CANOPY NET CARBON DIOXIDE EXCHANGE

BY BURNED AND UNBURNED TALLGRASS PRAIRIE

by

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

Others (Peet et al., 1975; Knapp, 1985) have measured
the photosynthetic rate of individual leaves of <u>Andropogon
gerardii</u>, the dominant grass species of the tallgrass

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prairie, but canopy photosynthetic rate has not been reported. Hence the need for this study. The present study measured net carbon exchange (NCE) of the plant canopy in burned and unburned tallgrass prairie.

MATERIALS AND METHODS

The experiment was conducted during the 1987 growing season at the Konza Prairie Resource Natural Area (KPRNA) in northeast Kansas (39 05' N, 96 35' W, Appendix Fig. 1). The study site was located on a clay upland site (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).

The south half of the experimental site had been burned on 8 April 1987, as well as the three previous springs. The north half had not been burned since 1985 and before that had been burned infrequently. By selecting a site with adjoining burned and unburned treatments, differences in exposure, precipitation, soil type, and vegetation were reduced. The dominant species in both treatments as determined by the modified step-point system (Owensby, 1973) was the warm-season perennial, big bluestem (<u>Andropogon gerardii</u> Vitman). Other species present in significant amounts were indiangrass (<u>Sorghastrum nutans</u> L.), little bluestem (<u>Andropogon scoparius</u> Michx.), and Kentucky bluegrass (<u>Poa pratensis</u>

L.). The occurrence of each species was strongly affected by the burning history of the site (Table 1). For example, _S. nutans_ composed 15% of the total vegetation in the burned treatment, while it composed <1% of the total vegetation in the unburned treatment. _P. pratensis_, a cool season perennial, composed 8% of the total vegetation in the unburned treatment compared to <1% in the burned treatment.

Six open-system plexiglas chambers (three on the burned area and three on the unburned area) were used in the experiment similar to those of Sij et al. (1972) (Appendix Fig. 2) but with slight modification. An aluminum angle frame was used to support the corners of the plexiglas. The plexiglas had a thickness on three sides of 3.2 mm. The plexiglas on the fourth side, which supported the air inlet duct, had thickness of 6.4 mm. The chambers were 1.21 m long by 0.91 m wide by 1.40 m tall (volume = 1.5 m^3). They had an arc dome at the top covered with 0.08 mm polyvinyl chloride (PVC) film. Inlet and outlet ducts were placed at opposite ends of the chamber. Air was blown into the chambers by a centrifugal blower fan located at the end of each air inlet tube. The inlet duct was placed at a height of 80 cm, while the outlet duct was placed at a height of 98 cm above the ground. The ducts were placed at different heights to

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Table 1. Percent botanical composition of burned
and unburned experimental sites in the tallgrass prairie.

	Experimental site	
Vegetation species	Burned	Unburned
Andropogon gerardii Vitman	55	71
Andropogon scoparius Michx.	12	--
Sorghastrum nutans (L.) Nash	15	--
Poa pratensis L.	--	8
Sporobolus asper Michx.	--	5
Others	18	16

ensure the air stream was thoroughly mixed within the chamber. PVC film (approximately 30 cm long) was stretched across the width of the chamber near the outlet duct to produce a baffle effect and further enhance air mixture within the chamber. A small blower fan placed at canopy level was used to improve the circulation of air within the chamber.

Airflow rates into each chamber were measured each day by determining an air velocity profile across the diameter of the inlet tube. The air velocity profile was measured with a portable air velocity meter (Teledyne Hastings-Raydist, Model AB-27, Hampton, VA). Air velocity was measured at seven points along the diameter of the tube. These points were used to divide the inlet tube into five concentric circles. Airflow through each circle was determined and this was used to calculate the flow rate through the entire inlet tube. In general, air exchange rates through the chambers were 2.2 to 3.0 m^3 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 (Appendix Fig. 3). The air samples, after entering the trailer, passed through a sam-

pling 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 (Cole Palmer, Model L37A3, Chicago, IL) 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 (Gilmont Instruments, Model No F1100, Great Neck, NY) 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 (LI-Cor Inc., LI-Cor 6200, Lincoln, NE). After leaving the sensor heads, the air passed through calcium sulfate drying columns. Finally, the air entered the infrared gas analyzer (IRGA) portion of the system. The analyzer was calibrated with standard concentrations of CO_2 gas (gas concentrations were 332.9 and 370.5 μL L^{-1} ± 2%, Scott Specialty Gases, Plumsteadville, PA) on a daily basis. Net carbon exchange rates (NCE) were calculated by taking the difference between the CO_2 concentrations of the chamber outlet and inlet ducts, multiplying by the chamber airflow

rate, and dividing by the ground area (Sestak et al., 1971; Wall, 1986).

Gas exchange measurements were made on individual leaves of A. gerardii at a similar range site 1500 m northeast of our experimental site using an ADC Portable Photosynthesis System (P.K. Morgan Instruments, Inc., Model LCA2, Landover, MA). The IRGA was calibrated for CO_2 with certified span gases (Scott Speciality Gases, Plumsteadville, PA). Gas exchange was measured with a narrow Parkinson leaf chamber (volume = 12 cm^3) 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 CST. Gas exchange rates were measured on 5 leaves in each of the treatments.

Carbon dioxide diffusion out of the soil was measured with a method similar to that described by Anderson (1982) with slight modification. Aerosol cans (6.7 cm diameter) 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 plexiglas chamber. 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 screwtype lid containing 10 ml of 1M 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 (V1) of 1M hydrochloric acid (HCl) needed to titrate the samples was noted. Phenolphthalein indicator was then added to the samples. The sample was titrated again with 1M HCl and the volume (V2) used was noted. The amount of CO_2 diffused from the soil could be found by subtracting V1 from V2 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 $0.1 \ m^2$ quadrats on each treatment. Leaf area measurements were made with an optical planimeter (Li-Cor Inc., Model 3100, Lincoln, NE). 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 midsummer using a Scholander-type pressure bomb (Soilmoisture Equipment Corp., Santa Barbara, CA). Six or more fully expanded leaves of A. gerardii were sampled from each treatment. These measurements were made from 1000 to 1400 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 2-4 min before the measurements were made.

Climatological data were recorded by an automatic meteorological weather station located 800 m northeast of the experimental site. Photosynthetically active radiation (PAR) was measured with PAR sensors (LI-190S, Li-Cor Inc., Lincoln, NE).

Statistical analysis of the data was accomplished 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, since the plots were similar and measurements were made on plants located within 30 m of each other.

RESULTS

Carbon exchange rates of the tallgrass prairie canopy were measured from July through October of 1987. Precipitation was unevenly distributed during the study period (Fig. 1). Rainfall for the month of June was 5.5 cm below normal and 6.7 cm below normal for July. Several small rainfall events totalled only 1 cm of precipitation
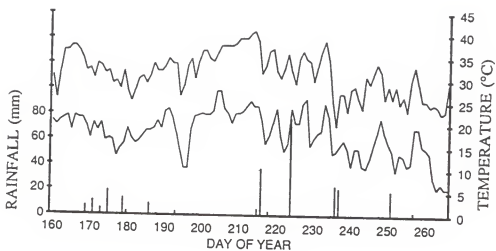
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Fig. 1. Maximum and minimum temperatures on the Konza
prairie during the summer of 1987 (Kansas State University
Weather Data Library). Also, along the bottom axis, the
seasonal precipitation recieved at the study site.

between 6 July and 2 August (DOY 187 and 214). Temperatures during July were slightly above average. During the latter part of this period, minimum leaf water potentials were <-4.0 MPa [pressure chamber limit] in both burned and unburned plots (Table 2). Between 3 August and 12 August, 12.2 cm of precipitation fell. No significant differences in leaf water potential existed between burned and unburned treatments on 11 August. Leaf water potentials were -1.79 and -1.83 MPa in burned and unburned treatments, respectively, on that date. Rainfall was 5.3 cm above average in August, but 6.7 cm below normal in September.

Relative rates of CO_2 exchange in burned and unburned treatments were compared and the results were mixed (Table 3). NCE was at its greatest on 11 July in the burned treatment, while the highest rate measured in the unburned treatment was 20 July. Included in the carbon exchange rates are CO_2 flux from the soil surface (root and soil respiration) and plant respiration. These CO_2 additions to the microenvironment within the chamber would cause the aboveground carbon exchange rate to be underestimated. Experimental results discussed later in this paper show soil CO_2 flux may be 10-30% of the total NCE.

On 11 July, NCE rates were significantly higher in

Table 2. Midday leaf water potential (MPa) of Andro-
pogon gerardii in burned and unburned treatments during
1987.

Date	(DOY)[a]	n	Burned	Unburned	p
			Treatment area		
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)	<.05
16 July	(197)	9	-2.87 (0.16)	-2.52 (0.13)	<.10
20 July	(201)	8	-3.32 (0.12)	-2.98 (0.13)	<.05
21 July	(202)	...[d]	<-4.0	<-4.0	
11 Aug.	(223)	9	-1.79 (0.18)	-1.83 (0.09)	ns
15 Aug.	(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
   Scholander chamber, so no measurements were available

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Table 3. Maximum NCE rates (mg CO_2 m^{-2} ground area s^{-1}) for both canopy and leaf measurements of burned and unburned treatments in the tallgrass prairie during 1987. Leaf area index (LAI, m^2 m^{-2}) is also included.

Date (DOY)	Canopy			Leaf			LAI	
	Burned	Unburned	p	Burned	Unburned	p	Burned	Unburned
11 July (192)	0.66 ± .06[a]	0.47 ± .07	.15[b]	1.21 .09[c]	0.74 -.13	.01	1.65 ± .22	1.83 .32
20 July (201)	0.38 ± .06	0.64 ± .13	n.s.	...[d]	...		1.00 ±.09	0.73 .22
28 July (209)	0.13 ± .04	0.10 ± .02	n.s.	...	...		0.69 ±.20	0.97 .25
15 Aug. (227)	0.37 ± .11	0.47 ± .14	n.s.	0.48 .08	0.44 .07	n.s.	1.16 ±.34	0.76 .09
23 Sept.(266)	0.50 ± .03	0.19 ± .02	<.10	...	...		1.17 ±.19	0.75 ±.24
6 Oct. (279)	0.11 ± .04	0.03 ± .03	<.15	...	...		0.25 ±.04	0.11 ±.06

a) Values represent mean ± standard error of 3 sampling chambers per treatment.

b) t-test significance level, Ho: the burned treatment had a higher NCE rate than the unburned treatment.
   n.s. = not significant at p = .20.

c) Values represent mean ± standard error of 5 individual leaves per treatment.

d) Data not available for theses dates.

the burned (0.66 mg CO_2 $m^{-2}sec^{-1}$) than the unburned plot (0.47 mg CO_2 $m^{-2}sec^{-1}$). NCE rates on 20 July was (0.38 mg CO_2 $m^{-2}sec^{-1}$) in the burned treatment compared to (0.64 mg CO_2 $m^{-2}sec^{-1}$) in the unburned treatment. The NCE maximum in the burned treatment on that day was 58% of the maximum measured on 11 July. Following approximately 12 cm of precipitation in the first two weeks of August, no significant differences in carbon exchange rates between treatments were measured on 15 August. Maximum photosynthetic rates on that date were 56% of the 11 July maximum (0.37 mg CO_2 $m^{-2}sec^{-1}$) in the burned treatment compared to 84% of the 20 July maximum (0.47 mg CO_2 $m^{-2}sec^{-1}$) in the unburned treatment. On 23 September, carbon exchange was significantly higher in burned (0.50 mg CO_2 $m^{-2}sec^{-1}$) than unburned plots (0.19 mg CO_2 $m^{-2}sec^{-1}$). These rates were 76 and 30% of the previously measured maximums in burned and unburned treatments, respectively. Rates were very low in both treatments by 6 October, ranging from 0.11 mg CO_2 $m^{-2}sec^{-1}$ in burned the burned treatment to 0.03 mg CO_2 $m^{-2}sec^{-1}$ in the unburned treatment.

Carbon exchange rates were measured on individual leaves of big bluestem at a range site comparable to that at which the chamber measurements were made. Photosynthetic rates of leaves on both burned and unburned treatments

were measured. The measurements were made on young, highly productive leaves of A. gerardii and would not account for less productive leaves that were included in the canopy measurements. These measurements, made on 11 July and 15 August, were compared to the maximum canopy exchange rates measured within the plexiglas chambers (Table 3). On 11 July, the maximum canopy exchange rates were 55% and 64% of those measured on individual leaves in burned and unburned treatments, respectively. The maximum leaf photosynthetic rate was significantly higher in the burned treatment (1.21 mg CO_2 m^{-2} ground area sec^{-1}) compared to the unburned treatment (0.74 mg CO_2 m^{-2} ground area sec^{-1}). On August 15, canopy exchange rates were 77 and 122% of those measured in burned and unburned treatments respectively. The maximum leaf photosynthetic rates were not significantly different in the burned treatment (0.48 mg CO_2 m^{-2} ground area sec^{-1}) compared to the unburned treatment (0.44 mg CO_2 m^{-2} ground area sec^{-1}) on that day.

NCE was measured as the change in CO_2 content of air flowing into and out of the plexiglas chambers. The change in CO_2 content quantified the amount of CO_2 taken up by plants for the photosynthetic process. This measurement underestimated the contribution of soil CO_2 flux to the photosynthetic process, which has been

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reported to be between 10 and 20% of the photosynthetic flux (Moss et al., 1961; Monteith et al., 1964).

The seasonal pattern of soil CO_2 flux from the soil followed trends similar to those of volumetric soil water content (Fig. 2). Rates declined in July (DOY 182 to 212) with drying soil from a maximum of 0.10 mg CO_2 $m^{-2}sec^{-1}$ on 11 July (DOY 192) to 0.06 mg CO_2 $m^{-2}sec^{-1}$ on 28 July (DOY 209), but more than doubled after precipitation in August (DOY 213 to 243), reaching 0.16 mg CO_2 $m^{-2}sec^{-1}$ on 6 August (DOY 218). As soils began to dry after precipitation, CO_2 evolution declined again.

CO_2 flux from the soil varies diurnally. Because our soil CO_2 flux measurements provide only an average flux for the day, it would not be entirely accurate simply 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 flux. To standardize the time length, all curves were integrated between times of 0830 and 1400 CST. By integrating the area under the curve, we were able to estimate the total amount of carbon fixed by the plants with a correction for soil CO_2 flux throughout each day.

Integrated CO_2 fixation rates, corrected for soil CO_2 flux, followed trends similar to the maximum NCE rates (Table 4). Carbon exchange rates on July 11 for a 5.5

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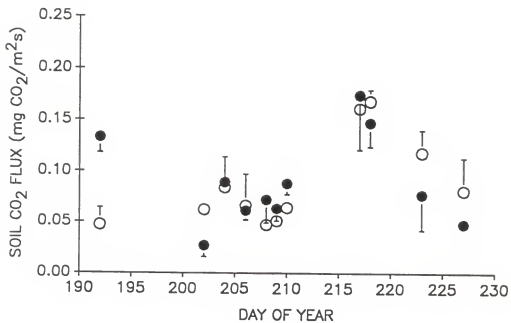
Fig. 2. Soil CO_2 flux in burned (o) and unburned (•)
treatments during 1987. Vertical bars represent + or −
standard error of the mean.

Table 4. Net carbon dioxide exchange rates on the Konza prairie during 1987. Values were obtained by integrating diurnal NCE curves for 5.5 hours (0830 to 1400 CST). Corrected NCE is the sum of daily NCE and soil CO_2 flux. Soil CO_2 is the soil CO_2 flux divided by the corrected NCE and represents the contribution of soil CO_2 flux to the net photosynthetic flux. All flux values are represented as g CO_2 m^{-2} ground area day^{-1}.

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 Aug. (227)				
Burned	4.06	1.61	5.67	28.4
Unburned	7.48	0.95	8.43	11.3

hour period were highest in the burned treatment at a rate of 13.0 g CO_2 $m^{-2}day^{-1}$. Maximum exchange rates in the unburned treatment occurred on 11 July at a rate of 10.5 g CO_2 m^{-2} day^{-1}. Exchange rates on 15 August in the burned treatment were 5.6 g CO_2 $m^{-2}day^{-1}$ compared to 8.4 g CO_2 m^2day^{-1} in the unburned treatment. The contribution of CO_2 diffusion from the soil to the net photosynthetic flux was estimated by dividing the daily soil CO_2 flux as measured in the alkali traps, by the integrated CO_2 fixation rates corrected for soil CO_2 flux. CO_2 diffusion from the soil ranged from 7.2 to 28.3% of the total NCE.

On 11 July and 20 July, plants seemed to be limited by factors other than light (Figs. 3 and 4). Both treatments reached maximum exchange rates and began to decline before PAR was a maximum for that date. This indicated that some other factor, probably water availability, was limiting production in both treatments. Leaf water potentials on 20 July were significantly lower in the burned -3.32 compared to unburned -2.98 MPa treatments (Table 2). On 15 August, CO_2 exchange was still increasing when PAR was at a maximum, indicating that the plants were not light saturated at 1900 μE m^{-2} sec^{-1} (Fig. 5). Leaf water potential was higher on this date; thus water was probably not a factor limiting growth. Leaf water potentials on this date averaged -1.9

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Fig. 3. Net carbon exchange (NCE) of burned (O) and unburned (●) treatments on 11 July, 1987 (DOY 192). Photosynthetically active radiation (PAR) is represented as (———). Vertical bars represent ± standard error of the mean.
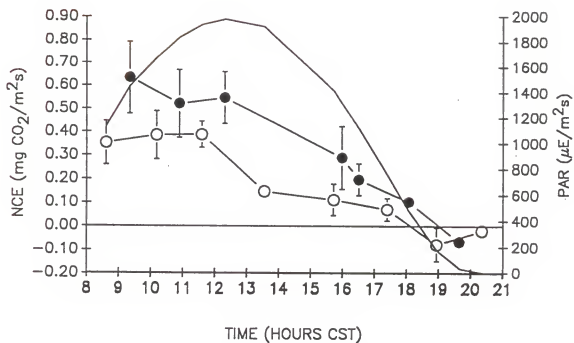
Fig. 4. Net carbon exchange (NCE) of burned (O) and unburned (●) treatments on 20 July, 1987 (DOY 201) Photosynthetically active radiation (PAR) is represented as (——). Vertical bars represent ±standard error of the mean.
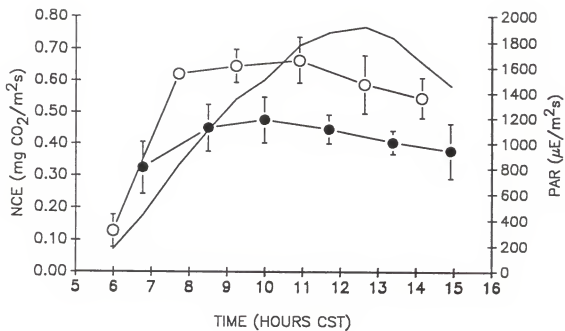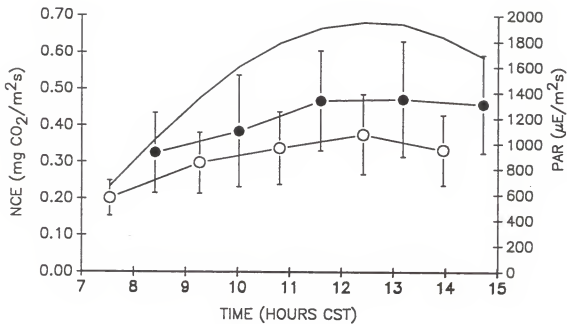
Fig. 5. Net carbon exchange (NCE) of burned (O) and unburned (●) treatments on 15 Aug., 1987 (DOY 227). Photosynthetically active radiation (PAR) is represented as (——). Vertical bars represent ± standard error of the mean.

and -2.0 MPa on burned and unburned treatments, respectively, and no significant difference between treatments was present.

A downward trend in leaf area index (LAI) was observed in both burned and unburned treatments throughout the experimental period (Fig. 6). LAI on 14 July (DOY 195) was 1.93 m^3m^{-3} in the burned treatment compared to 1.64 m^3m^{-3} in the unburned treatment. On 14 August (DOY 226), LAI had declined to 1.16 and 0.76 m^3m^{-3} in burned and unburned treatments, respectively. The LAI in both treatments was fairly constant during August and September (DOY 213 to 273).

DISCUSSION

The removal of dead plant material by fire alters the microclimate of the prairie grassland and causes a considerable shift in the water, nutrient, and energy flow through the prairie ecosystem. Knapp (1985) reported the dominant species in the tallgrass prairie, A. gerardii, had a greater photosynthetic yield after fire than before. The results presented in this study demonstrated that when moisture was not limiting to plant growth, photosynthetic rate was higher in the burned rather than the unburned plots, but at other times there were no significant differences in photosynthetic rate between the two treatments.
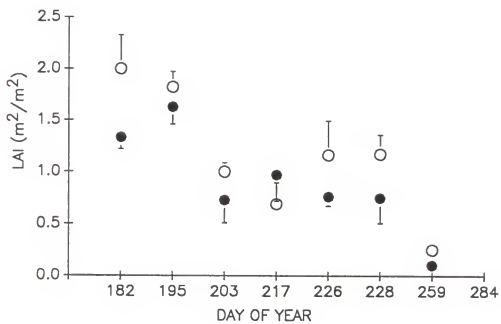
Fig. 6. Leaf area index (LAI) of burned (o) and unburned
(•) treatments during 1987. Vertical bars represent +
or - standard error of the mean. Some symbols exceeded
the size of the standard error bars.

The canopy NCE rates were generally lower than the photosynthetic measurements made on individual leaves of A. gerardii. Unlike the individual leaf measurements, the canopy NCE included leaves which were not producing at maximum levels. These less-productive leaves included senescent or damaged leaves, as well as those within the canopy that were partially shaded, and these leaves could also explain the lower exchange rate measured within the canopy.

Soil CO_2 flux into the chambers was a second reason for the lower values. Soil CO_2 flux ranged from 7 to 28% of the total CO_2 uptake, but the contribution of this component to NCE was unclear. By adding the soil CO_2 flux rate to the measured canopy NCE rate, one would get a canopy exchange rate closer to the photosynthetic rate measured on individual leaves.

Knapp (1985) reported photosynthesis decreased to zero when water stress was severe in 1983, but that leaves retained their chlorophyll under drought stress. Apparently, the photosynthetic apparatus was not damaged, since photosynthesis (measured on leaves present throughout the drought but with newly expanded tissue) increased substantially when water stress was alleviated. Similarly in our results, the NCE of the burned treatment on 20 July and 15 August were essentially identical.

NCE increased in the burned treatment between 15 August and 23 September while declining between those dates in the unburned plot (Table 3). Some of this increase might be attributed to variation within the treatment. Field notes indicate that the vegetation appeared vigorous near the chambers in the burned plot. Indiangrass, which composed 15% of the burned plot but less than 1% of the unburned plot, has been reported to undergo substantial growth of new tillers in late summer and early fall (McKendrick et al., 1975). The growth of tillers may contribute to the differences in NCE between burned and unburned treatments observed on 23 September.

Studies have shown soil CO_2 flux ranges from 0.04 to 0.65 mg CO_2 m^{-2}sec^{-1} in various cropped fields (Lundegardh, 1927; Monteith et al., 1964; Moss et al., 1961; Kanemasu et al., 1974). Kucera and Kirkham (1971) reported CO_2 evolution from the soil in a mid-Missouri tallgrass prairie to reach a maximum of 0.125 mg CO_2 m^{-2} sec^{-1} during the summer which is comparable to the rates measured here (Fig. 2). They noted that soil CO_2 flux declined as the water content of the prairie soil declined. This effect was similarly observed in forest soils (Wiant, 1967).

Brown and Trlica (1977) integrated exchange rate curves in terms of g of carbohydrates (CH_2O) m^{-2}grd area

day^{-1} for a blue grama (<u>Bouteloua</u> <u>gracilis</u> Lag.) canopy in northeast Colorado. Their values converted to CO_2 uptake, seemed similar to ours. On 28 to 29 June, they reported 24.2 g CO_2 m^{-2} day^{-1} compared to a maximum 13.0 g CO_2 m^{-2} day^{-1} measured in our experiment. Our values were obtained by integrating only a 5.5 hour interval, while Brown and Trlica reported values for the entire day. Brown and Trlica later reported integrated values for 6 to 7 July as 7.91 g CO_2 m^{-2}day^{-1}. By 11 to 12 August, plants under high soil water stress and high temperatures had integrated values of 5.72 g CO_2 m^{-2} 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 <u>A.</u> <u>gerardii</u> or <u>P.</u> <u>virgatum</u>, two dominant grasses in the tallgrass prairie, appeared to light saturate at 2200 μE m^{-2}sec^{-1} . These results are comparable to those found on 15 August when both burned and unburned treatments were still increasing in photosynthetic rate when PAR had reached a maximum of 1900 μE m^{-2}sec^{-1} (Figure 5). 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. 3 and 4).

Soil moisture has often been reported to be lower in burned than in unburned prairie late in the growing season (McMurphy and Anderson, 1965; Ehrenreich and Aikman, 1963; Anderson, 1965; Hulbert, 1969; Rice and Parenti, 1978). It might be reasoned that plants in an unburned prairie should be more productive than plants in a burned prairie during drought because soil water content is generally higher in the unburned plot. On 11 July, plants in both treatments had fairly low leaf water potentials. Each treatment reached a maximum NCE and began to decline in NCE before PAR was a maximum for that date (Fig. 3). In both canopy and individual leaf measurements, photosynthetic rate was significantly higher in the burned than the unburned treatment even under stressful conditions.

Knapp and Gilliam (1985) noted differences in photosynthetic pigments and structural characteristics in leaves of A. gerardii in unburned, low-irradiance sites compared to burned, high irradiance. Leaves in the unburned treatment had reductions in stomatal density, pore length, specific leaf mass and thickness as well as changes in leaf pigments and bundle sheath-vascular complex area. They concluded that these differences were adaptive for leaves in the unburned prairie, but by mid-season, when the leaves grew above the mulch into a high

irradiance environment, these characteristics limited production.

By 15 August, relative photosynthetic rate of the unburned compared to burned treatment had increased in both canopy and leaf measurements. Similarly, Knapp and Gilliam (1985) reported that photosynthetic rate of the unburned compared to burned treatments had increased during the latter half of the season. It appears that leaves may acclimatize to the high irradiance environment over time (Knapp and Gilliam, 1985; Hatch et al., 1969).

The present study was unique because it measured NCE on a canopy basis within the tallgrass prairie. Light is a critical factor in determining productivity; the data showed that plants were not light saturated at 1900 $\mu E\ m^{-2}\ sec^{-1}$. As other studies (Peet et al., 1975; Knapp, 1985) have shown, the burned treatment on certain days had a higher photosynthetic rate than the unburned treatment. However, the burned treatment did not always have a higher photosynthetic rate than the unburned treatment throughout the season. The differences in burned and unburned treatments are probably due to the interaction of several factors that have been discussed by other researchers, including differences in soil moisture and incident radiation as well as differences in leaf pigments and structural differences that occur when shoots emerge

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either into a low-irradiance or high-irradiance environment.

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APPENDIX

Appendix A

A REVIEW OF THE LITERATURE I. PHOTOSYNTHESIS IN THE
PRAIRIE ECOSYSTEM

The phototsynthetic process allows plants to
combine radiant energy with carbon dioxide (CO_2) to
produce an organic molecule with a relatively high energy
content through a series of complex biochemical
reactions. The carbon fixed by plants becomes food not
only for themselves, but also for other trophic levels
within the ecosystem (Risser et al., 1981).

The photosynthetic process for a particular species
of grass or forb in the tallgrass prairie may occur by one
of two biochemical pathways. Associated with these
pathways are morphological and physiological differences
between groups of species within the prairie. One pathway
for CO_2 fixation was described by Calvin and Bassham
(1962) in which CO_2 was incorporated into a 6-carbon
compound and rapidly converted into a 3-carbon compound
(C_3 photosynthesis). Hatch and Slack (1966, 1967)
described a second pathway for CO_2 fixation in which CO_2
was first incorporated into a 4-carbon compound (malic,
aspartic, or oxaloacetic acid) prior to transfer to sugars
(C_4 photosynthesis). Some plants possess features

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intermediate between the features characteristic of either the C_3 or C_4 plants. Kennedy and Laetsch (1974) reported _Mollugo verticillata_, an annual herb, had characteristics of both C_3 and C_4 plants. _Flaveria_ spp., annuals related to sunflowers, have shown a co-function of C_3 and C_4 cycles also (Monson et al., 1986).

Like almost all other physiological processes in plants, different species demonstrate different photosynthetic rates. Net photosynthetic rates of C_3 species have been reported to range from 0.4 to 1.0 mg CO_2 $m^{-2} sec^{-1}$ (Kanai and Black, 1972). Numerous researchers have reported C_4 plants exhibit higher rates, between 1.1 and 2.2 mg CO_2 m^{-2} sec^{-1} (Hesketh, 1962; Hesketh and Moss, 1963; Kanai and Black, 1972; and others).

Generally, grasses are divided into two broad groups: warm and cool season grasses. Warm season grasses are associated with C_4 photosynthesis. These grasses include such dominants of the tallgrass prairie as big bluestem (_Andropogon gerardii_), little bluestem (_Andropogon scorpius_), indiangrass (_Sorghastrum nutans_), and switchgrass (_Panicum virgatum_). These plants begin their growth in midspring and continue into late summer or early autumn. Cool season grasses are associated with C_3 photosynthesis. Cool season grasses include bluegrasses (_Poa_ spp.) and bromes (_Bromus_ spp.). They begin their growth in early

spring and complete it by early summer. Some may experience a second period of growth in late fall.

Although the biochemical and physiological characteristics of photosynthesis are reasonably well known, few data are available on the gas-exchange rates of prairie species. Additionally, the measurement of this process on a canopy basis is even less definite. Canopy photosynthetic measurements rely mostly on extrapolation from a limited number of leaf measurements, many of which were completed in the laboratory. Redmann (1971) measured photosynthetic rates of Sporobolus asper (A. Gray) A. gray growing in pots. He reported maximum photosynthetic rates of 10-12 mg CO_2 g^{-1} tissue dried weight hr^{-1}, but he gave no indication of the leaf area involved. Peet et al. (1975) found maximum photosynthetic rates of 0.25 mg CO_2 m^{-2} sec^{-1} for A. gerardii growing in the laboratory. These laboratory values may be significantly lower than field measurements. El-Sharkawy, Hesketh, and Muramoto (1965) indicated that plants grow less rapidly in glasshouses than in the field. Brown and Trlica (1977) compared photosynthetic rates of blue grama Bouteloua gracillis Lag.,a C_4 grass growing in the field and in greenhouses. They found photosynthetic rates in the greenhouse were approximately 65% of those determined in the field. They suggested these differences might have

been caused by adaptation of the greenhouse-grown plants to lower light intensities during their initial growth period.

Knapp (1985) measured photosynthetic rates of individual leaves of A. gerardii in burned and unburned field plots. He found the maximum photosynthetic rate was significantly higher in burned (1.83 mg CO_2 $m^{-2}sec^{-1}$) than unburned (1.23 mg CO_2 $m^{-2}sec^{-1}$) plots. Brown and Trlica (1977) made field CO_2 exchange determinations on a shortgrass prairie sod using a transparent dome which enclosed 0.3 m^2 of vegetation. They observed net photosynthetic rates as high as 1.80 mg CO_2 $m^{-2}sec^{-1}$ under optimum conditions.

A REVIEW OF THE LITERATURE II. FIRE-INDUCED CHANGES OF THE PRAIRIE ECOSYSTEM

Fire is an inherent feature of the tallgrass prairie (Vogl, 1974; Knapp, 1985). Both natural and man-caused fires probably have occurred throughout the 10,000 year history of the prairie (Weaver and Rowland, 1952; Old, 1969; Wells, 1970; Vogl, 1974). Natural fires were started by lightning and occurred at nearly any time of the year (Jackson, 1965).

Because fire was a natural and integral part of the ecosystem in which the tallgrass prairie developed, the

dominant prairie grasses are well adapted to regular burning (Knapp, 1984). Towne and Owensby (1984) reported annual late spring burns were not detrimental to species composition in a tallgrass prairie.

Many researchers have shown that properly timed burning improves herbage production in the prairie (Kucera and Ehrenreich, 1962; Hulbert, 1969; Towne and Owensby, 1984; and others). Unburned prairie deteriorates in both grass production and species composition (Towne and Owensby, 1984). Irradiance, temperature, soil water, and nutrient availability are four environmental variables which profoundly affect photosynthetic rates and are significantly influenced by fire. The C_4 species survive and may adapt better than many C_3 species under conditions of high irradiance, higher temperature, and high water stress associated with burned prairie (Risser et al., 1981).

In the absence of grazers or fire, mulch can accumulate to 1500 g m^{-2} (Weaver and Rowland, 1952). Hulbert (1969) reported the standing dead layer may exceed 40 cm on unburned, ungrazed tallgrass prairie. This mulch shades young shoots, reducing solar radiation and providing an unfavorable microclimate. Knapp (1984) found photosynthetically active radiation (PAR) incident on shoots was reduced by 58% by this thick layer of detritus.

During this period, aboveground production in unburned prairie was reduced by 55% compared to burned prairie. On a seasonal basis, direct loss of energy available to plants can be as much as 14%.

The photosynthetic response of individual leaves to light is generally hyperbolic (Kanemasu and Hiebsch, 1975). The response is nearly linear at low irradiance, with a steady increase until leveling out at a maximum rate under light saturation. The irradiance level at which light saturation occurs varies with species. In general, plants possessing the C_3 pathway become light saturated at irradiance levels less than those for the C_4 pathway, but this depends on light distribution within the canopy. Knapp (1985) compared the photosynthetic response of quantam flux of A. gerardii and P. virgatum. He found that photosynthetic rate was greatest in both grasses at high quantam flux in both burned and unburned treatments and that neither species appeared to light saturate at 2200 $\mu E \ m^{-2} sec^{-1}$.

As a consequence of less solar radiation reaching the soil surface, soil temperature is reduced on unburned sites (Hulbert, 1969; Old, 1969; Peet et al., 1975; Rice and Parenti, 1978). Knapp (1984) reported the cooler temperatures delayed the emergence of shoots in the spring and shortened the growing season. Compared to burned

sites, tillering was reduced, leading to lower shoot densities in unburned prairies.

The optimum air temperature for growth in C_4 species is typically 30 to 35°C (Black, 1973). Risser (1981) reported the optimum temperature for photosynthesis in A. gerardii was 35°C. Peet et al. (1975) found A. gerardii had a temperature optimum for photosynthesis between 25 and 30°C. Knapp (1985) reported that A. gerardii and P. virgatum had broad photosynthetic optimums. He found photosynthetic rate was 90% of the maximum at leaf temperatures from 28 to 41°C in A. gerardii and 33 to 41°C in P. virgatum. Brown and Trlica (1977) reported the optimum temperature for B. gracilis was 30°C.

Knapp (1984) reported windspeed in unburned plots was lowered by 89% by standing dead vegetation. The lower windspeed reduced convective cooling, and, as a result, leaf temperatures were higher in the unburned prairie than the burned prairie early in the season. An effect of higher leaf temperature is greater water loss resulting in lower leaf water potential. Knapp found leaf water potential was significantly lower in the unburned treatment than the burned treatment early in the year. He proposed that the lower leaf water potential and higher leaf temperature were significant in contributing to the lower production in unburned compared to burned prairie.

The reduced production of the unburned prairie may also be attributed to a reduction in available nutrients (Knapp and Seastedt, 1986). Detritus alters the forms and magnitude of nitrogen movement in the prairie. Dead foliage causes the conversion of immediately usable inorganic nitrogen in rainwater to less readily available organic nitrogen in microbial biomass (Seastadt, 1985). Nitrogen fixation by free-living microbes and blue green algae is inhibited by reduced phosphorus and/or light conditions in the unburned prairie (Eisele, 1985, cited by Seastadt, 1985). The combined effect of these differences in the microclimate may limit production in unburned prairie.

Reduction in soil moisture is one factor that may reduce production in the burned prairie. Hulbert (1969) reported soil moisture was 2 to 5% lower in plots denuded of litter (burned or clipped) compared to control plots. He felt that this difference was caused by increased evapotranspiration in the denuded plots. Anderson (1965) found that burning reduced soil moisture also. Old (1969) reported no difference in soil moisture caused by burning in an Illinois prairie.

Knapp (1985) studied A. gerardii during a midseason drought. He found midday leaf water potentials decreased to < -6.6 MPa (the limit of the pressure bomb)

and -5.74 MPa in burned and unburned plots, respectively. When water stress was most severe, photosynthesis decreased to near zero for both treatments. Following substantial late season precipitation, photosynthesis increased to 28 and 48% of the early season maximum in burned and unburned treatments, respectively. Brown and Trlica (1977) reported photosynthetic rates declined almost linerally with decreasing soil water potential from 0 to -3.0 MPa in shortgrass prairie. They attributed this decline to partial stomatal closure.

The differences in productivity of burned and unburned treatments also may be a result of morphological differences which exist between plants of the same species. The plants may adopt sun/shade adaptations similar to those documented for species growing either in forest understory environments and those in open, high irradiance sites (Boardman, 1977; Knapp and Gilliam, 1985). Knapp found leaves of A. gerardii in the low irradiance, unburned site had significantly lower stomatal density, pore length, and conductance, as well as specific leaf mass and thickness, than leaves from the high irradiance, burned site. Additionally, the chlorophyll a:b ratio, carotenoid content, and bundle sheath-vascular complex area were significantly lower in the plants at the unburned site.

An important source of CO_2 assimilated by plants is supplied by CO_2 transfer up from the soil. CO_2 is released by bacterial, fungal, algal, and protozoan cells in the soil as a result of both aerobic and anaerobic metabolism (Kucera and Kirkham, 1971). Additional CO_2 is added to this movement from carbonic acid reaction and variable diffusion rates. It has been reported that soil respiration can contribute 27-63% of the total CO_2 uptake of leaves (Nilouskaya et al., 1970). Other researchers have reported that respiration contributes only about 10 to 20 % of the net photosynthetic flux (Moss et al., 1961; Monteith et al., 1964) Because CO_2 flux may vary with location, it is important to determine CO_2 flux at the field site in experiments which measure gas exchange.

Historically, one of the oldest methods used to investigate the rates of CO_2 evolution from in situ soils is the titrametric analysis in which CO_2 moves from the soil and is absorbed by an alkali trap (Anderson, 1982). After a given period of time, the unreacted portion of the alkali is determined by titration. By means of subtraction, the amount of CO_2 that combines with the alkali may be determined.

Infrared analysis is a second method by which CO_2 flux from the soil may be measured. Chambers are placed over bare areas of the soil surface. In general, the

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alkali absorption technique yields CO_2 values which are less than the air flow method. Kucera and Kirkham (1971) reported CO_2 flux rates measured by alkali absorption to be 61% of those obtained by infrared analysis. They suggested that a lack of air turbulence within chambers used in the titrametric method and a decline in the absorption rates as the alkali is neutralized might be the cause of the lowered measurements.

Kucera and Kirkham (1971) reported CO_2 evolution from the soil in a mid-Missouri tallgrass prairie to reach a maximum of 0.125 mg CO_2 $m^{-2}sec^{-1}$ during the summer. As soil moisture in the surface soil approached the permanent wilting point, CO_2 evolution was reduced. Wiant (1967) found the effect of soil moisture extremes on CO_2 evolution to be similar in forest soils. Other researchers reported CO_2 flux ranging from 0.04 to 0.65 mg CO_2 $m^{-2}sec^{-1}$ in various cropped fields (Lundegardh, 1927; Moss et al., 1961: Monteith et al., 1964; Kanemasu et al., 1974).

A REVIEW OF THE LITERATURE III. OPEN CHAMBER MEASUREMENT OF PHOTOSYNTHETIC RATE

Gasometric methods are the most widely used methods for determining the gas exchange rates and photosynthetic activity of plants. The gas exchange system is composed of an assimilation chamber, a gas handling system, and a CO_2

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analyzer (Sestak et al., 1971). The assimilation chamber encloses a plant to facilitate measurement of gas exchange. The gas handling system transports reference and sample air streams from the assimilation chamber to the analyzer. It consists of leak-proof pumps and inert tubing. The CO_2 analyzer measures changes in gas concentration of the air entering the chamber and the air leaving the chamber. The measurement of CO_2 is based on the difference in intensity of infrared radiation (IR) passing through two sampling cells which contain either the reference or sample gases. Infrared radiation is transmitted through both cell paths, and the output of the analyzer is proportional to the difference in absorption between the two cells (Li-Cor, 1986). By calibrating the analyzer with known concentrations of gas, the difference in CO_2 between gases of unknown concentrations may be determined.

In the open gas exchange system, an airstream is passed through the assimmilation chamber at a constant flow rate. The carbon dioxide flux, F (kg $m^{-2} s^{-1}$), is then given by:

$$F = J * \frac{\triangle C}{A}$$

where

J = the rate of flow of air through the assimilation chamber

$(m^{-3}s^{-1})$

ΔC = the change in CO_2 concentration of the air as a result of passage through the chamber (kg m^{-3})

A = the area of leaf surface enclosed in the assimilation chamber (m^2) (Sestak, 1971 et al.)

The open chamber system has an advantage over other gas exchange systems (closed and semi-closed) in that it does not require a completely leak-free assimilation chamber. If the air is pushed through the system, rather than drawn, slight leakage is of little significance (Sestak et al., 1971). The disadvantages of the open system are a complex gas handling system and the need for an accurate measurement of flow rate through the system.

A major concern of the open chamber system is the effect it has on the microenvironment around the plant canopy. Differences depend on the design of the chamber, but plants receive 80 to 100% of natural full sunlight (Denmead, 1984). Some differences in the quality of light in the ultraviolet and near infrared regions do exist (Drake et al., 1985). In general, the microenvironment around the plant canopy is slightly warmer and more humid than outside the chambers. Baker and Kimball (1986) calculated that temperatures could be expected to rise 3.0 to 6.0°C in nearly transparent structures. Researchers at Kansas State University found temperatures to be a

maximum of 2.7 °C warmer inside open plexiglas chambers than outside (Burnett et al., 1985). Denmead (1984) estimated that transpiration rates may be affected by up to 100% depending on the combinations of environmental and physiological factors. Foster and Leuning (undated) reported transpiration rates within a ventilated chamber to be 10 to 15% higher than for undisturbed conditions according to both leaf energy budget and Penman-Monteith equation estimates. The seasonal rate of increase of growing degree days is higher inside chambers than outside (Surano and Shinn, 1984).

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RESEARCH TREATMENTS ON KONZA PRAIRIE RESEARCH NATURAL AREA

N = grazed by native grazers: bison, elk, pronghorn
K = ungrazed North Branch of Kings Creek (to allow comparison
    with the grazed South Branch)
C = grazed by cattle
1,2,4, and 10 = number of years between burning
3U3B = unburned for 3 years, then burned for 3 years
W = burned after years with more than 1.2 times the
    median precipitation
U = unburned
A, B, C, etc. = replications
Years indicate times the treatment began or is planned to begin.
Solid lines are fence locations, dashed lines fireguard locations.

Appendix Fig. 1.   Map of the Konza prairie and the
experimental site (Konza Prairie Office, Bushnell Hall,
Kansas State University, Manhattan KS).

Appendix Fig. 2. Diagram of the open chamber used to measure canopy NCE on the tallgrass prairie. Dimensions are given in cm.
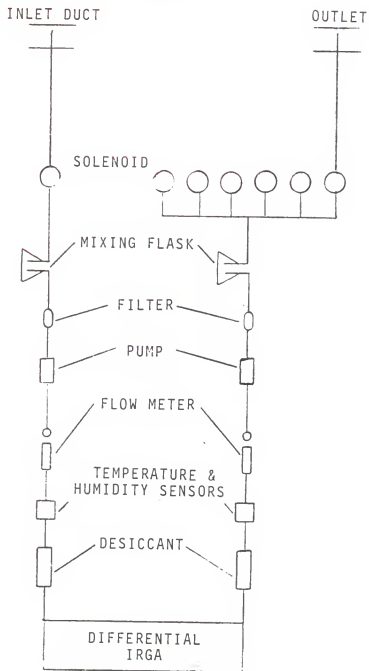
Appendix Fig. 3. Schematic of equipment used to measure CO_2 concentrations in the incoming and outgoing air streams of the plexiglas chambers.
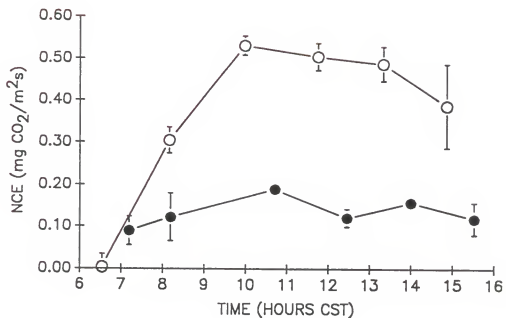
Appendix Fig. 3. Net carbon exchange (NCE) of burned (O)
and unburned (●) treatments on 23 Sept., 1987 (DOY 266).
Vertical bars represent ±standard error of the mean.

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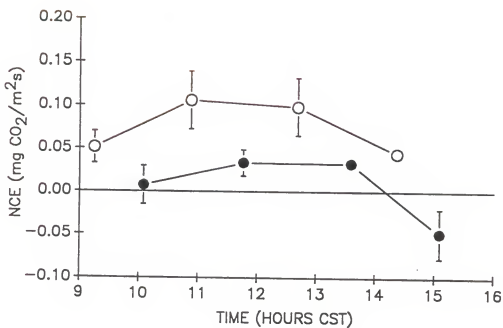
Appendix Fig. 4. Net carbon exchange (NCE) of burned (O) and unburned (●) treatments on 6 Oct., 1987 (DOY 279). Vertical bars represent ±standard error of the mean.
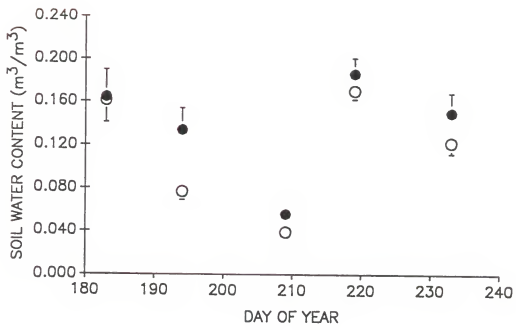
Appendix Fig. 5. Volumetric soil water content at 0 to 5 cm during 1987 in burned (o) and unburned (●) treatments. Vertical bars represent + or - standard error of the mean.
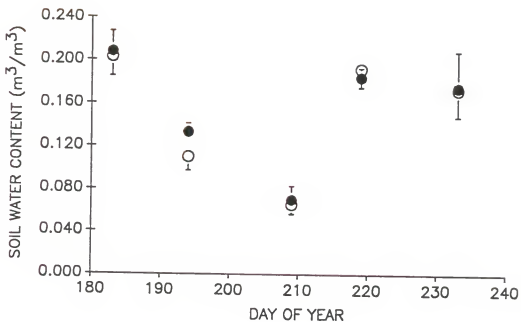
Appendix Fig. 6. Volumetric soil water content at 5 to 10 cm during 1987 in burned (o) and unburned (●) treatments. Vertical bars represent + or - standard error of the mean.

ADDITIONAL PAR MEASUREMENTS WITHIN THE PLEXIGLAS CHAMBERS

When reviewing this experimental method and considering the results, it should be kept in mind that the microclimate of the plants is altered, and, therefore, may present some difficulties in interpretations. One area of concern in this experiment was the effect that the chambers might have on light reaching the plants. The effect depends on the unique design of each chamber, but plants may receive 80 to 100% of full natural sunlight (Denmead, 1984). Additionally, some differences in the quality of light in the ultraviolet and infrared regions of the light spectrum may exist (Drake et al., 1985).

PAR sensors (LI-190S, Li-Cor, Lincoln, NE) were used to compare total incoming PAR, as well as diffuse light at the top of the plant canopy, both with and without the chamber in place at four different times of the day. The diffuse component of the PAR was measured by shading the sensors with circles cut from sheet metal and painted black. These circles were held in position about 0.6 m from the PAR sensors by clamps in such a way that no direct sunlight fell upon them.

Upon experimentation, we found that the total reduction of light was less than expected; however, the diffuse component of the light is greatly enhanced (Appendix Table

1). Over the entire day, total PAR was reduced by 5.4%. Over this same period of time, the diffuse component of this radiation was increased by 76.6%. With the chamber in place, diffuse light composed 27.7% of the total PAR at the top of the plant canopy, without the chamber it composed only 14.9%. This is significant because the diffuse light is better able to penetrate the plant canopy (by reaching leaves that might otherwise be shaded) and probably increases the photosynthetic rate.

Appendix Table 1. The influence of plexiglas chambers on PAR reaching the plant canopy.

Time (CST)	Total PAR[a,b]		%[c]	Diffuse PAR[d]		%[c]
	With Chamber	Without Chamber		With Chamber	Without Chamber	
0828				253.0	174.1	+45
0849	842.1	992.7	-15%			
1032	1241.5	1438.8	-14			
1034				386.1	222.1	+74
1301	1548.5	1568.0	- 1%			
1302				371.1	191.9	+93
1419				346.5	194.6	+78
1424	1388.9	1355.1	+ 3%			

a) $\mu E\ m^{-2}\ s^{-1}$
b) mean of 3 measurements.
c) % change with chamber in place. Increase (+), decrease (-).
d) mean of 6 measurements.

Appendix Table 2. NCE (mg CO_2 m^{-2} ground area s^{-1}) of burned and unburned treatments in the tallgrass prairie during 1987. Chambers 1 to 3 were located on the burned treatment; chambers 4 to 6 were located on the unburned treatment.

Chamber:	1	2	3	4	5	6
11 July	0.793	0.545	0.654	0.381	0.592	0.495
20 July	0.572	0.216	0.370	0.489	0.466	0.948
28 July	0.125	0.072	0.219	0.131	0.089	0.069
15 Aug.	0.502	0.470	0.157	0.221	0.693	0.490
23 Sept.	0.439	0.534		0.177	0.201	
6 Oct.	0.165	0.051	0.101	0.060	0.031	0.008

Appendix Table 3. Photosynthesis readings (mg CO_2 m^{-2} ground area s^{-1}) of individual leaves of A. gerardii on burned and unburned treatments of the tallgrass prairie during 1987.

Date	Burned	Unburned	t	p
11 July	1.16	0.24		
	0.98	0.65		
	1.53	1.00		
	1.09	0.85		
	1.30	0.93		
$\bar{x}$	1.21	0.74	3.96	<.01
15 Aug.	0.43	0.34		
	0.43	0.53		
	0.25	0.27		
	0.57	0.64		
	0.72	0.43		
$\bar{x}$	0.48	0.44	0.54	ns

Appendix Table 4. Midday leaf water potential (MPa) of A. gerardii in burned and unburned treatments in the tallgrass prairie.

Date	Burned	Unburned	t	p
5 July	1.70	1.88		
	1.50	2.15		
	1.50	2.12		
$\bar{x}$	1.57	2.05		
14 July	2.42	1.92		
	2.48	1.48		
	1.04	1.28		
$\bar{x}$	1.98	1.56	1.17	<.20
15 July	2.20	2.48		
	2.22	2.38		
	2.84	2.39		
	3.06	2.10		
	3.00	2.70		
	3.18	2.98		
	3.20	2.42		
	3.20	2.42		
	3.06	2.48		
$\bar{x}$	2.85	2.49	2.33	<.05
16 July	2.58	1.70		
	2.36	2.92		
	2.04	2.80		
	3.02	2.20		
	3.20	2.62		
	3.54	2.80		
	2.98	2.90		
	2.82	2.38		
	3.32	2.40		

Date	Burned	Unburned	t	p
$\bar{x}$	2.87	2.52	1.66	<.10
20 July	3.44	3.18		
	2.95	3.28		
	2.92	2.72		
	3.26	2.38		
	2.98	3.04		
	3.62	2.88		
	3.70	3.54		
	3.70	2.78		
$\bar{x}$	3.32	2.98	2.15	<.05
11 Aug.	1.30	1.70		
	0.88	1.68		
	1.24	1.30		
	2.52	1.62		
	1.80	2.04		
	1.80	2.20		
	2.20	1.88		
	2.18	1.90		
	2.22	2.18		
$\bar{x}$	1.79	1.83		
15 Aug.	1.88	1.66		
	1.98	1.92		
	2.04	2.00		
	2.06	1.92		
	1.72	2.10		
	2.02	2.36		
	1.68	1.80		
	2.08	1.90		
	2.04	2.38		
$\bar{x}$	1.94	2.04		

Appendix Table 5. Vegetative data of burned and unburned treatments on the tallgrass prairie during 1987. Three samples per treatment were taken on each day of year (DOY)

DOY	Burned			Unburned		
174	1.94[a]	2.92	1.50	1.75	3.63	2.08
	223.7[b]	253.4	169.9	212.0	274.2	261.7
	376.6[c]	481.8	314.1			
182	1.84	1.55	2.64	1.12	1.34	1.51
	166.4	161.9	239.3	135.2	141.3	152.9
	304.2	239.7	424.2			
191	1.96	1.77	1.22	2.08	1.21	2.24
	189.9	286	166.7	204.1	162.9	244.1
	284.9	543.7	287.1			
195	2.01	1.81	2.32	2.40	1.57	1.70
	276.7	257.6	226.2	289.9	198.2	191.3
	574.6	504.4	342.7			
203	1.02	.86	1.15	.84	.31	1.05
	124.6	217.1	210.0	136.0	78.8	188.4
	296.2	541	464.3			

DOY	Burned			Unburned		
				.77	1.47	.67
217	1.07	.36	.65			
				176.0	255.9	122.7
	156.0	53.9	96.9			
	364.1	213.5	347.4			
				.90	.60	.77
226	0.96	1.82	.71			
				187.3	107.3	112.5
	135.3	307.3	122.6			
	326.0	580.7	280.3			
				0.48	1.24	0.54
259	1.47	1.23	0.83			
				61.9	146.8	65.4
	192.9	175.6	87.4			
	601.4	409.5	306.7			
				.26	.28	.30
284	.20	.24	.32			
				45.4	8.47	18.8
	18.8	34.2	53			

a) Leaf area index ($m^2\ m^{-2}$).

b) Dry weight ($g\ m^{-2}$) of green grass leaves and stems.

c) Dry weight ($g\ m^{-2}$) of aboveground vegetation including standing dead, litter, and green grass leaves and stems.

Appendix Table 6. Change in CO_2 (ppm) as the air stream passed through the plexiglas chambers for burned and unburned treatments in the tallgrass prairie. Flow rates are given in m^3 min^{-1}. NCE may be calculated from these values using the following formula:

$$NCE = \frac{Flow\ rate\ (cm^3)\ *\ CO_2\ (ppm)\ *\ 0.4464}{ground\ area\ (11,140\ cm^2)}$$

Each line represents one sampling time. Values given in this paper are the mean of three chambers per treatment per sampling time.

| | July 11 | | | | | |
| | Burned | | | Unburned | | |
Chamber	1	2	3	4	5	6
	-.039	-2.0204	-2.2749	-3.116	-7.037	-4.0947
	-8.3425	-6.4122	-8.9886	-6.0471	-9.0646	-5.02436
CO_2 (ppm)	-10.0611	-5.889	-9.3933	-5.9011	-8.994	-6.142
	11.0238	-5.8916	-8.775	-6.7247	-8.169	-5.117
	-9.9728	-4.4226	-8.5679	-5.72	-6.8323	-5.36143
	-8.82935	-4.5641	-7.734	-4.7287	-8.3476	-3.75089
Flow rate (m^3/min)	2.44	3.14	2.53	1.96	2.23	2.74

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July 20

	Burned			Unburned	
1	2	3	4	5	6
-6.876	-3.343	-5.156	-7.874	-7.639	-12.983
-7.627	-3.786	-5.448	-7.441	-4.977	-10.941
-6.555	-5.238	-5.5064	-7.365	-6.811	-10.54
-2.6242	-1.9621	-1.9148	-4.023	-1.3344	-7.372
-3.094	-.0193	-1.4977	-1.7983	-2.4682	-4.478
-2.1622	-.8146	-.3251	-2.006	-1.2657	-1.4701
.0456	.2178	.1601	.6158	.4408	1.7728
.6119	-.2559	.4136	0	0	0
2.57	1.94	2.31	2.11	2.07	2.49

July 28

	Burned			Unburned	
1	2	3	4	5	6
-1.7489	-.83219	-2.8504	-2.0164	-1.3331	-1.125
-.436	-1.4796	-.4473	-1.4481	-2.4156	.0888
-.7133	-.1892	-.54484	-1.2979	-1.4114	-.8513
-.5246	-.409	-.1699	-1.6601	-1.382	-.3871
2.44	2.94	2.61	2.21	2.28	2.09

Aug. 15

	Burned			Unburned	
1	2	3	4	5	6
-4.2872	-3.0325	-4.329	-3.1785	-5.59	-3.644
-6.698	-4.541	-5.4102	-3.454	-7.099	-3.89646
-7.65	-5.2499	-5.7505	-3.991	-7.1805	-6.848
-8.9267	-5.5286	-6.473	-3.9326	-7.8724	-6.1293
-7.2941	-5.2719	-5.7898	-4.5364	-7.3485	-5.7912
1.91	2.89	2.46	1.88	3.28	2.43

Sept. 23

	Burned			Unburned	
1	2	3	4	5	
.4845	.0751	-.753	-.911	-1.7062	
-3.733	-3.223	-4.116	-2.95877	-.8963	
-5.638	-5.42	-6.274	-2.915	-2.7527	
-5.9977	-5.815	-6.5742	-1.6244	-1.9493	
-5.9686	-5.349	-6.3824	-2.8556	-1.9143	
-5.8617	-4.8442	-5.431	-2.5885	-1.0994	
3.05	2.56	2.76	2.07	2.48	2.03

Oct. 6

	Burned			Unburned	
1	2	3	4	5	6
-.671	-1.5788	-.2919	-.616	-.0287	-.0157
-2.909	-.5377	-1.146	-1.545	-.5681	-1.623
-3.661	-1.136	-1.741	-1.5013	-.1572	-1.0183
-3.819	-1.2102	-1.829	-1.436	-.525	-.751
2.21	2.23	2.55	2.31	2.66	0.77

CANOPY NET CARBON DIOXIDE EXCHANGE

BY BURNED AND UNBURNED TALLGRASS PRAIRIE

by

WILLIAM J. GALE

B.S.,B.A. Kansas State University, 1986

AN ABSTRACT OF A MASTER'S THESIS

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ABSTRACT

Net carbon exchange (NCE) was measured on a burned and unburned tallgrass prairie canopy during a four month period in 1987. NCE rates were higher on the burned treatment (0.66 mg CO_2 $m^{-2}sec^{-1}$) compared to the unburned treatment (0.47 mg CO_2 $m^{-2}sec^{-1}$) on 11 July. On 20 July NCE rates were higher in the unburned treatment (0.64 mg CO_2 $m^{-2}sec^{-1}$) than the burned treatment (0.38 mg CO_2 $m^{-2}sec^{-1}$). Maximum NCE rates on 15 August were 0.37 mg CO_2 $m^{-2}sec^{-1}$ and 0.47 mg CO_2 $m^{-2}sec^{-1}$ in the burned and unburned treatments, respectively, but no significant differences existed between treatments. Plants were not light saturated at 1900 μE m^{-2} sec^{-1} on 15 August. Canopy NCE rates were generally lower than rates measured on individual leaves of <u>Andropogon gerardii</u> (big bluestem).

No consistent differences in soil water content or leaf water potential were measured between burned and unburned treatments. The highest measured midday leaf water potential was -1.56 MPa in the unburned treatment on 14 July, but had declined to <-4.0 MPa in both treatments by 21 July. Soil CO_2 flux decreased as soil water content declined, reaching a low of 0.06 mg CO_2 $m^{-2}sec^{-1}$, but increasing under higher soil water content to 0.16 mg CO_2 m^{-2} sec^{-1}. Soil CO_2 flux was 7 to 28% of the net

photosynthetic flux.   Differences in photosynthetic rate
can probably be attributed to differences in incident
solar radiation as well as morphological differences
between plants emerging in sun (burned) or shade
(unburned) environments.