(Aus dem Bangladesh Institute of Nuclear Agriculture und aus dem Bereich Lebenswissenschaften des Österreichischen Forschungszentrums Seibersdorf)

Studies on drought resistance in *Sorghum bicolor* L. Muench
Leaf water parameters in different growth stages

By M. A. SALAM

(With 2 figures)

Summary

The different leaf water parameters, i.e., total leaf water potential (Ψt), leaf osmotic potential at full turgor (Ψs^{100}) leaf osmotic potential at zero turgor (Ψs^0), relative water content at zero turgor (RWC^0) and relative dry weight of the leaf (RDW) were studied during four growth stages in five varieties of sweet sorghum under various soil moisture regimes. In all the varieties, severely stressed plants under 30 % field capacity (FC) conditions showed the most negative noon Ψt, whereas plants grown under the highest soil moisture regimes (70 % FC) showed the least negative noon Ψt. The varieties X-8180 and 301 exhibited a similar potential to adjust osmotically in the dry environment. The range of their osmotic adjustment was from 0.20 to 0.50 MPa. Both varieties showed the highest sensitivity to drought during the dough stage of growth, but only in variety X-8180 the decrease in Ψs values was sufficient to maintain leaf turgor. The variety Red Top Candy was found to be moderately resistant, the extent of osmotic adjustment ranging from 0.10 to 0.25 MPa. This variety also showed less capacity for osmotic adjustment during the milk stage of growth. The variety Keller did not show any significant amount of osmotic adjustment. In the variety 405 only a weak tendency of osmotic adjustment was found during the flowering stage of growth.

Key-words: sorghum, drought, plant-water parameters, leaf water potential, osmotic adjustment.

Untersuchungen der Trockenresistenz von *Sorghum bicolor* L. Muench Wasserhaushaltsparameter in verschiedenen Wachstumsstadien

Zusammenfassung

In einem Gefäßversuch wurden die Auswirkungen von Wasserstreß auf verschiedene Wasserhaushaltsparameter wie Gesamtwasserpotential des Blattes (Ψt), osmotisches Potential des Blattes bei vollem Turgor (Ψs^{100}), osmotisches Potential des Blattes am Turgorverlustpunkt (Ψs^0), relativer Wassergehalt am

Turgorverlustpunkt (RWC^0) und relatives Trockengewicht des Blattes (RDW) bei Zuckerhirse in-situ untersucht. Die Messungen wurden bei fünf Sorten während verschiedener Entwicklungsstadien durchgeführt. Alle Sorten zeigten die niedrigsten Werte von Ψt bei einer Bodenfeuchte von 30 % der Feldkapazität (FC) und die höchsten bei 70 % FC. Bei den Sorten X-8180 und 301 war eine ähnliche genetische Fähigkeit zur osmotischen Anpassung bei Trockenstreß zu beobachten. Die osmotische Anpassung betrug 0,20 bis 0,50 MPa. Beide Sorten waren im Milchreifestadium trockenempfindlich, aber nur X-8180 konnte das osmotische Potential weit genug erniedrigen, um den Blattturgor zu erhalten. Die Sorte Red Top Candy erwies sich als mittelresistent. Die osmotische Anpassung bei dieser Sorte betrug jedoch nur 0,10 bis 0,25 MPa. Im Milchreifestadium zeigte Red Top Candy keine osmotische Anpassung. Bei der Sorte Keller war keine osmotische Anpassung nachzuweisen, bei der Sorte 405 gab es nur eine schwache Tendenz zur osmotischen Anpassung im Blütestadium.

Schlüsselworte: Sorghum, Trockenheit, Wasserhaushalt, Blattwasserpotential, osmotische Anpassung.

1. Introduction

Plant moisture conditions are crucial to growth and development of plants. Different types of environmental conditions can influence the status of plant moisture. For example, prolonged deficiency of rainfall may result in deficit soil moisture for crop plants. High ambient temperatures, low relative humidity and relatively high wind velocities on a clear day may also result in stress conditions for plants even under sufficient moisture conditions. Under these stress conditions, the uptake of water by roots may be insufficient to meet the transpirational loss in such dry air and soil environments. Due to the environmental demands the Ψt values of the leaves gradually decrease and leaf water content also declines. Ultimately, the leaves loose turgor, and in extreme cases, the plants may become wilted. In some cases, resistances to water flow from the root to shoot lead to plant stress conditions due to a reduced cross-sectional area of water conducting tissue or formation of tyloses in the xylem vessels (Hellkvist et al. 1974). Plants develop different mechanism to continue their growth or to survive water stress conditions. Some plants simply increase their root density and/or length. By penetrating deeper into the soil to reach moisture they thus enhance water absorption capabilities (Hsiao and Acevedo 1974, Turner and Begg 1981). Some plants have morphological characteristics which help to reduce absorbance of radiation, e. g. hairs (Quarrie and Jones 1977) or wax layers (Blum 1975). Increased stomatal resistances as a result of abscisic acid accumulation may also help to maintain constant leaf turgor by triggering the closing of stomata, thus keeping tissue water potential higher (Qarrie and Jones 1979, Pierce and Raschke 1980). Some plants have the capacity to maintain leaf turgor at low tissue water potentials and keep their stomata open. In these plants, active accumulation of osmotica in the cell sap occurs. Thus the osmotic potential is lowered and positive pressure potentials under depleted cell water content are maintained (Turner and Jones 1980). Genes that encode enzymes for steps in the synthesis of the osmolytes have also been identified (Bray 1993). Varietal differences in the ability of osmotic adjustment exist among field crops and trees (Morgan 1984, Barker 1991, Abrams et al. 1990, Premachandra et al. 1992). Increased cell wall elasticity (Elson et al. 1976) and reduction of cell sizes (STEUDLE et al. 1977) help to maintain leaf turgor by sustaining higher tissue water potentials at low tissue water content. C-4 plants such as maize, sorghum etc., are well known as plants of high energy content (starch, sugar etc.), higher photosynthetic rates (60 to 80 mg dm^{-2} h^{-1}) and high biomass production.

Strong efforts have been made to produce bioenergy from plant sources as an alternative to shortfalls of mineral oil. Bioenergy and industrial products based on biomass are generally considered to produce less CO_2 input into the atmosphere. There are dry areas in Austria where biomass production from sorghum and maize is low. The present study was carried out to measure leaf water parameters of sorghum under moist and dry conditions and to screen some varieties according to their ability of osmotic adjustment. The interaction between growth stage and varieties was also analysed.

2. Materials and methods

Two pot experiments were conducted in 1983 (May to October) and in 1984 (May to October) at the Institute of Agriculture, Austrian Research Centre, Seibersdorf, Austria. In 1983, five varieties of sweet sorghum (X-8180, 301, Red Top Candy, 405 and Keller) were grown. According to the first year performances, only three contrasting varieties (X-8180, Red top candy and Keller) were grown in 1984. Each pot contained 12 kg Seibersdorf chernozem. The pots were kept on wooden trolleys, on the cemented floor in ambient air. Five seeds were sown per pot; one plant only was allowed to grow beyond the four leaf stage. Three different soil moisture regimes (30 %, 50 % and 70 % field capacity [FC]) were carried out. Leaf water parameters were studied at four growth stages pre-flowering (pf), flowering (fl), milk (mi) and dough (dou). Each treatment was replicated twice in 1983 and three times in 1984. Usually the pots were irrigated three times a week, but during the periods of strongest evapotranspirative demand the plants were watered daily. Excess addition of water from rainfall was avoided by transferring the pots to a greenhouse according to the weather forecast. Total water potentials (Ψt) and pressure-volume (P-V) curves were determined from the same leaves. The fully expanded 2nd leaf from the apex position was used to measure Ψt. Measurements of Ψt were carried out between 11:00 and 14:00 hours using the pressure chamber technique (SCHOLANDER et al. 1965).

Determination of P-V curves: After measurement of the leaf water potential, the pressure within the chamber was released at a rate of 0.025 MPa (TURNER 1981) to avoid any injury of the tissue. The leaves were then removed from the chamber and resaturated by immersing the petioles in a glass jar containing a small amount of water. The inner surface of the glass jar was lined with wet filter paper to maintain high humidity. The jar was kept in the dark at room temperature. After attaining full saturation within 24 hours (TURNER 1981), the leaves were removed, their surfaces dried with tissue paper and weighed immediately. Thereafter, the leaves were placed into the pressure chamber and Ψt values were determined. The leaves were weighed again, the mean of the two weights was used to calculate the relative water content (RWC). The measurements were repeated several times until drought symptoms showed up on the blades. Beyond the turgor loss point of the leaf, five to ten measurements were taken so that linear regression lines could be easily established. Finally, the leaves were dried at 100 °C for 24 hours. The RWC of leaves was calculated using the following formula:

$$RWC = \frac{FW - DW}{TW - DW}$$

FW = Fresh weight of leaf
DW = Dry weight of leaf
TW = Turgid weight of leaf

From the P-V curves (Transformation type 1, RICHTER 1978) the osmotic potentials at full turgor (Ψs^{100}) and at zero turgor (Ψs^{0}) as well as the relative water content at zero turgor (RWC^{0}) were derived. The osmotic adjustment of the stressed plants (30 and 50 % FC) was calculated as the difference of Ψs^{100} values between the control (70 % FC) and the corresponding stress treatment. The relative dry weights of leaves (RDW) were calculated using the following formula:

$$RDW = \frac{DW}{TW - DW}$$

Considering the soil moisture regimes as factor A, and the growth stages as factor B, a two-way factorial analysis was completed for individual varieties. Least significant differences (LSD) tests were used to evaluate the data.

3. Results

3.1 1983 experiments

The effect of different soil moisture regimes on various leaf water parameters during different stages of growth is illustrated in figures 1a, b, c, d, and e for the varieties X-8180, 302, Red Top Candy, 405 and Keller, respectively. The 30 % treatment of variety X-8180 had a significantly lower Ψt value of −1.7 MPa at milk stage of growth. The flowering stage showed the least sensitivity to water stress as the Ψt decreased to −1.32 MPa only. Both the osmotic potentials at full turgor (Ψs^{100}) and at zero turgor (Ψs^{0}) were found to be significantly more negative in the stressed plants. The amount of osmotic adjustment was 0.22, 0.17, 0.40 and 0.25 MPa at pf, fl, mi and dou stages of growth, respectively. The RWC^{0} were always lesser in the plants of 30 % FC. The least RWC^{0} was found as 0.86 by 30 % FC at the mi stage of growth. The stressed plants yielded relatively higher RDW and the Ψt values also increased with the advance of age.

In the variety 301 (Fig. 1b), similar effects to that of X-8180 were observed for the different soil moisture regimes with respect to parameters Ψt, Ψs^{100}, Ψs^{0}, RWC^{0} and RDW values. Variety 301 showed also the most sensitivity toward stress during the dou stage of growth. At this stage and at 30 % FC the 301 plants exhibited noon Ψt values to −1.98 MPa which revealed the plants almost at the turgor loss point. The minimum amount of RWC^{0} values in this variety were observed as 0.83, 0.87 and 0.92 by 30 %, 50 % and 70 % FC plants, respectively. A significant amount of osmotic adjustment resulted in every growth stage of the stressed plants. The range of osmotic adjustment was from 0.17 to 0.44 MPa. The RDW values of the soil moisture treatments differed significantly and were found to be highest in 30 % FC plants.

The variety Red Top Candy (Fig. 1c) showed the Ψt value of −1.86 MPa in fl stage at 30 % FC. This variety reached Ψs^{0} values of −1.66 MPa on the same day which was less negative than the noon Ψt. The data were not taken in dou stage due to lack of plant material. The stressed plants (30 % FC) showed a significant reduction of Ψt compared to the 70 % FC plants. But only fl stage

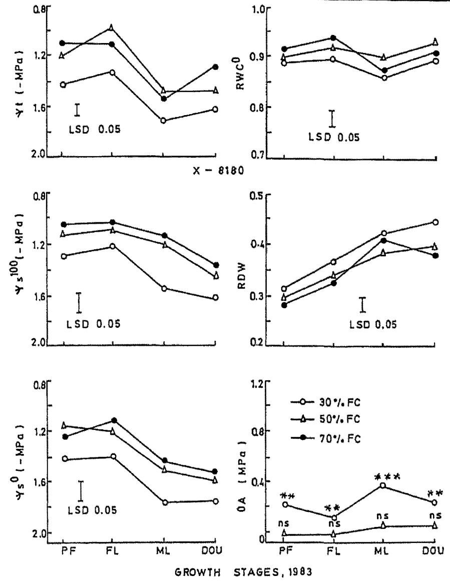

Fig. 1a: Leaf-water parameters of sweet sorghum variety X-8180 under different soil moisture regimes at different growth stages in 1983.
For details see fig. 1e

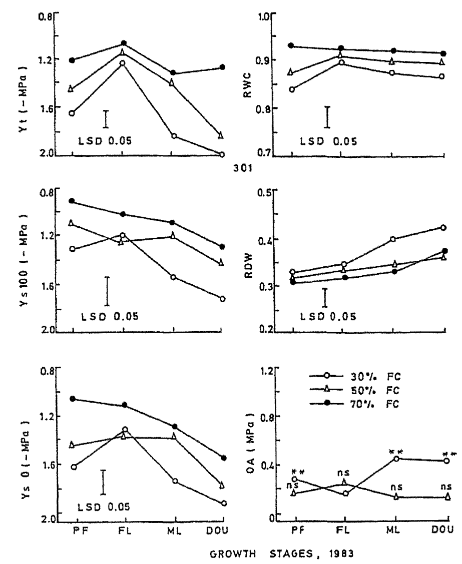

Fig. 1b: Leaf-water parameters of the sweet sorghum variety 301 under different soil moisture regimes at different growth stages in 1983.
For details see fig. 1e

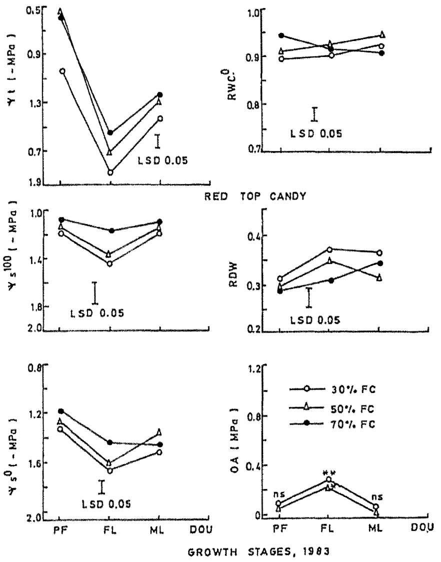

Fig. 1c: Leaf-water parameters of the sweet sorghum variety Red Top Candy under different soil moisture regimes at different growth stages in 1983.
For details see fig. 1e

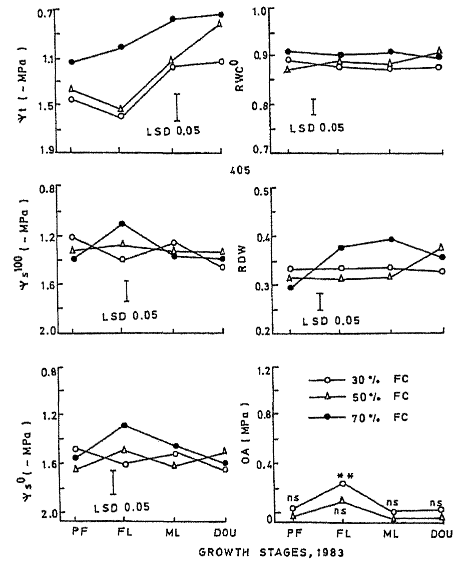

Fig. 1d: Leaf-water parameters of the sweet sorghum variety 405 under different soil moisture regimes at different growth stages in 1983.
For details see fig. 1e

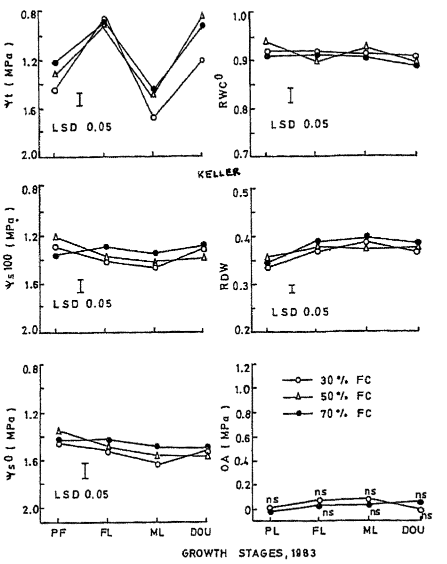

Fig. 1 e: Leaf-water parameters of the sweet sorghum variety Keller under different soil moisture regimes at different growth stages in 1983.
PF = Pre-flowering, FL = Flowering, ML = Milk and DOU=Dough
Ψt= Total leaf water potential,
Ψs^{100} = Leaf osmotic potential at full turgor, Ψs^0 = Leaf osmotic potential at zero turgor, RWC^0 = Relative water content of leaf at zero turgor,
RDW = Relative dry weight of leaf,
OA = Osmotic adjustment.
** = Significant at $P < 0.05$ level,*
*** = Significant at $P < 0.01$ level,*
**** = Significant at $P < 0.001$ level,*
ns = not significant and LSD 0.05 = Least significant difference at $P < 0.05$ level.

showed a significant amount of osmotic adjustment and yielded also higher ($P < 0.05$) RDW values in stressed treatments. In this variety no significant trends of changes of RWC^0 values were found as a result of cell water depletion.

The data on the different leaf-water, parameters of varieties 405 (Fig. 1d) and Keller (Fig. 1 e), respectively also showed a decrease in the Ψt values as the pot soil moisture was depleted. The variety Keller showed no significant differences in Ψt values among the different soil moisture regimes, except in the fl stage. The variety 405 showed significantly less negative Ψt values in 70 % FC plants than the other low moisture treatments. Both the varieties Keller and 405 did not show any ability to lower Ψs^{100}, Ψs^0 and RWC^0 and to increase RDW values in stress conditions. The only exception was found in the variety 405 which was able to show weak evidence of osmotic adjustment in fl stage.

3.2 1984 experiments

The variety X-8180 (Fig. 2a) confirmed the results obtained in 1983 experiments the values Ψt, of Ψs^{100}, Ψs^0 and RWC^0 being less negative than in the year before. For example, the lowest Ψt was – 1.7 MPa in 1983, whereas in 1984 it was –1.4 MPa only. Accordingly, the amount of osmotic adjustment was also less (0.3 MPa) than in 1983 (0.4 MPa).

The moderately drought resistant variety Red Top Candy (Fig. 2b) showed similar responses in decreasing the leaf water parameters in the stressed plants as in 1983. There were some dissimilarities regarding the growth stage interaction. The osmotic adjustment was found to be significant in pf, fl, and dou stages, but in 1983 only in the fl stage. After fl stage, further leaf water parameter studies in 1984 were not possible in the variety Keller due to lack of plant material. The data recorded from the two early growth stages did not show any significant differences of the treatments.

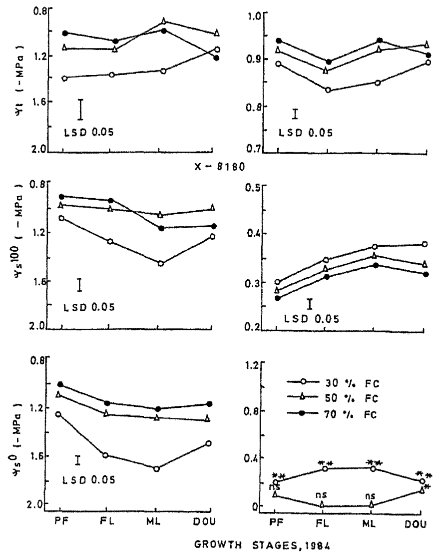

Fig. 2a: Leaf-water parameters of the sweet sorghum variety X-8180 under different soil moisture regimes at different growth stages in 1984. For details see fig. 1e

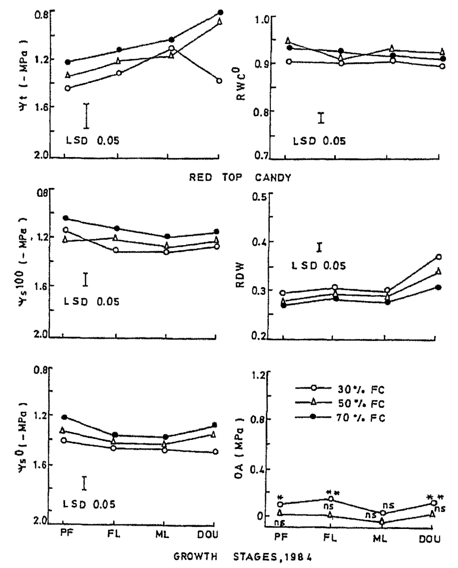

Fig. 2b: Leaf-water parameters of the sweet sorghum variety Red top candy under different soil moisture regimes at different growth stages in 1984. For details see fig. 1e

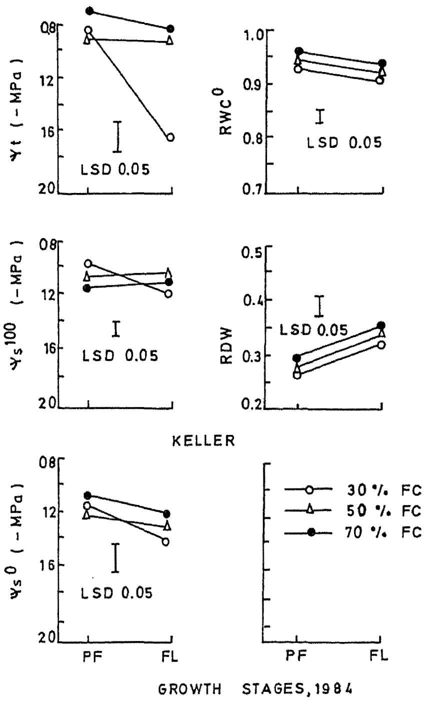

Fig. 2c: Leaf-water parameters of the sweet sorghum variety Keller under different soil moisture regimes at different growth stages in 1984. For details see fig. 1e

4. Discussion

All the varieties investigated reduced their noon Ψt values in the stressed plants. The most negative Ψt values were observed in the 30 % treatments. Medium stressed plants (50 % FC) showed medium ranges, and the highest Ψt values were measured in the plants of 70 % FC. The maximum differences in Ψt values between the 30 % FC and the 70 % FC water regimes were 0.37 MPa in X-8180 (Fig. 1a), 0.71 MPa in 301 (Fig. 1b), 0.45 MPa in Red Top Candy (Fig. 1c), 0.38 MPa in 405 (Fig. 1d) and 0.30 MPa in Keller (Fig. 1e). TURNER et al. (1978) reported the midday difference in Ψt values between irrigated and non-irrigated sorghum as 0.4 MPa. In the 1983 experiment, the noon Ψt, Ψs^{100}, Ψs^{0} and RWC^{0} values were comparatively lower and the osmotic adjustment values were higher than those obtained in the 1984 experiment which may be due to drier environments in the 1983 experiments (see Table 1).

Table 1

Selected meteorological data (from May 1, to October 2) of Seibersdorf in 1983 and 1984

Parameters	1983	1984
Solar radiation KJ/cm^2	68.13	61.73
Air temperature Absolute maximum	37.3 °C (19 July)	34.7 °C (12 July)
Relative humidity Absolute minimum	22 % (26 July)	27 % (3 Aug.)
Days below 40 %	50	44

Among the five varieties, only three (X-8180, 301, Red Top Candy) showed genetic capacity to adjust osmotically to water stress, i.e., their leaf osmotic potentials decreased at both full and zero turgor in response to lower Ψt and RWC values. The varieties X-8180 and 301 possessed a greater capacity for osmotic adjustment (0.4 MPa) than the moderately drought resistant variety Red Top Candy (0.25 MPA). This result agrees with observations of JOHNSON et al. (1984), FLOWER et al. (1990), and GRIMA and KRIEG (1992) increased in water stressed plants as well as RDW values of leaves of these three varieties in senescent plants. The RDW values were equivalent to the amount of dry matter per unit volume of water at the saturated condition. Dry matter per unit saturation is described in literature as an index of tissue elasticity. Previous research has shown that the higher the tissue elasticity, the lower the RDW values (WILSON et al. 1980, TYREE and JARVIS 1982). In this study, the bulk modulus model was not used to measure tissue elasticity. However, some deductions can be made from the differences between the values of Ψs^{100} und Ψs^{0} relative to the criterion of tissue elasticity. The difference was found to be bigger in more elastic tissues (CHEUNG et al. 1975). The difference between Ψ s^{100} and Ψs^{0} in this experiment as shown in table 2 was not remarkable. There is some evidence that in sorghum plants tissue elasticity decreases with increasing water stress (JONES and TURNER 1978). SOBRADO and TURNER (1983) and MYERS and NEALS (1986) observed that the ratio of turgid weight to dry weigth (TW/DW) declined with the reduction of Ψt. This evidence confirms our observation that increased

RDW values (DW/H20) are joined with reduced Ψt values. Higher RDW values are supposed to be accompanied by active accumulation of osmotica (osmotic adjustment). The osmotic adjustment resulted primarily from an active accumulation of inorganic solutes (HELLEBUST 1976, JONES et al. 1980), organic acids, ions etc. (FLOWERS and YEO 1986). RICHTER and WAGNER (1983) defined osmotic adjustment as an avoidance strategy in regard to water stress on photosynthetic rate, allowing to keep the stomata open despite of more negative leaf water potentials in dry condition. This condition is also beneficial for plants under stress as they become able to extract more water from the soil (MORGAN and CONDON 1986) and thereby have the capacity to maintain turgor during drought (PEACOCK et al. 1988). All these characteristics are beneficial for plant growth processes (WANG et al. 1991, PREMACHANDRA et al. 1992). Thus more dry matter under conditions of drought stress can be produced in sorghum (TANGPREMSRI et al. 1991). Genotypic variation of osmotic adjustment was found to be positively correlated with drymatter production and yield in wheat (MORGAN et al. 1986). HINCKLEY et al. (1980) showed that stomatal closure induced by water stress, occurred in several shrub species whenever Ψt values declined near to the tugor loss point.

Table 2

$\Psi s^{100} - \Psi s^{0}$ values of sweet sorghum at different growth stages under different soil moisture regimes

Varieties	Field capacity %	Growth stages Preflowering	Flowering	Milk	Dough
		MPa			
X-8180+	30	0.16	0.30	0.29	0.24
	50	0.15	0.24	0.19	0.17
	70	0.17	0.20	0.11	0.24
301*	30	0.33	0.09	0.20	0.31
	50	0.34	0.15	0.18	0.36
	70	0.18	0.14	0.20	0.24
Red top candy+	30	0.24	0.15	0.23	0.22
	50	0.15	0.22	0.17	0.22
	70	0.17	0.14	0.13	0.16

The values are calculated from the means.
+ 1984 experiment, 3 replications
* 1983 experiment, 2 replications

In the present study, genetic variation was found in maintaining noon leaf turgor with regard to decreasing Ψt values. The variety X-8180 maintained noon Ψt values above Ψs^0 values during all days of measurement. But in another study under field grown conditions, this variety showed turgor loss in the leaves at noon at 32 % FC (SALAM 1991). The variety 301 showed similar capability for osmotic adjustment as X-8180. Red Top Candy suffered from turgor loss during peak stresses in the summer. For example, in 1983 the minimum Ψt values were – 1.98 MPa and – 1.86 MPa in the varieties 301 (Fig. 1b) and Red Top Candy (Fig. 1c), respectively. Both varieties showed declining Ψs^0 values concomitantly to –1.94 and –1.66 MPa, which were less negative than their Ψt values. This indicates that the degree of stress was higher on those days which exceeded the capability of leaf osmotic adjustment within those varieties. JONES and TURNER (1978) found that Ψt values at the turgor loss point in sorghum were between –1.40 and –2.60 MPa.

Acknowledgements

The author is grateful to the Federal Government of Austria for financial assistance, and to tit. a. o. Univ.-Prof. Dr. E. HAUNOLD for providing the research facilities, to Dr. P. TUSCHL, Dr. S. KIKUTA, Dr. G. SOJA for their help to carry out this study and Dr. R. WITTER, Senior Res. Management Specialist, Intl. Service for Natl. Agric. Res. for improving the text.

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(Manuskript eingelangt am 29. Juni 1994, angenommen am 19. Jänner 1995)

Anschrift des Verfassers:

Dr. M. Abdus SALAM, Österreichisches Forschungszentrum Seibersdorf Ges. m. b. H., A-2444 Seibersdorf, und Bangladesh Institute of Nuclear Agriculture, P.O. Box No. 4, Mymensingh, Bangladesh