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**EVIDENCE FOR PANICLE CONTROL OF STOMATAL BEHAVIOUR IN
WATER-STRESSED PLANTS OF PEARL MILLET**

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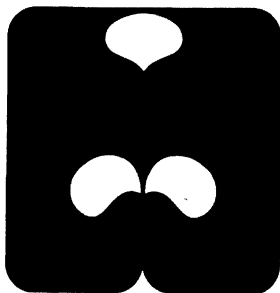
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mays (L.)), levels of stress causing marked stomatal closure in vegetative plants had little effect on stomatal conductance following flowering (Ackerson and Krieg, 1977; Ackerson et al., 1980). Similarly, in wheat (*Triticum aestivum* L. em. Thell.), stomatal sensitivity to stress was progressively reduced with advancing ontogeny (Frank et al., 1973; Morgan, 1977; Teare et al., 1982).

We have previously shown that in pearl millet, there is likewise a reduction in stomatal sensitivity to water stress as plants enter a reproductive phase (Henson et al., 1983, 1984). The tendency for stomata to be open at low leaf water potentials (ψ) which, in young vegetative plants result in very low stomatal conductance (g_s), was shown in millet to be related to the emergence of the panicle from the flag leaf sheath (Henson et al., 1984). Differences in g_s between plants with and without emerged panicles could not be explained by differences in bulk leaf turgor. However, the concentration of abscisic acid (ABA), a plant hormone which readily induces stomatal closure (Raschke, 1975), was found frequently to be lower in leaves of plants with emerged panicles (flowering plants), than in those without (non- or pre-flowering; Henson et al., 1983, 1984).

In the present investigation we have explored further the relationships between panicle growth and development and stomatal conductance of water-stressed pearl millet plants. Observations were confined to the flag leaf and were designed to investigate the possible influence of panicle sink activity on stomatal behaviour, via the regulation of ABA concentration in the leaf.

MATERIALS AND METHODS

Plant culture

Plants of pearl millet were grown in the field on a medium depth (ca. 1.0 m) Alfisol soil at ICRISAT Centre near Hyderabad, India, during the dry season (February to May) in 1983 and 1984. Seed was machine sown in rows 0.75 m apart and plants were later thinned to ca. 0.10 m apart within rows. Control plots were furrow irrigated at approximately weekly intervals. This maintained flag leaf ψ above ca. -0.8 MPa. To impose water stress, irrigation was discontinued after 19 (1983) or 13 (1984) days after sowing (DAS).

Sampling was confined to two cultivars; BJ 104, an early-flowering F_1 hybrid with a synchronous flowering habit even under stress, and B282, a later-flowering inbred of less synchronous habit.

Measurements

Fully emerged flag leaves were sampled for stomatal conductance, leaf water potential, and ABA concentration; all three measurements being made on the same leaves. Rates of ^{14}C -assimilate export were determined using separate sets of plants from the same populations. Most measurements were

made between 10.30 and 12.00 h Indian Standard Time, but some measurements of ^{14}C export and of conductance (in 1983) were made later in the day. In all cases, plants assigned to different treatments were sampled alternately. During sampling, screened air temperatures were ca. 35–37°C, and photosynthetic photon flux density was 1600–2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Conductance was measured on both leaf surfaces using an automatic diffusive resistance porometer in 1983 (Mark II porometer; Delta-T Devices, Burwell, Great Britain)*, or a steady state porometer in 1984 (Li-1600; Licor, Lincoln, NE, U.S.A.).

Leaf water potential was measured using a pressure chamber, with leaves protected against post-excision evaporative losses. Immediately after this measurement leaves were frozen in liquid nitrogen and subsequently freeze-dried. The freeze-dried material was later extracted and analysed for ABA using the method of Quarrie (1978).

To measure panicle growth, randomly-selected plants were tagged when in the boot stage and observed daily for the extent of panicle emergence. Other plants were tagged at flowering (stigma emergence). Panicles were harvested at different stages of development, oven dried, and weighed.

To obtain a measurement of assimilate export, attached flag leaves were exposed to ^{14}C -labelled CO_2 whilst sealed in a glass tube with a split rubber bung. Just prior to its insertion into the tube the tip of the leaf was cut off at right angles to the midrib so that the entire end window of a Geiger-Müller probe (see below) could be covered by the distal end of a treated leaf. Radioactive CO_2 was introduced into the tube by injecting either CO_2 generated externally from ^{14}C -barium carbonate, or ^{14}C -sodium bicarbonate solution followed by a solution of lactic acid. The gas or solutions were injected into the tube via a rubber septum mounted in an arm fixed near the tube base. As the tube was held on a slant with the base tilted downwards, solutions did not come into direct contact with the leaf.

Leaves were exposed to $^{14}\text{CO}_2$ for 2 min. The tubes were removed and the end 20 mm of the leaf mounted above the end window of a Geiger-Müller probe, connected to a pulse count ratemeter (Model 489-35 probe, Model 490 Thyac III ratemeter; Victoreen Inc. U.S.A.). Counts were initially recorded half-hourly over 2 or 3 h. For convenience, export from the monitored leaf portion was assessed in terms of the percentage decline in count rate during the first hour following dosing. The method did not allow for changes in the self-absorption characteristics of the leaf during measurement, but these were not expected to vary with the treatments which were being compared.

Flag leaves of some plants were heat-girdled near the base of the lamina using a battery-operated resistive-wire heater which was applied simultaneously to both leaf surfaces for 10–20 s.

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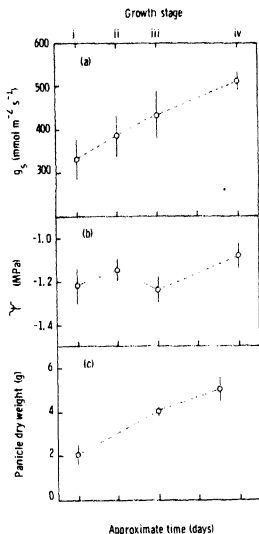


Fig. 1. Stomatal conductance (a) and water potential (b) of the flag leaf, and panicle dry weight (c), of plants of cv. BJ 104 at various stages of panicle development: viz. (i) boot stage, (ii) panicle half emerged from flag leaf sheath, (iii) panicle fully emerged, stigmas emerged, (iv) panicle with stamens, at anthesis. An approximate time scale is indicated. Data in (a) and (b) are means of six; in (c) are means of three batches, each of three panicles. Vertical bars indicate $2 \times$ standard error of mean.

RESULTS

Comparisons of panicle growth stages

In 1984, flag leaves of cv. BJ 104 were sampled from droughted plots for g_s and ψ 45 DAS (32 days after the last irrigation) when plants at various stages of panicle development were present. Conductance was found to increase progressively with stage of panicle growth (Fig. 1a). Differences in ψ did not appear to account for the differences in g_s (Fig. 1b). At anthesis, g_s of droughted plants was as high as 83% of that of irrigated control plants

TABLE 1

Stomatal conductance, water potential, and ABA content of flag leaves of cv. B282 at two stages of panicle growth^a

| | Stage of growth | |
|---|-----------------|------------------|
| | Boot | Panicles emerged |
| g_s (mmol m ⁻² s ⁻¹) | 153 | 413** |
| ψ (MPa) | -1.62 | -1.81 ns |
| [ABA] (ng g ⁻¹ dry weight) | 467 | 129* |

^aLeaves were sampled 51 days after sowing from droughted plots. Data are means of six leaves. Significance of differences between growth stages are indicated by * ($P < 0.05$) and ** ($P < 0.01$); ns = not significant.

TABLE 2

Rate of ¹⁴C-labelled assimilate movement and water potential of flag leaves of cv. B282 at two stages of panicle growth^a

| | Stage of growth | |
|-------------------------------------|-----------------|------------------|
| | Boot | Panicles emerged |
| Δ cpm (% min ⁻¹) | 0.45 | 0.78** |
| ψ (MPa) | -1.50 | -1.65 ns |

^aLeaves were sampled 49 or 50 days after sowing from droughted plots. Data are means of six leaves and are pooled from three separate experiments, each involving four plants (two per growth stage). Significance of differences between growth stages is indicated as in Table 1.

(which had a mean ψ of -0.7 MPa). Between the boot stage and anthesis, panicle dry weight increased by ca. 150–200% in droughted plants (Fig. 1c).

Using adjacent plots of cv. B282, further comparisons were made between plants at the boot stage and those which had just attained full panicle emergence. (Due to the delaying effects of drought on stem/panicle growth the latter stage coincided with stigma emergence.) At panicle emergence, flag leaf g_s was significantly higher than at the boot stage, despite ψ being similar in both groups (Table 1). This difference in g_s was also found on another occasion (data not presented). ABA concentration in the flag leaf was significantly lower at panicle emergence than at the boot stage (Table 1).

Separate groups of droughted plants were used to measure ¹⁴C-assimilate export (Table 2). Again, ψ did not differ with growth stage (Table 2). However, the rate of disappearance of ¹⁴C from the monitored portion of the flag leaf was considerably greater with panicles emerged, than when in the boot stage (Table 2).

Effects of panicle removal

Experiments in 1983 indicated that cutting off panicles of BJ 104 resulted in a decreased flag leaf conductance 3 days after removal, but not after 1 or 6 days when g_s of intact and treated plants was very similar (Fig. 2A). The panicles generally had grain present and the leaves had a low ψ (ca. -1.8 MPa) which was not altered by panicle removal. Also, while there was no effect of panicle removal on flag leaf ABA content after 1 or 6 days (Fig. 2A), at 3 days after removal ABA content was substantially increased in treated plants.

In 1984 similar experiments were conducted with BJ 104 but plants were

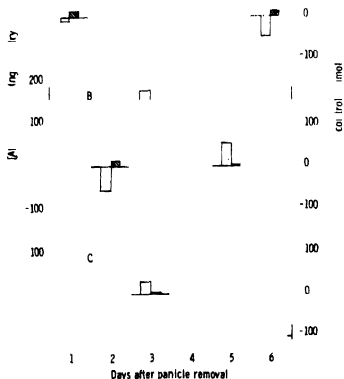


Fig. 2. Differences between control (panicles present) and treated (panicles removed) plants of cv. BJ 104 in flag leaf ABA concentration (unshaded bars) and conductance (shaded bars) at various times following panicle removal. (A) panicles with grains present, 1983; (B) panicles with stigmas emerged, 1984; (C) panicles with grains present, 1984. Mean values for ABA concentration and g_s of control plants were 260 ng g^{-1} dry weight and $303 \text{ mmol m}^{-2} \text{ s}^{-1}$ respectively. * above a bar indicates significance of difference at $P < 0.05$.

TABLE 3

Effect of removing the panicle on the rate of ^{14}C -labelled assimilate export (% min $^{-1}$) from flag leaves of cv. BJ 104^a

| Panicle growth stage | Approximate time of ^{14}C -labelling (h after panicle removal) | Treatment | |
|------------------------------|--|-----------------|-----------------|
| | | Panicle present | Panicle removed |
| Stigmas present ^b | 0.1 | 0.62 | 0.44* |
| | 24.0 | 0.93 | 0.54** |
| Grains present ^c | 0.1 | 0.77 | 0.71 ns |
| | 24.0 | 0.76 | 0.77 ns |

^aData are means of six leaves. Significance of differences between treatments is shown as in Table 1.

^bPanicle just emerged from flag leaf sheath.

^cGrains at soft dough stage.

less stressed (flag leaf ψ ca. -1.4 MPa) than in 1983. Panicles were removed at both stigma emergence and after grain set. Only when panicles were removed at stigma emergence (Fig. 2B) were any significant effects observed on g_s and ABA content. Relative to controls, g_s was lowest and ABA content highest 3 days after panicle removal. Between 3 and 5 days the effect of removal on both g_s and ABA content progressively diminished. All decreases in g_s resulting from removal were accompanied by increases in ABA concentration in the flag leaf (Fig. 2), the correlation between the two measurements being highly significant ($r = -0.94$; $P < 0.001$). In a separate experiment, no effect of panicle removal on g_s was found at 0.5, 1, 2 or 4 h after removal (data not presented). In no case did panicle removal have any significant effect on flag leaf ψ (data not presented).

Measurements of ^{14}C -labelled assimilate export from the flag leaf were made in 1984 immediately after panicle removal or 24 h later. Significant reductions in export rate were observed at both times for panicles removed at stigma emergence (Table 3). However, as with g_s and ABA content, ^{14}C export was not significantly affected when panicles were removed at early grain fill.

Effects of girdling

Heat girdling the base of the lamina resulted in a zone of dead cells ca. 2 mm wide across the leaf which prevented export from the leaf. No radioactivity was found to pass below the girdle following ^{14}C -dosing of the apical portion of the leaf. When performed early to mid-morning, girdling had no effect on leaf ψ (Table 4), though leaves girdled at noon or later showed some reduction in ψ below controls (data not presented). Irrespective of the

TABLE 4

Effect of heat girdling base of laminae of flag leaves of cv. BJ 104 on stomatal conductance, ABA concentration, and leaf water potential. Data are means of six leaves \pm s.e. mean

| | Time of sampling ^a | Control | Girdled ^b |
|--|-------------------------------|------------------|----------------------|
| g_s (mmol m ⁻² s ⁻¹) | 10.00 | 172 \pm 29 | 103 \pm 13 |
| | 11.00 | 335 \pm 30 | 118 \pm 13 |
| | 12.00 | 231 \pm 42 | 69 \pm 11 |
| ABA content (ng g ⁻¹ dry weight) | 10.00 | 270 \pm 43 | 664 \pm 58 |
| | 11.00 | 357 \pm 64 | 710 \pm 119 |
| | 12.00 | 303 \pm 37 | 622 \pm 130 |
| ψ (MPa) | 10.00 | -1.10 \pm 0.08 | -1.16 \pm 0.05 |
| | 11.00 | -1.32 \pm 0.08 | -1.40 \pm 0.11 |
| | 12.00 | -1.51 \pm 0.09 | -1.49 \pm 0.09 |

^aIndian Standard Time.

^bLeaves girdled at 09.00 h.

time of treatment girdling resulted in a decrease in g_s and an increase in ABA concentration. When girdling was done at 09.00 h the reduction in g_s was most apparent 2 h later, when g_s of untreated leaves was at a maximum (Table 4). ABA concentrations of girdled leaves were approximately twice those of ungirdled leaves.

DISCUSSION

High leaf conductance during water stress has been observed in plants of sorghum, maize and pearl millet during the reproductive phase, while vegetative plants of these species had, at the same ψ , much lower conductances indicative of stomatal closure (Ackerson and Krieg, 1977; Ackerson et al., 1980; Henson et al., 1983, 1984). In droughted plants of pearl millet, increased g_s of flag leaves was associated with emergence of the panicle from the flag leaf sheath (Henson et al., 1984). The present results extend this observation and demonstrate that at similar leaf ψ , g_s increased with growth and development of the panicle. Furthermore, g_s was positively related to the ability of the leaf to export recently-assimilated carbon and negatively correlated with the concentration of ABA in the leaf.

Maintenance of leaf turgor, rather than high ψ per se may be the more important for stomatal opening. However, it was previously shown (Henson et al., 1984) that differences in bulk leaf turgor did not account for differences in g_s between plants with and without emerged panicles. Leaf turgor was not measured in the present experiments but, judging from earlier results (Hen-

son, 1984), treatments such as panicle removal and heat girdling which decreased g_s , were likely to have *increased* leaf turgor due to a greater accumulation in the leaf of photosynthetic assimilates. This increased turgor should have favoured opening.

The increased g_s in water-stressed millet associated with panicle growth may result from an effect of the panicle itself or from correlated but independent changes within the leaf as it ages. However, differences in g_s were observed in similarly-aged leaves following either panicle removal or girdling. Hence, it is suggested that the opening of flag leaf stomata was the outcome of an increase in panicle sink strength and when sink demand was reduced by panicle removal, or eliminated by heat girdling, stomatal opening was reduced.

Increased sink demand could stimulate g_s via a feed-back effect on photosynthetic rate, so leading to a fall in intercellular CO_2 concentration (C_i). Alternatively, a lowering of the concentration of ABA, which accumulates in the leaf in response to water stress, might result from increased sink demand for ABA and so permit greater stomatal opening. Export of a minor constituent such as ABA may be influenced by the movement of bulk assimilate and the evidence presented is consistent with this possibility. The presence of ABA in the phloem and its rapid export from leaves has been demonstrated (Goldbach and Goldbach, 1977; Zeevaert, 1977; Hoad, 1978; Setter et al., 1981). Heat girdling, which causes the stomata to close and increases ABA content (Table 4), does not induce a rise in C_i in unstressed millet plants (Henson, 1984). Hence, stomatal closure in girdled millet leaves may be a direct response to ABA, as previously proposed by Setter et al. (1980a, b) for soybean.

The reduction in g_s following panicle removal was transient and not always readily apparent. A significant effect of removal at grain fill was observed in 1983 only, when the millet plants were more stressed ($\psi \approx -1.8$ MPa) than in 1984. In neither year was a response observed until 3 days after removal, after which time it disappeared. The lag in response may reflect the time required for ABA concentrations to build up, following a reduction in export rate, to sufficient levels to influence g_s . Disappearance of the effect could be due to the establishment of alternative sinks on the shoot, for in millet, both drought and damage in the main panicle encourage the development of secondary, aerial tillers. Development of such tillers might account for the weaker response to panicle removal at grain set in 1984. In that year, the combined dry weight of aerial tillers harvested from the four nodes below the main panicle was more than five times greater at early grain fill than at stigma exertion (data not presented). Tiller growth was not measured in 1983 but it may have been less than in 1984 due to lower plant water potential. The role of tillers as alternative sinks in millet requires further evaluation, as does the quantitative relationship between ABA export and assimilate export under conditions of water stress.

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