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ENVIRONMENTAL EFFECTS ON THE CO_2 FLUX AND CO_2—WATER FLUX RATIO OF ALFALFA*

DENNIS D. BALDOCCHI, SHASHI B. VERMA and NORMAN J. ROSENBERG

Center for Agricultural Meteorology and Climatology, Institute of Agriculture and Natural Resources, University of Nebraska, Lincoln, NE 68583 (U.S.A.)

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ABSTRACT

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Environmental effects on the CO_2 flux (F_c) and CO_2—water flux ratio (*CWFR*) of alfalfa (*Medicago sativa* L.) were studied using micrometeorological techniques. The study was conducted in the east central Great Plains of North America. F_c was dependent on solar radiation, turbulent mixing and air temperature. The response of F_c to increasing irradiance was described by a diminishing returns curve. Increasing turbulent mixing caused a reduction in the boundary-layer resistance to CO_2 transfer and increased light penetration into the canopy; both factors caused F_c to increase. Under high irradiance, F_c decreased with increasing air temperature in the range 23—32°C. This effect was due to both soil plus root and dark respiration increasing with air temperature. F_c was not limited by plant water potentials ranging between −7 and −17 bar. That alfalfa is relatively drought-tolerant is indicated by the fact that no significant stomatal closure seemed to have occurred at water potentials as low as −17 bars. *CWFR* was correlated with net radiation. Sensible heat advection, however, reduced *CWFR* since this additional source of energy contributed only to evapotranspiration.

INTRODUCTION

There is a continuing need for field tests of laboratory-developed relations between plant response and environmental conditions. This need arises since the field environment is non-steady and complex.

Micrometeorological methods have been used, in recent years, to study the CO_2 exchange and transpiration rates in field grown crops. The advantages of using micrometeorological methods to measure the exchanges of CO_2 and water vapor in the field are numerous. Measurements of CO_2 and water vapor exchange can be obtained on a continuous basis with minimal disturbance to the crop. In addition, sensors can be arranged in the field so as to obtain spatial averages. Monteith and Szeicz (1960), Saugier (1970), Brown and Rosenberg (1971) and Biscoe et al. (1975) are among the researchers who have used micrometeorological methods to measure the CO_2 and water vapor exchange between a crop canopy and the atmosphere.

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In this paper we attempt to examine the effects of environmental variables on the CO_2 and water vapor exchanges of field-grown alfalfa. Fluxes of CO_2 and water vapor were measured by means of micrometeorological methods. Environmental variables studied included net radiation, turbulent mixing and air temperature. Plant water potential was the physiological factor observed.

MATERIALS AND METHODS

The studies described below were conducted during the summer of 1978 at the University of Nebraska Agricultural Meteorology facility 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 site and instrumentation are described in detail by Baldocchi (1979) and Baldocchi et al. (1981).

Three separate studies were conducted on the crop stand 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; and Study 78-3, August 8—September 16.

CO_2 flux (F_c) was computed using flux-gradient theory. For this computation the gradient of CO_2 concentration was measured by means of infrared gas analysis (see Rosenberg and Verma, 1967; Baldocchi et al., 1981). F_c was corrected for density effects caused by the simultaneous flux of water vapor. F_c was also corrected for the effects of changes in pressure and air temperature that occurred between the field, where air was sampled, and the laboratory, where the air was analyzed for $[CO_2]$. F_c was computed using

$$F_c = (P/P_I)(T_I/T)\left[K_c \frac{\partial \bar{\rho}_c}{\partial z} + (\mu\, \bar{\rho}_c/\bar{\rho}_a)(1 + \mu\sigma)^{-1} E\right] \quad (1)$$

(see Webb et al., 1980) where P and T are the ambient pressure and temperature, respectively, P_I and T_I are the pressure and temperature of the air sample within the gas analyzer, K_c is the eddy exchange coefficient for CO_2 transfer, $\partial\bar{\rho}_c/\partial z$ is the mean vertical gradient of CO_2 density, μ is the ratio of the molecular masses of dry air and water vapor, $\bar{\rho}_c$ is the mean CO_2 density, $\bar{\rho}_a$ is the mean density of dry air, σ is the ratio of the densities of water vapor and dry air, and E is the mass flux of water vapor. K_c was assumed to be identical to K_w, the eddy exchange coefficient for water vapor. K_c was computed as

$$K_c = \frac{E}{(\bar{\rho}_a/P\mu)(\partial\bar{e}/\partial z)} \quad (2)$$

where $\partial\bar{e}/\partial z$ is the mean vertical gradient of the mean vapor pressure. E was measured directly with a precision weighing lysimeter (Rosenberg and Brown, 1970).

Water use efficiency is described in terms of an index, the CO_2—water flux ratio (*CWFR*), defined as

$$CWFR = F_c / E \qquad (3)$$

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

The water relations of the crop were monitored by measurements of plant water potential and stomatal resistance. Further details of the measurement methods are given in Baldocchi et al. (1981).

Apparent photosynthesis (AP) is defined as

$$AP = F_c + R_{s+r} \qquad (4)$$

where R_{s+r} is soil plus root respiration. Gross photosynthesis (gPs) is defined as

$$gPs = F_c + Rd + R_{s+r} \qquad (5)$$

where Rd is dark respiration. R_{s+r} and Rd are computed as functions of air temperature (T) using

$$R(T) = R_0 Q_{10}^{[(T-T_0)/10]} \qquad (6)$$

where R_0 is the respiration rate at a reference temperature ($T_0 = 20°C$) and Q_{10} is the increase in temperature. Values of R_0 and Q_{10} for R_{s+r} and Rd are listed in Table I.

TABLE I

Reference respiration rates (R_0) at 20°C and Q_{10} for dark respiration (Rd) and soil + root respiration (R_{s+r}). Values of R_0 and Q_{10} are from Baldocchi (1979)

	Respiration	
	Dark	Soil + root
R_0 (mg m^{-2} leaf area s^{-1})	0.53	0.12
Q_{10}	1.44	3.16

RESULTS AND DISCUSSION

Environmental effects on CO_2 flux

Net radiation

Net radiation (Rn) at the crop surface is partitioned into heating the air, soil and crop canopy, evaporating water and driving photosynthesis. Photosynthesis, however, is driven only by solar irradiation in the 0.4—0.7 μm portion of the electromagnetic spectrum — the photosynthetically active radiation (PAR).

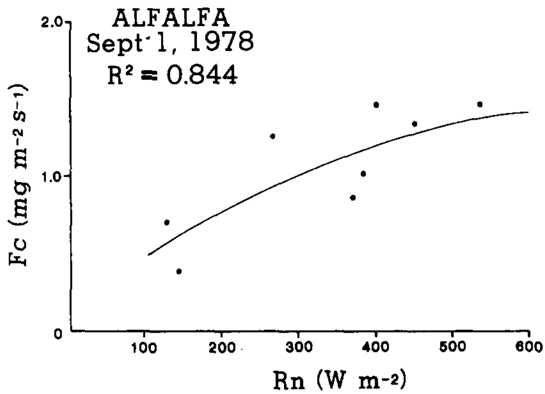

Fig. 1. Canopy CO_2 flux (F_c) of alfalfa as a function of net radiation (Rn) on September 1, 1978. The canopy leaf area index was 2.4. Data were fitted with a second-order polynomial.

The response of F_c to Rn, in field-grown alfalfa, is shown for a typical clear day in Fig. 1. The functional relationship between F_c and Rn is similar to that for photosynthesis and PAR. F_c responded strongly to increasing Rn under low levels of Rn. For high levels of Rn, however, F_c was not strongly dependent since the canopy was light-saturated. Light saturation occurred at about 400 W m^{-2}, which is within the range of values observed by Thomas and Hill (1949) for alfalfa. The magnitude of F_c at light saturation (1.35 mg m^{-2} s^{-1}) agrees well with Saugier's (1970) value (1.50 mg m^{-2} s^{-1}) for midday F_c in field-grown alfalfa. A review by Brown et al. (1972) indicated maximum stand photosynthesis in alfalfa, under high irradiance, between 1.6 and 2.5 mg m^{-2} s^{-1}.

Turbulent mixing

The literature is generally inconclusive on the question of whether CO_2 flux is affected by turbulent mixing. Lemon (1960) and Wright and Lemon (1966) were among the first to report a positive correlation between CO_2 flux and wind speed. Lemon (1960), Yabuki et al. (1974) and Uchijima (1976) contend that photosynthesis is limited on sunny days when wind speeds are low since a suppression of turbulence limits the supply of CO_2 to the crop. Yabuki and Miyagawa (1970) reported an increase in gross photosynthesis with increasing wind speed to about 0.60 m s^{-1}. With greater windspeeds, gross photosynthesis decreased. Denmead (1966) also found a positive correlation between wind speed and CO_2 flux. He hypothesized that increases in windspeed reduce the resistance to CO_2 diffusion. Denmead pointed out, however, that his observations may have been influenced by autocorrelation since CO_2 fluxes were computed by means of the aerodynamic method. More recently, Denmead (1976) stated that wind speed has negligible effects on the photosynthetic rate in temperate cereals. Brown and Rosenberg (1971) computed CO_2 flux in a field of sugar beets by a

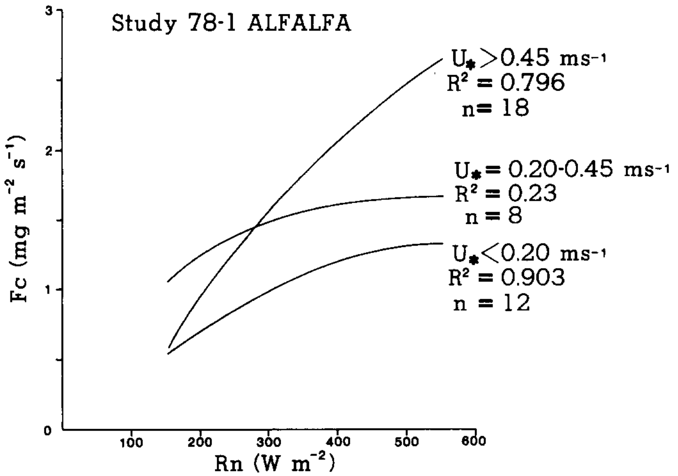

Fig. 2. Canopy CO_2 flux (F_c) as a joint function of net radiation (Rn) and turbulent mixing (U_*). Data were fitted with second-order polynomials for different regimes of turbulent mixing.

method independent of wind speed (the energy balance method). They found no relationship between CO_2 flux and wind speed. Monteith et al. (1964) concluded that, under most atmospheric conditions, turbulent mixing is vigorous enough to maintain a high CO_2 concentration ($[CO_2]$) near the leaf. The assimilation of CO_2 is, thus, dictated by irradiance, by the amount and distribution of foliage and by the crop's photosynthetic efficiency.

The data presented here suggest a relationship between turbulent mixing and CO_2 flux in an alfalfa field (Fig. 2). Autocorrelation is not a factor here since wind speed data were not used in the computation of F_c. Figure 2 shows the relationship between F_c and Rn for various regimes of turbulent mixing: $U_* < 0.20\ \mathrm{m\,s^{-1}}$, $0.20 < U_* < 0.45\ \mathrm{m\,s^{-1}}$ and $U_* > 0.45\ \mathrm{m\,s^{-1}}$. [When U_* was less than $0.20\ \mathrm{m\,s^{-1}}$, wind speed at 1.0 m was less than about $2\ \mathrm{m\,s^{-1}}$. When U_* was greater than $0.45\ \mathrm{m\,s^{-1}}$, wind speed at 1.00 m exceeded $3.2\ \mathrm{m\,s^{-1}}$.] Under low levels of Rn (less than about $300\ \mathrm{W\,m^{-2}}$) the turbulent mixing regime had no distinct effect on F_c. Under high levels of Rn, however, F_c increased with increasing turbulent mixing. There are two reasons for this effect. First, increasing wind speed reduces the boundary-layer resistance to CO_2 transfer, and thus enhances CO_2 flux. Second, higher wind speeds and wind gusts cause leaf flutter and temporary gaps in the canopy. This permits greater penetration of radiation into the canopy. Since leaves low in the canopy are usually light-saturated, increased light penetration should increase their rate of photosynthesis. The net result is an increase in canopy CO_2 flux.

Temperature

F_c is dependent on air temperature (T) under high levels of radiation ($Rn > 400\ \mathrm{W\,m^{-2}}$). Figure 3 shows that F_c decreased with increasing T in

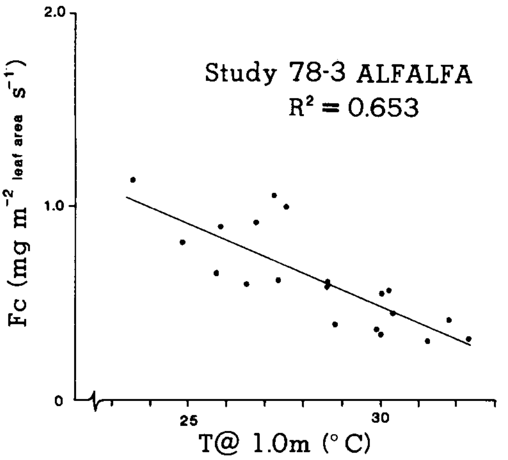

Fig. 3. Canopy CO_2 flux (F_c) during study 78-3 as a function of air temperature at 1.0 m. Data were selected from periods when net radiation exceeded 400 W m^{-2}.

the range 23 to 32°C. As the following calculations will show, such an effect can be due to the influence of temperature on soil plus root respiration (R_{s+r}) and dark respiration (Rd).

The large reduction in F_c with increasing T does not imply that apparent photosynthesis (AP) is inhibited to the same degree. Equation 4 indicates that both the atmosphere and rhizosphere are sources of CO_2 for AP. Therefore, the increase in R_{s+r} with temperature sustains appreciable rates of AP under a wider range of temperature.

The results in Fig. 3 are evaluated using calculations in Table II. Table II lists the values of F_c, Rd, R_{s+r}, AP and gPs at 25 and 30°C. The value of F_c at 25°C was obtained from Fig. 3. Rd and R_{s+r} were computed at 25 and 30°C using eq. 6; AP at 25°C was computed using eq. 4; and gPs at 25°C was computed using eq. 5.

In order to compute F_c and AP at 30°C, we assumed that gPs was constant in the temperature range 25 to 30°C. Thomas and Hill (1949) reported alfalfa photosynthesis to be virtually unaffected by temperature in the range

TABLE II

Effect of temperature on CO_2 flux (F_c), rate of dark respiration (Rd), rate of soil + root respiration (R_{s+r}), apparent photosynthesis (AP) and gross photosynthesis (gPs)

T (°C)	25	30
F_c (mg m^{-2} leaf area s^{-1})	0.90	0.61
Rd (mg m^{-2} leaf area s^{-1})	0.64	0.76
R_{s+r} (mg m^{-2} leaf area s^{-1})	0.21	0.38
AP (mg m^{-2} leaf area s^{-1})	1.11	0.99
gPs (mg m^{-2} leaf area s^{-1})	1.75	1.75

15—30°C. Based on this assumption, F_c at 30°C was computed using eq. 5. *AP* at 30°C was computed using eq. 4. The computed value of F_c at 30°C was 0.61 mg m^{-2} leaf area s^{-1} (Table II). This value agrees very well with the mean value of F_c at 30°C in Fig. 3.

As the Table and Figure show, F_c decreased by about 32% with a temperature increase from 25 to 30°C. *AP*, on the other hand, decreased by only about 11%.

These results should not be extrapolated to temperatures greater than 32°C. Delaney et al. (1974) and Pearson and Hunt (1972) reported that such elevated temperatures result in reductions in gross alfalfa photosynthesis.

Physiological effects on CO_2 flux

Plant water potential

Changes in plant water potential (Ψ) can affect CO_2 flux by inducing stomatal closure and by reducing chloroplast activity (Boyer, 1976). Stomatal conductance is reduced significantly only after Ψ decreases below a threshold level. The threshold water potential for stomatal closure varies among crops, but usually occurs between −8 and −20 bar (see Hsiao and Acevedo, 1974; Turner, 1974).

The dependence of alfalfa CO_2 flux and Ψ in periods of high irradiance ($Rn > 400$ W m^{-2}) is illustrated in Fig. 4. F_c was not inhibited by water potentials between −7 and −17 bar. Apparently, water stress represented by Ψ values as low as −17 bar was not sufficiently severe to induce stomatal closure and limit CO_2 flux.

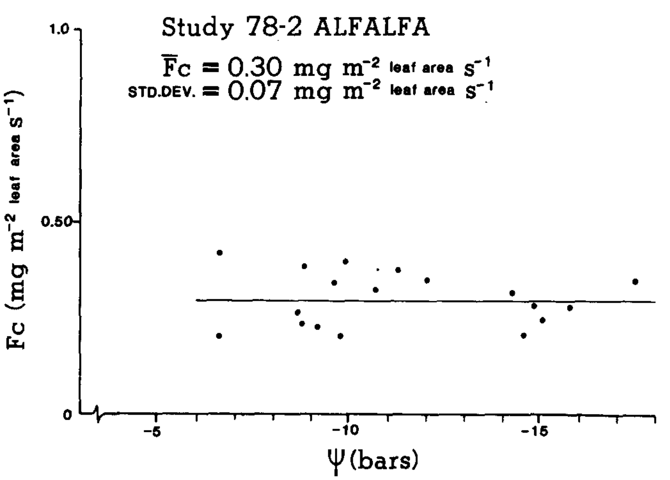

Fig. 4. Canopy CO_2 flux (F_c) during study 78-2 as a function of plant water potential (Ψ). These data were selected from periods when net radiation exceeded 400 W m^{-2}.

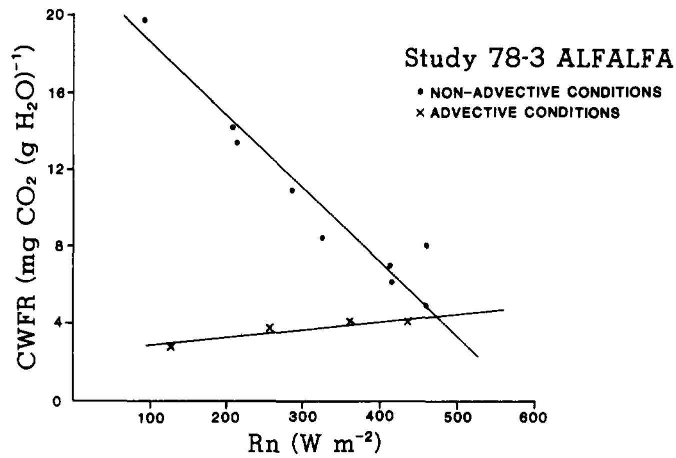

Fig. 5. CO_2 water flux ratio (*CWFR*) during study 78-3 as a function of net radiation (*Rn*) in non-advective (dots) and advective (crosses) conditions. Data were obtained during study 78-3.

CO_2—water flux ratio

Net radiation and sensible heat advection are the environmental factors that most greatly affect *CWFR*. *Rn* supplies energy which is used in the evaporative and photosynthetic processes, while sensible heat advection supplies additional energy that contributes only to evapotranspiration. [Under conditions of sensible heat advection, sensible heat flux is directed towards the crop since daytime temperature inversions prevail. For a detailed discussion of sensible heat advection, see Brakke et al. (1978) and Rosenberg and Verma (1978).]

Figure 5 shows the relationship between *CWFR* and *Rn* under non-advective and advective conditions. Under non-advective conditions, *CWFR* decreased linearly with increasing *Rn*. Under conditions of sensible heat advection, *CWFR* was relatively constant with increasing *Rn*. When irradiance was strong, *CWFR* was similar under advective and non-advective conditions. However, when irradiance was weak *CWFR* was much lower under advective than under non-advective conditions. Humid and cloudy conditions are, therefore, best for water use efficiency in alfalfa.

SUMMARY AND CONCLUSIONS

The CO_2 flux and CO_2—water flux ratio of alfalfa are related to a number of environmental variables. CO_2 flux (F_c) was controlled mainly by solar radiation, turbulent mixing and air temperature. The response of F_c to increasing net radiation was described by a "diminishing returns" curve.

Increasing turbulent mixing caused an increase in F_c by reducing the boundary-layer resistance to CO_2 transfer. Turbulent mixing also opened the canopy and allowed radiation to penetrate deeper into it. Since leaves low in the canopy are light-unsaturated, the increase in light penetration caused an increase in canopy CO_2 flux.

Under high irradiance, F_c decreased with increasing air temperature in the range 23—32°C. This effect was due to both soil-plus-root and dark respiration increasing with air temperature. Photorespiration may have also limited F_c. More research is needed, however, to investigate the degree to which photorespiration affects CO_2 exchange of alfalfa in the 23—32°C temperature range.

Alfalfa was rather tolerant of water stress since plant water potentials as low as −17 bar had no significant affect on F_c. CO_2—water flux ratio (*CWFR*) was dependent on net radiation and sensible heat advection. Under non-advective conditions, *CWFR* decreased with decreasing *Rn*. On the other hand, *CWFR* was relatively constant over a wide range of *Rn* when sensible heat advection prevailed.

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