

Physiological Basis for Increasing and Stabilising Yield under Drought in Sorghum*†

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Although drought causes more yield losses than combined effect of all biotic stress factors, the progress in increasing yield under water-limited environment is small. Major reasons for slow progress are listed and the relationships between crop productivity and drought resistance are examined. Adaptations to drought in sorghum are discussed in order of their utility in the immediate future: phenological, morphological, physiological and biochemical. Results of interdisciplinary research in understanding drought resistance are discussed with respect to available screening methods, genetic variability and breeding methods. Breeding and management strategies should be aimed at increasing transpirational water use throughout the season and decreasing injury caused by drought.

Key Words: *Sorghum bicolor*, Drought resistance, Grain yield, Adaptation

Introduction

Crop production is limited more by (Boyer 1982). Even in the United States of America, in spite of great deal of unfavourable physiochemical environments than by all other factors combined of research and use of inputs, the major

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cereal yields range from 1/4 to 1/7 of the potential yield (Wittwer 1975). In India, the average yields of major crops in the farmers' field are 10–20 folds less than those achieved by "Krishi Pandits" (award winning farmers selected by the government on the basis of crop growing competition).

Dudal (1976) has estimated that 90% of the global land area has significant problems for agriculture. Of these, most important is drought which is chronic on 28% of land with another 25.4% of land sporadically under drought, either due to the shallowness of the soil (24%) or due to mineral toxicity (23%), etc. All the national and international crop improvement programs are seriously concerned about the problems of drought. For instance, the sorghum improvement program at ICRISAT has given top priority in its 10-year research projections to work on genetic improvement for drought resistance, and on management research to increase yields in drought prone areas (ICRISAT 1982b).

Improvement for Drought Resistance: A Myth?

Breeding plants resistant to drought, or devising management strategies to increase water-use efficiency have been attempted since long ago, but the progress has not kept up with the expectations. Research on these areas, especially breeding for drought resistance, is very frustrating. To quote Arnon (1980) "Breeding for drought resistance has been a consistent theme for as long as I remember and probably the greatest source of wasted breeding efforts in the whole field of plant breeding".

Recent advances in our understanding of the problem makes us feel more optimistic, mainly on the following grounds:

Firstly, only fairly recently drought, with all its ramifications, has been systematically analyzed on all levels of biological organizations. Secondly, the breeders have not extensively used diverse germ-plasm and the novel breeding techniques such as the recurrent selection method, so far. Thirdly, the tools available to us today, such as remote sensing and dynamic modelling, are far more superior and powerful than those employed by previous workers. Furthermore tools for quantification of stress such as infrared thermometers will greatly assist the breeding efforts. The cost of these need not be prohibitively high, and such tools can be simplified. For example, simple temperature-sensitive adhesive paper can be used to measure and register leaf temperature. With the advance in electronics it should be soon possible to "video-tape" the leaf temperatures in the field and scrutinize the response quantitatively. Finally, in recent years new field screening techniques such as the line source sprinkler irrigation system (Hanks et al. 1976), have been introduced, and statistical methods have been improved to deal with increased field sampling variability under drought.

In this paper we will examine the problems and the prospects for increasing grain yields under drought. Although we have extensively used the data on sorghum [*Sorghum bicolor* (L.) Moench], which is one of the five most important cereals of the world, the physiological principles can be applied to other crops under appropriate situations.

Problems in Crop Improvement for Drought Resistance

Experimentally it is more difficult to incorporate drought resistance in crops, than it is to incorporate disease or pest

resistance. The former can be handled without affecting crop yields or adaptability, and in most cases the number of genes involved is quite small; in the case of drought resistance, crop productivity is linked to water which is a substrate, constituent (e.g. of hydrophilic proteins) and the medium in which all cellular processes take place. Water is also essential for evaporative cooling of the plant. Furthermore the flow of water in the soil-plant-atmospheric continuum (SPAC) is crucial for the flow of nutrients, hormones and other substances.

The specific problems in crop improvement for drought resistance are:

1. Even under the same management practices the profile of drought varies considerably from year to year, from location to location and on different soil types within a farm. Even when the soil and plant characteristics and management factors are known or controllable, the aerial environment (e.g. rainfall and atmospheric demand for water) is difficult to predict.
2. Several adaptations favouring water loss under drought seem to negate crop productivity. For example, both leaf rolling and stomatal closure conserve water, but reduce light interception and entry of carbon dioxide into the leaf.
3. Drought affects many morphological and physiological processes; hence consideration of a single character has not yielded any consistent results.
4. Sensitivity to drought varies considerably between stages of crop growth. Resistance at one stage (e.g. seedling stage) is not necessarily correlated with resistance at other stages.
5. In the absence of simple methods to quantitatively estimate the effects

of drought, the measurements of reduction in yield under drought as compared to yield under optimum moisture supply, is the only method available so far. This is very laborious and time-consuming.

6. Results from screening for drought resistance during 'rain-out' dry seasons should correspond to the performance under drought occurring during normal rainy season.
7. Some of the adaptations are difficult to transfer. For example, the Nigerian sorghums escape drought by completing heading at the end of rains regardless of their planting date because of their photosensitivity (Bunting & Curtis 1970), but this character is not universally acceptable and it cannot be easily transferred to other latitudinal zones.
8. Drought is frequently associated with high temperature stress, and at higher elevations with cold (which reduces water-uptake) and high radiation stress. Drought also reduces nutrient-uptake.

Approaches towards Improvement for Drought Resistance: Ecophysiological Considerations

The first and the foremost task of a drought researcher is to characterize the profile of water stress. The effectiveness of any attempts to improve drought resistance in a crop must be based on a thorough knowledge of, and an appreciation for locational and temporal specificity (rainfall, temperature, radiation, humidity, day length, soil characteristics, duration of crop growth, the stage at which stress occurs and the intensity and duration of stress) that characterizes a particular drought condition (O'Toole & Chang 1979, Seetharama et al. 1982b).

The best example is the case of the wheat variety Pitic-62, which performs well under terminal drought conditions of the Canadian prairie region, but is of no obvious advantage in Britain, where the periodic stresses occurring throughout the growing season are quite mild (Jones 1979). It can be further clarified by comparing the effect of soil moisture stress on transpiration under the following two environments:

1. Sorghum grown during the rainy season (*kharif*) at Anantapur on shallow Alfisol [Plant available water-holding capacity (PAWHC) = 5cm].
2. Sorghum grown during the postrainy season (*rabi*) on deep Vertisol at

Patancheru, Hyderabad (PAWHC = 23 cm.)

Figures 1 and 2 show the simulated relative transpiration rates (and hence degree of stress) of sorghum (flowering in 65 days) planted at the beginning of the season when the rainfall on the day of sowing exceeded 2 cms.

The date of sowing (rainfall > 2 cm) is very uncertain at Anantapur, while it is fairly definite at Patancheru. The inter-annual variability is very high at Anantapur though the water availability at the end of the season is comparatively more assured. At Patancheru, each year, in the beginning of the season water is relatively plentiful and stress increases

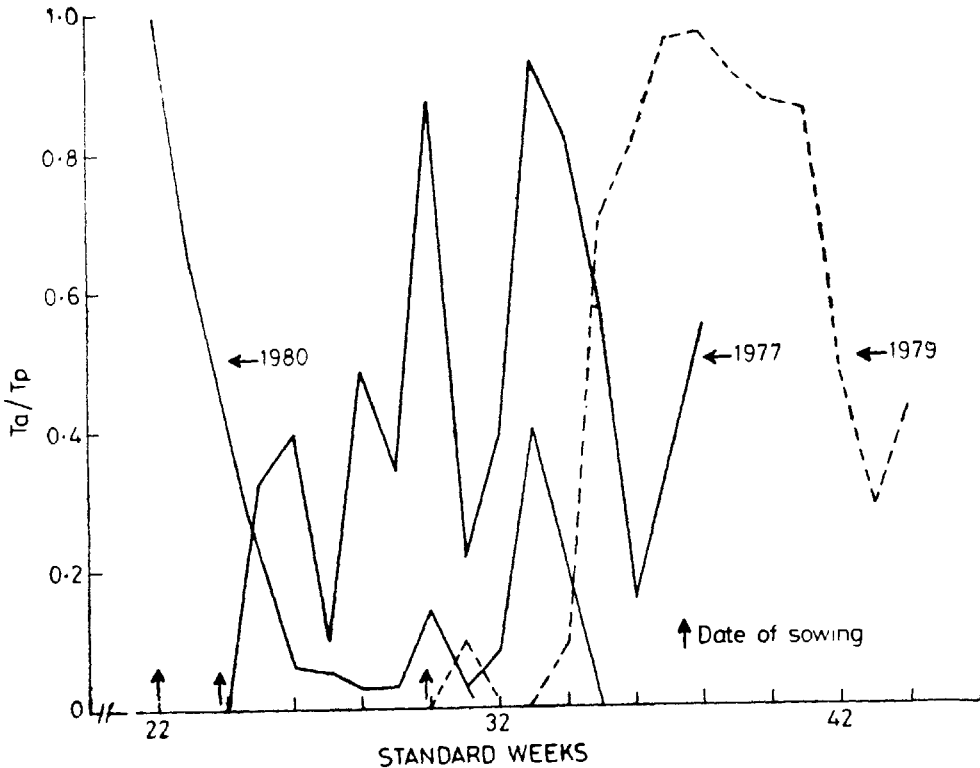


Figure 1 Relative transpiration during crop growth at Anantapur: 1977, 1979 and 1980 *kharif* (rainy season) T_a , transpiration possible with actual rainfall (mm/week); T_p , potential transpiration; based on ICSWAB model of SJ Reddy as modified by V Mahalakshmi and GDP Rao. Computations are on weekly basis

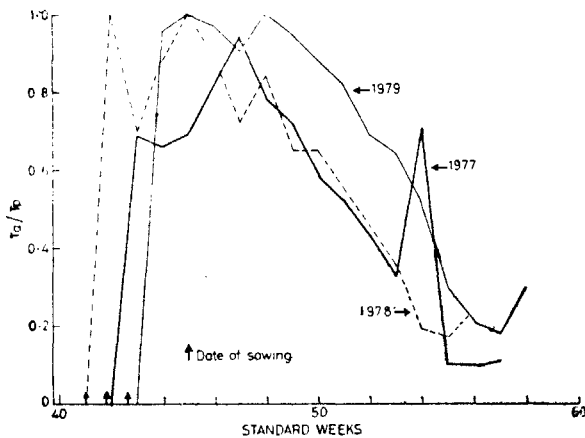


Figure 2 Relative transpiration during crop growth on deep vertisols at Patancheru, Hyderabad: 1977 (partially charged profile), 1978 and 1979 (fully charged) *rabi* seasons (post rainy). Based on ICSWAB model of SJ Reddy as modified by V Mahalakshmi and GDP Rao. Computations are on weekly basis

continuously throughout the season. During 1977, when the profile was not fully recharged, the stress was slightly more during early part of the season than during other years.

Thus, more uncertainty exists at Anantapur due to erratic rainfall and poor water-holding capacity of the soil (and higher evaporative demand; data not shown). At Patancheru, the moisture environment is more easily and accurately predictable and hence strategies to make best use of available water, and to stabilize production can be devised with greater confidence.

Empirical Screening in the Field

Repeatability in the field tests: The ultimate test of drought resistance is yield measured in the field under typical drought conditions. It is very difficult to develop field techniques to evaluate a large number of genotypes for drought resistance. In normal seasons in tropics,

rainfall is erratic and hence even at a given location it is very difficult to conduct field experiments which can provide results which are applicable over many years. Ideally field evaluations need one irrigated (non-stressed) control to compare the effect of stress *per se* on grain yield. The proportional reduction in yield under stress compared to the yield obtained under well watered conditions is more useful as a selection criteria (Blum 1974, Asana 1976, Seetharama & Bidinger 1977) than mere absolute yield estimates under stress.

When using the information from a multilocal testing program, care should be taken to compare the test sites (environments) with those of target regions; otherwise types which have a high degree of drought resistance across different environments, but much poorer local adaptability and productivity may be selected. For example, for *rabi* sorghum growing with stored moisture, it is more valid to select or test under different depths of soil in the post-rainy season than to rely on the results from multilocal trials during *kharif*. Selection of entries from field trials within a single season (even from several closely related sites) is often difficult. Selecting in large populations ensure better repeatability (Hurd 1976).

Ranking of genotypes in the drought screening trials for yield across years, or between similar locations, is occasionally found to be very poorly correlated. A major problem lies in developing field sites and irrigation techniques to produce the required pattern of stress. Also in handling the within-test variability, differences in soil texture, depth etc., which are not very evident under non-stress conditions become major problems under stress conditions. The coefficient of

variation (CV) of the trial mean (figure 3A) or CV of mean yield of a cultivar (figure 3B) increases as the stress level increases (or as mean yield decreases).

Successful field testing involves a careful selection of site, time of sowing, good control of irrigation and development of statistical methods to adjust for yield variability (e.g. use of covariance or moving mean using systematic checks). Use of 'hill plots' seems to be less

advantageous in sorghum since the plant produces the abnormal nodal or basal tillers under such conditions. The loss of competitive environment under hill plots may also increase the variability (work of Leisle quoted by Hurd 1976). With proper techniques, cultivar differences in drought resistance for rice (O'Toole & Chang 1978) and wheat (Fischer & Maurer 1978) have been demonstrated and this was repeatable over seasons. At ICRISAT we have reasonably sound techniques to screen sorghum and pearl millet for drought resistance in the field (ICRISAT 1982a).

Screening for drought resistance using line source: The Line Source (LS for short; Hanks et al. 1976), as described earlier (ICRISAT 1979, Seetharama et al. 1982b) continues to be useful for screening sorghum cultivars for drought resistance since it can be used for maintaining a stress gradient with a minimum land requirement and cost and with a great degree of precision. One experiment was conducted during the 1980 *rabi* with 18 cultivars. From each of the two replications (on either side of LS) each row was harvested for final yield and biomass estimation. Regression of final yields against water applied through LS plus rainfall received until physiological maturity of each genotype (figure 4) was used to estimate the yield potential (yield of rows nearest to LS; intercepts in figure four and drought susceptibility (slopes). Since the actual water applied through LS (six irrigations for early genotypes and seven for late ones) rather than distance from LS was used as independent variable, nearly a fortnight's difference in maturity was ignored.

The correlation coefficient between intercepts (yield potential) and slopes (drought susceptibility) in figure 4, was

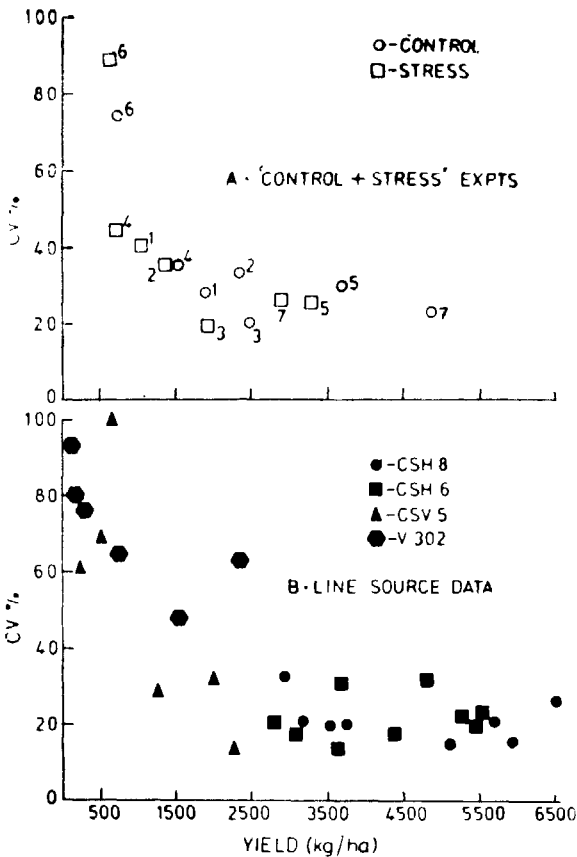


Figure 3 Relationship between coefficient of variation (CV %) and mean yield of cultivars: (A) CV (%) vs mean grain yields. The data are from different trials with irrigation treatments as main plots. The trial number appears within the treatment symbols; (B) CV (%) vs mean grain yields from the same irrigation level from a line source irrigation experiment

very highly significant ($r = -0.813$; $P < 0.001$). This apparently poses a serious problem to the breeders aiming at combining high yield potential with the low drought susceptibility. Hence the slopes from the regressions shown in figure 4 were regressed against intercepts (yield potential; figure five and genotypes showing above average yield potential (points on right hand side of broken vertical line) and slopes less than regression predicted values (points above regression lines) were selected as drought resistant types (least reduction in yield

per unit decline in water supply). Similarly the genotypes below the regression line and on the left hand side of the broken vertical line can be identified as susceptibles.

The entries in the drought-resistance group (e.g., CSH6, DJ1195 and SPV351) did not necessarily have a steeper slope than entries in the susceptible group (CSV5, V302 and D71463). D71463 and D71464 are sister lines derived from the same cross. In the field screen for leaf firing (ICRISAT 1981, Peacock 1982) under hot dry summer conditions D71464 was found to be more resistant than D71463; the former also recovered faster. In figures 4 and 5 it is apparent that while the difference in the yield potentials was very small, there was considerable variation in drought resistance. Studies conducted at Hissar indicated that the above differences may primarily be due to differences in phenology (D71463 is late, especially under stress).

To make direct comparison of drought susceptibility independent of yield potential, yields were expressed on a relative basis as fractions of the intercept (figure 6). Although the slopes of CSH6 and D71464 were vastly different in figure 4, they were similar when adjustment was made for the yield potential. Susceptible entries like V302 and CSV5 have a far steeper slope than resistant lines (e.g. CSH6, DJ1195, etc.). Distinct differences between the two sister lines can also be noted.

Since the applied irrigation water decreased continuously and linearly as the distance from LS increased, the stability analysis of Eberhart and Russels (1966) was adopted using each row as one 'moisture environment'. The regression coefficients indicating stability (b's)

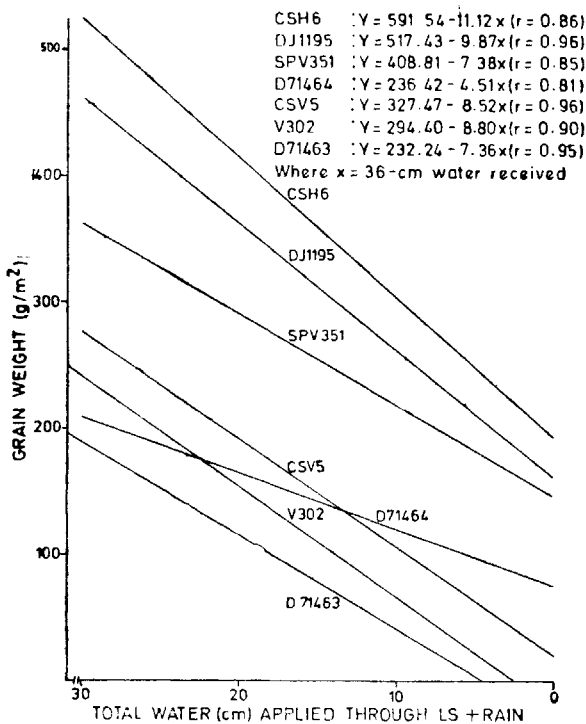


Figure 4 Genotype evaluation for drought resistance using line source (LS) sprinkler irrigation system: Relationship between irrigation water applied through LS plus rain (after 3 uniform furrow irrigations to recharge the profile during crop establishment phase) and grain yield. (Field RP11B, 1980 post-rainy season, regressions for only 7 (out of 18) genotypes are shown; for all correlations $n = 18$; $P < 0.001$)

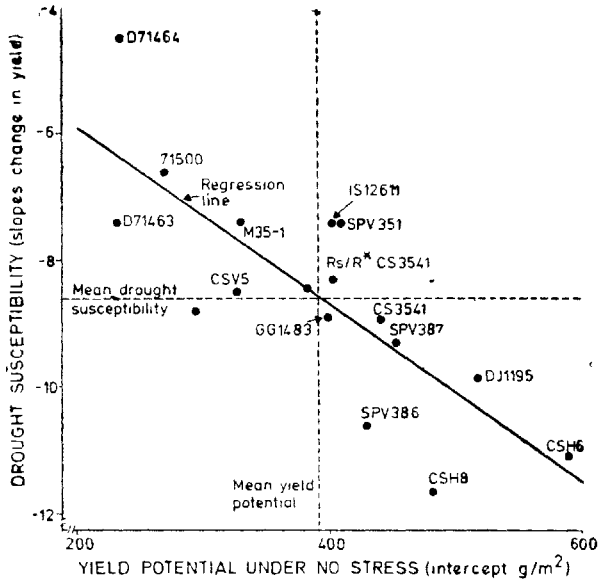


Figure 5 Relationship between yield potential and drought susceptibility (RP 11B, post-rainy season 1980 data for 18 genotypes are shown, unpublished data of N Seetharama)

and residuals were highly correlated with slopes ($r=0.976$; $P < 0.001$) and coefficient of determination ($r = 0.769$; $P < 0.001$), respectively, obtained in the analysis described earlier (figure 4). Thus the data collected on a small piece of land using LS in a single location can be used to select drought resistant (or 'stable') genotypes.

The hybrid check CSH6 showed the highest yield potential, and, inspite of having a steeper slope in figure 4 than other entries, out-yielded all varieties at all levels of water supply used in the experiment. This supports the common belief that hybrids are more productive than varieties even under stress.

Yield Potential vs Drought Resistance

Higher yield of advanced varieties (e.g., SPV351) or hybrids (e.g., CSH6) are highly related to their overall yield potential *per se* rather than drought resistance. Garrity et al. (1982) have quoted Quinby's earlier work (1974) which suggested that the higher yield of hybrids is related to their greater efficiency in dry matter production and to a higher harvest index. Literature is replete with examples of the trade-off between adaptability to drought and maximum growth or yield (Ahmed & Sankhla 1981, Bunce 1981, Gaff 1981, Johnson et al. 1981, Orians & Solberg 1977, Reitz 1974) which can be explained from the viewpoint of plant strategies or 'energy drain' caused by the production of a chemical or structural component regarded as unnecessary under non-stress conditions (Hanson & Nelson 1980). Sorghum plants with high drought tolerance are generally associated with decreased growth and development (Sullivan 1972). Some of the traits which reduce the loss of water from the plant such as decreased leaf area (either by

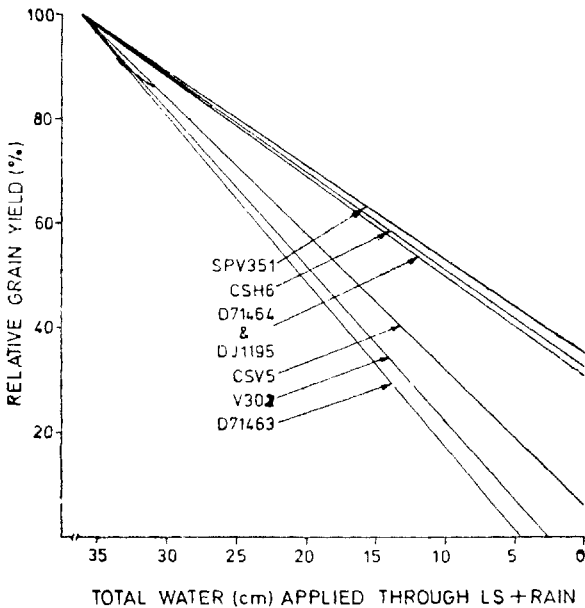


Figure 6 Relative grain yields at declining levels of water supply (RP 11B, postrainy season 1980, data shown only for 5 selected genotypes, unpublished data of N Seetharama)

production of smaller and fewer leaves or by rapid senescence), leaf rolling or stomatal closure, waxiness, etc., also reduce photosynthesis since less light is intercepted (table 2) Parson (1979) has pointed out that while selecting for drought resistance care must be taken not to select just for small plants which do not have high growth potential.

In figure 7 we have attempted to conceptualize the relationship between productivity and drought resistance. The relative growth efficiency of two hypothetical cultivars with or without drought resistance, but with high yield potential (RP and rP, respectively), and a third drought resistant one with low yield potential (Rp) are compared. The high yield potential cultivar RP always takes advantage of the growth opportunities (mostly limited by water supply), while

the low yield potential type (Rp) lags behind. However the latter may sometimes appear more efficient than the former: e.g., between 70 and 85 days. The RP would have a higher demand for water because of higher leaf area built and maintained over time. Rp on the other hand, may have less leaf area and hence more moisture remains untapped in the soil for later use. However, RP also has mechanisms to cut down its consumption temporarily when the supply is limiting (and again increase if the water becomes available later in the season). The susceptible cultivar rP, though has a higher growth rate under well watered conditions (before stress begins), and may run out of water at a critical stage when stressed and collapse.

The above arguments imply that any further increase in drought resistance is

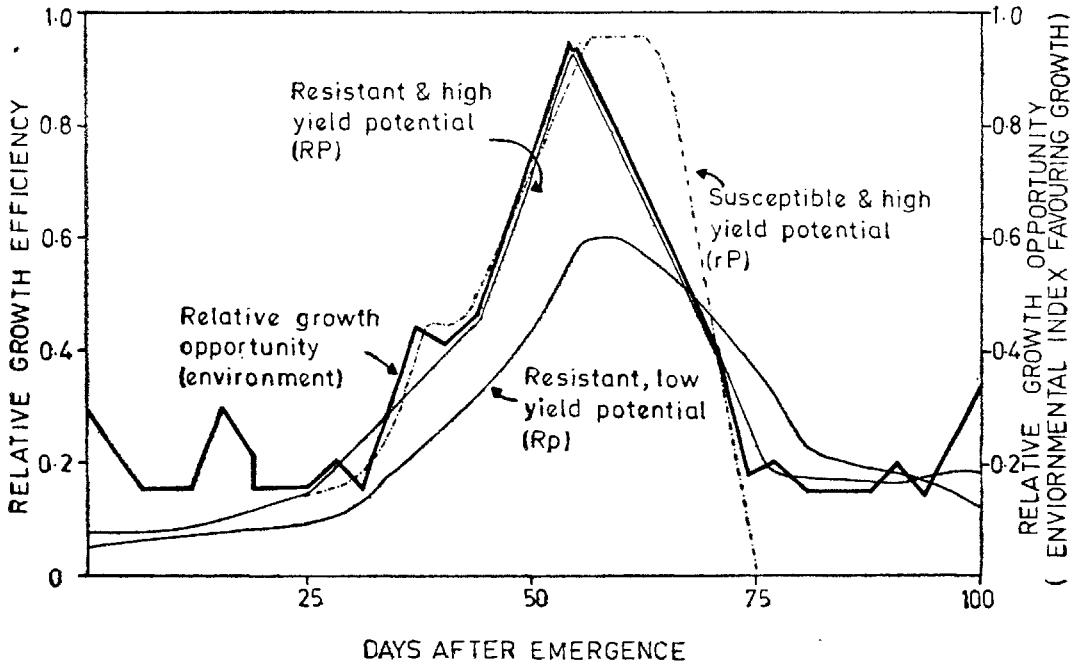


Figure 7 Resource use by various (hypothetical) sorghum genotypes (relationship between growth opportunity and growth efficiency, see text for explanations)

difficult at higher yield potentials. However this is not true under many instances. Seetharama and Bidinger (1979) have shown that the correlation between yield potential and drought resistance (measured as maintenance of yield under stress) becomes weaker as the stress level increases; only under severe stress are the drought resistance attributes completely expressed and yield 'maintained' in resistant types. It means that the survival mechanisms, become more important than maintenance of grain productivity (yield potential) if the stress intensity is high or duration is long, since few to several production steps in the developmental sequence will be totally disrupted. The observation of Mederski and Jeffer (1973) that soybean varieties had the same rank order regardless of whether they were grown under moist or water-deficient conditions, can thus be explained in terms of lack of substantial differences in the water regime under two treatments (Boyer & McPherson 1975).

In order to evaluate the relative importance of yield potential (as well as wide adaptability) and drought resistance, and to establish whether specific adaptability exists for the particular pattern of drought, direct selections were made in different stress environments (see below) from the So generation of NP9BR and Downs' populations, and from F2s derived from single crosses between two resistant and widely adapted cultivars (CSV3 and CK60B) with a susceptible one (CSV5), for two generations.

The selection environments (in F2s, F3s etc.) included the following:

- (i) *Kharif* (rainy season) stress (on light shallow Alfisol)
- (ii) *Rabi* stress (receding moisture situation on medium deep Vertisol during postrainy season)

(iii) Summer mid-season stress (crop not irrigated during panicle development stage, shallow soils)

(iv) Summer control (regularly irrigated summer crop).

Twenty-three selections made from each population and crosses during each of the seasons were tested for yield together with two checks, during *kharif*, *rabi* and summer of 1980-81, to see whether the selections made during any particular season are in reality best suited for that very season. The *rabi* selections were distinctly superior in *rabi* yield trial (table 1); they were also found to be better than *kharif* selections even during *kharif*. During the *kharif* test, terminal drought did occur because of lack of rains and the poor water-holding capacity of a shallow Alfisol. Thus the stress profile might have been more conducive for *rabi* selections for adaptation for terminal stress than for *kharif* types.

Table 1 Grain yields of selection made under different environments during *kharif* and *rabi* trials (1980). The phenological differences between groups of selections made under each environment were not significantly different (see text for details)

Selection environment	Mean grain yield (q/ha) during 1980 yield trials	
	<i>Kharif</i> trial	<i>Rabi</i> trial
<i>Kharif</i> (Shallow Alfisols)	38.9	10.6
<i>Rabi</i> (medium deep Vertisols)	40.1	13.3
Summer control (Alfisol, regularly irrigated)	38.4	9.4
Summer stress (as under control but 3 irrigations missed during panicle development stage)	37.7	9.0
Overall mean	38.8	10.6
LSD (5%)	1.2	2.0

Thus the existence of genotypes which can give relatively high yields consistently from place to place and from season to season can be found. However, at high input levels and near-optimum environments, a strong breeding program in every narrowly defined geographical area within the broad band of adaption is expected to result in distinctly superior types for each region. But in the semi-arid tropics, where seasonal fluctuations are great, wide adaption is really worth looking for. Seetharama et al. (1982) emphasized that the ideotype for any given location can never be more precise than the quantitative and probabilistic characterization of the seasonal moisture environment and other factors influencing growth and productivity. Arnon (1980) has pointed out that variability within a given ecological niche can be greater from year to year, than between locations in the old Palestine region, and hence argued that broadly adapted varieties must be introduced (Arnon 1975).

There was no difference in yield between the summer selections made under midseason stress or under regular irrigation. This pointed out the difficulty in selecting for each agroecological set of conditions. In India although several distinct agroclimatic divisions exist (Murthy & Pandey 1978) widely adapted cultivars such as CSH1, CSH6, CSV4 and SPV351 are found to be yielding far better in almost all years of testing in most of the locations than the best local cultivars. Hence the conclusion has been made that the whole part of the country growing grain sorghum during *kharif* can be treated as one zone (Rao et al. 1979). Only varieties with wide adaptability can be expected to be retained after such tests.

While we can reasonably succeed in

characterising a location on the basis of long term weather records, it is difficult to deal with the interannual variability. The problem is made more complex as the management factors also influence seasonal plant microenvironment (e.g., higher rates of fertilizer or plant population increasing water demand). As the seasonal rainfall decreases, the variations also increase (Cocheme & Franquin 1967) and hence the problem of breeding for a specific plant type adapted to that location becomes more difficult. The profile of drought the plant undergoes during the F₂ could be qualitatively and quantitatively far different from that for the selection of the F₃ generation. Hence only those adaptive features which are given a chance to express themselves during each year of the selection period are likely to be retained in the final selections.

Adaptative Mechanisms

To know which parameter best describes and explains plant response to water stress, and which adaptive feature is responsible for drought resistance requires an understanding of how plant water stress is transduced into plant performance (Steponkus et al. 1980). There has been a great deal of published material in the form of proceedings of various symposia and workshops (Durham et al. 1982, Goffdin & Northington 1979, IRRI 1982, ICRISAT 1980, 1982c, 1982d, Mussell & Staples 1979, Raper & Kramer 1983, Turner & Kramer 1980, Paleg & Aspinall 1981, Johnson 1981, Monteith & Webb 1981, Krizek 1981); books (Brown 1974, Christiansen & Lewis 1982, Hall et al. 1979, Lange et al. 1982, Lyons & Briedenbach 1980, Levitt 1980, Scott 1979) and reviews (Boyer & McPherson 1975, Behboudian 1977, Begg & Turner

1976, Parson 1979, Jordan & Monk 1980, Turner 1982a & b; Seetharama et al. 1982b, Hanson 1981) and hence we will confine ourselves to the general assessment of the significance of various mechanisms or adaptive features in the immediate as well as the distant future.

Several authors (Jordan & Monk 1980, (i) Phenological, (ii) Morphological, (iii) Physiological, and (iv) Biochemical.

Table 2 Phenological, morphological, physiological and biochemical changes reported to contribute to drought resistance of sorghum and a qualitative assessment of their cost in terms of biomass or grain productivity (modified from Turner 1979 and Jordan & Monk 1980)

Mechanism of drought resistance	Productivity reduced?	Reference
1. DROUGHT ESCAPE:		
A. Phenological response		
1. Rapid phenological development	No?	Blum 1970
2. Developmental plasticity	Depends on conditions	Seetharama & Bidinger 1979
3. Photoperiodic response	Mostly biomass only reduced with delayed planting	Bunting & Curtis 1970
B. Carbon assimilation & remobilization		
1. Remobilization of stem reserves	Biomass only reduced	Seetharama et al. 1982
2. High growth rates	No	Garrity et al. 1982
3. Low respiration rates	No	Rice 1979
2. DROUGHT AVOIDANCE (TOLERANCE AT HIGH WATER POTENTIAL):		
A. Reduction in water loss		
1. Increase in stomatal resistance	Yes	Henzell et al. 1975
2. Reduction in leaf area (death)	Yes	Seetharama et al. (unpublished)
3. Reduction in leaf area (rolling)	Yes	Begg 1980
4. Increase in epicuticular wax	No?	Ebercon et al. 1977
5. Increase in cuticular resistance	No	Blum 1979a
6. Glossy leaf	No?	Maiti 1980
B. Maintenance of water uptake		
1. Increased root density & depth	No?	Jordan & Miller 1980'
2. Increased liquid phase conductance	No?	_____
3. DROUGHT TOLERANCE (TOLERANCE AT LOW WATER POTENTIAL):		
A. Maintenance of turgor		
1. Osmotic adjustment	No?	Seetharama et al. 1982
2. Increase in cellular elasticity	No?	Turner & Jones 1980
3. Decrease in cell size	No?	Turner & Jones 1980
B. Dessication tolerance		
1. Protoplasmic tolerance	No	Sullivan & Blum 1970
2. Maintenance of chloroplast integrity	No	Sullivan & Blum 1970
3. Resistance to leaf firing	No	Seetharama et al. 1982
4. Heat resistance	No	Sullivan & Ross 1979

*Phenological Adaptations**Earliness*

The single most important and common change that occurs in high yielding cultivars bred for drought prone areas is earliness in maturity. Thus the early hybrids and varieties are rapidly replacing all locals in India under progressive farming, and thereby achieved a quantum jump in the yield of sorghum (Rao et al. 1979). Further, earliness has also made the crop more widely adapted across the country and offers better intercropping opportunities. However, earliness is not a universally successful strategy (see below).

Photoperiod sensitivity

In west African countries like Nigeria, Mali and Upper Volta, the rainfall in the beginning of the season is too erratic, while in the end of the season it ends rather abruptly. The length of wet season increases from north to south in Nigeria. The local farmers take advantage of the photosensitivity of the sorghum since the plants flower at the same time irrespective of sowing date (Curtis 1968). With an insensitive type this kind of flexibility in sowing date is not possible and the late sown crop would flower and fill the grains under severe moisture deficits (and under cold conditions) every year. When sown early during wet years the genotype will suffer from grain weathering. An additional advantage of the photosensitive type is the prevention of the severe buildup of pest populations (e.g. midge or earhead bug) since in all fields, irrespective of date of sowing, the crops flower simultaneously. If the insensitive types are grown, the early sown (and hence early flowering) crop will undoubtedly serve

as the source of severe epidemics on late sown crop.

However, in the case of India, earliness has been the most extensively used strategy in contrast to photoperiod sensitivity. Photosensitive varieties have a limited range of adaptation. Webster (1972) reported that a sensitive variety developed at Samaru, Nigeria was adapted to an ecological zone no more than 80 to 120 km wide north and south. Outside this zone the variety was too early or too late. Such an approach of breeding for extremely narrowly adapted varieties can only be useful if each location has a strong breeding program; otherwise the crop improvement in such places will lag behind the centralized programs where the widely adapted varieties are emphasized, at least initially.

Developmental plasticity

Stout et al. (1978) have described stress induced changes in the length of growth stages. Seetharama and Bidinger (1979) studied a set of 33 germplasm lines under well irrigated and midseason (approximately during panicle development stage or GS2) stress conditions and found that the days to flower under stress could be either hastened by a day or delayed as long as 33 days (figure 8A). There was a positive and significant correlation ($r=0.55$; $P<0.01$) between days to flower under control, and delay under stress. This association, however, appeared to be largely due to those cultivars which flowered earlier than about 80 days (figure 8A). In another experiment with 33 SI lines from NP9BR population, the correlation was not significant ($r=0.27$; figure 8B). In both cases the delay approximately follow the normal distribution. Thus this response seems to be, partly at least,

under genetic control and hence it may be possible to manipulate this character in a breeding program for a region where there is a good probability of adequate rains late in the season to complete an extended crop growth period.

Figure 9 shows the relationship between delay in flowering and grain yield under stress. In the first experiment, the stress yields were reasonably correlated with delay up to about 10 days in flowering. In the second experiment they were unrelated (figure 9B).

The common nontillering sorghum of India lacks the degree of plasticity exhibited by other tillering cereals like wheat and pearl millet, which can use tiller number (and size) to buffer against the available water for fairly long periods during the season. However, some sorghums produce nodal tillers and, if the midseason stress has reduced the main culm yield, the nodal tillers make up for the loss by producing grain rather quickly. During the 1976 summer experiment at ICRISAT, IS1037 under midseason stress produced 1.1 t/ha on the main shoot, and an additional 1.5 t/ha was produced on nodal tillers (the control produced 2.1 t/ha only).

Morphological adaptations

Morphological adaptations which increase water uptake (table 2) as well as reduce consumption of water have been extensively discussed in the literature (see above). At ICRISAT genotypes resistant to wilting, leaf tissue firing and recovery ability at seedling stage have been evaluated in the field, in wooden and brick flats, and in cylinders. Significant genotypic differences in response to drought were found both in the germplasm and breeder's elite lines (figure 10 A) as measured by scoring for wilting,

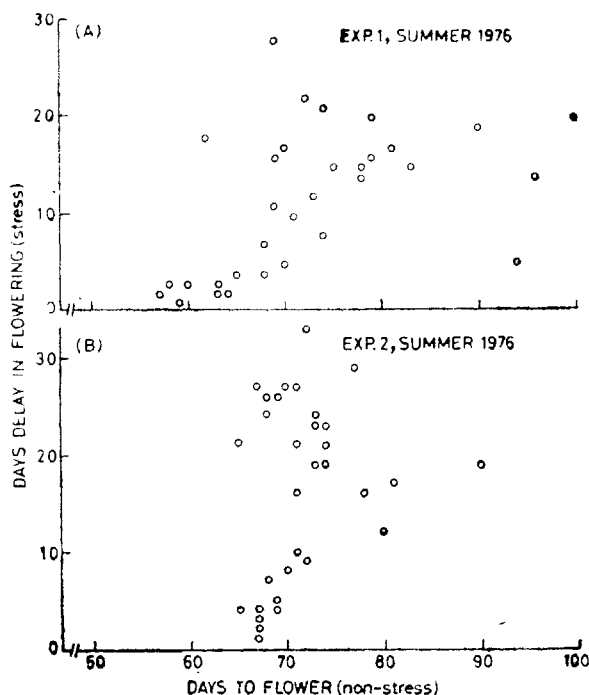


Figure 8 Relationship between days to flower (non-stress) and days delay in flowering under stress (Seetharama & Bidinger 1979)

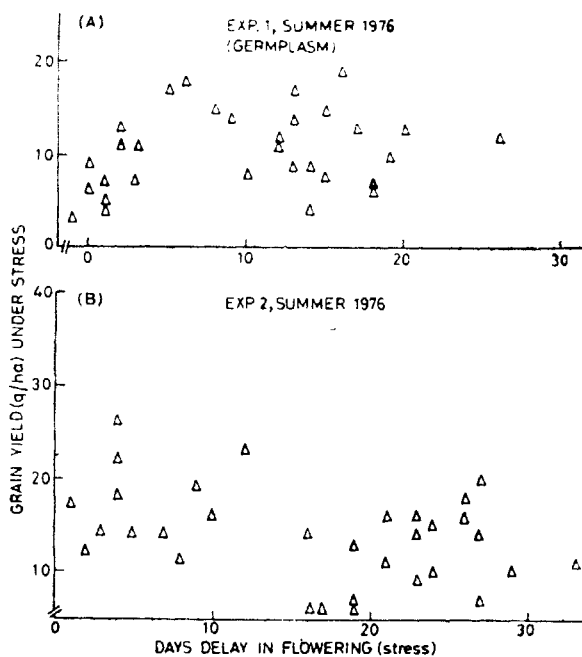


Figure 9 Relationship between days delay in flowering in stress and grain yield (Seetharama & Bidinger 1979)

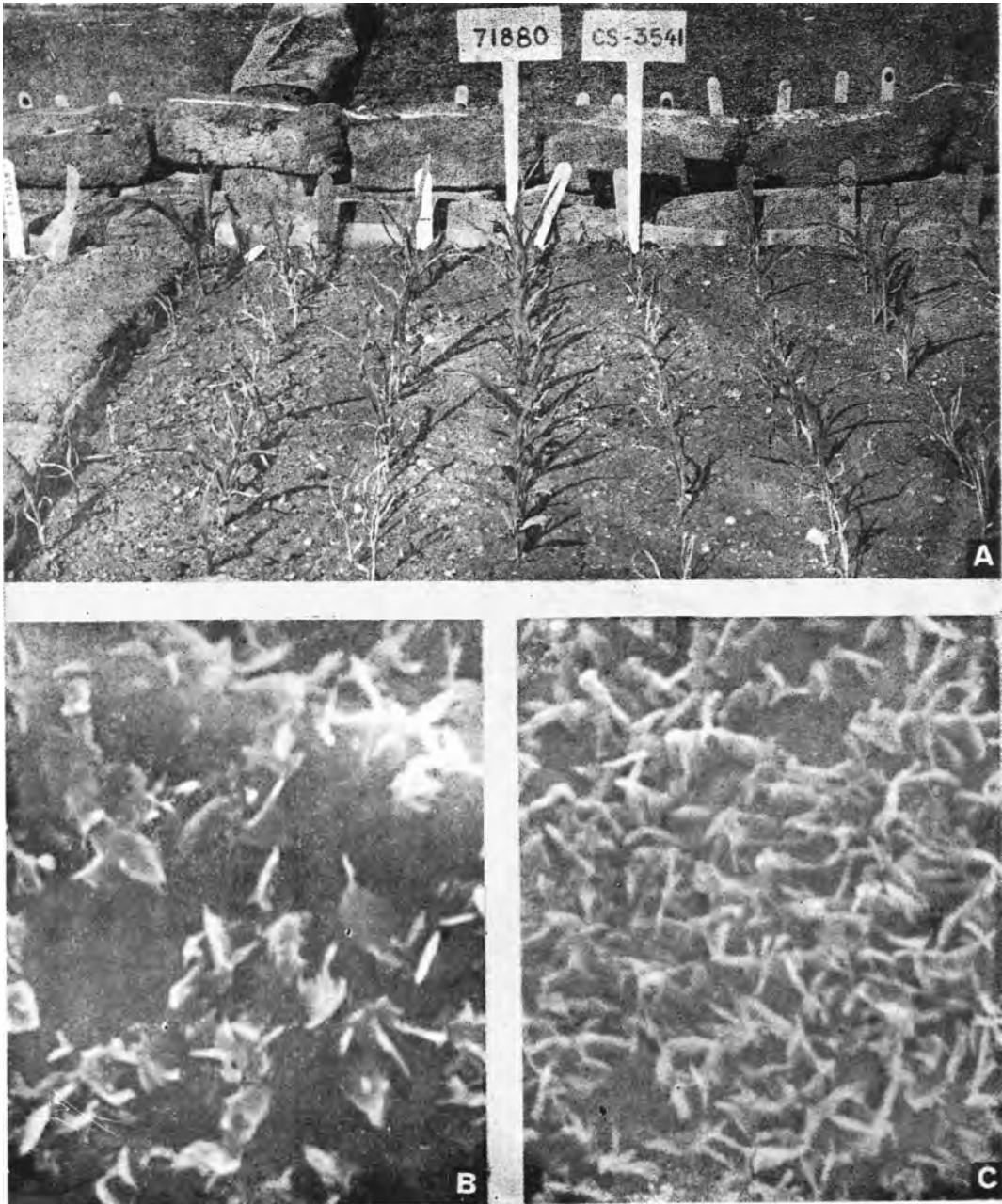


Figure 10 (A) Screening for seedling drought resistance in brick flats (picture was taken after the 'release' of stress by rewatering. CS3541, a susceptible entry in the trial was killed due to stress; IS1160, a resistant entry shows least damage due to stress and good recovery); (B) & (C) Scanning electron micrographs (SEM) of glossy (B) and non-glossy (C) sorghum leaf surfaces (Glossy leaf surface has flat wax plates forming large crystals; non-glossy surface has small needle shaped crystals; SEM by the courtesy of Dr Susan Woodhead, Centre for Overseas Pest Research, London)

recovery and survival after release of stress. Most of the seedling drought resistant lines had light green leaves with a 'glossy' surface, while the susceptible lines, in general, had dark green leaves (Maiti 1980). Scanning electron microscopy showed that the 'glossy' leaves (figure 10 B) have smooth wax plates forming large crystals, whereas the non-glossy ones have small needle shaped crystals (figure 10 c). Hull et al. (1978) have noted similar differences in wax structure among drought resistant and susceptible *Eragrostis* species.

Physiological Adaptations

Physiological adaptations have been under study for more than a century and the findings for sorghum are summarized

in several recent reviews (Jordan & Monk 1980, Jordan & Sullivan 1982, Garrity et al. 1982, Turner 1981a, Seetharama et al. 1982 b). Generally, any single physiological characteristic independent of others is unlikely to be directly correlated with drought resistance in the field. Table 3 shows the various physiological characteristics of 10 sorghum cultivars under typical *rabi* conditions at Patancheru. Although M35-1 and CSH8 are more resistant cultivars in the field than CSV5 and V302, no single physiological characteristic can match perfectly with that observation.

The physiological traits can be better used in screening genotypes by adapting the following:

Table 3 Plant water stress parameters of 10 sorghum cultivars (B2, 1979 *rabi*) seasonal water stress parameters measured around noon on 12 Feb 1980, 94 days after planting

Genotype	(i) Leaf water potential* (bars)	(ii) Solute potential** (bars)	Turgor*** (bars)	Stomatal conductance (cm/sec)	Leaf temperature (°C)
NK 300	±16.8	±11.2	5.6	0.58	28.6
CSH 8	±19.7	±12.1	7.6	0.52	28.3
CSV 5	±21.9	13.1	8.8	0.75	25.1
CS 3541	±20.5	±11.7	8.8	0.76	25.1
IS 1037	±20.9	±15.4	5	0.59	26.3
M 35-1	±25.9	±19.3	6.6	0.50	30.6
CSH 6	±17.8	±13.7	4.1	1.14	27.0
SPV 86	±24.1	±15.7	8.4	0.47	27.9
V 302	±20.4	±15.9	4.5	0.56	29.6
CSH 1	±16.0	±13.8	2.2	0.92	28.5
Mean	±20.41	±14.14	6.27	0.68	27.69
SE	±0.80	±0.39	±0.88	±0.15	±0.23
CV %	7.80	5.49	28.05	45.23	1.69

* Measured with pressure bomb; 4 plants/plot sampled

** Measured with Wescor osmometer, corrected by the procedure of Jones and Rawson, 1979; 4 plants/plot sampled

*** Differences between (i) and (ii); only 2 plants/plot sampled

1. Measure the traits diurnally and/or seasonally and use the integrated value, if needed, after "cleaning" data for field variability, etc. Figure 11 shows the seasonal pattern of differences in leaf temperature between different irrigation treatments over the fully irrigated control. The LI treatment had cooler leaves than the control during the later stages. This was because of reduced leaf area in LI compared with controls (and hence less stress). Even the dry matter yield of LI was marginally more than control suggesting that it is not merely total green leaf area, but also the activity of those leaves, which produce higher yield under stress. Thus the judicious loss of some leaf area is more beneficial than having a large area which subsequently exposes the plant to a more severe stress. Piara Singh (1981) has described the advantages of integrating various physiological stress parameters to predict yield quantitatively.
2. Use of several traits measured regularly or during critical stages: Devising a "battery of tests" for the given pattern of stress environment would tremendously stimulate breeders to use physiological parameters (L.R. House, ICRISAT, personal communication). Research at ICRISAT since 1976 has proved useful in formulating a hypothesis regarding such a "battery of tests" for *rabi* sorghum. For example, osmotic adjustment, remobilization of stem reserves to the grain, rapid phenological development (not delayed by stress) and deep roots-are all important for *rabi* sorghum along with proper management practices for high and

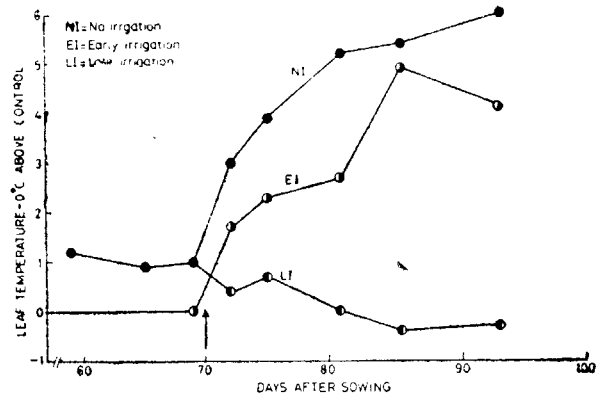


Figure 11 Seasonal (mid afternoon) leaf temperature of sorghum under different irrigation treatments. CSH8R sorghum was grown in RP 17 during *rabi* 1978 with uniform irrigation until 35 days. Control received two more irrigations on 47 and 70 DAS. Treatment EI received irrigation only 47 DAS and LI only 70 DAS. NI didn't receive any irrigation beyond 35 DAS FR Bidinger, unpublished

stable productivity (Seetharama et al. 1983).

Biochemical Adaptations

During the course of evolution of mesophytes, most of the changes that have taken place are either morphological or phenological but the basic biochemical apparatus has remained almost unchanged. Among higher plants there is a great variability among species or groups of species (e.g. C4 vs C3 pathway; Good & Bell 1980) in more efficient use of water, but difference between genotypes within a crop species is rare to find. However, there seem to be reasonable differences in the metabolism of small molecules: e.g. differential production of proline or betaine in response to stress (Hanson 1980) or changes in hormones (Milborrow 1981, Kannangara et al. 1981a). Figure 12 shows changes in abscisic acid (ABA), phaseic acid (PA) and 3-indolylacetic acid (IAA) as the stress levels vary. ABA increases

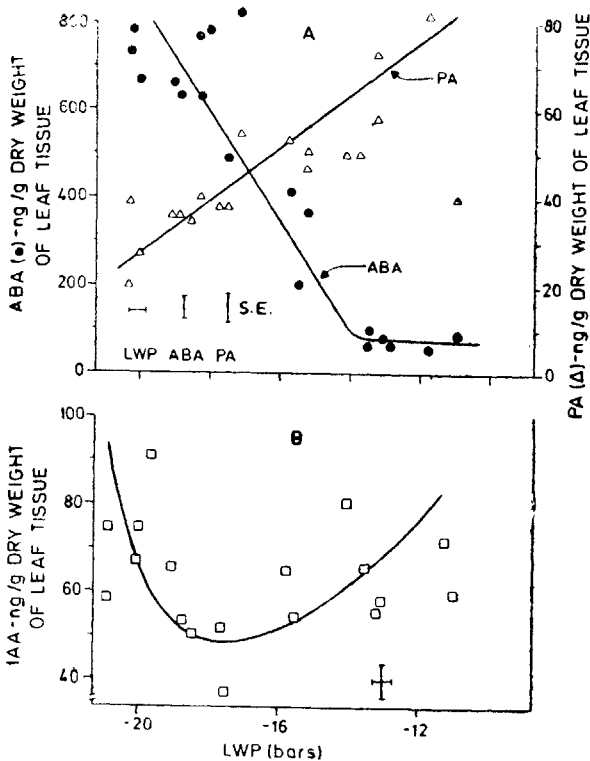


Figure 12 Relationship between leaf water potential (LWP) and (A) Abacisic acid (ABA), Phasoic acid PA, and (B) Indole-3 Acetic acid (IAA) concentrations, (CSH-8; R6, 1980 Rabi, Line source, unpublished data of T. Kannangara, R.C. Durley and G.M. Simpson)

rapidly in response to stress. Genotypic differences in hormonal levels are found under normal conditions, and the changes under stress also seem to be genotype-specific (Kannangara et al. unpublished). In a preliminary study with CSH8R under gradient of moisture stress levels (imposed by using a line source sprinkler), the correlation between ABA and yield ($r = -0.65$) was similar to the correlation between irrigation and grain yield ($r = +0.68$) except being opposite in sign. Thus leaf ABA content could be equally strongly correlated as irrigation water applied, to yield (Kannangara et al. 1981b). However at this stage the technique has to be

further perfected and simplified before being used on a large scale.

Physiologists envisage the control of transpiration by hormones to be dynamic (Jones 1979, Walton 1980) responding quickly and favourably to the onset of stress and reversing to the original level once the stress is removed. Thus it is possible to select for a low natural level of hormones with a tendency to produce large amounts at the onset of stress (e.g. accumulation of ABA in response to stress) or enhanced sensitivity under stress conditions (e.g. increased stomatal sensitivity to lower concentrations of ABA in pre-stressed crops). Such facultative adaptations are less costly, and more efficient than obligatory irreversible adaptations. Increased research in this area is expected to produce rich dividends. Obviously we need to know far more about the role of hormones in the various physiological processes and their interactions with the environment, and also how they are integrated during ontogeny to produce a particular magnitude of yield (or yield reduction under stress).

Studies with mosses has shown that the ability of the plant to mobilize enzymatic defence against lipid peroxidation (Dhindsa & Matowe 1981) and to conserve messenger RNA during drying (Dhindsa & Bewley 1978) were very useful in detecting differences in drought tolerance. Boyer (1981) and Lawlor (1981) have reviewed the potential for biochemical and physiological modifications of crops to yield under stress. Although they have identified a few areas for possible applications, the existing knowledge is not enough to be of immediate practical use in screening genotypes.

Walbot (1980) has regretted that agricultural sciences have captured the attention of too few molecular biologists.

However, Hsiao and Acevedo (1974) have cautioned that the basic work at cell and plant levels should not be ignored while attempting to identify specific attributes at molecular levels (Woolhouse 1981). The recent thrust in this direction to support suitable research by United Nations Industrial Development Organization (Stein 1981) and Government of India (GOI 1981) are encouraging.

Interdependence of Adaptive Mechanisms: Role of Intermediate and Integrating Adaptations

The above discussion of various adaptations under the respective four headings should not give the impression that each of these four are distinct categories, independent of each other. Sinha et al. (1981) have argued that crop productivity, including that under stress, is a total sum of several interacting factors varying in quality, quantity and duration. For example, short-term biochemical events such as ABA production have influences on both stomatal response (short term) and on vegetative and reproductive growth (long term; Quarrie & Jones 1977). Similarly many physiological responses to stress influence crop growth and yield through changes in phenology and morphology.

For the immediate future for crop improvement we should concentrate on those adaptive features, which are intermediary in character (e.g. leaf area) or an integrated effect (leaf area duration or leaf area/root length ratio, representing balance between water demand and supply) as illustrated below.

Leaf area

On 22nd April 1981, six cultivars of sorghum were planted and grown under irrigation for 10 days (5-leaf stage). From then-on one treatment (stress) received no further irrigation, while the other (control) was irrigated twice a week. The emergence, expansion and senescence of all leaves were measured daily. While the total number of leaves was unchanged under stress, it reduced their sizes. In CSH8, there was little delay in emergence of leaves under stress (figure 14) (delay of 0, 3 and 4 days under stress for 10th, 15th and

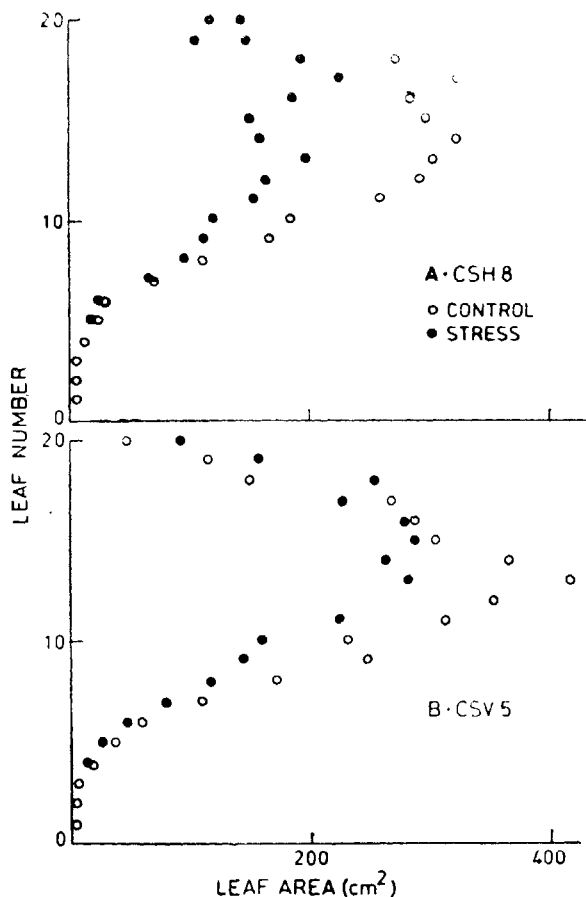


Figure 13 Area of individual leaves of two genotypes under irrigated (control) and unirrigated (stress) conditions (Botanical garden, Summer 1981; see text for details), (unpublished data of J M Peacock, P K Verma and N Seetharama)

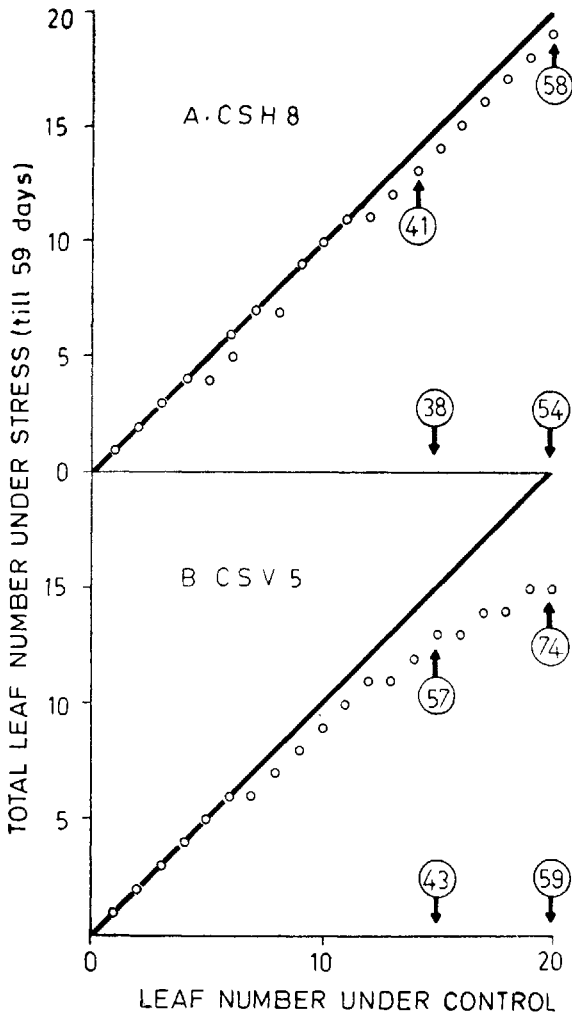


Figure 14 Relationship between number of leaves emerged in control and stress plots (Botanical garden 1981 summer; the final leaf under stress in CSH8 and CSV5 emerged respectively, 58 and 74 days after sowing; the circle with no. inside, denotes the no. of days from emergence of the particular leaf pointed out by the arrow under control (arrow pointing downwards) and stress (upwards) (See text for details)

20th leaf); however, the size of leaves under stress was reduced. On the other hand in CSV5, the emergence of leaves was delayed to a greater extent (figure 14) (by 2, 14 and 15 days for 10th, 15th and 20th leaf) under stress, and the

final few leaves emerged and expanded after the release of stress by the advent of monsoon rains during late June. Since the environmental conditions were optimum for leaf growth after the rains, the top several leaves of CSV5 actually grew bigger in size in the stress plots than under the control. Thus the phenological changes could markedly change the morphological (or even physiological) responses. If water availability is expected later during the development the postponement of development could be a better strategy than production of smaller leaves under stress.

Analysis of Change in Yield Components under Stress

During the *rabi* 1979, using a line source on medium deep Alfisol, the effect of three different patterns of stress during panicle and grain development was studied (figure 15). The seed number (figure 15A) as expected, was influenced only by stress during panicle development stage (GS2). A linear decline in seed number was noticed under the gradient of stress (treatments LS/LS or LS/UI) but under the third treatment (NI/LS) the seed number at different distances from line source was not significantly different, though drastically reduced (no irrigation during GS2; line source irrigation applied only during GS3). On the other hand, seed size differences were found only in the treatments receiving variable amounts of water during GS3 (in LS/LS and NI/LS; not in LS/UI). Such yield component analysis can help us to logically look back at the individual steps which occur sequentially during the season in order to understand the physiological basis of yield differences under stress.

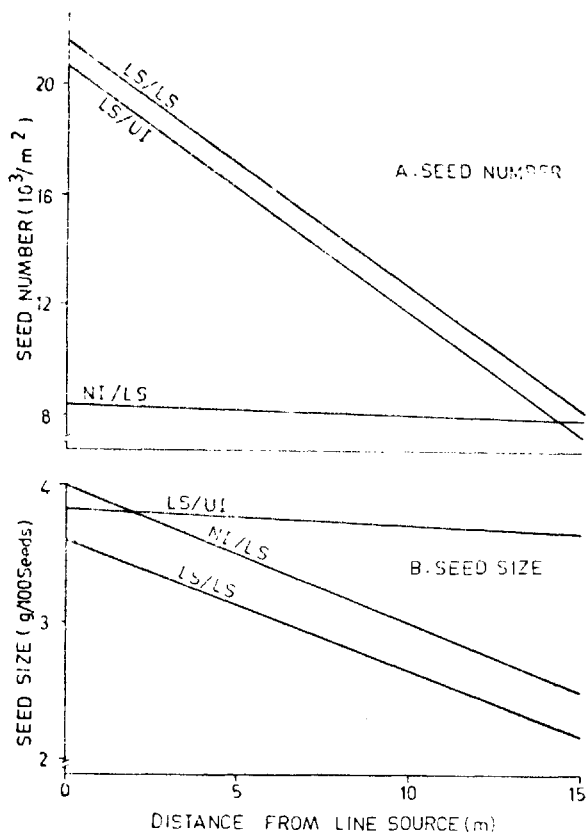


Figure 15 Changes in yield components as a function of distance from line source (LS) sprinkler and irrigation treatments (Line source experiment, 1979 *rabi*, LS/LS—Gradient of moisture stress using LS in GS₂ and GS₃. LS/UI—Gradient only during GS₂, uniform irrigation (no stress) during GS₃. NI/LS—Uniform stress in GS₂, (no irrigation) and gradient of stress with LS in GS₃. (unpublished data of R C Sachan)

Following the arguments of Sinha et al. (1981) it is also clear that phenological and morphological adaptations should be used more extensively as they represent greater integrating effects than physiological and biochemical adaptations. The use of physiological and biochemical parameter stipulate higher levels of commitment of time and resources (Swindale & Bidinger 1981) and hence the progress in using them will be slower.

Some of the morphological ('glossy') and developmental ('recovery ability') traits have more profound and integrating effect than others (table 2).

Even the drought resistance mechanisms (Levitt 1980) are not mutually exclusive. Sullivan (1972), discussing the basis of selection for drought resistance, suggested combining all the interacting mechanisms. Boyer and McPherson (1975) have argued that some 'avoidance' type of responses may also act as pretreatment for developing greater tolerance. Blum (1979b) has shown that early sorghum genotypes not only escape drought but also avoid it because of reduced transpiration demand as a result of decreased leaf area and high root length—leaf area ratio.

Summary and Conclusions

Assessment, prevention or amelioration of drought effects in various crops at different growth stages has remained as one of the most challenging problems of our time. Drought is the major limiting factor in sorghum production in most parts of the world, and in spite of its reputation as one of the most drought resistant crops, sorghum yields are considerably reduced by water stress. Hence a great deal of further research is needed in identifying and quantifying sorghum responses to stress, and in refining breeding methodology and management practices.

Both drought and the response of plants to it are highly location specific. Hence no single set of priorities should be advocated universally. Selection of the most appropriate method (or combinations of methods), is thus complicated; it must be based on environmental, economic, social, and other relevant factors prevailing in a certain region.

The introduction of crops and varieties endowed with a spectrum of drought resistant traits is not always the best and cheapest solution. The relative merits of high productivity and drought resistance (stability) will vary across regions. In most of the semi-arid tropics where sorghum is grown, the farmers have very limited resources and yield levels are very low; further varietal improvement with required alterations in the management is expected to raise the yield significantly above the current yield level (e.g., approximately 600 kg/ha in India, Seetharama et al. 1982) as well as stability across years of erratic rainfall.

Elucidation of location specific plant water stress profiles and the spectrum of responses should go hand in hand with field screening and breeding activities. In all dynamic agricultural systems there is always room for further improvements

and refinements; hence the absence of complete understanding of the problem of drought need not discourage us from initiating appropriate measures using empirical approaches which can be further refined by additional physiological and agroclimatological research.

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