

## EFFECT OF HEAT AND DROUGHT STRESS ON SORGHUM (*SORGHUM BICOLOR*). I. PANICLE DEVELOPMENT AND LEAF APPEARANCE

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### SUMMARY

Seven sorghum lines, flowering from 50 to 87 days after sowing, were subjected to early drought stress, late stress, and both early and late stress in the field during the dry season in India. Panicle initiation was delayed by 2–25 days and flowering by 1–59 days by the drought stress treatments, the greatest effect being in the treatment subjected to both early and late stress. Stress increased the period between panicle initiation and flowering by retarding the rate of panicle development; when stress was severe panicle development stopped. Upon relief of stress following irrigation, panicle development resumed at rates comparable to those in a fully irrigated control. The rate of leaf appearance was affected in a similar manner to panicle development soon after water was withheld. Rate of leaf appearance and panicle development decreased as pre-dawn leaf water potential decreased and ceased at water potentials of  $-0.55$  and  $-0.7$  MPa, respectively.

*Efecto del calor y la sequía en el sorgo (Sorghum bicolor) I. Desarrollo de panículas y aparición de hojas*

### RESUMEN

Siete variedades de sorgo, con florecimiento de 50 a 87 días a partir de la siembra, fueron sometidas en campo a una sequía temprana, y a una sequía temprana y tardía, durante la estación seca en India. Debido a los tratamientos de falta de agua, la iniciación de las panículas observó un retraso de 2-25 días, mientras que la floración presentó un retraso de 1-59 días. Los mayores efectos se vieron en las plantas sometidas a sequía temprana y tardía. La falta de agua incrementó el período entre la iniciación de las panículas y el florecimiento debido a la menor rapidez de desarrollo de las panículas, y cuando la falta de agua fue severa, el desarrollo de las panículas cesó por completo. Solucionada la falta de agua, luego de la irrigación, el desarrollo de las panículas se reinició con una intensidad comparable a las de las plantas de control que contaron con irrigación total. El índice de aparición de hojas fue afectado en forma similar, poco después de cortarse el agua. El índice de aparición de hojas y de desarrollo de panículas se redujo a medida que disminuyó el potencial de agua en la hoja antes del amanecer, y se detuvo por completo con potenciales de agua de  $-0,55$  y  $-0,7$  MPa, respectivamente.

### INTRODUCTION

Identifying the morphological, physiological and biochemical bases of resistance or tolerance to heat and drought stress has been given a high priority in many crop

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improvement programmes (for example, see Srivastava *et al.*, 1987; ICRISAT, 1988). It is well known, though frequently overlooked in drought experiments, that one of the most important traits conferring adaptation to drought is the selection of an appropriate flowering and maturity date or pattern of panicle development (Bidinger *et al.*, 1987; Ludlow and Muchow, 1988). It is surprising, therefore, that only a few studies have examined in detail the effect of heat and drought stress on panicle (apical) development in cereals (for example, Aspinall and Husain, 1970; Husain and Aspinall, 1970; Nicholls and May, 1963).

Development can be defined as 'progress towards maturity' and, in the context of this paper, refers to reproductive or panicle development, that is, to the change from a vegetative to a reproductive apex (panicle initiation) and to the increasing complexity of form and size thereafter until flowering. Stress from water deficits and high temperatures delays panicle initiation (Whiteman and Wilson, 1965; Downes, 1972; Rees, 1986; Mahalakshmi and Bidinger, 1985a; Matthews *et al.*, 1990), retards panicle development and flowering (Angus and Moncur, 1977; Husain and Aspinall, 1970; Whiteman and Wilson, 1965; Mahalakshmi and Bidinger, 1985a,b; Mahalakshmi *et al.*, 1987) and hastens flowering in cereals (Angus and Moncur, 1977; Stout *et al.*, 1978). However, the degree to which these effects of stress on the rate of panicle development are due to differences in temperature between stressed and non-stressed treatments, to differences in the response to temperature of different genotypes or to differences in the severity of the stress treatments is not clear.

We describe here the effects of the timing and severity of pre-flowering heat and drought stress on panicle development and leaf appearance in seven contrasting sorghum lines grown in the field in India. The effects of stress on panicle development are compared with the effects on leaf appearance using pre-dawn leaf water potential ( $\psi$ ) as an index of plant available water and hence of stress.

#### EXPERIMENTAL DETAILS

The experiment was conducted during the 1986 dry season, and extended into the monsoon season (March–July), at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India. The soil was a sandy clay with a loamy surface, defined according to USDA taxonomy as a fine, mixed, hypothermic Udic Rodustalf.

Seven lines of sorghum (*Sorghum bicolor* (L.) Moench), chosen for their contrasting responses to heat and drought stress based on their capacity to maintain green leaves during a drought (Peacock *et al.*, 1988), were examined. Drought resistance or susceptibility, days to maturity and the cardinal temperatures of seed germination are given in Table 1. Base temperature,  $T_b$ , is the temperature at and below which the rate of germination is zero; optimum temperature,  $T_o$ , is the temperature at which the rate of germination is fastest; and maximum or lethal temperature,  $T_m$ , is the temperature at and above which the rate of germination is zero.

The experiment was machine sown on 12 March and sprinkler irrigated three days later. The day of irrigation was taken as day zero for calculations of days after sowing (DAS) and accumulated thermal time ( $^{\circ}\text{Cd}$ ). Plot size was  $9 \times 12$  m. A basal dressing of  $200 \text{ kg ha}^{-1}$  of superphosphate (28:28:0) was applied before sowing, followed by a top dressing of  $100 \text{ kg ha}^{-1}$  urea at 19 DAS. Lodging, a common problem in susceptible lines, was prevented by supporting the plants with stakes.

The initial design of the experiment was a split block of two treatments with three replications; the seven sorghum lines constituted the sub-plots. Originally there were two treatments: a control, which was furrow irrigated at weekly intervals, and a drought treatment, where water was withheld after crop establishment (20 DAS). However, following 30 mm of rain between 40 and 43 DAS, the design was changed, creating four, instead of two treatments: a control (irrigated), an early stress treatment (20–42 DAS:  $310\text{--}657^{\circ}\text{Cd}$ ), a late stress treatment (47–69 DAS:  $730\text{--}1080^{\circ}\text{Cd}$ ) and an early plus late stress treatment (20–69 DAS:  $310\text{--}1080^{\circ}\text{Cd}$ ). From 43 DAS there were two replicates of the early stress treatment and late stress treatment, but only one replicate (plot) of the control and early plus late stress treatments. These two plots were divided in half so that an equal number of observations were collected in all treatments. The modification to the design meant that the stress treatment/line means could not all be compared statistically. An analysis of variance was carried out on the replicated treatments and the standard error from this analysis was used to give some indication of the variability.

#### *Leaf water potential*

Measurements of leaf water potential ( $\psi$ ) were made prior to dawn on the mid-portion of four to six of the youngest fully expanded leaves in each treatment. Measurements were made every seven days, starting 25 DAS. Leaves were excised and placed between moistened sheets of filter paper lined with muslin, then transported to an adjacent field laboratory. One side of the leaf (without the midrib) was then stripped and placed in a humidified pressure chamber (PMS Instruments Inc., Corvallis, Oregon, USA) for determination of leaf water potential.

#### *Leaf appearance*

The number of fully expanded leaves (those with visible ligules) was recorded on five plants per plot every seven days in all lines except IS 1347. The rate of leaf appearance was determined from linear regression of the number of leaves on accumulated thermal time (above  $T_b$ ) from sowing.

#### *Panicle development*

In all lines, four or six plants from each treatment were harvested every three to four days to monitor panicle development, starting 19 DAS. Harvesting continued to flowering (FL) or to 68 DAS. In the lines that had not reached panicle

initiation (PI) by 68 DAS, harvests were taken at seven day intervals thereafter to determine PI.

Each plant was dissected under a binocular microscope and the stage of development of the apex recorded. Panicle development was examined with reference to descriptions published by Eastin and Kit-Wah Lee (1985) (for the early stages) and Waddington *et al.* (1983) (for the later stages) using a scale analogous to that given for pearl millet by Craufurd and Bidinger (1988) in which the numerical stage of development is linear with accumulated temperature (above  $T_b$ ). The key stages of panicle development identified and their scores (in parentheses) were: vegetative apex (0), panicle initiation (1), primary branch initiation (2), secondary branch initiation (4), tertiary branch initiation (6), spikelet initiation (8), stamen initiation (10), pistil initiation (12), style initiation (14), stigmatic branch initiation (16); stigmatic branch differentiation and elongation (18), and, finally, first appearance of the anthers (20).

The phenology of the crop could therefore be divided into three phases: GS1, the phase from sowing to PI; GS2, the phase from PI to FL; and GS3, the phase from FL to maturity (M, black layer appearance). Panicle initiation was determined by dissection, and FL and M from observations in the field. Rate of development was calculated as the reciprocal of the duration (using accumulated thermal time) of GS2.

#### *Extractable soil water content*

The extractable soil water content at time  $t$  was calculated as:

$$\frac{\text{water content at time } t - \text{minimum water content}}{\text{maximum water content} - \text{minimum water content}} \times 100$$

where field capacity equals 100% and the permanent wilting point equals 0% (Ritchie, 1973). Water content was determined using a neutron probe, with gravimetric samples taken at the surface. The soil was, on average, 85 cm deep and it was assumed that all treatments had access to water at this depth.

#### *Accumulated temperature calculations*

To describe adequately panicle development and leaf appearance, both of which are temperature-dependent processes (Ong and Monteith, 1985), genetic variation in response to temperature ( $T_b$ ,  $T_o$  and  $T_m$ , Table 1) and variation in temperature between stress treatments have to be taken into account. The cardinal temperatures of seed germination used in these studies were obtained from the unpublished data of Flower, Rani and Peacock. These authors also confirmed for two of the lines that the cardinal temperatures determined from seed germination and leaf expansion were similar. All data in this paper are presented here in terms of accumulated thermal time ( $^{\circ}\text{Cd}$ ), calculated from leaf temperature using the equations of Garcia-Huidobro *et al.* (1982a,b). Leaf temperatures in the field were measured with thermocouples fixed to the abaxial

Table 1. Drought resistance or susceptibility, days to physiological maturity and cardinal temperatures (base,  $T_b$ ; optimum,  $T_o$ ; maximum,  $T_m$ ) of seed germination of a range of sorghum lines

Line	Resistant(R) or susceptible(S)†	Days to physiological maturity	Cardinal temperatures (°C)		
			$T_b$	$T_o$	$T_m$
IS 12739	S	78	9.3	37.0	45.9
IS 12744	S	84	—‡	—‡	—‡
IS 1347	R	75	9.8	37.8	46.9
IS 13441	R	88	10.6	37.7	47.8
IS 22380	R	115	—‡	—‡	—‡
ICSV 213	R	120	12.1	36.6	44.6
ICSH 109IN	R	100	—‡	—‡	—‡
Mean			10.5	37.3	46.3

†Based on Peacock *et al.* (1988); ‡no data available.

surface of the leaf. Temperature was logged every five minutes (CR7 data logger: Campbell Scientific Inc., Logan, Utah, USA) and mean hourly temperatures were used in the calculation of °Cd. No allowance was made for the effect of vapour pressure deficit (VPD) on crop growth or development (see Hamdi *et al.*, 1987).

## RESULTS

### Weather

Minimum and maximum temperatures, evaporation rates and solar radiation were all high for the first 90 days of the experiment (Table 2). The average maximum air temperature for this period exceeded the optimum temperature for sorghum, indicating that temperature had been a source of stress. The highest leaf temperature measured was 42°C on 60, 67 and 69 DAS. Rainfall was negligible during this period, except for 30 mm between 40 and 43 DAS. After 90 DAS, with the onset of the monsoon, maximum temperature, evaporation rate and solar radiation all declined as rainfall and cloud cover increased.

Table 2. Mean daily minimum and maximum air temperature (°C), total rainfall (mm), mean daily evaporation rate ( $\text{mm d}^{-1}$ ) and mean daily radiation ( $\text{MJ m}^{-2} \text{d}^{-1}$ ) during the periods 21–42 DAS (early stress period), 43–69 DAS (late stress period), 70–90 DAS and 91–110 DAS

DAS	Time (°Cd)	Temperature		Rainfall	Evaporation rate	Solar radiation
		Minimum	Maximum			
21–42	346–684	22.4 ± 3.6	37.7 ± 1.4	13.0	10.9 ± 1.2	22.4 ± 2.5
43–69	684–1124	24.1 ± 4.2	38.6 ± 1.8	27.5	13.0 ± 3.0	24.0 ± 2.0
70–90	1124–1424	24.5 ± 3.0	36.7 ± 3.1	7.0	12.6 ± 3.2	21.4 ± 4.3
91–110	1424–1738	23.3 ± 0.9	31.7 ± 2.1	97.0	6.7 ± 2.7	13.2 ± 5.9

*Pre-dawn leaf water potential and extractable soil water*

The pre-dawn water potential of leaves is the maximum level measured on any particular day and has been used as a measure of plant water status (Angus and Moncur, 1977). The relationship between leaf water potential and extractable soil water (soil water availability) shows that in this experiment mean leaf water potential was maintained at about  $-0.25$  to  $-0.3$  MPa until approximately 60–70% of the extractable soil water had been used, after which it declined sharply to  $-2.1$  MPa at 0% extractable water (Fig. 1). Values above  $-0.3$  MPa indicate that water for transpiration was still freely available and plants were able to recover overnight from deficits during the day (Stage I drought stress, Sinclair and Ludlow, 1986). Values of leaf water potential less than  $-0.3$  MPa indicate that water for transpiration was no longer freely available and plants could not recover overnight (Stages II and III drought stress: Sinclair and Ludlow, 1986).

The effect of the stress treatments on the time course of leaf water potential was similar in all lines (Flower *et al.*, 1990) and is illustrated by IS 13441 (Fig. 2). (Note that from sowing to 43 DAS ( $730^{\circ}\text{Cd}$ ) the control and late stress treatments, and the early and early plus late stress treatments are the same.) In IS 13441, the leaf water potential in the control treatment remained above  $-0.3$  MPa throughout the period of measurement, except at 67 DAS when temperature and evaporation rates were particularly high. In the first period of stress ( $310$ – $675^{\circ}\text{Cd}$ ), leaf water potential in the early and early plus late stress treatments declined from about  $-0.25$  to  $-0.4$  MPa, indicating that for most of the early stress period water was freely available for transpiration. During the late stress period ( $730$ – $1080^{\circ}\text{Cd}$ ), leaf water potential declined rapidly in both the early plus late and the late stress treatments as the available water was depleted. Minimum values of leaf water potential reached during this period in the early plus late stress treatment ranged from  $-1.27$  MPa in IS 12744 to  $-3.2$  MPa in ICSV 213,

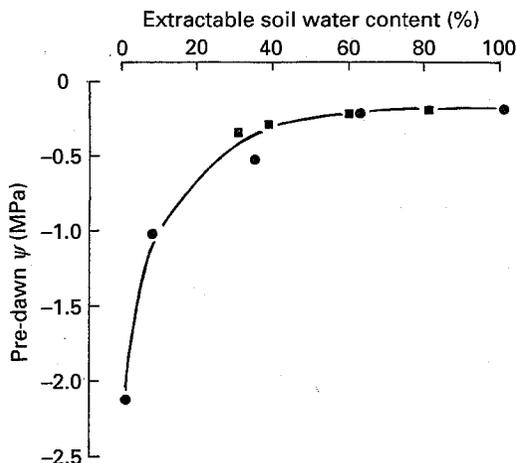


Fig. 1. Relation between pre-dawn leaf water potential ( $\psi$ ) and extractable soil water for early stress (■) and late stress treatments (●) (curve fitted by eye).

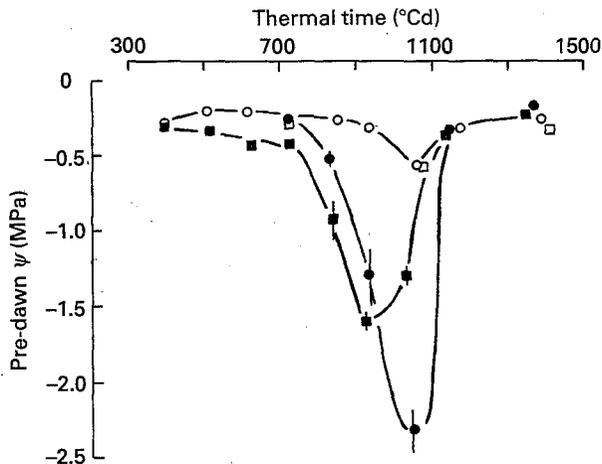


Fig. 2. Relation between pre-dawn leaf water potential ( $\psi$ ) and thermal time from sowing in IS 13441 for control (○), early (□), late (●), and early plus late (■) stress treatments (SEs are shown where they exceed the symbol; curve fitted by eye). (Source: Flower *et al.*, 1990.)

and in the late stress treatment from  $-1.42$  MPa in ICSV 213 to  $-2.29$  MPa in IS 13441 (Fig. 2). The very rapid decline in leaf water potential in the late stress treatment compared with the slow decline in the early stress treatment presumably reflected the greater leaf area at the time water was withheld and the increased evaporation rate during the drought stress period. The severity of the stress was therefore much greater in the late and early plus late stress treatments than in the early stress treatment. Following rewatering, leaf water potential quickly recovered to values typical of the control.

#### *PI, FL and the duration of GS2*

The stress treatments had marked effects on the time to PI and FL, which were dependent on whether the line was early or later flowering, and on the time and duration of the stress.

In the early flowering (50–60 d) lines, where PI occurred at the start (IS 1347) or midway (IS 12744, IS 12739) through the early stress treatments, PI and FL, and therefore the duration of GS2, were largely unaffected by the early and late stress treatments (Table 3). In the early plus late stress treatment, however, FL occurred 28 to 35 days later than in the control, and this was associated with a longer duration of GS2.

In the later flowering lines, where FL occurred 70 to 92 DAS in the control treatment, the stress treatments affected either or both days to PI and the duration of GS2 (Table 3). In all four of these lines, PI in the control treatment occurred between the end of the early stress treatment and the start of the late stress treatment (41 to 47 DAS). In the early stress treatment (which was not very severe compared with the late stress treatment) PI was nonetheless delayed in all lines (by 6 to 19 d), but with no subsequent effect on the duration of GS2. The late

Table 3. Days to panicle initiation (PI), flowering (FL), maturity (M), the duration of GS2 (PI to FL) and leaf number at PI in four stress treatments in a range of sorghum lines

Line	Stress treatment	Days to			Duration of GS2		Leaf no. at PI
		PI	FL	M	d	°Cd	
<i>Early flowering lines</i>							
IS 12739	Control	30	58	80	28	442	12.5
	Early	32	61	89	29	466	12.0
	Late	30	59	81	29	448	12.5
	Early + late	32	86	115	54	795	12.0
IS 12744	Control	29	60	85	31	488	11.5
	Early	33	66	90	33	539	11.5
	Late	29	69	94	40	538	11.5
	Early + late	33	88	118	55	848	11.5
IS 1347	Control	19	50	78	31	521	—†
	Early	19	57	83	38	685	—†
	Late	19	52	76	33	617	—†
	Early + late	19	85	118	66	1058	—†
<i>Later flowering lines</i>							
IS 13441	Control	41	70	99	29	458	18.3
	Early	51	84	112	33	522	17.7
	Late	45	99	124	44	821	19.1
	Early + late	86	129	161	43	610	22.1
IS 22380	Control	47	87	122	40	650	18.2
	Early	66	110	144	44	704	22.4
	Late	68	117	152	49	835	23.7
	Early + late	100	142	174	42	585	27.4
ICSV 213	Control	47	92	123	45	683	16.2
	Early	58	116	150	58	919	17.3
	Late	47	102	136	55	844	16.2
	Early + late	83	137	172	54	752	19.0
ICSH 109IN	Control	42	71	99	29	481	15.3
	Early	48	78	105	30	471	16.8
	Late	42	99	132	57	943	16.5
	Early + late	69	106	140	37	511	18.2
SE		—	5.6	5.5	—	—	0.29

†Data not available.

stress treatment had no marked effect on PI in three of the lines (IS 13441, ICSH 109IN and ICSV 213), since PI occurred at the start of this stress treatment, but did increase the duration of GS2, delaying FL by 10 to 29 days. In IS 22380, late stress delayed PI until the end of the stress period, with little subsequent effect on the duration of GS2. In the early plus late stress treatment, where leaf water potential started to decline at the end of the early stress period, PI was delayed in all lines until 0 to 31 days after the termination of the stress treatment.

The retardation of PI caused by the stress treatments was generally associated with a retardation in the rate of leaf appearance (Table 3), that is, PI occurred at a time when there were the same number of expanded leaves in most lines. The

exceptions to this were the later flowering lines in the early plus late stress treatment, where PI occurred at a higher leaf number.

The delay in FL of the early flowering lines in the early plus late stress treatment and of the later flowering lines in the late stress treatment was approximately proportional to the duration of the late stress period, that is, about 25 days. The accumulated temperature calculations, which take account of differences in leaf temperature between stress treatments and the known response of individual lines to supra-optimal temperatures, show clearly that the increase in the duration of GS2 was not due to differences in temperature.

The duration of GS3, which in nearly all line and treatment combinations occurred after the stress treatments had ended, was generally unaffected by earlier stress periods.

#### *Leaf appearance and panicle development*

The effect of stress on leaf appearance and panicle development was similar in all lines (allowing for differences in flowering time group) and is illustrated by IS 12739, an early flowering line, and IS 13441, a later flowering line (Fig. 3).

Rates of leaf appearance in the control treatments were linear with respect to accumulated temperature (Fig. 3, Table 4), and the mean accumulated temperature per leaf for all lines was 52°Cd, comparable to other published values in sorghum (Hamdi *et al.*, 1987). The imposition of stress, both in the early and late stress treatments, immediately resulted in a reduction in the rate of leaf appearance (Fig. 3, Table 4). As the severity of the stress increased, leaf appearance eventually ceased. When stress was relieved, the rates of leaf appearance rapidly returned to rates comparable to the control (Fig. 3, Table 4).

Stress affected panicle development in a similar manner to leaf appearance: rate of development (from PI) was initially slowed by stress until development ceased altogether, and no further development occurred until stress was relieved (Fig. 3). The other lines exhibited similar responses to stress: panicle development ceased at stage 14 in IS 1347 and stage 8 in IS 12744 in the late stress treatment, and at stage 6 in ICSV 213 and stage 4.5 in ICSH 109IN in the early plus late stress treatment. Clearly, stress can cause the cessation of panicle development at any stage of development from PI to FL, as well as delaying PI (see Table 3).

#### *Relation between rates of leaf appearance and development and leaf water potential*

Stress affected the appearance of leaves and panicle development in a similar manner, which was presumably related to the level of stress, or leaf water potential (see Fig. 2). This section examines the relation between leaf water potential and the rates of leaf appearance and panicle development.

To examine the relation between leaf water potential and leaf appearance, calculated rates of leaf appearance (Table 4) were normalized to the same mean rate in the control treatment (0.0193 leaves °Cd<sup>-1</sup>) and plotted against mean values of leaf water potential during the period of linear increase in leaf

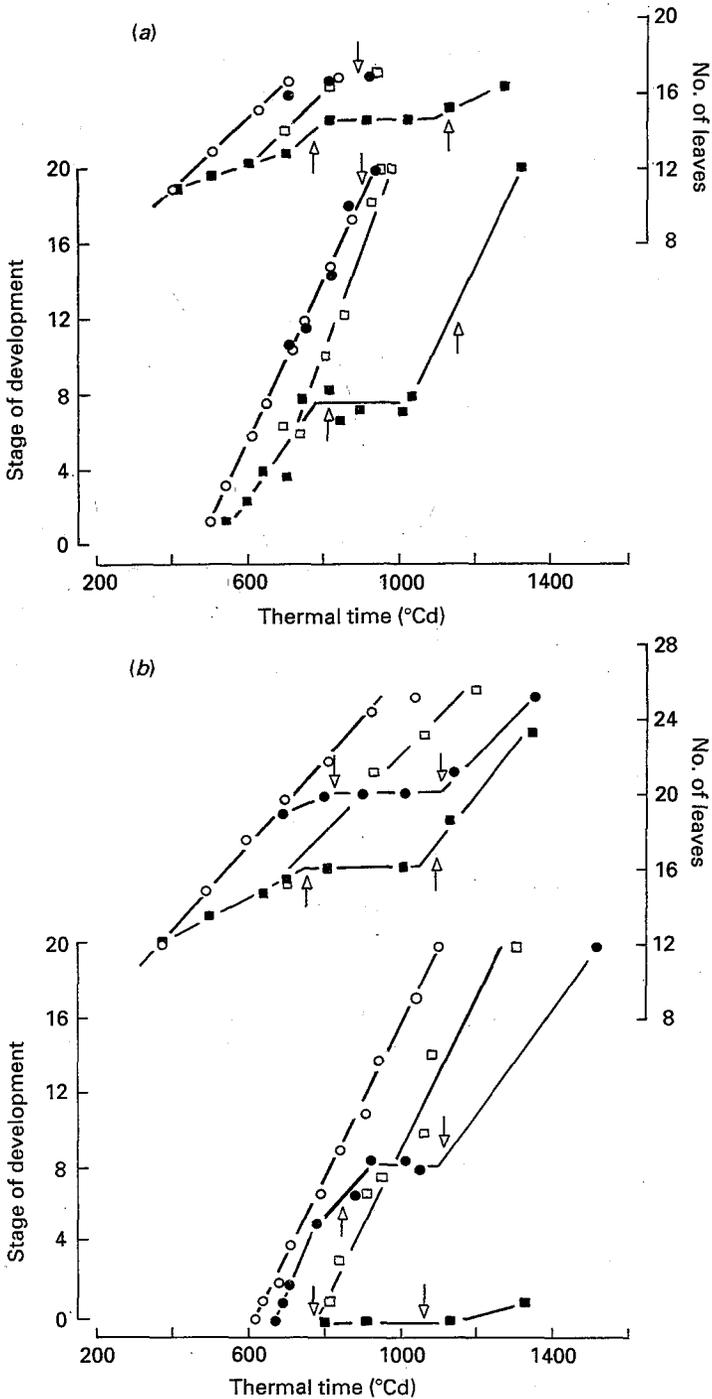


Fig. 3. Relation between number of leaves and stage of panicle development and thermal time from sowing in (a) IS 12739 and (b) IS 13441 for control (○), early (□), late (●), and early plus late (■) stress treatments; arrows show when the leaf water potential ( $\psi$ ) reached  $-0.55$  MPa (leaves) and  $-0.70$  MPa (panicle development).

Table 4. Rate of leaf appearance ( $\text{leaf}^\circ\text{Cd}^{-1}$ ) and the rate of development adjusted for periods when development stopped ( $1/\text{GS2}^* \times 10^{-3}$ ) in four stress treatments in a range of sorghum lines (see text for details on the calculation of rate of leaf appearance and development)

Line	Stress treatment	Rate of leaf appearance	Rate of development	
<i>Early flowering lines</i>				
IS 12739	Control	0.018	2.26	
	Early	—†	2.14	
	Late	—†	2.23	
	Early + late <sup>4</sup>	0.006	1.90	
IS 12744	Control	0.020	2.05	
	Early <sup>1</sup>	0.022	1.85	
	Late	—†	1.92	
IS 1347	Early + late <sup>2</sup>	0.006	1.59	
	Control	—†	1.73	
	Early	—†	1.42	
IS 13441	Late	—†	1.62	
	Early + late	—†	1.22	
	<i>Later flowering lines</i>			
	IS 22380	Control	0.024	2.18
Early <sup>1</sup>		0.020	2.16	
Late <sup>3</sup>		0.011	1.47	
Early + late <sup>2</sup>		0.009	1.64	
Early + late <sup>4</sup>		0.021	—	
ICSH 109IN	Control	0.019	1.54	
	Early <sup>1</sup>	0.018	1.42	
	Late <sup>3</sup>	0.009	1.77	
	Early + late <sup>2</sup>	0.005	1.70	
	Early + late <sup>4</sup>	0.026	—	
ICSH 213	Control	0.021	2.08	
	Early <sup>1</sup>	0.021	2.12	
	Late <sup>3</sup>	0.007	1.72	
	Early + late <sup>2</sup>	0.012	1.75	
	Early + late <sup>4</sup>	0.026	—	
ICSH 109IN	Control	0.014	1.46	
	Early <sup>1</sup>	0.016	1.59	
	Late <sup>3</sup>	0.010	1.38	
	Early + late <sup>2</sup>	0.004	1.33	
	Early + late <sup>4</sup>	0.019	—	

†Not calculated. <sup>1</sup>Rate following rewatering, 43 DAS onwards. <sup>2</sup>Rate during stress period, 20–69 DAS. <sup>3</sup>Rate during stress period, 43–69 DAS. <sup>4</sup>Rate following rewatering, 69 DAS onwards.

appearance (Fig. 4). Exponential (Equation 1) and linear (Equation 2) regression analyses on all the data ( $n = 20$ ) both adequately described the data:

$$y = 0.0345 - 0.0067 \times 0.053^x \quad r^2 = 0.66 \quad P < 0.001 \quad (1)$$

$$y = 0.0346 + 0.0561x \quad r^2 = 0.65 \quad P < 0.001 \quad (2)$$

The threshold ( $y = 0$ ) values of leaf water potential from these equations were  $-0.55$  for the exponential and  $-0.61$  MPa for the linear regression. Alternatively, rate of leaf appearance can be considered as constant at leaf water potential values above  $-0.3$  MPa, when water for transpiration is freely available (Sinclair and Ludlow, 1986). A linear regression fitted to data when leaf water potential values were less than  $-0.3$  MPa ( $n=8$ ) gave:

$$y = 0.0379 + 0.0665x \quad r^2 = 0.70 \quad P < 0.001 \quad (3)$$

The threshold leaf water potential for leaf appearance from this analysis was  $-0.57$  MPa, similar to the analyses using all the data. These thresholds agree with the observed data (see arrows in Fig. 3).

A comparison of rate of development and leaf water potential is less straightforward for two reasons. First, the rate of development as defined ( $1/GS2$ ) included periods of zero development (see Fig. 3), which were presumably due to

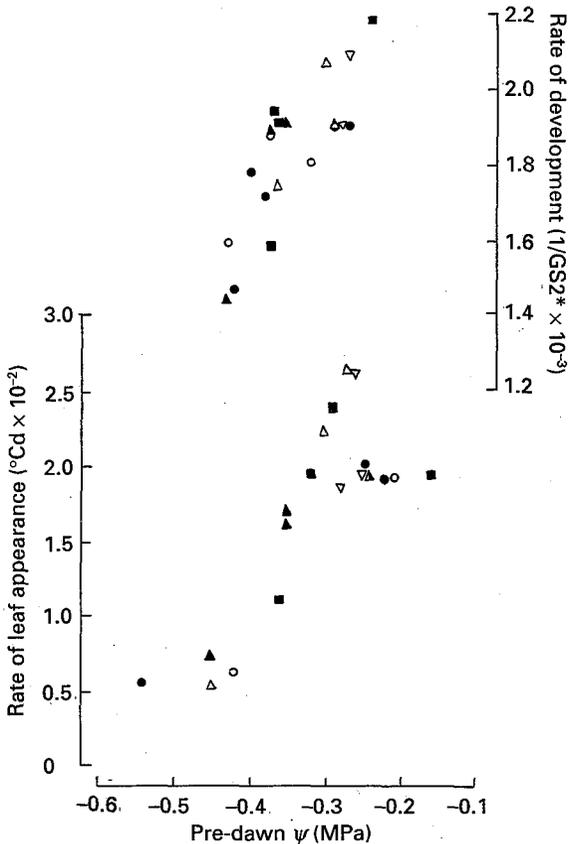


Fig. 4. Relation of (a) normalized rate of development adjusted for periods when development stopped ( $1/GS2^*$ ) and (b) normalized rate of leaf appearance to pre-dawn leaf water potential ( $\psi$ ) for IS 12739 (○), IS 12744 (●), IS 1347 (□), IS 13441 (▲), IS 22380 (▽), ICSV 213 (△), and ICSH 109IN (■).

leaf water potential values below the threshold values for development. Periods of zero development were therefore determined from plots of panicle development on accumulated temperature and these periods deducted from GS2 to give an adjusted GS2 ( $1/GS2^*$ , Table 4). Similarly, leaf water potential during these periods of zero development was ignored in calculating the mean value, that is, the relation between  $1/GS2^*$  and leaf water potential is for periods only when progress in development was occurring. Secondly,  $1/GS2^*$  varied between lines in the control treatment ( $1.46$  to  $2.26 \times 10^{-3}$ ; Table 4). Therefore  $1/GS2^*$  was normalized to give the same mean  $1/GS2^*$  in the control treatments ( $1.96 \times 10^{-3}$ ). The relation between rate of development and leaf water potential is also shown in Fig. 4.

Exponential and linear regressions fitted to all the data ( $n = 20$ ) adequately described the data:

$$y = 2.12 - 0.0079 \times 0.00004^x \quad r^2 = 0.65 \quad P < 0.001 \quad (4)$$

$$y = 2.78 + 2.77x \quad r^2 = 0.64 \quad P < 0.001 \quad (5)$$

but gave threshold leaf water potential values of  $-0.55$  and  $-1.00$  MPa, respectively. Linear regression analysis of the data when leaf water potential values were less than  $-0.30$  MPa ( $n=11$ ) gave:

$$y = 3.76 + 5.23x \quad r^2 = 0.74 \quad P < 0.01 \quad (6)$$

The threshold leaf water potential value for development from this analysis was  $-0.71$  MPa. This value is also shown in Fig. 3 by arrows and fits the data reasonably well. Thus it can be seen from Fig. 3 that in the late stress treatment in IS 12739 the threshold value was not reached until just before anthesis, and therefore panicle development did not cease in this treatment. In the early plus late stress treatment in IS 13441, stress was severe enough to delay panicle initiation, and it was only after leaf water potential values went above  $-0.71$  MPa that panicle initiation occurred.

## DISCUSSION

This paper shows that heat and drought stress can have considerable effects on panicle development in sorghum. These stresses can markedly delay panicle initiation (Whiteman and Wilson, 1965; Mahalakshmi and Bidinger, 1985a; Rees, 1986; Matthews *et al.*, 1990). Stress can also reduce the rate of panicle development (Whiteman and Wilson, 1965; Husain and Aspinall, 1970) and can cause the cessation of panicle development at any stage between panicle initiation and flowering. Upon relief of stress, panicle development resumes at rates comparable to those in the well watered control (Whiteman and Wilson, 1965). Both the rate of panicle development and leaf appearance respond in a similar manner to stress and are sensitive to changes in pre-dawn leaf water potential.

The effects of stress on PI require further investigation. Aspinall and Husain (1970) have shown in single cycle long and short day plants that stress can prevent flowering. Coaldrake and Pearson (1985, 1986) have shown in pearl millet that nitrogen deficiency can limit apex growth and panicle development. In all the early and late stress treatments, where PI was delayed by only 2–11 days, the number of expanded leaves at PI was constant (Table 3). This would suggest that stress affected induction in a quantitatively similar manner to its effect on leaf appearance. Whether this is a direct quantitative effect on induction or an indirect effect through the effects of stress on leaf and plant growth still needs to be determined. In the remaining lines and treatments, where PI occurred after more leaves had been initiated (Table 3), stress was severe enough to cause many leaves to become highly desiccated and fired. This may have delayed induction and/or translocation of a stimulus, and certainly would have limited assimilate availability until more leaves were expanded.

Once PI has occurred, rate of development when water and nutrients are not limiting is primarily a function of temperature (Fig. 3; Ong and Monteith, 1985; Roberts and Summerfield, 1987). The imposition of stress immediately reduces the rate of development (Husain and Aspinall, 1970), and in this experiment this was related to decreasing leaf water potential values. Indeed, panicle development ceased altogether when leaf water potential values reached  $-0.7$  MPa, irrespective of whether the apex was at an early or late stage of panicle development. This threshold value was lower (more negative) than that for leaf appearance and growth (Flower *et al.*, 1990), which both ceased at  $-0.55$  MPa, suggesting that development is less sensitive to leaf water potential than the appearance and growth of leaves. Munns *et al.* (1979) have shown that the apical meristem has a considerable capacity to maintain turgor at water potentials less than  $-0.5$  MPa, which might be expected to allow continued apical development after leaf appearance or growth ceased. However, the water potential of the youngest fully expanded leaf is not a direct measure of the water potential in the apical meristem, particularly when the meristem is small and still enclosed in the leaf sheaths (Barlow *et al.*, 1980), and therefore direct measurement of apical as well as leaf water potential values are required to confirm this.

These data also raise questions about whether the rates of leaf appearance and panicle development are responding to leaf water potential *per se* or, as seems more probable, responding to reductions in assimilate availability as growth rate is reduced (Coaldrake and Pearson, 1985, 1986). Equally, we need to know more about the response of leaf appearance, panicle development and growth to the fraction of extractable soil water. Using the general relation between pre-dawn leaf water potential and extractable soil water (ESW) it would appear that rates of development start to decline when approximately 70% of ESW has been used (that is, when the leaf water potential is less than  $-0.35$  MPa), which agrees with the data of Ritchie (1973) and Sinclair and Ludlow (1986). In the following paper we examine grain yield and harvest index of the same sorghum lines in relation to the timing of the stress.

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