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Reviewed work(s):

Source: *BioScience*, Vol. 55, No. 3 (March 2005), pp. 243-254

Published by: [University of California Press](#) on behalf of the [American Institute of Biological Sciences](#)

Stable URL: <http://www.jstor.org/stable/10.1641/0006-3568%282005%29055%5B0243%3AAEITCA%5D2.0.CO%3B2>

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An Ecosystem in Transition: Causes and Consequences of the Conversion of Mesic Grassland to Shrubland

JOHN M. BRIGGS, ALAN K. KNAPP, JOHN M. BLAIR, JANA L. HEISLER, GREG A. HOCH, MICHELLE S. LETT, AND JAMES K. McCARRON

Woody plant expansion is one of the greatest contemporary threats to mesic grasslands of the central United States. In this article, we synthesize more than 20 years of research to elucidate the causes and consequences of the ongoing transition of C₄-dominated grasslands to savanna-like ecosystems codominated by grasses and woody plants. This transition is contingent on fire-free intervals, which provide the opportunity for recruitment both of new individuals and of additional shrub and tree species into this grassland. Once shrubs establish, their cover increases regardless of fire frequency, and infrequent fires accelerate the spread of some shrub species. This process has resulted in a new dynamic state of shrub–grass coexistence in the mesic grasslands of North America. Important consequences of this shift in plant life-form abundance include alterations in plant productivity, species diversity, and carbon storage. Without drastic measures such as mechanical removal of shrubs, it is unlikely that management of fire and grazing regimes alone will be sufficient to restore historic grass dominance in these ecosystems.

Keywords: grasslands, tallgrass prairie, woody vegetation, fire, grazing

Graslands and savannas occupy more than 40% of the global terrestrial landscape (Chapin et al. 2001), and their rapid responses to changes in land management and climate can have dramatic ecological and social consequences (Lauenroth et al. 1999). Temperate grasslands are important from both agronomic and ecological perspectives. These grasslands are the basis of an extensive livestock production industry in North America and elsewhere. Grasslands sequester and retain large amounts of soil carbon (C) (Amthor et al. 1998), and thus they are an important component of the global C cycle (Schimel et al. 1994).

Historically, the major threat to the mesic grasslands of the United States (and of the world) was conversion to row-crop agriculture. Although the conversion of grasslands to agriculture continues today, the most significant loss of grassland is now due to changing land management coupled with other global change phenomena (Mitchell 2000). Understanding the mechanisms driving reductions in the extent and quality of grasslands, and forecasting the sustainability of the remaining tracts of these ecosystems, will be key to their successful management.

In this synthesis, we focus on the tallgrass prairies of North America and present evidence that this productive grassland is threatened by an increase in the abundance of native woody species—an expansion of woody plant cover originating both from within the ecosystem and from adjacent ecosystems.

Increased cover and abundance of woody species in grasslands and savannas have been observed worldwide (Archer et al. 1995), with well-known examples from Australia (Brown and Carter 1998), Africa (Moleele and Perkins 1998), and South America (Dussart et al. 1998). In North America, this phenomenon has been documented in mesic tallgrass prairies of the eastern Great Plains (Bragg and Hulbert 1976, Knight et al. 1994, Hoch and Briggs 1999, Briggs et al. 2002, Hoch et al. 2002, Heisler et al. 2003), subtropical savannas of Texas (Archer et al. 1988), desert grasslands of the Southwest (Schlesinger et al. 1990), and the upper Great Basin (Miller and Rose 1995). Purported drivers of the increase in woody plant abundance are numerous and include changes in climate, atmospheric carbon dioxide (CO₂) concentration, nitrogen (N) deposition, grazing pressure, and disturbance regimes (e.g., the frequency and intensity of fire) (Schlesinger et al.

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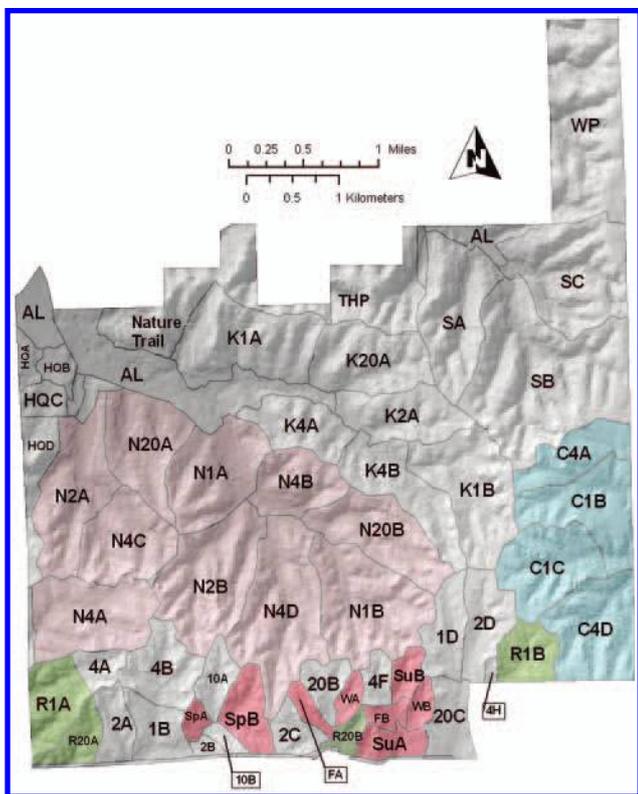


Figure 1. Konza Prairie experimental design and watershed-level fire and grazing treatments. Watersheds with bison (codes beginning with N) are highlighted in pink, and cattle-grazed watersheds (codes beginning with C) are blue. All other watersheds are ungrazed. Numbers in the watershed codes designate fire return intervals for spring-burned watersheds, and the letter A, B, C, or D at the end of a code identifies replicate watersheds of the same treatment (e.g., 4B = burned every 4 years, replicate B). Watersheds subject to different seasons of fire are highlighted in red, and the fire treatment reversal watersheds (codes beginning with R) are highlighted in green. Many plot-level experiments are located at the headquarters area (codes beginning with HQ) in the northwest portion of the site. Abbreviations: AL, alluvial soil; F, fall burns; K, Kings Creek watershed; Sp, spring burns; Su, summer burns; THP, Texas hog pasture; W, winter burns; WP, white pasture (leased for cattle grazing).

1990, Archer et al. 1995, Brown and Archer 1999, Van Auken 2000, Briggs et al. 2002, Hoch et al. 2002).

The tallgrass prairies of North America are particularly well suited for evaluating transitions from grassland to forest. Tallgrass prairie occupies a tension zone between more arid grasslands and more mesic forests (Axelrod 1985), making it particularly responsive to shifts in climate, land management, and fire regimes (Knight et al. 1994, Briggs and Gibson 1992, Hayden 1998). Although the expansion of trees and shrubs on prairies in the absence of fire was well documented long ago (Gleason 1913), the consequences of more moderate alterations in fire regime in these grasslands are less

certain, as is the potential for restoring grasslands after the conversion to shrub or forest dominance. In this article, we synthesize more than 20 years of field research, coupled with a 63-year record of aerial photographs from one of North America's most intensively studied grassland sites, the Konza Prairie Biological Station (KPBS; figure 1) in Kansas. Our goal is to provide a synoptic perspective on the transition of a C_4 graminoid ecosystem to one dominated by C_3 woody plants, with a focus on identifying key drivers, mechanisms of expansion and persistence, and consequences of displacement of grasses by woody plants. The highly productive mesic grasslands (tallgrass prairie) of the central United States are particularly appropriate ecosystems for studying this phenomenon, given that these grasslands are among North America's most endangered ecosystems, and woody plant expansion is a threat to the remaining tracts of this once expansive ecosystem.

Patterns of woody vegetation expansion

Historically, most of the tallgrass prairie in North America was lost when the land was converted to row-crop agriculture (Samson and Knopf 1994). Although the loss of native grasslands because of agricultural conversion is still occurring in some places, dramatic increases in the abundance of woody plants in tallgrass prairie threaten the remaining tracts of this grassland, and the expansion of woody vegetation into grasslands will continue to be a threat to grasslands in the future. Increases in woody plant cover can take several forms, including (a) expansion of bottomland hardwood forests from within the grasslands and (b) increases in shrub and conifer (*Juniperus* spp.) cover on slopes and uplands. In an analysis of the original land office surveys for KPBS, Abrams (1986) reported a dramatic increase in gallery forest (narrow bands of hardwood forest associated with deep, alluvial-colluvial soil deposits along major stream drainages) between 1859 and 1939. In 1859, only two areas of continuous forest, totaling about 5 hectares (ha), were noted. Because these surveys were conducted only along section lines (i.e., north-south and east-west), and the surveyors were from areas where forest cover was much greater, the forested area was probably underestimated. However, in general, the Flint Hills region in the 1800s was described as rolling prairie devoid of woody vegetation (Abrams 1986).

Knight and colleagues (1994) conducted a detailed spatial analysis of the extent of gallery forest on KPBS by digitizing aerial photographs taken over a 46-year period. Here we include data from 2002 to extend that study (figure 2). On the basis of a GIS (geographic information system) database that included spatial coverages of soil, a digital elevation model, and a fire history of KPBS, it is possible to perform a spatially explicit analysis of the historic expansion of the gallery forest. In contrast to the 5 ha of forest recorded in 1859 (Abrams 1986), more than 159 ha of forest was present on KPBS in 1939. By 2002, the area of mapped forest had increased to 274 ha (a 72% increase in areal extent in 63 years). More important, Knight and colleagues (1994) concluded that

availability of suitable landscape units would not limit the future expansion of gallery forest on KPBS, since only 10% to 15% of the alluvial–colluvial deposits along stream channels (the most common edaphic substrate for forest on KPBS) were forested. This suggests that other factors, such as fire or drought, had historically limited the extent of woody vegetation in this system, and that continued expansion is likely to occur in the future.

Using a long-term data set from upland topographic positions on KPBS, Heisler and colleagues (2003) quantified patterns of change in shrub cover, frequency, and species richness associated with three distinct fire regimes on Konza Prairie. From 1983 to 2000, shrub cover increased most dramatically in sites with a fire frequency of once every 4 years (intermediate frequency; increase of 28.6%), followed by sites in which fire occurred only once during the 18-year period (low frequency; increase of 23.7%). While annual spring fires effectively prevented the recruitment of new woody plant species, shrub cover still increased slightly (3.7%). Shrub species richness doubled (from three species to six, all of them native species) during this 18-year period in the intermediate and low-frequency fire sites. These data indicate that periods without fire are necessary for the recruitment both of new individuals and of additional shrub species within this grassland. However, once established, shrubs persist even in frequently burned areas, and shrub cover increases regardless of fire frequency, with the greatest rate of increase at low and intermediate frequencies. This discovery was surprising, as an intermediate fire frequency of 3 to 4 years is thought to be the historical fire frequency before extensive settlement by Europeans (Knapp et al. 1998a). These persistent shrub islands eventually become large enough to resist fire in their interior and can provide safe sites for fire-sensitive forest species, thus facilitating tree invasion of the grassland (figure 3).

Fire, grazing, and the increase in woody vegetation in grasslands

Changes in resource abundance and disturbance regimes have been implicated as critical for the establishment and spread of woody plants within grasslands, driven by changes in climate, livestock grazing, and fire regimes. Although fire regime is critically important in determining the cover and extent of woody vegetation in mesic grasslands (figure 4), the interaction of fire and livestock grazing can exacerbate the expansion of woody vegetation within tallgrass prairie. While chronic, high levels of herbivory by domestic animals are postulated to be a key driver of shrub expansion in semiarid grasslands (Van Auken 2000), the primacy of fire in mesic grasslands results in unique interactions between fire and grazing regimes. Long-term (20-year) data sets on the responses of woody plants to different fire frequencies and grazing on KPBS have been generated by mapping all trees and shrubs extending above the grass canopy in watersheds under a variety of grazing and burning treatments (figure 1;

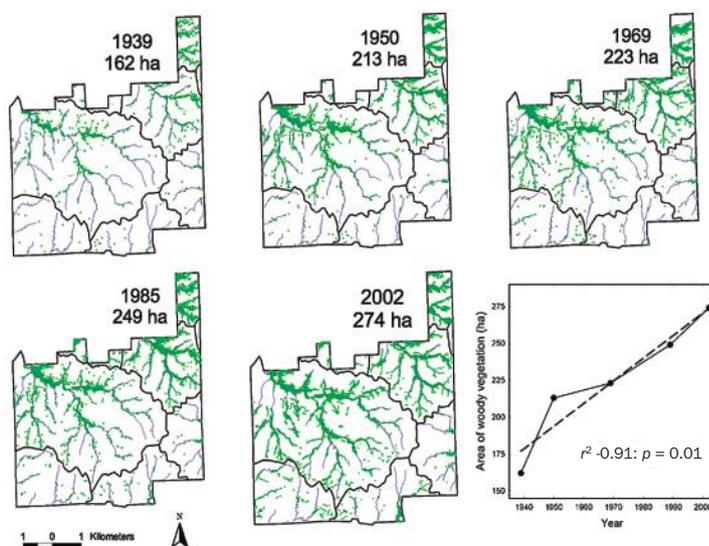


Figure 2. GIS (geographic information system) representation of gallery forest expansion, digitized from aerial photographs from 1939, 1950, 1969, 1985, and 2002. From 1939 to 2002, the extent of the gallery forest increased from 162 hectares (ha) to 274 ha (lower right panel). Major drainage boundaries at the Konza Prairie Biological Station are outlined in black; some of the major streams are outlined in blue. Updated from Knight and colleagues (1994).

Briggs and Gibson 1992, Briggs et al. 2002). Over a 20-year period, woody plant density increased by two- to tenfold, except in those watersheds that were burned annually. Although increased woody plant abundance was expected in watersheds protected from fire, tree and shrub density also increased substantially in watersheds burned once every 4 years, consistent with the results of Heisler and colleagues (2003). Surprisingly, this intermediate fire frequency actually increased the abundance of the common shrub *Cornus drummondii* more than did the almost complete fire exclusion (one fire in 15 years; figures 5, 6).

Four years after the addition of native herbivores (*Bos bison*) to a subset of the long-term experimental watersheds (infrequently and annually burned; figure 1), woody plant abundance increased by 4- and 40-fold, respectively, compared with corresponding ungrazed watersheds. Thus, the presence of large ungulate grazers in tallgrass prairie greatly accelerated the increase in woody plant abundance (figure 7).

The interactive effects of fire and grazing on the mortality of red cedar (*Juniperus virginiana*), a common and aggressive invader of tallgrass prairie, were experimentally examined by Hoch and colleagues (2002). Individuals of *J. virginiana* are easily killed by fire, and this sensitivity enabled us to determine whether grazing altered patterns of fire-induced mortality. Trees at the four study sites ranged in size from seedlings to individuals more than 2.5 meters (m) tall. Two sites had not been grazed for 3 years before 1999, and the other two sites had been grazed annually for at least 5 years. None of the sites had been burned for 3 to 4 years before the study. The potential fuel load on the ungrazed and grazed sites



Figure 3. A *Gleditsia triacanthos* tree within an island of *Cornus drummondii*. This shrub island became large enough to resist fire in its interior and provided a safe site for the germination and growth of this tree. Photograph: Alan K. Knapp.

was estimated from herbaceous biomass data obtained from comparable tallgrass prairie sites, and more than 1800 trees were sampled for postfire mortality. Grazing reduced potential fuel loads by 33%, and this reduction significantly affected red cedar mortality. For example, in ungrazed sites, fire-induced tree mortality averaged 94% (± 1.8 standard error [SE]), while in low-fuel, grazed sites, mortality was only 32% (± 6.4 SE). In the ungrazed areas, the mortality rate of trees in the smallest size class (0.6 to 1.4 m) was 100%, and mortality in the largest class size (2.8 m) averaged more than 80%. In contrast, the activities of grazers lowered mortality in the 0.6- to 1.4-m size class to less than 65%, and trees greater than 2 m had mortality rates of less than 20% in grazed areas (figure 8). These results confirm the mechanistic link between grazing, fuel load, and the success of woody vegetation in the fire-prone tallgrass prairie.

Resource availability and the expansion of woody vegetation in tallgrass prairie

Schlesinger and colleagues (1990) have argued that the redistribution of soil resources into resource-rich patches is the primary mechanism driving the expansion of woody vegetation in the arid Southwest. To determine whether soil resource redistribution and amount are important factors in woody plant expansion in tallgrass prairie, Heisler and colleagues (2004) manipulated the availability of soil N (the most limiting nutrient in tallgrass prairie; Blair et al. 1998) in

young shrub islands of the common species *C. drummondii*. Islands were randomly assigned to treatments in which they were (a) protected from annual spring burning (standing litter within the island remained undisturbed), (b) protected and provided additional N (10 grams [g] per m^2 in the form of ammonium nitrate applied to each island in late spring), (c) burned in the spring at the same time that the entire watershed was burned, (d) burned and provided additional N in late spring, or (e) burned with a litter addition following the fire. Grassland plots (with and without added N) that were devoid of woody vegetation were also established in adjacent areas.

Although the immediate effect of fire was 100% above-ground mortality of shoots of *C. drummondii*, postfire resprouting resulted in an increase of approximately 600% in stem density by the end of the second growing season. By comparison, in islands protected from fire, an increase of only about 200% was observed. The removal of the litter layer in burned islands was associated with important changes in resource availability, which included pulses in available soil N and light. Burned shrub islands that received a litter addition after fire showed dramatic reductions in soil temperature (by 6.5 degrees Celsius) and in light penetration to the soil surface (less than 3% of full sunlight), with both measures reaching levels similar to those of unburned islands, but stem density still increased by approximately 400%. This suggests that the direct effects of fire as well as alterations in the

radiation environment and microclimate following litter removal increased stem densities of *C. drummondii*. Surprisingly, N additions influenced neither new stem production nor aboveground net primary productivity (ANPP) in any treatment. Thus, changes in N availability following fire did not affect shrub expansion during this study, suggesting that soil resource redistribution (Schlesinger et al. 1990) is not important as a driver of increased shrub abundance in this ecosystem.

While 2 years of fire did not affect the total ANPP in *C. drummondii* shrub islands, it did shift the relative abundance of growth forms. Grass productivity (360.7 ± 20.1 g per m²) was stimulated by the high light conditions of the postfire environment, while *C. drummondii* ANPP (34.2 ± 2.4 g per m²) was reduced. The ANPP of *C. drummondii* was greatest (50.4 ± 2.2 g per m²) in shrub islands protected from fire, where graminoid ANPP was low (282.5 ± 19.9 g per m²). Despite 2 years of fire, an overall reduction in total ANPP occurred in burned shrub islands relative to the adjacent grassland. Consequently, early in the transition stage, when grasses and *C. drummondii* co-occur, productivity is at a minimum compared with the levels at sites in which either growth form dominates.

The response of larger, more mature shrub islands (figure 4, bottom panel) to fire was examined in another series of experiments (McCarron and Knapp 2003, McCarron et al. 2003) designed to test the hypothesis that postfire shrub resprouts may take advantage of the transient period of greater resource availability (light and N) and respond positively compared with shrubs in unburned grasslands. Fire may increase interspecific competition for light, water, and nutrients between resprouting shrubs and grasses (Knapp and Seastedt 1986). Small shrub islands are characterized by the co-occurrence of abundant grasses, whereas large islands exclude grasses from their understory as a consequence of light limitations (Lett and Knapp 2003). One goal of these studies was to assess the effect of the size of shrub islands on the abundance and vigor of resprouts and new ramets produced in burned and unburned tallgrass prairie. Small shrub islands were predicted to be more negatively affected by fire relative to large islands because of (a) greater fine-fuel loads in small shrub islands, (b) reduced belowground C reserves, and (c) potentially stronger competitive interactions with grasses (Davis et al. 1998). Responses were measured in both burned and unburned sites on KPBS.

Seasonal average net photosynthesis in *C. drummondii* was 20% higher in burned than in unburned shrubs, with no effect of island size. Shrubs in burned sites also produced shoots with higher leaf N concentrations than unburned shrubs, with leaves from small islands having higher N concentrations than leaves from large islands. Burning caused a decrease in late summer predawn xylem pressure potential (a measure of water stress) in small islands, whereas burned large islands did not differ from unburned shrub islands. Finally, postfire productivity of new shoots was significantly greater than that of shoots in unburned sites. These results indicate

that a transient period of high resource availability after fire allows for increased growth and rapid recovery of shrubs regardless of island size. Thus, although fire has a negative effect on the aboveground biomass of shrubs, the postfire increase in resource availability, which enhances growth in the dominant grasses, is also important for the recovery of



Figure 4. Top panel: A watershed at the Konza Prairie Biological Station (KPBS) that has been burned annually in the spring for more than 20 years. Note the complete lack of woody vegetation. Bottom panel: A watershed at KPBS that has been burned in spring every 4 years since 1971. Note the abundance of woody vegetation (*Cornus drummondii*). This photograph was taken in a year in which the watershed was burned. Note the charred stems surrounding many of the islands of *C. drummondii* and the extensive flowering, indicating that the fire did not burn through the island nor impair the vigor of *C. drummondii* following the burn. Both photographs are from watersheds that are ungrazed and therefore characterized by a heavy fuel load that would support an extensive, intense fire. Photographs: Top panel, Melinda D. Smith; bottom panel, John M. Briggs.

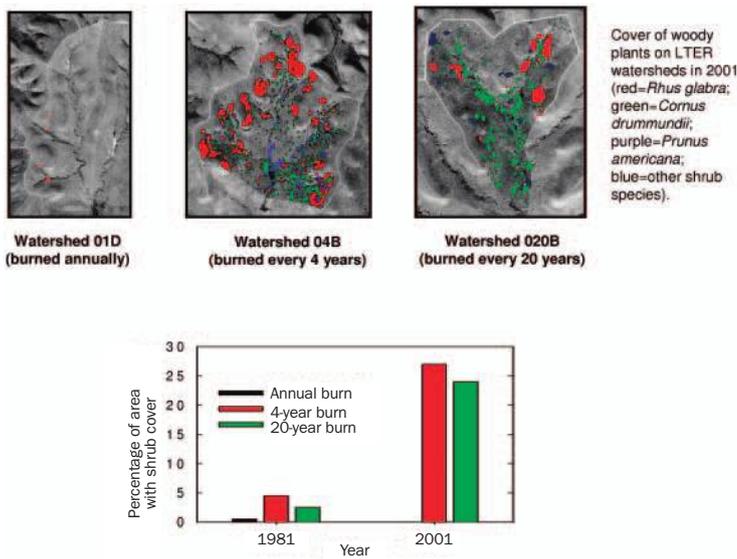


Figure 5. Top panels: Cover of woody plants on three LTER (long-term ecological research) watersheds at the Konza Prairie Biological Station in 2001 (red = *Rhus glabra*; green = *Cornus drummondii*; purple = *Prunus americana*; blue = other species). Bottom panel: Change in the percentage of total woody cover on the same three watersheds under three different burning treatments.

established woody species. These two experiments, coupled with extensive long-term monitoring (Heisler et al. 2003), support the view that, once established, infrequent fire may actually accelerate the expansion of some shrub species in grasslands by providing increased resources that evoke vigorous resprouting.

Community and ecosystem consequences of a change in life forms

The shift from a C_4 grass- to a C_3 shrub-dominated ecosystem is likely to significantly affect plant productivity and both pools and fluxes of C (Jackson et al. 2002). Tallgrass prairies are characterized by relatively high net primary productivity (NPP), high belowground allocation of NPP (> 50%), large quantities of soil organic matter, high microbial biomass and activity, and high soil CO_2 flux (Kucera et al. 1967, Zak et al. 1994, Briggs and Knapp 1995, Bremer et al. 1998, Knapp et al. 1998b, 1998c). As noted earlier, when shrubs first begin to displace the dominant grasses, ANPP may be reduced, but Lett and colleagues (2004) found that within large, established *C. drummondii* islands (figure 4, bottom panel), ANPP was 1035 ± 83 g per m^2 per year, nearly three times that within comparable areas of open grassland (356 ± 28 g per m^2 per year). As a result of greater aboveground biomass, aboveground C and N storage within shrub islands (3267 ± 465 g C per m^2 ; 37.8 ± 5.3 g N per m^2) was substantially greater

than that within open grassland (241 ± 33 g C per m^2 ; 6.1 ± 0.8 g N per m^2). No change in soil organic C or total N was evident at depths of up to 10 centimeters. The storage of C in aboveground biomass of *C. drummondii* islands represents a significant short-term increase in C storage relative to open grassland.

As expected, the expansion of woody vegetation into tallgrass prairie produces significant changes within the herbaceous community. Lett and Knapp (2005) found lower species richness and diversity within *C. drummondii* islands, relative to similar-sized areas of tallgrass prairie vegetation devoid of *C. drummondii*. Furthermore, shrub dominance may facilitate forest expansion (figure 3; Lett and Knapp 2005), and when forest species such as *J. virginiana* increase in abundance and cover, a strong negative relationship occurs between the richness of herbaceous species and the density of *J. virginiana* (Hoch et al. 2002). Thus, the shift from a C_4 grassland to an ecosystem dominated by C_3 woody species may impose dramatic changes in the tallgrass community structure and composition. A summary of the overall consequences of the expansion of woody vegetation into tallgrass prairie is provided in table 1.

What is the potential for restoration of grassland after shrub dominance?

Given (a) the long-term persistence of individual shrubs in annually burned sites (Heisler et al. 2003), (b) results that indicate intermediate fire frequencies accelerate woody plant expansion (Briggs et al. 2002, McCarron

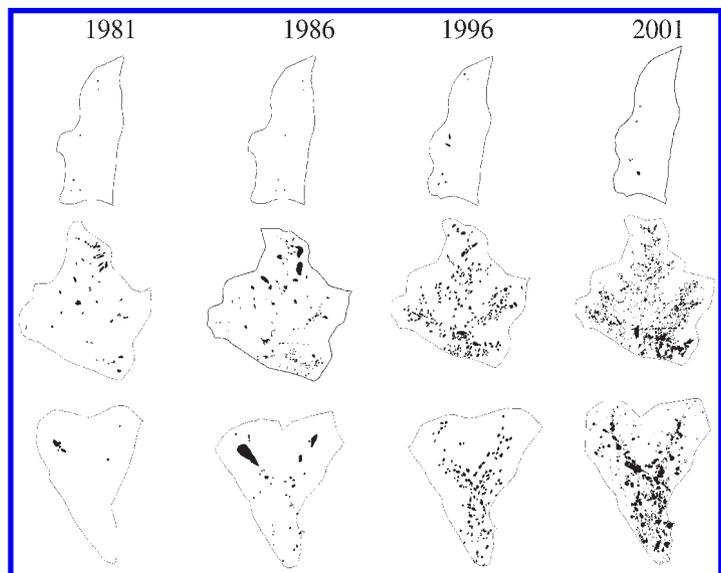


Figure 6. The change in woody vegetation over a 20-year time frame on three watersheds at the Konza Prairie Biological Station subjected to three different burning treatments: burned annually (top series), burned every 4 years (middle series), and burned once in 20 years (bottom series).

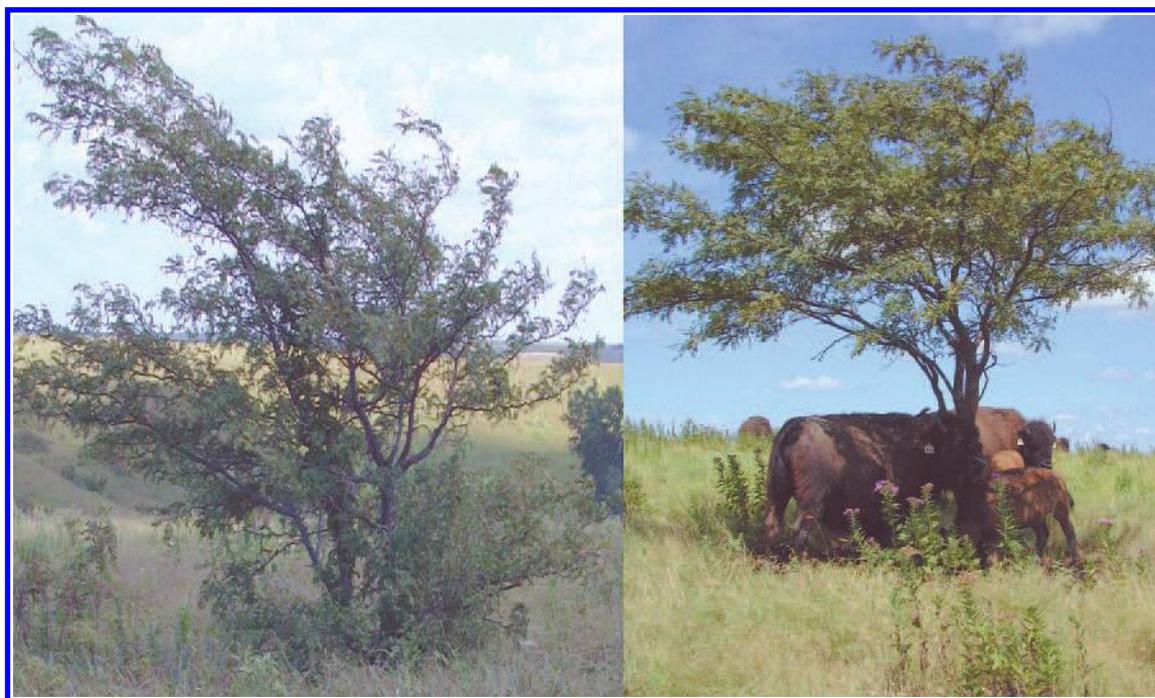


Figure 7. Left panel: *Gleditsia triacanthos* in an ungrazed watershed at the Konza Prairie Biological Station (KPBS). Note the large amount of standing biomass around the tree and the low hanging branches, which suggest that if a fire swept through this area, there is a good chance that the tree would be damaged. Right panel: *G. triacanthos* in a grazed watershed at KPBS. American bison (*Bos bison*) have reduced the amount of fuel around the tree, and there are no low-lying branches. Thus, if a fire swept through this area, there is a good chance that the tree would be minimally affected and would survive. Photographs: John M. Briggs.

and Knapp 2003), and (c) observations that large shrub islands do not burn (figure 4, bottom panel) and have not decreased in size even after 4 years of annual fire, thus providing safe sites for forest species (figure 3), it is clear that a return to a frequent fire regime may not be sufficient to eliminate most established woody vegetation (especially *C. drummondii*). Hence, these ecosystems may now be better described as “savanna grasslands,” defined by Scholes and Archer (1997) as ecosystems with a continuous grass layer and scattered shrubs and trees.

If frequent fire cannot reduce these woody species, mechanical or chemical removal of woody plants may be an alternative means for tallgrass prairie restoration following shrub expansion. To assess the potential for grassland ecosystem restoration in sites formerly dominated by shrubs, Lett and Knapp (2005) removed *C. drummondii* islands that had completely excluded grasses from their understory. Shrub removal in 14 islands was accomplished by cutting all *C. drummondii* stems at the base and applying herbicide to the cut surface of each stem. For comparative purposes, other shrub islands were left undisturbed, and adjacent, shrub-free grassland plots similar in size to the shrub islands were established.

Patterns of light and N availability were assessed to determine the mechanism by which shrub expansion and removal may affect the recovery of herbaceous vegetation. As expected, removal of the aboveground shoots of shrubs increased light penetration and created a pulse of available soil N in the first year. Levels of these resources decreased in the second year (although inorganic N levels remained greater

Table 1. Selected ecological consequences of the shift from a C_4 grass-dominated to a C_3 shrub-dominated ecosystem.

Ecological measure	Shrub island	Grassland
ANPP (g per m ² per year)	1284 ± 131	356 ± 28
Standing crop (g per m ²)	6711 ± 95	512 ± 70
Standing crop C (g per m ²)	3267 ± 465	241 ± 33
Standing crop N (g per m ²)	37.8 ± 5.3	6.1 ± 0.8
Soil organic C (g per m ²)	4740 ± 76	4721 ± 213
Inorganic soil N (μg per g)	1.81 ± 0.16	9.02 ± 0.65
Annual CO ₂ flux (kg per m ² per year) ^a	4.78	5.84
Soil CO ₂ flux (μmol per m ² per second)	5.0–6.2	6.2–8.5
Leaf chemistry (percentage N)	2.84 ± 0.06	1.57 ± 0.04
Species richness (numbers per m ²)	11.2 ± 0.9	20.12 ± 1.0

ANPP, aboveground net primary productivity; C, carbon; CO₂, carbon dioxide; N, nitrogen.

Note: Values represent means and standard error of the mean.

a. Only one measurement was calculated.

Source: Blair et al. 1998, Knapp et al. 1998c, McCarron et al. 2003, Heisler et al. 2004, Lett et al. 2004, Lett and Knapp 2005.

than in undisturbed grasslands plots in year 2; Lett and Knapp 2003). Graminoid ANPP in the first year after shrub removal was significantly higher than in the intact shrub islands but remained lower than in the grassland plots. In contrast, total ANPP in the shrub-removal plots, two years after removal, was equivalent to that in the grassland plots; however, this was the result of C_3 forb production rather than recovery by the previously dominant C_4 grasses. These results suggest that the apparent alternative stable state of *C. drummondii* codominance in the tallgrass prairie landscape is biotically maintained and driven by shrub-induced low light levels that eliminate the grasses, rather than by soil resource enrichment that allows shrubs to displace the grasses (Schlesinger et al. 1990). In areas where shrubs were removed, there were no long-term changes in soil resource availability. Thus, it appears that mechanical removal promotes the restoration of shrub-dominated areas to an ecosystem that is more representative of the tallgrass prairie, although the time required for recovery to graminoid dominance is currently unknown.

Contemporary woody plant expansion in grasslands

In the past, an increase in woody plant cover at the expense of native grasses and forbs might have been interpreted as a successional process (Oosting 1942). Indeed, the traditional

ecological view of ecosystems in transition from one state to another (e.g., from grassland to forest) has been framed within a disturbance–succession paradigm in which discrete disturbances lead to some quasi-predictable and repeatable path of ecosystem return to a predisturbance state (Pickett and White 1985). Although multiple or alternate “climax” ecosystem states have long been recognized (Holling 1973), these too include predictable and repeatable changes following disturbance events. But in many important ways, the changes in ecosystem structure and function associated with the ongoing increase in woody plant cover in grasslands do not fit the disturbance–succession paradigm, and we believe that the process of woody plant expansion into grassland, and the potential for reduction of the dominant grasses, should be viewed in a fundamentally different way.

Global change phenomena, like traditional disturbances, can lead to dramatic, and in some cases rapid, transitions in ecosystem structure and function (Bazzaz 1990, Mooney et al. 1991, Wedin and Tilman 1996, Vitousek et al. 1997, Allen and Breshears 1998, Alward et al. 1999). State transitions, driven by global change, are distinct from responses to disturbances because they are not initiated by discrete events; instead, they are characterized by persistent changes in the abundance and distribution of potentially limiting resources. Because global change drivers such as elevated atmospheric CO_2 or N deposition are chronic, new ecosystems develop that have dramatically different characteristics than the previous communities that occupied the area (Wedin and Tilman 1996), and there is often no apparent tendency to return to the previous state of the ecosystem.

In cases where the species composition of the ecosystem is altered, this too can significantly affect ecosystem structure and function, independent of the drivers of change (Hooper and Vitousek 1997). However, the most profound ecological consequences occur when changes in species composition involve the replacement of one dominant growth form by another. Perhaps there is no more dramatic example of this than the displacement of C_4 grasses by woody plants in grassland. The large-scale invasion of arid and semiarid grasslands by mesquite and creosote bushes is a well-documented example (Archer et al. 1988, Schlesinger et al. 1990), but in more mesic systems there can be complete replacement of C_4 grasslands with closed-canopy C_3 shrubs and trees (Bragg and Hulbert 1976, Hoch and Briggs 1999, Hoch et al. 2002). The ecological consequences of this conversion in dominance from one form of plant life to another are likely to be substantial and to manifest rapidly in mesic grasslands, where resource abundance and production potential are greater than in arid grasslands.

Before the widespread settlement of Europeans in North America, the tallgrass prairie was described as an ecosystem that was subject to frequent fire and mostly devoid of trees, with only a minor shrub component in the plant community. In addition, large numbers of ungulate grazers (mostly *B. bison*) were common (Knapp et al. 1999). Many contemporary studies in tallgrass prairie and especially at

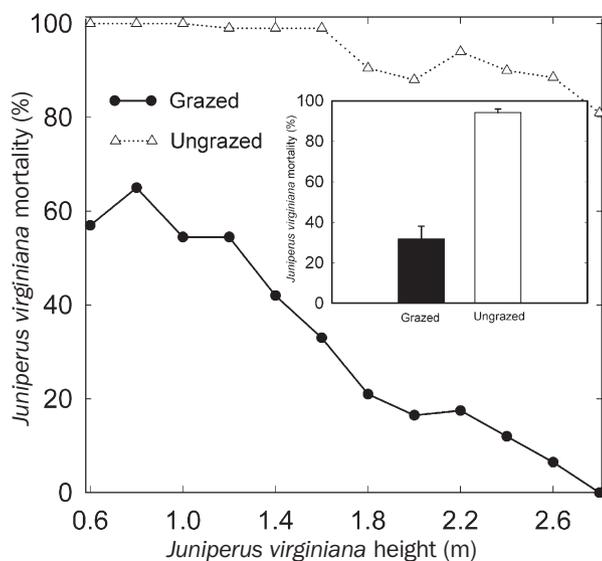


Figure 8. Eastern red cedar (*Juniperus virginiana*) mortality after fire as a function of tree height on grazed (circles) and ungrazed (triangles) tallgrass prairie. In two ungrazed sites, even the largest size classes had greater than 80% mortality, while the grazed sites had only 50% mortality at the 1-meter (m) size class. Inset shows average red cedar mortality in grazed and ungrazed tallgrass prairie. Red cedars in ungrazed tallgrass prairie had significantly higher mortality rates than in grazed tallgrass prairie (ANOVA [analysis of variance between groups]; $F = 210.4$, $P < 0.001$). Source: Hoch and colleagues (2002).



Figure 9. Aerial photograph illustrating the fragmented pattern of present-day forest and tallgrass prairie in northeastern Kansas. Photograph: Sara Baer.

KPBS have shown that both fire and grazing are critical for the maintenance of this ecosystem (Collins and Wallace 1990, Collins et al. 1998, Knapp et al. 1999). Yet even with frequent fire and grazing, and a very large population of browsers (white-tailed deer [*Odocoileus virginianus*]), shrub and woody plant abundance continues to increase in this mesic grassland. This contradiction cannot be resolved by invoking short-term climatic changes. There is no indication from the long-term (118-year) weather record that the increase in woody vegetation on KPBS is associated with any recent change in weather patterns. Instead, we believe that there are two key factors promoting the contemporary expansion of woody plants. The first is the fragmentation of the landscape as a result of land-use changes in the past 150 to 200 years. This fragmentation has decreased the frequency, intensity, and extent of fire and, more important, has increased the availability of seed sources from surrounding woody vegetation (figure 9; Hoch et al. 2002). In the past, woody vegetation was restricted to riparian areas or protected escarpments where fires were less frequent and less intense (Wells 1965). Thus, even when bison removed fine fuel by grazing, there was a low probability that seeds of woody plants would reach these patches. In the current fragmented landscape, which is characterized by a higher cover of woody plants (figure 9), there is a greater chance that the seeds of woody plants will reach a grazed area with low fire intensity. In addition, bison were migratory grazers; thus, grazing in any given area were probably not chronic. Fuels could accumulate in years when there were no

bison grazing in the area and therefore could support intense fires. Today, cattle graze the same areas every growing season, which precludes the accumulation of large amounts of fine fuel and results in low-intensity fires, even if they occur at a high frequency. In addition, although fires can (and historically did) occur throughout the year within the tallgrass prairie (Knapp et al. 1998a), most fires today are prescribed and conducted during moderate weather conditions in the spring. In contrast, fires that occur late in the summer, particularly in very hot and dry years, might be more intense and thus more effective in reducing the number and cover of woody plants. Thus, increased propagule availability and alterations in grazing and fire regimes (both spatial and temporal) are likely reasons that historic drivers, which previously maintained the grasslands in a state of low woody plant abundance, are no longer effective at doing so today.

Conclusions

Historically, woody plant expansion was constrained by widespread fire and an overall low abundance of woody vegetation. Our studies suggest that while different pathways characterize the conversion of this C_4 grass-dominated system to one codominated by grass and woody plant growth forms, only a single pathway exists by which the plant community that is characteristic of a mesic grassland ecosystem can be maintained. This pathway involves frequent fire and the absence of grazing or grazing at low intensity. It is important to note that once shrubs establish and a state of

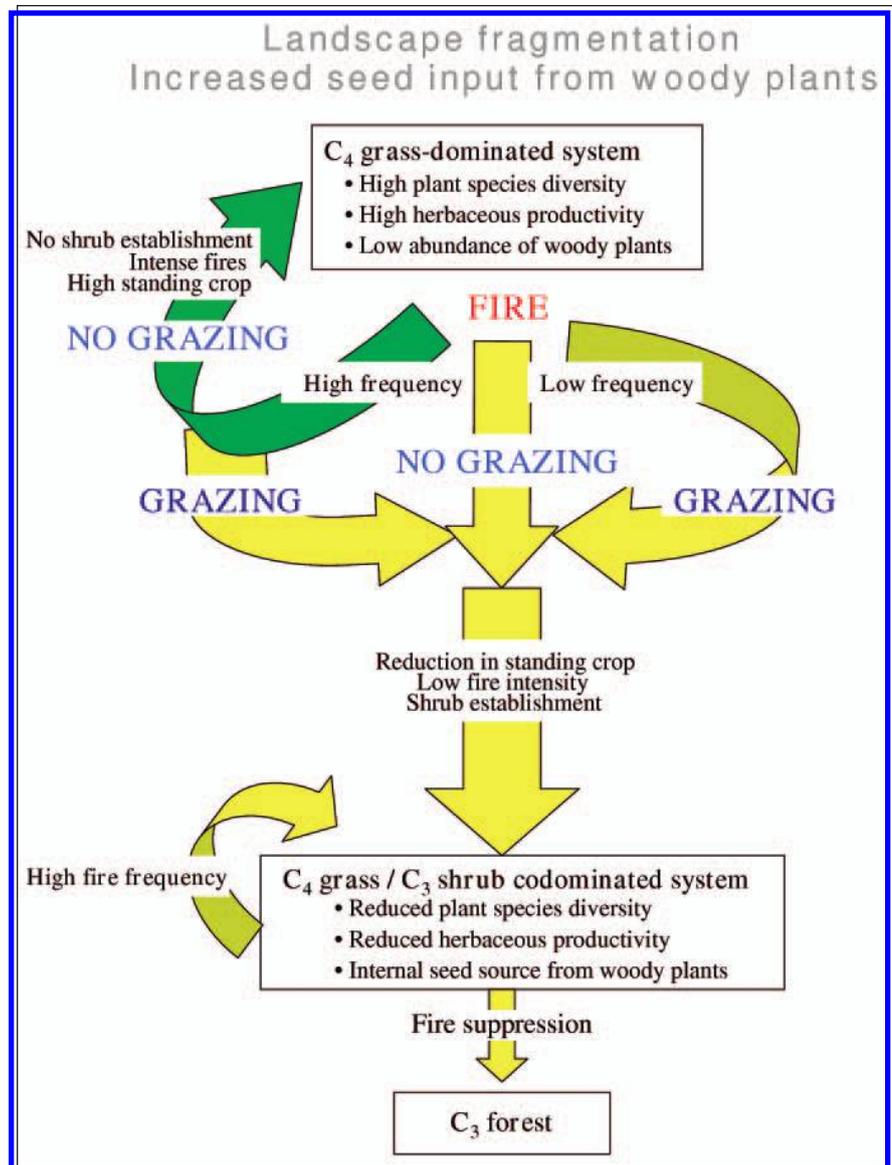


Figure 10. Flowchart illustrating the primary pathways by which native tallgrass prairie may be converted to a grass–shrub codominated system under the chronic pressures of landscape fragmentation and increased seed rain.

codominance is reached, frequent fire will maintain this state, but a return to a C_4 -dominated grassland is no longer possible. For these reasons, we believe that the expansion of native woody vegetation is a serious threat to the remaining tracts of tallgrass prairie.

There are varied pathways by which tallgrass prairie can be converted to a system that is dominated by woody vegetation (figure 10). This expansion of woody vegetation changes many, if not most, of the basic properties of the ecosystem. The fragmentation of the remaining grasslands in this area has been recognized as a key factor in reducing the frequency of fire (Knapp et al. 1998a), and as noted by Leach and Givnish (1996), reducing the frequency of fire contributes to the loss of species in tallgrass prairie. In addition, these fragmented

grasslands are susceptible to increased cover of woody plants caused by the expansion of nearby woody vegetation. Currently, most tallgrass prairie is better described as savanna grassland or mixed shrub and woodland. Restoring these systems to tallgrass prairie, even with a high fire frequency, is unlikely as the shift in dominant growth form renders substantial changes in ecosystem and community properties that fire alone cannot reverse. Thus, it is imperative that we understand what mechanisms drive the reduction in the extent and quality of tallgrass prairie and how further increases in woody plant abundance can be halted. This understanding will be critical to the successful management and conservation of this ecosystem and similar grasslands around the world.

Acknowledgments

The National Science Foundation's Long-Term Ecological Research, Ecological Biology, and Ecosystem Science programs; the National Aeronautics and Space Administration; and The Nature Conservancy supported the research summarized here. Jason Walker read and improved an earlier version of this manuscript. We would like to thank Brent L. Brock for his help with figures 1, 5, and 6. Comments made by Paul Zedler and two anonymous reviewers considerably enhanced the manuscript.

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