

Water Deficit Effects on Transpiration and Leaf Growth¹

W. D. Rosenthal, G. F. Arkin, P. J. Shouse, and W. R. Jordan²

ABSTRACT

Reductions of leaf development and transpiration are closely related to soil water deficits. Few studies have analyzed the effects of water deficits on both processes during different growth stages. A study was conducted to analyze and quantify the effects of water deficits during different growth stages on leaf development (number, extension, and senescence) and transpiration rates of sorghum [*Sorghum bicolor* (L.) Moench] and cotton (*Gossypium hirsutum* L.). The study was conducted at the Blackland Research Center at Temple, TX, in a glasshouse using covered pots and in the field using covered lysimeters. In the glasshouse, the sorghum and cotton pre-flowering treatments were irrigated at 60, 35, 15, and 0% of water used in the control pots. In the lysimeters, water deficit treatments of 50, 30, and 0% plant available water (PAW) were imposed on sorghum during the vegetative period (before panicle initiation and between panicle initiation and anthesis) and after anthesis. Leaf length and transpiration rates were measured two to three times per week. Leaf extension was reduced to 0% of well-watered sorghum and cotton when the PAW decreased from 50 to 0%. Transpiration per unit leaf area decreased from 100 to 0% of well-watered sorghum and cotton when PAW decreased from 28 to 0% for each stressed period. Sorghum leaf senescence was enhanced and leaf number increased in the 0% PAW treatments compared to the well-watered and 30% treatments. These relationships of leaf development, transpiration, and PAW compare favorably with other published results. The PAW threshold values when each process is affected would be useful in developing criteria for scheduling irrigation and in improving the accuracy of crop growth models in estimating leaf development and transpiration.

Additional index words: Sorghum, Cotton, Soil water deficit, Lysimeter, Dry matter, Plant available water, Leaf senescence, Growth stage.

A NUMBER of relationships have been published that describe the effects of water deficit on leaf growth (LG) and transpiration (T) (Meyer and Green, 1980; Acevedo et al., 1971; Ritchie et al., 1972). The percentage of plant available water (PAW) has been used to describe water status when T and LG decrease from the potential rate (Ritchie et al., 1972; Meyer and Green, 1980; Rosenthal et al., 1977; Tanner and Jury, 1976). At low PAW, reductions in T are generally accompanied by increased stomatal resistance and decreased photosynthetic rates, dry matter accumulation, and economic yield (Y) (Turner, 1974). Many relationships have been developed comparing Y to T (Hanks 1974; Garrity et al., 1982; Arkley, 1963). The sensitivity of Y to T relationships differ between growth stages, with the most sensitive period for sorghum [*Sorghum bicolor* (L.) Moench] being the early boot through anthesis growth stages when the potential number of seeds per panicle is determined (Eastin et al., 1983; Garrity et al., 1982; Meyers, et al. 1984; Vanderlip and Reeves, 1972; Whiteman and Wilson, 1965).

¹ Contribution from the Texas Agric. Exp. Stn., Texas A&M Univ., College Station, TX 77843. Contribution no. TA-22156. Received 14 Nov. 1986.

² Research scientist, Blackland Res. Ctr., Texas Agric. Exp. Stn., P.O. Box 6112, Temple, TX 76503-6112; associate director, Georgia Agric. Exp. Stn., Griffin, GA 30212; soil scientist, U.S. Salinity Lab., USDA-ARS, Riverside, CA 92501; and director, Texas Water Resources Inst., Texas A&M Univ., College Station, TX 77843, respectively.

Generally, the most sensitive period for cotton (*Gossypium hirsutum* L.) yield is during peak flowering (Marani and Horowitz, 1963; Marani and Fuchs, 1964).

Water deficits may also affect canopy development through effects on total leaf number and rates of individual leaf emergence from the whorl, and on leaf extension and senescence (Arkin et al., 1983). All of these components are important in determining the surface area available for transpiration and assimilate production (Meyers et al., 1984; Parameswara and Krishnaswamy, 1982; El-Sharkawy et al., 1965). Acevedo et al. (1971) and Hsiao et al. (1976) found corn (*Zea mays* L.) leaf extension to be more sensitive to water deficits than transpiration. Meyer and Green (1981) found the lower limit of PAW for maximum soybean [*Glycine max* (L.) Merr.] leaf extension to be approximately 25%. The lower threshold for maximum T is also a function of evapotranspiration and soil hydraulic conductivity (Slabbers, 1980).

In spite of the abundant literature on water deficit effects on leaf extension, few studies have investigated more than one plant process during water deficits applied at different growth periods (Hsiao, 1973; Ritchie, 1981). The purpose of our study was twofold: (i) analyze and quantify the effects of water deficit on sorghum leaf number and senescence, and sorghum and cotton leaf extension, and (ii) analyze and quantify water deficit effects on transpiration before flowering in cotton and sorghum, and after flowering in sorghum.

MATERIALS AND METHODS

Glasshouse Study. During 1982, a study was conducted in a ventilated glasshouse at the Blackland Research Center at Temple, TX, using thirty 50-L pots filled with Frio silt loam (fine, montmorillonitic, thermic Cumulic Haplustoll) (75%) and peat moss (25%). The pots were covered with polyethylene plastic sheets fitted around the base of each plant stem and covered with dry sand to minimize soil evaporation. Holes were drilled at the bottom of the pots to allow for free water drainage. Before planting, each pot was irrigated until water drained freely from the bottom. Weight changes were measured every other day using a 700-kg load cell, and were taken as transpiration rates. After anthesis, total plant weight was measured after plants remained wilted for 4 days. The changes of plant weight between measurements were small compared to the pot weight changes such that it resulted in less than 2% error and was ignored in the analysis.

Sorghum (cv. 100M) and cotton (cv. SP37-H) were planted in 15 pots on 1 July. After emergence, seedlings were thinned to two plants per pot. Adequate minerals to provide for growth throughout the season were supplied before planting.

The area of individual green sorghum leaves (LA) was determined from measurements of leaf length (LL) and maximum leaf width (LW) every second day using Eq. [1] suggested by Stickler et al. (1961):

$$LA = LL \times LW \times 0.75 \quad [1]$$

Measurements were taken from leaf emergence in the whorl until the leaf ligule had appeared. Leaves were numbered from the first leaf at plant emergence (Leaf 1) to the flag leaf

Table 1. Mean maximum cumulative leaf area (LA) and standard deviations (SD) for each plant available water (PAW) treatment during 1983 and 1984.

Year	Treatment	LA	
		m ²	
1983	control/control	0.2185	0.0304
	control/30% PAW	0.1697	0.0227
	control/0% PAW	0.1794	0.0329
	30% PAW/control	0.1433	0.0400
	30% PAW/30% PAW	0.0873	0.0358
	30% PAW/0% PAW	0.1093	0.0094
	0% PAW/control	0.0648	0.0125
	0% PAW/30% PAW	0.1387	0.0455
	0% PAW/0% PAW	0.0431	0.0129
	LSD(0.05)	0.0422	
1984	control	0.1499	0.0438
	30% PAW	0.1315	0.0250
	0% PAW	0.0974	0.0132
	LSD(0.05)	0.0310	

(Leaf *n*). Dates for 50% senescence (50% of the individual leaf yellow or necrotic) of individual leaves, leaf emergence, anthesis, and physiological maturity were also recorded.

The area of individual main stem cotton leaves was calculated using the method described by Constable (1981):

$$LA = 1.053(LL)^2 - 1.96(LL), \quad [2]$$

where LL is leaf length (cm). Leaf length was measured from emergence to maximum size, which was assumed to be attained when leaf length did not change between measurements.

The experimental design consisted of five irrigation treatments imposed before anthesis and three replications. After sowing, every pot was irrigated to field capacity. The control pots were maintained on an irrigation regime sufficient to replace the water lost during the 2-day period measurement interval. Pots in the four water stress treatments were irrigated when water loss during the previous 2 days decreased to 60, 35, 15, and 0% of the well-watered control pots. The treatments were based on water use rather than PAW because PAW could not be determined until after flowering and after all leaves had attained full size. Treatment pots were irrigated to field capacity and then irrigated every other day in amounts sufficient to replace water lost during the previous 2 days. Field capacity was determined 2 days after the irrigation at planting. The lower limit was determined for all pots by withholding water after anthesis. When pot

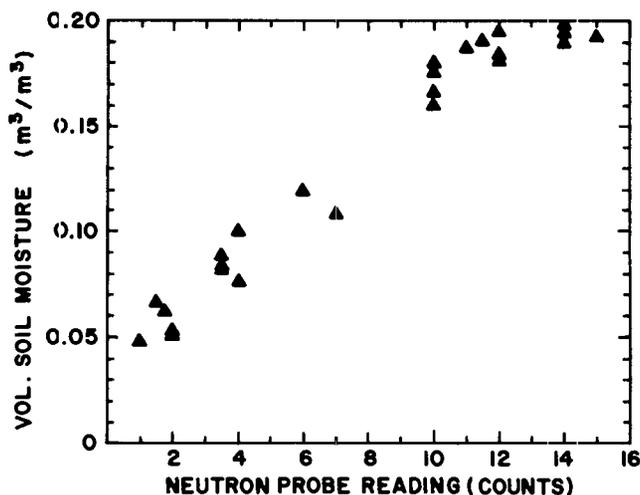


Fig. 1. Comparison of surface neutron probe data to measured volumetric soil moisture content in 0.25-m layers.

weight did not change and the leaves remained wilted over a 4-day period, the lower limit of soil water was assumed to have been reached. Plant available water was then calculated for each pot using the following equation:

PAW(%)

$$= [(WT_a - WT_l)/(WT_u - WT_l)] \times 100, \quad [3]$$

where WT_a is the weight of the pot on a given date, WT_l is the pot weight at the lower limit of plant available water, and WT_u is the pot weight at the drained upper limit.

Lysimeter Study. In 1983 and 1984, water deficit studies were conducted with sorghum at the Blackland Research Center using 24 lysimeters (1.7 m deep with horizontal dimensions of 0.6 by 0.18 m). Each lysimeter consisted of a steel chamber with one glass face, placed in concrete retaining liners. A complete description of the facility is given by Arkin et al. (1978).

Each lysimeter was filled with an alluvial loamy sand (subsoil of Patrick soil—clayey over sandy or sandy skeletal, carbonatic, thermic Typic Calcicustoll). While each lysimeter was being filled with soil, the lysimeter was periodically shaken and the soil tamped to approximate bulk densities of 1.2 to 1.3 Mg m⁻³. Six grams of 25-10-0 (N-P-K) fertilizer were incorporated into the surface 0.15 m of soil in the lysimeters. To reduce evaporation, each lysimeter was covered

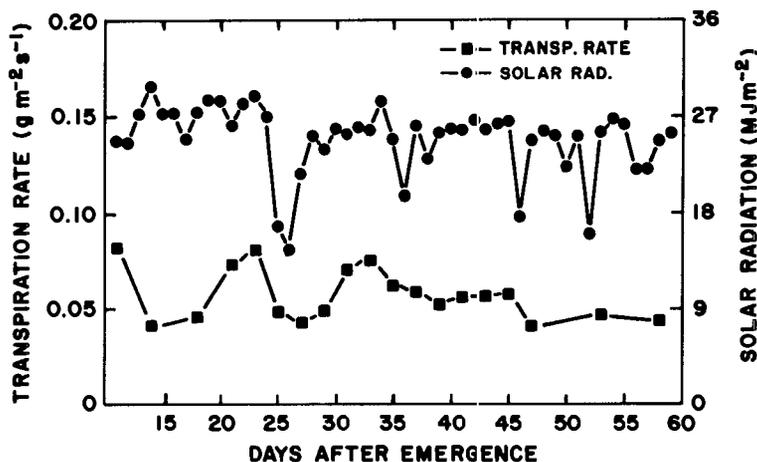


Fig. 2. Daily solar radiation and average 2-day sorghum transpiration rates per unit leaf area for the well-watered (100%) irrigation treatment in the glasshouse.

with sheets of polyethylene plastic and styrofoam. Two 0.05-m-diam holes were cut in the center of the plastic and styrofoam to allow for plant growth.

The grain sorghum hybrid 'ATx378 × RTx430' was sown in and around each lysimeter in rows 0.69 m apart on 31 Mar. 1983 and 15 Mar. 1984. After emergence, seedlings were thinned to two plants per lysimeter, which was equivalent to a density of 18 plants m^{-2} . Emergence, anthesis, and physiological maturity dates were recorded. The maximum rooting depth on the glass face was observed weekly by lifting the lysimeters out of the concrete liners, and was used in determining PAW in the root zone.

In 1983, the study consisted of a well-watered control and eight water deficit treatments imposed before anthesis. These treatments are listed in Table 1 where 30 and 0% PAW are the minimum PAW percentages allowed in the root zone before irrigation. Treatments within the table are listed as the minimum PAW before and after panicle initiation (e.g., "control/30%" is a control treatment before and irrigation at the 30% PAW treatment after panicle initiation). Panicle

initiation was assumed to have occurred when the eighth leaf had fully grown (Vanderlip and Reeves, 1972). Water deficits were assumed to equally affect the timing of panicle initiation and the eighth leaf stage. Soil moisture was maintained above 50% PAW in both the well-watered control and in the water deficit treatments after the final stress period. To attain the desired PAW percentage before panicle initiation, the soil was initially air-dried before being put into the lysimeters and then irrigated with 10 to 20 mm of water to permit plant emergence. Small amounts of water (60–70 mm) were carefully metered to each lysimeter after emergence. These amounts allowed PAW to decrease to the desired PAW percentages before panicle initiation. Pre-panicle initiation water deficits were removed by irrigating the lysimeters at panicle initiation, approximately 29 days after emergence. During the post-panicle initiation period, PAW within the lysimeters of the control treatment was maintained above 50% by irrigating with 60 to 150 mm of water; in the 30% PAW treatment, PAW was maintained above 30% by irrigating with 20 to 90 mm of water. After anthesis,

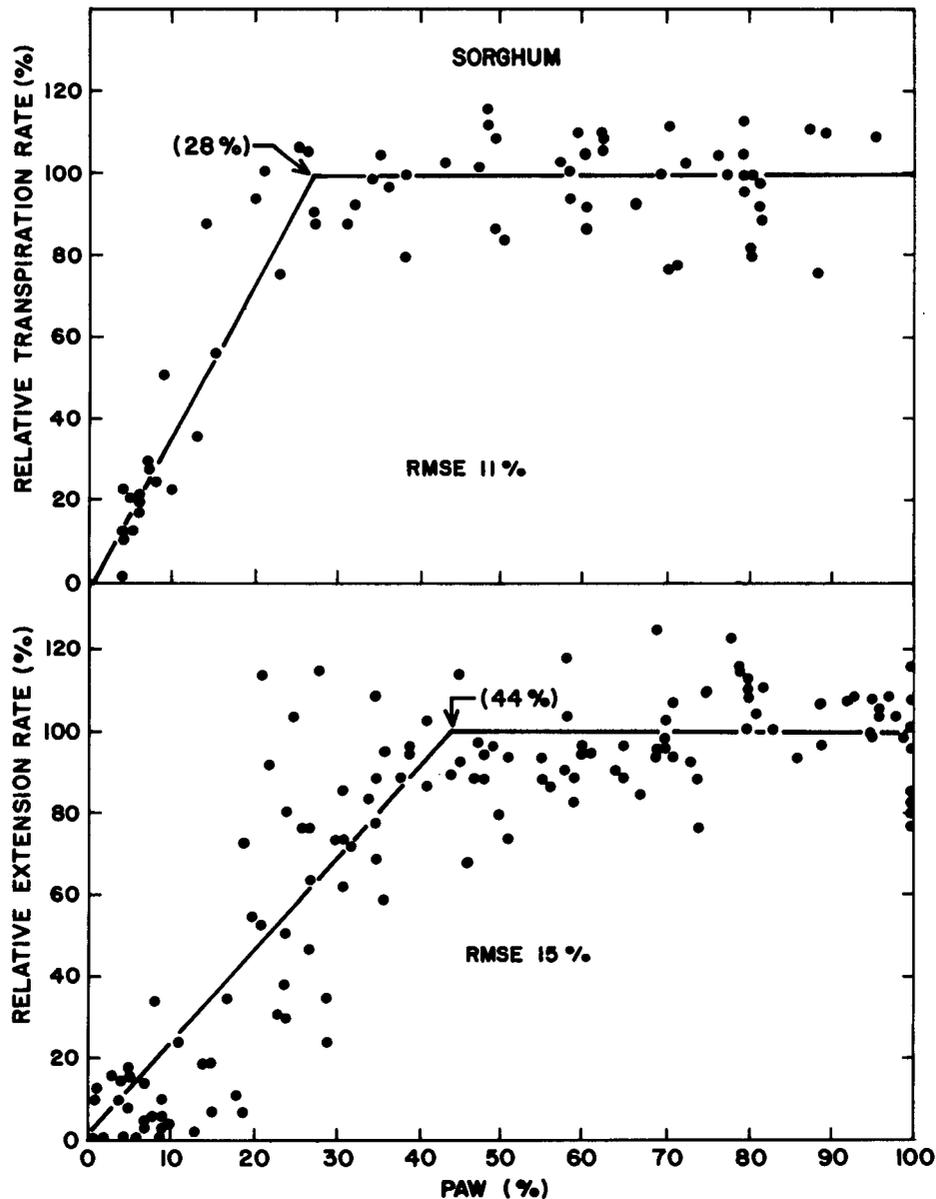


Fig. 3. Relative sorghum transpiration rates per unit leaf area and relative leaf extension rates as a function of plant available water (PAW). Plotted data represents relative transpiration and leaf extension data measured between 30 and 60 days after emergence in the glasshouse.

the lysimeters were irrigated to the drained upper limit throughout the profile. Any tillers that developed after irrigation were removed.

During 1984, water deficits were induced during the grain filling stage only. To eliminate water deficits during the vegetative stage, the soil was initially saturated and irrigated to the weight of the lysimeter at saturation every 7 to 20 days until anthesis. The same PAW percentages as those of the previous year were then imposed on plants in the lysimeters during the grain filling stage (Table 1). After anthesis, lysimeters in the control treatment were irrigated with 120 to 400 mm of water, while lysimeters in the 30% PAW treatment were irrigated with 50 to 90 mm of water.

Transpiration was calculated from neutron scattering with a surface moisture probe³ (Model 3411B; Troxler Electronics Laboratory, Inc., Research Triangle Park, NC) by summing the change in volumetric soil moisture percentages between measurements within each 0.25-m layer of the observed root zone on the glass face every 4 to 7 days. The 0.25-m layer

increment was selected because it corresponded to the length of the surface moisture probe. The neutron probe was calibrated for soil type by developing a relationship between volumetric soil moisture percentage determined gravimetrically in 0.25-m increments of the total soil profile and corresponding probe data. Gravimetric samples and the probe data were collected 2 and 7 days, respectively, after 260, 190, 160, and 0 mm of water were applied to four lysimeters, respectively, filled with air-dried soil. Volumetric water contents at soil water potentials of 0.01 and 1.5 MPa were determined using a pressure plate. Volumetric soil water content within a 0.25-m layer could be measured within $\pm 0.01 \text{ m}^3 \text{ m}^{-3}$, which equals $\pm 7.0 \text{ mm T}$ for the 1.7-m profile (Fig. 1). Drainage from the lysimeters was estimated from volumetric soil water percentage differences between measurements at the bottom layer, and was subtracted from total water lost from the lysimeters. The resulting water use estimates from the surface neutron probe data were compared to lysimeter weight changes during the same period as mea-

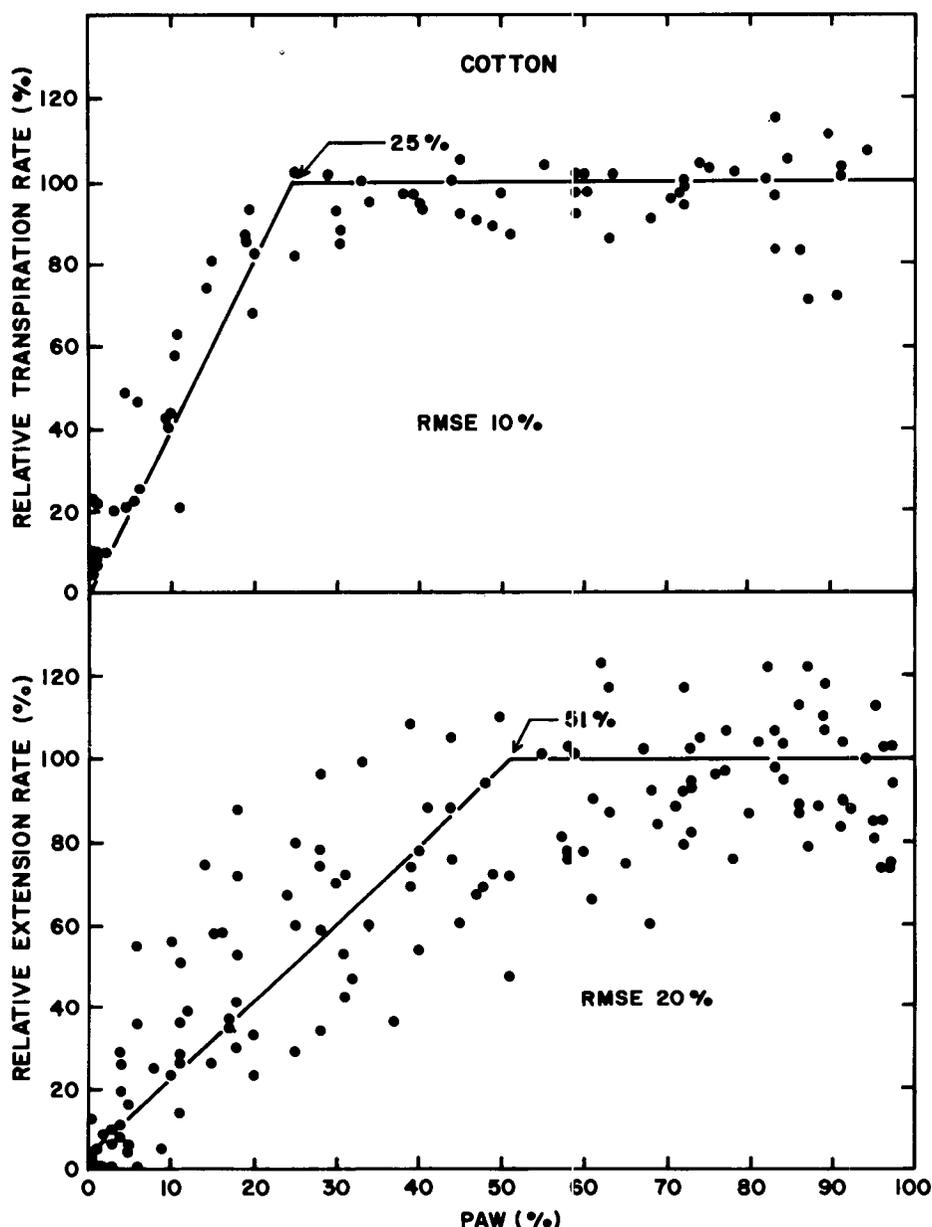


Fig. 4. Relative cotton transpiration and leaf extension rates plotted as a function of plant available water (PAW). The measurement dates were between 30 and 60 days after emergence in 1982, in the glasshouse.

sured by a load cell³ (T3P1-C 700-kg load cell; BLH Electronics, Inc., Waltham, MA).

Leaf area (LA) for each plant in the lysimeters was determined by measuring the length and maximum width of each green leaf three times per week in 1983 and once per week in 1984, and using Eq. [1]. Individual leaf senescence and leaf numbers were observed three times per week in 1983 and once per week in 1984.

Daily meteorological data collected with a micrologger³ (CR21; Campbell Scientific, Logan, UT 84321) were used to calculate potential evapotranspiration using the modified Penman equation (Dorrenbos and Pruitt, 1977). Transpiration from lysimeters was then compared to potential evapotranspiration rates during the period between measurements and between treatments.

To eliminate transpiration differences due to leaf area, the transpiration rate was calculated as water lost per unit of leaf area. Relative transpiration was then calculated as the ratio between transpiration from water-stressed and well-watered pots or lysimeters. Relative leaf extension was calculated as the ratio between leaf extension of water-stressed and well-watered pots or lysimeters. Relative transpiration and leaf extension were then compared to PAW in the stressed pots or lysimeters.

A nonlinear regression technique (Ray, 1982) was used to determine the inflection point (IP) where two linear functions describe relative leaf extension, transpiration, and PAW. One function is $T/T_{max} = 1$ for $IP < PAW < 100\%$; the other function is $T/T_{max} = PAW/IP$ for $0\% < PAW < IP$, where IP is the inflection point for the two functions. Other functions may better describe the relationships, but to compare the IP with published results, these linear functions were used to describe the relationships.

Aboveground dry weight was measured during 1983 at physiological maturity and was compared to cumulative transpiration. Sorghum midge [*Conterinia sorghicola* (coquillet)] reduced final grain yield, so grain weights in the water deficit treatments were not representative of plant water status. In 1984, grain and aboveground dry weights and cumulative transpiration were measured at physiological maturity. Dry weights were then compared to cumulative transpiration from emergence to physiological maturity.

RESULTS AND DISCUSSION

Glasshouse Study. Transpiration, defined as water lost between successive measurements per unit of leaf area, was significantly reduced as water deficits developed. Well-watered transpiration rates for sorghum were $8.0 \times 10^{-2} \text{ g m}^{-2} \text{ s}^{-1}$ (Fig. 2), which compared well to transpiration from well-watered plants having low plant resistances (Gates, 1980). The reduced transpiration with time is believed to be due to the percentage of the leaves being shaded and not transpiring at the potential rate. Measurements of shaded leaf area were not taken, however. Transpiration rates also decreased when solar radiation decreased during a 3-day period. Since only main stem cotton leaf area was measured, transpiration rates were calculated as water lost between successive measurements per unit of main stem leaf area. The relationship between cotton transpiration and time followed the same trend as that of sorghum transpiration.

Relative sorghum transpiration was significantly reduced at small PAW percentages (Fig. 3). The IP when

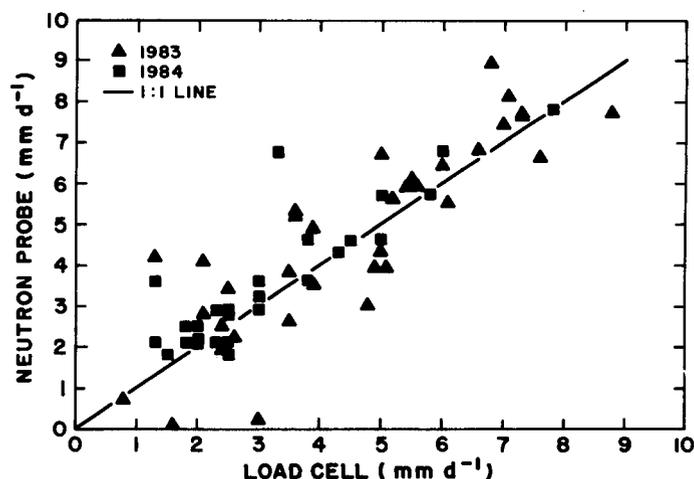


Fig. 5. Comparison of daily water use rates (mm day^{-1}) from lysimeters as measured by a surface neutron probe and a load cell. Plotted data represent rates during the following periods: 61–64, 73–78, and 89–96 days after emergence in 1983, and 35–41, 42–48, 52–55, 55–62, 70–76, 77–83, 84–91, 105–119, and 119–126 days after emergence in 1984.

relative transpiration decreased was $28 \pm 8\%$ PAW. Using the same regression techniques, the PAW percentage when cotton relative transpiration was reduced was not significantly different from that of sorghum ($25 \pm 6\%$ PAW) (Fig. 4).

Cumulative sorghum leaf area was significantly less for plants in the water deficit treatment when T decreased to 1% of the well-watered control pots (Table 1). Leaf growth was reduced due to water deficits approximately 30 days after emergence when PAW < 50%. These leaf area differences can be attributed to a reduction in leaf extension rates, fewer leaves, or enhanced leaf senescence. The relative sorghum leaf extension (ratio between water deficit and well-watered leaf extension rates) decreased when PAW percentages decreased below $44 \pm 10\%$, determined using the same linear regression technique for determining the IP (Fig. 3). The relative leaf extension rates of cotton decreased when PAW percentages were less than $51 \pm 15\%$ (Fig. 4). The effects of water deficits on the relative extension rates of both crops were statistically equivalent, which is somewhat surprising due to the fact that sorghum and cotton have different photosynthetic and transpiration efficiencies. Because water deficits were imposed after panicle initiation, no differences in total number of leaves were observed. The effect of water deficits on leaf senescence was not determined for cotton. For sorghum, enhanced leaf senescence rates were correlated to the periods when PAW was less than 30%. For example, as many as five leaves senesced in the treatment exposed to a minimum of 1% PAW from 30 to 40 days after emergence. Well-watered pots had three leaves senesce during the same period and had PAW greater than 50%. Leaf area differences between treatments were, therefore, attributed to reductions of leaf extension rates and enhanced leaf senescence rates.

Lysimeter Study. Water loss from lysimeters, as measured by the surface neutron probe and a load cell, were highly correlated (Fig. 5). Data in 1983 and 1984 were not significantly different at the 5% level. In addition, transpiration from the well-watered lysimeters

³ Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the Texas Agricultural Experiment Station and does not imply its approval to the exclusion of other products that also may be suitable.

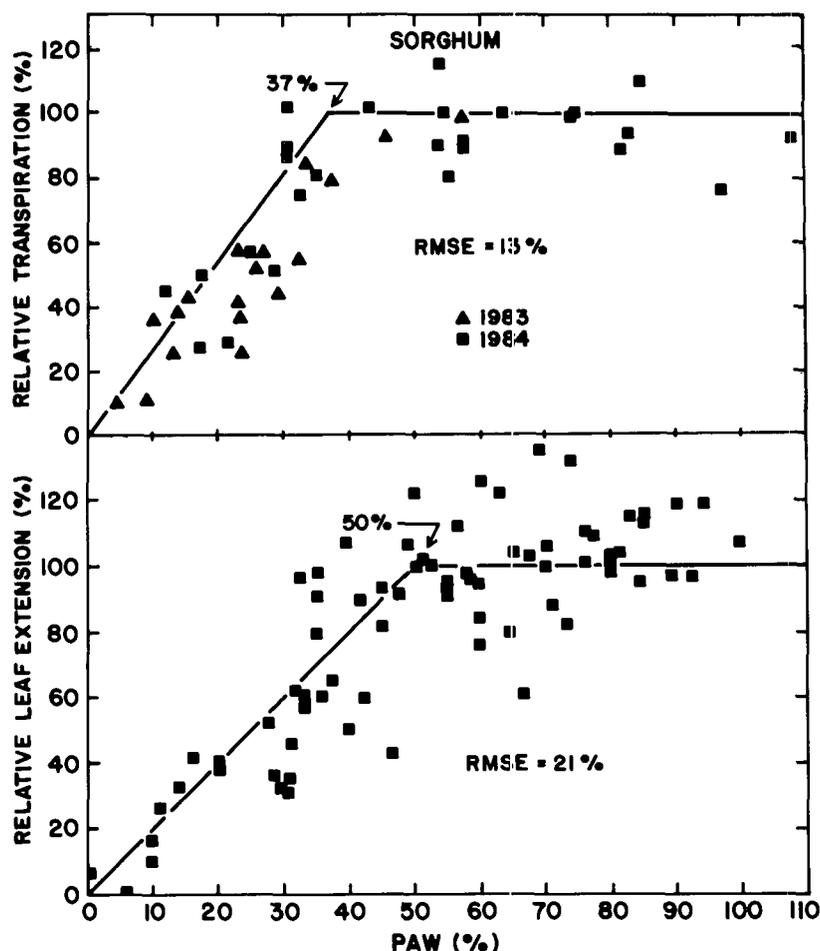


Fig. 6. Relative transpiration per unit leaf area and leaf extension rates as a function of plant available water (PAW) in the lysimeters. Data points represent 4- to 5-day transpiration rates from individual lysimeters measured, using the surface neutron probe during the periods 61-81 and 91-119 days after emergence during 1983 and 1984, respectively. Leaf data was collected between 31 and 60 days after emergence in 1983.

was within 1 to 2 mm of the daily potential evapotranspiration rates (average = 6 mm day⁻¹).

Using the same regression techniques for analyzing the glasshouse data, relative sorghum transpiration from the lysimeters decreased when PAW was less than 37 ± 8% (Fig. 6). The plotted points represent relative transpiration rates from lysimeters during 1983 and 1984 for PAW percentages in the root zone ranging from 5 to 100%. The effects of pre- and post-anthesis water deficits on transpiration were not significantly different (5% level). In addition, the IP when relative

transpiration decreased for sorghum was not significantly different (10% level) as determined from the lysimeters and glasshouse.

Water deficits imposed during the vegetative period significantly (5% level) reduced cumulative leaf area (Table 1). Average total plant leaf area for the well-watered control was more than five times that of the treatment exposed to 0% PAW. All observed leaf growth components (total leaf number, extension, and senescence) were affected by water deficits.

Severe water deficits (30 and 0% PAW) before pan-

Table 2. Mean delay in anthesis (PA), mean duration when PAW < 30% (D) before anthesis, and standard deviation (SD) for each plant available water (PAW) treatment in 1983.

Treatment	PA	SD	D	SD
	no. days			
control/control	0.0	0.0	0.0	0.0
control/30% PAW	3.3	5.8	1.3	2.3
control/0% PAW	4.0	0.7	4.5	2.1
30% PAW/control	13.3	1.5	15.3	3.8
30% PAW/30% PAW	13.0	5.7	13.5	9.2
30% PAW/0% PAW	9.5	5.0	11.5	6.4
0% PAW/control	19.0	4.2	24.0	5.7
0% PAW/30% PAW	11.7	2.9	12.3	2.5
0% PAW/0% PAW	22.0	7.0	20.3	5.5
LSD(0.05)	6.56		6.68	

Table 3. Mean total leaf number per plant (L) and standard deviations (SD) for each plant available water (PAW) treatment during 1983.

Treatment	L	SD
	no. leaves	
control/control	15.5	0.5
control/30% PAW	16.0	0.5
control/0% PAW	15.5	0.0
30% PAW/control	16.7	0.6
30% PAW/30% PAW	16.5	0.0
30% PAW/0% PAW	16.5	0.7
0% PAW/control	17.5	1.2
0% PAW/30% PAW	17.0	0.5
0% PAW/0% PAW	17.8	1.1
LSD(0.05)	1.22	

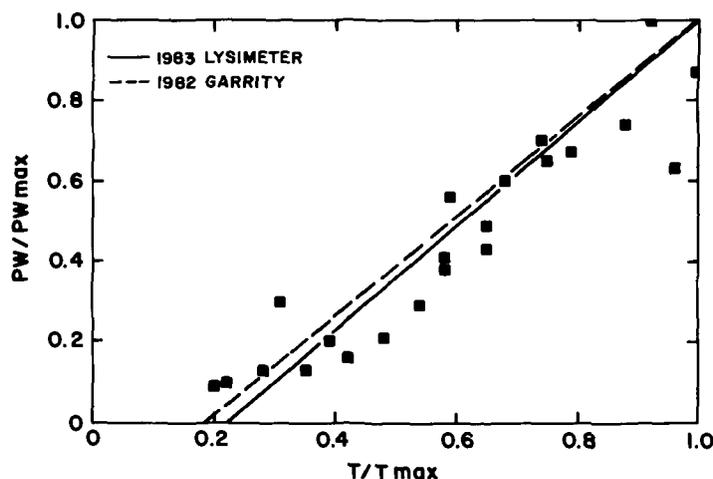


Fig. 7. Relative plant dry weight ($\Sigma PW/\Sigma PW_{max}$) as a function of relative cumulative transpiration ratio ($\Sigma T/\Sigma T_{max}$) at physiological maturity in 1983. The plotted points represent cumulative transpiration and total plant weight for plants exposed to water deficits.

icle initiation delayed anthesis (Table 2). The delay was highly correlated ($R=0.96$) to the period when plants were exposed to PAW percentages of less than 30%. Water deficit treatments that attained 0% PAW before panicle initiation had one to two more leaves than did control plants (Table 3), contrary to the findings of Whiteman and Wilson (1965). However, water deficits could have induced fewer leaves in that study if the delay caused by deficits before panicle initiation exposed plants to shorter daylengths.

Although the number of leaves increased with increasing water deficits, the primary effect of water deficits on cumulative leaf area was expressed through smaller individual leaves resulting from reduced leaf extension rates. Decreased leaf size with decreased PAW resulted from the decreased relative leaf extension rates when PAW was less than $50 \pm 10\%$ (Fig. 6).

The effect of water deficits on leaf senescence was most evident in cumulative leaf area differences at physiological maturity between each water deficit treatment imposed in the lysimeters during grain filling. The average cumulative leaf area for the 0% PAW treatment was significantly different from those for the other treatments at the 5% level (Table 1). These results imply that PAW less than 30% enhances leaf senescence, and agree with those of Fischer and Kohn (1966) where senescence was significantly enhanced by water deficits after anthesis. The enhanced senescence rate may be due to high carbohydrate and N demands in the grain, and the mobilization of those nutrients from older leaves to the grain (Fischer, 1979).

Water deficits during the vegetative period reduced plant dry weight in the lysimeters to 14% of maximum dry weight (Fig. 7). The relationship between relative plant weight, defined as the ratio between plant dry weight (PW) and the maximum plant dry weight (PW_{max}) in the control lysimeters, and the cumulative transpiration ratio, defined as the ratio between cumulative T and the maximum cumulative T (T_{max}) from lysimeters at physiological maturity, is given by the equation

PW/PW_{max}

$$= 1.29 (T/T_{max}) - 0.29, \text{ RMSE} = 0.113 \quad [5]$$

that was forced through the intersection where $PW/PW_{max} = 1$ and $T/T_{max} = 1$. The slope of the equation, 1.29, was not significantly different from the slope for the relationship between relative plant dry weight and the evapotranspiration ratio developed by Garrity et al. (1982) for field-grown plants subjected to water deficits during the vegetative period using a line-source irrigation technique (Fig. 7).

In 1984, grain and vegetative dry weight variability within and between lysimeters was great enough that there was no significant relationship between relative grain and plant dry weight and relative transpiration in each treatment.

SUMMARY

From our studies of cotton and sorghum using pots in a glasshouse and field lysimeters, we found that water deficits below 20 to 30% PAW reduced transpiration, enhanced leaf senescence, and increased leaf number. Deficits below 50% PAW reduced relative leaf extension rates. These results agree with those of Meyer and Green (1980, 1981) for wheat and soybean evapotranspiration and leaf extension, and Ritchie et al. (1972) for cotton and sorghum evapotranspiration. In addition, the results from the glasshouse study were not significantly different from those from the lysimeter study. The reduction in leaf extension induced by soil water deficit also reduced leaf area and total biomass and was highly correlated with a reduction in cumulative transpiration. The relationship between relative biomass and cumulative transpiration for plants exposed to water deficits during the vegetative stage was linear, with a slope not significantly different from the slope for sorghum transpiration and total biomass data collected by Garrity et al. (1982) using a line-source irrigation technique.

REFERENCES

- Acevedo, E., T.C. Hsiao, and P.W. Henderson. 1971. Immediate and subsequent growth responses of maize leaves to changes in water status. *Plant Physiol.* 48:631-636.
- Arkin, G.F., A. Blum, and E. Burnett. 1978. A root observation chamber field installation. *Texas Agric. Exp. Stn. Misc. Pub.* MP-1386.

- , W.D. Rosenthal, and W.R. Jordan. 1983. A sorghum leaf area model. ASAE Tech. Pap. 83-2098. American Society of Agricultural Engineers, St. Joseph, MI.
- Arkley, R.J. 1963. Relationships between plant growth and transpiration. *Hilgardia* 34:559-584.
- Constable, G.A. 1981. Carbon fixation and distribution in cotton: Implications of single leaf measurements to plant performance. Ph.D. diss. Australian National Univ., Canberra, A.C.T.
- Doorenbos, J., and W.O. Pruitt. 1977. Crop water requirements. FAO Irrig. and Drainage Pap. 24. Food and Agriculture Organization, Rome.
- Eastin, J.D., R.M. Castleberry, T.J. Gerik, J.H. Hultquist, V. Mahalakshmi, V.B. Ogunlela, and J.R. Rice. 1983. Physiological aspects of high temperature and water stress. In C.D. Raper, Jr., and P.J. Kramer (ed.) Crop reactions to water and temperature stresses in humid, temperate climates. Westview Press, Boulder, CO.
- El-Sharkawy, M., J.D. Hesketh, and H. Muramoto. 1965. Leaf photosynthesis and other growth characteristics among 26 species of *Gossypium*. *Crop Sci.* 5:173-175.
- Fischer, R.A. 1979. Growth and water limitations to dryland wheat yield in Australia. A physiological framework. *J. Aust. Inst. Agric. Sci.* 45:83-94.
- , and G.D. Kohn. 1966. The relationship of grain yield to vegetative growth and post-flowering leaf area in the wheat crop under conditions of limited soil moisture. *Aust. J. Agric. Res.* 17:281-295.
- Garrity, D.P., D.G. Watts, C.Y. Sullivan, and J.R. Gilley. 1982. Moisture deficits and grain sorghum performance: Evapotranspiration-yield relationships. *Agron. J.* 74:815-820.
- Gates, D.M. 1980. Biophysical ecology. Springer-Verlag, New York.
- Hanks, R.J. 1974. Model for predicting plant yield as influenced by water use. *Agron. J.* 66:660-665.
- Hsiao, T.C. 1973. Plant responses to water stress. *Ann. Rev. Plant Physiol.* 24:519-570.
- , E. Acevedo, E. Ferres, and D.W. Henderson. 1976. Water stress, growth and osmotic adjustment. In Discussion on water relations of plants. *Philos. Trans. R. Soc. London B.* 273:479-500.
- Marani, A., and Y. Fuchs. 1964. Effect of the amount of water applied as a single irrigation on cotton growth under dryland conditions. *Agron. J.* 56:281-282.
- , and M. Horowitz. 1963. Growth and yield of cotton as affected by the time of a single irrigation. *Agron. J.* 55:219-222.
- Meyer, W.S., and G.C. Green. 1980. Water use by wheat and plant indicators of available soil water. *Agron. J.* 72:253-257.
- , and ———. 1981. Plant indicators of wheat and soybean crop water stress. *Irrig. Sci.* 2:167-176.
- Meyers, R.J.K., M.A. Foale, and A.A. Done. 1984. Responses of grain sorghum to varying irrigation frequency in the Ord irrigation area. III. Water relations. *Aust. J. Agric. Res.* 35:43-52.
- Parameswara, G., and K.S. Krishnasastri. 1982. Variability in leaf elongation rate and reduction in green leaf length in sorghum genotypes under moisture stress and on alleviation of stress. *Indian J. Agric. Sci.* 52:102-106.
- Ray, A.A. 1982. SAS user's guide: Statistics. 1982 ed. SAS Institute, Inc. Cary, NC.
- Ritchie, J.T. 1981. Water dynamics in the soil-plant-atmosphere system. In J. Monteith and C. Webb (ed.) Soil water and nitrogen in Mediterranean-type environments. International Center for Agricultural Research in the Dry Areas, Aleppo, Syria.
- , E. Burnett, and R.C. Henderson. 1972. Dryland evaporative flux in a subhumid climate. 3. Soil water influences. *Agron. J.* 64:168-173.
- Rosenthal, W.D., E.T. Kanemasu, R.J. Raney, and L.R. Stone. 1977. Evaluation of an evapotranspiration model for corn. *Agron. J.* 69:451-464.
- Slabbers, P.J. 1980. Practical prediction of actual evapotranspiration. *Irrig. Sci.* 1:185-196.
- Stickler, F.C., S. Wearden, and A.W. Pauli. 1961. Leaf area determination in grain sorghum. *Agron. J.* 53:187-188.
- Tanner, C.B., and W.A. Jury. 1976. Estimating evapotranspiration and transpiration from a row crop during incomplete cover. *Agron. J.* 68:239-243.
- Turner, N.C. 1974. Stomatal behavior and water status of maize, sorghum, and tobacco under field conditions. II. At low soil water potential. *Plant Physiol.* 55:360-365.
- Vanderlip, R.L., and H.E. Reeves. 1972. Growth stages of sorghum [*Sorghum bicolor*, (L.) Moench]. *Agron. J.* 64:13-16.
- Whiternan, P.C., and G.L. Wilson. 1965. Effects of water stress on the reproductive development of *Sorghum vulgare*. *Pers. Univ. Queensl. Pap. Dep. Bot.* 4(14):233-239.