FIRE IN THE NEBRASKA SANDHILLS PRAIRIE

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ABSTRACT

The effect of a single fire on Nebraska Sandhills Prairie vegetation was evaluated in an ungrazed area using spring, summer, and fall burns on hilltops and on north-facing and south-facing slopes. Data from permanent plots collected before burning, and for each of 4 years following burning, indicated that the effect of fire was most pronounced within a year of burning. The longer-term response (i.e., 4 years postburn) generally did not differ significantly from observations in areas with no record of burning. For species where differences in number were substantial, they were greatest on summer-burned, north-facing slopes. Burned areas had two-six fewer species than unburned areas. Forb cover, in particular, decreased with summer burns (−25%) and remained significantly lower than other treatments throughout the study. Woody plant cover also declined dramatically (−25%) the year following summer burning but returned to preburn levels by the second year after burning. Species that were generally unresponsive to burning included umbrella sedge (*Cyperus schweinitzii*) and prairie goldenrod (*Solidago missouriensis*). Sand dropseed (*Sporobolus cryptandrus*), sedges (*Carex* spp.), prairie sandreed (*Calamovilfa longifolia*), stiff sunflower (*Helianthus rigidus*), western fleabane (*Erigeron bellidiastrum*), Missouri spurge (*Euphorbia missurica*), and hairy grama (*Bouteloua hirsuta*) are among those that tended to increase with burning although initial responses varied. Junegrass (*Koeleria pyramidata*), sand muhly (*Muhlenbergia pungens*), western ragweed (*Ambrosia psilostachya*), and narrow-leaved puccoon (*Lithospermum incisum*) tended to decrease. The high proportion of species responding favorably to burning is consistent with the concept that fire was a component of the historic grasslands of the region. Despite significant changes in several individual species, a subjective assessment of the results of Principal Components Analysis of 1984–1996 data did not suggest any substantive changes in community diversity although fall-burned plots seem to be most affected for the longest period of time. While the results of this study on a single fire event may differ from those with repeated burns, they provide an initial insight into the historic role of fire in the Nebraska Sandhills Prairie. In particular, the short-term response of many species to burning suggests that more frequent fires would have the potential to substantially affect species composition of this ecosystem.

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INTRODUCTION

The Nebraska Sandhills Prairie (*Andropogon-Calamovilfa*) (Küchler 1964) is the largest continuous sand prairie in North America. It covers approximately 5 million hectares in central and western Nebraska (Bleed and Flowerday 1990). Dominant vegetation of this region has been variously described as prairie sandreed (*Calamovilfa longifolia*), sand bluestem (*Andropogon hallii*), little bluestem (*Andropogon scoparius*), blue grama (*Bouteloua gracilis*), hairy grama (*Bouteloua hirsuta*), needle-and-thread (*Stipa comata*), and sand dropseed (*Sporobolus cryptandrus*) (Pound and Clements 1900, Pool 1914, Ramaley 1939, Frolik and Sheperd 1940, Brinegar and Keim 1942, Burzlaff 1962, Weaver 1965, Whitcomb 1989). In addition to regional variations in dominant species, substantial differences in overall species composition have been recorded between uplands, slopes, and lowlands (Wolfe 1973, Bragg 1978, Barnes et al. 1984) and between various stages of vegetation succession (Tolstead 1942). Extensive cattle grazing, which began in the early 1900's, may account for some of the variations noted between early and more recent observations, such as the decline of little bluestem and the increase of prairie sandreed (e.g., Brinegar and Keim 1942). Fire suppression, however, is just as likely to have had some impact on the herbaceous component of sandhills vegetation. Lack of fire has been reported to account for woody plant invasion, particularly along the margins of the region (Steinauer and Bragg 1987).

In the Nebraska Sandhills, lightning-caused fires have been reported since the early 1900's (Pool 1914, Ramaley 1939, Westover 1986) and were common in presettlement times as well (Bragg 1995); occurring, on average, every 4–5 years (Bragg 1985). Evaluations of fire effects in the sandhills, however, have been few. A May, lightning-caused fire in an ungrazed area resulted in a 26% reduction in end-of-year standing crop, although this reduction averaged only 8% after two growing seasons (Bragg 1978). A net decline (−23%) also was reported by Morrison et al. (1986) in response to a fall, lightning-caused fire. In addition to reduced standing crop, spring and summer fires were reported to remove the protective vegetation cover (Frolik and Sheperd 1940, Burzlaff 1962) and thus increase the frequency of blowout formation (Pool 1914). Postfire effects of wind erosion also generate concerns about fire application in the sandhills (Burzlaff 1962, Whitcomb 1989, Bragg and Steuter 1996).

Cosby (1971) and Wolfe (1973) considered the effects of fire on different plant groups and noted a decline in total plant cover with May burning, largely a reflection of the substantial decline in forb cover. Grass cover, however, was not substantially altered by fire. Pfeiffer and Steuter (1994) also reported no end-of-year reduction in standing crop of grasses. They observed that both bunchgrasses (e.g., needle-and-thread) and rhizomatous grasses (e.g., prairie sandreed and sand bluestem) increased with spring burns, although summer burns dramatically reduced bunchgrasses.

Effects of fire on individual plant species have also been reported. Cosby (1971) and Wolfe (1973), for example, reported reductions in the amount of sand bluestem and sand dropseed and an increase in prairie sandreed and needle-and-thread following a May, lightning-caused fire. Bragg (1978), however, indicated that prairie sandreed and needle-and-thread declined with burning at this time of the year, as did sand muhly (*Muhlenbergia pungens*) and yucca (*Yucca glauca*). Masters et al. (1988) also reported a decline in yucca following burning in sandy soils in Texas. Inconsistent results from different studies were expected, given the spatial variability of fire conditions and fire behavior. Furthermore, most of these studies were based on lightning-caused fires in which variables, such as the precise seasonal timing of the burn, could not be controlled.

There are few controlled, experimental efforts to evaluate the effect of fire on sandhills vegetation. For other grasslands, however, fire has been shown to affect a wide array of vegetation characteristics including productivity, species composition, density, phenology, plant size, root development, flowering activity, growth form, seed survival, seed germination, and nutrient content. In addition, physical effects of fire on grassland soil include higher soil temperatures and variations in soil moisture, pH, and nutrients. A comprehensive survey of these and other effects of fire in grasslands is provided by Daubenmire (1968), Vogl (1974), Wright and Bailey (1982), Collins and Wallace (1990), and Bragg (1995). In addition, Howe (1994, 1995) recently reported significant effects of fire season on prairie species, although not for those occurring in the sandhills region. The paucity of experimental fire studies in the sandhills prairie ecosystem and the need to understand fire effects, for both ecological and practical application, were the bases for the initiation of this study. Therefore, the objective of this study was to assess the effect of season-of-fire on individual plant species and plant community composition in a Nebraska Sandhills prairie.

METHODS

Study Site

The study was conducted at the Niobrara Valley Preserve, a 22,660 hectare site owned and managed by The Nature Conservancy. The preserve is located approximately 23 kilometers east of Valentine in north-central Nebraska (43°N × 100°W). Average monthly temperatures for the region range from −5 C in January to 24 C in July (National Oceanic and Atmospheric Administration 1984). Annual precipitation averages 5600 millimeters, most of which occurs in the summer months (Voightlander et al. 1992). For the years of the study (1984–1988), records maintained at the preserve indicated that precipitation varied considerably: 4610 millimeters in 1984, 5540 millimeters in 1985, 5670 millimeters in 1986, 6790 millimeters in 1987, and 6470 millimeters in 1988 (data provided by The Nature Conservancy, Niobrara Valley Preserve).

The study site was situated within a 295 hectare, fenced, research exclosure from which large grazers (e.g., cattle and bison) had been excluded since at least 1976, 7 years prior to the initiation of the study. Fires had not occurred in the study site for at least 20 years, and probably much longer. The exclosure was located within the Valentine Rolling Sands Range site that typifies an extensive soil-vegetation association of the Nebraska Sandhills Prairie. Soils of this range site are classified as mixed, mesic Typic Ustipsamments (Voightlander et al. 1992).

Field Methods

In 1984, twelve treatment areas were established within the research exclosure to provide three replicates of each of four treatments; spring-burned, summer-burned, fall-burned, and unburned. Treatment areas varied in size from 2–3 hectares in order to ensure that each incorporated three, suitable topographic locations: hilltop, north-facing slope, and south-facing slope. These three topographic locations were separately evaluated because of reported differences in species composition and biomass (Bragg 1978, Barnes et al. 1984), and hence the likelihood of differences in fire effects. For clarity, each treatment area is referred to as a "treatment-topographic area."

Burn treatment dates were selected to coincide with critical times of the growing season. Spring (May) burns were expected to have a greater impact on C_3 (cool-season) plants, which will have initiated growth by that time, than on C_4 (warm-season) plants, which will still be dormant. Summer (July) burns were expected to have the greatest impact on the dominant, warm-season plants which will have been actively growing for some time by then. July also is the month during which lightning-caused fires in the sandhills were most frequent (Westover 1986). Finally, fall (October) burns occur after most vegetative growth has ended for the year thus leaving the soil most exposed, for example to wind erosion, for the longest period of time.

A preburn evaluation of vegetation was conducted in all treatment-topographic areas in 1984. In 1985, headfire burns were conducted 1–2 May, 19 July, and 1 October. Several years of litter accumulation helped facilitate burning.

From the fall of 1985 through 1988, all treatments were evaluated annually except for 1985 when fall-burned treatment-topographic areas were not evaluated since they had not yet been burned. Evaluations were conducted in spring (approximately 1 June) and late summer (approximately 20 August). Spring evaluations included only selected species that, through experience, were known either to be dormant in the fall and without above-ground cover (e.g., spiderwort (*Tradescantia occidentalis*) and palm-leaved scurf-pea (*Psoralea digitata*)) or on which herbivory substantially reduces cover by fall (e.g., prairie dogbane (*Apo-*

Table 1. Pre-burn (1984) canopy cover of dominant species by topographic location.

Species	Canopy Cover (%) by topographic location		
	South-Facing Slope	Hilltop	North-Facing Slope
Carex spp.	41 ± 2.1	29 ± 1.6	26 ± 1.4
Woody Species	21 ± 2.3	9 ± 1.4	16 ± 1.6
Andropogon hallii	48 ± 2.0	36 ± 1.7	18 ± 1.6
Calamovilfa longifolia	20 ± 1.6	30 ± 2.0	8 ± 1.1
Ambrosia psilostachya	23 ± 1.4	24 ± 1.2	23 ± 1.2
Muhlenbergia pungens	5 ± 1.2	14 ± 1.6	tr.
Andropogon scoparius	21 ± 2.0	21 ± 2.3	52 ± 2.0
Eragrostis trichodes	7 ± 1.4	4 ± 1.2	22 ± 1.8
Average Number of Species per plot	25	25	26

cynum cannabinum) or skeletonweed (*Lygodesmia juncea*)). Since spring evaluations were not conducted in all years, only data from fall evaluations are included in this paper. Due to identification difficulties in the field, all sedges were grouped together for canopy cover assessment. Species nomenclature follows the Great Plains Flora Association (1986).

From 1989–1996, annual evaluations were reduced to one replicate of each treatment area. This provided continuous data during the study period for each of four treatment areas. These annual evaluations are planned to be continued indefinitely. Data for 1984–1996 were only evaluated in this study using Principal Components Analysis. Unless otherwise specified, all analyses refer to the replicated treatment data collected from 1984–1988.

Vegetation evaluations were conducted in ten, 1.0 by 0.5 meter plots equally spaced on alternate sides of a 21-meter long transect. The transect was centrally situated within each treatment-topographic area. Ten such plots have been found to be adequate for measuring dominant species in the Nebraska Sandhills (Bragg 1978). The 21-meter transect was marked with permanently emplaced metal stakes at each end. During annual evaluations, a meter tape was stretched between the stakes and the same point evaluated during each subsequent evaluation. Plant composition within each plot was evaluated by estimating canopy cover both by species and by general characteristics (i.e., total cover, litter, bare soil, graminoid, forbs, woody plants, and cacti). Coverage categories, modified from those of Daubenmire (1959), were 0%, <1%, 2–5%, 6–25%, 26–50%, 51–75%, 76–95%, 96–99%, and >99%.

In 1995, standing crop was measured by clipping all plant matter from within twelve, 30 by 50 centimeter plots. Plots were located in the vicinity of each of the twelve treatment-topographic transects being used for continuous data collection. This provided four samples of standing crop for each topographic location. Plant matter was separated into one of five categories (graminoid, forbs, woody plants, cacti, and litter), oven-dried, and weighed. These data were not intended to provide statistically comparable information but rather to generally characterize differences in end-

Table 2. End-of-season standing crop by topographic location for 1995. Data from one, 0.15 m^2 plot per treatment-topographic area (n = 4).

Topographic Location	Average Vegetation Height (cm)	Weight (g/m^2) by Vegetation Category				
		Grass	Forb	Woody Plant	Cacti	Litter
North	20	72.5	10.6	6.8	0.0	178.7
South	20	79.3	11.6	27.0	1.7	85.2
Hilltop	13	51.2	42.4	0.0	0.0	55.2
Depression	20	92.5	27.6	3.9	<0.5	110.2

of-year standing crop by topographic location from which to infer differences in fuel load.

Statistical Analysis and Ordination

Data were analyzed by year and by species. Only those species present in at least two of three replicates in at least three of four treatment-topographic areas were analyzed in order to ensure a sufficient number of values for both reasonable statistical testing and ecological significance. Twenty-two species met these criteria (Appendix 1).

Non-parametric procedures were used for analyses. The NPAR1WAY procedure, a one-factor, ranked Analysis of Variance (ANOVA) based on Wilcoxin scores, was used to assess significant differences among treatments by topographic area (Prob. ≥F=0.05) (SAS Institute Inc. 1989). The Student-Newman-Keuls multiple range test, a ranked multiple comparison test, was used to determine between which treatment-topographic areas significant differences occurred (P≤0.05) (Zar 1984). A nested ANOVA (SAS Institute Inc. 1989), with topography nested within treatment, was used to identify those species that were sufficiently common in all treatment-topographic areas that a significant effect of burning, irrespective of effects of topography and fire season, provided useful ecological insight. The nested ANOVA, however, is not the principal analysis used in this study since it does not provide for analysis of burn season and since it tends to minimize the effect of treatment on species that are limited in their normal topographic distribution (e.g., sand muhly, Table 1). Repeated Measures Analysis was not applied since it does not take into account natural changes that occur over time that could mask treatment effects.

NPAR1WAY analyses were run two ways, first with all treatment-topographic data and second with all but fall-burn data. These two analyses were necessary because of complications in assessing some results in the absence of 1985 fall-burn data. Specifically, interpretation of the results involved comparing ANOVA significance values for each species among treatments for one year with those values for each other year. Differences in statistical significance were used to indicate a response to burning. For example, no significant difference among treatments was determined for western ragweed (*Ambrosia psilostachya*) for 1984 but there was a significant difference among treatments for 1985. Moreover, these differences occurred at all three topographic locations. Thus, burning during spring and summer could be interpreted to have had a significant effect on western ragweed on all topographic locations, although the specific season of burn is not identified. By making such comparisons for all of the 22 species statistically evaluated and then considering the sum of such effects, one can obtain an additional assessment of the general effect of fire on the dominant plant community, both for the short term (1984 to 1985) and the longer term (1984 to 1988). This type of comparison requires that the number of treatment-topographic areas are the same for all years. Thus, the exclusion of fall treatment areas, which had not been evaluated in 1985, was required to meet this analytical design. Fall data, however, were eliminated only from this assessment. Analyses involving a comparison of ANOVA significance values by species, then, involved a total of 66 possible combinations (22 species × 3 treatments). An additional 21 combinations between general community characteristics (e.g., total cover, bare soil, and litter) and treatment were also analyzed statistically.

Temporal changes in the plant community of each treatment-topographic area were subjectively assessed by Principal Components Analysis (PCA) using PC-ORD (McCune and Mefford 1995). Correlation matrices that weight species evenly were selected. Species cover was the response variable with PCA plots being treatment-topographic areas for each year. Continuous data from 1984–1996 were collected only from one of each of the treatment replicates, thus, PCA was performed only on these four treatment-topographic areas. PCA was chosen over Detrended Correspondence Analysis (DCA) because its Euclidean features are preferable in studies incorporating short gradient lengths in which species response may be assumed to be linear (ter Braak and Prentice 1988).

Table 3. Comparison, between years, of within-year significance of treatment effects based on spring-burn, summer-burn, and unburned treatments only. *sig to ns* = significant effects occurred in the base year but not in the year to which the base year was compared; *ns to sig* = no significant difference in the base year but significant treatment effects were recorded for data for the year to which the base year was compared (Prob. > F = 0.05). H, N, or S (H = hilltop, N = north-facing slope, S = south-facing slope) are the treatment-topographic areas within which the change was noted. Blank cells = no change in significance. Only species analyzed by NPAR1WAY ANOVA are included.[1]

Species	1984 ANOVA results	1984 Compared to 1985		1984 Compared to 1988	
		sig to ns	ns to sig	sig to ns	ns to sig
Ambrosia psilostachya			HNS		HNS
Andropogon hallii	N		H		H
Andropogon scoparius	H	H	NS		
Artemesia ludoviciana	H			H	
Bouteloua hirsuta	H	H	S		S
Calamovilfa longifolia	HNS			S	
Carex spp.	S		N		N
Cyperus schweinitzii			NS		
Dalea villosa	HS	H		S	
Dichanthelium wilcoxianum	HN	H		H	
Eragrostis trichodes			HN		S
Erigeron bellidiastrum	N	N	H	N	
Euphorbia missurica			N		H
Helianthus rigidus			HN		H
Koeleria pyramidata			HN		
Liatris squarrosa			N		
Lithospermum incisum	S	S		S	
Muhlenbergia pungens	H				
Solidago missouriensis	NS	N	H	S	H
Sporobolus cryptandrus	HNS			HNS	
Stipa comata	S				
SUMMARY					
Hilltop		4	7	3	5
North-Facing Slope		2	9	2	2
South-Facing Slope		1	4	5	3

[1] Example: There is no significant difference among treatments for western ragweed for 1984 whereas there was a significant difference among treatments for 1985 and that difference was from not significant (ns) to significant (sig) for all topographic locations.

RESULTS

Of the 76 species found in study plots, 74 were native sandhill species of which 58 were perennial species and the remainder either annual or biennial. The two naturalized species, bugseed (*Corispermum nitidum*) and tumbleweed (*Salsola iberica*), are both annual species that were never found more frequently than as a single plant in a single plot every year or so. Both species composition and end-of-year standing crop differed by topographic location (Tables 1–2, Appendix 1). Specific effects of fire within this topographic and spatial variability were assessed both at the species-level and at the community-level.

Species-Level Effects

Short-term Effects of Burning

Between 1984 and 1985, changes in ANOVA significance (within topographic locations and between treatments) showed short-term effects of burning for 16 of the 22 species evaluated, these occurring in 27 of the 66 species-treatment-topographic combinations (Table 3). Of these, most differences (20 of the 27 treatment-topographic areas) changed from not significant to significant. A similar comparison over a longer term (1984–1988) showed differences for 15 species (20 of 63 treatment-topographic transects) although there was no trend toward significance or non-significance, as occurred with short-term effects. Stiff sunflower (*Helianthus rigidus*), western ragweed, and sand dropseed are some species that typify those with principally short-term effects (Figure 1, Appendix 1). These three are all native perennial species common throughout the study area. Stiff sunflower, however, flowers late in the growing season whereas western ragweed flowers earlier. Sand dropseed, a C_4 (warm-season) species, tends to occur in more disturbed sites than do the other two species. While no species was entirely consistent, overall responses allowed species to be categorized into one of three groups: fire-neutral, fire-positive, and fire-negative.

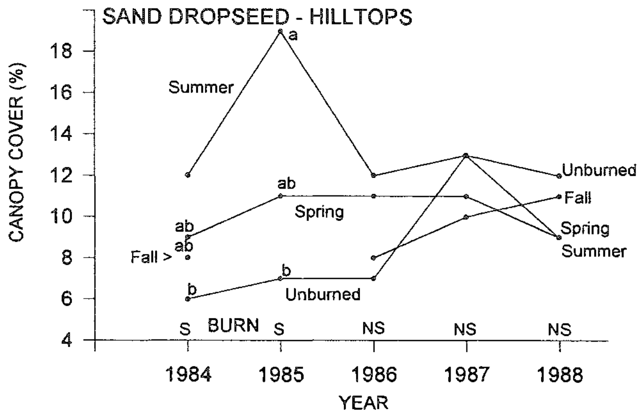

Fig. 1. Canopy cover of sand dropseed (*Sporobolus cryptandrus*) on hilltop locations. *Spring, Summer, Fall,* and *Unburned* refers to the burn season. Data points with either the same superscript, or without superscripts, do not differ significantly (ANOVA Prob. >F=0.05) from other cover values for the year indicated. *NS* or *S* above the x-axis indicates a significant difference among treatments based only on spring, summer, and unburned data for which there were data for all years (note the absence of fall-burn data for 1985).

Table 4. Probability results from nested ANOVA, by year. Only species with a significant treatment effect for at least one year are listed. Values shown indicate the level of significance of differences among treatments exclusive of effects of topographic location. Underlined values indicate P ≤ 0.05 which was considered a significant effect in this study.

Species or Plant Category	Probability				
	1984 (pre-burn)	1985 (1-year post-burn)[1]	1986	1987	1988
Total Cover	0.3698	0.0082	0.0640	0.0332	0.0615
Graminoid	0.1505	0.0083	0.0856	0.0353	0.0135
Forbs	0.1806	0.1369	0.2754	0.0305	0.4731
Litter	0.2708	0.0001	0.0001	0.2606	0.0253
Bare Soil	0.9502	0.0075	0.0052	0.0017	0.0204
Ambrosia psilostachya	0.4752	0.0059	0.0001	0.0005	0.0064
Euphorba missurica	0.5449	0.0323	0.2544	0.1284	0.7100
Sporobolus cryptandrus	0.0011	0.0036	0.0868	0.0303	0.0931
Lithospermum incisum	0.6472	0.0421	0.5701	0.5929	0.4606

[1] Does not include fall data.

Fire-neutral Species

Fire-neutral species are considered, here, to be those that did not differ noticeably from 1984 to 1988, although there may have been a brief change in cover, presumably in response to burning. Umbrella sedge and prairie goldenrod characterize this group. Neither of these species showed a significant response to burning or to fire season (Appendix 1). Umbrella sedge was particularly unresponsive with canopy cover averaging 2–3% higher in both burned and unburned areas during the 5 years of the study. Similarly, fire did not result in a decline in cover of prairie goldenrod although canopy cover increased most (+5%) on hilltops where this species was most common.

Fire-positive Species

In contrast to fire-neutral species, the canopy cover of seven species was found to increase with burning. Principal species of this group included sand dropseed, sedges, prairie sandreed, stiff sunflower, and hairy grama. Western fleabane (*Erigeron bellidiastrum*) and Missouri spurge (*Euphorbia missurica*), both small, native annual species, also appear to react positively to fire.

Sand dropseed, in the short term, was the most responsive of the fire-positive species with the effect of fire significant over all topographic locations and fire seasons (Table 4). Cover of this species the year following burning increased most (+7%) with summer burning. It also increased in all other treatments but more so with burning than without (Figure 1, Appendix 1). However, significant differences in canopy cover among treatments that were noted for both 1984 (preburn) and 1985 (immediate postburn) were no longer detected by 1988.

Sedge cover declined substantially from 1984 to 1985 in all topographic locations (−6%) but the decline was greater without burning (−23%) than with burning (−6%) (Appendix 1), thus its inclusion in this group of plants. The initial responses of prairie sandreed and stiff sunflower differed noticeably from sedges, and from each other. The canopy cover of prairie sandreed, a C_4 (warm-season) species, was substantially higher with summer burning in all topographic locations, both the year following burning (+10%) and four years following burning (+5%) (Appendix 1). These increases were greatest on hilltops (+12% 1-year postburn and +10% 4-years postburn). Burning did not result in significant declines in this species in any topographic location. In contrast, stiff sunflower, a species with relatively small canopy cover values, responded with a decline in cover in most treatment-topographic areas the year following burning (Appendix 1). However, in subsequent years, cover of this species was higher, often significantly so, than on the unburned area. This response was most noticeable on hilltops and north-facing slopes. Further, increases in canopy cover of this species were greater with than without burning.

Canopy cover of hairy grama decreased slightly (−3%) in all treatment-topographic areas, including the unburned area, the year following burning with the single exception of spring-burned, south-facing slopes (+3%). However, by 1988, canopy cover increased an average of +5% (range: 0–11%) in burned areas and only slightly (+1%) in the unburned areas; cover on spring burned south-facing slopes increased 11%.

Annual plants, which constitute a small but occasionally frequent component of sandhills flora, were expected to respond positively to the effects of fire, particularly to removal of litter and plant cover. Western fleabane and Missouri spurge are two small, annual species that seem to fit in the fire-positive group. While there are some differences in the response of these species to fire, both generally increased more

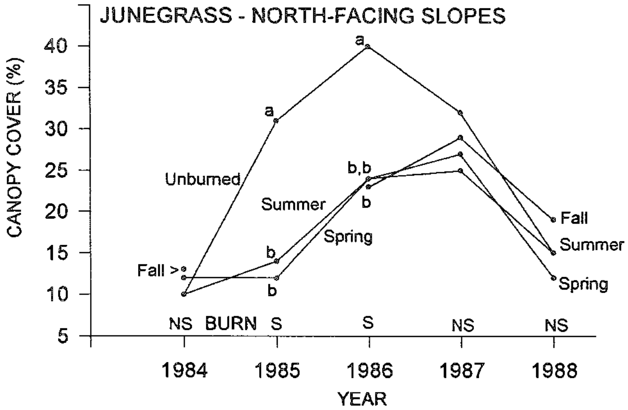

Fig. 2. Canopy cover of junegrass (*Koeleria pyramidata*) on north-facing slopes. *Spring, Summer, Fall,* and *Unburned* refers to the burn season. Data points with either the same superscript, or without superscripts, do not differ significantly (ANOVA Prob. >F=0.05) from other cover values for the year indicated. *NS* or *S* above the x-axis indicates a significant difference among treatments based only on spring, summer, and unburned data for which there were data for all years (note the absence of fall-burn data for 1985).

rapidly with than without burning, although the response was delayed until the second year following burning (Appendix 1). Canopy cover of western fleabane, for example, was greatest on hilltops 2 years after fall burning and, to a lesser extent, following summer burning. Missouri spurge cover also averaged highest 2 years following burning, particularly with summer burning. This species was also one of only four that showed a significant effect of burning irrespective of topographic location and fire season (Table 4). For 1985, however, this result may be an artifact of the absence of data for fall treatment-topographic areas.

Fire-Negative Species

Junegrass (*Koeleria pyramidata*), sand muhly, western ragweed, and narrow-leafed puccoon are the principal species evaluated that appear to be most adversely affected by burning. Junegrass, a C_3 (cool season) species found primarily on north-facing slopes, increased most (+21%) in the absence of burning with canopy cover remaining significantly higher than all burned treatments through the second year following burning (Figure 2, Appendix 1). However, this species also increased an average of 15% in all burn treatments for up to 2–3 years following burning. These increases may reflect the effect of higher-than-average rainfall that occurred during the last years of the study when annual precipitation (6470 millimeters) was second highest for the period. From 1987 to 1988, cover declined an average of 12% for all treatment-topographic areas with no significant differences recorded 4 years after burning.

Sand muhly, a species of hilltops and upper slopes, also declined in all treatment areas the year following burning but did so most sharply with fall burning. Between 1984 (preburn) and 1986 (one growing season after burning), cover in fall-burned treatments declined 10% on hilltops and 9% on south-facing slopes (Appendix 1). Three years following burning, the species had not yet recovered (−10% on hilltops and −7% on south-facing slopes). However, this species also declined between 1984 and 1988 without burning (−12% on hilltops and −3% on south-facing slopes).

Western ragweed was significantly affected by burning irrespective of the effects of topography and fire season ($P \leq 0.05$) (Table 4). However, while canopy cover declined significantly with burning (−17% cover), it also declined without burning (−12%) (Appendix 1). Summer burning appeared to have the greatest impact since only burning at that time of year reduced cover enough to result in significantly lower cover than other treatments, a response that continued throughout all years of the study. For spring burns, some, but not all, treatment-topographic areas showed significant effects of fire for this species.

Narrow-leaved puccoon, a frequent but small perennial species with consistently low canopy cover, was significantly affected by burning over all topographic and fire-treatment types, although the effect persisted for only 1 year (Table 4). Significant differences between fire season treatments within topographic-treatment areas, however, were noted only for 1986 (hilltop) and 1987 (south-facing slope) (Appendix 1).

Community-Level Effects

Both species composition (Table 1) and end-of-year standing crop (Table 2) differed among topographic locations. The effect of fire on community-level parameters is reflected in data from (1) general plot characteristics, (2) changes in the number of species in burned areas that differ from changes in the unburned area, and (3) ordination of data using PCA.

General Plot Characteristics (Total Cover, Litter, Bare Soil, Graminoid, Forbs, Woody Plants, and Cacti)

The effect of burning on general plot characteristics was often significant in the short-term (i.e., 1984–1985) (Table 4) but only summer burns seemed to have effects that extended through 1988. This trend is exemplified by forbs, woody plants, and litter. The greatest effect on forb cover occurred with summer burning for which the short-term effect was greatest on south-facing slopes. There, forb cover declined 25% from 1984 to 1985 remaining significantly lower than other treatments, including the unburned treatment, throughout the study period (Figure 3, Appendix 1). Average forb cover for all treatment-topographic areas, however, declined 14% from 1984 to 1988 although the decline was greater with burning (−16%) than without (−9%). Without burning, forb cover declined more on south-facing slopes (−16%) than north-facing slopes (−4%) or hilltops (−8%).

Dominant woody plants of the study site were smooth sumac (*Rhus glabra*), prairie wild rose (*Rosa arkansana*), poison ivy (*Toxicodendron rydbergii*), and, to a lesser extent, sand cherry (*Prunus pumila* var.

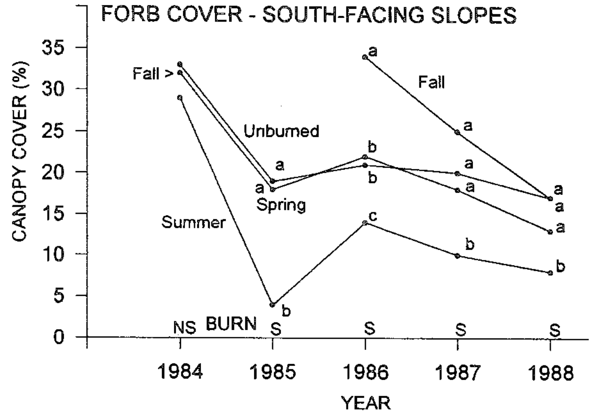

Fig. 3. Canopy cover of forbs on south-facing slopes. *Spring, Summer, Fall,* and *Unburned* refers to the burn season. Data points with either the same superscript, or without superscripts, do not differ significantly (ANOVA Prob. >F=0.05) from other cover values for the year indicated. *NS* or *S* above the x-axis indicates a significant difference among treatments based only on spring, summer, and unburned data for which there were data for all years (note the absence of fall-burn data for 1985).

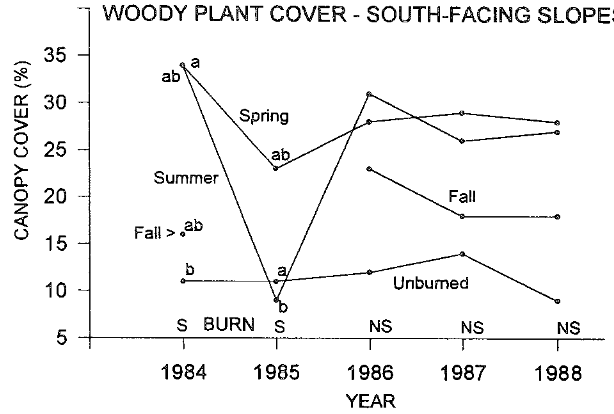

Fig. 4. Canopy cover of woody plants on south-facing slopes. *Spring, Summer, Fall,* and *Unburned* refers to the burn season. Data points with either the same superscript, or without superscripts, do not differ significantly (ANOVA Prob. >F= 0.05) from other cover values for the year indicated. *NS* or *S* above the x-axis indicates a significant difference among treatments based only on spring, summer, and unburned data for which there were data for all years (note the absence of fall-burn data for 1985).

besseyi). As with forbs, woody plants on south-facing slopes declined dramatically (−25%) the year following summer burning (Figure 4). However, unlike forbs, 2 years following burning woody plant canopy cover returned to levels at or near preburn conditions which did not differ significantly from cover in any of the other burned or unburned areas. Fall burning, in particular, appears to have increased woody plant cover, although not significantly.

Litter was one of five plot characteristics significantly affected by burning, irrespective of any effects of topography and fire season (Table 4). Litter canopy cover returned to preburn levels within 4 years of treatment except for fall-burned north- and south-facing slopes (Appendix 1). These exceptions most likely reflect that, in 1988, fall-burned plots had accumulated only 3 years of litter while summer- and spring-burned areas, having regrown some the year of the burn, had an accumulation of 4 years of litter. Changes in litter cover in fall-burned treatment-topographic areas were still increasing in 1988.

Change in Species Richness

Year-to-year changes in absolute Species Richness (the number of species) in the unburned treatment areas were used as a base to reflect expected changes due to factors other than fire treatment. This base was used even though the presence of fire in this ecosystem is likely to be historically more natural than is the absence of fire. Comparisons between years that differ from this expected change were used to suggest effects of burning on community diversity. An arbitrary difference of more than four species was used to indicate substantive changes.

Within the spatial variability afforded by differences in species composition and living+dead phytomass, and based on differences between observed and expected numbers of species, no dramatic change in overall Species Richness was observed in response to fire (Table 5). There was, however, a tendency for burned areas to have from two-six fewer species than unburned areas 4 years after burning. Summer and fall burns on south-facing slopes (+three species) were the only exceptions. Despite the general lack of substantial changes, some comparisons between 1984 (preburn) and 1988 (4 years following burning) are instructive.

Between 1984 and 1988, an increase in Species Richness occurred only on south-facing slopes with summer and fall burning (Table 5). The greatest decline in Species Richness occurred on summer-burned, north-facing slopes which averaged six fewer species than expected. This decline occurred concomitant with increases in cover for both C_3 (cool-season) species (e.g., needle-and-thread and junegrass) and C_4 (warm-season) species (e.g., sand dropseed) (Figure 1, Appendix 1).

Table 5. Difference in the number of species between the base year (1984) and the comparison year (1985, 1986, 1987, and 1988) by treatment-topographic area. H = hilltop, N = north-facing slope, S = south-facing slope. "–" = no data (not evaluated in Fall 1985).

		Year(s)				
Topographic Location	Treatment	1984 (base)	1984–1985	1984–1986	1984–1987	1984–1988
Hilltop	Spring Burn	38	−3	−1	−1	−2
	Summer Burn	34	−1	+3	0	+1
	Fall Burn	42	–	+1	0	−2
	Unburned	34	−1	+5	+4	+3
North Slope	Spring Burn	35	−2	+1	−1	−2
	Summer Burn	40	−7	−2	−9	−5
	Fall Burn	40	–	+4	−2	−1
	Unburned	41	−1	+3	−1	+1
South Slope	Spring Burn	35	−2	+3	+2	−1
	Summer Burn	33	−3	0	+3	+4
	Fall Burn	41	–	+3	+3	+4
	Unburned	38	−4	0	−1	−2

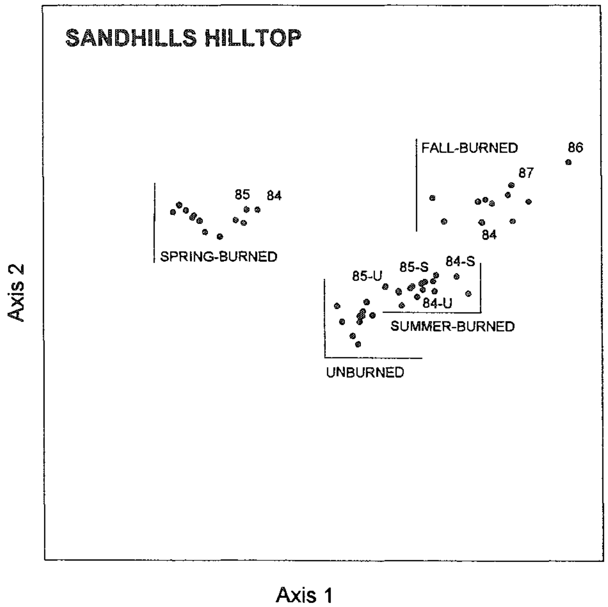

Fig. 5. Ordination of hilltop vegetation samples along the first two PCA axes. Each PCA plot (dot) represents data from mean values (n=10) of one treatment-topographic area for one year. Numeric superscripts on some PCA plots indicate the specific year represented. Little change in location of PCA plots indicates little change in community diversity. Eigenvalues: Axis 1 = 9.897 (17.4% of variance), Axis 2 = 6.396 (11.2% of variance).

A second, noteworthy decline between 1984 and 1988 occurred on both spring-burned and fall-burned hilltops (five less species than expected). The reduction in Species Richness on spring-burned hilltops was consistent throughout the study, occurring in all years. With fall burning, however, results varied considerably, from −4 in 1986 to +1 in 1987 to −5 in 1988 (Table 5).

Multivariate Comparisons

Despite significant changes in at least some individual species (Appendix 1), no substantive changes occurred in community composition from 1984 to 1996, as reflected subjectively by Principal Components Analysis (Figure 5). The greatest shift on the ordination plot between preburn and postburn occurred with fall burning. Fall burning also showed both the longest lasting effect of burning (1986–1987) and the greatest variability, reflected in the greater dispersion of plots. Interpretation of the results of ordination needs to be tempered with the consideration that only 29% of the variance is incorporated in Axes 1 and 2 of the ordination.

DISCUSSION

Species-level Effects

Within the spatially heterogeneous environment of the Nebraska Sandhills, single spring, summer, or fall burns generally were found to have the greatest impact within 1 year of burning with longer-term (e.g., 4 years postburn) effects generally not differing significantly from unburned areas (Appendix 1). The responses to burning, as affected by topographic location, varied among and between species, results that parallel the general variability in species responses previously reported in the region (Cosby 1971, Wolfe 1973, Bragg 1978).

Of the most clearly fire-neutral, fire-positive, or fire-negative species, the greater number (7 of 15) were fire-positive. While not conclusive, a higher proportion of fire-adapted species is consistent with the concept that fire was a natural component of the Nebraska Sandhills Prairie (e.g., Bragg 1995). Further, the greater number of warm-season-type species that were identified as fire-positive suggests, although again only by inference, that fire may have affected the C_3:C_4 ratio of species in the region, generally from C_3 (cool-season) to C_4 (warm-season) (but see Steuter 1987). Fire suppression may have caused changes in species composition. Such an effect would be difficult to determine today, due to the absence of quantitative historical records.

Not all species' responses to burning, however, support the idea that fire is the principal vector of change. Not unexpectedly, data from some species suggest fire to be only one factor. For example, western ragweed cover declined dramatically from 1984–1988, not only in burned areas (−17% cover) but also in unburned areas (−12%) (Appendix 1). Data collected during subsequent years show the canopy cover of this species to recover to near-preburn levels by 1991 (Bragg, unpublished data). Clearly, long-term fluctuations in this species are related primarily to factors other than those associated directly with fire. Fire, however, did play some role in western ragweed changes as evidenced by the significant decline in cover with summer burning, a significance that remained for at least 4 years following burning.

One important explanation for individual species responses to burning may be reflected in the effect of burning on litter. For example, following somewhat different initial responses, the canopy cover of junegrass (Figure 2), sand muhly, and sedges increased for the first 3 years but then decreased in the latter years, a time during which litter had accumulated to preburn cover (Appendix 1). While providing only inferential evidence, this response is consistent with the concept that fire's removal of litter improves conditions for the growth, and perhaps reproduction, of some species, a consequence that may affect long-term species diversity (Weaver and Rowland 1952, Carson and Peterson 1990).

Of particular importance in this study, are the results of burning on woody plant cover. Woody plants recovered to preburn levels of cover within 2 years after burning, this despite an initial 25% decline. A single fire, thus, appears to be able to temporarily suppress, but not eliminate, woody plants. More frequent fires may prove to be the most effective means by which to control woody plant encroachment, although rates of fuel accumulation, about which little is known for the Nebraska Sandhills, will certainly place a limit on such application. Further, higher-frequency fire prescription needs to be carefully considered in light of other impacts on the ecosystem, such as adverse effects on plant species composition (e.g., see Collins 1992) and prairie fauna, particularly invertebrates (e.g., see Bragg 1995). It may be that fire, in the end, is best used as a management tool to prevent the establishment of woody plants rather as one intended to eliminate them, although this issue clearly needs more careful study than was intended by the present study.

These results of burning on individual species are consistent with the general impression that a single fire has only a minimal direct effect on plant species composition, despite season-of-occurrence. Effects, however, most likely differ with repeated burning. Short-term species responses, such as are reported in this study, however, suggest the potential for longer-term effects where fires occur more frequently. The significant increase of sand dropseed the year following summer burning (Figure 1), for example, suggests the potential for this species to increase substantially with more frequent burning, particularly in the summer when fires were historically more frequent (Westover 1986). In contrast, sedges, hairy grama, and stiff sunflower, all of which decreased initially but increased by the end of the fourth year, may decline in the long term with higher fire frequency since they may not have time to recover to preburn levels before they are reburned. The degree to which such hypothesized effects are ecologically accurate, however, await the results of much needed, decades-long studies.

Community-Level Effects

As a group, forbs best reflect a community's response to burning since they are an important component of grassland diversity, being more dynamic and diagnostic of changes in moisture, grazing, and fire regimes than the perennial grass matrix (Biondini et al. 1989, Steuter et al. 1995). In this study, effects of fire differed both with respect to topographic setting and fire season. Generally, however, significant differences in forb cover did not persist longer than 2 years following burning, with the exception of summer burns, particularly those on south-facing slopes (Figure 3). There, summer-burned treatment-topographic areas remained significantly different from other treatments throughout the 4 years of the study. Notably, however, while Species Richness declined on summer-burned, north-facing slopes, perhaps a consequence of higher fuel loads (Table 2), it increased on south-facing slopes (Table 5). This increase was accompanied by a decline in forb canopy cover, suggesting that fire resulted in conditions that enabled additional species to become established. Since all except two of the species in this study were native sandhill species, this consequence supports the concept that natural community diversity over the long term may, at least in part, be maintained by fire, although results may vary for different topographic locations. Thus, there is at least some evidence to support the inclusion of summer treatments in fire prescriptions designed to approximate historic conditions, a suggestion made in other studies as well (e.g., Bragg 1991, Howe 1994).

The various effects of burning discussed in this study are limited in scope in that they represent the responses to a single fire event and, notably, one that followed a long period of fire suppression. Within this context, however, and despite short-term changes in individual species on various topographic locations and fire seasons, data support the conclusion that a single fire event did not substantially affect community diversity in the Nebraska Sandhills Prairie (Figure 5), a result consistent with Tilman's (1996) conclusions that individual population instability need not also affect community stability.

While focussing on the effects of a single fire event, this study also provides data from which to infer the effects of repeated burning which, most likely, parallel the short-term effects of fire on individual species. The frequent, and often significant, short-term effects, previously discussed in this paper, have the potential to become even greater when, for example, a second fire occurs before the community, or species within the community (e.g., sedges, hairy grama, and stiff sunflower), can return to preburn conditions. Such potentially greater long-term effects would, most likely, further differ depending on the topographic setting or season of burning. For example, PCA results suggest that more frequent fires in the fall may cause a shift in species diversity that persists for a longer period of time than it does in other burning seasons. The effects of fire season would be further influenced by responses that differ with respect to topographic variability, such as the opposite effect of fire on Species Richness on south-facing and north-facing slopes shown for summer fires.

Overall, this study shows that a single fire occurring in the variable landscape of the Nebraska Sandhills, irrespective of season-of-occurrence, appears to have little long-term effect. In contrast, however, data suggest that more frequent fires occurring in different seasons have the potential to maintain a highly diverse landscape through differentially affecting species occupying different topographic locations. More detailed study is clearly needed to most accurately assess the effects of fire on this ecosystem. Whether interested in a basic ecological understanding of the ecosystem or in management implications, this study provides further insight into the past and future role of fire in the Nebraska Sandhills Prairie, although much is yet to be learned about this extensive ecosystem.

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Appendix 1. Mean canopy cover ± Standard Error for those species present in at least two of three replicates in at least three of four treatment areas. "—" = not evaluated (burned Fall 1985). Mean values with either the same superscript or without superscripts do not differ significantly within that topographic-treatment area for the year indicated (Student-Newman-Keuls multiple comparison tests; $P < 0.05$). Comparisons include all treatment-topographic areas evaluated from 1984–1988.

Species or Group	Topographic Location	Treatment	Mean Canopy Cover ± Standard Error, by Year				
			1984	1985	1986	1987	1988
TOTAL PLANT COVER	Hilltop	Spring	88 ± 1.7	86 ± 1.7^{b}	85 ± 1.0	85 ± 0.4	85 ± 1.0
		Summer	87 ± 0.9	86 ± 0.6^{b}	85 ± 0.0	87 ± 0.8	88 ± 0.9
		Fall	87 ± 0.9	—	83 ± 1.3	86 ± 0.7	84 ± 1.2
		Unburned	89 ± 1.0	90 ± 1.1^{a}	86 ± 0.6	87 ± 0.9	87 ± 0.9
	North-Facing Slope	Spring	90 ± 1.5	89 ± 1.4^{b}	87 ± 1.2^{ab}	88 ± 0.9^{b}	88 ± 1.0^{ab}
		Summer	90 ± 1.1	85 ± 1.3^{c}	86 ± 0.7^{ab}	88 ± 0.9^{b}	87 ± 1.3^{ab}
		Fall	91 ± 1.1	—	85 ± 0.4^{b}	85 ± 0.4^{b}	86 ± 0.6^{b}
		Unburned	94 ± 1.1	94 ± 1.1^{a}	89 ± 1.0^{a}	93 ± 1.1^{a}	90 ± 1.1^{a}
	South-Facing Slope	Spring	86 ± 1.2^{b}	85 ± 1.0^{b}	87 ± 1.2	87 ± 0.8^{b}	87 ± 0.9^{b}
		Summer	91 ± 1.2^{a}	87 ± 1.5^{b}	88 ± 1.0	89 ± 1.1^{ab}	91 ± 1.1^{a}
		Fall	89 ± 1.1^{ab}	—	84 ± 2.0	86 ± 1.1^{b}	86 ± 1.1^{b}
		Unburned	91 ± 1.2^{a}	94 ± 1.1^{a}	89 ± 1.1	92 ± 1.1^{a}	92 ± 1.1^{a}
GRAMINOID	Hilltop	Spring	84 ± 0.8^{ab}	84 ± 1.4^{ab}	84 ± 1.1^{a}	85 ± 0.0^{a}	84 ± 0.8
		Summer	87 ± 0.8^{a}	82 ± 1.6^{b}	85 ± 0.0^{a}	84 ± 0.8^{a}	84 ± 1.1
		Fall	83 ± 1.3^{b}	—	78 ± 1.9^{b}	80 ± 1.7^{b}	84 ± 1.0
		Unburned	85 ± 1.8^{ab}	87 ± 0.8^{a}	84 ± 0.8^{a}	87 ± 0.8^{a}	86 ± 1.1
	North-Facing Slope	Spring	85 ± 1.4	83 ± 1.8^{b}	85 ± 1.4	86 ± 0.7^{b}	85 ± 0.0^{b}
		Summer	87 ± 0.9	83 ± 1.3^{b}	84 ± 0.8	86 ± 0.6^{b}	85 ± 1.0^{b}
		Fall	87 ± 0.9	—	84 ± 0.8	85 ± 0.0^{b}	84 ± 0.4^{b}
		Unburned	86 ± 1.5	92 ± 1.5^{a}	84 ± 0.8	89 ± 1.0^{a}	88 ± 0.9^{a}
	South-Facing Slope	Spring	84 ± 1.2^{ab}	82 ± 1.5^{b}	83 ± 1.7	85 ± 0.9^{b}	85 ± 1.0^{ab}
		Summer	88 ± 1.0^{a}	85 ± 1.9^{b}	85 ± 0.9	86 ± 0.6^{b}	84 ± 0.4^{ab}
		Fall	81 ± 2.0^{b}	—	80 ± 1.7	85 ± 1.3^{b}	84 ± 1.4^{b}
		Unburned	88 ± 0.9^{a}	91 ± 1.5^{a}	85 ± 1.0	89 ± 1.1^{a}	87 ± 0.9^{a}
FORB	Hilltop	Spring	37 ± 2.7^{a}	26 ± 3.4^{a}	32 ± 2.5	19 ± 1.9^{b}	19 ± 1.6
		Summer	29 ± 2.4^{ab}	10 ± 1.8^{b}	25 ± 2.2	16 ± 1.8^{b}	20 ± 1.7
		Fall	36 ± 2.8^{ab}	—	34 ± 2.0	30 ± 2.8^{a}	19 ± 1.9
		Unburned	28 ± 2.7^{b}	27 ± 2.8^{a}	28 ± 2.6	33 ± 3.5^{a}	24 ± 2.7
	North-Facing Slope	Spring	42 ± 3.6	34 ± 3.8^{a}	36 ± 2.5^{ab}	18 ± 1.6^{b}	18 ± 1.9
		Summer	35 ± 2.9	22 ± 2.2^{b}	36 ± 3.5^{ab}	22 ± 2.3^{b}	21 ± 2.4
		Fall	37 ± 2.4	—	40 ± 2.4^{a}	33 ± 2.8^{a}	27 ± 2.9
		Unburned	32 ± 2.7	22 ± 2.3^{ab}	27 ± 3.0^{b}	24 ± 2.6^{b}	24 ± 2.5
	South-Facing Slope	Spring	32 ± 2.1	18 ± 2.2^{a}	22 ± 2.6^{b}	18 ± 1.8^{a}	13 ± 1.3^{a}
		Summer	29 ± 3.6	4 ± 1.7^{b}	14 ± 3.4^{c}	10 ± 2.1^{b}	8 ± 1.3^{b}
		Fall	32 ± 3.0	—	34 ± 2.4^{a}	25 ± 3.1^{a}	17 ± 1.3^{a}
		Unburned	33 ± 2.7	19 ± 2.7^{a}	21 ± 3.0^{b}	20 ± 2.3^{a}	17 ± 2.4^{a}
WOODY PLANTS	Hilltop	Spring	14 ± 3.1^{a}	14 ± 3.1^{a}	18 ± 3.8^{a}	16 ± 3.6^{a}	16 ± 3.5^{a}
		Summer	15 ± 3.4^{a}	9 ± 2.7^{a}	15 ± 3.7^{a}	14 ± 3.0^{a}	12 ± 2.7^{a}
		Fall	9 ± 2.7^{a}	—	8 ± 2.5^{a}	9 ± 2.2^{a}	9 ± 2.2^{a}
		Unburned	1 ± 0.5^{b}	1 ± 0.5^{b}	1 ± 0.7^{b}	1 ± 0.7^{b}	1 ± 0.7^{b}
	North-Facing Slope	Spring	28 ± 3.4^{a}	27 ± 2.9^{a}	31 ± 3.4^{a}	28 ± 3.7^{a}	23 ± 2.7^{a}
		Summer	9 ± 2.9^{b}	6 ± 1.9^{b}	8 ± 2.9^{b}	12 ± 3.5^{b}	13 ± 3.2^{b}
		Fall	5 ± 1.6^{b}	—	9 ± 2.6^{b}	7 ± 2.2^{b}	6 ± 1.9^{b}
		Unburned	22 ± 2.6^{a}	17 ± 2.3^{a}	22 ± 2.6^{a}	21 ± 2.7^{a}	22 ± 2.5^{a}
	South-Facing Slope	Spring	34 ± 4.5^{a}	23 ± 3.7^{ab}	28 ± 5.1	29 ± 5.1	28 ± 4.5
		Summer	34 ± 5.8^{ab}	9 ± 1.9^{a}	31 ± 5.3	26 ± 4.4	27 ± 4.5
		Fall	16 ± 3.1^{ab}	—	23 ± 4.9	18 ± 3.5	18 ± 3.4
		Unburned	11 ± 3.0^{b}	11 ± 3.1^{b}	12 ± 3.1	14 ± 3.6	9 ± 2.4
CACTI	Hilltop	Spring	2 ± 0.8	2 ± 0.8	2 ± 1.4	2 ± 0.8	1 ± 0.7
		Summer	1 ± 0.5	tr.	tr.	1 ± 0.5	1 ± 0.7
		Fall	2 ± 1.4	—	1 ± 0.7	2 ± 0.8	2 ± 0.8
		Unburned	tr.	tr.	tr.	tr.	tr.
	North-Facing Slope	Spring	1 ± 0.7	tr.^{b}	tr.	1 ± 0.5	1 ± 0.7
		Summer	tr.	tr.^{b}	tr.	tr.	tr.
		Fall	tr.	—	tr.	1 ± 0.5	1 ± 0.5
		Unburned	2 ± 0.5	1 ± 0.5^{a}	1 ± 0.7	1 ± 0.7	1 ± 0.7
	South-Facing Slope	Spring	3 ± 1.0	1 ± 0.5	2 ± 1.4	3 ± 1.5	2 ± 1.4
		Summer	tr.	tr.	1 ± 0.2	1 ± 0.5	1 ± 0.5
		Fall	1 ± 0.5	—	tr.	1 ± 0.5	1 ± 0.5
		Unburned	3 ± 1.4	2 ± 1.3	2 ± 1.2	2 ± 0.9	1 ± 0.7

Appendix 1. Continued.

Species or Group	Topographic Location	Treatment	Mean Canopy Cover ± Standard Error, by Year				
			1984	1985	1986	1987	1988
LITTER	Hilltop	Spring	80 ± 1.8[a]	15 ± 0.9[c]	50 ± 2.6[c]	66 ± 2.8[a]	73 ± 3.1
		Summer	77 ± 2.3[a]	23 ± 2.4[b]	58 ± 1.7[b]	63 ± 1.4[a]	70 ± 3.4
		Fall	78 ± 2.0[a]	—	25 ± 3.0[d]	48 ± 3.4[b]	63 ± 2.4
		Unburned	68 ± 4.4[b]	68 ± 2.7[a]	77 ± 2.3[a]	64 ± 2.5[b]	70 ± 3.3
	North-Facing Slope	Spring	80 ± 1.8	12 ± 1.0[c]	53 ± 2.5[c]	65 ± 3.1[ab]	76 ± 3.3[a]
		Summer	80 ± 1.7	20 ± 2.3[b]	62 ± 1.8[b]	64 ± 2.3[ab]	74 ± 2.9[a]
		Fall	78 ± 2.0	—	36 ± 2.5[d]	60 ± 3.2[b]	60 ± 2.4[b]
		Unburned	76 ± 2.0	72 ± 2.6[a]	78 ± 2.8[a]	72 ± 2.4[a]	79 ± 2.3[a]
	South-Facing Slope	Spring	78 ± 2.0	20 ± 2.0[c]	48 ± 3.0[c]	69 ± 2.5[a]	76 ± 2.5[a]
		Summer	78 ± 2.0	33 ± 2.9[b]	62 ± 2.4[b]	67 ± 2.3[a]	79 ± 1.8[a]
		Fall	80 ± 1.7	—	33 ± 3.1[d]	58 ± 3.6[b]	68 ± 2.7[b]
		Unburned	78 ± 1.9	77 ± 2.0[a]	80 ± 1.9[a]	75 ± 2.9[a]	80 ± 2.0[a]
BARE SOIL	Hilltop	Spring	9 ± 1.2[b]	48 ± 3.5[a]	43 ± 4.1[c]	32 ± 3.5[a]	34 ± 3.8
		Summer	14 ± 2.1[ab]	39 ± 3.5[a]	53 ± 2.5[b]	33 ± 2.0[a]	31 ± 3.0
		Fall	13 ± 1.9[ab]	—	74 ± 2.4[a]	50 ± 3.2[a]	45 ± 3.6
		Unburned	16 ± 1.6[a]	22 ± 2.1[b]	48 ± 3.9[bc]	19 ± 3.0[b]	31 ± 2.8
	North-Facing Slope	Spring	9 ± 2.1	33 ± 4.2[a]	44 ± 4.4[b]	25 ± 3.0[b]	28 ± 3.4[b]
		Summer	8 ± 1.6	36 ± 2.5[a]	51 ± 3.2[ab]	29 ± 2.0[b]	24 ± 2.6[b]
		Fall	7 ± 1.6	—	63 ± 2.4[a]	39 ± 2.3[a]	44 ± 3.0[a]
		Unburned	8 ± 1.8	10 ± 2.2[b]	25 ± 4.2[c]	23 ± 3.0[b]	23 ± 2.8[b]
	South-Facing Slope	Spring	13 ± 1.6[a]	52 ± 3.7[a]	51 ± 4.8[b]	30 ± 2.4[b]	32 ± 3.2[a]
		Summer	7 ± 1.6[b]	31 ± 3.5[b]	40 ± 3.4[b]	19 ± 2.1[c]	14 ± 1.5[b]
		Fall	14 ± 2.1[a]	—	67 ± 2.9[a]	48 ± 4.2[a]	37 ± 3.2[a]
		Unburned	8 ± 1.6[b]	14 ± 2.0[c]	29 ± 2.9[c]	17 ± 2.8[c]	16 ± 2.2[b]
Ambrosia psilostachya (western ragweed)	Hilltop	Spring	23 ± 2.8[ab]	9 ± 1.5[b]	5 ± 1.5[b]	5 ± 1.2[a]	8 ± 1.2[a]
		Summer	20 ± 1.7[b]	1 ± 0.5[c]	1 ± 0.5[c]	2 ± 0.7[b]	3 ± 1.1[b]
		Fall	29 ± 2.4[a]	—	11 ± 1.8[a]	9 ± 1.3[a]	8 ± 1.3[a]
		Unburned	23 ± 2.2[ab]	16 ± 1.6[a]	10 ± 1.5[a]	9 ± 1.6[a]	8 ± 1.6[a]
	North-Facing Slope	Spring	20 ± 2.1	13 ± 2.6[a]	5 ± 1.1[b]	4 ± 1.0[b]	6 ± 1.3[b]
		Summer	20 ± 2.1	tr.[b]	1 ± 0.5[c]	1 ± 0.7[c]	4 ± 1.6[c]
		Fall	31 ± 2.5	—	11 ± 2.2[a]	8 ± 1.3[a]	12 ± 1.4[a]
		Unburned	22 ± 2.3	12 ± 1.7[a]	7 ± 1.5[ab]	9 ± 1.3[a]	12 ± 1.7[a]
	South-Facing Slope	Spring	22 ± 2.3[ab]	4 ± 1.1[b]	5 ± 1.5[b]	7 ± 1.3[ab]	7 ± 1.3[a]
		Summer	24 ± 3.4[b]	1 ± 1.2[c]	1 ± 0.5[c]	1 ± 0.7[c]	2 ± 0.9[b]
		Fall	18 ± 2.3[b]	—	8 ± 1.2[a]	5 ± 1.2[b]	10 ± 1.6[a]
		Unburned	30 ± 2.8[a]	11 ± 1.5[a]	8 ± 1.2[a]	11 ± 1.5[a]	8 ± 1.2[a]
Andropogon hallii (sand bluestem)	Hilltop	Spring	43 ± 4.0	38 ± 3.4	44 ± 3.8	40 ± 3.7	45 ± 2.9[a]
		Summer	35 ± 3.6	38 ± 4.1	38 ± 3.8	35 ± 4.0	33 ± 3.2[ab]
		Fall	32 ± 3.6	—	40 ± 4.3	34 ± 3.6	32 ± 3.3[b]
		Unburned	32 ± 2.4	26 ± 2.7	40 ± 2.5	32 ± 2.9	36 ± 2.5[a]
	North-Facing Slope	Spring	15 ± 2.9[b]	15 ± 2.9[a]	22 ± 3.4[b]	19 ± 3.1[b]	21 ± 3.2[bc]
		Summer	27 ± 3.9[a]	21 ± 3.3[a]	30 ± 4.2[a]	29 ± 3.6[a]	27 ± 3.8[ab]
		Fall	21 ± 3.2[a]	—	27 ± 2.9[a]	31 ± 2.5[a]	36 ± 2.9[a]
		Unburned	10 ± 2.1[b]	7 ± 1.9[b]	12 ± 3.3[c]	11 ± 2.3[c]	14 ± 3.3[c]
	South-Facing Slope	Spring	44 ± 4.2	44 ± 4.5	48 ± 4.3	48 ± 4.5	46 ± 3.8
		Summer	50 ± 3.9	46 ± 3.1	55 ± 4.0	51 ± 2.6	52 ± 3.2
		Fall	42 ± 4.2	—	50 ± 4.2	42 ± 3.9	42 ± 3.6
		Unburned	55 ± 3.5	44 ± 3.6	52 ± 3.7	48 ± 3.4	54 ± 3.5
Andropogon scoparius (little bluestem)	Hilltop	Spring	18 ± 4.6[b]	14 ± 3.0	12 ± 3.0[b]	11 ± 2.7[b]	11 ± 3.0[b]
		Summer	35 ± 5.1[a]	27 ± 4.2	30 ± 4.7[ab]	27 ± 4.2[a]	32 ± 5.2[a]
		Fall	12 ± 3.4[b]	—	9 ± 2.5[b]	11 ± 2.5[b]	14 ± 3.6[b]
		Unburned	19 ± 3.7[ab]	20 ± 3.8	20 ± 3.5[a]	16 ± 2.9[ab]	16 ± 2.8[ab]
	North-Facing Slope	Spring	50 ± 3.4	36 ± 3.4	40 ± 3.4	33 ± 2.6	33 ± 3.2
		Summer	51 ± 5.0	38 ± 4.1	33 ± 4.8	29 ± 4.3	33 ± 4.7
		Fall	55 ± 3.6	—	31 ± 3.2	32 ± 3.1	31 ± 2.8
		Unburned	51 ± 3.7	52 ± 4.2	42 ± 3.7	32 ± 3.0	33 ± 3.0
	South-Facing Slope	Spring	14 ± 3.9[b]	10 ± 2.7[b]	13 ± 3.7[b]	11 ± 3.1[b]	12 ± 3.6[b]
		Summer	23 ± 3.8[a]	16 ± 3.0[a]	21 ± 3.6[a]	20 ± 3.4[a]	23 ± 4.0[a]
		Fall	21 ± 4.4[ab]	—	16 ± 3.7[a]	16 ± 3.3[ab]	18 ± 3.7[a]
		Unburned	25 ± 3.8[a]	26 ± 3.3[a]	28 ± 3.8[a]	20 ± 2.8[a]	20 ± 3.2[a]
Artemisa ludoviciana (white sage)	Hilltop	Spring	9 ± 2.6[a]	4 ± 1.2[a]	4 ± 1.1[a]	4 ± 1.1[a]	2 ± 0.8
		Summer	0.0[b]	1 ± 0.5[b]	0.0[b]	2 ± 0.8[b]	2 ± 0.8
		Fall	5 ± 1.6[a]	—	7 ± 2.2[a]	6 ± 1.3[a]	5 ± 1.6
		Unburned	2 ± 1.3[b]	1 ± 0.7[b]	2 ± 0.9[b]	1 ± 0.7[b]	2 ± 0.9

Appendix 1. Continued.

Species or Group	Topographic Location	Treatment	Mean Canopy Cover ± Standard Error, by Year				
			1984	1985	1986	1987	1988
	North-Facing Slope	Spring	5 ± 1.3[b]	8 ± 2.0	9 ± 2.2	8 ± 1.7	6 ± 1.2
		Summer	8 ± 2.4[b]	7 ± 2.2	10 ± 3.0	10 ± 2.4	6 ± 1.6
		Fall	11 ± 1.6[a]	—	17 ± 3.2	11 ± 1.8	9 ± 1.3
		Unburned	3 ± 1.0[b]	3 ± 1.5	7 ± 2.2	6 ± 1.7	6 ± 1.3
	South-Facing Slope	Spring	9 ± 2.8	5 ± 1.6	7 ± 2.2	5 ± 1.2	5 ± 1.2[a]
		Summer	3 ± 1.5	2 ± 1.3	3 ± 1.4	3 ± 1.4	2 ± 0.9[b]
		Fall	10 ± 2.7	—	12 ± 2.8	8 ± 2.0	7 ± 1.7[a]
		Unburned	3 ± 1.5	3 ± 1.5	4 ± 1.8	4 ± 1.8	2 ± 1.4[b]
Bouteloua hirsuta (hairy grama)	Hilltop	Spring	23 ± 2.8	18 ± 2.7	24 ± 3.5	29 ± 3.6	33 ± 3.9
		Summer	16 ± 2.1	14 ± 2.7	14 ± 2.9	19 ± 2.8	21 ± 2.4
		Fall	22 ± 3.0	—	14 ± 2.3	17 ± 2.0	25 ± 2.5
		Unburned	30 ± 3.5	22 ± 2.7	25 ± 2.9	3 1± 3.5	30 ± 2.5
	North-Facing Slope	Spring	3 ± 1.1	3 ± 1.4	4 ± 1.2	6 ± 1.6	9 ± 2.6
		Summer	4 ± 1.1	3 ± 1.0	2 ± 0.7	7 ± 1.9	7 ± 1.9
		Fall	6 ± 1.9	—	2 ± 0.8	6 ± 1.3	10 ± 2.2
		Unburned	3 ± 0.9	5 ± 1.5	2 ± 0.8	4 ± 1.1	4 ± 1.1
	South-Facing Slope	Spring	9 ± 1.6[ab]	12 ± 2.2[ab]	15 ± 2.9	18 ± 3.1	20 ± 3.4
		Summer	6 ± 2.3[b]	6 ± 1.6[b]	5 ± 1.8	8 ± 1.9	11 ± 2.3
		Fall	13 ± 2.5[a]	—	8 ± 2.1	11 ± 2.3	13 ± 2.5
		Unburned	11 ± 2.0[a]	10 ± 1.5[a]	12 ± 2.2	13 ± 2.0	13 ± 1.9
Calamovilfa longifolia (prairie sandreed)	Hilltop	Spring	42 ± 4.2[a]	40 ± 4.2[a]	46 ± 4.3[a]	35 ± 4.3[a]	31 ± 3.9[a]
		Summer	22 ± 3.0[b]	34 ± 3.5[a]	38 ± 4.1[a]	34 ± 4.1[a]	32 ± 4.1[a]
		Fall	38 ± 4.0[a]	—	44 ± 3.6[a]	37 ± 3.1[a]	36 ± 3.0[a]
		Unburned	18 ± 3.0[b]	20 ± 2.5[b]	23 ± 2.7[b]	21 ± 2.1[b]	16 ± 2.0[b]
	North-Facing Slope	Spring	3 ± 0.9[b]	8 ± 2.5[b]	7 ± 1.9[b]	6 ± 1.6[b]	3 ± 1.0[b]
		Summer	13 ± 2.7[a]	22 ± 3.6[a]	25 ± 3.8[a]	17 ± 2.8[a]	17 ± 3.2[a]
		Fall	12 ± 2.4[a]	—	15 ± 2.9[a]	12 ± 2.0[a]	9 ± 1.9[a]
		Unburned	6 ± 1.6[a]	8 ± 1.2[ab]	9 ± 2.4[b]	8 ± 1.6[ab]	3 ± 1.1[b]
	South-Facing Slope	Spring	37 ± 3.3	33 ± 3.2[a]	35 ± 3.8[ab]	23 ± 2.8[b]	19 ± 2.8
		Summer	26 ± 3.2	34 ± 3.5[a]	44 ± 3.4[a]	37 ± 3.6[a]	28 ± 2.7
		Fall	27 ± 3.2	—	29 ± 3.4[b]	24 ± 3.5[b]	21 ± 2.9
		Unburned	25 ± 3.1	23 ± 3.7[b]	31 ± 3.8[ab]	30 ± 3.8[ab]	25 ± 3.0
Carex spp. (sedge)	Hilltop	Spring	30 ± 2.6	22 ± 2.6	25 ± 2.8	18 ± 1.7	14 ± 1.4
		Summer	27 ± 3.6	21 ± 1.9	24 ± 2.6	19 ± 1.6	16 ± 1.8
		Fall	28 ± 2.1	—	24 ± 3.6	20 ± 2.5	13 ± 1.8
		Unburned	27 ± 3.0	18 ± 2.2	19 ± 2.6	19 ± 2.5	16 ± 1.8
	North-Facing Slope	Spring	24 ± 2.8	22 ± 3.6[b]	24 ± 3.3[ab]	20 ± 3.2	12 ± 1.1[b]
		Summer	28 ± 2.9	27 ± 3.0[a]	29 ± 3.1[a]	22 ± 2.6	18 ± 1.4[a]
		Fall	24 ± 2.9	—	28 ± 3.2[a]	21 ± 2.1	12 ± 1.4[b]
		Unburned	34 ± 3.8	14 ± 1.5[b]	18 ± 2.5[b]	18 ± 2.1	12 ± 1.4[b]
	South-Facing Slope	Spring	39 ± 3.8[b]	24 ± 2.6[b]	36 ± 3.6[a]	26 ± 3.0[b]	19 ± 2.6[bc]
		Summer	40 ± 2.7[b]	35 ± 3.5[ab]	43 ± 3.5[a]	26 ± 3.1[b]	23 ± 2.1[ab]
		Fall	25 ± 3.9[c]	—	26 ± 4.2[b]	22 ± 3.8[b]	15 ± 2.6[c]
		Unburned	60 ± 3.6[a]	29 ± 2.3[a]	40 ± 2.8[a]	49 ± 3.7[a]	28 ± 2.5[a]
Cyperus schweinitzii (umbrella sedge)	Hilltop	Spring	1 ± 0.5	7 ± 1.6	3 ± 0.9	3 ± 0.8	4 ± 1.0
		Summer	3 ± 0.9	8 ± 1.9	3 ± 0.8	6 ± 1.2	4 ± 1.0
		Fall	2 ± 0.9	—	4 ± 1.0	3 ± 1.0	6 ± 1.2
		Unburned	2 ± 0.7	5 ± 1.1	3 ± 0.9	4 ± 1.0	6 ± 1.2
	North-Facing Slope	Spring	tr.[b]	tr.[b]	tr.[b]	tr.[b]	1 ± 0.5[b]
		Summer	1 ± 0.5[ab]	5 ± 1.5[a]	1 ± 0.5[ab]	2 ± 0.7[a]	2 ± 0.5[ab]
		Fall	1 ± 0.7[ab]	—	3 ± 0.8[a]	2 ± 0.7[a]	2 ± 0.8[ab]
		Unburned	2 ± 0.7[a]	6 ± 1.2[a]	2 ± 0.8[ab]	4 ± 1.1[a]	3 ± 0.8[a]
	South-Facing Slope	Spring	1 ± 0.5	6 ± 1.2[a]	1 ± 0.2[ab]	1 ± 0.7	1 ± 0.5
		Summer	1 ± 0.2	3 ± 1.0[b]	3 ± 0.9[ab]	2 ± 0.7	3 ± 0.8
		Fall	1 ± 0.5	—	4 ± 0.9[a]	3 ± 0.9	3 ± 0.9
		Unburned	1 ± 0.2	2 ± 0.8[b]	1 ± 0.2[b]	2 ± 0.8	1 ± 0.5
Dalea villosa (silky prairie clover)	Hilltop	Spring	7 ± 2.2	7 ± 2.2[a]	7 ± 2.4	3 ± 1.5	4 ± 1.9
		Summer	2 ± 0.8	2 ± 0.8[ab]	2 ± 1.3	2 ± 1.4	1 ± 0.5
		Fall	3 ± 1.4	—	3 ± 1.0	1 ± 0.5	1 ± 0.5
		Unburned	2 ± 0.8	1 ± 0.5[b]	1 ± 0.5	1 ± 0.7	1 ± 0.5
	North-Facing Slope	Spring	tr.	0.0	0.0	0.0	tr.
		Summer	0.0	0.0	0.0	0.0	0.0
		Fall	0.0	—	0.0	0.0	0.0
		Unburned	0.0	0.0	0.0	0.0	0.0

Appendix 1. Continued.

Species or Group	Topographic Location	Treatment	Mean Canopy Cover ± Standard Error, by Year				
			1984	1985	1986	1987	1988
	South-Facing Slope	Spring	2 ± 0.9[a]	3 ± 1.5[a]	3 ± 1.5	3 ± 1.5	2 ± 0.9
		Summer	0.0[b]	tr.[b]	1 ± 0.5	1 ± 0.5	1 ± 0.5
		Fall	2 ± 0.9[a]	—	3 ± 1.8	1 ± 0.5	1 ± 0.5
		Unburned	0.0[b]	0.0[b]	tr.	tr.	tr.
Dichanthelium wilcoxianum (Wilcox dichanthelium)	Hilltop	Spring	0.0	1 ± 0.5	1 ± 1.2	1 ± 0.5[b]	1 ± 0.5
		Summer	2 ± 0.8	1 ± 0.5	1 ± 0.5	2 ± 0.9[a]	2 ± 0.8
		Fall	0.0	—	0.0	0.0[b]	4 ± 1.2
		Unburned	0.0	0.0	0.0	0.0[b]	0.0
	North-Facing Slope	Spring	11 ± 1.2[a]	8 ± 1.6[a]	13 ± 2.2[a]	12 ± 1.1[a]	11 ± 1.2[a]
		Summer	6 ± 1.7[b]	5 ± 1.9[b]	8 ± 2.2[b]	6 ± 1.3[b]	7 ± 1.3[b]
		Fall	4 ± 1.2[b]	—	1 ± 0.7[c]	2 ± 0.8[b]	0.0[b]
		Unburned	6 ± 1.7[b]	1 ± 0.5[c]	3 ± 1.0[bc]	5 ± 1.3[b]	5 ± 1.3[b]
	South-Facing Slope	Spring	0.0	0.0	0.0	0.0	0.0
		Summer	0.0	0.0	0.0	0.0	0.0
		Fall	0.0	—	0.0	0.0	0.0
		Unburned	0.0	0.0	0.0	0.0	0.0
Eragrostis trichodes (sand lovegrass)	Hilltop	Spring	8 ± 3.5[a]	4 ± 1.9[a]	3 ± 1.0	2 ± 1.3	4 ± 1.9
		Summer	8 ± 3.3[a]	2 ± 0.8[a]	2 ± 1.4	1 ± 0.5	4 ± 2.2
		Fall	1 ± 0.5[ab]	—	1 ± 0.5	1 ± 0.5	2 ± 1.4
		Unburned	0.0[b]	0.0[b]	0.0	0.0	0.0
	North-Facing Slope	Spring	29 ± 3.3[a]	22 ± 2.5[a]	10 ± 2.1	21 ± 2.4[a]	32 ± 3.6[a]
		Summer	20 ± 3.5[ab]	7 ± 1.3[b]	10 ± 1.9	17 ± 2.8[ab]	22 ± 3.2[ab]
		Fall	17 ± 4.0[b]	—	8 ± 2.2	13 ± 3.0[b]	20 ± 4.3[b]
		Unburned	23 ± 3.4[ab]	26 ± 4.9[a]	19 ± 3.1	28 ± 3.7[a]	34 ± 4.9[a]
	South-Facing Slope	Spring	4 ± 1.6	2 ± 0.8	2 ± 0.8	2 ± 0.9	tr.[c]
		Summer	12 ± 3.9	2 ± 1.4	5 ± 1.9	6 ± 2.7	7 ± 2.2[a]
		Fall	8 ± 3.1	—	3 ± 1.5	3 ± 1.5	6 ± 1.9[ab]
		Unburned	5 ± 1.5	4 ± 1.8	2 ± 0.9	3 ± 1.5	1 ± 0.7[bc]
Erigeron bellidiastrum (western fleabane)	Hilltop	Spring	1 ± 0.5[b]	tr.[ab]	tr.[c]	1 ± 0.2[b]	tr.
		Summer	3 ± 0.9[a]	0.0[b]	6 ± 1.5[a]	6 ± 1.5[a]	tr.
		Fall	4 ± 1.1[a]	—	1 ± 0.7[c]	12 ± 3.2[a]	1 ± 0.5
		Unburned	1 ± 0.5[b]	1 ± 0.7[a]	4 ± 1.8[b]	6 ± 1.9[b]	1 ± 0.5
	North-Facing Slope	Spring	0.0[b]	tr.	0.0[b]	tr.[b]	0.0
		Summer	4 ± 1.5[a]	0.0	2 ± 0.8[b]	tr.[b]	0.0
		Fall	1 ± 0.2[a]	—	tr.[b]	0.0[b]	0.0
		Unburned	3 ± 0.9[a]	tr.	4 ± 1.5[a]	1 ± 0.5[a]	1 ± 0.5
	South-Facing Slope	Spring	2 ± 0.7[ab]	0.0	1 ± 0.2	3 ± 1.0[a]	tr.[b]
		Summer	1 ± 0.7[b]	0.0	1 ± 0.2	tr.[b]	1 ± 0.5[ab]
		Fall	4 ± 1.1[a]	—	2 ± 1.2	6 ± 1.6[a]	2 ± 0.7[a]
		Unburned	1 ± 0.5[b]	0.0	tr.	1 ± 0.5[b]	tr.[ab]
Euphorbia missurica (Missouri spurge)	Hilltop	Spring	1 ± 0.7	1 ± 0.7	1 ± 0.2[b]	2 ± 0.8[ab]	1 ± 0.5
		Summer	1 ± 0.5	tr.	6 ± 1.5[a]	0.0[b]	6 ± 1.9
		Fall	1 ± 0.5	—	4 ± 0.9[a]	5 ± 1.6[a]	2 ± 0.8
		Unburned	2 ± 0.7	1 ± 0.5	2 ± 0.9[b]	2 ± 1.2[a]	5 ± 1.6
	North-Facing Slope	Spring	tr.[ab]	2 ± 0.7[a]	tr.[b]	tr.	1 ± 0.5
		Summer	1 ± 0.5[a]	0.0[b]	1 ± 0.2[b]	tr.	1 ± 0.5
		Fall	1 ± 0.7[a]	—	2 ± 0.5[a]	tr.	3 ± 1.0
		Unburned	0.0[b]	0.0[b]	tr.[c]	1 ± 0.5	1 ± 0.7
	South-Facing Slope	Spring	1 ± 0.5[ab]	1 ± 0.5	3 ± 0.9[a]	tr.[b]	1 ± 0.7[b]
		Summer	2 ± 0.7[a]	0.0	4 ± 0.9[a]	1 ± 0.5[ab]	tr.[b]
		Fall	1 ± 0.7[ab]	—	6 ± 1.1[a]	5 ± 1.6[a]	3 ± 1.0[a]
		Unburned	tr.[b]	tr.	2 ± 0.8[b]	1 ± 0.7[b]	1 ± 0.5[b]
Helianthus rigidus (stiff sunflower)	Hilltop	Spring	6 ± 1.7	7 ± 1.7[a]	10 ± 2.4[a]	9 ± 1.9[a]	9 ± 1.6[a]
		Summer	6 ± 1.7	4 ± 1.2[ab]	6 ± 1.7[ab]	5 ± 1.3[ab]	7 ± 1.4[a]
		Fall	2 ± 0.8	—	2 ± 0.8[b]	3 ± 1.0[b]	2 ± 0.9[b]
		Unburned	2 ± 0.9	1 ± 0.7[b]	2 ± 0.7[b]	3 ± 1.1[b]	3 ± 1.4[b]
	North-Facing Slope	Spring	6 ± 1.7[ab]	6 ± 1.3[a]	10 ± 2.3[a]	8 ± 1.4[a]	8 ± 1.7
		Summer	5 ± 1.3[ab]	3 ± 1.0[b]	9 ± 2.6[a]	8 ± 1.7[a]	8 ± 1.7
		Fall	7 ± 1.7[a]	—	10 ± 2.5[a]	7 ± 1.4[a]	7 ± 1.3
		Unburned	2 ± 0.9[b]	2 ± 0.8[b]	2 ± 0.9[b]	3 ± 1.0[b]	4 ± 1.3
	South-Facing Slope	Spring	0.0	0.0	1 ± 0.5	1 ± 0.5	1 ± 0.5
		Summer	1 ± 0.7	0.0	1 ± 0.5	1 ± 0.7	2 ± 0.8
		Fall	1 ± 0.7	—	2 ± 0.8	2 ± 0.8	1 ± 0.7
		Unburned	1 ± 0.5	1 ± 0.8	2 ± 1.3	2 ± 1.3	2 ± 0.9

Appendix 1. Continued.

Species or Group	Topographic Location	Treatment	Mean Canopy Cover ± Standard Error, by Year				
			1984	1985	1986	1987	1988
Koeleria pyramidata (junegrass)	Hilltop	Spring	1 ± 0.5	0.0[b]	2 ± 0.8	2 ± 1.4[b]	2 ± 0.9
		Summer	1 ± 0.5	tr.[ab]	3 ± 1.1	5 ± 1.7[ab]	3 ± 1.1
		Fall	1 ± 0.7	—	2 ± 0.8	5 ± 1.3[a]	4 ± 1.2
		Unburned	1 ± 0.7	2 ± 0.9[b]	3 ± 1.4	5 ± 1.3[a]	4 ± 1.2
	North-Facing Slope	Spring	12 ± 1.7	12 ± 1.4[b]	24 ± 2.2[b]	27 ± 2.1	12 ± 0.9
		Summer	10 ± 1.6	14 ± 2.2[b]	24 ± 2.2[b]	25 ± 2.7	15 ± 1.6
		Fall	13 ± 1.3	—	23 ± 2.9[b]	29 ± 2.6	19 ± 1.6
		Unburned	10 ± 1.5	31 ± 3.3[a]	40 ± 3.5[a]	32 ± 2.4	15 ± 0.8
	South-Facing Slope	Spring	0.0	0.0	0.0	0.0	0.0
		Summer	0.0	0.0	0.0	tr.	1 ± 0.5
		Fall	tr.	—	1 ± 0.5	1 ± 0.5	1 ± 0.5
		Unburned	0.0	tr.	1 ± 0.5	1 ± 0.5	0.0
Liatris squarrosa (gay-feather)	Hilltop	Spring	1 ± 0.5	tr.[b]	1 ± 0.5	2 ± 0.8	1 ± 0.7
		Summer	0.0	tr.[b]	1 ± 0.5	1 ± 0.5	1 ± 0.5
		Fall	1 ± 0.5	—	tr.	tr.	2 ± 0.8
		Unburned	tr.	1 ± 0.2[a]	1 ± 0.5	2 ± 0.9	2 ± 0.8
	North-Facing Slope	Spring	1 ± 0.5	2 ± 0.8[a]	1 ± 0.5[ab]	1 ± 0.7[b]	1 ± 0.7
		Summer	tr.	tr.[b]	1 ± 0.5[b]	tr.[b]	2 ± 0.8
		Fall	1 ± 0.7	—	4 ± 1.0[a]	4 ± 1.1[a]	3 ± 1.0
		Unburned	tr.	1 ± 0.5[b]	1 ± 0.5[b]	1 ± 0.5[b]	2 ± 0.8
	South-Facing Slope	Spring	0.0	tr.	tr.	1 ± 0.5	0.0
		Summer	0.0	0.0	tr.	0.0	0.0
		Fall	1 ± 1.5	—	1 ± 0.5	1 ± 0.5	1 ± 0.5
		Unburned	0.0	tr.	tr.	0.0	1 ± 0.5
Lithospermum incisum (narrow-leaved puccoon)	Hilltop	Spring	1 ± 0.5	0.0	tr.[ab]	tr.	0.0
		Summer	1 ± 0.5	tr.	1 ± 0.7[a]	1 ± 0.5	tr.
		Fall	1 ± 0.5	—	0.0[b]	0.0	0.0
		Unburned	tr.	1 ± 0.5	tr.[ab]	1 ± 0.5	1 ± 0.5
	North-Facing Slope	Spring	tr.	tr.	tr.	tr.	tr.
		Summer	1 ± 0.5	tr.	tr.	tr.	1 ± 0.5
		Fall	1 ± 0.5	—	3 ± 1.0	3 ± 1.0	1 ± 0.2
		Unburned	1 ± 0.7	1 ± 0.5	1 ± 0.7	2 ± 0.9	1 ± 0.5
	South-Facing Slope	Spring	0.0[b]	tr.	tr.	tr.[b]	tr.
		Summer	1 ± 0.5[a]	tr.	1 ± 0.2	2 ± 0.8[a]	1 ± 0.5
		Fall	1 ± 0.5[ab]	—	1 ± 0.5	0.0[b]	tr.
		Unburned	tr.[b]	tr.	1 ± 0.5	1 ± 0.7[b]	2 ± 0.8
Muhlenbergia pungens (sand muhly)	Hilltop	Spring	8 ± 2.2	3 ± 1.5[b]	5 ± 2.6[b]	4 ± 1.6[b]	4 ± 1.9[b]
		Summer	10 ± 2.5	1 ± 0.5[b]	1 ± 0.5[b]	1 ± 0.7[b]	1 ± 0.5[b]
		Fall	17 ± 4.0	—	4 ± 1.5[b]	6 ± 1.6[a]	7 ± 1.9[a]
		Unburned	21 ± 3.2	21 ± 3.8[a]	13 ± 2.7[a]	10 ± 1.9[a]	9 ± 1.9[a]
	North-Facing Slope	Spring	0.0	0.0	0.0	0.0	0.0
		Summer	0.0	0.0	0.0	0.0	0.0
		Fall	0.0	—	0.0	0.0	0.0
		Unburned	tr.	0.0	0.0	0.0	0.0
	South-Facing Slope	Spring	4 ± 2.2[b]	1 ± 0.7	2 ± 1.3[b]	2 ± 1.3[b]	2 ± 1.3[b]
		Summer	0.0[b]	0.0	0.0[b]	0.0[b]	0.0[b]
		Fall	14 ± 3.3[a]	—	5 ± 1.9[a]	7 ± 2.0[a]	7 ± 2.0a
		Unburned	4 ± 1.8[b]	2 ± 1.4	1 ± 0.7[b]	1 ± 0.7[b]	1 ± 0.7[b]
Solidago missouriensis (prairie goldenrod)	Hilltop	Spring	1 ± 0.7[b]	1 ± 0.2[b]	2 ± 0.8[b]	3 ± 1.0[b]	3 ± 1.3[b]
		Summer	2 ± 0.8[ab]	2 ± 0.9[ab]	3 ± 1.1[ab]	4 ± 1.2[ab]	2 ± 0.8[b]
		Fall	3 ± 0.7[ab]	—	5 ± 2.4[b]	4 ± 2.2[b]	2 ± 0.9[b]
		Unburned	4 ± 1.1[a]	6 ± 1.9[a]	8 ± 2.5[a]	9 ± 2.5[a]	7 ± 1.9[a]
	North-Facing Slope	Spring	2 ± 0.8[ab]	1 ± 0.7[a]	3 ± 1.0[b]	3 ± 1.1[a]	4 ± 1.2[a]
		Summer	tr.[b]	tr.[ab]	1 ± 1.0[b]	1 ± 0.5[b]	tr.[b]
		Fall	2 ± 0.7[a]	—	7 ± 2.2[a]	5 ± 1.6[a]	3 ± 1.0[a]
		Unburned	0.0[b]	0.0[b]	0.0[b]	tr.[b]	0.0[b]
	South-Facing Slope	Spring	1 ± 0.5[b]	1 ± 0.5[b]	tr.[ab]	1 ± 0.7	1 ± 0.5
		Summer	0.0[b]	0.0[b]	0.0[b]	tr.	tr.
		Fall	0.0[b]	—	1 ± 0.5[ab]	1 ± 0.7	1 ± 0.7
		Unburned	3 ± 1.0[a]	3 ± 1.5[a]	4 ± 1.8[a]	3 ± 1.1	4 ± 2.2
Sporobolus cryptandrus (sand dropseed)	Hilltop	Spring	9 ± 1.2[ab]	11 ± 1.5[ab]	11 ± 1.8	11 ± 1.5	9 ± 1.2
		Summer	12 ± 1.7[a]	19 ± 3.1[a]	12 ± 2.2	13 ± 1.6	9 ± 1.6
		Fall	8 ± 1.6[ab]	—	8 ± 1.2	10 ± 1.2	11 ± 1.5
		Unburned	6 ± 1.2[b]	7 ± 1.2[b]	7 ± 1.8	13 ± 1.9	12 ± 1.8

Appendix 1. Continued.

Species or Group	Topographic Location	Treatment	Mean Canopy Cover ± Standard Error, by Year				
			1984	1985	1986	1987	1988
	North-Facing Slope	Spring	8 ± 1.2	13 ± 1.6[a]	8 ± 1.6	12 ± 1.5	9 ± 1.2
		Summer	11 ± 1.5	19 ± 2.7[a]	7 ± 1.2	12 ± 1.7	8 ± 1.6
		Fall	7 ± 1.2	—	6 ± 1.2	9 ± 1.6	10 ± 1.3
		Unburned	6 ± 1.1	7 ± 1.3[b]	5 ± 1.5	11 ± 1.5	10 ± 1.5
	South-Facing Slope	Spring	10 ± 1.2[a]	12 ± 2.2	9 ± 1.2	11 ± 1.7	9 ± 1.2
		Summer	14 ± 1.8[a]	21 ± 2.8	11 ± 1.8	12 ± 2.0	9 ± 1.6
		Fall	4 ± 1.1[b]	—	7 ± 1.2	10 ± 1.2	8 ± 1.3
		Unburned	7 ± 1.1[a]	13 ± 2.1	8 ± 1.8	14 ± 1.7	13 ± 1.9
Stipa comata (needle-and-thread)	Hilltop	Spring	2 ± 1.0	3 ± 1.0	2 ± 0.9	1 ± 0.7	2 ± 0.8
		Summer	2 ± 1.4	1 ± 0.7	3 ± 1.4	3 ± 1.5	2 ± 0.9
		Fall	1 ± 0.7	—	1 ± 0.7	2 ± 1.4	1 ± 0.7
		Unburned	1 ± 0.7	1 ± 0.7	2 ± 0.9	2 ± 1.3	3 ± 1.0
	North-Facing Slope	Spring	15 ± 3.0[a]	14 ± 3.0	19 ± 3.9[a]	13 ± 2.7[a]	9 ± 1.6[a]
		Summer	13 ± 2.9[ab]	10 ± 1.9	17 ± 3.0[a]	12 ± 2.0[a]	10 ± 1.9[a]
		Fall	4 ± 1.2[b]	—	3 ± 1.0[b]	4 ± 1.2[b]	4 ± 1.2[b]
		Unburned	7 ± 2.3[b]	15 ± 2.6	13 ± 2.6[a]	11 ± 2.7[a]	14 ± 2.8[a]
	South-Facing Slope	Spring	1 ± 0.7[b]	2 ± 0.8[ab]	1 ± 0.5[b]	1 ± 0.5[b]	0.0[b]
		Summer	4 ± 1.6[a]	6 ± 2.1[a]	6 ± 1.9[a]	8 ± 2.5[a]	6 ± 2.0[a]
		Fall	0.0[b]	—	0.0[b]	0.0[b]	0.0[b]
		Unburned	tr.[b]	tr.[b]	0.0[b]	0.0[b]	0.0[b]
Yucca glauca (yucca)	Hilltop	Spring	1 ± 1.2	1 ± 0.5	1 ± 0.5	1 ± 0.5	1 ± 0.5
		Summer	4 ± 1.8	3 ± 2.1	3 ± 2.2	2 ± 1.4	1 ± 1.2
		Fall	5 ± 2.5	—	1 ± 0.5	1 ± 0.5	1 ± 0.7
		Unburned	0.0	0.0	0.0	0.0	0.0
	North-Facing Slope	Spring	0.0	0.0	0.0	0.0	0.0
		Summer	2 ± 2.1	2 ± 1.3	1 ± 0.7	1 ± 0.7	2 ± 1.3
		Fall	1 ± 0.7	—	1 ± 0.5	1 ± 0.5	0.0
		Unburned	3 ± 1.8	3 ± 1.8	2 ± 0.8	3 ± 1.8	2 ± 0.8
	South-Facing Slope	Spring	3 ± 2.8[ab]	2 ± 2.1	3 ± 2.8	3 ± 2.8	3 ± 2.1
		Summer	0.0[b]	0.0	0.0	0.0	0.0
		Fall	4 ± 1.8[a]	—	tr.	1 ± 0.5	2 ± 1.3
		Unburned	2 ± 1.3[ab]	2 ± 1.4	2 ± 1.4	2 ± 1.4	1 ± 0.7