Influence of Water Stress on the Diurnal Exchange of Mass and Energy between the Atmosphere and a Soybean Canopy


ABSTRACT

A micrometeorological-physiological study was conducted at Mead, Nebr., during the summer of 1980 to examine the diurnal exchanges of mass and energy of well-watered and water-stressed soybean (Glycine max (L.) Merr. cv. Harosoy) canopies and to relate these exchanges to environmental and physiological variables. Data are presented for 2 clear days when the canopy was fully-developed. Measurements of CO$_2$ latent heat and sensible heat flux were made using the Bowen-ratio energy balance technique. The soil of the area is a Sharpsburg silty clay loam (a fine, montmorillonitic, mesic Typic Argiudoll). Water stress greatly influenced the partitioning of available energy between latent and sensible heat flux. When the crop was well-watered, sensible heat (H) was directed toward the crop and caused latent heat exchange (LE) to exceed net radiation (Rn). When the crop was water stressed, only two-thirds of Rn was consumed as LE; the remainder was converted into sensible heat. Since both Rn and vapor pressure deficit were greater on the day when the crop was water-stressed, stomatal closure appears to have been the primary cause of the reduction in LE.

Carbon dioxide exchange was not sensitive to water stress in the morning but was severely limited by such stress during midday. The midday reduction in CO$_2$ exchange appears to have been caused by a combination of high stomatal resistance limiting CO$_2$ diffusion to the cell chloroplasts and low leaf water potential coupled with high air temperature affecting the enzymatic reactions associated with photosynthesis. Water use efficiency (defined in terms of the CO$_2$-water flux ratio) was greater when the crop was well-watered than when it was stressed for water. A combination of water stress, a large vapor pressure deficit, and high air temperature reduced the CO$_2$-water flux ratio.

Additional index words: Glycine max (L.) Merr., Micrometeorology, Water use efficiency, Photosynthesis, Evapotranspiration, Canopy CO$_2$ exchange, Environmental physiology.

ENVIRONMENTAL and physiological variables affect mass and energy exchanges between a crop canopy and the atmosphere in a mutualistic, synergistic, or antagonistic manner. Micrometeorological measurements, supported with physiological data, provide one of the best means of examining these complex processes. The advantage of using micrometeorological techniques is the ability they afford to measure spatially integrated exchange rates on a continuous basis, without influencing the local microclimate.

Over the past 20 years, most comprehensive micrometeorological-physiological studies have been performed over crops in a well-watered condition—corn, wheat, alfalfa, and sugar beets (e.g., Lemon, 1960; Monteith and Szeicz, 1960; Denmead, 1969; Saugier, 1970; Brown and Rosenberg, 1971; Baldocchi et al., 1981a, 1981b). Only a few such studies have been attempted with water-stressed crops (Begg et al., 1964; Biscoe et al., 1975). There have also been very few detailed studies of the mass and energy exchanges between the atmosphere and soybeans, an economically important crop. Bailey and Davies (1981) is an exception to this statement.

The objective of the study reported here is to examine the diurnal exchanges of mass and energy of well-watered and water-stressed soybean canopies. The influence of environmental and physiological variables on these exchanges are discussed in detail. Results are compared with findings derived from chamber studies on soybeans.

MATERIALS AND METHODS

Experimental Details

The study was conducted during the summer of 1980 at the Univ. of Nebraska Agricultural Meteorology Laboratory at Mead, Nebr. (41° 09' N; 96° 30' W; alt. 354 m above msl). Soybeans (Glycine max L. Merr. cv. Harosoy) were planted on 22 May 1980, in an experimental field (65 m E-W by 210 m N-S) in 0.75 m wide north-south rows. Border fields to the east, south, and west were also planted in Harosoy cv. soybeans. Data used in this study were selected from periods when the fetch to height ratio exceeded 75 to 1. Between 20 July and 10 August the canopy was erect but was water-stressed. A storm on 10 August relieved the water stress but caused lodging in the crop.

Air temperature and vapor pressure were measured over the field at 1.25, 1.50, 1.75, 2.25, 2.75, and 3.25 m with an automatic, self-checking, multilevel psychrometer (Rosenberg and Brown, 1974). Once each hour the psychrometer assembly rotated automatically into a horizontal position for calibration.

Air was sampled to determine CO$_2$ concentration with a multilevel manifold at 0.30, 0.50, 0.70, and 0.90 m within the crop.
canopy and at 1.25, 1.50, and 1.75 m above it. The manifold had six intakes at each level. These were spaced equidistantly over a horizontal distance of 2.5 m. Carbon dioxide concentration was measured with a system which employed an absolute and a differential infrared gas analyzer (see Rosenberg and Verma, 1976, for details). Once each hour both analyzers were calibrated automatically with standard gases of known concentration.

Wind speed above the crop was measured at 0.25 m intervals between 1.25 and 2.50 m with three-cup anemometers. The anemometers were calibrated in a wind tunnel before and after the growing season.

Photosynthetically active radiation (PAR) was measured above the canopy with a quantum sensor. Net radiation was measured with a net radiometer at 1.85 m above the ground. Soil heat flux was measured with three soil heat flux plates at a depth of 0.01 m in the soil.

All micrometeorological data were recorded on magnetic tape with a computer controlled data acquisition system. Cup anemometer data were recorded as integrated counts over 5 min. Carbon dioxide concentrations were measured and recorded once every 7½ min. Signals from all other voltage producing sensors were sampled about two times per minute. Data were later averaged for the first 45 min of each solar hour. The remaining 15 min of each hour were reserved for calibration of psychrometers and infrared gas analyzers.

Leaf water potential was measured hourly with a pressure chamber. Stomatal resistance (r_s) was measured on both sides of six randomly selected leaves with a steady state porometer. Stomatal resistance was computed by assuming that the resistances on the top and bottom sides of the leaf act in parallel.

Moisture in the upper 0.30 m layer of the soil was determined using a gravimetric technique. A neutron probe was used to measure soil moisture below this level. Soil water potential (Ψ_s) was computed with the aid of moisture release curves developed in the laboratory.

The data presented in this paper were obtained on 2 clear days: 24 July and 19 Aug. 1980. On 24 July, the crop height was 1.00 m and the leaf area index (LAI) was 3.0. On 19 August, crop height and LAI were 0.80 m and 3.1, respectively. According to the Fehr and Caviness (1977) classification scheme for soybean development, the crop was at stage V15, R4 on 24 July and at stage V19, R6 on 19 August.

**Theoretical Considerations**

Fluxes of CO₂ (F_c), latent heat (LE), and sensible heat (H) were computed as the product of the appropriate vertical gradient and turbulent exchange coefficient (K). The turbulent exchange coefficients for CO₂ (K_c), water vapor (K_w) and sensible heat (K_H) were assumed identical and were computed using the Bowen-ratio energy balance technique:

\[ K = K_c = K_w = K_H = \rho \left( R_n + S \right) \left( C_p \frac{\partial T}{\partial z} + \frac{\partial P}{\partial z} \right) + \lambda \frac{\partial \theta_c}{\partial z} \]  

where \( R_n \) is net radiation, \( S \) is soil heat flux, \( \rho \) is the density of moist air, \( C_p \) is the specific heat of moist air, \( P \) is air pressure, \( L \) is the latent heat of vaporization, \( \epsilon \) is the ratio of the molecular masses of water vapor and dry air (\( \epsilon = 0.622 \)) and \( \lambda \) is the energy equivalent of CO₂ fixation. \( \frac{\partial P_c}{\partial z} \) are the vertical gradients of air temperature, vapor pressure, and CO₂ density, respectively. We recognize that the assumption of \( K_w = K_H \) may not hold under daytime inversion conditions and that such an assumption may lead to the underestimation of latent heat flux (Blad and Rosenberg, 1974; Verma et al., 1978). The qualitative concepts presented in this paper are, however, unaffected by reliance on this assumption. In fact, calculated differences in latent heat flux between well-watered and water-stressed conditions would be even greater if corrections were made for the inequality in K.

Both CO₂ flux (F_c) and latent heat flux (LE) were corrected for the effect of water vapor exchange on the fluctuations in density of dry air (see Webb et al., 1980 for further details):

\[ F_c = \frac{(P/P_1) (T_1/T_k)}{K_c \left( \frac{\partial P_c}{\partial z} + \frac{\partial P}{\partial z} \right)} \left[ 1 + \frac{\sigma}{\epsilon} \right] E \]  

\[ LE = \left( 1 + \frac{\sigma}{\epsilon} \right) \left[ 1 + \frac{L}{C_P} \right] \rho \frac{E}{P} K_w \frac{\partial \theta_c}{\partial z} \]  

where T_1 and P_1 are the respective absolute air temperature and pressure inside the cells of the infrared gas analyzer, \( \sigma \) is the ratio of the densities of water vapor (\( \rho_w \)) and dry air (\( \rho_b \)), \( \beta \) is the uncorrected Bowen-ratio, T_k is absolute air temperature, E is vapor flux. All other variables have been previously defined.

**RESULTS AND DISCUSSION**

The diurnal course of various mass and energy exchanges are presented in this section for a day when the crop was under water stress (24 July) and for a day when

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1 Cayuga Development, Ithaca, NY, Model WP-1.
2 Lambda Instrument Co., Lincoln, NE, Model LI-190S.
3 Swisteco Pty. Ltd., Melbourne, Australia, Type S-1.
6 Lambda Instr. Co., Lincoln, NE, Model LI-1600.
7 Fluxes directed toward the surface are positive, while those directed from the surface are negative.

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Fig. 1. a) Diurnal variation of leaf water potential (Ψ) for a day on which the soybean crop was water-stressed (WS) (24 July) and for a day on which it was well watered (NS) (19 August).

b) Same as a) except for stomatal resistance (r_s).
the crop was well watered (19 August). The water status of the crop on these 2 days is depicted in Fig. 1a and 1b by the diurnal course of leaf water potential ($\Psi$) and stomatal resistance ($r_s$), respectively. On the water stressed (WS) day, $\Psi$ values as low as $-1.7$ MPa and $r_s$ values on the order of $200$ sec m$^{-1}$ were observed during the midday hours. On the non-stressed (NS) day, $\Psi$ values as low as only $-1.1$ MPa and $r_s$ values on the order of $60$ sec m$^{-1}$ were observed. Soil moisture conditions for 24 July and 19 August are presented in Table 1. These data show that soil moisture was considerably depleted in the zero to $0.60$ m layer on 24 July and that root extraction was not yet significant at lower depths at this time. By 19 August, soil moisture had been replenished.

a) Diurnal Course of Net Radiation, Latent and Sensible Heat Flux

Figure 2 shows the diurnal course of net radiation ($R_n$), latent heat flux ($LE$) and sensible heat flux ($H$) for both 24 July (WS day) and 19 August (NS day). The diurnal course of $R_n$ was parabolic on both days indicating clear skies. The daily totals of $R_n$ were $17.6$ and $15.3$ MJ m$^{-2}$ for 24 July and 19 August, respectively. Greater values of $R_n$ were observed on 24 July since this day was nearer the summer solstice. The amount of $R_n$ partitioned into $LE$ was different on the NS and WS days. On the NS day, the energy consumed by $LE$ exceeded the amount of net radiation (the daily total of $LE$ from 0600 to 1845 hours was $-16.6$ MJ m$^{-2}$). Rosenberg (1969) and Rosenberg and Verma (1978) are among those who have previously reported that values of $LE$ over well-watered crops can equal or exceed $R_n$. On the WS day, however, only $66\%$ of $R_n$ was consumed by $LE$ (the daily total of $LE$ was $-11.6$ MJ m$^{-2}$). Bailey and Davies (1981) and Meyer and Green (1981) observed a similar reduction in water vapor exchange of a soybean canopy as it progressed from a well-watered to a water-stressed state.

Differences in $LE$ rates between any two canopies can be due to differences in leaf area, soil surface wetness, environmental conditions, or physiological status of the crop. In this study, the $LAI$ of the soybean canopy exceeded 3.1 on both the WS and NS day. Leaf area index likely did not affect $LE$ since $LE$ is considered to be independent of $LAI$ when $LAI > 2.9$ (Brun et al., 1972). Differences in soil surface wetness can also influence $LE$ values. However, the soil surface was dry on both days. Net radiation ($R_n$), vapor pressure deficit ($VPD$), air temperature ($T$), and wind speed ($U$) are the prime meteorological factors that affect latent heat exchange. Assuming that a crop canopy is fully-developed and well-watered, an increase in any one of these four variables will lead to an increase in $LE$. Figures 2, 3a, and 3b show

**Table 1. Soil moisture in terms of volumetric water content ($\theta_v$) and soil water potential ($\Psi$).**

<table>
<thead>
<tr>
<th>Depth</th>
<th>$\theta_v$ (%)</th>
<th>$\Psi$ (MPa)</th>
<th>$\theta_v$ (%)</th>
<th>$\Psi$ (MPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 - 0.30 cm</td>
<td>17.5</td>
<td>-1.5</td>
<td>36.3</td>
<td>-0.05</td>
</tr>
<tr>
<td>0.30 - 0.60 m</td>
<td>31.9</td>
<td>-0.3</td>
<td>34.4</td>
<td>-0.2</td>
</tr>
<tr>
<td>0.60 - 0.90 m</td>
<td>32.3</td>
<td>-0.10</td>
<td>29.7</td>
<td>-0.15</td>
</tr>
</tbody>
</table>

Fig. 2. Diurnal course of net radiation ($R_n$), latent heat flux ($LE$), and sensible heat flux ($H$) on the water-stress and non-stress days.

Fig. 3. Diurnal course of a) vapor pressure deficit and b) air temperature ($T_a$) (both at 1.50 m above-ground), and c) wind speed (at 2 m above-ground) on the water-stress and non-stress day.
made over the course of the entire day (Rawson et al., 1978; Turner et al., 1978; Vignes and Planchon, 1979; Larson et al., 1981). The studies cited report results similar to ours—e.g., that CO₂ exchange rates of soybeans are insensitive to water stress in the early morning and are severely suppressed after mid-morning. Prior to the above-cited investigations, most related studies had a) examined the effects of water stress on CO₂ exchange rates of soybeans grown only under controlled environmental conditions (e.g., Boyer, 1970a and 1970b; Silvius et al., 1977) or b) examined CO₂ exchange rates of water stressed soybeans only at midday (e.g., Ghorashy et al., 1971).

Midday values (from 1000 to 1400 hours) of Fₑ were on the order of 0.25 to 0.40 mg m⁻² leaf area sec⁻¹ when the crop was well-watered. Chamber studies (Sakamoto and Shaw, 1967; Jeffers and Shibles, 1969; Egli et al., 1970; Larson et al., 1981) gave similar CO₂ exchange rates for well-watered soybean canopies. Midday values of Fₑ were reduced to about 0.10 mg m⁻² leaf area sec⁻¹ when the crop was water-stressed. An integration of CO₂ flux values between 0600 and 1845 hours shows that Fₑ totals were 8.96 and 5.22 g m⁻² for the NS and WS days, respectively. Rawson et al. (1978) and Larson et al. (1981) have reported a similar difference between the CO₂ exchange rates of well-watered and water-stressed soybean leaves.

The mechanisms governing variations in Fₑ are complex, the explanations for the observed reduction in Fₑ on the WS day are considered below. Differences in Fₑ were not due to differences in photosynthetically active radiation (PAR) since more PAR was available on 24 July (Fig. 5).

Differences in Fₑ on the WS and NS days can be explained, to some degree, by differences in stomatal resistance (rₛ) since increases in stomatal resistance retard the diffusion of CO₂ from the atmosphere to the cell chloroplasts. Figure 1b shows that rₛ was substantially greater on the day of water stress. Boyer (1970a, 1970b), Ghorashy et al. (1971), Silvius et al. (1977), Rawson et al. (1978), and Vignes and Planchon (1979) are among those previously reporting that water stress limits CO₂ exchange in soybeans. Larson et al. (1981), however, reported that non-stomatal effects limited CO₂ exchange of water-stressed soybeans. Boyer (1970a, 1970b) and Hsiao

that Rn, VPD, and T were greater on the WS day and Fig. 3c shows that U was slightly greater on the NS day. Environmental conditions should have led to greater LE values on the WS day. This, however, was not the case. Stomatal resistances were greater on the WS day (Fig. 1b) and thus, restricted water vapor transfer to a greater degree than on the NS day.

Larger VPD values on the WS day did not result in larger values of water vapor exchange. These large VPDs were an artifact of water-stress and drier air. Rawson et al. (1978) and Bailey and Davies (1981) have previously observed large VPDs over water-stressed soybeans.

When a crop is fully-developed, the amount of Rn, VPD, and T were greater on the WS day and Fig. 3c shows that U was slightly greater on the NS day. Environmental conditions should have led to greater LE values on the WS day. This, however, was not the case. Stomatal resistances were greater on the WS day (Fig. 1b) and thus, restricted water vapor transfer to a greater degree than on the NS day.

b) Diurnal Course of CO₂ Flux

In Fig. 4, the diurnal course of CO₂ flux (Fₑ)¹⁰ on the water-stress and non-stress days are compared. The course of Fₑ on both days was similar until about mid-morning. After that time, a significant divergence in the values of Fₑ occurred. On the NS day, Fₑ increased to a maximum at about midday and then decreased as the afternoon progressed. Under water stress, Fₑ was suppressed throughout the remainder of the day. The mechanisms governing variations in Fₑ are complex, the explanations for the observed reduction in Fₑ on the WS day are considered below. Differences in Fₑ were not due to differences in photosynthetically active radiation (PAR) since more PAR was available on 24 July (Fig. 5).

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①Fₑ is reported on a per unit leaf area basis.
(1973) state that low leaf water potentials can limit CO₂ exchange by affecting certain enzymatic reactions associated with photosynthesis. Since Ψ values were as low as about −1.8 MPa on the WS day, it is quite plausible that such levels of water stress did affect certain associated enzymatic reactions and contributed to the reduction in Fₚ.

It is also possible that elevated air temperatures may have helped suppress Fₚ on the day of water stress. Afternoon air temperatures (Tₐ) were generally about 34 C and 32 C on the WS and NS days, respectively (Fig. 3b). In an earlier paper (Baldocchi et al., 1981a), we report that a significant reduction in Fₚ of soybeans occurs when air temperatures exceed 32 C. Larson et al. (1981), however, state that CO₂ exchange of soybean canopies are not correlated with air temperatures in the range 24 to 34 C.

A large reduction also occurred in Fₚ on August 19 between 1100 and 1200 hours (Fig. 4). The reduction in Fₚ was not attributable to changes in PAR, rₑ or Tₛ since these variables were relatively constant during this time interval. Since Fₛ was great during the previous hour, a rapid accumulation of phoyosynthate may have occurred in the leaves and inhibited photosynthesis during this period. We lack the data to test this hypothesis. However, such an effect has been observed in soybean leaves by Thorne and Koller (1974), Nafziger and Koller (1976) and Peet and Kramer (1980). Nafziger and Koller (1976) state that the accumulation of assimilate limits photosynthesis by impeding intracellular CO₂ transport. Turner et al. (1978), Mauney et al. (1979) and Potter and Breen (1980), on the other hand, report experiments in which the accumulation of starch in soybean leaves did not affect photosynthesis.

c) Diurnal Course of CO₂-Water Flux Ratio

The diurnal course of CO₂-water flux ratio (CWFR) is presented in Fig. 6. As expected from the previously presented results, CWFR was significantly greater when the crop was well-watered. Midday CWFR values ranged, generally, from 4 to 6 mg CO₂ (g H₂O)⁻¹ on the NS day and from 1 to 3 mg CO₂ (g H₂O)⁻¹ on the WS day. Rawson et al. (1978) reported similar values for well-watered and water-stressed soybean leaves. These workers contend that large rₑ and VPD values are among the factors most responsible for the reduction in CWFR when a crop is water-stressed. They found, for example, that water use efficiency of soybean leaves decreased with increasing soil moisture deficit because of stress-induced stomatal closure. This, in turn, reduced the rate of diffusion of CO₂ into the leaf and increased the vapor pressure deficit between the leaf and the atmosphere. Our results show that rₑ was greater on the WS day (Fig. 1b). We do not have direct measurements of the leaf to air vapor pressure difference. We do, however, have measurements of the atmospheric vapor pressure deficit at 1.5 m aboveground. As shown in Fig. 3a, the vapor pressure deficit was greater when the crop was water stressed.

The water-stress day was also characterized by high air temperatures (Fig. 3b) and low leaf water potentials (Fig. 1a). These two factors may have also contributed to the reduction in CWFR on this day since high air temperatures limit soybean canopy CO₂ exchange (Baldocchi et al., 1981a) and low water potentials can affect the enzymatic processes associated with photosynthesis (Boyer, 1970a, 1976; Hsiao, 1973).

SUMMARY

The influence of water stress on the diurnal course of mass and energy exchange between a soybean canopy and the atmosphere was examined. Water stress conditions greatly influenced the partitioning of Rn between LE and H. When the crop was well watered, all of Rn was consumed as latent heat flux. Only 66% of Rn was consumed as LE when the crop was water-stressed. Sensible heat was directed towards the surface when the crop was well-watered and away from the surface when the crop was water-stressed.

Carbon dioxide flux (Fₚ) was unaffected by water stress until about mid-morning since, until that time, both the stressed and non-stressed crops were at a state near hydraulic equilibrium with the soil. Fₛ was inhibited after mid-morning on the day that the crop was water-stressed. Relatively large stomatal resistance and high air temperatures are the most likely causes of this inhibition of Fₛ. Low values of leaf water potential may also have limited Fₛ, since severe water stress affects the enzymatic reactions associated with photosynthesis.

The CO₂-water flux ratio (CWFR) was greater on the NS day than on the WS day. The combination of water stress, high stress temperatures, and large VPD greatly reduced CWFR.

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LITERATURE CITED

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