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CAUSES OF FIRE EFFECTS IN TALLGRASS PRAIRIE[1]

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Abstract. Eleven experimental treatments were applied to 2 × 2 m plots over 2 yr at Konza Prairie Research Natural Area, Riley County, Kansas, to ascertain why burning tallgrass prairie causes increased production and flowering. Warming of the soil in unburned plots resulted in an increase in both total production and flower stalk production of dominant tall grasses, primarily big bluestem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans*), but the increase was small (34% increase in biomass; 78% increase in number of flower stalks) compared with that in burned plots (151% increase in biomass; 435% increase in flower stalks). Increased surface light intensity also appears to be a factor affecting changes in productivity following burning as suggested by the combined responses of increased productivity with removal of standing dead, whether by clipping or burning, and decreased productivity with shading. Further, the addition of ammonium nitrate increased yield 41% and flowering 168% for the dominant grasses, suggesting that any factor increasing nitrogen availability would affect these vegetative parameters. Neither ash left from burning nor heating of the soil surface during burning produced detectable effects on subsequent vegetative growth. Different results for some parameters between years and between species suggest that many complex interactions operate to affect the grassland's response to burning, but surface light, soil surface temperature, and nitrogen appear to be particularly important factors.

Key words: aboveground biomass; bluestem prairie; burning; fire; flowering; soil temperature; tallgrass prairie.

INTRODUCTION

The tallgrass (bluestem) prairie (*Andropogon-Panicum-Sorghastrum*) (Küchler 1964) is an ecosystem in which fire is an important factor and one that has been widely studied. The warm-season grasses, which dominate the ecosystem, respond to burning in a variety of ways. In general, they start growth earlier, grow faster early in the growing season, and produce more flower stalks than unburned areas (Curtis and Partch 1950, Ehrenreich 1959, Kucera and Ehrenreich 1962, Ehrenreich and Aikman 1963, Hulbert 1969, Old 1969, Adams and Anderson 1978, Henderson et al. 1983, Petersen 1983). Similarly, stem tiller density is greater in burned than in unburned areas (Kucera and Koelling 1964, Dokken and Hulbert 1978, Towne and Owensby 1984). When burned in late spring, as growth of the warm-season grasses is just starting, productivity of tallgrass species is higher than when unburned (Kucera and Ehrenreich 1962, Ehrenreich and Aikman 1963, Owensby and Anderson 1967, Hulbert 1969, Old 1969, Hill and Platt 1975). In addition to effects on vegetation, soil has been found to warm more rapidly in burned than in unburned areas and to remain warmer throughout much or all of the growing season (Kelting 1957, Ehrenreich 1959, Kucera and Ehrenreich 1962, Ehrenreich and Aikman 1963, Hulbert 1969, Adams and Anderson 1978, Rice and Parenti 1978, Petersen 1983).

Studies evaluating possible causes of fire effects have generally tended to seek single causes instead of recognizing that combinations of factors are most likely to control responses to burning. The importance of climate in affecting fire effects was discussed by Borchert (1950) and that of soil texture by Bell and Hulbert (1974). Soil moisture has been found to be lower in burned than in unburned areas (Hopkins 1954, Kelting 1957, Anderson 1965, Hulbert 1969, Owensby 1973, Petersen 1983) so the higher production recorded after burning cannot be attributed to a shortage of water in the unburned sites. Similarly, Rice and Parenti (1978) found no support for the hypothesis that toxic chemicals released from standing dead and litter lowered production in unburned prairie. Many factors other than the above also have been proposed as causes of fire effects in tallgrass prairie although they, too, have generally been single-factor studies. The objective of this study was to consider these additional causes in a single study. Specifically considered were the following: increased soil temperature by solar heating following fire, increased light intensity, ash effects, direct effects of heat of the fire, and changes in soil nitrogen.

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STUDY SITE

The experimental plots were established on Konza Prairie Research Natural Area, 9 km south of Man-

TABLE 1. Air, soil surface, and 10-cm soil temperatures in experimental plots in May and July 1982. Heating of soil in unburned-warmed plots was halted on 19 June. Values shown are averages of five measurements.

Location	Treatment				
	Clipped	Burned	Unburned	Unburned-warmed	Air
	Temperature (°C)				
17–24 May 1982					
Surface	20.3	20.6	16.7	···	18.3
10 cm below surface	18.8	18.9	16.1	20.0	18.3*
12–19 July 1982					
Surface	26.4	26.4	23.8	···	26.7
10 cm below surface	24.9	24.9	22.8	22.7	26.7*

* One air-temperature recording point was used for all treatments.

hattan, Riley County, Kansas. Vegetation is native tallgrass or bluestem prairie dominated by big bluestem (*Andropogon gerardii*), accompanied by Indian grass (*Sorghastrum nutans*) and little bluestem (*Andropogon scoparius*). The plots were established on a lowland, deep soil (Reading silt loam), with 1.3% slope (Jantz et al. 1975). Elevation is ≈340 m above mean sea level. Precipitation averages 814 mm annually, but amounts received for 1981 and 1982 were 896 and 886 mm respectively. In 1981 and 1982, 70 and 75% of the precipitation was received during April–September, the normal time for most rainfall in the region.

The area containing the study plots was last burned in 1979; thus 3–4 yr of standing dead vegetation (defined herein to include litter) had accumulated. The amount of oven dry, standing dead vegetation was 594 g in October 1981 and 890 g in October 1982; this material formed a fairly dense layer 20–30 cm deep. The treatments were applied 29 April–4 May in 1981 and 8–11 May in 1982.

TABLE 2. (A) Density (no./m²) of flower stalks in 1981. Averages of six replications. (B) Significance levels of treatment differences.

A) Density of flower stalks*

Species	Treatment							
	Burned (B)	Clipped (C)	Clipped torched (CT)	Clipped + ash (CA)	Burned shaded (BS)	Unburned warmed (UW)	Unburned + ash (UA)	Unburned (U)
Andropogon gerardii Big bluestem	64.7	48.0	63.2	42.7	34.2	25.2	14.5	15.5
Sorghastrum nutans Indian grass	31.8	15.8	24.5	7.8	2.3	10.0	6.0	7.7
Andropogon scoparius Little bluestem	60.3a	69.2a	32.5a	66.5a	3.3	30.3a	47.2a	37.3a
Bouteloua curtipendula Side oats grama	0.7a	1.0a	3.5b	1.7ab	0.2a	1.3ab	0.8a	1.7ab
Panicum virgatum Switchgrass	0.8a	0.5a	0a	2.0a	0a	0.2a	0.2a	0a
Sporobolus asper Tall dropseed	1.5a	0.2	0.7a	0.3a	0.3a	0.5a	1.3a	0.8a

B) Significance levels of treatment differences†

Andropogon gerardii

	B	C	CT	CA	BS	UW	UA	U
B		5	···	1	1	1	1	1
C			···	···	···	1	1	1
CT				5	1	1	1	1
CA					···	5	1	1
BS						···	5	5
UW							···	···
UA								···
U								

Sorghastrum nutans

	B	C	CT	CA	BS	UW	UA	U
B		5	···	1	1	1	1	1
C			···	···	···	···	···	···
CT				5	1	5	1	5
CA					···	···	···	···
BS						···	···	···
UW							···	···
UA								···
U								

* Treatment comparisons within each species are by Duncan's Multiple Range test (α = .05). For the last four species, values in a row with the same letter are not significantly different. The absence of a letter indicates a sample size too small to evaluate statistically.

† Significance levels for comparisons between treatments are indicated thus: 5 = $P < .05$, 1 = $P < .01$. Ellipses (···) indicate that the two treatments defining that cell did not differ significantly.

TABLE 3. (A) Density (no./m²) of flower stalks in 1982. Averages of 10 replications. (B) Significant levels of treatment differences.

A) Density of flower stalks*

Species	Treatment: Burned (B)	Clipped (C)	Clipped + N (CN)	Clipped + soil (CD)	Clipped torched (CT)	Burned shaded (BS)	Unburned warmed (UW)	Unburned + N (UN)	Unburned (U)
Andropogon gerardii Big bluestem	40.3	36.8	39.7	34.4	33.8	31.2	9.0	5.5	2.1
Sorghastrum nutans Indian grass	2.4	6.1	6.0	2.6	5.2	1.3	2.1	1.5	0.7
Above two grasses combined	42.7	42.9	45.7	37.0	39.0	32.5	11.1	7.0	2.8
Andropogon scoparius Little bluestem	12.3	11.3	12.2	18.8	11.0	2.6	2.0	2.7	1.8
Bouteloua curtipendula Side oats grama	0.5	1.5	0.8	1.7	0.6	0.1	1.4	0.6	0.4
Panicum virgatum Switchgrass	0.1a	0.2a	0.4a	0a	0.1a	0a	0a	0.5a	0a
Sporobolus asper Tall dropseed	3.4ab	4.7a	5.0a	3.0ab	2.9ab	1.1b	0.9b	0.5b	0.7b

B) Significance levels of treatment differences†

Andropogon gerardii

	B	C	CN	CD	CT	BS	UW	UN	U
B		···	···	···	···	···	1	1	1
C			···	···	···	···	1	1	1
CN				···	···	···	1	1	1
CD					···	···	1	1	1
CT						···	1	1	1
BS							1	1	1
UW								···	1
UN									···
U									

Sorghastrum nutans

	B	C	CN	CD	CT	BS	UW	UN	U
B		···	···	···	···	···	···	···	···
C			···	···	···	···	···	···	5
CN				···	···	···	···	···	5
CD					···	···	···	···	···
CT						5	5	5	5
BS							···	···	···
UW								···	···
UN									···
U									

A. gerardii and *S. nutans* combined

	B	C	CN	CD	CT	BS	UW	UN	U
B		···	···	···	···	···	1	1	1
C			···	···	···	···	1	1	1
CN				···	···	···	1	1	1
CD					···	···	1	1	1
CT						···	1	1	1
BS							1	1	1
UW								···	1
UN									···
U									

Andropogon scoparius

	B	C	CN	CD	CT	BS	UW	UN	U
B		···	···	···	···	···	5	···	5
C			···	···	···	···	···	···	5
CN				···	···	···	5	···	5
CD					···	1	1	1	1
CT						···	···	···	5
BS							···	···	···
UW								···	···
UN									···
U									

Bouteloua curtipendula

	B	C	CN	CD	CT	BS	UW	UN	U
B		···	···	···	···	···	···	···	···
C			···	···	···	5	···	···	···
CN				···	···	···	···	···	···
CD					···	5	···	···	5
CT						···	···	···	···
BS							5	···	···
UW								···	···
UN									···
U									

* Treatment comparisons within each species are by Duncan's Multiple Range test ($\alpha = .05$). For the last two species, values in a row with the same letter are not significantly different.

† Significance levels for comparisons between treatments are indicated thus: 5 = $P < .05$, 1 = $P < .01$. Ellipses (···) indicate that the two treatments defining that cell did not differ significantly.

METHODS

In 1981, 6 replications of 8 treatments, and in 1982, 10 replications of 9 treatments, were established. Each plot was 2 × 2 m in size with 1-m aisles between. Treatments, placed randomly within blocks, were as follows:

(U)	Unburned	1981	1982
(UW)	Unburned and soil warmed	1981	1982

(UA)	Unburned and ash added	1981	
(UN)	Unburned and NH_4NO_3 added		1982
(C)	Clipped	1981	1982
(CA)	Clipped and ash added	1981	
(CT)	Clipped and surface heated with propane torch	1981	1982
(CN)	Clipped and NH_4NO_3 added		1982
(CD)	Clipped and burned-area soil added		1982
(B)	Burned	1981	1982
(BS)	Burned and shaded	1981	1982

Unburned plots (U) received no kind of treatment. In the unburned-warmed plots (UW), the soil was heat-

TABLE 4. Average height (cm) of flower stalks in 1981. Values in a row followed by the same letter are not significantly different (α = .05, Duncan's Multiple Range test). The last two species had too few flower stalks to make calculation of significance useful.

	Treatment							
Species	Burned (B)	Clipped (C)	Clipped torched (CT)	Clipped + ash (CA)	Burned shaded (BS)	Unburned warmed (UW)	Unburned + ash (UA)	Unburned (U)
Andropogon gerardii Big bluestem	161a	154a	160a	153a	158a	154a	153a	150a
Sorghastrum nutans Indian grass	119a	116a	122a	120a	126a	114a	100a	99a
Andropogon scoparius Little bluestem	99a	97a	92a	90a	87a	106a	92a	93a
Bouteloua curtipendula Side oats grama	86a	91a	98a	75a	77a	88a	72a	90a
Panicum virgatum Switchgrass	108	...	...	101	97	...	83	...
Sporobolus asper Tall dropseed	82	92	82	80	70	82	88	77

TABLE 5. (A) Average height (cm) of flower stalks in 1982. (B) Significance levels of treatment differences. Species other than *Andropogon gerardii* had an insufficient number of flower stalks for statistical analysis.

A) Average height of flower stalks

	Treatment								
Species	Burned (B)	Clipped (C)	Clipped + N (CN)	Clipped + soil (CD)	Clipped torched (CT)	Burned shaded (BS)	Un-burned warmed (UW)	Un-burned + N (UN)	Un-burned (U)
Andropogon gerardii Big bluestem	128	123	133	131	129	119	136	140	118
Sorghastrum nutans Indian grass	113	120	124	113	116	94	110	104	123
Andropogon scoparius Little bluestem	66	67	63	69	65	56	68	69	74
Bouteloua curtipendula Side oats grama	51	66	91	78	81	71	80	77	87
Panicum virgatum Switchgrass	56	135	124	...	78	...	...	102	...
Sporobolus asper Tall dropseed	55	65	69	67	58	64	85	66	63

B) Significance levels of treatment differences*

Andropogon gerardii

B	C	CN	CD	CT	BS	UW	UN	U	
	...	...	...	...	...	...	5	...	B
		...	...	...	...	5	1	...	C
			...	...	5	...	...	1	CN
				...	5	...	...	5	CD
					5	...	...	5	CT
						1	1	...	BS
							...	1	UW
								1	UN
									U

* Significance levels for comparisons between treatments are indicated thus: 5 = $P < .05$, 1 = $P < .01$ (Duncan's Multiple Range test). Ellipses (···) indicate that the two treatments defining that cell did not differ significantly.

TABLE 6. (A) Average oven-dry mass (g/m²) of aboveground plant parts at end of 1981 growing season; averages based on 10 replications. FLST = flower stalks; VEG = vegetative biomass; TOTAL = total biomass. (B) Significance levels of treatment differences.

A) Average oven-dry mass of aboveground plant parts

Species	Plant component	Treatment: Burned (B)	Clipped (C)	Clipped torched (CT)	Clipped + ash (CA)
Andropogon gerardii	FLST	308	248	338	197
Big bluestem	VEG	222	258	237	272
	TOTAL	530	506	575	469
Sorghastrum nutans	FLST	77	44	70	22
Indian grass	VEG	129	95	139	58
	TOTAL	206	140	209	80
Andropogon scoparius	FLST	54	60	23	55
Little bluestem	VEG	53	48	22	55
	TOTAL	107	108	45	109
Bouteloua curtipendula	FLST	0.4	0.5	2.4	1.1
Side oats grama	VEG	0.9	4.5	2.3	3.6
	TOTAL	1.2	5.0	4.8	4.7
Panicum virgatum	FLST	1.4	2.4	0	5.2
Switchgrass	VEG	0.2	0.6	0.3	2.0
	TOTAL	1.6	2.9	0.3	7.2
Sporobolus asper	FLST	3.1	0.4	1.2	0.7
Tall dropseed	VEG	4.2	1.6	1.5	2.5
	TOTAL	7.2	2.1	2.6	3.2
Above 6 grasses combined	FLST	445	355	435	281
	VEG	409	408	402	393
	TOTAL	853	763	837	674
Dichanthelium oligosanthes v. *Scribnerianum* Scribner dicanthelium	TOTAL	0.6	3.8	0.8	2.0
Poa pratensis Kentucky bluegrass	TOTAL	0.2	0.4	0.1	0.1
Annuals	TOTAL	12.8	0.1	15.8	0
Perennial forbs and woody	TOTAL	36	24	46	36
All plants	TOTAL	903	793	900	714

B) Significance levels of treatment differences*

Andropogon gerardii

Flower stalks

B	C	CT	CA	BS	UW	UA	U	
	...	...	5	5	1	1	1	B
		...	...	...	5	1	1	C
			1	1	1	1	1	CT
				...	...	5	5	CA
					...	...	...	BS
						5	5	UW
							...	UA
								U

Vegetative

B	C	CT	CA	BS	UW	UA	U	
	...	...	...	1	...	...	...	B
		...	...	1	...	...	...	C
			...	1	...	...	...	CT
				1	...	...	5	CA
					1	5	...	BS
						...	...	UW
							...	UA
								U

Sorghastrum nutans

Flower stalks

B	C	CT	CA	BS	UW	UA	U	
	...	...	1	1	5	1	1	B
		...	...	...	...	...	...	C
			5	1	5	5	5	CT
				...	...	...	...	CA
					...	...	...	BS
						...	...	UW
							...	UA
								U

Vegetative

B	C	CT	CA	BS	UW	UA	U	
	...	...	5	1	1	1	1	B
		...	...	1	5	5	5	C
			1	1	1	1	1	CT
				...	...	...	...	CA
					...	...	...	BS
						...	...	UW
							...	UA
								U

Andropogon scoparius

Flower stalks

B	C	CT	CA	BS	UW	UA	U	
	...	...	...	5	...	...	...	B
		...	...	5	...	...	...	C
			...	...	...	...	...	CT
				5	...	...	...	CA

Vegetative

B	C	CT	CA	BS	UW	UA	U	
	...	...	...	1	...	...	...	B
		...	...	1	...	...	...	C
			5	...	...	5	...	CT
				1	...	...	...	CA

TABLE 6. Continued.

Treatment			
Burned shaded (BS)	Unburned warmed (UW)	Unburned + ash (UA)	Unburned (U)
181	143	83	82
121	224	200	187
302	367	283	270
9	30	19	20
6	39	27	39
15	69	46	59
2	50	58	47
1	28	62	37
4	77	121	84
0.1	0.8	0.5	1.1
0	0.8	1.8	0.5
0.1	1.6	2.3	1.6
3.7	0.2	0.5	0
2.7	0.5	1.4	0.5
6.4	0.7	2.0	0.5
0.6	1.0	3.8	2.1
0.1	1.1	6.5	0.7
0.7	2.1	10.3	2.7
196	224	165	152
131	293	299	265
327	517	464	417
0	0.5	0.5	0.6
0.02	1.3	3.4	2.1
0	0	0	10.1
20	61	75	72
347	582	545	510

Andropogon gerardii

Total

B	C	CT	CA	BS	UW	UA	U	
	...	...	...	1	5	1	1	B
		...	...	1	...	1	1	C
			...	1	1	1	1	CT
				5	...	5	5	CA
					...	...	...	BS
						...	...	UW
							...	UA
								U

Sorghastrum nutans

Total

B	C	CT	CA	BS	UW	UA	U	
	...	...	1	1	1	1	1	B
		...	...	1	...	5	...	C
			1	1	1	1	1	CT
				...	...	...	...	CA
					...	...	...	BS
						...	...	UW
							...	UA
								U

Andropogon scoparius

Total

B	C	CT	CA	BS	UW	UA	U	
	...	...	...	1	...	...	...	B
		...	...	1	...	...	...	C
			...	...	...	5	...	CT
				1	...	...	...	CA

ed by running warm water through 4.8 mm ID (inside diameter) vinyl tubing with 1.6 mm wall thickness. Tubes were spaced 10 cm apart in 1981 and 5 cm apart in 1982. The 2 m long tubes, inserted on the soil surface under the standing dead and litter, were connected to brass nipples in galvanized water pipes leading to a 113-L insulated water tank heated with a single, 1000-watt electric immersion heater in 1981 and with two such heaters in 1982. In 1981, the soil in the unburned-warmed plots could not be heated the same amount as in the burned plots, thus the use of closer tube spacing and greater heating capacity in 1982. Immersion pumps were used to pump the water through the system. Soil temperature was recorded automatically for five plots of each treatment during 17–24 May and 12–19 July 1982 (Table 1). These data were used to maintain soil temperature of the unburned-warmed plots at approximately the same average temperature as the burned plots.

The unburned (UA) and clipped (CA) plots with ash added, received three times the amount of ash that would result from burning the standing dead in place. This amount was applied to increase the chance of showing effects; previous studies had indicated that ash addition was not a cause of the observed effects (Hulbert 1969, Old 1969, Lloyd 1972). Ash was obtained by burning plant matter from clipped plots in a large metal tray. Ash was then scattered as uniformly as possible onto the treatment plots.

The treatment CT (clipped and surface heated with propane torch) was intended to evaluate the effect of heat generated during burning. After all vegetative material was removed, thereby ensuring no ash residue, the plots were heated with a plumber's propane torch. Based on results in 1981 that found differences, but none significant, the 1982 clipping/torch treatments were applied using two temperature ranges, 150°–300°C and 400°–600°. These are high and low temperatures that have been recorded at the soil surface during grassland burning. The high temperature was used to assess the maximum effects likely to occur naturally.

Plots were treated with nitrogen to assess the extent to which the hypothesized increase in nitrogen fixation or mineralization could account for increases in productivity. Nitrogen-fertilized plots (treatments UN and CN) received 12.75 g/m^2 of NH_4NO_3 or 4.06 g/m^2 (40.6 kg/ha) of nitrogen.

Clipping was accomplished with hand shears, and plant biomass was removed as close to the soil surface as feasible. All clipped material and litter was removed.

Soil for treatment CD (clipped and burned-area soil added) was obtained from a nearby burned area. The top few millimetres of soil were scraped off and uniformly scattered within the CD plots to assess whether a chemical change in the soil affected subsequent growth of the vegetation. The soil added was collected from an area approximately the same size as the treatment plot.

Burning was accomplished by wetting the aisle around

TABLE 6. Continued.

B) Significance levels of treatment differences* (continued)

Andropogon scoparius

Flower stalks

B	C	CT	CA	BS	UW	UA	U	
					5	5	5	BS
						…	…	UW
							…	UA
								U

Vegetative

B	C	CT	CA	BS	UW	UA	U	
					…	1	5	BS
						5	…	UW
							…	UA
								U

Bouteloua curtipendula

Flower stalks

B	C	CT	CA	BS	UW	UA	U	
	…	…	…	…	…	…	…	B
		…	…	…	…	…	…	C
			…	…	…	…	…	CT
				…	…	…	…	CA
					…	…	…	BS
						…	…	UW
							…	UA
								U

Vegetative

B	C	CT	CA	BS	UW	UA	U	
	5	…	…	…	…	…	…	B
		…	…	1	5	…	5	C
			…	5	…	…	…	CT
				5	…	…	…	CA
					…	…	…	BS
						…	…	UW
							…	UA
							…	U

A. gerardii, S. nutans, A. scoparius, B. curtipendula, P. virgatum, and *Sp. asper* combined

Flower stalks

B	C	CT	CA	BS	UW	UA	U	
	…	…	1	1	1	1	1	B
		…	…	1	1	1	1	C
			1	1	1	1	1	CT
				…	…	5	1	CA
					…	…	…	BS
						…	…	UW
							…	UA
								U

Vegetative

B	C	CT	CA	BS	UW	UA	U	
	…	…	…	1	1	1	1	B
		…	…	1	1	1	1	CT
			…	1	1	1	1	CA
				1	1	1	1	BS
					1	1	1	UW
						…	…	UA
							…	U

Dichanthelium oligosanthes

B	C	CT	CA	BS	UW	UA	U	
	1	…	5	…	…	…	…	B
		1	1	1	1	1	1	C
			5	…	…	…	…	CT
				1	5	5	5	CA
					…	…	…	BS
						…	…	UW
							…	UA
								U

Poa pratensis

B	C	CT	CA	BS	UW	UA	U	
	…	…	…	…	·	1	5	B
		…	…	…	·	1	…	C
			…	·	·	1	5	CT
				·	·	1	5	CA
					·	1	5	BS
						5	…	UW
							…	UA
								U

* Significance levels for comparisons between treatments are indicated thus: 5 = $P < .05$, 1 = $P < .01$ (Duncan's Multiple Range test). Ellipses (···) indicate that the two treatments defining that cell do not differ significantly. *P. virgatum* and *Sp. asper* had an insufficient number of flower stalks for statistical analysis.

the plot to be burned and then igniting the dead plant material with a torch. The resulting fire seemed comparable to a larger grassland fire with regard to speed and heat produced. In 1981, the plots were burned on 29 April with air temperature ranging from 24° to 38°, wind speed from 8 to 14 km/h, and relative humidity 25–40%. Burning was applied on 10 May in 1982 with air temperature 23°–27°, wind speed 0–2 km/h, and relative humidity 55–60%. In 1981, nine days had passed since the occurrence of a rain sufficient to wet the soil; four days had passed in 1982. The standing dead and litter were dry at the time of burning in both years.

The shading of burned plots was intended to simulate the interception of light by standing dead in the unburned plots. In 1981, this type of shading was attempted by placing a layer of clipped grass between two layers of chicken wire and supporting it on stakes ≈25 cm above the soil surface. The clipped grass matted quickly and thus differed from natural shading. The plants grew through this layer of dead vegetation, which was left in place throughout the growing season. In 1982, shade was produced by installing a layer of chicken wire ≈25 cm above the soil surface and overlaying this with two layers of burlap and a layer of white cotton muslin in order to simulate the change in irradiance as plants grow up through standing dead debris. The muslin was removed after the plants had grown 10–15 cm, and the burlap and wire were removed when the plants grew against the burlap. During

TABLE 6. Continued.

Andropogon scoparius

Total

B	C	CT	CA	BS	UW	UA	U	
					5	1	5	BS
						...	...	UW
							...	UA
								U

Bouteloua curtipendula

Total

B	C	CT	CA	BS	UW	UA	U	
	5	...	...	...	...	...	...	B
		...	...	1	...	...	...	C
			...	5	...	...	...	CT
				5	...	...	...	CA
					...	...	...	BS
						...	...	UW
							...	UA
								U

A. gerardii, S. nutans, A. scoparius, B. curtipendula, P. virgatum, and *Sp. asper* combined

Total

B	C	CT	CA	BS	UW	UA	U	
	...	...	1	1	1	1	1	B
		...	...	1	1	1	1	C
			1	1	1	1	1	CT
				1	1	1	1	CA
					1	5	...	BS
						...	5	UW
							...	UA
								U

the evaluation, however, it became obvious that neither the 1981 nor the 1982 procedures adequately simulated natural conditions.

Temperatures at 1.5 m above the soil surface, at the soil surface, and 10 cm beneath the soil surface were automatically recorded from five replicates of each treatment. Measurements were made using copper/constantan thermocouples with a Campbell Scientific CR-R recorder.

When flower stalks had ceased growth in late summer, the center square metre of each plot was clipped at the soil surface. In unburned plots, the dead material from previous years was separated from the current year's production. Current-year material was separated by species, and, for the dominant grasses, flower stalks plus attached leaves were separated from other vegetative production. The length of each flower stalk of warm-season grasses was recorded. All material was oven-dried at 60° and weighed.

Statistical analyses were performed by Dr. K. E. Kemp of the Department of Statistics, Kansas State University, using the standard complete randomized block ANOVA of the Statistical Analysis System (SAS); comparisons between treatments were performed using the Duncan Multiple Range Test ($\alpha = .05$) (SAS 1982). Scientific names follow the *Flora of the Great Plains* (Great Plains Flora Association 1986).

RESULTS AND DISCUSSION

Soil surface irradiance

One important effect of burning was the removal of standing dead and litter, which exposed the soil to sunlight. This result is shown by the combination of (1) no significant differences between burned and clipped plots, (2) increases in vegetative and reproductive productivity with litter removal, via burning and clipping, yet, (3) at least with 1981 data, a decrease in this productivity when burned areas where shaded (Tables 2–7). This overall result is reflected in the data in various, specific ways.

Comparing burned and clipped treatments, the production of both flower stalks and vegetative growth did not differ significantly for most species and species combinations (Tables 2–7). The principal exceptions were significant differences in the number of big bluestem and Indian grass flower stalks in 1981; both species had higher numbers with burning. In addition, Scribner dichanthelium (*Dichanthelium oligosanthes* v. *scribnerianum*) and side oats grama (*Bouteloua curtipendula*) both had higher aboveground biomass with clipping. The general similarity in the effects of burning and clipping are consistent with the findings of Hover and Bragg (1981) and support the idea that the physical removal of standing dead vegetation is an important consequence of burning.

The importance of increased surface light intensity, one environmental change that occurs with litter removal, was evaluated using the burned-shaded (BS) treatment. Data for 1981 on the six dominant grasses support the hypothesis that light intensity affects plant responses; significant differences were observed between burned and burned-shaded treatments, and no significant differences were recorded between burned-shaded and unburned treatments (Tables 2, 4, and 6). Opposite results were obtained in 1982, however (Tables 3, 5, and 7). This contradiction in effects is attributed to the different procedures used to shade the plots. The fact that one procedure resulted in significant effects, however, is sufficient to implicate increased incident solar radiation as an important factor in explaining causes of fire effects. It seems reasonable to

TABLE 7. (A) Average oven-dry mass (g/m²) of aboveground plant parts at end of 1982 growing season; averages based on 10 replications. FLST = flower stalks; VEG = vegetative biomass; TOTAL = total biomass; T = <0.1 g. (B) Significance levels of treatment differences.

A) Average oven-dry mass of aboveground plant parts

Species	Plant component	Treatment: Burned (B)	Clipped (C)	Clipped + N (CN)	Clipped + soil (CD)	Clipped torched (CT)
Andropogon gerardii	FLST	127	105	138	114	107
Big bluestem	VEG	249	244	327	274	260
	TOTAL	376	349	465	387	368
Sorghastrum nutans	FLST	6	18	17	6	13
Indian grass	VEG	16	24	34	22	26
	TOTAL	22	42	51	28	39
Andropogon scoparius	FLST	6	6	8	11	6
Little bluestem	VEG	10	10	19	19	16
	TOTAL	16	16	26	30	23
Bouteloua curtipendula	FLST	0.2	0.7	0.6	0.8	0.3
Side oats grama	VEG	0.7	2.5	1.4	2.8	1.1
	TOTAL	0.9	3.2	2.0	3.6	1.4
Panicum virgatum	FLST	0.1	0.6	1.4	0	0.1
Switchgrass	VEG	0	0.1	0.1	0.2	T
	TOTAL	0.1	0.7	1.5	0.2	0.2
Sporobolus asper	FLST	4.0	4.7	5.9	3.6	1.8
Tall dropseed	VEG	5.9	9.7	16.7	9.1	8.7
	TOTAL	10.0	14.3	22.6	12.7	10.5
Above 6 grasses combined	FLST	144	136	170	135	129
	VEG	282	290	398	326	312
	TOTAL	426	425	569	461	442
Dichanthelium oligosanthes v. *Scribnerianum* Scribner dichanthelium	TOTAL	4.6	2.8	4.8	3.0	2.7
Poa pratensis Kentucky bluegrass	TOTAL	0	0.4	0.4	0.07	0.04
Other perennial grasses	TOTAL	0.3	0.1	0.6	0	0.6
Carex spp. and *Cyperus* spp.	TOTAL	0.8	1.3	2.3	3.0	0.5
Perennial forbs	TOTAL	47	69	108	69	48
Annuals and biennials	TOTAL	37	10	24	12	24
All plants	TOTAL	515	509	709	548	517

B) Significance levels of treatment differences*

Andropogon gerardii

Flower stalks

B	C	CN	CD	CT	BS	UW	UN	U	
	...	...	...	...	5	1	1	1	B
		...	...	...	...	1	1	1	C
			...	...	5	1	1	1	CN
				...	...	1	1	1	CD
					...	1	1	1	CT
						...	5	1	BS
							...	1	UW
								5	UN
									U

Vegetative

B	C	CN	CD	CT	BS	UW	UN	U	
	...	5	...	...	...	1	1	1	B
		5	...	...	...	1	1	1	C
			...	5	5	1	1	1	CN
				...	...	1	1	1	CD
					...	1	1	1	CT
						1	1	1	BS
							...	...	UW
								...	UN
									U

Sorghastrum nutans

Flower stalks

B	C	CN	CD	CT	BS	UW	UN	U	
	...	...	...	...	...	...	...	...	B
		...	...	...	5	...	...	5	C
			...	...	5	...	...	5	CN
				...	...	...	...	...	CD
					5	...	...	5	CT
						...	...	...	BS
							...	...	UW
								...	UN
									U

Vegetative

B	C	CN	CD	CT	BS	UW	UN	U	
	...	...	...	...	...	...	...	...	B
		...	...	...	...	...	5	1	C
			...	...	5	1	1	1	CN
				...	...	...	...	5	CD
					5	5	1	1	CT
						...	...	...	BS
							...	...	UW
								...	UN
									U

TABLE 7. Continued.

Treatment			
Burned shaded (BS)	Unburned warmed (UW)	Unburned + N (UN)	Unburned (U)
76	34	28	6
239	118	139	117
315	151	167	123
3	8	4	2
11	9	5	0.4
14	17	9	2
1	2	2	2
3	4	8	6
4	5	10	8
T	1	0.4	0.3
0.1	1.3	1.2	0.1
0.2	2.3	1.6	0.4
0	0	1.4	0
0	0.4	0.6	0
0	0.4	2.0	0
1.2	1.7	1.1	0.9
2.8	0.8	1.1	0.8
4.0	2.5	2.2	1.8
81	46	37	11
256	132	155	124
338	179	192	135
2.9	0.01	0.3	0.03
0	1.4	1.7	0.5
0	0.1	0.2	T
0.8	0.8	1.1	0.4
43	60	47	91
53	0.4	18	7
437	241	260	234

Andropogon gerardii

Total

B	C	CN	CD	CT	BS	UW	UN	U	
	...	...	...	...	...	1	1	1	B
		5	...	...	...	1	1	1	C
			...	5	1	1	1	1	CN
				...	...	1	1	1	CD
					...	1	1	1	CT
						1	1	1	BS
							...	...	UW
								5	UN
									U

Sorghastrum nutans

Total

B	C	CN	CD	CT	BS	UW	UN	U	
	...	...	...	...	...	...	...	...	B
		...	...	...	...	...	5	1	C
			...	...	5	5	1	1	CN
				...	...	...	...	...	CD
					5	5	1	1	CT
						...	...	...	BS
							...	...	UW
								...	UN
									U

believe that the greatest effect of burning is to increase light intensity near the soil early in the growing season. Having ample light for early growth of grasses may be important partly because it stimulates growth at the time when water supplies are most favorable. In addition to increasing light intensity, however, other effects may result from litter removal. Knapp (1984), for example, found that daytime leaf temperatures are higher near the soil in burned than in unburned plots. Such differences may sufficiently affect physiological processes to result in increased growth.

Soil surface temperatures

Warming the soil in unburned areas (treatment UW), which was designed to approximate soil temperatures throughout the growing season in burned plots, resulted in a significant (28%) increase in combined productivity of the six most common grass species; productivity in burned plots, however, was increased by 121% (Tables 6–7). Similar increases were shown for individual species as well but not always at the 5% significance level. While not statistically evaluated, combined data for all species also showed an increase; 8% with warming soil compared with 98% with burning. In combination, these results support the hypotheses of Rice and Parenti (1978) and others that changes in soil temperature contribute to explaining fire effects on tallgrass vegetation.

As noted, the response to warming in unburned plots was small compared with the response in burned plots. Part of this difference may be that the methods used to warm the soil in unburned plots did not sufficiently duplicate the soil temperature of burned plots. For example, the soil surface in warmed plots did not get as hot in the daytime nor as cool at night as in burned plots. Such differences, however, occur primarily in the top few centimetres of soil. At the depth where roots and rhizomes occur, the difference in diel variation in soil temperature was small between burned and unburned-warmed plots (Table 1). The results of soil warming, therefore, suggest that soil temperature increases seem to be a minor cause of fire effects.

Soil nitrogen

Total vegetative production of big bluestem, the dominant grass, was significantly greater on both clipped and unburned plots receiving nitrogen (treatments CN and UN) than on untreated plots (treatments C and U) (Table 7). Similarly, while not tested statistically, total aboveground plant production averaged 39% greater in clipped and 11% greater in unburned plots to which nitrogen had been added. These results are consistent with the work of Owensby et al. (1970) who found an increase in productivity with addition of nitrogen to tallgrass prairie, although weedy species showed a greater response than did the native grasses.

Nitrogen is volatilized during the burning process,

TABLE 7. Continued.

B) Significance levels of treatment differences* (continued)

Andropogon scoparius

Flower stalks

B	C	CN	CD	CT	BS	UW	UN	U	
	···	···	···	···	···	···	···	···	B
		···	···	···	···	···	···	···	C
			···	···	···	···	···	···	CN
				···	1	1	1	1	CD
					···	···	···	···	CT
						···	···	···	BS
							···	···	UW
								···	UN
									U

Vegetative

B	C	CN	CD	CT	BS	UW	UN	U	
	···	···	···	···	···	···	···	···	B
		···	···	···	···	···	···	···	C
			···	···	1	5	···	5	CN
				···	1	5	···	5	CD
					···	···	···	···	CT
						···	···	···	BS
							···	···	UW
								···	UN
									U

Bouteloua curtipendula

Flower stalks

B	C	CN	CD	CT	BS	UW	UN	U	
	···	···	···	···	···	···	···	···	B
		···	···	···	···	···	···	···	C
			···	···	···	···	···	···	CN
				···	···	···	···	···	CD
					···	···	···	···	CT
						5	···	···	BS
							···	1	UW
								5	UN
									U

Vegetative

B	C	CN	CD	CT	BS	UW	UN	U	
	5	···	5	···	···	···	···	···	B
		···	···	···	1	···	···	1	C
			···	···	···	···	···	···	CN
				···	1	···	···	1	CD
					···	···	···	···	CT
						···	···	···	BS
							···	···	UW
								···	UN
									U

A. gerardii, S. nutans, A. scoparius, B. curtipendula, P. virgatum, and *Sp. asper* combined

Flower stalks

B	C	CN	CD	CT	BS	UW	UN	U	
	···	···	···	···	5	1	1	1	B
		···	···	···	5	1	1	1	C
			···	···	1	1	1	1	CN
				···	5	1	1	1	CD
					5	1	1	1	CT
						···	···	1	BS
							···	1	UW
								5	UN
									U

Vegetative

B	C	CN	CD	CT	BS	UW	UN	U	
	···	1	···	···	···	1	1	1	B
		1	···	···	···	1	1	1	C
			5	1	1	1	1	1	CN
				···	5	1	1	1	CD
					···	1	1	1	CT
						1	1	1	BS
							···	···	UW
								···	UN
									U

Dichanthelium oligosanthes Vegetative

B	C	CN	CD	CT	BS	UW	UN	U	
	···	···	1	···	···	···	···	···	B
		···	5	···	···	···	···	···	C
			···	5	1	···	···	···	CN
				1	···	1	5	1	CD
					···	···	···	···	CT
						···	···	···	BS
							···	···	UW
								···	UN
									U

Poa pratensis Vegetative

B	C	CN	CD	CT	BS	UW	UN	U	
	···	···	···	···	···	1	1	1	B
		···	···	···	···	5	5	5	C
			···	···	···	1	1	1	CN
				···	···	5	5	5	CD
					···	5	···	5	CT
						5	5	5	BS
							···	1	UW
								1	UN
									U

* Significance levels for comparisons between treatments are indicated thus: 5 = $P < .05$, 1 = $P < .01$ (Duncan's Multiple Range test). Ellipses (···) indicate that the two treatments defining that cell do not differ significantly. *P. virgatum* and *Sp. asper* had an insufficient number of flower stalks for statistical analysis.

but fire has been hypothesized to indirectly increase the nitrogen supply in other ways. Nitrogen fixation by blue-green algae, for example, might be stimulated by the higher light intensity or the greater solar heating of the soil in burned prairie as suggested in a review by Vogl (1974). Burning may also affect nitrogen fixation by increasing the population size of blue-green algae (Kragskow 1982). Other possibilities may be increased nitrogen availability from heterotrophic mineralization or differential effects of season-long surface warming that may interact with soil moisture to affect nitrogen mineralization. In this latter case, soil in unburned plots eventually reaches the same temperature as that in burned plots, although, being later in the growing season, surface moisture is usually lower. Thus fire might provide warmer temperatures when

TABLE 7. Continued.

Andropogon scoparius

Total

B	C	CN	CD	CT	BS	UW	UN	U	
	...	...	...	...	...	...	...	...	B
		...	...	...	...	...	...	...	C
			...	...	5	5	...	5	CN
				...	1	1	5	5	CD
					...	...	...	...	CT
						...	...	...	BS
							...	...	UW
								...	UN
									U

Bouteloua curtipendula

Total

B	C	CN	CD	CT	BS	UW	UN	U	
	5	...	5	...	...	...	...	...	B
		...	...	...	5	...	...	5	C
			...	...	...	...	...	...	CN
				...	1	...	...	1	CD
					...	...	...	...	CT
						...	...	...	BS
							...	...	UW
								...	UN
									U

A. gerardii, S. nutans, A. scoparius, B. curtipendula, P. virgatum, and *Sp. asper* combined

Total

B	C	CN	CD	CT	BS	UW	UN	U	
	...	1	...	...	...	1	1	1	B
		1	...	...	...	1	1	1	C
			5	5	1	1	1	1	CN
				...	5	1	1	1	CD
					5	1	1	1	CT
						1	1	1	BS
							...	5	UW
								1	UN
									U

Carex and *Cyperus* spp. Vegetative

B	C	CN	CD	CT	BS	UW	UN	U	
	...	...	1	...	...	...	...	...	B
		...	5	...	...	...	...	...	C
			...	5	...	...	...	...	CN
				1	1	1	5	1	CD
					...	...	...	...	CT
						...	...	...	BS
							...	...	UW
								...	UN
									U

soil is more moist thereby stimulating nitrogen fixation and decomposition.

While the results of this study are consistent with hypotheses that fire affects productivity by increasing nitrogen supply, they do not verify this effect. This is true in part because the extent to which nitrogen addition approximates natural fire conditions is unknown.

Ash addition

Overall, no significant differences were found in flower production and height of aboveground biomass with the addition of ash to clipped or unburned plots (Tables 2, 4, and 6) despite the addition of triple the amount of ash that would normally result. This result is shown by the absence of significant differences between clipped plots (C) and clipped, ash-added plots (CA) and between unburned plots (U) and unburned, ash-added plots (UA). These results support the findings of Old (1969), Hulbert (1969), and Lloyd (1972). A single exception was the suppressive effect of ash addition on biomass of Scribner dichanthelium. Long-term effects of increased ash were not addressed in the present study.

Direct surface heating

Based on the comparison between clipped (C) and clipped/torched (CT) treatments, direct heating of the soil surface by fire did not generally affect flower or total aboveground production (Tables 2–7); two exceptions were flower stem number of side oats grama, which was higher, and biomass of Scribner dichanthelium, which was lower, with surface heating. These results are contrary to the positive effect of heating proposed by Petersen (1983). Significant differences were not observed between the low- and the high-temperature clipped/torched treatments applied in 1982; therefore, these data were combined on all 1982 tables and figures.

Addition of soil from burned area

The addition of soil from a burned area did not affect any of the vegetative parameters measured; no significant differences were obtained between clipped (C) plots and plots to which soil from burned plots had been added (CD). There is, thus, no evidence to support the idea that the heat of a fire produces chemicals that indirectly affect subsequent growth, at least not in the short-term.

CONCLUSION

This study provides one additional step toward identifying the causes of fire effects by considering, at one time, a variety of factors. The results indicate the importance of increased incident solar radiation and nitrogen availability and the absence of significant, short-term effects of either ash addition or direct soil heating during burning.

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