Influence of Osmotic Adjustment on the Growth, Stomatal Conductance and Light Interception of Contrasting Sorghum Lines in a Harsh Environment*

D. J. Flower, A. Usha Rani and *J. M. Peacock*

International Crops Research Institute for the Semi-Arid Tropics,
Patancheru P.O., Andhra Pradesh 502 324, India.

Abstract

Two drought resistant lines of sorghum, IS 13441 and IS 1347, with a high capacity for osmotic adjustment and two susceptible lines, IS 12739 and IS 12744, were subjected to drought in the field during a summer season in the semi-arid tropics in India. During this season there is little rain, air temperatures reach 42°C, and pan evaporation rates may reach 20 mm d^{-1} providing a harsh environment for crop growth. Most of the osmotic adjustment occurred within 3 weeks after withholding water and at high predawn leaf water potentials, i.e. at values above $-1 \cdot 0$ MPa. As a result, resistant lines were able to maintain a positive turgor to lower leaf water potentials ($-2 \cdot 8$ MPa) than susceptible lines ($-2 \cdot 0$ MPa). Nevertheless, dry matter production was negligible in both resistant and susceptible lines when predawn leaf water potentials fell to $-0 \cdot 55$ MPa. Furthermore, throughout the drought period the leaf area of all water-stressed plants was similar when expressed relative to the control regardless of the level of osmotic adjustment. Resistant lines had similar stomatal response to leaf water potential as susceptible lines. Large changes occurred in stomatal conductance and leaf rolling soon after withholding water while there was considerable osmotic adjustment in the leaves. Leaf rolling coincided with a reduction in the ability of the plant to utilise radiation. Therefore, even if osmotic adjustment had delayed leaf rolling, the gain in productivity would be small. On the basis of these turgor related processes it can be concluded that there would be little advantage in selecting for plants with a higher capacity for osmotic adjustment in this harsh environment.

Introduction

Osmotic adjustment reduces the sensitivity of turgor-dependent processes, such as leaf expansion, stomatal conductance, and leaf rolling, to declining leaf water potentials (Jones and Turner 1980; Morgan 1984).

Osmotic adjustment permits plants to grow at otherwise inhibitory leaf water potential by contributing to the maintenance of turgor (Cutler *et al.* 1980; Meyer and Boyer 1981; Takami *et al.* 1982; Matthews *et al.* 1984; Westgate and Boyer 1985). Thus plants should remain productive for longer periods during a drought, provided soil water reserves are used conservatively. Nevertheless, a reduction in leaf growth rate can occur even though turgor is maintained, as the result of changes in tissue extensibility, yield threshold, and hydraulic conductivity (Matsuda and Raizi 1981; Meyer and Boyer 1981; Michelena and Boyer 1982; Matthews *et al.* 1984; Westgate and Boyer 1985).

Genotypic differences exist in both the capacity of sorghum leaves to adjust osmotically and in the stomatal response to leaf water potential (Henzell *et al.* 1976; Ackerson *et al.* 1980; Wright *et al.* 1983; Santamaria *et al.* 1986). A strong positive

correlation between the level of osmotic adjustment and the water potential at which stomatal closure occurred has been shown for some species (Turner *et al.* 1978; Ludlow 1980; Ludlow *et al.* 1983, 1985). This led to the suggestion that osmotic adjustment was the main trait responsible for stomatal adjustment to leaf water deficits (Ludlow *et al.* 1985). However, stomatal conductance is often only loosely related to the turgor potential (TP) of water-stressed leaves (Jones and Rawson 1979; Henson *et al.* 1982) and changes in stomatal conductance can occur independently of leaf water potential (Bates and Hall 1982; Blackman and Davies 1985; Gollan *et al.* 1986).

Sorghum genotypes differ in both the capacity for leaf rolling and in the water potential at which leaf rolling occurs (Wright *et al.* 1983; Santamaria *et al.* 1986). Leaf rolling occurs in sorghum when the turgor potentials of leaves approach zero (Wright *et al.* 1983). By maintaining turgor, osmotic adjustment reduces the water potential at which rolling occurs in excised rice leaves (Hsiao *et al.* 1984) and increases the amount of radiation intercepted by the water-stressed crop (Turner *et al.* 1986). When light use-efficiency is negligible, leaf rolling may be desirable if it reduces the risk of photoinhibition and lethal leaf temperatures (Barlow 1983).

This study determined the influence of leaf osmotic adjustment in contrasting sorghum lines on the growth rate, stomatal conductance and leaf rolling of water-stressed plants growing in a harsh environment. Information obtained may be used to evaluate the potential of osmotic adjustment as a selection criteria for plants in the semi-arid and arid tropics (Morgan 1983).

Methods and Materials

Crop Management and Experimental Design

The experiment was conducted during the 1986 summer and monsoon season at ICRISAT, Patancheru, India, on a sandy clay with a loamy surface, defined as a fine mixed hypothermic Udic Rodustalf with an average depth of 90 cm. Six sorghum lines chosen for their different responses to heat and drought stress (Peacock *et al* 1988) were sown in a split block design with three replicate 9 m × 12 m plots. Lines were IS 12744, IS 12739 (drought susceptible), IS 1347, IS 13441 (drought resistant) and two promising breeding lines ICSH 109IN (SPH 263) and ICSV 213. Resistant lines had a low incidence of leaf firing and exhibited yield stability relative to susceptible lines when subjected to mid-season drought (Peacock *et al* 1988). Seed was sown on 12 March at 12 plants m^{-2} in rows 0 6 m apart. At sowing, a basal dressing of superphosphate was applied at the rate of 200 kg ha^{-1} and 22 days later a top dressing of urea was applied at the rate of 100 kg ha^{-1}

Two treatments were used a water-stressed treatment and an irrigated control treatment. Both treatments were sprinkler-irrigated for 2 weeks after sowing to prevent soil crusting and ensure plant establishment. Thereafter, the control treatment was furrow irrigated at weekly intervals for the duration of the crops. Twenty days after sowing (DAS), irrigation was withheld from the water-stressed treatment for the next 46 days, stressed plants were then irrigated on a weekly basis as in control. From day 20 to day 43, maximum air temperatures and pan evaporation rates were stable at 38°C and 11 mm d^{-1}, respectively. After day 43 there was a progressive increase in air temperature until day 65 when maximum air temperatures reached 42°C. Likewise, pan evaporation rates increased to 20 mm d^{-1} during this period. There were 26 mm of rain on day 43.

Leaf Water Relations

Measurements of leaf water relations were made prior to dawn and near midday (1300 h) on the mid-portion of the youngest fully expanded leaf (YFEL). Leaves were excised and placed between moistened sheets of filter paper lined with muslin. At the field laboratory, one side of the leaf was stripped and placed in a humidified pressure chamber (PMS instruments) for leaf water potential (ψ_l) determination. The other side of the leaf was cut into three pieces, two of which were used for the measurement of relative water content (RWC) (Flower and Ludlow 1986). This leaf tissue was floated on demineralised water for 4 h at a temperature of 25°C and a photon irradiance of 20 μmol m^{-2} s^{-1} before the measurement of turgid weight. The remaining tissue was placed in a microcentrifuge vial and stored in liquid nitrogen. The tissue was then thawed in its vial and centrifuged at a speed of 19 000 g for 5 min and

the osmotic potential (OP) of the expressed sap was measured with a calibrated freezing point (Roebling) osmometer

Measurements of apoplastic water content were made on irrigated plants early in the season and on water-stressed plants at the end of the drought (Table 1) The apoplastic water content was determined on YFEL sampled predawn and rehydrated for 4 h in the dark Two strips, 2-3 cm in width, were taken from these leaves and their turgid weight was determined The leaf tissue was then dehydrated on the bench for up to 4 h with the tissue water content and potential being periodically measured Apoplastic water content (AWC) was calculated by extrapolation of the linear region of the inverse leaf water potential/relative water content relationship (Ritchie and Roden 1985)

Leaf OP was corrected for the dilution of the symplastic sap by apoplastic water which occurs when sap is expressed (Wright *et al* 1983) Turgor potential (TP) was calculated by subtraction of the corrected osmotic potential from the water potential reading Osmotic potential at full turgor was calculated according to the formula of Wilson *et al* (1979)

$$OP_{100} = OP(RWC - AWC)/(100 - AWC)$$

Osmotic adjustment is the difference between the osmotic potential at full turgor (OP_{100}) of unstressed and stressed leaves Changes in OP_{100} in the irrigated treatment were small (<0 3 MPa) and no significant difference between lines was detected 20 DAS, or at the same physiological stage of development (panicle initiation and anthesis) Therefore, an average value of OP_{100} irrigated (−1 09 MPa) was used for all lines

Light Interception

Incident solar radiation was measured with a LI-200SB pyranometer (400-1100 nm wavelength; Li-Cor Instruments Inc , Lincoln, Nebraska, USA) and the radiation transmitted through the crop was measured with two calibrated tube solarimeters connected in series and placed under the crop canopy normal to the row Intercepted radiation was calculated as the difference between the incident and transmitted values The data were logged every 5 min and hourly averages of these readings were made throughout the crop season The conversion efficiency was calculated as the ratio of above ground dry matter production to 0 5 times the integral of radiation intercepted The factor 0 5 was taken as the proportion of incoming radiation that was photosynthetically active

Growth Analysis

Measurements of green leaf area and above-ground dry weight were made at weekly intervals from 9 DAS Six plants of each sorghum line were selected from each plot or 18 per treatment Measurements of above-ground dry weight included any dead leaves that were still attached to the plant Growth rates were calculated for each day from second- and third-order polynomials fitted ($R^2 > 0$ 90) to the measurements of above-ground dry weight

Stomatal Conductance

In 1985 an experiment was conducted using the same lines planted on the same date and in the same field as that in 1986 Furthermore, cultural details were the same as in 1986 and water was also withheld 20 days after sowing Each week during the drought measurements of leaf conductance were made at 0830, 1230, and 1600 h using a diffusive resistance porometer (Delta-T Devices, mark III) On each occasion conductances were measured on three positions on the YFEL, i e near the base at the middle and tip and the mean value was calculated Eight measurements were collected per line

Results and Discussion

Influence of Osmotic Adjustment on the Maintenance of Leaf Turgor

Apart from early maturing lines during the later stages of grain filling, predawn ψ_l of all lines was maintained at −0·2 to −0·5 MPa throughout the experiment in the irrigated treatment (Fig. 1a). In contrast there was a progressive decline in midday ψ_l in this treatment, with the exception of the reading on day 46 when the soil was still wet from rain 3 days previously. This seasonal decline in ψ_l was associated with an increasing demand for water as a result of an increasing leaf area (Hochman 1982) coupled with a seasonal increase in pan evaporation.

Irrigation was withheld from plants in the water-stressed treatment 20 DAS and the first differential irrigation was given to the control treatment at 27 DAS. Considering the harsh environment, changes of ψ_l were comparatively small until the later stages of the experiment. By 32 DAS, there was a significantly ($P < 0.01$) lower midday ψ_l in the stress treatment than in the control (Fig. 1*b*). This $0.3-0.7$ MPa difference in ψ_l was maintained as the experiment progressed in all lines. The two susceptible lines, however, maintained a significantly ($P < 0.01$) higher ψ_l (although not always the case in IS 12739) than resistant lines, particularly towards the end of the drought. In this experiment susceptible lines had a slower rate of leaf area development in *both* treatments which presumably resulted in a slower rate of water use and higher midday ψ_l values in these lines. The first significant ($P < 0.01$) difference in predawn ψ_l occurred on day 39 when IS 12744, IS 13441, ICSH 109IN (data not presented) and ICSV 213 (data not presented) were $0.05-0.25$ MPa lower than the control (Fig. 1*a*). All lines were not significant ($P < 0.01$) until 60 DAS when ψ_l had declined to -1.0 to -1.6 MPa.
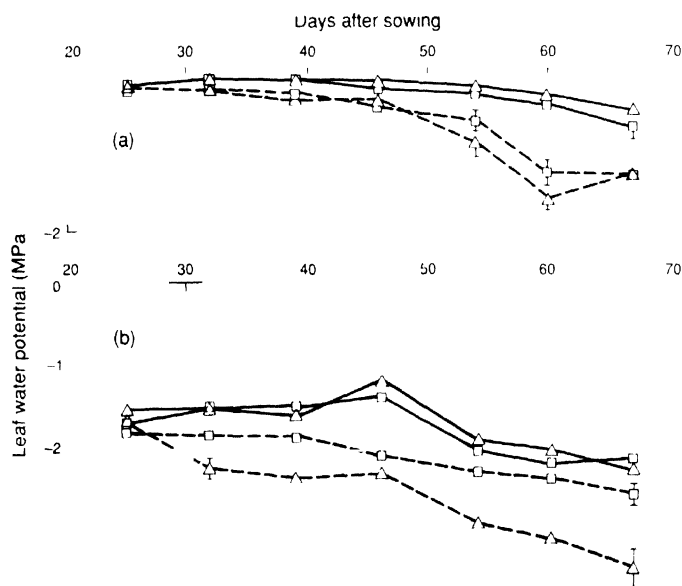

Fig. 1. Time trends in the predawn (*a*) and midday (*b*) leaf water potential of irrigated (———) and water-stressed (— — —) plants. Points are means of 4–6 measurements, and vertical bars where they exceed the size of the symbol indicate the standard error of the mean. [ ] IS 12744; ∧ IS 13441.

In response to stress all lines exhibited some degree of osmotic adjustment (Fig. 2*a*). Much of this adjustment occurred within 3 weeks of withholding water. During this period, resistant lines adjusted osmotically at a faster rate than corresponding susceptible lines of the same maturity type. From 25 to 39 DAS, resistant lines such as IS 13441 had adjusted at a rate of 0.044 MPa d^{-1} compared with a rate of < 0.011 MPa d^{-1} in IS 12744. The wet conditions preceding the measurement on day 46 resulted in a considerable loss of adjustment. However, by 54 DAS, leaves had again reached their maximum capacity for adjustment, and there was little diurnal adjustment in either resistant or susceptible lines (Fig. 2*a*).

Most of the osmotic adjustment occurred at high leaf water potentials in sorghum leaves (Fig. 2*a*). When predawn LWP had declined to -1.0 MPa, both resistant and

susceptible lines had reached the maximum capacity for osmotic adjustment. This is in contrast to the findings of Flower and Ludlow (1986) where predawn ψ_l values $< -4 \cdot 5$ MPa were required for maximum levels of osmotic adjustment in pigeonpea. Susceptible lines not only adjust osmotically at lower rate, they have a lower capacity
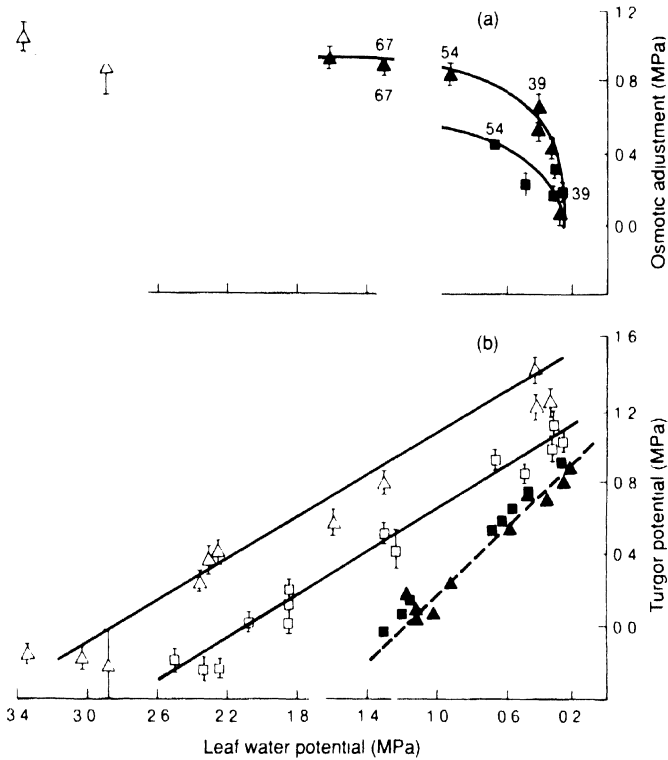

Fig. 2. Relationship between osmotic adjustment and leaf water potential (*a*), and turgor potential and leaf water potential (*b*) of IS 12744 (squares) and IS 13441 (triangles) plants subject to water stress in the field. Numbers refer to the days after sowing and the solid and open symbols in (*a*) are measurements made predawn and midday, respectively. Lines were fitted by eye and vertical bars indicate the standard errors of the mean. The dashed line represents the relationship obtained from leaves of IS 12744 and IS 13441 rapidly dehydrated on the bench to prevent osmotic adjustment. Data from day 46 have been deleted due to the occurrence of rain 3 days earlier, resulting in a loss of osmotic adjustment.

Table 1. Apoplastic water contents of contrasting sorghum lines

Sorghum line	Apoplastic water content (%)		
	Irrigated 26–52 DAS	Unirrigated 81 DAS	Mean
ICSV 213	$16 \cdot 2 \pm 3 \cdot 0$	$16 \cdot 1 \pm 5 \cdot 5$	$16 \cdot 2$
ICSH 1091N	$21 \cdot 4 \pm 2 \cdot 8$	$21 \cdot 7 \pm 5 \cdot 3$	$21 \cdot 6$
IS 22380	$11 \cdot 8 \pm 6 \cdot 0$	$13 \cdot 2 \pm 3 \cdot 2$	$12 \cdot 5$
IS 13441	$2 \cdot 3 \pm 4 \cdot 8$	$7 \cdot 0 \pm 1 \cdot 2$	$4 \cdot 7$
IS 12739	$12 \cdot 6 \pm 5 \cdot 6$	$12 \cdot 5 \pm 6 \cdot 4$	$12 \cdot 6$
IS 12744	$14 \cdot 4 \pm 9 \cdot 2$	$4 \cdot 9 \pm 4 \cdot 8$	$9 \cdot 7$
Mean	$13 \cdot 1$	$12 \cdot 6$	$12 \cdot 9$

for adjustment. The maximum levels of adjustment were 0·53, 0·63, 0·65, 0·65, 0·8 and 1·03 MPa for IS 12744, IS 12739, ICSH 109IN, ICSV 213, IS 13441, and IS 134? respectively. There was no apparent influence of maturity on the capacity for adjus ment, as found by Santamaria *et al.* (1986). The two earliest maturing lines, IS 134 and IS 12739, which had both initiated during the drought, exhibited the highest an second lowest levels of adjustment, respectively.

Negative turgor potentials are frequently measured in sorghum leaves using th expressed sap pressure chamber technique (Wright *et al.* 1983) and values as low a − 1·3 MPa (Shackel *et al.* 1982; Shackel and Hall 1983) have been reported. It has bee
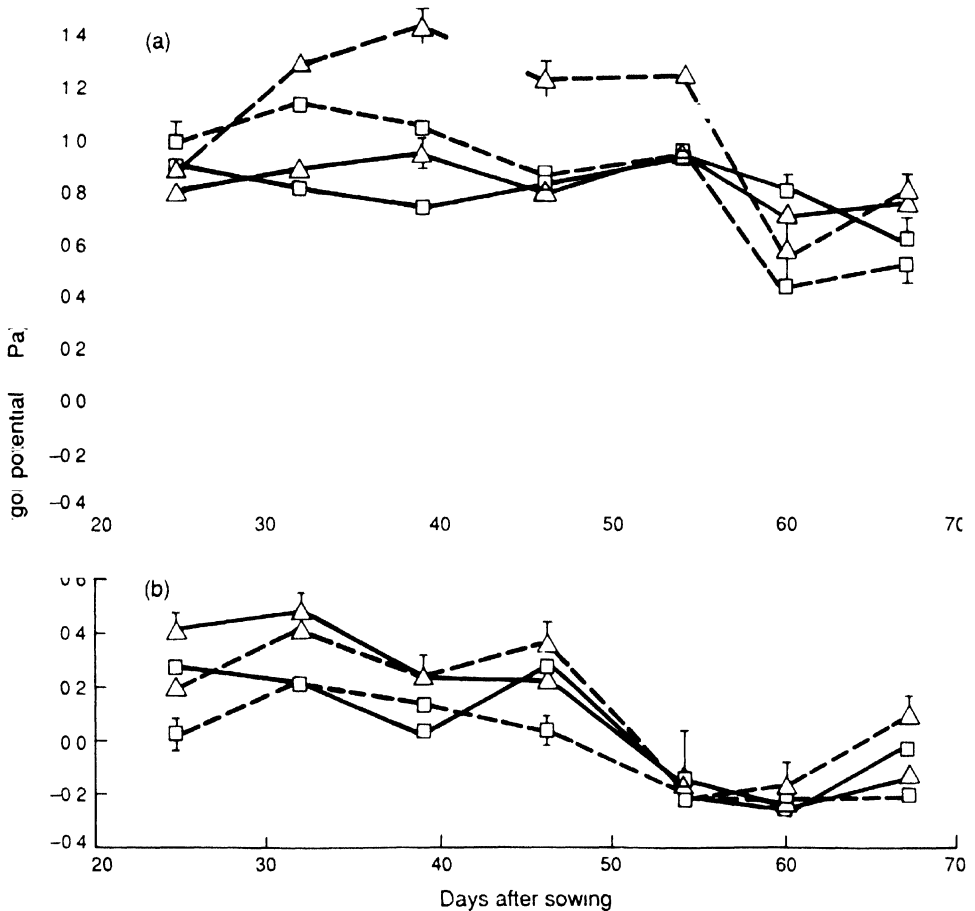

Fig. 3. Changes with time in the predawn (*a*) and midday (*b*) turgor potential of leaves in the irrigated (————) and unirrigated (— — —) treatments Points are means of 4–6 measurements, and vertical bar indicate the standard errors of the mean. ⊓ IS 12744, △ IS 13441

suggested that negative values of TP arise from the dilution of symplastic solutes b) apoplastic water (Tyree 1976; Sobrado and Turner 1983; Wright *et al.* 1983). No pub lished measurements of apoplastic water content (AWC) exist for sorghum, although i has been estimated to be $7 \pm 3\%$ in cv. TX610 (Turner *et al.* 1978). In the curren experiment there was no measurement of AWC made during the drought; however there was no appreciable difference between the mean AWC of irrigated plants anc stressed plants after the termination of the drought (Table 1). ICSH 109IN anc ICSV 213 had higher AWC than the other lines, although differences were no significant. Therefore, a common value of 12·9% was used to correct for dilutior errors.

Leaves of both IS 12744 and IS 13441, when rapidly dehydrated on the bench during measurements of AWC, thereby preventing osmotic adjustment, lost turgor when ψ_l fell to $-1 \cdot 2$ MPa (Fig. 2b). In the field at this ψ_l, stressed leaves of IS 12744 and IS 13441 had a TP which was 62 and 112% of that measured in irrigated leaves. The TP of leaves of IS 12744 in the field reached zero at a ψ_l of $-2 \cdot 0$ MPa compared with $-2 \cdot 9$ MPa in IS 13441. As changes in tissue elasticity were small (unpublished results), osmotic adjustment made a significant contribution to the maintenance of turgor in resistant lines such as IS 13441 and, to a smaller extent, in susceptible lines.

Throughout the season, the TP was maintained at $0 \cdot 8$–$1 \cdot 0$ MPa prior to dawn in the irrigated treatment and there was no consistent difference between lines (Fig. 3a). As a result of an increase in osmotic adjustment, the predawn TP of water-stressed leaves
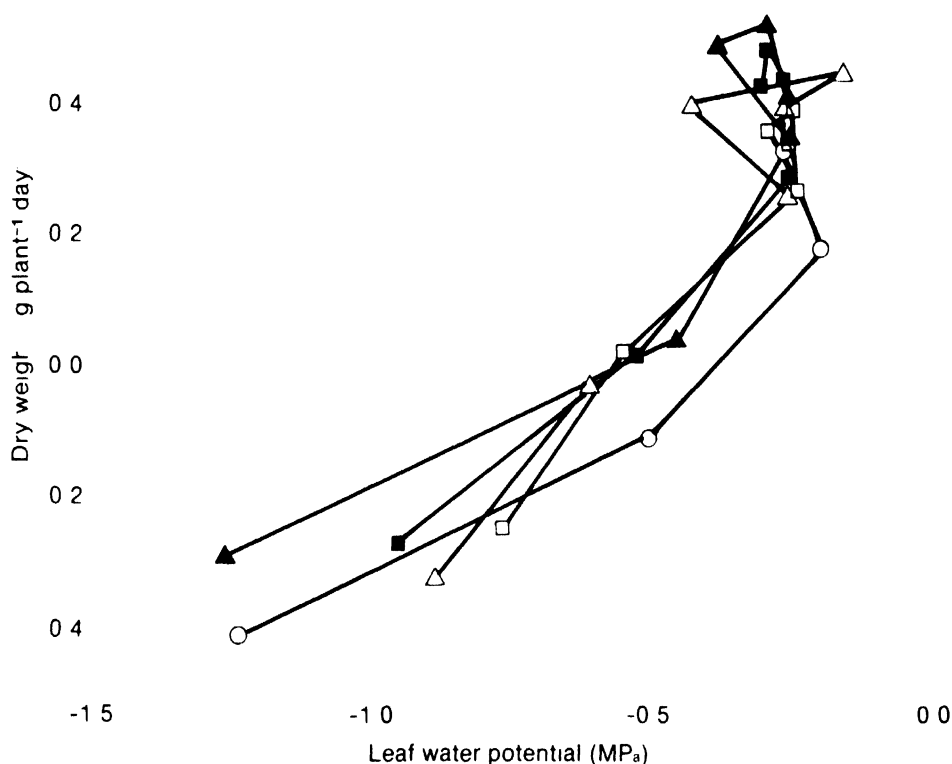

Fig. 4. Relationship between the rate of change in total above-ground dry weight, and predawn leaf water potential (———) Points are means of 4–6 measurements and the symbols refer to the following sorghum lines; ☐ IS 12744; ○ IS 12739; ■ ICSH 109IN, △ ICSV 213; ▲ IS 13441.

was significantly ($P < 0 \cdot 001$) greater prior to dawn than that measured in irrigated leaves. Lines with the highest capacity for osmotic adjustment had the highest predawn TP. On day 60, when predawn ψ_l had decreased to $-1 \cdot 1$ to $-1 \cdot 6$ MPa (Fig. 1a), three of the six lines had a significantly ($P < 0 \cdot 05$) lower TP than the control.

The TP of irrigated leaves was reduced to approximately $0 \cdot 2$ MPa by midday on day 25 (Fig. 3b). As the experiment progressed and ψ_l fell (Fig. 1b), midday TP of irrigated plants decreased until day 54 when it became negligible. Small negative readings were recorded in some lines after day 54 possibly as a result of a slight under estimation of AWC or as a consequence of experimental error. However, as no measurements of AWC were made during the drought, the cause of these negative readings cannot be ascertained. In general, there was no consistent significant difference in the midday TP of irrigated and water-streesed leaves.

Influence of Osmotic Adjustment on Dry Matter Production

The relationship between the rate of dry matter production and ψ_l in the stressed treatment is presented in Fig. 4. Twenty days after sowing the growth rate of irrigated plants increased linearly with time from $0 \cdot 3$ to $2 \cdot 0$ g plant^{-1} d^{-1} (data not presented). After water was withheld, the rate of dry matter production was reduced to zero as predawn ψ_l declined from $-0 \cdot 25$ to $-0 \cdot 55$ MPa, despite the TP of the YFEL of resistant lines being positive until a ψ_l of $-2 \cdot 8$ MPa. Also there was no appreciable difference in the predawn or midday ψ_l (data not presented) at which growth ceased in resistant or susceptible lines.

In Fig. 5, the ratio of the leaf area in stress relative to the control treatment is plotted against the level of osmotic adjustment of six sorghum lines. If osmotic adjustment was of benefit to leaf expansion during the drought then it would be expected that plants
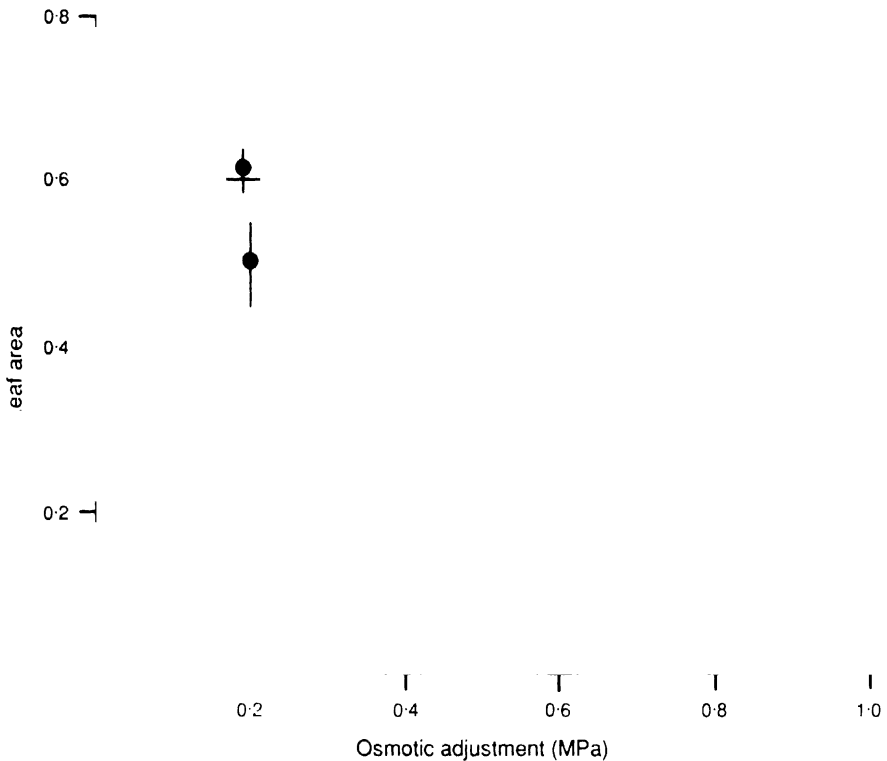

Fig. 5. Relationship between the ratio of the leaf area in the water-stressed/control treatments and the degree of predawn osmotic adjustment of six sorghum lines (IS 12744, IS 12739, ICSV 213, ICSH 109IN, IS 22380 and IS 13441). The solid symbols are for 37 DAS and the open symbols are for 58 DAS. Vertical bars represent the standard errors of the mean.

capable of high osmotic adjustment also have a higher leaf area ratio, which was clearly not the case. Osmotic adjustment neither maintained growth rates to lower ψ_l nor did increase the leaf area of stressed plants at any stage during the drought.

While measurements of TP in the elongating region cannot be inferred from measurements on the exposed blade of grasses (Michelena and Boyer 1982), available evidence suggests that the expanding tissue has a greater capacity to maintain turgor than the fully expanded tissue (Maxwell and Redman 1978; Radford 1980; Michelena and Boyer 1982; Westgate and Boyer 1985). Moreover, species capable of turgor maintenance in the exposed blade are also capable of turgor maintenance in expanding tissue (Radford 1980; Michelena and Boyer 1982).

Therefore it was highly likely that resistant lines were also capable of osmotic adjust-ment in the expanding regions of the leaf. Munns (1987) was able to demonstrate, using a root pressurisation technique, that maintenance of full turgor was insufficient to main-tain growth rates of water-stressed leaves as the soil in the pots dried out. Therefore, if turgor was not limiting to water-stressed plants, osmotic adjustment would be of little benefit. Our results from the field suggest that, regardless of the level of osmotic adjust-ment, the productivity of droughted plants would be similar.
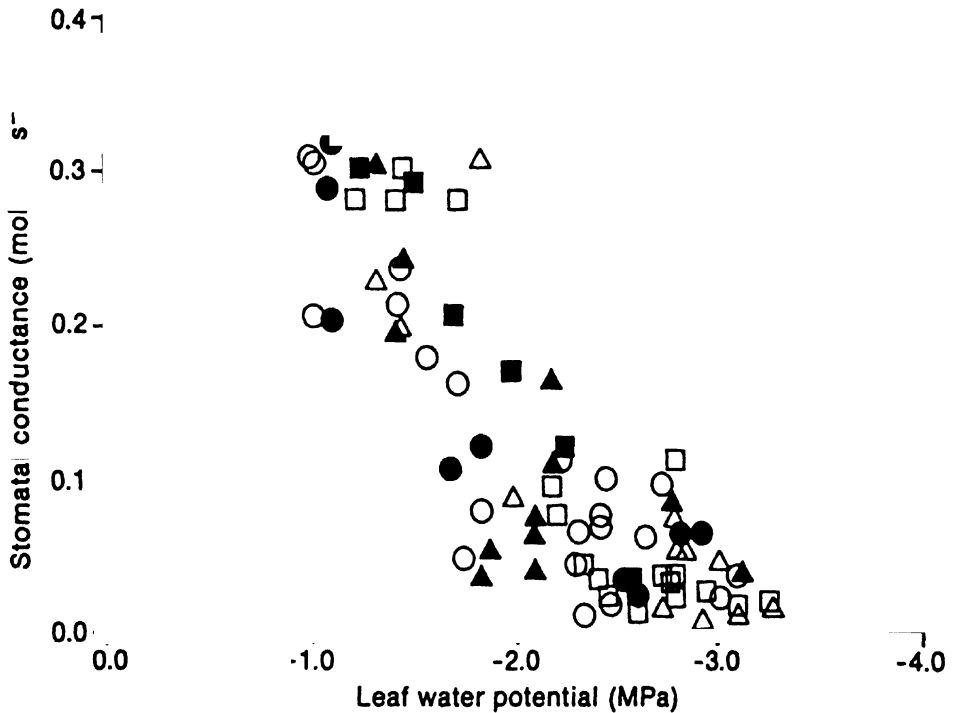

Fig. 6. Relationship between stomatal conductance and leaf water potential of contrasting lines. Points are individual measurements and the line was fitted by eye. The symbols refer to the following sorghum lines: ○ IS 12739; ● IS 1347; △ IS 12744; ▲ IS 13441; ■ IS 20969; and □ IS 17605.

Influence of Osmotic Adjustment on the Stomatal Response to Leaf Water Potential

In a similar experiment during the 1985 summer season, data were collected on the relationship between stomatal conductance and leaf water potential. The maximum stomatal conductance of 0.37 mol m^{-2} s^{-1} occurred at a ψ_l of -1.1 MPa (Fig. 6). Stomatal conductance fell to half this value when water potentials declined by 0.5 MPa and became negligible when water potentials were lower than -3 MPa. There was no appreciable difference in the stomatal conductance of the contrasting lines at either LWP.

No measurement of osmotic adjustment were made during the 1985 season. The level of osmotic adjustment in water-stressed crops is dependent on the rate of development of water deficits and the availability of assimilate (Jones and Rawson 1979). The rate of decline in midday ψ_l was the same in 1985 and 1986 and so was midday air tempera-ture, which influences stomatal and metabolic activity (Fig. 7). The growth and devel-opment of a crop, like osmotic adjustment, is also a function of the availability of

assimilates. The changes in leaf area index with time was the same in 1985 and 1986 in both irrigated and water-stressed treatments. Therefore, while some caution is required when examining data from different years, it is highly likely when we consider the environment and performance of the crops that similar levels of osmotic adjustment were present in both years.
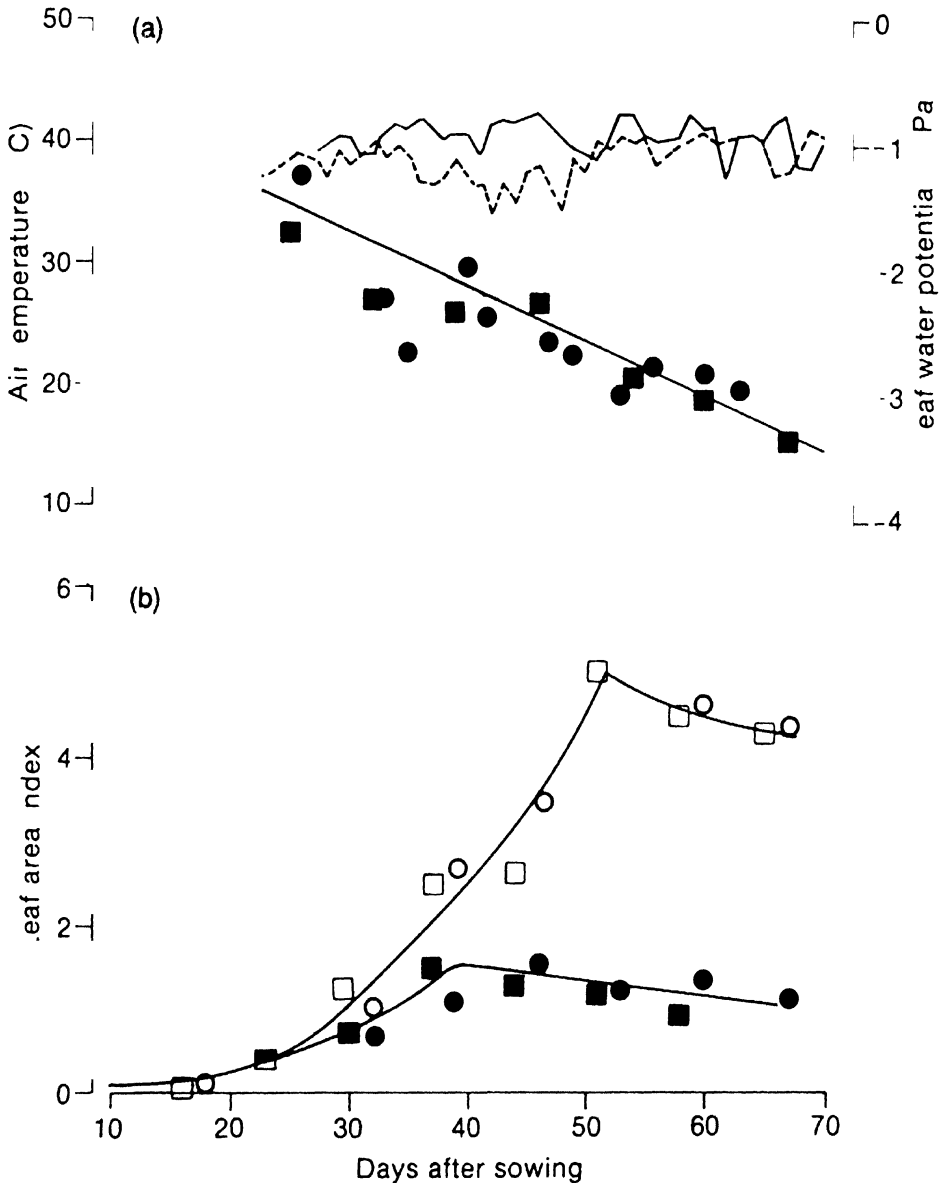

Fig. 7. Changes with time in (*a*) midday Stevensons screen air temperature (1985 ———; 1986 — — —) and leaf water potentials (1985, circles; 1986, squares) and (*b*) leaf area index of control (1985, open circles; 1986, open squares) and water-stressed (1985, closed circles; 1986, closed squares).

Soon after water was withheld, ψ_l began to decline (1985–1986), and growth rates (1985–1986) decreased. Commensurate with these reductions was an increase in the level of osmotic adjustment (1986). While resistant lines had a higher capacity for osmotic adjustment than susceptible lines, there was no difference in the stomatal

conductance-ψ_l relationship. Recent data of Blackman and Davies (1985) and Gollan *et al.* (1986) suggest that the decrease in stomatal conductance which occurs in potted plants as soil water content falls is not a consequence of a reduction in leaf turgor potential. Therefore, if turgor is not limiting stomatal conductance during a drought, then the influence of osmotic adjustment on stomatal conductance will be negligible.

Influence of Osmotic Adjustment on Leaf Rolling and Light Interception

Repeated failure of some tube solarimeters led to a lack of replication and data presented are a mean response (nine readings) rather than values for any particular line. However, these contrasting sorghum lines exhibit a similar relationship between light interception and leaf area index under irrigated conditions (R. B. Matthews, unpublished data).

Two days after the first differential irrigation the plants in the unirrigated treatment were intercepting a similar amount of light at 0800 h as plants in the control treatment (Fig. 8). As the day progressed and leaf water potentials declined in both treatments
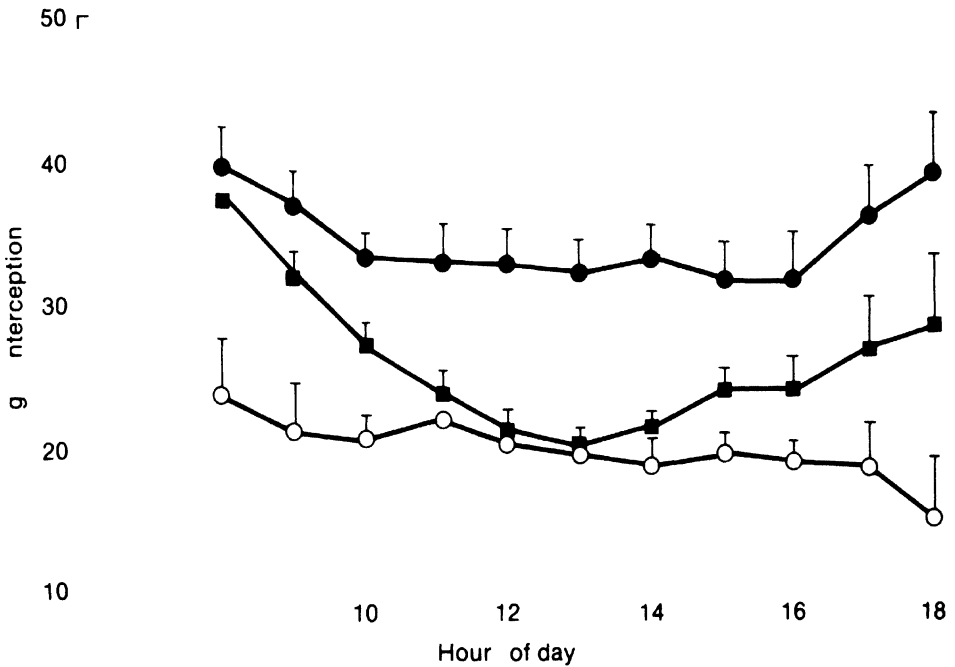

Fig. 8. Diurnal changes in percentage light interception of unirrigated plants 29 days after sowing (closed squares), and irrigated plants 24 (open circles) and 29 (closed circles) days after sowing. Vertical lines indicate the mean plus the standard error.

plants in the unirrigated treatment intercepted less light, and by midday plants were intercepting only 60% of the light of plants in the control treatment. Irrigated plants on day 24 (by interpolation), with a 34% ± 2·8 lower leaf area than stressed plants on day 29, intercepted the same amount of radiation at midday. This substantial reduction in the ability of the canopy to intercept radiation was the result of changes in leaf angle and leaf rolling.

Stressed leaves of all sorghum lines exhibited an osmotic adjustment at midday on day 32, which was greater than 76% of their maximum capacity. However, coincident with this increase in osmotic adjustment was a reduction in midday ψ_l at all times (0·3–0·7 MPa relative to controls) resulting in no significant ($P < 0·05$) difference between the TP of leaves in the two treatments (Fig. 5b). Therefore, while substantial

osmotic adjustment is apparent at midday on day 32, it is unable to delay the occurrence of leaf rolling.

From 24 to 40 DAS the irrigated crop had an average conversion efficiency of $2 \cdot 5$ g MJ^{-1} which is similar to that reported for sorghum grown in the summer and monsoon seasons in northern Australia (Muchow 1986). After irrigation was withheld from the stressed crop, on day 20, the conversion efficiency progressively declined until day 40 when it was $1 \cdot 3$ g MJ^{-1} (Fig. 9). From 24–40 DAS, the leaf area of the irrigated crop was linearly related to the percentage of light intercepted (LI). As this was not the case in the stressed crop, percentage leaf display index was calculated at each leaf area:

$$\text{Leaf display index} = \frac{LI_{stressed} - LI_n}{LI_{irrigated} - LI_{min}} \times \frac{100}{1} \text{ ,}$$

where LI_{min} is the lowest percentage light interception measured for a given leaf area in the stressed treatment. A low leaf display index was the result of changes in leaf angle
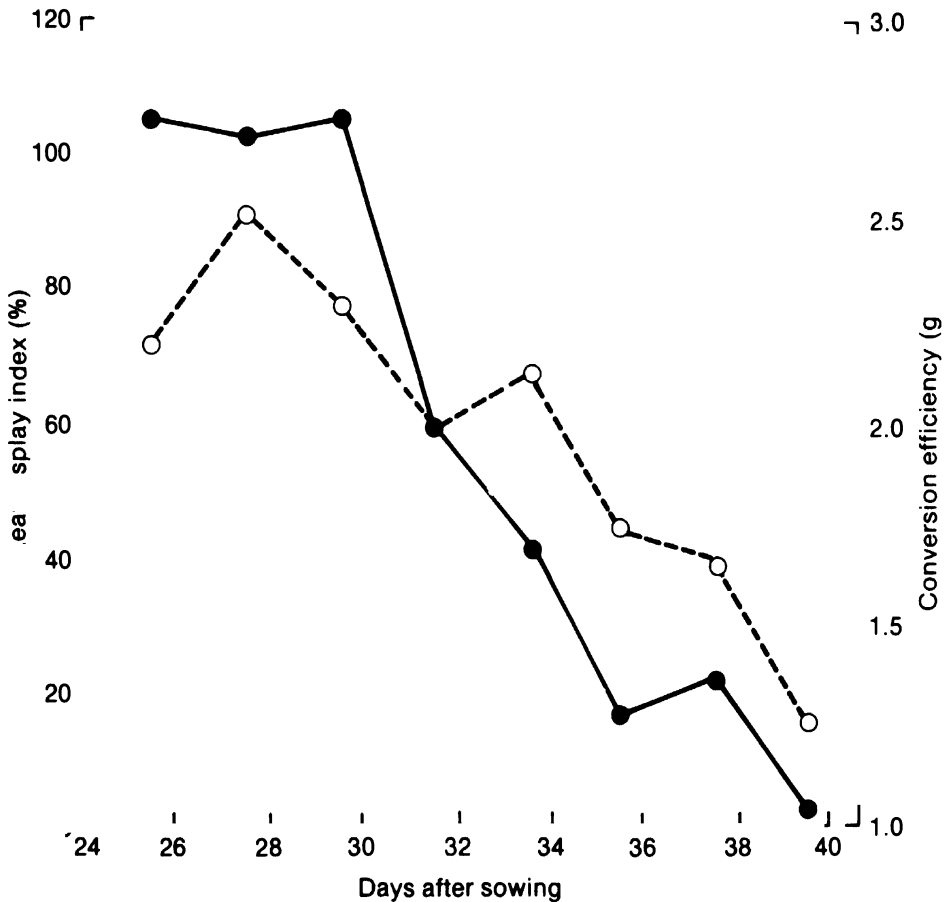

Fig. 9. Changes with time in the conversion efficiency (open circles) and leaf display index (closed circles) of water-stressed crops.

due to wilting and the occurrence of leaf rolling. Coincident with the decline in conversion efficiency was a reduction in leaf display index (Fig. 9). Therefore, a delay in the onset of leaf rolling and wilting without a change in conversion efficiency is unlikely to contribute substantially to an increase in productivity and may even result in higher transpiration rates.

Conclusions

Osmotic adjustment occurred at high leaf water potentials soon after water was withheld. Resistant lines adjusted at a faster rate and had a higher potential for adjustment than susceptible lines. Resistant lines were able to maintain turgor to lower leaf water potentials, but this had little influence on growth, stomatal conductance and light interception. Large changes in these factors occurred soon after water was withheld and at high leaf water potentials.

Two other possible roles of osmotic adjustment that have not been explored in this experiment. Resistant lines with a high capacity for adjustment also have a greater ability to maintain green leaves during a drought (Peacock *et al.* 1988). Substantial osmotic adjustment is apparent at low ψ_l which may promote the survival of leaves (Flower and Ludlow 1986). It has also long been suggested that osmotic adjustment may be beneficial to root growth (Sharpe and Davies 1979; Westgate and Boyer 1985) by allowing plants to utilise water in the soil at greater depths. Measurements made in 1985 and 1986 (unpublished results) indicated that resistant lines have a higher root/shoot ratio than susceptible lines. However, any extra water made available as a result of osmotic adjustment in the roots had little influence on productivity of plants during the drought period in this experiment.

Acknowledgments

References

Ackerson, R. C., Krieg, D. R., and Sung, F. J. M. (1980). Leaf conductance and osmoregulation in field grown sorghum genotypes. *Crop Sci.* **20**, 10–14.

Barlow, E. W. R. (1983). Water relations of the mature leaf. In 'The Growth and Functioning of Leaves'. (Eds J. E. Dale and F. L. Milthorpe.) pp. 332–33. (Cambridge University Press: London.)

Bates, L. M., and Hall, A. E. (1982). Stomatal closure with soil water depletion not associated with changes in bulk leaf water status. *Oecologia* **50**, 62–5.

Blackman, P. G., and Davies, W. J. (1985). Root to shoot communication in maize plants of the effects of soil drying. *J. Exp. Bot.* **36**, 39–40.

Cutler, J. M., Shahan, K. W., and Steponkus, P. L. (1980). Influences of water deficits and osmotic adjustment on leaf elongation of rice. *Crop Sci.* **20**, 314–18.

Flower, D. J., and Ludlow, M. M. (1986). Contribution of osmotic adjustment to the dehydration tolerance of water-stressed pigeonpea (*Cajanus cajan* (L.) Millsp.) leaves. *Plant Cell Environ.* **9**, 33–40.

Gollan, T., Passioura, J. B., and Munns, R. (1986). Soil water status affects the stomatal conductance of fully turgid wheat and sunflower leaves. *Aust. J. Plant Physiol.* **13**, 459–64.

Henson, I. E., Alagarswamy, G., Bidinger, F. R., and Mahalakshmi, V. (1982). Stomatal responses of pearl millet (*Pennisetum americanum* (L.) Leeke) to leaf water status and environmental factors in the field. *Plant Cell Environ.* **5**, 65–74.

Henzell, R. G., McRee, K. J., Van Bavel, C. H. M., and Shertz, K. F. (1976). Sorghum genotypic variation in stomatal sensitivity to leaf water deficits. *Crop Sci.* **16**, 660–2.

Hochman, Z. (1982). Effects of water stress with phasic development on yield of wheat grown in a semi-arid environment. *Field Crops Res.* **5**, 55–67.

Hsiao, T. C., O'Toole, J. C., Yambo, E. B., and Turner, N. C. (1984). Influence of osmotic adjustment on leaf rolling and tissue death in rice (*Oryza sativa* L.). *Plant Physiol.* **75**, 253–341.

Jones, M. M., and Rawson, H. M. (1979). Influence of rate of development of leaf water deficits upon photosynthesis, leaf conductance, water-use efficiency and osmotic potential in sorghum. *Physiol. Plant.* **61**, 122–6.

Jones, M. M., and Turner, N. C. (1980). Osmotic adjustment in expanding and fully expanded leaves of sunflower in response to water deficits. *Aust. J. Plant Physiol.* **7**, 181–92.

Ludlow, M. M. (1980). Adaptive significance of stomatal responses to water stress. In 'Adaptation of Plants to Water and High Temperature Stress'. (Eds N. C. Turner and P. J. Kramer.) pp. 123-37. (Wiley-Interscience: New York.)

Ludlow, M. M., Chu, A. C. P., Clements, R. J., and Kerslake, R. G. (1983). Adaptation of species of *Centrosema* to water stress. *Aust. J. Plant Physiol.* **10**, 119-30.

Ludlow, M. M., Fisher, M. J., and Wilson, J. R. (1985). Stomatal adjustment to water deficits in three tropical grasses and a tropical legume grown in controlled conditions and in the field. *Aust. J. Plant Physiol.* **12**, 131-49.

Matthews, M. A., Van Volkenburgh, E., and Boyer, J. S. (1984). Acclimation of leaf growth to low water potentials in sunflower. *Plant Cell Environ.* **7**, 199-206.

Matsuda, K., and Raizi, A. (1981). Stress induced osmotic adjustment in growing regions of barley leaves. *Plant Physiol.* **68**, 571-6.

Maxwell, J. O., and Redman, R. E. (1978). Water potential and component potentials in expanded and unexpanded leaves of two xeric grasses. *Physiol. Plant.* **44**, 383-7.

Meyer, R. F., and Boyer, J. S. (1981). Osmoregulation, solute distribution and growth in soybean seedlings having low water potentials. *Planta* **151**, 482-9.

Michelena, V. A., and Boyer, J. S. (1982). Complete turgor maintenance at low water potentials in the elongating region of maize leaves. *Plant Physiol.* **69**, 1145-9.

Morgan, J. M. (1983). Osmoregulation as a selection criteria for drought tolerance in wheat. *Aust. J. Agric. Res.* **34**, 607-14.

Morgan, J. M. (1984). Osmoregulation and water stress in higher plants. *Annu. Rev. Plant Physiol.* **35**, 299-319.

Muchow, R. C. (1986). The productivity of grain sorghum in the wet and dry seasons in northwest tropical Australia. (Eds M. A. Foale and R. G. Henzell.) pp. 4.64-4.72. *Proc. Aust. Sorghum Conf.*, Lawes, February 1986.

Munns, R. (1987). Does leaf turgor determine leaf expansion rates in dry or saline soils. In 'Physiology of Cell Expansion during Plant Growth'. (Eds D. J. Cosgrove and D. P. Knievel.) pp. 241-2. (Am. Soc. Plant Physiol.: Maryland.)

Peacock, J. M., Azam-Ali, S. N., and Matthews, R. B. (1988). Approach to screening for resistance to water and heat stress in sorghum (*Sorghum bicolor* (L.) Moench). In 'Arid Lands: Today and Tomorrow'. (Eds E. E. Whitehead, C. F. Hutchinson, B. N. Timmerman and R. G. Varady.) pp. 487-97. (Westview Press: London.)

Radford, S. P. (1980). Comparative responses to water deficits of three C_4 grasses grown in field and controlled environments. M. Agr. Sci. Thesis, University of Queensland.

Ritchie, G. A., and Roden, J. R. (1985). Comparison between two methods of generating pressure-volume curves. *Plant Cell Environ.* **8**, 49-53.

Santamaria, J. M., Ludlow, M. M., and Fukai, S. (1986). Drought resistance traits in hybrids and lines of *Sorghum bicolor* (L.) Moench. (Eds M. A. Foale and R. G. Henzell.) pp. 4.127-4.144. *Proc. Aust. Sorghum Conf.*, Queensland Agricultural College, Lawes, February 1986.

Shackel, K. A., and Hall, A. E. (1983). Comparison of water relations and osmotic adjustment in sorghum and cowpea field conditions. *Aust. J. Plant Physiol.* **10**, 423-35.

Shackel, K. A., Foster, K. W., and Hall, A. E. (1982). Genotypic differences in leaf osmotic potential among grain sorghum cultivars grown under irrigation and drought. *Crop Sci.* **22**, 1121-5.

Sharpe, R. E., and Davies, W. J. (1979). Solute regulation and growth by roots and shoots of water-stressed maize plants. *Planta* **147**, 43-9.

Sobrado, M. A., and Turner, N. C. (1983). Influence of water deficits on the water relations characteristics and productivity of wild and cultivated sunflowers. *Aust. J. Plant Physiol.* **10**, 195-203.

Takami, S., Rawson, H. M., and Turner, N. C. (1982). Leaf expansion of five sunflower (*Helianthus annuus* L.) cultivars in relation to water deficits. II. Diurnal patterns during stress and recovery. *Plant Cell Environ.* **5**, 279-87.

Turner, N. C., Begg, J. E., and Tonnet, L. M. (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.

Turner, N. C., O'Toole, J. C., Cruz, R. T., Namuco, O. S., and Sayeed Ahmad (1986). Responses of seven diverse rice cultivars to water deficits. I. Stress development, canopy temperature, leaf rolling and growth. *Field Crops Res.* **13**, 257-71.

Tyree, M. T. (1976). Negative turgor pressure in plant cells: fact or fallacy? *Can. J. Bot.* **54**, 2738-46.

Westgate, M. E., and Boyer, J. S. (1985). Osmotic adjustment and the inhibition of leaf, root, stem and silk growth at low water potentials in maize. *Planta* **164**, 540-9.

Wilson, J. R., Fisher, M. J., Schulze, E.-D., Dolby, G. R., and Ludlow, M. M. (1979). Comparison between pressure-volume and dewpoint hygrometry techniques for determining the water relation characteristics of grass and legume leaves. *Oecologia* **41**, 77-88.

Wright, G. C., Smith, R. C. G., and Morgan, J. M. (1983). Differences between two grain sorghum genotypes in adaptation to drought stress. III. Physiological responses. *Aust. J. Agric. Res.* **34**, 637-651.