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Net Carbon Dioxide Exchange in Canopies of Burned and Unburned Tallgrass Prairie*

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With 4 Figures

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Summary

Net carbon dioxide exchange (NCE) rates were measured in a tallgrass prairie, a grassland with high productivity, to determine photosynthetic rates of the canopy. Canopy measurements were made in large, plexiglass chambers (1.21 m long; 0.91 m wide; 1.40 m tall) placed on burned and unburned areas of the prairie. The NCE rates of the canopy were compared with those of individual leaves of *Andropogon gerardii* Vitman (big bluestem). In addition, CO₂ flux from the soil was quantified and compared with net photosynthetic flux. The canopy NCE rates were generally lower than those made on individual leaves. In mid-summer (11 July 1987), the maximum canopy NCE rates were 55% and 64% of those measured on individual leaves in burned and unburned treatments, respectively. Canopy NCE rates were lower than individual-leaf NCE rates for two reasons. First, the individual-leaf measurements were made on young, unshaded, healthy leaves, while the canopy measurements were made on all types of leaves including senescing, shaded, and damaged leaves. Second, soil CO₂ flux into the chambers lowered NCE values. The CO₂ flux from the soil ranged from 7.2% to 28.4% of the total NCE. One needs to add soil CO₂ flux rates to the measured canopy NCE rates to obtain canopy NCE rates closer to individual-leaf NCE rates. Soil CO₂ flux decreased when conditions became dry, reaching a low of 0.06 mg CO₂ m⁻² s⁻¹, but increased after rain to 0.16 mg CO₂ m⁻² s⁻¹. Also, after rain, when plants were well watered, they were not light saturated at 1900 μEm⁻² s⁻¹. The NCE rates on the burned treatment were either higher or similar to those on the unburned treatment. For example, on 11 July

1987, NCE rates were higher on the burned treatment (0.66 mg CO₂ m⁻² s⁻¹) compared to the unburned treatment (0.47 mg CO₂ m⁻² s⁻¹). During the rest of July and August, the rates of the two treatments were not significantly different. But in September and October, the NCE rates were again higher on the burned treatment compared to the unburned treatment. The results indicated that canopy NCE rates may be more indicative of the productivity of the prairie than individual-leaf measurements made only on young, highly productive leaves.

Introduction

The tallgrass prairie, a grassland noted for its high productivity, may produce annual yields greater than 400 g m⁻² (Towne and Owensby, 1984). The prairie is characterized by a relatively dry microclimate, which leads to slow rates of decomposition for the dead plant material (Knapp and Seastedt, 1986). The buildup of detritus may exceed 1500 g m⁻² (Weaver and Rowland, 1952). This accumulation of dry plant material is conducive to fire.

Many researches have emphasized the importance of fire for productivity in the tallgrass prairie and found that the removal of detritus through fire or grazing improves production (Weaver and Rowland, 1952; Kucera and Ehrenreich, 1962; Hulbert, 1969; Towne and Owensby, 1984). Burning may increase solar radiation available to new shoots by 50%, a factor that may contribute to

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the increased production of burned prairie (Knapp, 1984). Associated with increased radiation are differences in photosynthetic pigments and structural characteristics of leaves in burned and unburned prairie (Knapp and Gilliam, 1985).

The photosynthetic rate of individual leaves of *Andropogon gerardii* Vitman (big bluestem), the dominant, warm-season, perennial grass species of the tallgrass prairie, has been measured (Peet et al., 1975; Knapp, 1985), but canopy photosynthetic rate has not been reported. Therefore, the objective of this study was to determine net carbon exchange of the plant canopy in burned and unburned tallgrass prairie. Measurements made on the canopy were compared with those made on individual leaves. Another objective was to determine soil CO₂ flux as a percent of net photosynthetic flux.

Materials and Methods

The experiment was conducted during the 1987 growing season at the Konza Prairie Research Natural Area in northeast Kansas (39° 05' N lat, 96° 35' W long, 325 m). The study site was located on a clay upland soil (fine, mixed, mesic Udic Argiustolls). These soils are relatively thin, well drained, and have numerous chert fragments in the top soil (Jantz et al., 1975). Precipitation was unevenly distributed during the measurement period [11 July through 6 October or day of year (DOY) 192 through 279].

The southern half of the study site had been burned on 8 April 1987, as well as the three previous springs. The northern half had not been burned since 1985 and before that had been burned infrequently. The two halves were adjacent to each other. The site was about 300 m in the east-west direction and 500 m in the north-south direction. The occurrence of species at the site, determined by using the method of Owensby (1973), was affected by burning (Table 1).

Six open-system, plexiglass chambers (three on the burned area and three on the unburned area) were used in the experiment and were similar to those of Sij et al. (1972). The chambers were 1.21 m long by 0.91 m wide by 1.40 m tall (volume = 1.5 m³). Airflow rates into each chamber were measured one time each day in the morning by determining an air velocity profile across the diameter of the inlet tube. The air velocity profile

Table 1. *Percent Botanical Composition of Burned and Unburned Experimental Sites in the Tallgrass Prairie*

	Experimental site	
	Burned	Unburned
<i>Andropogon gerardii</i> Vitman (big bluestem)	55	71
<i>Andropogon scoparius</i> Michx. (little bluestem)	12	... ⁺
<i>Sorghastrum nutans</i> (L.) Nash (Indiangrass)	15	...
<i>Poa pratensis</i> L. (Kentucky blue grass) ...		8
<i>Sporobolus asper</i> Michx. (drop seed) ...		5
Others	18	16

+ Less than 1%

across the diameter of the inlet tube. The air velocity profile was measured with a portable air velocity meter (Model AB-27, Teledyne Hastings-Raydist, Hampton, Virginia, U.S.A.). Air exchange rates through the chambers were 2.2 to 3.0 m³ min⁻¹.

Air samples were drawn from across the entire width of the air outlet ducts. One intake sample was drawn from the inlet duct of a randomly-selected chamber to serve as a reference gas sample. These samples were pumped through copper lines (6.4 mm diameter; 45 m long) to a trailer at the site. The air samples, after entering the trailer, passed through a sampling manifold system controlled by electronic solenoids to allow selection of the chamber to be measured. The manifold directed the selected air stream to a common sampling line. Airtight metallic bellows pumps (Model L 37A3, Cole Palmer, Chicago, Illinois, U.S.A.) located within the trailer were used to circulate air throughout the system.

After passing through 0.5 L volumetric mixing flasks, which uniformly mixed the air, and 15 µm filters which removed dust and pollen, the air samples were directed through flow meters (Model No. F 1100, Gilmont Instruments, Great Neck, New York, U.S.A.), which kept flow rates through the air inlet and outlet sampling lines equal. Next the samples entered sensor heads, where air temperature and humidity were measured. These sensor heads were part of the portable photosynthesis system (Model 6200, Li-Cor, Inc., Lincoln, Nebraska, U.S.A.). After leaving the sensor heads, the air passed through calcium sulfate drying col-

umns. Finally, the air entered the infrared gas analyzer portion of the system. The analyzer was calibrated daily with standard concentrations of CO₂ gas. The standard concentrations were 332.9 and 370.5 $\mu\text{L L}^{-1} \pm 2\%$ (Scott Specialty Gases, Plumsteadville, Pennsylvania, U.S.A.). Net CO₂ exchange rates (NCE) were calculated by taking the difference between the CO₂ concentrations of the chamber outlet and inlet ducts, multiplying by the chamber airflow rate, and dividing by the ground area (Jarvis and Čatský, 1971).

Gas exchange measurements were made on individual leaves of *A. gerardii* at a similar, unsized site 1 500 m northeast of the northern part of the previously described site. Half of the unsized site had been burned, and half had not been burned. Measurements were taken throughout the summer of 1987 by using an ADC Portable Photosynthesis System (Model LCA2, The Analytical Development Co., Ltd., Hoddesdon, Herts., England; supplied by P. K. Morgan Instruments, Inc., Andover, Massachusetts, U.S.A.). The infrared gas analyzer was calibrated for CO₂ with certified span gases (Scott Specialty Gases, Plumsteadville, Pennsylvania, U.S.A.). Gas exchange was measured with a narrow Parkinson leaf chamber (volume = 12 cm³) clamped over the midleaf portion of a fully expanded leaf. On each leaf, five measurements, each lasting 10 seconds, were made. Measurements were made between 0900 and 1300 h, Central Standard Time (CST). Gas exchange rates were measured on five leaves in each of the treatments (burned and unburned). The unsized site was marked with flags, and the person who measured photosynthesis always returned to the same location (flag) (one on the burned part and one on the unburned part) to measure photosynthesis throughout the season. Measurements were taken on plants located within 30 m of each other. On two days (11 July and 15 August), the individual-leaf and canopy measurements overlapped, and results for these two days will be compared. (Even though it would have been desirable, individual-leaf and canopy measurements were never made side by side on leaves at the same site. We are not aware of literature describing side-by-side measurements of individual-leaf and canopy photosynthetic measurements).

Carbon dioxide flux out of the soil was measured with a method similar to that described by Anderson (1982). Aerosol cans (6.7 cm diameter;

12.4 cm long) with the bottom cut out were used for the airtight metal cylinders. These cans were placed over a bare surface of the soil near to or inside the plexiglass chambers. The open end of the can was pushed into the soil about 1 cm. A rubber stopper closed the opening at the top of the can. Suspended within the cylinder was a glass jar with a screwtype lid containing 10 ml of 1 M potassium hydroxide (KOH). The traps were set out in the morning and collected at the end of the day (8 to 10 hours).

In the laboratory, methyl red indicator was added to the exposed samples. The volume (V 1) of 1 M hydrochloric acid (HCl) needed to titrate the samples was noted. Phenolphthalein indicator was then added to the samples. The sample was titrated again with 1 M HCl, and the volume (V 2) used was noted. The mass of CO₂ that moved from the soil could be found by subtracting V 1 from V 2 and multiplying by the normality of the acid.

Vegetative data were taken in one-to-two-week intervals throughout the experiment. Leaf area index (LAI) was measured by clipping three 0.1 m² quadrats on each treatment. Leaf area measurements were made with an optical planimeter (Model 3100, Li-Cor, Inc., Lincoln, Nebraska, U.S.A.). The clippings were taken in the same location or directly adjoining the place where the chambers had been located the week before.

Midday leaf water potential was measured in mid-summer by using a pressure chamber (Soil-moisture Equipment Corp., Santa Barbara, California, U.S.A.). Six or more fully expanded leaves of *A. gerardii* were sampled from each treatment. These measurements were made from 1000 to 1400 h (CST). Care was taken to minimize water loss from the leaves after excision by sealing them in a humidified plastic bag immediately and storing them for no more than 2 to 4 min before the measurements were made.

Photosynthetically active radiation (PAR) was measured with PAR sensors (Model LI-190 S, Li-Cor, Inc., Lincoln, Nebraska, U.S.A.) at a weather station located 800 m northeast of the study site. The data logger was Model 21 X, made by Campbell Scientific (Logan, Utah).

Statistical analysis of the data was accomplished by using Student's *t*-test (Steel and Torrie 1960, p. 78–80). The measurements made in this experiment were not made in replicated burned and unburned plots. Replicated plots would have

required that three separate plots be marked off and burned individually. The size of the experimental area and the length of the copper tubing required to carry gas samples would have been impractical to do this. Differences were assumed to result from the fire treatment, because the unburned plots at both locations (where individual-leaf and canopy measurements were made) were similar, based on visual observation, and the burned plots at both locations looked similar.

Results

Rainfall for the month of June (DOY 152 through 181) and July (DOY 182 through 212) was 5.5 cm and 6.7 cm below the 30-year normal, respectively. (The normals for June and July are 13.4 cm and 8.1 cm, respectively.) Several rainfalls totalled only 1 cm of precipitation between 7 July (DOY 188) and 2 August (DOY 214) (Table 2). During the middle part of this period, minimum leaf water potentials were less than -4.0 MPa (pressure-chamber limit) in both burned and unburned plots (Table 3). Between 3 August (DOY 215) and 13 August (DOY 225), 12.5 cm of rain fell. No significant differences in leaf water potential existed between burned and unburned treatments on 11 August. Rainfall was 9.2 cm above normal in August, but 6.7 cm below normal in September. (The normals for August and September are 8.1 cm and 10.3 cm, respectively.)

Table 2. Daily Precipitation Received on the Konza Prairie During the Summer of 1987

Date	Day of year		Precipitation (mm)	
June	11	162	2	
	16	167	7	
	19	170	12	
	23	174	6	
	25	176	19	
	28	179	14	
	29	180	4	
	30	181	1	
	July	6	187	9
		8	189	2
12		193	4	
17		198	2	
18		199	2	
August	4	216	6	
	5	217	37	
	7	219	4	
	13	225	78	
	23	235	2	
	24	236	24	
	25	237	22	
September	5	248	2	
	6	249	2	
	8	251	20	
	14	257	4	

The maximum net CO₂ exchange (NCE) rates in burned and unburned treatments are shown in Table 4. Included in these rates are CO₂ flux from the soil surface (root and soil respiration) and

Table 3. Midday Leaf Water Potential (MPa) of *Andropogon gerardii* in Burned and Unburned Treatments During 1987

Date	(DOY) ^a	n	Treatment Area		p
			Burned	Unburned	
5 July	(186)	3 ^b	-1.57 (0.67) ^c	-2.05 (0.85)	ns
14 July	(195)	3	-1.98 (0.47)	-1.56 (0.19)	ns
15 July	(196)	8	-2.85 (0.14)	-2.54 (0.10)	<0.05
16 July	(197)	9	-2.87 (0.16)	-2.52 (0.13)	<0.10
20 July	(201)	8	-3.32 (0.12)	-2.98 (0.13)	<0.05
21 July	(202)	... ^d	< -4.0	< -4.0	
11 August	(223)	9	-1.79 (0.18)	-1.83 (0.09)	ns
15 August	(227)	9	-1.94 (0.05)	-2.00 (0.08)	ns

^a Day of year

^b Sample size

^c Values represent mean (standard error) of burned and unburned treatments

^d Leaf water potential exceeded pressure limits of the pressure chamber, so no measurements were available. Nine leaves were sampled on each treatment.

Table 4. Daily Maximum NCE Rates ($\text{mg CO}_2 \text{ m}^{-2} \text{ Ground Area s}^{-1}$) for Both Canopy and Leaf Measurements of Burned and Unburned Treatments in the Tallgrass Prairie During 1987

Date	(DOY)	Canopy			Leaf			LAI	
		Burned	Unburned	p	Burned	Unburned	p	Burned	Unburned
11 July	(192)	0.66 ± 0.06^a	0.47 ± 0.07	$<0.15^b$	1.21 ± 0.09^c	0.74 ± 0.13	<0.01	$1.65^e \pm 0.22$	1.83 ± 0.22
20 July	(201)	0.38 ± 0.06	0.64 ± 0.13	ns	... ^d	...		1.00 ± 0.09	0.73 ± 0.22
28 July	(209)	0.13 ± 0.04	0.10 ± 0.02	ns		0.69 ± 0.20	0.97 ± 0.25
15 August	(227)	0.37 ± 0.11	0.47 ± 0.14	ns	0.48 ± 0.08	0.44 ± 0.07	ns	1.16 ± 0.34	0.76 ± 0.09
23 September	(266)	0.50 ± 0.03	0.19 ± 0.02	<0.10		1.17 ± 0.19	0.75 ± 0.24
6 October	(279)	0.11 ± 0.04	0.03 ± 0.03	<0.15		0.25 ± 0.04	0.11 ± 0.06

The maximum usually occurred about midday. Instantaneous values from three chambers in each treatment were averaged together to determine the maximum value. Leaf area index (LAI, $\text{m}^2 \text{ m}^{-2}$) also is included.

^a Values represent mean \pm standard error of three sampling chambers per treatment.

^b t-test significance level, H_0 : the burned treatment had a higher NCE rate than the unburned treatment, ns = not significant at $p = 0.20$.

^c Values represent mean \pm standard error of five individual leaves per treatment.

^d Data not available for these dates.

^e LAI based on measurement of three 0.1 m^2 quadrats on each treatment.

plant respiration. These CO_2 additions to the microenvironment within the chamber cause the above-ground NCE rate to be underestimated. Experimental results discussed later in this paper show that soil CO_2 flux may be 10% to 30% of the NCE rate. On 11 July, 23 September, and 6 October, maximum NCE rates were significantly different (higher) in the burned canopy than in the unburned canopy.

The individual-leaf measurements, made on 11 July and 15 August, were compared to the maximum canopy NCE rates measured within the plexiglass chambers (Table 4). The measurements were made on young, highly productive leaves of *A. gerardii* and do not account for less productive leaves that were included in the canopy measurements. On 11 July, the maximum canopy NCE rates were 55% and 64% of those measured on individual leaves in the burned and unburned treatments, respectively.

The maximum leaf NCE rate was significantly higher in the burned treatment compared to the unburned treatment. On 15 August, canopy NCE rates were 77% and 122% of those measured on individual leaves in the burned and unburned treatments, respectively. The maximum leaf NCE rate in the burned treatment was not significantly different from that in the unburned treatment.

The seasonal pattern of CO_2 flux from the soil is shown in Fig. 1. Rates declined in July (DOY

192 to 212) with drying soil, but more than doubled after rain on August 4, 5, 7, and 13 (DOY 216, 217, 219, and 225). As soil began to dry after this rain, the CO_2 evolution declined again.

The NCE measurement underestimated the contribution of soil CO_2 flux to photosynthesis. We quantified the flux of CO_2 flux from the soil as follows. The CO_2 flux from the soil varies diurnally. Because our soil CO_2 -flux measurements provided only an average flux for the day, it was not accurate to add the average CO_2 flux to the maximum photosynthetic rate. Instead, the NCE curves were integrated over time, and this daily CO_2 uptake was then added to the daily soil CO_2

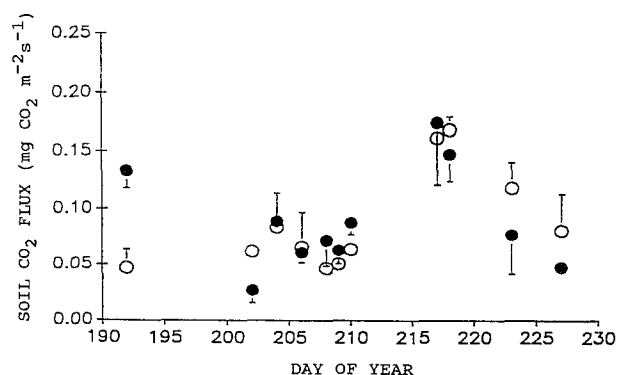


Fig. 1. Soil CO_2 flux in burned (open circles) and unburned (closed circles) treatments during 1987. Vertical bars represent \pm standard error of the mean. If a dot has no bar, the bar fell within the dot.

Table 5. Net Carbon Dioxide Exchange Rates on Burned and Unburned Areas on the Konza Prairie During 1987

Date	(DOY)	NCE	Soil CO ₂ flux	Corrected NCE (NCE + Soil CO ₂ flux)	Soil CO ₂ % of photosynthetic flux (Soil CO ₂ /Corrected NCE)
11 July (192)					
Burned		12.07	0.93	13.00	7.2
Unburned		7.90	2.63	10.53	25.0
15 August (227)					
Burned		4.06	1.61	5.67	28.4
Unburned		7.48	0.95	8.43	11.3

Values were obtained by integrating diurnal NCE curves for 5.5 hours (0830 to 1400 CST). Soil CO₂ flux is also based on 5.5 hours. Corrected NCE is the sum of daily NCE and soil CO₂ flux. Soil CO₂ is the soil CO₂ flux divided by the corrected NCE and represents the contribution of soil CO₂ flux to the net photosynthetic flux. All flux values are represented as g CO₂m⁻² ground area day⁻¹.

flux. To standardize the length of time, all values (NCE and soil CO₂) were integrated between the times of 0830 h and 1400 h CST. By integrating, we were able to estimate the total amount of carbon fixed by the plants with a correction for soil CO₂ flux throughout each day.

Integrated CO₂ fixation rates, corrected for soil CO₂ flux, followed trends similar to the maximum NCE rates (Table 5). Carbon exchange rates on 11 July for a 5.5-h period were highest in the burned treatment (13.0 g CO₂ m⁻² day⁻¹). The contribution of CO₂ from the soil to the net photosynthetic flux was estimated by dividing the daily soil CO₂ flux by the integrated CO₂ fixation rates corrected for soil CO₂ flux. The CO₂ flux from the soil ranged from 7.2% to 28.4% of the total NCE.

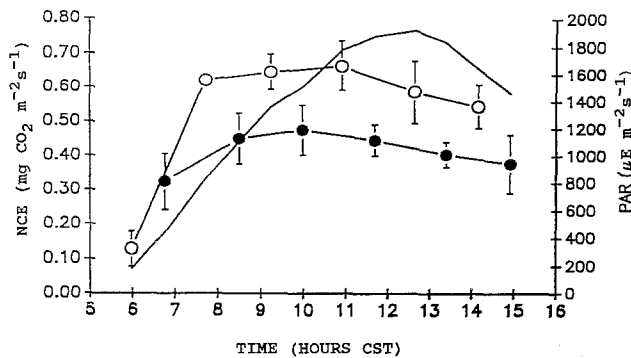


Fig. 2. Net carbon dioxide exchange (NCE) of burned (open circles) and unburned (closed circles) treatment on 11 July 1987 (DOY 192). Photosynthetically active radiation (PAR) is represented as (—). For vertical bars, see legend of Fig. 2

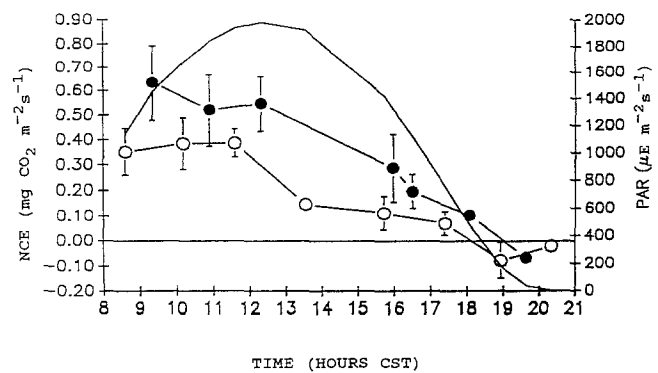


Fig. 3. Net carbon dioxide exchange (NCE) of burned (open circles) and unburned (closed circles) treatment on 20 July 1987 (DOY 201). Photosynthetically active radiation (PAR) is represented as (—). For vertical bars, see legend of Fig. 2

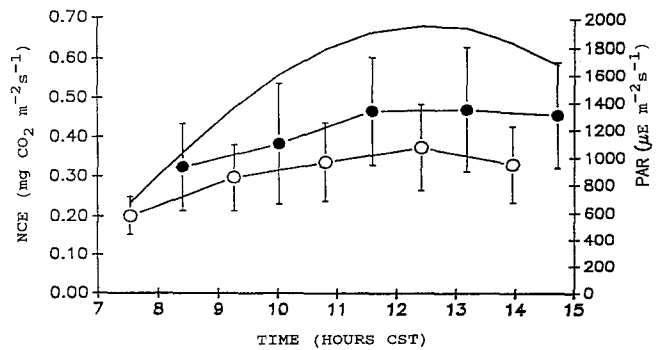


Fig. 4. Net carbon dioxide exchange (NCE) of burned (open circles) and unburned (closed circles) treatments on 15 August 1987 (DOY 227). Photosynthetically active radiation (PAR) is represented as (—). For vertical bars, see legend of Fig. 2

On 11 July and 20 July, both treatments reached maximum NCE rates and began to decline before PAR was a maximum for that date (Figs. 2 and 3). This indicated that some other factor, perhaps water availability, was limiting production in both treatments. Leaf water potentials on 20 July were significantly lower in the burned (-3.32 MPa) compared to the unburned (-2.98 MPa) treatments (Table 3). On 15 August, NCE was still increasing when PAR was at a maximum, indicating that at least some of the plants were not light saturated at $1900 \mu\text{E m}^{-2} \text{s}^{-1}$ (Fig. 4). Leaf water potentials on this date averaged -1.94 MPa and -2.00 MPa on the burned and unburned treatments, respectively, and water was probably not a factor limiting growth.

Discussion

The present study was unique because it measured NCE on a canopy basis within the tallgrass prairie. The canopy NCE rates were generally lower than those made on individual leaves of *A. gerardii*. Rates were lower for two reasons. First, unlike the individual-leaf measurements, the canopy NCE measurements included leaves that were not producing at maximum levels. The less-productive leaves were senescent or damaged leaves, as well as those within the canopy that were partially shaded. These leaves could explain the lower NCE rates measured within the canopy. Second, soil CO_2 flux ranged from 7% to 28% of the total daily CO_2 flux into the chambers lowered values. Canopy NCE rates would be closer to the NCE rates measured on individual leaves, if one added the soil CO_2 flux rate to the measured canopy NCE rate. In our experiment, soil CO_2 flux ranged from 7% to 28% of the total daily CO_2 uptake, values similar to those reported by others (between 10% and 20%) (Moss et al., 1961; Monteith et al., 1964). However, the contribution of this soil CO_2 component to each NCE value throughout the day could not be determined, but our CO_2 flux values can be compared to those determined by others. Studies have shown that soil CO_2 flux ranges from 0.04 to $0.65 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in cropped fields (Lundegardh, 1927; Moss et al., 1961; Monteith et al., 1964; Kanemasu et al., 1974). Kucera and Kirkham (1971) reported CO_2 evolution from the soil in a mid-Missouri (U.S.A.) tallgrass prairie to reach a maximum of $0.125 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ dur-

ing the summer, which is comparable to the rates measured here (Fig. 1). Brown and Trlica (1977) integrated exchange rate curves in terms of g of carbohydrates m^{-2} ground area day^{-1} for a blue grama (*Bouteloua gracilis* Lag.) canopy in north-east Colorado (U.S.A.). Their values converted to CO_2 uptake seemed similar to ours, even though our values were obtained by integrating only a 5.5-hour interval, while they determined values for the entire day. On 28 to 29 June 1972, they reported $24.2 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ compared to a maximum of $13.0 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ measured in our experiment. On 6 to 7 July, they obtained an integrated value of $7.91 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$. In our experiment, by 11 to 12 August, plants had integrated values of $5.72 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$.

Most grass species in the tallgrass prairie utilize the C_4 photosynthetic pathway. C_4 species usually require full solar irradiances for light saturation, and some may not saturate even in full sunlight. Knapp (1985) reported that neither *A. gerardii* nor *Panicum virgatum*, two dominant grasses in the tallgrass prairie, appeared to light saturate at $2200 \mu\text{E m}^{-2} \text{s}^{-1}$. These results are comparable to those found on 15 August, when plants had increasing photosynthetic rates, even though PAR had reached a maximum of $1900 \mu\text{E m}^{-2} \text{s}^{-1}$ (Fig. 4). On two previous dates, 11 July and 20 July, a midday decline in NCE occurred before maximum PAR was reached, presumably caused by stomatal closure induced by water stress (Figs. 2 and 3).

Even though fire often elevates productivity of a prairie, as noted in the Introduction, our results showed that burning may not always increase growth. We found that, on certain days, the burned treatment had a higher photosynthetic rate than that of the unburned treatment. On other days, however, the burned treatment had a photosynthetic rate similar to that of the unburned treatment. Differences were probably due, in part, to rainfall. But it was not the only factor determining photosynthetic rate, because both during a dry period and after a large rainfall, photosynthetic rates were not different between the burned and unburned treatments. Interaction of several factors, including rainfall, incident radiation, type of leaf pigments, and leaf structure (Knapp and Gilliam 1985) affects productivity. All these factors must be assessed in deciding whether or not to burn a prairie for increased production.

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References

- Anderson, J. P. E., 1982: Soil respiration. In: Page A. L., Miller R. H., Keeney, D. R. (eds.) *Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties*. 2nd ed. American Society of Agronomy, Soil Science Society of America, Madison, Wisconsin, pp. 831–871.
- Brown, L. F., Trlica, M. J., 1977: Carbon dioxide exchange of blue grama swards as influenced by several ecological variables in the field. *J. Appl. Ecol.*, **14**, 204–213.
- Hulbert, L. C., 1969: Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology*, **50**, 874–877.
- Jantz, D. R., Harner, R. F., Rowland, H. T., Gier, D. A., 1975: Soil survey of Riley County and part of Geary County, Kansas. United States Department of Agriculture, Soil Conservation Service and Kansas State University Agricultural Experiment Station, Manhattan, Kansas, 71 pp. + maps.
- Jarvis, P. G., Čatský, J., 1971: Gas exchange systems. In: Šesták, Z., Čatský, J., Jarvis, P. G., (eds), *Plant photosynthetic production. Manual of Methods*. Dr. W. Junk, The Hague, The Netherlands, pp. 50–56.
- Kanemasu, E. T., Powers, W. L., Sij, J. W., 1974: Field chamber measurements of CO₂ flux from soil surface. *Soil Sci.*, **118**, 233–237.
- Knapp, A. K., 1984: Post-burn differences in solar radiation, leaf temperature and water stress influencing production in a lowland tallgrass prairie. *Am. J. Bot.*, **71**, 220–227.
- Knapp, A. K., 1985: Effect of fire and drought on the co-physiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology*, **66**, 1309–1320.
- Knapp, A. K., Gilliam, F. S., 1985: Response of *Andropogon gerardii* (Poaceae) to fire-induced high vs. low irradiance environments in tallgrass prairie: leaf structure and photosynthetic pigments. *Am. J. Bot.*, **72**, 1668–1671.
- Knapp, A. K., Seastedt, T. R., 1986: Detritus accumulation limits productivity of tallgrass prairie. *BioScience*, **336**, 662–668.
- Kucera, C. L., Ehrenreich, J. H., 1962: Some effects of annual burning on central Missouri prairie. *Ecology*, **43**, 334–336.
- Kucera, C. L., Kirkham, D. R., 1971: Soil respiration studies in tallgrass prairie in Missouri. *Ecology*, **52**, 912–915.
- Lundegardh, H., 1927: Carbon dioxide evolution of soil and crop growth. *Soil Sci.*, **23**, 417–454.
- Monteith, J. L., Szeicz, G., Yakuki, K., 1964: Crop photosynthesis and the flux of carbon dioxide below the canopy. *J. Appl. Ecol.*, **1**, 321–337.
- Moss, D. N., Musgrave, R. B., Lemon, E. R., 1961: Photosynthesis under field conditions. III. Some effects of light, carbon dioxide, temperature and soil moisture on photosynthesis, respiration and transpiration of corn. *Crop. Sci.*, **1**, 83–87.
- Owensby, C. E., 1973. Modified step-point system for botanical composition and basal cover estimates. *J. Range Manage.*, **26**, 302–303.
- Peet, M., Anderson, R., Adams, M. S., 1975: Effects of fire on bluestem production. *Am. Midland Natur.*, **94**, 15–25.
- Sij, J. W., Kanemasu, E. T., Teare, I. D., 1972. Stomatal resistance, net photosynthesis, and transpiration in PMA-treated sorghum: a field study. *Crop. Sci.*, **12**, 733–735.
- Steel, R. G. D., Torrie, J. H., 1960: *Principles and Procedures of Statistics*. McGraw-Hill, New York, 481 pp.
- Towne, G., Owensby, C., 1984: Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. *J. Range. Manage.*, **37**, 392–397.
- Weaver, J. E., Rowland, N. W., 1952: Effects of excessive natural mulch on development, yield and structure of native grassland. *Bot. Gaz.*, **114**, 1–19.

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