

Genetic Relationship Between Turgor Maintenance and Growth in Cotton Germplasm¹

J. E. Quisenberry, G. B. Cartwright, and B. L. McMichael²

ABSTRACT

Seventeen photoperiodic sensitive cotton (*Gossypium hirsutum* L.) stocks were grown for 2 years (1980 and 1981) at Big Spring, Tex. to evaluate the relationship between turgor maintenance and shoot dry matter accumulation (growth). During each year, leaf-cutter thermocouple psychrometers were used to measure predawn and midday leaf water and osmotic potentials and to estimate turgor pressure at 50 and 80 days after planting (DAP). Shoot dry weights were measured also at 50 and 80 DAP. The 1st year was hot and dry while the 2nd year had about average temperatures and rainfall. Linear regressions between predawn and midday water and turgor potentials were used to estimate turgor maintenance as i) the change in turgor pressure per unit change of water potential (slope) and, ii) the osmotic potential where zero turgor pressure occurred (X intercept). Significant differences did not occur among the stocks for changes in turgor pressure per unit change in water potential (slope), but they did occur among stocks for osmotic potential at zero turgor (π_0) at all four sampling dates. Analysis over-all of the sampling dates, identified a consistently low (T178) and high (T292) stock for π_0 . Linear correlation and regression coefficients between shoot dry weights and π_0 were negative and statistically significant during the sampling period (80 DAP, 1980) when the plants were water-stressed. The linear correlation and regression coefficients were negative, but not statistically significant during the other sampling periods (50 DAP, 1980, and 50 and 80 DAP, 1981). Linear correlation coefficients between the change in shoot dry weights between 50 and 80 DAP in 1980 and the change in π_0 were negative ($r = -0.82$) and statistically significant. These relationships suggest that if selection pressure is directed towards enhancing osmotic adjustment under water stress, a reduced growth potential may result.

Additional index words: Osmotic potential, Water potential, Shoot dry weights, *Gossypium hirsutum* L., Osmotic adjustment, Physiological genetics.

SEVERAL physiological and biochemical adjustments have been shown to occur when plants are grown with insufficient water (5). One such response is the maintenance of turgor pressure at low water potential through the adjustment of osmotic potential (1,2,4). Turgor maintenance has been shown to be related to the ability of a plant to reduce the osmotic potential as water potential is reduced (10). The reduced osmotic potential results from either the passive concentration of solutes due to dehydration, increases in cellular elasticity and thus passive concentration of cell solutes, or an increase in the net accumulation of cellular solutes. The exact cause of the change in osmotic potential is difficult to determine, and probably all of these events occur at different stages in the adaptation process. In each case, however, turgor pressure will be maintained at a reduced water potential.

The maintenance of turgor pressure is essential for

cell elongation and for open stomata (3,9). Cell elongation is related to expansive growth and perhaps cell division, while the maintenance of open stomates is related to the diffusion of carbon dioxide and subsequently continued carbon fixation by the photosynthetic process. The additional photosynthate produced through this process should produce increased growth in water stressed environments.

Radin (8) has defined criteria for identifying the different types of turgor maintenance from plots of turgor pressure vs. water potential. From these criteria, it can be deduced that the active accumulation of cellular solutes will significantly shift the intercepts of such plots while leaving the slope unchanged. Changes in either cellular elasticity or water partitioning will significantly affect the slope of the line. Turner and Jones (10) have suggested that the degree of osmotic adjustment can be measured as the change in osmotic potential at a particular water potential or water content. They suggested that for the purpose of comparison, osmotic potential should be estimated at either full turgor (i.e. where $\Psi = 0$, and $\rho = \pi$) or zero turgor (i.e. where $\rho = 0$, and $\Psi = \pi$), where Ψ is the total water potential, π is the osmotic potential, and ρ is the turgor pressure.

The objectives of this study were i) to determine the amount of genetic variability in turgor maintenance among exotic cotton germplasm and, ii) to relate this variability in turgor maintenance to growth under water deficient field conditions. This information should be useful in determining the potential benefits expected from selecting cotton germplasm with an enhanced ability for turgor maintenance.

MATERIALS AND METHODS

Seventeen photoperiodic sensitive (short-day) cotton stocks were grown during 2 years (1980 and 1981) at the USDA-ARS field station at Big Spring, Tex. The 17 non-flowering stocks were from the World Collection of *Gossypium* germplasm maintained by USDA-ARS scientists at College Station, Tex. These stocks represented four of the *G. hirsutum* L. races (Table 1) and were chosen to represent a cross-section of growth and morphological characters observed during several years of testing numerous photoperiodic stocks from the World Collection. Nonflowering stocks were used to reduce the variability in growth associated with changing sink-source relationships.

The 17 stocks were planted in three replications in a randomized complete block design on 20 May 1980 and 2 June 1981. A commercial cultivar, Tamcot SP-37, was used to border each of the 17 test entries. Within each replication, plots were a single row, plot length was 11 m and was divided into 3×3.7 m sections. Data were taken from one section at 50 days after planting (DAP), from another section at 80 DAP, and the center section was used to monitor soil water extraction with a neutron probe. Conventional tillage and cultural operations were performed. The soil type was an Amarillo sandy clay loam (fine-loamy, mixed,

¹ Cooperative investigations among the USDA-ARS, the Texas Agric. Exp. Stn., and Texas Tech Univ., Lubbock, TX 79401. Received 3 Aug. 1983.

² Research geneticist, biological laboratory technician, and plant physiologist, respectively. Plant Stress and Water Conservation Research Unit, USDA-ARS, Route 3, Lubbock, TX 79401.

Table 1. Means and mean separation for shoot dry weights for 17 exotic cotton stocks measured at two time periods in 1980 and 1981.

		1980		1981	
Stocks	Race	50 DAP	80 DAP	50 DAP	80 DAP
<i>g</i>					
T 79	latifolium	5.6 bc†	9.5 d-f	5.7 c-e	24.1 bc
T 95	latifolium	3.3 c	5.8 f	4.7 d-f	19.7 b-e
T 168	latifolium	4.2 bc	8.3 d-f	3.9 ef	21.6 b-e
T 178	latifolium	4.0 bc	7.9 ef	5.1 c-f	16.1 de
T 186	latifolium	3.9 c	8.3 d-f	3.8 ef	14.9 e
T 191	morrilli	3.9 c	10.0 b-f	4.7 d-f	21.5 b-e
T 192	morrilli	4.8 bc	9.9 c-f	6.7 cd	23.0 b-d
T 196	latifolium	4.5 bc	11.8 b-e	7.4 bc	21.4 b-e
T 209	latifolium	4.9 bc	12.8 b-d	5.9 c-e	22.3 b-e
T 215	latifolium	6.3 b	8.9 d-f	6.1 c-e	26.3 b
T 217	latifolium	3.8 c	8.1 ef	3.0 f	18.0 c-e
T 222	latifolium	6.8 b	17.2 a	9.6 ab	24.1 bc
T 223	latifolium	5.0 bc	10.2 b-f	6.7 cd	19.5 b-e
T 257	morrilli	5.0 bc	11.0 b-e	6.3 c-e	22.5 b-d
T 292	morrilli	5.1 bc	14.5 ab	5.4 c-f	20.3 b-e
T 461	richmondi	8.4 a	14.4 a-c	10.6 a	36.8 a
T 684	yucatanense	5.4 bc	12.3 b-e	7.5 bc	22.8 b-d
Mean		5.0	10.6	6.1	22.1

† Means within columns followed by the same letter are not statistically different at the 0.05 probability level based on a Duncan's Multiple Range Test.

thermic Aridic Paleustalfs). Irrigation water was not applied.

The 2 test years differed in rainfall and temperatures. In 1980, 19.1 cm of rainfall occurred prior to planting, 13.0 cm between planting and 50 DAP (most of this rainfall occurred in May and early June), and only 0.4 cm between 50 and 80 DAP. The average monthly temperatures were 28.3°C in June, 31.1°C in July, and 28.3°C in August. These values compare with the long-term averages of 26.7°C in June, 28.3°C in July, and 27.2°C in August. Plant growth was severely reduced by insufficient soil water (11 g dry mass per plant at 80 DAP). The year was hot and dry. In 1981, 26.9 cm of rainfall occurred prior to planting, 15.2 cm between planting and 50 DAP, and 5.1 cm from 50 to 80 DAP. Monthly temperature averages were 26.1°C in June, 28.9°C in July, and 26.7°C in August. This year was about average in rainfall and temperatures. Plant growth was not affected seriously by water limitations (22 g dry mass per plant at 80 DAP).

At 50 and 80 DAP, Merrill leaf-cutter thermocouple psychrometers³ were used at predawn and midday to measure total water and osmotic potentials of the upper-most fully expanded leaves. Each psychrometer was calibrated with NaCl solutions at 30°C in a water bath controlled to $\pm 0.1^\circ\text{C}$. All readings were made in the 30°C water bath. Leaf samples were taken from intact plants, sealed in the psychrometer chambers, and allowed to equilibrate for 4 h prior to measuring water potential. After water potential was determined the psychrometer chambers were placed in liquid N for one minute, reequilibrated for one hour, and osmotic potential was read. Turgor pressure was estimated as the difference between total water potential and osmotic potential. Four plants were measured from each plot at predawn and midday. These four values were averaged to estimate plot water status. Following the estimates of water status, 10 plants were harvested from each plot. Leaf area and dry weights were measured and the data were summarized on a per plant basis.

³ Mention of a trademark or proprietary product does not infer any endorsement or preferential treatment of the product by the USDA.

Table 2. Water potentials (Ψ) and osmotic potentials (π) measured during 2 years, two time periods during each year, and two times during the day for 17 exotic cotton stocks.

Year	Sampling time	Predawn		Midday	
		Ψ	π	Ψ	π
MPa					
1980	50 DAP†	-0.9*	-1.5*	-1.9	-2.1*
	80 DAP	-2.3	-2.9*	-3.4	-3.4*
1981	50 DAP	-1.3**	-1.7**	-2.3*	-2.3*
	80 DAP	-0.6	-1.3	-1.5	-1.7*

*,** Indicates statistically significance levels 0.05 and 0.01, respectively, for the stock mean squares from an analysis of variance.

† DAP = days after planting (data taken on 9 July and 14 Aug. 1980, and 22 July and 20 Aug. 1981).

Linear regressions of turgor pressure (y) on predawn and midday total water potential (x) were calculated to estimate i) the change in turgor potential per unit water potential (slope), and ii) the osmotic potential at zero turgor potential (π_0) (X intercept). Analysis of variance and Duncan's multiple range test were used to determine differences among the stocks. Regression analyses were used to estimate effects of turgor maintenance on growth (shoot dry weights).

RESULTS AND DISCUSSION

Shoot dry weights averaged 5.0 and 6.1 g at 50 DAP and 10.6 and 22.1 g at 80 DAP in 1980 and 1981, respectively (Table 1). Quisenberry et al. (7) reported that irrigated (water applied at—50 cb based on tensiometers placed at 46 cm) shoot dry weights taken at Big Spring in 1978 from 15 exotic nonflowering cotton strains averaged 2.7 g at 44 DAP, 8.5 g at 58 DAP, 15.6 g at 72 DAP, and 21.5 g at 86 DAP. A comparison of the 50 DAP dry weights in 1980 and 1981 and the 80 DAP dry weight in 1981 with these 1978 values suggests that the plants were not subjected to water stress prior to these sampling dates. Prior to the 80 DAP sampling in 1980, the plants were subjected to water stress and the lack of available water (only 0.4 cm at 64 DAP) reduced dry matter production about 50%.

The stocks differed in shoot dry weights at all four sampling dates (Table 1). One stock, T461, tended to produce the most shoot dry weight. The only sampling time when T461 was not significantly larger than the other 16 stocks was at 80 DAP in 1980. In an across years analysis of variance, the three-way interaction between years-sampling time-stocks was statistically significant at the 0.01 probability level (analysis not shown). When the analysis was conducted without the data from 80 DAP in 1980, none of the interactions were significant. The results suggested that some stocks did produce proportionally more dry weight under water stress. Two stocks noted were T222 and T292. It should be stated that we did not measure root dry weights since we do not know of an acceptable method for these field measurements. In greenhouse pot studies, we have found that roots from nonflowering cottons account for about 10 to 20% of the total biomass (unpublished data).

Mean total water and osmotic potentials averaged over the 17 stocks for the predawn and midday time periods, the 50 and 80 DAP sampling times, and for the two years are given in Table 2. Rainfall data, soil

Table 3. Mean squares from the analyses of variance of linear regression coefficients (b_1) from water potential regressed on turgor potential and osmotic potentials at zero turgor potential (π_o) for 17 cotton stocks.

SOV	df	1980				1981			
		50 DAP		80 DAP		50 DAP		80 DAP	
		b_1	π_o	b_1	π_o	b_1	π_o	b_1	π_o
Replications	2	0.019	0.024	0.037	0.341	0.037	0.104**	0.001	0.100**
Stocks	16	0.013	0.135*	0.023	0.705*	0.008	0.125**	0.012	0.109**
Error	32	0.009	0.063	0.014	0.321	0.014	0.043	0.012	0.031
CV (%)		20.1	11.2	21.7	16.6	27.4	8.8	17.0	9.6
Mean	MPa	0.46	-2.3	0.54	-3.4	0.43	-2.4	0.57	-1.8

*, ** Significant at the 0.05 and 0.01 probability level, respectively.

Table 4. Means for osmotic potential at zero turgor potential (π_o) for 17 exotic cotton stocks measured at two time periods in each of 2 years.

Stocks	1980		1981		Average
	50 DAP	80 DAP	50 DAP	80 DAP	
T 79	2.4 b†	4.1 ab	2.5 ab	1.9 a-c	2.7 ab
T 95	2.4 b	3.7 a-d	2.4 ab	1.9 a-c	2.6 a-c
T 168	2.1 bc	3.6 a-d	2.4 ab	1.9 a-c	2.5 a-c
T 178	2.9 a	4.3 a	2.6 a	2.2 a	3.0 a
T 186	2.1 bc	3.3 a-d	2.5 ab	1.8 bc	2.4 a-c
T 191	2.1 bc	3.5 a-d	2.2 b	1.6 c	2.4 a-c
T 192	2.2 bc	3.2 a-d	2.2 b	1.8 bc	2.3 a-c
T 196	2.3 bc	3.1 a-d	2.4 ab	2.0 ab	2.5 a-c
T 209	2.3 bc	3.0 b-d	2.4 ab	2.0 ab	2.4 a-c
T 215	2.5 ab	3.9 a-c	2.6 a	1.7 bc	2.7 ab
T 217	2.2 bc	3.4 a-d	2.6 a	1.7 bc	2.5 a-c
T 222	2.3 bc	2.6 d	2.3 ab	1.7 bc	2.2 bc
T 223	2.1 bc	3.6 a-d	2.3 ab	1.7 bc	2.5 a-c
T 257	2.3 bc	3.6 a-d	2.2 b	1.9 a-c	2.5 a-c
T 292	2.1 bc	2.6 d	1.8 c	1.3 d	1.9 c
T 461	2.1 bc	3.4 a-d	2.3 ab	1.7 bc	2.4 a-c
T 684	1.9 c	2.8 cd	2.5 ab	1.9 a-c	2.3 a-c

† Means within columns followed by the same letter did not differ statistically at $P = 0.05$ by Duncan's Multiple Range Test.

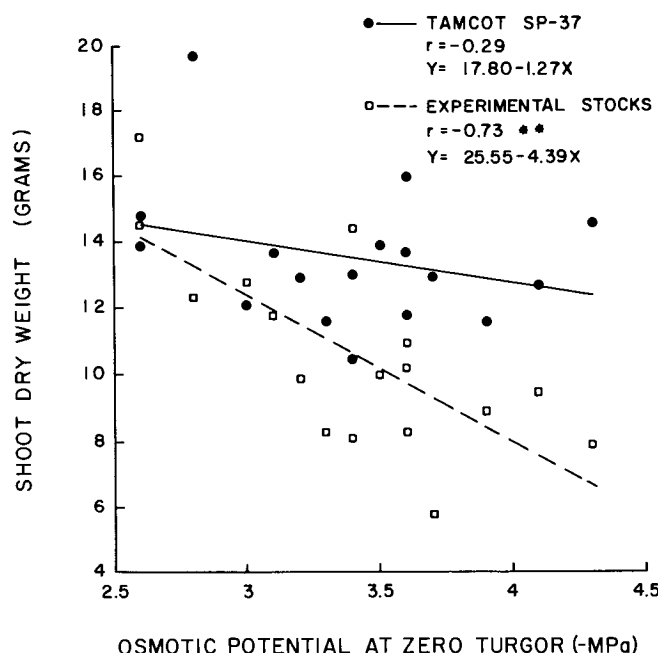
water estimates from neutron probes (data not shown), and the shoot dry weights (Table 1) taken at 50 DAP in 1980 and 50 and 80 DAP in 1981 showed that the plants had not been water stressed prior to these sampling times. In 1980, the same data showed that plants at 80 DAP were water stressed prior to the sampling.

The stocks differed in predawn water potential at 50 DAP in both 1980 and 1981 and in midday water potentials at 50 DAP in 1981 (Table 2). The stocks differed in osmotic potential at all predawn and midday estimates, except predawn at 80 DAP in 1981.

Analyses of variance on the change in turgor potential per unit change in water potential (linear regression coefficients) revealed that the stocks did not differ significantly in this parameter (Table 3). The average change in turgor potential per -1 MPa water potential was 0.5 MPa. Similar analyses of osmotic potentials at zero turgor (π_o) showed that the stocks differed at each of the sampling dates. The mean values at 50 DAP in 1980 and 50 and 80 DAP in 1981 were similar at -2.3 , -2.4 , and -1.8 MPa. The value at 80 DAP in 1980 was -3.4 MPa. The change in π_o from 50 to 80 DAP in 1980 was due to water stress.

Means for π_o for the 17 stocks for the four sampling times are given in Table 4. Differences between two stocks are obvious: T178 always had the lowest π_o , while T292 generally had the highest value.

In an analysis of variance across years on π_o , stocks


Fig. 1. Osmotic potential at zero turgor potential regressed on shoot dry weights for 17 exotic cottons and their border plots of Tamcot SP-37 at 80 DAP in 1980.

were significantly different but none of the two-way or three-way interactions was significant (analysis not shown). Linear correlation coefficients were calculated on the stock π_o means between 80 DAP in 1980 (plants grown under water stress) and 50 DAP in 1980, and 50 and 80 DAP in 1981 (plants not grown under water stress). The linear correlation coefficients (r) were 0.62 , 0.52 , and 0.49 , respectively. All coefficients were significantly different from zero ($P = 0.05$). The lack of significant interactions and the significant correlation coefficients suggest that certain germplasms, such as T178, maintain a low osmotic potential at zero turgor potential, regardless of plant water stress. Ladyman et al. (6) have drawn the same conclusion for the accumulation of glycinebetaine in barley (*Hordeum vulgare* L.).

The relationship between plant dry weights and π_o at 80 DAP for the 17 stocks in 1980 is shown in Fig. 1. The dry weights from the border rows of Tamcot SP-37 regressed on the π_o for the experimental stock are also shown. The Tamcot SP-37 dry weights were used to confirm that the relationship among the experimental stocks was genetic and not due to spatial

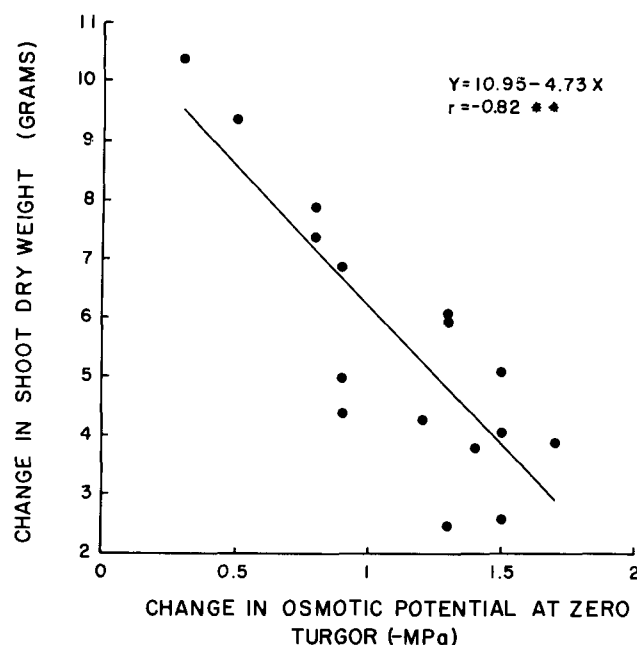


Fig. 2. Changes in osmotic potential at zero turgor regressed on changes in shoot dry weights from 50 to 80 DAP in 1980 for 17 exotic cottons.

variability of soil water among the plots. Changes in soil-water content over the season (data not shown) further supported the genetic nature of the relationship. A statistically nonsignificant linear regression coefficient existed between the experimental stock π_0 and the adjacent dry weights of Tamcot SP-37. The negative relationship between the stock dry weights and π_0 was highly significant. Stocks that had the lowest osmotic potential at zero turgor produced the least amount of shoot dry weights.

These results were further confirmed when changes in shoot dry weights (growth) from 50 to 80 DAP in 1980 were regressed on changes in π_0 (Fig. 2). Again those stocks that maintained the most turgor had the least amount of growth. Comparisons of the relationships at 50 DAP in 1980 and 50 and 80 DAP in 1981 showed that although the correlation and regression coefficients were generally not significant statistically, the direction of the relationship remained constant (i.e. reduced growth was associated with low π_0).

The results we obtained in this study did not meet our expectations based on prior physiological studies on turgor maintenance. Most of these studies have been conducted with a single crop cultivar (3). In these studies, water optimal and water deficient conditions were compared to estimate the relationships between turgor maintenance and continued growth under water deficit conditions. Under these experimental conditions, turgor maintenance at low water potentials has been shown to be used by plants to

avoid temporarily the detrimental effects on growth associated with deficient available water. In this study, all the stocks increased their π_0 from 50 to 80 DAP in 1980. Each stock maintained turgor at lower water potentials.

Two explanations can be used to interpret our results. The first would be that growth inhibition and turgor maintenance are both manifestations of water stress i.e., parallel but not related responses. If so, then selection for turgor maintenance would result in strains that would not grow well under water stress. In fact, selection would be for stress-susceptible germplasm. Perhaps, as the results suggest, we should select against turgor maintenance.

Another possible explanation would be that turgor maintenance and growth inhibition are related responses. Turner and Jones (10) have considered the cost of osmotic adjustment and concluded that accumulation of osmotically active solutes will be at the expense of some growth processes. In addition, since we did not measure the dry matter of the root system, it is possible that those stocks with low shoot dry weights may have put proportionally more dry weight into roots. Regardless of the explanation used to interpret the results, we are hesitant to develop a selection program based upon the ability of a plant to maintain turgor at low water potentials without additional research on the phenomena.

REFERENCES

1. Ackerson, R.C. 1981. Osmoregulation in cotton in response to water stress. *Plant Physiol.* 67:489-493.
2. Coyne, P.I., J.A. Bradford, and C.L. Dewald. 1982. Leaf water relations and gas exchange in relation to forage production in four asiatic bluestems. *Crop Sci.* 22:1036-1040.
3. Cutler, J.M., and D.W. Rains. 1978. Effects of water stress and hardening on the internal water relations and osmotic constituents of cotton leaves. *Physiol. Plant* 42:261-268.
4. ———, ———, and R.S. Loomis. 1977. Role of changes in solute concentration in maintaining favorable water balance in field-grown cotton. *Agron. J.* 69:773-779.
5. Hsiao, T.C., E. Acevedo, E. Fereres, and D.W. Henderson. 1976. Water stress, growth, and osmotic adjustment. *Philos. Trans. R. Soc. London, Ser. B* 273:479-500.
6. Ladyman, J.A.R., K.M. Ditz, R. Grumet, and A.D. Hanson. 1983. Genotypic variation for glycinebetaine accumulation by cultivated and wild barley in relation to water stress. *Crop Sci.* 23:465-468.
7. Quisenberry, J.E., W.R. Jordan, B.A. Roark, and D.W. Fryrear. 1981. Exotic cottons as genetic sources for drought resistance. *Crop Sci.* 21:889-895.
8. Radin, J.N. 1983. Physiological consequences of cellular water deficits: Osmotic adjustment. In H.M. Taylor, W.R. Jordan, T.R. Sinclair (ed.) *Limitation to efficient water use in crop production*. Am. Soc. of Agron. Madison, Wis.
9. Steponkus, P.L., K.W. Shahan, and J.M. Cutler. 1982. Osmotic adjustment in rice. p. 181-195. In *Drought resistance in crops with emphasis on rice*. Inter. Rice. Res. Int., Los Banos, Laguna, Philippines.
10. Turner, N.C., and M.M. Jones. 1980. Turgor Maintenance by osmotic adjustment: A review and evaluation. p. 87-103. In N.C. Turner and P.J. Kramer (ed.) *Adaptation of plants to water and high temperature stress*. John Wiley and Sons, New York.