Mass and Energy Exchanges of a Soybean Canopy under Various Environmental Regimes¹

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ABSTRACT

The environment of the east central Great Plains of North America can be very extreme during the course of a growing season. A field study was thus conducted during the summer of 1979 to examine the exchange of mass and energy between the atmosphere and a soybean canopy [Glycine max (L.) Merrill] for various environmental conditions experienced in the east central Great Plains of North America. The crop was planted in a Typic Argiudoll (Sharpsburg silty, clay loam) soil. Measurements of mass and energy balance technique. Hot, clear days dominated by sensible heat advection

Hot, clear days dominated by sensible heat advection limited CO_2 exchange but increased latent heat flux. As a result, the CO_3 -water flux ratio (CWFR), a measure of water-use efficiency, was low. Cloudy days suppressed both CO_3 and latent heat flux. This effect caused CWFR to be greater. Optimal conditions for photosynthesis and CWFR occurred in the absence of sensible heat advection on clear days with moderate temperatures.

Our measurements indicate that a developed soybean canopy (LAI of 4.1) did not become light saturated at photosynthetically active radiation (PAR) levels exceeding 400 Wm⁻³. Optimal air temperatures for CO_2 exchange ranged between 29 and 32 C. Higher temperatures led to a reduction in CO_2 exchange. The CWFR was found to be dependent on both net radiation and sensible heat advection.

Additional index words: Photosynthesis, Latent heat flux, Sensible heat flux, CO₃-water flux ratio, Water-use efficiency.

C ROP production depends upon exchanges of matter and energy that occur between the crop canopy and the atmosphere. Dry matter production depends upon CO_2 exchange. The temperature of the plant and cell turgor depend upon the rate at which water is evaporated into the air. Metabolic rates are also affected by plant temperature which is controlled by the the partitioning of net radiation into latent and sensible heat.

The soybean [Glycine max (L.) Merrill] is one of the world's major economic crops. There is considerable literature concerning CO_2 exchange from fieldgrown soybeans using chamber methods (Sakannoto and Shaw, 1967; Jeffers and Shibles, 1969; Egli et al., 1970; Dornhoff and Shibles, 1970; Beuerlein and Pendleton, 1971; Sinclair, 1980). However, of these only Sinclair (1980) has studied soybean CO_2 exchange on a diurnal basis. Rosenberg (1972), Pallas (1973), Rawson et al. (1978), and Vignes and Planchon (1979) have examined, on a diurnal basis, the simultaneous exchanges of CO_2 and water vapor between a soybean canopy and the atmosphere. The exchange of sensible heat between a soybean canopy and the atmosphere has not been studied extensively.

Here we report diurnal measurements of mass and energy exchange that occur between the atmosphere and a soybean crop canopy under three conditions typical of the Great Plains climate: (i) a clear, hot day dominated by regional advection of sensible heat,³ (ii) a cool, cloudy day and, (iii) a non-advective day with clear skies and moderate temperatures. The dependence of CO_2 exchange in the canopy on photosynthetically active radiation and temperature and the dependence of the CO_2 -water flux ratio (CWFR) on net radiation and sensible heat flux are also examined.

MATERIALS AND METHODS

Experimental Details

Experiments were conducted during the summer of 1979 at the University of Nebraska Agricultural Meteorology Laboratory at Mead, Nebraska (41° 09' N; 95° 30' W; altitude 354 m above mean sea level). Soybeans ('Clark') were planted in the main experimental field (105 m E-W; 210 m N-S) in 0.75 m wide rows. The soil in this field was a Typic Argiudoll (Sharpsburg silty, clay loam). The field was irrigated. Border fields to the east, south, and west were planted with 'Woodworth' soybeans having similar growth characteristics as Clark. These latter fields were not irrigated. Data reported in this paper were selected from periods during which the fetch to height ratio in the main experimental field exceeded 60 to 1.

Air temperature and vapor pressure profiles were measured 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). The differential thermopiles of the psychrometer provided a 0.013 C temperature resolution. Once each hour, the psychrometer assembly rotated automatically into a horizontal position for calibration. Within-canopy air temperature and vapor pressure profiles were measured at three locations at 0.10, 0.30, 0.50, 0.70, and 0.90 m with mini-psychrometers adapted from the design of Stigter and Welgraven (1976).

Carbon dioxide concentrations were measured at 0.10, 0.30, 0.50, 0.70, and 0.90 m within and at 1.25, 1.50, 1.75, and 2.00 m above the canopy. Air was sampled in the field with a multi-level manifold. The manifold had six intakes at each level. These were spaced equidistantly over a horizontal distance of 2.5 m. Carbon dioxide concentrations were measured with a

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^a Under conditions of regional sensible heat advection, the sensible heat flux (H) is directed towards the crop and daytime temperature inversions prevail. For a detailed discussion of sensible heat advection, see Brakke et al. (1978) and Rosenberg and Verma (1978).

system which employed an absolute and a differential infrared gas analyzer (Rosenberg and Verma, 1976). The accuracy of the CO_2 gradients were about ± 0.2 ppm while the absolute CO_2 concentrations were measured with an accuracy of ± 1 to 2 ppm. Once each hour, both analyzers were calibrated automatically with standard gases of known concentration.

Wind speed was measured at 0.25 m intervals between 1.25 and 2.75 m with Cayuga three-cup anemometers (Cayuga Development, Ithaca, NY, Model WP-1). 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 Lambda quantum sensor (Lambda Instru-ments Co., Lincoln, Neb., LI-190S). Net radiation was measured



Fig. 1. Energy and mass fluxes and environmental variables over a soybean canopy on 4 Aug. 1979 at Mead, Nebraska.

- a) Diurnal course of canopy CO₂ flux (\mathbf{F}_c) and photosynthetically active radiation (PAR). b) Diurnal course of net radiation (Rn), latent heat flux
- (LE), and sensible heat flux (H).

d) Diurnal course of CO2 water flux ratio (CWFR).

with two Swissteco net radiometers (Swissteco Pty. Ltd., Melbourne, Australia, Type S-I) 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 (Science Associates Inc., Princeton, N.J., Model 632(1)).

All micrometeorological data were sampled with a computer controlled data acquisition system and were recorded on magnetic tape. Cup anemometer data were recorded as integrated counts over 5 min. Carbon dioxide concentrations were measured every 5 min. Signals from all other voltage producing sensors were sampled three times per min. Data were later averaged over 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.

Plant water potential was measured hourly on a number of days with a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, Calif., Model 3005). Six to eight leaves from the upper canopy were selected for this purpose. Each leaf was placed in a plastic bag after excision and was then immediately placed within the pressure chamber.

Theoretical Considerations

Fluxes of CO₂, latent heat, and sensible heat were computed using the flux-gradient theory (Rosenberg, 1974). Both CO_2 flux (F_e) and latent heat flux (LE) calculations were corrected for the effect of water vapor exchange on the density of dry air (Webb et al., 1980). The eddy exchange coefficients for CO_2 (K_c), water vapor (K_w), and sensible heat (K_B), as-sumed to be identical, were computed by means of the Bowenratio energy balance (BREB) method.

Water-use efficiency was expressed in terms of the CWFR which is the ratio of CO_2 flux to water vapor flux.

RESULTS AND DISCUSSION

Diurnal Course of Mass and Energy Exchange -Weather Related Differences

Figures 1a through d show the diurnal course of mass and energy exchange⁴ between crop and atmosphere and associated environmental and physiological variables on 4 Aug. 1979. This was a clear day characterized by strong winds, extreme temperatures, and a considerable advection of sensible heat. Carbon dioxide flux $(F_c)^5$ increased in the morning in response to increasing photosynthetically active radiation (PAR) (Fig. 1a). The F_c reached a maximum of about 1.5 mg m⁻² s⁻¹ at about 1100 hours. The peak value of F_c agrees with the results of chamber measurements reported by Sakamoto and Shaw (1967), Jeffers and Shibles (1969), Beuerlein and Pendleton (1971), and Sinclair (1980).

A dramatic reduction in F_c occurred after 1100 hours even though the flux density of PAR remained great. Rawson et al. (1978) observed a midday depression in soybean CO_2 exchange that they attributed to the effects of low leaf water potential. In our studies, however, water stress was not a factor on 4 August since leaf water potential (Ψ) was greater than -6 bars throughout the day (Fig. 1c). Air temperature (T_a), measured at 0.7 m⁶ exceeded 35 C at midday (Fig. 1c) and this may have been the factor limiting \dot{CO}_2 flux. A similar temperature effect on soybean CO₂ flux at midday has been noted by Vignes and

Diurnal course of air temperature at 0.7 m (T), plant C) water potential (Ψ), and wind speed at 2 m.

^{*}Fluxes directed toward the surface are positive, while those directed from the surface are negative.

⁸ Carbon dioxide flux is expressed on a per unit ground area basis.

[&]quot;Air temperature at 0.7 m was used instead of above-canopy air temperature since the former more closely approximates leaf temperature.

Planchon (1979). After 1600 hours, F_c became less than zero. Low irradiance conditions accompanied by high temperature limited the CO₂ uptake from the atmosphere. The relationship between F_c and T_a is shown in Fig. 2 for a fully developed canopy (LAI = 4.1) under conditions of high irradiance (PAR > 300 Wm⁻²). It is seen that F_c is limited when T_a exceeds about 32 C. Figure 2 is discussed in further detail later.

The diurnal course of net radiation (Rn) (Fig. 1b) was approximately sinusoidal with a midday maximum of about 560 Wm⁻². The magnitude of latent heat flux (|LE|) increased rapidly until 0900 hours but remained between 540 and 660 Wm⁻² until about 1700 hours and decreased thereafter. Energy consumed in LE was greater than that supplied by Rn during the day. This was as a result of regional sensible heat advection contributing energy to drive the evaporative process.

Since high temperatures limited F_c and sensible heat advection increased evapotranspiration, CWFR was low throughout the day (Fig. ld). A maximum CWFR of 5.6 g CO₂ (kg H₂O)⁻¹ occurred at 1100 hours, when F_c reached its maximum value. For the remainder of the day, CWFR was less 2.4 g CO₂ (kg H₂O)⁻¹. Rosenberg (1972) reported that the CWFR of a soybean canopy ('Amsoy') was about 5.0 g CO₂ (kg H₂O)⁻¹ under similar advective conditions. The CWFR values less than zero are shown after 1600 hours since F_c was negative (away from the surface).

Figures 3a through d show the diurnal course of the variables displayed in Fig. 1a through d with the exception of Ψ data. The 16 Aug. 1979 was cool, windy and overcast. The F_c was suppressed and never exceeded 0.75 mg m⁻² s⁻¹. This occurred since PAR (Fig. 3a) was limited by heavy cloud cover and air temperature (Fig. 3c) did not exceed 24 C. Our results differ from those of Sinclair (1980), who states that the CO₂ exchange of soybean leaves is relatively insensitive to synoptic weather changes. The F_c was limited by air temperature since the air temperature was below the optimal range of 25 to 30 C reported for soybean CO₂ exchange by Jeffers and Shibles (1969). The cloud cover also reduced Rn and thus latent heat flux was small (Fig. 3b). The midday value of Rn



Fig. 2. Relationship between canopy CO₂ flux (F_c) and air temperature (T). The T was measured at 0.70 m. Data were obtained from periods when PAR exceeded 350 Wm²⁻.

was about one third that on 4 August, the clear day shown in Fig. 1b. Since latent heat flux was less than Rn on 16 August, H was directed away from the crop. The midday value of latent heat flux was one-fourth of that on the clear day, 4 August (Fig. 1b).

The CWFR, however, was very high on 16 August, ranging between 7.6 and 10.0 g CO_2 (kg $H_2O)^{-1}$ during the period 0900 to 1400 hours (Fig. 3d). Although F_c was suppressed, it proceeded at a substantial rate under moderate irradiance while evapotranspiration was greatly reduced due to the low levels of Rn and the absence of sensible heat advection. As a result, the average CWFR value between 0900 hours and 1400 hours was more than three times greater than during the same hours on 4 August (Fig. 1d).



Fig. 3a, b, c, d. Same as Figures 1a through d except data are from 16 Aug. 1979, and no plant water potential data are presented in Fig. 3c.

Results presented above help us define the environmental conditions that make for most optimal water use in soybeans. For example, hot, windy days (Fig. 1) are not desirable since these conditions cause \dot{CO}_2 exchange to be suppressed and latent heat to be increased. Cloudiness reduced both Fc and latent heat flux since irradiance and air temperatures were low. Thus, a clear sky, moderate temperature, and the absence of sensible heat advection should favor both soybean photosynthesis and water-use efficiency. Figures 4a through d present data for 3 September, a day during which, in general, these criteria were met. On 3 September the flux density of PAR was great (over 400 Wm^{-2} at midday; Fig. 4a) and air temperature at 0.7 m was moderate (about 32 C at midday; Fig. 4c). As a result, peak F_c was greater than 1.5 mg m⁻² s⁻¹. The Rn (Fig. 4b) reached a midday value of about 520



Fig. 4a, b, c, d. Same as Figures 3a through d except data are from 3 September 1979.

Wm⁻². Latent heat flux did not exceed Rn until the onset of regional sensible heat advection at about 1500 hours.

Since F_c was great and latent heat flux was moderate on 3 September, CWFR (Fig. 4d) remained high until the onset of sensible heat advection. The average CWFR between 0900 and 1700 hours was 6.8 g CO₂ (kg H₂O)⁻¹. This value was greater than the average for the advective day [2.86 g CO₂ (kg H₂O)₂⁻¹ (Fig. Id)] but less than that for the cloudy day [9.2 g CO₂ (kg H₂O)⁻¹ (Fig. 3d)]. Rawson et al. (1978) observed that the CWFR of field-grown soybean leaves ranged between 11.7 and 6.4 g CO₂ (kg H₂O)⁻¹ on a clear day with a maximum air temperature of 32 C (meteorological conditions for this experiment are reported in Turner et al. (1978) and indicate a non-advective situation).

Specific Environmental Effects on F_c and CWFR

Effect of Irradiance on F_c . Figure 5 shows the dependency of F_c on PAR when LAI was 4.1 and air temperature ranged between 20 and 32 C. The correlation between F_c and PAR was good (r = 0.90). The light compensation point for the canopy had a value of about 40 Wm⁻² under these conditions. This value agrees with that reported by Sakamoto and Shaw (1967) for a soybean canopy. Our data do not indicate that the canopy reached a condition of light saturation. Sakamoto and Shaw (1967) found soybean canopies to become light saturated in the field at PAR values between about 250 and 290 Wm⁻². Jeffers and Shibles (1969) found that a soybean canopy with LAI exceeding 4 did not become light saturated in the field while one with an LAI of 2 was saturated at about 280 Wm⁻². Egli et al. (1970) also reported that soybean canopies do not become light saturated in the field.

Effect of Air Temperature on F_c . Figure 2 illustrates the strong dependence of F_c on air temperature at 0.70 m during periods of high irradiance. Optimal air temperatures in these experiments ranged between about 29 and 32 C. Above 32 C, F_c rates were limited and approached zero as T_a increased to about 36.4 C.



Fig. 5. Relationship between canopy CO_2 flux (E_c) over soybeans and photosynthetically active radiation (PAR). Data were obtained from periods when air temperatures ranged between 20 and 32 C.



Fig. 6. Relationship between CO₂ water flux ratio (CWFR) over soybeans and net radiation (Rn). The CWFR data are presented from periods with lapse and inverted temperature profiles.

With air temperatures above 36.4 C, F_c was negative, probably because of increases in photo- and dark respiration rates. High temperatures also adversely af-fect chloroplast activity. Zero or negative values of F_c , however, do not always indicate that apparent photosynthesis was zero, since the crop could have been fixing CO_2 released from the rhizosphere.

Effect of Net Radiation and Sensible Heat Advection on CWFR. The CWFR depends upon net radiation (Fig. 6) but the relationship is strongly affected by the occurrence of sensible heat advection. Under non-advective conditions, CWFR decreased linearly with increasing Rn because of increasing evapotranspiration. This effect has also been noted in field grown soybean leaves by Rawson et al. (1978). Under conditions of sensible heat advection, however, CWFR was considerably reduced because sensible heat advection supplies additional energy for the evaporative process. Under such conditions, CWFR actually appears to increase slightly with increasing Rn. This effect can probably be attributed to the fact that the magnitude of sensible heat advection is greater late in the afternoon when irradiance is diminished (Brakke et al., 1978).

SUMMARY AND CONCLUSION

The diurnal course of energy and mass exchange between the atmosphere and a soybean canopy is compared on three typical, but different kinds of days. On clear, hot, windy days, under sensible heat advection, F_c and CWFR are suppressed while LE is increased. Cool, cloudy days limit F_c and LE but the ratio of the two is improved. Optimal conditions for photosynthesis and good water-use efficiency exchange occur on clear days with air temperatures near 30 C and in the absence of sensible heat advection. Our findings suggest that, contrary to Sinclair's (1980) observation, F_c of soybeans is sensitive to weather changes on the synoptic scale.

The response of a soybean canopy F_c to PAR indicates that the crop is not light saturated at an LAI of 4.1. Most data available in the literature support this finding. The Fe is also strongly dependent on air temperature. Air temperatures between 29 and 32 C provide the optimal range for photosynthesis.

The CWFR depends upon Rn and the occurrence of sensible heat advection. Under non-advective conditions, CWFR decreased with increasing Rn. With the occurrence of sensible heat advection, CWFR is greatly reduced but appears to increase slightly with increasing Rn. This latter effect is probably an artifact caused by the coincidence of maximum sensible heat advection and diminishing irradiance in the late afternoon.

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LITERATURE CITED

- Beurlein, J. E., and J. W. Pendleton. 1971. Photosynthetic rates and light saturation curves of individual soybean leaves under field conditions. Crop Sci. 11:217-219.
- Brakke, T. W., S. B. Verma, and N. J. Rosenberg. 1978. Local and regional components of sensible heat advection. J. Appl. Meteorol. 17:955-963
- Egli, D. B., J. W. Pendleton, and D. B. Peters. 1970. Photosynthetic rate of three soybean communities as related to CO₂ levels and solar radiation. Agron. J. 62:411-414. Jeffers, D. L., and R. M. Shibles. 1969. Some effects of leaf
- area, solar radiation, air temperature, and variety on net photoysnthesis in field grown soybean. Crop Sci. 9:762-764. Pallas, J. E., Jr. 1973. Diurnal changes in transpiration and
- daily photosynthetic rate of several crop plants. Crop Sci. 13:82-8
- Rawson, H. M., N. C. Turner, and J. E. Begg. 1978. Agronomic and physiological responses to soybean and sorghum crops to water deficits IV. Aust. J. Plant Physiol. 5:195-209. Rosenberg, N. J. 1972. Simultaneous estimations of short period
- photosynthesis and evaporation in soybeans. Nebraska Water
- Res. Res. Inst. Proj. A-017-NEB. ———. 1974. Microclimate: The biological environment. John Wiley and Sons, New York. ——, and K. W. Brown. 1974. Self-checking psychrometer
- system for gradient and profile determinations near the ground. Agric. Meteorol. 13:215-226.
- ground. Agric. Meteorol. 1976. A system and program for monitoring CO_2 concentration, gradient, and flux in an ag-ricultural region. Agron. J. 68:414-418. _____, and _____. 1978. Extreme evapotranspiration by ir-
- rigated alfalfa: A consequence of the 1976 midwestern drought. J. Appl. Meteorol. 17:934-941. Sakamoto, C. M., and R. H. Shaw. 1967. Apparent photosyn-thesis in field soybean communities. Agron. J. 59:73-75. Sinclair, T. R. 1980. Leaf CER from post-flowering to senes-conce of field errorm soybean continuer. Crop Sci. 20:106 200.
- cence of field-grown soybean cultivars. Crop Sci. 20:196-200.
- Turner, N. C., J. E. Begg, H. M. Rawson, S. D. English, and A. B. Hearn. 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits III. Com-ponents of leaf water potential, leaf conductance ${}^{4}CO_{s}$ pho-tosynthesis, and adaption to water deficits. Aust. J. Plant Physiol. 5:169-177.
- Stigter, C. J., and A. D. Welgraven. 1976. An improved radiation protected differential thermocouple psychrometer for crop environment. Arch. Met. Geoph. Biokl., B, 24:177-181. Vignes, D., and C. Planchon. 1979. Structure, eclairement et echanges gazeux d'une culture de Soja (Glycine max) Photo-
- synthetica 13:136-145. Webb, E. K., G. I. Pearman, and R. Leuning. 1980. Correction of flux measurements for density effects due to heat and water vapor transfer. Quart. J. R. Met. Soc. 106:85-100.