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Expansion of Woody Plants in Tallgrass Prairie: A Fifteen-year Study of Fire and Fire-grazing Interactions

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ABSTRACT.—Temporal changes in the abundance of trees and a common shrub, *Cornus drummondii*, were quantified for 15 y (1981–1996) in seven tallgrass prairie watersheds in Northeast Kansas. Woody plant responses to different fire frequencies and grazing were assessed with a data set that included >9000 individuals. Although 15 tree species were included in this data set, only four (*Juniperus virginiana, Celtis occidentalis, Gleditsia triacanthos* and *Ulmus americana*) were sufficiently abundant for detailed analysis. Over the 15 y study tree density increased by two- to 10-fold, except in watersheds burned annually where woody plants remained almost completely absent throughout the study. Although increased woody plant abundance was expected in watersheds protected from fire, tree and shrub density also increased substantially in watersheds burned only once in 4 y. An intermediate fire frequency (burned every 3–5 y) actually increased the abundance of *C. drummondii* relative to a low fire frequency (burned only once in 15 y). Moreover, a severe wildfire in 1991, which affected all watersheds, did not markedly reverse this pattern of increase in abundance in most tree species. Four years after the addition of native herbivores (*Bos bison*) to three of the long-term experimental watersheds (infrequently and annually burned) woody plant abundance increased by four- and 40-fold, respectively, compared to corresponding ungrazed watersheds. Thus, the presence of large ungulate grazers in tallgrass prairie resulted in a significant increase in woody plant abundance. The most parsimonious explanation for this phenomenon is that fire intensity and extent was reduced in grazed grasslands allowing greater success of woody species.

INTRODUCTION

In the last 100 y the abundance of woody plants has increased substantially in savannas and grasslands worldwide (Bragg and Hulbert, 1976; Knight *et al.*, 1994; Archer *et al.*, 1995; Wilson and Kleb, 1996; McPherson, 1997; Hoch and Briggs, 1999). Changes in disturbance regimes and resource abundance have been implicated as critical for the establishment and spread of woody plants within the grassland matrix, with changes in climate, CO_2 concentration, livestock grazing and fire frequency specifically proposed as drivers (Schlesinger *et al.*, 1990; Bahre and Shelton, 1993; Archer *et al.*, 1995; Brown and Archer, 1999; Bond and Midgley, 2000).

The tallgrass prairies of North America are particularly valuable for evaluating tree/grass interactions because this biome occupies a tension zone between forest and grassland (Axelrod, 1985) and historically this tension zone has been quite sensitive to shifts in climate, land management and fire regime (Manogaran, 1983; Grimm, 1984; Knight *et al.*, 1994; Briggs and Gibson, 1992; Hayden, 1998). In some sites changes in land management (fire suppression, a regional phenomenon) have resulted in the conversion of native tallgrass prairie to closed canopy forest in as little as 35 y (Hoch and Briggs, 1999). Conversely, annual fires minimize the abundance of woody species in this and most other grasslands (Bragg and Hulbert, 1976; Briggs and Gibson, 1992; Hartnett and Fay, 1998). Little is known about the responses of woody species to less extreme fire regimes, yet infrequent fires (3–

4 y intervals between fires) are regionally more common than either annual fire regimes or complete fire suppression and the interactive effects of fire and ungulate grazing, in particular, must be evaluated if the ecological consequences of shifting land management and regional changes in land cover are to be assessed.

There is no doubt that, historically, grazing by large ungulates such as bison (*Bos bison*) was important in grasslands such as the tallgrass prairie (Axelrod, 1985; Knapp *et al.*, 1999). Today, domestic cattle (*Bos bos*) have replaced bison in much of the remaining tallgrass prairie, although substantial bison herds now exist in public and private preserves (Knapp *et al.*, 1999). Bison (and cattle) are primarily graminoid feeders (Hartnett *et al.*, 1997) and, thus, might be expected to have few direct effects on woody plants (but *see* Coppedge and Shaw, 1997). However, bison grazing removes aboveground biomass (the fine fuel needed for fires) in a patchy fashion and thus can alter fire intensity and behavior (Knapp *et al.*, 1999). Because bison preferentially graze in recently burned sites (Coppedge and Shaw, 1998; Briggs *et al.*, 1998; Knapp *et al.*, 1999), these effects should be most pronounced in frequently burned sites where woody plants would be least abundant in the absence of grazers.

The goals of this research were to: (1) assess the long-term effects of different fire frequencies on the abundance of several tree species and a common shrub, *Cornus drummondii*, in tallgrass prairie and (2) evaluate the interactive effects of fire and bison grazing on the temporal dynamics of woody plant abundance. Our research was based on the long-term experimental research program at the Konza Prairie LTER site in NE Kansas. We took advantage of a unique sequence of experimental treatments and events in which 10 y of woody plant abundance was mapped in seven watersheds exposed to high, intermediate and low fire frequencies in the absence of grazing. Bison were then introduced to a subset of the watersheds allowing for fire-grazing interactions to be assessed.

MATERIALS AND METHODS

Konza Prairie Biological Station (KPBS) includes over 3487 ha of native tallgrass prairie located 10 km south of Manhattan, Kansas (Knapp and Seastedt, 1998). Konza Prairie is representative of the Flint Hills, a dissected upland with chert-bearing limestone layers and steep-sided hills. Elevation on KPBS ranges from 320 m to 444 m and the climate is temperate midcontinental with 75% of the annual precipitation (35-y mean = 835 mm) occurring during the growing season [April to September; Hayden (1998)].

The flora of Konza Prairie is dominated by big bluestem (*Andropogon gerardii*), Indian grass (*Sorgastrum nutans*), little bluestem (*Schizachyrium scoparius*) and switch grass (*Panicum virgatum*) (Freeman and Hulbert, 1985; Freeman, 1998). Under an experimental plan initiated in 1971 and expanded in 1981, each of 60 watersheds (catchment basins) have been assigned grazing (by bison, cattle) or ungrazed and prescribed burning (mid-April) treatments with fire frequencies ranging from annual, 2-, 4-, 10- and 20-y intervals (Knapp and Seastedt, 1998). Before the purchase of KPBS by the Nature Conservancy in 1972, cattle grazed most of the area and it is estimated that the area was burned at intervals of 1–3 y (Knapp and Seastedt, 1998).

On seven watersheds that encompassed a range of burning treatments (annual burning to long-term fire exclusion), detailed mapping of all woody vegetation has occurred at 5-y intervals. Although a few watersheds have been mapped since 1973, most watersheds were first mapped in 1981, thus we restricted our analyses to the 1981 to 1996 time period so that comparable data were available for all watersheds. Detailed sampling methodology is presented in Briggs and Gibson (1992), but, briefly, each watershed was surveyed in transects 15–20 m wide. The locations of all trees and shrubs extending above the grass canopy were marked on a mylar overlay on a large-scale aerial photograph of the area. Each individual was identified and tree heights were estimated to the nearest meter. The aerial extent of shrub patches was also recorded on the map overlay. This information was subsequently digitized into a Geographic Information System (ARC/INFO).

Four watersheds in this study were consistently exposed to three fire frequency treatments and protected from grazing since 1972. These included an annually burned watershed (high fire frequency); a watershed burned at 4-y intervals or six times before 1996 (infrequently burned) and 2 low fire frequency watersheds (burned only once since 1972). The three other watersheds used in this study were protected from fire from 1973 to 1988 before high and intermediate fire frequency treatments were imposed. Since 1992 these watersheds have also been grazed by bison (Collins *et al.*, 1998). The bison herd (ca. 220 individuals) on Konza Prairie is resident throughout the year, has access to 10 watersheds burned at various frequencies and is not actively managed (Knapp *et al.*, 1999). The target level of biomass consumption by the herd is ca. 25% of aboveground biomass (Hartnett *et al.*, 1997).

Although watersheds were mapped in 1981, 1986, 1991 and 1996, data from 1991 were omitted because an April 1991 wildfire burned over 2160 ha of KPBS (62% of the area; Briggs *et al.*, 1994) including all seven watersheds mapped for woody vegetation. Although many individuals likely survived this fire and resprouted basally (pers. observ.), they were difficult to locate during the 1991 mapping effort.

To assess how fire frequency affected tree and shrub abundance, those individuals and species that persist in tallgrass prairie primarily because they grow in protected areas or along riparian corridors (*i.e.*, *Populus deltoides*, *Salix* sp.) were excluded from detailed analyses. This is because fires seldom burn or do so at a lower intensity in such sites. Thus, we constructed a spatial model with a combination of GIS coverages of the watersheds that included stream drainages, elevation, slope, aspect and soil types to calculate the proportion of the watersheds that would be exposed to fire and eliminate those areas where fires would not likely impact woody plants. With this model, we delineated a buffer around all stream channels with the width of the buffer determined by the order of the stream, the slope around the stream channel and the soil type. Rocky areas with thin soils also had buffers constructed around them. Although watershed size varied substantially, the proportion of each watershed that was excluded from analyses was similar (27–34%). With these buffers identified, individuals mapped within them could then be excluded from analysis. Because four tree species (*Ulmus americana*, *Gleditsia triacanthos*, *Celtis occidentalis* and *Juniperus virginiana*) accounted for over 90% of all individuals mapped, these species were assessed in more detail to determine their responses to fire and grazing treatments over the 15-y period.

A statistical analysis of the effects of fire frequency on woody plant abundance was problematic because of the trade-offs inherent in our choice of mapping a few large watersheds vs. many replicated small plots. The low density of trees and their random occurrence (Briggs and Gibson, 1992) dictated the former approach. Using the 1981, 1986 and 1996 mapping campaigns as replicates, we ranked the abundance of each of the four most abundant tree species among the three fire frequency treatments (n = 12 rankings) and tested the null hypotheses that the ranking of species would not differ among the treatments. A Kruskal-Wallis test using the Wilcoxon option of the Nparlway procedure in SAS with Wilcoxon scores was performed (SAS, 1989). These methods were then used to determine if the widespread shrub species, *Cornus drummondii*, responded similarly and if grazing altered responses of trees and shrubs to fire. The latter comparisons were possible because before bison were introduced to the grazed watersheds, these sites were included in the analysis with the other ungrazed watersheds.

TABLE 1.—The most common tree species mapped from 1981 to 1996 on Konza Prairie Biological Station. Also shown noted is the capability of a species to resprout after fire, the maximum density of trees in watersheds and the number of watersheds (#) in which the species was recorded(#)

Species	Resprout after fire	Maximum Density/ha	#
Gleditsia triacanthos	Yes, and root suckering	52.8	6
Ulmus americana	Yes	48.0	6
Populus deltoides	Yes	13.6	7
Celtis occidentalis	Yes	12.2	4
Juniperus virginiana	No	5.1	3
Quercus muehlenbergii	Yes	3.0	3

RESULTS AND DISCUSSION

The 15-y data set included >9000 individual trees recorded on KPBS. A total of 15 tree and 12 shrub species (not including short-statured shrubs within the grass canopy or subshrubs) were encountered, with six trees species exceeding a mean density of one individual per ha (Table 1). These six species accounted for over 98% of all individuals recorded. Other tree species noted on KPBS included: *Gymnocladus dioica*, *Morus rubra* and *Cercis canadensis*. Only one species (*Populus deltoides*) was found on all seven watersheds over the 15-y period. This species was restricted to stream channels (Fowells, 1965). In addition to *Cornus drummondii*, the most abundant shrub species recorded included: *Rhus glabra*, *Prunus americana*, *R. aromatica* and *Zanthoxylum americanum*.

Fire effects on woody plant abundance.—In general, tree density increased on KPBS during the 15-y study (Fig. 1) with the exception of watersheds burned frequently (annual fire). There was also a general increase in the area of the shrub *Cornus drummondii* over time (Fig. 2), again with the exception of annually burned watersheds. The area of this shrub also increased dramatically 5 y after the 1991 wildfire in both intermediate and high fire frequency watersheds that were grazed by bison.

In watersheds without bison, fire frequency had a dramatic impact on tree density (Fig. 1). As expected from previous work (Briggs and Gibson, 1992; Hartnett and Fay, 1998), tree density on the high fire frequency watersheds was lowest ($P < 0.05$) among the three treatments (Fig. 1) and this was also true when tree species were considered individually (Table 2). Similarly, tree densities were highest ($P < 0.05$) at the lowest fire frequency (Fig. 1) and of intermediate density at the intermediate fire frequency in all three sampling efforts. Only one exception to this pattern occurred when tree species were considered individually (Table 2; *Ulmus americana* in 1996).

Of the four most common tree species, the two least abundant (*Juniperus virginiana* and *Celtis occidentalis*) were found only in watersheds where fire frequencies were low (Table 2). *Juniperus virginiana* with its thin bark, its inability to resprout after fire (Table 1) and its shallow roots that can be injured by light surface fires (Arend, 1950), is not well adapted to survive a grassland fire, thus this pattern is not surprising. *Celtis occidentalis* also has a thin bark and although it can resprout after fire, it only persists in areas when fire is eliminated for a long time.

In contrast, *Ulmus americana* and *Gleditsia triacanthos* were the most abundant trees (Table 1) in watersheds with an intermediate as well as a low fire frequency (Table 2). Both of these tree species resprout vigorously after fire or cutting (Stoutemyer *et al.*, 1944;

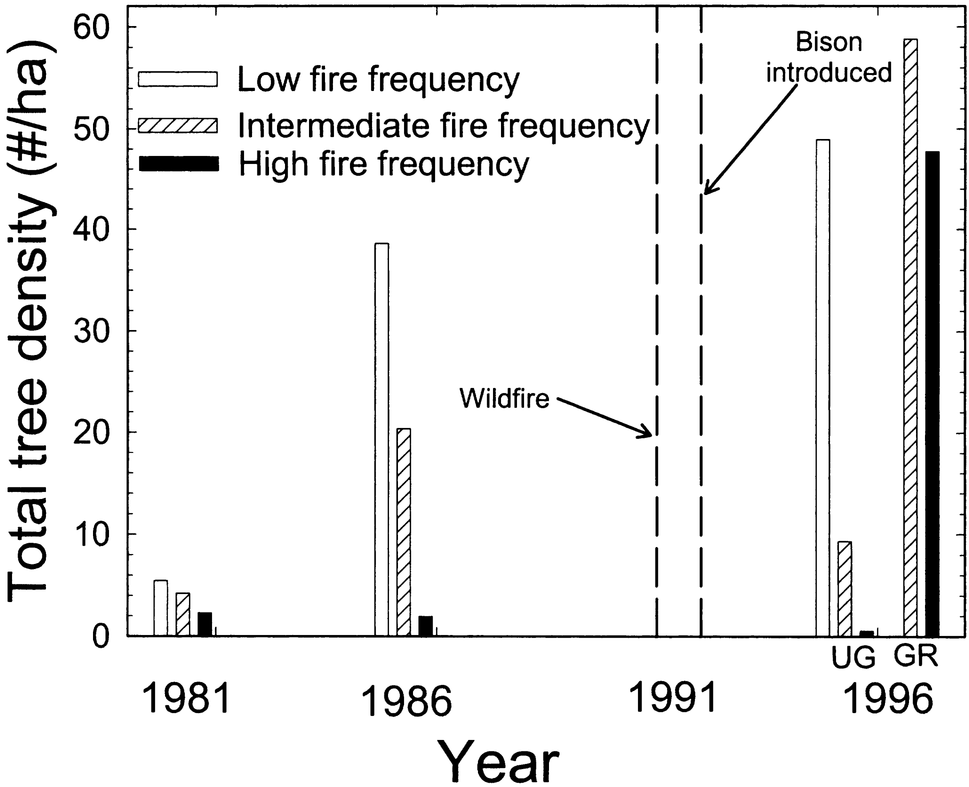

FIG. 1.—Total tree density on Konza Prairie Biological Station from seven selected watersheds under three burning treatments from 1981 to 1996. High fire frequency = annual spring burning; intermediate fire frequency = burned every 3 to 5 y; low fire frequency = burned once during this study. The two dashed vertical lines denote the wildfire of 1991 and the reintroduction of *Bos bison*. UG = Ungrazed; GR = Grazed watersheds in 1996

Abrams, 1988) and this vegetative response is probably responsible for their ability to survive more frequent fires.

Based on the observed responses of trees to fire frequency and previous work by Abrams (1988), an abundance ranking of low > intermediate > high fire frequency was expected for the common shrub *Cornus drummondii* in this grassland. Although annual fire frequencies did maintain this shrub at very low levels, intermediate fire frequency actually increased the area of *C. drummondii* relative to a low fire frequency (Fig. 2). Clearly, a fire frequency of every four years is not sufficient to slow the expansion of this species in tallgrass prairie.

Grazing–fire interactions.—No watersheds were exposed to a low fire frequency and grazed by bison, but grazed watersheds with high and intermediate fire frequencies can be compared with ungrazed watersheds in order to determine if grazing altered the effects of fire. Although statistical comparisons were not possible due to a lack of replicate watersheds, the greater density of trees in grazed vs. ungrazed watersheds with an intermediate fire frequency and the 40-fold increase in trees in the annually burned grazed watershed strongly suggests that the presence of bison has resulted in a greater increase in tree abundance

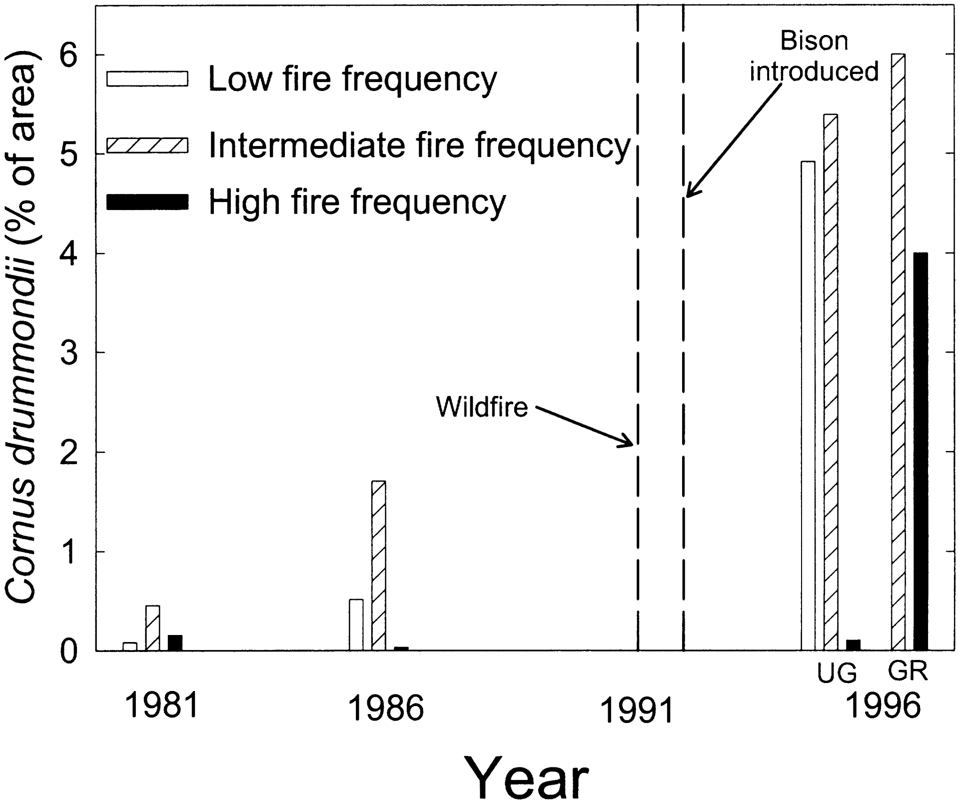

FIG. 2.—Percentage of area occupied by *Cornus drummondii* on seven selected watersheds exposed to a variety of burning treatments from 1981 to 1996 on Konza Prairie Biological Station. High fire frequency = annual spring burning; intermediate fire frequency = burned every 3 to 5 y; low fire frequency = burned once during this study. The two dashed vertical lines denote the wildfire of 1991 and the re-introduction of *Bos bison*. UG = Ungrazed; GR = Grazed watersheds in 1996

TABLE 2.—Mean densities (#/ha) of the four most abundant tree species on Konza Prairie Biological Station from selected watersheds under a variety of burning and grazing treatments from 1981 to 1996. Low = low fire frequency, burned once during this study; Inter = Intermediate fire frequency, burned every 3–5 y; High = High fire frequency, annual spring burning

	1981			**1986**			**1996**				
	Ungrazed			Ungrazed			Ungrazed			Grazed	
Species	Low	Inter	High	Low	Inter	High	Low	Inter	High	Inter	High
Gleditsia triacanthos	0.0	0.3	0.0	7.7	1.4	0.0	30.2	2.3	0.0	14.7	40.8
Ulmus americana	1.7	3.2	0.0	20.0	10.2	0.0	4.0	6.9	0.0	28.5	12.7
Celtis occidentalis	0.8	0.0	0.0	6.5	0.0	0.0	7.3	0.0	0.0	2.8	3.1
Juniperus virginiana	0.0	0.0	0.0	3.6	0.0	0.0	0.8	0.0	0.0	0.3	0.3

on KPBS than occurred on ungrazed sites (Fig. 1). It is important to note that these grazed watersheds were included in the 1986 mapping campaign before the introduction of bison, thus these results cannot be attributed to different watersheds being sampled during the study. This general increase in woody species in frequently burned watersheds as a result of grazing activities can be seen in each of the four tree species analyzed individually, even those very sensitive to fire (*Celtis occidentalis* and *Juniperus virginiana,* Table 2) as well as in *Cornus drummondii* (Fig. 2).

With grazing, the abundance of woody plants in tallgrass prairie increased over time regardless of the fire frequency. Although ungulates could be responsible for dispersing seeds of woody plants and enhancing their establishment by reducing herbaceous competition (Van Auken, 1989; Archer, 1995), the most parsimonious explanation for this phenomenon is that fire intensity and extent is reduced in grazed grasslands due to the heterogeneous reduction fuel loads (Knapp *et al.*, 1999). This coexistence of trees and grasses in annually burned and grazed tallgrass prairie today is not consistent with early descriptions of this biome as treeless despite the historical prevalence of fire and large herds of native ungulates (Axelrod, 1985; McHugh, 1972). Instead, its likely that the extreme fragmentation of the remaining tracts of tallgrass prairie (Samson and Knopf, 1994; Leach and Givnish, 1996) and the resultant increase in seed source from adjacent populations of woody species is driving this fire-grazing interaction. Thus, conserving the remaining tracts of tallgrass prairie as primarily herbaceous-dominated systems may require more frequent fire if ungulate grazers are present.

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LITERATURE CITED

ABRAMS, M. D. 1988. Effects of prescribed fire on woody vegetation in a gallery forest understory in Northeastern Kansas. *Trans. Kans. Acad. Sci.,* **91**:63–70.

ARCHER, S. 1995. Tree-grass dynamics of savanna vegetation: reconstructing the past and predicting the future. *EcoScience,* **2**:83–99.

———, D. SCHIMEL AND E. H. HOLLAND. 1995. Mechanisms of shrubland expansion: land use, Climate or CO_2. *Climatic Change,* **29**:91–99.

AREND, J. L. 1950. Influence of fire and soil on distribution of eastern redcedar in the Ozarks. *J. For.,* **48**:129–130.

AXELROD, D. I. 1985. Rise of the grassland biome, central North America. *Bot. Rev.,* **51**:163–201.

BAHRE, C. J. AND M. L. SHELTON. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *J. Biogeography,* **20**:489–504.

BOND, W. J. AND G. F. MIDGLEY. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biol.,* **6**:865–869.

BRAGG, T. B. AND L. C. HULBERT. 1976. Woody plant invasion of unburned Kansas bluestem prairie. *J. Range Manage.,* **29**:19–23.

BRIGGS, J. M. AND D. J. GIBSON. 1992. Effect of burning on tree spatial patterns in a tallgrass prairie landscape. *Bull. Torrey. Bot. Club,* **119**:300–307.

———, J. T. FAHNESTOCK, L. WARD AND A. K. KNAPP. 1994. Aboveground biomass in tallgrass prairie: effect of time since last fire, p. 165–170. *In:* R. G. Wickett, P. D. Lewis, A. Woodliffe and P. Pratt (eds.). Proceedings 13th North America Prairie Conference, Windsor, Ontario CA.

———, M. D. NELLIS, C. L. TURNER, G. M. HENEBRY AND H. SU. 1998. A landscape perspective of patterns and processes in tallgrass prairie, p. 265–279. *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, New York.

BROWN, J. R. AND S. ARCHER. 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology,* **80**:2385–2396.

COLLINS, S. L., A. K. KNAPP, J. M. BRIGGS, J. M. BLAIR AND E. M. STEINAUER. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science,* **280**:745–747.

COPPEDGE, B. R. AND J. H. SHAW. 1997. Effects of horning and rubbing behavior by bison (*Bison bison*) on woody vegetation in a tallgrass prairie landscape. *Am. Midl. Nat.,* **138**:189–196.

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

FOWELLS, H. A. 1965. Silvics of forest trees of the United States. Agricultural Handbook No. 271. Forest Service U.S.D.A. Washington, DC. 772 p.

FREEMAN, C. C. AND L. C. HULBERT. 1985. An annotated list of the vascular flora of Konza Prairie Research Natural Area, Kansas. *Trans. Kans. Acad. Sci.,* **88**:84–115.

———. 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, New York.

GRIMM, E. C. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. *Ecol. Monogr.,* **54**:291–311.

HARTNETT, D. C., A. A. STEUTER AND K. R. HICKMAN. 1997. Comparative ecology of native and introduced ungulates, p. 72–101. *In:* F. Knopf and F. Samson (eds.). Ecology and conservation of great plains vertebrates. Springer-Verlag, New York.

——— AND P. A. FAY. 1998. Plant populations: patterns and processes, p. 81–100. *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, New York.

HAYDEN, B. P. 1998. Regional climate and the distribution of tallgrass prairie, p. 19–34. *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, New York.

HOCH, G. A. AND J. M. BRIGGS. 1999. Expansion of eastern red cedar (*Juniperus virginiana*) in the northern Flint Hills, Kansas, p. 9–15. *In:* J. T. Springer (ed.). Proceedings 16th North American Prairie Conference. University of Nebraska, Kearney.

KNAPP, A. K. AND T. R. SEASTEDT. 1998. Grasslands, Konza Prairie and long-term ecological research, p. 3–15. *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, New York.

———, 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.

KNIGHT, C. L., J. M. BRIGGS AND M. D. NELLIS. 1994. Expansion of gallery forest on Konza Prairie Research Natural Area, Kansas, USA. *Landscape Ecol.,* **9**:117–125.

LEACH, M. K. AND T. J. GIVINISH. 1996. Ecological determinants of species loss in remnant prairies. *Science,* **273**:1555–1561.

MCHUGH, T. 1972. The time of the buffalo. Knopf, New York. 339 p.

MCPHERSON, G. R. 1997. Ecology and management of North American savannas. University of Arizona Press, Tucson.

MANOGARAN, C. 1983. The prairie peninsula: a climatic perspective. *Physical Geography,* **4**:153–166.

SAMSON, F. AND F. KNOPF. 1994. Prairie conservation. *BioScience,* **44**:418–421.

SAS INSTITUTE INCORPORATED. 1989. SAS/STAT User's Guide, Version 6, 4th ed. Vol. 1 and 2. 1842 p.

SCHLESINGER, W. H., J. F. REYNOLDS, G. L. CUNNINGHAM, L. F. HUENNEKE, W. H. JARRELL, R. A. VIRGINIA AND W. G. WHITFORD. 1990. Biological feedbacks in global desertification. *Science,* **247**:1043–1048.

STOUTEMYER, V. T., F. L. O'ROURKE AND W. STEINER. 1944. Some observations on the vegetative propagation of honeylocust. *J. For.,* **42**:32–36.

VAN AUKEN, O. W. AND J. K. BUSH. 1989. *Prosopis glandulosa* growth: influence of nutrients and simulated grazing of Bouteloua curtipendula. *Ecology,* **70**:512–516.

WILSON, S. D. AND H. R. KLEB. 1996. The influence of prairie and forest vegetation on soil moisture and available nitrogen. *Am. Midl. Nat.,* **136**:222–231.

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