RANGE ECOLOGY OF BISON ON TALLGRASS

PRAIRIE IN OKLAHOMA

By

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CHAPTER I

INTRODUCTION

Tallgrass prairie once extended from southern Manitoba southward through eastern Oklahoma, covering some 57 million hectares of the central Great Plains of North America (Risser et al. 1981, Sims 1988). With the arrival of European settlers in the late 19th century, most of this expansive, fertile prairie was transformed into farms and cropland. Today, only an estimated 5 million hectares of unplowed tallgrass prairie exists, and most of this is in small patches or remnants such as cemeteries and small parks (Joern and Keeler 1995). The only remaining large, contiguous tracts of virgin tallgrass prairie are located in the Flint and Osage Hills of Kansas and Oklahoma (Risser et al. 1981, Reichmann 1987).

When European settlers arrived on the Great Plains, they not only found vast areas of fertile prairie, but a population of bison (*Bison bison* L.) estimated at 30 (McHugh 1972) to 60 million (Seton 1929). However, the large herds were nearly exterminated through overhunting (Roe 1970, Dary 1974), and by the early 1900's fewer than 2000 scattered individuals remained (Garretson 1938).

Tallgrass prairie and bison, like many of the earth's natural resources, were nearly eliminated by man's abuse. Today, however, both are the focus of numerous conservation efforts across the country. There are now about 67 tallgrass prairie sites set aside for preservation in the United States (Pankratz

1994), and bison now number over 200,000 in North America (Hodgson 1994). One of the largest tallgrass prairie-bison restoration efforts is underway in northcentral Oklahoma. On November 8, 1989, the Nature Conservancy, a non-profit conservation organization, purchased the 14,000 hectare Barnard Ranch in northcentral Osage County, Oklahoma (Madson 1990). Renamed the Tallgrass Prairie Preserve, the ranch became the core of the largest conservation effort ever attempted by the Nature Conservancy, and capped a decades-long national effort to preserve a part of the tallgrass prairie ecosystem for future generations (Pierce 1985, Hulsey 1988, Wallace 1989). With additional purchases and leases, the Tallgrass Prairie Preserve now encompasses approximately 15,342 hectares (R. G. Hamilton, personal communication).

The Present Study: Bison and Tallgrass

As part of the ecosystem restoration process at the Tallgrass Prairie Preserve, two naturally occurring but lacking components were reintroduced to the preserve - seasonal fire and bison grazing. On September 5, 1993, a spatially- and seasonally-variable prescribed burning program was initiated. The intent of this program is to simulate the mosaic of naturally occurring fires that were known to occur historically in tallgrass prairie (Collins and Wallace 1990). In addition, a herd of 300 bison donated to the Nature Conservancy by Ken-Ada Ranches in Bartlesville, Oklahoma was reintroduced to a 1,973 hectare portion of the preserve on October 18, 1993. This study was designed to evaluate various ecological processes in relation to the bison reintroduction, including evaluations of the (1) patterns of bison-fire interactions; (2) the effects of bison grazing and seasonal fire on tallgrass

prairie vegetation; and (3) the physical effects of bison reintroduction on specific landscape components of the preserve where bison had not been present in a wild state for over 150 years (Shaw and Lee 1995). Specific objectives of my study are outlined below.

Study Objectives

1) To determine the botanical composition of bison diets on a seasonal basis.

2) To document seasonal patterns of bison grazing relevant to the seasonally- and spatially-variable prescribed burning program.

3) To assess the effects of environmental interactions such as fire, grazing, and climate on the composition of tallgrass prairie vegetation.

4) To conduct a comprehensive study on the wallowing behavior of bison, and investigate the process of wallow site selection and formation.

5) To conduct a comprehensive study on the horning behavior of bison and the effects of this behavior on the woody vegetation of the study area.

The next five chapters of this dissertation are manuscripts formatted for publication, followed by a brief summary chapter. Each manuscript chapter is a separate study addressing one of the five objectives presented above. Chapter II, "Botanical composition of bison diets on tallgrass prairie on Oklahoma," and Chapter III, "Bison grazing patterns on seasonally burned tallgrass prairie," are formatted for the *Journal of Range Management.* Chapter IV, "Vegetation-environment relationships in tallgrass prairie: plant guild responses to seasonal fire and climatic variation," is formatted for the journal *Vegetatio.* Chapter V, "Characterization of bison wallowing behavior and wallow formation sites on tallgrass prairie in Oklahoma," is formatted as a note for the *Southwestern Naturalist.* Chapter VI, "Effects of horning and

rubbing behavior by bison (*Bison bison*) on woody vegetation in a tallgrass prairie landscape," is formatted for the *American Midland Naturalist*. The manuscripts are complete as written, and need no supporting material.

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CHAPTER II

BOTANICAL COMPOSITION OF BISON DIETS ON TALLGRASS PRAIRIE IN OKLAHOMA

Abstract. - Diets of bison (*Bison bison* L.) were examined in a 2-yr study on a tallgrass prairie site in northcentral Oklahoma. Graminoids comprised at least 99% of the diet across all seasons. Bison showed strong feeding selectivity; grasses and sedges formed a significantly higher proportion of diets than was generally available in herbage on the landscape. Bison avoided forbs, which were ≤ 1% of the diet. Significant seasonal variation in diet composition was found. Sedges were a large (20-39%) diet component in winter and spring but decreased substantially during summer and fall (11-15%). These changes in sedge use corresponded to seasonal variation in sedge availability. Our results support the general contention that bison are primarily grazers in prairie habitats and play a significant role in shaping structure and function of tallgrass prairie.

Introduction

The American bison (*Bison bison* L.) is the largest native herbivore in North America. Estimates of historic populations range from 30 to 60 million (Shaw 1995), but overhunting late in the 19th century virtually eliminated the species (Garretson 1938). Today, scattered populations of bison can be found throughout the continent. Numerous contemporary studies have been conducted on bison diets to understand the ecological role of bison grazing in

the development and maintenance of central North American grasslands (Axelrod 1985). There are three major types of grasslands in central North America: shortgrass prairie, mixed-grass prairie, and tallgrass prairie (Risser et al. 1981). However, bison diet studies have been conducted only on shortgrass (Peden et al. 1974, Peden 1976, Kautz and Van Dyne 1978, Schwartz and Ellis 1981) and mixed-grass (Wydeven and Dahlgren 1985, Plumb and Dodd 1993) prairies. Knowledge of dietary habits of bison on tallgrass prairie is lacking because most tallgrass prairie has been eliminated by conversion to farms and croplands (Risser et al. 1981). With continued efforts and interest in restoring and preserving this grassland ecosystem (Joern and Keeler 1994), a study on the diets of bison on a tallgrass site was needed.

In 1989, the Nature Conservancy, a private conservation organization, established the Tallgrass Prairie Preserve in Oklahoma. As part of their efforts to restore a functioning tallgrass prairie ecosystem, a bison population was established on the site in 1993. This provided us with the opportunity to conduct a baseline study on the dietary preferences of bison in a tallgrass prairie landscape. Because studies from shortgrass and mixed-grass prairies have shown that grasses comprise the majority of bison diets on those sites (Kautz and Van Dyne 1978, Schwartz and Ellis 1981, Plumb and Dodd 1993), we hypothesized that graminoids also would dominate bison diets on tallgrass prairie. But because bison generally select for warm-season grasses while avoiding cool-season graminoids and forbs (Plumb and Dodd 1993), we further hypothesized that bison would exhibit seasonal selectivity in response to forage availability, preferentially grazing warm-season grasses even when cool-season graminoids and forbs were abundant.

Study Area and Methods

The study was conducted in 1994 and 1995 on the Nature Conservancy's Tallgrass Prairie Preserve (TPP), a 15,342-ha tallgrass prairie site in the Osage Hills of northern Oklahoma (36°50'N, 96°25'W). Vegetation of the area was dominated by big bluestem (*Andropogon gerardii* Vitman), indiangrass (*Sorghastrum nutans* [L.] Nash), switchgrass (*Panicum virgatum* L.), and little bluestem (*Schizachyrium scoparium* [Michx.] Nash). Subdominant species included tall dropseed (*Sporobolus asper* (Michx.) Kunth) and sedges (*Carex* spp.). Common forbs were western ragweed (*Ambrosia psilostachya* DC.) and annual broomweed (*Gutierrezia dracunculoides* (DC.) Nutt.). Average monthly temperatures ranged from a low of -5.0° C in January to a high of 34.4° C in July. Average total annual precipitation was 877 mm; 70% occurred between April and September (Bourlier et al. 1979). Maintenance of tallgrass prairie is dependent on periodic burning (Collins and Wallace 1990), so preserve management included prescribed burning 20% of the area each year.

Three hundred bison were reintroduced into a 1,973-ha part of the preserve in October 1993. Following natural herd recruitment and the release of additional animals, the area allocated to bison was expanded by 292-ha in August 1995 to maintain a stocking density of 6-7 ha AU^{-1} during our study. Herd management was limited to annual roundups for inoculations, weighing, and culling.

Field work was conducted during 4 seasonal periods: winter (15 January - 15 February), spring (15 April - 15 May), summer (15 July - 15 August) and fall (15 October - 15 November). Composition of available herbage was estimated for each seasonal period with the dry-weight-rank method (Gillen and Smith 1986) conducted along 10 100-m transects in areas frequented by bison and where fecal collections were made. Herbage components estimated

were grasses and grasslike (Gramineae and Juncaceae), sedges (Cyperaceae), and forbs (all non-woody Dicotyledonae). Because woody browse was a minor component of the vegetation and is infrequent in bison diets (Plumb and Dodd 1993), its availability was not measured.

Bison diets were estimated with microhistological fecal analysis conducted by the Composition Analysis Laboratory, Ft. Collins, Colorado, following the methods of Sparks and Malechek (1968). Plant fragments were identified to the lowest possible taxon, which in most cases was to genus. Six composite fecal samples were collected during each period. Each sample consisted of 10 g of fresh fecal material from 4-6 fecal pats. Because of potential differences in diets due to sexual segregation of adults (McHugh 1958, Main and Coblentz 1990), we analyzed fecal samples only from mixed groups of bison. These groups were composed of cows, yearlings, calves, and young (< 5 yrs. of age) bulls and comprised > 90% of the population. The remainder of the population was comprised of mature bulls (> 5 yrs. of age) that were segregated into bull-only groups except during the July mating season (McHugh 1958).

To evaluate hypotheses of variation in both forage availability and bison diets, data were tested with a 2-way multivariate analysis of variance (MANOVA) using year and season as independent variables and percent herbage and diet composition of grasses, sedges, and forbs as dependent variables. The overall significance of independent terms in MANOVA models was tested at $\alpha = 0.05$ with Wilk's λ (Johnson and Wichern 1992). To assess selectivity of bison diets, an index (Plumb and Dodd 1993) was calculated for each forage class as the ratio of each class percentage in the diet to its percentage availability in the herbage. An index value of 1.0 indicated nonselective use of a forage class, while values > 1.0 or < 1.0 indicated grazing selectivity for or against a particular class, respectively. Selectivity was tested

by calculating a 95% confidence interval around each mean selectivity value. Significant selectivity was indicated when the interval did not contain the value 1.0 (Plumb and Dodd 1993). Although Loehle and Rittenhouse (1982) criticized selectivity indices for their lack of predictive power in diet studies, Lechowicz (1982) concluded that such indices were appropriate when used as an assessment of general feeding patterns. Because our goal was to describe relative feeding preferences of bison and not to make predictions of future diets, we deemed this descriptive index suitable for our purposes.

Results

Composition of available forage varied significantly by year ($p < 0.02$). During 1994, herbage composition estimated from transects averaged ($\pm$ 1 SE) 73.1 $\pm$ 3.4% grasses, 1.6 $\pm$ 1.0% sedges, and 25.3 $\pm$ 3.3% forbs. During 1995, herbage composition averaged 62.1 $\pm$ 2.4% grasses, 4.3 $\pm$ 0.7% sedges, and 33.6 $\pm$ 2.4% forbs. Thus, there were 10% fewer grasses, 3 times more sedges, and 10% more forbs in 1995 as compared to 1994. Seasonal variation in forage composition was significant ($p < 0.001$), but no year by season interaction was detected ($p > 0.6$). Grasses were most abundant (80% of herbage) during winter and fall, decreasing to 50% during spring and summer when forbs became more prevalent (Fig. 1). Sedges were most abundant during the winter and spring periods, comprising 10 to 20% of the herbage, but decreased to half these levels during summer and fall.

Bison diet composition did not differ significantly between years ($p > 0.1$). Diets did vary significantly by season ($p < 0.02$), but no interaction of season and year on diets was detected ($p > 0.2$). Grasses generally formed the majority (60-88%) of bison diets (Table 1). Many of the dominant tallgrasses in the study area were indistinguishable in fecal samples; therefore, these

grasses were grouped into a 'bluestem' category that was consistently the single largest dietary component. Other common grasses in the diet included *Sporobolus, Muhlenbergia*, and the *Panicum/Dicanthelium* complex; the latter two genera were indistinguishable from one another in fecal samples. Sedges, primarily composed of *Carex*, were a large (21-39%) component of winter and spring diets but decreased substantially during summer and fall (11-15%). Forbs never comprised > 1% of any diet.

Seasonal trends in diet selectivity of bison were evident. Grasses were consumed either in equal proportion to or slightly above their seasonal availability in the herbage (Fig. 2). Sedges were strongly and consistently selected for by bison in all seasons. Forbs were a significant herbage component (Fig. 1) but were strongly avoided by bison during all seasons (Fig. 2).

Discussion

Bison diets on tallgrass prairie were composed primarily (99%) of graminoids, thus supporting our hypothesis that this forage type would dominate bison diets on tallgrass prairie. The single largest dietary category was the bluestem complex, comprised of the warm-season tallgrasses and little bluestem. Other grasses prevalent in the diet included tall dropseed, switchgrass, and muhly (*Muhlenbergia*). Several studies of bison grazing behavior on tallgrass prairie in Kansas have shown that bison preferentially graze many of these species after recent burning (Hartnett et al. 1996, Pfeiffer and Hartnett 1995, Vinton et al. 1993). However, repeated defoliation by bison can be detrimental to these grasses by reducing growth rates and cover and altering population structure (Vinton and Hartnett 1992, Pfeiffer and Hartnett 1995). Preferential grass herbivory by bison can incidentally benefit some

prairie vegetation. Ungrazed forbs often are released from competition with nearby grazed grasses, which increases their growth and productivity (Fahnestock and Knapp 1994). Bison grazing also increases plant species diversity and spatial heterogeneity of vegetation (Hartnett et al. 1996). Thus, bison grazing alone is an important influence on tallgrass prairie vegetation, reducing the cover of preferentially grazed species while conversely increasing plant heterogeneity. But bison grazing effects are amplified when coupled with fire (Pfeiffer and Hartnett 1995, Vinton et al. 1993) by significantly altering both the structure and diversity of tallgrass prairie vegetation (Hartnett et al. 1996).

Bison either exhibited selectivity for grasses or consumed them in proportion to their availability, while consistently avoiding forbs. This partially supports our hypothesis of bison selectivity for warm-season grasses and avoidance of cool-season graminoids and forbs. However, the consistent seasonal preference of bison for sedges does not. Because a recent comprehensive study of mixed-grass prairie forages found no significant differences in digestibility between sedges (*Carex* sp.) and grasses in general (Plumb and Dodd 1993), we do not believe that the dietary composition of sedges in our study is the result of bias from differential digestibility. Instead, we believe bison may be utilizing sedges because they are the most nutritious forage option available to the animals during some seasonal periods. The study area is dominated by warm-season tallgrasses that have major vegetative growth during the latter part (summer) of the growing season (Howe 1994). Sedges are cool-season graminoids with primary growth during cooler, wetter periods of the year (Howe 1994), a pattern supported by our herbage availability estimates. Studies have shown that tallgrasses are most nutritious during spring, but are nutritionally undesirable for large grazers during the

remainder of the year (Waller et al. 1972). Bison use of sedges, therefore, may be linked to a simple nutritional need for digestible forage (Fryxell and Sinclair 1988), which sedges could provide during periods when warm-season grasses are either inactive or unpalatable. This would be especially important for lactating cows during late winter and early spring (March-April), when bison calves are usually born in Oklahoma (Halloran 1968). In our study, calving and associated nutritional demands correspond to a time when sedge availability was highest (spring), which was when the only major seasonal shift in diet composition occurred. We suggest that future studies should consider evaluating the seasonal nutritional properties of sedges relative to grasses in studies of herbivore ecology on tallgrass prairie.

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Table 1. Seasonal diet composition (%, $\bar{x}$ ±1 SE) as determined from composite fecal samples from bison on tallgrass prairie in Oklahoma. Because year effects were insignificant, data from both years (1994-1995) were pooled for each season (n = 12). Fecal samples are from bison mixed groups, which comprised >90% of the study population and were composed of cows, yearlings, calves, and young bulls.

| | Season | | | | | | | |
| | Winter | | Spring | | Summer | | Fall | |
Taxon	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Grasses and Grasslike								
Agropyron	0.4	0.4	0.1	0.1	0.9	0.3	0.2	0.2
Aristida	1.3	0.6	1.0	0.5	0.8	0.4	1.3	0.2
Bluestems[1]	38.8	2.3	36.5	2.7	61.6	1.3	53.1	2.0
Bromus	2.5	0.8			0.3	0.2	0.1	0.1
Cynodon					0.4	0.2	0.3	0.2
Elymus	0.4	0.2	0.2	0.1	0.2	0.1	1.6	0.5
Juncus	1.0	0.4	1.5	0.5	0.3	0.3	0.1	0.1
Leptoloma	0.1	0.1	0.4	0.3	0.8	0.3	0.3	0.2
Miscellaneous[2]			0.1	0.1			0.2	0.2
Muhlenbergia	6.5	1.4	0.8	0.2	2.1	0.4	2.6	0.4
Panicum/ Dicanthelium	3.2	1.0	3.1	0.6	5.3	0.7	3.4	0.8
Poa	0.4	0.2	0.6	0.3	0.8	0.5	1.3	0.5
Setaria			0.1	0.1	0.3	0.2	0.6	0.3
Sporobolus	22.7	1.4	15.1	1.0	13.7	0.4	16.9	1.2
Tridens	1.2	0.6	0.1	0.1	0.5	0.2	0.2	0.2

Table 1 cont.

Tripsacum			0.1	0.1	0.5	0.2	1.0	0.5
Unknowns[3]	0.1	0.1	0.3	0.3	0.2	0.1	0.4	0.1
TOTAL GRASSES	**78.6**	**2.2**	**60.0**	**2.7**	**88.0**	**1.1**	**83.6**	**1.2**
Sedges								
Carex	19.5	1.9	31.2	1.8	9.6	0.8	13.5	1.0
Eleocharis	1.3	0.6	8.2	1.2	0.8	0.4	1.9	0.6
Unknowns	0.1	0.1						
TOTAL SEDGES	**20.9**	**2.2**	**39.4**	**2.8**	**11.0**	**1.0**	**15.4**	**1.2**
Forbs								
Desmodium			0.2	0.1	0.6	0.2		
Miscellaneous[4]	0.3	0.2	0.2	0.2	0.2	0.1	0.4	0.2
Unknowns	0.2	0.1	0.2	0.1	0.2	0.2	0.6	0.1
TOTAL FORBS	**0.5**	**0.2**	**0.6**	**0.2**	**1.0**	**0.3**	**1.0**	**0.4**

[1] Includes *Andropogon*, *Paspalum*, *Sorghastrum*, *Sorghum*, and *Schizachyrium*.

[2] Items that did not exceed 0.1% in any diet; includes *Agrostis*, *Bouteloua*, *Festuça*, and *Phleum*.

[3] Includes unknown grass seeds and glumes.

[4] Includes a negligible browse component. Comprised of items that did not exceed 0.2% in any diet; includes *Croton*, *Artemisia*, *Juniperus*, *Melilotus*, *Medicago*, *Plantago*, and *Quercus*.

Fig. 1. Mean percent relative composition of seasonal herbage components

available to bison on the Tallgrass Prairie Preserve, Oklahoma, 1994-

1995, as determined by the dry-weight-rank method (Gillen and Smith

1986). Error bars represent 1 SE.
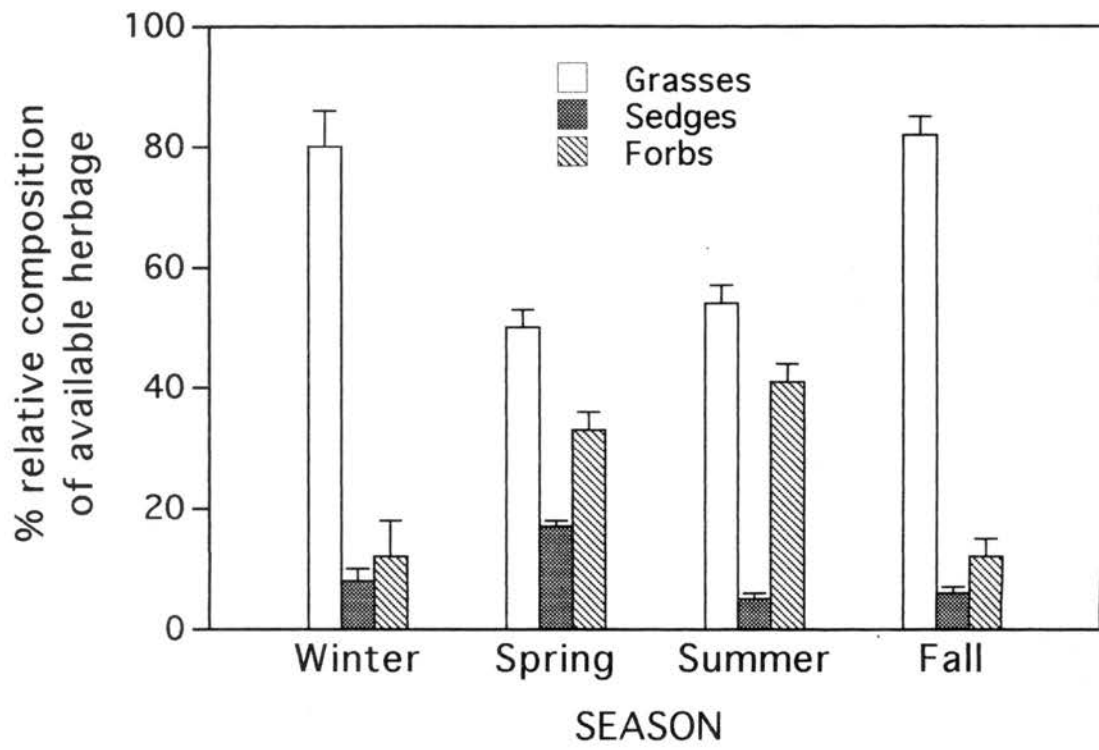
Fig. 2. Mean selectivity index values and 95% confidence intervals for

seasonal bison diets on tallgrass prairie in Oklahoma. Means with

intervals that do not overlap 1.0 indicate selection (> 1.0) or avoidance (<

1.0) of the respective forage class (Plumb and Dodd 1993).
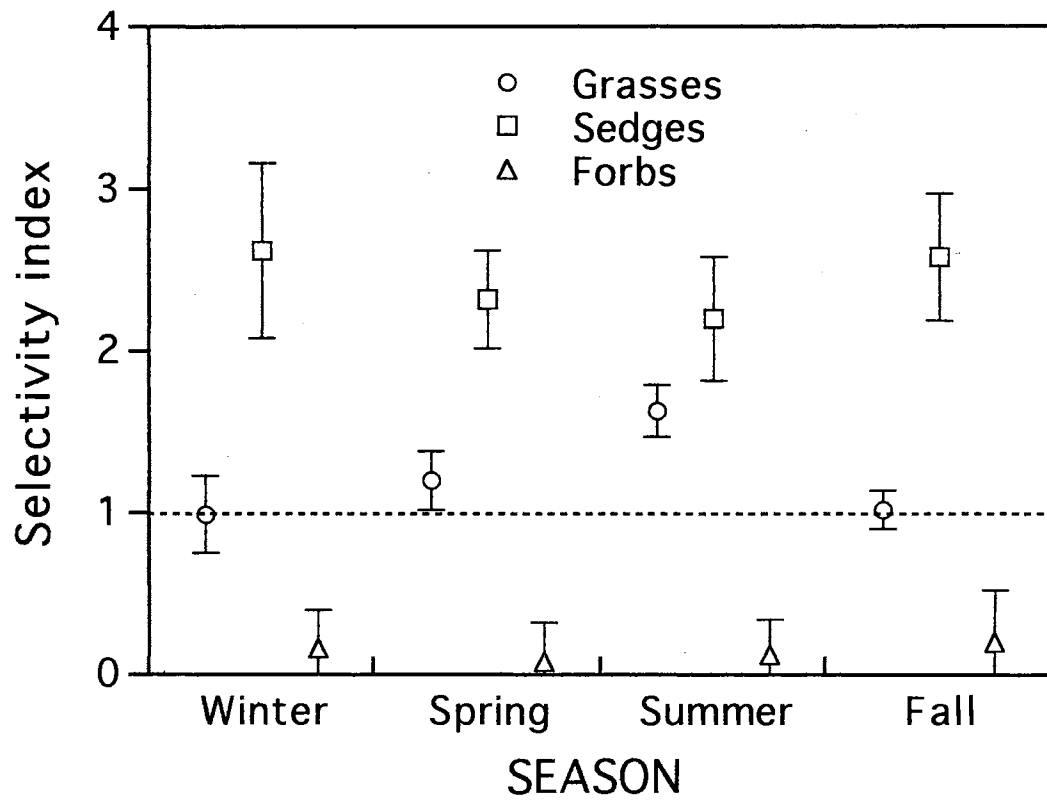
CHAPTER III

BISON GRAZING PATTERNS ON SEASONALLY BURNED TALLGRASS PRAIRIE

Abstract. - Patterns of bison (*Bison bison* L.) grazing were examined in a 2-yr study on a tallgrass prairie site in Oklahoma subjected to a seasonally and spatially variable burning regime. Mixed groups of bison, composed of cows, yearlings, calves, and young (< 5 yrs. of age) bulls, comprised 90% of the study population and showed selectivity by using burned areas significantly more than expected 23% of the time. Mixed groups avoided unburned areas 62% of the time. In contrast, bull groups of mature bulls > 5 yrs. of age selected unburned areas for grazing 29% of the time and burned areas only 6% of the time. Temporal patterns in bison grazing were evident; selective use of burns persisted for only a short period during the first post-fire growing season, after which burns were grazed in proportion to availability and then selectively avoided as bison shifted grazing efforts to newer burns. Regression analysis verified that bison grazing was negatively related to burn age. Regression also showed that grazing patterns were positively related to burn patch size. Although burn types varied significantly in total graminoid to forb ratios and overall vegetative composition, bison exhibited only limited preference for any burn type, choosing those with higher cover of annual *Bromus* spp. and sedges. It appears that bison select burned areas with relatively low graminoid biomass for grazing, presumably choosing these areas based on forage quality rather than quantity.

Introduction

Most North American prairies developed under the influence of fire and bison (*Bison bison* L.) grazing (Axelrod 1985), and numerous studies have documented the interaction between these phenomenon. Bison are strongly attracted to recently burned areas (Coppock and Detling 1986, Shaw and Carter 1990, Vinton et al. 1993, Pearson et al. 1995), presumably because of increases in forage quality (Coppock et al. 1983) and quantity (Wallace et al. 1995). In tallgrass prairie, fires were frequent and seasonally-variable (Bragg 1982). However, even slight differences in the seasonal timing of burning can have profound effects on vegetation response (Towne and Owensby 1984). In general, fires that occur during the dormant season favor those species that are not actively growing, such as the warm-season grasses that now dominate tallgrass prairie (Collins and Wallace 1990). However, fires during the growing season when these warm-season species are active reduces their competitive ability and favors cool-season species (Howe 1994). What is not well understood is how burning tallgrass prairie at different times of the year, during both active and dormant growing seasons, affects both the vegetative response and the subsequent grazing use by native herbivores.

This study reports on the grazing patterns of bison in a tallgrass prairie landscape subjected to seasonally-variable prescribed burns. Study objectives were to investigate spatial and temporal patterns of bison grazing in relation to the burning regime. Specifically, we were interested in testing hypotheses that 1) seasonal burns differ significantly in vegetative parameters and 2) bison grazing patterns are influenced by variations in burn patch parameters such as vegetative, spatial and temporal characteristics. Because bison on this site are almost exclusively gramnivorous (Coppedge 1996), we specifically hypothesized that grazing preferences would be closely tied to areas with high

cover of graminoids. We also evaluated habitat use by different bison social groups. Bison, like many ungulates, practice sexual segregation where adult males and females remain spatially and/or temporally separated for most of the year (McHugh 1958, Main and Coblentz 1990). Because differential habitat use in bison social groups has received little research attention, we compared grazing patterns of bison social groups in this study to test the hypothesis that segregation results in different overall grazing patterns.

Methods

The Study Area

The study was conducted from January 1994 to December 1995 on the Nature Conservancy's Tallgrass Prairie Preserve (TPP), a 15,342-ha tallgrass prairie site in the Osage Hills of northern Oklahoma (36°50'N, 96°25'W). The Osage Hills are a southward extension of the Flint Hills region that lies primarily in Kansas. The Flint Hills are an upland area characterized by hilly topography and rocky soils that prevented extensive cultivation and contain the largest remaining tracts of native tallgrass prairie in North America.

Vegetation is dominated by big bluestem (*Andropogon gerardii* Vitman), indiangrass (*Sorghastrum nutans* [L.] Nash), switchgrass (*Panicum virgatum* L.), and little bluestem (*Schizachyrium scoparium* [Michx.] Nash). Subdominant graminoids include rough dropseed (*Sporobolus asper* (Michx.) Kunth) and sedges (*Carex* spp.). Common forbs are western ragweed (*Ambrosia psilostachya* DC.) and annual broomweed (*Gutierrezia dracunculoides* (DC.) Nutt.). Average monthly temperatures range from a low of -5.0° C in January to a high of 34.4° C in July. Average total annual precipitation is 877 mm; 70% occurs between April and September (Bourlier et al. 1979). Before establishment in 1989 the Tallgrass Prairie Preserve was

grazed by cattle and burned in early spring every 1 to 2 years. It was never plowed.

Three hundred bison were reintroduced into a 1,973-ha part (the study area) of the preserve in October 1993. Following natural herd recruitment and the release of additional animals, the area allocated to bison was expanded by 292-ha in August 1995 to maintain a stocking density of 6-7 ha AU^{-1} during the study. Herd management was limited to annual roundups for inoculations, weighing, and culling.

Burning Regime

Beginning in September 1993 (1-mo. before to bison reintroduction), preserve management began a prescribed burning program. Burns were conducted during 3 seasonal periods: summer (September); fall (November and December); and spring (March and early April). Burns were conducted as headfires under conditions of low relative humidity, heavy fuel loads, and relatively high air temperatures (Table 1). Burn patch juxtaposition and burning history through the duration of this study was documented (Fig. 1).

Bison grazing patterns

The study area was surveyed during daylight hours 4 to 12 times per month. To assure temporal independence of observations (Swihart and Slade 1985), surveys were conducted only once per day, alternating between morning (0600 to 1200) and afternoon (1200 to dark). The location, size, and type of all bison herds were recorded. Bison generally form two types of social groups: bull groups of mature (> 5 yrs. of age) bulls and mixed groups of cows, yearlings, calves, and young (< 5 yrs. of age) bulls. The activity in which the majority of individuals in the herd were engaged was recorded, and locations

mapped on 1:24,000 USGS topographic quadrangles. Grazing use of burns and the remaining unburned portion of the study area was assessed in relation to availability with χ^2 analysis (Neu et al. 1974). To detect selection or avoidance of specific burn types and assess the significance of grazing patterns, 95% Bonferroni confidence intervals were constructed (Byers et al. 1984). Because the herding behavior of bison may lead to violation of statistical assumptions (Alldredge and Ratti 1986), we used both herds and individual animal counts as observations. Data were pooled for each year into seasonal study periods for analysis, defined as winter (Jan.-Mar.); spring (Apr.-Jun.); summer (Jul.-Sep.); and fall (Oct.-Dec.). To evaluate patch-specific grazing trends, observations were also summarized for individual burn patches (Fig. 1). These data were subjected to analysis by simple linear regression analysis to assess relationships between bison group observations and spatial-temporal burn patch characteristics. We followed the general protocol for regression analysis presented by Senft et al. (1983). Characteristics evaluated were burn patch age (in months), size (in ha), distance to permanent water (in km), and mean interpatch distance (in km). Because of small sample sizes from bull groups, we limited the analysis to mixed group data (Neter et al. 1989).

Vegetation

Vegetation was assessed by establishing 20 (1994) and 23 (1995) 1-ha plots in the study area each year. Plot locations were stratified to represent as many individual burn patches, burn types, and unburned areas as possible: thus, all but 2 burn patches present in the study area (Fig. 1) were sampled. Composition of the standing crop of current year's growth was estimated with the dry-weight-rank method (Gillen and Smith 1986), with herbage components grouped into 7 categories: tallgrasses (big bluestem, switchgrass,

indiangrass), little bluestem, all other perennial grasses, annual grasses, sedges, legumes, and forbs (Table 2). Sampling dates represented the broad seasons of plant phenology - early growing season (June) and late growing season (August). To estimate biomass, all aboveground herbage in 20-25 20 x 50 cm quadrats was clipped in each plot on each sampling date. Herbage was separated into current year's growth, litter, and mulch, and dried at 70° C to a constant weight. Total graminoid to forb ratios also were calculated by pooling composition data. The significance of variation in biomass and ratios was tested with a 3-way ANOVA, using burn type (spring, summer, fall, unburned), sample date (June and August), and year (1994 and 1995) as independent variables. Composition data were similarly tested using a MANOVA model with percent composition of the seven forage groups as a multivariate dependent variable. Significance of terms in the model was tested at $\alpha = 0.05$ with Wilk's λ (Johnson and Wichern 1992).

Results

Grazing Patterns

Group and animal count analyses were similar 66% of the time (Tables 1-2). There were no situations of opposite indications of grazing selectivity; the only differences were whether an area was grazed in proportion to availability or whether it was selected/avoided. Because of potential bias from individual observations due to lack of independence, we focus our interpretations only on group count observations and analyses.

Bison showed a limited selectivity for fall burns, with 17% of observations showing selection for this burn type, 15% showing selectivity for summer burns, and 11% showing selectivity for spring burns. Patterns of avoidance, however, were more substantial. Thirty-five percent of bison

observations indicated avoidance of fall burns, compared to 28% for spring burns and 15% for summer burns. Using the magnitude of differences between avoidance and selection observations to gauge bison preferences, bison appeared to most favor summer burns, followed by fall then spring burns.

Temporal trends in grazing patterns were apparent. Older burns from 1993 and 1994 were generally used only in proportion to availability or avoided by bison during 1995 (Table 2). When newer and presumably more attractive burns appeared on the landscape (Fig. 1), bison shifted to these newer burns in 1995, regardless of burn season (Table 3). Regression analysis of grazing patterns on individual burn patches in relation to spatial-temporal characteristics verified that temporal trend. Although regression accounted for only 12-31% of the variation in bison grazing (Table 4), grazing observations were negatively related to burn age ($p < 0.002$) and positively related to burn size ($p < 0.001$).

Bull groups and mixed groups did not have similar grazing patterns. Bull selectively grazed burns only 6% of the time, compared to a 23% rate of burn selection for mixed group observations. Use of unburned areas showed similar trends. Observations indicated bison showed a 62% rate of avoidance for unburned areas for mixed groups, while bull groups avoided unburned areas only 29% of the time. In contrast, bull groups selected for unburned areas 29% of the time while mixed groups never exhibited selection for unburned areas. Overall, pairwise seasonal comparisons for both study years (Tables 1-2) showed only 46% agreement between grazing patterns of bulls and mixed groups. Thus, the majority of observations (54%) indicate that grazing patterns differed between bison social groups (Tables 1-2).

Vegetative characteristics

Biomass did not vary significantly between burn types and unburned areas ($p > 0.1874$). However, total graminoid to forb ratios did ($p < 0.0182$). Unburned areas had the highest mean ($\bar{x} \pm 1$ SE) ratio (34.8 ± 11.9) of total graminoids to forbs, followed by spring burns (4.7 ± 1.1), fall burns (2.0 ± 0.2), and summer burns (1.8 ± 0.3). There was a significant burn type by season interaction (p < 0.016) for vegetation composition. Spring burns and unburned areas had the highest mean relative composition of tallgrasses and little bluestem (Table 5). Summer burns had the highest levels of annual grasses, forbs, and legumes, but sedges were most prominent on fall burns.

Discussion

Bison in this study showed preferences for grazing on burned areas, consistent with previous studies of bison habitat use (Coppock and Detling 1986, Shaw and Carter 1990, Vinton et al. 1993, Pearson et al. 1995). However, what remained unknown until now was how different seasonal burn patches that possess varying vegetative properties influenced bison grazing patterns. The trend in mean graminoid to forb ratios proceeded from a high ratio on unburned areas, followed by spring burns, fall burns and finally summer burns; this is exactly opposite of the grazing preference trend exhibited by bison in this study. This suggests an increase in grazing selection by bison with a decrease in graminoids and an increase in forbs. Bison, however, are primarily gramnivorous (Plumb and Dodd 1993) and usually avoid areas with abundant forbs (Trammel and Butler 1995). More importantly, our study of food habits for bison on this site have shown almost exclusive gramnivory, with graminoids comprising ≥ 99% of the diet (Coppedge 1996). This lead to our hypothesis that grazing patterns would be related to high levels of graminoids

on the landscape, which the graminoid to forb ratio trend does not support. However, there is a plausible explanation for this apparent contradiction. Selective grass herbivory by bison, by removing the competition between grasses and forbs, is known to favor forb growth and productivity in tallgrass prairie (Fahnestock and Knapp 1993, 1994). Because our sampling was done at the midpoint of broad phenological periods and used a technique that provided a relative measure of composition, we believe that we were measuring the ungrazed forb response to the removal of graminoids by bison and that bison are not actually selecting areas in response to an increase in forbs.

Bison may be maintaining graminoids on burn patches at a relatively low biomass with frequent regrazing. Because of a general decrease in forage quality with increases in maturity level and biomass (Van Soest 1982), grazers in many situations face a trade-off between forage quality and forage quantity (Hobbs and Swift 1988). The "forage maturation hypothesis" (Fryxell 1991) suggests that frequent regrazing by large herbivores maintains areas of low to intermediate biomass as "grazing lawns" (McNaughton 1984, 1986), which contain forage of both acceptable quality and sufficient quantity to meet their foraging requirements (Stephens and Krebs 1986). The tallgrasses that dominate our study site are quite variable in their nutritive content with changes in phenology (Waller et al. 1972, Adams and Wallace 1985), so bison may be selectively regrazing areas with low graminoid biomass based on nutritional cues and forage quality. These regrazed areas would subsequently have a relatively high forb cover resulting from frequent grass herbivory by bison. Vinton et al. (1993) reported high grass to forb ratios on patches selected for grazing by bison on tallgrass prairie in Kansas. However, because burns with low graminoid biomass seem to be preferred by bison in our study,

total graminoid to forb ratios were not a reliable indicator of bison grazing patterns on our study site.

Burn types varied significantly for most vegetative parameters, supporting our hypothesis that burn season results in different vegetative characteristics. Bison showed some selectivity among burn types. Most preferred were summer burns, characterized by a low graminoid to forb ratio, but having a relatively high cover of annual grasses, namely *Bromus* spp. These are a common diet item for bison on this site (Coppedge 1996). Bison also have been shown to choose burned tallgrass prairie sites in Kansas that were characterized by high levels of these exotic, cool-season grasses (Vinton et al. 1993). It appears that annual grasses are somewhat desired by bison, thus partially influencing their choice of grazing location. Fall burns also were preferred by bison. The only unique vegetative characteristic of this burn type was a higher cover of sedges. These are a highly desired forage item for this bison population (Coppedge 1996). These results support our hypothesis that bison choose areas for grazing based at least partially on vegetative characteristics.

Two spatial factors shown to be important in similar studies of large grazers were not significant in this study. Foraging theory predicts that both large patches and patches more isolated or with longer travel times (in this study measured by mean interpatch distance) tend to have longer residence time by grazers (Stephens and Krebs 1986). Instead, we found that only burn size was important, supporting only part of the optimal foraging hypothesis. We suspect that a simple effect of scale may explain the lack of importance for mean interpatch distance. The animals can traverse the study area in only a few hours, thereby likely preempting the importance of travel time and its potential influence on grazing patterns. Similarly, distance to water,

important in some studies of cattle grazing distribution (Senft et al. 1985, Pinchak et al. 1991), was unimportant in this study. Again, the size of the study area and the relatively uniform distribution of permanent water (Fig. 1) may have reduced the importance of this variable.

This study also found an interesting temporal trend in bison grazing patterns that had not been documented before -- bison preference for newer burns while avoiding older patches. However, because the study area is an unusual situation with a prescribed burning program that is spatially and temporally variable, it is likely that similar trends could be observed for other herbivores in other locations under similar conditions. Our results showing a temporal grazing trend for bison supports recent suggestions that herbivores have accurate spatial memory based on previous foraging experiences and can remember locations of and return to productive sites while avoiding unproductive areas where foraging experiences were poor (Bailey et al. 1996).

Significantly different grazing patterns between mixed and bull groups of bison supports the hypothesis that sexual segregation results in differential habitat use. Main and Coblentz (1990) concluded that sexual segregation among ungulates arose as the result of different reproductive strategies, with females selecting areas best suited for rearing offspring and males choosing habitats to maximize body condition. Differences in grazing patterns between bison social groups were most disparate in spring when calves are born and nutritional demands on females are highest and the period immediately before the rut when males will compete for breeding opportunities (McHugh 1958). Thus, spring grazing patterns of bison certainly indicate this pattern of social segregation may apply to bison as well.

Conclusions

Bison grazing is influenced by temporal, spatial, and vegetative characteristics of the landscape. Temporal variation in the seasonal burning regime influenced the length of time that bison were attracted to and grazed on burned patches. Size of a burn patch influenced how much bison utilized the patch. Timing of seasonal burns influenced the vegetative community, which in turn affected bison grazing patterns as bison selected for patches with higher relative cover of annual grasses and sedges. Total graminoid levels, however, were not a suitable indicator of bison grazing preferences because bison appeared to select for areas with low quantities of presumably high quality graminoids. Bison social groups had different grazing patterns. Although bull groups were a small part of the population (<10%), they showed less attraction to burned areas than mixed groups of cows, calves, and yearlings. Conversely, bull groups showed more preference for unburned prairie while mixed groups avoided these areas.

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Table 1. Average burning conditions for the 3 types of seasonal burns conducted at the Tallgrass Prairie Preserve, Oklahoma.[1]

Burn Type	Air temp. (°C)	Rel. hum. (%)	Windspeed (km h⁻¹)	Fuel load (kg ha⁻¹)	Ave. size (ha) (range)
Spring	19	24	16	8,200	86 (66 - 98)
Summer	28	39	8	7,990	26 (14 - 49)
Fall	16	43	11	8,920	91 (51 - 137)

[1] Data courtesy R.G. Hamilton and J.S. Crockett.

Table 2. Seasonal grazing patterns in 1994 by bison social groups in relation to available burn types and unburned areas on tallgrass prairie in Oklahoma. Grazing use is expressed as a percentage of total observations on groups and as counts of individual animals.

Burn type	Group type	Winter (Jan.-Mar.)		Spring (Apr.-Jun.)		Summer (Jul.-Sep.)		Fall (Oct.-Dec.)	
		Groups	Animals	Groups	Animals	Groups	Animals	Groups	Animals
Summer 1993	Bull	0.0-[1]	0.0-	25.0	1.3	11.1	7.7+	2.2	4.0
	Mixed	19.1+	26.2+	15.0+	12.7+	22.2+	26.4+	7.9	9.0+
Fall 1993	Bull	0.0-	0.0-	20.0	18.2	27.8+	36.5+	8.8	19.0+
	Mixed	2.9-	2.6-	37.0+	50.9+	29.6+	36.3+	16.5	22.2+
Spring 1994	Bull			25.0	18.2	16.7	13.5	24.4	33.0+
	Mixed			23.3+	29.7+	24.1+	29.8+	4.7	7.3
Summer 1994	Bull							2.2	2.0
	Mixed							9.4	9.2+
Fall 1994	Bull							2.2-	10.0-
	Mixed							5.5	7.2-
Unburned	Bull	100.0+	100.0+	30.0-	62.3-	44.4-	42.3-	60.2	38.0-
	Mixed	78.1-	71.2-	24.7-	6.7-	24.1-	7.5-	56.0	45.1-

[1] Indicates significant selection (+) or avoidance (-) relative to availability as estimated from simultaneous 95% Bonferroni confidence intervals (Byers et al. 1984).

Table 3. Seasonal grazing patterns in 1995 by bison social groups in relation to available burn types and unburned areas on tallgrass prairie in Oklahoma. Grazing use is expressed as a percentage of total observations on groups and as counts of individual animals.

Burn type	Group type	Winter (Jan.-Mar.)		Spring (Apr.-Jun.)		Summer (Jul.-Sep.)[1]		Fall (Oct.-Dec.)	
		Groups	Animals	Groups	Animals	Groups	Animals	Groups	Animals
Summer 1993	Bull	15.2	12.1+[2]	6.7	10.6			0.0-	0.0-
	Mixed	9.5	17.7+	0.0-	0.0-	10.0	2.3-	3.2	1.5-
Fall 1993	Bull	15.2	6.9	20.0	23.4			0.0-	0.0-
	Mixed	10.1	8.8	1.4-	0.6-	0.0-	0.0-	5.3	2.2-
Spring 1994	Bull	18.2	12.1	0.0-	0.0-			0.0-	0.0-
	Mixed	9.0	7.1	5.8	1.1-	3.3	1.1-	1.1-	0.4-
Summer 1994	Bull	3.0	6.9	0.0-	0.0-			0.0-	0.0-
	Mixed	9.0	9.5+	18.8+	17.8+	13.3	21.5+	4.3	3.3
Fall 1994	Bull	3.0	0.9-	40.0+	21.3			0.0-	0.0-
	Mixed	7.4	12.4+	42.0+	35.9+	13.3	14.9+	12.8	10.4
Spring 1995	Bull			0.0-	0.0-			0.0-	0.0-
	Mixed			16.0	35.5+	10.0	9.9+	6.4	16.5+
Summer 1995	Bull							18.2	6.9
	Mixed					6.7	8.7+	9.6	13.7+
Fall 1995	Bull							0.0-	0.0-
	Mixed							0.0-	0.0-
Unburned	Bull	51.4	61.1	33.3	44.7			81.8+	93.1+
	Mixed	55.0-	44.5-	16.0-	9.1-	43.4	41.6-	57.3	52.0+

[1] Due to small sample sizes, no analyses were conducted for bull groups during this season.

[2] Indicates significant selection (+) or avoidance (-) relative to availability as estimated from simultaneous 95% Bonferroni confidence intervals (Byers et al. 1984).

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Table 4. Results of regression analysis of spatial and temporal trends in bison grazing patterns. The percentage of total grazing observations from each burn patch was used as the dependent variable, with the burn patch age (in months), size (in ha), distance to permanent water (in km), and mean interpatch distance (in km) as independent variables. Only data from mixed groups were used in the analysis because these groups constituted the majority (90%) of the population. Observations on bull groups were too few in some seasons and from many burn patches to conduct regression analysis.

Variable	Equation	P	R^2
Burn size	$\hat{y} = 2.5 + 0.1x$	<0.002	0.12
Mean interpatch distance	$\hat{y} = 7.3 - 0.7x$	>0.715	0.00
Distance to permanent H_2O	$\hat{y} = 5.8 + 1.8x$	>0.579	0.00
Burn age	$\hat{y} = 12.6 - 0.6x$	<0.001	0.31

Table 5. Herbage composition (%, $\bar{x}$ ±1 SE) of seasonally burned and unburned tallgrass prairie in Oklahoma, 1994-1995, as determined by the dry-weight-rank method (Gillen and Smith 1986).

Vegetation component	Season	Spring $\bar{x}$	SE	Summer $\bar{x}$	SE	Fall $\bar{x}$	SE	Unburned $\bar{x}$	SE
Tallgrasses	June	34.3	4.5	21.4	3.3	21.7	3.4	24.3	3.5
	August	29.3	5.7	21.0	2.9	21.6	2.3	41.7	3.5
Little bluestem	June	28.6	3.8	16.7	4.3	19.1	4.1	33.3	4.6
	August	32.8	2.4	18.8	5.3	17.2	3.8	25.8	4.3
Other perennial grasses	June	8.4	1.9	16.6	4.6	16.0	3.2	15.2	1.6
	August	11.3	2.2	13.0	1.7	17.4	3.0	12.1	1.5
Annual grasses	June	0		5.7	2.6	0.7	0.5	1.2	0.6
	August	0		0.6	0.4	0		0.1	0.1
Sedges	June	2.0	1.2	2.5	0.9	10.6	2.9	8.6	2.5
	August	0.7	0.4	1.7	0.5	3.0	1.4	2.8	0.9
Forbs	June	25.2	4.7	32.9	4.8	30.1	3.0	15.9	2.9
	August	24.9	4.6	42.3	4.8	39.5	2.2	15.4	3.7
Legumes	June	1.5	0.7	4.2	1.0	1.9	0.7	1.6	0.7
	August	1.0	0.3	2.6	0.8	1.4	0.6	2.2	1.0

Fig. 1. Burning history of the bison unit of the Tallgrass Prairie Preserve,

Oklahoma at the conclusion of the study in December 1995. Numbers

refer to the order in which burns were conducted.
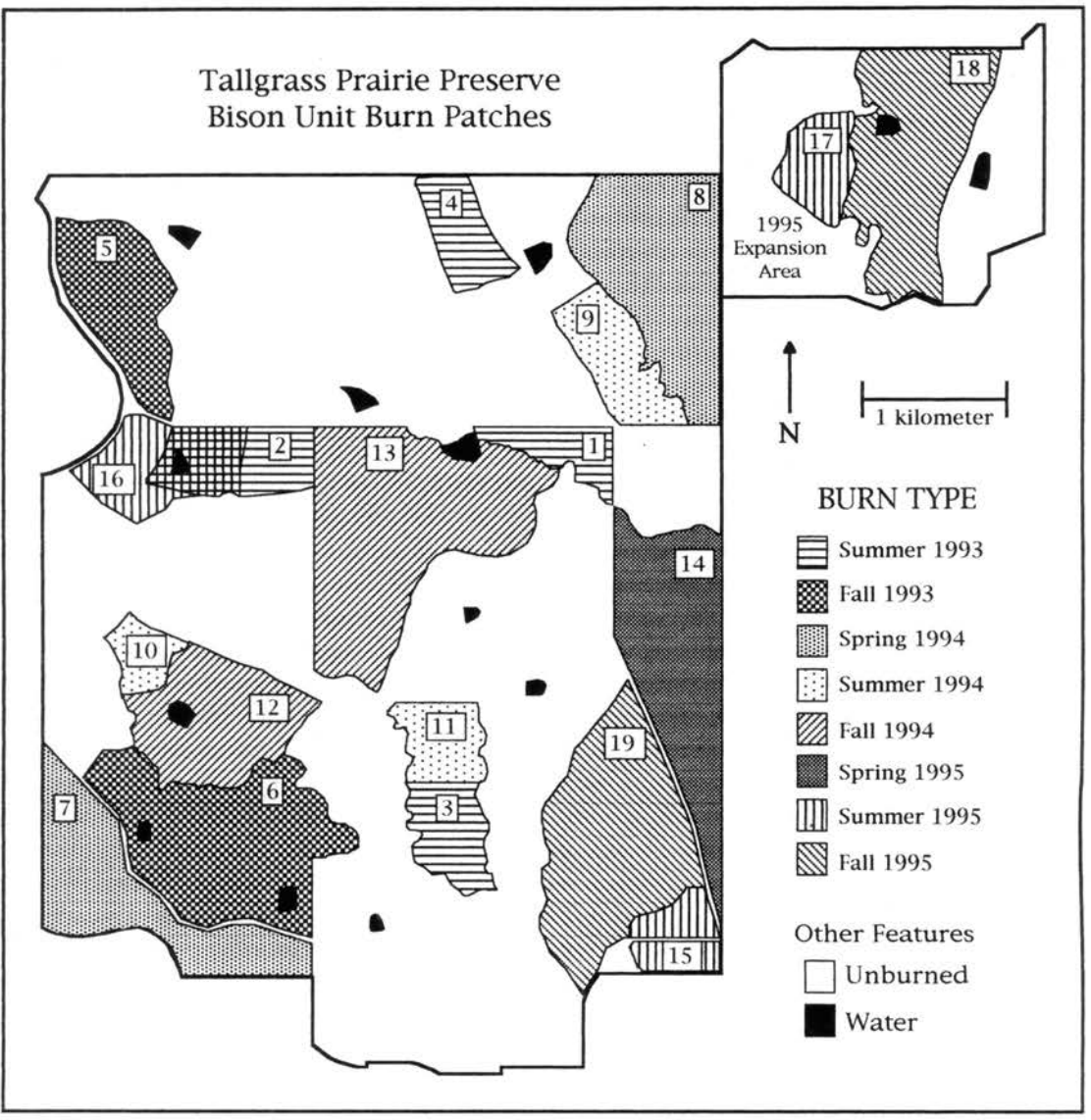
Tallgrass Prairie Preserve
Bison Unit Burn Patches

1995 Expansion Area

N

1 kilometer

BURN TYPE

Summer 1993
Fall 1993
Spring 1994
Summer 1994
Fall 1994
Spring 1995
Summer 1995
Fall 1995

Other Features

Unburned
Water

CHAPTER IV

VEGETATION-ENVIRONMENT RELATIONSHIPS IN TALLGRASS
PRAIRIE: PLANT GUILD RESPONSES TO SEASONAL
FIRE AND CLIMATIC VARIATION

Abstract. - Multivariate techniques were used to evaluate vegetation-environment relationships for plant guilds on a tallgrass prairie site in northern Oklahoma, USA grazed by bison. The objective of the study was to identify environmental variables that were associated with variation in guild abundances. Canonical Correspondence Analysis (CCA) was used to directly relate vegetation patterns to environmental variables such as seasonal fire, grazing, and topoedaphic variation. CCA ordination revealed that some guilds were most closely associated with particular seasonal fires; other guilds were most strongly associated with either the length of time since fire or with grazing. Some guilds were not associated with any measured environmental gradients, indicating they were either equally affected by measured parameters or that important environmental variables were omitted. The abundance of some prairie plant guilds appeared to be determined primarily by seasonal and/or climatic variation. Results also suggest that occurrence of some plant guilds was principally determined by a single factor; others are influenced by the interactions of several environmental phenomenon.

Introduction

Fire is a necessity for the maintenance of North American tallgrass prairie (Collins & Wallace 1990). Without recurrent burning, litter accumulates which decreases productivity (Knapp & Seastedt 1986) and changes community composition (Abrams & Hulbert 1987; Gibson & Hulbert 1987). Fires occurred historically in tallgrass prairie throughout the year (Bragg 1982) but most prescribed burning is done now in spring (Towne & Owensby 1984). Relatively few studies exist on the effects of fire seasonality on tallgrass prairie. Spring fires occur when warm-season species are not actively growing, and burning during spring generally favors warm-season tallgrasses (Howe 1994a; Towne & Owensby 1984). In contrast, summer fires usually favor forbs and cool-season species like annual grasses and sedges (Ewing & Engle 1988; Howe 1994a). Thus, fire seasonality in tallgrass prairies is important in determining vegetation composition and productivity (Ewing & Engle 1988; Towne & Owensby 1984).

Along with seasonality, fire frequency (Gibson 1988) and the length of time since fire occurrence also significantly affect tallgrass prairie floristics (Gibson & Hulbert 1987). Additional influences include variations in topography and soils (Abrams & Hulbert 1987; Gibson & Hulbert 1987; Towne & Knapp 1996), grazing (Vinton & Hartnett 1992; Vinton et al. 1993) and climatic fluctuations (Briggs & Knapp 1995; Gibson & Hulbert 1987; Knapp 1985). While understanding the individual effects of these factors on tallgrass prairie is important, rarely, if ever, do they act independently on the vegetation. Fire influences grazing patterns (Vinton et al. 1993), which in turn affects the likelihood of another fire (Hobbs et al. 1991). Tallgrass prairie response to fire varies with topography and soils (Abrams et al. 1986; Briggs & Knapp 1995). Fire, topography, and grazing in turn affect vegetation differently under

varying climatic conditions (Briggs & Knapp 1995; Gibson & Hulbert 1987; Knapp 1985). Clearly, studies of variation in tallgrass prairie community composition must control or account for numerous potential interactions to understand effects of a single phenomenon of interest. As such, there are few studies that have attempted to address the simultaneous effects of multiple factors on tallgrass prairie. Collins' (1987) study of cattle grazing and spring fire concluded that their interaction was important in determining community structure of tallgrass prairie, including both species diversity and composition. In a study on mixed-grass prairie, Collins & Barber (1985) concluded that the interactions of climatic, pyric, and biotic factors were of overriding importance in comparison to their individual influences. In one of the most comprehensive studies to date, Gibson & Hulbert (1987) identified time since burning as the single most important influence on species composition of tallgrass prairie, followed by topoedaphic differences and climatic variation. Their study also emphasized interactions between these variables and the influence of this interaction on the abundance of particular species.

Earlier studies were conducted with single-season fires (Collins 1987), with either non-native grazers (Collins 1987) or no grazing at all (Gibson & Hulbert 1987), or on fundamentally different grassland communities such as mixed-grass prairie (Collins & Barber 1985). Comprehensive studies are still needed on effects of seasonally variable fire, native grazers, topoedaphic and climatic variations, and their interactions on tallgrass prairie vegetation. We had the opportunity to conduct such a study when the Nature Conservancy established the 15,342-ha Tallgrass Prairie Preserve (TPP) in northern Oklahoma, USA in 1989. As part of the preserve restoration effort, a population of the native grazer of North American prairies, bison (*Bison bison* L.), was established, accompanied by a seasonally-variable burning regime. The

objectives of our research were to assess patterns of variation in abundance of tallgrass prairie plant guilds in relation to interacting environmental factors. We used multivariate direct gradient techniques to investigate the role of seasonal fire, length of time since burning, bison grazing, topoedaphic variation, and intra- and interseasonal climatic variation in determining tallgrass prairie community composition. We hypothesized that we would find some guilds that were primarily associated with a single environmental factor, while others would show simultaneous associations with several factors.

Methods

Study area

The study was conducted during 1994 and 1995 on the Nature Conservancy's Tallgrass Prairie Preserve, a tallgrass prairie in the Osage Hills of northern Oklahoma, USA (36°50'N, 96°25'W). The Osage Hills are a southern extension of the Flint Hills region lying primarily in Kansas. The Flint Hills are an upland area characterized by hilly topography and rocky soils that historically prevented extensive cultivation and contain the largest remaining tracts of native tallgrass prairie in North America. The preserve is only a few kilometers southeast of the Osage Site, a tallgrass prairie intensively studied by Risser et al. (1981).

Average total annual precipitation was 877 mm; 70% occurred between April and September (Bourlier et al. 1979). Total precipitation during the study was 1,058 mm in 1994 and 939 mm in 1995. The area was grazed by bison at a stocking density of 6-7 ha AU^{-1}. Preserve management included prescribed burning of 20% of the area annually with fires conducted during late summer (September), fall (November and December), and spring (March).

Vegetation sampling

Eighteen 1-hectare (100 x 100m) study plots were established in patches of the vegetation mosaic in March 1994. Plot locations were stratified to represent as many different combinations of environmental characteristics as possible. Seven additional plots were established on new burned patches in 1995 to achieve this goal. Plots were sampled in early June and mid-August each year to account for seasonal variation in phenology between cool-season and warm-season species (Howe 1994). Percent composition of phytomass of each plot was assessed with the dry-weight-rank method (Gillen & Smith 1986) based on 25-0.1 m^2 (10 x 50 cm) quadrats located randomly within each plot. Ranking was performed on 7 categories of functional plant guilds. We chose our guild designations *a priori*, and they were similar to those recently presented by Kindscher & Wells (1995) for tallgrass prairie sites in Kansas. The three perennial C_4 (warm-season) tallgrasses that codominated the study area and typically constituted the matrix of the vegetation on most sites formed the first guild (Table 1). A closely associated C_4 species, little bluestem (*Schizachyrium scoparium* [Michx.] Nash), was also a codominant in the study area, but as a perennial bunchgrass (as compared to the rhizomatous tallgrasses) it is heavily used by bison after burning (Pfeiffer and Hartnett 1995). Due to this difference in growth form and its negative response to summer fire (Ewing & Engle 1988), we chose to designate a separate category for this species. Remaining grasses were relegated to either a perennial grass or annual grass guild. The non-Gramineae C_3 (cool-season) sedges (Cyperaceae) and rushes (Juncaceae) formed a fifth guild (Table 1). Due to the positive response of legumes to burning (Towne & Knapp 1996), they were separated from all remaining non-woody dicots (forbs) to form the remaining guilds (Table 1). The different phenological forb guilds presented by

Kindscher & Wells (1995) were grouped in our study because forbs generally respond positively to selective grass herbivory by bison (Fahnestock & Knapp 1994), they are relatively unimportant in bison diets (Plumb & Dodd 1993), and they play a lesser role in the overall productivity of tallgrass prairie than do grasses (Gibson & Hulbert 1987).

Environmental variables

In conjunction with a concurrent study of bison grazing patterns in relation to the prescribed burning program, observations of bison grazing distributions were made 4 to 20 times per month (Coppedge 1996). Bison locations were mapped on 1: 24,000 scale USGS topographic quadrangles. Plot locations were determined by a global positioning system and entered into a geographic information system (GIS). Bison locations also were digitized into the GIS, along with date of observation and number of animals observed. We used the GIS to tabulate all bison grazing observations taken 3 months before each sampling date for a 100-m radius around each plot center. Although that area was beyond the actual plot boundaries used for vegetation sampling, we assumed that animals in the general vicinity of a plot likely grazed on the plot to some extent. The cumulative number of grazing bison was then divided by the total number of animals present in the population during the sampling month to derive an index of bison grazing intensity, one of the environmental variables. Other environmental variables used in the analysis included the number of growing seasons since each study plot had been burned; the dry weight of litter present on each plot, estimated by collecting all litter and standing dead material (except current year's senesced material) in 10, 0.1-m^2 quadrats per plot per sampling date and drying to a constant weight at $70°$ C; topoedaphic site, defined by soil texture (Bourlier et al. 1979) and topographic

position (Coppedge 1996); sampling date; sample year of the study; and burn type, determined by the dates of the burns on which the plots were established (Table 2).

Data analysis

We used Canonical Correspondence Analysis (CCA) to examine relationships between plant guild abundance and environmental factors. We used CANOCO version 3.1 (ter Braak 1990) for all ordination analyses. CCA is a direct gradient analysis that constructs ordination axes that are orthogonal linear combinations of the environmental variables (ter Braak 1987a). The algorithm used in CCA is reciprocal averaging, a form of eigenanalysis, and linear least-squares regression (Palmer 1993). In CCA, the total amount of variation in guilds that can be explained by the environmental variables is calculated by dividing the sum of canonical eigenvalues by the sum of all unconstrained eigenvalues (ter Braak 1986). The resulting value approximates R^2 because CCA is a special type of multiple regression. The value is inferred, however, so no *p*-value is directly associated with it. However, effects of included environmental variables on guild variation can be tested (i.e., the probability of randomly obtaining the same relationship) by conducting Monte Carlo permutations on the guild-environment relationship (ter Braak 1987a). To assess the importance of individual environmental variables, the intra-set correlations were calculated by dividing the inter-set correlations by *R*, the species-environment correlation of the axis (ter Braak 1986). Guild abundance data were square-root transformed before analysis to dampen the effects of dominant guilds (Palmer 1993). The resulting ordination is a bi-plot showing the relationship between guild abundances and environmental variables (ter Braak 1986, Palmer 1993).

Results and Discussion

The first two CCA axes from the full set of environmental variables accounted for 76.8% of the variation between guild abundances and environmental variables (Table 3). The total amount of guild variation accounted for by this analysis was 39%. Monte Carlo permutations ($n = 500$) indicated that the eigenvalues for the CCA axes constructed with the environmental variables were significant ($F = 5.28$; $p < 0.01$), which indicated a strong relationship between plant guilds and environmental variables. Vectors in the bi-plot (Fig. 1) visually represent the correlation between the continuous environmental variables and the CCA axes (Table 3). The points representing categories of nominal environmental variables are the centroids (the weighted averages) of that category (ter Braak 1986) and are an approximation of the correlation between the variable and the axes (Table 3). The correlation between an environmental variable and an axis is a measure of the relative importance of that particular environmental variable (Table 3). Environmental vectors also extend in the opposite direction from the origin, possibly indicating a negative relationship between a guild and an environmental variable. The position of a guild point relative to an arrow or categorical point indicates how strongly that guild was associated with that particular environmental variable.

The most obvious relationship was between annual grasses and summer burns. These were closely associated but both points were outside the scale of the bi-plot needed to clearly orient the remaining guild and environmental data (Fig. 1). Although to a lesser extent, annual grasses also were associated with lowland sites and June sampling dates. Sedges and rushes clearly orient with the 1995 sample year and to a lesser extent with fall burns, June sample

dates, and litter. At first it appears that legumes do not clearly relate to any environmental variable, but their position opposite the arrow representing number of growing seasons since burning (GSNU) may indicate the legume guild had a negative relationship with this variable. Tallgrasses and little bluestem were closely associated with bison grazing intensity and to a lesser extent with August sampling dates, spring burns, upland topoedaphic sites, and the 1994 sample year. Forbs and perennial grasses were not clearly associated with any of the environmental variables (Fig. 1).

Precipitation patterns during the study may also explain trends in the orientation of some plant guilds (Fig. 2). During 1994, there was above-average precipitation in July and August, a period of substantial growth for many warm-season species (Howe 1994a; Kindscher & Wells 1995). This might have lead to the association of the warm-season tallgrass and little bluestem guilds with both the 1994 and August (late-growing season) centroids (Fig. 1). During 1995, there was above-average rainfall during the early part of the growing season, especially before and during the June sampling (Fig. 2). The positive sedge and rush guild association with the 1995 centroid and to a lesser extent with the June centroid is probably due to the timing of this abundant moisture. This guild is composed primarily of C_3 or cool-season species with most of their active growth during the early, cooler period of the growing season (Kindscher & Wells 1995). This group also is favored by very early spring and winter (December) burning (Towne & Owensby 1984). It was not surprising, therefore, to find this group closely associated with fall fires in our study, which were conducted during November and December.

Tallgrasses and little bluestem make up a large portion of bison diets on this site (Coppedge 1996). Vinton & Hartnett (1992) reported that these species have reduced growth rates when repeatedly defoliated by bison. Pfeiffer &

Hartnett (1995) reported that little bluestem was grazed three times as frequently in burned areas as compared to unburned areas. Recently, Hartnett et al. (1996) reported that these species usually decrease in cover under the influence of bison grazing. All of this evidence suggests that the true underlying relationship between bison grazing and residual phytomass of these dominant grass guilds is negative. In partial support of our hypothesis of interacting environmental effects, these guilds also show simultaneous relationships with several factors. These include sampling date and year, an indication of the phenologic affiliation of these species (warm-season) and response to short-term precipitation patterns (Knapp 1984); spring burns, which have been shown favor these species and has lead to spring burning of the landscape around the study area becoming established as a grazing management tool (Towne & Owensby 1984); and upland sites. The association with upland sites contradicts the results of Abrams & Hulbert (1987) that reported no difference in cover between upland and lowland sites for big bluestem and indiangrass, but did report a topographic effect on switchgrass cover. This emphasizes the importance of interactions of environmental variables on these guilds, and also indicates that there are species-specific responses that may be masked by guild-level analyses.

Summer fire has less of an effect on the species that have already had a substantial portion of their annual growth and have either seeded or stored resources for the next year (Howe 1994a). These would be mostly C_3 species like some annual grasses and sedges (Kindscher & Wells 1995). Our annual grass guild was composed primarily of *Bromus* spp., namely Japanese brome (*B. japonicus* Thunb.). This exotic annual is known to respond favorably at times to summer fire in tallgrass prairie (Ewing & Engle 1988) which would likely explain its strong association with summer fire.

Gibson & Hulbert (1987) reported that time since burning was one of the principal agents determining species composition in tallgrass prairie. It was surprising, therefore, that only legumes showed a strong relationship with our equivalent variable of number of growing seasons since burning (GSNU). Because tallgrass prairie can be a nitrogen-limited system for some species (Hulbert 1988, Ojima et al. 1994), nitrogen-fixing legumes are a vital part of the functioning of this ecosystem (Seastedt et al. 1991). Towne & Knapp (1996) found that legume densities were significantly higher in annually burned tallgrass prairie as compared to unburned sites. One of the most common legumes in our study, leadplant [*Amorpha canescens* (Nutt.) Pursh] is known to increase under all annual burning conditions (Towne & Owensby 1984). The negative relationship between number of growing seasons since burning and legumes indicated by our results supports the general contention of these earlier studies that most legumes are either fire tolerant or at least respond favorably to fire, further emphasizing the importance of recurrent fire to components of tallgrass prairie structure and function such as nutrient cycles (Knapp & Seastedt 1986).

Our results support those of previous studies that concluded that patterns of both productivity (Briggs & Knapp 1995) and composition (Gibson & Hulbert 1987) in tallgrass prairie are driven by the interactions of numerous factors, including fire, grazing, topography, soils, and climate. We also have supported the hypothesis that for some groups of prairie plants, a single environmental factor is most influential in determining its abundance (i.e., annual grasses with summer fire), while other groups are influenced by numerous interactions (i.e., tallgrasses and little bluestem with grazing, spring fire, and late growing season periods). However, our use of large, inclusive guilds for perennial grasses and forbs may have masked species-

level responses to the environmental variables, especially when forbs exhibit species-specific responses to yearly climatic variation and fire season in mixed-grass prairie (Biondini et al. 1989) and selective grass herbivory by bison is known to favor forb growth in tallgrass prairie (Fahnestock & Knapp 1994). Our results show that guild-level analysis is a useful approach for studying general vegetative trends (Kindscher & Wells 1995), but our failure to find clear environmental associations for all guilds may be an indication that this analyses is not appropriate for all studies, especially those concerned with species-specific and biodiversity issues (Howe 1994b).

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Table 1. Tallgrass prairie plant guilds and representative species.

Guild	Representative species
1. Tallgrasses	*Andropogon gerardii, Sorgastrum nutans, Panicum virgatum*
2. Little bluestem	*Schizachyrium scoparium*
3. Perennial grasses	*Sporobolus* spp., *Tridens* spp., *Paspalum* spp.
4. Annual grasses	*Bromus* spp., *Festuca* spp.
5. Sedges & rushes	*Carex* spp., *Cyperus* spp., *Juncus* spp., *Eleocharis* spp.
6. Forbs	*Ambrosia* spp., *Aster* spp., *Helianthus* spp., *Solidago* spp.
7. Legumes	*Amorpha* spp., *Desmodium* spp., *Lespedeza* spp.

Table 2. Environmental variables used for multivariate analysis of tallgrass prairie plant guilds.

Variable	Units/categories	Acronym
Number of growing seasons since burned	-	GSNU
Bison grazing intensity index	-	BGII
Litter weight	gm/m^2	LITT
Burn date	late summer (September)	SUMB
	fall (November - December)	FALB
	spring (March)	SPRB
Topoedaphic site	upland (loams)	UPLD
	run-in (silt loams)	RNIN
	lowland (silty clay loams)	LOWL
Sampling year	-	1994
	-	1995
Sampling date	early growing season (June)	JUNE
	late growing season (August)	AUGU

Table 3. Summary of the relationship of environmental variables to CCA axes.

	Axes	
	1	2
Eigenvalues	0.051	0.032
Guild-environment correlations	0.734	0.652
Cumulative percentage variance of:		
Guild data	18.2	29.5
Guild-environment	47.3	76.8
Intra-set correlations with environmental variables[1]		
GSNU	-0.0558	-0.4862
BGII	0.2098	0.0031
LITT	-0.2275	-0.4172
SUMB	-0.4891	0.7040
FALB	-0.1281	-0.2991
SPRB	0.5272	-0.3466
UPLD	0.3583	0.0706
RNIN	-0.0055	-0.6181
LOWL	-0.3256	0.5414
1994	0.4768	0.4218
1995	-0.4768	-0.4218
ERGS	-0.5095	-0.1181
LTGS	0.5095	0.1181

[1] Underlined values are for those variables with the strongest + and -
correlations with the respective axis. Acronyms are from Table 2.

Fig. 1. Bi-plot depicting the first two axes of the canonical correspondence analysis. Continuous environmental variables are represented by vectors, categories of nominal environmental variables are represented by closed triangles, and guilds are represented by open circles. Open arrows either identify points that were too close for labeling or the approximate direction of a data point that was outside the scale of the plot. Acronyms for environmental variables are taken from Table 2.
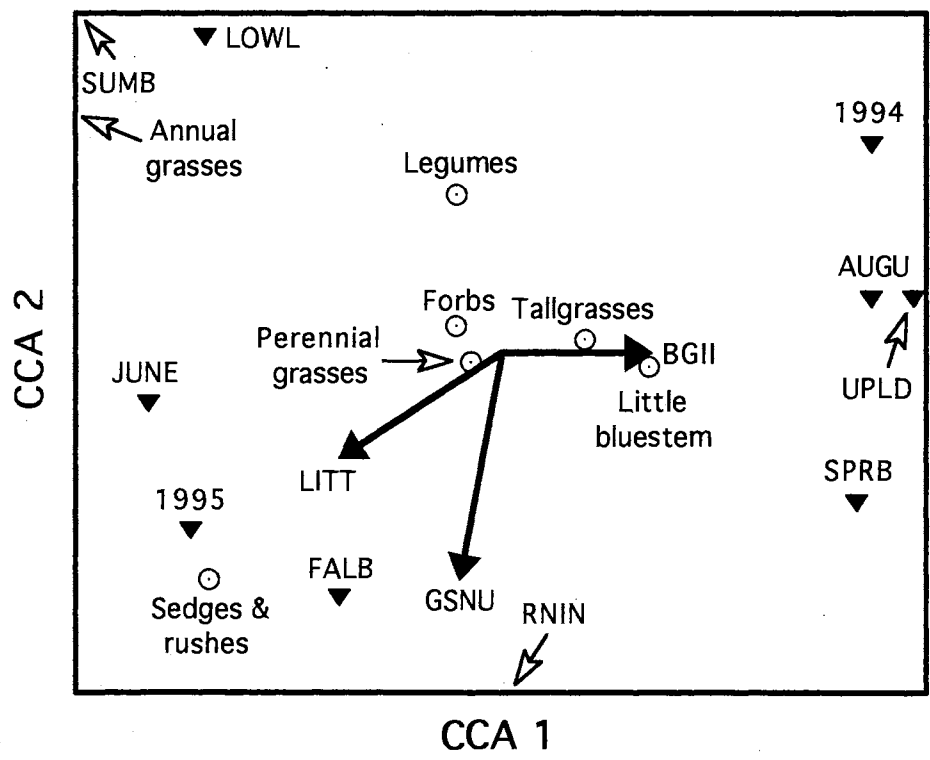
Fig. 2. Growing season precipitation by month during the study period, 1994-1995, relative to the long-term (1951-1974) average (Bourlier et al. 1979).
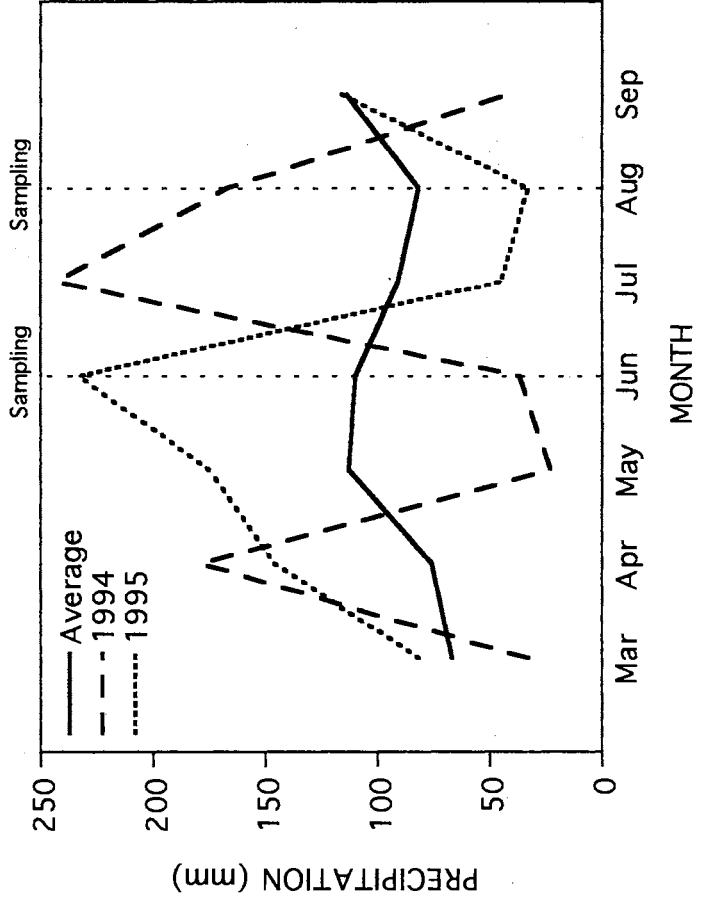
CHAPTER V

CHARACTERIZATION OF BISON WALLOWING BEHAVIOR AND WALLOW

FORMATION SITES ON TALLGRASS PRAIRIE IN OKLAHOMA

One of the most conspicuous behaviors of American bison (*Bison bison* L.) is their dust-bathing or 'wallowing' in loose soil (McHugh, 1958). Wallowing is thought to serve as both a socially aggressive behavior during the mating season (McHugh, 1958; Lott, 1974) and a grooming or comfort activity (Reinhardt, 1985). Reinhardt's (1985) quantitative study on seasonal and social patterns of wallowing behavior is the most comprehensive to date. However, that study was conducted on a small herd under confined conditions. We still do not know how larger populations of bison select wallowing sites in natural landscapes under free-ranging conditions.

Frequent wallowing by bison on the same site can form characteristic soil depressions called wallows. Wallows were once a distinctive feature of North American prairies (England and DeVos, 1969) before the near-extermination of bison (Garretson, 1938). Wallows are important components of prairie ecosystems because they provide moist microhabitats that increase plant biodiversity (Collins and Barber, 1985; Gibson, 1989; Umbanhowar, 1992).

We had the opportunity to evaluate bison wallowing behavior and wallow formation when the Nature Conservancy established the 15,342-ha Tallgrass Prairie Preserve (TPP) in Oklahoma. As part of a restoration effort, bison were reintroduced after an absence from the area of almost 140 years

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(Shaw and Lee, 1995). Our objectives were to quantify wallowing activity on a seasonal and social basis and characterize sites used by bison for wallow formation.

The TPP is located 25 km northwest of Pawhuska in northern Oklahoma (36°50'N, 96°25'W). TPP is situated in the Osage Hills, an area characterized by hilly topography and rocky soils that prevented extensive cultivation. Vegetation of the TPP is native tallgrass prairie dominated by big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schizachyrium scoparium*). Prior to its establishment in 1989, the TPP was grazed by cattle and spring-burned every 1-2 years. It was never plowed. Current management practices include burning 20% of the area annually with spring, summer, and fall prescribed burns.

Three hundred bison were reintroduced into a 1,973-ha part of the TPP in October 1993. To assess temporal and social patterns in wallowing behavior, we observed wallowing activity during daylight hours from November 1993 to October 1995. Observation periods ranged in length from 1 to 3 hours, and alternated between morning and afternoon periods. Data recorded during observations included age/sex class (bull, cow, yearling or calf) of the animal performing the behavior and any aggressive interactions with other herd members that accompanied the behavior. These interactions included bunts, lunges, and displacements (Rothstein and Griswold, 1991). By recording the total number of animals of each age/sex class during each observation period, we quantified wallowing by calculating a rate as the number of wallowing incidents observed per animal per hour. Rate data were pooled by seasonal periods, which were defined as winter (Jan.-Mar.), spring (Apr.-Jun.), summer (Jul.-Sep.), and fall (Oct.-Dec.). Ideally, we also would have quantified

wallowing by age/sex class during each season, but the scarcity of observations on some age/sex classes prevented the calculation of proper statistical tests. Therefore, social patterns of wallowing activity were analyzed by pooling all observations by age/sex class and testing against the expected distribution based on population proportions with χ^2 analysis. A concern that arose during the analysis was that smaller segments of the population might be underrepresented in observations. However, a preliminary test found no significant difference between the total number of animals of each age/sex class observed and in the population as a whole ($\chi^2 = 1.12, P > 0.25$)

To assess characteristics of sites used by bison for wallowing, the study area was surveyed prior to reintroduction in 1993 by conducting 10-m wide belt transects across the study area on foot or on all-terrain vehicle when possible. The purpose of this preliminary survey was to locate and map any existing soil anomalies that might be confused at a later date with bison wallows. The area was resurveyed in late October 1995 to locate wallows formed by bison during the study. Wallow locations were mapped on 1: 24,000 USGS topographic quadrangles with the aid of aerial photographs. To assess spatial distribution trends in wallow locations, maps were digitized into a geographic information system. Wallow locations were analyzed with respect to elevation, surface soil (A-horizon) texture groups (Bourlier et al. 1979), and burning history. Statistical analyses for this study included tests for: (1) seasonal variation in observed wallowing rates (ANOVA); (2) differences in observed and expected distribution of wallowing activity by age/sex class (χ^2 analysis); and (3) tests for differential distribution of wallows in relation to spatial variables (χ^2 analysis).

Wallowing rate did not vary significantly by season ($F_{3,39} = 1.30, P = 0.288$). This was unexpected considering that previous studies on bison

wallowing reported an increase in activity during summer, thought to be associated with insect harassment and rut (McHugh, 1958; Lott, 1974; Reinhardt, 1985). Insect harassment of bison can be severe in some locations (Melton et al., 1989), and although we did not make a formal attempt to quantify levels of insect harassment, we did not make any incidental observations of insect harassment during our observations either. Another possible factor preempting the increase in summer wallowing was the sex structure of the study population. The male: female ratio during the study was 1: 7. Thus, competition for mates might not have been as severe as in some populations, decreasing the need for aggressive wallowing displays by bulls (Lott, 1974). As compared to earlier findings (Reinhardt, 1985) where 13% of wallowing was accompanied by aggression, wallowing appears to be primarily a grooming or comfort behavior in our population. The increased aggression noted in that study was likely the result of the confined conditions of the study population (Reinhardt, 1985). In our free-ranging population, we only observed 5 cases (3% of total) where aggressive behavior accompanied wallowing. In each case, a younger, subordinate cow was displaced from a wallow by an older, higher ranking cow. We observed no aggression near wallows among bulls.

Most observations (89%) of wallowing were limited to adult animals (bulls and cows), which comprised only 58% of the population. As a result, wallowing was not distributed proportional to the age/sex class structure of the population (χ^2 = 52.9, $P < 0.001$). Bulls and cows wallowed more than expected, while yearlings and calves wallowed much less frequently. These findings support previous studies that also noted an increase in wallowing behavior with an increase in age (McHugh, 1958; Reinhardt, 1985).

The transect surveys found 43 new wallows formed by bison during the study. Wallow distribution was not random with respect to soils ($\chi^2 = 34.5$, $P < 0.001$) or elevation ($\chi^2 = 18.6$, $P < 0.001$). Wallows were formed 3 times more frequently than expected on loam soils (Table 1), and were found more frequently than expected at higher elevations (Table 1). However, it must be noted that most upland soils in the study area are loam soils (Bourlier et al., 1979), thus, it is unclear whether bison are selecting these sites for wallowing based on soil characteristics or topography. Burn history also influenced bison wallow formation and distribution ($\chi^2 = 73.1$, $P < 0.001$), as all new wallows were located on burned areas (Table 1). This is likely a simple reflection of the influence of fire on bison habitat use in tallgrass prairie. Vinton et al. (1993) found that bison graze almost exclusively on burns, while ignoring unburned areas. Thus, wallow formation was not spatially random, but influenced by both topoedaphic factors and fire.

Because abandoned wallows can retain moisture and harbor vegetative communities different from that of surrounding prairie (Polley and Collins, 1984), the trend towards upland distribution of wallows on our site has an interesting implication. Vegetation on upland sites generally becomes more stressed in drier periods than vegetation in moister lowlands (Abrams et al., 1986). Abandoned wallows may therefore alleviate moisture stress in some upland locations, providing a refugia for drought-intolerant species. Wallows are also important as disturbance sites, allowing the colonization of ruderal and ephemeral species (Collins and Uno, 1983). Their widespread distribution can also increase local habitat heterogeneity (Polley and Wallace, 1986). Thus, through some lesser known activities such as wallowing and horning (Coppedge and Shaw, *in press*), bison can influence habitat diversity on

several scales (Risser, 1990) and be a major influence on prairie vegetation structure and function.

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Table 1. Distribution of bison wallows on the Tallgrass Prairie Preserve in relation to the spatial variables of soil, elevation, and burn history.

Spatial variables	% of area occupied	observed # of wallows formed (expected)
SOILS[1]		
Loams	17	21 (7)
Silt loams	19	4 (8)
Silty clay loams	41	14 (18)
Mixed/misc.	23	4 (10)
ELEVATION		
High (above 338 m)	36	24 (15)
Moderate (337- 324 m)	32	1 (14)
Low (below 323 m)	32	18 (14)
BURN HISTORY		
Spring burns	13	17 (6)
Summer burns	12	3 (5)
Fall burns	19	23 (8)
Unburned	56	0 (24)

[1] Based on A-horizon soil textures listed by Bourlier et al. (1979).

CHAPTER VI

EFFECTS OF HORNING AND RUBBING BEHAVIOR BY
BISON (*Bison bison*) ON WOODY VEGETATION
IN A TALLGRASS PRAIRIE LANDSCAPE

Abstract. - Horning and rubbing behaviors of American bison (*Bison bison*) and effects on woody vegetation were investigated for 2 years on a herd of 300+ animals reintroduced to a 1973-ha tallgrass prairie site in Oklahoma. Horning and rubbing activity was significantly higher in summer than in other seasons. Whether this increase was associated with rut, shedding of winter pelage, insect harassment, or a combination of these factors was unclear; however, these behaviors did have measurable impacts on the woody vegetation of the area. Bison injury to trees was minimal, although one willow (*Salix nigra*) was uprooted and killed during the study, and several other trees were seriously injured. Bison horning had the most effect on saplings and shrubs, killing or severely injuring 4% of the woody plants documented within the study area and causing moderate injury to 13% and light injury to 12%. Bison showed a strong preference for small willows, killing or severely injuring 17% of the saplings and shrubs of this species during the study. Bison also used artificial, man-made objects present on the landscape such as utility poles and fenceposts. Results suggest that horning and rubbing by bison, along with fire and drought, may have influenced the historical distribution of woody vegetation in prairie environments.

Introduction

Bison (*Bison bison* L.), like many large mammals (Snyder and Janke, 1976; Inouye *et al.*, 1994), are capable of severely impacting woody vegetation. England and DeVos (1969) suggested that herds of bison in North American prairies once influenced the distribution of woody vegetation by horning, rubbing, grazing, and trampling. Soper (1941) noted that wood bison (*B. b. athabascae*) destroyed trees by horning and rubbing against them to reduce insect irritation. Similar behavior has been observed in populations of plains (*B. b. bison*) bison (McHugh, 1958; Meagher, 1973). Moss (1932) and Campbell *et al.* (1994) concluded that the near extinction of bison from overhunting in the northern plains contributed to the expansion of aspen (*Populus tremuloides*) woodland into prairies during the late 1800's.

Few studies have documented quantitatively the effects of bison on woody vegetation. Edwards (1978) found that bison in private midwestern herds destroyed woody plants by horning, rubbing, and feeding on bark. In one case, 15 bison in a 36-ha enclosure had debarked 80% of the 600 trees in a 1-ha grove in one year, killing most by the following year. He noted that bison exhibited species preferences in their horning, rubbing, and feeding activities. McHugh (1958) found that 14% of a small sample of lodgepole pines (*Pinus contorta*) horned by bison in Yellowstone National Park (YNP) were girdled and killed. Horning and rubbing of lodgepole pine by an estimated 2500 bison spending the summer of 1992 in the Hayden Valley of YNP resulted in extensive tree mortality (M. Meagher, personal communication).

We conducted a study of the effects of bison on woody vegetation in the Nature Conservancy's 15,342-ha Tallgrass Prairie Preserve (TPP) in Oklahoma. Bison were reintroduced to the preserve after an absence from the area of almost 140 years (Shaw and Lee, 1995). The objectives of our research were to:

(1) quantify horning and rubbing activity of bison; (2) characterize objects selected for use by bison during these behaviors; and (3) examine effects of bison horning and rubbing on woody vegetation.

Materials and Methods

The TPP is located *ca.* 25 km northwest of Pawhuska in northern Oklahoma (36°50'N, 96°25'W) in the Osage Hills, an extension of the Flint Hills that lie primarily in Kansas. The Flint Hills have hilly topography and generally rocky soils that historically prevented extensive cultivation. Vegetation of the area is native grassland dominated by big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schizachyrium scoparium*). Woody vegetation is limited to steep rocky slopes, some uplands, and larger drainages. The principal species are post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), green ash (*Fraxinus pennsylvanica*), American elm (*Ulmus americana*), black walnut (*Juglans nigra*) and Kentucky coffeetree (*Gymnocladus dioca*). Black willow (*Salix nigra*), sycamore (*Platanus occidentalis*) and hackberry (*Celtis occidentalis*) are common along drainages.

Prior to its establishment in 1989, TPP was grazed by cattle and burned every 1-2 years during spring. It was never plowed. A management plan was initiated in 1993 which included prescribed burning in summer, fall, and spring. About 20% of the preserve is burned annually. Three hundred bison were reintroduced into the study area, a 1973-ha part of the TPP, in October 1993. We counted and measured woody plants and other vertical objects in parallel, 10-m wide belt transects across the study area from June to October 1993, before bison release. Surveys were conducted on foot or on all-terrain vehicle when possible. Objects encountered during the surveys were recorded

and mapped on 1:24,000 USGS topographic quadrangles with the aid of black-and-white aerial photographs taken in 1991. Existing damage to objects such as broken limbs and damage from insects, deer (*Odocoileus virginianus*) and fire were noted.

Objects were categorized as trees, small woody species, or miscellaneous objects. Trees were live woody plants ≥ 5 cm in diameter at 1.4 m height and $\geq$ 1.8 m tall; data collected on trees included species, diameter, height to first limb, distance to the nearest tree (a measure of spatial isolation), bark texture (rough or smooth), and the presence of aromatic substances detectable by us. Small woody species were live saplings or shrubs < 5 cm diameter at 1.4 m height and ≥ 1.8 m tall; saplings were single-stemmed and shrubs were multi-stemmed. Data recorded for saplings and shrubs included species, bark texture, and presence of aromatics. Miscellaneous objects were non-living structures ≥ 0.5 m tall. Naturally-occurring objects were rock outcrops, stumps, and logs; artificial structures included wooden and metal poles (≥ 2 m tall), posts (< 2 m) such as fenceposts and signposts, and other items such as oil field equipment and cement bridge abutments. Data recorded for miscellaneous objects included physical descriptions and the presence or absence of detectable aromatics.

The study area was resurveyed in September and October 1995 and all objects checked for evidence of bison use. Criteria indicating bison use included the presence of shed hair; hoofprints around the base of the object; horn scratches; and broken limbs, stems, or damaged bark not attributable to other causes. Bison damage to live vegetation was quantified by the area of stem girdled on trees and saplings and the percentage of shrub stems broken (light damage = 0-33%, moderate damage = 34-66%, severe damage = 67-100%).

Plants killed by bison were noted. As damage to non-living objects could not be quantified, bison use of these objects was recorded as positive or negative.

We gathered data on horning and rubbing activity by observing animals under natural conditions during daylight hours from November 1993 to October 1995. Bison were observed during 194 periods totaling 331 hours. Because we could not always distinguish between horning and rubbing, we grouped horning and rubbing as a single behavior (referred to as horning) in which animals made contact with an object with parts of their head and/or neck and shoulders. Data recorded during observations included the age/sex class (bull, cow, yearling or calf) of the animal and the identity of the object horned. Data were analyzed for: (1) seasonal variation in observed horning activity (ANOVA); (2) expected distribution of horning activity by age/sex class (χ^2 goodness-of-fit test); and (3) differences in characteristics between objects used for horning and those that were not [Student's t-test and the two sample Z test for proportions (Zar, 1984)].

Results

Horning activity varied significantly by season ($F = 5.93$; $P < 0.002$). The mean ($\pm$ 1 SE) number of horning incidents observed per animal per hour was highest in summer (July-September; $\bar{x} = 0.35 \pm 0.10$), intermediate in spring (April-June; $\bar{x} = 0.13 \pm 0.10$) and fall (October-December; $\bar{x} = 0.10 \pm 0.14$) and lowest in winter (January-March; $\bar{x} = 0.04 \pm 0.15$). Observations of horning behavior were not distributed as expected across age/sex classes based on the proportion of each class in the total population ($\chi^2 = 13.5$; $P < 0.005$). Bulls, cows and yearlings performed horning behavior more than expected, while calves did so less than expected.

Bison exhibited preferences for certain objects during horning behavior. Based on the ground survey, bison preferred to use miscellaneous objects and small woody vegetation for this behavior but selected against trees (Table 1). Based on our observations of behavior, bison preferred objects in the miscellaneous category but selected against use of trees and small woody vegetation (Table 1). These conflicting results concerning small woody vegetation may have been a result of the distribution of objects on the landscape. Most woody vegetation was limited to certain topographic features such as draws, drainages, and ponds, whereas miscellaneous objects were distributed at all locations within the study area. Thus, because locations for behavioral observations were made at random whenever bison were encountered, our observations may have inadvertently overrepresented bison use of miscellaneous objects but underestimated bison use of woody plants. Nevertheless, two trends in horning behavior were still apparent; bison preferred the widely available miscellaneous objects and selected against the use of trees (Table 1).

Although trees were not used in proportion to their availability among object types, bison did prefer to horn certain species. Green ash, sycamore, and black willow were used significantly more than expected based on their availability on the landscape; post oak and blackjack oak were used significantly less than expected (Table 2). Bison also selected for some tree characteristics. The average ($\pm$ 1 SE) diameter for trees horned by bison was 25 $\pm$ 1 cm, which was significantly (t = 2.85; P < 0.005) less than the average diameter for all trees (29 $\pm$ 1 cm). Bison also selected trees with smooth bark, using them in a higher proportion than they were generally available (Z = 3.13; P < 0.001). There was no difference between trees used for horning and those generally available in either height to first limb (P > 0.3) or distance to

the nearest tree ($P > 0.7$). The presence of odors also did not appear to influence bison choice, since trees with aromatics were not used out of proportion to their availability ($P > 0.1$).

Several trees were severely injured by bison. A moderate-sized (25-cm dbh) eastern redcedar (*Juniperus virginiana*) appeared girdled but remained alive, while a small (9 cm dbh) willow was uprooted and killed. A large, low-hanging limb on a large (41 cm dbh) blackjack oak was pushed against so hard that it broke, causing severe damage to the trunk. Several green ash trees received moderate damage to the bark. However, most trees used by bison had only light damage.

Bison horning had the most impact on small woody vegetation. Of all saplings and shrubs surveyed for this study, 4% were severely injured, 13% had moderate injury, and 12% had light injury. Bison showed a strong preference for black willow (Table 3). Bison use of small willows was so severe that 17% of the saplings and shrubs of this species were top-killed (resulting in root-sprouting) or killed outright. Plants of sycamore, false indigo (*Amorpha fruticosa*), and persimmon (*Diospyros virginiana*) were used less than expected. There was no disproportional use of small woody vegetation based on bark texture ($P > 0.2$) or presence of aromatics ($P > 0.2$).

Bison use of items in the miscellaneous category for horning was higher than expected. Most of this use was focused on metal and wooden poles and posts (Table 4). Bison use of other miscellaneous objects, both natural and artificial, was not disproportional to their availabilities, except for oil well rigs, which were avoided. Only wooden utility poles exhibited any detectable odors, and these were heavily used by bison ($Z = 2.95$; $P < 0.002$). In fact, horning use of a few (~5) of these poles was so severe that they were loosened

from the ground and leaning, forcing local utility companies to install additional support and apply metal wire deterrents to discourage bison use.

Discussion

Bison at the TPP had measurable effects on only a few trees, but significantly affected shrubs and saplings (especially willows). Willows (*Salix*) are a major diet component for some populations of bison (Waggoner and Hinkes, 1986); however, our preliminary studies of diets show that willows are not a major food component for this population. Because willows and most of the woody vegetation in the study area was adjacent to water, we did not attempt to access the importance of distance to water as a factor in bison use of an object. However, woody vegetation near water bodies were most affected by bison in other studies (McHugh, 1958, England and DeVos, 1969). Unfortunately, our study area also contained numerous man-made objects that were readily used for horning, especially utility poles. This preference is consistent with historical accounts that mention bison rubbing and toppling of telegraph poles (McHugh, 1972). The presence of these objects undoubtedly affected the level of use and overall impact bison had on the naturally occurring woody vegetation in our study area. Removal of these artificial objects might substantially increase bison use of woody vegetation and thereby more closely restore presettlement conditions and associated biotic interactions.

Results from previous studies (McHugh, 1958; Meagher, 1973; Edwards, 1978) indicate that bison prefer to horn aromatic species such as cedars and pines. Although we found no bison selection for trees that we detected as aromatic, bison in our study horned (and nearly killed) a single large eastern redcedar tree and horned treated utility poles that were aromatic. Thus, bison

appear to prefer aromatic objects as horning stations. Presumably these aromatic substances have insecticidal or repellent properties desired by the animals to provide relief from insect harassment. The increased rate of horning in summer when insects are most prevalent lends support to this idea, as do Soper's (1941) observations that insect harassment of bison was often followed by horning and rubbing behaviors. Many woody species that have invaded prairie sites such as pines (Steinauer and Bragg, 1987) and eastern redcedar (Blewett, 1986) have aromatics. Although the invasion of these species is attributed to fire suppression (Arend, 1950), they also may have been used by bison as horning and rubbing stations.

McHugh (1958) postulated that horning was a socially-motivated aggressive behavior similar to wallowing during the rut. Reinhardt (1985) reported that wallowing was associated only with shedding and not with insect harassment or rutting behavior. Shedding, rut and insect harassment all occur simultaneously in summer, therefore, it may be a combination of these factors that result in horning and wallowing behaviors. Carefully designed studies would be needed to distinguish between these possible causes.

High moisture requirements (Abrams, 1986; Steinauer and Bragg, 1987; Knight et al., 1994), droughts (Albertson and Weaver, 1945) and fire (Briggs and Gibson, 1992; Grimm, 1984) are all known to affect tree distribution in prairies. The lack of fire allows woody plant invasion of prairie sites (Bragg and Hulbert, 1976; Anderson and Schwegman, 1991), and most studies attribute the cause of invasion only to fire suppression (Abrams, 1986; Steinauer and Bragg, 1987; Briggs and Gibson, 1992). As burning has been a part of the management practices of our study site during most of this century, bison effects on woody vegetation appear to complement those of fire. With estimates of historic populations ranging in the tens of millions (Shaw, 1995),

roaming herds of bison could have caused extensive damage and mortality to woody vegetation. We concur with earlier studies (Edwards, 1978; Campbell *et al.*, 1994) that suggest that bison, in conjunction with other factors such as fire and drought, may have significantly limited the historic distribution of woody vegetation in the Great Plains.

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Table 1. Use of objects for horning and rubbing by bison as determined by 1) ground survey and 2) behavioral observations. Positive Z values indicate selection, whereas negative Z values indicate avoidance. All Z values were significant at $P <$ 0.001 unless otherwise noted.

Object category	% of total available objects ($n = 1692$)	Ground Survey		Behavioral Observations	
		% used by bison ($n = 466$)	Z value	% used by bison ($n = 69$)	Z value
Trees	62	37	- 9.7	12	-8.3
Small woody species	24	34	4.4	12	-2.3*
Miscellaneous	14	29	7.8	76	13.8

*$P < 0.02$

Table 2. Tree species used by bison for horning and rubbing. A significant positive Z value indicates selection, whereas a significant negative value indicates avoidance.

Tree Species	% of used trees ($n = 172$)	% of available trees ($n = 1043$)	Z value
Green ash (*Fraxinus pennsylvanica*)	36.0	21.1	4.29**
Sycamore (*Platanus occidentalis*)	20.3	10.3	3.78**
Black willow (*Salix nigra*)	19.7	9.7	3.88**
Black walnut (*Juglans nigra*)	5.8	5.8	0
American elm (*Ulmus americana*)	4.1	3.1	0.69
Post oak (*Quercus stellata*)	3.5	11.4	- 3.15**
Hackberry (*Celtis occidentalis*)	2.9	5.4	- 1.38
Blackjack oak (*Quercus marilandica*)	1.7	21.4	- 6.15**
Eastern cottonwood (*Populus deltoides*)	1.2	1.8	- 0.56
Chittamwood (*Bumelia lanuginosa*)	1.2	0.5	1.10
Poplar (*Populus nigra*)	1.2	0.3	1.67*
Plum (*Prunus* sp.)	0.6	0.5	0.17
Eastern redcedar (*Juniperus virginiana*)	0.6	0.2	0.96
Bitternut hickory (*Carya cordiformis*)	0.6	0.1	1.47
Catalpa (*Catalpa bignonioides*)	0.6	0.1	1.47
Kentucky coffeetree (*Gymnocladus dioca*)	0	4.0	- 2.69*
Redbud (*Cercis canadensis*)	0	1.3	- 1.52
Chinkapin oak (*Quercus muehlenbergii*)	0	1.2	- 1.46
Persimmon (*Diospyros virginiana*)	0	0.8	- 1.17
Red mulberry (*Morus rubra*)	0	0.4	- 0.83
Osage orange (*Maclura pomifera*)	0	0.2	- 0.54
Honeylocust (*Gleditsia triacanthos*)	0	0.2	- 0.54
Dogwood (*Cornus drummondii*)	0	0.1	- 0.41
Black oak (*Quercus velutina*)	0	0.1	- 0.41

*$P < 0.05$
**$P < 0.001$

Table 3. Small woody species used for horning and rubbing by bison. A significant
positive Z value indicates selection, whereas significant negative values indicate
avoidance.

Woody Species	% of used plants ($n = 158$)	% of available plants ($n = 407$)	Z value
Black willow (*Salix nigra*)	60.8	28.2	7.20***
Green ash (*Fraxinus pennsylvanica*)	13.3	11.3	0.66
Sycamore (*Platanus occidentalis*)	11.4	23.0	-3.11***
Buttonbush (*Cephalanthus occidentalis*)	11.4	14.4	-0.92
Plum (*Prunus* sp.)	2.5	4.2	-0.95
False indigo (*Amorpha fruticosa*)	0.6	5.4	-2.61**
Persimmon (*Diospyros virginiana*)	0	7.6	-3.55***
Smooth sumac (*Rhus glabra*)	0	2.5	-2.09*
Osage orange (*Maclura pomifera*)	0	1.0	-0.90
American elm (*Ulmus americana*)	0	0.5	-0.79
Honeylocust (*Gleditsia triacanthos*)	0	0.5	-0.79
Post oak (*Quercus stellata*)	0	0.5	-0.79
Black walnut (*Juglans nigra*)	0	0.3	-0.71
Eastern cottonwood (*Populus deltoides*)	0	0.3	-0.71
Chittamwood (*Bumelia lanuginosa*)	0	0.3	-0.71

*$P < 0.05$
**$P < 0.01$
***$P < 0.001$

Table 4. Use of miscellaneous objects for horning and rubbing by bison. Significant positive Z values indicate selection, whereas significant negative Z values indicate avoidance.

Category & description	% of used objects ($n = 136$)	% of available objects ($n = 242$)	Z value
Natural			
Rock outcrops	10.3	9.5	0.25
Stumps & logs	3.7	3.7	0
Artificial			
Wooden poles & posts	29.4	19.0	2.31*
Metal poles & posts	41.9	30.6	2.21*
Oil well rigs	0	19.8	-5.54**
Other	14.7	17.4	-0.68

*$P < 0.02$
**$P < 0.001$

CHAPTER VII

SUMMARY

Significant findings

Bison diets on tallgrass prairie appear to be composed almost exclusively of graminoids. Some of the grasses that dominate the study area, namely big and little bluestem and indiangrass, were not distinguishable from each other with the microscopic technique used for plant fragment identification. Nonetheless, this 'bluestem complex' was consistently the single largest diet item. Sedges were another common diet item, which was surprising because bison in mixed-grass prairie selectively avoid foraging on this type of cool-season graminoid. Bison showed strong feeding selectivity; grasses and sedges formed a significantly higher proportion of diets than was generally available. Bison avoided feeding on forbs, which were ≤ 1% of the diet. Diets also varied by season. Sedges were a large diet component in winter and spring but decreased substantially during summer and fall. These changes in sedge use corresponded to seasonal variation in sedge availability.

Mixed groups of bison showed grazing selectivity by using burned areas significantly more than expected while generally avoiding unburned areas. In contrast, bull groups often selected unburned areas for grazing while rarely selectively grazing burned areas. Spatial and temporal patterns in bison grazing were evident. Bison used larger burns more, and overall use of

burns persisted for only a short time, after which bison generally shifted grazing efforts to newer burns. Although burn types varied significantly in vegetative parameters, bison exhibited only limited preference for any burn type. Bison apparently select areas with low graminoid biomass because of forage quality.

Canonical Correspondence Analysis (CCA) was used to relate variation in abundance of tallgrass prairie vegetation guilds to environmental variables such as seasonal fire, grazing, and topoedaphic variation. Annual grasses were most closely associated with summer fires, while sedges were most closely associated with fall fires. Legumes were most associated with the length of time since fire, while tallgrasses and little bluestem were associated with grazing. Forb and perennial grass guilds were not associated with any measured environmental gradients, indicating they were either equally affected by measured parameters or that important environmental variables were not measured. Sedges and tallgrasses appeared to be affected by climatic variation.

Bison exhibited wallowing behavior consistently throughout the year, which contradicted presumed patterns and those found by an earlier study. The majority of wallowing was done by adult animals (cows and bulls). There was little aggression observed in association with the behavior, which again contradicted the findings of earlier studies. Instead, wallowing appeared to be primarily a comfort or grooming behavior. Bison did form new wallows on higher elevation sites, which were characterized by loamy soils.

Horning and rubbing activity was observed more in summer than in other seasons. These behaviors had measurable impacts on woody vegetation. Although bison injury to trees was minimal, horning had a significant effect on saplings and shrubs. Bison showed a strong preference for willows, and

also used artificial, man-made objects present on the landscape for horning and rubbing.

Conclusions

Fire was an important driving force in the range ecology of bison on tallgrass prairie. Fires influenced bison grazing patterns, which in turn acted in concert with the original seasonality of the fire, topography, and climate to affect the abundance of specific components of the vegetation. This modified vegetative community in turn affected bison grazing preferences, which shifted to newer burns. This will, in time, affect the likelihood of fire returning to these sites because of litter buildup. Because fire patterns on the landscape affected the distribution of bison, it also indirectly affected the distribution of their physical effects such as horning and wallowing. These bison behaviors in turn foster vegetational diversity by either selective removal of preferred forages, damage or death to horned and trampled woody vegetation, and creation of moist microhabitats that harbor less common species. Thus, the constant, cyclic series of interactions between bison and fire help determine the natural structure and functioning of tallgrass prairie.

Management recommendations

Mature bulls only comprised about 10% of the study herd at the Tallgrass Prairie Preserve. This study has shown that these bulls, as groups, use burn patches present on the landscape in a significantly different manner than the majority of the herd. Assuming that historic bison populations were balanced with a 1:1 sex ratio, the alteration of herd structure to one favoring females (7:1) such as the study herd could have several important ecological implications. No consistent nor noteworthy aggressive activity was observed

to accompany wallowing and horning behaviors. Because previous studies have reported that these behaviors are often exhibited in antagonistic encounters among bulls, the lack of aggressive behavioral displays may be the result of an altered sex structure. There are enough cows in the population so that there is no need for aggressive competition among bulls. This in turn could affect the attempts of restoration of this site to one mimicking pre-settlement conditions if, for example, trees are not damaged and wallows not formed at rates that would have been present historically. With different grazing patterns than mixed groups, the spatial distribution of the physical effects of these bulls and the indirect effects of grazing by the larger sex are not achieved. To assure the closest approximation to pre-settlement conditions, the sex structure of the population should remain as close as possible to 1:1.

Follow-up studies to this one on the Tallgrass Prairie Preserve will need to address issues of scale effects as the area allocated to the growing bison herd expands. To adequately assess spatial components of the landscape, some alteration of the prescribed burning regime is recommended. As the burning regime is structured now, spring and fall burns are consistently large patches, being on average four to five times as large as summer burns. With this design, effects of scale cannot be separated from those of season, because small burns are only conducted during summer, and large burns only during dormant spring and fall periods. Because a set amount of the preserve is burned each year, future burning patterns should attempt to vary scale equally across all seasonal burns. For example, all burns in one year should be of about equal size, but in several separate, smaller patches. During the next year, the same amount of total area could be burned during each season, but this time each seasonal burn could be conducted on a single large patch. Although the historical effects of scale will probably never be fully

understood and those scales will likely never be achieved, adding this variation to the burning regime will take full advantage of the size, ecological setting and scientific opportunities of the preserve.

Finally, the affinity of bison for horning and rubbing on artificial objects was surprising. This certainly suggests that removal of as many artificial vertical objects as is practically possible is warranted if the full suite of natural conditions and behaviors are to be achieved. Obviously, not every object can be removed; fences and posts, utility poles, and traffic signs are an inherent part of the society in which we live and a necessary part of the preserve landscape. However, it is recommended that these objects be kept to an absolute minimum so that the natural objects that would have been used by bison historically for these behaviors, trees and shrubs, will again be subjected to the full set of natural forces that shaped tallgrass prairie.

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