

EFFECT OF HEAT AND DROUGHT STRESS ON SORGHUM (*SORGHUM BICOLOR*). II. GRAIN YIELD

By P. Q. CRAUFURD† and J. M. PEACOCK‡

*Cereals Program, International Crops Research Institute for the Semi-Arid Tropics
(ICRISAT), Patancheru, Andhra Pradesh 502 324, India*

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SUMMARY

Three early and four later flowering lines of sorghum were subjected to three drought stress treatments (early, late and early plus late stress) in the field during the dry season at Hyderabad in India. Mean diurnal temperature and evaporation rate were uniformly high throughout the experiment. The late and early plus late stress conditions were severe, while the early stress was mild.

Grain yield was affected by both the timing and the severity of the stress. The largest reduction (87%) in grain yield resulted from stress imposed during booting and flowering (late stress) in the early flowering lines; the same stress treatment on vegetative plants had no effect on grain yield. Increasing the duration of severe stress on vegetative plants (early plus late stress) reduced grain yield by 50–60%.

Grain yield was strongly and positively correlated with the number of grains m^{-2} . Variation in grain yield was associated with variation in total dry matter rather than with harvest index, which was only reduced when stress occurred at flowering. Treatment effects on thermal growth rates ($g\ m^{-2}\ ^\circ C d^{-1}$) during the phase from booting to flowering confirmed that growth during this phase is the major determinant of yield potential (number of grains). The importance of phenology in research into drought resistance is discussed.

Efecto del calor excesivo y la falta de agua en el sorgo

RESUMEN

Tres variedades tempranas y cuatro variedades tardías de sorgo con floración fueron sometidas en campo a tres tratamientos de falta de agua (temprano, tardío, y temprano y tardío) durante la estación seca en Hyderabad, India. La temperatura media diurna y el índice de evaporación presentaron cifras uniformemente elevadas durante todo el experimento. Las condiciones de falta de agua en el tratamiento tardío, y temprano más tardío, resultaron severas, mientras que las del tratamiento temprano fueron ligeras.

El rendimiento de grano se vio afectado tanto por el momento en que se produjo la falta de agua, como por la severidad de la misma. La mayor reducción (87%) en el rendimiento de grano fue el resultado de la falta de agua infligida durante el establecimiento y la floración (falta de agua tardía) en las variedades de florecimiento temprano, mientras que el mismo tratamiento aplicado a las plantas vegetativa no produjo efecto alguno en el rendimiento de grano. Una mayor duración del período de severa falta de agua en las plantas vegetativas (tratamiento temprano y tardío) redujo el rendimiento de grano en un 50–60%.

La variación del rendimiento de grano estuvo relacionada con la masa seca total, y no con el índice de cosecha, el cual sólo se redujo cuando la falta de agua se produjo durante el

floreCIMIENTO. Los efectos del tratamiento en los índices de crecimiento térmico ($\text{g m}^{-2} \text{ } ^\circ\text{Cd}^{-1}$) durante la fase del establecimiento hasta la floración confirmaron que el crecimiento durante esta fase constituye el mayor determinante de potencial de rendimiento (cantidad de grano). Se discute la importancia de la fenología en la investigación sobre la resistencia a la sequía.

INTRODUCTION

The timing of stress (for example, shortage of water and/or extremes of temperature) in relation to crop development has a significant effect on grain yield (Salter and Goode, 1967; Doorenbos and Kassam, 1979). In most cereals, stress experienced during the two weeks before flowering (booting) and during flowering reduces grain yield significantly more than stress either during vegetative and early reproductive growth or during grain filling (Lewis *et al.*, 1974; Mahalakshmi *et al.*, 1987). Grain yield is, nonetheless, usually proportional to total dry matter accumulation (Sinclair, 1988; Sinclair *et al.*, 1990); only when stress is severe (that is, when total dry matter is reduced by more than 50%) is harvest index also reduced.

Craufurd *et al.* (1993) have demonstrated that heat and drought stress in the pre-flowering phase can markedly delay panicle initiation and flowering in sorghum. Here, we describe the consequences for grain yield of such variation in phenology in relation to the timing of the stress, and examine the relation between growth and number of grains (yield potential). Breeding for drought resistance is discussed in relation to these data and the other findings reported in papers from the same experiment (Craufurd *et al.*, 1993; Flower *et al.*, 1990; Sivaramakrishnan *et al.*, 1988).

EXPERIMENTAL DETAILS

Full details of the experiment, including the design, treatments, sorghum lines, weather and recording of crop development, are given in Craufurd *et al.* (1993). Briefly, three early and four later flowering lines of sorghum (*Sorghum bicolor* (L.) Moench) were grown in the field during the dry season at Hyderabad in India and various stress treatments imposed (Table 1). Initially, there were three replicates of each of two treatments: a control, furrow irrigated every seven days, and a stress treatment, where irrigation was withheld from 20 days after sowing (DAS). However, since 30 mm of rain fell between 40 and 43 DAS, the experiment was subsequently modified, creating four instead of two treatments: a control; early stress (no irrigation 20–42 DAS); late stress (no irrigation 43–69 DAS); and an early plus late stress treatment (no irrigation 20–69 DAS). The early and late stress treatments were replicated twice but the control and early plus late stress treatments were unreplicated and could not therefore be analysed statistically.

Dry matter accumulation was measured every seven days from nine DAS until reproductive maturity in all lines, except in the case of IS 1347 where measurements did not start until 51 DAS. Six plants from each line were harvested from a fully guarded area in each plot. Measurement of above-ground dry matter

Table 1. Stage of panicle development at the end of the stress period in the early and later flowering lines (numerical stages of development (Craufurd *et al.*, 1993) in parentheses)

Line	Stress treatment		
	Early	Late	Early + late
	<i>Early flowering lines</i>		
IS 12739	Tertiary branch (6)	Flowering + 10 days	Spikelet initiation (8)
IS 12744	Tertiary branch (6)	Flowering	Spikelet initiation (8)
IS 1347	Stamen initiation (10)	Flowering + 17 days	Style initiation (14)
	<i>Later flowering lines</i>		
ICSH 109IN	Vegetative	Secondary branch (4)	Vegetative
ICSV 213	Vegetative	Secondary branch (4)	Vegetative
IS 13441	Vegetative	Spikelet initiation (8)	Vegetative
IS 22380	Vegetative	Panicle initiation (1)	Vegetative

included dead leaves that were attached to the plant. Polynomials were fitted to describe the relation between dry matter per plant and thermal time from sowing. (The calculation of thermal time is described in the previous paper, Craufurd *et al.*, 1993.) In all sorghum lines except IS 22380 values of r^2 were at least 90% and often greater than 95%. In IS 22380 the regression lines were fitted by eye. In IS 1347 dry matter prior to 51 DAS was assumed to be the same as in IS 12744; both these lines were early maturing and had similar total dry matter yields at maturity. The thermal growth rate (TGR, $\text{g plant}^{-1} \text{ }^\circ\text{Cd}^{-1}$) from 14 days before flowering until seven days after flowering was calculated from the fitted values. Values of TGR per plant were then multiplied by the number of plants m^{-2} to give TGR m^{-2} .

Grain yield at maturity and various yield components were determined from an area of 30 m^2 . The number of plants and panicles was first counted, and the total above-ground dry matter measured. After threshing, all the grain was oven dried at 80°C for 48 hours and weighed to give grain yield m^{-2} . Three sub-samples of 100 grains were weighed to determine the 100-grain mass. Harvest index (HI), the ratio of grain to total recoverable above-ground dry matter, and number of grains m^{-2} were derived by division.

RESULTS

Stage of panicle development during the stress periods

Plants were at various stages of panicle development during the periods of stress (Table 1), as a result of inherent differences in their relative time of flowering and the consequences of stress in retarding panicle development (Craufurd *et al.*, 1993). For example, stress occurred during flowering and early grain filling in the three early flowering lines (IS 12739, IS 12744 and IS 1347) in the late stress treatment. In contrast, plants of the later flowering lines (ICSH

Table 2. Total above-ground dry matter (TDM, $g\ m^{-2}$), grain yield (GY, $g\ m^{-2}$), harvest index (HI), number of panicles m^{-2} , number of grains panicle $^{-1}$ and grain wt (mg) in the control and stress treatments

Treatment	TDM	GY	HI	Panicle number	Grain number	Grain weight
<i>Early flowering lines</i>						
IS 12739						
Control	638	76	13	12	443	14.3
Early	776	94	12	13	492	14.7
Late	382	10	2	5	214	9.3
Early + late	190	36	19	6	276	21.7
IS 12744						
Control	774	53	7	12	311	14.2
Early	774	52	7	10	328	15.9
Late	453	1	0	2	77	9.0
Early + late	378	39	10	6.5	285	21.0
IS 1347						
Control	819	216	26	12	1000	18.0
Early	746	319	43	11	1421	20.4
Late	333	49	15	7.5	733	9.1
Early + late	438	53	12	4	716	18.5
Means						
Control	744	115	15	12	585	15.5
Early	765	155	20	11.3	747	17.0
Late	389	20	7	4.8	341	9.1
Early + late	335	43	14	5.5	426	20.4
<i>Later flowering lines</i>						
ICSH 109IN						
Control	1050	247	23	12.5	915	21.6
Early	1494	458	31	13.5	1682	20.2
Late	954	276	29	9	1411	21.7
Early + late	592	99	17	6.5	725	21.0
IS 13441						
Control	1292	162	12	14	548	21.1
Early	1324	197	15	10.5	745	25.0
Late	768	115	15	9	566	22.7
Early + late	947	48	5	11	216	20.2
ICSV 213						
Control	1243	120	10	10	538	22.3
Early	1940	254	14	13	955	19.9
Late	1106	118	10	9	673	18.6
Early + late	677	69	10	6.5	489	21.7
IS 22380						
Control	1730	151	9	12	546	23.1
Early	1296	35	3	7.5	238	19.1
Late	982	65	7	9.5	381	19.9
Early + late	592	54	9	7	295	26.4
Means						
Control	1329	170	13	12.2	637	22.0
Early	1513	236	16	12.3	905	21.0
Late	952	143	15.2	9	757	20.6
Early + late	702	67	10	8	431	22.3
SE†	81.2	25.3	1.9	1.2	98.8	0.93

†Standard error of mean for comparing early and late stress treatments.

109IN, IS 13441, IS 22380 and ICSV 213) remained vegetative throughout the early and early plus late stress treatments.

Grain yield in relation to the timing of stress

The effects of stress on total above-ground dry matter, grain yield, harvest index (HI) and components of yield are given in Table 2. Grain yields of IS 22380 were particularly variable. Two lines, IS 1347 and ICSH 109IN, had notably larger grain yields in the control treatment as a result of increased partition. Nonetheless, their response to stress was similar to that of other lines with the same time of flowering, so the means for each group are shown.

The overall effects of the timing and duration of stress on the early and later flowering lines are summarized in Table 3, omitting IS 22380 from the later flowering group means. The pre-dawn values of leaf water potential (ψ) (Craufurd *et al.*, 1993) indicate that the intensity of the early stress treatment was weak (values of ψ were greater than -0.35 MPa) and water was still available for transpiration. The intensity of stress in the late and early plus late stress treatments was severe (values of ψ were less than -0.6 MPa) and all the transpirable water was exhausted. It is therefore not surprising that grain yields were not reduced (in fact, they were increased) by the early stress treatment, especially as stress did not occur close to flowering (Table 1).

In the early flowering lines, the late stress treatment caused the largest reduction (87%) in grain yield (Table 3). In this treatment stress occurred during the phase from booting through flowering to early grain filling. The largest individual reduction in grain yield (98%) occurred in IS 12744, when stress terminated at flowering. The later stress was terminated relative to flowering, the correspondingly less severe were the reductions in grain yield (IS 12739 and IS 1347). In the early plus late stress treatment, which was of longer duration and equally severe, grain yield was only reduced by 52%. In this treatment plants were at an early to midway stage of reproductive development during the stress.

In the later flowering lines the late stress treatment occurred when plants were

Table 3. *The effect of stress on the mean grain yield (%) relative to the control and the time (d) that stress ended relative to flowering of the early and later flowering groups*

Stress treatment			Grain yield		Time stress ended	
Timing	Duration	Intensity	Early flowering	Later flowering	Early flowering	Later flowering
Early	23 days	Low	125	155	-15	-48
Late	23 days	Severe	13	111	+ 9	-31
Early + late	46 days	Severe	48	43	-17	-54

in the early stages of reproductive development and grain yield was not reduced. This response is in marked contrast to the effects of the late stress treatment on the early maturing lines. The longer duration early plus late stress treatment, which occurred when plants were still in a vegetative stage, reduced grain yield by 65%. This was similar to the yield reduction that occurred when the same treatment was imposed on the early maturing lines.

Grain yield, dry matter yield and thermal growth rate

The number of panicles m^{-2} and grains panicle $^{-1}$ were both reduced by the late and early plus late stress treatments (Table 2). Increases in the number of grains panicle $^{-1}$ compensated for fewer panicles m^{-2} to a limited extent. Grain size was only reduced in the early flowering lines subjected to the late stress treatment, that is, when stress occurred during grain filling. Over all lines and treatments, grain yield was strongly and positively correlated ($r^2 = 0.97$) with number of grains m^{-2} (Fig. 1). These data are consistent with findings published elsewhere (for example, Mahalakshmi *et al.*, 1987; Bidinger *et al.*, 1987a).

Stress markedly reduced total dry matter at maturity, and in some sorghum line and treatment combinations, HI was also reduced significantly (Table 2). The largest reduction in total dry matter occurred in the longest duration early plus late stress treatment. The most significant reduction in HI occurred in the early maturing lines where stress occurred during flowering. There was, however, no relation between relative reduction in total dry matter (%) and HI (see for example, IS 12744 and IS 12739 in the late and early plus late stress treatment). Indeed, partitioning was increased in the most severe conditions. Furthermore, there was no relation between individual plant size and HI, as Rees (1986) has reported from Botswana.

To examine further the relation between grain yield and growth (dry matter accumulation), the thermal growth rates (TGRs) during the phase of maximum reproductive growth, during booting and flowering, were calculated. The yield potential (number of grains) of several crops has already been correlated quantitatively with growth (or radiation interception) during this phase under conditions of adequate moisture and nutrient supply (Hawkins and Cooper, 1981; Ong and Squire, 1984; Craufurd and Bidinger, 1989). The relation between the number of grains m^{-2} and TGR for the sorghum lines in this experiment is presented in Fig. 2.

There was a strong and positive relation between number of grains m^{-2} and TGR for all lines except ICSV 213 ($r^2 = 0.36$). Thermal growth rates were in the range 1.77–10.24 $\text{g m}^{-2} \text{ }^\circ\text{Cd}^{-1}$, excluding ICSH 109IN where the number of grains m^{-2} was very high, possibly because of late tillering. These data support the concept that poor grain yields during and after water stress are due to slow growth rates during booting and flowering, caused by the general adverse effect of stress on dry matter accumulation. There was no evidence that grain yield was reduced as a result of stress occurring at a particular 'critical stage' during the period, such as microsporogenesis (Ogunlela and Eastin, 1984), even though

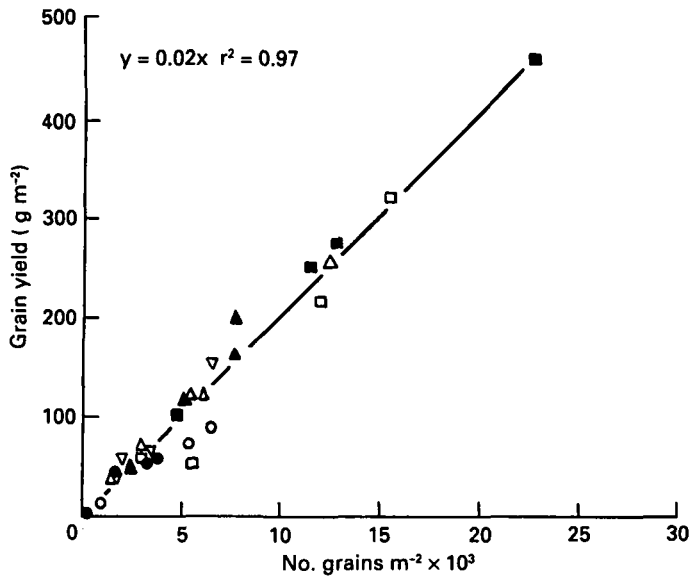


Fig. 1. Relation between grain yield and number of grains m^{-2} for sorghum lines IS 12739 (○), IS 12744 (●), IS 1347 (□), ICSH 109IN (■), IS 13441 (▲), ICSV 213 (△) and IS 22380 (▽).

temperatures were supra-optimal and leaf water potential was very low (Craufurd *et al.*, 1993). The larger yields observed following early stress can similarly be explained by more rapid growth rates during the booting and flowering phase, presumably because conditions for growth were more favourable later in the experiment and after the monsoon started (see Table 2 in Craufurd *et al.*, 1993 for

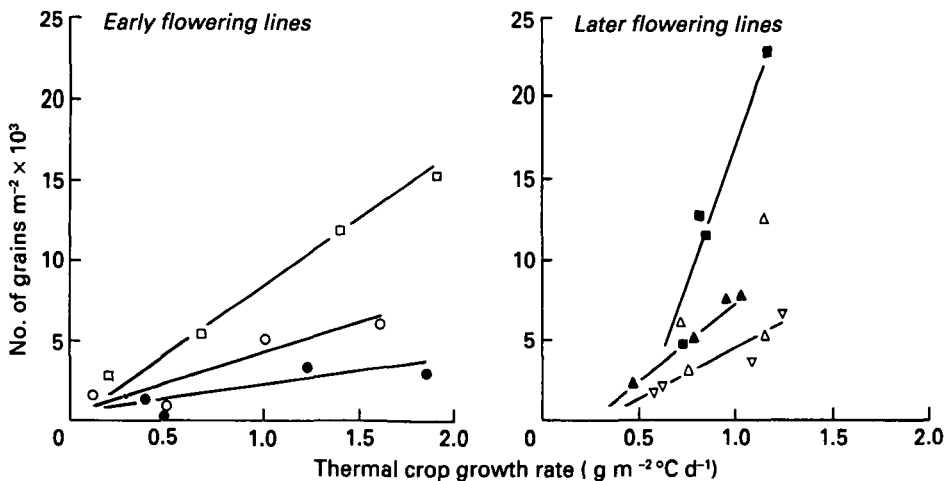


Fig. 2. Relation between number of grains m^{-2} and thermal growth rate for IS 12739 (○) $y = 0.43 + 3.70x$, $r^2 = 0.89$; IS 12744 (●) $y = 0.50 + 1.77x$, $r^2 = 0.58$; IS 1347 (□) $y = 8.37x$, $r^2 = 0.98$; ICSH 109IN (■) $y = -19.48 + 36.16x$, $r^2 = 0.94$; IS 13441 (▲) $y = -2.65 + 10.24x$, $r^2 = 0.97$; IS 22380 (▽) $y = -1.93 + 6.15x$, $r^2 = 0.87$.

climatic data). The greater yield potentials of IS 1347 and ICSH 109IN were associated with improved partitioning of dry matter to grain, rather than more rapid growth rates *per se*.

DISCUSSION

This and the previous paper (Craufurd *et al.*, 1993) demonstrate the importance of understanding the effect of stress on phenology and the relation between phenology and grain yield in cereals (Mohammad Saeed and Francis, 1983; Bidinger *et al.*, 1987a,b; Ludlow and Muchow, 1988). They also illustrate several common problems in physiological experiments intended to measure 'drought resistance'.

The effects of the timing of stress are similar to other published data on sorghum (Lewis *et al.*, 1974; Inuyama *et al.*, 1976) and millet (Mahalakshmi *et al.*, 1987). Other researchers have also shown that sorghum survives a severe stress best when still in the vegetative stage (Rees, 1986; Matthews *et al.*, 1990). This is probably related to plant size (small leaf area and consequently a slow rate of water loss) and the unique position and properties of the apical meristem (Barlow *et al.*, 1980), which has a high solute potential, can maintain turgor at much lower water potentials than leaves, and is protected from direct water loss within the leaf whorls.

Yield potential (number of grains) is strongly correlated with growth during reproductive development under conditions of adequate moisture and nutrient supply (Hawkins and Cooper, 1981; Ong and Squire, 1984). This paper illustrates that the same principle can be applied to yield potential and growth during the following drought stress. Further data are now needed to verify this principle, preferably for as many lines and as great a range of stress treatments as possible. Physiologists and breeders should therefore concentrate on selecting traits that maximize growth under stress, rather than worrying about stress effects on particular developmental events.

The importance of choosing cultivars with appropriate phenologies for specific environments is recognized (Ludlow and Muchow, 1988), for example, avoiding early maturing cultivars when mid-season stress is likely to occur. The adaptive value of developmental plasticity (that is, variation in the duration of the development period in response to stress), particularly for environments where the timing of the stress is unpredictable (and the season length is extended), is also recognized and clearly demonstrated in these papers. All the sorghum lines exhibited developmental plasticity in response to increasing values of leaf water potential (Craufurd *et al.*, 1993). Whether or not there is useful variation in this response in sorghum germplasm requires further investigation.

Physiologists often study landrace and other accessions rather than cultivars because these materials exhibit variation in traits of interest. The range of flowering times and yield potentials under optimum conditions of the 'resistant' and 'susceptible' lines under test in this experiment were large, but not atypical. A multiple regression of grain yield under stress against flowering time and yield in

the control gave r^2 values of 0.84, 0.50 (0.57 for flowering only) and 0.75 in the early, late and early plus late stress treatments, respectively. Thus, even among so few lines, a significant proportion of the variation in grain yield is accounted for by these two parameters alone. Given the importance of the timing of stress and the growth rate during flowering, it is difficult to make valid comparisons or to draw useful conclusions on the value of particular physiological traits in relation to grain yield. As others have argued elsewhere (Ludlow and Muchow, 1988; Richards, 1987), physiologists must collaborate with breeders to demonstrate genetic variability and heritability of traits, and evaluate those traits in as similar a genetic background as possible in order to remove the confounding effects of phenology and inherent yield potential.

These papers, and others from the same experiment on the role of osmotic adjustment (Flower *et al.*, 1990) and proline accumulation (Sivaramakrishnan *et al.*, 1988), also demonstrate the importance of a quantitative assessment of drought intensity, and of relating the effects of measured traits to productivity. For example, we were able to demonstrate that rate of development and leaf appearance slowed in response to falling values of leaf water potential (Craufurd *et al.*, 1993). Similarly, Flower *et al.* (1990) found differences in osmotic adjustment between 'resistant' and 'susceptible' lines, but were able to demonstrate that this trait did not contribute to increased productivity; all lines stopped leaf growth when their leaf water potential reached the same critical value.

In conclusion, we emphasize again the primary importance of understanding the role of phenology, particularly in relation to stress (water and temperature), in adapting sorghum (and other crops) to harsh environments. The contribution of other physiological traits to grain yield must then be evaluated in suitably matched material, but research on these topics should be secondary to research into identifying appropriate phenologies for different production environments.

REFERENCES

- Barlow, E. W. R., Munns, R. E. & Brady, C. J. (1980). Drought responses of apical meristems. In *Adaptation of Plants to Water and High Temperature Stress*, 191–206 (Eds N. C. Turner and P. S. Kramer). New York: John Wiley.
- Bidinger, F. R., Mahalakshmi, V. & Rao, G. D. P. (1987a). Assessment of drought resistance in pearl millet (*Pennisetum americanum* [L.]Leeke). 1. Factors affecting yields under stress. *Australian Journal of Agricultural Research* 38:37–48.
- Bidinger, F. R., Mahalakshmi, V. & Rao, G. D. P. (1987b). Assessment of drought resistance in pearl millet (*Pennisetum americanum* [L.]Leeke). 2. Estimation of genotype resistance to stress. *Australian Journal of Agricultural Research* 38:49–59.
- Craufurd, P. Q. & Bidinger, F. R. (1989). Potential and realized yield in pearl millet (*Pennisetum americanum*) as influenced by plant population density and life-cycle duration. *Field Crops Research* 22:221–225.
- Craufurd, P. Q., Flower, D. J. & Peacock, J. M. (1993). Effect of heat and drought stress on sorghum (*Sorghum bicolor* L. Moench). I. Panicle development and leaf appearance. *Experimental Agriculture* 29:61–76.
- Doorenbos, J. & Kassam, A. H. (1979). Yield response to water. *FAO Irrigation and Drainage Paper No. 33*. Rome: FAO.

- Flower, D. J., Usha Rani, A. & Peacock, J. M. (1990). Influence of osmotic adjustment on the growth, stomatal conductance and light interception of contrasting sorghum lines in a harsh environment. *Australian Journal of Plant Physiology* 17:91–105.
- Hawkins, R. C. & Cooper, P. J. M. (1981). Growth, development and grain yield of maize. *Experimental Agriculture* 17:203–207.
- Inuyama, S., Musick, J. T. & Dusek, D. A. (1976). Effect of plant water deficits at various growth stages on growth and grain yield and leaf water potential of irrigated grain sorghum. *Proceedings of the Crop Science Society of Japan* 45:298–307.
- Lewis, R. B., Hiler, E. A. & Jordan, W. R. (1974). Susceptibility of grain sorghum to water deficit at three growth stages. *Agronomy Journal* 66:589–591.
- Ludlow, M. M. & Muchow, R. C. (1988). Critical evaluation of the possibilities for modifying crops for high production per unit precipitation. In *Drought Research Priorities for the Dryland Tropics*, 179–211 (Eds F. R. Bidinger and C. Johansen). Patancheru, India: International Crops Research Institute for the Semi-Arid Tropics.
- Mahalakshmi, V., Bidinger, F. R. & Raju, D. S. (1987). Effect of timing of water deficit on pearl millet (*Pennisetum americanum*). *Field Crops Research* 15:327–339.
- Matthews, R. B., Reddy, D. M., Rani, A. U., Azam-Ali, S. N. & Peacock, J. M. (1990). Response of four sorghum lines to mid-season drought. I. Growth, water use and yield. *Field Crops Research* 25:279–296.
- Mohammad Saeed & Francis, C. A. (1983). Yield stability in relation to maturity in grain sorghum. *Crop Science* 23:683–687.
- Ogunlela, V. B. & Eastin, J. D. (1984). Effect of elevated night temperature during panicle development on sorghum (*Sorghum bicolor* L.) yield components. *Cereal Research Communications* 12:245–251.
- Ong, C. K. & Squire, G. R. (1984). Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.). VII. Final number of spikelets and grains. *Journal of Experimental Botany* 35:1233–1240.
- Rees, D. J. (1986). Crop growth, development and yield in semi-arid conditions in Botswana. I. The effects of population density and row spacing on *Sorghum bicolor*. *Experimental Agriculture* 22:153–167.
- Richards, R. A. (1987). Physiology and breeding of winter-grown cereals for dry areas. In *Drought Tolerance in Winter Cereals*, 133–149 (Eds J. P. Srivastava, E. Porceddu, E. Acevedo and S. Varma). Chichester, UK: John Wiley.
- Salter, P. J. & Goode, J. E. (1967). *Crop Response to Water at Different Stages of Growth*. UK: Commonwealth Agricultural Bureau.
- Sinclair, T. R. (1988). Selecting crops and cropping systems for water-limited environments. In *Drought Research Priorities for the Dryland Tropics*, 87–94 (Eds F. R. Bidinger and C. Johansen). Patancheru, India: International Crops Research Institute for the Semi-Arid Tropics.
- Sinclair, T. R., Bennett, J. M. & Muchow, R. C. (1990). Relative sensitivity of grain yield and biomass accumulation to drought in field grown maize. *Crop Science* 30:690–693.
- Sivaramakrishnan, S., Patell, V. Z., Flower, D. J. & Peacock, J. M. (1988). Proline accumulation and nitrate reductase activity in contrasting sorghum lines during mid-season drought stress. *Physiologia Plantarum* 74:418–426.