Influence of Fire Frequency and Burning Date on the Proportion of Reproductive Tillers in Big Bluestem and Indian Grass

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Abstract. Big bluestem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans*) were censused for two seasons in ungrazed tallgrass prairie to investigate the influence of fire frequency and seasonality on tiller density and flowering. For big bluestem, the highest percentage of reproductive tillers (43.7%) occurred in plots burned after 3 years without burning ($P < 0.001$). As burning frequency increased, the proportion of reproductive tillers declined to 23.9% in plots burned after 1 year without burning and 14.5% in plots burned annually in late spring. The proportion of reproductive tillers was significantly lower in unburned plots than in any burn treatment. Seasonality of annual burns did not affect the percentage of reproductive tillers. For Indian grass, the proportion of reproductive tillers (14.8%) was highest in plots burned annually in late spring. Long-term unburned plots and plots burned every 4 years had the lowest percentage of tillers producing an inflorescence (0.6% and 1.4%, respectively). Results of this study indicate that annual fires in tallgrass prairie stimulate approximately 15% of big bluestem and Indian grass tillers to produce inflorescences, when ample precipitation occurs during the growing season. Burning once every 4 years reduces big bluestem tiller density compared to annual burning, but maximizes the number and percentage of reproductive tillers. In contrast, quadrennial burning drastically reduces the proportion of Indian grass tillers producing an inflorescence.

Key words: fire frequency, fire seasonality, reproductive effort, grass inflorescence, tallgrass prairie

Introduction

Reproduction by dominant, warm-season, perennial grasses in tallgrass prairie is primarily vegetative. Sexual reproductive effort varies from year-to-year, but profuse flowering of big bluestem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans*) is infrequent, often occurring only two or three times per decade (Cornelius 1950). Removing litter with fire increases reproductive stem density (Curtis and Partch 1950; Kucera and Ehrenreich 1962; Ehrenreich and Aikman 1963; Knapp and Hulbert 1986; Hulbert 1988). However, interactions among fire frequency, fire seasonality, and independent environmental factors such as growing season precipitation can influence flowering dynamics of warm-season grasses. In native prairie, a seemingly high proportion of big bluestem and Indian grass tillers occasionally produce an inflorescence. Although various studies have examined inflorescence production in tallgrass prairie, the proportion of tillers that produce an inflorescence generally has been ignored. This study evaluated the influence of fire frequency and seasonality on tiller density and inflorescence production of big bluestem and Indian grass during 2 successive flowering years. The hypothesis was that these dominant warm-season grasses would respond to fire, particularly infrequent fire, with significant increases in both total and reproductive tillers.

Materials and Methods

An ungrazed tallgrass prairie area on Konza Prairie Research Natural Area (KPRNA) was partitioned into 10 x 25 m plots in 1982 to investigate long-term effects of fire at different seasons and intervals between fire. In addition to unburned plots, fire regimes included: annual burning in early spring (mid March), late spring (late April), and fall (mid November); late spring burning every 2 years (two different treatments for year-of-fire); and late spring burning every 4 years (four different treatments for year-of-fire). Each treatment was replicated four times across a topoedaphic gradient ranging from silty clay lowland soils to clayey upland soils. Since the initiation of treatments, seasonality and frequency of fire have visibly influenced the vegetative composition, but big bluestem and Indian grass are relatively common in most plots.

Tillers and flowering culms of big bluestem and Indian grass were censused in 10 quadrats (0.1 m^2) along a transect within each plot. To avoid edge effects, quadrats were located at least 1 m from plot borders. Tillers were counted in September 1992 and 1993.

For statistical analysis, densities of tillers and flowering culms were log transformed to equalize variances and reduce skewness within the data. The proportions of big bluestem and Indian grass tillers that produced an inflorescence were arcsine transformed before analysis (Zar 1974). Transformed data were analyzed as a two-way analysis of variance with means separated by least significant difference ($P < 0.05$).

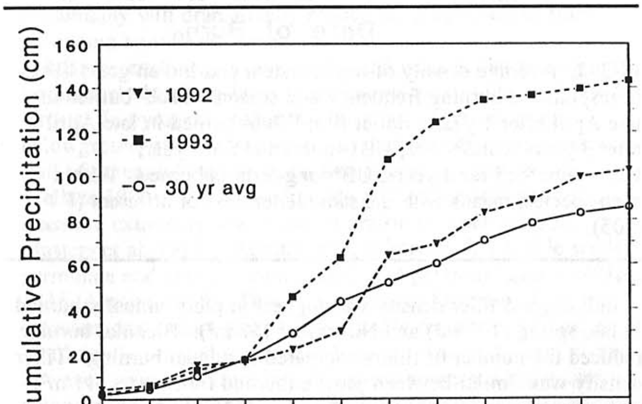

FIG. 1. Cumulative precipitation pattern of 1992 and 1993 compared with the 30-year average.

Results

Precipitation in 1992 was below the 30-year mean in the early part of the growing season (May-June). However, rainfall in July was the third highest on record (33.6 cm), and the year ended 17 cm above the long-term average (Fig. 1). In 1993, precipitation was above the 30-year mean throughout the growing season, and the year ended as the second wettest on record (143 cm).

Both 1992 and 1993 were considered "flowering years" in which perceptibly high numbers of big bluestem and Indian grass tillers produced flowering culms. However, inflorescence production was significantly higher for both grasses in 1993 than in 1992. Tiller density and the proportion of tillers producing an inflorescence also were higher for most treatments in 1993 than in 1992.

Tiller Density

Big bluestem tiller density was highest (212/m^2) in plots annually burned in late April (Fig. 2). Tillers were more numerous in plots annually burned in March (121 tillers/m^2) or November (114 tillers/m^2) than in any unburned treatment ($P < 0.001$). Biennial burning tended to increase ($P = 0.09$) tillers in the year that fire occurred (85/m^2) compared to plots unburned for 1 year (63/m^2).

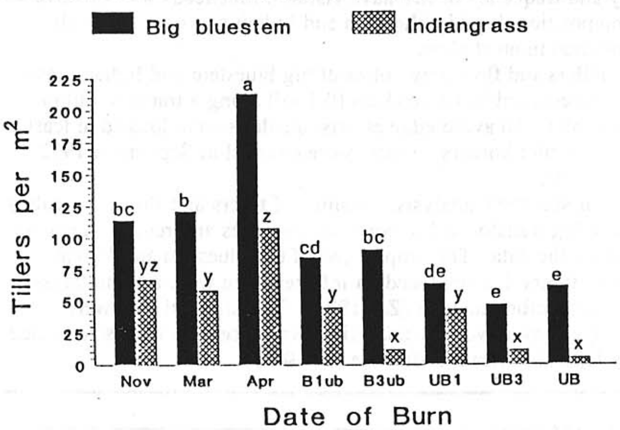

FIG. 2. Average density of big bluestem and Indian grass tillers in response to burning frequency and season. B1ub=burned in late April after 1 year without fire; B3ub=burned in late April after 3 years without fire; UB1=unburned for 1 year; UB3=unburned for 3 years; UB=long-term unburned. Within each species, means with the same letter are not different ($P > 0.05$).

Indian grass tiller density was highest in plots annually burned in late spring (107/m^2) and November (67/m^2). Biennial burning reduced the number of tillers compared to annual burning. Tiller density was similar between plots unburned for 3 years (11/m^2) and plots burned after 3 years of no fire (12/m^2). Long-term unburned plots had the lowest number of tillers (5/m^2).

Reproductive Stem Density

The greatest density of big bluestem flowering culms (39/m^2) occurred in plots burned after 3 years without fire (Fig. 3). Annual burning in late April produced more inflorescences (30/m^2) than annual burning in March or November (13/m^2 and 15/m^2, respectively). Flowering density was significantly lower ($P < 0.001$) in unburned plots than in any fire treatment.

Flowering density of Indian grass culms was greatest in plots annually burned in late April (26/m^2). In biennially burned plots, inflorescence density was 16 culms/m^2 in the year that fire occurred, but only 6 culms/m^2 in plots unburned for 1 year ($P < 0.001$).

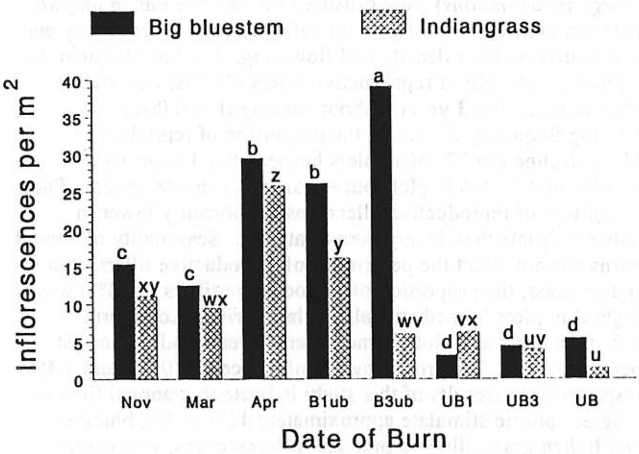

FIG. 3. Average density of big bluestem and Indian grass flowering culms in response to burning frequency and season. B1ub=burned in late April after 1 year without fire; B3ub=burned in late April after 3 years without fire; UB1=unburned for 1 year; UB3=unburned for 3 years; UB=long-term unburned. Within each species, means with the same letter are not different ($P > 0.05$).

Percentage of Reproductive Stems

The mean proportion of big bluestem tillers that produced an inflorescence (43.7%) was higher ($P < 0.001$) in plots burned after 3 years without fire than any other treatment (Fig. 4). The proportion of reproductive tillers decreased to 23.9% in plots burned after 1 year without fire and to 14.5% in plots annually burned in late spring. In unburned plots, the percentage of tillers producing an inflorescence was significantly lower than in any burn treatment. Seasonality of annual burns did not affect the proportion of reproductive tillers.

Annual burning in late April stimulated the greatest proportion of Indian grass tillers to produce an inflorescence (14.8%). Burning in different seasons reduced the percentage of tillers that flowered (5.9% in November and 3.8% in March). Long-term unburned plots and plots burned every 4 years had the lowest percentages of tillers producing an inflorescence.

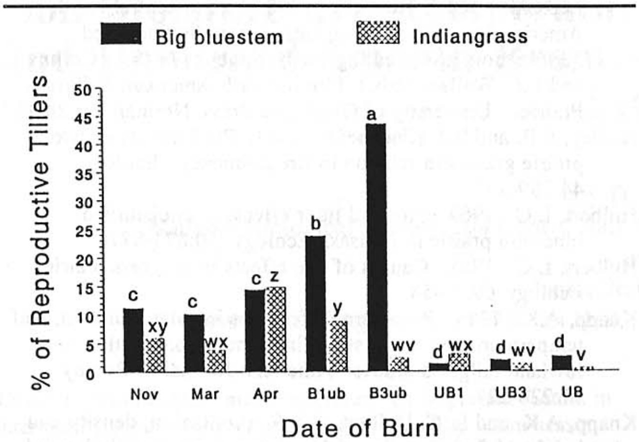

FIG. 4. Average proportion of big bluestem and Indian grass tillers producing an inflorescence in response to burning frequency and season. B1ub=burned in late April after 1 year without fire; B3ub=burned in late April after 3 years without fire; UB1=unburned for 1 year; UB3=unburned for 3 years; UB=long-term unburned. Within each species, means with the same letter are not different ($P > 0.05$).

Discussion

Annual fire, particularly in late spring, favors big bluestem (Svejcar 1990). Higher tiller density in burned than in unburned plots may be due to increased light levels from litter removal (Knapp 1984; Svejcar and Browning 1988). Although fire stimulates vegetative propagation of big bluestem, its influence is mediated by environmental conditions. Glenn-Lewin *et al.* (1990) concluded that weather is responsible for greater year-to-year fluctuations in tiller production than is fire.

Indian grass also is favored by annual fire, but tiller counts included numerous newly emerged shoots. In a separate late September census, 51.7% of all Indian grass tillers were < 10 cm tall (Table 1). These tillers arise throughout the growing season from established parent tillers and usually are short-lived (McKendrick *et al.* 1975). In unburned plots, light limitation from litter apparently is more inhibitory to the intermittently emerging tillers of Indian grass than the synchronized spring tillering of big bluestem. After 3 years without fire, litter buildup significantly reduced ($P < 0.001$) Indian grass tillers compared with other treatments. However, removing litter accumulations with quadrennial fire did not stimulate tiller or inflorescence production. Thus, Indian grass is much more dependent on frequent fire than is big bluestem.

Table 1. Height of Indian grass tillers measured in late September.

Height (cm)	Number of tillers	%
0.1 - 4.9	179	31.6
5 - 9.9	114	20.1
10 - 29.9	150	26.5
> 30	123	21.7

n = 566

Burning removes litter and usually stimulates inflorescence production in warm-season grasses (Curtis and Partch 1950; Weaver and Rowland 1952; Hulbert 1969). The flowering response is proportional to the detritus thickness and the length of time it is present (Old 1969). Inflorescence density is higher when the fire occurs in late spring than at other times. Benning and Bragg (1993) reported highest reproductive response to burning if fire occurred in mid to late May when photosynthetically active leaves were elongating. Other reports have shown that the influence of fire on inflorescence production decreased in the year after burning but remained higher than in unburned areas (Ehrenreich and Aikman 1963; Hadley and Kieckhefer 1963). In this study, however, flowering density of big bluestem was not different ($P > 0.1$) between plots unburned for 1 year and long-term unburned plots, suggesting that the stimulus of fire in the previous year did not have a carryover effect.

Although burning stimulates inflorescence production, the response is augmented by precipitation (Cornelius 1950). Generally, a wet year that follows a hot, dry year is favorable for stimulating flowering in big bluestem and Indian grass (Knapp and Hulbert 1986). Old (1969) suggested that the flowering response is controlled by environmental conditions at the beginning of the growing season. However, the high number of flowering tillers in this study suggests that precipitation during July and August, when the warm-season grasses are initiating flowering culms, may be a more critical influence. Circumstantial support for the influence of summer moisture on flowering density also can be gleaned from long-term records of inflorescence data on KPRNA. Yearly precipitation totals for 1981, 1982, 1983, and 1984 all were above the 30-year average, but only in 1981 and 1982 did profuse flowering occur. Both years received abundant moisture in July and August, with no extended periods of high temperature. In contrast, 1983 and 1984 were wet in the spring but hot and dry during the summer, and the warm-season grasses produced few or no inflorescences (Knapp and Hulbert 1986). The two successive wet years in this study stimulated a relatively high percentage of big bluestem and Indian grass tillers to produce an inflorescence, and flowering likely approached the upper limits in unfertilized native prairie. Precipitation deficits in the summer of more "typical" years presumably will dramatically reduce the proportion of tillers producing an inflorescence.

Inflorescence formation in perennial grasses that propagate vegetatively has long-term ramifications on survival of individual ramets. In pyrogenic habitats, allocation of resources to belowground storage in lieu of aerial structures is an adaptive trait of perennial grasses to conserve nutrients (Adams and Wallace 1985). Viable seed yields of big bluestem and Indian grass are extremely low in native prairie (Cornelius 1950; Masters et al. 1993). Additionally, relatively few viable seeds germinate and survive amid established perennial grasses (Blake 1935; Abrams 1988). Thus, inflorescence formation from big bluestem and Indian grass tillers usually represents wasted or inefficiently utilized resources. In quadrennially burned plots, however, removing litter buildup opens numerous microsites for colonization and may increase the likelihood of seedling survival. Big bluestem responds to infrequent fire with a high proportion of reproductive tillers, a strategy that could increase genet diversity in the population, if the probability of successful seedling establishment concomitantly increases.

Inflorescence production of big bluestem and Indian grass may reflect transient responses to recurring shifts in limiting resources. Nonequilibrium conditions created by infrequent fire stimulates the flowering response in a high proportion of big bluestem tillers, because both energy and nitrogen availability are increased (Seastedt and Knapp 1993). Nitrogen availability likely was not a limiting factor in 1992, because the previous year was relatively dry (18.3 cm precipitation below normal). Timely and abundant precipitation during the 1993 growing season saturated the soil to the point where the roots probably never experienced water stress, and the grasses responded with profuse tillering and inflorescence production.

In summary, yearly fires in tallgrass prairie stimulated approximately 15% of big bluestem and Indian grass tillers to produce inflorescences. In unburned sites, less that 3% of big bluestem and Indian grass tillers flowered. Floral induction in big bluestem is maximized (44% of the tillers) when burning occurs following 3 years without fire. However, the proportion of Indian grass tillers producing an inflorescence is reduced drastically with quadrennial burning (< 2% of all tillers).

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