# DROUGHT RESISTANCE OF Sorghum bicolor. 5. GENOTYPIC DIFFERENCES IN THE CONCENTRATIONS OF FREE AND CONJUGATED ABSCISIC, PHASEIC AND INDOLE-3-ACETIC ACIDS IN LEAVES OF FIELD-GROWN DROUGHT-STRESSED PLANTS.

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DURLEY, R. C., KANNANGARA, T., SEETHARAMA, N. AND SIMPSON, G. M.1983. Drought resistance of Sorghum bicolor. 5. Genotypic differences in the concentrations of free and conjugated abscisic, phaseic and indole-3-acetic acids in leaves of field-grown drought-stressed plants. Can. J. Plant Sci. 63: 131-145.

Concentrations of free and conjugated abscisic acid (AbA), phaseic acid (PA) and indole-3-acetic acid (IAA) were measured in leaves of sorghum (Sorghum bicolor (L.) Moench) genotypes grown in the field. Hormone levels were compared and related to grain yield stability under drought, expressed as the percentage reduction in grain yield (percent RGY) of drought-stressed compared to irrigated plants. Although hormone concentrations were similar in irrigated plants, there was considerable genotypic variation in drought-stressed plants. In a four genotype comparison during the panicle initiation stage, mean leaf AbA concentrations in drought-stressed plants were positively related to percent RGY. Furthermore, the slopes of regression lines of AbA on leaf water potential in stressed genotypes were also positively related to percent RGY. In contrast, PA and total AbA metabolite concentrations were negatively related to percent RGY, implying a higher efficiency of conversion of AbA to its metabolites in drought resistant than in drought-susceptible genotypes. There was genotypic variation in free and conjugated IAA concentration in leaves of stressed plants, but these concentrations were not directly related to percent RGY. Nevertheless, high levels of free and conjugated IAA were found at some periods in leaves of drought-susceptible genotypes. The positive relationship between free AbA concentration and percent RGY was confirmed in a nine genotype comparison. Mean leaf AbA concentrations during flowering and early grain filling in drought-stressed plants were found to be a significantly correlated  $(r=0.86^{**})$  with percent RGY. It is concluded that it is possible to evaluate genotype drought resistance to a given stress treatment in sorghum by examination of AbA, PA and IAA concentations in leaves. The potential of the method as a tool for plant breeders is discussed.

Key words: Sorghum bicolor, drought stress, abscisic acid, phaseic acid, indole-3-acetic acid, yield

[Résistance à la sécheresse du Sorghum bicolor. 5. Différences génotypiques des concentrations à l'état libre et conjugué des acides abscisique, phaséïque et indole-3-acétique dans les feuilles de plante cultivées dans des champs soumis au stress sécheresse.]

Can. J. Plant Sci. 63: 131-145 (Jan. 1983)

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Titre abrégé: Hormones dans le sorghum soumis à la sécheresse

Les concentrations en acides abscisique, phaséïque et indole-3-acétique sous forme libre ou conjuguée ont été mesurées dans des feuilles de génotypes de sorgho (Sorghum bicolor L. Moench) cultivés au champ. Ces concentrations ont été confrontées avec le degré de stabilité du rendement de grain, en condition de sécheresse. Ce degré de stabilité était exprimé par le pourcentage de réduction de rendement grainier en conditions sèches par rapport à un régime irrigué. Bien que les concentrations étaient semblables dans les plantes irriguées, on a observé une variation génotypique considérable en régime de culture sèche. Lors d'une comparaison de 4 génotypes au stade d'exsertion de la panicule, les concentrations foliaires moyennes en acide abscisique, AAb chez les plantes de culture sèche étaient positivement reliées au pourcentage de réduction du rendement grainier; ce dernier était également positivement relié aux pentes des lignes de régression de AAb sur le potentiel hydrique des feuilles. En revanche, les concentrations en acide phaséique (AP) et en métabolites totaux de AAb étaient négativement reliés au pourcentage de réduction de rendement, ce qui laisse sopçonner une conversion plus efficace de AAb en ses métabolites chez les génotypes résistants à la sécheresse. On a observé une variation génotypique des concentrations foliaires en acide indole acétique (AIA) libre et conjuguée chez les plantes privées d'eau, mais ces concentrations n'étaient pas directement reliées au pourcentage de réduction de rendement grainier. Il reste que de fortes concentrations de cet acide (libre et conjugué) ont été observées aussi, à certaines époques, dans les feuilles de génotypes sensibles à la sécheresse. Le rapport positif constaté entre la concentration en AAb libre et le pourcentage de réduction de rendement de grain s'est vérifié dans une comparaison faite, cette fois, sur neuf génotypes. Les concentrations foliaires moyennes en AAb au cours de la floraison et du début de la phase de remplissage du grain, chez les plantes privées d'eau, étaient positivement corrélées ( $r = 0.86^{**}$ ) avec le pourcentage de réduction de rendement. Il apparaît donc possible d'évaluer la résistance génotypique à une contrainte hydrique donnée d'après les concentrations foliaires en AAb, AP et AIA. Les possibilités que la méthode offre aux sélectionneurs sont passées en revue.

Mots clés: Sorghum bicolor, stress de sécheresse, acide abscisique, acide phaseïque, acide indole-3-acétique, rendement

Recently there has been a great deal of interest in breeding for improved drought resistance in crop plants (Simpson 1981). Since drought resistance is generally assessed by grain yield performance under drought stress, it is this parameter that is almost exclusively used as a selection index. However by using this complex character alone the selection of desirable physiological components can be overlooked (Hurd 1976).

Alternative indicators of plant performance during drought stress have, therefore, been investigated. A good indicator is one which changes markedly in relation to drought and which can be easily measured. Proline (Hanson et al. 1979), betaine (Hanson 1980), nitrate reductase (Pal et al. 1976) and measurement of net photosynthesis (Kaul and Crowle 1974) have been suggested as indicators.

Since hormones are involved in waterstress-sensitive processes and since plants respond to drought by changes in growth, it is believed that hormones play a major role in plant drought resistance mechanisms (Durley 1981). Measurement of hormone concentrations could, therefore, be used to develop an index for the selection of drought resistant genotypes. In wheat, the accumulation of one of these hormones, abscisic acid (AbA), which is associated with growth inhibition and stomatal closure, was shown to be a heritable trait (Quarrie 1981; Quarrie and Henson 1982).

Several studies have indicated that genotypic differences in crop plants can be observed in terms of AbA concentrations in leaves of stressed plants or in detached leaves which have been given stress treatment. For example, in both spring wheat (Quarrie 1981) and millet (Henson et al. 1981a), a genotypic variation of about three- to fourfold was observed in accumulation of AbA in stressed leaves.

Furthermore, in some crop plants drought resistance has been associated with hormone changes under drought stress. In maize (Larqué-Saavedra and Wain 1976), sorghum (Larqué-Saavedra and Wain 1976), soybean (Samet et al. 1980) and millet (Henson et al. 1981a) high accumulation of leaf AbA was claimed to be associated with drought-resistant types. In contrast, however, the opposite was implied for wheat (Quarrie and Jones 1979; Quarrie 1980, 1981) where low accumulation of leaf AbA was associated with drought resistant types. These contrary associations may be due to species differences or to drought response type. The latter point was recently illustrated in a comparison of two field-grown sorghum genotypes (Simpson et al. 1979; Kannangara et al. 1982b). A drought-tolerant genotype was found to contain higher levels of leaf AbA, but lower levels of phaseic acid (PA and indole-3-acetic acid (IAA), than a drought-avoidant genotype. Since both genotypes had some drought-resistance qualities, one responding to drought by delaying (tolerant) and the other by hastening (avoidant) floral initiation (Stout and Simpson 1978; Stout et al. 1978), it is possible that leaf hormone levels are dependent on the specific genotypic response to drought. In all these studies the yield data, with which drought resistance could be assessed were not given.

We have previously demonstrated that leaf AbA, PA and IAA concentrations in sorghum change according to the degree and timing of drought stress (Kannangara et al. 1982a,b, 1983). In this report the genotypic variation of drought-induced changes in AbA, PA and IAA concentrations is examined. The significance of these hormone changes in relationship to grain yield stability under drought stress conditions is discussed.

### MATERIALS AND METHODS

The experiments were conducted at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Centre near Hyderabad, India ( $17^{\circ}$  32' N Lat) during December-March 1979/1980 and 1980/1981. Plants were field-grown with a split-plot experimental design in which irrigation and stress treatments were the main plots and genotypes were the subplots. Each treatment for each genotype was replicated three times. Each subplot consisted of four rows 4 m long and 75 cm apart. Seeds were sown on raised ridges and irrigation was effected by flooding the furrows between rows. Plants were thinned to 10 cm apart 16 days after sowing (DAS).

#### Four Genotype Comparison

Genotypes CSH6, CSH8, M-35 and CSV5 were grown for this experiment. CSH6 and CSH8 are hybrids. CSH6 is early maturing and has some drought-resistant qualities. M-35 is a commonly used genotype in India and has known droughttolerance qualities (Stout and Simpson 1978). CSV5 is a drought-susceptible type.

Seeds were sown on a light medium-deep alfisol (red soil). This soil had low water retention properties. Control plots were irrigated 4, 13, 35, 48, 61, 70, 82, 91 and 97 DAS. Stress plots were irrigated 4 and 13 DAS. In addition, rain fell on 38 and 45 DAS. Harvests were taken at 44, 47, 52, 55, 58 and 63 DAS for hormone analysis. At the same time six leaf water potential ( $\psi_w$ ) measurements per subplot were taken as previously described (Kannangara et al. 1983). The remaining plants were allowed to reach maturity, and their seed number and grain yields were determined.

#### Nine Genotype Comparison

Genotypes NK300, IS1037, CSH1, CSH6, CSH8, M-35, V302, CSV5 and CS3541 were grown. NK300, CSH1, CSH6 and CSH8 are hybrids. NK300, IS1037, CSH1 and CSH6 are early-maturing types. M-35 has some drought tolerance qualities. CSV5, V302 and CS3541 are believed to be susceptible to drought.

Seeds were sown on black clay soil. This soil had much greater water retention properties than the alfisol. Control plots were irrigated 7, 27, 46 and 73 DAS. Stressed plots were irrigatd at 7 DAS. In addition, rain fell on 40 DAS. Six harvests were taken between 50 and 85 DAS for hormone analysis; at the same time leaf  $\psi_w$ measurements were taken (data not shown). The remaining plants were allowed to reach maturity and grain yield was determined.

#### **Hormone Analysis**

The top three leaves from each of six plants were combined to constitute a replicate. These leaves were chosen since they contained the highest levels of AbA and IAA (Kannangara, Durley and Simpson, unpubl. obs.). The time of harvest was between 1200 and 1400 h (local time), since although AbA and PA levels change diurnally, they are relatively constant during that time (Kannangara et al. 1982a). The leaves were frozen in dry-ice and immediately transported to the laboratory. The tissue was freezedried below 0°C until most of the water was removed, then allowed to dry fully at ambient temperature inside the freeze dryer for 4 h. The freeze-dried tissue was ground to a powder and batches of 1.25 g were extracted in methanolwater (4:1) for examination of free and conjugated (alkali hydrolysable) AbA, IAA and PA. Full details of the method have been presented (Durley et al. 1982). Briefly the method involved ether extraction, then filtration of the hormones as ammonium salts through insoluble polyvinylpyrrolidone, preparative high performance liquid chromatography (HPLC) with  $C_{18}$  reverse-phase columns, and analytical HPLC on silica (AbA, PA) or C<sub>18</sub> reverse-phase columns (IAA). The overall recoveries of the hormones were  $75 \pm 3\%$  for both abscisins and  $64 \pm 3\%$  for IAA. All the hormone data were adjusted for extraction losses.

#### **Statistical Analysis**

Variances of mean values indicated in each figure were tested for homogeneity. If they were homogenous a pooled standard error was calculated to represent the variability around each mean. If the variances were nonhomogenous standard errors of individual mean values were given.

### RESULTS

#### Four Genotype Comparison

Leaf  $\psi_w$  declined over the period 44–63 DAS in both control and stressed plants of all genotypes (Fig. 1). In stressed plants the decline was more rapid. The lowest leaf  $\psi_w$  was observed on day 58. There was no significant genotypic difference in leaf  $\psi_w$ on any given occasion.

In leaves of stressed plants free AbA concentrations were generally higher and varied more than in controls (Fig. 2) Also, genotypic differences could more easily be observed in stressed plants. In particular, from 52 DAS onwards CSH6 had lower free AbA concentrations in leaves of stressed plants than the other genotypes.

On day 47 the AbA concentrations in leaves of stressed plants were similar to controls due to rain 2 days earlier (Fig. 2). A high concentration of AbA was observed in all genotypes on day 58. Since leaf  $\psi_w$ was low on this day, it is likely that the threshold leaf  $\psi_w$  value for rapid AbA synthesis had been reached (Kannangara et al. 1983).

For each cultivar the AbA content in leaves of stressed plants was significantly negatively correlated with leaf  $\psi_w$  (Fig. 3). Furthermore, there were genotypic differences between the slopes ( $\beta$ ) of the linear regressions of AbA on leaf  $\psi_w$  (Fig. 3); the slope for CSH6 was significantly less steep (P < 0.05) than those for the other three.

As observed for free AbA, genetic differences in other hormone concentrations were much larger in stressed plants than controls. Therefore, in the following comparison, only stressed plants are considered.

There was little difference between genotypes in levels of conjugated AbA except when stress was severe (Fig. 4). On days 58 and 63 conjugated AbA concentration was high in three genotypes, with larger concentrations in CSH8 and M-35 than the others. It is possible that the metabolite is simply a deactivation product of AbA rather than a storage product (Walton 1980;

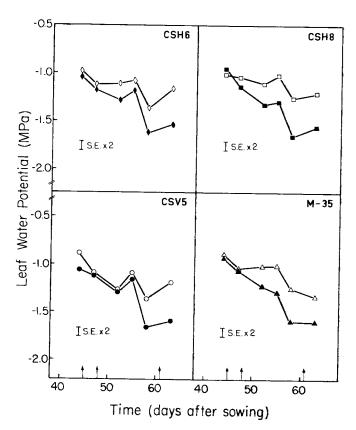


Fig. 1. Variation of leaf  $\psi_w$  during the panicle initiation stage of four sorghum genotypes. Open symbols, irrigated controls; closed symbols, drought stressed. Arrows shown on the 48th and 61st day after sowing indicate days of irrigation of controls. The arrow shown on the 45th day after sowing indicates rain fell on that day. Values are means of 18. SE represents pooled standard error.

Pierce and Raschke 1981) and its level increases as free AbA concentration increases.

The concentration of free PA, a major metabolite of AbA (Walton 1980), in leaves of stressed plants was noticeably higher in CSH6 than in other genotypes (Fig. 5). A similar situation also existed with conjugated PA (Fig. 6). Thus, the leaves of genotype CSH6 contained the lowest AbA and highest PA concentrations.

There were some genotypic differences in the concentration of free IAA in leaves of stressed plants (Fig. 7). Concentrations were similar in CSH8 and CSV5 and did not significantly change with increasing stress. The concentration of free IAA in leaves of M-35 was similar to those of CSH8 and CSV5, except that under severe stress (observed on days 58 and 63) the concentration in M-35 was substantially increased. Genotype CSH6 had low free IAA levels at the early-panicle-initiation stages (observed on days 44 and 47), but levels gradually rose with time and the onset of stress.

The highest concentration of conjugated IAA was observed in genotype CSV5 (Fig. 8). Moderate concentrations were observed

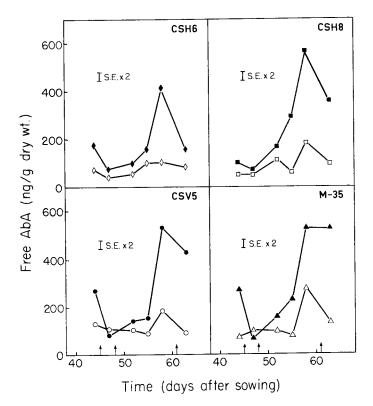


Fig. 2. Variation of leaf AbA content during the panicle initiation stage of four sorghum genotypes. Open symbols, irrigated controls; closed symbols, drought stressed. For explanation of arrows see Fig. 1. Values are means of three. SE represents pooled standard error.

in CSH6 and low concentrations in CSH8 and M-35. There is, therefore, a marked genotypic variation of conjugated IAA concentration independent of stress.

The effects of drought stress on the genotypes was evaluated by examination of the stability of grain yield to drought, which is expressed as the percentage reduction in grain yield (percent RGY) of stressed plants compared to irrigated plants. In Table 1 the genotypes are arranged in order of percent RGY. CSH6 had the lowest and CSV5 the highest percent RGY. A similar ordering is found in the comparison of the percentage reduction in seed numbers in stressed plants compared to irrigated plants (Table 1).

A positive relationship was present be-

tween genotype mean AbA levels (the mean of all AbA leaf concentrations in stressed plants made during the panicle initiation stage) and percent RGY (Table 1). Thus, CSH6, which had the lowest percent RGY, also had the lowest mean AbA level, whereas M-35 and CSV5, which exhibited high percent RGY, had the highest mean AbA levels. CSH8 was intermediate between these.

In contrast, genotype mean PA levels, measured in leaves of stressed plants during the panicle initiation stage, were negatively related to percent RGY (Table 1). Thus, CSH6 (low percent RGY) had high PA levels in leaves, whereas M-35 and CSV5 (high percent RGY) had low PA levels in leaves, with CSH8 being inter-

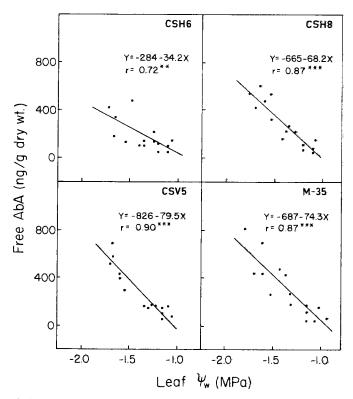


Fig. 3. The relationship between leaf AbA content and leaf  $\psi_w$  in drought-stressed plants of four sorghum genotypes. Lines are fitted linear regressions. d.f. = 13. Correlation coefficients (r) are indicated.

mediate in both PA and percent RGY. A similar negative relationship existed between AbA metabolite (PA + conjugates of AbA and PA) concentrations and percent RGY.

There was no clear relationship between mean free IAA or conjugated IAA concentrations in leaves of stressed plants and percent RGY. However, the genotype CSV5, which had the highest concentration of conjugated IAA also had the highest percent RGY (Table 1).

## Nine Genotype Comparison

The positive relationship between mean leaf AbA levels in stressed plants and percent RGY was reexamined with nine genotypes. As stress in the black clay soil developed slowly, plants were more advanced (flowering and early grain filling) when the six harvests for measurement of leaf AbA concentrations were made. When percent RGY for each genotype was regressed on the mean of these six AbA levels in drought stressed plants, a significant positive correlation ( $r = 0.86^{**}$ ) was observed (Fig. 9). Unlike AbA the magnitude of the change in leaf  $\psi_w$  to stress was small and hence a low correlation between  $\psi_w$  and percent RGY was observed.

## DISCUSSION

Although there are some difficulties in comparison of genotypic hormone concentrations in field-grown plants due to diurnal changes (Kannangara et al. 1982a), variations due to severity of drought (Kannan-

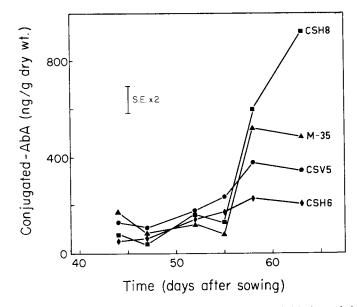


Fig. 4. Variation of leaf conjugated AbA content during panicle initiation of drought-stressed plants of four sorghum genotypes. Values are means of three. SE represents the pooled standard error.

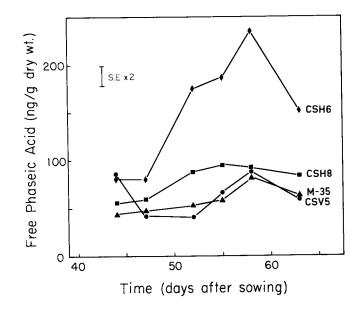


Fig. 5. Variation of leaf free PA content during panicle initiation of drought-stressed plants of four sorghum genotypes. Values are means of three. SE represents the pooled standard error.

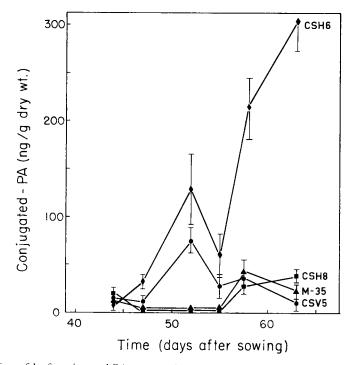


Fig. 6. Variation of leaf conjugated PA content during panicle initiation of drought-stressed plants of four sorghum genotypes. Values are means of three. SE of each point is indicated.

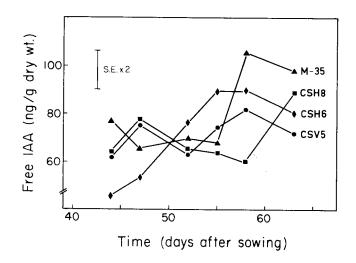


Fig. 7. Variation of leaf free IAA content during panicle initiation of drought-stressed plants of four sorghum genotypes. Values are means of three. SE represents pooled standard error.

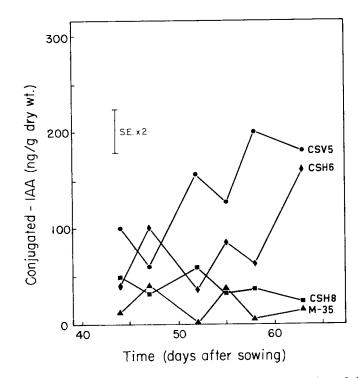


Fig. 8. Variation of leaf conjugated IAA content during panicle initiation of drought-stressed plants of four sorghum genotypes. Values are means of three. SE represents pooled standard error.

gara et al. 1983), as well as field variations, measurements in the field are a more accurate evaluation of the genotypic response to drought than growth chamber or other nonfield estimations. Furthermore, genotypic variation in field adjustment to drought would be expected to alter the spectrum of hormone concentrations. Besides AbA, which is most commonly associated with water stress, we have examined AbA metabolites, free IAA and conjugated IAA in order to make the evaluation of genotypic response to drought as comprehensive as possible.

The slopes of the linear regressions of AbA on leaf  $\psi_w$  in the four-genotype comparison corresponded positively with percent RGY (compare Fig. 3 and Table 1). In particular, the slope of the regression line for CSH6 was significantly less steep (P < 0.05) than the other three and it was

this genotype that had the lowest percent RGY.

Furthermore, the mean leaf AbA concentration in the four-genotype comparison was positively related to percent RGY and again in the nine-genotype comparison. Thus, for these genotypes leaf AbA concentrations could be used to predict genotype performance under drought.

The general relationship between leaf AbA and percent RGY was maintained in both four-and nine-genotype comparisons even though individual genotype performance differed in each experiment. Thus, CSH6 contained low leaf AbA concentrations and had the lowest percent RGY in the four-genotype comparison, whereas it contained moderate leaf AbA concentrations and had an average percent RGY in the nine-genotype comparison. Also, CSV5 contained high leaf AbA concentra-

	מוות	and mean normore levels in leaves of stressed plants of four sorghum genotypes	leaves of stressed play	nts of four sorghum ge	notypes	
Genotype	Percent RGY <sup>+</sup>	Percent reduction in seed no.‡	Mean AbA (ng/g dry wt)\$	Mean PA (ng/g dry wt)\$	Mcan total AbA metabolites (nM/g dry wt)§¶	Mean conjugated IAA (ng/g dry wt)§
CSH6 CSH8	$49.0 \pm 3.8$ 61 3 + 2 7	22.7±2.8 41.7+3.0	$179 \pm 27$	$158 \pm 13$	$1.32 \pm 0.18$	75.5 ± 16.1
M-35	$67.0 \pm 2.9$	$54.7 \pm 5.8$	$217 \pm 30$	/0.4 ± 4.7 59 8 + 3 9	$1.05 \pm 0.21$ 0 81 + 0 17	37.0± 4.5
CSV5	$71.3 \pm 3.2$	$65.7 \pm 5.1$	$293 \pm 39$	$64.5 \pm 4.5$	$0.82 \pm 0.11$	$142 \pm 17$
†Defined as [(gr (±SE).	Defined as [(grain yield (irrigated) — grain yield (stressed))/grain yield (irrigated)] $\times$ 100%. Calculated from three replicate irrigated and nonirrigated plots $\pm$ SE).	tin yield (stressed))/grain	yield (irrigated)] × 1	00%. Calculated from	three replicate irrigated	1 and nonirrigated plots
$\pm Defined$ as [(se plots ( $\pm$ SE).	Ebefined as [(seed number (irrigated) — seed number (stressed))/seed number (irrigated)] $\times$ 100%. Calculated from three replicate irrigated and nonirrigated olds ( $\pm$ SE).	eed number (stressed))/se	ed number (irrigated)]	$  \times 100\%$ . Calculated	from three replicate in	igated and nonirrigated
§Mcans of 18 me	$\$$ M cans of 18 measurements of hormone concentrations ( $\pm$ SE) in the top three leaves of stressed plants in three replicate plots (six values per plot). M casurements	ncentrations ( $\pm$ SE) in the	top three leaves of stre	ssed plants in three rep	olicate plots (six values J	per plot). Measurements

of mean free PA and conjugates of PA and AbA concentrations ( $\pm$ SE)

taken during panicle initiation (44-63 DAS).

Sum o

The percentage reduction in grain yield (percent RGY) and percentage reduction in seed number of drought-stressed compared to irrigated plants, and mean hormone levels in leav Table 1.

tions and had the highest percent RGY in the four-genotype comparison, but contained low leaf AbA concentrations and had a low percent RGY in the nine-genotype comparison. The reason for the low percent RGY of CSV5, which is normally considered to be drought susceptible, in the nine-genotype comparison, was probably due to the lack of severe stress in the heavy water-retaining soil until late in the season. Thus, leaf AbA levels are a sensitive indicator of the degree and type of drought stress experienced by each genotype. In contrast to free AbA, the concentrations of metabolites of AbA were negatively related to percent RGY. In particular, CSH6, which had the lowest percent RGY in the four-genotype comparison, could easily be distinguished from the other genotypes by its high leaf PA or total AbA metabolite concentrations. We have

previously observed high leaf PA levels in drought-avoider NK300 (Kannangara et al. 1982b) which also had a low percent RGY (Fig. 9). These results imply that the highyielding genotypes were able to metabolize AbA more efficiently than the other genotypes tested. A high rate of metabolism of AbA may assist in moderating excessive AbA production during drought stress. There were only slight genotypic varia-

tions in the concentration of free IAA in stressed plants (Fig. 7). However, much larger variations were observed in conjugated IAA concentrations. For example, in the four-genotype comparison (Fig. 8 and Table 1) and from other experiments (Durley et al. 1981) we have found that M-35 contains very low concentrations of conjugated IAA, whereas CSV5 contains much higher concentrations of conjugated IAA.

It is believed that concentrations of conjugated IAA depend on an equilibrium between free and bound IAA (Nowacki and Bandurski 1980). Whether this equilibrium is associated with drought resistance is not known. However, we have noted that drought-susceptible genotypes such as CSV5 (Table 1), V302, SPV86 and

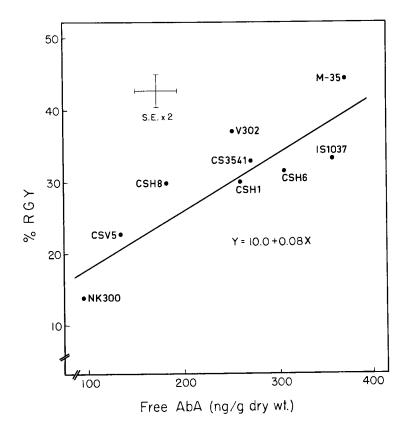


Fig. 9. The relationship between the percentage reduction in grain yield (percent RGY) of plants grown under drought-stressed conditions compared to irrigated plants and mean free AbA content in leaves of drought-stressed plants of nine sorghum genotypes. The line represents the fitted linear regression,  $r = 0.86^{**}$ . Each point represents means of six AbA concentration values. SE are the pooled standard errors.

CS3541 (Durley et al. 1981) contain moderately high free and very high conjugated IAA concentrations during vegetative and early-panicle-initiation stages. It is noteworthy that the overall increase in concentration of free IAA in drought resistant CSH6 was greater than for the other genotypes (Fig. 7).

It is not possible to conclude from these findings that high free and conjugated IAA concentrations are associated with high percent RGY. Spraying the sodium salt of IAA on intact plants of *Vicia faba* increased ethylene levels (Hall et al. 1977). Thus, under severe drought stress, if endogenous IAA concentrations increase this, in turn, could induce ethylene formation, which favors leaf senescence.

It is likely that AbA levels are an indication of cellular turgor pressure. Thus, the stimulus for rapid AbA synthesis is related to a lowering of the turgor pressure (Pierce and Raschke 1980, 1981). In sorghum, we have found that AbA levels rise rapidly when turgor pressures are near zero (Kannangara et al. 1983). At low turgor pressure leaf metabolic functions dependent on turgor would be impaired and if this were sustained over a long period, yield would suffer. Genotypic variation in changes in turgor potentials per unit change in leaf  $\psi_w$  have been reported in field grown sorghum (Ackerson et al. 1980).

Assuming AbA is a major controlling factor of stomatal aperture (Walton 1980), an increase of AbA concentration in leaves of water-stressed plants would assist in controlling water loss. Genotypic variation of leaf stomatal conductance in pearl millet has been associated with the amount of AbA accumulation (Henson et al. 1981b). Although control of water loss would be beneficial in the short term, large and sustained concentrations of AbA would prevent stomates opening, thus causing a lowering of leaf gas exchange (Mittelheuser and van Steveninck 1969) and contributing to a rise in leaf temperature. Both these effects would impair normal leaf function. Furthermore, high AbA concentrations have been reported to reduce seed set in wheat (Morgan 1980; Radley 1980). Thus, genotypes which are able to maintain sufficient turgor so that large increases in AbA do not occur, even under extreme drought, will suffer less detrimental effects from the hormone. This has been discussed in relation to AbA accumulation in wheat (Quarrie 1980). In this case it was suggested that in some genotypes, low drought-induced AbA accumulation could confer improved drought resistance qualities.

These and our data are in contrast to those of Larqué-Saavedra and Wain (1976) working with maize and sorghum, Samet et al. (1980b) working with soybean and Henson et al. (1981a) working with millet, all of whom have indicated that high drought-induced AbA accumulation is associated with drought-resistant genotypes. The reasons for these differing conclusions may be due to the specific type of drought resistance. In sorghum, drought avoidance is associated with early maturity, maintenance of high turgor and low leaf AbA concentrations (Kannangara et al. 1982b). Drought tolerance, on the other hand, is associated with late maturity and

high leaf AbA concentrations, which may be beneficial in some circumstances in delaying floral development (Quarrie 1980; Kannangara et al. 1982b). In this report we have attempted to avoid these drought response characters by simply relating hormone levels to percent RGY.

It can be expected that genotypic hormone variations are associated with many factors, not all of which are related to percent RGY. Nevertheless the data indicate that measurement of leaf AbA, and PA concentrations is effective in evaluating genotypic variation of percent RGY. This could have some potential as a tool for plant breeders. According to our results selections would be made on the basis of low free AbA and low free and conjugated IAA concentrations in leaves of droughtstressed plants. Although the examination of hormones in field trials is a time-consuming process, if used in conjunction with determination of seed number and final grain yield, it could provide the breeder with additional information for the selection of genotypes for specific types of drought resistance. Furthermore, measurement of hormones in droughted seedlings could allow evaluation of a large number of genotypes in a relatively short period of time.

#### ACKNOWLEDGMENTS

The authors thank Dr. J. Peacock and Dr. F. R. Bidinger, for the use of facilities at ICRISAT and Mrs. J. Montgomery and Messrs. A. Ma, D. M. Reddy, K. Reddy and H. Rao for excellent technical assistance. Prof. J. A. D. Zeevaart (Michigan State University) is thanked for generously providing a sample of phaseic acid. This research was funded by a grant from the International Development Research Centre, Ottawa.

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