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Effects of Water Stress on Growth and Panicle Development of Grain Sorghum

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ABSTRACT. A solution culture experiment was conducted at the University of Queensland, Australia, from 1988/89 to study the effects of water stress, imposed during various growth stages (GS I and GS II) on the panicle development of grain sorghum cv. Texas 610 SR. Polyethylene glycol (PEG) 6000 was used to decrease the osmotic potential of the solution.

Water stress (−0.4 MPa of solution osmotic potential) caused substantial reductions in panicle development of grain sorghum. Water stress imposed during early stages of plant growth (before panicle initiation) reduced the dimensions of the shoot apices. However, the number of primary branches initiated from the surface of the shoot apices was not changed by the imposed stress. The fertility of the primary branches was reduced when stress was imposed at or before panicle initiation.

The number of whorls was reduced gradually from 12 to 10 when water stress was imposed at or before panicle initiation. The panicle produced a greater number of primary branches per whorl to compensate for the lost whorls. The total number of secondary branches was reduced only when water stress was imposed at or before panicle initiation. Both total and fertile tertiary branches were more susceptible to the water stress than the secondary branches. Water stress had a marked effect on upper than on lower whorls in the panicle. When imposed early they caused primary branches in the lower whorls to abort, thereby reducing the number of secondary and tertiary branches which resulted in a reduction in the number of fertile florets.

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INTRODUCTION

Water stress is a major limiting factor to grain sorghum production in the semi-arid tropics. Water stress at any stage of growth may have a detrimental effect on crop vigour and on ultimate crop yield (Wright and Smith, 1983; Wright *et. al.*, 1983). Field studies reveal that under water stress conditions sorghum may experience a loss in grain yield through both abortion of florets and sterilization of florets in the panicle (Herbert, 1984). However, the exact timing of the events causing these effects is unknown. Therefore a series of experiments were initiated to study the effects of water stress on the growth and panicle development of sorghum. In the present study, water stress was imposed using PEG 6000 as an osmoticum. Firstly, an experiment was conducted to find a suitable level of osmotic potential for further studies. Another experiment was then conducted to study the effects of water stress imposed at five different growth stages on growth and panicle structure of sorghum.

MATERIALS AND METHODS

Sorghum bicolor *cv.* Texas 610 SR was grown in an evaporatively cooled glass-house using solution culture techniques during the months of October to December 1988. Seeds were sterilized, aerated overnight and germinated in an incubation room for 2 days at 28 C. Two seedlings with radicles about 2-3 cm long were planted in each seedling container of culture vessels. On day 3, the seedlings were thinned to two per pot. All the treatments were replicated three times; the pots were completely randomized within four rows in the centre of the glass-house. The daily maximum glass-house temperature ranged from 26 C to 35 C, and the minimum from 20 C to 23 C during the night. The plants were grown by the Programmed Nutrient Addition technique (Asher and Blamey, 1986) using the "NUTRADD" program to calculate the daily demand for each nutrient element for the duration of each experiment. The nitrate to ammonium ratio was maintained at 8:1 to help stabilize solution pH (Clark, 1982).

In Experiment 1, there were four nominal solution osmotic potentials, *viz.* 0, −0.2, −0.4 and −0.6 MPa, in combination with four rates of daily approach to these potentials *via* increments of 0.05, −0.1, −0.15, and −0.2 MPa per day. The treatments of Experiment 2 are

given in Table 1. Water stress was imposed every 7 days starting from day 14 (7 days before panicle initiation). A nominal solution osmotic potential of −0.3 MPa was obtained within 2 days.

The amounts of PEG 6000 needed to reach the above osmotic potentials were calculated using a previously established calibration curve (Rego, 1986, personal comm.). These impositions were made between 0600 h and 0800 h. After 14 days the water stress was relieved from some of the pots to study recovery from the water stress.

There was only one harvest in Experiment 1; this was taken on day 42. The schedule of harvest times for plants grown in Experiment 2 is shown in Table 2. At harvest the panicles were dissected and the fresh panicles were stored in a cold room until they could be examined in detail. Panicles less than 1 cm in length were preserved in 100% amyl acetate for Scanning Electron Microscopy (SEM). The panicles larger than 1 cm in length were examined under a large magnifying lens to enable the panicle components to be counted.

RESULTS

Experiment 1 was an exploratory experiment designed to identify a solution osmotic potential which would cause a considerable reduction in growth, and find an addition procedure which would allow water stress to be imposed rapidly but with minimal osmotic shock and to help in selecting a suitable level of stress for Experiment 2. There was no clear effect of the rate of change of solution osmotic potential on the leaf osmotic potential measured on day 41 (Table 3). However, lowering the solution osmotic potential significantly lowered leaf osmotic potentials.

In both Experiments, the control plants remained green and healthy in appearance throughout. In Experiment 2, when water stress was imposed on days 14 or 21, the plants produced only 12 or 13 leaves, but in the remaining treatments they produced approximately 15 leaves.

The earlier the water stress was imposed, the greater was the reduction in growth of the sorghum plants (Table 4). Also, water stress prolonged the length of the vegetative period. Panicle initiation was delayed by about 2 and 5 days when water stress was imposed on day 14 and day 21 respectively; control plants initiated on day 23.

Table 1. Times of imposition and relief of −0.3 MPa osmotic potential and harvest of sorghum plants which were water stressed and which had water stress relieved 14 days after its imposition (Expt. 2).

Treatments		Times of harvest (days after transplanting)	
Water stress imposed days after transplanting)	Water stress relieved (days after transplanting)	Stressed plants	Plants from which stress was relieved
14	28	14[A], 21, 28, 35, 42	28[B], 35, 42
21	35	21[A], 28, 35, 42, 49	35[B], 42, 49
28	42	28[A], 35, 42, 49, 56	42[B], 49, 56
35	49	35[A], 42, 49, 56, 63	49[B], 56, 63
42	56	42[A], 49, 56, 63, 70	56[B], 63, 70
Control		49[A], 56[A],63[A],70[A]	

A Control plants which were never water−stressed
B Plants which were water stressed for 14 days, and harvested immediately prior to the relief of water stress.

Table 2. Effects of solution osmotic potential and rates of increase of solution osmotic potential on the leaf osmotic potential of the youngest fully−opened blade of sorghum on day 41 (Expt. 2).

Rate of daily decrease in solu. osmo. poten. (MPa day $^{-1}$)	Leaf osmotic potential (MPa) at indicated solution osmotic potentials (MPa)			
	−0.1	−0.3	−0.5	−0.8
Control	−0.8			
−0.05		−1.1	−1.3	−1.8
−0.1		−1.0	−1.2	−2.0
−0.15		−1.2	−1.4	−2.0
−0.2		−1.2	−1.4	−1.8
Mean		−1.1	−1.3	−1.9
l.s.d. (P = 0.05)		−0.14		

Table 3. Effect of relieving water stress on the dry matter yield (g pot^{-1}) in various parts of sorghum cv. Texas 610 SR (Expt. 2).

Plant part		Dry matter yield of various plant parts on indicated days (P=0.05)					l.s.d.
		D42	D49	D56	D63	D70	
Total C[A]	13.7	29.8	71.1	118.9	144.6		4.7
	R[B]	18.7	34.7	79.5	122.8	151.7	
Shoot C	10.2	23.3	55.0	89.8	112.8		3.4
	R	14.2	26.9	61.4	92.5	118.3	
Stems C	1.3	3.7	12.7	21.9	27.6		1.3
	R	2.1	5.4	14.6	22.8	29.9	
Leaves	C	8.8	17.6	27.1	36.7	36.7	2.1
	R	12.0	19.5	28.3	38.7	38.4	
Inflore-scence	C	0.05	1.9	15.2	28.4	48.5	1.6
	R	0.08	2.1	18.4	31.0	52.1	
Roots C	3.5	6.5	16.1	29.1	31.9		1.1
	R	4.5	7.8	18.1	30.3	32.7	

[A] C refers to plants which were subjected to continuous water stress 28 days prior to the indicated harvest day.

[B] R refers to plants which were water stressed for a 14 day period commencing 28 days prior to the indicated harvesting day.

Table 4. Effects of solution osmotic potential and the rate of change of solution osmotic potential on panicle length of sorghum cv. Texas 610 SR on day 42 (Expt. 1).

Rate of change in osmotic potential MPa day^{-1}	Panicle length (mm) at solution osmotic Potential (MPa) of			
	−0.1 (Control)	−0.3	−0.5	−0.8
Control	287			
−0.05		210	143	60
−0.1		215	150	55
−0.15		220	127	60
−0.2		218	115	55
Mean		216	134	58
l.s.d. (P=0.05)		12	2	57

In Experiment 1, the control plants developed a leaf osmotic potential of about −0.8 MPa. As the solution osmotic potential decreased, the leaf osmotic potentials also gradually decreased to a mean value of −1.9 MPa in the −0.8 MPa treatment (Plate 1).

Plate 2 shows the appearance of the panicles in Experiment 1 on day 42. Imposed water stress reduced the length of the panicle significantly (Table 5). The rate at which the treatment solution osmotic potential was reached had no significant effect on panicle length.

In Experiment 2, relief of the water stress by transfer of plants to fresh nutrient solutions after 14 days had no effect on the panicle components. Water stress had a significant effect on the number of whorls only when it was imposed on day 28 or earlier (Table 5).

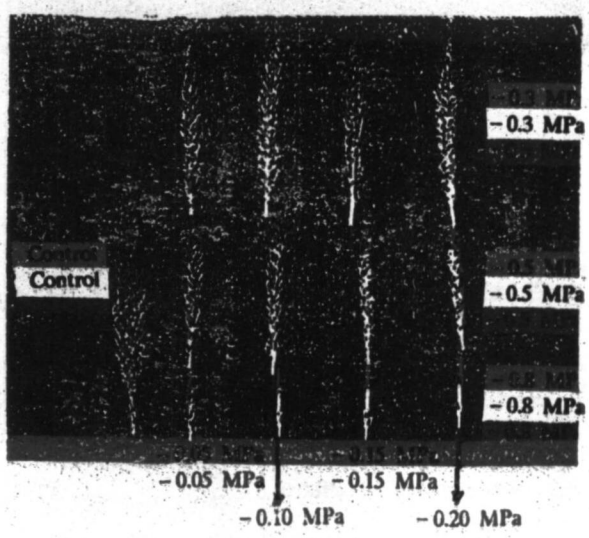

Plate 1. Effects of final solution osmotic potential and rate of change in solution osmotic potential on panicles of sorghum cv. Texas 610 SR at day 42 after transplanting (Experiment 1).

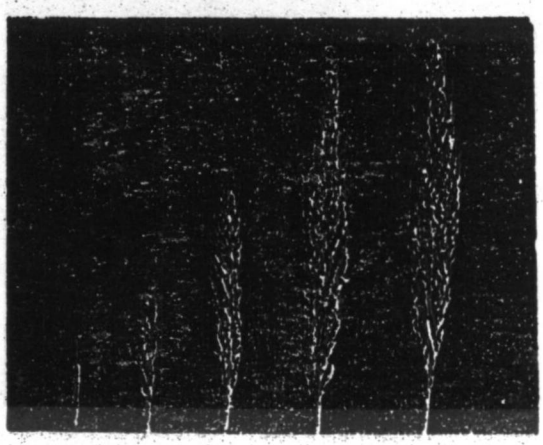

Plate 2. Effects of water stress on the panicle development of sorghum cv. Texas SR on day 42. (From left to right: water stress imposed on day 14, day 21, day 28, day 35,and unstressed control, Experiment 2.

Table 5. Effects of water stress, continuously maintained for 28 days, on the panicle components of sorghum cv. Texas 610 SR (Expt. 2).

Parameter	Day from which water stress was imposed					l.s.d
	(Control)	D21	D28	D35	D42	(P=0.05)
Number of whorls	11.7	10.0	10.3	11.7	11.7	1.01
Number of primary branches						
Total number	64	62	62	63	64	2.14
Fertile number	62	52	62	62	63	5.47
Number of secondary branches						
Total number	412	253	381	377	386	67.5
Fertile number	395	110	295	272	335	82.4
Number of tertiary branches						
Total number	331	143	296	311	305	48.2
Fertile number	300	40	103	157	152	31.7
Number of fertile florets	2206	579	1361	1545	1683	152

Control plants and plants in which water stress was imposed later than day 28 had an average of 11.7 whorls per panicle. The number of whorls was significantly reduced from 11.7 to 10.0 and 10.3, when water stress was imposed continuously for 28 days starting from day 21 or day 28 respectively.

The imposition of water stress had no significant effect on the number of primary branches, irrespective of whether it was imposed before panicle initiation, or later on during the growth of the panicle. The mean number of primary branches per panicle was 63. However, the number of fertile primary branches when water stress was imposed on day 21 was reduced to 52 compared with 62 in the control treatment (Table 5).

The unstressed control plants produced 412 secondary branches; this number was not significantly different from that produced by plants which were water stressed on day 28, day 35, or day 42 (Table 5). However, earlier imposition of the water stress (day 21) reduced the number of secondary branches to 253. The fertility of secondary branches increased as the imposition of water stress was delayed. The number of fertile secondary branches increased from 110 when water stress was imposed on day 21, to 395 in the panicles of the control plants (Table 5). The percentage of secondary branches that were fertile increased from 43% when plants were stressed on day 21 to 96% in the control plants.

The total number of tertiary branches was reduced below that of the control only when water stress was imposed on day 21 (Table 5), the number being approximately 43% of that of the controls. However, there was a much more substantial effect of the water stress treatments on the number of tertiary branches that were fertile. This number was significantly below that of the control plants in all stress treatments; the reduction in number of fertile tertiary branches was greater the earlier the water stress was imposed. Water stress reduced the number of fertile florets in all treatments. The reduction was greater when the water stress was imposed earlier in the growth cycle (Table 5). Water stress imposed on day 21, *i.e.* before panicle initiation, reduced the number of fertile florets by approximately 74% whereas water stress imposed after panicle initiation on day 28, day 35 or day 42 reduced the number of fertile florets by 38%, 30% and 24% respectively.

DISCUSSION

The total dry matter of the plants was reduced as the level of water stress increased. This was again shown by the leaf water potential of different water stress levels. Similar observations were made by several other workers both in soils and water culture (Ludlow and Powles, 1988; Rego *et. al.*, 1986, 1988). Thus leaf water potential provides an indication of the degree of water stress experienced by the plant.

Brown (1978) studied the effects of water stress on panicle development in sorghum *cv.* E 57. He found that this cultivar is capable of compensating for potential yield loss after experiencing adverse conditions by increasing individual seed weight or by rejuvenating 'aborted' florets, which otherwise would have failed to set seed. Similar results have been observed by Wright *et. al.*, (1983) with E 57 when they compared that variety with another variety Texas 671. They reported that E 57 tolerates water stress conditions, because of its ability to continue normal panicle development under severe water stress. E 57 achieves this by having a low level of floral abortion, maintaining longer leaf area duration, and possibly by a higher root to shoot ratio. They also found that up to 50% of the florets had either aborted or were sterile when Texas 671 was grown under drought conditions. The present study showed that Texas 610 SR also had high rates of floret abortion or sterility when water stress was imposed at any stage of its growth (Table 5) but particularly when water stress was imposed before panicle initiation. Relief of water stress after 14 days had no beneficial effect on fertility of the florets.

In the present experiment, the plants were grown up to a final harvest on day 70, at which point they were still in the grain filling stage. The final harvest was too early to enable any conclusions to be drawn about the effects of water stress on grain size of Texas 610 SR.

It is clear from the present study that the number of primary branches of the panicle is not affected by water stress. It was shown that even with severe nitrogen stress, the total number of primary branches was not affected (Dias, 1990). However, when nitrogen stress or water stress was imposed before panicle initiation, it affected the fertility of the primary branches. This indicates that even though the

number of primary branches initiated they appear to be unaffected by stress. However, a phase following soon after appeared very susceptible to stress effects. It may also be concluded that the fertility of the primary branches depends to a large extent on the nutrient supply and water available to the plant following panicle initiation.

In the present study, the fertility of primary branches was reduced only when water stress was imposed before panicle initiation, *viz.* on or before day 21. It would thus appear that imposition of water stress on sorghum, during the period from day 21 to day 42 will reduce grain yield, through effects on the number and fertility of the secondary and tertiary branches rather than through the effects on the primary branches (Table 5).

After the primary branches have been initiated, their continued development depends on the nutrient or assimilate distribution to them. The lower primary branches which have more higher order branches usually receive a lower priority in distribution of assimilates because of the inter-whorl competition within the panicle. Several investigators reported that there is an apical dominance in the assimilate flow into the growing grains of sorghum (Fischer and Wilson, 1975a,b; Hamilton *et. al.*, 1982). Fischer and Wilson (1975a,b) found that the grain yield of sorghum was not limited by the translocation of photosynthate from stem to grains. They found that removal of increasing portions of the apical spikelets produced a higher percentage in compensation of grains in the remaining basal region. This suggests that in the case of the inter-spikelet competition, the presence of apical spikelets will hinder the translocation of assimilates to the basal spikelets. Hamilton *et. al.*, (1982) reported that grains in the apical region attract more photosynthate than a similar number of grains located in the basal part. Michael and Seiler-Kelbitch (1972) observed that changes in the concentration of hormones in the developing grains in barley also alter the grain number in the panicle. Therefore, it may be concluded that in the present study, the primary branches in the lower whorls were more susceptible to any kind of stress, and more likely to lose the ability to produce any fertile florets. Similar results have been observed by Brown (1978), who reported that if the top whorls were affected by water stress, the lower part of the panicle was able to set seeds to compensate for the lost yield.

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