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SEASONAL AND DIURNAL VARIATION IN THE CO_2 FLUX AND CO_2—WATER FLUX RATIO OF ALFALFA*

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ABSTRACT

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The seasonal and diurnal variation of CO_2 flux (F_c) and CO_2—water flux ratio (*CWFR*) of alfalfa were studied using micrometeorological techniques during the summer of 1978 at a location in the east central Great Plains.

Significant seasonal variation was found in both F_c and *CWFR*. F_c and *CWFR* were large in value during late spring. F_c and *CWFR* decreased and reached a minimum during midsummer but recovered with the approach of fall.

F_c was great during late spring as a result of optimal environmental conditions and the spring growth flush. The midsummer minimum in CO_2 flux appears to have been due to a reduced [CO_2] gradient between the chloroplast and atmosphere, to oxygen inhibition of CO_2 uptake and thermal pre-conditioning.

The diurnal course of F_c was affected by irradiance and, possibly, by an accumulation of starch in the leaves. The diurnal course of *CWFR* was affected by net radiation and by sensible heat advection.

INTRODUCTION

Many micrometeorological studies have shown that the CO_2 and water vapor exchanges of crops are affected by environmental variables (e.g. Lemon, 1960; Begg et al., 1964; Denmead, 1966; Saugier, 1970). During the course of the growing season CO_2 and water vapor exchange of the crop is affected by changing environmental, physiological and developmental conditions. Yet few micrometeorological studies exist in which the CO_2 and water vapor exchange of a crop have been investigated over the length of the growing season. Among the few noteworthy studies in which this has been done are those of Monteith and Szeicz (1960) and Brown and Rosenberg (1971) over sugar beets and Biscoe et al. (1975) over barley.

Here we report results of a study made with alfalfa at a location in the east central Great Plains of North America. Work by Rosenberg (1969), Blad and Rosenberg (1974) and Rosenberg and Verma (1978) has shown that alfalfa grown in this region can experience extreme rates of evapotranspiration as a result of strong sensible heat advection. Little is known, however,

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how the environment of this region affects the CO_2 flux and water use efficiency of alfalfa over the course of the entire growing season.

The objective of this study was to investigate the seasonal and diurnal variation in the CO_2 flux (F_c) and CO_2—water flux ratio ($CWFR$) of alfalfa and to relate these variations to seasonal and diurnal changes in environmental and physiological factors and to the stage of crop development.

MATERIALS AND METHODS

Experimental details

The studies described below were conducted during the summer of 1978 at the University of Nebraska Agricultural Meteorology Laboratory near Mead, Nebraska (41° 09′ N; 96° 30′ W; altitude 354 m above m.s.l.). A three-year old alfalfa crop (*Medicago sativa* L., cv. Dawson) was used. The main field (105 m east—west, 210 m north—south) was irrigated. Border fields to the east, south and west were planted with non-irrigated alfalfa of the same cultivar. A uniform fetch of about 400 m (north—south) was maintained for winds between the southwest and southeast directions due to ample spring and summer rains in 1978.

Three separate studies were conducted during the 1978 growing season. Each study lasted from cutting to cutting: Study 78-1, May 12—June 27; Study 78-2, June 28—August 7; Study 78-3, August 8—September 16.

Concentrations and gradients of CO_2 were measured with a system comprised of an absolute and a differential infrared gas analyzer (IRGA)* in tandem. Details of the system and calibration procedures are given in Rosenberg and Verma (1976). Air was sampled through a multi-level manifold. Each level of the manifold had six intakes spaced equidistantly over a length of 2.5 m. Air was sampled at heights of 0.50, 0.75 and 1.00 m when the crop was shorter than 0.40 m. After the crop height exceeded 0.40 m, air was sampled at 0.75, 1.00 and 1.25 m. The CO_2 sampling cycle was repeated every five minutes. During each cycle, specific samples were measured every 17 s. This was an adequate interval for the IRGA cells to be purged and for the analyzer to reach equilibrium, since the time constant of the IRGA was about 8 s. Once each hour and the absolute and differential IRGAs were calibrated with gases of known concentration.

Above-canopy vertical profiles of air temperature and vapor pressure were determined with a self-checking aspirated, multi-level psychrometer at 0.50, 0.75, 1.00 and 1.50 m. When the crop grew taller than 0.40 m, each level on the psychrometer was raised by 0.25 m. Once each hour the psychrometer was rotated into a horizontal position for calibration (see Rosenberg and Brown, 1974, for details).

Two precision weighing lysimeters (van Bavel—Myers type, modified by

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* Beckman Instruments Models 315A and 315B.

Rosenberg and Brown, 1970) with soil bins 1 m^2 in area and 1.6 m in depth were used to measure evapotranspiration rate. Net radiation was measured with two Swissteco net radiometers*. Windspeed profiles were measured with Cayuga 3-cup anemometers** and soil heat flux was measured with two soil heat flux plates*** buried at 0.01 m.

Data were sampled and recorded with a computer controlled data acquisition system. IRGA signals were recorded every five minutes. Other instrument signals were recorded three times a minute. All data were later averaged for the first 45-minute period of each solar hour. The last 15 minutes of each hour was reserved for calibration of the psychrometers and infrared gas analyzers.

Stomatal resistance and plant water potential were measured hourly on selected days. Stomatal resistance was measured with a diffusion resistance meter**** on the top and bottom sides of six randomly selected leaves in the upper sunlit portion of the canopy. Stomatal resistance was calculated by assuming that the top and bottom sides of the leaf acted as parallel resistors to the flow of water vapor. Plant water potential was determined using a "pressure chamber"***** device. Six randomly selected plants, cut at the fourth internode below the apical meristem, were used in the pressure chamber.

Leaf area index (*LAI*) and dry matter accumulation (*DM*) were sampled periodically. *LAI* and *DM* were determined from six random samples, each 0.25 m × 0.25 m in size. *LAI* was measured with a Hayashi-Denco automatic area meter. *DM* was determined from the weight of oven dried plant samples.

Theoretical considerations

CO_2 flux (F_c) was calculated using flux-gradient theory

$$F_c = fK_c(\partial c/\partial z) \tag{1}$$

where K_c is the eddy exchange coefficient for CO_2, $\partial c/\partial z$ is the vertical gradient of CO_2 concentration (ppm m^{-1}) and f is a proportionality constant to convert ppm to specific weight. K_c was assumed to be equal to the eddy exchange coefficient for water vapor (K_w) and was computed by the lysimetric method (Rosenberg, 1974)

$$K_c = K_w = LE\bigg/\left(\bar{\rho}_a \ \frac{\epsilon}{P}\ L\ \frac{\partial e}{\partial z}\right) \tag{2}$$

where $\bar{\rho}_a$ is the mean density of dry air, LE is latent heat flux, measured directly with a lysimeter, ϵ is the ratio of the molecular weights of water

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* Swissteco Pty. Ltd., E. Hawthorne, Vic., Australia (Type S-1).
** Cayuga Development, Ithaca, NY (Model WP-1).
*** Science Associates, Inc., Princeton, NJ (Model G32(1)).
**** Lambda Instruments Co., Lincoln, NE (Model LI-50).
***** Soil Moisture Equipment Corp., Santa Barbara, CA (Model 3005).

vapor (M_w) and dry air (M_a) ($\epsilon = 0.622$), P is atmospheric pressure, L is the latent heat of vaporization and $\partial e/\partial z$ is the vertical gradient in water vapor pressure.

Fluxes of both latent and sensible heat (H) have been shown to be great in the east central Great Plains as a result of sensible heat advection (Rosenberg, 1969; Rosenberg and Verma, 1978). Because of these strong fluxes, considerable error can occur in the flux estimates of minor constituents, such as CO_2, since the fluxes of LE and H can cause significant variation in the density of dry air. An expression was thus developed to correct eq. 1 for the effects of LE and H [see Baldocchi (1979) for the derivation]

$$F_c = \underbrace{fK_c \frac{\partial c}{\partial z}}_{\mathrm{I}} + \underbrace{\frac{\bar{\rho}_c M_a LE}{\bar{\rho}_a M_w L[1 + (\bar{\rho}_w M_a/\rho_a M_w)]}}_{\mathrm{II}} + \underbrace{\frac{\bar{\rho}_c H}{\bar{\rho}_a^2 \bar{T} C_p}\left(\frac{M_a \bar{\rho}_w}{M_w} + \rho_a\right)}_{\mathrm{III}} \quad (3)$$

where $\bar{\rho}_c$ is the mean density of CO_2, $\bar{\rho}_w$ is the mean density of water vapor, C_p is the specific heat of dry air at constant temperature, $\bar{T}$ is the mean absolute temperature. The first term (I) is the uncorrected CO_2 flux, the second term (II) corrects CO_2 flux for the effect of water vapor flux on the density of dry air and the third term (III) corrects for the effect of sensible heat flux on the density of dry air.

Other corrections for CO_2 flux have been presented by Webb and Pearman (1977) and Jones and Smith (1978). Webb and Pearman, however, corrected only for water vapor flux. Jones and Smith derived an expression that corrected CO_2 flux for both H and LE but their equation can be applied only when CO_2 flux is measured by eddy concentration.

Water use efficiency was calculated in terms of an index — the CO_2—water flux ratio ($CWFR$) defined as

$$CWFR = F_c/E \quad (4)$$

where E is the mass flux of water vapor.

Turbulent mixing was described in terms of friction velocity (u_*) and was calculated from flow level drag coefficients derived from wind profile data (for details see Deacon and Swinbank, 1958; Bradley, 1972; Verma et al., 1976).

RESULTS AND DISCUSSION

Seasonal trends

A. Environmental and physiological variables

Midday averages (computed during the period 1000 to 1345 h) of F_c, $CWFR$, net radiation (Rn), latent heat flux (LE), air temperature (T), friction velocity (u_*), CO_2 concentration ($[CO_2]$) and plant water potential (Ψ) were computed for those days during each study for which a sufficient fetch

TABLE I

Midday averages and standard deviations of CO_2 flux (F_c), CO_2—water flux ratio ($CWFR$), net radiation (Rn), latent heat flux (LE), CO_2 concentration ([CO_2]), air temperature (T), friction velocity (u_*) and plant water potential. Meteorological measurements were made over alfalfa during the summer of 1978 at Mead, Nebraska. n denotes sample size

Variables	Units	Study 78-1* mean ±s.d.	Study 78-2* mean ±s.d.	Study 78-3* mean ±s.d.
F_c	10^{-6} kg(m^{-2} leaf area)s^{-1}	0.63 ±0.28	0.24 ±0.07	0.78 ±0.34
$CWFR$	g CO_2(kg H_2O)$^{-1}$	6.95 ±2.65	2.82 ±1.36	5.98 ±1.96
Rn	W m^{-2}	559 ±38	543 ±27	464 ±66
LE	W m^{-2}	−752 ±217	−768 ±219	−507 ±98
[CO_2]**	ppm	322 ±2.4	300 ±7.7	311 ±4.0
T**	°C	26.1 ±4.0	27.9 ±3.1	29.4 ±2.0
u_*	m s^{-1}	0.45 ±0.23	0.39 ±0.16	0.34 ±0.12
Ψ	bar	−9.9 ±3.4	−11.8 ±3.2	—
n	—	16	22	31

*Data for the following days were used in averaging: Study 78-1, June 2, 10, 13, 19; Study 78-2, July 17, 24, 25, 28, August 4, 5, 6; Study 78-3, August 16, 20, 21, 22, 24, September 1, 7, 8, 9.
** Measured at 1.00 m.

to height ratio existed (Table I). Net radiation and latent heat flux were unchanged (variables were tested for differences on the 5% level of significance) during the first two studies but were significantly reduced during the third study. The average midday CO_2 concentration was greatest during study 78-1, reached a minimum during study 78-2 and increased during study 78-3. There was no significant change in temperature and friction velocity throughout the summer. Plant water potential increased significantly between the first and second studies. No data on plant water potential were available for the third study.

B. CO_2 flux

CO_2 flux of alfalfa (on a leaf area basis) showed a significant seasonal variation. CO_2 fluxes were great during the late spring and late summer and showed a minimum during midsummer. Delaney et al. (1974) observed a similar pattern for alfalfa. We observed no significant differences, however, between late spring and late summer CO_2 fluxes (studies 78-1 and 78-3). Furthermore, the magnitudes of alfalfa CO_2 flux agreed with reported values in the literature (see Brown et al., 1972, for a review).

The high values of CO_2 flux during study 78-1 may stem from a number of causes. Irradiance exceeded the light saturation point [between 384 and 558 W m^{-2} for alfalfa (Thomas and Hill, 1949)]. Temperature, turbulent mixing, [CO_2] and plant water potential were also not rate limiting. High values of alfalfa CO_2 flux during study 78-1 may also be attributed to the spring growth flush noted by Brown et al. (1972) and Delaney et al. (1974).

The midsummer CO_2 flux minimum may have been due to a combination of physiological and environmental factors. Net radiation, temperature and turbulent mixing (represented by u_*) were not, however, significantly changed during the first two studies. These then were probably not the factors that limited CO_2 flux. The reduction in $[CO_2]$ may have had a two-fold effect on CO_2 flux. A reduction in the ambient $[CO_2]$ causes a reduction in the CO_2 concentration gradient from the atmosphere to the cell chloroplast. This would lead to a reduction in F_c since flux is proportional to the concentration gradient. The reduction in CO_2 may also have affected the oxygen inhibition of CO_2 uptake. Ehleringer and Bjorkman (1977) showed that a decrease from 400 to 300 ppm in the intercellular $[CO_2]$ of a C_3 species causes an increase in the oxygen inhibition of CO_2 uptake and a reduction in quantum yield. Delaney et al. (1974) previously suggested that photorespiration may have been responsible for the midsummer reduction in photosynthesis and yield observed in alfalfa grown in Arizona, although they presented no direct evidence of this effect.

A decrease in plant water potential occurred during the second study. However, the observed change in Ψ did not increase stomatal resistance to a degree that would limit CO_2 flux (see Baldocchi et al., 1981b).

Thermal pre-conditioning can reduce photosynthetic rates (Ku and Hunt, 1977). This effect may have reduced F_c since air temperature exceeded 37°C on four days during study 78-2. These high temperatures may have damaged the photosynthetic machinery of the crop to such a degree that photosynthesis was suppressed for the remainder of the second study.

CO_2 fluxes recovered during the third study probably because environmental and physiological variables were not rate limiting.

The period of minimum F_c corresponded with the period of minimum $[CO_2]$ (Fig. 1). Verma and Rosenberg (1976, 1981), however, have reported that the period of maximum F_c, at a multi-cropped location in the east central Great Plains, corresponded with the period of minimum $[CO_2]$. The relationship between F_c and ambient CO_2 concentration is different for alfalfa from that for the large agricultural region discussed by Verma and Rosenberg (1976, 1981), since alfalfa, a perennial crop, is established and photosynthesizing actively in the spring before most other crops of the region (e.g. corn, sorghum and soybeans) are even planted. CO_2 concentration is high in the spring since biomass has decayed and released CO_2 over the winter.

C. CO_2—water flux ratio

The midday CO_2—water flux ratio (*CWFR*) also showed a significant seasonal variation: a maximum during late spring, a minimum during midsummer and an upswing during late summer. *CWFR* values in Table I are

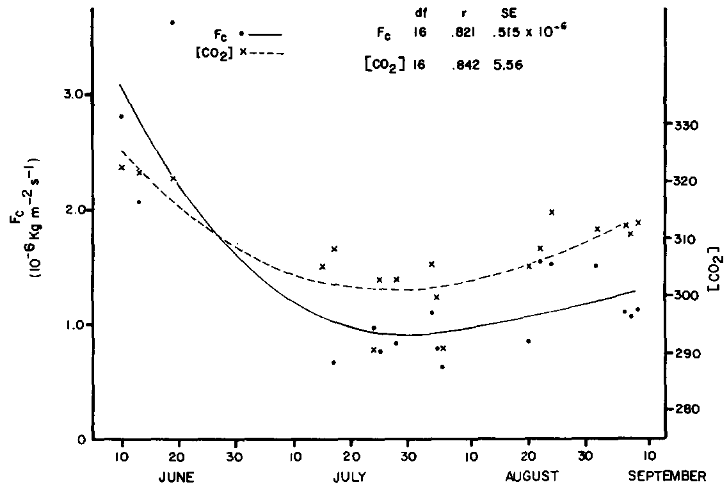

Fig. 1. Seasonal variation in canopy CO_2 flux (F_c) and $[CO_2]$ at 1.0 m over alfalfa at Mead, Nebraska. Data were fitted with a second-order polynomial regression.

higher than other reports of water use efficiency (*WUE*). Briggs and Shantz (1914) found alfalfa *WUE* to range from 0.97 to 2.38 g dry matter (kg $H_2O)^{-1}$. *CWFR* is higher than *WUE* since some of the photosynthate is consumed by nocturnal respiration and some is translocated to the roots; therefore, not all of the photosynthate is harvestable as dry matter (Hunt et al., 1970).

D. Growth

The seasonal variation in leaf area index and dry matter accumulation are shown in Figs. 2 and 3, respectively. *LAI* (Fig. 2) exceeded 4 at maturity during the first two studies. During study 78/3, however, *LAI* did not exceed 2.5. Dry matter accumulation (Fig. 3) exceeded 0.40 kg m^{-2} during each of the first two studies but did not exceed 0.30 kg m^{-2} during the third study. *LAI* and dry matter accumulation were reduced during the third study, probably because a large portion of assimilated carbon was translocated to the roots during this period. The work of Hunt et al. (1970) found, for example, that root growth was 6 and 9% of top growth during the first two cuttings of an alfalfa crop. During the third cutting root growth increased to 35% of top growth.

Although total accumulated dry matter was similar for the first two studies, Fig. 3 shows that between 15 and 40 days after cutting the first crop accumulated dry matter at a faster rate than did the second crop (1.41×10^{-2} vs. 1.15×10^{-2} kg m^{-2} day $^{-1}$).

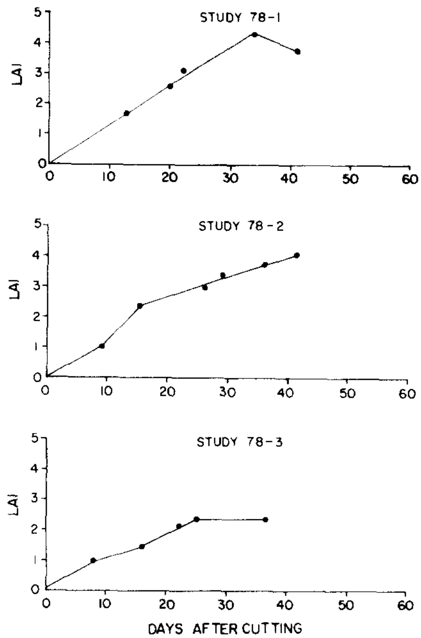

Fig. 2. Leaf area index (*LAI*) as a function of days after cutting. Data were fitted by eye.

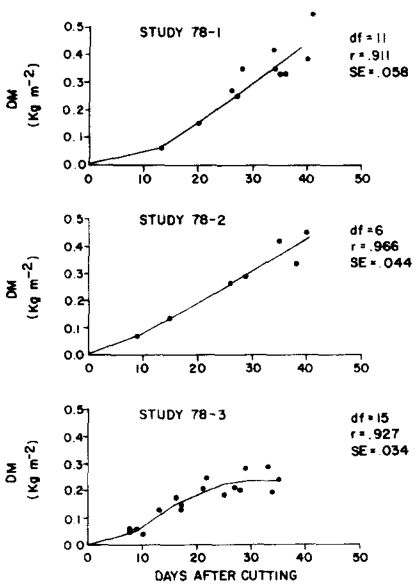

Fig. 3. Change in dry matter accumulation (*DM*) with time after cutting. Data were fitted with a second-order polynomial regression.

Diurnal effects

A. CO_2 flux

Figure 4 shows the diurnal course of F_c on a clear day: a rapid increase after sunrise, reaching a plateau about mid-morning and then a decrease during the afternoon. The diurnal course for F_c was similar to that of Rn.

Brown et al. (1972) indicate that the diurnal course of alfalfa photosynthesis can be affected by a rapid accumulation of starch in the leaves during the morning. In Fig. 5 the reduction in F_c between 0845 and 0945 may have been due, partly, to a rapid accumulation of starch causing a reduction in photosynthesis. During this period there was a 38% reduction in F_c even though irradiance had increased. The diurnal course shown in Fig. 5 was more typical of the second than the first and third studies.

The diurnal interaction between F_c and physiological environmental variables is shown for August 5 in Fig. 6. Both Rn and LE increased during the morning. Midday fluctuations in Rn and LE were due to cumulus clouds reducing available solar energy. Sensible heat flux was directed from the surface throughout the day. Therefore, H did not enhance LE, as would be the case during sensible heat advection. Stomatal resistance (r_s) and plant water potential (Ψ) both increased in magnitude until about 1400 h and then remained relatively constant thereafter. The increases in r_s between 1000 and 1300h seemed not to reduce F_c, however. Results indicate that the changes in r_s may not have been significant in comparison to other factors which controlled photosynthesis. The reduction in F_c between 0900 and 1000 h was probably due to an accumulation of starch in the leaves, for a reduction in F_c occurred even though irradiance increased.

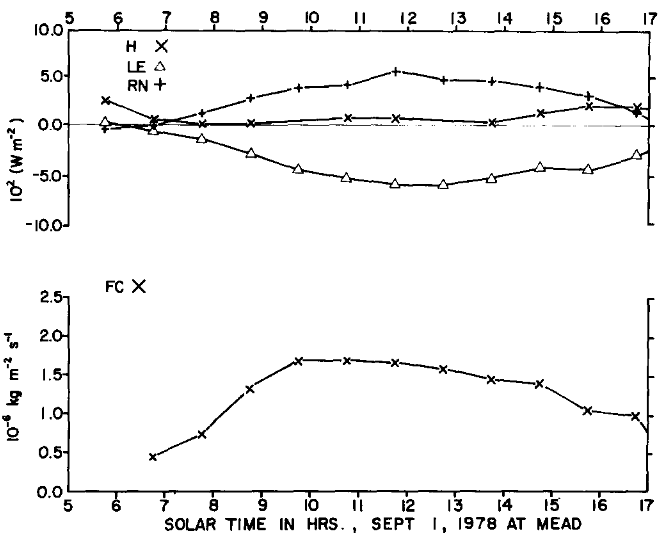

Fig. 4. The diurnal course of canopy CO_2 flux, sensible and latent heat fluxes and net radiation on September 1, 1978 over alfalfa at Mead, Nebraska.

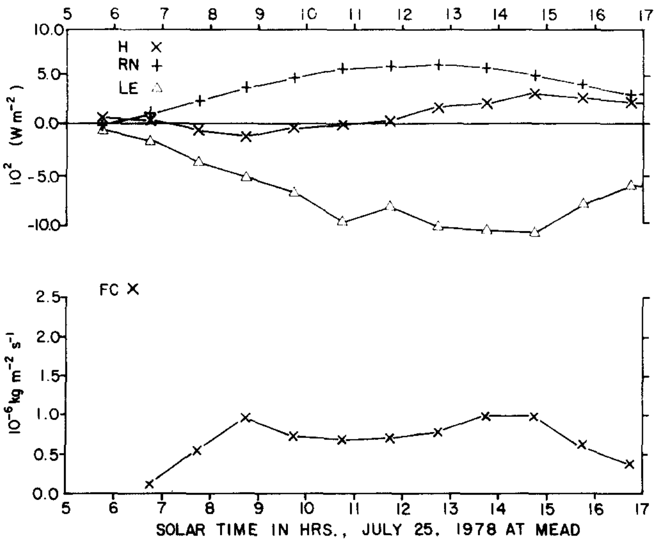

Fig. 5. Same as Fig. 4, except for July 25, 1978.

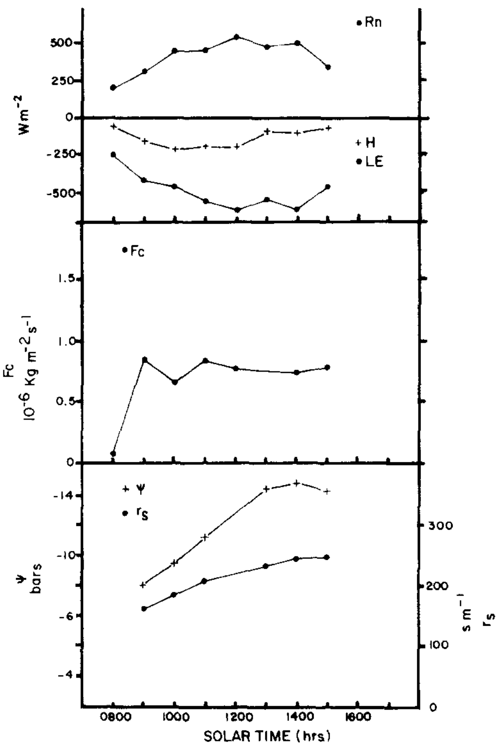

Fig. 6. The diurnal course of canopy CO_2 flux, plant water potential (Ψ), stomatal resistance (r_s), net radiation (Rn), sensible (H) and latent (LE) heat fluxes on August 5, 1978.

B. CO_2—water flux ratio

The diurnal course of *CWFR* was affected mainly by net radiation and sensible heat advection. The diurnal course of *CWFR* is plotted in Fig. 7 for two cases — a day with sensible heat advection (July 25) and a day without (August 5). The maximum *CWFR* value, for both cases, was achieved at about 0900 h. CO_2 flux then is maximal since irradiance is near the light saturation level. Evapotranspiration, on the other hand, reaches its maximal value sometime after solar noon.

After the morning maximum, the diurnal course of *CWFR* depended on the occurrence of sensible heat advection. For the "non-advective" day (August 5), *CWFR* decreased from the morning maximum to a minimum at midday and then recovered in the afternoon as irradiance and latent heat flux were reduced. For the "advective" case (July 25) *CWFR* decreased rapidly from its morning maximum to a minimum at midday. *CWFR* then remained near the minimum value for the remainder of the day. *CWFR* did not recover in the afternoon of the "advective" day since sensible heat advection contributed to the maintenance of a strong latent heat flux.

Figure 7 also shows that the occurrence of sensible heat advection causes a lower absolute *CWFR* value. At 1445 h, for example, *CWFR* was 3.98 g CO_2 (kg H_2O)$^{-1}$ on August 5 and 2.22 g CO_2 (kg H_2O)$^{-1}$ on July 25. Net radiation and stage of growth were similar during these two periods. Sensible heat flux, however, was -63 W m^{-2} on August 5 and 300 W m^{-2} on July 25 at 1445 h.

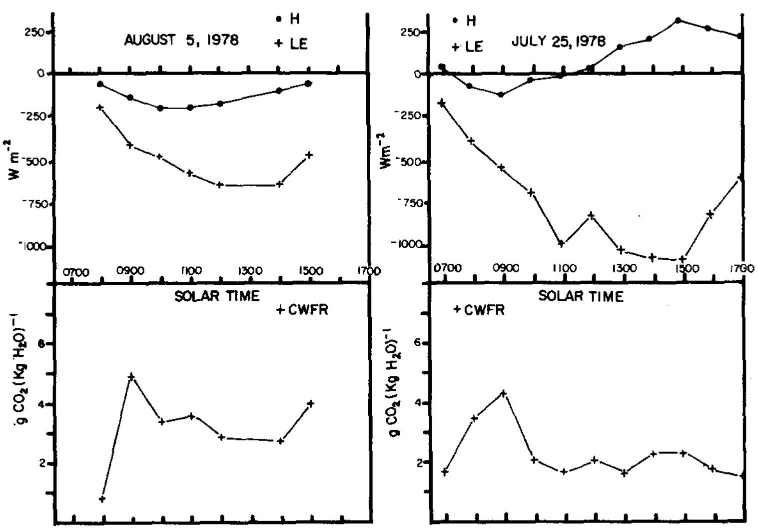

Fig. 7. The diurnal course of CO_2—water flux ratio (*CWFR*) for a "non-advective case" (August 5, 1978) and an "advective" case (July 25, 1978).

SUMMARY AND CONCLUSIONS

Significant seasonal variation was found in both CO_2 flux (F_c) and CO_2-water flux ratio (*CWFR*) of alfalfa grown in an east central Great Plains location. Large values of F_c and *CWFR* occurred during late spring. Values then decreased and reached a minimum during midsummer. With the approach of fall, both F_c and *CWFR* recovered.

F_c was large during late spring as a result of optimal environmental conditions and the spring growth flush. The midsummer reduction in F_c may have been due to a combination of various factors — a low ambient [CO_2] reducing the gradient between the ambient air and chloroplast and affecting the oxygen inhibition of CO_2 uptake and a thermal pre-conditioning adversely affecting the photosynthetic machinery of the crop. A possible accumulation of starch in the leaves may also have limited F_c during the second study, since a midmorning reduction in F_c occurred constantly during this period.

The diurnal course of F_c was directly linked to net radiation although a mid-morning depression in F_c may have been caused by an accumulation of starch in the leaves.

The diurnal variation of *CWFR* was determined by the regimes of net radiation and sensible heat advection. In the absence of sensible heat advection *CWFR* decreased from a morning maximum to a minimum at midday. *CWFR* then recovered as the afternoon progressed and irradiance and latent heat flux diminished. When sensible heat advection was significant, *CWFR* decreased rapidly from its morning maximum value and remained low throughout the day. Sensible heat advection was also shown to cause a significant reduction in the absolute value of *CWFR*.

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