Effects of Irrigation History on Responses of Cotton to Subsequent Water Stress¹

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ABSTRACT

Experiments were designed to test the hypothesis that the internal water relations and stomatal and growth responses to water status of cotton plants (Gossypium hirsutum, 'Acala SJ 2') can be modified by prior tissue water deficits. Different levels of stress conditioning were achieved by varying irrigation frequency during a

pretreatment period.

Growth was limited by water stress under conditions of low and moderate irrigation frequency during the pretreatment period. During the final drought period, tissue water desorption characteristics, stomatal closure thresholds, and (inferentially) turgor sensitivity were different in stress-conditioned plants from those in plants not subjected to prior stress. Analysis of the relationships of water potential to relative water content suggested that osmotic adjustment might play a role in the reduced sensitivity of hardened plants. The altered behaviors of prestressed plants were in the right direction to explain differences observed between the responses of controlled-environment and field-grown plants and suggest that stress-conditioned plants are less sensitive to tissue water deficits.

Additional index words: Diffusion resistance, Leaf elongation, Leaf water potential, Growth, Dry weight partitioning, Hardening.

MANY physiological processes of plants are affected by water deficits (Hsiao, 1973). Among the most important of the affects of water deficits on productivity are a reduction in C fixation, mediated at least partly by stomatal closure, and a reduction in leaf expansion, with attendant effects on leaf area development, influenced in part by cellular turgor. It is clear that any alteration of these responses might influence production significantly.

Despite the voluminous research on the sensitivity of plants to water stress, relatively little attention has been paid to the capacity of plants to adjust so as to reduce or prevent water stress injury. The concept of "adaptation" (or "hardening") to water deficits is a relatively old one (Maximov, 1929), but investigations of the phenomenon and its manifestations are quite limited, especially with modern techniques and understanding.

Most crop plants are regularly subjected to moderate dehydration on a daily basis and to larger deficits during irrigation or rainfall cycles. Many plants subjected to periods of water stress are found to be "hardened" and thus able to survive subsequent drought with less injury than plants not previously

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stressed (Levitt, 1972). Indeed, some direct evidence (McCree, 1974; Brown et al., 1976) and a variety of indirect evidence suggest that plants grown under occasional stress show a lessened sensitivity of several physiological processes to subsequent water deficits.

This study examined the response of cotton plants (Gossypium hirsutum L.) to moisture stress following an initial growth period during which the plants were exposed to a wide range of irrigation frequency. These pretreatments were designed to supply a hardening stimulus. The plants were sampled periodically during the pretreatment period to examine several aspects of growth. Following the conditioning growth period, all of the plants were exposed to drought by withholding water. Stomatal opening, leaf blade elongation, and tissue water desorption characteristics were examined during the final drought period in order to document some of the effects of moisture history on the responses to subsequent drought.

MATERIALS AND METHODS

Plant Materials. 'Acala SJ-2' cotton plants were sown in early May in a greenhouse in 12-liter plastic pots containing sand. Light intensities during the experiment were 60 to 85% of full sun. Day temperatures were maintained at 30 ± 5 C, and night temperatures at 18 ± 5 C. Six seeds were sown per pot, and the seedlings were periodically harvested to a final density of two plants per pot. The harvested plants were used to determine leaf area and the dry weight of leaves and tops. Fifteen pots per pretreatment were used and these were spaced so that no mutual shading of plants occurred. The pots were watered to excess with half-strength Johnson's solution (Johnson et al., 1957) and flushed every third irrigation with distilled water to prevent salt accumulation. For the first 12 days of growth the pots were irrigated daily, and thereafter during the preconditioning period were watered every 1, 4, 6, and 8 days [respectively termed control (pretreatment 1) and pretreatments 4, 6, and 8]. When the plants were 55 days old and had 10 to 11 expanded leaves they all received a final irrigation, terminating the preconditioning period. Water was thereafter withheld from all treatments and the control, initiating the final drought period which lasted 5 days.

Measurements. At each harvest, the height of 15 plants from each pretreatment was measured from the soil surface to the mainstem growing point with a meter stick, and the leaf area of six plants per pretreatment with a Hayashi-Denko (Hayashi-Denko Co., Tokyo, Japan) photoelectric leaf-area meter. These same six plants were then dried to constant weight, partitioned, and weighed.

At 0600 and 1200 hours during the final drought period three plants from different pots from each pretreatment and the control were examined and harvested. The diffusive resistances ($r_{\rm L}$) of the lower and upper surfaces of three exposed leaves from three insertion positions (generally the third, and ninth nodal positions) from three different pots from each pretreatment were determined with a Lambda (Lambda Instrument, Inc., Model No. L160, Lincoln, Neb.) diffusion porometer using a horizontal sensor (Kanemasu et al., 1969). The water potential of these same leaves ($\psi_{\rm L}$) was estimated as the negative hydrostatic xylem sap pressure in a pressure bomb (Jordan, 1970), and immediately afterward the relative water content (RWC)

	Irrigation pretreatment†								
Day	1	4	6	8					
	Le	af area [cm² (one s	ided)/plant]						
20	102 ± 23.6‡	98 ± 17.6	100 ± 15.5	96 ± 4.4					
34	519 ± 27.1	461 ± 59.1	442 ± 80.6	322 ± 42.9					
55	1,930 ± 171.0	1,290 ± 222.0	1,354 ± 122.0	517 ±84.1					
		Leaf weight (g/	plant)						
20	0.50 ± 0.19	0.45 ± 0.11	0.54 ± 0.06	0.53 ± 0.01					
34	3.22 ± 0.21	3.04 ± 0.28	2.72 ± 0.40	2.20 ± 0.35					
55	11.84 ± 0.73	8.92 ± 0.93	9.15 ± 0.61	4.63 ± 0.60					
		Top weight (g/	plant)						
20	0.67 ± 0.29	0.59 ± 0.16	0.75 ± 0.07	0.72 ± 0.01					
34	5.63 ± 0.39	5.19 ± 0.78	5.22 ± 0.92	3.90 ± 0.74					
55	23.50 ± 1.27	18.70 ± 2.43	18.24 ± 1.36	7.85 ± 1.03					
		Plant height ((cm)						
20	16.9 ± 0.6	17.2 ± 0.7	17.0 ± 0.5	17.8 ± 0.5					
34	34.8 ± 0.9	35.4 ± 1.1	29.6 ± 0.6	29.7 ± 0.9					
55	65.2 ± 1.3	56.6 ± 1.7	51.8 ± 1.2	37.5 ± 2.0					
		Mainstem nod	e No.						
20	4.3 ± 0.4	4.7 ± 0.4	5.0 ± 0.2	5.0 ± 0.4					
34	7.1 ± 0.6	7.3 ± 0.2	7.6 ± 0.4	6.9 ± 0.6					
55	11.6 ± 0.7	11.2 ± 0.5	10.8 ± 0.7	9.3 ± 0.9					

† Pretreatments 1, 4, 6, and 8 received irrigation every 1, 4, 6, and 8 days (respectively) during the preconditioning period. \ddagger Mean \pm standard errors (N = 15 for plant height and node number; N = 6 for leaf area, leaf weight, and top weight).

was determined by a method similar to that described by Barrs (1968). Duplicate samples of five leaf discs (2.0 cm in diameter) were cut from between the veins of leaves and immediately weighed. The discs were then floated on distilled water for 26 hours in an incubator maintained at 30 C and illuminated with a 40-watt incandescent light. Excess moisture was blotted before turgid weight measurements. No waterlogging of the cut edges was apparent in the floated discs. Dry weights were determined after drying in an oven for 48 hours at 70 C.

All fitted curves were statistically compared by use of a two-tailed F test (Steel and Torrie, 1960), and differences stated to be significant were different at the 5 or 10% level. All other data were statistically compared by a t-test and confidence levels are explicitly stated.

RESULTS AND DISCUSSION

Growth. Table 1 shows that height, dry weight of tops and leaves, and leaf area were all less with less frequent irrigation. These effects are typical of the responses of both field- and laboratory-grown cotton (Hearn, 1972; Bieloria and Hopmans, 1975) and indicate that growth was limited relative to the control by water stress in all pretreatments. The first significant reductions (10% level) in growth were apparent 34 to 40 days after sowing, depending on the parameter measured and the irrigation frequency. The plants subjected to the less frequent irrigation were the first to exhibit slower growth. The number of mainstem nodes for each treatment was significantly different only at day 55 for pretreatment 8. This finding contrasts with field data of Hearn (1972) showing a consistent, though small, reduction in node number with decreasing water status. These differences may reflect the shorter duration of the present experiment.

In Fig. 1 the mean rate of mainstem elongation of 15 plants from each pretreatment (relative to the

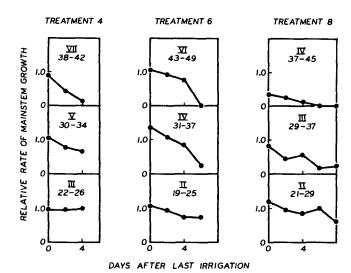


Fig. 1. Mainstem growth rate during the preconditioning period (expressed as a fraction of control) as affected by irrigation frequency and the number of the irrigation cycle. Roman numerals within graphs indicate the number of the irrigation cycle shown and arabic numerals, the time interval (in days after sowing) during which the cycle occurred.

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control) is shown as a function of time after irrigation for the three pretreatments for three different irrigation cycles during the pretreatment period. In each case, the relative rate of mainstem elongation tended to decrease with time after irrigation. Within each treatment, the decrease was greater with increasing age. With pretreatments 4 and 6, the rates returned to about the control rate after each irrigation, whereas plants of pretreatment 8 failed to recover to the control rate after the second cycle of irrigation. The mean relative rate of mainstem elongation of pretreatment 6 on rewatering during the fourth irrigation cycle, and of pretreatment 8 on rewatering during the second irrigation cycle are both significantly greater (5% confidence level) than 1.0. These results suggest that a sort of compensatory growth may accompany recovery from long term stress, as has been observed for the recovery of elongation of leaf blades from short term water stress (Acevedo et al., 1971). The ability to recover was thus a function of stress intensity and/or duration.

Leaf Growth. Leaf growth was affected by the conditioning treatments more than was mainstem growth. Mainstem lengths at the final harvest in pretreatments 4, 6, and 8 were respectively 13, 20, and 42% less than in controls, whereas the corresponding leaf areas were 33, 29, and 73% less.

Leaf area is important in determining potential productivity and interacts with root absorption, through its influence on transpiration, in determining water balance (Levitt, 1972). The influence of water status on leaf growth plays a central role in the determination of ultimate yield. The smaller leaf area observed for pretreatments 4 and 6 (Table 1) was due largely to reductions in leaf size since mainstem node number was not significantly affected. In addition, the plants of pretreatment 8 had fewer leaves through reductions of both branch stem development and stress-induced leaf abscission.

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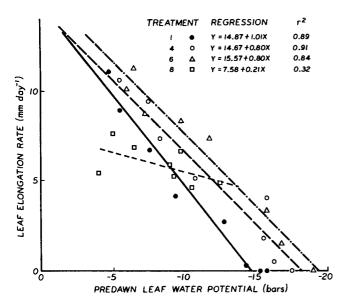


Fig. 2. Leaf blade elongation rate during the final drought period (days 56 to 60) as related to the predawn leaf water potential of the next lower leaf. Each data point represents one observation.

The high sensitivity of leaf enlargement to water deficits may be understood in part from the influence of water status on cellular turgor and the effects of turgor on cellular enlargement (Hsiao, 1973). During the 5 day final drought period, leaf blade length was measured daily with a millimeter rule on individually tagged mainstem leaves 10 or 11, which were 40 to 60 mm long. Leaves in this size range were elongating at about their maximum rate. Water potentials were estimated by predawn pressure bomb measurements on the next lower leaf. Figure 2 depicts leaf elongation rate (on a daily basis) as a function of the predawn water potential on the same day. In all cases except pretreatment 8, the data are fitted well by a linear regression. This is a surprising result since a number of experimental observations suggest that growth rate should be more closely correlated with turgor pressure, a quantity which for cotton is a markedly nonlinear function of water potential (Gardner and Ehlig, 1965). We will not speculate on the cause of this anomaly other than to note that the time scale of the present experiment is large (days) and any single value chosen cannot, on this scale, realistically represent water status or elongation rate. Both leaf water potential and leaf blade elongation rate vary diurnally, and the parameters we have documented are, at best, integrated measures of the effect of water status on leaf elongation.

The data of Fig. 2 may be interpreted on the basis of the cell extension turgor model of Lockhart (1965). The extrapolated interception of the fitted lines can be taken as a threshold leaf water potential for leaf enlargement. In this experiment, leaf elongation continued at quite low values of leaf water potential, suggesting that the threshold for growth might be lower than for most other plants (Hsiao, 1973). The shift in the extrapolated threshold (significant at the 5% level for both pretreatments 4 and 6 relative to

Table 2. Distribution of dry weight at the end of the pretreatment period (day 55) on an absolute and percentage basis as influenced by irrigation frequency.

	Irrigation pretreatment								
Plant part		1		4		6		8	
	Dry weight (g/plant)								
Total leaves	11.8	±0.7+	8.9	± 1.1	9.1	± 0.7	4.6	± 0.7	
Stems	11.7	± 0.8	9.8	± 1.4	9.1	±0.7	3.2	± 0.5	
Roots	12.4	±0.7	15.8	± 2.1	17.9	±1.7	7.9	± 0.9	
Total	35.9	± 1.9	34.5	±4.5	35.4	± 2.9	15.9	± 2.1	
	Dry weight distribution (% of total)								
Total leaves	31.8	± 0.7	25.7	±0.6	25.5	±0.6	28.4	± 1.4	
Stems	33.7	± 1.0	28.7	±0.6	24.3	±0.7	20.5	± 1,1	
Roots	34.6	±0.6	45.5	±0.4	50.2	±0.9	51.1	± 1.9	
	g/g								
Root/shoot ratio	0.53 ± 0.01		0.84 ± 0.01		1.01 ± 0.04		1.01 ± 0.0		
Root/leaf ratio	1.09 ± 0.03		1.77 ± 0.04		1.98 ± 0.04		1.80 ± 0.0		

[†] Mean ± standard deviation (N = 8)

the control) indicates that it is affected by stress history, with a trend suggesting a progressive adaptation to water stress. Unfortunately, the plants of pretreatment 8, with a greatly reduced leaf area, never attained low values of water potential during the final drought period, and the growth response at severe water deficits could not be evaluated. We might infer from the above that plants subjected to stress and recovery (if not too severe) adapt in such a way as to maintain positive turgor (a requisite for growth) to lower values of water potential than plants not so treated. Several other investigators have found some evidence for similar adjustment (Hsiao et al., 1976), which is presumably of an osmotic nature (Hsiao, 1973). This observation might have great significance with regard to the growth of plants in the field, where moderate stresses are recurrent, suggesting a need for further critical studies on stress hardening and adjustment.

In all cases except pretreatment 8, leaf blade growth rates extrapolate to similar values at high water potentials. This suggests that recovery of leaf elongation rate from mild to moderate water stresses was rapid and nearly complete as also noted by Acevedo et al. (1971). The response of pretreatment 8 suggests that severe stress will delay recovery of growth. Similar prolonged effects were noted from the analysis of mainstem growth (Fig. 1) and have been noted by investigators studying the effects of water stress on stomatal activity (Fischer et al., 1970). It is obvious that the ability to recover from water stress will depend on the severity of the stress.

Dry Weight Distribution. Roots supply many essentials for shoot growth, among which water and nutrients are quantitatively the most important. Shoots, in return, supply roots with essentials not produced by the roots themselves, of which carbohydrates are quantitatively most important. Brouwer and de Wit (1968) have shown that the relative availability of the aforementioned macronutrients (in large part determined by the environment) serve as a functional balance system which regulates the partitioning of dry weight in the plant. Much ecological work suggests that a reduction in transpiring leaf area and/

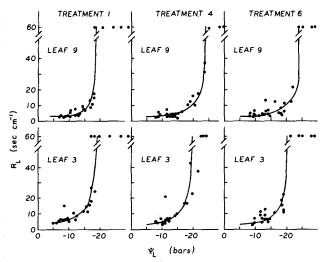


Fig. 3. Composite leaf diffusive resistance (both sides considered in parallel) as a function of leaf water potential during the final drought period (days 56 to 60) as influenced by prior irrigation frequency and leaf insertion position on the mainstem. Each data point represents a single observation and curves were drawn as described in text.

or an increase in root absorbing surface play an important role in drought adaptation (Parker, 1968). Table 2 illustrates, on an absolute and relative basis, the distribution of dry weight within the plants at the end of the pretreatment period (day 55) as affected by irrigation history.

Total stem weight was progressively smaller with decreasing irrigation frequency, whereas root weight was greatest for the two intermediate irrigation frequencies. Thus, total dry weight at final harvest was similar for all pretreatments except pretreatment 8. The near equality of total dry weight of the plants of pretreatments 1, 4, and 6 at the final harvest is very interesting, especially in view of the larger leaf area of plants of pretreatment 1. Self-shading or a reduced assimilation efficiency of the plants of pretreatment 1 may explain this apparent anomaly.

Leaf weight and stem weight, as a fraction of total plant weight, decreased with decreasing irrigation frequency while the root weight percentage increased. Similar trends can be inferred from data of Lawlor (1969). Root/shoot and root/leaf ratios increased dramatically with moderate stress (pretreatments 4 and 6), illustrating a strong influence of irrigation frequency on net dry weight partitioning, in agreement with the functional balance hypothesis of Brouwer and de Wit (1968).

Leaf Diffusive Resistance. Leaf water status affects leaf diffusive resistance, although the mechanisms of the responses remain in doubt (Raschke, 1975). The response of the leaf diffusive resistance of cotton has been investigated in the laboratory and field by many investigators (Bielorai and Hopmans, 1975; Jordan and Ritchie, 1971; and others). From these studies, cotton would seem to conform to the threshold-response model (i.e., a rapid and complete closure of stomata at leaf water potentials of about —15 to —18 bars). It is becoming increasingly evident, however, that environment, age, and a complex of other fac-

tors can dramatically alter a variety of stomatal parameters (Jordan et al., 1975; Brown et al., 1976).

Several investigators have noted that field-grown cotton is much less sensitive in stomatal response than growth chamber- or greenhouse-grown cotton and tends to maintain open stomata to much lower values of water potential (Jordan and Ritchie, 1971). Jordan and Ritchie hypothesized that this modification might be stimulated by prolonged exposure to water deficits in the field. McCree (1974) has shown such an effect in growth chamber-grown sorghum as have Brown et al. (1976) for cotton.

Figure 3 shows the effects of prior stress on the response of leaf diffusive resistance to water deficits for leaves at mainstem nodes 9 and 3 during the final 5 day drought period. The resistance of each surface is combined in parallel to calculate a total leaf resistance. Sharpe (1973) found that under field conditions, the adaxial and abaxial stomata differed in response to light, temperature, and water stress. The curves shown, except that for leaf 9 of pretreatment 6, were statistically fit to a linear equation relating leaf conductance (1/r_L) to leaf water potential (Cowan, 1972). The scatter of data for leaf 9 of pretreatment 6 precluded a significant linear transformation and the curve was eye-fitted. The threshold response of the stomata at nodes 3 and 9 was maintained in plants subjected to stress during growth but the thresholds for stomatal closure appear to shift to lower values of leaf water potential (significant at both nodes for pretreatment 4 at the 5% level relative to the control).

Control plants began to close stomata on leaves at node 9 at water potentials of about —18 bars, whereas plants from treatments subjected to stress during development maintained open stomata at the same nodal position to water potentials as low as —22 to —24 bars. The diffusive resistance of older leaves at node 3 was slightly greater throughout the range of water status studied, and in these leaves stomatal closure took place at slightly higher values of water potential (significant for pretreatment 4) than in leaves at node 9. The node-position response resembles that found by other researchers (Jordan et al., 1975; Nagarajah, 1975).

The variability in response is characteristic of such data (Jordan et al., 1975), indicating the complexity of the interactions involved, including the individual nature of stomatal response and variations from leaf to leaf. A close relationship is not necessarily to be expected, however, since stomatal opening is related most intimately to turgor potential differential between guard cells and adjacent epidermal cells, not to any measure of bulk tissue water status (Raschke, 1975). The observed changes attendant on previous stress are in the right direction to explain differences between well-watered greenhouse and growth chamber plants and field-grown plants, although factors other than stress history may also operate in the field. No single value of water potential could be characterized as a critical value for stomatal closure in cotton.

These observations present a dilemma in terms of understanding the nature of plant control of wa-

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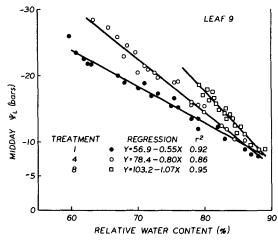


Fig. 4. Water potential isotherms during the final drought period (days 56 to 60) for leaves at node 9 as affected by preconditioning irrigation regime. Each data point represents the mean of two replicates on the same leaf for RWC and a single observation of water potential.

ter loss and balance. Extension of the threshold for stomatal closure, although advantageous in terms of allowing continued photosynthesis to take place, should inevitably lead to situations of severe water deficits unless other physiological adjustments take place (Levitt, 1972). These adjustments must facilitate the maintenance of gradients for water absorption without allowing loss of turgor. Such adjustments would presumably be of an osmotic nature (Levitt, 1972; Hsiao, 1973).

Water Potential Isotherms. From the preceding discussion it is clear that previously stressed cotton plants display a number of responses to subsequent stress which are quantitatively different from those of plants not so conditioned. The "hardened" plants continued elongation growth and appeared to maintain open stomata to lower values of water potential than did control plants. Our present understanding of the water relations of plants suggests that the maintenance of turgor (of which both growth and stomatal opening are local manifestations) to lower values of water potential can be facilitated by a decrease in osmotic potential, generated either by dehydration or solute accumulation (Hsiao, 1973), or by a high cell wall elasticity (Sanchez-Diaz and Kramer, 1971).

The importance of osmotic adjustment in plants exposed to saline media has long been recognized (Bernstein, 1961, 1963). Cotton exposed to such conditions takes up salt and adjusts osmotically, thus maintaining potential gradients for water absorption and turgor (Boyer, 1965; Hoffman et al., 1971). Earlier there was little direct evidence for parallel adjustment in plants subjected to nonosmotic water stress (Hsiao, 1973) but more recent results suggest that such adjustments may be more common than realized, especially in the field (Hsiao, et al., 1976) or in plants subjected to repeated stress (Brown et al., 1976).

Several researchers have attempted to characterize the drought tolerance of different species or of plants of a single species collected from different environ-

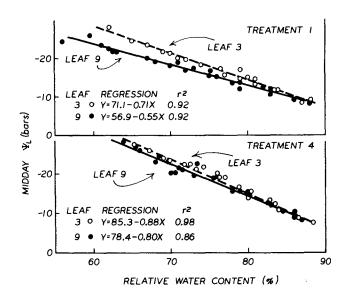


Fig. 5. Water potential isotherms during the final drought periods (days 56 to 60) as affected by nodal position and irrigation history. Each data point represents the mean of two replicates on the same leaf for RWC and a single observation of water potential.

ments by analysis of water potential isotherms (Noy-Meir and Ginzburg, 1969; Sanchez-Diaz and Kramer, 1971). This isotherm relates the water potential of a leaf to its water content, and changes may be interpreted to reflect changes in the osmotic or hydration properties of the tissue (Noy-Meir and Ginzburg, 1967). Figure 4 shows the isotherms during the final 5 day drought period for leaves at node 9 for the various pretreatments. All leaves were collected at noon (about the time of minimum water potential) to eliminate the complex influence of diurnal variation in this relationship (Jordan and Ritchie, 1971).

Over the range of water contents investigated, the relation is well-characterized by a linear regression (Fig. 4) although divergence should be expected at more extreme values. The shift in the isotherm with different irrigation regimes (significant at the 5% level for all pretreatments relative to the control) suggests that plants subjected to prestress had a larger decrease in leaf water potential per unit decrease in RWC than did the control (i.e., a smaller water loss from leaves of prestressed plants for a given decrease in leaf water potential). The response of pretreatment 6 (not shown) was quite similar to that of pretreatment 4, and for every pretreatment the divergence from control behavior increased as water was lost from the tissue. Similar results have been noted by other researchers (Knipling, 1967). Sanchez-Diaz and Kramer (1971) compared the water potential isotherms of sorghum and corn and found that sorghum lost less water per unit decrease in water potential than did corn. Those workers felt that this was an important factor in the higher drought resistance of the former crop.

Figure 5 shows the effect of nodal position on the water potential isotherm of cotton leaves. The desorption curve shifted with nodal position for both of the pretreatments illustrated and for pretreatment

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6. The change was significant (at the 10% level) only for pretreatment 1 and was not found at all for pretreatment 8. Over the range studied, leaf aging (nodal position) had less effect (although in the same direction) as preconditioning stress. Similar effects of leaf age have been noted in sorghum by Whiteman and Wilson (1963), in barley by Millar et al. (1968), and in dogwood leaves by Knipling (1967). Decreased cell wall elasticity and increased cell wall surface area are known to occur with leaf aging (Esau, 1967), and these changes are hypothesized to influence the transposition of the isotherm (Knipling, 1967, Sanchez-Diaz and Kramer, 1971). Neither alternative was evaluated in the present study.

Several workers have suggested that the shifts in the water potential isotherm upon stress conditioning are likely to be caused by a decreased osmotic potential in conditioned plants, and Knipling (1967) has shown this to be the case for dogwood leaves. Such a decrease is likely to be explained by solute accumulation rather than dehydration, since water potential at a given RWC, is decreased in prestressed plants. Changes in other cellular parameters which might affect the hydration properties of the cell (e.g., decreased cell wall elasticity, increased cell wall surface, or increased colloidal materials) might also contribute to the observed response. These cannot be ruled out as effectors, although the magnitude of such effects is generally thought to be insignificant within the range of water contents observed in our experiment (Hsiao et al. 1976). We have explored this further in other experiments (Cutler, 1976).

CONCLUSIONS

Cotton plants subjected to various irrigation frequencies were studied for altered responses to subsequent water deficits. Periodic sampling during the pretreatment period disclosed a progressive inhibition of various plant growth parameters with decreasing irrigation frequency. Recovery of growth was rapid and nearly complete for the intermediate pretreatments and slower and incomplete for the dry pretreatment. Net distribution of dry matter was modified with irrigation frequency with a greater partitioning into root growth for the pretreatments with lower frequency.

Several of the responses to subsequent water deficits were influenced by irrigation history in directions which suggest that plants subjected to water stress during development have a lessened sensitivity to later stresses. Leaf elongation and in some cases stomatal opening were maintained to lower values of leaf water potential in prestressed plants. Analysis of water potential isotherms indicated that prestressed plants had a smaller reduction in leaf water content per unit decrease in leaf water potential that did controls. These results suggest that cotton subjected to water stress during development is less sensitive to subsequent drought.

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