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Diurnal Changes in Endogenous Abscisic Acid in Leaves of Pearl Millet (*Pennisetum americanum* (L.) Leeke) under Field Conditions

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ABSTRACT

Diurnal variation in leaf abscisic acid (ABA) content was investigated in pearl millet (*Pennisetum americanum* (L.) Leeke) growing in the field in the semi-arid tropics and subjected to varying degrees of water stress.

There was a two- to three-fold change in ABA content during the photoperiod in three groups of 'severely' stressed plants of the genotype BJ 104. Maximum ABA occurred mid-morning (1030 h). ABA levels then declined to a minimum at 1500 h. Changes in ABA content of 'moderately' stressed and fully irrigated plants were smaller, but still significant. Though, when averaged over the day, levels of ABA of the five groups were positively related to the degree of water stress, relationships between ABA concentration and total water (Ψ) or turgor (Ψ_p) potentials varied considerably with time of sampling. Within groups, changes in ABA contents during the day were not always accounted for by changes in Ψ or Ψ_p.

Temporal changes in leaf ABA content similar to those found in BJ 104, and largely unrelated to Ψ, were observed in the genotypes Serere 39 and B282 in a subsequent year.

Leaf ABA content of droughted plants (BJ 104) did not decline appreciably overnight despite a marked increase in Ψ. However, a large reduction in ABA content with increase in Ψ did occur following heavy rainfall.

Diurnal changes in stomatal conductance (g_l) of BJ 104 could not be simply accounted for by temporal changes in total leaf ABA content, even when allowance was made for effects of irradiance and other environmental variables on g_l. It is suggested that the sensitivity of stomata to ABA, or accessibility of the hormone to the stomatal complex, changes during the day.

INTRODUCTION

The dramatic increase in levels of abscisic acid (ABA) in plants exposed to water stress has been observed in many experiments (Milborrow, 1974; Wright, 1978; Walton, 1980). Most such experiments have involved container-grown plants cultured in protected environments. Relatively few studies have been conducted to determine changes in ABA concentrations in plants grown in the field, although it is known that plant responses to water stress in the field may differ considerably from those in a glasshouse or growth chamber (Begg and Turner, 1976). The few investigations reported (McMichael and Hanny, 1977; Quarrie, 1980;

Henson, Mahalakshmi, Bidinger, and Alagarswamy, 1981*b*), show that ABA contents, even of severely stressed plants, are considerably lower in the field than in protected environments.

The factors which influence the ABA content of plants growing in the field have yet to be fully evaluated. Thus, relatively little information is available concerning relationships between ABA content and leaf water status in the field. There are also few published data on the relationships under field conditions, between ABA content and stress-induced responses such as stomatal closure.

Diurnal variation in water status can be pronounced under field conditions but it is uncertain to what extent this variation influences ABA content. Studies with several species suggest, however, that significant changes in ABA content can occur during the course of the day (Hiron, 1974; McMichael and Hanny, 1977; Davies and Lakso, 1978; Simpson, Durley, Kannangara, and Stout, 1979; Quarrie, 1980; Xiloyannis, Uriu, and Martin, 1980).

In the present study we examine diurnal changes in ABA in leaves of pearl millet (*Pennisetum americanum* (L.) Leeke) growing in the field in the semi-arid tropics, and relate the data to leaf water status and leaf conductance. Further aspects of crop water relations studied in the present experiments are described elsewhere (Henson *et al.*, 1981*a*, *b*; Henson, Alagarswamy, Bidinger, and Mahalakshmi, 1982).

MATERIALS AND METHODS

Experiments were conducted in the field at ICRISAT (International Crops Research Institute for the Semi-arid Tropics) Center, near Hyderabad, India, in the dry season (February to May) of 1980 and 1981.

In 1980, measurements of ABA content, leaf water potential (Ψ), osmotic potential (Ψ_s), and leaf conductance (g_l), were made on single, upper, fully expanded leaves of pearl millet (*Pennisetum americanum* (L.) Leeke) genotype BJ 104. Samples were taken from five groups of plants, one of which was fully (weekly) irrigated (treatment 1) while the remaining four groups experienced varying degrees of drought stress prior to sampling. Plants receiving treatments 1 and 2 (the latter being the least stressed of the droughted treatments in terms of leaf Ψ) were grown on a deep alfisol soil (site 1), while the remaining three groups were grown at a separate site (site 2) on a shallower soil which exacerbated the effects of water shortage. Plants at site 2 received water from a line source sprinkler system (Hanks, Keller, Rasmussen, and Wilson, 1976), with decreasing amounts from treatments 3–5. All three treatments were water stressed at the time of sampling (Fig. 2B). Although plants at the two sites were sown on different dates (24th January, site 1; 5th February, site 2), plants at both sites were the same age when sampled (43 d after sowing).

In 1981, three genotypes, BJ 104, B282, and Serere 39, subjected to drought stress, were similarly sampled but for Ψ and ABA content only. BJ 104 was irrigated with varying amounts of water using the line source sprinkler; for the other genotypes, water was withheld completely following stand establishment 14 d after sowing.

Conductance was measured on both surfaces of the leaf using an automatic diffusion resistance porometer (Mark II, Delta-T Devices, Burwell, U.K.). The separate conductances obtained were summed to give a total g_l. To determine Ψ the leaf was enclosed in moist muslin, excised just above the ligule, and rapidly transferred to a pressure chamber. The muslin wrapping was left in position throughout the operation to minimize evaporative losses and adiabatic heating. After removal from the pressure chamber the leaf was frozen by encasing between blocks of solid CO_2 (1980), or by immersion in liquid nitrogen (1981). In 1980 the leaves were divided longitudinally and the two halves frozen separately, one half being used to determine Ψ_s and turgor potential (Ψ_p), while the other portion was used for analysis of ABA.

Ψ_s was determined using a Roebling micro-osmometer (Camlab Ltd., Cambridge, U.K.) to measure cryoscopically the osmolality of sap expressed after thawing the frozen leaf portions. Ψ_p was calculated as the difference between Ψ and Ψ_s.

Samples for ABA analysis were stored temporarily at −20 °C, lyophilized, and the ground, dried material was later extracted in acetone:water (9:1, v/v) using 1·0 ml per 20 mg dry weight. Aliquots of the extract supernatant were analysed for free ABA using the procedure of Quarrie (1978).

Total irradiance (ca. 300–3000 nm), leaf temperature, and atmospheric vapour pressure deficit were determined as previously described (Henson *et al.*, 1982).

RESULTS

Changes in ABA content and leaf water status during the day

For BJ 104 sampled in 1980, an indication of the degree of water stress imposed by the different drought treatments was obtained by measuring mean plant height at time of sampling. Height decreased with decreasing water supply and was directly related to the minimum mid-day Ψ (Fig. 1A).

The mean ABA content for each treatment (i.e. mean of all harvests on the day of sampling) was likewise related to the minimum Ψ (Fig. 1B), with the least stressed plants having the lowest ABA levels. Data shown in Fig. 1B resemble those obtained by sampling plants at mid-day on a weekly basis during the development of drought stress (Henson *et al.*, 1981*a*).

All treatments exhibited significant changes in ABA content during the day (Fig. 2A). For the two treatments at site 1 (1 and 2), ABA levels were low (<175 ng g^{-1} dry weight) and changes were smallest (1·8-fold) ($P < 0{\cdot}05$). For treatments 3–5, however, ABA levels were

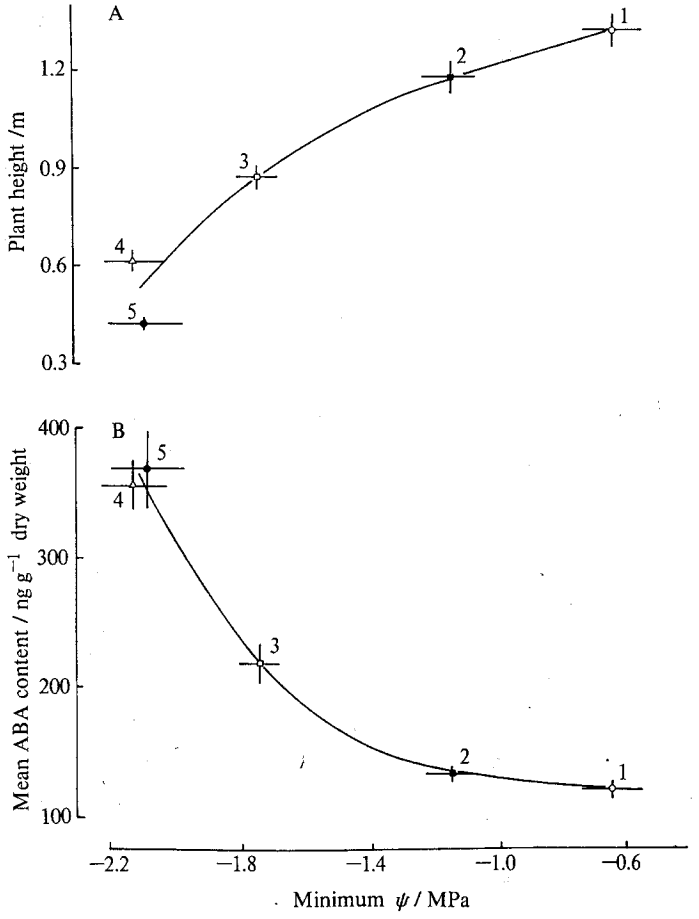

FIG. 1A. The relationship between plant height, (an indicator of drought-stress history), and the minimum mid-day Ψ. B. The relationship between the mean ABA content of upper, fully expanded leaves and the minimum mid-day Ψ. Data are for genotype BJ 104 sampled in 1980, 43 d after sowing. Plant heights were determined at 6 randomly chosen positions amongst plants sampled for ABA. Treatments are numbered 1–5 (see text), and represent decreasing water availability during growth. Bars on symbols indicate 2 × s.e. mean. Curves were fitted by eye.

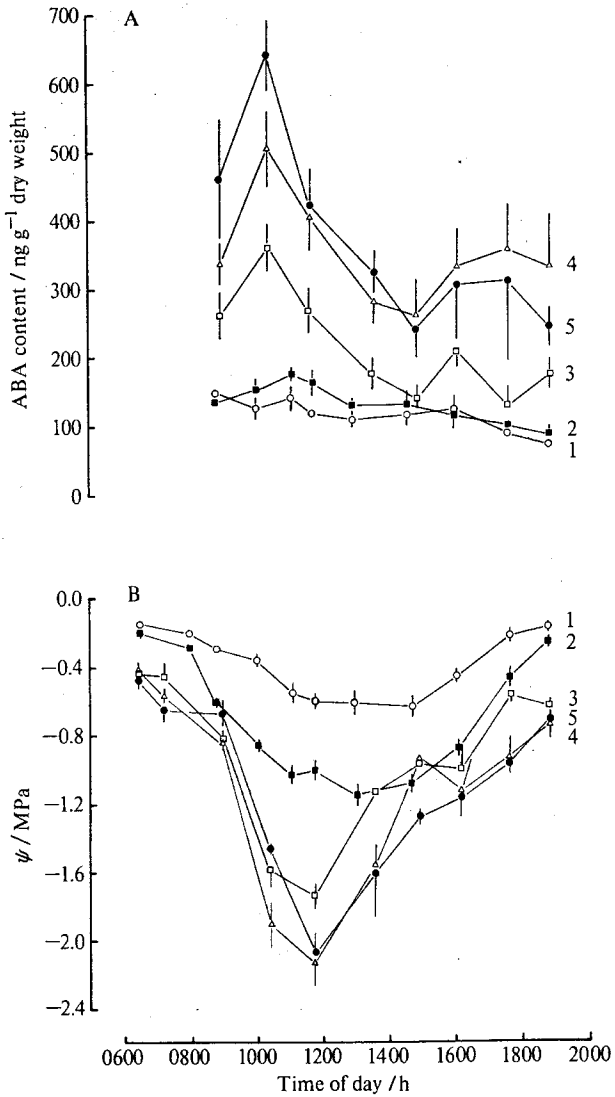

FIG. 2. Changes in (A) ABA content and (B) Ψ, of upper, fully expanded leaves of five groups of BJ 104 during the photoperiod. Treatments (see text) are numbered 1–5. Data are means for six (treatments 3–5) or four leaves (treatments 1, 2). Vertical bars, where they exceed the size of the symbols, indicate 2 × s.e. mean.

much higher and a 2–3-fold variation in ABA content occurred with time of day, significant at $P < 0{\cdot}01$ (treatment 4) or $P < 0{\cdot}001$ (treatments 3, 5). Patterns of change were similar for these latter three treatments.

Within treatments, the temporal changes in ABA content were not always closely related to Ψ or Ψ_p. Although ABA contents were at a maximum in samples taken at 1030 h (treatments 3–5) or 1110 h (treatments 1, 2) in line with falling Ψ and Ψ_p at these times (Fig. 2B; Henson *et al.*, 1982), the ABA levels then declined even though potentials were still falling and minimum Ψ and Ψ_p were not reached until 1200 h or later. Correlations between ABA content and both concurrent Ψ and Ψ_p using pooled diurnal data, were most significant in treatments with intermediate levels of stress and ABA concentration (Table 1).

TABLE 1. *Correlation between leaf ABA content and Ψ, Ψ_p and g_l for five groups of pearl millet BJ 104 during the course of a photoperiod*

Data are correlation coefficients (r) calculated for individual leaves from all sampling occasions. Significance of r at $P < 0.05$ (*), < 0.01 (**) and < 0.001 (***) is indicated; n.s. = not significant. d.f. = 34 (treatments 1, 2) or 46 (treatments 3, 4, 5). The correlation between ABA and g_l was calculated after logarithmic transformation of ABA data.

Treatment[a]	ABA vs Ψ	ABA vs Ψ_p	Ψ_p vs Ψ	ABA vs g_l
1	−0·27$^{n.s.}$	−0·43**	0·79***	0·40*
2	−0·41*	−0·53***	0·90***	0·36*
3	−0·60***	−0·63***	0·91***	0·49***
4	−0·43**	−0·41**	0·94***	0·14$^{n.s.}$
5	−0·16$^{n.s.}$	−0·06$^{n.s.}$	0·94***	0·45**

[a] For details see text.

Examination of combined data for treatments 1–5 showed that relationships between ABA content and Ψ at different sampling times were not constant but changed dramatically during the course of the photoperiod (Fig. 3). At 0900 h (3 h after dawn) ABA content was largely independent of Ψ, while with the approach of mid-day a significant negative relationship was established between ABA content and Ψ, similar to that obtained using mean values for the whole day (Fig. 1B). In the afternoon hours, while Ψ increased, ABA contents declined only slightly. This resulted in a given ABA concentration being associated with progressively higher values of Ψ as the photoperiod progressed. Only at 1150 h was ABA significantly ($P <$

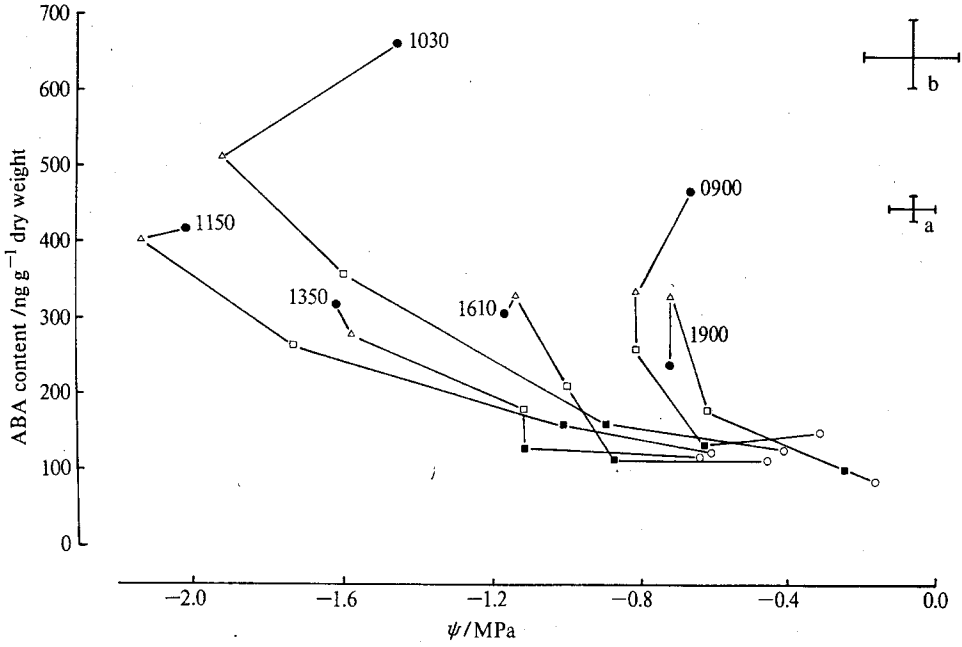

FIG. 3. Relationships between leaf ABA content and leaf Ψ for upper, fully expanded leaves of BJ 104 at different times during the photoperiod. Symbols for treatments are as in Figs 1 and 2. Times of sampling (h) are indicated. Data for samples taken at 1500 h and 1750 h are omitted for clarity. Some values for treatments 1 (○) and 2 (■) were obtained by interpolation (Fig. 2). Bars indicate 2 × pooled s.e. mean for (a) treatments 1 and 2 (○, ■,) and for (b) treatments 3–5 (□, △, ●).

0·001) negatively correlated with Ψ. Relationships between ABA and Ψ_p (not presented) were similar to those between ABA and Ψ.

Droughted plants of genotypes B282 and Serere 39 sampled in 1981 exhibited changes in leaf ABA content during the day somewhat similar to those of BJ 104 (Figs 4A and B). ABA levels again reached a peak in mid-morning before declining to a minimum during the afternoon despite Ψ remaining low throughout this period. The rise in Ψ which occurred towards the end of the photoperiod was, moreover, accompanied by an *increase* in ABA in both genotypes. As with BJ 104, therefore, the changes in ABA were not obviously related to the prevailing leaf water status assessed in terms of Ψ.

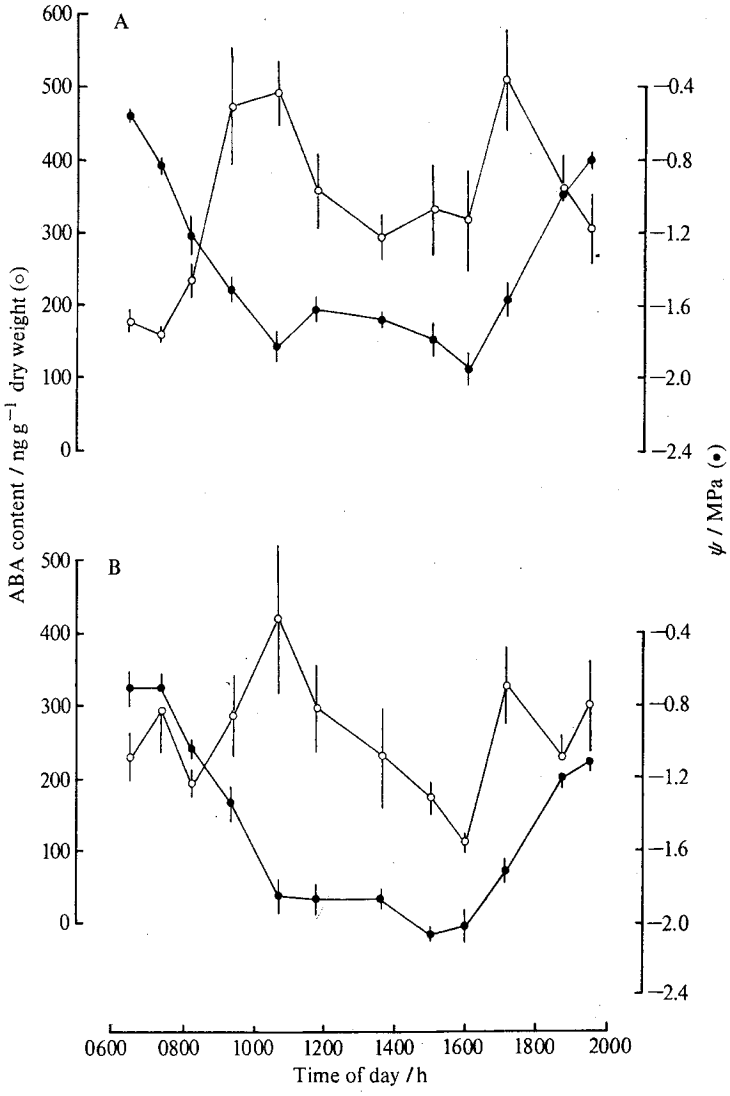

FIG. 4. Changes in ABA content (○) and Ψ (●) of upper, fully expanded leaves of droughted plants of (A) Serere 39 and (B), B282, during the photoperiod. Data are means for six leaves. Vertical bars indicate 2 × s.e. mean. Plants were sampled on 2/4/81, 63 d after sowing.

Effect of overnight rehydration and rewatering on ABA content

Changes in Ψ and ABA content overnight were examined in BJ 104 plants in 1981. Unseasonal rainfall (38 mm) between 1500 h and 2000 h the day following the start of sampling provided an opportunity to assess the effect of rewatering on ABA content.

While there was a gradual increase in leaf Ψ during the night the mean ABA level at around dawn did not differ significantly from that 12 h previously (Table 2). Conversely, rainfall, though only raising Ψ to an extent similar to that promoted by a night period, did result in a significant reduction in ABA content.

TABLE 2. *Changes in Ψ and ABA content of upper, fully expanded leaves of pearl millet BJ 104 overnight and following rewatering*

Plants were sampled at four positions along a water supply gradient resulting in a range of Ψ on any one sampling occasion. As the separate positions exhibited similar trends and there was no significant position × time interaction, data from all positions are combined for clarity. Values given are means for 16 leaves. The photoperiod was approximately 12 h (0600 h–1800 h). Plants were 51–53 d old when sampled.

Date and time of sampling[a]		Ψ (MPa)	ABA content (ng g^{-1} dry weight)
10/3/81	1800 h	−1·24	615
	2400 h	−0·67	702
11/3/81	0600 h	−0·52	538
	0900 h	−1·36	527
	1200 h	−1·77	565
12/3/81	0900 h	−0·79	222
LSD ($P = 0·05$)		0·17	141

[a] 38 mm rain fell between 1500 and 2000 h on 11/3/81.

Stomatal conductance and its relation to ABA content

Stomatal conductance was determined for genotype BJ 104 in the 1980 experiments. As reported elsewhere (Henson *et al.*, 1982) temporal changes in g_l were most closely related to changes in irradiance and were only partly dependent on leaf water status. High ABA levels in the morning were not, therefore, associated with appreciable stomatal closure at this time. Stomata opened in the morning as irradiance increased (and ABA levels were high) and generally closed after mid-day, at a time when ABA levels were declining. Thus, when significant correlations over time were obtained between ABA content and conductance, within treatments these were all *positive* (Table 1). Even allowing for the effects of irradiance and other variables (leaf vapour pressure deficit, Ψ, Ψ_p, leaf temperature) on g_l using multiple linear regression analysis, no significant negative relationships between g_l and ABA over time were revealed, and, as previously shown (Henson *et al.*, 1982), temporal changes in g_l were largely a function of irradiance and vapour pressure deficit. Significant *negative* correlations between g_l and ABA did, however, exist for individual sampling times across treatments. As for the relationships between ABA content and Ψ, those between g_l and ABA were not constant but changed in a systematic way with time of day (Fig. 5).

DISCUSSION

Large diurnal changes in ABA content were observed in leaves of pearl millet plants subjected to water stress. While it is not known how typical the observed changes are, or how they might vary with climatic conditions, similarly phased changes in ABA content have also been

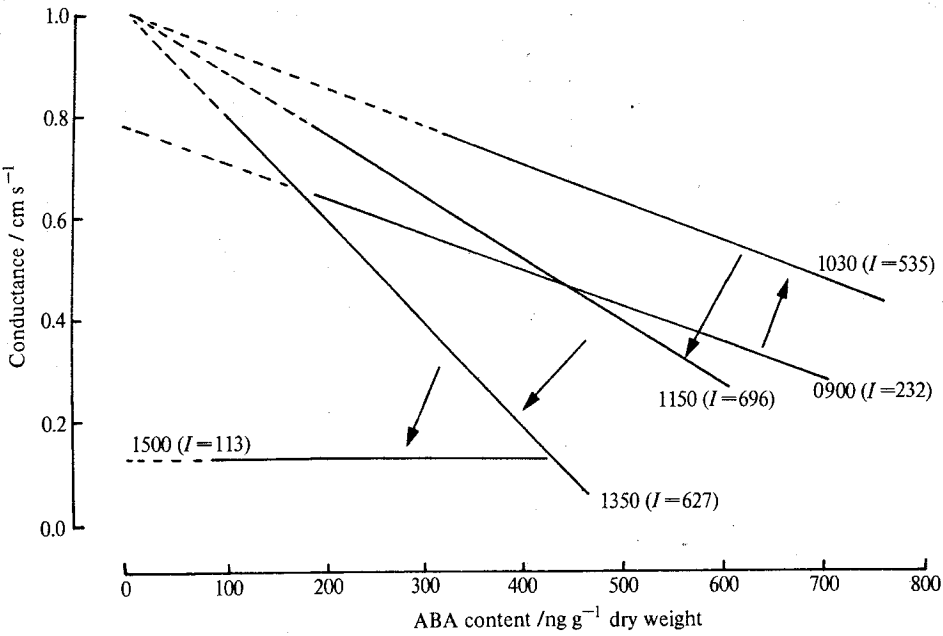

FIG. 5. Relationships between total leaf conductance (g_l) and leaf ABA content for upper, fully expanded leaves of BJ 104 at different sampling times during the photoperiod. Lines are fitted linear regressions for individual leaves of treatments 3–5 only, sampled 43 d after sowing. Solid portions indicate range of data, dashed portions are extrapolations to zero ABA. Data points are omitted for clarity. Times of sampling (h) and mean irradiances (I, W m^{-2}) are indicated for each line. Correlation coefficients (r) and levels of significance were: 0900 h, $r = -0{\cdot}58$, $P < 0{\cdot}05$; 1030 h, $r = -0{\cdot}57$, $P < 0{\cdot}05$; 1150 h, $r = -0{\cdot}58$, $P < 0{\cdot}05$; 1350 h, $r = -0{\cdot}68$, $P < 0{\cdot}01$; 1500 h, $r = 0{\cdot}04$, not significant. Regressions for later sampling times were similar to that for 1500 h.

reported to occur in leaves of wheat (Quarrie, 1980) and sorghum (Simpson *et al.*, 1979) subjected to water stress.

ABA contents of pearl millet determined at mid-day at weekly intervals as drought stress intensified, were previously shown to be closely related to the degree of water stress (Henson, *et al.*, 1981*a*, *b*). The same was true in the present study for mid-day samples of BJ 104 (Fig. 3), or when mean ABA contents for the whole photoperiod were related to minimum mid-day Ψ (Fig. 1B). By contrast, short-term changes in ABA during the photoperiod (Figs 2 and 4) could not be entirely accounted for in terms of simple linear regressions of ABA on leaf Ψ or Ψ_p. Neither were increases in Ψ during the night accompanied by the expected decline in ABA content (Table 2).

Although water stress is a major factor determining ABA content of leaves of mesophytic species, there are nevertheless a number of reasons why leaf ABA content may be apparently 'uncoupled' from leaf water status. Thus, changes in the amount of ABA exported from the leaf, movement of ABA between cells or sub-cellular compartments with differing metabolizing capacities, differences in temperature coefficients of enzymes involved in synthesis and metabolism of ABA, together with time lags between changes in Ψ or Ψ_p and their effects on ABA content, could all explain the absence of a close coupling between ABA content and bulk leaf water status.

The data for BJ 104 show, nevertheless, that the *mean* ABA level over the day was a reflection of the general degree of water stress imposed; the latter being exemplified both by the extent of growth inhibition (Fig. 1A) and the internal leaf water status (Fig. 1B). This was

true also of the *maximum* ABA concentration (Fig. 2) which, as it occurred prior to the minimum Ψ at mid-day, was more a reflection of previous than of current water stress.

Both mean and maximum ABA contents might be affected by previous water stress in two ways. ABA could be continuously accumulated; the current day's synthesis therefore augmenting that remaining from previous 'stress days'. Alternatively, previous stress conditioning could lead to a greater capacity to accumulate ABA in response to a further episode of stress. Both mechanisms could operate, and in the latter case ABA levels might be entirely depleted during the night due to the re-establishment of leaf turgor, only to increase again during the day with the reduction in Ψ and Ψ_p. In leaves of cotton (Ackerson, 1980), although there was evidence for some 'carry-over' of ABA following several stress and recovery cycles, the number of previous stress episodes did not greatly alter the extent of ABA accumulation in response to further stress. Data presented in Table 2 suggest that in pearl millet substantial 'carry-over' of ABA from day to day probably occurred in droughted plants. This agrees with the observation (Fig. 2) that substantial, though differing amounts of ABA were present in the three most droughted groups of BJ 104 at 0900 h, when Ψ (and Ψ_p) were: (i) still high, prior to their reduction to the mid-day minimum, and (ii) similar in all three treatments. Values of Ψ (and Ψ_p) were, in fact, not far below those of fully irrigated plants (Fig. 2B). Furthermore, moderately high levels of ABA were present in leaves of B282 at dawn (Fig. 4B). There was also no evidence from examination of regression analyses of ABA on Ψ or Ψ_p (data not presented), of any change, as a result of stress history, in capacity to accumulate ABA in response to a given stress.

While an overnight increase in Ψ failed to reduce ABA content significantly, a rise in Ψ following rain did result in lower ABA levels (Table 2). The latter finding is consistent with results of a pot experiment (Henson, 1981) which showed that ABA levels in leaves of droughted millet declined rapidly following rewatering. The difference in response to overnight rehydration and to rewatering does, however, require further investigation, though it is possible that the longer period for recovery which followed the rainfall (18 h maximum) could account for this.

Diurnal changes in leaf conductance (reported in detail elsewhere; Henson *et al.*, 1982) could not be accounted for by diurnal changes in ABA, at least in terms of a simple, *negative*, linear correlation model (Table 2). This was so even when allowance was made for the effects of irradiance, vapour pressure deficit, and other environmental variables likely to affect g_l. One explanation for this is suggested by Fig. 5 which shows how the relationship between g_l and total leaf ABA content for BJ 104 in treatments 3–5 changed with time of day. It is quite evident that these changes were only partly explicable in terms of changes in irradiance, the dominant environmental variable influencing g_l (Henson *et al.*, 1982). Thus, although the increase in mean g_l between 0900 h and 1030 h could be ascribed to increased irradiance, at later times stomata became progressively more responsive to ABA at a similar irradiance. This suggests either an increase in the inherent sensitivity of the guard cells to ABA, or a 'leakage' of ABA out of storage sites so that more of the hormone became available to act on the stomata. Insensitivity to ABA was once more restored (at 1500 h) as irradiance fell below a critical level such that stomata were closed even at a low ABA content. The view (Raschke, 1975) that light affects stomatal aperture and therefore g_l primarily via its effects on photosynthesis and intra-cellular CO_2 concentration (C_i), and that C_i and ABA interact positively to regulate g_l, should be considered in the context of the present results. It is noteworthy that for leaves of pearl millet *within* the canopy (which received a reduced irradiance and may therefore have had a higher C_i) g_l at mid-day was reduced to a considerably greater extent by water stress than was the case for upper leaves (Henson *et al.*, 1982) despite similar, or even greater levels of ABA in the latter leaves (unpublished results).

Hence, for a better evaluation of the influence of ABA on the daily course of conductance, data on C_i may be required. This, together with information on the distribution of ABA within the leaf, should help to clarify the role of ABA in stomatal regulation under field conditions.

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