# Growth and gas exchange of *Andropogon gerardii* as influenced by burning

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**Abstract**

**Late spring burning response of the dominant big bluestem *(Andropogon gerardii)* was studied on a tallgrass site in central Oklahoma (USA) during a dry (1984) and a wet (1985) year. During active growth (May and June) when temperatures were not limiting, photosynthesis (PS) was higher for burned (25–27 $\mu$ moles$^{-2}$ s$^{-1}$) relative to unburned plants (20–25 $\mu$moles m$^{-2}$ s$^{-1}$); but during summer drought, PS declined to <10 $\mu$ moles m$^{-2}$ s$^{-1}$ and treatment rank reversed. However, the 2 treatments had similar transpiration per unit leaf area, and burned plots had much higher peak big bluestem leaf area indices (6.4 in 1984 and 4.5 in 1985) than unburned plots (2.0 both years). Apparently higher transpirational demand in burned plots lowered soil moisture, thereby increasing late season moisture stress and lowering PS relative to unburned plots. Burning resulted in a doubling of big bluestem tiller numbers (997–1,034 and 498–600 tillers m$^{-2}$ for burned and unburned plots, respectively). Peak aboveground biomass of big bluestem was about 3 times higher on burned relative to unburned prairie during both years. During both years burned vs. unburned big bluestem had higher peak values of % leaf nitrogen (N) and more total leaf N (%N* leaf mass). Thus, burning big bluestem increased leaf area during the active growth period and stimulated PS, resulting in higher carbon uptake of burned relative to unburned plants.**

**Key Words: prescribed burning, tallgrass prairie, water potential**

The tallgrass prairie of North America has been classified as a fire-derived and fire-maintained ecosystem (Stewart 1951). Suppression of fire often reduces productivity of tallgrass species (Kucera and Ehrenheich 1962, Hadley and Hieckhefer 1963, Hulbert 1969, Rice and Parenti 1978, Knapp 1985). However, in a number of studies productivity was unaffected or reduced by burning (Kelting 1957, Owensby and Anderson 1967, Anderson et al. 1970). Several factors could explain the contradictory results obtained from burning studies: (1) in some ecosystems burning during wet years has a positive effect on primary productivity but the opposite is true for dry years (Wright 1974); (2) species response to fire varies, and thus the effect of fire may depend on the species composition of a particular tallgrass prairie site; and (3) timing of burning can affect species composition and primary production (Towne and Owensby 1984). Research from the Flint Hills of Kansas, where tallgrass prairie sites were burned annually since 1928, shows that time of burning has a major effect on community response to fire (Towne and Owensby 1984). Burning in late spring rather than at 1 of 3 earlier dates favored big bluestem (*Andropogon gerardii* Vitman) and Indiangrass (*Sorgastrum nutans* L.) Nash over other species. These 2 $C_4$ grasses are dominants in much of the tallgrass prairie region. Towne and Owensby (1984) further state that only 3 weeks difference in timing of a spring burn can have substantial long-term effects on the plant community.

Although there is a good deal of information concerning primary productivity and response to burning of tallgrass prairie species, few studies have concentrated on seasonal trends in physiological and morphological attributes of these species (Risser et al. 1981). During a drought year, Knapp (1985) found that big bluestem exhibited higher photosynthetic rates on burned compared to unburned prairie during the active growth period (May and June). The same author also showed that big bluestem has a high capacity for osmotic adjustment (Knapp 1984a), apparently a mechanism allowing this species to tolerate the summer drought common in the Central and Southern Great Plains.

To determine the effects of burning on big bluestem, we chose to burn a tallgrass prairie site at a time that favors productivity of this species. The objective was to monitor seasonal trends in physiological and morphological characteristics of burned and unburned big bluestem.

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## Materials and Methods

### Study Site

Research was conducted during 1984 and 1985 at the USDA/-ARS Forage and Livestock Research Laboratory (98°0′ W, 35° *40′N; elevation* = 450 m) near El Reno, Oklahoma. Vegetation on the study site was typical of native tallgrass prairie, with big bluestem, Indiangrass, and little bluestem *(Schizachyrium scoparium* (Michx.) Nash as dominants. Soils were silt loams classified as either Udic Paleustolls or Pachic Arguistolls. These soils tend to be well drained, relatively deep (150 cm), and have high available water capacity (Fisher and Swafford 1976). The mean annual precipitation is 762 mm, of which 68% (520 mm) occurs during the April through September growing season. Precipitation was below average during 1984, when yearly and growing season total were 724 and 349 mm, respectively; the opposite was true for 1985 when yearly (969 mm) and growing season (602 mm) precipitation were both well above average. Mean annual temperature is 15.6 C. The site had not been burned for at least 15 years prior to the initiation of the study. Livestock grazed the site during the dormant period (late fall and winter) until February 1983.

### Study Design

Three 30 by 60 m blocks were established in a 90 ha pasture. Half of each block was burned on 23 April 1984 and 10 April 1985, the remaining portion served as an unburned control. Data were analyzed using a randomized complete block model. Burning was conducted when leaves of big bluestem were 2 to 4 cm in length. This criterion was selected because it ensured that soil temperatures would be sufficient to support growth of native perennial grasses immediately following burning. Plots were not grazed during the study period.

### Gas Exchange and Xylem Water Potential

Net photosynthesis (PS), transpiration (TR), leaf temperature, and photsynthetic photon flux density (PPFD) were measured on recently expanded leaves of big bluestem from burned and unburned treatments with an LI-6000 portable photsynthesis meter (Li-Cor, Inc., Lincoln, NE) equipped with a 0.25 l leaf chamber. Measurements were taken between 1300 and 1500 hrs on clear days. Leaves were monitered for $CO_2$ uptake and water vapor losses over a 30-s period. About 20 minutes after being removed from the leaf chamber the leaf was wrapped with a moist paper towel, excised, and xylem water potential ($\psi$) measured with a pressure chamber (3000 Series, Soil-moisture Equip. Corp., Santa

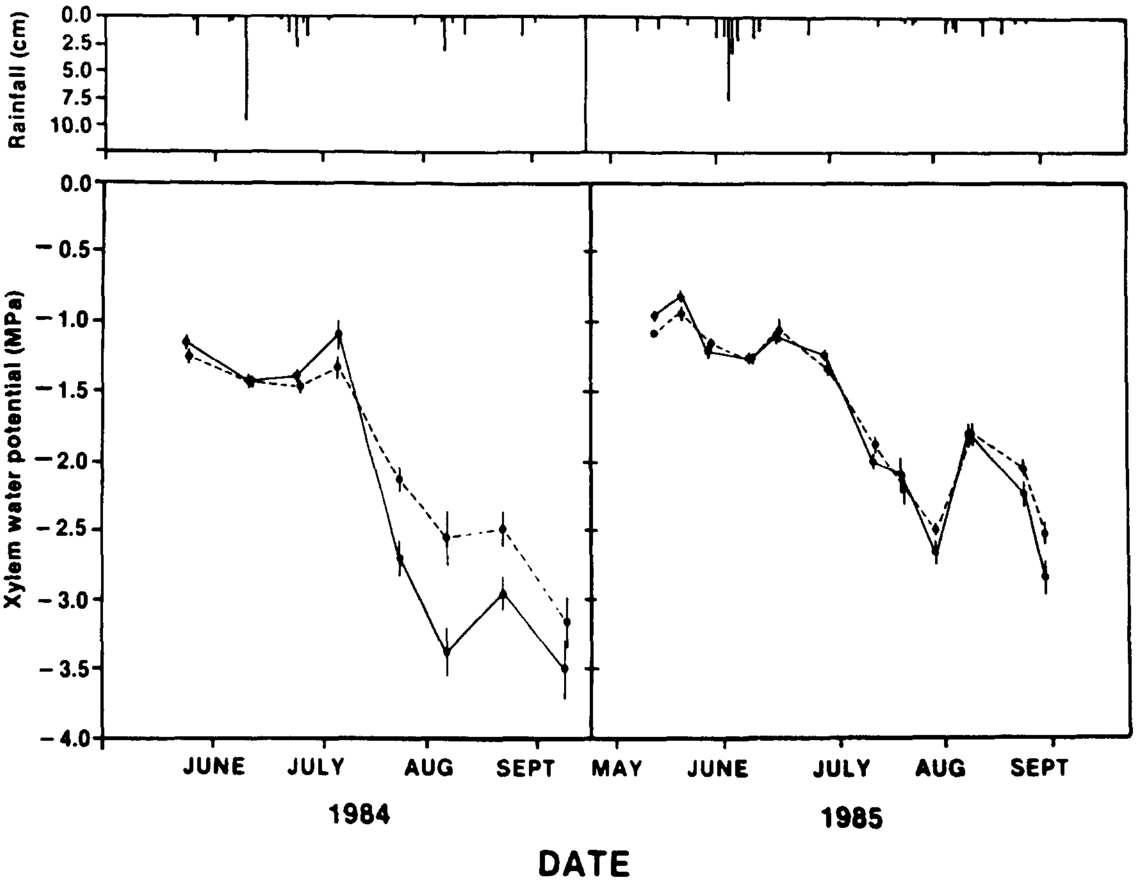


**Fig. 1.** *Seasonal trends in precipitation, and big bluestem xylem water potential (measured 1300 to 1500 h, CDT) from burned (solid lines) and unburned (dashed lines) tallgrass prairie during 1984 and 1985 growing seasons. Vertical lines are ± one standard error of the mean (n = 12). Treatment differences were significant (P≤.05) during the last half of 1984 and for the first two sampling dates of 1985.*

Barbara, Calif.) Leaves were stored between layers of moist towels and upon return to the laboratory measured for area with an LI-3000 area meter with conveyer belt assembly (Li-Cor, Inc., Lincoln, Nebr.). These values were used to calculate PS and TR on a leaf area basis. Measurements were taken on 8 occasions during May to September, 1984, and on 13 occasions during the same period in 1985.

**Phytomass, Tillers, Leaf Area and Nitrogen**

To assess the effect of burning on phytomass and morphological attributes of big bluestem, 15 × 25-cm quadrats were sampled on 3 dates in 1984 (4 quadrats per treatment/block combination on each date) and 8 dates in 1985 (6 quadrats per treatment/block combination on each date). Number of big bluestem tillers per quadrat were counted, then clipped to ground level. A portion of the tillers were selected at random and leaves removed and placed in glass jars over moist toweling. The remaining tillers were placed in paper bags. Phytomass of other species were also sampled. Leaves collected in glass jars were scanned on an LI-3000 area meter, dried at 50° C for 48 h, and weighed, and specific leaf weights (dry mass per leaf area) calculated. The remaining portion of the big bluestem sample was separated into leaf and stem (stem plus sheath) components. Oven-dry weights were deteremined for leaf and stem of big bluestem and total phytomass of other species. Leaf area index (LAI) of big bluestem was calculated from leaf mass and specific leaf weight. Leaf nitrogen (N) was determined by micro-Kjeldahl analysis (A.O.A.C. 1970) and total leaf N calculated from % N and leaf mass.

Data were analyzed using the Statistical Analysis System (SAS) analysis of variance procedures. Years were analyzed separately, and because treatments and time generally interact, we also analyzed the data by sampling date within each year.

## Results

**Xylem Water Potential, Gas Exchange, and Nitrogen**

The 2 years differed in rainfall distribution with a more severe late summer stress period in 1984 than in 1985 (Fig. 1). Minimum $\psi$ for burned big bluestem prior to senescence was -3.50 MPa in 1984 and -2.70 MPa in 1985. During both years $\psi$ was declining at the end of the measurement period. Measurements were continued until we could no longer find leaves which appeared alive and exhibited a positive carbon balance. From long-term weather records, it appeared that the pattern in 1984 was relatively typical, i.e., May and June were moist, followed by summer drought in July and early August, with sporadic thunderstorms in late August. However, 1985 was the fourth wettest in the past 30 years. There were more cloudy days and thus evaporation potential was assumed to be lower in 1985 than in 1984. Burned big bluestem was generally under slightly less water stress early in the season, and more stress later in the season than unburned plants. Late season differences between treatments were particularly evident in 1984 (e.g., in early August the difference between treatments was 0.75 MPa).

Photosynthetic rate exhibited a treatment crossover during the season; burned plants had PS rates 11% higher than unburned plants during the moist portion of the season, but rates were 36% lower during the dry portion (Fig. 2). The actual difference between treatments was 2.5 $\mu$moles $m^{-2} s^{-1}$ and 2.87 $\mu$moles $m^{-2} s^{-1}$ during the wet and dry parts of the growing season. Early in the growing season $\psi$ was fairly high for both treatments, and during this period TR appeared to be more affected by evaporative demand than by internal plant water relations (Figs. 1 and 2).

However, during the latter portion of the growing season as soil moisture declined and temperatures increased it appeared that internal plant water relations rather than evaporative demand controlled TR.

Seasonal trends in 1985 were not as clearly defined as in 1984 (Fig. 2). Certainly the mid- to late-summer drought was less well defined in 1985 relative to 1984, and in addition, May and June temperatures on the second and fifth sampling dates of 1985 appeared to have a definite impact on both TR and PS. Minimum temperatures the 2 days preceding the second measurement date averaged 8.5° C, whereas, those preceding the first and third sampling dates were 14.5 and 13.5° C, respectively. Minimum

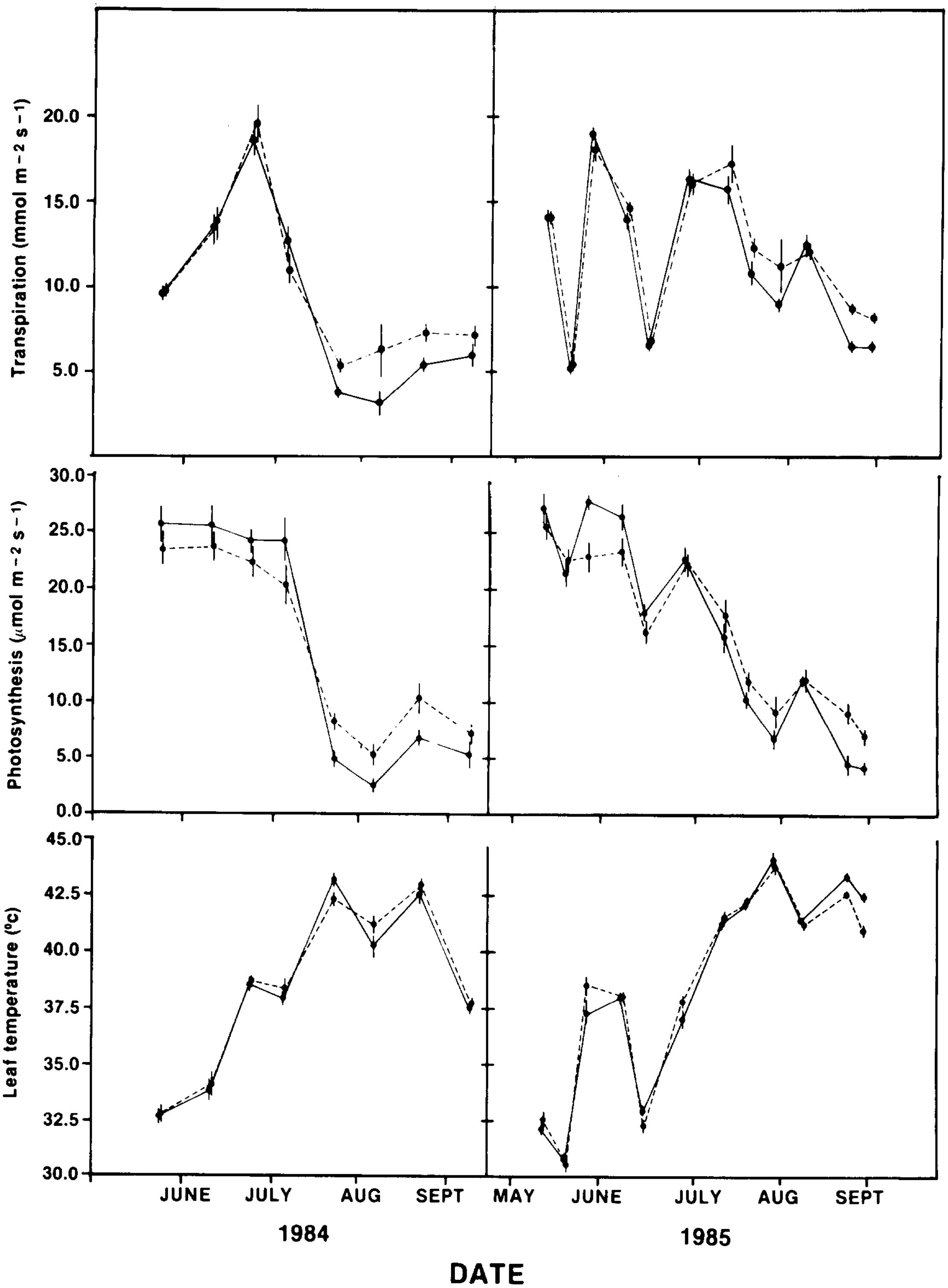


**Fig. 2.** *Transpiration, photosynthesis, and leaf temperature of big bluestem (measured 1300 to 1500 h, CDT) from burned (solid lines) and unburned (dash lines) tallgrass prairie during 1984 and 1985 growing season. Vertical lines are ± one standard error of the mean (n = 12). Treatment differences were significant (P≤.05) for photosynthesis during the moist portion (first 4 sampling dates) of 1984, and the third sampling of 1985 and for both photosynthesis and transpiration during the last 2 sampling dates of 1985.*

temperatures for the 2 days prior to the fourth, fifth, and sixth sampling dates in 1985 were 19, 11, 19.5° C, respectively. During 1984 there were no unusually cool nights prior to a sampling date.

Although moisture stress was not as severe in 1985 as it was in 1984, PS of both burned and unburned plants declined during July. There was an increase in PS in early August, which presumably was associated with reduced water stress (Fig. 1 and 2) resulting from a late summer thunderstorm. However, the increase in PS was brief, and by late August 1985 PS reached values similar to

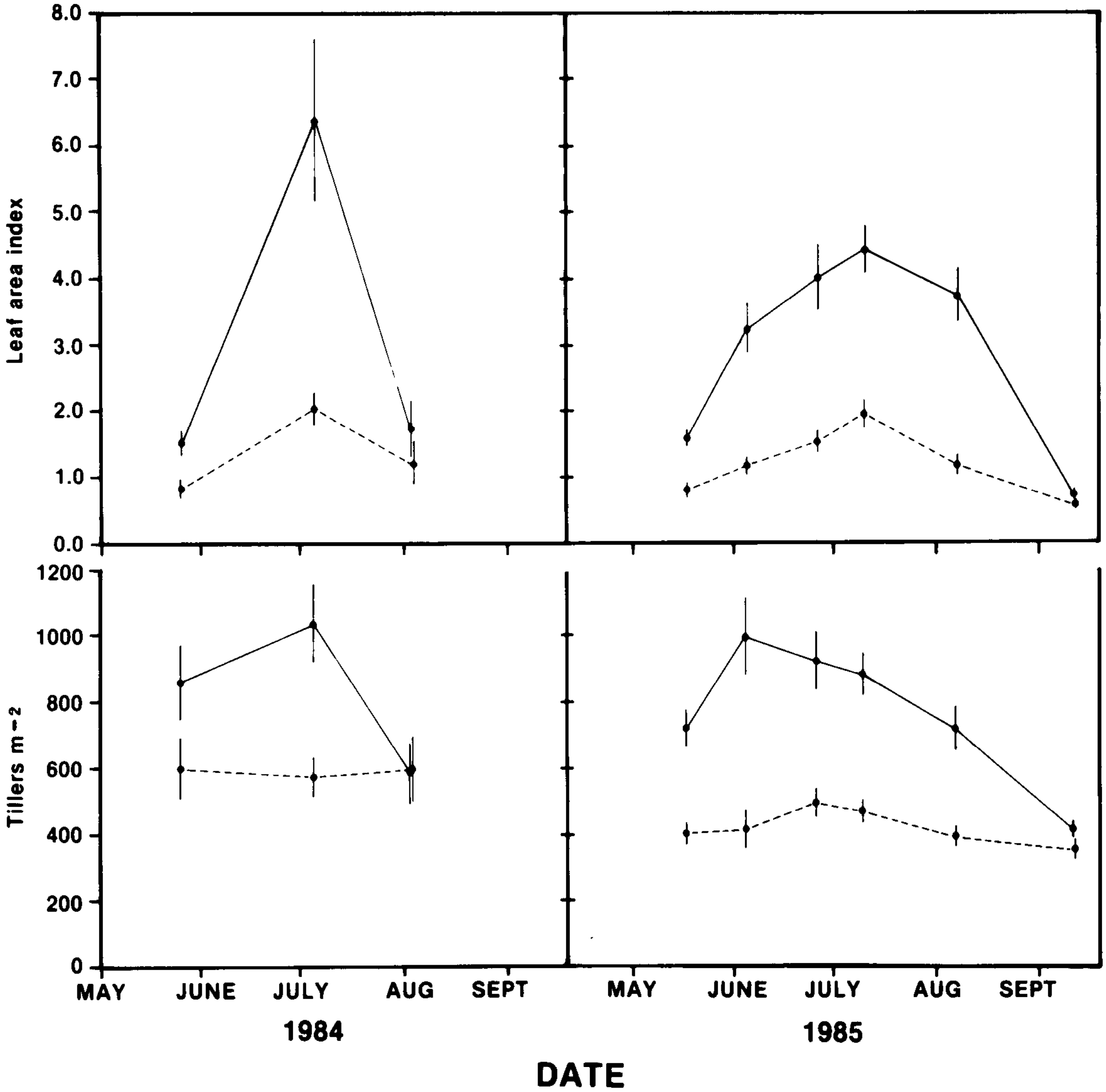


**Fig. 3.** *Leaf area index and tillers* $m^{-2}$ *of big bluestem from burned (solid lines) and unburned (dashed lines) tallgrass prairie during 1984 and 1985 growing seasons. Vertical lines are* ± *one standard error of the mean* (n = *12 for 1984,* n = 18 for 1985). Treatment differences were statistically significant ($P \leq .01$) *for leaf area index on the first 2 sampling dates of 1984, and all but the last sampling date in 1985. Treatments were different for tillers* $m^{-2}$ *on the second sampling date of 1984* ($P \leq .05$) *and on the first, second, fourth, and fifth sampling dates of 1985* ($P \leq .01$).

**Table 1. Season trends in nitrogen and phytomass components of big bluestem from burned (B) and unburned (U) tallgrass prairie; LN = % leaf nitrogen, TLN = total leaf nitrogen (% leaf nitrogen * leaf weight), LWT = leaf weight, SWT = stem and sheath weight, TWT = total weight. Phytomass of species other than *A. gerardii* (WT OTHER SPECIES) appears at the bottom of the table.**[1]

| | 1984 | | | | | | 1985 | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | May 25 | | July 5 | | Aug 3 | | May 17 | | June 5 | | June 26 | | July 10 | | Aug 7 | | Sept 11 | |
| Variable | B | U | B | U | B | U | B | U | B | U | B | U | B | U | B | U | B | U |
| LN (%) | 2.3** | 2.0 | 1.2 | 1.3 | 0.9 | 0.9 | 1.7* | 1.5 | 1.4 | 1.3 | 1.1 | 1.2 | 0.8 | 1.0 | 0.7* | 0.8 | 0.6** | 0.7 |
| TLN ($g\ m^{-2}$) | 1.9** | 0.9 | 5.2* | 1.8 | 1.9 | 1.3 | 1.5** | 0.8 | 2.7** | 1.0 | 3.0** | 1.3 | 3.0** | 1.5 | 1.8** | 1.0 | 0.6 | 0.6 |
| LWT ($g\ m^{-2}$) | 83.8* | 47.8 | 425.3* | 139.6 | 213.1 | 141.8 | 92.1** | 53.4 | 201.9** | 79.0 | 280.4** | 108.4 | 365.8** | 155.4 | 261.1** | 127.4 | 94.5 | 75.6 |
| SWT ($g\ m^{-2}$) | 21.8 | 17.6 | 177.0** | 42.2 | 232.8* | 64.9 | 24.8** | 12.8 | 73.7** | 24.0 | 125.8** | 40.1 | 235.8** | 49.7 | 328.4** | 40.0 | 238.4** | 47.8 |
| TWT ($g\ m^{-2}$) | 105.7 | 65.4 | 602.5** | 181.8 | 445.9* | 206.7 | 117.0** | 65.4 | 275.4** | 102.6 | 406.1** | 148.3 | 602.1** | 205.2 | 535.2** | 167.3 | 332.9** | 123.3 |
| WT OTHER SPECIES ($g\ m^{-2}$) | 34.3 | 55.6 | 202.6 | 178.7 | 246.2 | 93.3 | 33.9** | 94.3 | 89.2 | 124.9 | 134.8 | 110.7 | 106.6 | 157.4 | 87.7 | 110.3 | 82.7 | 87.5 |

[1]Asterisks indicate significant differences (* = $P < .05$, ** = $P < .01$) between burned and unburned treatments on a particular sampling date ($n$ = 12 and 18 for 1984 and 1985, respectively).

those measured during the dry portion of 1984. Transpiration rates remained relatively high (>10.0 mmole $m^{-2}$ $s^{-1}$) until the end of August; this contrasted with the late season response in 1984, especially for plants from the burned prairie.

Concentration of N in leaves of big bluestem from burned plots was generally higher than in unburned leaves during late May and early June. After mid June % N was similar between treatments or slightly lower in leaves from burned prairie (Table 1). The total amount of N (g $m^{-2}$) contained in big bluestem leaves was generally 2 to 3 times higher in burned relative to unburned prairie. The greatest total amount of N in leaf material was 5.2 g N per $m^{-2}$ ground area on burned prairie in early July, 1984.

**Leaf Area Index, Tiller Numbers, and Phytomass**

During both years LAI increased rapidly during late May and June, peaked in early July, declined in late summer (Fig. 3). However, peak LAI was 2 to 3 times greater for burned relative to unburned big bluestem and the stimulation of LAI from burning was greater in 1984 than 1985. During both years, LAI of unburned big bluestem peaked at 2.0, whereas peak values for burned plants were 6.4 and 4.5 in 1984 and 1985, respectively. Leaf folding occurred during August 1984, and leaf area values presented in Figure 3 are folded leaf area. We physically unfolded the leaves to determine what total leaf area would have been had the leaves not been folded. Folding resulted in a 26 and 29% reduction in leaf area for unburned and burned big bluestem, respectively.

Number of big bluestem tillers $m^{-2}$ were relatively static throughout the growing season on unburned plots, ranging from 577 to 600 in 1984, and 355 to 498 in 1985 (Fig. 3). There would probably have been more of a decline in tillers $m^{-2}$ in 1984 had we continued to sample past early August. There was, however, a great deal of seasonal variation in tillers $m^{-2}$ of big bluestem from burned prairie, with numbers ranging from 600 to 1,037 in 1984 and 416 to 997 in 1985.

Burning greatly stimulated production of big bluestem leaves and stems. The increase in stem production following burning was relatively greater than the increase in leaf production, thus the leaf to stem ratio was less for burned than unburned plants (Table 1). However, the proportion of leaf and stem contributing to peak standing crop was different between years, with more leaf in 1984 than in 1985. Burned plots had significantly ($P \leq .05$) more big bluestem phytomass than unburned plots on all sampling dates except 25 May 1984. In early July of both years, burned plots yielded about 3 times more big bluestem phytomass than unburned plots.

## Discussion

Burning has been shown to affect plant growth in the tallgrass prairie, but only recently have the mechanisms responsible been examined. We found that burning elevated PS rate during the active growth period (late spring and early summer), which generally agrees with the findings of Knapp (1985). The mechanism responsible for the increase in early season PS with burning is not completely clear. The removal of standing dead and litter by burning improves the light environment of emerging shoots (Knapp 1984b). All leaves we measured received full sunlight during the sampling period; however, Knapp and Seastadt (1986) suggest that differences in morphology between burned and unburned big bluestem leaves as a result of initial light environment helps explain the lower PS rates of unburned prairie. Another potential explanation for the higher PS rates is that the release of dormant buds created a higher demand for photosynthate, thus increasing PS rates. Burning doubled the number of big bluestem tillers produced during the active growth phase (Fig. 3). Two previous studies also measured a doubling of big bluestem tiller numbers as a result of spring burning (Hulbert 1969, Knapp 1984b).

The increase in peak tiller number resulting from burning has been attributed to both light levels and soil temperature. Knapp (1984b) found that burning increased PPFD reaching emerging shoots by almost 60% during the initial 30 days of growing season. Deregibus et al. (1985) have shown that increased red light at crown level increased the tillering rate of 2 humid grassland species. Increased tillering as a result of burning has also been attributed to higher soil temperature (Rice and Parenti 1978). Nitrogen nutrition may also be important in explaining tillering response. Burned plants had higher leaf %N than unburned plants (Table 1). Langer (1963) suggests that one of the main effects of N nutrition is on duration of tillering, and plants with an inadequate N supply stop producing new tillers at an early date. If Langer's conclusion applies to our conditions, lower N levels in unburned plants would explain the relatively stable tiller numbers on unburned prairie and the increase into late spring and burned prairie. The trend in leaf N among burned and unburned treatments is consistent with results from other locations in the tallgrass prairie (Old 1969, Owensby et al. 1970, Hayes 1985, Knapp 1985). Burned plots appear to initially have more available N, but the flush of growth uses N and as plant maturity occurs, there is a "dilution" of N as structural material accrues (Hayes 1985). Total leaf N was higher for burned relative to unburned big bluestem on a number of dates when burned plants had lower % leaf N, as a result of the increased leaf mass with burning.

The model used by Risser and Parton (1982) predicted that root uptake of N was higher on burned compared to unburned tallgrass prairie the first 2 years of burning, but that N uptake would be depressed by continuous annual burning. In the present study total leaf N of big bluestem declined about 40% from the first to second year of burning, whereas peak values were similar for the 2 years on unburned treatment. The results presented by Towne and Owensby (1984) showed that 56 years of continuous late-spring burning was not detrimental to tallgrass prairie in Kansas, which suggests any decline in N must have leveled off before detrimental effects on the plant community were manifested. A good deal of uncertainty exists in our understanding of the tallgrass prairie N-cycle (Risser and Parton 1982) and a better understanding of uptake, soil transformations, and internal conservation (see Hays 1985) of N will be necessary before accurate predictions of N-cycling can be made.

Leaf area is a functionally important factor that is not routinely measured on rangeland. The relationship between gas exchange and leaf area determines total carbon uptake and transpirational water loss. For example, the high LAI values for burned compared to unburned prairie, yet comparable TR rates among treatments, indicates soil moisture would probably be depleted more quickly on burned prairie. Trends in $\psi$ (Fig. 1) and soil moisture measurements (unpublished data) support this conclusion. In the same vein, burned prairie should have a good deal more carbon available for growth given slightly higher early season PS rates and much higher LAI compared to the unburned treatment. Most aboveground growth occurred during May and June based on standing crop data (Table 1). We think our data support Knight's (1973) contention that leaf area development is most important during the early part of the growing season when LAI is relatively low and soil moisture is available.

In general, mass of tallgrass prairie vegetation increases with burning (Hadley and Kieckhefer 1963, Peet et al. 1975, Knapp 1984, Towne and Owensby 1984), although the magnitude of the increase is affected by timing of burn, climatic conditions, prior site, history, community composition, etc. Our results show peak mass of big bluestem is increased almost 3-fold by burning (Table 1). There is a trend over the 2-year period for lower production of species other than big bluestem on burned plots, but the difference between treatments is not statistically significant. The increase in production of big bluestem more than compensates for the decline in productivity of other species with burning, and thus total aboveground primary production was greatly stimulated by late-spring burning.

Measurement of whole canopy physiological function is difficult in complex native communities, and does not allow evaluation of response of individual species. We suggest that response to environment can best be explained when both physiological and morphological attributes of a species are considered. In this study, burning influenced leaf area PS rate of big bluestem, but there was a much greater effect on tiller numbers and LAI. It would have been difficult to account for the 3-fold increase in big bluestem production resulting from burning based on a slight stimulation in PS rate. The stimulation of leaf N with burning may also help explain big bluestem response to fire; however, the mechanisms responsible for higher leaf N are not completely understood. We feel that the relationship between physiological and morphological attributes, which has been studied quite extensively in crop species, deserves more attention in the ecological literature.

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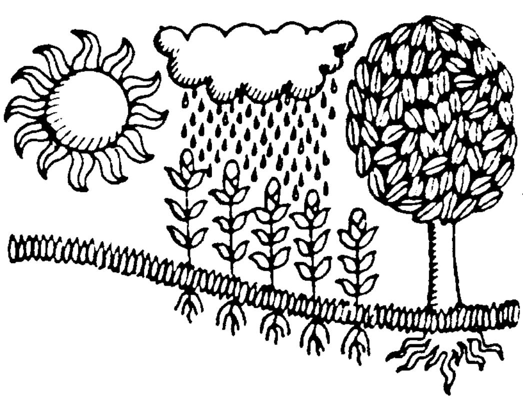
# Range Research: Basic Problems and Techniques

editors: C. Wayne Cook and James Stubbendieck



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