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Acclimation of CO_2 Assimilation in Cotton Leaves to Water Stress and Salinity[1]

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ABSTRACT

Cotton (*Gossypium hirsutum* L. cv Acala SJ2) plants were exposed to three levels of osmotic or matric potentials. The first was obtained by salt and the latter by withholding irrigation water. Plants were acclimated to the two stress types by reducing the rate of stress development by a factor of 4 to 7. CO_2 assimilation was then determined on acclimated and nonacclimated plants. The decrease of CO_2 assimilation in salinity-exposed plants was significantly less in acclimated as compared with nonacclimated plants. Such a difference was not found under water stress at ambient CO_2 partial pressure. The slopes of net CO_2 assimilation *versus* intercellular CO_2 partial pressure, for the initial linear portion of this relationship, were increased in plants acclimated to salinity of −0.3 and −0.6 megapascal but not in nonacclimated plants. In plants acclimated to water stress, this change in slopes was not significant. Leaf osmotic potential was reduced much more in acclimated than in nonacclimated plants, resulting in turgor maintenance even at −0.9 megapascal. In nonacclimated plants, turgor pressure reached zero at approximately −0.5 megapascal. The accumulation of Cl^- and Na^+ in the salinity-acclimated plants fully accounted for the decrease in leaf osmotic potential. The rise in concentration of organic solutes comprised only 5% of the total increase in solutes in salinity-acclimated and 10 to 20% in water-stress-acclimated plants. This acclimation was interpreted in light of the higher protein content per unit leaf area and the enhanced ribulose bisphosphate carboxylase activity. At saturating CO_2 partial pressure, the declined inhibition in CO_2 assimilation of stress-acclimated plants was found for both salinity and water stress.

Drought and salinity in the root environment of plants are frequently considered as imposing similar effects on plants due to the decrease in Ψ_{we}.[2] The conditions of salinity, however, differ from those of water stress in three main respects: salt ions are readily taken up and can thus be responsible for osmotic adjustment; salt ions, mainly sodium, may have adverse and toxic effects; and the drop in total soil water potential due to salinity in contrast to water deficit has no direct effect on soil hydraulic conductance. The response of many plant processes to given Ψ_{we} caused by salinity may thus differ from an identical Ψ_{we} caused by water stress.

Several reviews (*e.g.* 14, 21) have outlined the diminished rate of net CO_2 assimilation in water-stressed plants, which can be found for a wide spectrum of species (6, 8, 13, 25). The decrease of CO_2 assimilation in salinity-exposed plants was not as unequivocally outlined (3, 17, 19). A direct comparison of water stress and salinity showed (15) that water stress was much more inhibitory to CO_2 assimilation than salinity at an identical Ψ_{we}, which was attributed mainly to the difference in osmotic adjustment under the two stress conditions. Because osmotic adjustment may lead to stress acclimation, this study should be carried out under actual conditions allowing acclimation.

Repeated cycles of water deficit in cotton reduced the sensitivity of photosynthesis to a subsequent water deficit, which was attributed to altered stomatal response to a given Ψ_{wl} (1) or to reduced chloroplast response (12). The capability of chloroplasts to acclimate to water stress was also confirmed by the findings that under decreased Ψ_{wl} chloroplast volume was maintained and that the rise in their solute concentration exceeded that of the whole leaf (14).

The capability of field-grown plants to acclimate to water stress is greater than that of plants grown in small containers, probably because of the lower rate of moisture withdrawal from the root zone. It was in fact shown that the faster the rate of stress development, the more drastic was the decrease in net photosynthesis and leaf conductance (9). Acclimation obtained at a low rate of Ψ_{we} decrease was associated with solute accumulation, whereas this did not occur at a high rate of Ψ_{we} decrease.

The response of photosynthesis to stress in salinity-acclimated plants is much less documented, and it is quite possible that the more limited inhibition of photosynthesis by salinity (7, 10, 15, 16, 19) is related to such acclimation.

The purpose of this study was thus to determine salinity and water-stress effects on CO_2 assimilation in acclimated and nonacclimated cotton plants. Acclimation to both stress factors was imposed by controlling the rate of decrease in Ψ_{we}. This can be obtained by the rate of salinization of the growth media and, in the case of water stress, by changing the rate of transpiration and, thus, the withdrawal of soil moisture.

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[2] Abbreviations: Ψ_{we}, external water potential; A, Net CO_2 assimilation rate; C_i, intercellular CO_2 partial pressure; WUE, water use efficiency; ψ_{se}, external osmotic potential; ψ_{sl}, leaf osmotic potential; Ψ_{wl}, leaf water potential; RuBP, ribulose bisphosphate.

MATERIALS AND METHODS

Cotton plants (*Gossypium hirsutum* L. cv Acala SJ-2) were grown in loess-type soil (*Calcic Haploxeralf*) placed in plastic cylindrical pots 22 cm in diameter. The pots were filled with the equivalent of 3 kg of oven-dried soil to a height of 6 cm giving a soil specific weight of approximately 1.32 g/cm^3. Irrigation before planting was up to 0.25 of dry soil weight (equivalent to approximately 0.005 MPa) with deionized water containing half-strength Hoagland solution. This allowed uniform distribution of water and left approximately 35% of the total pore volume filled with air. Plants were thinned to one per pot, and the soil surface was covered with a thin layer of polyethylene. The cylinders were weighed daily, and the water lost by transpiration was replenished. Half-strength Hoagland solution was used once every 10 d.

Other seeds from the same batch were germinated in vermiculite prewetted with distilled H_2O. Six-day-old seedlings were then transplanted into plastic containers (28 × 18 × 12 cm) filled with 6 L of half-strength Hoagland solution and were grown hydroponically. Iron was added as 20 mg/L of 138 Fe-Sequestrene (Ciba-Geigy, Switzerland). The containers were covered with 1-cm-thick polystyrene sheets, and the roots were placed through holes into the solution. The nutrient solution was aerated continuously, and deionized water was added regularly to replace the water lost by transpiration. The solution was replaced approximately once in 14 d, and its pH was maintained between 5.5 and 6.5. All plants were grown in a naturally illuminated and temperature-controlled glasshouse at 28 ± 3°C air temperature. Plants were grown to a stage of five leaves under uniform, unstressed conditions. This required approximately 30 days in soil and 25 days in hydroponics.

Three Ψ_{we} levels, of -0.3, -0.6, and -0.9 MPa, were applied in soil by withholding irrigation water for different time periods and in nutrient solution by adding NaCl. As the water retention curve of the soil and the rate of daily water loss were known, the time needed to reach the predetermined Ψ_{we} was calculated to be 5, 7, and 8 d, respectively. Irrigation schedule was planned to obtain the different levels of Ψ_{we} on the same day. Plants were then covered with transparent polyethylene bags for 2 d and were kept in the shade to minimize further water loss, followed by 2 h under standard conditions. Three similar levels of ψ_{se} were obtained by adding NaCl to the nutrient solutions. The salt was added in steps so that the changes in ψ_{se} simulated those in Ψ_{we} under water stress. Plants were then maintained under similar conditions of minimal transpiration.

In the nonacclimation treatment, the rate of water extraction was enhanced by an additional planting of approximately 100 wheat seedlings 10 d before the final irrigation. This enhanced the rate of water withdrawal and the time required to reach the predetermined Ψ_{se} in soil to 1, 2, and 2.5 d, respectively. These plants were used shortly thereafter for the determination of CO_2 assimilation. The time allowed for the development of stress was thus reduced by a factor of 4 to 7.

Salinization of nonacclimated plants was done in one step for the -0.3 MPa salinity level and in two steps for the higher levels, extending 1 and 2 d, respectively, and were also used for the determination of CO_2 assimilation shortly thereafter.

Net CO_2 assimilation rates were measured with a Li-Cor 6000 portable system equipped with a 1.0-L chamber (Li-Cor, Lincoln, NE). Measurements of water- and salt-stressed plants were conducted on different days and included unstressed controls. A fixed leaf area between 12.0 and 14.0 cm^2 was confined by inserts, and the flow rate was 12 mL s^{-1}. The CO_2 analyzer was calibrated daily with a series of standard CO_2-air mixtures. Four consecutive measurements were taken at 15-s intervals which were then extrapolated back to zero time. Measurements were replicated on six different plants, conducted between 8:30 AM and 3:30 PM on fully sun-exposed leaves at a PAR intensity of 1300 to 1500 μmol/m$^2\cdot$s at the leaf surface and ambient p(CO_2) of 34 ± 2 Pa. Net CO_2 assimilation was calculated by using the computer program developed by Leuning and Sands (11).

One experiment was conducted to obtain A/C_i curves. Assimilation rates were similarly determined extrapolating to zero time but at six levels of ambient p(CO_2) between 7 and 40 Pa. Preliminary studies showed that nearly linear rates of CO_2 assimilation were obtained at least up to 40 Pa. The rates were very similar when the leaf was maintained between 3 and 25 min at a given p(CO_2) in this range. The CO_2 in the chamber was thus scrubbed by soda lime and was then gradually raised by injecting pure CO_2 with a microsyringe. The assimilation rate was determined at each step after maintaining the leaf for 3 to 4 min at the new p(CO_2). These measurements were conducted on three replicate plants. Intercellular p(CO_2) was calculated by the method of von Caemmerer and Farquhar (24), and WUE was calculated on a molar basis of H_2O and CO_2. Leaves were sampled for the determination of Ψ_{wl} and ψ_{sl} immediately after the determination of CO_2 assimilation. These were conducted by using a pressure chamber and freezing point depression osmometry for the leaf sap.

Homogeneity of CO_2 fixation over the leaf surface was determined by exposing leaves to $^{14}CO_2$ in air at ambient p(CO_2) in a 1-L leaf chamber for 1 min. Leaves were immediately clamped between two perforated aluminum plates, frozen in liquid N_2, lyophilized, and placed in contact with x-ray film which was then developed. An additional experiment was conducted to determine the rate of CO_2 fixation with a mixture of $^{14}CO_2$ and $^{12}CO_2$ with a known specific activity (18). These measurements were conducted on 1-cm^2 leaf discs on different leaves and at different locations of each leaf.

Chl was determined in 80% acetone extracts by the method of Arnon (2). Tissue chloride content was determined by coulometric-amperometric titration (5) conducted on extracts of dried leaf samples. Other ions were determined on H_2SO_4 digests of dried leaf samples: Na^+ and K^+ by flame photometry and Ca^{2+} plus Mg^{2+} by atomic absorption spectrophotometry. Glucose and sucrose were analyzed colorimetrically with glucose oxidase and *O*-dianisidine dihydrochloride (26) before and after hydrolysis with boiling 1 M HCl and were then neutralized. Amino acids were determined spectrophotometrically with ninhydrin. All amino acids, excluding proline, at 570 nm with leucine as standard and proline at 410 nm. The content of all of the solutes was presented as concentration in

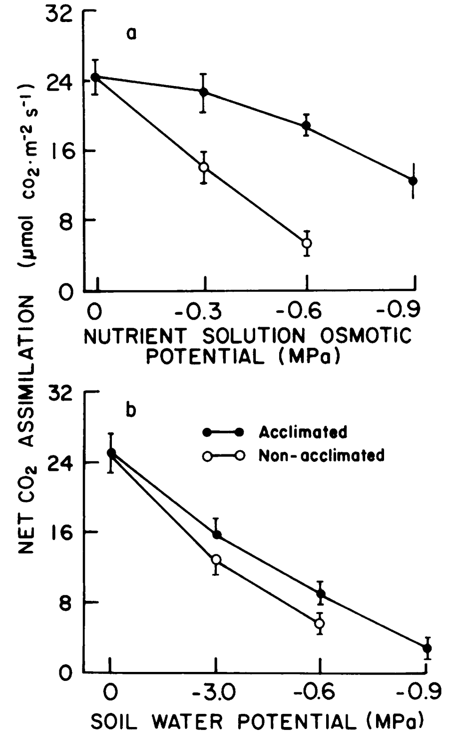

Figure 1. Rate of net CO_2 assimilation of cotton leaves as related to nutrient solution osmotic potential or to soil water potential. Assimilation rates were determined on acclimated and nonacclimated plants. Net CO_2 assimilation was determined at ambient $p(CO_2)$ of 34 ± 2 Pa and at PAR intensity of 1300 to 1500 $\mu mol \cdot m^{-2} s^{-1}$. a, Salinity-stressed plants; b, water-stressed plants.

cellular water, assuming for all treatments 15% of extracellular water out of total leaf water which presumably contains very low solute content.

RESULTS AND DISCUSSION

The different response in net CO_2 assimilation between acclimated and nonacclimated plants was marked in salt-stressed plants but much less in water-stressed plants (Fig. 1a and b). Although the decrease in net assimilation rate was much less in salt-acclimated as compared with nonacclimated plants, the decrease was very similar in water-stressed plants. The nonacclimated plants became severely wilted at −0.9 MPa under both salt and water stress, and net CO_2 assimilation could not be determined. Although the decrease in CO_2 assimilation of plants under stress was diminished in acclimated plants, the decrease in apparent transpiration was similar for both groups of plants (not presented). This difference is probably because of the fact that CO_2 assimilation is controlled by both stomatal conductance and biochemical activity, whereas transpiration is controlled only by stomata. Matthews and Boyer (12), studying drought acclimation of a different species and using a different procedure for acclimation, also concluded that chloroplast activity contributed

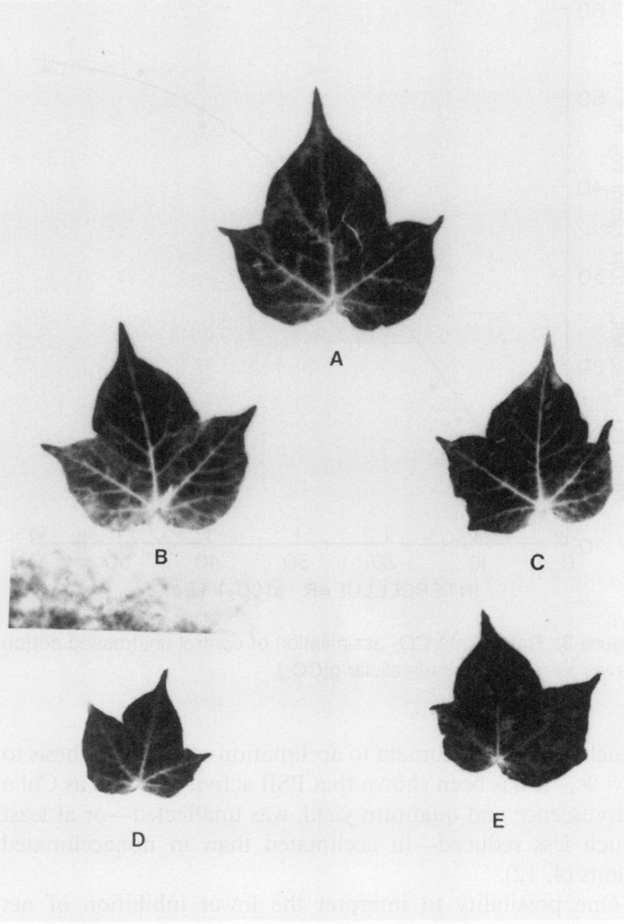

Figure 2. Autoradiograms of cotton leaves after fixation of $^{14}CO_2$ for 1 min, immediate freezing, and lyophilization. A is a control leaf, B and D are salinity acclimated at −0.3 and −0.6 MPa, and C and E are salinity nonacclimated and exposed to identical ψ_{se}, respectively.

Table I. *Rates of CO_2 Fixation in Leaves of Salinity-Acclimated and Nonacclimated Cotton Plants and the Distribution of These Rates Between Locations Within a Leaf and Between Leaves*[a]

Treatment	Mean $^{14}CO_2$ Fixation Rate	Average SD	
		Between locations	Between leaves
	μmol·m^{-2}·s^{-1}		
Control	28.3 E	2.99	2.89
Acclimated			
−0.3 MPa	26.1 D	2.76	2.67
−0.6 MPa	23.4 C	2.43	2.34
Nonacclimated			
−0.3 MPa	21.7 B	2.24	2.20
−0.6 MPa	14.8 A	1.61	1.54
F values		*Treatment*	*Replication*
Leaves		228	0.18
Locations		229	0.17
Individual measurements		222	0.09

[a] Leaf discs (area = 1 cm^2) were removed from the leaf immediately after being exposed to $^{14}CO_2$ for 30 s, and the incorporated ^{14}C was extracted and analyzed. Numbers followed by different letters differ significantly at P = 0.05 (according to Duncan's Multiple Range Test).

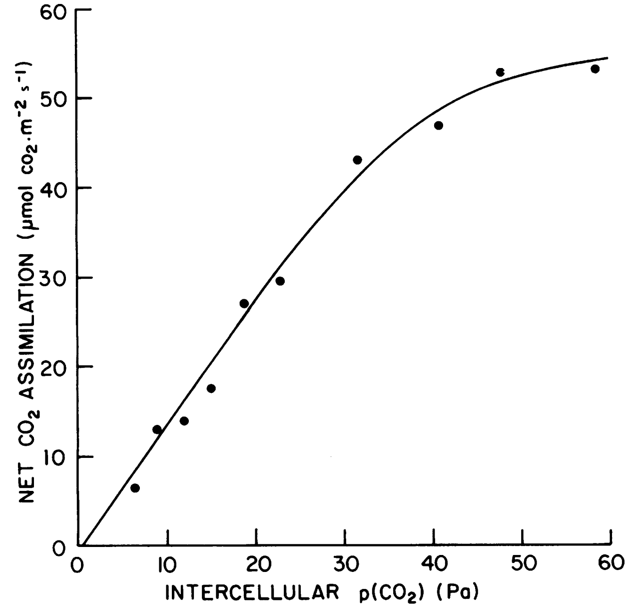

Figure 3. Rate of net CO_2 assimilation of control unstressed cotton leaves as related to intercellular $p(CO_2)$.

much more than stomata to acclimation of photosynthesis to low Ψ_{wl}. It has been shown that PSII activity, as well as Chl a fluorescence and quantum yield, was unaffected—or at least much less reduced—in acclimated than in nonacclimated plants (4, 12).

One possibility to interpret the lower inhibition of net assimilation as compared with transpiration mainly in plants acclimated to salinity is by enhanced biochemical activity in the chloroplasts. The ability of chloroplast acclimation can be evaluated much better by plotting net assimilation rate against internal $p(CO_2)$. However, the work of several investigators, who showed a nonhomogeneous distribution of open stomates known as patchiness, could lead to incorrect estimates of $p(CO_2)$ (22, 23) and might raise a problem in the determination of A/C_i relationship. We therefore tested the distribution of stomatal conductance over leaves of different salinity levels. This was done with autoradiograms prepared after brief exposure to $^{14}CO_2$ (Fig. 2) and by measuring the distribution of CO_2 fixation within a leaf *versus* the differences between leaves (Table I). Patchiness was not enhanced by salinity, as shown, for instance, in the case of water-stressed beans (22), excluding the −0.6 MPa of the nonacclimated leaf in which slight patchiness may be visible. The rate of labeling around major veins was lower than in the rest of the leaf, due either to a deeper location of the label which could not be seen on the x-ray film or to a lower density of stomates.

In another experiment, the rate of $^{14}CO_2$ fixation was determined at seven different locations within a leaf, each on seven leaves at different stages of development. The mean rate of $^{14}CO_2$ fixation differed significantly between salinity levels and between acclimated and nonacclimated plants

Table II. *Linear Regression Coefficient Between Net CO_2 Assimilation Rates A and Internal $p(CO_2)$ of Cotton Leaves, Determined on Salinity- and Water-Stress-Acclimated and Nonacclimated Plants*[a]

Stress Type and Intensity		Acclimated			Nonacclimated		
		Slope	Intercept	r^2	Slope	Intercept	r^2
				MPa			
Salinity							
control	−0.02	1.34	−1.2	0.94			
	−0.30	2.10	−2.2	0.90	1.21	−1.8	0.92
	−0.60	1.65	−1.5	0.89	0.91	−1.4	0.91
	−0.90	0.98	−0.8	0.92			
Water stress							
control	−0.04	1.36	−4.6	0.95			
	−0.30	1.42	−2.5	0.95	0.95	−1.8	0.96
	−0.60	0.85	−3.3	0.91	0.61	−1.8	0.88
	−0.90	0.53	−1.7	0.89			

[a] Rates of net assimilation were determined in a range of $p(CO_2)$ between 7 and 40 Pa. Units of slopes are in $mol \cdot m^{-2} \cdot s^{-2} \cdot Pa^{-1}$ and of intercepts in $mol \cdot m^{-2} \cdot s^{-1}$.

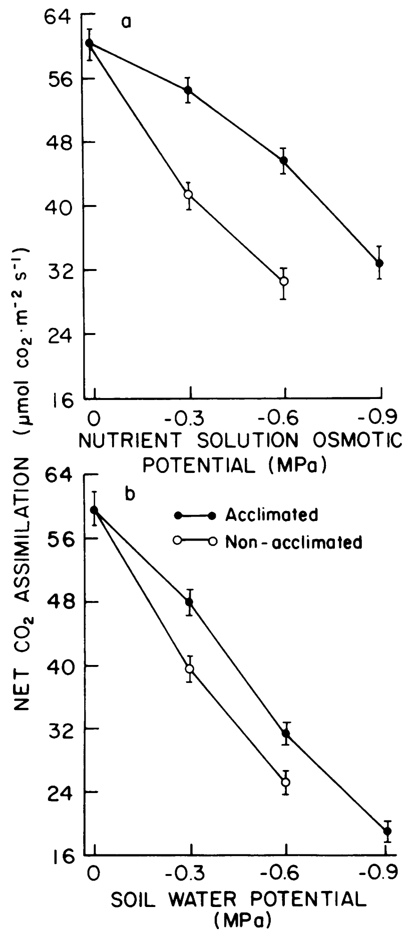

Figure 4. Rate of net CO_2 assimilation of cotton leaves as related to nutrient solution osmotic potential or to soil water potential. Assimilation rates were determined on acclimated and nonacclimated plants. Net CO_2 assimilation was determined at ambient $p(CO_2)$ of 70 ± 5 Pa and at PAR intensity of 1300 to 1500 $\mu mol \cdot m^{-2}s^{-1}$. a, Salinity-stressed plants; b, water-stressed plants.

Table III. *Dry Weight, Protein, and Chl Content Per Unit Leaf Area and RuBP Carboxylase Activities of Leaves Acclimated to Salinity and Water Stress*[a]

Stress Type and Intensity		Dry Wt	Protein	Chl	RuBP Carboxylase
	MPa	*g·m^{-2}*		*mg·m^{-2}*	*µmol of CO_2·mg of protein^{-1}*
Salinity					
control	−0.02	19.0 ± 0.6	3.96 ± 0.92	291 ± 7	28.9 ± 2.1
	−0.30	20.9 ± 0.7	4.85 ± 0.31	342 ± 11	34.9 ± 3.3
	−0.60	22.8 ± 0.6	4.74 ± 0.24	374 ± 9	20.9 ± 1.6
	−0.90	24.1 ± 0.8	4.61 ± 0.25	269 ± 8	17.5 ± 1.4
Water stress					
control	−0.04	43.6 ± 1.8	3.21 ± 0.15	210 ± 18	33.3 ± 2.8
	−0.30	48.6 ± 1.2	3.59 ± 0.20	278 ± 17	29.1 ± 2.5
	−0.60	63.2 ± 1.7	3.54 ± 0.19	291 ± 9	35.2 ± 2.2
	−0.90	56.5 ± 0.9	3.45 ± 0.18	259 ± 7	11.2 ± 1.2

[a] Values are means ± SE of five replicates.

(Table I). The ^{14}C distribution within a leaf was the same as among leaves, as can be seen from the similar SD, which were also relatively the same at the different treatments. The analysis of variance, conducted once defining leaves and once defining locations as replicates, also showed very similar *F* values, which were markedly small as compared with the *F* values between treatments.

An A/C_i curve for a control plant grown in nutrient solution (Fig. 3) shows that this was linear up to a C_i of 23 Pa. The slopes for these linear portions were increased in salinity-acclimated plants at −0.3 and −0.6 MPa, mainly at the former (Table II). This increase was minimal in plants acclimated to soil water stress and was nonexistent in nonacclimated plants. The initial slope of A/C_i is assumed to be a function of the concentration or activity of RuBP carboxylase, whereas the response of assimilation to p(CO_2) at high CO_2 partial pressures to RuBP regeneration (24). The higher initial slopes calculated for the A/C_i curves in acclimated plants must thus be due either to larger amounts of the enzyme per unit leaf area or to higher carboxylation efficiency. Provided the fraction of RuBP carboxylase out of total protein was not affected by stress, then the rise of approximately 20% in protein content at −0.3 and −0.6 MPa, in salinity-acclimated leaves (Table III) can explain at least part of the enhanced CO_2 assimilation rate of these plants. Seemann and Critchley (20) showed that, in beans, nitrogen content of RuBP carboxylase, out of total leaf nitrogen, was reduced by approximately 22% at 150 mM NaCl. This might not, however, be the case in cotton, which is much more salt tolerant, mainly when acclimated as in this present study and at a much lower NaCl concentration than 150 mM. Moreover, an increase in RuBP carboxylase concentration was also found in beans in the range of 60 to 120 mM NaCl (Fig. 6B in ref. 20). The rise in protein content in plants acclimated to soil water stress was approximately only 11%, insignificant from the control. RuBP carboxylase activity of salinity-acclimated plants was also enhanced at −0.3 MPa, by approximately 20% (Table III). This was not found when plants were acclimated to higher salinity levels or to water stress.

A rise in chlorophyll concentration occurred in salinity-

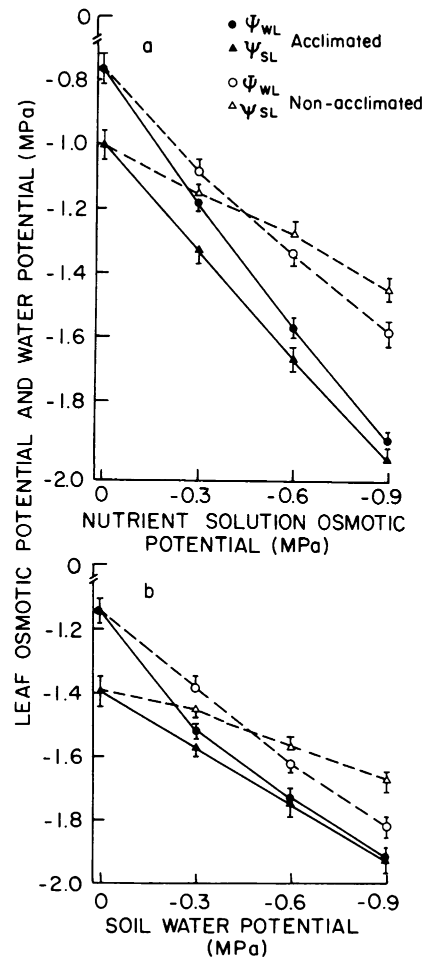

Figure 5. Water and osmotic potentials of cotton leaves as related to nutrient solution osmotic potential or to soil water potential. Cotton plants were grown in soil or in nutrient solution and were either acclimated or not acclimated to external water or osmotic potentials.

Table IV. *Effect of Salinity and Water Stresses on WUE of Cotton Leaves at Two Partial Pressures of* CO_2[a]

Stress Type and Intensity		$p(CO_2) = 34 \pm 2$ Pa		$p(CO_2) = 70 \pm 5$ Pa	
		Acclimated	Nonacclimated	Acclimated	Nonacclimated
	MPa				
Salinity					
control	−0.02	1.23 ± 0.16		4.98 ± 0.23	
	−0.30	2.32 ± 0.18	1.52 ± 0.09	5.92 ± 0.26	4.82 ± 0.42
	−0.60	2.40 ± 0.18	0.77 ± 0.08	6.13 ± 0.19	4.49 ± 0.25
	−0.90	2.07 ± 0.15		5.70 ± 0.40	
Water stress					
control	−0.04	1.86 ± 0.16		4.62 ± 0.27	
	−0.30	1.86 ± 0.15	1.41 ± 0.15	5.71 ± 0.20	4.76 ± 0.15
	−0.60	1.42 ± 0.16	0.85 ± 0.12	5.25 ± 0.15	4.40 ± 0.14
	−0.90	0.57 ± 0.08		3.65 ± 0.11	

[a] The control values serve as control for both acclimated and nonacclimated plants. Values of WUE are micromoles of net assimilated CO_2 divided by millimoles of transpired H_2O. Measurements of net assimilation and transpiration rates were conducted on acclimated and nonacclimated plants. Values are means ± SE of five replicates.

and water-stress-acclimated plants (up to −0.6 MPa). Provided that light was at saturation level, then this may be responsible for enhanced photosynthetic electron transport which could, in turn, result in a higher rate of RuBP regeneration. This may stimulate carbon assimilation only if $p(CO_2)$ is not rate limiting but will have no effect at the linear portion of the A/C_i curve. An additional experiment was therefore conducted in which net CO_2 assimilation was determined at an ambient $p(CO_2)$ of 70 ± 5 Pa (Fig. 4), which was close to saturation. Assimilation rate of unstressed plants was approximately 2.5-fold higher than at ambient $p(CO_2)$. The relative change in net assimilation of salinity-acclimated plants at the different ψ_{sc} was similar to ambient $p(CO_2)$ of 34 Pa. In nonacclimated plants, the relative decrease was less, namely, 33 and 49% as compared with 48 and 77% at 34 Pa for −0.3 and −0.6 MPa, respectively. It should be noted that, at $p(CO_2) = 70$ Pa, a response of CO_2 assimilation to acclimation was also found in the case of water stress, in contrast to the lower $p(CO_2)$. Drought acclimation of photosynthetic electron transport activity was also found by Conroy *et al.* (4) under a $p(CO_2)$ of 60 Pa, despite a marked decrease in leaf conductance and relative water content. The difference in stress acclimation between the two CO_2 levels is also demonstrated by the higher WUE of acclimated as compared with nonacclimated plants (Table IV). At ambient $p(CO_2)$ of 34 Pa, WUE was significantly higher than the control in salinity-acclimated plants but not in water-stress-acclimated plants. At ambient $p(CO_2)$ of 70 Pa, WUE was increased in both salinity- and water-stress-acclimated plants.

The exposure of plants to salinity and water stress resulted in a significant decrease in Ψ_{wl} and ψ_{sl}, and both decreases were steeper in acclimated than in nonacclimated plants (Fig. 5). The decrease in Ψ_{wl} was more marked than the decrease in ψ_{sl}, regardless of acclimation or stress type. This implies that there was a drop in turgor pressure from approximately 0.25 MPa in control plants to 0.02 to 0.08 MPa at Ψ_{wc} of −0.6 or −0.9 MPa. The decrease in Ψ_{wl} of nonacclimated plants was somewhat less than that of acclimated plants, but, as the decrease in ψ_{sl} was only partial, turgor pressure reached zero at approximately ψ_{sc} or $\Psi_{we} > -0.6$ MPa and was negative at −0.9 MPa.

The decrease in ψ_{sl} under salinity was similar to that in ψ_{sc}, whereas in soil-grown plants exposed to water stress the decrease in ψ_{sl} was much smaller. This decrease in ψ_{sl} under salinity can be accounted for by the increase in total ions and organic solutes concentration (Figs. 6 and 7). The increase in concentration exceeded somewhat the actual decrease in ψ_{sl} up to 0.6 MPa, but not at −0.9 MPa. This can probably be

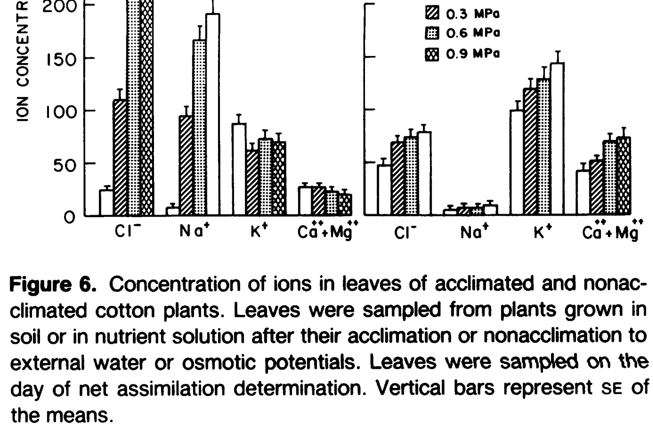

Figure 6. Concentration of ions in leaves of acclimated and nonacclimated cotton plants. Leaves were sampled from plants grown in soil or in nutrient solution after their acclimation or nonacclimation to external water or osmotic potentials. Leaves were sampled on the day of net assimilation determination. Vertical bars represent SE of the means.

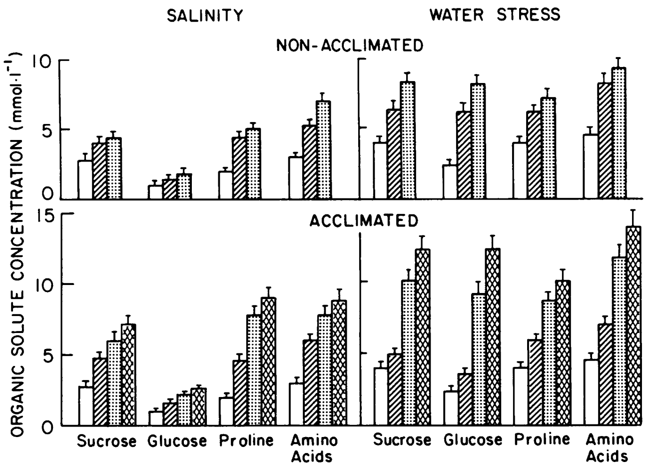

Figure 7. Concentration of organic solutes in leaves of acclimated and nonacclimated cotton plants. Leaves were sampled from plants grown in soil or in nutrient solution after their acclimation or nonacclimation to external water or osmotic potentials. Leaves were sampled on the day of net assimilation determination. Symbols of columns are as described for Figure 2. Vertical bars represent SE of the means.

interpreted by unequal fractions of extracellular water having a low solute content. The increase in total leaf solute content accounts, however, for only 50 ± 8% of the decrease in ψ_{sl} in the soil-grown plants which acclimated to water stress. This implies that some solutes were not determined or that the volume of cellular water out of the total leaf water was less in soil-grown plants. In the control unstressed plants, the total content of analyzed solutes contributes only approximately 35% to ψ_{sl}, so that a significant fraction of solutes was not identified.

The osmotic adjustment of salinity-exposed plants was almost entirely by uptake of Cl^- and Na^+. Organic solutes contributed only 5% to total solute concentration in acclimated plants and 7 to 9% in nonacclimated plants (Figs. 6 and 7). The concentration of K^+ was slightly reduced by Na^+, whereas the concentration of Ca^{2+} + Mg^{2+} was unchanged. Even in water-stressed plants, the contribution of Cl^- to osmotic adjustment was approximately 25% and that of organic solutes was only in the range of 10 to 20%.

The full osmotic adjustment which was found in salinity-acclimated plants was thus achieved mainly by the uptake of Cl^- and Na^+, whereas the organic solute contributed only 8 to 10% to this adjustment. This increase in organic solutes would be more than sufficient to provide compatible solutes to the chloroplasts which comprise a much smaller fraction of the cell and would thus ensure the maintenance of chloroplast volume and activity. It was earlier shown that stomatal volume can be maintained even with a marked decline of leaf water.

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