

WATER RELATIONS IN DIFFERENT GUAR (*CYAMOPSIS TETRAGONOLOBA* (L.) TAUB) GENOTYPES UNDER WATER STRESS

BARKAT KHANZADA, M. YASIN ASHRAF*, S. AHMED ALA**, S.M. ALAM, M.U. SHIRAZI AND R. ANSARI

*Plant Physiology Division,
Nuclear Institute of Agriculture, Tandojam, Sindh, Pakistan.*

Abstract

Water relations of four guar genotypes viz., S-807, Esser, Brooks and S-1183 under different water regimes at pre-flowering, post-flowering and terminal drought were studied in cemented tanks under natural conditions. Water deficit reduced yield relative water content (RWC), leaf osmotic potential (OP), leaf water potential (WP), turgor potential (TP) in all four guar genotypes used. However, the genotypes S-807 and Esser had comparatively higher yield RWC, turgor potential under all water stresses than Brooks and S-1183. Maximum reduction in all parameters were recorded under terminal drought. The differences between pre- and post-flowering stresses were non-significant in case of yield and RWC but significant in other parameters. Genotypes with higher RWC and turgor potential had higher seed weight.

Introduction

Guar (*Cyamopsis tetragonoloba* (L.) Taub), an important legume crop of Pakistan is grown over an area of about 242.6×10^3 hectares with seed production of 220.7×10^3 tons/year on an average yield of 909.7 kg/ha (Anon., 1993). It is a multipurpose crop and is used as a vegetable for human consumption, forage for cattle and is also used as a green manure crop (Hymowitz & Matlock, 1964). It improves the soil fertility through adding nitrogen in soil as its roots have nitrogen fixing bacteria. Its seed is also a rich source of agro-based industry to obtain galactomanin gum, which is used in food processing, paper manufacturing, textile printing and in pharmaceutical industries (Alexander *et al.*, 1988). In Pakistan, field crops are mainly irrigated by canals, however, about 1/3rd of the total cultivable land is rainfed, which is variable and unpredictable (Anon., 1992). In addition, the crops near the tail end of the canals generally face water shortage in their life cycle.

Various forces acting on plant growth through soil, plant atmosphere continuum, which allow the uptake and loss of water, constitute the water relations. The components of water relations consist of water potential (WP), osmotic potential (OP), turgor potential (TP) and relative water content (RWC). The study of water relations of cell/tissue are important since the differences in water relation characteristics reflects the difference between species and cultivars and are considered as an indicator of drought resistance or adaptation to drought (Sobrado & Turner, 1983). Particularly, osmotic adjustment i.e., active lowering of osmotic potential in response to drought is regarded as mechanism that significantly contribute to increase drought resistance (Morgan, 1984; Blum & Sullivan; 1986, Ludlow & Muchow, 1990). The transfer of water in the soil, plant atmosphere continuum is commonly regarded as a catenary flow process, the rate of which is

*Nuclear Institute of Agriculture and Biology, Faisalabad.

**Department of Botany, University of Sindh, Jamshoro, Sindh, Pakistan.

determined by potential gradients (driving force) and resistance. Besides, turgor has been considered as the driving force for cell elongation and expansion of growth (Turner, 1986). However, recent research has underlined the role of other factors than just turgor in determining the expansion growth (Termaat *et al.*, 1985; vanVolkenburgh & Boyer, 1985). The present study was therefore conducted to investigate the physiological aspect of water relations of guar genotypes under different water regimes.

Materials and Methods

The experiment was conducted in four cemented tanks, each tank measuring 9 m² (3 x 3 m) and 1 m in depth. Individual tank was separated by a 15 cm thick cemented wall which acted a buffer zone on each side to prevent seepage. Prior to sowing, the soil of the tanks were carefully levelled to ensure the even distribution of water. Soil samples from individual tanks were collected from 0-15, 16-30 and 31-60 cm depths before sowing the seeds and then analyzed for various physio-chemical properties (Table 1). A basic dose of urea (70 kg N/ha) and diammonium phosphate (35 kg P₂O₅/ha) were broadcast and mixed with the surface layer (0-15 cm) immediately prior to sowing.

Table 1. Soil characteristics of experimental site.

Characteristics	Soil profile		
	0-15 cm	16-30 cm	31-60 cm
	-----Depth-----		
A. Physical			
Sand %	45.96	46.00	46.00
Clay %	29.50	28.86	28.06
Silt %	24.54	25.14	25.94
Texture	Sandy clay loam	Sandy clay loam	Sandy clay loam
Bulk Density (g cm ⁻³)	1.40	1.40	1.40
Water Holding Capacity (%)	39.20	39.00	39.00
Field Capacity (-0.03 MPa)	28.20	28.00	28.00
Wilting Point	14.00	13.94	13.69
B. Chemical			
Nitrogen (%)	0.05	0.05	0.05
Available P (ppm)	6.50	5.00	4.00
Exchangeable K (ppm)	160.00	155.00	155.00
Organic Matter (%)	0.74	0.71	0.54
ECe (mS cm ⁻¹)	0.20	0.21	0.20
pH	7.20	7.10	7.10
HCO ₃ (meq-l)	2.21	2.25	2.15
Cl (meq-l)	6.20	6.34	6.86
SO ₄ (meq-l)	12.46	11.76	11.68
Ca+Mg (meq-l)	12.40	11.26	11.36
Na (meq-l)	10.42	10.42	10.45

Table 2. Effect of water stress on 100 seed weight (g) and relative water contents (RWC%) of different guar genotypes.

Variety	Treatment				Mean
	Control	Preflowering stress	Postflowering stress	Terminal stress	
	Seed weight				
	A	B	B	C	
S-807	3.78 b	3.56 b	3.48 b	2.75 a	3.39 b
	A	B	C	D	
ESSER	3.96 a	3.79 a	3.62 a	2.79 a	3.54 a
	A	B	C	D	
Brooks	3.79 b	3.50 b	3.39 c	2.15 c	2.88 d
	A	B	B	C	
S-1183	3.75 b	3.44 c	3.36 c	2.25 b	3.25 c
	A	B	B	C	
Mean	3.56	3.40	3.36	2.42	
	R.W.C.				
	A	B	B	C	
S-807	86.75 a	67.86 a	68.02 a	52.73 b	68.84 a
	A	B	B	B	
ESSER	71.64 b	64.58 a	63.70 ab	62.35 a	65.57 ab
	A	B	B	C	
Brooks	71.69 b	63.75 a	62.04 ab	49.45 b	61.73 ab
	A	B	B	C	
S-1183	75.00 b	65.37 a	67.00 a	52.51 b	64.84 ab
	A	B	B	C	
Mean	76.27	65.38	65.19	54.26	

Means in the same column and same row sharing the same letters did not differ significantly according to Duncan's New Multiple Range Test at 5% level.

Four guar genotypes viz., S-807, Esser, Brooks and S-1183 were used. The experiments were laid out in a complete randomized block design, with irrigation regimes in the main plots and genotypes in the sub-plots with three replications. The pre-sowing irrigation (75 mm) was applied. Seeds were hand drilled after the soil become into field capacity conditions, each genotypes was allotted three rows of 0.8 m length and having row to row distance of 0.30 m. The plants were grown up to maturity and when needed (75 mm) irrigation water was applied. The following stress treatments were imposed to simulate the type of drought generally encountered in the region.

1. Control = Normal irrigation as recommended for guar. Irrigation was applied after 30, 45 and 60 days of sowing using 75mm per irrigation, the quantity was measured by a water meter.
2. Preflowering = No irrigation up to flowering initiation.
3. Postflowering = No irrigation after flowering.
4. Terminal drought = No irrigation.

The seed weight of the respective treatments were recorded to study the differences between the treatments.

Before maturity, but at the grand growth period normally 45 days of sowing, water potential (estimated by pressure bomb), osmotic potential (by Micro Osmometer), turgor potential ($WP-OP=TP$) and relative water content (according to Weatherley, 1950) were determined. After harvest, 100 seed weight was also calculated. Analysis of variance was applied to determine the significance of differences among the treatments and /or genotypes. Differences were compared by Duncan's Multiple Range Test (DMRT) at 5% probability (Steel & Torrie, 1980).

During the growth period, all cemented tanks were protected from rain by manually operated shelter equipped with movable sheet of transparent flexible plastic sheet. Normal cultural practices were carried out and the tanks were hand weeded and hoed whenever necessary.

Results

Seed yield progressively decreased due to increase of water stress in all genotypes (Table 2). Under control condition, the genotypes had similar values except Esser, which had significantly higher yield. Similarly, under preflowering stress, again Esser had the higher values for 100 seed weight and lowest was in S-1183. Under postflowering stress, Esser had the higher seed weight while genotype S-1183 was lowest. Under terminal drought Esser and S-807 showed maximum seed weight with no significant differences whereas, Brooks and S-1183 had minimum seed weight, with significant differences. The treatment mean indicated non-significant differences between pre- and post-flowering stress. The highest seed weight was recorded under control condition and lowest under terminal stress. In genotype highest values for 100 seed weight were recorded in Esser followed by S-807, S-1183 and Brooks.

The relative water content (RWC) significantly reduced with the induction of water stress in all the genotypes (Table 3). Under control condition, S-807 had significantly higher RWC than in all the other genotypes. Under pre- and post-flowering stress, the differences among all the genotypes were non-significant. Under terminal drought the genotype Esser had the maximum RWC (62.35%), followed by S-807 (52.73%), S-1183 (52.51%) and Brooks (49.45%). However, the differences among the genotypes were non-significant, except that of Esser. The overall treatment mean showed significant differences, but the differences between pre-and post-flowering treatments were non-significant. The varietal mean values showed maximum RWC in S-807 (68.84%), followed by Esser (65.57%), S-1183 (64.84%) and Brooks (61.73%).

Similarly osmotic potential (OP), significantly reduced due to induction of different water regimes (Table 3). Under control the genotype had similar value except Brooks which has significantly higher values as compared to others. Under pre-and post-flowering stresses, the genotypes generally formed two groups, S-807 and Esser with lower OP and Brooks and S-1183 with higher OP whereas under terminal stress the differences among the genotypes were non-significant. The treatment mean showed reduction in OP due to the application of water stresses. Significant differences were recorded in all the treatments, but the differences between control and pre-flowering stress were non-significant. Genotypic mean again formed two groups, S-807 and Esser with lower OP values, Brooks and S-1183 with higher values.

Table 3. Effect of water stress on leaf Osmotic Potential (-Mpa), Water Potential (-Mpa) and Turgor Potential (Mpa) in different guar genotypes.

Variety	Treatment				Mean
	Control	Preflowering stress	Postflowering stress	Terminal stress	
Osmotic Potential (-Mpa)					
	C	C	B	A	
S-807	2.56 a	2.45 a	3.60 a	3.90 a	3.12 a
	C	C	B	A	
ESSER	2.62 a	2.51 a	3.77 a	4.01 a	3.23 a
	C	C	B	A	
Brooks	2.37 b	2.18 b	3.23 b	3.81 a	2.89 b
	C	C	B	A	
S-1183	2.65 a	2.23 b	3.16 b	3.74 b	2.94 b
	C	C	B	A	
Mean	2.55	2.34	3.44	3.87	
Water Potential (-Mpa)					
	C	C	B	A	
S-807	1.65 a	1.73 a	2.95 a	3.42 ab	2.44 a
	D	C	B	A	
ESSER	1.68 a	1.81 a	3.04 a	3.51 a	2.51 a
	C	C	B	A	
Brooks	1.48 b	1.49 b	2.66 b	3.39 ab	2.25 b
	C	C	B	A	
S-1183	1.67 a	1.57 b	2.62 b	3.38 ab	2.31 b
	C	C	B	A	
Mean	1.62	1.65	2.82	3.42	
Turgor Potential (Mpa)					
	A	B	C	D	
S-807	0.91 bc	0.72 a	0.65 b	0.48 a	0.69 a
	A	B	B	C	
ESSER	0.94 b	0.70 ab	0.73 a	0.50 a	0.72 a
	A	B	C	D	
Brooks	0.89 cb	0.69 ab	0.57 c	0.42 b	0.64 b
	A	B	C	D	
S-1183	0.98 a	0.66 cb	0.54 c	0.36 c	0.63 b
	A	B	C	D	
Mean	0.93	0.69	0.62	0.44	

Means in the same column and same row sharing the same letters did not differ significantly according to Duncan's New Multiple Range Test at 5% level.

Water stress significantly reduced the water potential in all the genotypes (Table 3). Esser showed significantly higher values as compared to others. Under pre- and post-flowering the genotypes S-8-7 showed lower WP whereas Brooks and S-1183 with higher WP. Under terminal drought the lowest WP was recorded in Esser (-3.51 Mpa) followed by S-807 (-3.42 Mpa), Brooks (-3.39 Mpa) and S-1183 (-3.38 Mpa), the differences

among S-807, Brooks and S-1183 were non-significant. The treatment means showed significant differences. The genotype means again constituted two groups as observed under pre- and post-flowering water stress conditions.

Like RWC, OP and WP, the turgor potential (TP) also significantly decreased due to the induction of water stress (Table 3). Plants grown under controlled condition showed significant differences among the genotypes. However, S-807 and Brooks had non-significant differences. Under pre-flowering stress the genotypes Esser and Brooks had similar values, but the maximum TP was observed in S-807 and minimum in S-1183. Under post-flowering conditions, the highest TP was recorded in Esser (0.73 Mpa) followed by S-807 (0.65 Mpa), Brooks (0.57 Mpa) and S-1183 (0.54 Mpa). Under terminal drought the genotypes S-807 and Esser did not differ significantly. On the other hand, the differences between Brooks and S-1183 were significant. Overall, the treatment means showed significant differences among the treatments. Genotypic means formed two groups, S-807 and Esser with higher turgor potential and Brooks and S-1183 with lower turgor potential.

Discussion

The importance of plant water status for the maintenance of turgidity which is required for plant growth and its survival has been widely recognised. Sanchez-Diaz & Kramer (1971) and Levitt (1972) have shown that drought resistant plants have smaller water deficit per unit decrease in leaf water potential than drought-susceptible plants. Kirkham *et al.*, (1980); Clark & McCraig (1982), Schonfeld *et al.*, (1988) and Ashraf & Khan (1990) evaluated the excised leaf water retention capabilities of wheat cultivars and found that genotypes with higher RWC were more drought resistant. In the present study, the RWC reduction in all the genotypes was recorded under water stress whereas, S-807 and Esser showed lower reduction in RWC at all water stress treatments (Table 3). The highest reduction was at terminal drought followed by postflowering and preflowering droughts. The difference between pre- and postflowering droughts was not significant. The genotypes, S-807 and Esser showed less reduction in yield under different water stress treatments. Such similar pattern for RWC has been observed on soybean (Carter & Patterson, 1985), barley, (Martin *et al.*, 1989) and groundnut (Joshi *et al.*, 1988). Flower & Ludlow (1986) reported that leaf survival which is essential for assimilation is determined by RWC, rather than by leaf water potential. RWC could be used as an indicator of drought resistance is supported by the present study and also by the authors quoted above.

Ludlow & Muchow (1990) based on the work of Flower & Ludlow (1986); Sinclair & Ludlow (1986) viewed low lethal water status as a mechanism for survival rather than having effect on yield components. However, indirectly it does contribute to dehydration tolerance and to leaf survival thus contributing to yield stability at least under intermittent water stress. They were of the view that high desiccation tolerance would not contribute substantially in terminal stress environments. It may be noted that there is a subtle difference between RWC and lethal water status. One indicates the degree of hydration and the other the hydration level at which the leaves of the plant die. Thus, the conclusions drawn on the basis of one's finding cannot be applied to the other. There is also a subtle difference in what is called terminal drought. Literally, it should mean where

no water is added to the growth medium from planting to harvesting, but in many studies some water was added by way of rainfall. Perhaps, this may be one of the reasons for different results obtained by different researchers.

Some workers are of the opinion that leaf water potential estimates over the whole stress period, provide the best information about the genotypic response rather than a single measurement obtained at peak stress under drought condition. Although, genotypes usually maintain their relative ranking as leaf water potential decreases with the stress intensity in sorghum (Blum, 1974), rice (O'Toole & Moya, 1978) and wheat (Blum, 1980; Ashraf & Khan, 1990). Variations in leaf water potential among wheat cultivars under moisture stress have also been reported (Fischer & Sanchez, 1979; Blum *et al.*, 1981; Aggarwal & Sinha, 1987; Ashraf & Khan, 1990). Sullivan & Estin (1974) and Levitt (1972) have suggested that leaf water potential may differentiate between drought resistant and susceptible cultivars. In the present study genotypes having lower leaf water potential showed higher seed yield (Table 2) with similar results observed in wheat as reported by Winter *et al.*, (1988).

Ludlow & Muchow (1990) suggested that osmotic adjustment results from the accumulation of solutes within cell which lowers the osmotic potential and helps to maintain turgor of plants experiencing water stress. The mechanism of compensation is essential for the survival of the plants as with decreasing water supply or soil potential also decreases. Faster decrease in osmotic potential is therefore, essential to maintain the potential difference to allow water uptake by the roots. Viewed in terms of energy potentials, reduction in the water potential induced by changes in the environments, are immediately off-set by reduction in the osmotic potential through an increase in the solute contents. In the present study when leaf water potential fell in response to a reduction in soil water, there was a parallel fall in the osmotic potential also. The pattern was observed in all genotypes tested in the present study (Table 3). The fall in S-807 and Esser was more clear than the others in all the treatments, which indicated their better adaptability to water stress environment. One of the mechanisms for reduction in osmotic potential is due to solute accumulation. In the present study, all the genotypes with lower osmotic potential had higher solute concentrations. Genotypes S-807 and Esser had the lowest leaf osmotic potential whereas Brooks and S-1183 the highest. These are the two groups of genotypes showing tolerant and non-tolerant response to various plant characteristics chiefly related to water stress tolerance.

Many important physiological and morphological processes such as leaf enlargement, stomatal opening and associated photosynthesis are directly affected by the leaf turgor potential. Under water stress condition, plants loose their turgor to a point restricting cell expansion (Turner, 1986). The plants must adjust their internal osmotic potential and sufficiently increase turgor to resume cell expansion and growth (Kramer, 1983). In contrast Munns (1988), reported that the major mechanism of turgor maintenance in plant growth system is osmoregulation. Here solutes accumulate, decreasing in the process the osmotic potential. The osmotic potential of the cell decreases allowing the uptake of water for maintaining the turgor potential of the cell. In the present study, the genotypes with lower osmotic potential had higher turgor under stress conditions (Table 3). The genotypes S-807 and Esser favourably maintained their turgor potential. The results of the present study showed that maintenance of turgor in plant system plays a significant role in the growth and seed weight of genotypes. The genotypes with higher turgor generally had

higher seed weight (Table 2). Turner *et al.*, (1978); Ackerson *et al.*, (1980) and Ludlow *et al.* (1985) observed that the maintenance of an optimum turgor range is very helpful for stomatal opening which is necessary for photosynthetic activity, which ultimately increase the productivity of plant. Water relations could thus be used for screening drought tolerant genotypes. Higher relative water content and turgor potential may be the causative factor for enhancing yield of a genotype under soil water deficit conditions.

Acknowledgement

Sincere thanks are due to Mr. Maraj Hussain Siddiqi, Stenographer of the Atomic Energy Agricultural Research Center Tandojam for composing this manuscript.

References

- Ackerson, R.C., D.R. Krieg and F.J.M. Sung. 1980 Leaf conductance and osmoregulation of field-grown sorghum genotypes. *Crop Sci.*, 20:10-14.
- Aggarwal, P.K. and S.K. Sinha. 1987. Response of droughted wheat to mid season water application, recovery in leaf area and its effect on grain yield. *Aust. J. Agric. Res.*, 14: 227-237.
- Alexander, W.L., D.A. Bucks and R.A. Backhaus. 1988. Irrigation water management for guar seed production. *Agron. J.*, 80: 447-453.
- Anonymous, 1992-93. Agriculture, In: *Pakistan Statistical Year Book*. Federal Bureau of Statistics. Economic Affairs and Statistics Division, Government of Pakistan, pp. 125-170, 1993.
- Ashraf, M.Y. and A.H. Khan. 1990. Effect of drought on wheat varieties during vegetative stage. *Sci. Int.*, 2: 325-327.
- Blum, A. 1974. Genotypic responses in sorghum to drought stress. 11. Leaf tissue water relations. *Crop Sci.*, 14:691-692.
- Blum, A. 1980. Drought avoidance in wheat and its rapid estimation by remote infrared thermal leaf canopy measurements. *Proc. 3rd. Inter. Wheat Conf.*, May 22- June 3. Madrid, Spain. *Crop Science*, 21: 43-47.
- Blum, A., G. Gozlan and J. Mayer. 1981. The manifestation of dehydration avoidance in wheat breeding germplasm. *Crop. Sci.*, 21: 495-499.
- Blum, A. and C.Y. Sullivan. 1986. The comparative drought resistance of land races of sorghum and millet from dry and humid regions. *Annals of Botany*, 57: 835-846.
- Carter, J.S. Jr. and R.P. Patterson. 1985. Use of relative water content as a selection tool for drought tolerance in soybean. In: *Agronomy Abstract*. pp.7. ASA, Madison, WI.
- Clark, J.M. and T.N. McCraig. 1982. Evaluation of techniques for screening for drought resistance in wheat. *Crop Sci.*, 22: 503-506.
- Fischer, R.A. and M. Sanchez. 1979. Drought resistance in spring wheat cultivars. II. Effects on plant water relations. *Aust. J. Agric. Res.*, 30: 801-814.
- Flower, D.J. and M.M. Ludlow. 1986. Contribution of osmotic adjustment to the dehydration tolerance of water stressed pigeon pea (*Cajanus cajan* (L.) Mills) leaves. *Plant Cell and Environ.*, 9: 33-40.
- Hymowitz, T. and R.S. Matlock. 1964. Guar seed plant and population studies, Oklahoma. *Agric. Exp. Stn. Tech. Bull.*, B108.
- Joshi, Y.C., P.C. Nautiyal, V. Ravindra and R.S. Dwivedi. 1988. Water relations in two cultivars of groundnut (*Arachis hypogea* L.) under soil water deficit. *Trop. Agric.*, (Trinidad), 65: 182-184.
- Kirkham, M.B., E.L. Smith, C. Dhanasobhen and I.I. Drake. 1980. Resistance to water loss of winter wheat flag leaves. *Cereal Research Communication*, 8: 393-399.

- Kramer, P.J. 1983. *Water relations in plants*. Academic Press New York.
- Levitt, J. 1972. *Responses of plants to environmental stress*. Academic Press, New York.
- Ludlow, M.M. and R.C. Muchow. 1990. A critical evaluation of traits for improving crop yields in water limited environments. *Adv. Agron.*, 43: 107-153.
- Ludlow, M.M., M.J. Fisher and J.R. Wilson. 1985. Stomatal adjustment to water deficits in three tropical grasses and a tropical legume in controlled conditions and in the field. *Aust. J. Plant Physiol.*, 12: 131-149.
- Martin, M.A., J.A. Brown and H. Ferguson. 1989. Leaf water potential, relative water content, and diffusive resistance as screening techniques for drought resistance in barley. *Agron. J.*, 81: 100-105.
- Morgan, J.M. 1984. Osmoregulation and water stress in higher plants. *Ann. Rev. Plant Physiol.*, 35: 299-319.
- Munns, R. 1988. Why measure osmotic adjustment? *Aust. J. Plant Physiol.*, 15: 717-726.
- O' Toole, J.C. and T.B. Moya. 1978. Genotypic variation in maintenance of leaf water potential in rice. *Crop. Sci.*, 18: 873-876.
- Sanchez-Diaz, M.F. and P.J. Kramer. 1971. Behavior of corn and sorghum under water stress and during recovery. *Plant Physiol.*, 48: 613-616.
- Schonfeld, M.A., R.C. Johnson, B.F. Carver and D.W. Mornthinweg. 1988. Water relation in winter wheat as drought resistance indicator. *Crop Sci.*, 28: 526-531.
- Sinclair, T.R. and M.M. Ludlow. 1986. Influence of soil water supply on water loss of four tropical grain legumes. *Aust. J. Plant Physiol.*, 13: 329-341.
- Sobrado, M.A. and N.C. Turner. 1983. A comparison of water characteristics of *Helianthus annuus* and *Helianthus petiolaris* when subjected to water deficit. *Oecologia*, 58: 309-313.
- Steel, R.G.D. and J.H. Torrie. 1980. *Principles and procedures of statistics*. McGraw-Hill, New York.
- Sullivan, C.Y. and J.D. Estin. 1974. Plant Physiological responses to water stress. *Agric. Meteorol.*, 14: 113-127.
- Termaat, A., J.B. Passioura and R. Munns. 1985. Shoot turgor does not limit shoot growth of NaCl affected wheat and barley. *Plant Physiol.*, 77: 869-872.
- Turner, N.C. 1986. Adaptation to water deficits.: a changing perspective. *Aust. J. Plant Physiol.*, 13: 175-190.
- Turner, N.C., J.E. Begg and M.L. Tonnet. 1978. Osmotic adjustment of sorghum and sunflower crops in response to water deficits and its influence on the water potential at which stomata close. *Aust. J. Plant. Physiol.*, 5: 597-608
- Van Volkenburgh, E. and J.S. Boyer. 1985. Inhibitory effect of water deficits on maize leaf elongation. *Plant Physiol.*, 77: 190-194.
- Weatherley, P.E. 1950. Studies in the water relations of the cotton plant. I. The field measurement of water deficits in leaves. *New Phytol.*, 49: 81-97.
- Winter, S.R., J.T. Musick and K.B. Porter. 1988. Evaluation of screening techniques for breeding drought resistant winter wheat. *Crop Sci.*, 28: 512-516.

(Received for publication 17 August 1998)