Effect of Water Stress on Canopy Senescence and Carbon Exchange Rates in Cotton[1]

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ABSTRACT

The work reported here was done as part of an effort to develop a physiological process level data base for the simulation of cotton (*Gossypium hirsutum* L.) growth and yield. The effects of water stress on vegetative growth and on carbon exchange rate (CER) in cotton canopies were investigated in naturally illuminated, controlled environment cabinets (SPAR units). The control treatment was irrigated daily. In the other treatments, irrigation was stopped just before the appearance of the first blooms. An extra low water treatment was allowed to dry much faster than the low water treatment. Water stress had a strong effect on vegetative growth. Rate of increase in plant height and leaf area declined when midday leaf water potential was lower than -1.4 MPa, and they were almost zero at -2.0 to -2.5 MPa. Water stress had a similar effect on the CER over a wide range of radiation intensities. CER started to decline < 2 weeks after irrigation was stopped, and it was about 50% of the control when midday leaf water potential reached -2.0 to -2.5 MPa. Two different mechanisms are suggested for the effect of water stress on canopy photosynthesis. A direct effect on single leaves may have closed stomata, increased mesophyll resistance, or decreased Hill reaction activity. Additionally, there was the long-term effect of reduced leaf growth, which produced a canopy consisting mainly of old, less photosynthetically efficient leaves.

Additional index words: CER, *Gossypium hirsutum* L., Leaf growth, Leaf water potential, Plant height.

WATER regime is one of the most important factors in cotton (*Gossypium hirsutum* L.) production. With irrigation, an attempt is made to optimize moisture conditions by controlling amounts and the timing of water application. Still, periods of water stress of variable durations and intensities frequently affect cotton yield.

Leaf water potential, a commonly accepted index of plant water stress, is relatively easy to measure in the field (23) and gives repeatable results either at 1200 h or before dawn. It is a function of both availability of soil water to the plant and prevailing climatic conditions, especially radiation, air temperature, relative humidity, and wind speed. Minimum values of leaf water potential generally occur shortly after 1200 h and can be used as indicators of water stress. In cotton, predawn measurements are usually 0.8 to 1.2 MPa higher than midday measurements under field conditions (10,20).

Delaying early irrigation reduces the rate of elongation of the main stem (12,19) and the rate of leaf growth (19,25) of cotton plants in field experiments. A relatively mild water stress delays the vegetative growth of many crop plants (1,6), e.g., leaf elongation

is significantly retarded at leaf water potentials of -0.3 to -0.4 MPa and stops at -0.35 to -1.0 MPa. Top growth of cotton plants ceases entirely when early morning leaf water potential decreased to < -0.5 to -0.7 MPa (17).

The effect of water stress on the rate of photosynthesis of single leaves is associated with closing of the stomata (2,9,14), with reduced Hill reaction activity (11), or with high mesophyll resistance (21). Although quantitative relationships between leaf water potentials and the rate of photosynthesis of single leaves of cotton have been reported (3,5,14,16,21), information is scarce on the effect of water stress on the carbon exchange rates (CER) of whole canopies (4,20). Thus, the purpose of the work reported here was to quantify effects of water stress on the CER of cotton canopies and related parameters of plant growth and development. This work was done as part of an effort to develop a physiological process level data base for the simulation of cotton growth and yield.

MATERIALS AND METHODS

The experiment was conducted in five naturally illuminated controlled environment soil-plant-atmosphere research (SPAR) (22) units at Mississippi State, MS. Each unit had 0.5 by 2.0 m ground area. The Plexiglas[3] aboveground enclosure was 1.5 m high. The SPAR unit soil bin, constructed of steel with a glass face for root observation, was surrounded by styrofoam insulation to reduce diurnal temperature fluctuations and to provide a soil temperature near average outside air temperature. The substrate in the 1.0-m deep soil bin was vermiculite.

A computerized system was used both to control various SPAR environmental parameters and to automatically record data. Temperature was controlled within 1 of 32°C during the day (14 h) and 20°C during the night. Atmospheric CO_2 concentration was monitored with a Bendix[3] infrared gas analyzer and maintained at a level of 330 μL L^{-1} via CO_2 injections through solenoid valves and rotameters. Solar radiation, SPAR unit atmospheric CO_2 concentration, and air, leaf, and soil temperatures were automatically recorded. Thermocouples were used for the temperature measurements and an Eppley[3] pyranometer was used outside the SPAR units for measurement of solar radiation. Independent measurements indicated that the Plexiglas transmitted 97% of the incident photosynthetically active radiation (PAR). Solar radiation and temperature measurements were averaged over 15-min periods. The cumulative length of CO_2 injections during each 15-min period were also recorded. Rotameter flow rates were entered manually. Gas law corrections of the volumetric CO_2 data were made, and the CER data were reported as μmol CO_2 m^{-2} ground area s^{-1}. Algebraic adjustments in the CER data were made for changes in the mass of CO_2 held in the cabinet air from the beginning to the end of the period.

Cotton ('Stoneville 213') was planted on 8 June 1980 in three rows in each cabinet. Each row was 0.5 m long with

0.8 m between rows. Emergence occurred on 16 June, and 2 weeks later the rows were thinned to six plants each. All SPAR units were kept open to outside air during the first month of the experiment. On 10 July, 1 week before appearance of the first squares, the cabinets were closed and kept under controlled temperature and CO_2 conditions.

The units were irrigated daily. A complete Hoagland solution was added to the irrigation stream three times per week. Also, a N fertilizer (ammonium nitrate) was applied several times during the season. These nutrient amendments were enough to constitute a luxury supply in all units. Two of the units were irrigated continuously and served as the control ("C") treatment. In the other three units, irrigation was stopped on 13 August, just before the appearance of the first blooms. At that time, the volumetric water content of the vermiculite medium was 0.39 m^3/m^3. No water was added to those units until 25 September. Two of these units dried out slowly and served as the low water ("L") treatment. The third dried much faster because it was kept open to the outside air from 13 August to 8 September. This cabinet served as the extra low water ("XL") treatment.

Beginning on 12 August, each cabinet was opened twice weekly at 1200 h for a short period, during which pressure bomb (23) measurements were made of the water potentials of three young fully expanded leaves from the fifth or sixth nodes from the top of the plant. The heights of the six plants in the center row of each cabinet were measured. On 29 August, 10 small leaves with maximum widths between 0.02 and 0.06 m were tagged in each unit. The maximum widths of these leaves were recorded twice weekly until 17 September. The area of each leaf was calculated as 0.7 of the squared leaf width. The 0.7 factor was based on previously unpublished data. Carbon exchange rate and growth increments for the 3- to 4-day periods were related to the averages of the leaf water potentials measured at the beginning and end of each period.

Black mesh screens, graduated in density as a function of depth in canopy, were hung around the sides of each

SPAR unit cabinet on 12 August. They were adjusted daily to the height of the enclosed crop to simulate within and between row light competition in field plantings. Measurements of CER were made from 22 August to 26 September in treatments C and L, and from 8 to 22 September in treatment XL (after temperature control was established and that chamber was closed). Carbon exchange rate data taken at 15-min intervals for each SPAR unit were pooled into 10 periods of 3 to 4 days each. Within each of these periods, a second-degree polynomial was fitted to relate CER to corresponding 15-min values of average solar radiation. For comparisons among moisture regimes, CER values at 698 W m^{-2} (1 langley min^{-1}) were computed from these polynomials. Canopy light capture was measured throughout the experiment by means of traversing PAR sensors at ground level referenced to a PAR sensor above the crops in the chambers. Light interception ranged from 0.92 on 22 August to 0.97 on 14 September with no significant differences among treatments.

RESULTS AND DISCUSSION

Average leaf water potential values (at 1200 h) are presented in Fig. 1. The fluctuations within each of the treatments are due to variations in cloud cover prior to and during the measurement period. Standard errors of estimate were calculated on the basis of the error mean squares for the leaves in each sample on each period. Values for the continually watered SPAR units ranged from -1.3 to -1.8 MPa during the measurement period. After 22 August they ranged from -1.6 to -2.1 and -1.8 to -2.5 MPa in treatments L and XL, respectively.

Plants in the well-watered units grew steadily until they reached the top of the cabinet (1.5 m). An immediate effect of water stress on vegetative growth in the other three units was observed. Final plant height in treatments L and XL was 1.13 m and 1.04 m, respectively. Rate of increase in plant height is plotted against leaf water potential for each measurement period in Fig. 2. The rate declined in re-
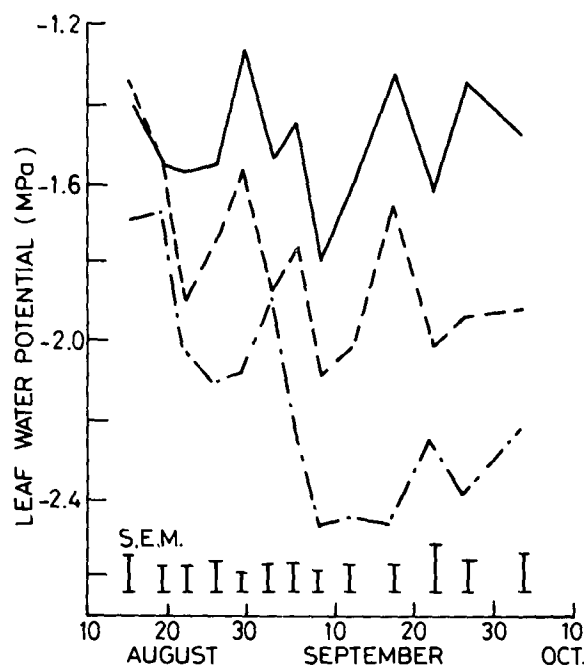

Fig. 1. Midday values of leaf water potentials of the three irrigation treatments. ————, treatment C; — — — —, treatment L; —·—·—, treatment XL; S.E.M. = standard error of the mean of three measurements for each date.
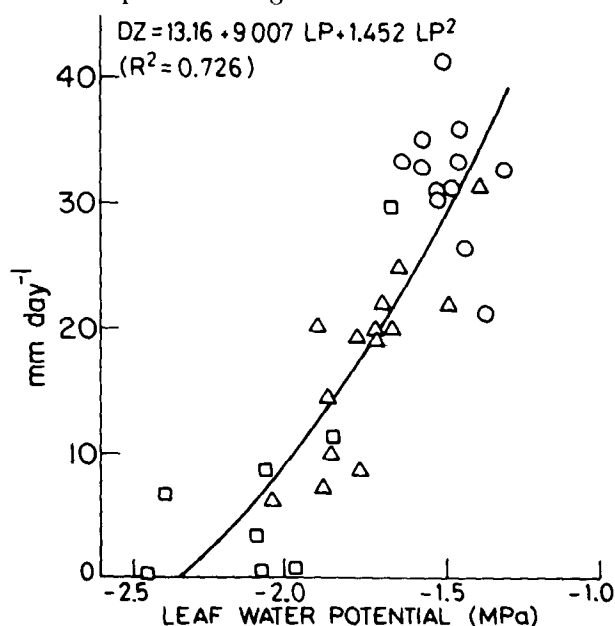

Fig. 2. The relationship between growth rate of plant height (DZ) and midday values of leaf water potential (LP). O = treatment C; $\triangle$ = treatment L; $\square$ = treatment XL.

$$DZ = 13.16 + 9.007\ LP + 1.452\ LP^2$$
$$(R^2 = 0.726)$$

sponse to water stress until it was nearly zero at -2.0 to -2.4 MPa. A second degree polynomial regression was calculated for the rate of stem elongation, DZ (m per day), on midday leaf water potential, LP (MPa). This function (Fig. 2) indicates no growth at -2.4 MPa, and an estimated growth rate of 44 mm day^{-1} at -1.2 MPa, which is probably the highest midday value found in cotton under field conditions. Grimes and Yamada (13) reported a linear regression, with somewhat lower rates of growth at the higher levels of leaf water potential, probably because high leaf water potentials are frequently associated with lower temperatures under field conditions.

Water stress also had a very large effect on the growth rate of leaves. Final area per leaf averaged 120, 58, and 27×10^{-4} m^2 in treatments C, L, and XL, respectively. The average growth rates exhibited

$$DL = 44.89 + 33.98\,LP + 6.38\,LP^2$$
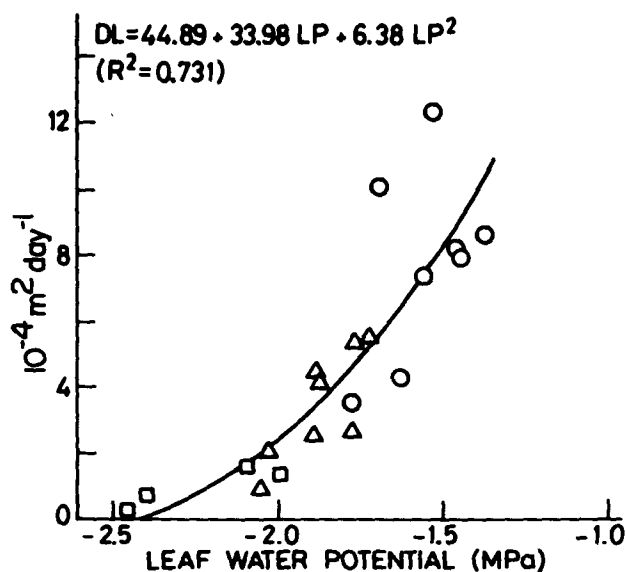$$(R^2 = 0.731)$$

Fig. 3. The relationship between growth rate of leaf area of tagged leaves (DL) and midday values of leaf water potential (LP), treatments marked as in Fig. 2.

the same relationships to leaf water potential for all the treatments (Fig. 3). Leaf growth rate declined in response to water stress and approached zero at -2.0 to -2.5 MPa. A second degree polynomial regression was calculated for the rate of growth of leaf area, DL (m^2 day^{-1}), on midday leaf water potential, LP (MPa). This function (Fig. 3) indicates no leaf growth at -2.43 MPa and a growth rate of 13.3×10^{-4} m^2 day^{-1} at -1.2 MPa. Jordan (15) found that the threshold for leaf growth of cotton seedlings was -0.8 MPa, and Klepper et al. (17) reported that top growth of cotton ceased entirely when early morning potentials were below -0.5 to -0.7 MPa. Cutler and Rains (9) found that the threshold for cotton leaf enlongation was -1.5 MPa, and for preconditioned plants it was -1.9 MPa. The discrepancies among the results reported in the literature are probably because some authors refer to instantaneous rates of growth and leaf water potentials, whereas others relate daily increments of growth to midday values of leaf water potentials. Also, osmotic adjustment has a pronounced effect on the response to water stress (2,3,9,10,24), and therefore different results may be obtained when the drying is gradual or immediate. The results of our experiment were obtained under gradual drying (Fig. 1), and it may be assumed that osmotic adjustment occurred.

Carbon exchange rates for three out of the 10 measurement periods (Fig. 4) show that differences between the well-watered control and the drier treatments increased continuously from 2 September to 22 September. The CER of treatment XL was lower than that of L whenever it was measured. Radiation varied from 150 to 1000 W m^{-2} (0.2–1.4 langley min^{-1}), and the effect of radiation intensity on CER was large in all cases. Light saturation was not approached in the irrigated treatment. This was also reported by Baker et al. (4).

The effect of water stress on CER was similar over a wide range of radiation levels. The radiation level of 698 W m^{-2} (1 langley min^{-1}) was taken as a basis
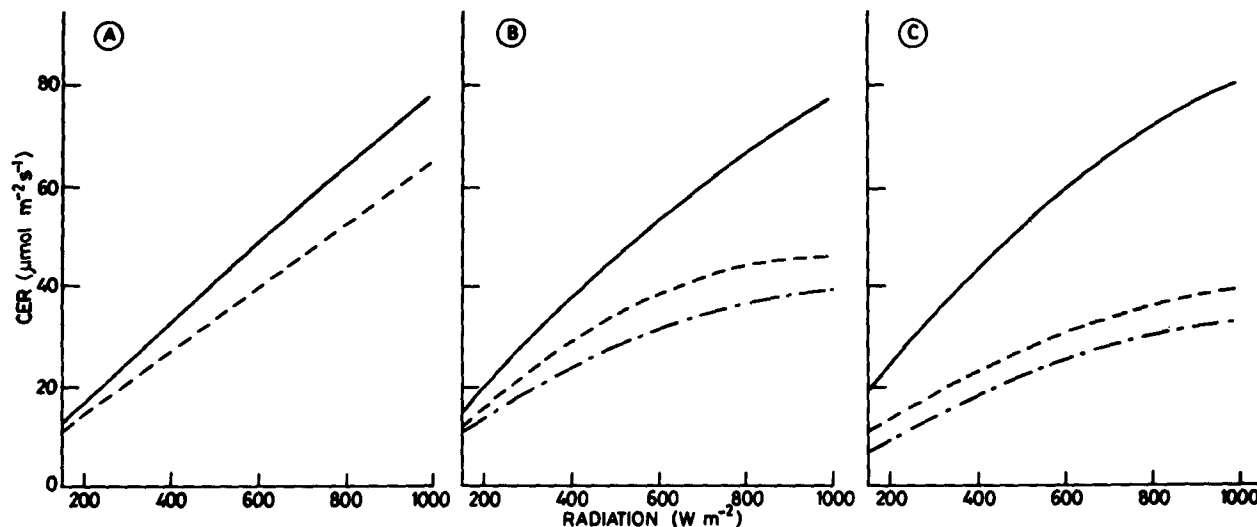

Fig. 4. Fitted response curves, relating CER (μmol CO$_2$ m^{-2} s^{-1}) to solar radiation. Each case represents the pooled data of 3-day periods around the following dates: A, 2 September; B, 12 September; C, 22 September. ———, treatment C; – – – – –, treatment L; — — —, treatment XL; S.E.M. = standard error of the mean of three measurements for each date. R^2 values for C, L, and XL were, respectively: A, 0.75, 0.78; B, 0.88, 0.78, and 0.75; C, 0.71, 0.60, and 0.76.

for comparing moisture treatments. Although the stressed crops abscised more leaves than did the non-stressed crops, canopy light capture at 1200 h remained in excess of 92% in all units throughout the experiment. The values of CER, as predicted by the regression equations for 698 W m^{-2}, are presented in Fig. 5. The CER of treatment C was nearly steady at 50 to 70 μmol CO_2 m^{-2} s^{-1}. In treatment L it declined after 29 August and reached values of 35 to 40 μmol CO_2 m^{-2} s^{-1} at the end of the measurement period. In the extremely dry treatment XL, CER was approximately 7 μmol CO_2 m^{-2} s^{-1} lower than in treatment L.

Carbon exchange rate at 698 W m^{-2} is plotted against midday leaf water potential (LP) in Fig. 6. Before 17 September, when leaf water potential decreased from -1.4 to -2.5 MPa, CER was decreased from 65 to 35 μmol CO_2 m^{-2} s^{-1}. The later data of treatment C followed the same pattern, but in treatments L and XL much lower CER values were found after 17 September. The entire data set from treatment C and the data from the other treatments prior to 17 September were pooled, and a second degree polynomial as fitted to the pooled data set (Eq. [1], Fig. 6). The results of treatments L and XL after 17 September followed a quite different pattern, with CER values being much lower than those predicted
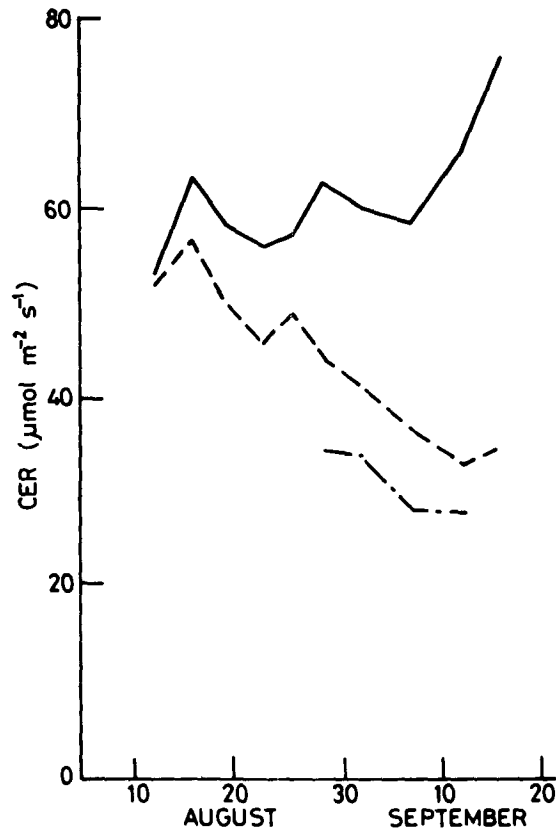
by this equation. Another polynomial was fitted to these data (Eq. [2], Fig. 6). It should be noted that canopies from the L and XL treatments after 17 September consisted almost entirely of old leaves because leaf growth had stopped at about 4 weeks before this date.

Constable and Rawson (7,8) reported that maximum photosynthesis per unit leaf area was obtained 13 to 15 days after leaf unfolding when the leaf was 75 to 90% of its maximum size. Krieg (18) found this when the leaf was 60 to 70% of its maximum size. Maximum rates of photosynthesis were maintained for an additional period of 13 to 15 days (7), or 20 to 35 days (18), before declining linearly. The rates declined to 50% of the maximum when the leaves were 50 days old (18) and to 20% of the maximum when the leaves were 70 days old (7).

The results in Fig. 6 indicate that there are probably two distinct mechanisms causing the decline of CER in cotton canopies as a consequence of water stress. There is a direct effect on the photosynthetic rate of each leaf, which may be attributed to the closing of stomata, high mesophyll resistance, or reduced Hill reaction activity. In addition to that, there is a long-term effect probably caused by canopy senescence. After a period of about 4 weeks of reduced leaf growth, there were very few young fully active leaves in the canopy. Solar radiation was mainly intercepted by older leaves that presumably were less efficient in their photosynthesis (7,18). The effect of water stress may be enhanced by a heavy boll load or by other factors causing a reduced leaf growth or an earlier leaf senescence.
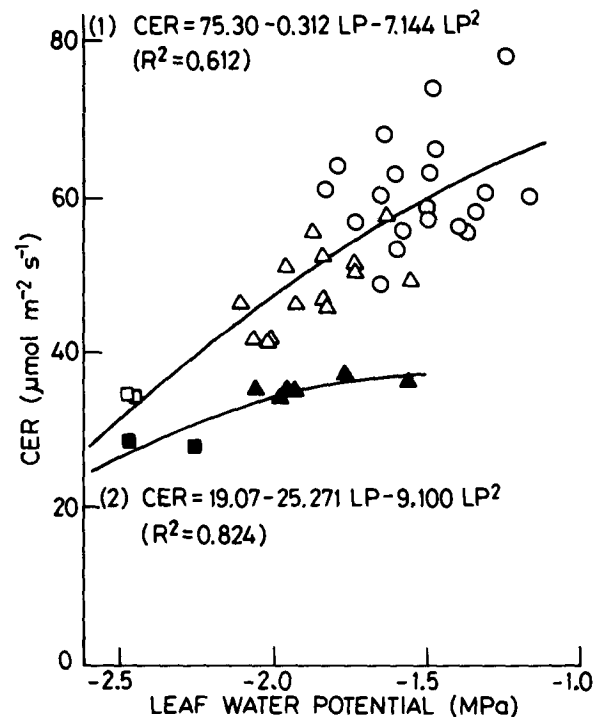

Fig. 5. Carbon exchange rate at a radiation level of 698 W m^{-2}, as predicted from fitted light response curves for the three irrigation treatments. ———, treatment C; — — — — —, treatment L; — — -, treatment XL; S.E.M. = standard error of the mean of three measurements for each date. Each point is derived from a second degree polynomial fitted for the pooled data of 3 or 4 days.

(1) CER = 75.30 $-$0.312 LP$-$7.144 LP^2
(R^2 =0.612)

(2) CER = 19.07$-$25.271 LP$-$9.100 LP^2
(R^2=0.824)

Fig. 6. The effect of midday leaf water potential (LP) on CER at a radiation level of 698 W m^{-2}, as predicted from fitted light response curves for each SPAR unit. Treatments are marked as in Fig. 3; full data points indicate observations made after 17 September in treatments L and XL.

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