

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Papers in Natural Resources

Natural Resources, School of

1990

Carbon Dioxide Exchange in a Temperate Grassland Ecosystem

S. B. Verma

University of Nebraska - Lincoln

Follow this and additional works at: <https://digitalcommons.unl.edu/natrespapers>



Part of the [Natural Resources and Conservation Commons](#), [Natural Resources Management and Policy Commons](#), and the [Other Environmental Sciences Commons](#)

Verma, S. B., "Carbon Dioxide Exchange in a Temperate Grassland Ecosystem" (1990). *Papers in Natural Resources*. 1205.

<https://digitalcommons.unl.edu/natrespapers/1205>

This Article is brought to you for free and open access by the Natural Resources, School of at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Papers in Natural Resources by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

CARBON DIOXIDE EXCHANGE IN A TEMPERATE GRASSLAND ECOSYSTEM¹

JOON KIM and SHASHI B. VERMA²

Department of Agricultural Meteorology, University of Nebraska-Lincoln, Lincoln, NE 68583-0728, U.S.A.

(Received in final form 16 January, 1990)

Abstract. Carbon dioxide exchange was measured, using the eddy correlation technique, over a tallgrass prairie in northeastern Kansas, U.S.A., during a six-month period in 1987. The diurnal patterns of daytime and nocturnal CO₂ fluxes are presented on eight selected days. These days were distributed throughout most of the growing season and covered a wide range of meteorological and soil water conditions. The midday CO₂ flux reached a maximum of 1.3 mg m⁻² (ground area) s⁻¹ during early July and was near zero during the dry period in late July. The dependence of the daytime carbon dioxide exchange on pertinent controlling variables, particularly photosynthetically active radiation, vapor pressure deficit and soil water content is discussed. The nocturnal CO₂ flux (soil plus plant respiration) averaged -0.4 mg m⁻² (ground area) s⁻¹ during early July and was about -0.2 mg m⁻² s⁻¹ during the dry period.

Introduction

The North American grassland, which extends from Saskatchewan to Mexico and from the Rockies to the Mississippi river, may be primarily divided into the tallgrass prairie, mixed grasslands and the shortgrass prairie (Clements and Shelford, 1939). Generally, tallgrasses and forbs occupy the eastern portion and moister habitats while shorter vegetation occupies western and drier habitats (Bazzaz and Parrish, 1982).

Global atmospheric CO₂ studies and models have generally lacked reliable information on CO₂ exchange in various terrestrial ecosystems, including the grasslands. A number of field and laboratory studies have been conducted on the physiological and morphological adaptations of individual grass species (e.g., Risser, 1985). Very few measurements, however, exist on the carbon dioxide exchange and its seasonal variation in this ecosystem.

We employed the eddy correlation technique to measure fluxes of moisture, heat and carbon dioxide at a tallgrass prairie site near the Konza Prairie Research Natural Area in Kansas, U.S.A. during the First ISLSCP³ Field Experiment (FIFE) in 1987. Information on the surface energy budget components and canopy surface and aerodynamic conductances was reported in a previous paper (Kim and

¹ Published as Paper No. 9061, Journal Series, Agricultural Research Division, University of Nebraska-Lincoln, U.S.A.

² Research Associate and Professor, respectively.

³ ISLSCP: International Satellite Land Surface Climatology Project (for details, see Sellers *et al.*, 1988).

Verma, 1990). Here we present results on carbon dioxide exchange in this ecosystem. The objectives of this paper are to evaluate the diurnal and seasonal variations in daytime and nocturnal CO₂ fluxes and to study their dependence on pertinent environmental variables.

2. Materials and Methods

2.1. SITE AND VEGETATION

The study site (latitude 39° 03'N, longitude 96° 32'W, 445 m above sea level) was located near Manhattan, Kansas. Soil at the site is predominantly Dwight silty clay loam (Typic Natrustolls). The soil bulk density averaged about 1.15 Mg m⁻³ for the top 0.30 m. The prairie was burned annually in early spring. The experimental area was not grazed in 1986 and 1987.

Percent species composition at the study site was estimated using the modified step-point method (Owensby, 1973). The vegetation is composed principally of three C₄ grass species: *Andropogon gerardii*, *Sorghastrum nutans*, and *Panicum virgatum* (Table I).

2.2. PLANT AND SOIL MEASUREMENTS

Leaf area index (LAI) was measured with an area meter (LI-COR⁴, Inc., Lincoln, NE, Model LI-3000). The surface soil water content (0–0.1 m) was monitored gravimetrically and subsurface water content (0.1–1.4 m) was measured with a neutron probe (Campbell Pacific Nuclear Co., Pacheco, CA, Model 503) on a weekly basis. The neutron probe was calibrated at the field site prior to the experiment.

TABLE I

Percent species composition at the experimental site (flowering stage, 1987) estimated by the modified step-point method (Owensby 1973)

Species	%
<i>Andropogon gerardii</i> (Big bluestem) (C ₄)	27.1
<i>Sorghastrum nutans</i> (Indiangrass) (C ₄)	22.2
<i>Panicum virgatum</i> (Switchgrass) (C ₄)	16.6
<i>Sporobolus asper</i> (Tall dropseed) (C ₄)	7.0
<i>Schizachyrium scoparium</i> (Little bluestem) (C ₄)	4.7
<i>Bouteloua gracilis</i> (Blue grama) (C ₄)	4.3
<i>Dichanthelium oligosanthes</i> (Scribner panicum) (C ₃)	4.0
<i>Agropyron smithii</i> (Western wheatgrass) (C ₃)	1.2
Other grasses	2.4
Sedges	6.3
Forbs and woody plants	4.2

⁴ Trade names and company names are included for the benefit of the reader and imply no endorsement or preferential treatment.

2.3. MICROMETEOROLOGICAL MEASUREMENTS

The eddy correlation instrument array included: a rapid response CO₂ sensor with a 0.2 m path length (Bingham *et al.*, 1978; Anderson *et al.*, 1984), a Lyman alpha hygrometer (A.I.R. Inc., Boulder, CO, Model LA-1) with a 5 mm path length, and a one-dimensional sonic anemometer (Kaijo Denki Co., Tokyo, Japan, Model DAT-100), mounted on a horizontal boom at 2.25 m above ground. The data were low-pass filtered using 8-pole Butterworth active filters with 12.5 Hz cutoff frequency and were sampled at 20 Hz. Sampling, recording, and near real-time processing of data were done with an IBM PC-AT microcomputer (details are available in previous reports e.g., Verma *et al.*, 1986, 1989). Fluxes were obtained from covariances computed over 30-min averaging periods. Values of CO₂ flux were corrected for the effects of spatial separation of sensors following Moore (1986) and the variation in air density due to simultaneous transfers of latent and sensible heat following Webb *et al.* (1980).

Photosynthetically active radiation (PAR) was measured with quantum sensors (LI-COR, Inc., Lincoln, NE, LI-190SB) located at 2.0 m above ground. Mean air temperature and humidity were measured with an aspirated ceramic wick psychrometer at 2.25 m above ground. Mean soil temperature (0–0.05 m) was measured with platinum resistance thermometers. Mean horizontal wind speed was measured with a three-cup anemometer (Cayuga Development, Ithaca, NY, Model WP-1) located at 2.25 m above ground.

3. Results and Discussion

3.2.1. Daytime CO₂ Flux

Figure 1 shows the seasonal variations in green LAI, rainfall and soil water content. Stages in the annual life cycle of the prairie vegetation are also indicated in Figure 1. The green LAI reached its maximum of about 3.2 toward the end of June during the peak growth stage, and gradually decreased with senescence of the prairie vegetation. Precipitation was generally ample from May to September, except during three weeks in late July–early August. The volumetric water content (θ_v) of the top 0.3 m of soil was generally above 0.25 m³m⁻³ during May through September, except for the dry period. During the dry period, θ_v reached as low as 0.16 m³m⁻³ in late July and moisture stress conditions prevailed.

3.2. DIURNAL AND SEASONAL VARIATIONS

3.2.1. Daytime CO₂ Flux

The diurnal patterns of the atmospheric CO₂ flux⁵ (Fc) and the incoming photosynthetically active radiation⁶ (PAR) for eight selected days are presented in Figures

⁵ The sign convention employed here is such that the CO₂ flux directed toward the surface is positive. CO₂ fluxes are reported on a per ground area basis.

⁶ The conversion factor of photon units ($\mu\text{Ei m}^{-2} \text{s}^{-1}$) to radiometric units (W m^{-2}) is approximately: $4.6 \mu\text{Ei m}^{-2} \text{s}^{-1} \approx 1 \text{ W m}^{-2}$.

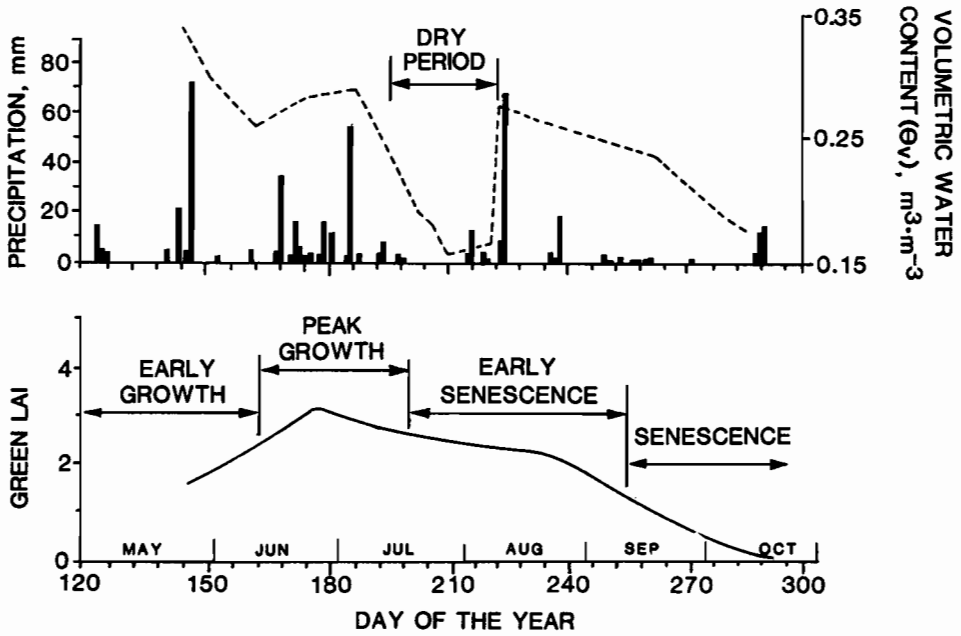


Fig. 1. Seasonal variations in green leaf area index, precipitation, and volumetric soil water content (0–0.3 m depth).

TABLE II

Midday (averaged during 1230–1430 hr, Central standard time) values of mean air temperature (T), vapor pressure deficit (D), wind speed (U) on selected days in 1987. These variables were measured at a height of 2.25 m above the ground. The values of the volumetric soil water content (0–0.3 m depth) (θ_v) and the green leaf area index (LAI) are also included

Date	Annual life cycle stage	T	D	U	θ_v	LAI
		°C	kPa	m s^{-1}	$\text{m}^3\text{-}^3$	
5 June	Early Growth	27.1	1.89	4.0	0.28	1.9
2 July	Peak Growth	33.2	1.25	3.3	0.34	3.0
23 July*	Early Senescence	33.3	2.82	5.9	0.19	2.7
30 July*	Senescence	37.1	4.30	5.5	0.16	2.6
10 August*		29.9	2.42	2.9	0.19	2.5
15 August		33.7	2.33	5.6	0.34	2.4
4 September		31.1	2.61	6.2	0.24	1.7
8 October	Senescence	20.0	1.70	7.8	0.13	0.3

* Day from the dry period (see Figure 1).

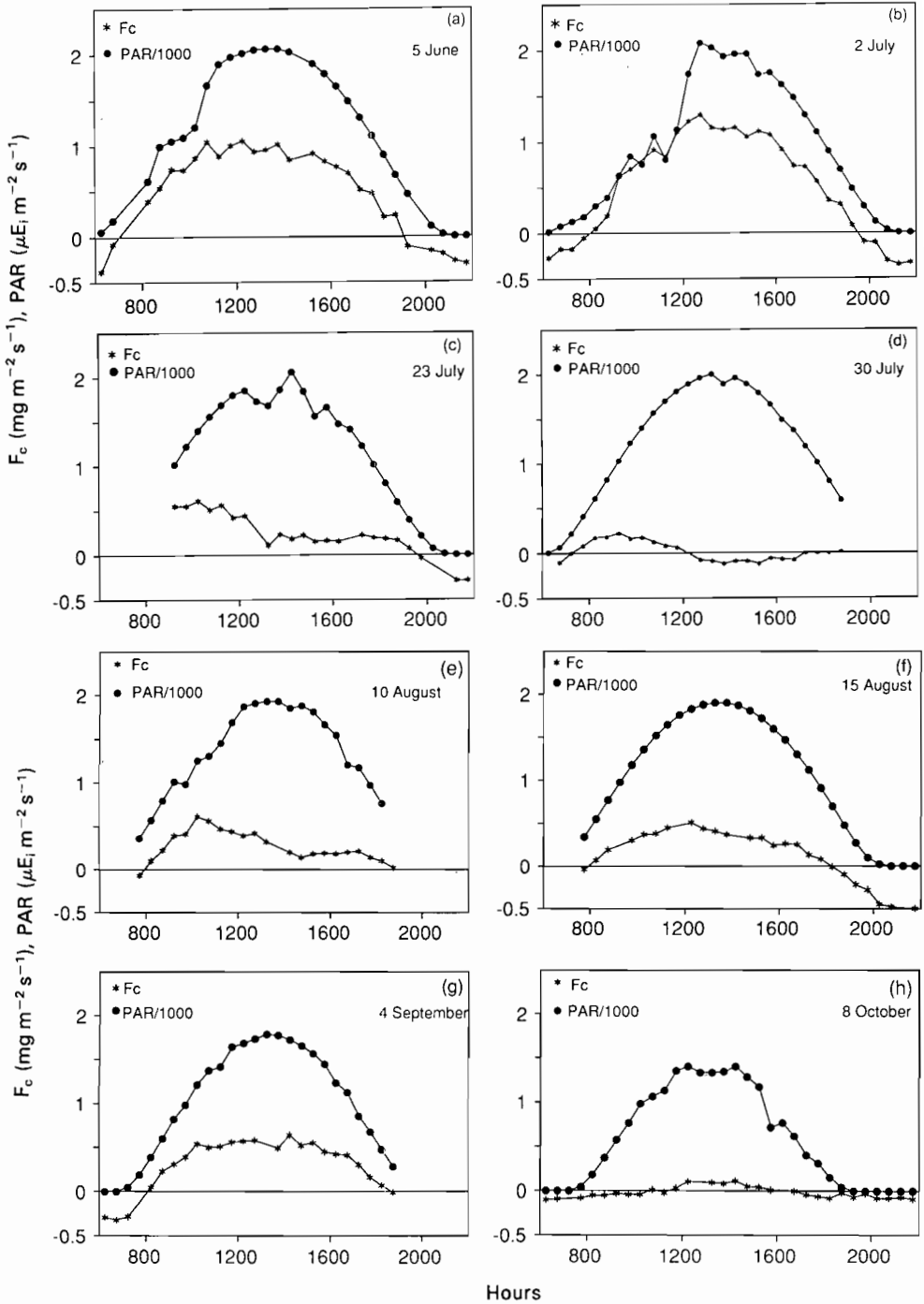


Fig. 2. Diurnal variation of the daytime CO₂ flux (F_c) and photosynthetically active radiation (PAR) on 8 selected days. Central standard time is shown.

2a-h. Meteorological and soil water conditions and LAI are summarized in Table II. On 5 June (early growth), the green LAI was 1.9 and θ_v was $0.28 \text{ m}^3 \text{ m}^{-3}$. In response to increasing PAR, F_c increased rapidly after sunrise until about noon and then decreased with diminishing radiation load later in the day (Figure 2a). Peak F_c of $1.1 \text{ mg m}^{-2} (\text{ground area}) \text{ s}^{-1}$ occurred at noon, whereas PAR reached its peak of $2060 \mu \text{Ei m}^{-2} \text{ s}^{-1}$ at 1330 hr.

It was partly cloudy on 2 July (peak growth) in the morning and became clear in the afternoon. The diurnal pattern of F_c followed that of PAR quite closely (Figure 2b). Both F_c and PAR reached their peaks at about 1300 hr with values of $1.3 \text{ mg m}^{-2} \text{ s}^{-1}$ and $2084 \mu \text{Ei m}^{-2} \text{ s}^{-1}$, respectively. Greater leaf area (LAI ≈ 3.0) and ample soil water ($\theta_v = 0.34 \text{ m}^3 \text{ m}^{-3}$) on this day resulted in somewhat greater CO_2 exchange as compared to that on 5 June. As will be discussed later, the small vapor pressure deficit on 2 July (see Table II) may have also contributed to this result.

With the onset of the dry period toward the end of the peak growth stage (late July), the magnitudes and patterns of F_c changed. Soil moisture decreased significantly (Figure 1) and θ_v on 23 July was about $0.19 \text{ m}^3 \text{ m}^{-3}$. On this day, the vapor pressure deficit (D) increased rapidly in the morning and reached up to 3.2 kPa in the afternoon. Midday air temperature (T) was around 33°C . The CO_2 flux reached its peak ($0.6 \text{ mg m}^{-2} \text{ s}^{-1}$) at 1000 hr and then decreased thereafter even though PAR continued to increase until the midday hours (Figure 2c). The value of F_c was around $0.2 \text{ mg m}^{-2} \text{ s}^{-1}$ during most of the afternoon.

As the dry period progressed, the peak F_c shifted further toward the morning hours. On 30 July the soil water availability was low ($\theta_v = 0.16 \text{ m}^3 \text{ m}^{-3}$), and the atmospheric evaporative demand was very high (Table II). The CO_2 flux was suppressed drastically and the maximum F_c of $0.2 \text{ mg m}^{-2} \text{ s}^{-1}$ occurred at 0900 hr (Figure 2d). The CO_2 flux in the afternoon averaged about $-0.1 \text{ mg m}^{-2} \text{ s}^{-1}$ (directed away from the vegetation).

The soil moisture conditions improved in early August due to frequent rainfall. On 10 August (Figure 2e) F_c was directed back toward the vegetation during the day with a peak of $0.6 \text{ mg m}^{-2} \text{ s}^{-1}$ occurring in late morning. With 67 mm of rainfall on 13 August (Figure 1) the soil water condition improved further. On 15 August the peak F_c ($0.5 \text{ mg m}^{-2} \text{ s}^{-1}$) shifted toward noon (Figure 2f) and the diurnal pattern of F_c generally followed that of PAR.

Midday F_c on 4 September (Figure 2g) was $0.6 \text{ mg m}^{-2} \text{ s}^{-1}$, about 50% of the early season rates observed during the peak growth stage. The peak F_c shifted back toward the midday hours and the diurnal pattern of F_c followed that of PAR quite closely. The photosynthetic rates diminished as the prairie vegetation senesced (Figure 2h). On 8 October (senescence stage), the value of F_c was less than $0.1 \text{ mg m}^{-2} \text{ s}^{-1}$ during the day.

These diurnal and seasonal patterns of F_c are similar to the results reported by Ripley and Saugier (1974) from their study of a shortgrass prairie in Saskatchewan, Canada. They found that F_c reached a peak of $0.3\text{--}0.4 \text{ mg m}^{-2} (\text{ground area}) \text{ s}^{-1}$

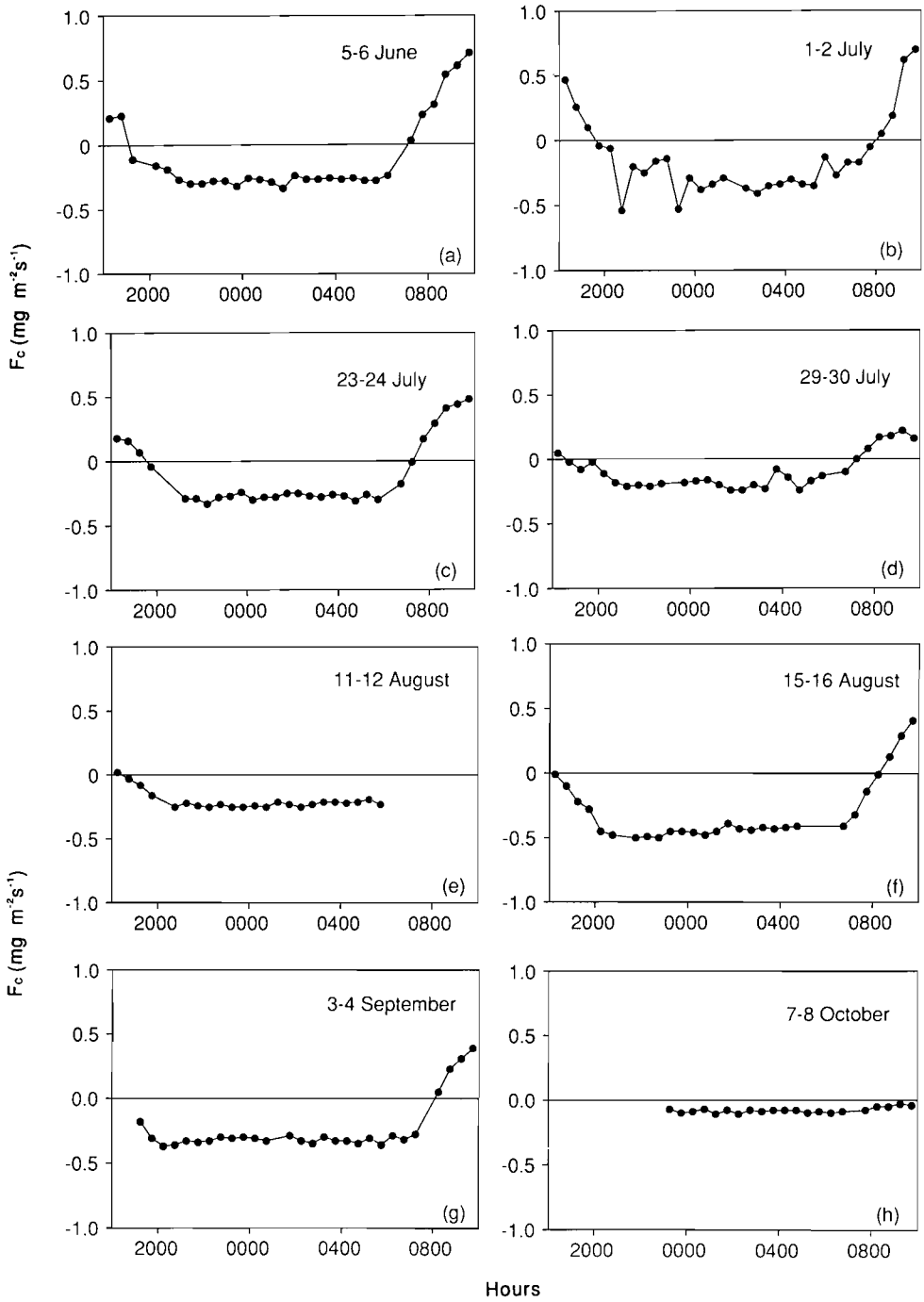


Fig. 3. Nocturnal CO₂ flux on 8 selected nights. Central standard time is shown.

TABLE III

Nocturnal (averaged during 2200–0600 hr, Central standard time) values of mean air temperature (T) and wind speed (U) on selected days in 1987. The values of the volumetric soil water content and the green leaf area index are given in Table II

Date	Annual life Cycle stage	T	U
		°C	m s ⁻¹
5–6 June	Early Growth	16.9	3.8
1–2 July	Peak Growth	18.4	2.0
23–24 July*	Early	24.7	3.9
29–30 July*	Senescence	26.3	3.8
11–12 August*		24.9	3.7
15–16 August		27.9	6.9
3–4 September		21.8	3.8
7–8 October	Senescence	6.5	3.8

*Day from the dry period (see Figure 1).

in early July and decreased with increasing plant water stress and senescence later in the season. Their values were lower than the values for the tallgrass prairie studied here, primarily because of a smaller leaf area ($LAI \approx 1.0$) and the dominance of C_3 grasses in their study.

3.2.2. Nocturnal CO_2 Flux (Soil plus Plant Respiration)

The CO_2 flux (F_c) measured on eight selected nights are presented in Figures 3a–h. Meteorological conditions are summarized in Table III. Generally, F_c decreased rapidly between 1900 and 2000 hr. Values of F_c were relatively stable between about 2200 hr and about an hour before sunrise. Excluding the transition periods near sunrise and sunset, the respiration (plant and soil) rates during the early growth (Figure 3a) and peak growth stages (Figure 3b) ranged from -0.3 to $-0.5 \text{ mg m}^{-2} (\text{ground area}) \text{ s}^{-1}$.

During the dry period, the extreme weather conditions and low availability of soil water (Table II) affected plant growth and reduced the rate of respiration from the plants and soil. The respiration rate during this period averaged about $-0.2 \text{ mg m}^{-2} \text{ s}^{-1}$ (Figures 3c–e). In response to improved soil moisture conditions during mid August and early September, the respiration rate increased and ranged from -0.3 to $-0.5 \text{ mg m}^{-2} \text{ s}^{-1}$ (Figures 3f and g). The increase in the respiration rate was due to the enhanced photosynthetic activity after the rain and to the increased activity of soil microorganisms. The respiration rate diminished as the season progressed. During the senescence stage (Figure 3h), the respiration rate averaged about $-0.1 \text{ mg m}^{-2} \text{ s}^{-1}$.

These patterns of nocturnal F_c are similar to those reported by Ripley and

Saugier (1974). The magnitudes in their shortgrass prairie were smaller (0.1–0.2 mg m⁻² s⁻¹ in early July), however.

3.3. FACTORS CONTROLLING DAYTIME CO₂ FLUX

3.3.1. Photosynthetically Active Radiation

Figure 4 shows the relationship between F_c and PAR for different stages in the annual life cycle of the prairie vegetation. Data were selected when the soil water condition was favorable [θ_v (0–0.3 m depth) > 0.25 m³m⁻³] and when the vapor pressure deficit (D) was low (0–1.5 kPa). As expected, a hyperbolic relationship existed between F_c and PAR during the early growth, peak growth and early senescence stages. Data in Figure 4 were fitted with a rectangular hyperbola (commonly used in physiological studies; see e.g. Landsberg, 1977) of the form:

$$F_c = \frac{(F_{cm})(b)(PAR- PAR^*)}{F_{cm} + (b)(PAR- PAR^*)}$$

where F_{cm} is the maximum F_c , PAR^* is the value of PAR at the light compensation

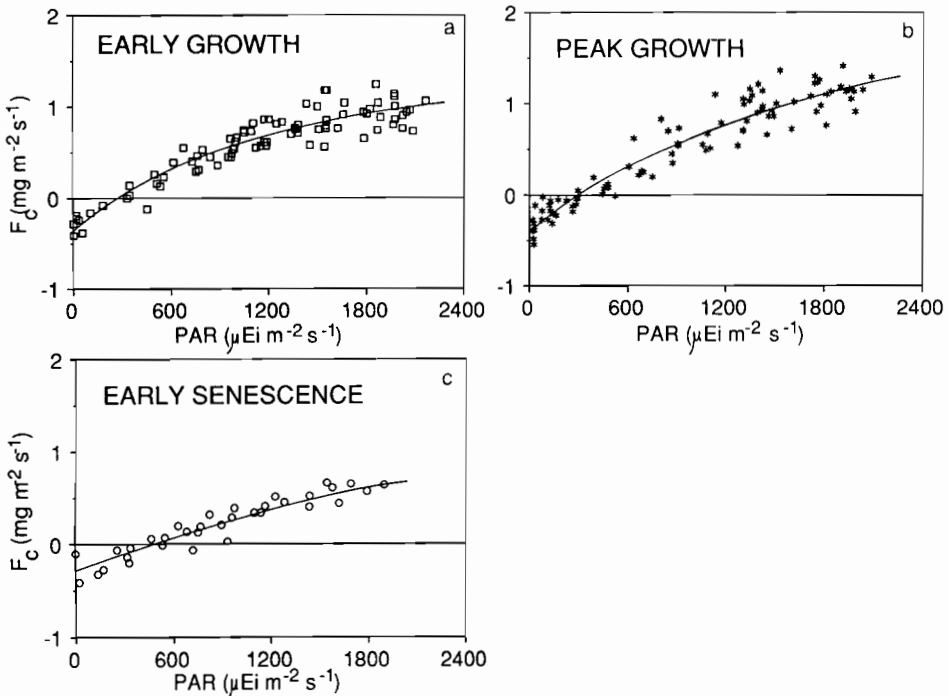


Fig. 4. Daytime CO₂ flux as a function of photosynthetically active radiation (PAR) at different annual life cycle stages of the prairie vegetation. Data were fitted with a rectangular hyperbola, $F_c = F_{cm}b (PAR- PAR^*)/[F_{cm} + b (PAR- PAR^*)]$. Data were selected when $\theta_v > 0.25$ m³m⁻³ and $0.0 < D < 1.5$ kPa.

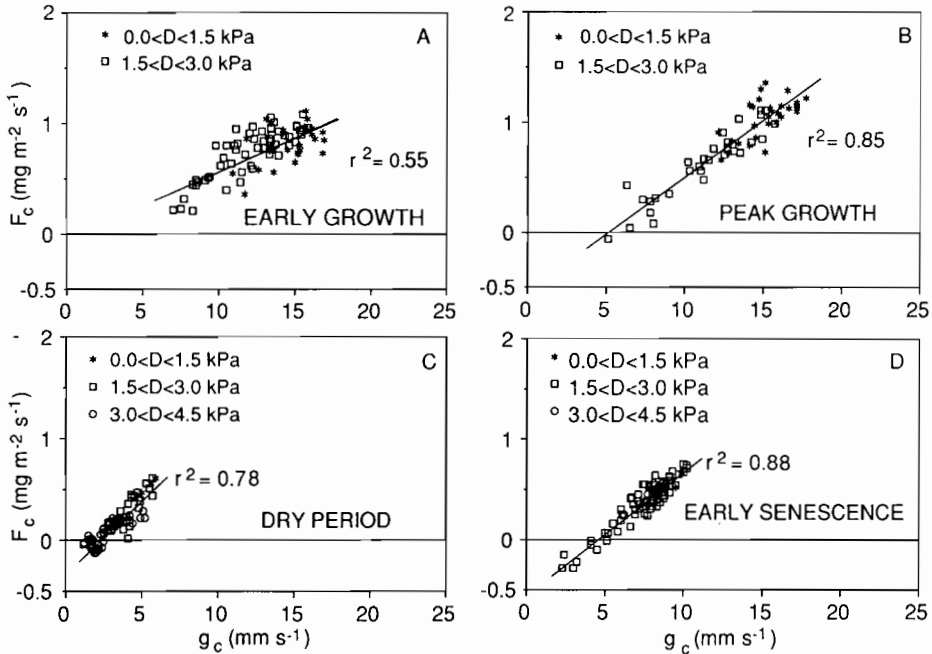


Fig. 6. Relationship between the daytime CO₂ flux (F_c) and the canopy surface conductance (g_c). Linear regression lines are included.

and vapor pressure deficit, using the Penman-Monteith equation (see Kim and Verma, 1990, for details). Figures 6a-d show the relationship between F_c and g_c . The data are grouped in three intervals of D . Data on rainy days and days after rain were excluded; and to minimize the confounding effect of dew on leaves, data before 1000 hr were excluded.

Although there is some scatter in the data, the relationship between F_c and g_c appears to be linear throughout the season (Figures 6a-d) (this relationship does not appear to have been affected by the values of D , although low g_c values were usually associated with large values of D). Similar F_c - g_c relationships have been reported in previous studies on individual leaves. For example, Knapp (1985) reported parallel changes between net photosynthesis and leaf conductance of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie.

It should be noted that parallel changes shown in Figures 6a-d do not necessarily suggest cause and effect relationships between F_c and g_c . However, these results further substantiate the physiological significance of g_c , as has been pointed out earlier.

3.4. FACTORS CONTROLLING NOCTURNAL CO₂ FLUX

Temperature and soil water availability are the primary environmental factors that control the nocturnal CO₂ emanating from the soil and from the plant (Kucera

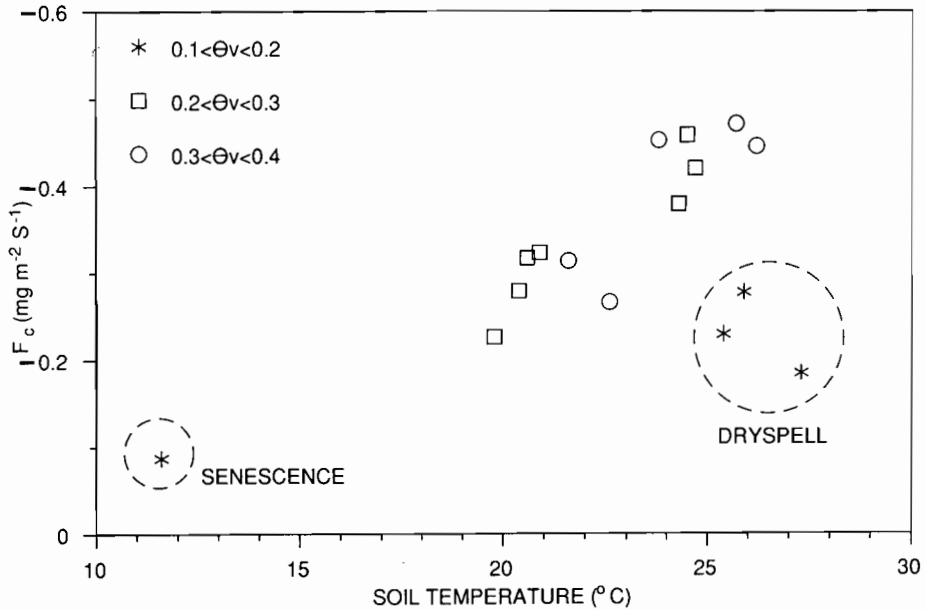


Fig. 7. The nocturnal CO_2 flux (F_c) as a function of soil temperature.

and Kirkham, 1971; Redmann, 1978). The response of the nocturnal CO_2 exchange to soil temperature (T measured at 0–0.05 m depth) is given in Figure 7 (data were averaged from 2200 to 0600 hr to minimize the confounding effect during the transition periods near sunrise and sunset). The data are grouped in three different intervals of soil moisture content (θ_v). Except for the period of low soil moisture ($0.1 < \theta_v < 0.2 \text{ m}^3 \text{ m}^{-3}$; see encircled data in Figure 7), the magnitude of

TABLE IV

Multiple regression analysis of the relationship of nocturnal CO_2 flux (F_c) to soil temperature (T_{soil}) soil moisture (θ_v) and wind speed (U). All coefficients of determination (r^2) were statistically significant (0.01 level)

Variables	Coefficient of determination (r^2)
<i>Dependent</i>	
Nocturnal CO_2 flux	
<i>Independent</i>	
T_{soil}	0.31
θ_v	0.56
U	0.35
$T_{\text{soil}}, \theta_v$	0.71
$T_{\text{soil}}, \theta_v, U$	0.91

nocturnal F_c appeared to increase with increasing T_{soil} . A linear regression through the data (nocturnal F_c and T_{soil}), however, yielded a coefficient of determination (r^2) of only 0.31 (Table IV). The soil moisture availability (θ_v) accounted for 56% of the variability in the nocturnal CO_2 exchange. The inclusion of θ_v with T_{soil} increased the r^2 value to 0.71.

The dependence of the nocturnal CO_2 exchange on wind speed (U) was also examined. A regression with wind speed alone yielded r^2 of 0.35, a small but significant value. A multiple regression, computed with T_{soil} , θ_v , and U as independent variables, accounted for about 91% of the variation in nocturnal CO_2 fluxes (Table IV).

4. Summary and Conclusions

Results are reported on the carbon dioxide exchange measured in a temperate grassland ecosystem near Manhattan, Kansas during the growing season of 1987.

During the most vigorous stage of plant growth (June-July), the midday CO_2 flux (F_c) reached a seasonal peak of 1.3 mg m^{-2} (ground area) s^{-1} and the nocturnal F_c (soil + plant respiration) averaged about $-0.4 \text{ mg m}^{-2} \text{ s}^{-1}$.

The dry period encountered during late July-early August, a rather typical feature of the climate of this region, caused F_c to decline to almost zero during the day. Nocturnal F_c averaged about $-0.2 \text{ mg m}^{-2} \text{ s}^{-1}$ during this dry period.

With frequent rainfall in mid-August to early September, the daytime F_c recovered to about 30–50% of the early season rates whereas the nocturnal F_c recovered almost fully. In October, plant senescence, low temperature and low soil water availability reduced the midday F_c to less than $0.1 \text{ mg m}^{-2} \text{ s}^{-1}$, while the nocturnal F_c was around $-0.1 \text{ mg m}^{-2} \text{ s}^{-1}$.

Under nonlimiting soil moisture conditions, the major determinant of the daytime CO_2 flux was photosynthetically active radiation. Examination of our data under both nonlimiting and limiting soil moisture conditions indicated that the CO_2 flux was suppressed significantly by high vapor pressure deficit. The daytime F_c and the canopy surface conductance were strongly correlated over a wide range of environmental conditions throughout the season. The nocturnal F_c seemed to be dependent primarily on soil moisture availability and also on soil temperature and wind speed.

Acknowledgements

This study was supported by the National Aeronautics and Space Administration under Grant NAG5-890 and by the National Science Foundation under Grant ATM-8519026. Messrs. H. D. Earl and Sheldon Sharp provided valued assistance in maintenance of instruments and data acquisition systems. Mr. James Hines assisted in data computation. We wish to express our sincere appreciation to Mr. Robert Clement for his valuable help in data collection and processing, and to

Mr. Randall Kennedy and Dr. Joseph Shinn of the Lawrence Livermore National Laboratory for their help in proper maintenance of the rapidresponse CO₂ sensor. We thank Dr. James Stubbendieck for his help in estimating species composition; Mrs. Sharon Kelly for the stenographic work; and Drs. John M. Norman, James Stubbendieck and Charles Y. Sullivan for their review of this manuscript.

References

- Anderson, D. E., Verma, S. B., and Rosenberg, N. J.: 1984, 'Eddy Correlation Measurements of CO₂, Latent Heat and Sensible Heat Fluxes Over a Crop Surface', *Boundary-Layer Meteorol.* **29**, 263-272.
- Bazzaz, F. A. and Parrish, J. A. D.: 1982, 'Organization of Grassland Communities', in J. R. Estes, R. J. Tyre, and J. N. Brunken (eds.), *Grasses and Grassland*, University of Oklahoma, Norman, pp. 234-254.
- Bingham, G. E., Gillespie, C. H., and McQuaid, J. H.: 1978, 'Development of a Miniature, Rapid Response CO₂ Sensor', Report UCRL52440, Lawrence Livermore National Laboratory.
- Clements, F. E. and Shelford, V. E.: 1939, *Bioecology*, John Wiley, New York.
- Kim, J. and Verma, S. B.: 1990, 'Components of Surface Energy Balance in a Temperate Grassland Ecosystem', *Boundary-Layer Meteorol.* **51**, 401-417.
- Knapp, A. K.: 1985, 'Effect of Fire and Drought on the Ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a Tallgrass Prairie', *Ecology* **66**, 1309-1320.
- Kucera, C. L. and Kirkham, D. R.: 1971, 'Soil Respiration Studies in Tallgrass Prairie in Missouri', *Ecology* **52**, 912-915.
- Landsberg, J. J.: 1977, 'Some Useful Equations for Biological Studies', *Expl. Agric.* **13**, 273-288.
- Monteith, J. L.: 1965, 'Evaporation and Environment', in G. E. Fogg (ed.), *The State and Movement of Water in Living Organisms*, Academic Press, New York. pp. 205-234.
- Monteith, J. L.: 1981, 'Evaporation and Surface Temperature', *Quart. J. Royal Meteorol. Soc.* **107**, 1-27.
- Moore, C. J.: 1986, 'Frequency Response Corrections for Eddy Correlation Systems', *Boundary-Layer Meteorol.* **37**, 17-35.
- Owensby, C. E.: 1973, 'Modified Step-Point System for Botanical Composition and Basal Cover Estimates', *J. Range Management* **26**, 302-303.
- Redmann, R. E.: 1978, 'Seasonal Dynamics of Carbon Dioxide Exchange in a Mixed Grassland Ecosystem', *Canadian J. Botany* **56**, 1999-2005.
- Ripley, E. A. and Saugier, B.: 1974, 'Energy and Mass Exchange of a Native Grassland in Saskatchewan,' *Proceedings of the 1974 International Seminar on Heat and Mass Transfer in the Environment of Vegetation*, Dubrovnik, pp. 311-325.
- Risser, P. G.: 1985, 'Grassland', in B. F. Chabot and H. A. Mooney (eds.), *Physiological Ecology and North American Plant Communities*, Chapman and Hall, New York, pp. 232-256.
- Sellers, P. J., Hall, F. G., Asrar, G., Strebel, D. E. and Murphy, R. E.: 1988, 'The First ISLSCP Field Experiment (FIFE)', *Bull. Amer. Meteorol. Soc.* **69**, 22-27.
- Shuttleworth, W. J.: 1976, 'A One-Dimensional Theoretical Description of the Vegetation-Atmosphere Interaction,' *Boundary-Layer Meteorol.* **10**, 273-302.
- Thom, A. S.: 1975, 'Momentum, Mass, and Heat Exchange of Plant Communities,' in J. L. Monteith (ed.), *Vegetation and the Atmosphere*. Vol. 1, Academic Press, New York, pp.57-109.
- Verma, S. B., Baldocchi, D. D., Anderson, D. E., Matt, D. R., and Clement, R. J.: 1986, 'Eddy Fluxes of CO₂, Water Vapor and Sensible Heat Over a Deciduous Forest,' *Boundary-Layer Meteorol.* **36**, 71-91.
- Verma, S. B., Kim, J., and Clement, R. J.: 1989, 'Carbon Dioxide, Water Vapor and Sensible Heat Fluxes Over a Tallgrass Prairie,' *Boundary-Layer Meteorol.* **46**, 53-67.
- Webb, E. K., Pearman, G. I., and Leuning, R.: 1980, 'Correction of Flux Measurements for Density Effects Due to Heat and Water Vapor Transfer,' *Quart. J. Royal Meteorol. Soc.* **106**, 85-100.

1

2