ENVIRONMENTAL EFFECTS ON THE CO₂ FLUX AND CO₂—WATER FLUX RATIO OF ALFALFA*

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(Received May 20, 1980; revision accepted March 3, 1981)

ABSTRACT


Environmental effects on the CO₂ flux ($F_c$) and CO₂—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 CO₂ 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 CO₂ exchange and transpiration rates in field grown crops. The advantages of using micrometeorological methods to measure the exchanges of CO₂ and water vapor in the field are numerous. Measurements of CO₂ 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 CO₂ and water vapor exchange between a crop canopy and the atmosphere.

* Paper No. 5999, Journal Series, Nebraska Agricultural Experiment Station. The work reported was conducted under Regional Research Project 11-33 and Nebraska Agricultural Experiment Station Project 11-49.
In this paper we attempt to examine the effects of environmental variables on the CO₂ and water vapor exchanges of field-grown alfalfa. Fluxes of CO₂ 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.

CO₂ flux \( (F_c) \) was computed using flux-gradient theory. For this computation the gradient of CO₂ 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 [CO₂]. \( F_c \) was computed using

\[
F_c = \frac{P}{P_1} \frac{T_1}{T} \left[ K_c \frac{\partial \bar{\rho}_c}{\partial z} + \left( \mu \frac{\bar{\rho}_c}{\bar{\rho}_a} \right) (1 + \mu \sigma)^{-1} E \right] 
\]

(see Webb et al., 1980) where \( P \) and \( T \) are the ambient pressure and temperature, respectively, \( P_1 \) and \( T_1 \) are the pressure and temperature of the air sample within the gas analyzer, \( K_c \) is the eddy exchange coefficient for CO₂ transfer, \( \partial \bar{\rho}_c / \partial z \) is the mean vertical gradient of CO₂ density, \( \mu \) is the ratio of the molecular masses of dry air and water vapor, \( \bar{\rho}_c \) is the mean CO₂ density, \( \bar{\rho}_a \) is the mean density of dry air, \( \sigma \) 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

\[
K_c = \frac{E}{(\bar{\rho}_a/P\mu)(\partial \bar{\sigma} / \partial z)} 
\]

where \( \partial \bar{\sigma} / \partial z \) 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 CO₂—water flux ratio (CWFR), defined as
\[ CWFR = \frac{F_c}{E} \]  

(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

\[ AP = F_c + R_{s+r} \]  

(4)

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

\[ gPs = F_c + Rd + R_{s+r} \]  

(5)

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

\[ R(T) = R_0 Q^{(T-T_0)/10} \]  

(6)

where \( R_0 \) is the respiration rate at a reference temperature \( (T_0 = 20^\circ C) \) 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\(^\circ\)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)

<table>
<thead>
<tr>
<th></th>
<th>Dark</th>
<th>Soil + root</th>
</tr>
</thead>
<tbody>
<tr>
<td>( R_0 ) (mg m(^{-2}) leaf area s(^{-1}))</td>
<td>0.53</td>
<td>0.12</td>
</tr>
<tr>
<td>( Q_{10} )</td>
<td>1.44</td>
<td>3.16</td>
</tr>
</tbody>
</table>

**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 \( \mu \)m 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 ($R_n$) 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 $R_n$, in field-grown alfalfa, is shown for a typical clear day in Fig. 1. The functional relationship between $F_c$ and $R_n$ is similar to that for photosynthesis and PAR. $F_c$ responded strongly to increasing $R_n$ under low levels of $R_n$. For high levels of $R_n$, 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 wind speeds, 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
method independent of wind speed (the energy balance method). They found no relationship between CO₂ flux and wind speed. Monteith et al. (1964) concluded that, under most atmospheric conditions, turbulent mixing is vigorous enough to maintain a high CO₂ concentration ([CO₂]) near the leaf. The assimilation of CO₂ 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 CO₂ flux in an alfalfa field (Fig. 2). Autocorrelation is not a factor here since wind speed data were not used in the computation of Fₖ. Figure 2 shows the relationship between Fₖ and Rₙ for various regimes of turbulent mixing: \( U_* < 0.20 \text{ m s}^{-1} \), \( 0.20 < U_* < 0.45 \text{ m s}^{-1} \) and \( U_* > 0.45 \text{ m s}^{-1} \). [When \( U_* \) was less than \( 0.20 \text{ m s}^{-1} \), wind speed at 1.0 m was less than about 2 m s⁻¹. When \( U_* \) was greater than \( 0.45 \text{ m s}^{-1} \), wind speed at 1.00 m exceeded 3.2 m s⁻¹.] Under low levels of \( Rₙ \) (less than about 300 W m⁻²) the turbulent mixing regime had no distinct effect on \( Fₖ \). Under high levels of \( Rₙ \), however, \( Fₖ \) increased with increasing turbulent mixing. There are two reasons for this effect. First, increasing wind speed reduces the boundary-layer resistance to CO₂ transfer, and thus enhances CO₂ 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 CO₂ flux.

Temperature

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

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 $F_c$, $R_d$, $R_{s+r}$, $AP$ and $gPs$ at 25 and 30°C. The value of $F_c$ at 25°C was obtained from Fig. 3. $R_d$ 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

<table>
<thead>
<tr>
<th>$T$ (°C)</th>
<th>25</th>
<th>30</th>
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</thead>
<tbody>
<tr>
<td>$F_c$ (mg m$^{-2}$ leaf area s$^{-1}$)</td>
<td>0.90</td>
<td>0.61</td>
</tr>
<tr>
<td>$R_d$ (mg m$^{-2}$ leaf area s$^{-1}$)</td>
<td>0.64</td>
<td>0.76</td>
</tr>
<tr>
<td>$R_{s+r}$ (mg m$^{-2}$ leaf area s$^{-1}$)</td>
<td>0.21</td>
<td>0.38</td>
</tr>
<tr>
<td>$AP$ (mg m$^{-2}$ leaf area s$^{-1}$)</td>
<td>1.11</td>
<td>0.99</td>
</tr>
<tr>
<td>$gPs$ (mg m$^{-2}$ leaf area s$^{-1}$)</td>
<td>1.75</td>
<td>1.75</td>
</tr>
</tbody>
</table>
$15-30^\circ\text{C}$. Based on this assumption, $F_c$ at 30$^\circ\text{C}$ was computed using eq. 5. AP at 30$^\circ\text{C}$ was computed using eq. 4. The computed value of $F_c$ at 30$^\circ\text{C}$ 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$^\circ\text{C}$ in Fig. 3.

As the Table and Figure show, $F_c$ decreased by about 32% with a temperature increase from 25 to 30$^\circ\text{C}$. AP, on the other hand, decreased by only about 11%.

These results should not be extrapolated to temperatures greater than 32$^\circ\text{C}$. 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 ($\Psi$) can affect CO$_2$ flux by inducing stomatal closure and by reducing chloroplast activity (Boyer, 1976). Stomatal conductance is reduced significantly only after $\Psi$ 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 $\Psi$ in periods of high irradiance ($R_n > 400$ 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 $\Psi$ values as low as $-17$ bar was not sufficiently severe to induce stomatal closure and limit CO$_2$ flux.

![Study 78-2 ALFALFA](image)

**Fig. 4.** Canopy CO$_2$ flux ($F_c$) during study 78-2 as a function of plant water potential ($\Psi$). These data were selected from periods when net radiation exceeded 400 W m$^{-2}$.
CO₂—water flux ratio

Net radiation and sensible heat advection are the environmental factors that most greatly affect CWFR. \( R_n \) 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 \( R_n \) under non-advective and advective conditions. Under non-advective conditions, CWFR decreased linearly with increasing \( R_n \). Under conditions of sensible heat advection, CWFR was relatively constant with increasing \( R_n \). 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 CO₂ flux and CO₂—water flux ratio of alfalfa are related to a number of environmental variables. CO₂ 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 CO₂ 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 $R_n$. On the other hand, $CWFR$ was relatively constant over a wide range of $R_n$ when sensible heat advection prevailed.

ACKNOWLEDGEMENTS

This study was conducted with the support of the Atmospheric Research Section, National Science Foundation, under Grant ATM 77-27533. Mr. Dale E. Sandin, Manager, Agricultural Meteorology Laboratory, was responsible for maintenance of the CO$_2$ sampling and analysis system. Our thanks to Messrs. Thomas Keber and James Hines who assisted in the field observations and data computations, to Mrs. Roberta Sandhorst, Mrs. Nancy Brown and Mrs. Betty James for the stenographic work and to Drs. John Norman and Raymond Chollet for their critical reviews of this paper. Special thanks are due Mr. Thomas Harris of Air Resources Laboratory, NOAA, Boulder, Colorado, for calibrating our primary standard gases. Figures were prepared by Sheila Smith and Bruce Sandhorst.

REFERENCES


