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Response of four sorghum lines to mid-season drought. II. Leaf characteristics

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ABSTRACT

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Four sorghum lines were visually selected on the basis of degree of leaf desiccation for resistance and susceptibility to mid-season drought stress. An association between leaf-rolling and degree of resistance based on this method of selection had previously been observed, prompting this study to identify the physiological contribution of characteristics at the leaf level to mid-season drought resistance.

During the drought period, the resistant lines showed more leaf-rolling than the susceptible lines, reducing the effective area of the uppermost leaves by about 75%. Leaf-rolling in the resistant lines occurred over a very narrow range of leaf water-potentials (-2.0 to -2.2 MPa) compared to the susceptible lines. The strong correlation between the light-extinction coefficient k and leaf-rolling indicated that changes in k over the season were in part due to differing abilities of the lines to roll their leaves. However, expected differences in leaf temperature between lines due to radiation shedding were not found. Lines exhibiting leaf-rolling had higher leaf conductances, although transpiration rates per unit leaf area were similar. It is suggested that leaf-rolling may alter the leaf surface microclimate so that stomata may remain open and growth continue without associated high rates of water loss.

INTRODUCTION

Part I of this series (Matthews et al., 1990, this volume) described work in which four lines of sorghum were visually selected for resistance or susceptibility to mid-season drought, and physiological traits at the crop level associated with this resistance or susceptibility were identified. It emerged that the resistant lines were able to maintain a higher plant water-status as the drought intensified, probably because of their higher root:shoot ratio. As a result, re-

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productive development, even though it occurred after release of drought in most lines, was less affected in the resistant lines than in the susceptible.

During the course of selection, rolling of leaves was observed to occur mainly in the lines resistant to drought; as one of the aims of the work was to identify traits that might make selection of drought-resistant lines easier, a more detailed investigation of a possible physiological basis of leaf-rolling was initiated.

There are two possible ways in which a plant in a droughted environment may benefit from rolling its leaves. Firstly, damage by increased leaf temperatures resulting from high levels of solar radiation incident on leaf surfaces could be minimised by reducing the effective leaf area presented to the sun's rays, so that less radiation is intercepted by leaf tissue (Begg, 1980). Secondly, transpiration rates could be reduced through the creation, by leaf-rolling, of a microclimate with both higher humidity and boundary layer resistances near the leaf surfaces, thereby conserving scarce water resources (Oppenheimer, 1960). This second paper in the series describes measurements of leaf-rolling in the four sorghum lines, and assesses its importance in relation to resistance to mid-season drought stress.

MATERIALS AND METHODS

Experiment management

Over a two-year period, 700 sorghum lines were screened for resistance to mid-season drought stress, with particular emphasis on their ability to withstand leaf-firing and to recover to produce grain after drought was relieved. From these, an early-maturing susceptible (IS12739), a late-maturing susceptible (IS17605), an early-maturing resistant (IS1347), and a late-maturing resistant line (IS20969) were selected for detailed physiological measurements; these lines are referred to as ES, LS, ER and LR, respectively. The four lines were sown on 12 March 1985, and were grown during the summer and monsoon seasons (March–August) at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, central India. Two treatments were imposed, one a control which was irrigated at weekly intervals throughout, and the second a stress, in which water was withheld from 20 days after sowing (DAS) until the onset of the monsoon rains at 84 DAS, after which weekly irrigation was resumed. Within the stress treatment there were four replications of each line. Complete details of the method of selection of the lines and the design and management of the experiment are given in Part I (Matthews et al., 1990). The following analysis is restricted to data from the stress treatment only.

Leaf-area index

At weekly intervals starting 18 DAS, four plants were randomly harvested from each plot, and their green leaf area measured using a Licor 3100¹ leaf-area meter. Leaf-area index (L) was calculated as the product of the mean leaf area per plant (m^2) and the population (plants m^{-2}), the latter being determined three times during the season – after establishment, at 56 DAS, and at final harvest of each line. Dry-weights of both green and dead leaf tissue were also recorded. As dead leaf material attached to the plant still intercepts solar radiation, the standing leaf area, both living and dead, was used for the analysis. While this does not necessarily represent the total leaf area produced, as dead leaves detached from the plant were not measured, it does give an estimate of the area of intercepting surfaces within the canopy.

Solar radiation

The horizontal distribution of light in each canopy was recorded using an instrument which measured light at 2-cm intervals across a transect normal to the direction of the crop rows. Two measurements were taken per plot. From these, the fraction of ground area shaded by vegetation, or fractional ground cover (C_g), was calculated. The instrument, termed a 'mouse', and the method of calculating C_g , are described in Matthews et al. (1987). Measurements were made at approximately weekly intervals from 20 to 84 DAS around midday on cloudless days.

Extinction coefficient (k)

Measurements of C_g were used to estimate k of each canopy in the stress treatment, using the equation (Jackson and Palmer, 1979):

$$T = T_f + (1 - T_f)e^{-kL'}$$

describing light transmission in row crops, where $T = (1 - C_g)$ from mouse measurements; $T_f = 1 - w/S_r$, where w is the mean canopy width (estimated from aerial photographs taken at regular intervals), and S_r is the inter-row spacing; and L' is the leaf area per unit ground area covered by the canopy, where $L' = LS_r/w$.

Leaf-rolling and leaf width

Estimates of the leaf-rolling index (RI_1) were made at 20, 27, 34, 43, 56, 64 and 75 DAS on ten plants within each plot in the stress treatment, in a manner similar to that described by Begg (1980). The width of the shadow cast by a leaf on a flat surface held normal to the direction of the sun's rays was measured, and expressed as a fraction of the leaf width at the same point when

¹Reference to commercial products does not imply endorsement or recommendation by ICRISAT in preference to other similar products.

the leaf was fully unrolled. A point midway between tip and base of the youngest fully expanded leaf was used to standardise this measurement.

Temperatures

Air temperature were measured with a 20-swg copper-constantan thermocouple positioned within a Stevenson screen. Leaf temperatures were measured with 38-swg copper-constantan thermocouples, located on the undersides of the leaves to avoid undue heating by direct-beam solar radiation, and held in place with plastic clips. These were placed on the youngest fully expanded leaf, and were checked regularly and repositioned when necessary. In each plot, three thermocouples were connected in parallel to give an average reading.

Soil temperatures in each plot were measured using 20-swg thermocouples buried 5 cm deep at regular intervals across a unit row width. The soldered junctions of the thermocouples were water-proofed to prevent shorting. As with the leaf thermocouples, three were joined in parallel to give an average reading per plot. All thermocouples were connected to a data logger (Campbell Scientific, Logan, Utah), and hourly averages of their outputs recorded.

Leaf water-potentials, conductance and transpiration

Midday leaf water-potentials (ψ_1) were measured in all plots twice weekly throughout the drought period (20–84 DAS), using a pressure chamber (PMS Instruments, Corvallis, Oregon). Within each plot, four plants were selected at random; the youngest fully expanded leaf and another leaf midway down the canopy were excised at a point midway along the leaf, and enclosed in a moist cloth to minimise water loss during transfer to the pressure chamber.

Weekly between 33 and 110 DAS, measurements of leaf conductance were made at mid-day using a diffusive resistance porometer (Mk II, Delta-T Devices, Cambridge, Great Britain). Two leaves per plant, one the youngest fully expanded leaf, the other midway down the canopy, were selected from two plants in each plot. Both adaxial and abaxial conductances were measured at three positions along the selected leaf, i.e. near the base, at the mid-portion and near the tip. Conductance at each position was calculated as the sum of the ad- and abaxial conductances, and the mean leaf conductance per plant as the mean of these three conductances.

Mean transpiration rates per unit leaf area were calculated by dividing the weekly crop water use of each plot (as measured by the neutron probe; for details, see Part I) by its green leaf area.

RESULTS

Radiation avoidance

Figure 1 shows seasonal changes in k for each of the lines. Although the resistant lines appeared to have higher k values than the susceptible lines at

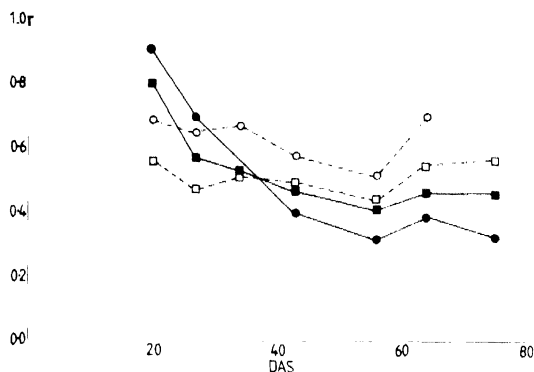


Fig. 1. Changes in the light-extinction coefficient (k) between 20 and 75 DAS. Symbols: LS, \square — \square ; ES, \circ — \circ ; LR, \blacksquare — \blacksquare ; ER, \bullet — \bullet . Vertical bars represent $LSD_{0.05}$.

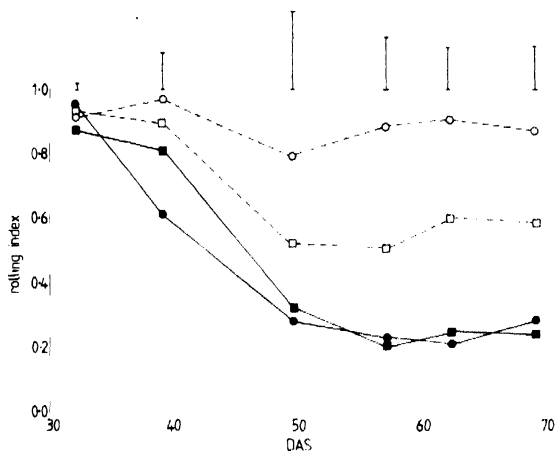


Fig. 2. Changes in the rolling index during the drought period. Symbols as in Fig. 1.

the beginning of the season, k declined markedly in the former as drought stress became more severe, so that from 32 DAS, values of k were lower for both than in the susceptible lines. There was little change in the value of k of the susceptible lines during the drought.

Leaf-rolling

The effect of leaf-rolling on the reduction of effective leaf surface area is shown in Fig. 2. Initially, there was very little difference between the lines in the degree of leaf-rolling, but after 42 DAS the resistant lines reduced their

effective leaf area much more than did the susceptible lines. Although some leaf rolling occurred in one of the susceptible lines (LS), in the other (ES) it did not, even under severe drought stress ($RI_1=0.9$). In the resistant lines, leaf-rolling of the uppermost leaf reduced its effective area by about 75% ($RI_1=0.25$). There was also an association between leaf-rolling ability and leaf width. Mean leaf widths at 69 DAS were 6.51, 7.45, 4.98 and 5.89 cm, for ES, LS, ER and LR, respectively. The resistant lines had significantly narrower leaves ($P < 0.01$, $LSD_{0.05}=0.45$) than the susceptible throughout the drought period.

The correlation between RI_1 and k (Fig. 3) indicates the capacity of leaf-

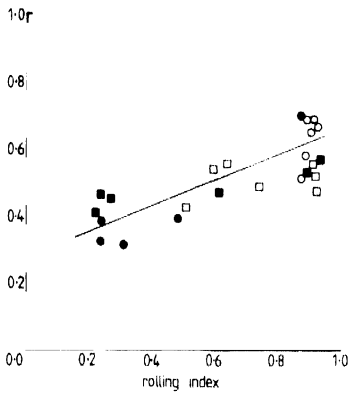


Fig. 3. Relation between the extinction coefficient (k) and rolling index (RI_1). Symbols as in Fig. 1. Regression line is $k=0.28+0.37 RI_1$ ($r^2=0.57$, $P < 0.01$).

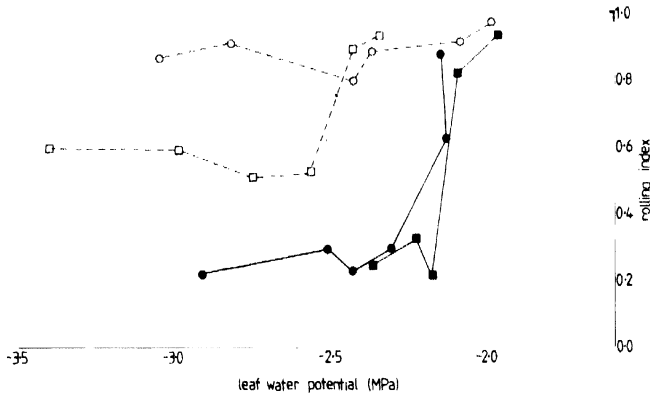


Fig. 4. Relation between leaf-rolling index (RI_1) and midday leaf water-potential (ψ_1) of the youngest fully expanded leaf. Symbols as in Fig. 1.

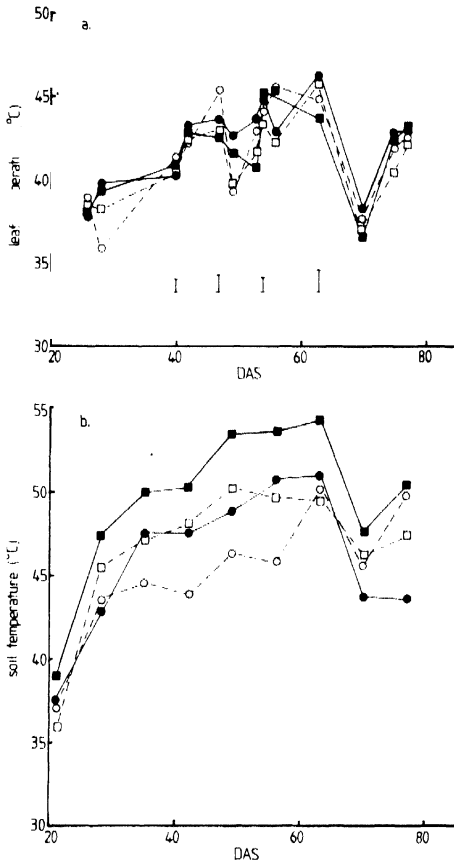


Fig. 5. (a) Temperatures of the youngest fully expanded leaf between 20 and 80 DAS, measured with copper-constantan thermocouples on the underside of the leaf. (b) Temperatures under each canopy at 5-cm soil depth between 20 and 80 DAS. Symbols as in Fig. 1.

rolling to substantially reduce radiation interception without reducing actual leaf area. Figure 4 shows the relation between the rolling index and leaf water potential (ψ_1). In the resistant lines, leaf-rolling appeared to occur very suddenly between -2.0 and -2.2 MPa. In contrast, rolling occurred between -2.4 and -2.6 MPa in LS, and hardly at all in ES. Consequently, there was a strong correlation between k and ψ_1 in the resistant lines, but not in the susceptible lines:

of radiation shedding; Trenbath and Angus (1975) list a number of cases where the reduction of radiation interception has resulted in small decreases in leaf temperature. Similarly, Shackel and Hall (1979) noted a reduction of 5.5°C due to leaf-folding in *Vigna unguiculata*. On the other hand, Turner et al. (1986) noted an increase in leaf temperature associated with leaf rolling in rice, possibly as a result of reduced transpiration. In the present experiment, however, there were no consistent differences in leaf temperatures between those lines in which rolling occurred and those in which it did not.

A reduction in k by leaf-rolling results in more radiant energy passing through the canopy to the soil. Whereas with a wet soil surface most of this energy would be dissipated as latent heat of evaporation, considerable heating of the soil may occur if it is very dry. Certainly in the dry soil surfaces in this experiment, soil temperatures were higher under the canopies of the resistant lines than those of the susceptible lines. It is likely that the elevated soil temperatures would result in an increase in the upward sensible-heat flux, swamping any small reduction in leaf temperatures caused by a reduction in the intercepted radiation by leaf-rolling. Therefore, it would seem unlikely that leaf-rolling plays a major part in maintaining lower leaf temperatures in droughted crop stands, particularly in short crops where leaf surfaces are near to the ground.

It is more likely that the effect of leaf-rolling is to alter the microclimate surrounding the leaf surfaces. Although the reduction in transpiration found in some grasses that roll their leaves (Oppenheimer, 1960) did not occur, leaf conductances were unexpectedly higher in the resistant lines, resulting in their lower $E_1:g_1$ ratios. Low $E_1:g_1$ ratios could be due either to an increased boundary-layer resistance (r_a) or to a decreased humidity gradient between leaf and atmosphere ($\chi_l - \chi_a$). Both these effects could be caused by leaf-rolling, the first by protecting the air within the rolled leaf from rapid removal by outside air-currents, and the second by a buildup of humidity from transpiration within the 'tube' so formed. It may be that, by altering the leaf microclimate in response to drought rather than closing the stomata, water loss can still be regulated while photosynthesis and growth continue. However, the increase in water-use efficiency expected from such changes near the leaf surfaces (Johns, 1978) did not occur; indeed, water-use efficiency was lower (see Part 1) in the resistant lines which exhibited the most leaf-rolling. Thus, it is unclear whether leaf-rolling is an adaptation to aid survival or merely a passive response of certain lines to changes in leaf water-potential.

Whatever mechanisms were involved, the lines visually selected as resistant to mid-season drought had the greatest ability to roll their leaves, and also the narrowest leaves. While there is a need to test a much larger selection of lines to establish a definite correlation, the evidence does suggest that variation between lines in these leaf characteristics may be a basis on which to select for resistance to mid-season drought stress. Leaf-rolling has been used

previously to select for drought resistant rice lines (Chang et al., 1975), although selection was made for lines whose leaves remain unrolled on the basis that they are better able to maintain leaf water-potentials for longer periods during a drought. In contrast, the present work indicates that in sorghum the reverse is true; lines that roll their leaves are able to maintain higher leaf water-potentials.

In conclusion to the series, it would seem that a key factor involved in survival during the drought period, and probably also in production of grain afterwards, is the maintenance of plant water status. It is likely that the higher root:shoot ratios of the resistant lines contributed to this by maximising the supply of water from the roots in relation to loss from the canopy. This in turn prevented leaf water status from falling below the critical value at which leaf death occurs (Flower and Ludlow, 1986; Ludlow and Muchow, 1988), and also mitigated the effect of the drought on subsequent reproductive development. Leaf-rolling which showed a differential response to leaf water-potential between resistant and susceptible lines, may enable stomata to remain open and growth to continue longer into the drought without associated high rates of water loss. It seems, therefore – at least on the basis of the four lines studied – that selection based on visual screening of desiccation, and possibly also of leaf-rolling, may provide a rapid and reliable method of selection for resistance to mid-season drought.

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