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DROUGHT STRESS EFFECTS ON THE GRAIN YIELD AND PANICLE DEVELOPMENT OF SORGHUM

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Many studies have reported responses to drought stress in sorghum (*Sorghum bicolor* (L.) Moench) but little is known about its effects on panicle development. To determine the stage of development most susceptible to water deficiency, in terms of grain yield components, eight plants of two sorghum lines were subjected to each of 10 single, successive drought stress treatments covering the entire life cycle. In each stress treatment, water was withheld until half of the plants remained wilted at sunrise. Effects on panicle development were also studied. Single sorghum plants were grown in pots containing a 3:1 soil (Typic Argiustoll)-sand mixture in a polyethylene greenhouse at Chapingo, México. Drought stress during microsporogenesis destroyed the whole panicle. Prior to this stage, drought produced abortion of the panicle-branch primordia, and a reduction of 25–55% in the number of grains per mature panicle. Later drought stress periods did not reduce the number of grains per panicle, but reduced individual grain weight by as much as 50%. Consequently, the yield was reduced by drought stress periods at all stages of panicle development before physiological maturity. Furthermore, drought stress before anthesis slowed the subsequent developmental rate of the panicle; drought stress after anthesis accelerated it. The proportion of fertile pollen grains remained above 90% in all drought stress periods. It is concluded that microsporogenesis and the milk dough stage are the most sensitive stages of sorghum panicle development to water deficits.

Key words: *Sorghum bicolor* (L.) Moench, grain sorghum, yield components, pollen sterility, sorghum cold-tolerance, microsporogenesis

[Effets du stress hydrique sur le rendement grainier et sur le développement des panicules du sorgho.]
Titre abrégé: Effets du stress hydrique sur le rendement et le développement des panicules du sorgho.
Les réactions du sorgho (*Sorghum bicolor* (L.) Moench) au stress hydrique ont fait l'objet de nombreuses études mais les effets de ce stress hydrique sur le développement des panicules sont encore très peu connus. Afin de déterminer le stade de développement le plus sensible à un manque d'eau, en fonction des composantes du rendement grainier, huit plants de deux lignées de sorgho ont été soumis à dix traitements successifs de stress hydrique couvrant l'ensemble du cycle vital. Dans chaque traitement, l'approvisionnement en eau était coupé jusqu'à ce que la moitié des plantes demeurent fanées au lever du jour. Les effets des traitements sur le développement des panicules ont également été étudiés. Des plants uniques de sorgho ont été cultivés en pots contenant un mélange de trois parties de sol (Argiustoll typique) pour une partie de sable dans une serre de polyéthylène à Chapingo (Mexique). Le stress hydrique

subi pendant la microsporogénèse a détruit la panicule entière. Les conditions de sécheresse subies avant ce stade ont provoqué l'interruption de la croissance de l'ébauche de la panicule et une réduction de 25 à 55% du nombre de graines par panicule mature. Les périodes de stress hydrique subies plus tard n'ont pas réduit le nombre de graines par panicule mais ont provoqué une baisse du poids des graines individuelles atteignant jusqu'à 50%. En conséquence, le rendement a été réduit par les périodes de stress hydrique à toutes les étapes du développement de la panicule précédant la maturité physiologique. En outre, le stress hydrique subi avant l'anthèse a provoqué un ralentissement du développement subséquent de la panicule alors que le stress hydrique après l'anthèse accélérait ce développement. La proportion de grains de pollen fertiles est demeurée supérieure à 90% pour toutes les périodes de stress hydrique. Nous concluons que la microsporogénèse et le stade laiteux-pâteux sont les deux stades du développement des panicules de sorgho les plus sensibles au manque d'eau.

Mots clés: *Sorghum bicolor* (L.) Moench, sorgho-grain, composantes du rendement, stérilité du pollen, tolérance au froid du sorgho, microsporogénèse

The effects of drought stress on grain yield and its components will depend, among other factors, on the stage of development in which the water deficit occurs. Grain yield reductions of 17, 34 and 10% were found in sorghum (*Sorghum bicolor* (L.) Moench) when water deficiency occurred before the boot stage, from the boot stage to anthesis, and from the milk dough stage to the soft dough stage, respectively (Lewis et al. 1974). Inuyama (1978) reported a 61% reduction in grain yield when drought occurred at the boot stage. In sorghum, however, the specific stage of panicle development which is most susceptible to water deficits is unknown, although microsporogenesis has been reported as the most critical stage in wheat (*Triticum aestivum* L.) (Saini and Aspinall 1981). Microsporogenesis also has been found to be a critical stage of development in sorghum for both high temperature stress (Dhopte 1984; Eastin et al. 1984; Ogunlela and Eastin 1984), and low temperature stress (González-Hernández 1977; González-Hernández et al. 1986).

Reductions of sorghum grain yield due to drought stress before anthesis are related to decreases in grain number, while a smaller grain size is responsible for yield losses when water deficits occur after anthesis (Mirhadi and Kobayashi 1980; Eastin et al. 1983). However, compensation between grain number and grain size makes it difficult to assess the specific effects in several cases. In wheat, certain drought treatments have been found to affect pollen viability, which in turn reduces seed number (Saini and Aspinall 1981).

The effects of water deficits on plant development will also vary according to the crop and to other environmental factors. In this regard López-Castañeda (1979) found that anthesis was retarded in barley (*Hordeum vulgare* L.) and wheat by previous moisture deficits, whereas physiological maturity was accelerated. On the other hand, Wong et al. (1983) found that anthesis was accelerated in sorghum by previous drought, and the length of the grain filling period was not affected.

In this study, we evaluated the grain yield and rate of panicle development responses of two cold-tolerant sorghum lines to drought stress at ten successive growth stages under greenhouse conditions.

MATERIALS AND METHODS

This study, performed in a polyethylene-covered greenhouse in Chapingo, México, involved two experimental cold-tolerant sorghum lines, CPTF-1 (L_1) and CPTF-2 (L_2), developed by the Sorghum Breeding Program of the Colegio de Postgraduados at Chapingo. In 1983, after suffering a moderate soil moisture deficit under field conditions, the two lines flowered and matured at the same time, but L_1 showed a higher grain yield than L_2. In unstressed conditions, both lines had identical grain yields and maturity. To determine their most sensitive developmental stage to drought stress in

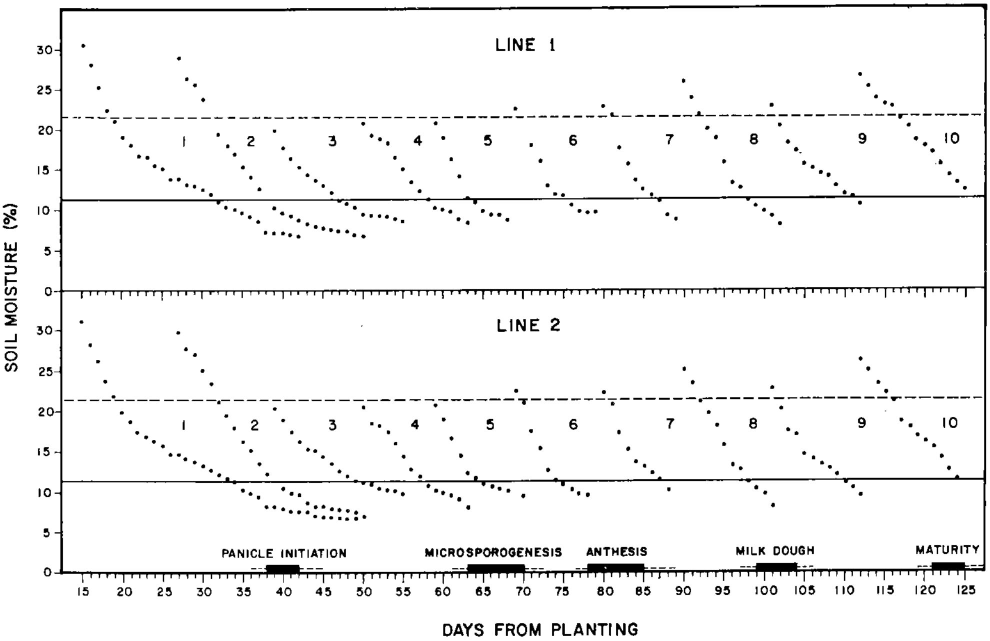

Fig. 1. Soil moisture depletion of 10 drought stress periods (1–10) imposed on two cold-tolerant sorghum lines, L_1 and L_2, across their life cycles. The bars at the bottom represent the time of developmental stages, averaged between the two lines, of panicle initiation (DS_2), microsporogenesis (DS_7) anthesis (DS_{11}), milk dough (DS_{13}) and physiological maturity (DS_{16}). Field capacity (------) and permanent wilting point (_______).

terms of grain yield components, plants of these two sorghum lines were subjected to single drought stress treatments at each of 10 successive stages of development covering the entire life cycle.

Single sorghum plants, planted on 22 May 1984, were grown in 11-L pots containing 10.13 kg (dry weight) of a 3:1 soil-sand mixture (the soil being of the Series Chapingo, a Typic Argiustoll), whose final composition was 47% sand, 18% silt, and 35% clay. The field capacity and permanent wilting point constants were 21.4 and 11.4%, respectively, as determined with two moisture extractors from Soilmoisture E. Corp. (a 5-bar pressure plate extractor, Mod. 1600; and a pressure membrane extractor, Mod. 1000) in the Soil Physics Laboratory of the Colegio de Postgraduados. Therefore, there were 1.01 liters of available water per pot at field capacity.

Each drought stress treatment began by withholding water in a group of eight plants per genotype until half of them remained wilted at sunrise. Thus, presumably, all plants received a physiologically similar water stress treatment, even in different panicle developmental stages, since according to Slatyer (1967), in any one plant-soil system, leaf permanent wilting represents the condition of zero turgor pressure in the leaves, and has a close association with growth cessation. The first drought period began with 15-d-old seedlings. The intervals between the beginning of one drought period and the beginning of the next varied from 10 to 12 d. Data in Fig. 1 show the average daily soil moisture levels and the duration in days for the 10 drought stress treatments.

Eight additional plants per genotype were used as controls for each drought period. Control plants were watered every day to keep the soil above 80% of field capacity. Soil moisture levels were monitored daily in each pot during the treatment period, both in stressed and unstressed plants, by recording the pot weight (± 25 g accuracy). Since the stressed (treated) plants were well-watered before and after the treatment period, any significant difference between controls and treated plants should be considered as an effect of the single water stress treatment. Except during the stress periods, every plant was provided with 3 L per week of a complete nutrient solution, whose composition has been reported by González-Hernández (1982).

Short-term effects of drought stress on the panicle developmental stage of sorghum were measured by dissecting: (a) four unstressed plants at the beginning of each treatment, (b) four unstressed control plants at the end of each treatment, and (c) four drought-stressed plants at the end of each treatment. Plant development was described using the morphological changes of the shoot apex outlined by González-Hernández (1977) (Table 1). (See Paulson (1969) and Lee et al. (1974) for previous descriptions of the sorghum shoot apex.)

Grain yield (grams per plant) and its components, grain number per panicle and grain weight (milligrams per grain), were recorded at harvest. Grain distribution in the panicle involved counting the number of grains per branch at different positions on the main rachis. Branches were numbered from the bottom to the top of the panicle. Other recorded data per plant included the number of branches on the panicle rachis, panicle length (cm), days to initiation of anthesis, and days to initiation of physiological maturity, as determined by the appearance of the black layer in the grain (Eastin et al. 1973). The duration of the grain-filling period was calculated by subtracting days to anthesis from days to physiological maturity.

In addition, the effects of drought on pollen fertility were evaluated in anthers detached from the middle portion of the main panicle in two plants per treatment; each anther was cut in two and squashed while in a drop of acetocarmine to extract

Table 1. Developmental stages of the shoot tip on the first and on the last day of 10 drought stress periods. Average of two sorghum lines

Drought stress period	First day	Last day of treatment	
		Watered plants	Stressed plants
1	DS_1†	DS_4	DS_2
2	DS_1	DS_5	DS_3
3	DS_2	DS_6	DS_4
4	DS_3	DS_7	DS_5
5	DS_6	DS_9	DS_7-DS_8
6	DS_9	DS_{11}	DS_{11}
7	DS_{11}	DS_{12}	DS_{12}
8	DS_{12}	DS_{13}	DS_{13}
9	DS_{13}	DS_{15}	DS_{15}
10	DS_{15}	DS_{16}	DS_{16}

†Codes for development stages (DS) (adapted from the thesis of González-Hernández 1977):

DS_1, shoot apex with leaf primordia only.

DS_2, very young panicle with acropetal branch differentiation. The primary branch primordia may have secondary and even tertiary branch primordia.

DS_3, young panicle with basipetal spikelet differentiation. Spikelets at the top show glume primordia.

DS_4, anther primordia appear in florets of the upper part of the panicle; glumes partially cover these florets.

DS_5, florets completely covered by colorless glumes in the top of the panicle. Pistil primordia, still without styles, are surrounded by three half-grown anthers.

DS_6, in the upper part of the panicle the glumes have light green veins, and young pistils support two small style primordia.

DS_7, microsporogenesis occurs in the upper florets of the panicle, and the upper pistils have pairs of elongated styles with stigma primordia.

DS_8, young pollen grains are found in the upper half to two thirds of the panicle. Stigmas are not fully developed yet. Glumes of the top florets are fully green.

DS_9, fully developed stigmas in the uppermost florets. This corresponds to the boot stage.

DS_{10}, fully developed stigmas almost in the whole panicle. This corresponds to panicle emergence from the flag leaf.

DS_{11}, anthesis in the upper half of the panicle, where fertilized and partially swollen ovaries can be seen.

DS_{12}, grains of the upper third of the panicle are swollen and contain a transparent liquid. Anthesis in the lower part of the panicle.

DS_{13}, grains in the milk dough stage at the top of the panicle.

DS_{14}, grains in the soft dough stage at the top of the panicle.

DS_{15}, grains in the hard dough stage at the top of the panicle.

DS_{16}, grains have reached physiological maturity (with a black layer) in the upper third of the panicle.

and stain the pollen grains (Sharma and Sharma 1965). Sterile and fertile pollen grains were then counted in 10 different microscope fields, and converted to percentage of the total number of pollen grains.

Each drought stress period corresponded to a completely randomized design with four treatments in a factorial arrangement and four replications (one plant, one replication). Since each drought period included its own control treatment, statistical analyses for most variables consisted of an analysis of variance for each period. Comparisons of means were performed with the Tukey's test when the interaction of genotype × drought stress level was significant, while the LSD test was applied when only two means were involved.

RESULTS

Drought Stress Effects on Panicle Developmental Rate

A severe soil moisture deficit at any time between panicle initiation and anthesis caused a delay in the development of the shoot apex (Table 1), which was equivalent to two phases (stages) of the developmental scale proposed by González-Hernández (1977) (see Table 1). On the other hand, a similar drought stress imposed at anthesis or during the grain filling period usually did not produce significant changes in the rate of panicle development. No differences were detected between the two sorghum genotypes with respect to panicle developmental rates for most of the drought stress periods.

Consequently, in the first five periods of drought stress, anthesis for the stressed plants was delayed when compared to the controls (Table 2), whereas panicle development was unaffected by drought stress imposed during or after anthesis except for Line 1 in period 8. The greatest delay in panicle development in terms of calendar days occurred after the fifth period of drought stress which affected microsporogenesis. Actually in this fifth period the panicles of the main shoots collapsed completely after rewatering both sorghum lines; nonetheless, all these plants

Table 2. Effects of 10 drought stress periods on days to anthesis and length of grain-filling period of two sorghum lines

Drought stress period	Line$_1$		Line$_2$	
	Unstressed	Stressed	Unstressed	Stressed
		Days to Anthesis†		
1	80*b*	80*b*	79*b*	86*a*
2	79*b*	84*a*	79*b*	84*a*
3	78*b*	83*a*	77*b*	83*a*
4	78*b*	86*a*	79*b*	86*a*
5	79	—	79	—
6	79*a*	77*a*	79*a*	78*a*
7	79*a*	79*a*	79*a*	79*a*
8	79*a*	79*a*	79*a*	79*a*
9	79*a*	79*a*	79*a*	79*a*
10	79*a*	79*a*	79*a*	79*a*
		Length of grain-filling period‡		
1	37*b*	44*a*	35*b*	43*a*
2	37*b*	43*a*	34*b*	42*a*
3	36*a*	37*a*	34*a*	37*a*
4	37*a*	36*a*	34*a*	35*a*
5	38	—	35	—
6	36*a*	41*a*	34*a*	37*a*
7	37*a*	35*a*	35*a*	30*a*
8	38*a*	26*b*	38*a*	37*a*
9	36*a*	32*a*	33*a*	31*a*
10	37*a*	37*a*	34*a*	34*a*

†Days to anthesis at the top of the panicle (average of four plants).

‡Days from anthesis to appearance of black layer in the grain of the top of the panicle (average of four plants).

a,*b* Figures with the same letter within a drought stress period are not statistically different (Tukey at 0.05).

remained alive and usually formed three tillers, each producing a panicle that reached anthesis about 24 d after anthesis of control plants. The length of the grain-filling period was increased significantly by water deficits only in the first two drought periods.

Drought Stress Effects on Grain Yield and Yield Components

Grain yield per plant, grain number per plant, and grain size, averaged over the two genotypes (since there were no statistical differences between them), are shown in Fig. 2. Drought stress caused significant reductions of grain yield in all periods, except the tenth, which occurred during physiological maturity. Clearly, the most sensitive stage of sorghum panicle development to drought stress was microsporogenesis (Period 5), since during this stage a severe water deficit produced a complete collapse and subsequent death of the main panicle. Consequently, grain yield of the main panicle in this treatment was zero. However, panicle death was always accompanied by the emergence and growth of several tillers on each plant, which combined were able to produce fertile panicles that yielded 13% more grain per plant compared to controls. Tillering induced by the other treatments was negligible.

Before microsporogenesis (Periods 1–4), water deficiency resulted in yields per plant that were 70–83% of the controls. After microsporogenesis, drought stress at the milk dough stage of grain development gave a grain yield of 44% of the control.

In addition, data in Fig. 2 show that yield reductions due to drought imposed prior to or during anthesis (Periods 1–6) are explained mostly by losses in grain number per panicle, while yield reductions due to drought stress imposed after anthesis (Periods 7–9) are explained by reductions in grain size. A considerable increase in grain size, up to 79%, was observed when drought occurred in the early stages of panicle development (Periods 1 and 2), although this increase did not fully compensate for the losses in grain number.

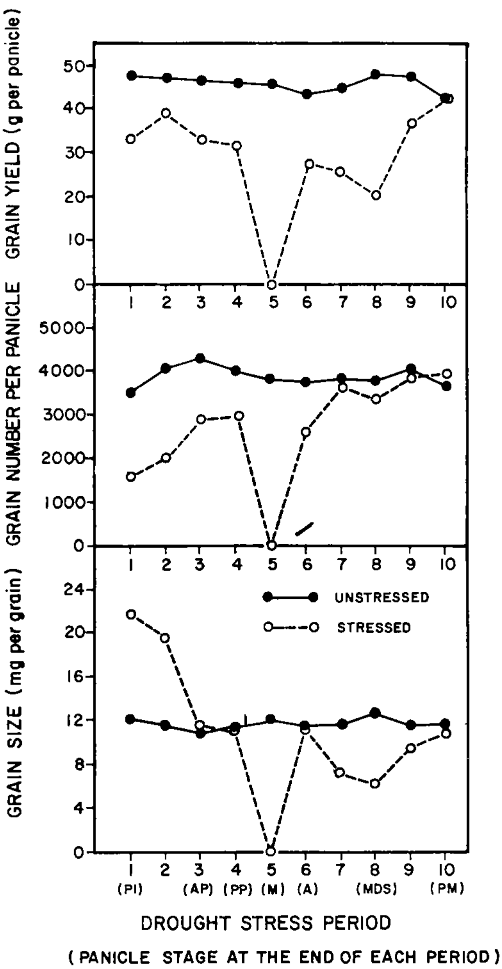

Fig. 2. Effects of drought stress imposed at 10 successive developmental stages of sorghum, on grain yield, grain number, and grain size. Averaged over two genotypes. (PI = panicle initiation; AP = anther primordia; PP = pistil primordia; M = microsporogenesis; A = anthesis; MDS = milk dough stage; PM = physiological maturity.)

Drought Stress Effects on Panicle Size

In both cultivars, drought stress significantly diminished the number of primary rachis branches in mature panicles only after periods 1, 4, and 5 (Table 3). These periods involve the differentiation of rachis branches in the panicle, the initiation of pistil primordia, and microsporogenesis, respectively. In period 1,

Table 3. Panicle responses to a severe drought stress period imposed at 10 different development stages. Average of two sorghum lines

Drought stress period	Branch number per panicle		Panicle rachis length (cm)	
	Unstressed	Stressed	Unstressed	Stressed
1	60*a*	47*b*	15.6*a*	14.5*a*
2	60*a*	54*a*	15.1*a*	14.7*a*
3	59*a*	57*a*	14.6*a*	13.1*b*
4	60*a*	43*b*	14.6*a*	10.0*b*
5	60	—	14.6	—
6	61*a*	58*a*	14.9*a*	15.5*a*
7	58*a*	57*a*	14.9*a*	14.9*a*
8	59*a*	55*a*	14.9*a*	14.9*a*
9	58*a*	56*a*	14.4*a*	14.5*a*
10	54*a*	55*a*	15.2*a*	15.2*a*

a,b Figures with the same letter within the same period are not statistically different (LSD at 0.05).

drought stress apparently inhibited branching whereas in periods 4 and 5, drought stress caused a partial or complete collapse of panicle branches which were already differentiated. Panicle length also was reduced significantly by drought stress in periods 3, 4, and 5.

Data in Table 4 show the relative number of seeds contained on primary rachis branches at three different positions in the panicle, with respect to their controls, averaged over two lines. Note that when water deficits affected the initiation of pistil primordia (Period 4), or affected earlier stages of panicle development (Periods 1–3), the inhibitory effects of drought stress on the number of grains per branch were statistically significant only on the middle and upper branches of the panicle. The losses ranged up to 73%. On the other hand, when drought affected anthesis (Period 6) or the next stage, the loss of grains was statistically significant only on branch 3, with losses up to 65%. During microsporogenesis, drought stress prevented any production of grain since the panicle collapsed entirely.

Drought Stress Effects on Pollen Viability

Plants subjected to water deficits had up to 9% of sterile pollen in two genotypes, while unstressed plants had about 4% of sterile pollen. Pollen sterility in the panicles of tillers after the Period 5 treatment was 6% for line L_1 and 28% for line L_2. These percentages of sterile pollen, however, did not seem to affect their grain set.

DISCUSSION

Microsporogenesis emerges as the most susceptible stage of sorghum development to drought stress, because in this stage water deficiency caused collapse and death of the whole panicle. Panicle death in sorghum was also observed by other workers (Hultquist 1973; González-Hernández 1982) after imposing a severe drought stress between anther differentiation and the boot stage. Additionally, microsporogenesis in sorghum is a very sensitve developmental stage for other adverse factors, such as high temperature (Dhopte 1984; Eastin et al. 1984; Ogunlela and Eastin 1984) and low temperature (González-Hernández 1977; González-Hernández et al. 1986; Brooking 1976). In those studies, however, grain yield reductions were not associated with panicle death, but were correlated with increases in pollen sterility.

Similarly, microsporogenesis has been detected as a very critical stage under stress conditions in other cereal crops. By successively imposing seven short drought stress periods during the development of the spike, Saini and Aspinall (1981) found that water deficiency during microsporogenesis induced male sterility and reduced grain yield in wheat plants. Furthermore, male sterility of wheat was induced by heat stress or exogenous application of abscisic acid during meiosis of the pollen mother cells (Saini et al. 1984). Pollen sterility and severe grain yield reductions due to low temperatures during the microsporogenetic stages of rice (*Oryza sativa* L.) plants

Table 4. Mean number of grains in branches 3, 30 and 50 of sorghum main panicles, as affected by drought stress imposed at 10 successive developmental stages during the life cycle. Average of two sorghum lines

Drought stress period	Branch 3			Branch 30			Branch 50		
	Unstressed	Stressed	(%)	Unstressed	Stressed	(%)	Unstressed	Stressed	(%)
1	125*a*	88*a*	(70)†	59*a*	16*b*	(27)	22*a*	11*b*	(50)
2	121*a*	84*a*	(69)	60*a*	22*b*	(37)	23*a*	9*b*	(39)
3	117*a*	84*a*	(72)	62*a*	47*a*	(76)	25*a*	24*a*	(96)
4	123*a*	101*a*	(82)	61*a*	41*a*	(67)	23*a*	13*b*	(57)
5	—	—	—	—	—	—	—	—	—
6	112*a*	39*b*	(35)	58*a*	47*a*	(81)	23*a*	19*a*	(83)
7	121*a*	80*b*	(66)	62*a*	60*a*	(97)	21*a*	24*a*	(114)
8	123*a*	115*a*	(93)	55*a*	58*a*	(105)	25*a*	20*a*	(80)
9	120*a*	109*a*	(91)	68*a*	59*a*	(87)	25*a*	22*a*	(88)
10	136*a*	130*a*	(96)	52*a*	58*a*	(112)	22*a*	23*a*	(105)

†Figures in parentheses are percentages of controls.

a,b Values with the same letter within the same stress period are not statistically different (LSD at 0.05).

also have been reported (Satake and Hayase 1970; Ito et al. 1970).

Other researchers claim that the interval between the boot stage or panicle emergence and anthesis of sorghum is the stage most vulnerable to water deficits (Lewis et al. 1974; Inuyama 1978; Mirhadi and Kobayashi 1979). However, their water stress treatments were applied in rather wide intervals and the developmental stages of the panicle were not defined with enough accuracy, so they might have overlooked microsporogenesis as a critical stage. Furthermore, genetic diversity among the sorghum cultivars used in the quoted investigations may explain their different results.

In our study, prior to microsporogenesis, severe soil moisture deficits produced 45–74% of the number of grains per panicle, in relation to that of unstressed plants. Probably due to a compensatory effect, grain size increased up to 180% as the seed number decreased to 45%, as compared to controls. Consequently grain yield losses of stressed plants were maintained between 20 and 30%. Note that water deficits during the early stages of panicle development may be useful for improving grain quality and vigor for sowing.

During anthesis we found that a drought stress caused a 31% reduction in grain number per head while grain size remained constant, so the loss in grain yield per panicle was about 36%. These results suggest that losses in grain number in this stage cannot be compensated for by increases in grain size, as in previous stages.

During the grain-filling period, grain number was only slightly inhibited by water stress, whereas grain size was considerably diminished, particularly for drought during the milk dough stage of grain development. In this stage losses in grain size reached 50% which almost accounts for the 56% reduction in grain yield. Therefore, in terms of grain yield, the early stages of grain development appear to be more susceptible to drought stress than the remaining stages of panicle development, excluding microsporogenesis. However, if the growing season is long enough, even a severe drought stress during microsporogenesis may not reduce the final grain yield of these sorghum genotypes because their tillers can produce as much grain as the unstressed plants, although they require 3 or 4 wk longer to reach physiological maturity.

We emphasize the close relationship between the stages of panicle development and the effects of water deficts on grain yield, a relationship which can be detected by recording the yield components and the distribution of primary rachis branches and grains in the panicle. For example, when plants were subjected to drought during panicle branch differentiation (drought periods 1 and 2), grain yield losses could be accounted for mostly by the reductions in the number of primary rachis branches and in the number of grains per branch. These reductions were specially strong in the upper half of the panicle, since at those stages the panicle differentiation is acropetal, so the branch primordia were younger above than below (Lee et al. 1974). At subsequent stages of formation, the spikelet and floret differentiation is basipetal; in these stages drought stress could still reduce the number of grains per panicle, but not grain size. Water deficits during anthesis (Periods 6 and 7) caused floret abortion in the lower branches of the panicle, thus producing losses in grain number. After anthesis (Periods 8 and 9) drought stress did not affect grain or branch number but reduced grain size. However, during microsporogenesis (Period 5), a severe drought stress killed the whole panicle, and during pistil initiation (Period 4) killed the top of the panicle. In these two cases panicle death occurred after drought stress was terminated (i.e., during the recovery period) by a still unknown mechanism.

Panicle developmental rate was also affected by water deficits, the magnitude of this effect depending on the stage of panicle development during the drought stress treatment. Drought stress before anthesis slowed subsequent development; after anthesis, it was accelerated. These results may explain the apparently conflicting reports about drought effects on panicle developmental rate of sorghum and other crops. In this study, a longer grain-filling period was associated with larger grains.

Finally, although the two sorghum cultivars showed a different response to a moderate soil moisture deficit in the field, our present results indicate that both lines had similar reactions to a very severe drought stress in the greenhouse where experimental conditions were carefully controlled.

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