Studies on water deficits on apical development and panicle initiation of grain sorghum (*Sorghum bicolor* L. Moench) in controlled temperature glasshouse conditions

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SUMMARY

Controlled temperature glasshouse experiments were performed to determine the influence of water deficits, imposed during the period between seedling emergence and panicle initiation, on leaf primordium production, apex growth, and panicle initiation of grain sorghum (*Sorghum bicolor* L. Moench). The consequence of these water deficits on the duration of subsequent growth stages as well as grain yield was examined after transferring plants to an ordinary glasshouse at panicle initiation. Leaf primordium production was severely inhibited by periods of water deficit, with apparent cessation occurring around a dawn water potential of -1.0 MPa. Panicle initiation was delayed according to the duration of water deficit and the period of cessation of leaf primordium production. The duration of growth stages two and three were not altered appreciably by the treatments. Panicle initiation occurred earlier when plants were grown in 25/20 and 30/25 °C than in 20/15 and 35/30 °C day/night temperature regimens. Higher grain yields were obtained for plants previously grown at 20/15 and 35/30 °C compared with those grown at 25/20 and 30/25 °C.

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RÉSUMÉ

J. A. ADJETEY & G. L. WILSON: *Les études sur les deficits d'eau sur le developpement spical et l'initiation de panicle de sorgho grain* (Sorghum bicolor L. Moench dans les conditions de température contrôleé en sone.Des expériences ont été menées en serre dans les conditions de température controllée, pour déterminer l'inflence du déficit hydrique qui s'impose pendant la période entre la levée et le début épiaison, sur la production de jeune feuilles, sur la croissance apicale, et sur la grainaison du sorgho (*Sorghum bicolor* L. Moench). Les effects de ce déficit hydrique sur la durée des stades consécutifs de croissance ainsi que l'effect sur le rendement en grains ont été examiné après avoir transferé les plantes dans une serre ordinarie au moment du début d'épiaison. La production de jeunes feuilles est sévèrement affectée pendant les périodes de déficit en eau, se manifestant par un arrêt apparent au environ d'un potential hydrique de - 1.0 MPa de feuilles prélevées à l'aube. L'épiaison est retardée en fonction de la durée du déficit en eau, et la période de l'arrêt de production de jeunes feuilles. La durée du deuxième stade de croissance et du troisième stade de croissance n'a pas été aaffectée de façon significative par les traitements. Le début d'épiaison intervient plus tôt dans les régimes à 25/20 et 30/25 °C que dans ceux à 20/15 et 35/30 °C. Il en résulte un rendement en grains supérieur pour celles plantes au régime 20/15 et 35/30 °C comparé à celles qui ont été soumises aux régime à 20/15 et 30/25 °C.

Introduction

Although grain sorghum (*Sorghum bicolor* L. Moench) is able to withstand spells of drought at different stages of growth (Jordan & Miller, 1980), it can suffer significant yield losses as a result of severe moisture deficit at the booting and grain-filling stages (Lewis, Hiler & Jordan, 1974). The effect of water deficits on the development of grain

sorghum and other cereals has been largely studied for the following periods: after panicle initiation; between panicle initiation and anthesis, i.e. growth stage two (GSII) when potential grain number is determined (Donatelli, Hammer & Vanderlip, 1992); and between anthesis and grain yield, i.e. growth stage three (GSIII) when kernel weight is determined. There has been little study of the period between seedling emergence and panicle initiation, i.e. growth stage one (GSI), although any influence of water deficit on leaf number in particular and plant size in general, as well as size of the reproductive apex, may be important in determining grain yield. Also, the scanty report available on this growth stage (Whiteman & Wilson, 1965) apparently lacks clear descriptions, in terms adequate by contemporary standards, of the degree of water deficits imposed.

Plant responses to various treatments are subject to changes in environmental conditions. It is, therefore, important to examine the responses during GSI under a wider set of conditions in which an environmental factor like temperature can be varied. Temperature has a strong, independent effect on GSI (Doggett, 1970; Wilson & Diczbalis, 1982), as does rate of development of water deficits in general (Bassetti & Westgate, 1993).

The objectives of the study were as follows: (1) to describe the morphological changes that take place at the shoot apex under severe water deficits during GSI, and how these affect panicle initiation and the duration of subsequent growth stages; and (2) to examine the response of sorghum to water deficits during GSI when grown under varying temperatures, and also determine the consequences of these treatments on grain yield and some yield components after transferring plants to an ordinary glasshouse at panicle initiation and growing them to maturity under well-watered conditions.

Materials and methods

The study comprised three glasshouse experiments carried out using soils from the University of Queensland Redland Bay Research Farm which contain a red loam (Kraznozem) with 60 per cent clay, 15 per cent silt, and 25 per cent sand. Field capacity and wilting point water contents, determined by the pressure plate technique (Black, 1965), were 37.7 and 19.0 per cent, respectively. The available moisture content was 18.7 per cent.

Experiment 1

Plants were grown in 10-*l* plastic pots of 25 cm diameter. Calculated volumes of water were added to known weights of air-dried soil and thoroughly mixed in a rotating concrete mixer. The initial soil water potential was - 0.8 MPa (GWC ≈ 22 per cent) for all drying treatments. Seedlings were raised in 100-ml plastic pots, half-filled with a mixture of 50 per cent peat, 50 per cent coarse sand, and a complete nutrient solution. Seven days after sowing, five seedlings were transferred to each 10-*l* pot with intact roots in the potting mix. Plants were grown in a controlled temperature glasshouse with day/night temperatures of 25/ 20 °C under a 14-h photoperiod.

The experiment was factorial combination of five hybrids and four watering regimens laid in a randomized complete block design with three replicates. Each treatment within a replicate comprised five 10-*l* pots and hence the experimental setup consisted of 60 pots. Each treatment had 25 sample plants per replicate. The watering treatments consisted of well-watered controls starting from field capacity and droughted treatments with an initial soil water potential of - 0.8 MPa (GWC ≈ 22 per cent). Watering was withheld for 8, 14, and 21 days in the droughted treatments, bringing plants to water potentials of about, -1.0, -1.5, and -2.2 MPa, respectively, and designated as T1, T2, and T3. Plants were rewatered at 2-3-day intervals on reaching the respective water potentials until panicle initiation occurred in each treatment. The cultivars used were TX610 SR, Dorado A, DK 38, Gunsynd, and Pacific 610. The soil surface of each pot was covered with white polyethylene beads to a depth of 2 cm to minimize evaporation. Dawn leaf water potential of the youngest fully expanded leaf was measured at 2-day intervals using a pressure cham-

ber. Stomatal resistance of the leaf was recorded near noon, 11 days from the start of treatments using a LI-COR, Inc. LI-1600 steady state porometer.

Fresh plant samples were collected at 2-3-day intervals commencing 20 days from sowing and dissected under a binocular microscope with magnification up to 40 × using a mounted needle and scalpel. Panicle initiation was judged to have occurred when the apical meristem elongated, becoming dome-shaped, with the appearance of first protuberances representing the primary branch primordia (Lee, Lommasson & Eastin, 1974).

Experiment 2

This experiment focussed on the responses of leaf primordium formation and apex elongation to water deficits. Only one cultivar (TX610 SR) was used to allow a more critical examination. Plant culture and treatments were similar to those of Experiment 1. An additional treatment (T4) in which plants were growth on soil which was initially at field capacity and without further watering over the duration of GSI was included. Plants were dissected under a binocular microscope and records of the total number of leaf primordia were kept. The length of the stem apex was measured on each sampling occasion using a calibrated eye-piece. After panicle initiation, plants were transferred to a normal glasshouse and allowed to grow to maturity with adequate water supply. The times to anthesis and maturity were recorded.

Experiment 3

Seedlings of the cultivar TX610 SR were raised under 30/25 °C conditions for 7 days for uniformity and then transferred into controlled temperature glasshouse of 20/15, 25/20, 30/25, and 35/30 °C day/night temperatures. Four watering regimens consisting of a well-watered control plus three drying treatments in which plants were rewatered when the water potential of the youngest fully-expanded leaf dropped to between -1.0 and -1.3, -1.35 and -1.55, and -2.6 and -3.3 MPa, respectively, were superimposed. Due to the fixed nature of the glasshouses, the watering treatments were randomized within each temperature regimen. All treatments were replicated three times, with five pots per treatment per replicate and five plants per pot. Data were analyzed as a split plot design with temperature as main plot effect and watering treatments as subplot treatments.

Dawn water potential was recorded at 2-3-day intervals. Twenty days from sowing, plant samples were harvested at 2-3-day intervals and dissected for visual observation of the apex, for evidence of panicle initiation. Panicle length was recorded at initiation. Plants were transferred at panicle initiation to an ordinary glasshouse, watered every other day and allowed to grow to maturity, keeping only one plant per pot. Data on grain yield and yield components were collected.

Results and discussion

Experiment 1

The response of leaf water potential to the water deficit treatments was similar across hybrids in Experiment 1. Also, the variation in dawn water potential was similar for Experiments 1 and 2; hence, only a representative set of data for the hybrid TX610 SR is presented (Fig. 1). At the start of the treatments, dawn leaf water potential was high, reflecting the well-watered condition of the plants. When plants were transferred to soil of low water

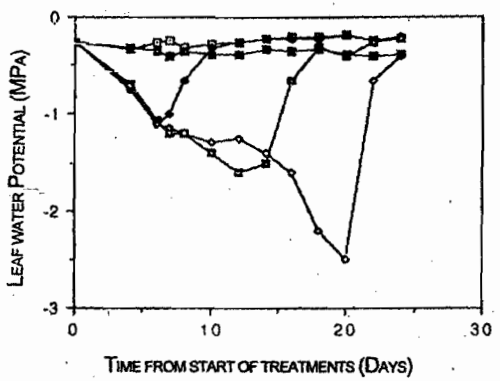

Fig. 1. Variations in dawn leaf water potential of sorghum grown under five watering regimes—□— control; —◆— T1; —□— T2; —◇— T3; —■— T4.

potential, the leaf water potential declined rapidly. After reaching -1.0 MPa, however, the rate of fall in plant water potential declined to values between a third and half that of the 1st week's. Plants were, therefore, adjusting to slow down the rate of water loss most probably by stomatal closure; hence, the high stomatal resistances (22 - 30 sec cm^{-1}) recorded near noon on the 11th day of treatments. After 14 days of drying, the leaf water potential of T3 declined very rapidly. On being rewatered, plants in all the droughted treatments recovered fully within 3 days with leaf water potential similar to the control treatment.

TABLE 1

Effect of Water Deficits on Time to Panicle Initiation in Five Early-maturing Sorghum Hybrids

Hybrid	*Time from sowing to panicle initiation (days)*			
	Control	*T1*	*T2*	*T3*
TX610 SR	26 (±0.33)	28 (±1.15)	33 (±0.00)	37 (±0.33)
Gunsynd	25 (0.00)	26 (±0.33)	33 (0.00)	36 (±0.33)
Pacific 710	26 (0.00)	29 (±1.00)	33 (±0.33)	39 (±0.33)
DK 38	24 (±0.33)	27 (0.00)	38 (±0.33)	NA
Dorado A	29 (0.00)	32 (0.00)	36 (±1.00)	40 (0.00)

Standard error of means shown in brackets.
T1: stressed to - 1.0 MPa, T2: stressed to - 1.5 MPa, T3: stressed to - 2.2 MPa.

Panicle initiation occurred earliest in the control treatments in all the hybrids (Table 1). The droughted treatments initiated panicles later, in times related to the durations of the water deficits imposed. Similar observations of inhibition of panicle initiation in grain sorghum have been reported by Whiteman & Wilson (1965).

Experiment 2

There were five leaf primordia at seedling emergence (Fig. 2). This number agrees with the reported presence of several embryonic leaves in cereals (Abbe & Phinney, 1951; House, 1980). After seedling emergence, primordium production in control plants occurred in a uniform fashion with an average plastochron of 2.5 until panicle initiation, when further leaf initiation ceased. House (1980) reported that about 4 to 5 days are required to lay down a leaf in the meristematic apex of grain sorghum, a time nearly double that observed in this study. The difference between that report and this study is attributed to the differences in cultivar and growing conditions. All treatments had similar leaf numbers at 4 days after the commencement of stress, although the controls and the slow-drying treatment (T4) had reached a dawn water potential of -0.25 and -0.33 MPa, respectively, in comparison with -0.60 MPa for the other drying treatments. It is, therefore, suggested that the water potential attained by the apex during the day, at this point in the drying cycle, was higher than the leaf water potential because of anatomical protection offered to the apex by the newly developing leaves or sheath of older leaves against evaporative water loss; hence, the apical water status was not inhibitory to leaf primordium production.

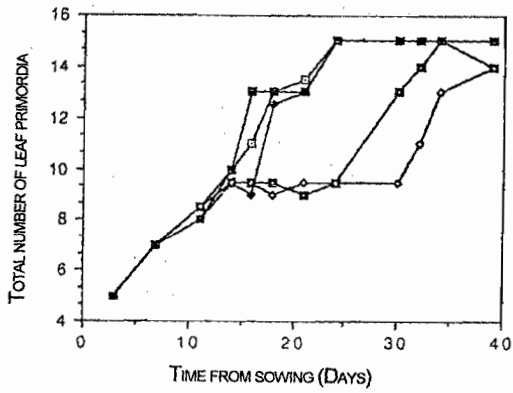

Fig. 2. Effect of five moisture regimens on time course of leaf primordium initiation. —□— control; —◆— T1; —□— T2; —◇— T3; —■— T4.

Attempts to measure the differences between leaf and apex water potentials using a thermocouple psychrometer failed, as the values obtained suggested a dehydration of the apical samples in the psychrometer chamber possibly due to a large chamber volume compared with apex sizes. Also, it has been reported that the apex is a strong sink, allowing for orderly accumulation of photosyn-

thates during water deficit. This enables osmotic adjustment to occur, resulting in the maintenance of turgor (Munns, Brady & Barlow, 1979; Barlow, Munns & Brady, 1980). Cessation of primordium initiation occurred when plants attained a leaf water potential of -1.0 MPa, and scope for resumption was lacking until plants were rewatered. As no reliable data were obtained for apex water potential, the exact apex water status at which initiation ceased could not be determined, but it occurred around a leaf water potential of -1.0 MPa.

The pattern of leaf primordium production with varying plant water status has been interpreted with dawn water potential values. These values are the daily maxima, and during the day, they fall to values which depend on the evaporative conditions. Certainly, the plants must respond to potentials other than the maximum which is reached in the cycle, but this study does not address whether it is the mean value, the low extreme, or some aspect of water potential below a critical value. The dawn value is one reliable point in this cycle, approximating to soil water potential, which does not immediately vary with environmental fluctuations; hence, its use in this study.

The ability of the apex to resume primordium production is dependent on the duration and degree of water deficits imposed. However, once primordium production has resumed, it proceeds at a slightly higher rate than the control treatments. Although plants in T3 reached a dawn leaf water potential of -2.6 MPa, as compared to -1.5 MPa for T2, the recovery pattern of plants in the two treatments was similar.

The difference in total leaf numbers among treatments was small, and this shows that upon the relief of early water deficits, plants would recover and be reproductive without necessarily attaining the same numbers observed for well-watered controls. Thus, the ultimate leaf number attained before panicle initiation is not critical in determining the time to initiation.

The treatments had no influence on apex length within the 1st week of stress (Fig. 3). This response is similar to that of leaf primordia production to the plant water status, and so are the explanations underlying them. As water deficits progressed and reached -1.0 MPa or lower, apex length did not increase until plants were rewatered. Control plants

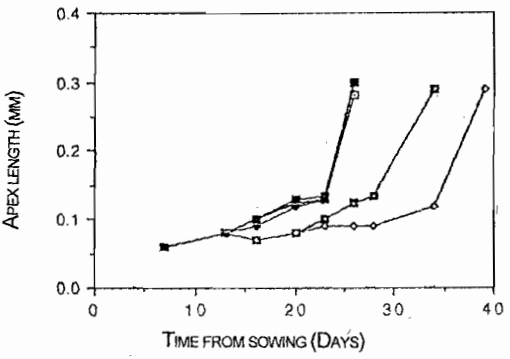

Fig. 3. Effect of moisture regimen on growth of apex. —□— control; —◆— T1; —□— T2; —◇— T3; —■— T4.

and those of T4 continued elongating at comparable rates until panicle initiation, indicating that the lowest level of water deficit reached in T4 could not inhibit the process.

The increase in panicle length in the control and T4 was small until 26 days from sowing, followed by a sudden and rapid increase in size which coincided with the time of panicle initiation. The transition from the vegetative to reproductive phase is reportedly characterized by marked increases in size of apices (Goldsworth, 1970; Lee, Lommasson & Eastin, 1974; Moncur, 1981). No differences in apex lengths were observed at initiation among treatments, indicating that apices recovered fully from the deficits imposed.

As in Experiment 1, time to panicle initiation was substantially delayed according to the duration of the water deficits (Table 2). Morphological development at the apex, judged by leaf primordium initiation, was delayed for 1, 8 and 14 days in T1, T2 and T3, respectively, and panicle initiation was also delayed by similar times. This suggests a closer dependence of time to panicle initiation on the cessation of morphological development at the

TABLE 2

Effect of Water Deficits on Leaf Primordium Formation and Panicle Initiation of Grain Sorghum

Treatment	Days			
	Cessation of leaf primordium initiation	*Time from sowing to last primordium initiation*	*Time from sowing to panicle initiation*	*Delay in initiation*
T1	1	24	27	2
T2	8	31	34	9
T3	14	36	39	14
T4	NA	23	26	1
Control	NA	23	25	NA
LSD (5 %)		0.8	1.2	

T1: stressed to - 1.0 MPa, T2: stressed to - 1.5 MPa, T3: stressed to - 2.6 MPa, T4: lowest water potential was - 0.45 MPa.

TABLE 3

Effect of Water Deficits during GSI on the Duration of GSII, GSIII, Times from Sowing to Anthesis and Maturity of Grain Sorghum

Treatment	Days			
	Duration of GSII	*Duration of GSIII*	*Time from sowing to anthesis*	*Time from sowing to maturity*
T1	30	33	57	90
T2	29	32	63	95
T3	28	32	67	99
T4	31	35	57	92
Control	32	33	56	90
LSD (5 %)	4.2	3.8	2.2	3.5

T1: stressed to - 1.0 MPa, T2: stressed to - 1.5 MPa, T3: stressed to - 2.6 MPa, T4: lowest water potential was 0.45 MPa.

apex rather than on the whole period when water deficits were imposed. The suspension of leaf primordium production positively indicates cessation of progress to panicle initiation.

The difference between the drier treatments and the control plants in durations of GSII and GSIII was not significant (Table 3). Thus, for practical purposes, the durations of these growth stages were unaltered by water deficits during GSI. Consequently, the times to anthesis and maturity were prolonged according to the duration of water deficits during GSI.

Experiment 3

Control plants maintained the highest leaf water potentials throughout the study (Fig. 4). However, those in the highest temperature regimen were marginally lower due to the high vapour pressure deficit associated with high temperatures. In the treatments subjected to water deficits, the pattern of plant response to soil water was similar to those in Experiments 1 and 2. In general, however, the rate of decline in leaf water potential was faster at the highest temperature.

Panicle initiation was delayed according to the duration of water deficits at all temperatures (Table 4), suggesting that the results of Experiments 1 and 2 were not unique to the temperature that was adopted. Plants grown in the 25/20 and 30/25 °C regimens initiated panicles earlier than those in the 20/15 and 35/30 °C regimens. The effect of temperature on panicle initiation has been documented (Wilson & Diczbalis, 1982; Cao & Moss, 1989).

Total leaf number at panicle initiation was significantly higher ($P<0.05$) in the 35/30 °C temperature regimen, irrespective of level of water deficits (Table 5). In the lowest (20/15 °C) and highest (35/30 °C) temperature regimens, apparent differences were lacking between dehydrated and control plants. In the 25/20 and 30/25 °C temperature regimens, however, the differences between severely dehydrated and control plants were small. Differences in leaf numbers among treatments are attributed to variations in rate of leaf initiation among temperatures. The differences in leaf numbers caused by both differences in temperature and water treatments suggest that leaf number is not critical to panicle initiation. Leaf numbers were not altered as much by water deficits during GSI as by variations in temperature.

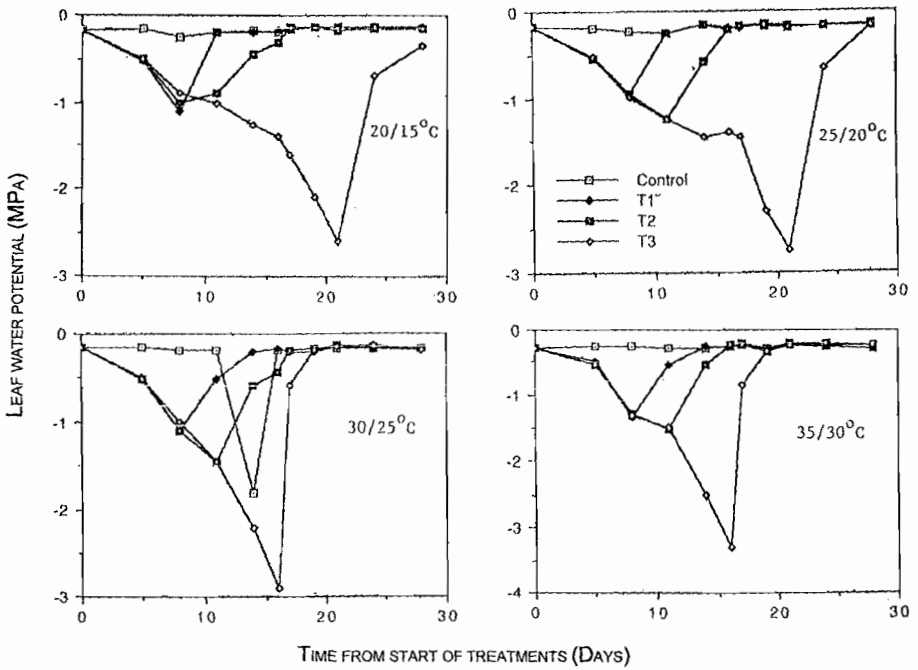

Fig. 4. Variations in dawn leaf water potential with time under different temperature regimens.
—□— Control; —◆— T1; —□— T2;—◇— T3.

TABLE 4

Effect of Water Deficits on Time to Panicle Initiation under Four Temperature Regimens

Treatment	*Time from sowing to panicle initiation (days)*				*Watering mean*
	20/15 °C	*25/20 °C*	*30/25 °C*	*35/30 °C*	
T1	36	29	28	37	32.5[x]
T2	37	33	30	38	34.5[y]
T3	46	37	33	40	39.0[z]
Control	34	28	27	35	31.0[y]
Temperature means	38.3[c]	31.8[b]	29.5[a]	37.5[c]	

Temperature and watering means with identical letters are not significantly different ($P<0.05$).
T1: stressed between -1.0 and -1.30 MPa, T2: stressed between -1.35 and -1.55 MPa, T3: stressed between -2.60 and -3.33 MPa.

TABLE 5

Effect of Water Deficits on Total Leaf Number under Four Temperature Regimens

Treatment	*Number of leaves*				*Watering mean*
	20/15 °C	*25/20 °C*	*30/25 °C*	*35/30 °C*	
T1	14.0	13.0	14.7	20.3	15.5[y]
T2	14.5	13.0	13.7	20.3	15.4[y]
T3	13.8	12.0	13.0	21.0	15.0[y]
Control	14.0	13.0	15.0	20.3	15.6[y]
Temperature means	14.1[b]	12.8[a]	14.1[b]	20.5[c]	

Temperature and watering means with identical letters are not significantly different ($P<0.05$).
T1: stressed between -1.0 and -1.30 MPa, T2: stressed between -1.35 and -1.55 MPa, T3: stressed between -2.60 and -3.33 MPa.

Grain yield and yield components

There were no significant differences in grain yield between control plants and those that experienced various levels of severe water deficits down to -3.33 MPa during GSI (Table 6). This is due to the inability of water deficits to cause very pronounced shifts in leaf numbers, hence leaf area at anthesis, of the kind induced by temperatures prior to panicle initiation. Thus, any effect of water deficit during GSI is of little importance for grain yield development than corresponding deficits on other growth stages. For example, Lewis, Hiler & Jordan (1974) reported 10-34 per cent reduction in yield when water deficit occurred near booting or milk to soft dough stage. Also, in maize, water deficits inhibit silk growth (Westgate & Boyer, 1986) and decrease kernel set (Schoper *et al.*, 1987; Schussler & Westgate, 1991; Bassétti & Westgate, 1993).

On the other hand, large yield differences ($P<0.05$) were observed between temperatures, with the lowest yield occurring in the 25/20 °C temperature regimen and highest in the 35/30 °C temperature regimen. These differences were attributed to differences in leaf area (Table 6) arising from the large differences in leaf number. Generally, grain yield in determinate crops like sorghum and maize has been reported to be directly related to leaf area at anthesis (Fisher & Wilson, 1971), with most post anthesis assimilate translocated into grain filling.

Water deficit pre-treatments had no visible influence on panicle length at initiation or maturity. Similarly, no influence on primary branches, grain numbers or grain size was observed among watering treatments. This observation strengthens earlier assertion that any detrimental influence of water deficits during GSI is only transitory if a subsequent period of adequate watering is maintained.

Unlike water deficits during GSI, temperature treatments altered some of the above components. Plants in the 20/15 and 35/30 °C temperature regimens had higher grain numbers and grain weights compared with the 25/20 and 30/25 °C temperature regimens due to high leaf areas. A possible reason for the high grain number especially at the highest temperature is the high number of primary branches and hence, an increase in the potential grain sites in the inflorescence. Whether this high number of primary branches at 35/30 °C temperature regimen is due to an enhanced panicle development at initiation is unclear as plants in the 20/15 °C which had a similar duration of GSI had less number of primary branches.

TABLE 6

Effect of Water Deficit and Temperature during GSI on Grain Yield, Leaf Area and Infloresence Characteristics of Grain Sorghum

Parameter	*Temperature regimen*				*Watering treatment*				
	20/15 °C	*25/20 °C*	*30/25 °C*	*35/30 °C*	*T1*	*T2*	*T3*	*Control*	
Grain weight per plant (g)	*64.2 c*	*39.9 a*	*48.5 b*	*81.3 b*	*59.8*	*57.6*	*56.9*	*59.78*	*(NS)*
Leaf area per plant (cm²)	*1876 c*	*1183 a*	*1483 b*	*3522 d*	*2094 y*	*1912 x*	*1883 x*	*2164 y*	
Kernel weight (mg)	*30.0 b*	*23.9 a*	*25.6 a*	*30.1 b*	*27.5*	*27.9*	*27.1*	*27.1*	*(NS)*
Grain number per plant	*2140 c*	*1674 a*	*1899 b*	*2711 d*	*2152*	*2029*	*2064*	*2178*	*(NS)*
Number of primary branches	*52.2 b*	*49.4 a*	*52.5 b*	*60.4 c*	*52.3*	*53.1*	*55.8*	*53.3*	*(NS)*
Panicle length at initiation (mm)	*0.265*	*0.275*	*0.265*	*0.288 (NS)*	*0.269*	*0.271*	*0.279*	*0.273*	*(NS)*
Panicle length at maturity (cm)	*23.3*	*23.0*	*23.7*	*24.1 (NS)*	*23.8*	*23.4*	*23.5*	*23.3*	*(NS)*

For either temperature or watering means, treatments with identical letters within a row are not significantly different ($P<0.05$). NS = Not significantly different at $P = 0.05$.

T1: stressed between -1.0 and -1.30 MPa, T2: stressed between -1.35 and -1.55 MPa,

T3: stressed between -2.60 and -3.33 MPa.

Conclusion

Results of this study and other reports on other growth stages suggest that water deficit during GSI is only important in inhibiting both apex elongation and leaf primordium production, and this causes a delay in panicle initiation. The knowledge that GSI is less susceptible to water deficits than corresponding deficits during other growth stages can be incorporated into irrigation timing, particularly in situations of limited water supply. When plants have established as at the start of treatments in this study, they could be allowed to grow without further irrigation. Under field conditions, with large soil volumes for root expansion and soil moisture extraction, the low water status achieved by plants may not occur easily. Thus, under limited water supply conditions, irrigation may be reserved for later growth states which are more critical in grain yield determination.

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