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Response of four sorghum lines to mid-season drought. I. Growth, water use and yield

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ABSTRACT

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Four sorghum (*Sorghum bicolor* L. Moench) lines were visually selected to represent the most resistant and most susceptible in terms of desiccation tolerance and ability to produce new leaves and grain after release from drought. The lines, representing early- and late-maturing lines in both classes, were grown during the summer and part of the monsoon season at Patancheru, Central India, in a study to investigate the physiological basis of the visual assessments. A control treatment was irrigated throughout, while a stress treatment had water withheld from 20 to 84 days after sowing.

During early growth in both irrigation treatments, the resistant lines had slower shoot and root growth rates, slower soil-water-extraction rates, but higher root:shoot ratios than the susceptible lines, which may have been responsible for their higher ψ_w of water-potentials in the stress treatment. Dry-matter production per unit of water transpired was also lower in the resistant lines. As drought became more severe, there was greater leaf death in the susceptible lines. In all lines, panicle initiation was delayed by mid-season drought stress, but once it did start, the length of the reproductive period was increased in the resistant lines but decreased in the susceptible. In both treatments, the resistant lines within each maturity group had higher grain yield than the susceptible lines; in the stress treatment this was largely due to better grain set and tillering.

INTRODUCTION

In areas of the semi-arid tropics where sorghum is grown, drought at some stage of crop growth is often the main factor causing low yields. To address this problem, the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) has initiated a research programme to study the broader

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aspects of drought resistance in sorghum. As part of this programme, the work described in this series of papers focuses on drought occurring during the intermediate stages of crop growth. Mid-season drought stress, starting at about the time of panicle initiation, can interfere with reproductive development and thereby severely reduce the final grain-yield.

From a large number of sorghum accessions subjected to mid-season drought, four lines were selected on the basis of visual screening for resistance or susceptibility to desiccation and the ability to recover and produce grain after the onset of rains (Peacock et al., 1988). These lines were to be used in a detailed study to investigate the physiological basis of the visual assessments, with the hope that any further traits identified might potentially be used also to aid selection of resistant lines in a drought-resistance breeding programme. Although a number of physiological measurements were made, only those which showed differences between the visually identified susceptible and resistant lines are reported. This is done in two parts. In this paper, the relationships at the crop level between dry-matter production and allocation, water uptake, and reproductive development, are described, and the relevance of these to the assessed degree of drought resistance is discussed. In part II (Matthews et al., 1990, this volume), the contribution to drought resistance by characteristics at the leaf level are investigated.

The close relationship between water uptake and dry-matter production has been well documented for a number of crops. Similarly, the importance of the timing of water uptake in relation to reproductive development and hence final yield, when water is limited, has been emphasised by Passioura (1972). Rates of water use and plant water status at each stage of crop growth are influenced by the relative sizes of the evaporative leaf surfaces and the roots. Differences between lines in these relative sizes may result in patterns of water use better or less suited for a given drought environment, in terms of both survival and grain production, by maintaining a favourable plant water status at critical stages of crop growth.

MATERIALS AND METHODS

Background

In 1983, 700 sorghum lines from a wide range of taxonomic groups were selected from more than 24 000 germplasm accessions and advanced breeding lines maintained at ICRISAT, Patancheru, Central India. These were grown at Patancheru in the summer season (March to June), during which water was withheld from emergence until the rains in June. Lines were visually screened for desiccation tolerance, i.e. the proportion of leaf area that remained green or 'unfired', and for the ability to produce new leaves and grain after release of stress. From these lines, 266 were selected, representing those most susceptible and resistant to mid-season drought. For detailed study,

TABLE 1

Description of the four sorghum lines¹

Line	Origin	Race	Altitude (m)	Rainfall (mm)	Height at maturity (cm)	Days to		Maturity class
						— PI	PM	
Susceptible								
ES (IS12739)	China	CB	n.a.	n.a.	220 (med)	51	78	early
LS (IS17605)	Yemen	D	1970	600	350 (tall)	131	174	late
Resistant								
ER (IS1347)	Egypt	CB	n.a.	n.a.	98 (short)	49	75	early
LR (IS20969)	Kenya	C	1100	1500	255 (med)	115	147	late

¹Line numbers are ICRISSAT accession numbers. Race: D—Durra; C—Caudatum; CB—Caudatum bicolor. Altitude and rainfall refer to regions of origin (n.a.—not available). Height at maturity, days to 50% panicle initiation (PI) and 50% physiological maturity (PM) are in the control treatment of the present experiment.

an early-maturing susceptible (IS12739), a late-maturing susceptible (IS17605), an early-maturing resistant (IS1347), and a late-maturing resistant line (IS20969) were selected. These are referred to as ES, LS, ER, and LR, respectively. Details of the responses to drought, the recovery on release from stress, and the environments from which these lines originated, are shown in Table 1. Full details of the selection procedure are given by Peacock et al. (1988).

Design and layout

The four lines were grown during the summer and monsoon seasons (March–August) in 1985, at Patancheru. Two treatments, one drought-stressed and an irrigated control, were imposed with the four lines arranged in a randomised-block design within each treatment. There were four blocks in the stress treatment and two in the control. Plot size was 9 m × 9 m.

The soil, a sandy clay with a loamy surface, is defined according to United States Department of Agriculture taxonomy as a fine mixed isohyperthermic Udic Rhodustalf. Bulk density in the surface 10 cm was 1.55 g cm⁻³, and below that, 1.65 g cm⁻³. A murrum layer was present at depths varying from 50 cm to 150 cm.

Experiment management

Before sowing, a basal dressing of 56:56:0 kg ha⁻¹ N:P:K was applied. The plots were sown on 12 March 1985, in 60-cm rows at about 120 plants m⁻², and irrigated 2 days later. The day of this irrigation was taken as 0 days after sowing (DAS). At 18 DAS, plots were thinned to 12 plants m⁻², and top-dressed with urea (40 kg ha⁻¹). To control shootfly (*Atherigona soccata*), Endosulphan (0.35%) was applied at 13, 20, 36, 43 and 64 DAS. The plots were hand-weeded at 12, 43, 80 and 117 DAS.

Irrigation

To ensure uniform establishment, both treatments were lightly irrigated with sprinklers approximately every four days until 20 DAS. Thereafter, water was withheld in the stress treatment until 84 DAS. There was no rain during this period. The control treatment was furrow-irrigated at weekly intervals throughout the season. Trenches were built around each block to prevent movement of water to the stress plots. To minimise runoff, each irrigation was split into two 1-h applications, one in the morning and one in the afternoon. The amount of water applied was not measured, but was assumed sufficient to recharge the profile to near field capacity. When the onset of the rains was imminent, both treatments were irrigated at weekly intervals from 84 DAS to minimise water stress due to erratic rainfall during the recovery period.

Growth analysis

At weekly intervals from 18 DAS, four plants were randomly harvested from each plot. For each plant, the green leaf area, total dry-weight and total grain-weight were recorded. Later, after the onset of the rains at 84 DAS, similar measurements were made on tillers, if present. Physiological maturity in each line was taken as the black-layer stage, and the final harvest was made shortly after this was observed. On 19, 40, 62, 89 and 102 DAS, roots were sampled by taking soil cores of 20-cm diameter from the top 30 cm of the profile, and 10-cm diameter for the next 60 cm. Four cores were taken from each plot, from beneath the plants that had been harvested for growth analysis. Cores were divided into 30-cm segments and soaked overnight in water. The roots in each segment were separated from the soil by hand-washing, then were dried and weighed.

Leaf firing

'Leaf firing', or the percentage of desiccated leaf, was measured weekly on the youngest fully expanded leaf of each line in the stress treatment from 39 to 81 DAS. Desiccated tissue was separated from green leaf tissue, and both measured with a leaf area meter (Licor 3100¹, Lincoln, Nebraska).

Water-uptake measurements

Two neutron-probe access tubes were installed in each plot, one on a crop row and the other between rows, to a maximum depth of 150 cm. In some plots, the murrum layer prevented penetration to this depth. Soil water-content was measured at weekly intervals in both the stress and control treatments during the drought period from 20 to 84 DAS, and immediately before

¹Reference to commercial products does not imply endorsement or recommendation by IC RISAT in preference to other similar products.

and after each irrigation during the recovery period (84 DAS to final harvest). Water content in the upper 30 cm of the profile was determined gravimetrically, and below 30 cm, at 15-cm depth increments, with a neutron probe. The probe was calibrated against gravimetric measurements from a single soil core adjacent to the access tubes installed in border rows of the crop.

As there was no irrigation or rainfall in the stress treatment during the drought period, both drainage and evaporation from the soil surface were assumed to be small in comparison to the total amount of water extracted by the crops. Thus, measured changes in soil water-content were assumed to be due mainly to transpiration, E_p . In this paper, the results using neutron-probe data refer only to the stress treatment during the drought period.

The position of the water-extraction front was estimated from the time at which there was a marked decline in the soil water-content in each layer, following the method described by McGowan (1974).

Environmental measurements

Throughout the season, an automatic data-logger (Campbell Scientific, Logan, Utah) recorded the hourly averages of ambient dry- and wet-bulb temperatures and incident solar radiation. Dry- and wet-bulb temperatures were measured with copper-constantan thermocouples in a Stevenson screen at 2 m height. Saturation deficit (e) was calculated using the equation given by Campbell (1977). Incident solar radiation was measured with a Kipp en Zonen (Delft, The Netherlands) solarimeter. The thermal time experienced by the crop from sowing until n days later was calculated as

$$\sum_0^n (T_i - T_b)$$

where T_i is the mean daily air temperature, and T_b the base temperature for sorghum, taken as 10 °C (Harris et al., 1987).

Leaf water-potentials

Midday leaf water-potentials (ψ_l) were measured in all plots twice-weekly throughout the experiment using a pressure chamber (PMS Instruments, Corvallis, Oregon). Within each plot, four plants were selected at random, and the youngest fully expanded leaf and another leaf midway down the canopy were excised at a point midway along the leaf, and enclosed in a moist cloth to minimise water loss during transfer to the pressure chamber.

RESULTS

Environment

Environmental conditions during the season are summarised in Fig. 1. Daily irradiance, maximum saturation deficit and air temperatures were constantly

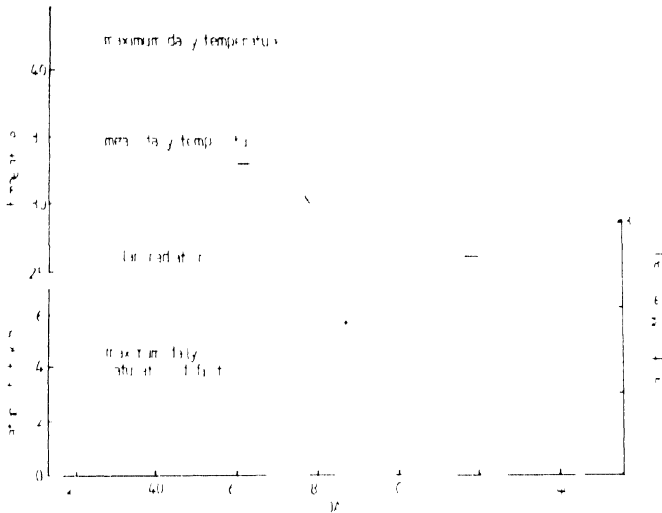


Fig. 1. Summary of the environmental conditions during the period of the experiment.

high for the first part of the season, but declined after 70 DAS due to increased cloud cover as the monsoon approached.

Dry-matter production

Shoot dry-weights at 39 DAS (representing the first part of the season), 88 DAS (effect of mid-season drought), and final harvest, are shown in Table 2. In the stress treatment, drought delayed maturity considerably in all four lines.

Up to 39 DAS in the control treatment, the susceptible lines had produced more dry-matter than the resistant lines. Thereafter, the growth of FS slowed, so that at 88 DAS its dry-weight was not significantly different from those of the resistant lines. Line LS maintained the fastest growth throughout the experiment. After the onset of the monsoon, LR continued to grow, approaching the dry-matter production of LS. Having already reached maturity, the early lines ES and ER showed little increase in dry-matter after 88 DAS.

In the stress treatment, the susceptible lines had again accumulated more dry-matter than the resistant lines by 39 DAS. Growth then slowed in all lines, especially in ES in which there was a significant loss of dry-matter due to leaf death. This line did not recover from the effect of drought, even when water became available. Throughout the stress period, LS was able to maintain its lead in dry-matter production gained early in the season, so that at 88 DAS it still had produced more than the resistant lines, despite having lost more leaf tissue from leaf-firing (Fig. 3). After the onset of the rains, it recovered substantially, although not reaching the same level of dry-matter production as

TABLE 2

Shoot dry-weights (g m^{-2}) at 39 DAS, 88 DAS and final harvest (FH)¹

DAS	Sorghum line				<i>t</i> (DF)	LSD (%)
	ES	IS	ER	LR		
Control						
39	334.4	349.6	219.4	189.2	7.0 (3.3)	
88	892.5	1712.7	1090.6	960.5	18.8 (3.3)*	250.4
FH	1039.5 [102]	2851.6 [179]	1408.3 [102]	2294.0 [179]	3.4 (3.3)	-
Stress						
39	212.2	193.0	117.8	128.3	9.7 (3.9)**	42.6
88	106.6	296.2	155.3	195.0	2.5 (3.9)	
FH	194.9 [116]	2484.6 [179]	1617.1 [151]	2464.1 [179]	23.3 (3.9)**	694.4

¹[] indicates DAS of final harvest. *t*-values from analysis of variance are shown. Least significance difference (LSD) is given only where *t*-values are significant. Levels of significance: ***P* < 0.01, **P* < 0.05.

in the control treatment. The resistant lines also recovered markedly after the arrival of the rains, producing even more dry-matter at final harvest than in the control treatment.

Tillers were produced only by ER and only during the recovery period, accounting for 70% of the total dry-matter at final harvest in the stress treatment, and 50% in the control treatment.

Roots

In the control treatment, the susceptible lines had greater root weights by 40 DAS than the resistant lines (Table 3), although differences were not significant. Shortly after this time, root growth slowed in the early-maturing lines as physiological maturity was reached, so that by 89 DAS, the late-maturing lines had significantly greater root weights. After 89 DAS, only LR continued to increase its root weight, to twice that of the other lines.

In the stress treatment, root growth appeared to be restricted at about the same time as shoot growth, so that at 40 DAS, root weights were only about half those in the control treatment. At this point, the resistant lines had lower root weights than the susceptible lines, and the early-maturing less than the later-maturing, reflecting the rankings of shoot weight (Table 2), although again these differences were not significant. From 40 DAS, there was little or no increase in root weight in the two susceptible lines, but weights continued to increase in the resistant lines, so that by 89 DAS there was little difference in root weights between all lines. After 89 DAS, in all lines except ES, there was a substantial increase in root weights to values similar to or higher than those in the control treatment.

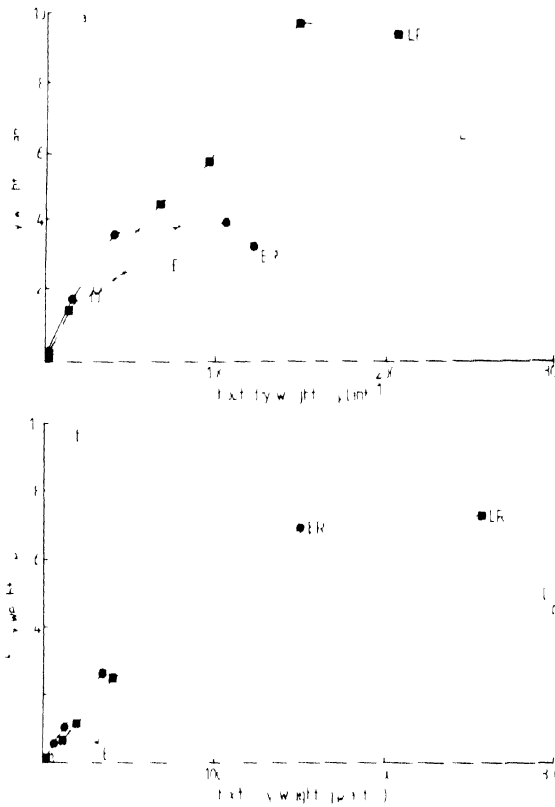


Fig. 2. Relation between root and shoot dry weights over the whole season in the control (a) and the stress treatment (b).

TABLE 3

Root dry weights (g) recovered from cores to 90-cm soil depth at 40 DAS, 89 DAS and final harvest (FH)

DAS	Sorghum line				F (DF)	LSD (5%)
	FS	LS	ER	LR		
Control						
40	1.84	1.64	1.59	1.33	1.5 (3,3)	-
89	3.10	5.46	3.93	5.60	68.7 (3,3)**	0.42
FH	4.43	4.48	3.22	9.39	7.9 (3,3)	-
Stress						
40	0.76	0.84	0.46	0.63	3.8 (3,3)	-
89	0.67	1.06	0.91	1.10	0.6 (3,3)	-
FH	-	4.49	6.88	7.21	0.7 (3,3)	-

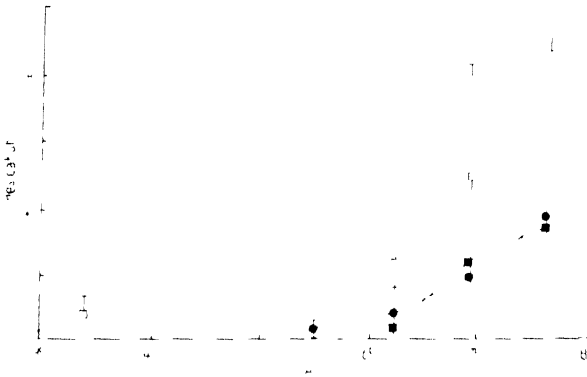


Fig. 3. Percentage desiccation of the youngest fully expanded leaf of the four lines between 39 and 81 days: —○— LS; —●— ES; —■— ER. Vertical bars indicate least significant differences (LSD, $P = 0.05$).

In general, there was a strong correlation between root and shoot weight in all lines before root growth ceased after flowering, although the slope of the relation differed markedly between lines and treatments (Fig. 3). Early in the season there were clear differences in both treatments between resistant and susceptible lines, the former having a greater root weight for a given shoot weight. In the control treatment (Fig. 2), root growth in ER ceased after flowering, but this decline was not apparent in the stress treatment (Fig. 3), although it may have been masked by infrequent sampling around flowering. In any case, the resistant lines maintained a greater root/shoot ratio throughout. Comparisons between treatments indicate that drought stress reduced root/shoot ratios, particularly in the susceptible lines.

Leaf-firing

The percentage desiccation of the youngest fully expanded leaf for each line is shown in Fig. 3. Desiccation was significantly higher in both the susceptible lines and was visible at 39 days in LS. The onset of 'firing' was delayed until about 60 days for the other three lines. Despite the delay in desiccation in ES, the final amount was significantly higher. There was no significant difference between the early- and late-resistant lines. In all lines, desiccation started at the tip and moved progressively towards the base of the leaf.

Water extraction

The cumulative water extracted by each line in the stress treatment is shown in Fig. 4a. From the start of the season, the susceptible lines extracted water considerably faster than the resistant lines. These rates declined towards the

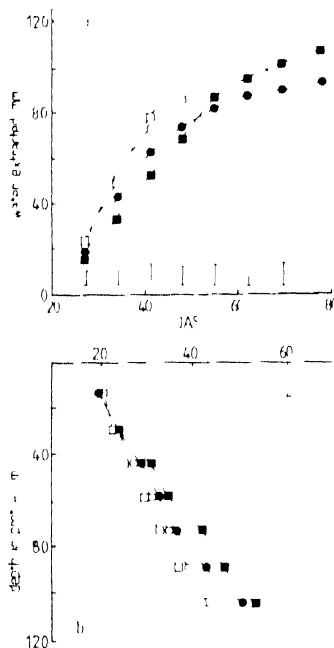


Fig. 4 (a) Cumulative soil water extracted by each line and (b) movement of the water-extraction front down the soil profile between 20 and 80 DAS. Symbols as in Fig. 2.

end of the drought period, especially in the susceptible line ES, which extracted virtually no water after 55 DAS, corresponding to its decline in dry-matter production. The other susceptible line, LS, declined to rates similar to those of the resistant lines, but due to its higher initial rate it had extracted the most water of all the lines by the end of the drought period.

Figure 4b shows the descent of the water-extraction front for each line in the stress treatment. There was a faster descent in the susceptible than the resistant lines. The extraction rates from each zone in the week following the arrival of the water-extraction front at that zone are shown in Table 4, again, the susceptible lines were faster at all depths. Thus, not only did the water-extraction front of the susceptible lines descend faster, but extraction at any particular depth was also faster. This faster extraction rate is consistent with the pattern of root growth, which showed that early in the season there was more root in the susceptible than the resistant lines (Table 3).

Dry-matter water ratio

The pattern of water extraction reflected that of shoot growth, with the faster-growing susceptible lines also extracting water faster, implying that the

TABLE 4

Rates of water extraction¹ (mm day⁻¹) during the week following arrival of the water-extraction front (Fig. 4b) in a given profile layer

Layer (cm)	Susceptible			Resistant			T (3.9)	LSD (5%)
	ES	LS	mean	FR	LR	mean		
7.5-22.5	1.10	0.93	1.02	1.00	0.67	0.84	0.7	
22.5-37.5	1.71	1.82	1.77	1.66	0.90	1.28	1.9	
37.5-52.5	1.37	1.87	1.62	1.12	1.14	1.13	2.2	
52.5-67.5	1.45	1.07	1.26	0.88	0.85	0.87	3.8*	0.41
67.5-82.5	0.82	0.94	0.88	0.81	0.83	0.82	1.0	
82.5-97.5	0.78	0.62	0.70	0.50	0.80	0.65	2.4	

¹Differences between means of the groups were significant ($P < 0.05$) in the 37.5-52.5 cm and 52.5-67.5 cm layers.

dry-matter water ratio (q) was conservative for all lines. However, the susceptible lines in fact produced more dry-matter per unit of water extracted than the resistant lines. The mean values of q , based on regressions of shoot dry-matter (biomass, B) on extracted water, were 3.12 ± 0.08 , 2.91 ± 0.01 , 2.26 ± 0.05 , and 2.35 ± 0.04 g B kg⁻¹ water. (\pm SE) for ES, LS, FR and LR, respectively. Differences between the susceptible and resistant groups were significant ($P < 0.05$), but not within each group. Although root:shoot ratios were higher in the resistant lines, their absolute root weights were smaller (Table 3), which, if included in the analysis, would tend to increase the differences in q . Similarly, it is unlikely that differences in q were due to differences in soil evaporation. In order for their values of q to be equivalent, the resistant lines would have had to lose about 15-20 mm more water from the soil surface than the susceptible lines. Assuming only water in the top 20 cm of soil is lost by direct evaporation, and that 26 mm is contained in this layer at field capacity (Russell, 1980), differences of 15-20 mm in soil evaporation are unlikely. Therefore, differences in q between resistant and susceptible lines appear to be real.

Leaf water-potential

Leaf water potential (ψ_1) was lowest in the LS from the time measurements started, and there was a marked decline in ES after 60 DAS, so that by 75 DAS, both susceptible lines had lower ψ_1 than the resistant lines (Fig. 5). There was no difference in ψ_1 for all lines during the recovery period.

Effect of stress on maturity

Table 5 presents data on the reproductive period from the time of panicle initiation to physiological maturity for each of the four lines in both treat-

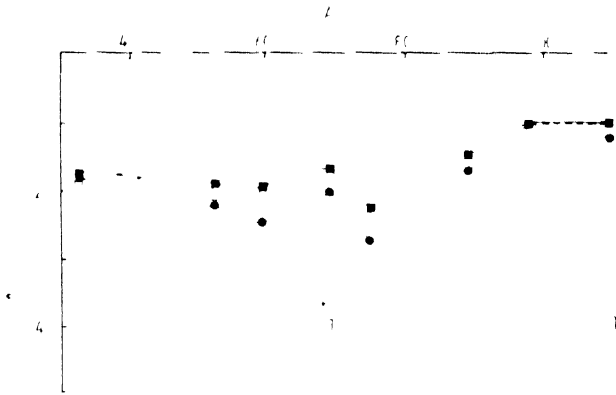


Fig. 5. Mean daily water-potential between 33 and 108 DAS. Symbols as in Fig. 2. Vertical bars indicate least significant differences (LSD, $P = 0.05$).

ments. The effect of variable ambient temperature during the reproductive period (Fig. 1) is taken into account by using thermal time instead of chronological time. In every line, panicle initiation was delayed by mid-season stress, even in the late-maturing lines LS and LR, where initiation in the control treatment occurred after the rains. Except in ER, panicle initiation in the stress treatment was delayed until after the monsoon. There was no relation between the length of delay in panicle initiation due to stress and whether or not the line was classed as resistant or susceptible. In terms of thermal time, the length of the reproductive period from panicle initiation to physiological maturity (PI-PM) was significantly shortened by drought stress in the two susceptible lines, and lengthened in the resistant lines. In both groups, these differences were due mainly to changes in the length of the period from panicle initiation to flowering (PI-F) and, to a lesser extent, from flowering to physiological maturity (F-PM).

Grain production

Table 6 shows grain-yield for each line in both treatments. Except for LR, grain production was less in the stress than in the control treatment, although in LS this difference was small. Line ES failed to produce any grain at all. In this control treatment, within each susceptibility group, the early lines out-yielded the late lines. Similarly, in both treatments, within each maturity group, the resistant lines out-yielded the susceptible lines by a factor of two or more.

In the control treatment, the superior grain-yield of the resistant lines in each maturity class was due to both increased mean grain weights and total grain number per unit area, the latter in turn being due to significantly more

TABLE 5

Effect of mid-season drought on the reproductive period

	Control				Stress				T (313)	SD (5%)
	ES	LS	ER	LR	ES	LS	ER	LR		
Days										
Panicle initiation (PI)	29.8	47.8	30.8	43.8	112.8	127.8	70.0	124.0	289.0**	3.0
Flowering (F)	80.8	131.0	48.8	118.0	129.3	183.0	97.3	181.3	82.0**	8.3
Physiological maturity (PM)	77.8	174.0	74.8	147.0	160.8	191.3	131.3	190.0	84.4**	7.4
PI-F	21.0	33.8	18.0	21.8	16.8	28.3	27.3	27.3	13.1**	4.6
F-PM	27.0	43.0	26.0	32.0	31.3	38.8	34.0	37.8	2.3	-
PI-PM	48.0	76.8	44.0	53.8	47.8	64.0	61.3	66.0	14.4**	7.0
Day-degrees¹										
Panicle initiation (PI)	844	1918	868	1883	2161	2398	1408	2343	317.8**	60
Flowering (F)	986	2446	948	2196	2419	2763	1907	2737	189.1**	78
Physiological maturity (PM)	1868	3098	1804	2678	2880	3384	2447	3329	63.8**	112
PI-F	442	830	380	348	288	368	498	394	167**	78
F-PM	879	649	888	472	460	890	840	891	3.8*	104
PI-PM	1024	1179	936	122	718	986	1038	988	177**	110

¹Thermal time is calculated using a base temperature of 10°C. Accumulated day-degrees up to the rains at 84 days were 1700°C d.

TABLE 6

Components of grain-yield at final harvest

	Sorghum line				<i>F</i> (3, 3)	LSD (5%)
	ES	LS	ER	LR		
Control						
Total grain wt. (g m ⁻²)	191.0	57.0	494.5	123.0	118.0**	51.5
MS ¹ grain wt. (g m ⁻²)	191.0	57.0	231.8	123.0	26.1*	13.8
Tiller grain wt. (g m ⁻²)		-	262.6			
Panicles m ⁻²	11.4	3.0	21.5	5.7	60.5**	3.1
Grains panicle ⁻¹	10678	8814	10417	11566	0.7	-
Total grain no. (m ⁻²)	120965	25684	222884	65777	107.8**	23746
Mean grain wt. (mg)	15.7	12.6	21.7	18.7	13.1*	3.1
Stress						
Total grain wt. (g m ⁻²)		46.1	138.4	123.6	13.5**	50.4
MS grain wt. (g m ⁻²)		46.1	64.7	123.6	15.0**	37.4
Tiller grain wt. (g m ⁻²)			73.8	-		
Panicles m ⁻²		4793	18055	38329	2.1	
Grains panicle ⁻¹		4793	18055	38329	2.1	-
Total grain no. (m ⁻²)		18317	99624	99066	23.3**	30835
Mean grain wt. (mg)		13.0	13.7	12.4	22.1**	3.9

¹main stem

panicles per unit area rather than to the number of grains per panicle. In ER, tillers contributed 53% of the total grain-yield in both treatments.

The higher grain-yield of the resistant lines in the stress treatment was mainly due to their setting four to five times as many grains as the susceptible lines. In contrast to the control treatment, this was in turn mainly from setting more grains per panicle rather than greater numbers of panicles. Both resistant lines produced more grains per panicle under stress than in the control treatment. Differences in mean grain weights in the stress treatment, though significant, were small.

DISCUSSION

The slower initial growth of both shoots and roots in the resistant lines was also reflected in their patterns of water uptake. Early in the season in the stress treatment, the resistant lines extracted water later and more slowly from a given depth than the susceptible lines. However, from about 50 DAS, both growth and extraction rates of the latter fell, and in the case of ES declined to almost zero. It seems that the high initial growth rates and associated fast rates of water extraction of the susceptible lines could not be sustained as drought became more severe.

Although initial growth was slower in the resistant lines, their pattern of allocation of dry-matter between shoots and roots resulted in higher root:shoot

ratios. A greater fraction of dry-matter allocated to the roots must necessarily result in a slower development of leaf area, reduced light interception, slower growth rates and therefore less dry-matter in both roots and shoots, as observed. However, it is likely that the higher root/shoot ratio of the resistant lines was responsible for their more favourable plant water status towards the end of the stress period, by maximising the supply of water by the roots in relation to its loss by the leaves. The data of Favis and Taylor (1979) reveal a similar positive relation between the root-length/leaf-area ratio and leaf water-potential. However, the relationship between plant water status and survival capacity is less clear. The higher proportion of leaf death in both susceptible lines may have been due to their lower ψ_1 , but whereas FS died, LS survived and was still able to maintain higher shoot weights than both resistant lines.

It has been argued that leaf death is an adaptation to provide some flexibility when soil water status is variable, in that a crop can maximise leaf area when water is not limiting, but can reduce its transpiring area to maintain a favourable water status when water becomes scarce (Stout and Simpson, 1978). However, in the susceptible lines, leaf death represented loss of dry-matter that could have been more profitably invested in root tissue earlier to give higher root/shoot ratios (as in the resistant lines). Thus, rather than an adaptation, it is more likely that their higher leaf death was a penalty that the susceptible lines had to pay for excessive leaf production earlier in the season, a conclusion also reached by Wright et al. (1983). Indeed, despite reducing the green leaf area to below that of the resistant lines, leaf death still failed to maintain leaf water-status when drought was severest (Fig. 5).

The resistant lines had a significantly lower q than the susceptible lines. Genotypic differences in q have been reported before for sorghum (Faci and Fereres, 1980; Garrity et al., 1982; Owonubi and Kanemasu, 1982). Various authors have pointed out that drought resistance and water-use efficiency are not synonymous (Hsiao and Acevedo, 1973; Reitz, 1974). It appears from our results and those of Owonubi and Kanemasu (1982) that those lines with higher water-use efficiencies also use the most water, and may therefore be less suited to prolonged periods without rainfall. Selection for high water-use efficiency may be desirable in maximising productivity under medium water stress, but for many crops in the semi-arid tropics, survival from severe drought stress during parts of their growing-season is the most important concern. It may be counter-productive, therefore, to select for plants with higher water-use efficiency alone.

Drought stress delayed the onset of reproductive development in all lines, and until after the rains in all except ER. Seetharama et al. (1984) observed that, when the onset of drought occurred after panicle initiation, flowering was delayed but physiological maturity was advanced. The timing of drought in relation to reproductive development is therefore important. It seems that,

once reproductive development commences, the plant is committed to seed production, and in order to produce some grain, maturity is hastened by stress. If, on the other hand, drought is imposed before panicle initiation, as in the present work, then the plant delays its entire reproductive development until conditions become more favourable. These effects on maturity highlight the need to match lines to specific patterns of drought. Where water deficits occur late in the season, the selection of early-maturing lines has resulted in considerable improvements in yield (Turner, 1979), but these same lines may not perform well when subjected to mid-season drought. If reproductive development is delayed until the release of drought, there would appear to be little advantage in selecting for early-maturing lines. Indeed, the lines in which stress had the least relative effect on grain production were the late-maturing lines (Table 5).

In the control treatment, there was an inverse relation between the length of the reproductive period (C d from panicle initiation to physiological maturity) and the grain-yield at final harvest of the lines, in the stress treatment, however, this relationship was positive – the longer the grain-filling period the higher the yield. This is in direct contrast to the observation by Blum (1970) that yield potential is proportional to grain-fill duration under non-stress conditions, but inversely proportional under stress. Comparing treatments indicates that the length of the reproductive period (C d) was increased by drought in the resistant lines but decreased in the susceptible, a factor which may have been influential in determining their respective grain-yields.

The higher grain-yields of the resistant lines under stress were due not so much to differences in the size of grain, but rather to the setting of more grains per unit area, this in turn being due to more panicles from tillering in the case of LR, and more grains per panicle in both ER and LR. Indeed, tillers contributed 50% of the final grain-yield in FR in the stress treatment. The importance of tiller production in compensating for reductions in grain numbers has been pointed out by Wright et al. (1983), while Mahalakshmi and Bidinger (1986) showed that high tillering in pearl millet is the main mechanism by which the crop overcomes loss of grain-yield due to drought stress during panicle development. However, although drought stress during reproductive development has been shown to reduce potential yields by inducing floral abortion (Wright et al., 1983; Morgan and King, 1984), in the present work drought stress occurred in most lines before reproductive development began. The reduction in grain numbers in the susceptible lines is therefore unlikely to be a direct effect of drought on floral abortion. Nevertheless, it is clear, from comparison of control with stress treatments, that subsequent reproductive development under stress was in some way affected by the drought that preceded it. It is possible that the higher root/shoot ratios of the resistant lines and resulting more favourable plant water-status towards the end of the

stress period may have caused less meristem damage thereby influencing the numbers of grains set later, although possible mechanisms must remain conjectural in the context of the present work.

While there is a need to test a wider number of lines, there can be little doubt that, at least in the four lines studied, the visual assessments of resistance to mid-season drought on the basis of degree of leaf desiccation are supported by differences in a number of physiological traits. This suggests that visual screening for mid-season drought stress on the basis of leaf firing and recovery potential may be a reliable method of rapidly evaluating large numbers of lines.

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