatments ($Z = 1.96$, $P = .02$). During both years, grazing significantly increased species diversity on the burned treatments ($Z = 1.53$ and 1.96 , $P = .05$ and $.02$, for 1985 and 1986, respectively). The highest diversity values occurred on the treatment with a combination of disturbances (+G+B). Based on paired t tests, diversity ($t = 0.44$, $P = .34$) and evenness ($t = 1.55$, $P = .08$) values were not significantly different between years. The diversity and evenness values from the two sample years were then combined, and each index was analyzed with two-way ANOVA to deter-

mine whether or not burning, grazing, or their interaction significantly affected diversity and evenness.

Based on the two-way ANOVA, burning and grazing interacted to significantly increase species diversity ($F = 5.09$, $P = .03$). A Tukey-Kramer unplanned comparisons test indicated that the interactions reflected a significant increase in diversity by grazing on the burned treatments and a significant reduction in diversity by burning on the ungrazed treatments. Although richness increased with increasing disturbance intensity, the differences in diversity were primarily a function of evenness (Table 2). Burning significantly reduced evenness ($F = 22.5$, $P < .001$), but grazing and interaction effects were not significant. The lower evenness values reflect increased dominance of *Andropogon gerardii* on burned grasslands. In fact, diversity was significantly negatively correlated with cover of *A. gerardii* ($r_s = -0.65$, $P < .001$).

DISCUSSION

As disturbances, burning and grazing had significant effects on the invariant structure of this tallgrass prairie. These effects were evident at the level of species, plant life-history characteristics, and community structure. Historically, both grazing and burning were important components during the evolution of North American grasslands (Stebbins 1981, Axelrod 1985). Individual species, however, were differentially affected by these disturbances. For example, in this study burning increased cover of *Dicanthelium oligosanthos* but decreased cover of *Bromus tectorum* (Table 1), both of which are nonmatrix grasses. Collectively, however, the results were more predictable. Fire increased cover of matrix-forming grasses, while grazing decreased cover of matrix grasses and increased cover of ruderal forbs such as *Conyza canadensis*.

Productivity, tillering, and flower number of matrix grasses are often increased following spring burning in mesic, *Andropogon*-dominated grassland (Curtis and Partch 1950, Kucera and Ehrenreich 1962, Peet et al. 1975, Adams and Anderson 1978, Hulbert and Wilson 1983, Knapp and Hulbert 1986). In this study, cover of *A. gerardii* was significantly greater during both years on the burned treatments. The other matrix grasses were less stimulated by burning (Table 1). Svejcar and

Christiansen (1986) reported no increase in tillering of *Schizachyrium scoparium* following spring burning at this site. The limited response of other grasses may indicate that *A. gerardii* outcompetes species such as *S. scoparium* and *Sorghastrum nutans* after spring burning (see Rabinowitz et al. 1984). In contrast, the abundance of the annual grass *Bromus tectorum* was significantly lower on the burned grassland. Most seeds of this annual germinate in the fall (Mack and Pyke 1983) and few individuals survive burning.

Grazing has been shown to alter the botanical composition of grasslands in North America (Voigt and Weaver 1951, Dyksterhuis 1958, Sims et al. 1978) and elsewhere (Austin et al. 1981, Persson 1984, Smart et al. 1985, Sala et al. 1986). In general, compositional changes reflect a decrease in palatable grasses and an increase in unpalatable grasses and forbs (Dyksterhuis 1958). In this study, grazing reduced cover of the dominant matrix grass, *A. gerardii*, by 27% on the burned treatment in 1986. The combined cover of matrix species in 1986 was reduced 19.5 and 26.3% by grazing on the burned and unburned treatments, respectively. Decreased cover of superior competitors by grazing frees space for colonization and/or growth by less vigorous competitors (Connell 1978, Sousa 1984b). In grasslands, however, the effects of grazing are often patchy (Bakker et al. 1984, Senft et al. 1985). Ungulates tend to regrazed previously grazed areas while other patches receive little or no herbivory (McNaughton 1984). At a larger scale, grazing in tallgrass prairie increases species diversity due to dynamics within grazed and ungrazed patches (Collins and Barber 1985).

Species richness increased with increasing disturbance intensity (Table 2). This pattern suggests that richness is enhanced by fire and grazing (Daubenmire 1968, Anderson and Bailey 1980, Risser et al. 1981). These results agree with the model of Denslow (1980), which predicts that richness will be higher subsequent to frequently occurring natural disturbances. In the absence of these disturbances, species richness decreases in grasslands primarily because of the development of a thick litter layer (Knapp and Seastedt 1986). Burning during the early part of the growing season opens space by removing canopy cover, standing dead material, and litter. Following fire, warmer soil temperatures and increased light at the soil surface may stimulate seed germination and productivity (Hassan and West 1986). In addition, the belowground portions of many grassland perennials often survive after fire. As a result, species richness is enhanced after burning in the spring. Because the number of grass species remains relatively constant (Fig. 1D), the increase in richness is primarily a function of more forb species (Fig. 1A).

Species diversity, however, did not have the same relationship to disturbance as did species richness (Table 2). Instead, diversity was lowest on the ungrazed, burned treatment and was highest on the grazed, burned treatment. Huston's (1979) model predicts that diver-

sity will be low in systems where the superior competitor has a rapid growth rate. Because burning stimulates the growth of *A. gerardii* (Knapp 1984), a dense canopy of grasses forms rapidly after fire. In the absence of grazing, many of the forb species that are present shortly after burning are eliminated later in the growing season. This probably results from competitive exclusion by *A. gerardii* because several forb species remain on artificial soil disturbances after disappearing from patches dominated by matrix grasses (S. Collins, *personal observation*). Thus, the decrease in forb richness reflects competition with matrix grasses, not phenological change. The overall effect is increased dominance by *A. gerardii*, which decreases diversity.

A. gerardii is highly palatable (Dyksterhuis 1958). Grazing lowers the rate of canopy development by this grass, which in turn reduces dominance and increases evenness. The high richness and diversity on the grazed, burned treatment reflects increased survival of forbs as dominance by grasses such as *A. gerardii* and *S. nutans* is reduced by herbivory. The initial effects of enhanced richness following fire are maintained by grazing. Therefore, as predicted by the model of Collins and Barber (1985), species diversity will be highest in grasslands that experience a combination of natural disturbances.

Although this study was conducted in a managed system grazed by domestic cattle, similar results may occur in systems with native herbivores such as *Bison bison*. Unlike cattle, the diet of *Bison* is composed almost exclusively of grasses (Schwartz and Ellis 1981, Krueger 1986). Therefore, dominance by the matrix grasses is likely to be reduced more by *Bison* than by cattle. This inference is further substantiated by similar results from a study in burned and unburned mixed-grass prairie grazed by bison, elk, and longhorn cattle (Collins and Barber 1985).

Together, these and other studies (e.g., Dyer et al. 1982, Coppock et al. 1983) clearly document the important role of natural disturbance in North American prairies (Collins and Uno 1985). Fire, grazing, and soil disturbance by animals, however, are important factors in many different grassland systems (Burggraaf-van Nierop and van der Meijden 1984, Kruger 1984, Persson 1984, Taylor and Friend 1984, Belsky 1985, McNaughton 1985). Simple models such as the intermediate disturbance hypothesis (Connell 1978) cannot address the variable interactions among disturbances in communities with complex disturbance regimes.

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