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The Keystone Role of Bison in North American Tallgrass Prairie

Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes

Alan K. Knapp, John M. Blair, John M. Briggs, Scott L. Collins, David C. Hartnett, Loretta C. Johnson, and E. Gene Towne

Throughout the history of Great Plains grasslands, North American bison (*Bos bison*, also known as *Bison bison*; Jones et al. 1992) and other large herbivores were abundant and conspicuous components of the biota (Wedel 1961, Stebbins 1981). Many of the earliest herbivores, particularly those that were primarily browsers, are now extinct, but their consumption of woody vegetation is thought to have played a critical role in the post-Pleistocene rise of the grassland biome and the subsequent increase in bison populations (Axelrod 1985, Hartnett et al. 1997). Indeed, the large herds of bison encountered by early Europeans on the Great Plains were likely the result of the rapid early-Holocene proliferation of this ungulate into a relatively young and expanding "treeless" grassland biome (Stebbins 1981, Axelrod 1985). In the most productive regions of the Great Plains, the eastern tallgrass prairies, abundant bison herds were noted by early explorers (Shaw and Lee 1997). Although herds were larger in the western shortgrass steppe, some have speculated that a greater density of bison could be supported in eastern tallgrass prairies than elsewhere in the plains (McHugh 1972). It is unfortunate, then, that despite the historic abundance of bison in tallgrass prairies, their ecological effects in these mesic grasslands are poorly understood.

Ungulate grazing activities and fire are key to conserving and restoring the biotic integrity of the remaining tracts of tallgrass prairie

Knowledge of the bison's role in tallgrass prairies is lacking because the extent of this grassland and the abundance of its dominant ungulate have declined dramatically and in tandem over the last 150 years. Although there is debate over the numbers of bison inhabiting the Great Plains before the 1800s (estimates range from 30 million to 60 million; McHugh 1972, Flores 1991), it is well documented that from 1830 to 1880 the slaughter of bison in the Great Plains reduced their numbers to an estimated low of a few thousand individuals. Widespread cultivation of the plains, which accompanied the near extirpation of the bison, reduced the once-vast tallgrass prairie (approximately 68 million hectares) to less than 5% of its presettlement range (Samson and Knopf 1994). The near-simultaneous reduction in herbivore abundance and grassland extent left little opportunity to assess bison–tallgrass prairie interactions.

Today, thanks to conservation efforts (Berger and Cunningham 1994), bison numbers in the Great Plains have rebounded (to approximately 150,000), and significant public and private herds are maintained in several mixed- and shortgrass prairie preserves and ranches. It is from these semi-arid grasslands, many of which escaped cultivation, that the most extensive knowledge of bison–grassland interactions has been generated (Peden et al. 1974, Coppock et al. 1983). By contrast, the current understanding of tallgrass prairie structure and function has been developed almost exclusively from studies of ungrazed tracts or from sites grazed by domestic cattle (Risser et al. 1981, Collins 1987, Howe 1994, Leach and Givnish 1996). Only recently have bison been reintroduced to tallgrass prairie sites that are large enough to assess both their influence on other biota and ecosystem processes, as well as their interactions with other important features of these grasslands, particularly fire (Collins et al. 1998, Coppedge and Shaw 1998, Knapp et al. 1998b).

The Konza Prairie Research Natural Area in the Flint Hills of northeastern Kansas is the largest tract of unplowed tallgrass prairie (3500 ha) in North America dedicated to research (Knapp et al. 1998b). Konza Prairie was one of the original sites selected in 1981 for inclusion in the

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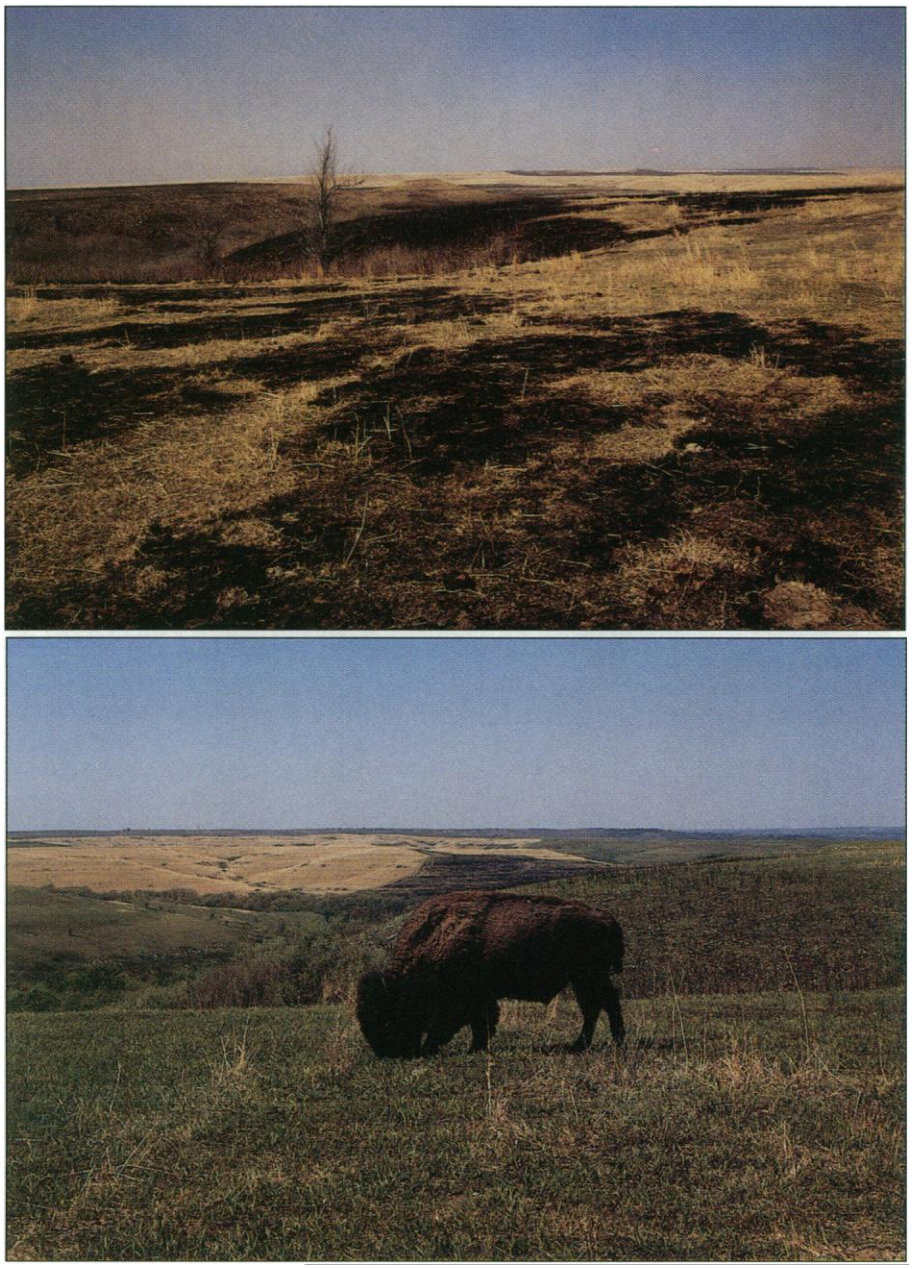


Figure 1. Grazing by bison increases spatial variability in tallgrass prairie. Immediately after fire (April) in grazed watersheds on the Konza Prairie, a native tallgrass prairie in northeastern Kansas, the uneven consumption of fuel by fire in grazed areas (upper photo) is caused by the patchiness of bison grazing the previous year. Dark areas indicate sites where bison did not graze or where grazing was light, and fuel loads were therefore sufficient to carry a fire through the patch. Lighter areas are patches that were grazed repeatedly by bison, such that fuel loads were reduced and the impact of fire was minimal. Later in the season, bison graze preferentially in recently burned watersheds (lower photo). In this late spring (May) view of a burned watershed, unburned watersheds can be seen in the background. Bison at Konza Prairie have access to 10 watersheds that differ in fire regime.

National Science Foundation's Long Term Ecological Research (LTER) program, and ongoing experimental treatments on some parts of the site date to 1972. Past syntheses of research at Konza Prairie have focused on the effects of fire and climatic variability (Knapp and Seastedt 1986, Knapp et al. 1998b), but a majority of these data were collected in the absence of bison grazing.

In 1987, 30 bison were reintroduced to Konza Prairie, and the herd was allowed to increase until 1992. Since that time, the herd has been maintained at approximately 200 individuals, who have had unrestricted access to a 1012 ha portion of the landscape. Within this area are 10 watersheds that are subjected to different frequencies of late-spring prescribed fire. The target animal density of 200 animals was selected so that approximately 25% of aboveground primary production is consumed annually. This consumption rate is approximately half that of tallgrass prairie managed for domestic cattle. The bison herd at Konza Prairie is not provided supplemental feed in winter, nor is it actively managed. Thus, this herd provides an opportunity to document the impact of bison on a native tallgrass prairie ecosystem.

Although research on bison–tallgrass prairie interactions began soon after bison were reintroduced to Konza Prairie, comprehensive studies spanning scales from the leaf to the landscape level began in the early 1990s. In this article, we provide the first synthesis of these research efforts, with the goal of highlighting the keystone role (sensu Power et al. 1996) that bison played in the tallgrass prairies of the past. Within this overview, we address two general questions: What are the direct and indirect effects of bison on patterns and processes in tallgrass prairie? What factors influence the spatial and temporal patterns of grazing activities by bison? Perhaps as important as addressing these questions, the data that we present indicate that large-ungulate herbivory can, and should, play a key role in the management and conservation of the remaining tracts of this once-widespread grassland.

Bison grazing activities and plant responses

Like all large herbivores, bison do not graze indiscriminately across the landscape or even within a local area (Senft et al. 1987, Wallace et al. 1995). Rather, they graze in two patterns in tallgrass prairie, creating both distinct grazing patches (typically 20–50 m^2 in Flint Hills tallgrass prairie; Catchpole 1996) and more extensive grazing lawns (larger than 400 m^2; McNaughton 1984). In both

cases, bison revisit grazed sites throughout the season, such that repeated defoliation of grazed plants is the norm and relatively sharp boundaries between grazed and ungrazed vegetation become evident (Figure 1). Bison are primarily graminoid feeders and consume higher proportions of the dominant grasses than would be predicted based on grass availability in the landscape (Peden et al. 1974, Van Vuren and Bray 1983, Steuter et al. 1995). Bison tend to avoid forbs and woody species, which usually constitute less than 10% of their diet. Thus, within a bison grazing area, forbs are often conspicuously left ungrazed and are surrounded by grazed grasses (Fahnestock and Knapp 1993, Damhoureyeh and Hartnett 1997).

Preferential grazing of the dominant grasses by bison sets the stage for significant alterations in competitive interactions among the C_4 grasses and the C_3 forbs. Such shifts are important for plant community structure because in ungrazed and frequently burned prairie, a small group of grass species (*Andropogon gerardii*, big bluestem; *Sorghastrum nutans*, Indian grass; *Panicum virgatum*, switchgrass; and *Andropogon scoparium*, little bluestem) account for most biomass, density, leaf area, and resource consumption (Knapp 1985, Briggs and Knapp 1995). However, it is the species-rich forb component (more than 350 species are recorded on Konza Prairie; Freeman 1998) that is critical for the maintenance of high levels of biotic diversity in tallgrass prairie (Gibson and Hulbert 1987, Glenn and Collins 1990, Turner et al. 1995). Thus, by grazing on grasses and allowing forbs to flourish, bison have the potential to significantly influence biodiversity in these grasslands (Collins et al. 1998).

The short-term effects of bison herbivory on the most abundant prairie grass, *A. gerardii*, are different from the long-term effects. At the leaf level, short-term responses to leaf removal are typical of many graminoids in grazing systems (McNaughton 1983). Wallace (1990) reported a postgrazing enhancement of photosynthesis in *A. gerardii* in Oklahoma. Similarly, on Konza Prairie, midseason photosynthetic rates averaged 53% higher in grazed tillers (individual grass stems) than in ungrazed plants, with a maximum stimulation of 150% (Figure 2a). Mechanisms for this enhancement of photosynthesis include increased light availability and reduced water stress for all species in grazed patches (Fahnestock and Knapp 1993) and greater tissue nitrogen concentration in *A. gerardii* leaves as nitrogen is reallocated from roots.

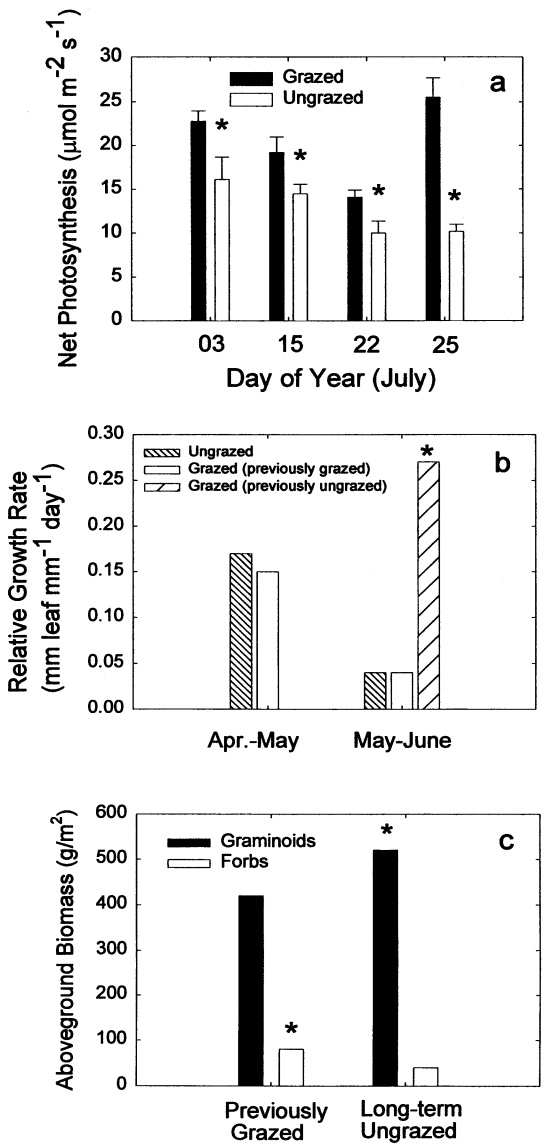


Figure 2. Response of tallgrass prairie vegetation to bison herbivory at three temporal scales. (a) Instantaneous leaf-level photosynthetic responses of *Andropogon gerardii* to grazing (Erin Questad and Alan K. Knapp, unpublished data). (b) Relative growth rates of tillers of *A. gerardii* in sites that differ in grazing history (data from Vinton and Hartnett 1992). Both ungrazed tillers and grazed tillers with a history of grazing had similar growth rates, whereas grazed tillers without a history of grazing had significantly greater growth rates. (c) End-of-season aboveground biomass in ungrazed sites that differ in grazing history (data from Knapp et al. 1998a). Asterisks in panels (a) and (b) indicate significantly different values ($P < 0.05$) for comparisons at specific dates; in panel (c) they indicate comparisons within growth forms.

These potential compensatory increases in photosynthesis after grazing may be augmented by the translocation of carbon reserves from belowground to aboveground tissues. Vinton and Hartnett (1992) found that in the first year of grazing, growth and biomass of grazed *A. gerardii* tillers had completely compensated for the loss to grazing by season's end. But after several years of grazing, the ability of tillers to compensate for lost tissue was reduced (Figure 2b). Vinton and Hartnett (1992) attributed these differences in short- and long-term responses to reductions in belowground carbon allocation and stored carbohydrate reserves after several years of grazing. Turner et al. (1993) also demonstrated the importance of grazing history on productivity in tallgrass prairie by measuring aboveground primary production in a number of sites with different grazing histories. They found that compensatory regrowth of biomass occurred in sites with little history of grazing but not in sites that had been grazed heavily in previous years.

Some researchers have argued that the inability of tallgrass prairie grasses to compensate for the biomass lost in frequently grazed areas is evidence that prolonged, intensive bison grazing did not occur in these grasslands (Shaw and Lee 1997). If this hypothesis were true, then grass abundance would decline continually following repeated grazing. However, the tallgrass prairie's loss of production potential due to grazing is short lived. At Konza Prairie,

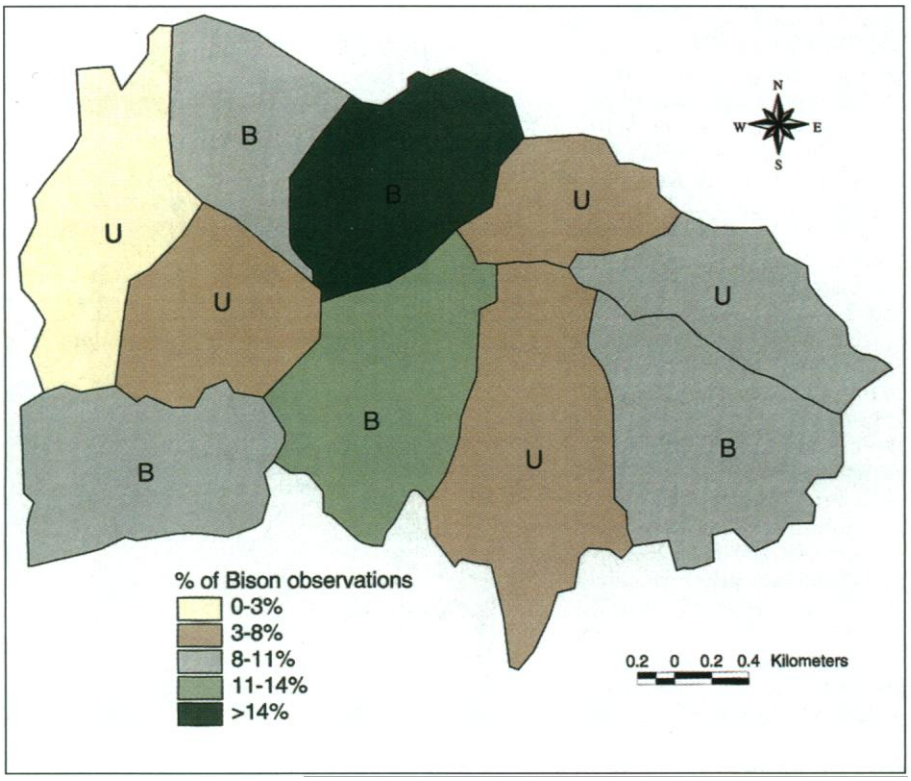


Figure 3. Spatial distribution of bison in 10 watersheds in the central portion of Konza Prairie after the completion of spring burning. During the months of April, May, and June 1992, bison locations were determined twice per week and recorded on large-scale, spatially rectified aerial photographs overlaid with a 30-meter grid. Bison were observed most frequently in the recently burned watersheds. B, burned watersheds; U, unburned watersheds.

permanent fenced exclosures have excluded bison from experimental plots within grazed watersheds for several years. When adjacent grazed sites were also protected from grazing with temporary exclosures, aboveground production in the first year in these newly protected sites was reduced relative to that in the adjoining long-term ungrazed areas (Figure 2c); however, these sites recovered their production potential by the second year. Thus, production potential can recover if bison grazing is sufficiently dynamic, either spatially or temporally, such that sites are grazed intermittently.

Removal of grass leaf area by bison, and reductions in the capability of the dominant grasses to compensate for tissue lost after multiple years of grazing, suggest that the cooccurring subdominant forbs may benefit from bison grazing. Indeed, comparisons of forbs inside grazing patches with those in adjacent ungrazed prairie have shown that gas exchange and aboveground biomass production, density, and cover can be enhanced by the selective consumption of grasses by bison (Fahnestock and Knapp 1993, Hartnett et al. 1996, Damhoureyeh and Hartnett 1997). Given the importance of past grazing pressures to the direct responses of grasses to herbivory and the indirect responses of forbs, identifying those factors that influence the selection and reselection of grazing patches by bison in tallgrass prairie is critical for understanding the long-term consequences of bison grazing patterns.

Factors influencing bison selection of grazing sites

Historical information regarding bison grazing patterns in the Great Plains is replete with anecdotal accounts of herds attracted to recently burned grasslands (Figure 1; McHugh 1972, Pyne 1982), but quantitative evidence of this preference in tallgrass prairie has been lacking until recently (Coppedge and Shaw 1998). As noted earlier, bison at Konza Prairie have free access to 10 watersheds that are subject to different fire frequencies. Since 1991, twice-weekly observations of the distribution of bison within this area have been made to assess patterns of bison grazing (Nellis et al. 1992). The results confirm that bison do graze preferentially within burned watersheds from April (burning takes place in late March–early April) through June and July, and, in some years, through August (Figure 3; Vinton et al. 1993, Nellis and Briggs 1997). In addition to grazing preferentially in burned sites, bison increase their selective consumption of some grass species in burned sites relative to unburned sites (Pfeiffer and Hartnett 1995). Late in the summer, lowland topographic positions with deeper soils (and therefore greater soil moisture and plant productivity; Knapp et al. 1993) in burned watersheds become preferred grazing locations as the uplands dry. This preference for burned areas in tallgrass prairie is consistent with postfire responses in mixed grass prairie (Coppock and Detling 1986), as well as with large ungulates' winter preference for burned sites in the northern mixed grasslands of Yellowstone National Park (Pearson et al. 1995).

Within a watershed or at a specific topographic position in tallgrass prairie, several factors may influence initial patch selection and reselection (see also Wallace et al. 1995). In addition, patch selection has several long-term consequences. When bison were first reintroduced to Konza Prairie, they encountered a mosaic of burned and unburned watersheds, with significant differences among watersheds in the spatial heterogeneity of plant community composition. For example, frequently burned but ungrazed watersheds are dominated by C_4 grasses and have low species richness and diversity, whereas less frequently burned sites have higher species richness and forb cover (Gibson and Hulbert 1987, Collins 1992). Initial studies on Konza Prairie indicated clearly that bison established grazing patches in areas strongly dominated by C_4 grasses and that these patches were reselected at a high rate (Vinton et al. 1993). Six years later, a survey of floristic composition indicated that established bison grazing patches had

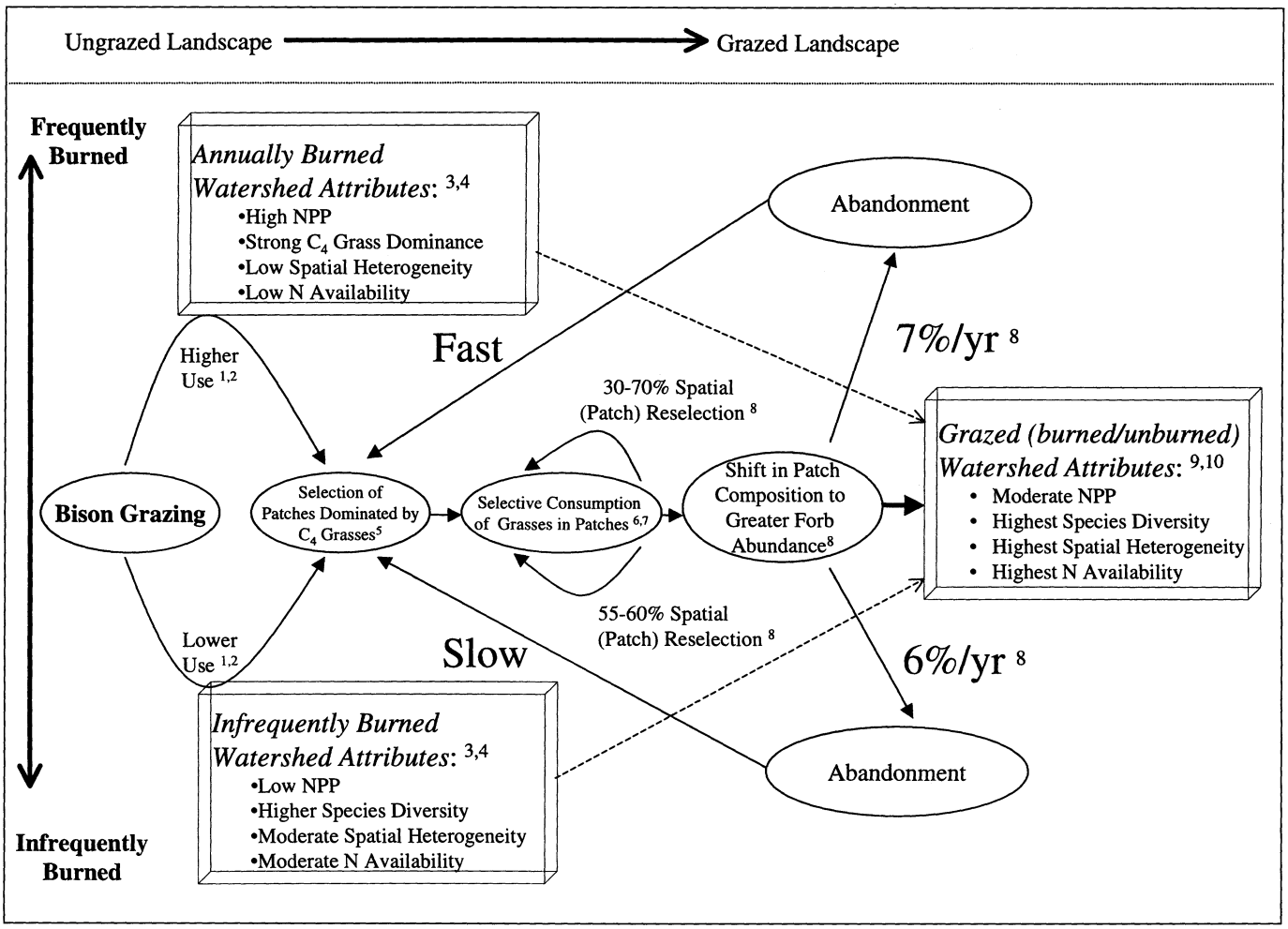


Figure 4. Conceptual model of the spatial and temporal dynamics of bison grazing activities and the responses of tallgrass prairie to the reintroduction of bison. Before the reintroduction of bison, watershed attributes at Konza Prairie differed strongly depending on the fire regime imposed, with frequently burned sites notable for their high productivity but low plant species diversity. Selective bison grazing at the watershed level (preference for burned sites, particularly in the spring) and the patch level (selection of patches dominated by C_4 grasses) has led to increased similarity in watershed attributes despite differences in fire history. Moreover, significant increases in plant species diversity and spatial heterogeneity have been noted in all watersheds. Superscripts denote studies on which this synthesis is based: 1, Nellis and Briggs (1997); 2, Vinton et al. (1993); 3, Briggs and Knapp (1995); 4, Collins (1992), Collins et al. (1995); 5, Vinton and Hartnett (1992), Vinton et al. (1993); 6, Hartnett et al. (1997); 7, Fahnestock and Knapp (1993, 1994); 8, Catchpole (1996); 9, Collins and Steinauer (1998); 10, Hartnett et al. (1996).

a higher abundance of forbs and a lower cover of grasses than adjacent ungrazed patches (Catchpole 1996). Similar small-scale patterns of forb and grass abundance were observed by comparing the floristic composition inside and outside grazing exclosures in grazed watersheds at Konza Prairie (Hartnett et al. 1996). These observations suggest that bison alter plant community composition at the patch scale by selecting species-poor, grass-dominated sites and converting them to sites of locally higher diversity (Figure 4).

A second factor that may influence patch selection and reselection by bison is plant quality. The foliar nitrogen content of plants is highly variable, both spatially and temporally. Bison contribute to this patchiness through deposition of nitrogen-rich urine. Steinauer (1994) applied synthetic bovine urine at randomly selected locations along eight transects at Konza Prairie (four each in grazed and ungrazed areas). In ungrazed areas, grass cover was significantly higher in plots that were fertilized with urine than in plots without urine. But in the grazed area, by contrast, grass cover was significantly lower on the urine-treated plots than in plots without urine because bison preferentially grazed the grasses on the urine-treated plots. Day and Detling (1990) have shown that grasses growing on urine patches in mixed-grass prairie have higher leaf nitrogen content, and are therefore more nutritious per bite, than grasses growing on patches without urine. Not only was grass cover lower on urine patches at Konza Prairie, but the total area of grazed patches on the urine-treated transects was significantly larger than the area of grazed patches on transects that were not treated with urine (Steinauer 1994). Thus, the enhanced productivity of grasses growing on urine patches represents a potential stimulus for the initiation and reselection of grazing patches by bison.

Given that bison prefer grazing patches that are initially dominated by C_4 grasses, but that their selective foraging and reselection habits convert these patches to sites with a greater abundance of nonforage species, it is likely that patch locations are spatially dynamic across the landscape. Patches can "move" by two mechanisms: patch abandonment, followed by selection of a new patch; or patch migration, wherein portions of a patch are abandoned and the patch expands into adjacent areas. Over a 3-year period, Catchpole (1996) found the rate of patch abandonment to be approximately 6–7% per year in both burned and unburned watersheds; thus, at least portions of previously established grazing patches were reselected at a high rate (Figure 4). However, when grazing patches were mapped and compared across years, the extent of spatial reselection—although highly variable due to differences in total burned area available to bison in any one year—averaged approximately 50% per year. Thus, grazing patches in both burned and unburned watersheds appear to migrate significantly from year to year. This local migration permits periodic release of portions of the grassland from grazing pressures (Figure 4) and provides a mechanism for recovery of belowground carbohydrate storage reserves and production potential.

At the watershed and landscape scales, the long-term consequences of bison activities include a reduction in cover, dominance, and productivity of grasses; the competitive release of many subdominant species, resulting in an increase in the abundance of forbs; an overall increase in plant species richness and diversity; and increased spatial heterogeneity (Figure 5; Hartnett et al. 1996). Although alterations in plant community composition can be attributed, in large part, to the direct effects of grazing by bison, increased plant species richness is also likely to be a product of increased microsite diversity generated by nongrazing activities, such as dung and urine deposition, trampling, and wallowing. These and other bison activities contribute significantly to the increase in spatial heterogeneity that is characteristic of grazed tallgrass prairie (Figure 5).

Other impacts of bison in tallgrass prairie

Effects of ungulates, especially grazing, on plant community composition and structure have been studied in many grasslands worldwide (McNaughton 1984, Milchunas et al. 1988, Frank and McNaughton 1992, Milchunas and Lauenroth 1993). Ungulate activities, however, affect many other aspects of grassland structure and function, including the physical structure of the environment and the rates of a number of ecosystem-level processes (McNaughton 1993, Frank and Evans 1997, McNaughton et al. 1997). There are several other important mechanisms by which bison alter ecosystem-level processes and physical habitat structure in tallgrass prairie.

Nutrient redistribution and cycling. Bison can substantially alter nutrient cycling processes and patterns of nutrient availability in tallgrass prairie. Their effects on nitrogen cycling are critical because nitrogen availability often limits plant productivity in these grasslands (Seastedt et al. 1991, Blair 1997, Turner et al. 1997) and influences plant species composition (Gibson et al. 1993, Wedin and Tilman 1993). Simulation models of tallgrass prairie responses to grazing (Risser and Parton 1982) and studies of grazers in other grasslands (Frank and Evans 1997, McNaughton et al. 1997) have demonstrated a disproportionate influence of ungulates, including bison, on the regulation of nitrogen cycling processes. Preliminary data from Konza Prairie suggest that bison are similarly important in controlling nitrogen cycling in tallgrass prairie.

Bison influence nitrogen cycling, conservation, and availability in tallgrass prairie ecosystems by altering several soil and plant processes. Ungulates in grasslands consume relatively recalcitrant plant biomass and return labile forms of nitrogen (i.e., urine) to soils (Ruess and McNaughton 1988), thus bypassing the otherwise slow mineralization of nitrogen in plant litter. Nitrogen in bison urine is largely urea, which can be hydrolyzed to ammonium in a matter of days (Ruess and McNaughton 1988). Indeed, application of synthetic bison urine increased concentrations of ammonium and nitrate in Konza Prairie soils over 130-fold and 30-fold, respectively, 8 days after application (J. R. Matchett and Loretta C. Johnson, unpublished data).

Bison grazing can decrease the export of nitrogen from tallgrass prairie by altering the magnitudes of two major pathways of nitrogen loss—combustion and ammonia volatilization. Fire is the major pathway of nitrogen loss from ungrazed tallgrass prairie (Dodds et al. 1996, Blair 1997); nitrogen loss from burning averages 1–4 $g \cdot m^{-2} \cdot yr^{-1}$ (Blair et al. 1998). Grazing lowers combustion losses of nitrogen in tallgrass prairie by reducing the aboveground plant detritus and increasing the patchiness of a prairie fire (Figure 2; Hobbs et al. 1991). Although volatilization of ammonia can be increased by grazing in other types of grassland (Detling 1988), Hobbs et al. (1991) suggested that any increase in ammonia volatilization in tallgrass prairie will be more than compensated for by a reduction in combustion losses of nitrogen.

Finally, bison grazing affects the amount and quality of plant litter returned to soils. Grazing increases plant uptake of nutrients (Ruess 1984) and shoot nitrogen content in many grasslands (Holland and Detling 1990, Milchunas et al. 1995), including tallgrass prairie (Turner et al. 1993). However, the effects of grazers on root growth and chemistry vary among grasslands (Milchunas and Lauenroth 1993). On Konza Prairie, root productivity and root biomass were 30% and 20% lower, respectively, in bison grazing lawns than in ungrazed exclosures. In addition, the nitrogen concentration of new root growth in bison grazing lawns at Konza Prairie increased significantly, from 0.6% to 0.9%, and the C:N ratio of roots decreased. A lower C:N ratio reduces microbial immobilization and enhances nitrogen availability within grazed areas. Indeed, recent studies on Konza Prairie indicated that net nitrogen mineralization in bison grazing lawns was 153% greater, and net nitrification 126% greater, than in ungrazed prairie (Figure 6). Furthermore, net nitrogen mineralization rates were proportional to the intensity of bison use of a given area. Thus, the

net effect of bison grazing appears to be increased rates of nitrogen cycling, coupled with a significant increase in spatial heterogeneity in nitrogen availability; together, these effects can alter patterns of plant productivity and species composition in tallgrass prairie (Figure 5; Steinauer and Collins 1995).

Wallowing. One aspect of bison behavior that differs from that of cattle, and is primarily a physical activity, is wallowing. Wallows in Flint Hills tallgrass prairie, which are established primarily in level upland or lowland sites, dramatically alter the patch structure of this prairie. Bison wallows develop as the animals paw the ground and roll in the exposed soil. Continued use of wallows by bulls, cows, and calves creates a soil depression of 3–5 m in diameter (and 10–30 cm in depth) that is devoid of vegetation. These denuded patches either gradually revegetate or remain as bare soil, depending on the frequency of revisitation by bison. With the vast numbers of bison that once occupied the Great Plains, these soil depressions were probably abundant and widespread features of the landscape (England and DeVos 1969). For example, a number of relic wallows had to be filled to level the playing field for the first University of Oklahoma home football game in 1895 (University of Oklahoma Athletic Department 1986). Relic wallows still exist in many areas where bison have not occurred in the past 125 years.

Environmental conditions in relic and newly established wallows strongly influence prairie patch dynamics (Polley and Collins 1984, Polley and Wallace 1986). Because of soil compaction, wallows often retain rainwater in the spring, creating localized habitats that are suitable for ephemeral wetland species, similar to vernal pools in California (Holland and Jain 1981, Uno 1989). In the summer, however, the same wallows support only plants that can tolerate severe drought. Vegetation composition and structure in wallows is different from that in the surrounding prairie (Polley and Collins 1984), and these differences are enhanced by fire (Collins and Uno 1983), which may not spread through wallows because of low fuel loads. Consequently, at larger spatial scales, grazed prairie that contains bison wallows has higher plant species diversity than grazed prairie without wallows (Collins and Barber 1985). Thus, bison can physically alter grasslands in ways that increase environmental heterogeneity and enhance both local and regional biodiversity (Hartnett et al. 1997).

Bison carcasses. Bison not only affect vegetation patterns and soil processes through their grazing activities but also have profound and lasting localized effects after they die. Although legal requirements and management practices dictate the removal of carcasses of domestic herbivores from public and private grasslands, native herbivores routinely die of natural causes and their bodies remain in situ. As part of the minimal management strategy at Konza Prairie, bison that die on site are not removed. As a result, these carcasses create unique local disturbances (Figure 7) that are the focus of studies to assess their effects on soil nutrients and vegetation responses in tallgrass prairie.

When an individual bison dies, copious quantities of fluids (with high nitrogen concentration) are released during decomposition. Adult bison can weigh more than 800 kg, and these carcasses typically kill underlying and adjacent plants, creating a denuded zone of 4–6 m^2 (Figure 7). Although the fluids that are initially released are toxic to vegetation, these sites eventually become zones of high fertility. For example, soil cores extracted from the center of carcass sites on Konza Prairie 3 years after death had inorganic nitrogen concentrations that were two to three times higher than the surrounding prairie. This nutrient enrichment may extend up to 2.5 m away from the original carcass site and results in patches dominated initially by early successional species. The aboveground primary production in these patches is two to three times higher than in undisturbed prairie.

Although disturbances created by bison carcasses are sporadic and localized on Konza Prairie, they provide nutrient pulses that exceed all other natural processes, even urine and fecal deposits. Overall, we can only speculate about historical rates of bison mortality. Given the enormous size of the bison population before their widespread slaughter in the 1800s, annual mortality was probably high. High death rates would have been especially common during droughts, when there would be the potential for large numbers of carcasses to occur across the landscape. Even though predators and scavengers may have consumed and relocated many of these carcasses, decomposition of the remaining and partial carcasses would still have resulted in patches of locally high nutrient concentration. Thus, although it was variable, bison mortality would have led to a continual cycle of disturbance and recovery of these patches in presettlement grasslands.

Are bison keystone species?

The net effects of selective bison grazing activities at the landscape, patch, and individual plant level include shifts in plant species composition, alterations of the physical and chemical environment, and increased spatial and temporal heterogeneity in vegetation structure, soil resource availability, and a variety of ecosystem processes (Figures 4, 5, and 6). Before bison reintroduction at Konza Prairie, the long-term burning experiments produced clear patterns of response in the vegetation. As fire frequency increased, the dominance of C_4 grasses increased, and the cover of C_3 grasses, forbs, and woody species decreased (Figure 4; Gibson and Hulbert 1987). Overall, plant species diversity declined as fire frequency increased in ungrazed tallgrass prairie (Collins et al. 1995).

These patterns in community structure, which had developed over 20 years of burning treatments at Konza Prairie, are being rapidly and dramatically altered by the grazing activity of the reintroduced bison. In particular, grazing by bison has lowered the abundance of the dominant C_4 grasses, increased the abundance of the subdominant C_3 grasses and forbs, and markedly increased plant species diversity (by 23%), richness (by 38%), and community heterogeneity (by 13%) relative to ungrazed sites, even under annual burning conditions (Hartnett et al. 1996, Collins and Steinauer 1998, Collins et al. 1998).

Because of the multiple and dramatic effects of bison on this landscape, we believe that bison are keystone species in the tallgrass prairie. Other authors have noted the potential of large grazing mammals to act as "keystone herbivores" capable of maintaining open grassland vegetation that would otherwise undergo succession to shrubland or woodland (Owen-Smith 1987). Indeed, the disappearance of a grazing megafauna at the end of the Pleistocene may have played a major role in the widespread transition from steppe to tundra at that time (Zimov et al. 1995). However, the concept of keystone species has been controversial since its inception (Power et al. 1996). One of the problems with this concept has been the variable interpretation of criteria by which species are determined to be keystone. Power et al. (1996) consider a keystone species to be "one whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance." To make this definition operational, these authors proposed a measure of community importance (CI) to be used as an index of the strength of the impact of a given species:

$$CI = [(t_N - t_D)/t_N][1/p_i]$$

where t_N is a quantitative measure of a trait (e.g., diversity) in an intact community, t_D is the measure of the trait when species *i* has been deleted, and p_i is the proportional abundance (biomass) of species *i* before it was deleted. CI values "much greater than 1" indicate that a species is keystone. We estimate bison biomass at Konza Prairie to be approximately 11–12 $g \cdot m^2$ (Collins and Steinauer 1998), which is approximately 1% of the total vegetative biomass. On Konza Prairie, diversity is significantly higher (10–33%) on grazed sites than ungrazed sites (Hartnett et al. 1996), and these values yield a range of CIs from 6 to 25. For this reason and others, we consider bison to be keystone species in tallgrass prairie ecosystems.

Are bison and cattle functional equivalents in tallgrass prairie?

The historical presence of immense herds of large ungulates in Great Plains grasslands is undisputed (McHugh 1972), and we have emphasized the keystone role that bison played in determining the structure and function of tallgrass prairies at multiple spatial and temporal scales. With the replacement of native bison by domesticated cattle in the remaining grasslands, an obvious issue is the degree of similarity between these two ungulates with respect to their effects on tallgrass prairie. In other words, can bison and cattle be considered ecological equivalents?

There have been several previous attempts to answer this question, but the results have been equivocal at best (Plumb and Dodd 1993, Hartnett et al. 1997). The primary barrier to resolving this issue rests with a lack of comparative studies in which management is held constant and the type of grazer is varied. Such studies have recently been initiated at Konza Prairie. Results after 3 years indicate that the abundance and richness of annual forbs, and the spatial heterogeneity of biomass and cover, are higher in sites with bison than in sites with cattle. No dramatic differences have been detected, however, between cattle- and bison-grazed sites in cover of the dominant C_4 grass, *A. gerardii*, or the dominant forb, *Ambrosia psilostachya*; total plant species richness is also not dramatically different (E. Gene Towne and David C. Hartnett, unpublished data).

Results at Konza Prairie are consistent with previous assessments (e.g., Schwartz and Ellis [1981], Van Vuren and Bray [1983], and Plumb and Dodd [1993] in mixed and shortgrass prairie), which noted that both bison and cattle are generalist herbivores that graze preferentially on graminoids. Nevertheless, some differences in the foraging patterns of bison and cattle have been documented that may have long-term implications for grasslands. For example, bison have a higher proportion of graminoids in their diet than do cattle; consequently, forb and browse species are more common in cattle diets (Van Vuren and Bray 1983, Hartnett et al. 1997). Also, bison spend less time grazing than cattle and more time in nonfeeding activities (Plumb and Dodd 1993), and bison strongly prefer open grassland areas for grazing, whereas cattle use wooded and grassland habitats opportunistically (Hartnett et al. 1997).

Studies that have focused exclusively on cattle generally concur that their grazing activities increase spatial heterogeneity and enhance plant species diversity, so long as stocking density is not too high (Collins 1987, Hartnett et al. 1996). Because bison grazing in tallgrass prairie has a similar effect, one could conclude that either herbivore can alter resource availability and heterogeneity and reduce the cover of the dominant grasses sufficiently to enhance the success of the subdominant species. Perhaps of greater importance than differences in foraging patterns between bison and cattle, however, are the number of nongrazing activities, such as wallowing and horning (i.e., rubbing on trees) that are associated exclusively with bison (Coppedge and Shaw 1997, Hartnett et al. 1997). These activities, when combined with the spatial redistribution of nutrients and selective consumption of the dominant grasses, may further increase plant species richness and resource heterogeneity, particularly at the landscape scale.

Nevertheless, it is likely that because bison and cattle are functionally similar as large grass-feeding herbivores, management strategies (stocking intensity and duration) will have a greater influence on the degree of ecological equivalency achieved than inherent differences in these ungulates (Hartnett et al. 1997). Clearly, the degree of overlap in diet and foraging patterns is greater between bison and cattle than between cattle and other historically important native herbivores (Hartnett et al. 1997), such as antelope (*Antilocapra americana*), deer (*Odocoileus virginianus*), and elk (*Cervus canadensis*). Indeed, the loss of antelope and elk from the tallgrass prairie, coupled with dramatic increases in deer populations, presents additional challenges for managing these ecosystems.

Conservation implications

Conserving small and moderate-sized tracts of once-vast biomes, such as the tallgrass prairie, presents a unique set of problems that are distinct from those associated with spatially re-

stricted ecosystems because many of the defining forces that historically were important in structuring these systems occurred at spatial scales that no longer exist. For example, in pre-1900s grasslands, fires were not plot-level or even watershed-level events but operated at spatial scales encompassing thousands of hectares. This large spatial scale resulted in potentially high fire frequencies throughout the tallgrass prairie because any point of ignition in this "inland sea of grass" could affect grasslands hundreds of kilometers distant.

Today, the fragmentation of Great Plains grasslands is recognized as a key factor in reducing the frequency of fire, which in turn contributes to species loss (Leach and Givnish 1996). Indeed, the primary management strategy for small prairie preserves, which are most prone to invasion by woody vegetation and exotic species, is to burn them as frequently as possible to suppress invasion by undesirable plants (Leach and Givnish 1996). Unfortunately, frequent (annual or biannual) spring fire maintains dominance by C_4 grasses but reduces plant species diversity relative to grasslands that are burned infrequently. One alternative is to conduct burns at different times of the year (Howe 1994), but summer fires, for example, may not prevent invasion or reduce the abundance of woody vegetation (Adams et al. 1982). In addition, burning in late summer may be difficult because of other considerations, including reduced ability to control the fire under dry, windy conditions. Not only are prairies threatened by fragmentation and invasion by undesirable species, but grasslands throughout the Great Plains are now affected by increased atmospheric nitrogen deposition (Wedin and Tilman 1996). Thus, remnant grasslands are subjected to a variety of anthropogenic factors that can reduce the diversity of native prairie species.

The spatial and temporal impacts of bison grazing activities caused by the historically large and nomadic herds are also best characterized as landscape-level forces. These too are difficult to replicate in today's fragmented grassland remnants. Yet just as some of the ecological characteristics of natural fires can be reintroduced to grasslands through prescribed fire, the key elements of bison grazing activities can and should be incorporated into conservation and restoration strategies for remnant prairies (Steuter 1997). One approach to accomplish this goal is the substitution of cattle for bison. Plumb and Dodd (1993) argued that the choice of whether to use cattle or bison as a management tool in grasslands is scale and context dependent. Clearly, reintroducing bison may not be appropriate for small prairie remnants with public access and low economic resources. But cattle, managed for their ecological rather than their economic value, may be suitable in such cases.

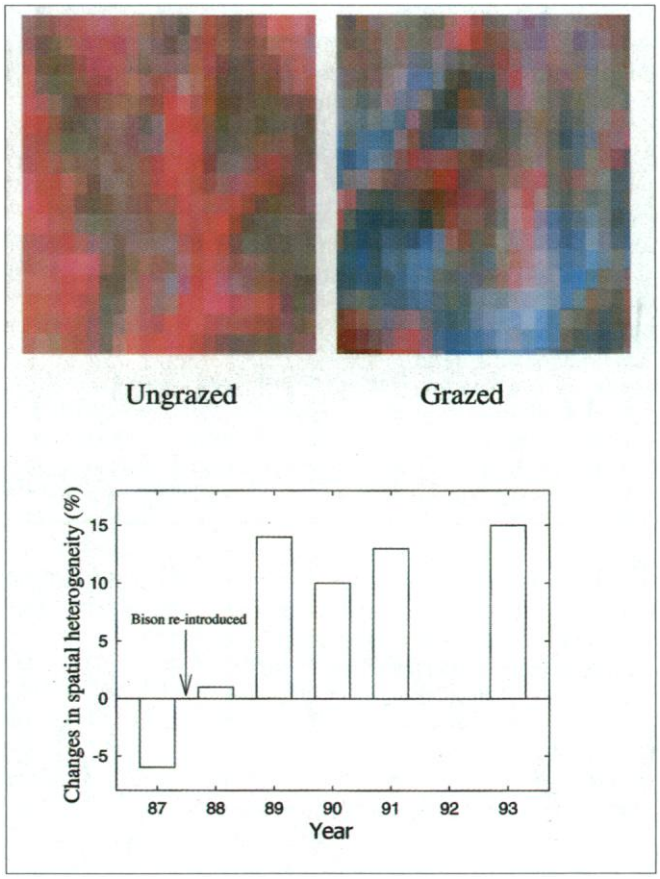


Figure 5. Landscape-level changes in spatial heterogeneity in tallgrass prairie induced by bison grazing activities. False-color composite of Thematic Mapper (TM) data from an area on Konza Prairie grazed by bison (upper left) and from a nearby area protected from grazing (upper right). Both sites were burned and have similar soil types, aspect, and slopes. Red colors represent areas of high productivity, and blue colors correspond to areas of low productivity or bare ground. (lower panel) Percentage difference in spatial heterogeneity of biomass (estimated from remotely sensed spectral reflectance data) between areas grazed by bison and adjacent ungrazed areas on Konza Prairie. Before bison reintroduction, watersheds scheduled to remain ungrazed appeared to have greater spatial heterogeneity than those scheduled to be grazed (negative values in 1987). After the reintroduction of bison in 1988, spatial heterogeneity in the grazed watersheds increased substantially. Spatial heterogeneity was assessed using the TEXTURE algorithm, which involves passing a moving 3 × 3 pixel window through the images and determining the differences between the minimum and maximum values for each subset of pixels (Briggs and Nellis 1991). Pixels represent derived Normalized Difference Vegetation Index (NDVI) values from TM data (30 m^2 spatial resolution) from 1988 to 1991 and from 1993 (TM data were not available for 1992). Previous studies have confirmed that the use of the TEXTURE algorithm with NDVI data is useful for estimating patterns of spatial heterogeneity in tallgrass prairie (Nellis and Briggs 1989, Briggs and Nellis 1991).

Alternatively, mowing can be used to reduce the dominance of the tall grasses and to enhance species richness (Gibson et al. 1993, Collins and Steinauer 1998). Results from a long-term experiment at Konza Prairie incorporating annual fire, nitrogen addition, and mowing (Collins et al. 1998) indicated that on annually burned and fertilized treatment plots, productivity of the grasses was higher, and plant species diversity lower, than in control plots. However, on burned, fertilized plots that were mowed (with removal of the foliage; a rough substitute for grazing), plant species diversity was restored to levels similar to control plots (Collins and Steinauer 1998).

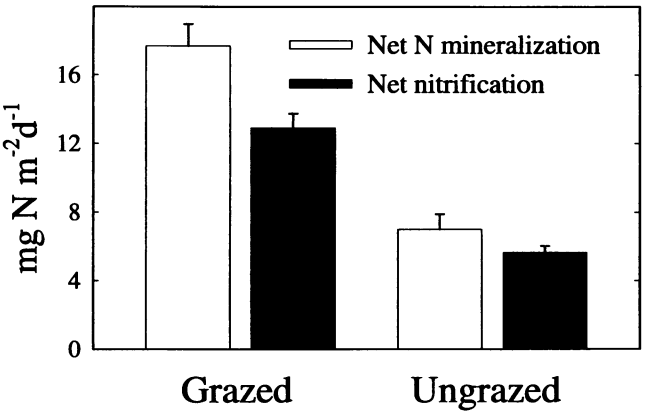


Figure 6. Net nitrogen mineralization and net nitrification rates in grazed and ungrazed areas of Konza Prairie. Measurements were made in situ for a 1-month period in June 1996 and May 1997 using a modified buried soil core technique (Raison et al. 1987). Replicate study plots were located on upland areas of adjacent grazed and ungrazed annually burned watersheds. Values are means ± 1 SE and are significantly different ($P < 0.05$, n = 120 per grazing treatment).

A combination of frequent spring fire to maintain populations of the desirable C_4 prairie grasses, decrease nitrogen availability (Blair 1997), and suppress growth of weedy annuals and woody vegetation, coupled with mowing portions of the site to reduce the competitive dominance of C_4 grasses, can enhance the abundance of forbs and maintain high plant species diversity in small remnant prairies. Ultimately, management designed to increase the spatial heterogeneity of resources in a manner analogous to that imposed by ungulate activities is essential if significant and sustainable biotic diversity in tallgrass prairie is a goal.

Conclusions

Despite less than a decade of research at Konza Prairie on bison–tallgrass prairie interactions, the keystone role that bison must have historically played in this grassland is clear. Moreover, much as fire is now recognized as an essential component of tallgrass prairie management (because without fire this grassland disappears), the need for reintroducing the forces of large ungulate herbivory to this grassland is evident. Indeed, it is the interaction of ungulate grazing activities and fire, operating in a shifting mosaic across the landscape, that is key to conserving and restoring the biotic integrity of the remaining tracts of tallgrass prairie.

Before bison were reintroduced to Konza Prairie, Knapp and Seastedt (1986) speculated that bison grazing and fire could act in similar ways by reducing the accumulation of detritus in this system. It is primarily the blanketing effect of the accumulation of dead plant material above ground that limits productivity in undisturbed tallgrass prairie. Like fire, bison grazing reduces aboveground standing dead biomass. But it is now clear that the unique spatial and temporal complexities of bison grazing activities (Figure 5) are critical to the successful maintenance of biotic diversity in this grassland. This grazing-induced heterogeneity contrasts sharply with the spatial homogeneity induced by fire in an ungrazed landscape (Figure 6).

Tallgrass prairie, by virtue of its inherently variable climatic, grazing, and fire regimes, is an ecosystem that requires long-term study to document patterns and quantify processes (Knapp et al. 1998b). Through the partnership of The Nature Conservancy, the National Science Foundation's LTER program, and Kansas State University, ongoing studies at this site will continue to explore the ecological interactions of fire and grazing in the tallgrass prairie landscape. Such research is timely because conservation and management issues have intensified in the remaining tracts of this once-vast biome, particularly in response to predicted alterations in global climate and land-use changes. Interdisciplinary ecological research, such as that ongoing at Konza Prairie, will provide the basic information necessary for designing optimal conservation, restoration, and management strategies in this and other grasslands.



Figure 7. Bison carcass approximately 9 months after death in burned tallgrass prairie. In this spring (May) photo, vegetation is completely lacking within the area in which the animal died. A zone of high fertility exists around the edge of this disturbance, and within 1–2 years the site will be dominated by early successional (annual) species.

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