Great Plains Research: A Journal of Natural and Social Sciences

Great Plains Studies, Center for

Spring 2003

Migrations of Grassland Communities and Grazing Philosophies in the Great Plains: A Review and Implications for Management

Joe C. Truett
Turner Endangered Species Fund

Truett, Joe C., "Migrations of Grassland Communities and Grazing Philosophies in the Great Plains: A Review and Implications for Management" (2003). *Great Plains Research: A Journal of Natural and Social Sciences*. 646.
https://digitalcommons.unl.edu/greatplainsresearch/646

Great Plains Research 13 (Spring 2003): 3-26

MIGRATIONS OF GRASSLAND COMMUNITIES AND GRAZING PHILOSOPHIES IN THE GREAT PLAINS: A REVIEW AND IMPLICATIONS FOR MANAGEMENT

Joe C. Truett

Turner Endangered Species Fund
P.O. Box 211
Glenwood, NM 88039
jtruett@gilanet.com

ABSTRACT—Ecologists commonly separate Great Plains grasslands communities into types based on grass height: shortgrass prairie, mixed-grass prairie, and tallgrass prairie. Grass height correlates directly with precipitation and thus lessens with distance westward and with drought. Grass height correlates inversely with grazing intensity and thus shortgrasses expand eastward when grazing pressures are great and shrink westward when grazing pressures relax. Evidence about past distributions of shortgrasses, coupled with the prehistoric and historic abundances of large grazers and the black-tailed prairie dog (a shortgrass indicator), suggest a far-eastward occurrence of shortgrass prairie in the late Pleistocene (despite a relatively wet climate), a shrinkage westward by late prehistoric and early historic times, and a farther shift westward in response to the bison's demise in the 19th century. After cattle arrived in the late 1800s, shortgrass prairie expanded and contracted depending on the prevailing grazing philosophies, resulting grazing intensities, and periodic drought. Currently, taller grasses have prevailed for over a half century, and shortgrass prairie may be more restricted than it has been for millennia, because of a grazing philosophy that promotes moderate grazing. An emerging change in grazing philosophy may presage a gradual return of heavier grazing and another expansion eastward of the shortgrass prairie. Such an expansion, particularly if accompanied by grazing regimes patterned on early historic and prehistoric grazing, may enhance biodiversity, the stability of some soils, and under some circumstances, economic returns from ranching.

KEY WORDS: bison, grasslands distribution, grazing, Great Plains, history, mixed-grass, prairie dogs, shortgrass

Introduction

One of the more puzzling phenomena reported by early-day travelers in the Great Plains was the apparent dominance of shortgrass prairie far east of where plant ecologists now portray its limits. For example, Ambrose (1996:165) asserted that Meriwether Lewis and William Clark on their westward journey in September 1804 entered the shortgrass country where the Missouri River borders northeastern Nebraska. The explorers' reports of the fauna bear this out. The expedition already had begun to encounter bison (*Bison bison*), killing its first on 23 August. Bison abundance quickly escalated—the travelers marveled at a herd of 400 on 9 September. Two days earlier, in present-day Boyd County, NE, they first had seen that classic marker of shortgrass prairie, the black-tailed prairie dog (*Cynomys ludovicianus*).

Bison and prairie dogs quickly became commonplace. On 17 September, about 300 km southeast of present-day Pierre, SD, Lewis hiked away from the river and came upon a scene oft to repeat itself in the coming weeks. He described a plain, nearly 25 km^2 in extent, that was

> intirely occupyed by the burrows of the barking squril [prairie dog]. . . . this anamal appears here in infinite numbers, and the shortness and virdure of grass gave the plain the appearance throughout it's whole extent of beatifull bowlinggreen in fine order. . . . this scenery already rich pleasing and beatiful, was still farther hightened by immence herds of Buffaloe deer Elk and antelopes which we saw in every direction feeding on the hills and plains. I do not think I exagerate when I estimate the number of Buffaloe which could be compreed [comprehended] at one view to amount to 3000. (Moulton 1987:80, 81).

Modern maps portraying Great Plains grassland types (e.g., Bell 1973:11; Wright and Bailey 1980:4; Licht 1997:3; Seig et al. 1999:279) indicate that taller grasses should have prevailed and that the expedition should not have entered shortgrass prairie for another 150 km or more to the west (Fig. 1). How can this seeming contradiction be explained?

Biogeography of Grass Height

In the affairs of humans and other animals of the Great Plains, few qualities of grass are more important than its height. Grass height correlates

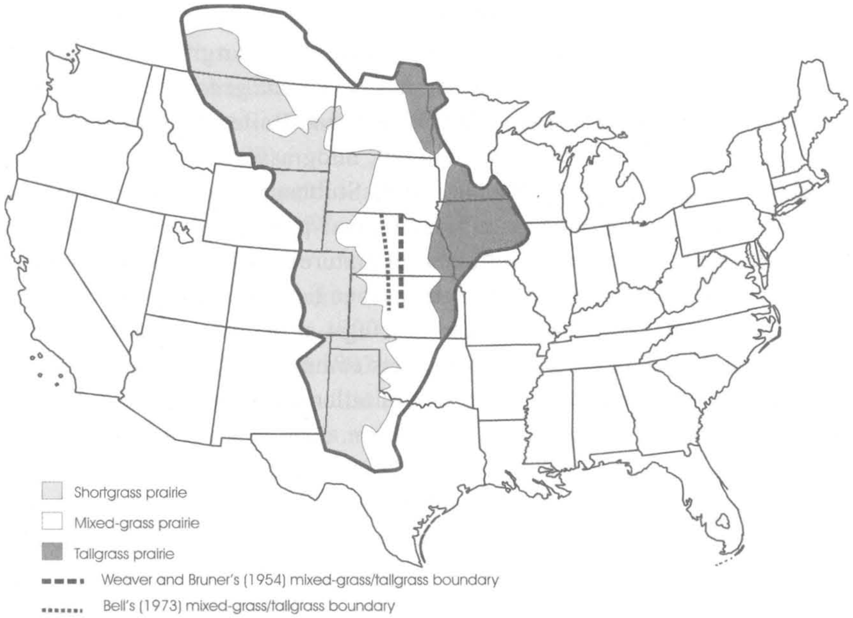

Figure 1. Distribution of shortgrass prairie, mixed-grass prairie, and tallgrass prairie types within the Great Plains as depicted by Licht (1997:3), and mixed-grass/tallgrass boundaries as presented by Weaver and Bruner (1954) and Bell (1973). The three different mixed-grass/tallgrass boundaries exemplify different assessments among ecologists about type boundary locations.

with soil productivity and carrying capacity of range for livestock (Weaver 1954; Sala et al. 1988). It determines the frequency of wildfire (Wright and Bailey 1980; Seig 1997) and the utility of burning as a livestock management tool (Shaw and Carter 1990). It can regulate the diversity and composition of mammal (Grant et al. 1982) and bird (Wiens 1973) communities.

Great Plains grassland ecologists traditionally have recognized three general grassland types based on height of the dominant species: tallgrass prairie, mixed-grass prairie, and shortgrass prairie (Weaver 1954; Sala et al. 1988; Licht 1997). Different ecologists have presented somewhat different maps of grassland type distributions. Disagreements on locations of type boundaries (see Fig. 1) no doubt resulted partly from differences in precipitation and grazing regimes in effect when ecologists gathered field data to verify maps.

The grass species themselves commonly are classed by growth form as tallgrasses (e.g., big bluestem, *Andropogon gerardii*; indiangrass, *Sorghastrum nutrans*), mid-height grasses or midgrasses (e.g., little bluestem, *Schizachrium scoparium*; western wheatgrass, *Agropyron smithii*), and shortgrasses (e.g., blue grama, *Bouteloua gracilis*; buffalograss, *Buchlöe dactyloides*) (Weaver 1954; Wright and Bailey 1980). Commonly dominant tallgrasses grow 90-300 cm tall, midgrasses 20-100 cm tall, and shortgrasses 5-60 cm tall (Brown 1993; Stubbendieck et al. 1997). By definition, tallgrass species dominate tallgrass prairies; shortgrass species dominate shortgrass prairies; and some admixture of tallgrasses, midgrasses, and shortgrass co-dominate in mixed-grass prairie (Weaver 1954).

Two factors—precipitation and grazing—strongly influence the average height of grasses in Great Plains grass communities. In general, height within species as well as the proportion of taller species present are directly proportional to average annual precipitation, such that the declining grass stature from east to west follows the gradient of declining moisture (Weaver and Bruner 1954; Lauenroth et al. 1999). Grass height is inversely proportional to grazing intensity; for example, heavy, frequent grazing by cattle or bison can convert tallgrass prairie to mixed-grass, or mixed-grass to shortgrass (Weaver and Bruner 1954; Hartnett et al. 1996; Gillen et al. 2000).

Other factors also influence grass height. Burning temporarily reduces grass height and kills some grasses. But given its historic infrequency—perhaps once in 1-5 years in tallgrass prairie and once in 5-30 years in mixed-grass prairie (Seig 1997)—and the resilience to fire of most dominant Great Plains grasses (Wright and Bailey 1980; Ford 1999), fire probably has never directly influenced grassland type as much as precipitation or grazing (Wright and Bailey 1980). Soil type, slope, and mean temperature exert additional influences (Lauenroth et al. 1999) that change relatively slowly over time. The temporal and spatial complexity of precipitation, grazing, fire, soils, and other factors create great interdigitation and patchiness, or a mosaic of types (Lauenroth et al. 1999), rather than sharp lines of demarcation where one grassland type grades into another.

Precipitation and grazing influence grass height by two important mechanisms. In the short term they affect the height, and often the cover, of the grasses without much effect on the species composition (McNaughton 1984; Milchunas et al. 1995). In the longer term they can induce a change in the species composition such that short-statured species are replaced by taller species, or vice versa (Weaver and Bruner 1954; Wilson and Macleod 1991; Vinton et al. 1993).

Changes in height occur within years or even seasons as precipitation or grazing change; changes in composition take longer but may be remarkably short. For example, Albertson and Weaver (1946) and Weaver

(1954:253-54) described shifts in species dominance from tallgrasses to midgrasses and from midgrasses to shortgrasses over large areas during the 1934-41 drought. Similarly rapid shifts in species dominance caused by intensive grazing also are well known (Weaver 1954:286; Hartnett et al. 1996; Gillen et al. 1998).

Rapid increases in species initially rare or absent depend on sources of seeds or other propagules. Weaver (1954) described two general sources: plants already present in the community (tallgrasses, midgrasses, and shortgrasses commonly co-occur) and windborne seeds from outside. Soil seed banks (Kinucan and Smeins 1992) or relict plants in favorable microhabitats (Fuhlendorf and Smeins 1997) can initiate rapid compositional changes in response to changing conditions. Some species persist or spread more commonly by vegetative parts such as rhizomes and stolons than by seeds (see Stubbendieck et al. 1997).

In the following sections we examine east-west migrations over time of tallgrass, mixed-grass, and shortgrass types and assess potential causes for these shifts. We delineate the types on the basis of grass height, which is strongly influenced by species composition, precipitation, and grazing. In particular, we assess changes in grazing by large herbivores as a causative factor. We evaluate how changes in lifeways and philosophies by hunting and pastoral peoples have affected grazing and thus grassland type distributions. Finally, we assess emerging changes in philosophy and their implications for future grassland type distributions and conservation.

Pastures of the Pleistocene

The initial rise of extensive grasslands in central North America probably took place 5 to 7 million years ago (Axelrod 1985). By the late Pleistocene (10,000-40,000 years ago), grasslands dominated what we now call the Great Plains (Holliday 1987; Barnosky 1989; Hall and Valastro 1995). At this time, the grass species present in the Great Plains were, with the possible exceptions of some C_4 (warm-season) species, the same as exist today (Stebbins 1981; Hall and Valastro 1995). However, species assemblages at given locations probably were different than they are today (Thompson 1988; Hall 2000).

Given the cooler, moister climate of the Great Plains in the late Pleistocene (Bryson 1974; Hall and Valastro 1995), one might expect shortgrass communities to have been spatially more restricted then than they are today. We cannot readily make direct inferences about this because the fossil records of the grasses themselves are notoriously incomplete (Brown 1993;

Hall and Valastro 1995). However, the late Pleistocene distribution of the black-tailed prairie dog (Goodwin 1995), a shortgrass-dependent species (Koford 1958; Hoogland 1981), can be used as an indicator. Prairie dogs need shortgrass because it enables them to see and avoid approaching predators (Hoogland 1981).

The range of the black-tailed prairie dog in the late Pleistocene extended east of its historic limit (Goodwin 1995; Graham et al. 1996), far into what we have come to know as tallgrass regions (cf. Figs. 1 and 2). Given the direct correlation between moister conditions and taller grasses (Weaver 1954; McNaughton 1984; Sala et al. 1988), one may suspect that late Pleistocene grazing rather than climate promoted the expansive distribution of black-tailed prairie dogs. Indeed, shortgrass swards, or "grazing lawns," seem to be a common evolutionary component of mid- or tallgrass regions that sustain large, wild grazers (McNaughton 1984). The great diversity of large grazers that populated the Great Plains in the late Pleistocene (Graham and Lundelius 1984), coupled with the far-eastward distribution of black-tailed prairie dogs at the same time, suggest that shortgrass prairie prevailed over larger areas and farther eastward than today, despite a wetter climate.

Human survival strategies may have altered grassland type distributions as early as the end of the Pleistocene. At least eight large North American grazers plummeted to extinction at that time (Graham and Lundelius 1984), with undoubted influence on the grasslands. Paul Martin's (1967) hypothesis that newly arrived humans were implicated in the extinctions gains more support as the sophistication of analysis increases (Alroy 2001). What led humans to exterminate large grazers will of course be forever veiled by time, although some insight may be gained from motivations leading to later overharvests, such as the 19th-century slaughter of bison.

These end-of-Pleistocene extinctions ushered in 10,000 years of bison domination among the grazers of the Great Plains (Mack and Thompson 1982). How did bison and their human hunters influence the distribution of grassland types during this period? This can best be inferred from historical evidence collected as Europeans entered the Plains and bison numbers began to decline.

The Bison Plains

More than 60 years ago Floyd Larson (1940) argued that bison, before their 19th-century demise, had maintained vast areas of Weaver and Clements's (1938) "mixed-grass prairie" in shortgrass condition. He believed the shortgrass region under the influence of bison to be a more "natural" depiction of its extent than that based on the ungrazed condition as proposed by Weaver and Clements (1938). His challenge of these two icons of prairie science had little effect at the time and, until recently, range managers steeped in Clementsian dogma dictated proper grass and proper grazing in the Great Plains.

Independent assessments of what early-19th-century travelers reported seeing have led numerous others (e.g., England and DeVos 1969; Roe 1970:361-62; Hart and Hart 1997; Thomas 2000; Hart 2001) to echo Larsen's (1940) belief that grazing by bison kept grasses short over vast regions. In terms of grassland type distributions, this view holds that bison grazing kept the shortgrass/mixed-grass boundary substantially east of where modern maps depict it (e.g., Wright and Bailey 1980; Omernik 1987; Licht 1997:3). Horses of bison-hunting tribes undoubtedly added to the grazing impact after the mid-1700s (Hämäläinen 2001). As today, spatial heterogeneity in grazing pattern (see Fuhlendorf and Engle 2001), in combination with variation in soils and topography (Lauenroth et al. 1999), undoubtedly created a wide mosaic of types rather than a distinct line where shortgrasses gave way to taller grasses.

A look at the historic distribution of the black-tailed prairie dog likewise suggests shortgrass prairie in the early 19th century extended farther east than today. Naturalists delineated the eastern boundary of prairie dog distribution (Fig. 2) based on the eastern limit of historic collections. Curiously, this boundary more nearly approximates the currently accepted mixed-grass/tallgrass boundary than it does the shortgrass/mixed-grass boundary (cf. Figs. 1 and 2). Prairie dogs do exist today in a few locations near the eastern limits of their historic range. But in such locations they appear to require either intensive, frequent grazing by livestock (C. Knowles, FaunaWest, Boulder, MT, pers. comm.; M. Fritz, Nebraska Game and Parks Commission, pers. comm.) or predator-unfriendly environments such as human settlements or small relict grasslands within extensive croplands (Sidle et al. 2001; M. Fritz pers. comm.).

Once intensive grazing or other disturbances that limit grass height are removed, colonies in mixed-grass or tallgrass regions shrink and often disappear within a few years (Osborn and Allan 1949; Koford 1958:65; Smith 1967; Snell and Hlavachick 1980; Knowles 1982:156; Snell 1985). The rate of colony shrinkage varies directly with the growth rate of herbaceous vegetation (Knowles 1982:156; Snell 1985) and thus the amount of precipitation (Cable and Timm 1987). Even when grazing maintains shortgrasses, colony growth often proceeds more slowly than colony shrinkage

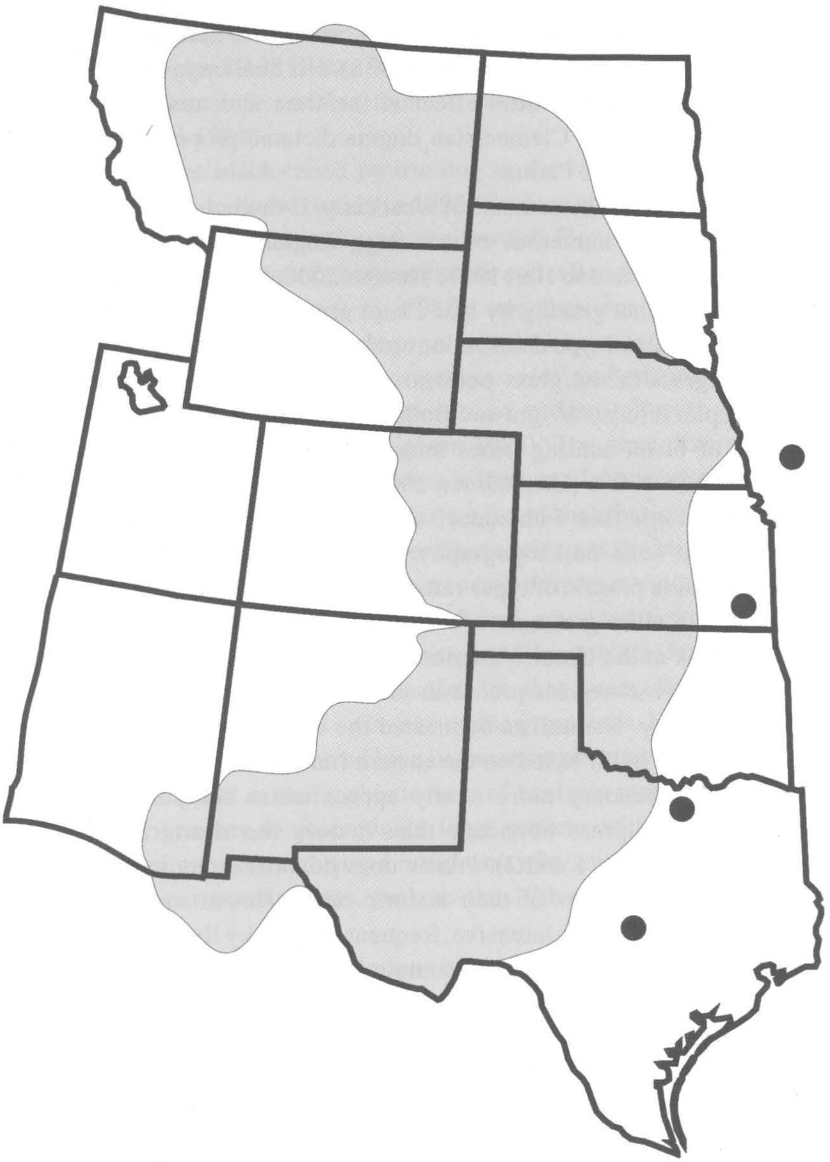

Figure 2. Historic range of the black-tailed prairie dog (shaded) (Hall 1981; Goodwin 1995) and late Pleistocene records of remains of the species east of historic range (dots) (Goodwin 1995).

does without grazing (cf. Knowles et al. 2002; Snell 1985). Recolonization of dense, tall swards of grass will not occur unless other colonies exist within a few kilometers as a source of immigrants (Knowles 1985) and grass height once again is reduced (Koford 1958:65; Knowles 1986).

To some extent the prairie dogs themselves can keep the grass short. They reduce vegetation height by clipping much more than they consume (Tileston and Lechleitner 1966; Whicker and Detling 1988). However, in mixed-grass or tallgrass regions, rapidly growing grasses overwhelm their trimming abilities, not only preventing colony expansion (Truett and Savage 1998) but also soon "choking out" existing colonies (Osborn and Allan 1949; Snell and Hlavachick 1980). Thus, prairie dog survival in eastern portions of their range depends on frequent heavy grazing by large herbivores, or some other frequent disturbance (e.g., fire, mowing), to keep the grass short.

Perhaps predictably, extensive prairie dog populations in mixed-grass regions in the 19th century seem to have been associated with abundant bison. For example, railroad surveyor Arthur Ferguson, moving west up the Platte River in 1865, encountered a "vast prairie dog village" 10 miles long near present-day Kearney, NE (White 2002), as he entered a region of bison abundance (Hart 2001). Large numbers of bison persisted the longest in Kansas (to about 1860) (West 1995:65) in the northwestern part of the state, the same region in which Mead (1899) noted that prairie dogs were particularly abundant in 1859. The final slaughter of the southern bison herd in the late 1870s took place in the same north-central Texas area (Gard 1959; Meinzer 1988) that Bailey (1905) later described as hosting by far the largest prairie dog colony ever documented — about 65,000 km^2 in extent. This last area, unlike most in the Great Plains, filled with cattle immediately upon the demise of bison such that grazing by a large herbivore continued almost uninterrupted (Dale 1930; Gard 1959; Meinig 1969:66; Isenberg 2000).

Some early-day naturalists left accounts of how grass and prairie dogs responded to the demise of bison. W. A. Bell (1870), traversing the plains west of Salina, KS, in 1867, wrote:

> Doubtless no grass [except buffalograss] could bear so well the heavy tramp of thousands of buffalo continuously passing over it; but it is a good thing for the land that, as settlers advance, and domestic herds take the place of big game, the coarser, more vigorous, and deeper rooted grasses destroy it, and take its place.

Naturalist J. R. Mead (1899) kept a Kansas journal in the 1850s and lived to comment on the changes that accompanied bison extermination during the next 40 years. He told attendees at the annual meeting of the Kansas Academy of Science in 1898 (Mead 1899) that prairie dogs in the 1850s were "innumerable," but that by the end of the century, "Prairie dogs, except for a few remnants, disappeared. The foot of the buffalo was necessary for their existence. As soon as the ground ceased to be tramped hard and the grass and weeds grew they perished."

Thus, one may deduce that the plain of "beatifull bowlinggreen in fine order" encountered by Lewis in northeastern Nebraska in 1804 had been kept that way not only by prairie dogs but also by bison and perhaps elk (*Cervus elaphus*) and horses. The poor dispersal ability (Knowles 1985) and slow colony growth (Knowles et al. 2002) of prairie dogs and their rapid demise without grazing (Osborn and Allan 1949; Snell 1985) suggest that such sites in mixed-grass or tallgrass regions probably had been heavily and frequently grazed for decades, or even centuries, by bison. The historic abundance of prairie dogs in mixed-grass and tallgrass regions supports Hart's (2001) contention that bison exerted frequent, rather than occasional, intensive grazing at some Great Plains localities. Thus, the demise of bison that began in the late 1700s and early 1800s (Flores 1991; Isenberg 2000; Hämäläinen 2001) may help explain the retreat 150-240 km westward of the shortgrass prairie thereafter (see Brown 1993).

Disagreement between Knowles et al. (2002) and Virchow and Hygnstrom (2002) about the abundance of prairie dogs encountered by 19th-century travelers may have a basis partly in the spatial and temporal differences in the abundance of bison. During this period, overhunting and perhaps disease (Altenhofen 1999) and other factors caused rapid declines in bison and thus undoubtedly of prairie dogs. Indeed, overhunting of bison with adverse effects on prairie dogs may have been going on long before Lewis and Clark.

Bison hunting by Great Plains tribes constituted a major subsistence economy during pre-European times, but increasingly in the 1800s tribal hunting also became market oriented (Hämäläinen 2001). Europeans and aboriginal Americans collaborated from the early 1800s to the early 1880s to exterminate bison in the Great Plains (West 1995; Isenberg 2000; Hämäläinen 2001). Killing for the market economy (e.g., hide hunting), and purposeful elimination of the food source of Plains Indians, seemed to be prime motivations of Euro-Americans.

Whether some of the tribes associated the impacts of their own hunting with the bison's demise is not clear (Hämäläinen 2001). Some Euro-

Americans saw the impacts of hunting and foretold the end but viewed extermination as beneficial because it would help drive Plains Indians to reservations and make way for white settlement (Licht 1997:12; Box 2001). Other Euro-Americans regretted the slaughter but probably viewed it as unstoppable (Dary 1974; Isenberg 2000). Thus, the transformation of the prairie that followed the removal of bison seems to be the by-product of an economic motivation unmitigated by any effective conservation philosophy.

Killing to the limits of human ability may have restricted the abundance of bison for centuries or even millennia before Europeans precipitated the 19th-century slaughter. Shaw and Lee (1997) suggested the historic scarcity of bison in the eastern tallgrass extremes of the central Great Plains may have resulted from overharvest by aboriginal groups sustained at high densities by crops grown in that relatively moist region. Truett (1996) likewise blamed hunting by farming peoples for the late prehistoric absence of bison in the Trans-Pecos Southwest. Martin and Szuter (1999) believed chronic overhunting by aboriginal tribes probably had long kept bison numbers low near tribal population centers more or less throughout the Great Plains.

Cattle

Cattle in large numbers entered the Great Plains initially from Texas, coming north in "cattle drives" primarily to prairie railheads such as Abilene, Wichita, and Dodge City, KS. Droves of Texas cattle began penetrating the central and northern Great Plains by the late 1860s (Dale 1930; Webb 1931:232). They reached their zenith in numbers coming north about 1882 (Webb 1931:236). By the late 1880s, barbed wire, sodbusters, and the coming of railroads to Texas ranges collaborated to strangle the short-lived glory of the cattle drive.

The romance of the open range and lure of free grass attracted cattlemen and would-be cattlemen to the Great Plains from the eastern United States and from Canada, England, Scotland, and other "wet" regions of the world (Webb 1931:234). These new pastoralists moved largely to the mixed-grass and shortgrass regions because by the late 1800s most of the tallgrass already had fallen to the homesteader and the plow (Licht 1997:12). By the early 1880s cattle brought north by Texas drovers and to a lesser extent by settlers moving west occupied much of the Great Plains that remained unplowed (Dale 1930; Webb 1931); the southern Plains had been heavily stocked earlier because of their proximity to the Texas source (Dale 1930).

Unsustainably heavy stocking, along with blizzards and drought, led to the death of 30% to 90% of the cattle on the Plains between 1884 and 1894 (Box 2001). Given the tendency of prairie dogs to proliferate with heavy grazing, no wonder C. Hart Merriam (1902) could say in 1901 that "on many parts of the Plains prairie dogs are now more abundant than formerly and their colonies have overspread extensive areas previously unoccupied." Although prairie dog numbers undoubtedly did increase with the entry of cattle, the species' poor dispersal ability suggests it did not spread many kilometers from preexisting colonies (see Knowles 1985; Knowles et al. 2002).

Cattle abundance remained generally at unsustainable levels through the 1930s (Licht 1997:15-16). Cattle grazing undoubtedly played a part in the reported shift eastward 160-240 km of the central Plains mixed-grass/tallgrass boundary during the 1934-41 drought (Weaver and Bruner 1954). Prairie dogs, though initially increasing with the influx of cattle, declined precipitously in the 1920s and 1930s as rodent poisoning programs escalated at the urging of Merriam (1902) and others (see Oakes 2000).

The unsustainable assault by early cattlemen on the semiarid grasslands resulted largely from a grazing philosophy born in wetter regions. These people came from tallgrass prairie and other high-rainfall areas that could sustain a higher density of grazers and were more resilient to grazing than grasses of the western Plains (Ellison 1960:5). They overestimated how many cattle the range could carry. An "eat out, get out" attitude may have exacerbated the problem. Thad Box (2001) quotes a Great Plains rancher saying in 1897, "[N]one of us know, or care to know, anything about grasses. . . . [W]e are after getting the most out of them while they last."

Clements's Climax

Following the 1930s "dust of shame" (Box 2001), science-based management of grasslands took root and proliferated. Strident voices had risen against the heedless gobbling of grass as early as the late 1800s, but cattlemen largely had ignored them. It so happened that the 1930s drought culminated a half-century of bad grazing management. The resulting "dust bowl" opened the door for acceptance of F. E. Clements's (1916) theory of plant succession as the basis for regulating grazing.

Briefly, Clements (1916, 1936) proposed that plant communities naturally developed through successional stages to a relatively stable climax condition governed by climate. Grazing and other disturbances caused "retrogression" from climax. Others elaborated (Sampson 1917; Dyksterhuis 1949; Parker 1954), proposing that climax conditions were most desirable in grasslands and that stockmen should strive to retain plant communities as near climax as possible. In general, this philosophy taught that the taller the grass, the better the range. Clements's concept caught on, and shortgrasses began a retreat westward. The condition of Great Plains grasslands today reflects adherence for a half-century and more to this grazing philosophy (Laycock 1989).

Not surprisingly, given the grazing impacts of bison, prairie dogs, and Indian horses in the early 1800s and the consequences today of a half-century of Clementsian philosophy on the range, the eastern limit of shortgrass dominance appears to have migrated far westward in the intervening two centuries. Brown (1993) concluded that "tallgrasses appear to have expanded westward in the Central Plains as much as 240 km" for reasons "contrary to the climatic determinism cause that rests on water as the limiting factor." In other words, differences in precipitation regimes between the early 1800s and now could not explain the change. This review suggests that differences in grazing pressure could.

Return of the Shortgrass?

In 1995, following growing criticism of the Clementsian approach to managing grazing (e.g., Wilson and Tupper 1982; Laycock 1989; Smith 1989; Borman and Pyke 1994), the Society for Range Management abandoned the concept. The Task Group on Unity in Concepts and Terminology (1995) conceded that the relationship of a plant community to an actual or theoretical "climax" condition often had little relationship to its ability to sustain livestock, wildlife, or biodiversity, or to meet other human needs. They determined that different vegetation types meeting different human desires on a particular site were equally acceptable as long as they did not compromise the potential of the site to sustain future, perhaps different, uses. They concluded that the ability of the vegetation to protect the soil base and prevent erosion, and not its relationship to climax, was the best measure of its acceptability.

How do shortgrasses compare with taller grasses in terms of their ability to protect soils from erosion? In locations not readily colonizable by shortgrasses because of unsuitable soil texture, lack of propagules, or other reasons, reductions in midgrasses or tallgrasses might exacerbate soil erosion and thus be undesirable. But in many situations, grazing-induced increases of shortgrasses over midgrasses or tallgrasses will increase the basal ground cover (Rhoades et al. 1964; Smoliak et al. 1972; McNaughton 1984; Task Group on Unity in Concepts and Terminology 1995; Hart and

Ashby 1998; Sims and Gillen 1999) as it replaces bunchgrasses with mat-forming ones (Albertson and Weaver 1946; Hart and Ashby 1998). The extent of ground cover may be a good measure of resistance to erosion (Smith 1989). The commonly greater near-surface root mass of shortgrasses (Smoliak et al. 1972; Sims et al. 1978) also suggests greater resistance to erosion. However, Thurow et al. (1986) and Thurow (1991) maintained that, given similar cover, midgrasses resist erosion better than shortgrasses. Thus, the grass type that best resists erosion may vary among sites and circumstances.

Why would a Great Plains land manager embrace a transition to shorter grass? In some cases, higher-than-conventional (i.e., heavy) stocking rates and the resulting shorter grasses yield greater sustainable profits from livestock than do moderate stocking levels (Manley et al. 1997; Sims and Gillen 1999). Furthermore, grazing the grass short may be locally unavoidable — the naturally patchy grazing habits of large herbivores will result in heavy grazing and shortgrass on some sites even when stocking levels are moderate on average (McNaughton 1984; Plumb and Dodd 1993; Hartnett et al. 1996). Such patchy grazing tends to enhance biodiversity (Fuhlendorf and Engle 2001; Truett et al. 2001), which may appeal to many government and some private land managers. Restoration of black-tailed prairie dogs and the biodiversity associated with them (Truett et al. 2001), a current priority with some agencies and nongovernmental organizations (Van Putten and Miller 1999), will require maintenance of shortgrass dominance.

Increases in grazing intensity sometimes can lead to undesirable changes. That grazing reduces the abundance of palatable, grazing-sensitive species and increases that of less palatable and more grazing-resilient ones ranks among the foremost axioms of modern range management (see Stoddart and Smith 1955:122-24; Ellison 1960). Two other kinds of potential changes attract much current attention: invasions by exotic species and shifts to alternative ecosystem "states."

Invasive exotics such as cheatgrass (*Bromus tectorum*) and Lehmann lovegrass (*Eragrostis lehmanniana*) now dominate some Great Basin and Sonoran Desert grasslands, respectively, that historically were grazed heavily (Anable et al. 1992; D'Antonio and Vitousek 1992). Although exotic plants also occur in the Great Plains (Seig et al. 1999) and some may invade at least tallgrass prairie (Lauenroth et al. 1999), few ecologists suggest that grazing has caused widespread shifts in dominance to exotics in mixed-grass or shortgrass regions. Heavy grazing may in fact increase the resistance of some of these Great Plains grasslands to invasions (Milchunas et al. 1989; Hart and Ashby 1998), a phenomenon perhaps related to their coevolution with large grazers (Mack and Thompson 1982).

The currently popular "state and transition" model of ecosystem change suggests that disturbances such as grazing can under some circumstances cause more or less irreversible shifts in the structure and composition of grasslands (Westoby et al. 1989; Friedel 1991; Laycock 1991). For example, heavy grazing in some southwestern grasslands apparently has triggered their conversion to shrubland or woodland (Archer 1989) that will not revert to grassland without greater intervention than simple control of grazing. Existing literature (e.g., Westoby et al. 1989; Laycock 1991; D'Antonio and Vitousek 1992) and regional examples of such shifts can help managers understand whether intensive grazing in their areas could cause such transitions.

Whether changing philosophies and land-use practices will stimulate a return eastward of shortgrass dominance in the Great Plains remains to be seen. Changes on the ground tend to substantially lag changes in thinking among progressive scientists and policymakers (Smith 1989; Box 2001). Thanks to Clements and his followers, grazing the grass nearly to the ground has come to symbolize poor management, and this perception may change slowly. But the long coevolution of grasslands and large herbivores in the central grasslands of North America, and the resulting ecological dynamism (Howe 1999), suggest that in the longer term, adverse impacts of heavy grazing will prove to be less important than many now envision.

Summary and Implications for Management

We have seen how grassland types in the Great Plains shifted eastward and westward over time in response to changes in moisture availability and grazing. Droughts gave advantage to shorter grasses and wet periods favored taller grasses, resulting in spatial shifts in boundaries between shortgrass, mixed-grass, and tallgrass types. Grazing by now-extinct mammals of the Pleistocene, by bison, and eventually by cattle favored shortgrasses and pushed the type boundaries eastward of where they would have occurred without grazing.

The long coevolution of grasses and grazers on the Great Plains made the grasslands as a whole highly resilient to grazing. Shortgrasses expand when increased grazing intensities reduce competition from taller grasses; the trend reverses when grazing slackens. Grazing does not necessarily "degrade" the grasslands, it simply alters the structure and composition of the community.

Emerging changes in grazing philosophies hold that these shifts are good or bad only to the extent they affect soil erosion and the biological community desired by people. Shortgrasses may hold soil as well or better than taller grasses, sometimes provide greater sustainable economic return from grazing, and better support some wildlife of current public interest (e.g., prairie dogs). Thus, the traditional Clementsian view of a grazing-induced short stature as overgrazed (Wilson and Macleod 1991) seems destined to change. If so, shortgrass prairie could begin to replace, at least locally, mixed-grass or even tallgrass prairie under a more intensive, more nearly "pristine" grazing regime. Such changes of course will have to accommodate site differences; coarse-textured soils, for example, may erode under heavy grazing (Pfeiffer and Steuter 1994).

The evolutionary history and the resulting resilience to grazing of Great Plains grasslands suggest many sites can sustain heavy grazing without damage to their long-term productivity. Increasing numbers of rangeland scientists are proposing that grazing management shift from the traditional Clementsian model of light to moderate, uniformly distributed grazing by one species to a regime based more on evolutionary grazing patterns. Such a new regime might include more patchy grazing to promote biodiversity (Seig et al. 1999; Fuhlendorf and Engle 2001), heavier grazing, especially in mixed-grass regions, to benefit shortgrass flora and fauna (Truett et al. 2001), and replacement of the dominant exotic grazer (cattle) with the native bison (Wuerthner 1998). Local mosaics of grazing intensity could preserve both grazing-sensitive species and species benefiting from grazing.

How might such changes evolve? That land managers tend to embrace new paradigms slowly (Thomas and Burchfield 2000; Box 2001) suggests that models prescribing radical change at the landscape scale will not be immediately accepted. Purposeful imposition of heavier and more patchy grazing may begin, even on public lands, as cautious experimentation at small scales by a few managers. Others may follow suit if early trials demonstrate few adverse effects and, especially for private landowners, if the changes promise increased economic returns from such sources as greater livestock production (Manley et al. 1997), increased recreational use (Holechek 2001), or conservation incentives (e.g., US Fish and Wildlife Service 2002). The declining profitability in conventional ranching (Holechek 2001) may speed the acceptance of such new ideas and the return eastward of the shortgrass in the Great Plains.

Acknowledgments

The author thanks R.E. "Ted" Turner and the Turner family for their continuing interest in the Great Plains and their support of grasslands research, including preparation of this paper. Managers of Turner-owned ranches influenced this paper with their practices, ideas, and knowledge; among these, John Hansen, Keith Yearout, Tom LeFaive, David Vackar, Tom Waddell, Steve Dobrott, Brian Ward, and Mark Kossler contributed through discussions or written commentary. David Vackar contributed important historical insight. Biologists Dustin Long, Kristy Bly Honness, and Kevin Honness contributed ideas and information. Kyran Kunkel constructively reviewed an early draft of this paper. Mike Phillips encouraged preparation of the paper and offered constructive guidance. Judy Truett, Alice Damon, and Janis Marston processed several revisions of the manuscript.

References

Albertson, F.W., and J.E. Weaver. 1946. Reduction of ungrazed mixed prairie to short grass as a result of drought and dust. *Ecological Monographs* 16:449-63.

Alroy, J. 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinctions. *Science* 292:1893-96.

Altenhofen, K.J. 1999. Catastrophic events in North American bison populations. Master's thesis, South Dakota State University, Brookings.

Ambrose, S.E. 1996. *Undaunted Courage: Meriwether Lewis, Thomas Jefferson, and the Opening of the American West.* New York: Simon and Schuster.

Anable, M.E., M.P. McClaran, and G.B. Ruyle. 1992. Spread of introduced Lehmann lovegrass (*Eragrostis lehmanniana* Nees) in southern Arizona, USA. *Biological Conservation* 61:181-88.

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? *American Naturalist* 134:545-61.

Axelrod, D.I. 1985. Rise of the grassland biome, central North America. *Botanical Review* 51:113-201.

Bailey, V. 1905. *Biological Survey of Texas.* North American Fauna no. 25. Washington, DC: US Bureau of Biological Survey.

Barnosky, C.W. 1989. Postglacial vegetation and climate in the northwestern Great Plains of Montana. *Quaternary Research* 31:57-63.

Bell, H.M. 1973. *Rangeland Management for Livestock Production.* Norman: University of Oklahoma Press.

Bell, W.A. 1870. *New Tracks in North America: A Journal of Travel and Adventure.* London: Chapman and Hall.

Borman, M.M., and D.A. Pyke. 1994. Successional theory and the desired plant community. *Rangelands* 16:82-84.

Box, T. 2001. From the dust of shame. *Rangelands* 23:23.

Brown, D.A. 1993. Early nineteenth-century grasslands of the midcontinent plains. *Annals of the Association of American Geographers* 83:589-612.

Bryson, R.A. 1974. A perspective on climate change. *Science* 184 (4138): 753-60.

Cable, K.A., and R.M. Timm. 1987. Efficacy of deferred grazing in reducing prairie dog reinfestation rates. In *Proceedings of the Eighth Great Plains Wildlife Damage Control Workshop*, ed. D.W. Uresk, G.L. Schenbeck, and R. Cefkin, 46-49. Ft. Collins, CO: US Forest Service Rocky Mountain Forest and Range Experiment Station.

Clements, F.E. 1916. *Plant Succession.* Washington, DC: Carnegie Institute Publication 42.

Clements, F.E. 1936. Nature and structure of the climax. *Journal of Ecology* 24:252-84.

Dale, E.E. 1930. *The Range Cattle Industry.* Norman: University of Oklahoma Press.

D'Antonio, C.M., and P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.

Dary, D.A. 1974. *The Buffalo Book.* New York: Avon Books.

Dyksterhuis, E.J. 1949. Condition and management of range land based on quantitative ecology. *Journal of Range Management* 2:104-15.

Ellison, L. 1960. Influence of grazing on plant succession of rangelands. *Botanical Review* 26:1-78.

England, R.E., and A. DeVos. 1969. Influence of animals on pristine conditions on the Canadian grasslands. *Journal of Range Management* 22:87-94.

Flores, D. 1991. Bison ecology and bison diplomacy: The southern plains from 1800 to 1850. *Journal of American History* 78:465-85.

Ford, P.L. 1999. Response of buffalograss (*Buchlöe dactyloides*) and blue grama (*Bouteloua gracilis*) to fire. *Great Plains Research* 9:261-76.

Friedel, M.H. 1991. Range condition assessment and concept of thresholds: A viewpoint. *Journal of Range Management* 44:422-26.

Fuhlendorf, S.D., and D.M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* 51:625-32.

Fuhlendorf, S.D., and F.E. Smeins. 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus-Quercus* savanna. *Journal of Vegetation Science* 8:819-28.

Gard, W. 1959. *The Great Buffalo Hunt.* New York: Alfred A. Knopf.

Gillen, R.L., J.A. Eckroat, and F.T. McCollum III. 2000. Vegetation response to stocking rate in southern mixed-grass prairie. *Journal of Range Management* 53:471-78.

Gillen, R.L., F.T. McCollum III, K.W. Tate, and M.E. Hodges. 1998. Tallgrass prairie response to grazing system and stocking rate. *Journal of Range Management* 51:139-46.

Goodwin, H.T. 1995. Pliocene-Pleistocene biogeographic history of prairie dogs, genus *Cynomys* (Sciuridae). *Journal of Mammalogy* 76:100-122.

Graham, R.W., and E.L. Lundelius Jr. 1984. Coevolutionary disequilibrium and Pleistocene extinctions. In *Quaternary Extinctions: A Prehistoric Revolution,* ed. P.S. Martin and R.G. Klein. Tucson: University of Arizona Press.

Graham, R.W., E.L. Lundelius Jr., M.A. Graham, E.K. Schroeder, R.S. Toumey III, E. Anderson, A.D. Barnosky, J.A. Burns, C.S. Churcher, D.K. Grayson, R.D. Guthrie, C.R. Haringon, G.T. Jefferson, L.D. Martin, H.G. McDonald, R.E. Morlan, H.A. Semken Jr., S.D. Webb, L. Werdelin, and M.C. Wilson. 1996. Spatial response of mammals to late Quaternary environmental fluctuations. *Science* 272:1601-6.

Grant, W.E., E.C. Birney, N.R. French, and D.M. Swift. 1982. Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover. *Journal of Mammalogy* 63:248-60.

Hall, E. 1981. *The Mammals of North America,* vol. 1. New York: John Wiley and Sons.

Hall, S.A. 2000. Was the high plains a pine-spruce forest? *Rangelands* 22:3-5.

Hall, S.A., and S. Valastro Jr. 1995. Grassland vegetation in the southern Great Plains during the last glacial maximum. *Quaternary Research* 44:237-45.

Hämäläinen, P. 2001. The first phase of destruction: killing the southern plains buffalo, 1790-1840. *Great Plains Quarterly* 21:101-14.

Hart, R.H. 2001. Where the buffalo roamed — or did they? *Great Plains Research* 11:83-102.

Hart, R.H., and M.M. Ashby. 1998. Grazing intensities, vegetation, and heifer gains: 55 years on shortgrass. *Journal of Range Management* 51:392-98.

Hart, R.H., and J.A. Hart. 1997. Rangelands of the Great Plains before European settlement. *Rangelands* 19:4-11.

Hartnett, D.C., K.R. Hickman, and L.E.F. Walter. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Journal of Range Management* 49:413-20.

Holechek, J.L. 2001. Western ranching at the crossroads. *Rangelands* 23:17-21.

Holliday, V.T. 1987. A re-examination of late-Pleistocene boreal forest reconstruction for the southern High Plains. *Quaternary Research* 28:238-44.

Hoogland, J.L. 1981. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology* 62:252-72.

Howe, H.F. 1999. Dominance, diversity, and grazing in tallgrass restoration. *Ecological Restoration* 17:59-66.

Isenberg, A.C. 2000. *The Destruction of the Bison: An Environmental History, 1750-1920.* Cambridge, UK: Cambridge University Press.

Kinucan, R.J., and F.E. Smeins. 1992. Soil seed bank of a semiarid grassland under three long-term grazing regimes. *American Midland Naturalist* 128:11-21.

Knowles, C.J. 1982. *Habitat affinity, populations, and control of black-tailed prairie dogs on the Charles M. Russell National Wildlife Refuge.* Ph.D. diss., University of Montana, Missoula.

Knowles, C.J. 1985. Observations on prairie dog dispersal in Montana. *Prairie Naturalist* 17:33-40.

Knowles, C.J. 1986. Some relationships of black-tailed prairie dogs to livestock grazing. *Great Basin Naturalist* 46:198-203.

Knowles, C.J., J.D. Proctor, and S.C. Forrest. 2002. Black-tailed prairie dog abundance and distribution in the Great Plains based on historic and contemporary information. *Great Plains Research* 12:219-54.

Koford, C.B. 1958. Prairie dogs, whitefaces, and blue grama. *Wildlife Monographs* no. 3:1-78.

Larson, F. 1940. The role of the bison in maintaining the short grass plains. *Ecology* 21:113-21.

Lauenroth, W.K., I.C. Burke, and M.P. Gutman. 1999. The structure and function of ecosystems in the central North American grassland region. *Great Plains Research* 9:223-59.

Laycock, W.A. 1989. Secondary succession and range condition criteria: Introduction to the problem. In *Secondary Succession and the Evaluation of Rangeland Condition,* ed. W.K. Lauenroth and W.A. Laycock, 1-15. Boulder, CO: Westview Press.

Laycock, W.A. 1991. Stable states and thresholds of range condition on North American rangelands: A viewpoint. *Journal of Range Management* 44:427-33.

Licht, D.S. 1997. *Ecology and Economics of the Great Plains.* Lincoln: University of Nebraska Press.

Mack, R.N., and J.N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. *American Naturalist* 119:757-73.

Manley, W.A., R.H. Hart, M.J. Samuel, M.A. Smith, J.W. Waggoner Jr., and J.T. Manley. 1997. Vegetation, cattle, and economic responses to grazing strategies and pressures. *Journal of Range Management* 50:638-46.

Martin, P.S. 1967. Prehistoric overkill. In *Pleistocene Extinctions: The Search for a Cause,* ed. P.S. Martin and H.E. Wright Jr., 75-120. New Haven, CT: Yale University Press.

Martin, P.S., and C.R. Szuter. 1999. War zones and game sinks in Lewis and Clark's West. *Conservation Biology* 13:36-45.

McNaughton, S.J. 1984. Grazing lawns: Animals in herds, plant form, and coevolution. *American Naturalist* 124:863-86.

Mead, J.R. 1899. Some natural history notes of 1859. *Transactions of the Kansas Academy of Science* 16:280-81.

Meinig, D.W. 1969. *Imperial Texas: An Interpretive Essay in Cultural Geography.* Austin: University of Texas Press.

Meinzer, W.P. 1988. Slaughter of the ancients. *Texas Parks and Wildlife* 46:24-31, 45.

Merriam, C.H. 1902. The prairie dog of the Great Plains. In *Yearbook of the United States Department of Agriculture, 1901,* 257-70. Washington, DC: Government Printing Office.

Milchunas, D.G., W.K. Lauenroth, P.L. Chapman, and M.K. Kazempour. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* 80:11-23.

Milchunas, D.G., A.S. Varnamkhasti, W.K. Lauenroth, and H. Goetz. 1995. Forage quality in relation to long-term grazing history, current-year defoliation, and water resource. *Oecologia* 101:366-74.

Moulton, G.E., ed. 1987. *The Journals of the Lewis and Clark Expedition,* vol. 3. Lincoln: University of Nebraska Press.

Oakes, C.L. 2000. History and consequence of keystone mammal eradication in the desert grasslands: The case of the Arizona black-tailed prairie dog (*Cynomys ludovicianus arizonensis*). Ph.D. diss., University of Texas, Austin.

Omernik, J.M. 1987. Ecoregions of the conterminous United States. *Annals of the Association of American Geographers* 77:118-25.

Osborn, B., and P.F. Allan. 1949. Vegetation of an abandoned prairie-dog town in tallgrass prairie. *Ecology* 30:322-32.

Parker, K.W. 1954. Application of ecology in the determination of range condition and trend. *Journal of Range Management* 7:14-23.

Pfeiffer, K.E., and A.A. Steuter. 1994. Preliminary response of Sandhills prairie to fire and bison grazing. *Journal of Range Management* 47:395-97.

Plumb, G.E., and J.L. Dodd. 1993. Foraging ecology of bison and cattle on a mixed prairie: Implications for natural area management. *Ecological Applications* 3:631-43.

Rhoades, E.D., L.F. Locke, H.M. Taylor, and E.H. McIlvain. 1964. Water intake on a sandy range as affected by 20 years of differential cattle stocking rates. *Journal of Range Management* 17:185-89.

Roe, F.G. 1970. *The North American Buffalo*. Toronto: University of Toronto Press.

Sala, O.E., W.J. Parton, L.A. Joyce, and W.K. Lauenroth. 1988. Primary production of the central grassland region of the United States. *Ecology* 69:40-45.

Sampson, A.W. 1917. Succession as a factor in range management. *Journal of Forestry* 15:593-96.

Seig, C.H. 1997. The role of fire in managing for biological diversity on native rangelands of the northern Great Plains. In *Conserving Biodiversity on Native Rangelands: Symposium Proceedings*, ed. D.W. Uresk, G.L. Schenbeck, and J.T. O'Rourke, 31-38. Washington, DC: US Government Printing Office.

Seig, C.H., C.H. Flather, and S. McCanny. 1999. Recent biodiversity patterns in the Great Plains: Implications for restoration and management. *Great Plains Research* 9:277-313.

Shaw, J.H., and T.S. Carter. 1990. Bison movements in relation to fire and seasonality. *Wildlife Society Bulletin* 18:426-30.

Shaw, J.H., and M. Lee. 1997. Relative abundance of bison, elk, and pronghorn on the southern plains, 1806-1857. *Plains Anthropologist* 42, *Memoir* 29:163-72.

Sidle, J.G., D.H. Johnson, and B.R. Euliss. 2001. Estimated areal extent of black-tailed prairie dogs in the northern Great Plains. *Journal of Mammalogy* 82:928-36.

Sims, P.L., and R.L. Gillen. 1999. Rangeland and steer responses to grazing in the southern plains. *Journal of Range Management* 52:651-60.

Sims, P.L., J.S. Singh, and W.K. Lauenroth. 1978. The structure and function of ten western North American grasslands: 1. Abiotic and vegetational characteristics. *Journal of Ecology* 66:251-85.

Smith, E.L. 1989. Range condition and secondary succession: A critique. In *Secondary Succession and the Evaluation of Rangeland Condition*, ed. W.K. Lauenroth and W.A. Laycock, 103-41. Boulder, CO: Westview Press.

Smith, R.E. 1967. *Natural History of the Prairie Dog in Kansas*. Lawrence, KS: University of Kansas Museum of Natural History and State Biological Survey Miscellaneous Publication no. 49.

Smoliak, S., J.F. Dormaar, and A. Johnston. 1972. Long-term grazing effects on *Stipa-Bouteloua* prairie soils. *Journal of Range Management* 25:246-50.

Snell, G.P. 1985. Results of control of prairie dogs. *Rangelands* 7:30.

Snell, G.P., and B.D. Hlavachick. 1980. Control of prairie dogs — the easy way. *Rangelands* 2:239-40.

Stebbins, G.L. 1981. Coevolution of grasses and herbivores. *Annals of the Missouri Botanical Garden* 68:75-86.

Stoddart, L.A., and A.D. Smith. 1955. *Range Management*. New York: McGraw-Hill.

Stubbendieck, J., S.L. Hatch, and C.H. Butterfield. 1997. *North American Range Plants*, 5th ed. Lincoln: University of Nebraska Press.

Task Group on Unity in Concepts and Terminology. 1995. New concepts for assessment of rangeland condition. *Journal of Range Management* 48:271-82.

Thomas, H.S. 2000. Bison: America's wild cow. The final installment — grazing and overgrazing on prehistoric rangelands. *North American Bison Journal* 2:12-14.

Thomas, J.W., and J. Burchfield. 2000. Science, politics, and land management. *Rangelands* 22:45-48.

Thompson, R.S. 1988. Vegetation dynamics in the western United States: Modes of response to climatic fluctuations. In *Vegetation History*, ed. B. Huntley and T. Webb III, 415-58. Boston: Kluwer Academic Publishers.

Thurow, T.L. 1991. Hydrology and erosion. In *Grazing Management: An Ecological Perspective*, ed. R.K. Heitschmidt and J.W. Stuth, 141-59. Portland, OR: Timber Press.

Thurow, T.L., W.H. Blackburn, and C.A. Taylor Jr. 1986. Hydrologic characteristics of vegetation types as affected by livestock grazing systems, Edwards Plateau, Texas. *Journal of Range Management* 39:505-9.

Tileston, J.V., and R.R. Lechleitner. 1966. Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado. *American Midland Naturalist* 75:292-316.

Truett, J.C. 1996. Bison and elk in the American Southwest: in search of the pristine. *Environmental Management* 20:195-206.

Truett, J.C., M. Phillips, K. Kunkel, and R. Miller. 2001. Managing bison to restore biodiversity. *Great Plains Research* 11:123-44.

Truett, J.C., and T. Savage. 1998. Reintroducing prairie dogs into desert grasslands. *Restoration and Management Notes* 16:189-95.

US Fish and Wildlife Service. 2002. Fiscal year 2002 private stewardship grants program. *Federal Register* 67:61649-62.

Van Putten, M., and S.D. Miller. 1999. Prairie dogs: the case for listing. *Wildlife Society Bulletin* 27:1113-20.

Vinton, M.A., D.C. Hartnett, E.J. Finck, and J.M. Briggs. 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. *American Midland Naturalist* 129:10-18.

Virchow, D.R., and S.E. Hygnstrom. 2002. Distribution and abundance of black-tailed prairie dogs in the Great Plains: A historical perspective. *Great Plains Research* 12:197-218.

Weaver, J.E. 1954. *North American Prairie*. Lincoln, NE: Johnson Publishing.

Weaver, J.E., and W.E. Bruner. 1954. Nature and place of transition from true prairie to mixed prairie. *Ecology* 35:117-26.

Weaver, J.W., and P.E. Clements. 1938. *Plant Ecology*. New York: McGraw Hill.

Webb, W.P. 1931. *The Great Plains*. Lincoln: University of Nebraska Press.

West, E. 1995. *The Way to the West: Essays on the Central Plains*. Albuquerque: University of New Mexico Press.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266-74.

Whicker, A.D., and J.K. Detling. 1988. Ecological consequences of prairie dog disturbances. *BioScience* 38:778-85.

White, T. 2002. On unsettled plains. *Nebraskaland,* October, 18-25.

Wiens, J. 1973. Pattern and process in grassland bird communities. *Ecological Monographs* 43:237-70.

Wilson, A.D., and N.D. Macleod. 1991. Overgrazing: Present or absent? *Journal of Range Management* 44:475-82.

Wilson, A.D., and G.J. Tupper. 1982. Concepts and factors applicable to the measurement of range condition. *Journal of Range Management* 35:684-89.

Wright, H.A., and A.W. Bailey. 1980. *Fire Ecology and Prescribed Burning in the Great Plains: A Research Review*. Ogden, UT: US Forest Service General Technical Report INT-77.

Wuerthner, G. 1998. Are cows just domestic bison? Behavioral and habitat use differences between cattle and bison. In *International Symposium on Bison Ecology and Management in North America*, ed. L. Irby and J. Knight, 374-83. Bozeman: Montana State University.