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The effect of fire season and frequency on the plant community of a restored tallgrass prairie.

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THE EFFECT OF FIRE SEASON AND FREQUENCY ON

THE PLANT COMMUNITY OF A RESTORED TALLGRASS PRAIRIE

A Thesis

Presented to the

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and the

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Nathaniel David Birks

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Chairperson _[signature]_

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THE EFFECT OF FIRE SEASON AND FREQUENCY ON

THE PLANT COMMUNITY OF A RESTORED TALLGRASS PRAIRIE

Nathan D. Birks, MA

University of Nebraska, 2003

Advisor: Dr. Thomas Bragg

The effect of fire season and frequency was evaluated in 2001 at a 65 ha restored tallgrass prairie in eastern Nebraska using permanent plots established in 1978 and first evaluated in 1979. Treatments included annual and quadrennial burning in spring, summer, and fall as well as unburned plots. Overall, the number of species increased from 28 in 1979 to 30 in 2001, with a shift from ruderal to native species. Shannon diversity (H') increased significantly across all treatments during this time. Canopy cover of grasses (+19%) and forbs (+18%) increased significantly. However, only forbs showed a significant difference among treatments in 2001 with the lowest value occurring in the annual spring treatment (6%) and the highest value occurring in the annual variable-season treatment (35%).

The canopy cover of individual species showed varying responses to treatment. Native perennial grasses, such as big bluestem (*Andropogon gerardii*) and Indiangrass (*Sorghastrum nutans*), generally increased with more frequent burning, although there was considerable variation among seasonal treatments. Cool-season native sedges (*Carex* spp.) also increased significantly, although they did not show a differential response to treatment. In contrast, cool-season, non-native grasses, such as Kentucky bluegrass (*Poa pratensis*), increased significantly with quadrennial burns but remained

low or absent with frequent fire, irrespective of season. The response of forb species differed from that of grasses in that higher cover generally occurred with less frequent burning, or with annual fall or variable-season burning.

This study suggests that variation in fire season and frequency in the tallgrass prairie has the potential to affect diversity, species composition, species groups, and individual species. Overall, this study shows that fire management with different seasons and frequencies of burning can be used to maintain prairie diversity. More specifically, varying plant responses suggest that fire management should be applied with a more random and less systematic season and frequency than is typically applied in prescribed burning of tallgrass prairies in order to maximize diversity.

Introduction

Fire has long been an important factor in the dynamics and evolution of the Bluestem Prairie (*Andropogon – Panicum – Sorghastrum*), (Küchler, 1964), an ecosystem that extends from central Canada to northern Texas. Effects of fire include removal of litter (Aldous, 1934; Ehrenreich, 1959; Hover and Bragg, 1981; Hulbert, 1988), invigoration of prairie plants (Ehrenreich and Aikman, 1963; Hadley and Kieckhefer, 1963; Hulbert, 1988), and control of woody plants (Aldous, 1934; Anderson *et al.*, 1970; Bragg and Hulbert, 1976; Hover and Bragg, 1981) and exotic species (Aldous, 1934; Hulbert, 1986; Hickey, 1992; Leach and Givnish, 1996). Historically, lightning-caused and anthropogenic fires, occurred throughout the year, although summer fires most likely were less intense and smaller in size than dormant season burns (Aldous, 1934; Ehrenreich and Aikman, 1963; Anderson *et al.*, 1970; Hulbert, 1972; Moore, 1972; Hulbert, 1986; Ewing and Engle, 1988). The frequency with which fires occurred in the region is estimated to have varied from 1-7 years (Bragg and Hulbert, 1976; Hulbert, 1986; Frost, 1999). This variation in season and frequency of burning may account for much of the diversity in the tallgrass prairie.

Studies on fire frequency in the tallgrass prairie suggest that a 3-5 year burn interval best maintains a diverse tallgrass prairie community (Frost, 1999). Burning more frequently than this, for example annually, increases native warm-season grasses at the expense of forbs (Kucera, 1962; Hulbert, 1986; Collins, 1992). Burning less frequently allows for woody plant encroachment (Bragg and Hulbert, 1976; Hulbert, 1986).

The season during which fires occur is equally as important as fire frequency in affecting species composition (Anderson *et al.*, 1970; Towne and Kemp, 2003). Spring burns occuring after cool-season grasses have emerged, but while the warm-season grasses are still dormant, favor the latter. For example, spring burns (late April – early May) increase production in warm-season grasses such as big bluestem (*Andropogon gerardii*), little bluestem (*Andropogon scoparius*), and Indiangrass (*Sorghastrum nutans*), although they also have been reported to decrease diversity (Hulbert, 1986). In contrast to spring burns, summer burns (July or early August) decrease overall tallgrass prairie primary production, reflecting a decline in dominant warm-season grasses that is not offset by the resulting increase in production of cool-season grasses (Hover and Bragg, 1981; Hulbert, 1986). Fall burns (November - early March) occur after warm-season plants are dormant and result in an increase in forbs and cool-season plants, but at the expense of warm-season grasses (Hulbert, 1986; Bragg *et al.*, 1999).

European settlement of the tallgrass prairie region in the mid 1800's resulted in loss of much of the tallgrass prairie to agriculture and urbanization. In addition, the historic fire season and frequency were altered with the advent of active fire suppression resulting in various plant community responses, particularly woody plant encroachment (Bragg and Hulbert, 1976). Today, less than 1% of the tallgrass prairie remains (Samson and Knopf, 1996). Recent efforts, however, have worked to restore tallgrass prairie in various locations throughout its historic range (Masters, *et al.*, 2001; Brye, *et al.*, 2002). In addition, these efforts have been accompanied by studies on how to best manage restorations, with fire season and frequency being among the principal considerations

(Hover and Bragg, 1981; Hulbert, 1986; Ewing and Engle, 1988; Frost, 1999). Most

studies on fire-effects in restorations, however, have lacked a long-term perspective that

may give results that differ from inferences made from short-term studies (Kucera and

Ehrenreich, 1962). This study was initiated to provide such a long-term perspective with

a particular focus on variations in fire season and frequency. Specifically, I tested the

hypothesis that different regimes of fire season and frequency, applied between 1979 and

2001, would differentially affect plant diversity, species composition, species groups, and

individual species of a restored tallgrass prairie.

Materials and Methods

Study Site

The study was conducted at Allwine Prairie Preserve, a 65 ha restored prairie in eastern

Nebraska (41° 20′ 19″ N, 96° 08′ 30″ W) (Becic and Bragg, 1978) (Fig. 1). The preserve,

situated within the region described by Küchler (1964) as potential *Bluestem Prairie*

(*Andropogon – Panicum - Sorghastrum*), was variously cultivated with soybeans, corn,

and red clover for many years before its donation to the University of Nebraska at Omaha

in 1959 (Bragg, 1978). In 1970, five species of native grasses were drilled through

soybean stubble across much of the preserve: big bluestem, little bluestem, Indiangrass,

sideoats grama (*Bouteloua curtipendula*), and switchgrass (*Panicum virgatum*) (Bragg,

1978). No forbs were planted in the seed mix, although efforts to introduce forbs to the

preserve have been ongoing since 1972 (Bragg, personal communication).

N

Research
Plots

Fig. 1. Aerial photograph of Allwine Prairie in 1993 showing the general location of research plots. Several of the recently burned plots are clearly visible in the photo.

Since 1974, the preserve has been managed using a 3-year fire return interval of spring

burns (late April – early May) with occasional haying in early July.

Soils of the site are primarily Marshal-Ponca soils of the Mollisol soil order

(Bartlett, 1975). These are deep, well-drained, and nearly level to moderately sloping

silty loam to silty clay loam soils on loess uplands. Slopes range from 7-17%. Small

areas of Steinauer silty-clay loam soils, developed from glacial till, are also found within

the study area at the site. Annual precipitation for the region averages 758 mm with

approximately 67% occurring during the growing season (High Plains Regional Climate

Center, 2001; NOAA, 2001). During 2001, precipitation was near normal from January

to April, 211% above normal for May, 33% of normal for summer (June – August), and

normal for the remainder for the year.

Experimental Design

In 1976, a 5 ha area was set aside for a study designed to test the hypothesis that

long-term fire treatments, applied at different seasons and frequencies, could significantly

alter species composition and productivity. The study area, located on a generally north

facing slope, was divided into 57 plots (Fig. 1). While individual plot size varied because

of terrain characteristics, none was smaller than 15 by 20 m. In the spring of 1978, a 10-

m long transect, oriented up-slope to down-slope, was established in the center of each

plot. The plot-length was extended to 11-m in 2002. Transects were a minimum of 5

meters from any plot boundary. The endpoints of each transect were permanently

marked with metal, electrical conduit to facilitate relocation in subsequent years.

In order to enhance plant community diversity, and to better allow for extrapolation of results to native prairie, additional tallgrass prairie species were added to each plot. In early summer of 1978, three individual porcupine grass (*Stipa spartea*) plants, a cool-season species, were transplanted from a nearby tallgrass prairie and placed at the midpoint of each of the 10-m transects in all plots. These transplants also appear to have inadvertently introduced sedges (*Carex* spp.), primarily Mead's sedge (*Carex meadii*), another cool-season genus. In 1979, locally collected seeds from eight species of prairie forbs were systematically scattered in rows at right angles to each transect throughout each plot. Forb species scattered were: black-eyed Susan (*Rudbekia hirta*), downy gentian (*Gentiana puberulenta*), white aster (*Aster ericoides*), Illinois tickclover (*Desmodium illinoense*), leadplant (*Amorpha canescens*), tall cinquefoil (*Potentilla arguta*), white prairie clover (*Dalea candida*), and wild white indigo (*Baptisia lactea*). No burns occurred two years before or three years after the introduction of these species.

In 1979, each of the fifty-seven plots was randomly assigned one of nineteen treatments. Treatments included annual through decennial burns applied in the spring (ca. 1 May), summer (ca. 1 July), fall (ca. 1 Nov.), or with the season varied on a rotating schedule (variable-season plots). In addition, a control treatment remained unburned. Each treatment was replicated three times. Non-prairie, woody vegetation has been regularly removed from all plots.

All plots were first evaluated in 1979 by quantifying plant-community characteristics in each of ten, 30 by 50 cm microplots systematically located along a meter tape stretched between the two metal stakes (Bragg, unpublished). The size and

number of microplots evaluated was determined from a previous study on a nearby, native, tallgrass prairie in which 90% of all species found in larger samples were identified in 10, 30 × 50 cm microplots (Bragg, 1991). The first microplot was placed at the 0.5-m mark on the west (or north) side of the tape starting at the upper (base) metal stake. Plots were oriented so that the long axis of the microplot was perpendicular to the tape. Subsequent microplots were at 1-m intervals on alternating sides of the tape, ending with the last microplot on the east (or south) side of the tape at the 9.5-m mark. Within each microplot, canopy cover was evaluated using categories modified from Daubenmire (1959): 0%, <5%, 5-25%, 25-50-%, 50-75%, 75-95%, and >95%. The midpoint of each group was used for statistical analysis. Canopy cover data were collected both for individual species and for species groupings: grasses, forbs, and woody vegetation. Nomenclature for this study is from Great Plains Flora Association (1986).

In 2001, nine of the initial 19 treatments, each replicated three times, were selected for study: no-burning and annual or quadrennial burns applied during spring, summer, fall, or with the season of burning varied from year to year. Treatment plots were evaluated from June 3-7, 2001 and again from August 6-10, 2001. Sampling protocol in 2001 was the same as that used in 1979 except that canopy cover categories varied somewhat: 0%, <1%, 1 - 5%, 5 - 25%, 25 - 50%, 50 - 75, 75 - 95%, 95 - 99%, and >99%. The change in <5% cover was made to distinguish between trace cover (<1%) and small cover (1 - 5%) rather than lumping both groups in the <5% category. The change in >95% cover was made to separate those species whose cover was continuous from those nearly so.

Statistical Analysis

Statistical analyses were based on average canopy cover values obtained by combining raw data from all three replicates of each treatment. Differences in average canopy cover of each species or species group between 1979 and 2001 were tested using a *t*-test (Zar, 1984). Differences in species cover among treatments in 1979 and in 2001 were tested using the parametric ANOVA and the non-parametric Student-Newman-Keuls (SNK) tests. ANOVA was used because it is a procedure that is robust, both with regard to heterogeneity of variance and assumptions of normality, so long as sample sizes are equal (Zar, 1984, page 170). The non-parametric SNK test was used because parametric multiple comparison tests are not as robust. Significant differences in species diversity between years and among treatments were calculated using the Shannon-Wiener Diversity Index (H') following procedures described by Zar (1984). This procedure involves testing each community against each other community, one pair at a time. No procedures are available to provide among-treatment multiple comparison tests based on the Shannon-Wiener Index.

Results and Discussion

Two overall results were apparent from this study. First, there was an increase in native and a decrease in non-native species from 1979 to 2001, although Species Richness did not change substantially. Second, different types of management resulted in significantly different grassland plant communities as reflected in species diversity, community composition, and individual species cover.

Effect on Diversity

For combined treatments, the number of native prairie species (i.e. Species Richness) increased from 17 in 1979 to 27 in 2001, although total Species Richness increased only from 28 to 30 (Table 1). This difference largely reflects the offsetting effect of an increase in native and a decline in ruderal species. While the increase in total Species Richness between 1979 and 2001 is only slight, there is a more pronounced increase in diversity when assessing species composition based in the Shannon-Wiener Diversity Index (H'), a measure of evenness. Based on this index, average species diversity increased from 1979 (H' = 0.5171) to 2001 (H' = 0.7700), a difference that was significant for all treatments, including the control ($P \leq 0.05$, t-test) (Zar, 1984) (Table 2).

The increase in native prairie species was expected, in part because of their intentional introduction to the plots immediately following the 1979 evaluation and in part because of the natural immigration, over time, of other native species such as prairie goldenrod (*Solidago missouriensis*) and white-eyed grass (*Sisyrinchium campestre*). The general shift from early seral species, such as common dandelion (*Taraxacum officinale*), goat's beard (*Tragopogon dubius*), and wild lettuce (*Lactuca* spp.), to native prairie species more characteristic of mature communities, such as prairie violet (*Viola pedatifida*), white-eyed grass, and downy gentian (Tables 3-4), characterize the process of directional ecological succession that may have typified historic regional community dynamics.

No significant differences in Shannon diversity were found among treatment plots in 1979 (Table 2). By 2001, however, all differed significantly ($P \leq 0.05$, t-test) (Zar,

Table 1. Species Richness by treatment and year for all species and for all native prairie species.

Burn Treatment		All Species		Prairie Species	
Frequency	Season	1979	2001	1979	2001
Annual	Spring	14	7	5	7
	Summer	16	15	8	15
	Fall	16	19	9	16
	Variable	11	18	6	18
Quadrennial	Spring	12	18	8	15
	Summer	13	19	8	18
	Fall	12	15	8	14
	Variable	11	16	9	14
Control	Unburned	14	13	9	11
Total		28	30	17	27

Table 2. Shannon-Wiener Diversity Index (H′) values for 1979 and 2001. No significant differences were found among treatments in 1979; each treatment differed significantly from each other treatment in 2001 ($P \leq 0.05$, t-test) (Appendix Table 1). * = a significant difference between 1979 and 2001 (Zar, 1984).

Burn Treatment		1979	2001
Annual	Spring*	0.5676	0.6639
	Summer*	0.5273	0.7462
	Fall*	0.4858	0.8316
	Variable*	0.5111	0.8455
Quadrennial	Spring*	0.5167	0.7829
	Summer*	0.4058	0.8463
	Fall*	0.5606	0.7336
	Variable*	0.5631	0.7598
Control	Unburned*	0.5162	0.7203

Table 3. Canopy cover by species for annually burned and control treatment areas in 1979 and 2001. tr = ≤0.5%. SE = Standard Error. For each species, P = probability values from t-test between 1979 and 2001; mean values indicated with a single asterisk (*) are considered to differ significantly between years (P ≤ 0.05). No significant differences were found among treatments for any species in 1979 (P ≤ 0.05). For each species, Student-Newman-Keuls (SNK) test results are indicated beneath t-test P-values; different letters indicate significant differences among treatments with Table 4 considered a continuation of Table 3. ** = native species. Species are ordered alphabetically by genus.

| | | Annual | | | | | | | | | Control | | | | | |
| | | Spring | | | Summer | | | Fall | | | Variable | | | Unburned | | |
Species	Year	X̄	SE	P / SNK	X̄	SE	P / SNK	X̄	SE	P / SNK	X̄	SE	P / SNK	X̄	SE	P / SNK
Total Cover	1979	83	1.3	<0.0001	82	1.4	<0.0001	81	1.6	<0.0001	82	1.4	<0.0001	83	1.3	<0.0001
	2001	100*	0.0	A	100*	0.0	A	100*	0.0	A	100*	0.0	A	100*	0.0	A
Litter	1979	62	1.4	<0.0001	61	1.2	<0.0001	62	1.6	<0.0001	58	1.7	<0.0001	64	1.0	<0.0001
	2001	3*	0.6	D*	10*	1.5	C	8*	1.5	C	17*	2.8	B	100*	0.0	A
Bare Soil	1979	tr		<0.0001	tr		<0.0001	1	0.5	<0.0001	2	0.8	<0.0001	tr		0.0261
	2001	39*	2.4	A	36*	2.3	A	26*	2.7	B	30*	3.0	B	0*	3.0	C
Grass	1979	81	1.6	<0.0001	83	1.3	<0.0001	81	1.7	<0.0001	80	1.8	<0.0001	81	1.6	<0.0001
	2001	100*	0.0	A	100*	0.0	A	100*	0.0	A	99*	0.1	B	100*	0.0	A
Forbs	1979	tr		0.0405	tr		0.0012	tr		<0.0001	tr		<0.0001	tr		0.0269
	2001	6*	2.5	C	13*	3.6	A,B,C	26*	4.6	A	35*	6.5	A,B	10*	4.3	C
Woody Vegetation	1979	tr		0.3215	0			0			0			0		0.3215
	2001	0		B	0		B	0		B	0		B	tr		B
Moss	1979	0			0			0		0.0003	0			0		
	2001	0		B	0		B	tr*		A	0		B	0		B

Table 3. Canopy cover by species for annually burned and control treatment areas in 1979 and 2001.

Species	Year	Annual												Control		
		Spring			Summer			Fall			Variable			Unburned		
		X̄	SE	P (SNK)	X̄	SE	P (SNK)	X̄	SE	P (SNK)	X̄	SE	P (SNK)	X̄	SE	P (SNK)
Box Elder	1979	0			0			0			0			tr		0.3215
Acer negundo	2001	0		B	0		B	0		B	0		B	0		B
Leadplant **	1979	0			0		0.2292	0		0.0646	0		0.3215	0		0.0965
Amorpha canescens	2001	0		A	3	2.1	A	5	2.4	A	1	0.5	A	11	2.6	A
Big Bluestem **	1979	12	2.5	<0.0001	10	2.3	<0.0001	11	2.6	<0.0001	15	3.2	<0.0001	9	1.8	<0.0001
Andropogon gerardii	2001	70*	5.9	A	75*	4.4	A	52*	6.0	A	63*	6.5	A	84*	4.1	A
Little Bluestem **	1979	41	4.3	0.8413	44	4.7	<0.0001	42	5.2	0.0338	37	4.8	0.9966	44	4.8	<0.0001
Andropogon sccparius	2001	39	6.2	A,B,C	17*	4.2	B,C,D	59*	6.0	A	39	6.0	A,B	16*	4.6	B,C,D
Field Pussy-toes **	1979	0			0		0.0779	0			0		0.1249	0		
Antennaria neglecta	2001	0		A	tr		A	0		A	1	0.7	A	0		A
White Aster **	1979	0			0			0		0.2143	0		0.0079	0		0.1555
Aster ericoides	2001	0		C	0		C	3	2.1	A,B,C	7*	2.4	A	1	0.7	B,C
Missouri Milk-vetch **	1979	0			0			0		0.2519	0			0		
Astragalus missouriensis	2001	0		A	0		A	1	0.7	A	0		A	0		A
White Wild Indigo **	1979	0		0.1555	0			0		0.0599	0		0.0255	0		0.1249
Baptisia lactea	2001	1	0.7	A	0		A	2	0.8	A	11*	5.0	A	1	0.7	A
Sideoats Grama **	1979	6	1.5	0.0001	13	2.4	<0.0001	7	2.1	0.0019	13	2.9	<0.0001	9	2.1	<0.0001
Bouteloua curtipendula	2001	0*		A	1*	0.7	A	tr*		A	tr*		A	tr*		A

Table 3. Canopy cover by species for annually burned and control treatment areas in 1979 and 2001.

Species	Year	Annual — Spring X	SE	P / SNK	Annual — Summer X	SE	P / SNK	Annual — Fall X	SE	P / SNK	Annual — Variable X	SE	P / SNK	Control — Unburned X	SE	P / SNK
Smooth Brome	1979	tr		0.1555	tr		0.0779	tr		0.3199	0			tr		0.0021
Bromus inermis	2001	0		B	0		B	1	0.5	B	0		B	9*	2.7	A
Sedge **	1979	0		<0.0001	tr		0.0009	tr		0.0006	0		<0.0001	0		0.001
Carex species	2001	19*	3.9	A	14*	3.9	A	15*	4.3	A	18*	3.5	A	6*	1.6	A
Horse-weed **	1979	tr		0.1555	tr		0.3215	tr		0.3215	tr		0.3215	tr		0.0779
Conyza canadensis	2001	0		A	0		A	0		A	0		A	0		A
White Prairie-clover **	1979	0		0.0317	0		0.1335	0		0.0095	0		0.0019	0		
Dalea candida	2001	4*	1.9	A,B	2	1.3	A,B	10*	3.8	A	18*	5.5	A	0		B
Illinois Tickclover **	1979	0			0			0		0.083	0		0.3215	0		0.3215
Desmanthus illinoensis	2001	0		B	0		B	5*	2.9	A,B	1	0.5	A,B	0		B
Scribners Panic Grass **	1979	0			tr		0.3215	0		0.3215	0		0.3215	tr		
Dicanthelium oligosanthes	2001	0		B	0		B	0		B	0		B	0		B
var. scribnerarum																
Purple Lovegrass **	1979	0			0		0.0081	0			0			0		
Eragrostis spectabilis	2001	0		B	7*	2.7	A	0		B	0		B	0		B
Daisy Fleabane **	1979	tr		0.0779	tr		0.3215	0			0		0.3215	tr		0.3215
Erigeron strigosus	2001	0		A	0		A	0		A	tr		A	0		A

Table 3. Canopy cover by species for annually burned and control treatment areas in 1979 and 2001.

Species	Year	Annual												Control		
		Spring			Summer			Fall			Variable			Unburned		
		X̄	SE	P (SNK)	X̄	SE	P (SNK)	X̄	SE	P (SNK)	X̄	SE	P (SNK)	X̄	SE	P (SNK)
Flowering Spurge **	1979	0			0			0			0			0		0.3215
Euphorbia corollata	2001	0		A	0		A	0		A	0		A	tr		A
Spurge **	1979	0			0			tr		0.3215	0			0		
Euphorbia species	2001	0		A	0		A	0		A	0		A	0		A
Downy Gentian **	1979	0			0			0			0			0		
Gentian puberulenta	2001	0		B	0		B	0		B	0		B	0		B
Junegrass **	1979	0			0		0.1249	0			0			0		
Koeleria pyramidata	2001	0		B	1	0.7	A	0		B	0		B	0		B
False Boneset **	1979	0			tr		0.3215	0			0			0		
Kuhnia eupatoroides	2001	0		A	0		A	0		A	0		A	0		A
Lettuce	1979	tr		0.0192	tr		0.0019	tr		0.0093	tr		0.0093	tr		<0.0001
Lactuca species	2001	0*		A	0*		A	0*		A	0*		A	0*		A
Sweet Clover	1979	0			0			tr		0.2383	0			0		
Melilotus species	2001	0		B	0		B	1	0.5	B	0		B	0		B
Grey-green Wood Sorrel	1979	tr		0.0093	tr		0.1555	tr		0.1555	tr		0.3215	tr		0.0779
Oxalis dillenii	2001	0*		A	0		A	0		A	0		A	0		A
Switchgrass **	1979	tr		<0.0001	1	0.5	0.5216	tr		0.0002	tr		0.0013	tr		0.0458
Panicum virgatum	2001	29*	4.2	A	2	1.3	C	14*	3.5	B	9*	2.4	B,C	5*	2.4	B,C

Table 3. Canopy cover by species for annually burned and control treatment areas in 1979 and 2001.

Species	Year	Annual — Spring X̄	SE	P	SNK	Summer X̄	SE	P	SNK	Fall X̄	SE	P	SNK	Variable X̄	SE	P	SNK	Control — Unburned X̄	SE	P	SNK
Ground Cherry ** *Physalis species*	1979	0				0				0				0				0			
	2001	0			A	0			A	0			A	0			A	0			A
Virginia Ground Cherry ** *Physalis virginiana*	1979	tr		0.3215		0				0				0				0			
	2001	0			A	0			A	0			A	0			A	0			A
Kentucky Bluegrass *Poa pratensis*	1979	0				tr		0.0011		tr		0.5614		tr		0.3215		2	1.2	<0.0001	
	2001	0			D	9*	2.6		C	tr			D	0			D	38*	5.6		A
Whorled Milkwort ** *Polygala verticillata*	1979	0				0				0				0				0			
	2001	0			A	0			A	0			A	0			A	0			A
Black-eyed Susan ** *Rudbeckia hirta*	1979	0				0				0				0				0			
	2001	0			B	0			B	1	0.5	0.1473	A	tr		0.0779	A,B	0			B
White-eyed grass ** *Sisyrinchium campesure*	1979	0				0				0				0				0			
	2001	0			A	1	0.5	0.1099	A	tr		0.3215	A	1	0.5	0.1473	A	0			A
Prairie Goldenrod ** *Solidago missouriensis*	1979	0				0				tr				0				0			
	2001	0			A	tr*		0.039	A	0		0.3215	A	tr		0.3215	A	1	0.5	0.3215	A
Indiangrass ** *Sorghastrum nutans*	1979	7	1.6			6	1.8			6	1.2			5	1.1			9	2.6		
	2001	10	2.7	0.4123	B	16*	2.8	0.0042	A,B	10	2.4	0.1998	B	14*	3.8	0.0202	B	8	2.2	0.8721	B
Porcupine-grass ** *Stipa spartea*	1979	tr				1.0	0.5			1	0.5			tr				tr			
	2001	0		0.1555	A	2	2.1	0.5114	A	1	0.7	0.5358	A	2	2.1	0.3454	A	0		0.1771	A

Table 3. Canopy cover by species for annually burned and control treatment areas in 1979 and 2001.

Species	Year	Annual												Control		
		Spring			Summer			Fall			Variable			Unburned		
		X̄	SE	P	X̄	SE	P	X̄	SE	P	X̄	SE	P	X̄	SE	P
				SNK			SNK			SNK			SNK			SNK
Common Dandelion	1979	tr		0.0779	tr		0.3215	tr		0.0779	tr		0.3215	0		
Taraxacum officinale	2001	0		A	0		A	0		A	0		A	0		A
Field Pennycress **	1979	0			0		0.0504	0			0		0.3215	0		
Thlaspi arvense	2001	0		B	tr		A	0		B	tr		B	0		B
Goat's Beard	1979	0			0			0			0			0		
Tragopogon dubius	2001	0		A	0		A	0		A	0		A.	0		A
Elm	1979	tr		0.1555	0			0			0			0		
Ulmus species	2001	0		A	0		A	0		A	0		A	0		A
Prairie Violet **	1979	0			0			0			0			0		
Viola pedatifida	2001	0		B	0		B	0		B	0.		B	0		B

Table 4. Canopy cover by species for quadrennially burned and control treatment areas in 1979 and 2001. tr = ≤0.5%. SE = Standard Error. For each species, P = probability values from *t*-test between 1979 and 2001; mean values indicated with a single asterisk (*) are considered to differ significantly between years (P ≤ 0.05). No significant differences were found among treatments for any species in 1979 (P ≤ 0.05). For each species, Student-Newman-Keuls (SNK) test results are indicated beneath *t*-test P-values; different letters indicate significant differences among treatments with Table 4 considered a continuation of Table 3. ** = native species. Species are ordered alphabetically by genus.

Species	Year	Quadrennial																Control			
		Spring				Summer				Fall				Variable				Unburned			
		X̄	SE	P	SNK	X̄	SE	P	SNK	X̄	SE	P	SNK	X̄	SE	P	SNK	X̄	SE	P	SNK
Total Cover	1979**	83	1.3	<0.0001	A	79	2.2	<0.0001	A	81	1.6	<0.0001	A	81	1.6	<0.0001	A	83	1.3	<0.0001	A
	2001	100*	0.0		A	100*	0.0		A	100*	0.0		A	100*	0.0		A	100*	0.0		A
Litter	1979	57	2.0	<0.0001	A	57	2.2	<0.0001	A	60	1.4	<0.0001	A	58	1.7	<0.0001	A	64	1.0	<0.0001	A
	2001	100*	0.0		A	100*	0.0		A	100*	0.0		A	100*	0.0		A	100*	0.0		A
Bare Soil	1979	tr		0.0013	C	1	0.5	0.031	C	1	0.5	0.0472	C	tr		0.0008	C	tr		0.0261	C
	2001	0*			C	0*			C	0*			C	0*			C	0*			C
Grass	1979	81	1.7	<0.0001	A	78	2.2	<0.0001	A	81	1.6	<0.0001	A	81	1.7	<0.0001	A	81	1.6	<0.0001	A
	2001	100*	0.0		A	99*	0.1		A	100*	0.0		A	100*	0.0		A	100*	0.0		A
Forbs	1979	tr		0.0005	A,B,C	tr		<0.0001	A	tr		0.0015	B,C	1	0.5	0.0008	A,B,C	tr		0.0269	C
	2001	17*	4.7		A,B,C	22*	4.9		A	15*	4.5		B,C	20*	5.3		A,B,C	10*	4.3		C
Woody Vegetation	1979	0		0.0779	A	tr		0.3215	B	tr		0.3215	B	0			B	0		0.3215	B
	2001	tr			A	0			B	0			B	0			B	tr			B
Moss	1979	0				0				0				0				0			
	2001	0			B	0			B	0			B	0			B	0			B

Table 4. Canopy cover by species for quadrennially burned and control treatment areas in 1979 and 2001.

Species	Year	Quadrennial Spring X̄	SE	P SNK	Summer X̄	SE	P SNK	Fall X̄	SE	P SNK	Variable X̄	SE	P SNK	Control Unburned X̄	SE	P SNK
Box Elder	1979	tr		0.0779	tr		0.3215	0			0			tr		0.3215
Acer negundo	2001	0		A	0		B	0		B	0		B	0		B
Leadplant **	1979	0		0.0424	0		0.0967	0		0.0738	0		0.0474	0		0.0965
Amorpha canescens	2001	9*	4.3	A	7	3.9	A	7	4.1	A	8*	3.9	A	11	2.5	A
Big Bluestem **	1979	14	2.2	<0.0001	7	2.4	<0.0001	11	2.3	<0.0001	9	2.3	<0.0001	9	1.8	<0.0001
Andropogon gerardii	2001	80*	3.6	A	79*	4.0	A	87*	4.0	A	88*	2.1	A	84*	4.1	A
Little Bluestem **	1979	35	5.2	0.0002	49	4.5	<0.0001	33	4.2	<0.0001	36	5.0	<0.0001	44	4.8	<0.0001
Andropogon scoparius	2001	12*	2.8	C,D	20*	4.1	A,B,C,D	5*	1.6	C,D*	10*	3.1	D	16*	4.6	B,C,D
Field Pussy-toes **	1979	0			0			0			1	0.5	0.3215	0		
Antennaria neglecta	2001	0		A	0		A	0		A	0		A	0		A
White Aster **	1979	0			0		0.1146	0		0.0269	0		0.173	0		0.1555
Aster ericoides	2001	0		C	5	2.9	A,B,C	3	1.5	A,B*	2	1.3	A,B,C	1	0.7	B,C
Missouri Milk-vetch **	1979	0			0			0			0			0		
Astragalus missouriensis	2001	0		A	0		A	0		A	0		A	0		A
White Wild Indigo **	1979	0		0.0628	0		0.1004	0		0.2905	0		0.2486	0		0.1249
Baptisia lactea	2001	2	0.8	A	2	1.4	A	1	1.2	A	3	2.9	A	1	0.7	A
Sideoats Grama **	1979	13	2.5	<0.0001	9	1.8	<0.0001	16	2.8	<0.0001	14	2.9	<0.0001	9	2.1	<0.0001
Bouteloua curtipendula	2001	tr*		A	tr*		A	1*	0.5	A	tr*		A	tr*		A

Table 4. Canopy cover by species for quadrennially burned and control treatment areas in 1979 and 2001.

Species	Year	Quadrennial												Control		
		Spring			Summer			Fall			Variable			Unburned		
		X̄	SE	P / SNK	X̄	SE	P / SNK	X̄	SE	P / SNK	X̄	SE	P / SNK	X̄	SE	P / SNK
Smooth Brome	1979	tr		0.5654	0			0			0		0.1417	tr		0.0021
Bromus inermis	2001	tr	2.0	B	0		B	0		B	1	0.7	B	9*	2.7	A
Sedge **	1979	tr		0.0004	tr		<0.0001	tr		<0.0001	0		0.0019	0		0.001
Carex species	2001	8*	2.0	A	16*	3.1	A	7*	1.7	A	3*	1.0	A	6*	1.6	A
Horse-weed **	1979				tr		0.1555	tr		0.039	tr		0.241	tr		0.0779
Conyza canadensis	2001	0		A	0		A	0*		A	0		A	0		A
White Prairie-clover **	1979	0		0.2519	0		0.0849	0		0.0646	0		0.0815	0		
Dalea candida	2001	1	0.5	B	4	2.2	A,B	3	1.5	B	4	2.4	B	0		B
Illinois Tickclover **	1979	0		0.0495	0		0.1935	0		0.3215	0		0.1555	0		
Desmanthus illinoensis	2001	3*	1.5	A	2	1.3	A,B	tr		A,B	1	0.7	A,B	0		B
Scribner's Panic Grass **	1979	0		0.173	tr		0.3215	0			0			tr		0.3215
Dicanthelium oligosanthes var. scribnerianum	2001	2	1.3	A	0		B	0		B	0		B	0		B
Purple Lovegrass **	1979	0			0			0			0			0		
Eragrostis spectabilis	2001	0		B	0		B	0		B	0		B	0		B
Daisy Fleabane **	1979	0			0			tr		0.1555	tr		0.3215	tr		0.3215
Erigeron strigosus	2001	0		A	0		A	0		A	0		A	0		A

Table 4. Canopy cover by species for quadrennially burned and control treatment areas in 1979 and 2001.

Species	Year	Quadrennial — Spring				Quadrennial — Summer				Quadrennial — Fall				Quadrennial — Variable				Control — Unburned			
		X̄	SE	P	SNK	X̄	SE	P	SNK	X̄	SE	P	SNK	X̄	SE	P	SNK	X̄	SE	P	SNK
Flowering Spurge **	1979	0		0.3215		0				0				0				0		0.3215	
Euphorbia corollata	2001	1	0.5		A	0				0			A	0			A	tr			A
Spurge **	1979	0				0				0				tr				0			
Euphorbia species	2001	0			A	0			A	0			A	0		0.3215	A	0			A
Downy Gentian **	1979	0				0		0.0779		0		0.3215		0		0.2519		0			
Gentian puberulenta	2001	0			B	1	0.7		A	tr			B	1	0.5		B	0			B
Junegrass **	1979	0				0		0.3215		0				0				0			
Koeleria pyramidata	2001	0			B	tr			B	0			B	0			B	0			B
False Boneset **	1979	0				0				0				0				0			
Kuhnia eupatoriodes	2001	0			A	0			A	0			A	0			A	0			A
Lettuce	1979	tr		0.0001		1	0.5	0.1527		tr	0.5	0.0043		tr		0.0799		tr		<0.0001	
Lactuca species	2001	0*			A	0			A	0*			A	0			A	0*			A
Sweet Clover	1979	0		0.3215		0				0				0				0			
Melilotus species	2001	1	0.5		B	0			B	0			B	0			B	0			B
Grey-green Wood Sorrel	1979	tr		0.3215		tr		0.039		tr		0.0192		tr		0.0043		tr		0.0779	
Oxalis dellenii	2001	0			A	0*			A*	0*			A	0*			A	0			A
Switchgrass **	1979	tr		0.0061		tr		0.0316		1	0.5	0.0169		1	0.5	0.0237		tr		0.0458	
Panicum virgatum	2001	10*	3.5		B,C	7*	2.9		B,C	11*	4.1		B,C	8*	2.9		B,C	5*	2.4		B,C

Table 4. Canopy cover by species for quadrennially burned and control treatment areas in 1979 and 2001.

Species	Year	Quadrennial — Spring X̄	Spring SE	Spring P (SNK)	Summer X̄	Summer SE	Summer P (SNK)	Fall X̄	Fall SE	Fall P (SNK)	Variable X̄	Variable SE	Variable P (SNK)	Control — Unburned X̄	Unburned SE	Unburned P (SNK)
Ground Cherry **	1979	tr		0.1625	0		0.2519	0			0			0		
Physalis species	2001	1	0.7	A	1	0.5	A	0		A	0		A	0		A
Virginia Ground Cherry **	1979	0			0			0			0			0		
Physalis virginiana	2001	0		A	0		A	0		A	0		A	0		A
Kentucky Bluegrass	1979	tr		<0.0001	tr		<0.0001	0		<0.0001	0		<0.0001	2	1.2	<0.0001
Poa pratensis	2001	65*	5.5	A	24*	4.3	A	40*	7.8	B	48*	5.3	A	38*	5.6	A
Whorled Milkwort **	1979	0			0			0			tr		0.3215	0		
Polygala verticillata	2001	0		A	0		A	0		A	0		A	0		A
Black-eyed Susan **	1979	0		0.3215	0			0			0			0		
Rudbeckia hirta	2001	tr		B	0		B	0		B	0		B	0		B
White-eyed grass **	1979	0			0		0.1555	0		0.0779	0			0		
Sisyrinchium campestre	2001	0		A	tr		A	tr		A	0		A	0		A
Prairie Goldenrod **	1979	0		0.0886	0		0.039	0			0		0.1555	0		0.3215
Solidago missouriensis	2001	2	1.4	A	tr*		A	0		A	tr		A	1	0.5	A
Indiangrass **	1979	5	1.5	0.0001	1	0.2	<0.0001	7	1.8	0.0273	7	1.6	<0.0001	9	2.6	0.8721
Sorghastrum nutans	2001	24*	4.2	A,B	18*	2.9	A,B*	17*	4.1	A,B	27*	4.1	A	8	2.2	B
Porcupine-grass **	1979	tr		0.0604	1	0.7	0.5352	tr		0.1303	tr		0.3389	tr		0.1771
Stipa spartea	2001	0		A	1	0.5	A	4	2.4	A	3	2.8	A	0		A

Table 4. Canopy cover by species for quadrennially burned and control treatment areas in 1979 and 2001.

Species	Year	Quadrennial												Control		
		Spring			Summer			Fall			Variable			Unburned		
		X̄	SE	P (SNK)	X̄	SE	P (SNK)	X̄	SE	P (SNK)	X̄	SE	P (SNK)	X̄	SE	P (SNK)
Common Dandelion	1979	0			0			0			0			0		
Taraxacum officinale	2001	0		A	0		A	0		A	0		A	0		A
Field Pennycress **	1979	0			0			0			0			0		
Thlaspi arvense?	2001	0		B	0		B	0		B	0		B	0		B
Goat's Beard	1979	0			tr		0.3215	0			0			0		
Tragopogon dubius	2001	0		A	0		A	0		A	0		A	0		A
Elm	1979	0			0			tr		0.1555	0			0		
Ulmus species	2001	0		A	0		A	0		A	0		A	0		A
Prairie Violet **	1979	0			0			0			0			0		
Viola pedatifida	2001	0		B	2*	0.7	0.0244 A	0		B	0		B	0		B

1984). Differences in species diversity among treatments in 2001 suggest two general trends, one relevant to annual burns and the other to quadrennial burns. The first trend noticed is that annual burns occurring later in the season, or with a varied season, resulted in significantly higher diversity than those occurring in the spring or summer (Table 2). In the absence of burning, however, diversity was lower (H' = 0.7203) than all annual burn treatments except those occurring in the spring (H' = 0.6639) (Table 2). The results of annual burning are consistent with the conclusions of earlier studies (Anderson et al., 1970; Hulbert, 1986; Towne and Kemp, 2003). It is also worth noting that annual, early-spring burns are commonly used to manage most grazing lands in tallgrass prairies of the Kansas Flinthills. Decreased diversity that may result from such early-spring burns is likely to be related to the decline in forbs that occur with frequent burning, particularly since forbs contribute the most to prairie plant community diversity (Bragg and Steuter, 1996).

The second trend observed in species diversity is that, among quadrennial treatments, the highest diversity occurs with mid-season (summer) rather than late-season (fall) burns as was shown for annual burning. Among quadrennial burns, summer burns, for example resulted in the greatest diversity (H' = 0.8463) and the greatest increase in diversity (+109%) (Table 2, Fig. 2). In addition, all quadrennial treatments (average H' = 0.7807) resulted in significantly higher diversity than the unburned control (H' = 0.7203).

The difference in plant community responses to annual or quadrennial burning at any one time of the year may be related to litter accumulation or microclimatic changes
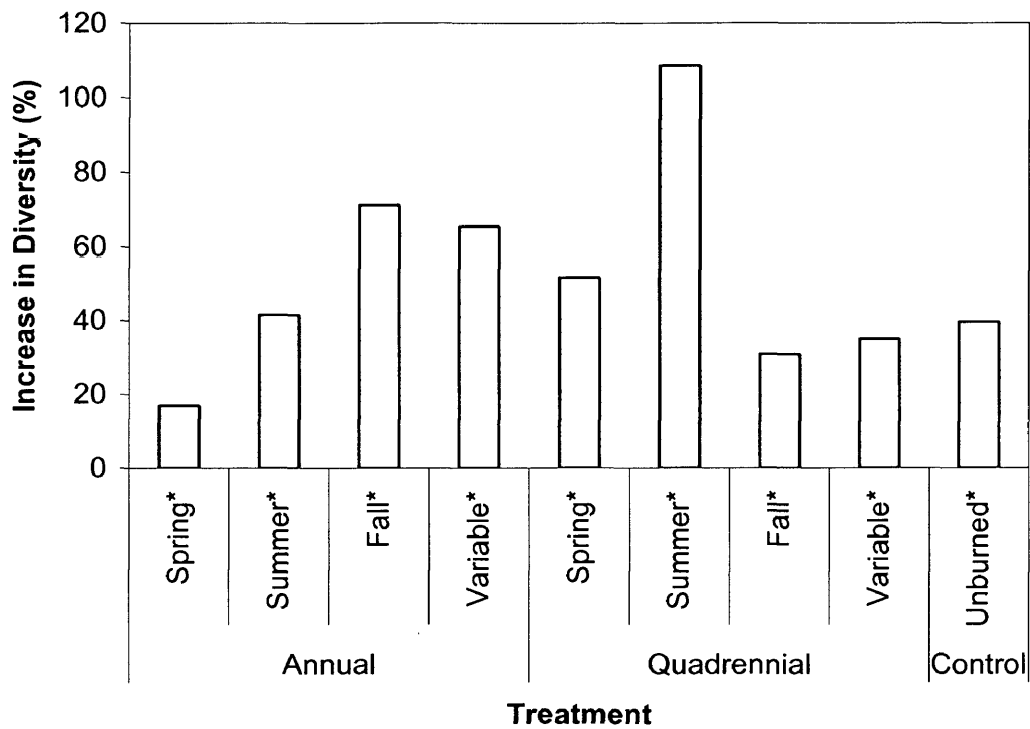
Fig. 2. Percent increase in Shannon diversity (H') between 1979 and 2001. * = significant difference between 1979 and 2001 ($P \le 0.05$, t-test) (Table 2).

that accompany litter accumulation (Tables 3-4). Less frequent burning, for example, allows for sufficient litter accumulation to intercept solar radiation thereby delaying emergence of some species. Frequent burning, however, would expose the soil surface earlier in the season, thereby speeding emergence. In addition, fall burns, even those occurring occasionally, are more likely to adversely affect seedlings or seeds in the litter. Seed longevity, time of dispersal, and need for stratification by fire are among other variables that may alter the effect of different seasons and frequencies of burning.

Effect on Canopy Cover of Species Groups

Grasses. -- There were no significant differences in grass cover among treatment plots in 1979 (Tables 3-4). During the following twenty-two years of study, though, total grass cover for all treatments increased significantly from an average of 81% in 1979 to 100% in 2001. While the increase over time was significant, grass cover in 2001 differed significantly among treatments only for the annual variable-season treatment, where the difference (<1%) is probably not biologically meaningful. The increase in grass cover is not surprising as, over time, plants were expected to fill canopy openings as established individuals increased in size and as additional plants were successfully established.

Forbs. -- The increase in forb cover was significant between years from an average for all plots of <1% in 1979 to 18% in 2001 (Tables 3-4). This increase parallels the overall increase in Shannon diversity observed during the same time period (Fig. 2) and, thus, is consistent with the idea that the majority of plant diversity in the tallgrass

prairie resides in the forb component as suggested by Bragg and Steuter (1996). The increase in overall forb cover from 1979 to 2001 was expected due to the intentional introduction of forbs in 1979 and the likelihood that, with time, additional species would immigrate into the plots.

As with grass cover, the mean percent canopy cover of forbs did not differ significantly among treatment plots in 1979 (Tables 3-4, Fig. 3). Differences, however, were significant among all treatments in 2001, reflecting the response to long-term treatment. These differences are best explained by dividing treatment effects into three general comparisons: (1) the effect of burning versus not burning, (2) the effect of season of burning among annual and among quadrennial treatments, and (3) the effect of variable-season versus single season burning.

Burning vs. Not Burning: Except for annual spring burning (cover = 6%), forb cover for all burn treatments in 2001 averaged higher (21%) than the control (10%) (Tables 3-4, Fig. 3). Differences from the control, however, were significant only for annual fall (26%), annual variable-season (35%), and quadrennial summer (19%) treatments, none of which differed significantly from any other. This result indicates first, that long-term fire treatments have the potential to alter forb cover significantly and second that, except for annual spring burns, some type of burning is needed to maintain prairie forb diversity. A greater number of significant responses to treatment might occur after a longer period of time or if treatments were applied in a more diverse tallgrass
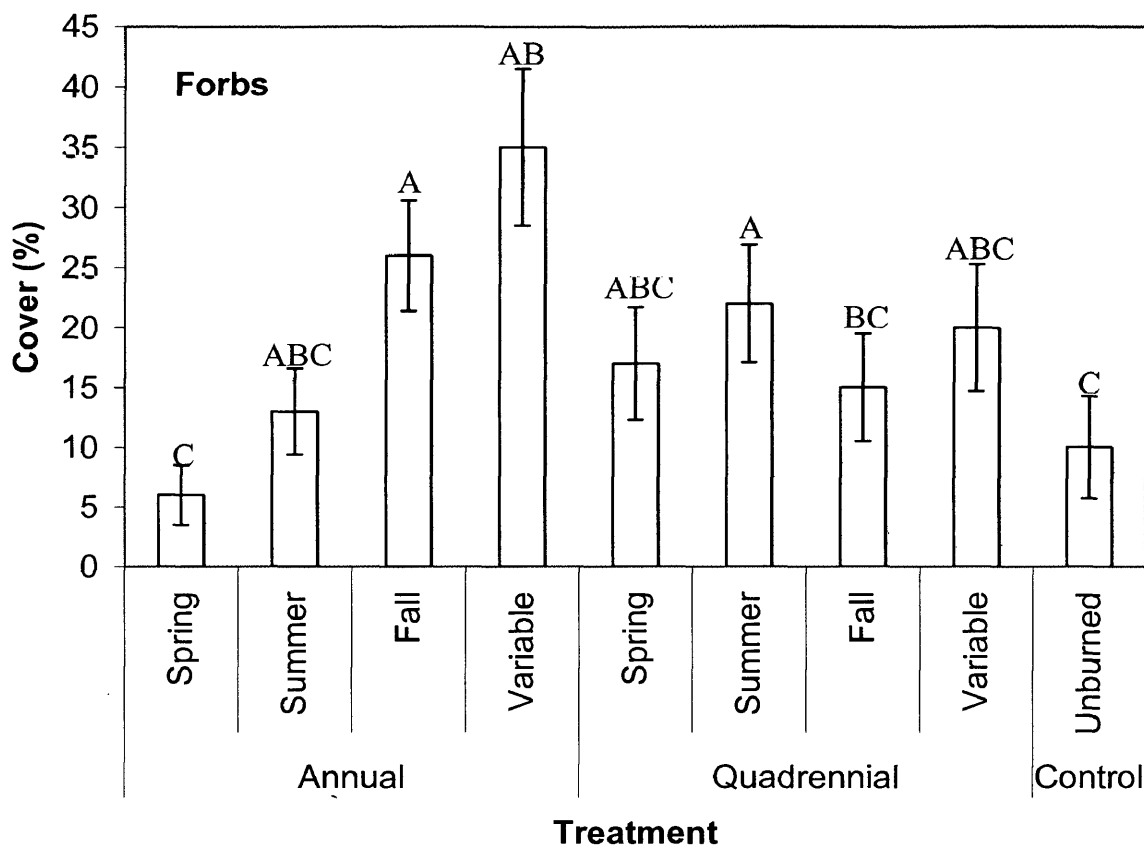
Fig. 3. Mean canopy cover of forbs in 2001. Letters above each bar indicate significant differences in mean canopy cover among treatments; bars with the same letter do not differ significantly ($P \leq 0.05$, Student-Newman-Keuls Test). Vertical lines within each bar represent the standard error.

prairie, but these possibilities could not be ascertained from the results of the present study.

Annual vs. Quadrennial Burns: As with Shannon diversity, in 2001 there was a trend of increasingly higher forb cover as annual burns occurred later in the year (Tables 3-4, Fig. 3). This increase, however, was not significant among all treatments although it is comparable to that observed by Hulbert (1986). Forb cover in unburned areas was significantly lower than either fall or variable-season treatments.

Unlike annual burns, quadrennial burns did not result in a general trend of increasing forb cover with increasingly later season burns. There were, however, significant differences in treatment with quadrennial summer burns resulting in significantly more forb cover (22%) than either quadrennial fall burns (15%) or in the absence of burning (10%) (Tables 3-4, Fig. 3). In combination, these results suggest that the season of quadrennially prescribed burning is less critical in affecting plant response than is the frequency of burning.

Variable-Season vs. Single-Season Burns: Given the relationship between diversity (Table 2) and cover (Fig. 3), forb diversity may be enhanced by variable-season burns. For example, the highest forb cover among all treatments occurred with annual variable-season burns (35%), although it was significantly higher than only three of the eight other treatments: annual spring (6%), quadrennial fall (15%), and unburned control (10%) (Tables 3-4). This high forb cover, however, was largely attributable to two species, white wild indigo and white prairie clover (Tables 3-4). This result, while not

conclusive, implies that annually or quadrennially burned treatments applied in different

seasons, over time, are likely to result in forb cover either equal to or greater than that in

treatments either burned at the same time of the year or not burned. This irregular

occurrence of fire is consistent with historic accounts of fire in the Great Plains (Moore,

1972). In addition, these data suggest that variable-season burning is capable of

maintaining forb cover equal to or significantly greater than single-season burns or in the

absence of burning.

Effect on Individual Species

Of the 40 species recorded in this study, 19 showed a significant ($P \leq 0.05$; t-test)

change in canopy cover between 1979 and 2001 in at least one treatment with changes in

ten species exceeding 10%: big bluestem (+79%), little bluestem (-28%), Indiangrass

(+20%), sideoats grama (-16%), switchgrass (+29%), Kentucky bluegrass (*Poa pratensis*)

(+65%), sedges (+19%), wild white indigo (+11%), leadplant (+11%), and white prairie

clover (18%) (Tables 3-4). Sixteen species, including some of the 19, also showed a

significant difference among treatments in 2001. The maximum cover for ten of these 16

species occurred in annual burn treatments, four in quadrennial burn treatments, one in

both annual and quadrennial treatments, and one in the unburned control. Four of the ten

species whose maximum cover occurred in an annual treatment were annual or biennial

species; purple lovegrass (*Eragrostis spectabilis*), sweetclover (*Melilotus* spp.), black-

eyed Susan, and field pennycress (*Thaspe arvense*). Together, these results indicate a

variety of responses of individual species to fire season and frequency that may best be described by dividing the plants into functional groups.

Warm-Season Grasses. -- The principal warm-season grass species of the study area may be divided into those that are either tall-statured or short-statured. The principal tall-statured species include big bluestem, Indiangrass, and switchgrass. Short-statured species include little bluestem and sideoats grama. An evaluation of species response by plant height provides a possible explanation for the different responses observed since taller-statured species tended to increase whereas short-statured species generally decreased. These trends, however, varied somewhat for specific treatments.

Warm-season grasses, whose cover increased significantly over time, included big bluestem, Indiangrass, and switchgrass (Tables 3-4). Of these, big bluestem was most responsive, increasing significantly in all treatments, from an average cover of 11% in 1979 to 75% in 2001 ($P \leq 0.05$, t-test) (Fig. 4). An increase with burning would be consistent with fire-related increases in big bluestem noted in numerous studies (*e.g.* Kucera and Ehrenreich, 1962; Hulbert, 1969; Towne and Kemp, 2003). In this instance, however, no significant differences in canopy cover were detected among treatments, including the unburned control. At least in this restoration and with this species composition, fire season or frequency do not alone account for the difference in the response of big bluestem.

The canopy cover of Indiangrass, another tall-statured, warm-season grass, also increased with burning between 1979 and 2001, although both the initial cover (6%) and
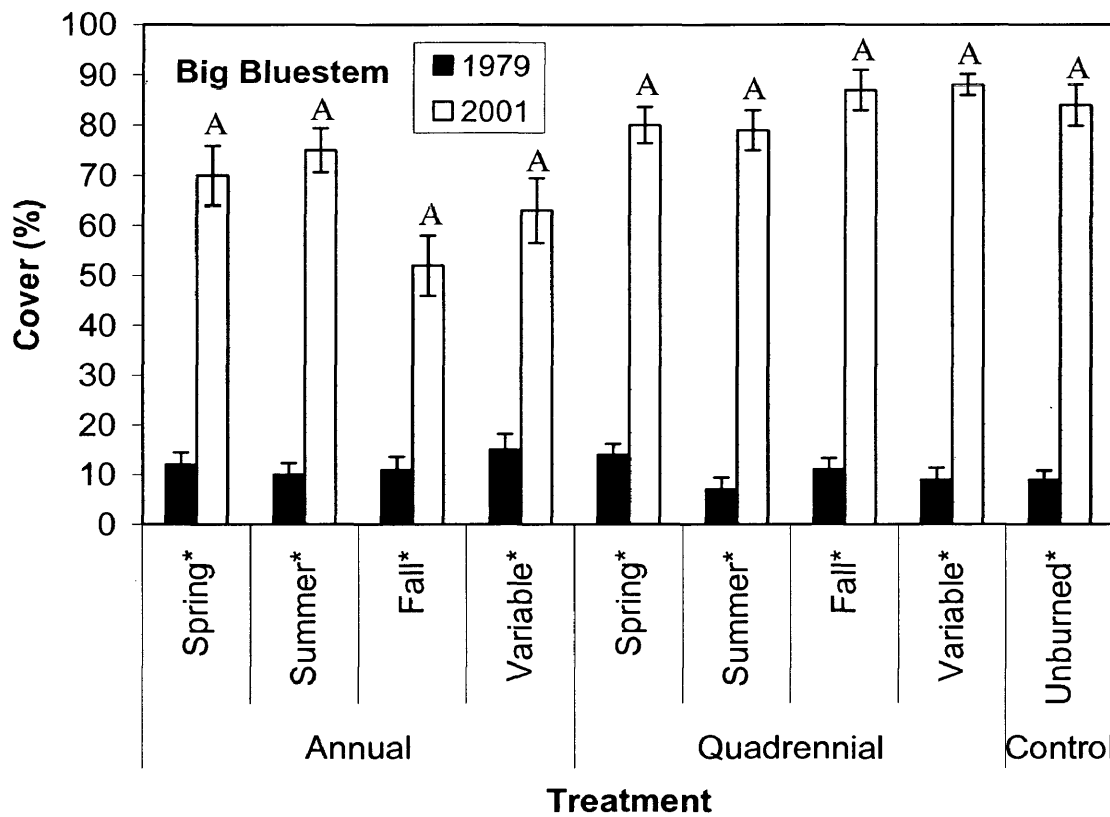
Fig. 4. Mean canopy cover of big bluestem (*Andropogon gerardii*) in 1979 and 2001.
* = significant difference between 1979 and 2001 ($P \leq 0.05$, t-test); there were no significant differences among treatments in either 1979 or 2001. Letters above each bar indicate significant differences in mean canopy cover among treatments in 2001. Bars with the same letter are not significantly different ($P \leq 0.05$, Student-Newman-Keuls test). Vertical lines shown for each bar indicate the standard error.

the cover in 2001 (16%) averaged lower than that of big bluestem (Tables 3-4). The change in cover between 1979 and 2001 was significant for all treatments except the annual spring (+3%), annual fall (+4%) and unburned control (-1%) ($P \leq 0.05$, t-test) (Fig. 5). In contrast to big bluestem, however, significant differences among some treatments were noted for Indiangrass. Canopy cover with annual treatments (13%) averaged consistently lower than with quadrennial treatments (22%), although differences were significant only between the quadrennial variable-season treatment (27%) and annual spring (10%), fall (10%), and variable-season (14%) treatments. Cover in the unburned control was also significantly lower (8%) than with quadrennial variable-season burning. No significant differences were observed among annual treatments or among quadrennial treatments despite substantial differences in average cover.

As with big bluestem and Indiangrass, the canopy cover of switchgrass generally increased significantly between 1979 and 2001, averaging +10% ($P \leq 0.05$, t-test) (Tables 3-4, Fig. 6). The one exception was annual summer burning where the increase was not significant. The greatest increase (+29%) occurred with annual spring treatment, where canopy cover was significantly higher than all other treatments. Among annual treatments, canopy cover of switchgrass with summer burning (2%) was significantly lower than with fall burning (14%), although neither treatment differed significantly from variable-season burning (9%). No significant differences were observed among quadrennial treatments, or between quadrennial treatments and the unburned control.

Little bluestem, a short-statured, warm-season grass, characterizes those warm-season grasses that generally declined with burning over time. This species appears to be

Fig. 5. Mean canopy cover of Indiangrass (*Sorghastrum nutans*) in 1979 and 2001. * = significant difference between 1979 and 2001 ($P \le 0.05$, t-test); there were no significant differences among treatments in 1979. Letters above each bar indicate significant differences in mean canopy cover among treatments in 2001. Bars with the same letter are not significantly different ($P \le 0.05$, Student-Newman-Keuls test). Vertical lines shown for each bar indicate the standard error.
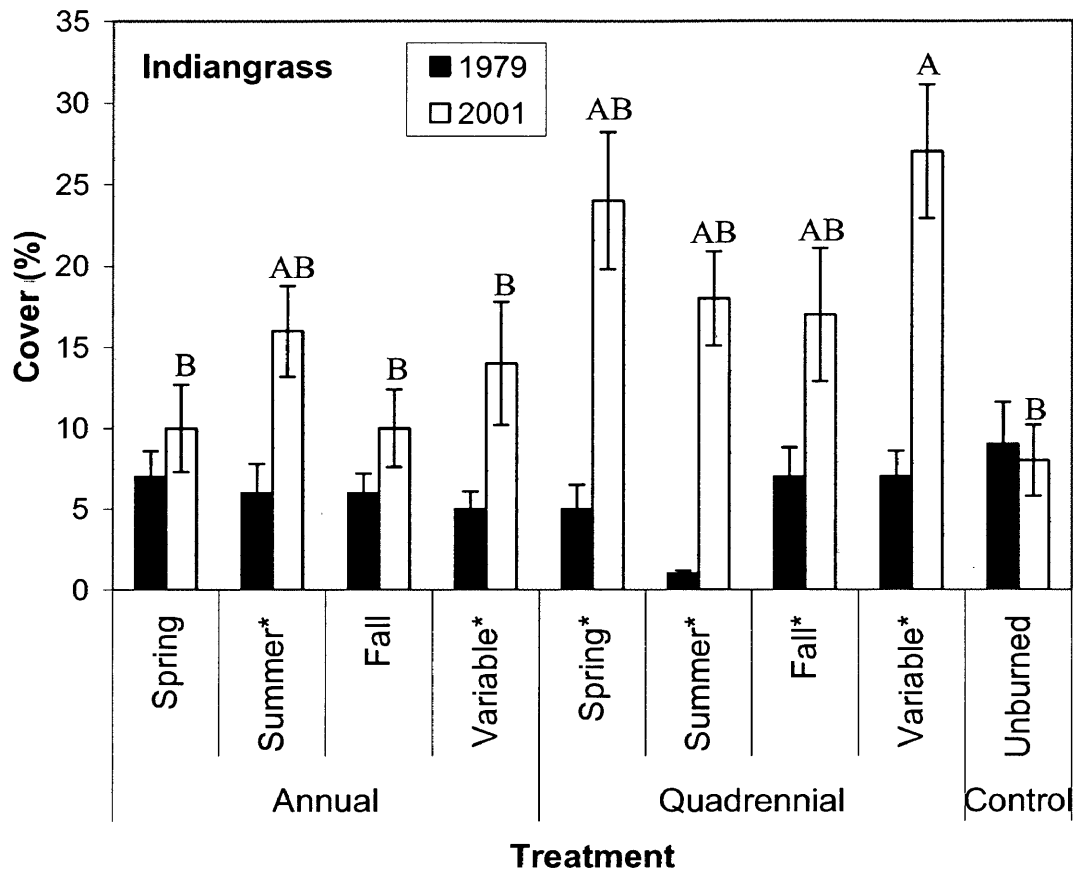
Fig. 6. Mean canopy cover for switchgrass (*Panicum virgatum*) in 1979 and 2001. * = significant differences between 1979 and 2001 ($P \leq 0.05$, t-test); there were no significant differences among treatments in 1979. Letters above each bar indicate significant differences in mean canopy cover among treatments in 2001. Bars with the same letter are not significantly different ($P \leq 0.05$, Student-Newman-Keuls test). Vertical lines shown for each bar indicate the standard error.
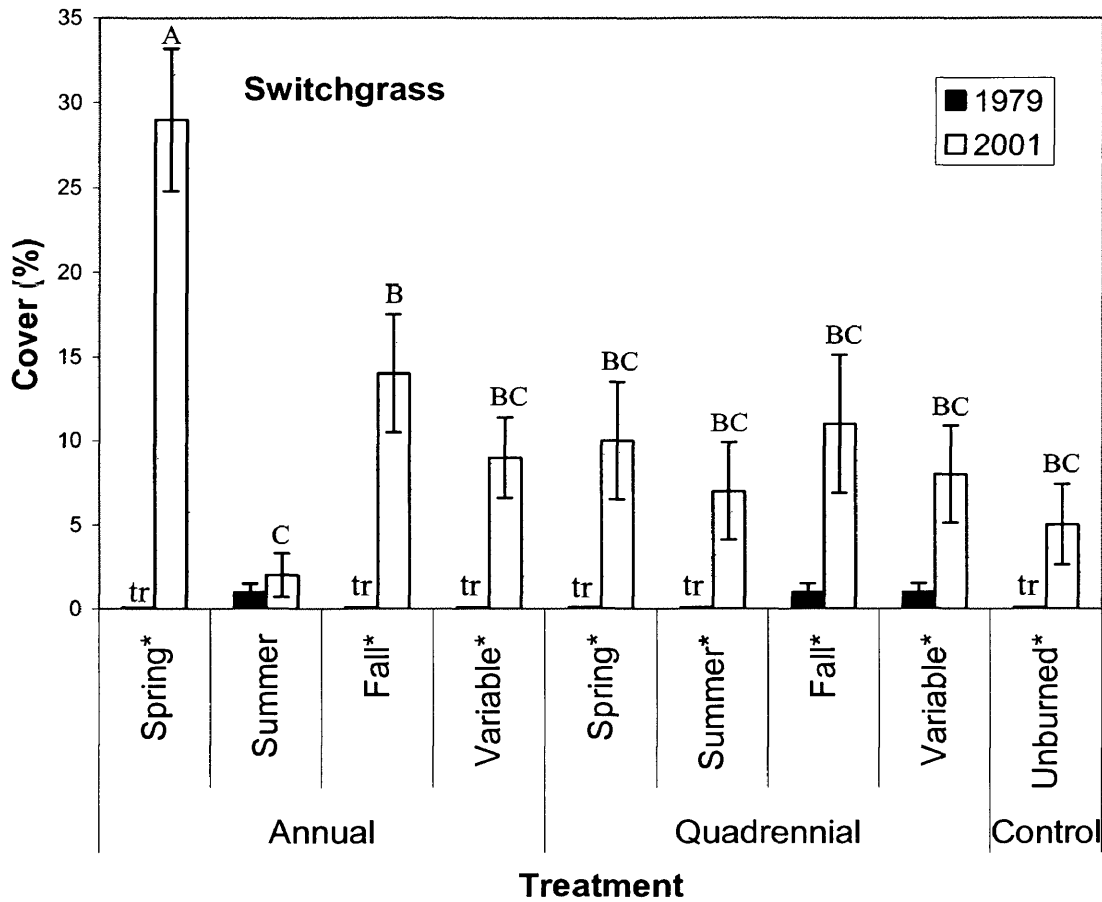
the most sensitive of the principal warm-season grasses of any stature to the effects of variation in treatment, with responses varying from significant increases to significant decreases ($P \leq 0.05$, t-test) (Tables 3-4, Fig. 7). Little bluestem dominated the canopy cover in all treatments in 1979 (average cover = 40%). Cover values among treatments did not differ significantly. By 2001, however, cover had decreased an average of 16% although there were exceptions. Significant declines in little bluestem between 1979 and 2001 were recorded for annual summer burns (-27%), all quadrennial burns (average -27%), and the unburned control (-28%). Little bluestem declined with annual spring burning as well, but this decline was not significant. Increases in cover were observed for both annual fall and annual variable-season burn treatments, although the increase was significant only with annual fall burns (+17%).

Sideoats grama, an early-flowering warm-season, short-statured grass responded to treatment in a manner similar to that of little bluestem, with significant declines (average -11%) between 1979 and 2001 (Tables 3-4, Fig. 8). Unlike little bluestem, however, no treatments resulted in an increase in cover.

The diversity of response of warm-season grasses to variation in fire season and frequency appears to have a common denominator. Fire treatments in general maximize growth, including stature, of taller grasses such as big bluestem (Benning and Bragg, 1993). This, in turn, reduces the amount and quality of light available for shorter grasses. Over the long term, reduced photosynthesis would reduce the vigor of short-statured grasses resulting in the kind of reduced cover of these species observed in this study. A similar logic could be applied to litter accumulation that would also reduce incident light
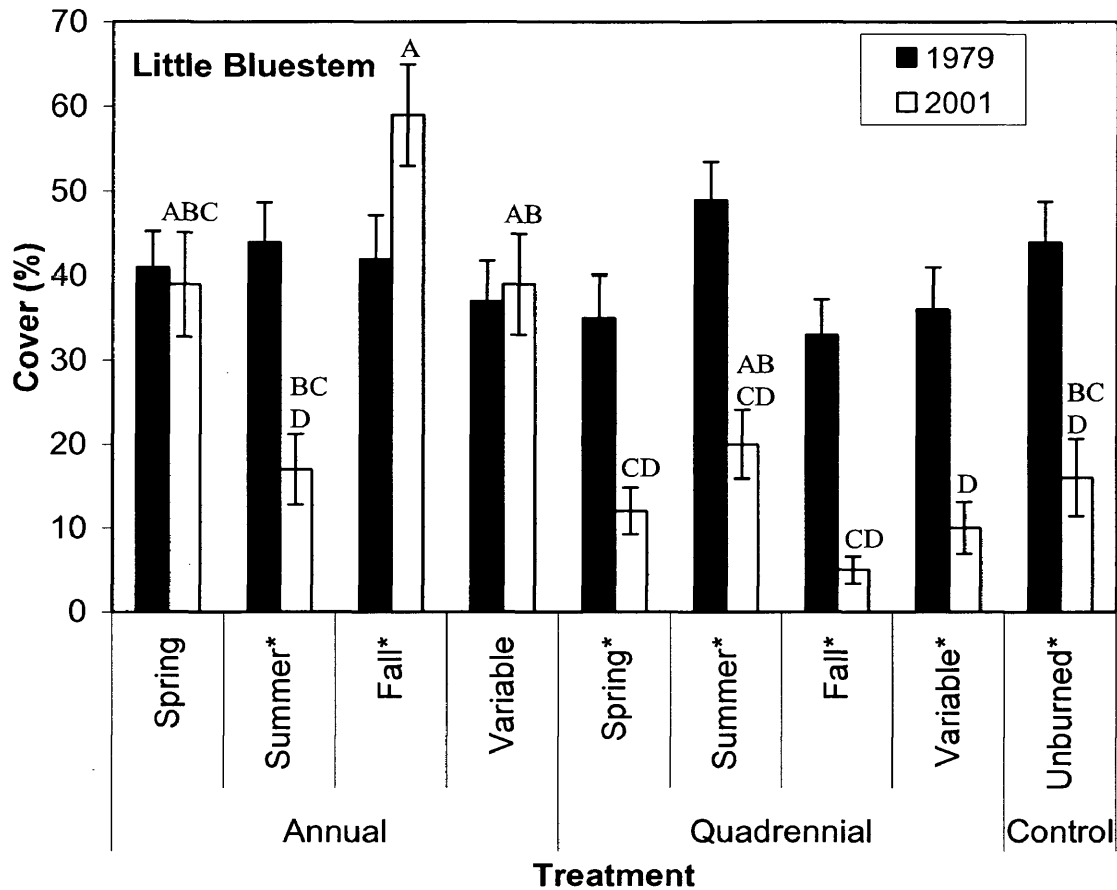
Fig. 7. Mean canopy cover of little bluestem (*Andropogon scoparius*) in 1979 and 2001. * = significant differences between 1979 and 2001 ($P \leq 0.05$, *t*-test); there were no significant differences among treatments in 1979. Letters above each bar indicate significant differences in mean canopy cover among treatments in 2001. Bars with the same letter are not significantly different ($P \leq 0.05$, Student-Newman-Keuls test). Vertical lines shown for each bar indicate the standard error.

Fig. 8. Mean canopy cover for sideoats grama (*Bouteloua curtipendula*) in 1979 and 2001. Letters above each bar indicate significant differences in mean canopy cover among treatments in 2001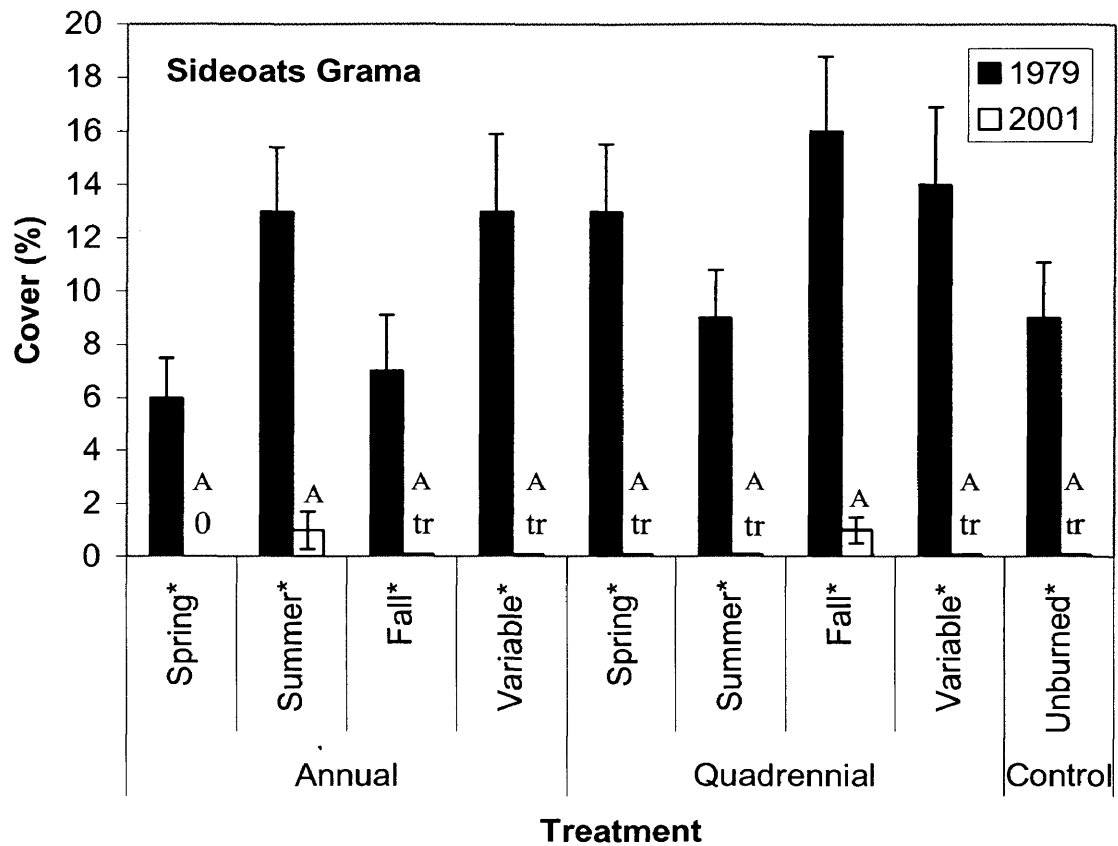. Bars with the same letter are not significantly different ($P \leq 0.05$, Student-Newman-Keuls test); there were no significant differences among treatments in 1979. Vertical lines shown for each bar indicate the standard error.

and otherwise effect microclimate conditions. For example, in quadrennially burned and control treatments where litter cover was highest (100%), short-statured species consistently declined. However, where litter cover was lowest (10%), such as in annually burn treatments, short-statured species increased (Tables 3-4). Together, increased vigor of taller-statured species and changes in the microclimate associated with the accumulation of litter are likely to be among explanations for why short-statured, warm-season species are likely to be at a disadvantage under mesic conditions that favor tall, warm-season grasses.

The historic persistence of sideoats grama, little bluestem, and other short-statured species in the tallgrass prairie region (Weaver, 1954) may have been at least partially accommodated by the grazing effect of large animals. Such grazing would have reduced litter and prevented tall-statured species from substantially overtopping shorter species. Other explanations for their persistence may be related to the morphological or physiological adaptation of shorter-statured species to particularly xeric areas, such as those resulting from frequent burning or those reflecting environmental differences such as aspect (Bragg, personal communication). The dominance of sideoats grama, little bluestem, and other short-statured species in the more xeric mixed- and short-grass prairie of the western Great Plains (Weaver, 1954) and on the xeric southwest-facing slopes of the Loess Hills Prairie of western Iowa (Bragg, 1991) are consistent with this logic.

Cool-Season Graminoids. -- In contrast to warm-season grasses, cool-season graminoids were observed to increase in all plots, although the amount of the increase

varied by treatment (Tables 3-4). Of this group, sedges and Kentucky bluegrass were the most frequent.

Sedges are cool-season, native, grass-like plants that were introduced to the research plots in plugs of porcupine grass (*Stipa spartea*) transplanted from a native prairie in 1978. Found in trace amounts in 1979, the average cover for sedges increased significantly in all treatments by 2001 (+12%) ($P \leq 0.05$, *t*-test) (Tables 3-4, Fig. 9). While no significant differences were observed among treatments in 2001, the average increase in cover among annual treatments (+17%) was higher than that of quadrennial and control treatments (+8%), despite great differences in average values, suggesting that this species is better suited to conditions resulting from more frequent fire. Lower cover of sedges in quadrennial burn plots may be a reflection of the same negative response of short-statured, warm-season grasses to increases in cover and litter accumulation. That is, plants beneath the litter layer may receive less solar energy and thus expand more slowly than those receiving full sunlight a greater proportion of the time. Annually burned areas, in which litter does not accumulate, would provide these conditions. The low cover of sedges in the unburned area reinforces the logic of this explanation. At the same time, however, this logic is inconsistent with the general explanation that cool-season species are better suited to lower light conditions than are warm-season species. The significant increase of sedges in all treatment areas, however, suggests that at least some species are likely to be maintained to some extent, irrespective of fire season or frequency. This result is consistent with the persistence of sedges in the tallgrass prairie where fire season and frequency most likely varied considerably over the years.
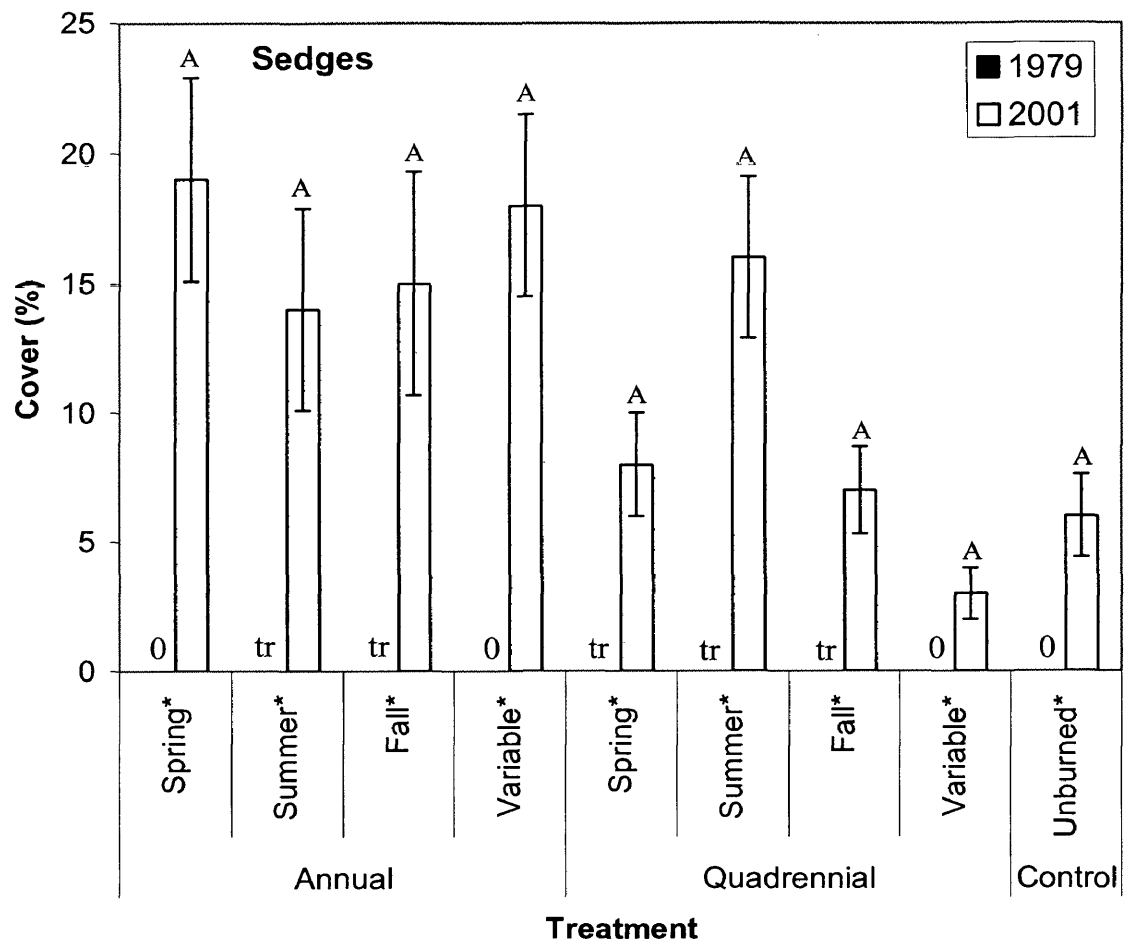
Fig. 9. Mean canopy cover for sedges (*Carex* spp.) in 1979 and 2001.
* = significant differences between 1979 and 2001 ($P \le 0.05$); there were no significant differences among treatments in 1979 or 2001. Letters above each bar indicate significant differences in mean canopy cover among treatments in 2001. Bars with the same letter are not significantly different ($P \le 0.05$, Student-Newman-Keuls test). Vertical lines shown for each bar indicate the standard error.

Kentucky bluegrass is a non-native, invasive, short-statured, cool-season grass that, like sedges, was present in only trace amounts in 1979 with no significant differences among treatments (Tables 3-4, Fig. 10). By 2001, this species had increased significantly but, unlike sedges, the increase occurred primarily either with quadrennial treatments (average +44%) or in the absence of fire (+36%), both of which differed significantly from all annual treatments (+2%) (Fig. 10). Annual fires generally tended to suppress Kentucky bluegrass, although suppression was less effective with annual summer burns where there was a significant increase (+9%) between 1979 and 2001. Fires at this time of the year occur past the time of active growth of cool-season species and also consume less phytomass because of the high proportion of green matter in the fuel (Bragg, 1982). Together, these factors appear to result in conditions allowing for at least some increase in Kentucky bluegrass with the annual summer burn treatment.

Overall, quadrennial burns, appear to result in microclimatic conditions more similar to those occurring without burning than to those resulting from annual treatments, at least to the extent that they favor Kentucky bluegrass. Unlike sedges, Kentucky bluegrass seems more suited to microclimatic conditions associated with increased litter cover, such as lower incident light, reduced soil temperature resulting from the interception of solar radiation by litter, or more mesic conditions occurring below the litter layer resulting from higher humidity, lower temperature, and lower evaporation rates. Alternatively, Kentucky bluegrass may simply be more adversely affected by fire than are other species, such as sedges. The opposite response of sedges and Kentucky bluegrass to treatments resulting in litter accumulation suggest that different
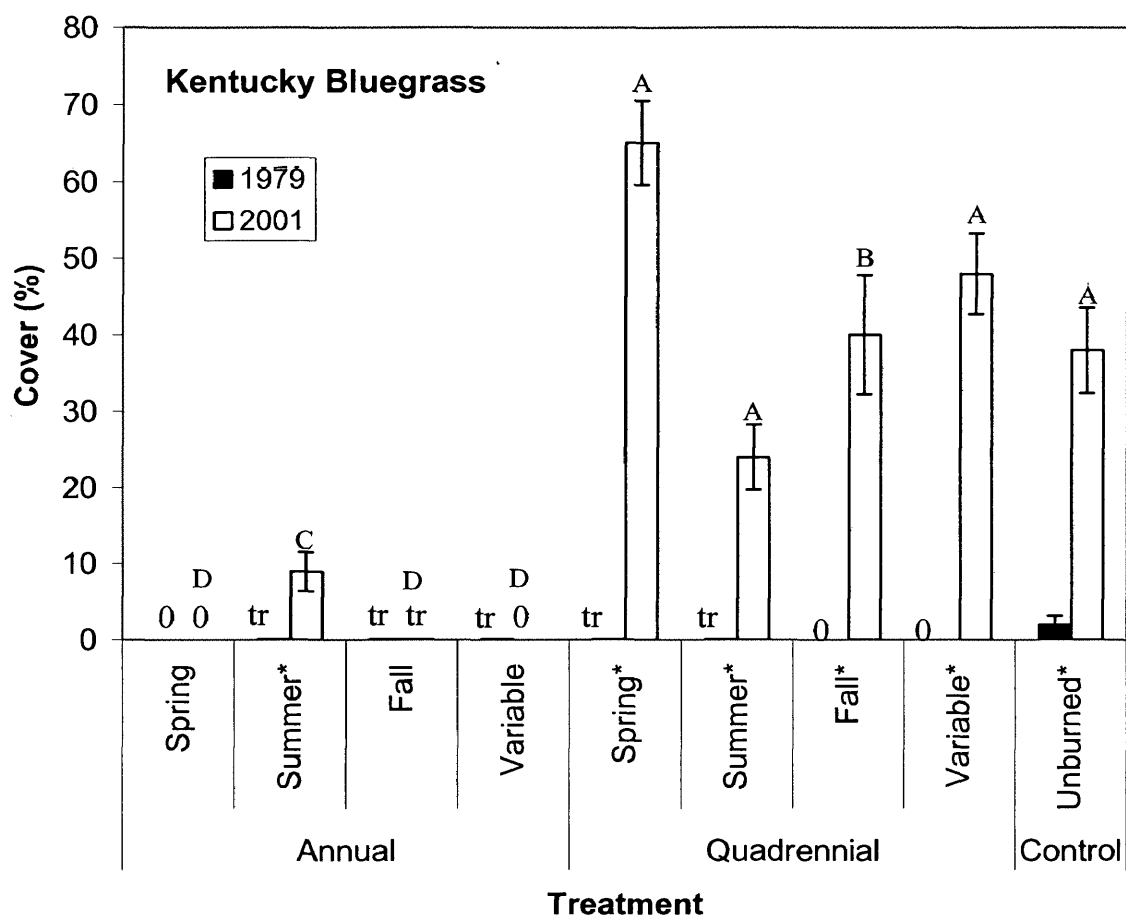
Fig. 10. Mean canopy cover for Kentucky bluegrass (*Poa pratensis*) in 1979 and 2001. * = significant differences between 1979 and 2001 ($P \leq 0.05$) ; there were no significant differences among treatments in 1979. Letters above each bar indicate significant differences in mean canopy cover among treatments in 2001. Bars with the same letter are not significantly different ($P \leq 0.05$, Student-Newman-Keuls test). Vertical lines shown for each bar indicate the standard error.

environmental factors may differentially affect the response of native and non-native

cool-season species to variations in fire season and frequency.

Smooth brome, also a cool-season, non-native grass, was only a minor species in

the treatment area. It occurred in trace amounts in five of nine treatments in 1979 and

increased significantly only in the absence of burning (+9%) ($P \leq 0.05$, t-test) (Tables 3-

4). This increase, while small, is consistent with the results of a study by Bragg *et al.*

(1999) in which smooth brome, a substantial proportion of the initial plant community,

increased significantly with all but annual spring burn treatments. This response of

smooth brome to frequent fire, in combination with somewhat similar responses of

Kentucky bluegrass, suggests that some annual treatments may discourage the invasion of

some cool-season grasses. It is important to recall, however, that frequent fires have also

been shown to reduce plant diversity (Hulbert, 1986; Collins, 1992).

Forbs. -- The response of individual forb species varied substantially. For

example, some species increased significantly with summer treatments (*e.g.* prairie

goldenrod and prairie violet (*Viola pedatifida*)) while others increased significantly with

spring treatments (*e.g.* leadplant and white prairie clover). Some species increased more

with annual burns (*e.g.* white prairie clover) while others did so with quadrennial burns

(*e.g.* Illinois tickclover). These observations clearly indicate the differential response of

different species to different fire regimes. Understanding these differences, then, allows

for a more refined generalization of fire effects on the prairie as a whole, even though

there almost certainly are yet undetermined interactions that may account for some of the responses observed.

Canopy cover of individual forb species was generally low although a few were sufficiently frequent or high enough in cover to provide information useful in assessing the effect of different fire treatments (Tables 3-4). Significant differences either in mean canopy cover between 1979 and 2001 or among treatments in 2001 were observed for all eight native species seeded into plots in 1979. Of these, five species occurred in at least five of the nine treatments: white prairie clover, leadplant, wild white indigo, white aster, and Illinois tickclover.

White prairie clover was not found in treatment plots in 1979 (Tables 3-4). By 2001, however, this species had increased to an average cover of 5%. While treatment effects differed significantly among all treatments in 2001 ($P \leq 0.05$, ANOVA), no significant differences were observed among annual or among quadrennial burns (Fig. 11). Based on these differences, white prairie clover, like little bluestem and sedges, appears to benefit from microclimate conditions resulting from the reduction in both litter and canopy cover associated with frequent fire. For example, the greatest increases in white prairie clover occurred with annual fall and annual variable-season burn treatments. An increase with annual fall burning is a logical response for a species such as white prairie clover that is among those growing earliest in the spring (ca. May) (Lommasson, 1973). An explanation for the significantly greater cover of this species in response to variable-season burns is not apparent but is likely to be related to variables associated
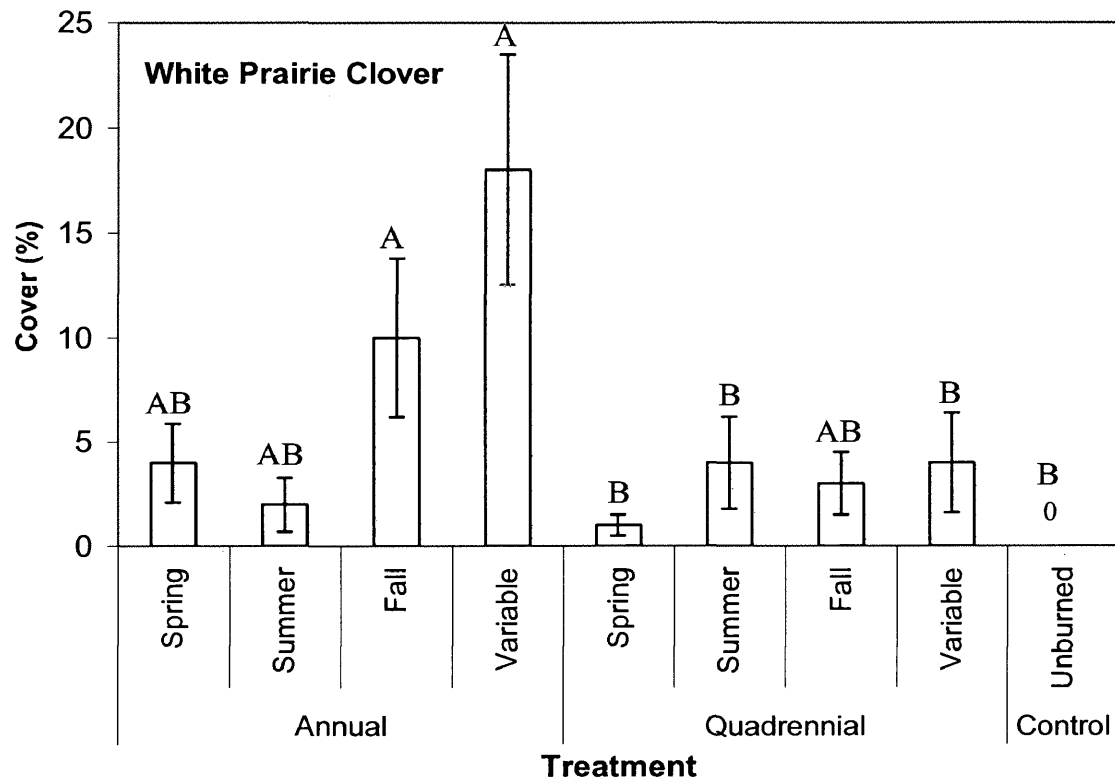
Fig. 11. Mean canopy cover for white prairie clover (*Dalea candida*) in 2001. This species was not recorded in 1979. Letters above each bar indicate significant differences in mean canopy cover among treatments ($P \leq 0.05$, Student-Newman-Keuls test). Vertical lines shown for each bar indicate the standard error.

with reduced litter in the spring resulting from occasional fall and summer fires. This explanation is supported by the absence of any white prairie clover in the unburned control where litter had not been removed at any time during the study period.

Leadplant is a native, woody prairie plant often discussed with forbs to distinguish it from non-prairie woody plants simply as a procedural convenience. As with most forbs, leadplant was absent from 1979 microplots but generally increased in cover by 2001 (Tables 3-4). The single exception to increases in this species was its absence from the annual spring treatment plots in 2001. Unlike white prairie clover, there were no significant differences among treatments in 2001, perhaps because average cover values were never significantly greater than zero (Fig. 12). In general, though, canopy cover of leadplant averaged higher with quadrennial treatments (8%) than with annual treatments (2%), suggesting that this species may ultimately prove to be better suited to fires occurring less frequently than annually, a result also noted by Briggs *et al.* (2002). The absence of leadplant from the annual spring treatment seems logical, since this species, which emerges and flowers relatively early in the season (early summer), could be expected to be more adversely affected by fire at this time of the year than by fires occurring at later dates (Bragg, 1991).

Wild white indigo, a tall legume, increased in cover with all but annual summer burning (Tables 3-4). The increase in cover of this species was expected given that fire is known to be important in preventing seed predation by weevils (Leach and Givnish, 1996), which are known to occur at the preserve (Bragg, personal observation). The only
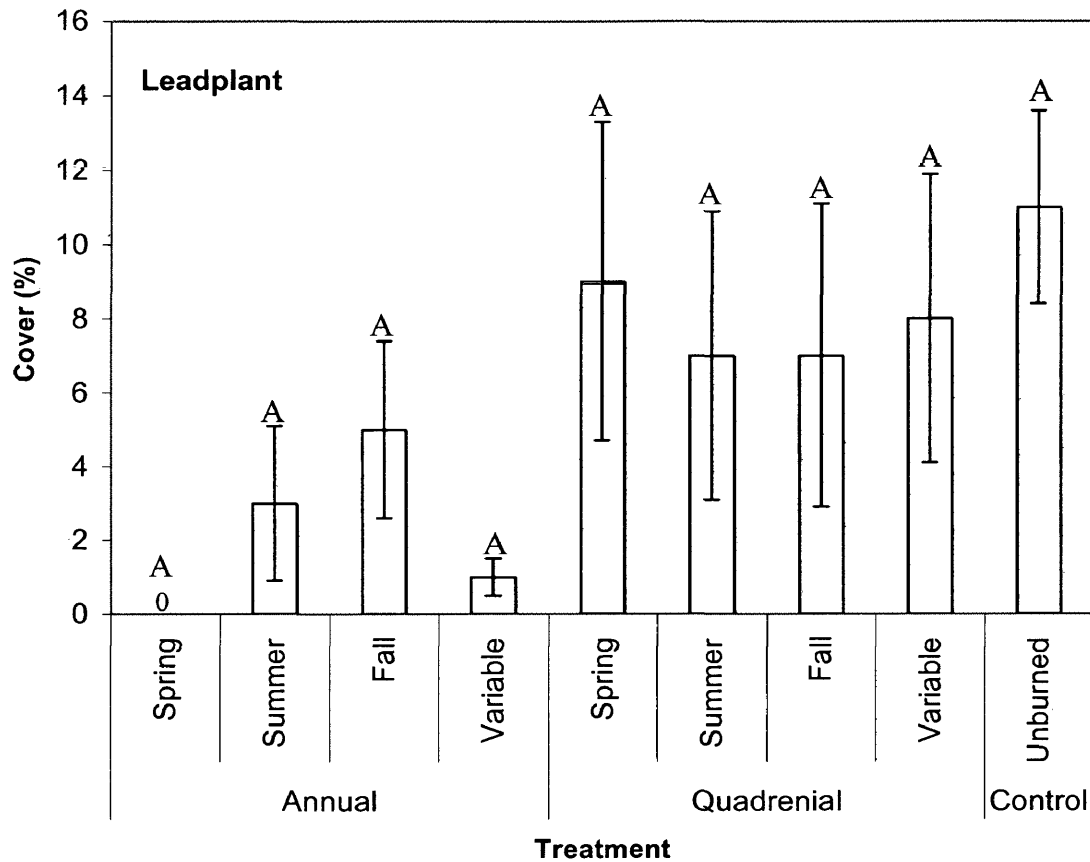
Fig. 12. Mean canopy cover for leadplant (*Amorpha canescens*) in 2001. This species was not recorded in 1979. Letters above each bar indicate significant differences in mean canopy cover among treatments ($P \leq 0.05$, Student-Newman-Keuls test). Vertical lines shown for each bar indicate the standard error.

significant differences among treatments were observed between annual variable-season

burning and four other treatments, of which all were either quadrennially burned or not

burned. Small canopy cover values, however, suggest that these may not be biologically

significant differences. General trends among annually burned treatments show the

greatest increase in cover to occur with variable-season burning (+11%) (Fig. 13).

Similarly, the greatest increase among quadrennial burning occurred with the variable-

season treatment (+3%).

The response of white aster and Illinois tickclover to variation of fire treatment

was similar to that of several of the other forb species that occurred in sufficient numbers

to be statistically evaluated (Tables 3-4), with each species increasing in most of the

treatment areas. For white aster, burning resulted in the greatest increase among annual

treatments with a general trend shown for an increase in cover as fire occurred later in the

season (Fig. 14). Among quadrennial burns the greatest cover occurred with summer

burning (5%). For Illinois tickclover, however, there were a few significant differences

among treatments but the only trend was a non-significant decline in cover as quadrennial

burns occurred later in the year (Fig. 15). As with other species, statistically significant

differences among treatment where cover value is low may not be biologically

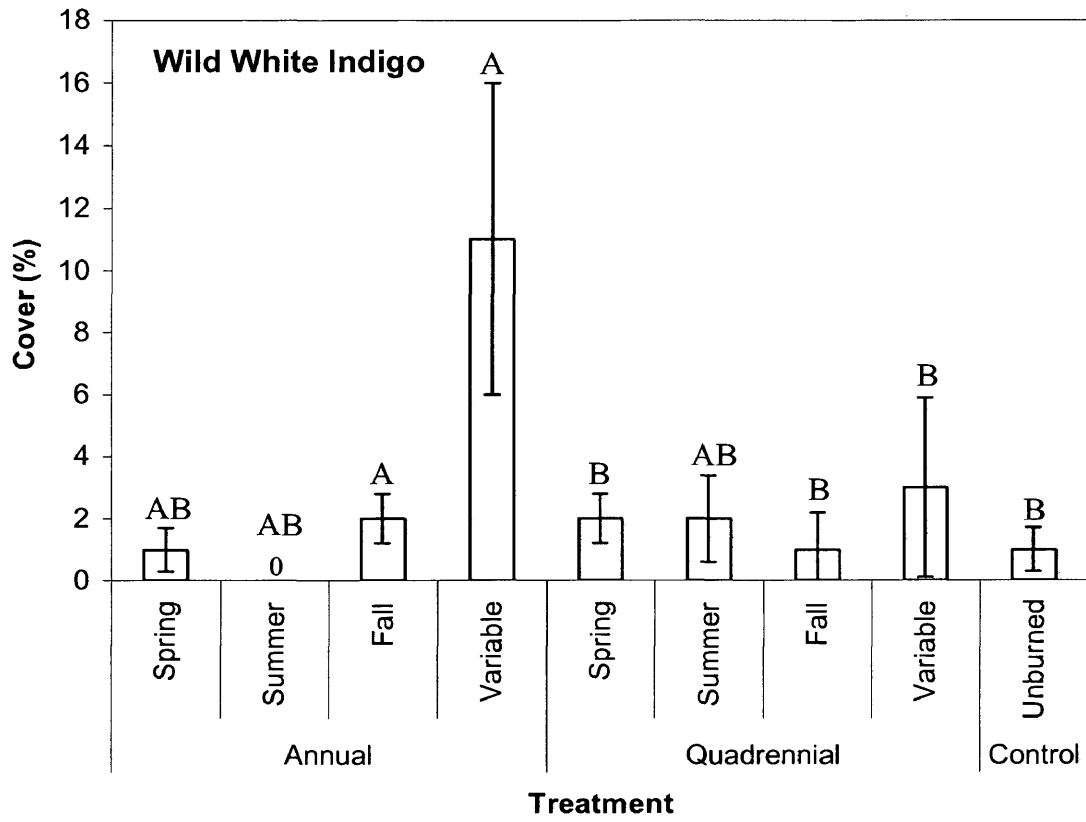meaningful, at least not at this point in the study.

Fig. 13. Mean canopy cover for wild white indigo (*Baptisia lactea*) in 2001. This species was not recorded in 1979. Letters above each bar indicate significant differences in mean canopy cover among treatments ($P \leq 0.05$, Student-Newman-Keuls test). Vertical lines shown for each bar indicate the standard error.
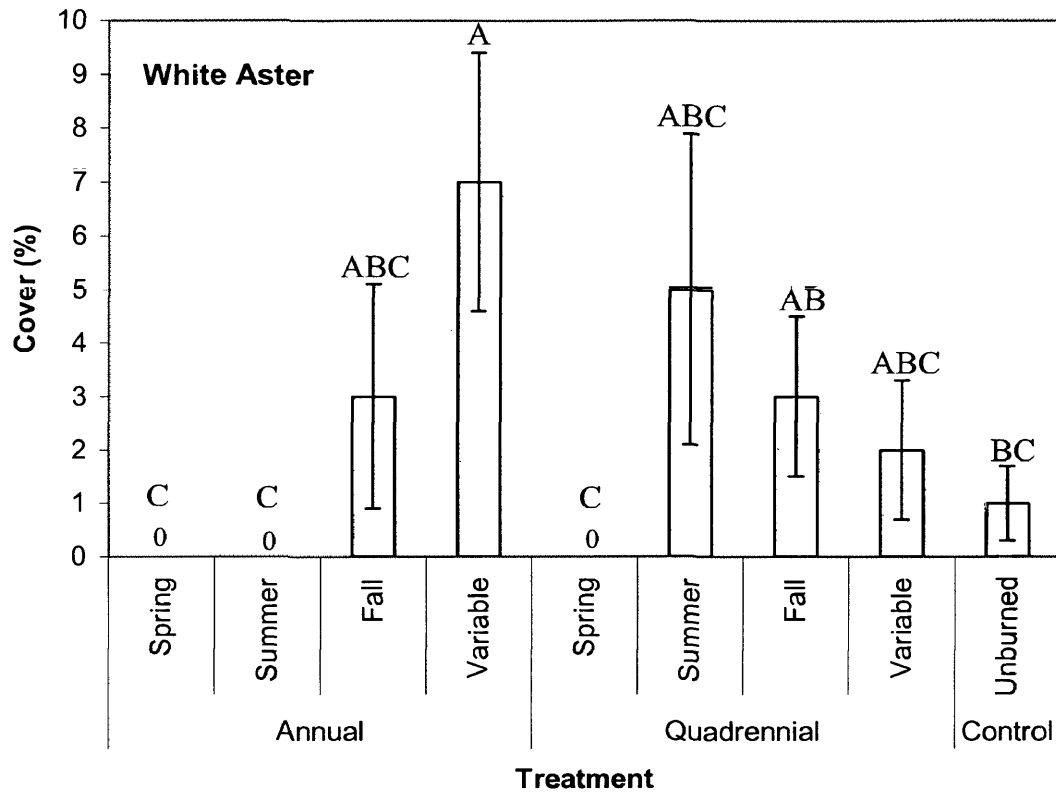
Fig. 14. Mean canopy cover for white aster (*Aster ericoides*) in 2001. This species was not recorded in 1979. Letters above each bar indicate significant differences in mean canopy cover among treatments ($P \leq 0.05$, Student-Newman-Keuls test). Vertical lines shown for each bar indicate the standard error.
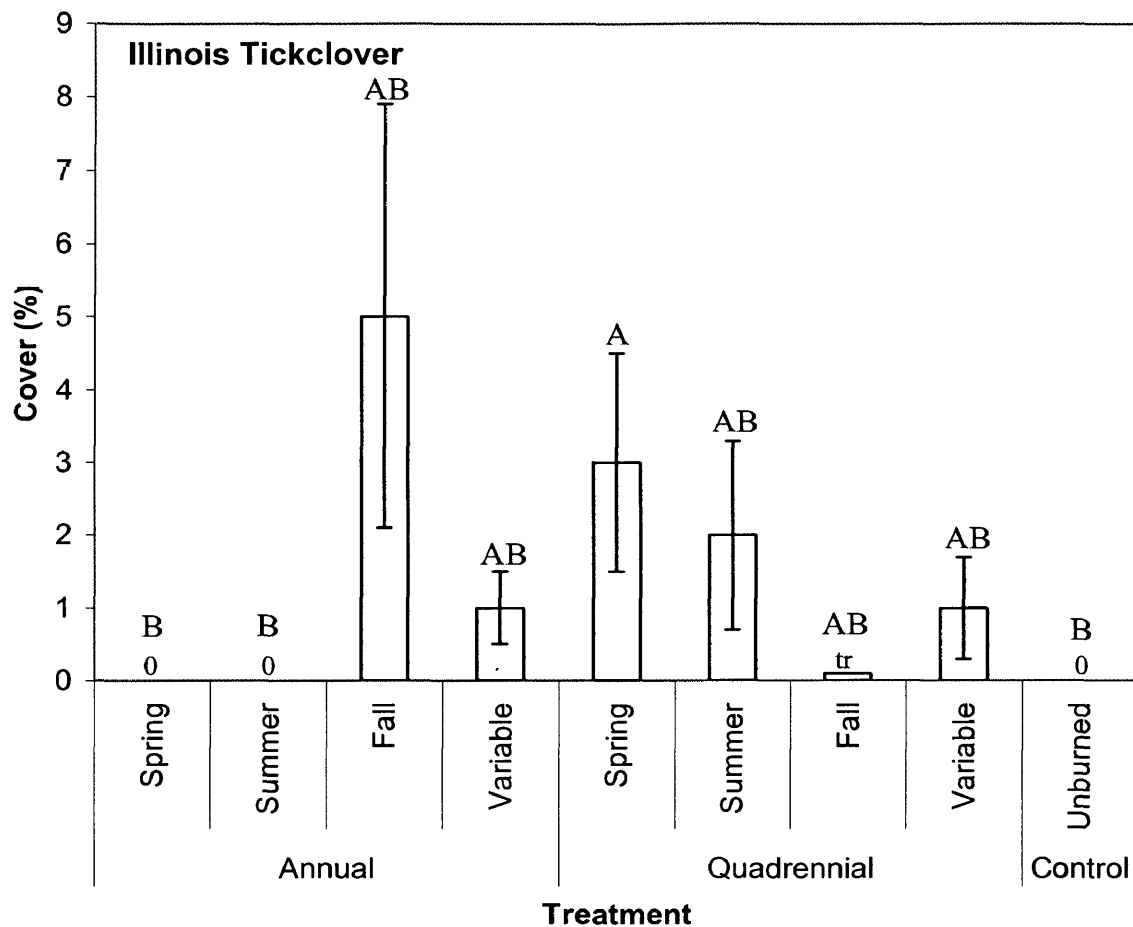
Fig. 15. Mean canopy cover for Illinois tickclover (*Desmodium illinoense*) in 2001. This species was not recorded in 1979. Letters above each bar indicate significant differences in mean canopy cover among treatments ($P \leq 0.05$, Student-Newman-Keuls test). Vertical lines shown for each bar indicate the standard error.

Conclusion

This study documents both (1) the increase in cover of prairie species following their initial introduction and (2) significant differences in species cover resulting from a variety of annual or quadrennial burning treatments applied at different seasons of the year. Changes in canopy cover of individual prairie species are accompanied by significant increases in plant diversity, although these increases also varied with season and frequency of treatment. As a group, grasses generally increased with frequent fires while forbs decreased. Ruderal species, on the other hand, generally declined significantly as prairie species increased. Overall, this study shows that different seasons and frequencies of fire management may be used to effectively maintain prairie diversity. The variation of plant responses suggests that, to provide high ecosystem diversity, fire management should be applied with a more random and less systematic season and frequency than is typically applied in prescribed burning of tallgrass prairies.

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APPENDIX

Appendix Table 1. *t*-values and *v*-values from *t*-test on comparison of Shannon diversity between all combinations of 2001 treatment areas (Zar, 1984). Shannon diversity for every treatment differed significantly from that of every other treatment.

			Annual				Quadrennial				Control
			Spring	Summer	Fall	Variable	Spring	Summer	Fall	Variable	Unburned
Annual	Spring	*t*-value	-								
		v-value									
	Summer	*t*-value	-3.4944								
		v-value	255								
	Fall	*t*-value	-5.8044	-5.2267							
		v-value	291	158							
	Variable	*t*-value	-6.6561	-5.7483	-6.2695						
		v-value	278	136	117						
Quadrennial	Spring	*t*-value	-4.9183	-4.2061	-6.3830	-7.1606					
		v-value	312	205	190	162					
	Summer	*t*-value	-6.0722	-5.4488	-6.4349	-6.9066	-6.6294				
		v-value	299	161	121	106	195				
	Fall	*t*-value	-3.5691	-3.4956	-4.0680	-6.0528	-4.3136	-4.9015			
		v-value	298	165	142	157	199	126			
	Variable	*t*-value	-4.2585	-4.0124	-4.5762	-5.1467	-4.9601	-5.3693	-3.9765		
		v-value	311	158	135	206	193	121	187		
Control	Unburned	*t*-value	-2.1245	-3.3234	-3.9083	-4.3146	-4.1406	-4.7618	-3.1783	-2.7914	
		v-value	290	157	135	200	189	121	184	151	