

Influence of Water Stress on the Diurnal Exchange of Mass and Energy between the Atmosphere and a Soybean Canopy¹

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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 CO₂, 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 CO₂ exchange appears to have been caused by a combination of high stomatal resistance limiting CO₂ 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 CO₂-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 CO₂-water flux ratio.

Additional index words: *Glycine max* (L.) Merr., Micrometeorology, Water use efficiency, Photosynthesis, Evapotranspiration, Canopy CO₂ 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 ad-

vantage 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 CO₂ concentration with a multilevel manifold at 0.30, 0.50, 0.70, and 0.90 m within the crop

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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, 1975, 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.³ 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.⁴ Net radiation was measured with a net radiometer⁵ 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.⁶

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.⁷ Four to six leaves from the upper part of the canopy were selected for this purpose. After excision, each leaf was inserted into a plastic bag and placed immediately within the pressure chamber.

Stomatal resistance (r_s) was measured on both sides of six randomly selected leaves with a steady state porometer.⁸ 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 3.6. 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 canopy was at stage V15, R4 on 24 July and at stage V19, R6 on 19 August.

Theoretical Considerations

Fluxes⁹ 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:

$$K = K_c = K_w = K_H = \frac{(R_n + S)}{\rho \left[C_p \frac{\partial T}{\partial z} + \frac{\epsilon}{P} L \frac{\partial e}{\partial z} \right] + \lambda \frac{\partial \rho_c}{\partial z}} \quad [1]$$

where R_n is net radiation, S is soil heat flux, ρ 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, ϵ is the ratio of the molecular masses of water vapor and dry air ($\epsilon = 0.622$) and λ is the energy equivalent of CO₂ fixation. $\partial T/\partial z$, $\partial e/\partial z$, and $\partial \rho_c/\partial z$ 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):

$$F_c = (P/P_1)(T_1/T_k) \left[K_c \frac{\partial \rho_c}{\partial z} + (\rho_c/\epsilon \rho_a) \left(1 + \frac{\sigma}{\epsilon} \right)^{-1} E \right] \quad [2]$$

$$LE = \left(1 + \frac{\sigma}{\epsilon} \right) \left[\left(1 + \frac{L}{C_p} \right) (\rho_v \beta / \rho T_k) \right] \rho \frac{L \epsilon}{P} K_w \frac{\partial e}{\partial z} \quad [3]$$

where T_1 and P_1 are the respective absolute air temperature and pressure inside the cells of the infrared gas analyzer, σ is the ratio of the densities of water vapor (ρ_v) and dry air (ρ_a), β 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

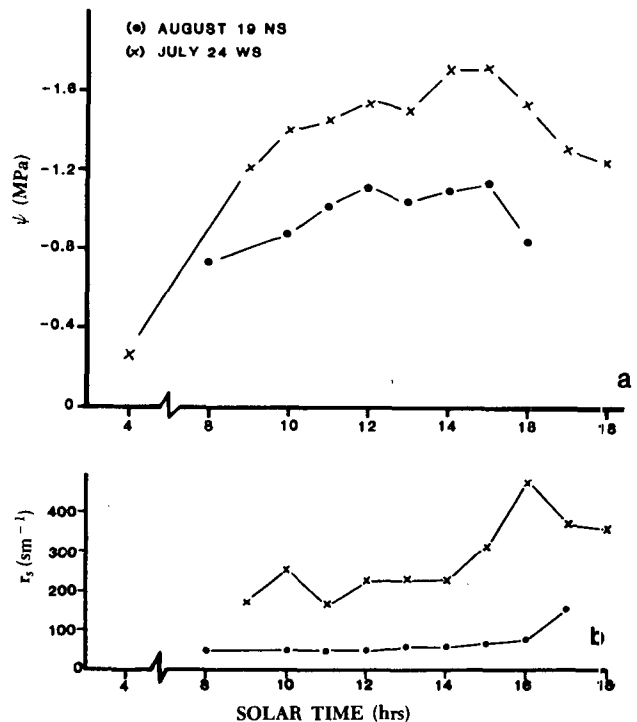


Fig. 1. a) Diurnal variation of leaf water potential (Ψ) for a day on which the soybean crop was water-stressed (WS) (24 July) and for a day on which it was well watered (NS) (19 August).
b) Same as a) except for stomatal resistance (r_s).

³ Cayuga Development, Ithaca, NY, Model WP-1.

⁴ Lambda Instrument Co., Lincoln, NE, Model LI-190S.

⁵ Swissteco Pty. Ltd., Melbourne, Australia, Type S-1.

⁶ Science Associates Inc., Princeton, NJ, Model 632 (1).

⁷ Soil Moisture Equip. Co., Santa Barbara, CA, Model (3005).

⁸ Lambda Instr. Co., Lincoln, NE, Model LI-1600.

⁹ Fluxes directed toward the surface are positive, while those directed from the surface are negative.

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 (Ψ) and stomatal resistance (r_s), respectively. On the water stressed (WS) day, Ψ 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, Ψ 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 (Rn), latent heat flux (LE) and sensible heat flux (H) for both 24 July (WS day) and 19 August (NS day). The diurnal course of Rn was parabolic on both days indicating clear skies. The daily totals of Rn were 17.6 and 15.3 MJ m^{-2} for 24 July and 19 August, respectively. Greater values of Rn were observed on 24 July since this day was nearer the summer solstice.

The amount of Rn 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

Table 1. Soil moisture in terms of volumetric water content (θ_v) and soil water potential (Ψ_s).

Depth	24 July		19 August	
	θ_v (%)	Ψ_s (MPa)	θ_v (%)	Ψ_s (MPa)
0 -0.30 cm	17.5	-1.5	36.3	-0.05
0.30-0.60 m	31.9	-0.3	34.4	-0.2
0.60-0.90 m	32.3	-0.10	29.7	-0.15

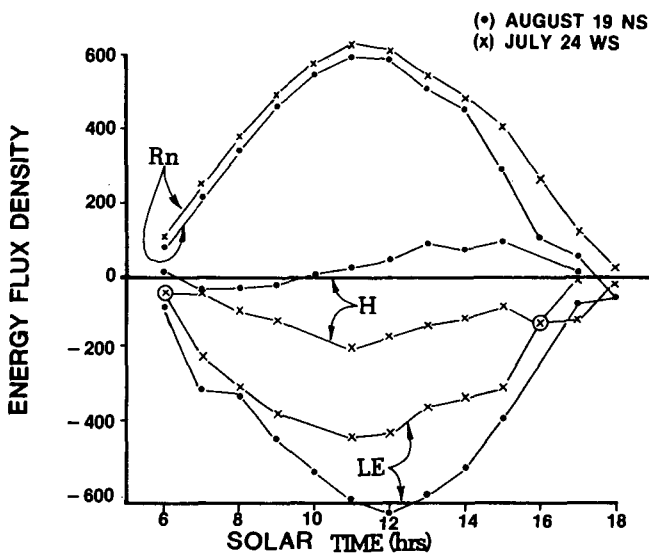


Fig. 2. Diurnal course of net radiation (Rn), latent heat flux (LE), and sensible heat flux (H) on the water-stress and non-stress days.

that values of LE over well-watered crops can equal or exceed Rn. On the WS day, however, only 66% of Rn 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 (Rn), 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

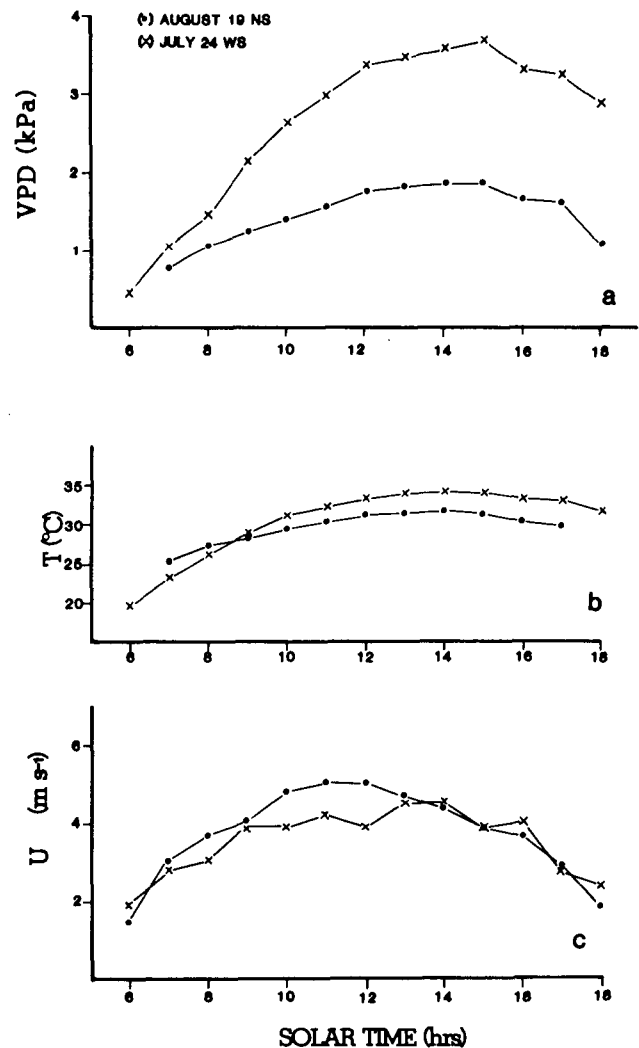


Fig. 3. Diurnal course of a) vapor pressure deficit and b) air temperature (T_a) (both at 1.50 m above-ground), and c) wind speed (at 2 m above-ground) on the water-stress and non-stress day.

that R_n , 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 $R_n + S$ converted to sensible heat (H) can be approximated as the residual after the energy requirement for latent heat transfer is met (Shaw and Decker, 1979). Figure 2 shows the diurnal course of H on the WS and NS days. The daily totals of H were, respectively, -4.8 and 1.34 MJ m^{-2} on these days. Generation of H was greater on the WS day since the high values of r_s (Fig. 1b) helped reduce the possibility for high rates of evapotranspiration. A similar effect has previously been noted over soybeans by Sumayao and Kanemasu (1979).

b) Diurnal Course of CO_2 Flux

In Fig. 4, the diurnal course of CO_2 flux (F_c)¹⁰ on the water-stress and non-stress days are compared. The course of F_c on both days was similar until about mid-morning. After that time, a significant divergence in the values of F_c occurred. On the NS day, F_c increased to a maximum at about midday and then decreased as the afternoon progressed. Under water stress, F_c was suppressed throughout the remainder of the day. On the morning of 24 July, water stress effects were not evident since the water stressed crop was at a state approaching hydraulic equilibrium with the soil: as shown in Fig. 1a the pre-dawn leaf water potential was -0.26 MPa on 24 July.

Only recently have comparisons of the CO_2 exchange rates in well-watered and water-stressed soybeans been

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 CO_2 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 CO_2 exchange rates of soybeans grown only under controlled environmental conditions (e.g., Boyer, 1970a and 1970b; Silvius et al., 1977) or b) examined CO_2 exchange rates of water stressed soybeans only at midday (e.g., Ghorashy et al., 1971).

Midday values (from 1000 to 1400 hours) of F_c 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 CO_2 exchange rates for well-watered soybean canopies. Midday values of F_c were reduced to about 0.10 $mg\ m^{-2}$ leaf area sec^{-1} when the crop was water-stressed. An integration of CO_2 flux values between 0600 and 1845 hours shows that F_c 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 CO_2 exchange rates of well-watered and water-stressed soybean leaves.

The mechanisms governing variations in F_c are complex, the explanations for the observed reduction in F_c on the WS day are considered below.

Differences in F_c were not due to differences in photosynthetically active radiation (PAR) since more PAR was available on 24 July (Fig. 5).

Differences in F_c on the WS and NS days can be explained, to some degree, by differences in stomatal resistance (r_s) since increases in stomatal resistance retard the diffusion of CO_2 from the atmosphere to the cell chloroplasts. Figure 1b shows that r_s 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 CO_2 exchange in soybeans. Larson et al. (1981), however, reported that non-stomatal effects limited CO_2 exchange of water-stressed soybeans. Boyer (1970a, 1976) and Hsiao

¹⁰ F_c is reported on a per unit leaf area basis.

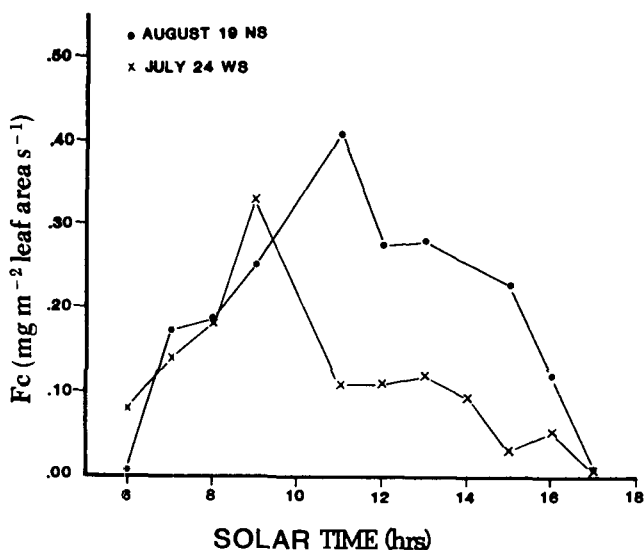


Fig. 4. Diurnal course of canopy CO_2 flux (F_c) on the water-stress and non-stress days.

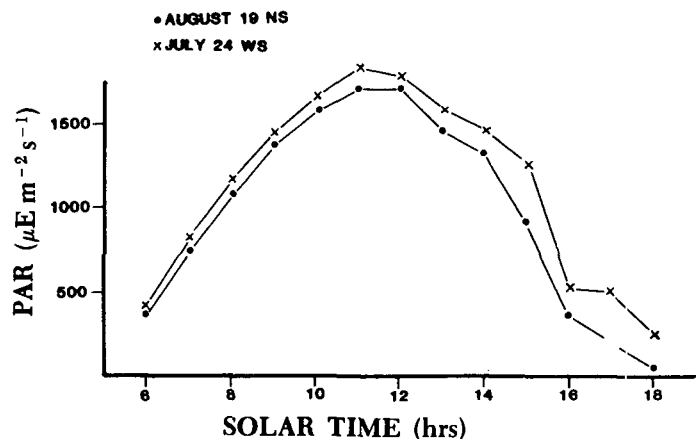


Fig. 5. Diurnal course of photosynthetically active radiation (PAR) on the water-stress and nonstress day.

(1973) state that low leaf water potentials can limit CO_2 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 F_c .

It is also possible that elevated air temperatures may have helped suppress F_c on the day of water stress. Afternoon air temperatures (T_a) 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 F_c of soybeans occurs when air temperatures exceed 32 C. Larson et al. (1981), however, state that CO_2 exchange of soybean canopies are not correlated with air temperatures in the range 24 to 34 C.

A large reduction also occurred in F_c on August 19 between 1100 and 1200 hours (Fig. 4). The reduction in F_c was not attributable to changes in PAR, r_s or T_a since these variables were relatively constant during this time interval. Since F_c 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 CO_2 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 CO_2 -Water Flux Ratio

The diurnal course of CO_2 -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 $\text{mg CO}_2 (\text{g H}_2\text{O})^{-1}$ on the NS day and from 1 to 3 $\text{mg CO}_2 (\text{g H}_2\text{O})^{-1}$ on the WS day. Rawson et al. (1978) reported similar values for well-watered and water-stressed soybean leaves. These work-

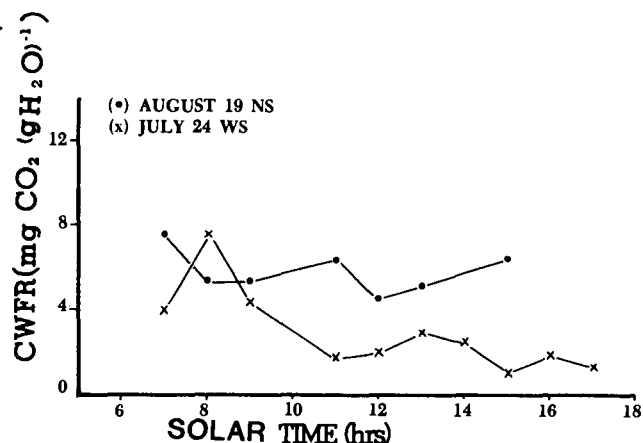


Fig. 6. Diurnal course of CO_2 -water flux ratio (CWFR) on the water-stress and non-stress day.

ers contend that large r_s 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 CO_2 into the leaf and increased the vapor pressure deficit between the leaf and the atmosphere. Our results show that r_s 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 CO_2 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 R_n between LE and H. When the crop was well watered, all of R_n was consumed as latent heat flux. Only 66% of R_n 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 (F_c) 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. F_c 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 F_c . Low values of leaf water potential may also have limited F_c , since severe water stress affects the enzymatic reactions associated with photosynthesis.

The CO_2 -water flux ratio (CWFR) was greater on the NS day than on the WS day. The combination of water stress, high temperatures, and large VPD greatly reduced CWFR.

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