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Effects of Late Summer Fire on Tallgrass Prairie Microclimate and Community Composition¹

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ABSTRACT: Two tallgrass prairie sites with different grazing histories and fuel accumulation were burned to investigate vegetation response to wild fires of differing intensity. Headfires were ignited 5 September 1985 under wildfire weather conditions (37 C air temperature, 36% relative humidity and wind gusts to 40 km/h). One of the burned plots had not been grazed for the past 3 years and had 1000 g/m² fine fuel load; the other had been grazed moderately and had 450 g/m² fine fuel. Fire intensity at the soil surface on the high fuel-load plot was four times that on the low fuel burn plot. Microhabitat and vegetation responses were monitored the year following burning. Measured vegetative parameters, including tiller density, basal area and production, indicated that rhizomatous tallgrasses revegetated both burned plots quickly. Bunchgrasses decreased in both basal area and production on the high fuel plot. Community composition and productivity differences persisted 1 yr after the fires and were mainly attributable to bunchgrass mortality and microhabitat improvement for ruderal species. The data suggest that fire intensity is an important factor to consider when developing fire disturbance theory for tallgrass prairie.

INTRODUCTION

The tallgrass prairie ecosystem is often cited as an example of a fire-tolerant system which evolved with fire as a part of its natural disturbance regime (Adams *et al.*, 1982). Tallgrass prairie is not regarded as a strict "fire type" but it has been shown that fire protection results in loss of productivity by the dominant grasses (Weaver and Rowland, 1952; Aikman, 1955; Ehrenreich, 1959; Hulbert, 1969; Anderson *et al.*, 1970) and eventual replacement by woody species (Weaver, 1968; Bragg and Hulbert, 1976). Aboriginal and lightning-set fires are believed to have maintained the northern and eastern borders of this grassland well into climatic regions where forest would be considered climax vegetation (Vogl, 1974; Vankat, 1979; Axelrod, 1985).

Most controlled experimental fires in tallgrass prairie have been conducted in the spring for a variety of reasons, including: (1) Researchers have long been interested in the increased productivity and renewed vigor of dominant grasses such as *Andropogon gerardii* Vit. following a spring burn (Curtis and Partch, 1950; Dix and Butler, 1954; Ehrenreich, 1959; Kucera and Ehrenreich, 1962; Hadley and Kieckhefer, 1963; McMurphy and Anderson, 1965; Old, 1969; Kucera, 1970; Launchbaugh and Owensby, 1978; Knapp, 1984a); (2) spring burns can be conducted in relative safety (Anderson, 1982; Wright and Bailey, 1982); (3) it had been incorrectly perceived that fire in other seasons, particularly summer, was not possible because of green or insufficient fuel (Bragg, 1982) and low probability of lightning-caused ignition (Hulbert, 1973), and (4) summer fire is not desirable because it removes forage valued for livestock grazing (Bragg, 1982). Prescribed spring burning does little damage to dominant warm-season grasses (C₄) while reducing the vigor of cool-season plants (C₃), thus giving the vegetation a boost toward theoretical tallgrass climax. This is a much studied and well-documented phenomenon (Anderson *et al.*, 1970). Additionally, there is a stimulatory effect on the rhizomatous tallgrasses due to the fire, by the removal of litter and timely microclimate improvement (Old, 1969; Knapp, 1984a).

However, the intensity of spring fires may differ from that of fires occurring in summer and autumn. Historical fire accounts (Higgins, 1986) show that 85% of the

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lightning-set fires in the northern Great Plains occurred in June, July and August; and that Indian-set fires occurred in nearly all months with a majority in late summer and autumn. Most written discussions of fire as a natural disturbance in ecosystems cite high temperature, low humidity, heavy fuel accumulation and thunderstorm frequency as important factors in wildfire development (Anderson, 1982; Wright and Bailey, 1982; Sousa, 1984; Axelrod, 1985). These conditions occur in late summer and autumn for the tallgrass prairie and generate wildfires of greater intensity than the prescribed spring burns generally studied. Mid- to late-growing season fires are more likely to damage the climax dominants because rapid plant growth is occurring, meristems are elevated and plants may already be under stress because soil water content is declining (Risser *et al.*, 1981).

With the exception of a study by Adams *et al.* (1982) in which woody plant response was recorded after a low intensity July burn, there have been few controlled investigations into the effects of late summer fire on prairie vegetation. Our objectives were: (1) To quantify simulated wildfire effects on community composition and production of key prairie population groups, and (2) to quantify the fire-induced microclimate which results in habitat changes for the two population groups (warm-season dominants and cool-season ruderals).

MATERIALS AND METHODS

Study sites.—The study sites, approximately 3.5 km apart, were located on the Oklahoma Agricultural Experiment Station's Agronomy Research Range, 15 km SW of Stillwater, Oklahoma. Vegetation on the sites is tallgrass prairie dominated by C₄ tallgrasses (*Andropogon gerardii* Vit., *Sorghastrum nutans* (L.) Nash and *Panicum virgatum* (L.) and C₄ midgrasses (*Schizachyrium scoparium* (Michx.) Nash and *Bouteloua curtipendula* (Michx.) Torr.). Paired plots (burned and unburned) were established on each of two similar upland sites (Grainola-Lucien soils; subsoil at 10 to 40 cm) on the basis of differences in recent grazing use by domestic cattle and the resultant differences in accumulated litter. One site had been moderately grazed in recent years and the year of burning and will be referred to as the low fuel site. The other site had not been grazed for at least 3 years before the study and will be referred to as the high fuel site. Average annual precipitation at Stillwater is 831 mm with 75% occurring during the April through October growing season. Growing season precipitation in 1985 was approximately 17% greater than average. Vegetation on both study sites was dominated by a mixture of C₄ grasses although tallgrasses were proportionally more abundant on the ungrazed site than on the grazed site. Grazing was excluded during the study.

Burning conditions.—On each site, two 10 x 20 m plots were established with a SW-NE orientation to match the SW wind direction which prevails in late summer. On 5 September 1985, after fire retardant was applied to mowed 2 m plot borders, line headfires (ignited by driptorch) were set on one of the plots for each study site. The unburned plots were left undisturbed to serve as reference areas. Fuel loading and several weather variables were sampled immediately before each burn. Fuel loading was measured by clipping aboveground herbage to ground level in 10 randomly placed 0.5 m² circular quadrats per plot. Samples were oven-dried at 70 C for 72 h. Fuel moisture was calculated on the basis of dry weight. Fire temperature was sampled at 2-sec intervals using chromel-alumel thermocouples connected to a Campbell Scientific datalogger. Thermocouples were grouped in three sets per plot to measure temperatures at three vertical positions: at the soil surface, and at 15 and 30 cm above the soil surface. Fire intensity measures including degree seconds were calculated from each thermocouple temperature trace using a program in Turbo Pascal for IBM compatible microcomputers. The program included a discrete summation algorithm to arrive at an estimate of degree seconds, which is the area above the preburn and postburn ambient temperatures and under the time-temperature curve. The points of definite temperature rise and drop for computing residence time were numerically determined by sequential reverse progression through 10-sec intervals of the time-temperature curve to points of 2

C or greater departure from the postburn ambient temperature.

Vegetation response.—Vegetation characteristics were measured on both burned and unburned plots. On 10 September 1985, 10 soil samples (20 cm² x 1 cm deep) were taken from each plot and spread on top of sterilized potting medium in the greenhouse to determine the resident winter-annual seedbank. Emergent annual grass seedlings (*Bromus* spp.) were counted for 3 wk. Annual grass seedling densities were sampled in the field (10-20 cm² quadrats per plot) on three dates during the growing season. Difference in growth form of the rhizomatous tallgrasses and the tufted midgrasses required different sampling methods; tiller density of tallgrasses and basal area of midgrasses were sampled in 10 permanent 0.125 m² quadrats per plot, three times during the growing season. Basal area was measured by cutting brown paper to fit the basal area of the grasses in the field and then running it through a leaf area meter in the laboratory. Herbage was clipped to ground level in 10 randomly placed 50 x 50 cm quadrats per plot on 18 June and 26 August 1986, the approximate dates of peak C₃ and C₄ plant production, respectively. Current year's biomass was then separated into tallgrass, midgrass, cool season annual grass and dicotyledonous components. Herbage was oven-dried at 70 C for 72 h.

Microclimate.—Soil water content was measured indirectly with a neutron probe (Troxler) at least monthly for 1 yr. Soil water contents at three depths (15, 30 and 45 cm) were summed to estimate profile soil water content on a cm H₂O/cm vertical profile basis. Soil surface (-1 cm), canopy (+10 cm) and leaf (lower epidermis) temperatures were measured every 2 h on several cloud-free days during autumn and winter, beginning in September 1986, with fine wire copper-constantin thermocouples. Soil surface and canopy temperatures were measured with four *in situ* psychrometers per plot. Leaf temperatures of *Andropogon gerardii* were measured by inserting a thermocouple junction into the lower epidermis of five young, fully expanded upper canopy leaves in each plot. Diurnal trends of soil surface, canopy and leaf temperatures were measured in the autumn to determine peak temperature and stress periods. Temperature sampling during the following summer was done on three dates during the anticipated peak temperature period (1400-1500 CDT). Afternoon leaf water potential was measured on 8 cloud-free days using leaf cutter psychrometers (J.R.D. Merrill, Logan, Utah). Leaf disk samples taken from young, fully expanded leaves of 10 *A. gerardii* plants on each plot were transported to the laboratory and processed using a Wescor HP-115 water potential data system (Logan, Utah) as described by Johnson *et al.* (1986).

Statistical comparisons of burned and unburned samples within a litter type were made using Student's *t*-test.

RESULTS AND DISCUSSION

Direct effects of the fires.—The low fuel plot had less than half the accumulated fuel load of the high fuel plot (Table 1). Weather conditions on the day of the burn were typical of wildfire conditions; the weather was hot (37 C), dry (RH = 36%) and windy (gusts up to 40 km/h). Fire intensity measures calculated from fire temperatures and fire duration demonstrate that the fire on the high fuel plot was roughly four times as intense at the soil surface as that on the low fuel plot (Table 1). Nearly complete combustion of biomass occurred and the plots had a general aspect of blackened and bare soil with a dusting of ash.

Tiller counts before and 2 months after the fires showed that the rhizomatous tallgrasses recovered well after the fire on the low fuel plot (Table 2). Most of the regrowth came from existing tillers which had been completely defoliated but had not suffered apical meristem damage during the fire. Existing tillers which survived the fire had burned leaf tips whereas newly initiated tillers exhibited no evidence of fire damage. Some stimulation of tallgrass tillering may have occurred as a result of standing biomass removal. Conversely, extensive damage to existing tallgrass tillers occurred on the high

fuel plot (Table 2). Highly significant reductions in tallgrass tiller densities were still apparent 2 months after the fire. Regrowth on the high fuel plots consisted largely of newly initiated tillers.

Basal area of the tufted midgrasses was significantly reduced by both fires (Table 2). *Schizachyrium scoparium*, which elevates a high proportion of apical meristems to near or aboveground level (Branson, 1953), was especially sensitive to the high intensity of these fires and suffered 58 and 95% reduction in basal area on the low and high fuel plots respectively. Regrowth during the 2 mo after the burn was primarily from surviving tillers. Because few new tillers were initiated on either burn plot, regrowth was minimal on the low fuel plot and very slight on the high fuel plot.

Germinable annual grass seed was nonexistent in the soil samples taken from the high fuel site (Table 3). This was a notable and unexpected finding although rather easily explained. Litter build-up in recent years had been so dense that no suitable habitat existed for natural establishment and regeneration of annual grasses. On the low fuel site, germinable annual grass seed was abundant in soil samples (Table 3). Resident seed density for *Bromus* spp. was greater than 11,000 seeds/m². Burning decreased seed density by ca. 74%. This reduction in seed source was reflected throughout the winter-

TABLE 1. — Burning conditions and fire behavior of simulated wildfires, 5 September 1985

	Low fuel	High fuel
Total fuel (g/m ²) ($\bar{x} \pm SE$)	443 \pm 74	1032 \pm 60
Fuel moisture (%)	22	20
Weather		
Air temperature (C)	37	37
Relative humidity (%)	36	36
Windspeed (average-gusts, km/h)	23-40	13-30
Degree seconds (C sec)		
Soil surface ($\bar{x} \pm SE$)	10,400 \pm 1900	43,600 \pm 3200
15 cm above soil surface ($\bar{x} \pm SE$)	6300 \pm 40	29,600 \pm 2100
30 cm above soil surface ($\bar{x} \pm SE$)	3900 \pm 180	20,300 \pm 1400

TABLE 2. — Tallgrass tiller density (number/m²) and midgrass based area (cm²/m²) on plots burned 5 September 1985

	Low fuel		High fuel	
	Before burn (8/15/85)	After burn (10/22/85)	Before burn (8/15/85)	After burn (10/22/85)
Tiller density				
<i>Andropogon gerardii</i>	23	45	89	17**
All tallgrasses ^a	70	98	162	74**
Basal area				
<i>Schizachyrium scoparium</i>	213	90*	274	14**
All midgrasses ^b	268	141**	274	14**

*Before burn and after burn means significantly different ($P < 0.05$) within a fuel type

**Before burn and after burn means significantly different ($P < 0.01$) within a fuel type

^aIncludes: *Andropogon gerardii*, *Sorghastrum nutans* and *Panicum virgatum*

^bIncludes: *Schizachyrium scoparium* and *Bouteloua curtipendula*

spring growing season during which *Bromus* spp. seedling densities were at least 54% lower on the burned plot. It is clear that similar reductions would have occurred on the high fuel plot had a seedbank existed.

Microclimate alteration immediately following the fires. — During the autumn regrowth period (9/27/85-10/25/85) the diurnal course of air, soil and leaf temperatures differed on burned and unburned plots (Fig. 1a). Air temperature in the leaf canopy (+ 10 cm) was significantly higher at midday on the unburned plots of both sites. Burned and unburned plot canopy air temperatures converged late in the day and became equal overnight. The moderating effect of a litter layer on air flow and the maintenance of higher daytime canopy temperatures has been reported by Old (1969) and Knapp (1984a). To test whether or not this holds true for extremes in temperature, we sampled on an extremely cold winter day (1/27/86) and the pattern differed slightly (Fig. 1a). Significant differences in canopy air temperatures always occurred on the burned and unburned plots from the high fuel site. High litter continually moderated the environment whereas low litter moderated the environment significantly only at midday.

TABLE 3. — Seedling density (no. seedlings X 10³/m²) of *Bromus* spp. taken from soil samples germinated in the greenhouse and from field plots on three dates

	Low fuel		High fuel	
	Unburned	Burned	Unburned	Burned
Greenhouse germinated soil sample, 9/10/85	11.4	3.0**	0	0
Field samples				
9/27/85	8.1	3.7**	0	0
10/25/85	16.6	3.1**	0	0
5/13/86	9.0	2.5**	0	0

**Row means significantly different (P < 0.01) within fuel type

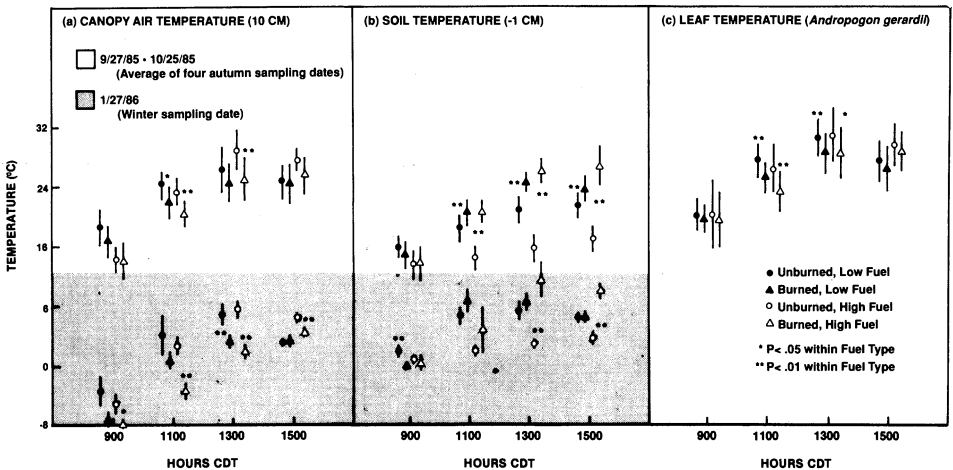


Fig. 1 — Diurnal course of canopy air, soil and *Andropogon gerardii* leaf temperatures during autumn and winter on burned and unburned plots. Vertical bars are 1 sd about the mean

Daytime soil temperatures (-1 cm) during the autumn regrowth period were nearly always significantly higher on the burned plots compared to the unburned plots (Fig. 1b). Differences generally increased through the day as heat from solar radiation accumulated in the blackened soil and then temperatures converged overnight as heat was reradiated back to the atmosphere. High litter maintained much cooler soil temperature than low litter. The difference in soil temperature modification by the two different litter accumulation levels was greatest on the winter sampling date (Fig. 1b). High litter was a much better insulator and continued to maintain significantly lower soil temperature on the unburned than the burned plots while soil temperature from burned and unburned low fuel plots were similar throughout the day.

Andropogon gerardii leaf temperatures reflected canopy air temperatures on all plots (Fig. 1c). Midday leaf temperatures were significantly higher on unburned plots for both sites. A similar trend was observed by Knapp (1984a), who sampled *A. gerardii* leaf temperatures in summer following a prescribed spring burn of a Kansas tallgrass prairie.

Due to variation in grazing management and the resultant effects on litter, the high fuel site had nearly twice as much water in the soil profile as the low fuel site on 5 September 1985 (Fig. 2). Differences disappeared during the autumn and winter rainy period when prairie soil profiles are typically recharged with water (Risser *et al.*, 1981). Leaf water potential of *Andropogon gerardii* leaves sampled at midday during that time indicate that little or no water stress existed and that differences due to treatment effects were not distinguishable (Fig. 3). Autumn midday leaf water potentials were similar to nonstressed *A. gerardii* leaves sampled by Knapp (1984b).

Carryover effects of the fires. — Significant differences in midday canopy air temperatures between burned and unburned plots tended to disappear over the growing season as burned plots revegetated (Fig. 4a). Midday differences in soil temperatures found on burned and unburned plots persisted and intensified as summer temperatures got hotter and sunlight became more direct (Fig. 4b). Leaf temperatures followed no particular pattern over the course of the growing season and no simple relationship of leaf temperature to treatment developed (Fig. 4c).

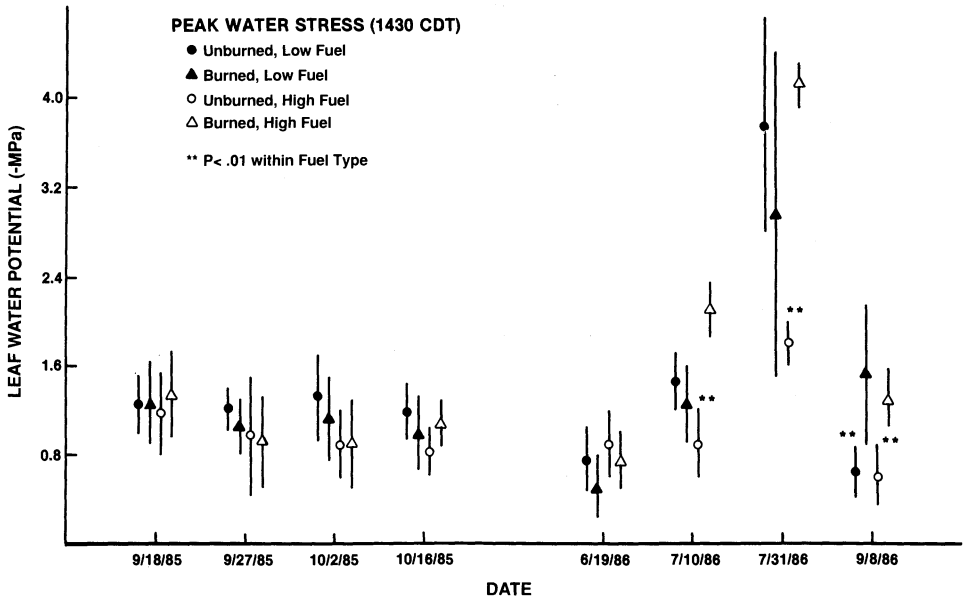


Fig. 2 — Soil water content from burned and unburned plots

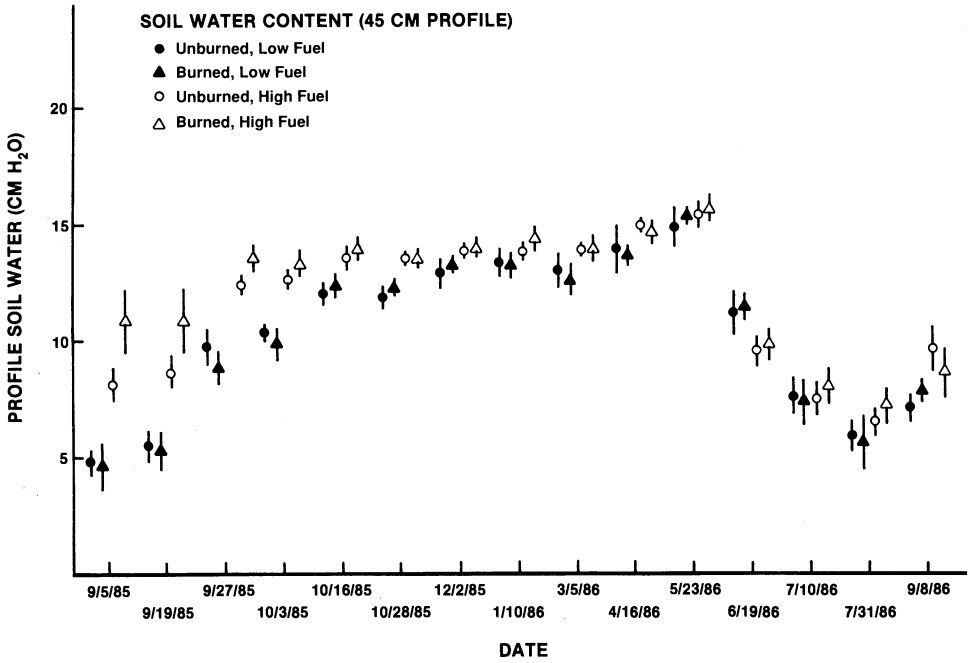


Fig. 3—*Andropogon gerardii* leaf water potential at peak stress (afternoon) on burned and unburned plots. Vertical bars are one standard deviation about the mean

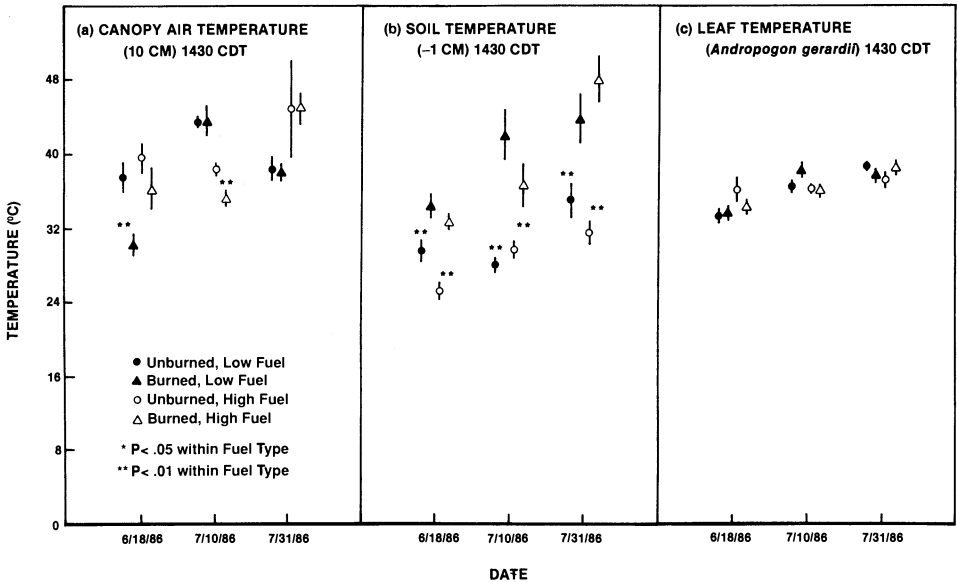


Fig. 4—Canopy air, soil and *Andropogon gerardii* leaf temperatures at midday on burned and unburned plots. Vertical bars are 1 SD about the mean

During the rapid growth period for C₄ grasses (June-August) the role of litter in maintaining improved leaf water status during the day became evident (Fig. 3). Leaves sampled on 10 and 31 July 1986 showed greater leaf water stress in plants growing on the burned plots than in those on the unburned plots from the high fuel site. A similar pattern did not develop on the low fuel site until 8 September 1986. During the same period, soil water content decreased in the usual fashion, reaching a minimum in late summer (Fig. 2). However, significant treatment differences in soil profile water content never developed and it is reasonable to assume that for a deep-rooted species like *Andropogon gerardii*, growing on shallow soils like the Grainola-Lucien series, water was equally available on all plots. Because these observed treatment differences in leaf water potential cannot be related to observed differences in water availability, evaporative loss must be considered. Knapp (1984a) reported 290% higher windspeed adjacent to tillers in burned prairie compared to ungrazed, unburned prairie. Indeed, leaves sampled from burned plots in this study were often wilted and/or rolled and appeared wind-desiccated.

Tallgrasses performed similarly throughout the growing season on burned and unburned low fuel plots on which tiller densities were roughly equal for all three summer sampling dates (Table 4). On the high fuel site, significant fire-induced reductions in tallgrass tiller densities early in the growing season disappeared by September. Tiller densities on unburned plots at the end of the growing season were consistent with densities measured the year before and there was no perceptible change in the relative proportion of the three tallgrass species over time.

In general, midgrasses did not recover as well as the tallgrasses on burned plots. Basal area of midgrasses decreased on the unburned plots as the growing season progressed and plants became reproductive (Table 4). Basal tillers of *Schizachyrium scoparium* that do not initiate inflorescences often senesce during the droughty period of late summer. Therefore, the observed convergence of midgrass basal area on burned and unburned plots over the summer was not so much a result of recovery by burned plants as it was an artifact of midgrass tillering behavior. Large differences may have persisted between burned and unburned plots from the high fuel site even after 1 yr; however, due to large sample variance, statistically significant differences were detected only in May.

The effects of all the vegetation parameters discussed to this point are reflected in the data collected on biomass production (Table 5). Cool season annual grasses showed a 450% increase in June production on the burned plot where seed was available (low fuel). Although the fire had reduced seed and seedling densities, winter growing conditions were improved by burning (greater insolation and higher soil surface temperatures). Individual *Bromus* spp. plants appeared more robust. Peak biomass production by tallgrasses was not significantly different between burned and unburned plots. If production was reduced on burned plots, it may be due in part to reduced photosynthesis and cell enlargement resulting from greater leaf tissue water stress during late summer. There were no significant differences in peak biomass production by *Schizachyrium scoparium* on the burned and unburned low fuel plots. However, *S. scoparium* biomass production on the burned high fuel plot was only 5% that on the unburned plot. The high fuel burn nearly eliminated basal area of midgrasses and *S. scoparium* biomass production.

Total biomass production was similar for paired plots during both June and August sampling. Any postfire reductions in production by grasses were offset by increases in herbaceous dicot production. This was especially evident during the June sampling period. *Rudbeckia hirta* L., which had been a minor component of the vegetation, dominated the burned high fuel plot in June. Burning of the low fuel plot reduced production of two herbaceous species which were abundant on the unburned plots, namely *Ambrosia psilostachya* DC. and *Xanthocephalum dracunculoides* DC. (Shinners). This reduction was offset in total by increased annual grass biomass production.

TABLE 4. — Tallgrass tiller density (number/m²) and midgrass basal area (cm²/m²) on burned and unburned plots the growing season following simulated wildfires

	5/13/86				7/10/86				9/8/86			
	Low fuel		High fuel		Low fuel		High fuel		Low fuel		High fuel	
	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned
Tiller density	162	186	382	176*	116	126	192	92*	149	143	203	292
Basal area	357	113*	92	14*	231	108	105	31	89	93	43	8

*Burned and unburned means significantly different (P < 0.05) within a date and fuel type

TABLE 5. — Current year's biomass (g/m²) on plots burned 5 September 1985

	18 June 1986				26 August 1986			
	Low fuel		High fuel		Low fuel		High fuel	
	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned
Tallgrasses ^a	10	16	118	82	40	30	153	106
<i>Schizachyrium scoparium</i>	20	13	17*	1	36	56	25*	1
Other perennial grasses ^b	168*	116	97	53	271	254	56	50
Cool season annual grasses ^c	32**	142	8	1	8**	32	1	0
Herbaceous dicots ^d	48*	23	93**	254 ^e	32	50	130	153
Total	278	310	333	391	387	422	365	310

*Row means significantly different (P < 0.05) within date and fuel type

**Row means significantly different (P < 0.01) within date and fuel type

^aIncludes *Andropogon gerardii*, *Sorghastrum nutans* and *Panicum virgatum*

^bIncludes *Bouteloua curtipendula*, *B. gracilis*, *B. hirsuta*, *Bothriochloa saccharoides* and *Sporobolus asper*

^cLargely *Bromus* spp.

^dIncludes *Ambrosia psilostachya*, and *Xanthocephalum dracunculoides*

^e*Rudbeckia hirta* dominant in burned plot

Fire effects on community composition: a summary.—Conventional wisdom is that forage production by the dominant prairie grasses decreases after a summer prairie wildfire. Launchbaugh and Owensby (1978) recommended that cattle stocking rates be reduced by 25-75% the 1st yr and 25-50% the 2nd. Direct effects on individual plants and microclimate alteration have been offered as reasons for the decline. We attempted to evaluate the relative importance of these effects with this experiment.

Previous studies on microclimate alteration after prescribed spring prairie burning have focused on timely microclimate improvement for the C₄ populations. Old (1969), Peet *et al.* (1975) and Knapp (1984a) concluded that part of the increase in tallgrass productivity after a spring burn is a result of increased insolation, more optimal leaf temperatures for photosynthesis and improved water status early in the growing season. The microclimate changes resulting from the late summer burn carried well into the following summer and agreed closely with the results from other experiments. The only time C₄ plant growth conditions may not have been more favorable on the burned plots was mid to late summer when evaporative loss was high and leaf water potential was low at midday. However, important differences exist between this and the other fire-microclimate studies. Cool season (C₃) plants experienced growth enhancement due to litter removal prior to germination and no disturbance of their life cycle or reproduction occurred. The major microclimate improvement was timely for C₃ rather than C₄ species. Population dynamics and community composition postfire reflected this difference.

We did not see the postfire flush of growth commonly expected from tallgrasses because the fire was conducted at a time which inflicts maximum damage to C₄ species. However, tallgrass productivity the following August was in the seasonally normal range because tiller densities were not much reduced and microclimate changes were generally favorable. The rhizomatous habit of tallgrasses may be an important protective characteristic in the event of wildfire. Bunchgrasses, the growing points of which are not as well-protected, were damaged or killed outright depending upon fire intensity. Spring burns result in greater abundance of the tallgrasses relative to the bunchgrasses through differing competitive abilities (Svejcar and Christiansen, 1986; Collins, 1987). In this study, tallgrasses achieved relatively greater abundance through a fire-resistant growth habit. This indicates there is a major difference in disturbance response within the matrix grasses of the community depending upon the season and intensity of the disturbance. Nonmatrix ruderals which are frequently favored by opening the canopy either with fire or grazing (Grime, 1979) had a decided advantage after a late summer fire and in a manner different from that seen after a spring burn.

Researchers tend to regard fire in prairie as a simple defoliation event (Old, 1969; Hulbert, 1969; Collins, 1987) unless considering woody plant response within the community when it is regarded as a potentially lethal event (Adams *et al.*, 1982). However, late season fires should not be considered a simple defoliation event for herbaceous species, because defoliation is not the main source of community alteration. Where litter build-up is high, mortality of grasses may be a significant part of subsequent community change. Microclimate alteration, although similar to that following a spring burn, is not as important for the matrix grasses. Microclimate changes resulting from defoliation are significant improvements for the non-matrix cool season ruderals.

This study provides evidence that late summer fire may be sufficiently intense to be considered a major disturbance causing shifts in community composition away from C₄ plant dominance. Season of a prairie fire is a critical factor in individual plant and community effects because different population groups are vulnerable. Residual litter and accumulated fuel are also critical factors because they affect fire intensity. We have shown that a higher intensity fire induced greater community change through matrix grass mortality and ruderal (*i.e.*: *Bromus* spp. and *Rudbeckia hirta*) establishment. Therefore, development of disturbance theory concerning prairie community structure such as proposed by Collins (1987) should include consideration of disturbance season and intensity. This is true concerning all types of defoliation processes (Heady, 1975). Al-

though we did not measure species richness, a community attribute discussed by Collins (1987), observation suggests that richness did not vary with fire intensity to the degree that species abundance varied.

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