Genotypic Variation in Pearl Millet (*Pennisetum americanum* (L.) Leeke), in the Ability to Accumulate Abscisic Acid in Response to Water Stress

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ABSTRACT

Variation between genotypes in the ability to accumulate abscisic acid (ABA) in response to water stress was investigated in pearl millet (*Pennisetum americanum* (L.) Leeke). Using a detached leaf test a more than four-fold variation in accumulation capacity was observed amongst a set of 16 genotypes grown in a controlled environment. Two genotypes which contrasted in their accumulation capacity, BJ 104 and Serere 39 (the latter accumulating most ABA), maintained the difference over a range of leaf water contents and potentials.

Some of the genotypes were grown in the field in the semi-arid tropics with and without irrigation, and sampled for ABA content. In two experiments, substantial genotypic variation in ABA accumulation was observed, which could not be attributed to differences in leaf water potential (ψ). In a field experiment comparing three genotypes (Serere 39, BJ 104, and B282), differences in ABA accumulation were also shown to be largely independent of genotypic differences in turgor potential (ψ_p).

For a set of six of the genotypes, the amounts of ABA accumulating in leaves of intact, droughted plants, in the field, when adjusted for differences in ψ, were found to be significantly ($P < 0.05$) correlated with amounts of ABA accumulated in detached, water-stressed leaves. It is concluded that the detached leaf test adequately reflects the ability of pearl millet genotypes to accumulate ABA under field conditions.

INTRODUCTION

The rise in the level of the plant hormone abscisic acid (ABA) in plant tissues subjected to water stress, first reported by Wright (1969) for wheat, has since been demonstrated to occur in a large number of species (Wright, 1978; Walton, 1980), and, at least for mesophytes, appears to be a general response to water deficit. The effects of applied ABA on stomatal aperture, shoot development, and morphology of plants bear a close resemblance to many of the effects of water stress (Quarrie and Jones, 1977; Aspinall, 1980; Walton, 1980), and imply that ABA is directly involved in mediating several stress responses. Also, the increase in water-use

efficiency following ABA application (Jones and Mansfield, 1972; Mizrahi, Scherings, Malis-Arad, and Richmond, 1974; Raschke, 1974; Dubbe, Farquhar, and Raschke, 1978) testifies to the benefits likely to be conferred by the hormone under certain conditions of water stress.

In view of such findings the possibility arises that plant performance during drought may be related quantitatively to the capacity to accumulate ABA. This possibility appears first to have been examined by Larqué-Saavedra and Wain (1974, 1976) who found varieties of maize and sorghum regarded as drought-resistant to accumulate more ABA under water stress (imposed on detached leaves) than did drought-susceptible types. Similar results have since been obtained by Ibragimov, Igamberdyeva, and Saidova (1978) with cotton and by Samet, Sinclair, and Cortes (1980) with soybean, but in each case only a few genotypes were compared, and the nature of the drought resistance was not defined precisely. Genotypic variation in ABA accumulation during water stress has recently been more extensively investigated in spring wheat (Quarrie, 1978a, 1980, 1981; Quarrie and Jones, 1979) and in rice (Henson, unpublished results). In both these cereals there appears to be a negative relationship between drought resistance (as assessed by yield performance and/or visual estimates of drought injury) and ABA accumulation. Possible reasons for such species differences have been discussed by Quarrie (1980).

The present work was concerned with identifying within-species variation in the ability to accumulate ABA in response to water stress, in pearl millet (*Pennisetum americanum* (L.) Leeke), a cereal of major importance in semi-arid tropical agriculture (Ferraris, 1973), and which is regarded as being highly drought-resistant. Identification of such intraspecific variation is a necessary preliminary to exploring its consequences for plant functioning and for yield performance under drought. The ability to accumulate ABA was evaluated both under laboratory conditions with detached leaves, and under field conditions in the semi-arid tropics using intact plants.

MATERIALS AND METHODS

Detached leaf tests

Plant culture. Seeds of pearl millet genotypes (*Pennisetum americanum* (L.) Leeke) obtained from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) were sown at Cambridge in John Innes no. 2 potting compost, three per 9·0 cm diameter pot. The seedlings were reduced to one plant per pot at the two-leaf stage.

Plants were grown in a controlled environment cabinet operated to give a 12 h photoperiod, a 27·5 °C day and a 25 °C night temperature. Relative humidity was maintained constant at 86 ± 2%. The light source, consisting of a combination of fluorescent tubes and incandescent lamps, provided a total irradiance of 120 W m^{-2} at plant height, 25% of which originated from the incandescent lamps.

Throughout growth, plants were kept well-watered by means of a water-conducting wick threaded through the base of each pot. The wicks were fed from troughs in which a constant depth of water was maintained by means of a float valve. Under these conditions plants were maintained at high water status, as evidenced by high values of leaf water potential (ψ) (c. −0·3 MPa) and relative water content (RWC) (c. 97–98%).

Imposition of water stress. The fifth leaf was selected on the day of ligule emergence (15–19 d after sowing depending on genotype), rapidly weighed to the nearest mg using an analytical balance, and exposed for about 10–15 min at room temperature to an air stream from a laboratory air blower

(Jencons (Scientific) Ltd., Hemel Hempstead, U.K.). Weight loss was monitored by reweighing the leaf at frequent intervals until a loss of $7 \pm 0.5\%$ of the initial fresh weight had been attained. Leaves were then individually placed in sealed tubes lined with moist filter paper. The amount of water to be added to the filter paper to minimize changes in leaf weight during incubation was determined by preliminary experimentation. Leaves were incubated in the dark at 28 °C for 5 h. Changes in weight during incubation were less than 1% of the initial fresh weight for the majority (93%) of samples. The procedure adopted has been shown to favour maximum ABA accumulation (Henson and Quarrie, 1981).

Apart from the drying treatment control leaves were incubated and otherwise handled in the same way as stressed samples.

Following incubation the leaves were divided longitudinally into two halves, each of which was immediately weighed. One half was used to determine relative water content (RWC) as described below, while the other was chopped into 2–3 mm slices which were rapidly frozen in liquid N_2 and stored at below -20 °C prior to ABA analysis.

Assessment of leaf water relations. RWC of leaves at the end of incubation was calculated for leaf halves as:

$$\text{RWC} = \frac{\text{fresh weight–dry weight}}{\text{turgid weight–dry weight}} \times 100.$$

Turgid weight was determined after imbibition of leaf portions in distilled water in sealed test tubes for 4 h at room temperature followed by overnight storage at 5 °C, and dry weight was determined after 48 h at 80 °C.

Changes in water potential and its components solute potential (ψ_s), and turgor potential (ψ_p) with loss of fresh weight were determined by a pressure-volume technique, using a procedure similar to that described by Wilson, Fisher, Schulze, Dolby, and Ludlow (1979) but with some modifications. Briefly, the method entailed making paired measurements for individual leaves of water potential (using a pressure chamber) and leaf weight. A leaf was initially enclosed by a plastic film ('Parafilm') to restrict evaporative losses, detached near the ligule, and its base inserted, with the leaf still in the plastic wrapping, through a slit rubber bung. After determining the initial balance pressure the leaf was weighed and immediately returned to the chamber for a further determination of ψ. This procedure was repeated until linearity between $1/\psi$ and weight loss was established and resulted in 7–8 points covering the full to zero ψ_p range. Reduction in ψ was promoted following the initial loss of turgor by removing the plastic wrapping from the leaf. 'Overpressure' was not used to promote water loss. Care was taken to increase and release chamber pressure slowly (<0.01 MPa s^{-1}) to minimize temperature changes.

Field experiments

Field experiments were conducted at ICRISAT Center, near Hyderabad, Andhra Pradesh, India (17°30′N) during the dry season (late January to May) in 1979 and 1980. In 1979, maximum day temperatures during March, when plants were sampled for ABA, ranged from 30 to 36 °C, minimum temperatures from 17 to 21 °C, and open pan evaporation from 7 to 10.5 mm per day. There was no rainfall during this period. Weather conditions during March 1980 were similar to 1979.

Experimental design. A split-plot design with irrigation (irrigated and droughted) treatments constituting main plots, and genotypes, sub-plots was adopted. The genotypes grown were chosen to represent a range in ability to accumulate ABA as shown in detached leaf tests. Each treatment × genotype combination was replicated three times. In the 1979 experiment each sub-plot contained four rows 0.75 m apart and 4 m long. Sampling was confined to the inner two rows. In 1980 sub-plots contained six 4 m rows at the same spacing with sampling being confined to the inner four rows. Genotypes were randomly located within main plots.

Cultural treatment. Seed was direct sown in late January on slightly raised ridges. The soil was a deep alfisol. Plants were subsequently thinned to about 10 cm apart within rows.

Irrigation was applied by flooding furrows between rows at approximately weekly intervals; continuously throughout crop growth in the case of the irrigated (control) treatment. To impose drought irrigation was withheld from the 11th day after sowing (DAS) in 1979 and from the 14th DAS in 1980.

Sampling for ψ and ABA content. Samples were taken at approximately weekly intervals on three

occasions in 1979 (36, 43, and 50 DAS) and on five occasions in 1980 (29, 36, 45, 52, and 59 DAS), following withholding water from the droughted plots. The youngest fully expanded leaf was selected from two randomly chosen plants per sub-plot on each occasion. Sampling was carried out between 11.30 and 12.30 h Indian Standard Time. The leaves were detached at the lamina base, enclosed between damp muslin to reduce evaporative losses, and transferred to a pressure chamber to determine ψ. Slightly different procedures were used in the two years. In 1979 leaves were first divided longitudinally, one half being used to measure ψ, while the other half was rapidly frozen by enclosing in a plastic bag and placing between blocks of solid CO_2. This portion was subsequently used for ABA analysis. In 1980, ψ was measured prior to dividing the leaf, and greater care was taken to minimize evaporative losses by keeping the leaf wrapped in damp muslin throughout measurement of ψ. One half of the lamina was used to determine ψ_p as described by Henson, Mahalakshmi, Bidinger, and Alagarswamy (1981*a*), while the other half was used for ABA analysis.

Analysis of abscisic acid

Leaf slices (detached leaf tests) were extracted in water:acetone (1:9, by vol.) using $1 \cdot 0$ ml solvent per 100 mg fresh weight. Field samples, after initial storage at below $-20\,°C$, were lyophilized, ground to a coarse powder, and extracted in the same solvent using $1 \cdot 0$ ml per 20 mg dry weight. Increasing the proportion of water in the solvent mixture used to extract dried samples did not affect recovery. All samples were initially homogenized using an ultrasonic disintegrator. Extracts were purified by thin-layer chromatography following the procedure of Quarrie (1978*b*).

RESULTS

Detached leaf tests

The ABA contents of unstressed leaves and of leaves subjected to a 7% loss of fresh weight were determined for 16 genotypes. The genotypes were of diverse genetic and geographic origin (Table 1) and growth habit. In all the genotypes ABA levels were low in unstressed leaves, being close to the lower limit of detection by the assay ($\simeq 10$ ng g^{-1} fresh weight), and ranged from 13 to 24 ng g^{-1} fresh weight. There were no significant differences between genotypes in the levels of ABA present in unstressed leaves, nor any significant correlation between these levels and those accumulated following water stress, and hence these data are not presented.

As a result of stress treatment the mean ABA content of all genotypes, expressed on the basis of initial fresh weight, increased 12-fold over the mean control level (mean for control leaves = 17 ng g^{-1} fresh weight, for stressed leaves = 201 ng g^{-1} fresh weight). Between genotypes, the ABA content of stressed leaves varied $4 \cdot 7$-fold (Table 1). Analysis of variance showed that the interaction, and the main effects of treatment and genotype, were all highly significant ($P < 0 \cdot 001$).

Although care was taken to impose a uniform degree of water loss (as measured by loss of fresh weight) and to maximize initial water content of the plants, there were small but significant ($P < 0 \cdot 05$) differences between genotypes in the RWC of stressed leaves, ABA content being negatively correlated ($r = -0 \cdot 44$, $P < 0 \cdot 001$) with RWC. However, allowing for such differences by covariance analysis did not greatly change the significance of the variance ratio for genotypes, and substantial genotypic differences were still present (Table 1).

Differences between genotypes in the ability to accumulate ABA might, nevertheless, have arisen from differences in ψ or, more probably, ψ_p (Pierce and Raschke, 1980) between genotypes. Such differences could be present even if equal reductions in fresh weight of initially turgid leaves were achieved. This aspect was

T A B L E 1. *The accumulation of ABA in detached leaves of 16 pearl millet genotypes*

Genotypes are ranked in order of ABA accumulation (adjusted means). Data are means of six replicates. Means assigned the same letter are not significantly different at $P = 0.05$ (Duncan's multiple range test). BJ 104 was tested on three separate occasions, designated (1), (2), (3).

Genotype	Genetic constitution	Country of origin	ABA accumulation (ng g^{-1} initial fresh weight)	
			Unadjusted	Adjusted for RWC
Kano Gero 40	Breeding line	Nigeria	119 ab	129 a
BK560	F$_1$ hybrid	India	91 a	131 a
BJ 104 (1)	F$_1$ hybrid	India	142 abc	147 a
B282[a]	Germplasm accession	Botswana	150 abc	148 a
SCI	Breeding composite	Uganda	145 abc	156 a
IP2788	Germplasm accession	Chad	160 abc	157 a
BJ 104 (2)	F$_1$ hybrid	India	159 abc	158 a
700112-5	Breeding line	Nigeria	164 abc	171 a
Ex Bornu	Landrace population	Nigeria	173 abc	175 a
BJ 104 (3)	F$_1$ hybrid	India	194 abc	175 a
700256	Breeding line	Nigeria	172 abc	177 a
B211[a]	Germplasm accession	Unknown	197 abc	195 a
700251	Breeding line	Nigeria	211 bc	209 ab
Mali NKK	Open pollinated variety	Mali	232 cd	221 ab
B816[a]	Germplasm accession	Unknown	238 cd	233 abc
WC9-27	Composite progeny	Nigeria	328 d	307 bc
½ Hainei Khirei	Open pollinated variety	Niger	320 d	324 c
Serere 39	Breeding line	Uganda	430 e	413 d

[a] IP (International Pennisetum) lines, redesignated B (Bankok) lines in Thailand.

thus investigated using BJ 104 (a 'low' ABA accumulator), and Serere 39 (a 'high' accumulator) by (a) comparing ABA accumulation by the two genotypes over a range of reductions in initial fresh weight (0–15%), and (b) evaluating relationships between ψ, ψ_p, and RWC and fresh weight loss, using a pressure–volume technique. The latter approach failed to reveal any significant differences between the two genotypes in the shape of the curves relating ψ and ψ_p to water content (Fig. 1). Except in unstressed leaves, Serere 39 accumulated more ABA than BJ 104 at all levels of ψ (Fig. 2A). Further, there was a consistent difference in accumulation ability between the genotypes over a range of turgor (Fig. 2B). The curves relating ABA accumulation to RWC (not presented), were similar to those in Fig. 2A.

Field experiments

Six genotypes were sampled in 1979 for leaf ψ and ABA. During the sampling period ψ declined progressively in both irrigated and non-irrigated plants from -1.44 and -1.70 MPa respectively at 36 DAS to -1.56 and -2.10 MPa 50 DAS (values meaned over all genotypes), the changes being significant at $P < 0.05$ and 0.001 respectively. On each occasion treatment differences were significant ($P < 0.05$). There was a highly significant ($P < 0.001$) effect of genotype on ψ 36 DAS
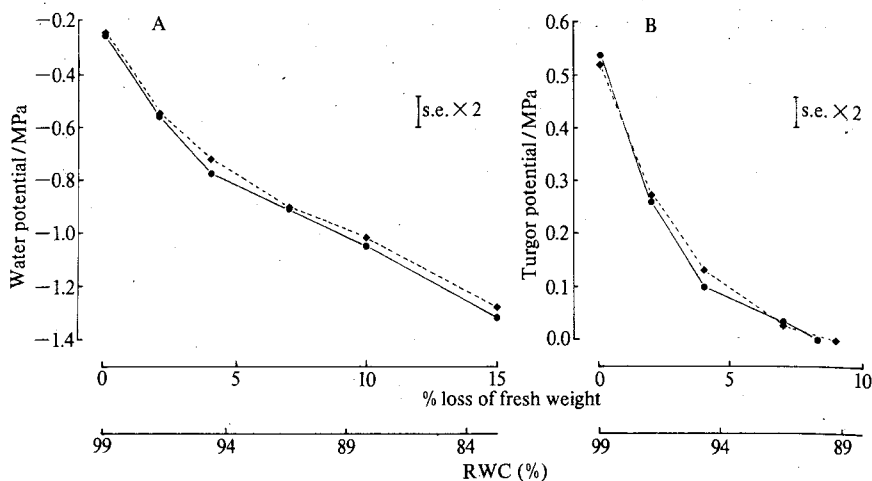
FIG. 1. Relationships between ψ and water content (A), and ψ_p and water content (B), for the fifth leaf of pearl millet genotypes BJ 104 ($\blacklozenge$) and Serere 39 ($\bullet$) as determined by a pressure–volume technique. Points, means of six, were derived by interpolating individual curves of $1/\psi$ versus fresh weight loss at positions corresponding to 0, 2, 4, 7, and 10% reduction in initial fresh weight, and (for B) at zero ψ_p.
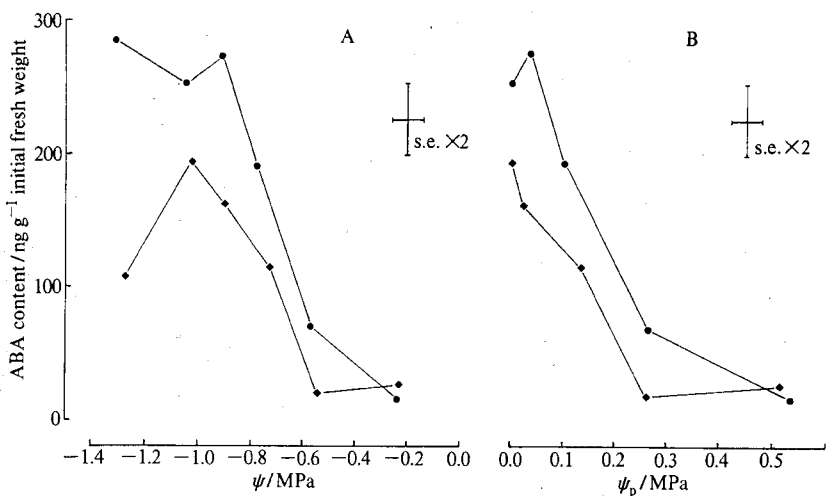

FIG. 2. Relationships between ABA content and ψ (A), and ABA content and ψ_p (B), for the fifth leaf of pearl millet genotypes BJ 104 ($\blacklozenge$) and Serere 39 ($\bullet$). Points are means of six.

when mean ψ of B816 and 1/2 Hainei Khirei (1/2 HK) were higher than other genotypes. However, these genotype differences in ψ had disappeared by the last sampling date when all six genotypes exhibited similar mean leaf ψ (the range being -1.44 to -1.64 MPa for irrigated, and -1.99 to -2.24 MPa for droughted plants). Averaging ψ over all sampling dates it was found that B816, BJ 104, and 1/2 HK maintained a significantly ($P < 0.05$) higher ψ than Mali NKK which had

TABLE 2. *Leaf water potentials (MPa) and ABA contents (ng g^{-1} dry weight) of six pearl millet genotypes grown in the field*

Data are means for samples taken 36, 43, and 50 d after sowing from plants grown near Hyderabad, India during the 1979 dry season. The analyses were done using data for individual leaves harvested on the three occasions.

Genotype	Leaf water potential			Leaf ABA content		
	Control	Droughted	Mean	Control	Droughted	Mean
BJ 104	−1·54	−1·81	−1·68	139	398	269
BK560	−1·51	−2·02	−1·77	197	558	377
Serere 39	−1·52	−1·94	−1·73	249	796	523
B816	−1·46	−1·88	−1·67	146	691	419
Mali NKK	−1·59	−1·98	−1·79	144	632	388
1/2 HK	−1·48	−1·90	−1·69	237	794	515
Mean	−1·52	−1·92	−1·72	185	645	415
LSD ($P = 0.05$)						
Treatment		0·071			103	
Genotype		0·088			77	
Interaction		not significant			130	

the lowest mean value (Table 2). However, there was no significant interaction between treatment and genotype in the maintenance of leaf ψ.

Drought resulted in a substantial increase in levels of ABA in leaves of all genotypes (Table 2). Averaged over genotypes, ABA levels changed little between sampling dates; grand means (both treatments) being: 430 ng g^{-1} dry weight 36 DAS, 424 ng g^{-1} dry weight 43 DAS, and 391 ng g^{-1} dry weight 50 DAS. There were highly significant ($P < 0.001$) differences in ABA content between genotypes on the first two sampling occasions but not on the third occasion (50 DAS) when varietal differences were smaller and standard errors larger. However, the ranking of genotypes for ABA content on this date was very similar to the previous occasion (43 DAS), and the correlation between ABA levels of individual genotypes on the two occasions was highly significant ($r = 0.94$, $P < 0.01$).

Averaging over all sampling occasions there was a strong effect of genotype, as well as of treatment, on ABA content, together with a significant ($P < 0.001$) genotype × treatment interaction. In droughted plants ABA levels were highest in Serere 39 and 1/2 HK, intermediate in B816 and Mali NKK, and lowest in BK 560 and BJ 104. Serere 39 and 1/2 HK also accumulated the most ABA in the control.

Adjustment of data by means of covariance analysis, to allow for differences in leaf ψ, did not significantly change the mean ABA contents of the genotypes. The level of significance of genotypic differences in ABA content was unaffected by such adjustment. This suggests that variations in ABA accumulation between genotypes did not arise because of differences in ψ.

ABA content was significantly negatively correlated with ψ for each genotype (Table 3) while linear regressions of ABA content on leaf ψ showed an improvement

TABLE 3. *Correlation (r) and linear regression (β) coefficients relating ABA content to leaf water potential of six pearl millet genotypes*

Data ($\pm$s.e.) refer to samples of pearl millet leaves taken 36, 43, and 50 d after sowing (DAS) from plants in the field near Hyderabad, India during the 1979 dry season. Statistical significance at $P < 0.05$, <0.01 and <0.001 is indicated by *, **, and *** respectively. d.f. for genotypes (all dates) = 34, and for dates (all genotypes) = 70.

Genotypes (all dates)	r	$\beta \pm$ s.e. (ng ABA g^{-1} dry weight MPa^{-1})
BJ 104	-0.49**	337 ± 103
BK560	-0.52***	404 ± 114
Serere 39	-0.74***	878 ± 138
B816	-0.56***	529 ± 135
Mali NKK	-0.73***	769 ± 124
1/2 HK	-0.54***	630 ± 166
Dates (all genotypes)		
6/3 (36 DAS)	-0.52***	653 ± 129
13/3 (43 DAS)	-0.65***	750 ± 106
20/3 (50 DAS)	-0.71***	666 ± 79

in goodness to fit with time. Genotypic differences in ABA content were reflected in the slopes of the regression equations, with BJ 104 having the shallowest, and Serere 39 the steepest, slope. Slopes of these two genotypes differed significantly ($P < 0.01$). The slope of BJ 104 was also significantly ($P < 0.05$) less steep than that of Mali NKK, but did not so differ from the remaining genotypes.

In the field experiment in 1980, three genotypes (BJ 104, Serere 39, B282) were compared and both ψ and ψ_p were measured. There were significant differences between genotypes in the slope (β) of linear regressions relating (i) ABA to leaf ψ and (ii) ABA to ψ_p (Fig. 3). For the former relationship the slope for Serere 39 was significantly ($P < 0.001$) steeper than that of either BJ 104 or B282. For the regression of ABA on ψ_p, although the ranking of genotypes for the magnitude of β was the same as with ABA v ψ, differences in β were only significant ($P < 0.001$) comparing Serere 39 with B282. When genotype differences in ψ_p and ψ were allowed for by covariance analysis (Table 4), the significance of the large difference in mean ABA contents of droughted plants, between Serere 39 and both the other two genotypes, was not affected.

Correlations between the detached leaf test and field experiments

For the genotypes in the 1979 field experiment the correlation between the mean amounts of ABA accumulated by stressed, detached leaves (adjusted for RWC), and the mean amounts detected in leaves of droughted plants in the field (adjusted for ψ), was significant ($r = 0.86$, $P < 0.05$). For the 1980 field experiment, as shown in Table 4, there was a close relationship between the mean amounts of ABA accumulated by the three genotypes in the field, and that accumulated in a further detached leaf test (cf. also data in Table 1).
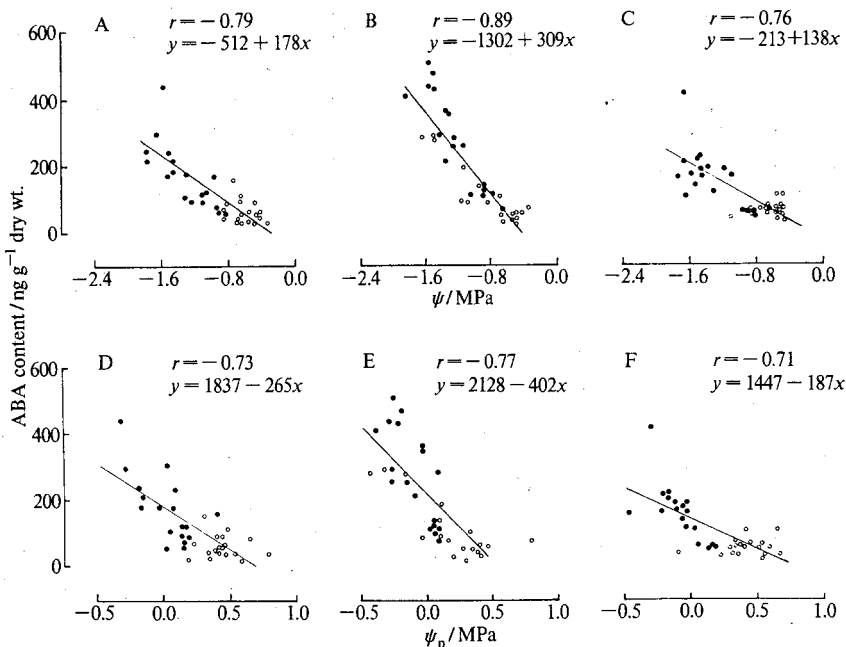
FIG. 3. Relationships between leaf ABA content and ψ (A, B, C), and leaf ABA content and ψ_p (D, E, F) for pearl millet genotypes BJ 104 (A, D), Serere 39 (B, E) and B282 (C, F) grown in the field in 1980 with (O) or without (●) irrigation. Correlation coefficients (r) are given for each graph; d.f. = 34. Lines are fitted linear regressions.

TABLE 4. *The relative capacity of three pearl millet genotypes to accumulate ABA in response to water stress; detached leaves compared with intact plants in the field*

ABA accumulation in detached leaves was determined after incubation at 28 °C in darkness for 5 h at a 7% loss of initial fresh weight. ABA contents of attached leaves are means for unirrigated plants grown in the field near Hyderabad, India, during the 1980 dry season, and sampled 45, 52, and 59 d after sowing. The data were adjusted for differences in Ψ or Ψ_p by covariance analysis.

Genotype	Detached leaves (ng ABA g^{-1} fresh wt.)	Attached leaves (ng ABA g^{-1} dry wt.)		
		Unadjusted	Adjusted for Ψ	Adjusted for Ψ_p
BJ 104	253	176	175	195
B282	209	165	158	155
Serere 39	483	277	285	267
LSD ($P = 0.01$)	120·1	61·9	59·1	59·2

DISCUSSION

The accumulation of ABA in response to water stress is a variable phenomenon which may be influenced by several factors. In pearl millet large variations in the amount of ABA accumulating in detached leaves can occur within a single

genotype, and accumulation is affected by environmental conditions both before and after detachment, as well as by leaf age (Henson and Quarrie, 1981; Quarrie and Henson, 1981; Henson, unpublished results). Thus, differences observed between genotypes need to be regarded with some caution until they are shown to be sustained under different conditions. The present study has indicated that for certain genotypes of pearl millet there is a consistent relationship between the amount of ABA accumulated in detached leaves following a rapidly-induced water deficit, and the amount of the hormone found in leaves of intact plants experiencing a slowly developing water stress under field conditions. As far as we are aware this is the first report of such a comparison. This result suggests that the detached leaf procedure provides a useful indication of differences likely to be encountered in intact, field-grown plants of pearl millet and that it can usefully be employed as an initial step in locating genotypic variation in the ability to accumulate ABA.

The differences between Serere 39, which accumulated high levels of ABA, and BJ 104 and B282, both of which had a lower accumulation capacity, were confirmed on a number of occasions in both laboratory and field experiments, and were shown not to be due to differences in leaf ψ (Figs 2, 3; Tables 3, 4) or ψ_p (Figs 2, 3; Table 4). In the field the above three genotypes differed in the ability to maintain turgor at a given ψ. This was a consequence of their differing capacity to adjust osmotically in response to water stress (Henson *et al.*, 1981*a*). Although a greater loss of turgor was observed in Serere 39 than in either BJ 104 or B282, this did not account for the enhanced capacity of this genotype to accumulate ABA (Table 4). However, as measured, ψ and ψ_p are bulk properties of the whole laminae and it is possible that local differences in the ψ and/or ψ_p of individual cells or tissues might account for the observed genotypic variation in ABA accumulation.

Differences in the capacity to accumulate ABA could arise from variation in the rate of ABA synthesis or in the rate of metabolism, or both. There are few definitive experiments (Walton, 1980) indicating which of these processes controls ABA accumulation and there are no data for pearl millet. Exploitation of genotypic differences may be useful for investigation of this problem.

Differences in ABA accumulation between BJ 104 and Serere 39 were not apparent when ABA content was determined during the course of rapid drying imposed by detaching the shoot from the root system (Henson, 1981). The absence of genotypic differences following this treatment contrasts with the results from both the detached leaf test in which stress is *more* rapidly imposed (but is then maintained constant for several hours), and the intact plants in the field where stress develops slowly. The reason for this disparity is unclear, but it may involve the lack of opportunity afforded in the detached shoot experiment for the 'system' governing ABA accumulation to 'equilibrate' with the rapid and continuous changes in ψ.

Whether the differences observed between genotypes in the ability to accumulate ABA are of functional significance is currently under investigation. Data on stomatal responses to water stress (Henson *et al.*, 1981*b*) do suggest that the ability to accumulate high levels of ABA results in a reduction in water use due to a reduced stomatal conductance during stress.

Whether the genotypic differences observed in the ability to accumulate ABA are also related to general agronomic performance under drought cannot, however, be answered with any certainty at present. Insufficient data are available on the drought 'resistance' of the genotypes, and objective and quantitative assessment of such resistance is extremely difficult (Hanson and Nelson, 1980). For the field experiment conducted in 1979, genotypes accumulating most ABA also displayed the greatest yield stability under drought (i.e. a smaller percentage reduction in total grain yield; results not presented). Further work is, however, necessary, both to confirm this result and to investigate the reasons for any such association.

The cross-pollinating nature of the species inevitably leads to appreciable potential variability in pearl millet within existing genotypes, some of which are, in any case, 'populations' (Table 1). This adds to the difficulties of determining between-genotype differences. During testing, substantial variation in ABA accumulation by individual plants was occasionally detected. If found to be heritable this variation could be exploited to determine the significance of such differences for water use and performance under drought. Alternatively, genotypes of contrasting capacity for ABA accumulation, such as identified here, could be utilised in a breeding programme for the same purpose, as has been done for spring wheat (Quarrie, 1981). These possibilities are currently under investigation.

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