

Modulation of Diversity by Grazing and Mowing in Native Tallgrass Prairie

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Species diversity has declined in ecosystems worldwide as a result of habitat fragmentation, eutrophication, and land-use change. If such decline is to be halted ecological mechanisms that restore or maintain biodiversity are needed. Two long-term field experiments were performed in native grassland to assess the effects of fire, nitrogen addition, and grazing or mowing on plant species diversity. In one experiment, richness declined on burned and fertilized treatments, whereas mowing maintained diversity under these conditions. In the second experiment, loss of species diversity due to frequent burning was reversed by bison, a keystone herbivore in North American grasslands. Thus, mowing or the reestablishment of grazing in anthropogenically stressed grasslands enhanced biodiversity.

In North American tallgrass prairie, diversity and productivity are controlled to a large extent by nitrogen availability (1). Historically, the spatial and temporal dynamics of nitrogen availability in prairies were driven by interactions between fire frequency and grazing by large herbivores (2–4). In general, spring fires enhance the growth of dominant C_4 grasses, and herbivores such as bison preferentially graze these grasses (2–4). Extirpation of native grazers, habitat fragmentation, elevated atmospheric nitrogen deposition, and altered fire frequency have disrupted the ecosystem structure and function of grasslands worldwide (5). To evaluate the interactive effects of grazing, nitrogen enrichment, and fire frequency on plant species diversity in native tallgrass prairie, we established two long-term field experiments at the Konza Prairie Long-Term Ecological Research site in northeastern Kansas, United States. We predicted that top-down forces, namely grazing by bison at the watershed scale or its surrogate, mowing at the plot scale, would maintain species diversity under conditions of high potential productivity. This prediction is counter to prevailing theory and experimental results which demonstrate that productivity and diversity are negatively related (6).

In the first experiment, four replicate 12 m by 12 m plots in annually burned (April) lowland prairie were established in 1986 with the following treatments: burned only; nitrogen addition at a rate of 10 g of N per square meter per year ($\text{g N m}^{-2} \text{ year}^{-1}$) as

NH_4NO_3 (7); mowing in late June with cut biomass removed; and N addition plus mowing. An unmanipulated (no burning) control treatment was included for comparison. Aerial cover of each species was visually estimated in one 10-m² circular quadrat centered in each treatment plot in July of 1989 and 1994. Aboveground biomass was measured by harvesting all plants in two 0.1-m² quadrats per replicate in early September of each year. Biomass was sorted to graminoids and forbs, dried, and weighed.

The addition of N resulted in a greater than 10-fold increase in inorganic soil nitrogen pools in the fertilized plots (Table 1). Aboveground biomass production in 1989 and 1994 was highest on the N-addition plots. In both 1989 and 1994, grasses accounted for greater than 95% of the total biomass on these plots. In contrast, aboveground biomass on the control plots was low in both years, and grasses accounted for only 56 to 68% of the total in 1989 and 1994.

In 1989, no significant differences in species richness occurred among the experimental plots (Table 1). In 1994, after 9 years of treatment, species richness on annually burned, N-addition plots was 48% lower than richness from this treatment in 1989, and nearly 66% lower than on the control plots. Mowed, annually burned, N-addition plots had more than double the species richness of plots that were not mowed, and species richness in these mowed, fertilized, burned plots was not significantly different from the control (Table 1). Thus, mowing prevented the loss of richness under conditions that otherwise led to a reduction in species diversity.

Light is often a limiting resource in highly productive herbaceous communities (6). We measured midday light levels at 10 cm above the soil surface in each treatment plot (8). Light availability on burned, N-

addition plots was one-tenth that of burned, mowed plots (Table 1). Light availability on burned, N-addition, mowed plots was significantly greater than on burned, N-addition plots that had not been mowed, but it was not significantly different from the control. This increase in light within the canopy of mowed plots may be a major mechanism by which species richness is maintained.

High species diversity in these grasslands is due to a large number of C_3 species, especially forbs (9). There were no significant differences in species richness in C_3 functional groups among treatments in 1989, but by 1994, richness differed among treatments in all functional groups except for woody species (Table 1). For all functional groups, the lowest richness occurred on N-addition, burned plots, whereas richness on burned, fertilized, mowed plots was not significantly different from the control.

In 1994, no C_3 grasses or woody species were recorded on annually burned, or burned plus N-addition treatments (Table 1). Thus, two of four functional groups were lost under conditions of both high fire frequency and N availability. In contrast, the

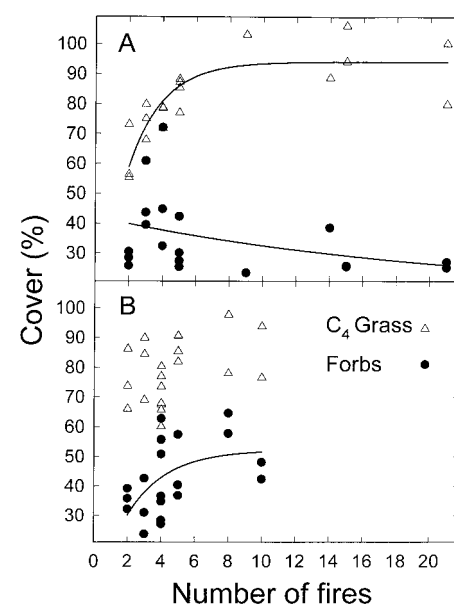


Fig. 1. Effect of fire frequency on abundance (cover per 10 m²) of C_4 grasses and forbs on ungrazed watersheds (A) and watersheds grazed by bison (B). Regression statistics are based on angular transformed cover data. C_4 grass abundance was significantly positively related to fire frequency on ungrazed treatments ($r^2 = 0.80$, $F = 46.83$, $P < 0.0001$, $n = 19$; r^2 is the correlation coefficient, and F and P were calculated from ANOVA) but not on grazed treatments. Forb abundance was significantly positively related to fire frequency on grazed treatments ($r^2 = 0.25$, $F = 6.09$, $P = 0.024$, $n = 20$), and negatively related to fire frequency on ungrazed treatments ($r^2 = 0.16$, $F = 3.42$, $P = 0.08$, $n = 19$).

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Table 1. Effects of burning, nitrogen addition, and mowing on biomass, species richness, extractable soil nitrogen, and light availability. Biomass and richness were measured in 1989, 3 years after the start of the experiment, and in 1994. Mowing occurred in late June of each year. Nitrogen data were averaged from June samples from 1993 to 1995. Light was measured in September. Differences among means in each row were determined by

analysis of variance (ANOVA) and Least significant difference (LSD) tests ($n = 4$ in all cases). Treatment means with different superscripts (a, b, c) in each row are significantly different from each other. Treatment means in rows without superscripts were not significantly different from each other (NS). (C_4 and C_3 plants have as their first product of photosynthesis a four-carbon and a three-carbon acid, respectively.)

	Control	Burned only	Burned + mowed	Burned + N	Burned + N + mowed	P
<i>1989 Assessment</i>						
Biomass (g/m ²)						
Grass	178.3 ± 81.2 ^a	336.4 ± 88.1 ^{ab}	296.0 ± 44.5 ^a	440.92 ± 213.2 ^{ab}	678.6 ± 180.4 ^b	0.0049
Forb	85.6 ± 99.9	15.2 ± 14.7	5.0 ± 3.1	2.3 ± 3.3	3.5 ± 7.8	NS
Richness (no./10 m ²)						
C ₄						
Grass	4.3 ± 1.0	5.5 ± 0.6	5.8 ± 1.0	4.3 ± 1.3	6.0 ± 0.8	NS
C ₃						
Grass	1.3 ± 1.5	0.3 ± 0.5	0.8 ± 0.5	0.8 ± 1.0	1.3 ± 0.5	NS
Forb	9.0 ± 2.6	9.0 ± 2.9	9.5 ± 3.4	5.3 ± 3.6	7.0 ± 2.9	NS
Woody	0.5 ± 0.6	0.0	0.0	0.3 ± 0.5	0.0	NS
Total	15.0 ± 1.4	14.8 ± 3.4	16.0 ± 3.4	10.5 ± 4.6	14.2 ± 2.9	NS
<i>1994 Assessment</i>						
Biomass (g/m ²)						
Grass	152.2 ± 98.2 ^a	275.9 ± 185.9 ^a	345.2 ± 73.0 ^a	757.4 ± 375.5 ^b	785.5 ± 292.1 ^b	0.0001
Forb	121.2 ± 116.6 ^a	4.9 ± 7.1 ^b	1.3 ± 1.5 ^b	0.0	36.0 ± 8.2 ^b	0.0009
Richness (no./10 m ²)						
C ₄						
Grass	5.0 ± 0.8 ^a	4.3 ± 0.5 ^{ab}	5.3 ± 1.0 ^a	2.8 ± 0.5 ^b	5.5 ± 0.6 ^a	0.0003
C ₃						
Grass	1.5 ± 1.9	0.0	0.5 ± 0.6	0.0	1.5 ± 0.6	0.074
Forb	8.2 ± 2.5 ^{ab}	9.5 ± 3.3 ^a	9.2 ± 3.0 ^a	2.8 ± 1.3 ^b	5.2 ± 1.5 ^{ab}	0.0055
Woody	0.5 ± 0.6	0.0	0.0	0.0	0.0	NS
Total	15.3 ± 3.1 ^a	13.8 ± 3.0 ^a	15.0 ± 2.8 ^a	5.6 ± 1.0 ^b	12.2 ± 2.2 ^a	0.0003
Light (μmol m ² s ⁻¹)	237.5 ± 120.2 ^{ab}	416.8 ± 205.1 ^{ab}	965.7 ± 83.5 ^c	78.8 ± 29.3 ^b	480.2 ± 247.2 ^a	0.0001
N (μg g ⁻¹ soil)*	7.3 ± 3.6 ^a	3.9 ± 1.9 ^a	2.7 ± 1.5 ^a	38.6 ± 33.2 ^b	43.5 ± 35.3 ^b	0.0001

*Concentrations of 2 M KCl-extractable inorganic nitrogen (NO₃⁻ and NH₄⁻N) in 0- to 5-cm-deep soil cores.

richness of C₃ grasses on burned, N-addition, mowed plots was equal to the richness on the control, and mowing maintained a low number of C₃ grasses on annually burned sites. Consequently, mowing prevented the loss of C₃ grasses under conditions that otherwise led to local extinction of this functional group. Woody species were not found on mowed plots.

In the second experiment, watersheds on Konza Prairie were subjected to various combinations of prescribed burning in early April and grazing by bison (*Bos bison*) (10). This was a split-plot design with random assignment of fire frequencies to watersheds in either grazed or ungrazed portions of

Konza Prairie. Some burning treatments were initiated in 1972, others in 1981. Bison were reintroduced onto a portion of Konza Prairie in October 1987, and the area grazed was increased to its current size in 1992 (11). Vegetation cover was estimated in 1995 in 40 permanently marked 10-m² circular quadrats in two replicate watersheds of each treatment.

Total species richness was highest on grazed watersheds and lowest on annually burned watersheds (Table 2). As in the experimental plots, grasses accounted for greater than 80% of aboveground biomass on annually burned sites (12). Total species richness on grazed and burned watersheds

was significantly greater than on annually burned sites and the unmanipulated watersheds (Table 2). These patterns occurred despite the fact that grazed grasslands have higher N availability than ungrazed grasslands (13).

The richness of C₃ species (grasses, forbs, and woody plants) was lowest on watersheds that were burned but not grazed (Table 2). Forb richness was highest on grazed watersheds regardless of burning treatment. The richness of C₃ grasses and forbs on burned and grazed watersheds was nearly double that on watersheds that were burned but not grazed. The richness of C₄ species was also higher on grazed, burned sites compared with the control. Thus, similar to results from mowing the experimental plots, grazing by native herbivores led to higher species richness under conditions that otherwise reduced diversity.

The abundance of plant species and functional groups in tallgrass prairie is also a function of fire frequency (14). The abundance (cover per 10 m²) of C₄ species increased as fire frequency increased in ungrazed watersheds (Fig. 1), but there was no relation between C₄ abundance and fire frequency in grazed watersheds. Forb abundance in response to fire frequency was altered by grazing as well. On watersheds

Table 2. Effect of annual fire and grazing by bison in native tallgrass prairie on plant species richness. Richness was measured in 1995 in eight 50-m² transects within each watershed. Statistical notation as in Table 1.

	Control	Grazed only	Burned only	Burned + grazed	P
Richness (no./50 m ²)					
C ₄					
Grass	6.6 ± 1.2 ^a	9.4 ± 3.2 ^b	8.3 ± 1.1 ^{ab}	9.9 ± 1.4 ^b	0.0001
C ₃					
Grass	6.4 ± 1.4 ^a	8.3 ± 2.1 ^b	3.6 ± 0.8 ^c	6.6 ± 2.0 ^a	0.0001
Forb	29.1 ± 7.4 ^a	41.5 ± 10.0 ^b	23.2 ± 5.5 ^a	40.8 ± 11.4 ^b	0.0001
Woody	4.2 ± 1.9 ^{ab}	4.8 ± 1.9 ^a	1.9 ± 0.8 ^c	3.6 ± 1.0 ^b	0.0001
Total	46.2 ± 9.8 ^a	64.2 ± 14.4 ^b	36.9 ± 10.7 ^c	60.9 ± 14.2 ^b	0.0001

where bison were excluded, there was a negative relation between abundance of forbs and fire frequency. In contrast, there was a positive relation between fire frequency and forb abundance on watersheds that were grazed by bison (Fig. 1). Thus, grazing increased the abundance of forbs under conditions that would otherwise promote dominance by C_4 grasses and lower species diversity.

Although burning is essential to maintain tallgrass prairie (15), fire alone is not a sufficient management solution for restoring prairie biodiversity as some have proposed (16). More frequent fires are now needed to resist invasion by exotics and woody species in remaining grassland fragments (16), but as shown here frequent burning dramatically increases the dominance of C_4 grasses and reduces plant species diversity (17). Whereas fire is used as a conservation tool throughout much of the tallgrass region, the use of grazing by bison or cattle as a management tool for maintaining species diversity is less common (18). Yet herbivores such as bison historically served as keystone species in tallgrass ecosystems because they reduced the competitive dominance of the C_4 grasses, increased habitat heterogeneity, and increased species diversity (19).

One consequence of anthropogenically driven global change has been the extinction or dramatic reduction in populations of keystone species (20). The role that keystone species play in community structure and ecosystem functioning is now widely recognized (21). In some systems, loss of a keystone species may decouple the critical interplay between trophic interactions and community structure (20). Our research demonstrates that by adding or maintaining top-down forces such as grazing, at least in ecosystems like grasslands that were affected historically by keystone herbivores (22), diversity in native vegetation can be retained under conditions that would otherwise lead to a decline in species richness.

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12 December 1997; accepted 16 March 1998

Anterior Cingulate Cortex, Error Detection, and the Online Monitoring of Performance

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An unresolved question in neuroscience and psychology is how the brain monitors performance to regulate behavior. It has been proposed that the anterior cingulate cortex (ACC), on the medial surface of the frontal lobe, contributes to performance monitoring by detecting errors. In this study, event-related functional magnetic resonance imaging was used to examine ACC function. Results confirm that this region shows activity during erroneous responses. However, activity was also observed in the same region during correct responses under conditions of increased response competition. This suggests that the ACC detects conditions under which errors are likely to occur rather than errors themselves.

It has been proposed that the ACC plays a prominent role in the executive control of cognition (1). This hypothesis is based, in part, on functional neuroimaging studies that show ACC activity during tasks that engage selective attention, working memory, language generation, and controlled information processing (2). Disturbances in this brain region have been reported in disorders associated with cognitive impairment, including schizophrenia and depression (3). This account of ACC function is

consistent with the rich anatomical connectivity of this region with association, limbic, and motor cortices (4). However, it is lacking in detail regarding the precise contribution of the ACC to cognitive control.

To date, the most explicit hypothesis regarding ACC function comes from event-related brain potential (ERP) studies during speeded response tasks. These studies have reported an error-related negativity (ERN), peaking 100 to 150 ms after