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DROUGHT RESISTANCE IN CROPS WITH EMPHASIS ON RICE

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SORGHUM IMPROVEMENT FOR DROUGHT RESISTANCE

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Drought is the major limiting factor in most of the sorghum-growing areas of the world, especially in the semiarid tropics. At the International Crops Research Institute for the Semi-Arid Tropics, sorghum improvement for drought resistance involves using a range of techniques for screening germplasm and elite breeding material. Selections are advanced to multilocation trials in drought-prone areas. The need to incorporate drought-resistance mechanisms in addition to escape and to tailor the plant to suit the target environment is emphasized. Field and laboratory techniques are used to study specific adaptations such as leaf-area adjustment (drought avoidance) and heat and desiccation tolerance and adjustment in osmotic potential (drought tolerance). Future problems and prospects in crop improvement for drought resistance are considered. The requirements for tackling the locational and temporal specificity of drought by problem-oriented training, by better cataloguing of environments coupled with requisite adaptations, and by modeling are noted.

Sorghum, grown on 51 million ha in both tropical and temperate zones, is one of the 5 most important cereals in the world (Doggett 1970). The major ecological zone for sorghum lies between the humid forests near the equator and the deserts

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of the arid and semiarid tropics (SAT). Recently FAO carried out a more complete agroecological description of the sorghum-growing areas of Africa, Southwest and Southeast Asia, and Central and South America (Higgins 1978). The rainfall probability and moisture availability indices for many SAT regions have been compiled and published by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) (Virmani et al 1980a,b). But much more has to be done to delineate agroecological zones of the SAT regions of the world.

In Africa, sorghum is grown on 14 million ha in the group of drought-prone countries that extend across the continent between latitudes 10° and 20° N (Motha and Sakamoto 1979), bordered on the north by the Sahara Desert in the Sahelian-Sudanian zones, down through East Africa, and into Central and Southern Africa. It is the major source of food calories in many countries, but yields average only 690 kg/ha (FAO 1979).

In Asia, sorghum grown on 26 million ha yields an average of less than 880 kg/ha. In India, where it is the third major cereal, it is grown on 16 million ha, of which 50% is cultivated on stored moisture during the postrainy season. Regions growing sorghum during the rainy season fall between the wheat- and pearl millet-growing environments in the north and the rice- and finger millet-growing regions in the south (S. J. Reddy, ICRISAT, pers. comm.). They are classified as agricultural subdivisions II and III (Murthy and Pandey 1978). Sorghum usually is intercropped with pigeon pea during the rainy season in India.

In Latin America, especially in Mexico and Argentina, the rate of increase in area sown and yield has been impressive (3.5 t/ha in Mexico and 2.9 t/ha in Argentina in 1979). In Latin America, as in Africa, sorghum is intercropped with other cereals such as pearl millet or maize (depending upon the rainfall) and with a variety of legumes. A ratoon crop also is grown in many countries.

Most countries of the semiarid tropical belt of Africa, Asia, and Latin America have exhibited a dramatic downward trend in levels of food self-sufficiency over the last 15 years. This decline has been reflected by both a general decline in total annual rainfall (Motha and Sakamoto 1979) and large year-to-year fluctuations in the amount of rainfall. These two conditions together have brought drought. The impact has been compounded by population increases.

Drought limits the yield of sorghum, reputedly one of the most drought-resistant crops. Surveys conducted by ICRISAT and the Semi-Arid Food Grain Research and Development (SAFGRAD) show that drought is the major problem limiting sorghum production in SAT (House 1980). Even in high-rainfall (>80 cm) areas, short periods of drought can decrease yield considerably.

The objectives of this paper are:

1. to examine approaches to screening for drought resistance in sorghum, with particular reference to the complexity of the SAT environment and the vast range of germplasm available;
2. to examine the usefulness of different techniques of selection for drought resistance; and
3. to speculate on future problems and prospects of success.

Other authors (Garrity et al, this volume) also deal with sorghum. This paper will be confined to sorghum in the SAT and work at ICRISAT.

SCREENING AND BREEDING FOR DROUGHT RESISTANCE

Approaches to screening

The various approaches to screening for drought resistance may be grouped as direct (agronomic or empirical) or indirect (physiological or analytical). Direct selection for resistance implies either selection for absolute performance (growth rate or yield) under actual moisture stress or selection for only a small reduction in performance under stress. Indirect selection implies screening for morphological or physiological characteristics that may be correlated with or that contribute to drought resistance.

An important aspect of the sorghum improvement program at ICRISAT is the availability of more than 18,000 accessions of sorghum germplasm. The diversity of sorghum-growing environments and the resulting plant adaptations suggest that there is scope for using the germplasm to improve drought resistance. To identify the various traits that individually and in combination contribute to drought resistance, accessions have to be grown in the field. Such direct field screening probably can be done only where and when there is little or no rainfall or where moisture supply to the crop can be controlled through use of irrigation and rain-out shelters. Fortunately, this is possible at many sites in the SAT during the dry season, provided irrigation facilities are available.

The complexity of drought has led to the comment that empirical selection may remain the most effective procedure for some time (Evans 1980). Indirect selection and short-term measurements in the field or under controlled environments also are useful.

Selection for tolerance for desiccation and heat (Sullivan and Ross 1979) and selection for stomatal sensitivity to stress (Henzell et al 1975) are examples of indirect selection in sorghum. It is probably unrealistic to expect a correlation between individual physiological responses and final yield or yield maintenance under moisture stress. However, such responses should consistently confer at least some advantages during stress.

To establish the usefulness of such adaptations in reducing moisture stress, direct field screening and yield estimates are essential. For evaluation of a large number of germplasm and breeders' lines, field screening should have priority. The selected lines can be subjected to individual tests so that the diverse components and underlying mechanisms contributing to stress resistance can be identified and better understood. In the long run, the two approaches are complementary, not mutually exclusive.

Strategies for breeding

Strategies for breeding for drought resistance have been widely discussed (Blum 1979a, Hurd 1976, Sharma and Saxena 1979, Townley-Smith and Hurd 1979, Reddy et al 1980, Fischer 1981). At ICRISAT, it has been postulated that the genes for yield, adaptability, and resistance to stress are separate, at least at some of the loci, and that stress resistance can be further improved without sacrificing yield or adaptability. Segregating materials grown under stress environments can be selected for drought resistance. Selections should be tested repeatedly under environments where the seasonal and interacting patterns of temperature and water stress are similar to those in the target regions.

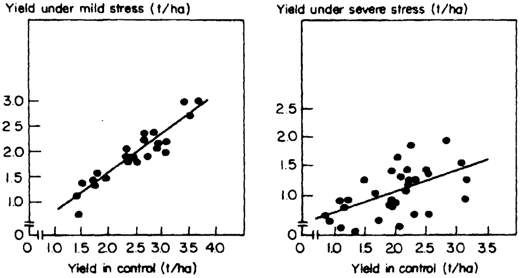
RESEARCH AT ICRISAT

Field screening methods

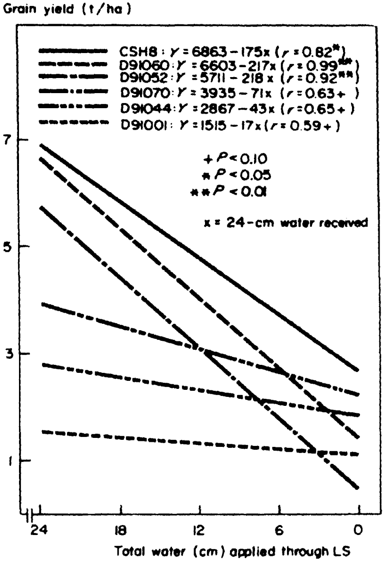
Since 1975, attempts have been made at ICRISAT to evolve simple and direct empirical drought screening methods to evaluate large germplasm accessions and breeder's lines. The experiments were conducted under soil moisture stress in the postrainy (rabi: October-February) and summer (March-June) seasons. Initially, two conditions were imposed: drought during the panicle development stage and receding soil moisture conditions in Vertisols. The first condition represents the midseason drought pattern of the rainy season in many parts of SAT, the second the pattern in rabi crops in India similar to that in crops grown under receding soil moisture conditions in the Mediterranean region (Israel and Yemen) as well as parts of West Africa (Lake Chad area in Nigeria and in Mali).

Screening for midseason stress. Comparison of results of early experiments (Seetharama and Bidinger 1979) in postrainy and summer seasons revealed an important aspect of the screening technique (Fig. 1). Yields under moderate stress were closely related to yields without stress. The mean absolute deviation of the measured yield under stress was only 9% of the predicted yield (obtained by regressing stress yield on control yield). This suggests that mild moisture stress is not sufficient for the expression of genotype differences in response to stress. However, severe stress during the summer caused larger deviations from the predicted yield. The mean absolute deviation equaled 26% of the predicted yield and the range of deviation was from −59 to +63%. This provided an opportunity to tentatively identify a number of genotypes which might have different responses to stress.

The stress treatment used did not produce an abnormal crop (despite lower yields). Correlations of yield and other variables (such as yield components, dry weight, and harvest index) were similar in stress and no-stress treatments. How-



1. Relationship between sorghum yields and stress and no stress.



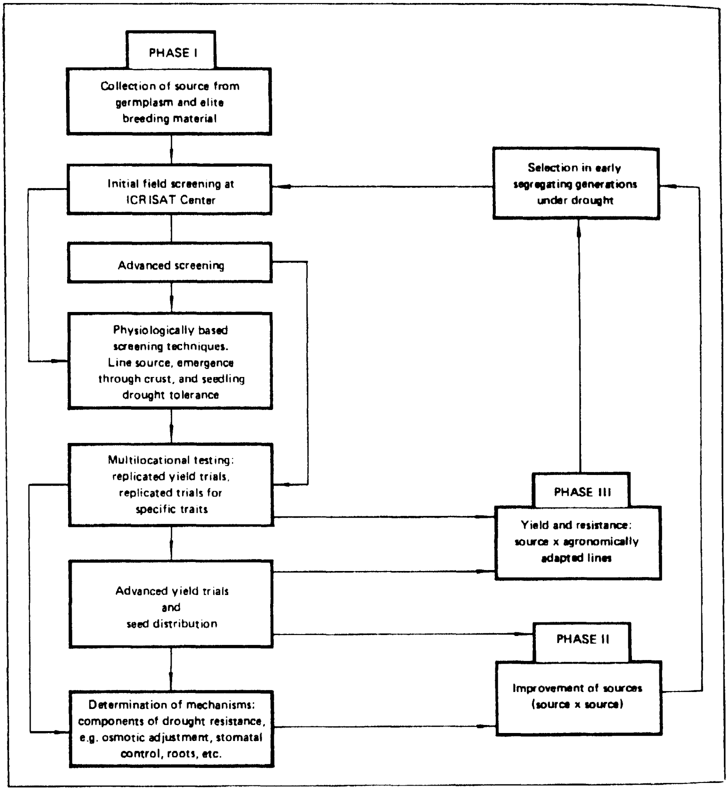
2. Relation between grain yield and irrigation water applied through line source (LS) sprinkler irrigation system (after 3 uniform furrow irrigations to recharge the profile during crop establishment phase). Field RA9C; 9.4 cm water available up to 130-cm depth.

ever, phenology differences are important in this type of approach and estimates of cultivar performance under stress may need to be adjusted for them. Simple indices have been proposed for assessing drought resistance in the field which are independent of cultivar yield potential and correlated to yield under stress. The procedure is similar to that described for pearl millet (Bidinger et al, this vol.).

Screening for rabi pattern of stress. Comparison of yields on shallow Vertisols or on partially saturated deep Vertisols with yields for an irrigated control can be used to screen genotypes for drought resistance in receding-soil-moisture environments.

Line source sprinkler irrigation system. Line source (LS) sprinkler irrigation (Hanks et al 1976) is useful in maintaining a stress gradient at minimum land requirement and cost. A series of test rows of different genotypes planted at right angles to the LS is exposed individually to a uniform gradient of water — from zero to any desired maximum (or adequate to satisfy plant requirements) — from a single row of overhead sprinklers. This technique was used in 1980-81 to screen 64 advanced F_6 progenies (using 8 checks) from the drought-resistance breeding project.

Genotypic differences in response to the water gradient by LS (after the initial three uniformly applied irrigations needed for crop establishment) can be seen when the yield is plotted against the water applied through LS (Fig. 2). The



3. Flow chart of steps in sorghum improvement for drought resistance at ICRISAT (from Reddy et al 1980).

intercepts indicate the yield potential and the slopes indicate susceptibility to decline in water supply. Genotypes with higher intercept and lower degree of slope are selected. When comparing entries such as D91052 and D91070, the areas under regression lines (or overall mean yield across all levels of water supply) are used. Note that, because of its very high yield potential (intercept), the hybrid check CSH8 yielded more than all other entries at all levels of water supply, although it has a steeper slope than D91070, D91044, and D91001. This technique is used at ICRISAT to select for more resistant genotypes (less slope) with high yield potential (intercept) in each maturity group.

Identification of resistance sources and breeding

The crop improvement strategy at ICRISAT consists of essentially three phases (Fig. 3):

Phase I: identification and characterization of sources of drought resistance.

Phase II: improvement of the sources, for example by bringing together the various genes distributed in germplasm into a smaller number of lines.

Phase III: production of agronomically acceptable types by combining yield and adaptability with drought resistance.

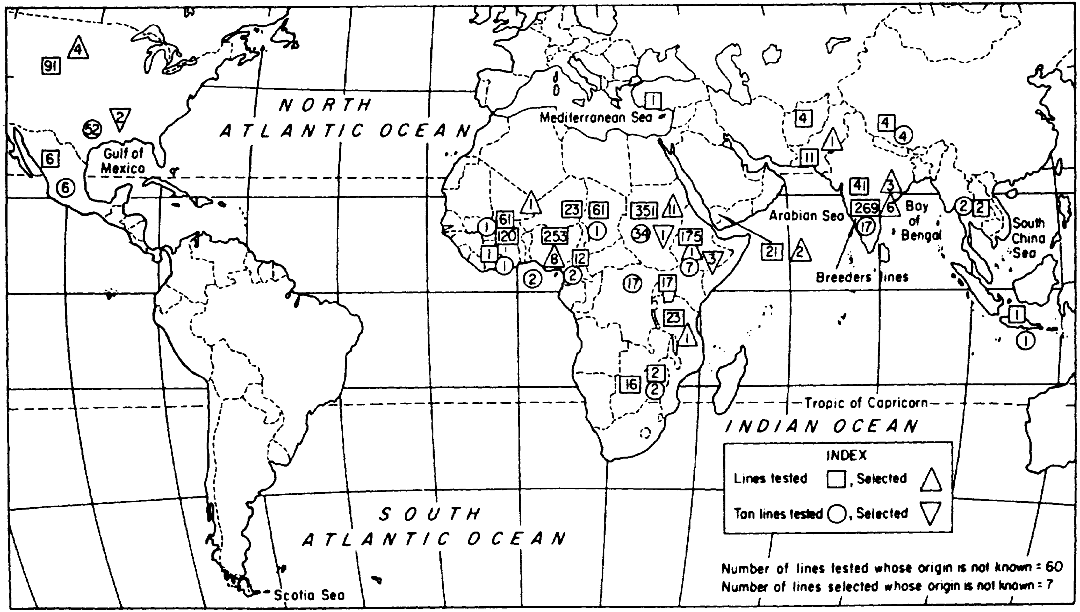
The success of the scheme depends upon the selection of suitable test sites for screening. Both the wet and postrainy dry seasons with controlled irrigation at the ICRISAT center and other sites in India and Africa are used. These sites or environments represent the major patterns of stress being dealt with: 1) intermittent rainy-season drought with emphasis on crop establishment during the first growth stage, and 2) leaf and reproductive growth during the second and third growth stages.

Germplasm screening. During 1978 and 1979, 1,255 germplasm accessions from the drier regions (Fig. 4) of SAT and about 600 advanced breeding stocks were subjected to empirical field screening. Based on field performance during drought, 150 promising lines with suitable checks were organized into 3 separate trials and tested at 8 sites. Some promising selections are listed in Table 1.

Crossing, selection, and testing. Promising lines were identified and crosses were made with agronomically desirable high-yielding lines. Large populations of early generations were grown at the ICRISAT center during the rainy season. Selections were based on agronomic eliteness and resistance traits such as glossy leaves, mold-free grains, and freedom from pests and diseases. Advanced generations were placed in different trials during all seasons and across many sites wherever water deficits were expected to occur during crop growth. The most promising selections were used in crossing for improving various resistance traits and adaptation (Phase III). They were also crossed among themselves and with new sources to improve the level of resistance to drought (Phase II). Final selections were subjected to special screening under the line source sprinkler irrigation system and were tested for seedling drought resistance.

MECHANISMS OF DROUGHT RESISTANCE

Crop plants, unlike most of the xerophytes, use more than one mechanism to resist moisture stress (O'Toole and Chang 1978, Gaff 1980). The complete exploitation of genetic diversity requires evaluating mechanisms that ameliorate internal stresses and those that minimize drought injury (Steponkus et al 1980). Investigations on mechanisms of drought resistance of ICRISAT have two objectives: 1) to establish simple field or laboratory screening methods to handle a large number of genotypes, and 2) to study which of the plant attributes or mechanisms contribute



4. Lines screened for drought resistance (1977 and 1978 cycles). Source: ICRISAT Sorghum Breeding annual reports 1977-78.

Table 1. Genotypes selected for drought resistance at 2 sites and their origins. ISDRON[a], 1979 entries[b].

Genotype	Origin	Selection made at
(NP × E65352-1)-2-1-1[c]	ICRISAT[c]	ICRISAT, India, and Sudan
IS-2312	Sudan	ICRISAT, India, and Sudan
IS-3581	Sudan	ICRISAT, India, and Sudan
15-6	USA[d]	ICRISAT, India
IS-8344	Pakistan	ICRISAT, India
11-9	USA	ICRISAT, India
IS-8595	Sudan	ICRISAT, India
3-40	USA	ICRISAT, India
IS-7525	Nigeria	ICRISAT, India
IS-2321	Sudan	Sudan
IS-2311	Sudan	Sudan
IS-8662	USA	Sudan
DJ-1195	India	Sudan
M35-1 (variety check)	Rabi, India	Sudan
CSH6 (hybrid check)	India	Sudan

[a] International Sorghum Drought Observation Nursery. [b] Reddy et al 1980. [c] From Karper's Nursery, Texas, USA. [d] Line derived from Nebraska population.

to resistance for a particular pattern of drought (for example, midseason stress vs postrainy season terminal stress). The mechanisms described are escape, avoidance, and tolerance (Levitt 1972).

Drought escape

Three escape mechanisms enable crop plants to resist drought: early maturity, developmental plasticity, and remobilization to grain of stem reserves stored before anthesis (Turner 1979).

Early maturity and remobilization of stem reserves. In the Indian Peninsula, the replacement of traditional 130- to 180-day sorghums with early hybrids and varieties of 100-110 days duration, which mature before the rains end or before soil moisture is depleted, has resulted in a remarkable increase in sorghum production (Rao et al 1979). The character concerned (maturity) is detected visually.

Under terminal water stress during the postrainy season, early maturing sorghum genotypes such as CSH6, CSH1, and NK300 escape drought. They produce equal grain but less dry matter than late (100-110 days) cultivars such as M35-1, CSH8, and SPV86 (Table 2). The late cultivars also extract more soil water. CSH8, which has a large seed number, shows maximum remobilization of stem reserves, suggesting that retranslocation of stem reserves depends on potential sink strength.

Developmental plasticity. Most of the sorghums grown in SAT (especially in India) do not produce (basal) tillers. They lack the advantage of adjusting tiller number in response to drought. Many sorghum lines delay or postpone their development during stress and resume their development with the start of rain (Seetharama and Bidinger 1977). This kind of plasticity in phenology during midseason stress is useful where there is a good probability of adequate rains to

Table 2. Genotypic differences in grain yield and dry matter production; estimates of retranslocation of stem reserves to the grain and associated seasonal water use.

Genotype	Days to physiological maturity	Grain yield (t/ha)	Dry matter production (t/ha)		Retranslocation from stem[b] (equivalent wt) (t/ha)	Seasonal water use (mm)
			Seasonal	In GS3[a]		
CSH1	100	4.06	9.23	4.36	—	276
CSH6	95	3.16	8.20	3.02	0.14	166
CSH8	105	4.05	9.89	2.79	1.26	215
M35-1	105	1.94	11.38	4.51	—	272
SPV86	108	2.95	10.47	3.23	—	197
CS3541	105	3.18	8.01	2.42	0.76	322
IS-1037	98	2.07	8.01	3.51	—	270
CSV5	105	3.69	8.58	2.64	1.05	309
V302	105	3.15	8.98	2.76	0.39	231
NK300	88	4.03	9.44	5.08	—	264

[a] GS3 = grain-filling period (anthesis to physiological maturity). Values for GS3 are estimated as the difference between dry matter at physiological maturing and flowering. [b] Values represent differences between dry matter at physiological maturity and flowering.

complete an extended crop period. Sometimes even the nodal tillers produced during the recovery period contribute toward grain yield.

Drought avoidance

Although modern cultivars can escape drought, most crops in the SAT undergo some periods of water shortage. Plants avoid low tissue water potentials by one or more quite discrete mechanisms, such as a change in rooting pattern or an adjustment in leaf area.

Root pattern. Drought avoidance achieved by increased root growth draws considerable interest since it does not unduly hamper the productive processes, unlike reduction in leaf area or stomatal closure. Genotypic differences in sorghum roots have been noted (Blum et al 1977a,b; Jordan et al 1979). Screening methods using nutrient culture (Jordan et al 1979) or brick chambers (ICRISAT 1976) are available. However, while these techniques are useful in screening parent lines in a breeding program, selection of segregating material may be better carried out in deep soils when rainfall is absent or meager (Wayne Jordan: Temple, Texas, pers. comm.).

Leaf area adjustment. Leaf area adjustment has been suggested as one of the most powerful means of avoiding stress (Passioura 1976). 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). Many have felt that physiologists have not given sufficient attention to the processes determining leaf area, especially in the field (Elston 1980, Kramer 1979). Because of the high sensitivity of leaf extension to change in turgor, several authors (Orshan 1954, Boyer and McPherson 1975, Karamanos 1979, Hsiao and Acevedo 1974) have suggested that leaf extension rate be used as the criterion for evaluating drought sensitivity. Culm (stem and leaf) extension rates are being used as an index of drought avoidance in the maize program at the International Maize and Wheat Improvement Center (CIMMYT) (K. S. Fischer, pers. comm.). Table 3 shows the range in genotypic variation in leaf extension rates with respect to stress. Note that CSV5 and V302, which are sensitive to water stress, show more marked reduction in extension rates than M35-1 or CSH8, which are more drought resistant.

Other adaptations. During the 1979 rainy season at ICRISAT, a severe drought occurred on shallow Alfisols during the boot stage. Many elite entries (which yielded more than 7 t on deep Vertisols during the same season) gave very low yields on Alfisols because under stress they failed to exsert their panicles through the boot (sheath of flag leaf). The entries can be easily screened for such a failure of stem and peduncle extension under stress and susceptible ones discarded. Further genotypes whose panicles are damaged (for example, aborted spikelets) during stress also can be eliminated.

A decrease in radiation absorption by the leaf by leaf rolling (Begg 1979) or by light reflection and a decrease in cuticular loss of water normally save only small amounts of water. But, under conditions of severe stress, gains are substantial. Sorghum shows all these adaptations (Blum 1975, Chatterton et al 1975) but the traits have been incompletely quantified.

Table 3. Extension rates of culm (leaf + stem; Ter) and of leaf (Ler) under control (irrigated) and stress during the panicle development stage.

Genotype	Ter[a] (mm/h)		Reduction (%)	Ler[a] (mm/h)		Reduction (%)
	Control	Stress		Control	Stress	
CSV5	2.42	1.42	41.3	2.18	1.23	43.6
V302	2.37	1.53	35.4	1.76	1.11	36.9
CSH8	2.09	1.79	14.4	1.74	1.47	15.5
M35-1	2.45	2.28	6.9	1.95	1.70	12.8
IS-12611	4.05	2.67	34.1	2.42	1.72	28.9
CS3541	3.08	1.49	29.5	1.49	1.16	22.2
CSH-1	2.55	1.72	32.6	1.30	0.88	32.3
CSH-5	2.87	2.20	23.3	2.06	1.65	19.9
Mean ± S.E.	2.61 ± 0.22	1.89 ± 0.16	27.19 ± 4.10	1.86 ± 0.13	1.37 ± 0.11	26.51 ± 3.80
Range	2.08-4.06	1.42-2.67	6.9-41.3	1.30-2.42	0.88-1.72	12.8-43.6

[a] Data for period 1600 h on 31 Jan 1981 to 1530 h on 2 Feb 1981. Field RP 16A Patancheru (Seetharama, unpubl.).

Genotypes were compared for drought avoidance through short-term measurements of leaf water potential, leaf temperature, and stomatal conductance. While repeatable genotypic differences are found, there is no simple way they can be related to final yield reduction under stress (Seetharama et al, unpubl.), although these studies help in understanding the various mechanisms.

Drought tolerance

In spite of a plant's efforts to avoid drought, low tissue water potential will occur during prolonged periods of water stress. It is necessary, under SAT conditions where chances of prolonged drought are high, to distinguish between the tolerance mechanisms that enable the protoplasm to survive and allow the plant to recover from stress after the rains (for example, heat and desiccation tolerance) and those that enable the plant to adapt to low tissue water potential (for example, osmotic adjustment) so that it can continue to grow and develop at reasonable rates (Turner 1979).

Heat and desiccation tolerance and recovery ability. Conditions of high temperature and evaporative demands are more conducive to drought resistance screening than milder conditions (Fig. 1).

Three hundred and sixty-four advanced selections from the drought resistance breeding project were evaluated in replicated trials at Sangareddy (20 km west of ICRISAT center) during the hot summer (Apr-May) of 1980, when the maximum daily temperature varied between 35° C and 43° C. The plots were irrigated at planting, then subjected to severe desiccation and heat stress. The leaves rolled

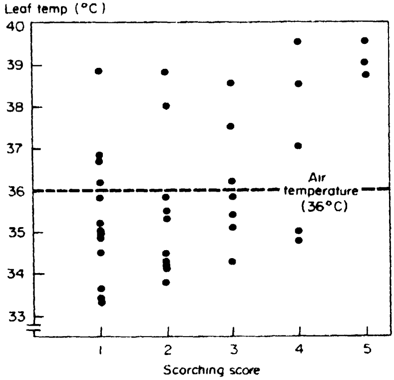
5. Screening of *Sorghum bicolor* for heat and drought resistance; genotypic differences in leaf firing. Selection D71305 (left) shows severe leaf firing: D71152 (right) has dark green leaves.

and growth practically ceased in most of the genotypes during the stress period. The cumulative effect of heat and water stress was more apparent 20 days after the onset of the monsoon, by which time a total of 60 mm of rainfall had been received. Genotypes that were severely damaged because of stress did not recover and part of or whole leaves remained white or fired (Fig. 5). In contrast, other genotypes with little fired leaf area showed varying ability to recover and resume growth (Reddy et al 1980).

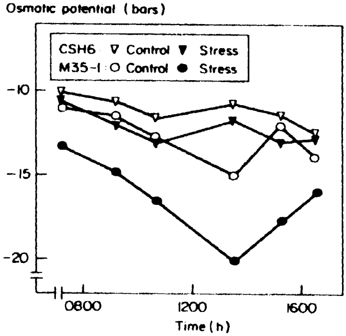
Genotypes were scored on a 1-5 scale (1 = least firing). One trial had an additional treatment and received 2 more irrigations at 3-week intervals after initial establishment. The leaf and air temperatures were measured on two occasions and correlated with leaf firing. Entries receiving a score of one (least scorching) had leaves cooler than air and entries receiving a higher score (more scorching) had hotter leaves (Fig. 6). Many entries showing resistance to leaf firing were also agronomically good. Preliminary results showed good correlations ($P < 0.01$) between scores for leaf firing and ability to recover at Sangareddy in summer (off-season) and at Anantapur (14°7'N) during the normal rainy season under natural drought.

Sullivan and Ross (1979) have cited seven reports in which heat tolerance tests were used to select for drought resistance. It should be possible to screen large numbers of breeding lines and germplasm for resistance to heat and desiccation tolerance in the field during summer. Arnon (1975) and Sullivan and Ross (1979) have pointed out certain instances in which correlation between heat and desiccation tolerance was poor, but it is generally agreed that heat tests can be used to reduce the number of genotypes to a small group which then can be subjected separately to both heat and desiccation tests.

Osmotic adjustment. Diurnal and seasonal osmotic adjustments to water stress have been noted in sorghum (Jones and Turner 1978) and genotypic differences are known to exist (Stout and Simpson 1978). A decrease in osmotic potential



6. Relationship between scorching score and leaf temperature. Leaf temperature was measured with infrared thermometer during stress on 21 May 1980 between 1420 and 1440 h; scorching was scored after recovery period of 18 July 1980; score 1 = leaf firing. Each point represents one genotype.



7. Diurnal variations in osmotic potentials in sorghum cultivars CSH6 and M35-1. Standard error of the mean is less than 0.5 bar.

contributes to leaf expansion in sorghum during conditions of high atmospheric demand for water (Acevedo et al 1979). At ICRISAT, genotypic differences have been detected in predawn osmotic potentials even under mild stress. Postrainy season cultivars such as M35-1 and CSH8 which encounter terminal water stress have a greater capacity to decrease their osmotic potential under stress than the rainy-season type CSH6 (Fig. 7). A regression approach (Ackerson et al 1980) showed that the leaf water potential at zero turgor was 4 bars less for M35-1 than for CSH6.

FUTURE PROSPECTS AND PROBLEMS

The first step in planning any crop improvement program for drought-prone areas is the comprehensive diagnosis of direct (a water deficit which depends upon the rainfall pattern and the soils' capacity to store and supply water between rainfall events) and indirect (attendant physical, chemical and biological, and cultural changes) factors determining the locational and temporal specificity of drought (Gotoh et al 1979, Jordan and Monk 1980). However, it must be understood that our concept of an ideal plant for a given environment cannot be more accurate than the prediction of the climate (within confidence limits) for an average year. The rabi sorghum environments in the Indian Deccan plateau under deep Vertisols can be well defined and greater progress can be expected toward bridging the gap between potential and actual yield in these environments. In contrast, great seasonal fluctuations within an adaptation zone exist in vast areas of the SAT.

The progress in producing genotypes that have the maximum flexibility to adjust to a wide range of seasonal conditions will be understandably slow. Any international or regional breeding program aiming to serve a large number of adaptation zones (such as ICRISAT) should have a broad spectrum of drought-resistant genetic material differing in maturity and plant type. The breeders in local and national programs could then evaluate the most promising progeny for their own use.

Table 4. Constitutive adaptation, facultative adaptation, and management practices that confer drought resistance. prospects in a sorghum improvement program

Remarks	Examples	Existing variability	Basic information or techniques	Prospects for breeding
	Constitutive adaptation			
Mostly irreversible and lifelong	*Morphological or phenological*			
	1 Maturity	High	High	High
	2 Developmental plasticity	Meager (tillering not considered)	Scant	Moderate-low
	3 Glossy leaf	High	Scant	High
	4 Number, shape, and size of leaf	Moderate	Moderate-low	Moderate
	Physiological			
	5 Desiccation tolerance	High	Moderate	High
	6 Heat tolerance	High	Moderate	High
	7 High growth rates	Moderate among elite breeding stocks	Moderate	Moderate
	8 Low respiration	Moderate	Scant	Low
	9 Recovery rate after stress	High	Moderate	High
	10 Anatomical features	Low	Scant	Low
	11 Root-shoot ratio	Moderately high	Scant	Low
	12 Liquid phase resistance	Low	Scant	Low
	13 Deep roots	Moderate	Scant	Low

	Facultative adaptation			
Shorter term responses, more dynamic, some (1-2) almost completely reversible, others (4-8) irreversible	1. Stomatal closure	Moderate to high	Moderately high	Low
	2. Leaf rolling	High	Moderate	Low
	3. Increase in wax content of epidermis	Moderate	Moderate	Low-moderate
	4. Leaf area increase	Moderate to high	Moderate	Moderate to high
	5. Leaf senescence	High	Moderate	High
	6. Remobilization of stem reserves	Moderate (up to 30%)	Moderate	High
	7. Plant hormones	Low	Scant	Low-unknown
	8. Osmotic adjustment	Moderate	Scant to moderate	Moderate
	9. Relative increase in root growth	Moderate	Scant	Moderate
	Management factors			
Application of antitranspirants is not within means of small farmers.	1. Time of planting	Genotype-management interactions well documented but information not enough for initiating special breeding program.		Except in case of change in planting date where thermo-sensitivity and photoperiod sensitivity may be involved, screen only the advanced material, at least in the near future.
	2. Plant population			
	3. Row spacing			
	4. Fertilizer application			
	5. Tillage practices			
	6. Use more than one variety			
	7. Intercrop midseason correction by ratooning			

Multicriteria approach: breeders' dilemma

Control of water loss from the shoot can be curtailed by one or more mechanisms (Table 4). Undoubtedly, drought escape is a first line of defense but other mechanisms should be used for any further improvement. Because crops use several of these mechanisms to varying degrees in field conditions, it is necessary to incorporate at least some of them for a high degree of drought resistance.

It is important to show that all the adaptive mechanisms that have been advocated are heritable. In sorghum, the inheritance of traits such as waxy bloom (Blum 1975) is simple, but others are expected to be governed by several genes. Some of these traits (such as net carbon dioxide exchange rate/transpiration rate 6-14% higher in lines having blooms than in bloomless ones, Chatterton et al 1975) apparently contribute little in isolation, but the collective contribution may be substantial. For example, waxiness, glossy appearance, and narrowness of leaf individually may contribute little but collectively the contribution to water economy may be considerable, especially under severe stress. Some useful traits seem to occur together in some local germplasm lines. For example, M35-1 has glossy leaves and deep roots and is heat resistant, besides being less susceptible to diseases such as charcoal rot and to shoot fly. It is advisable to thoroughly examine the value of such traits before trying to accumulate the corresponding genes in a breeding population.

At present, our understanding of metabolic traits such as osmotic adjustment and hormonal regulation is incomplete. At the beginning, screening for physiological and metabolic traits could be confined to parents used in the crossing program or in hybrid development. It should be used only to complement the more important, easier, and inexpensive techniques. In breeding, the emphasis also must be on traits that apparently have no or minimal deleterious influence on yield.

This approach poses another problem: how to bring together several of the traits, sometimes linked and sometimes mutually exclusive. Conventional breeding techniques, such as selections in single cross and backcross progenies, can be used to accumulate a few genes at a time. The population breeding method, which allows simultaneous incorporation of several genes or traits (Doggett 1977), is advocated. However, progress with such an approach is slow. Because it is generally agreed that sorghum hybrids are superior to other varieties, even under stress (Rao and Harinarayana 1969, Blum 1979a), reciprocal recurrent selection may allow concentrating a set of characters in each of two B- and R-populations. Two sorghum drought-resistant populations (NP9BR and Downes) are available for further improvement.

Other traits closely related to drought. Good management practice is a precondition for more efficient use of water. Physiologists and breeders are aware that genotypes interact differently with various management factors (Table 4), especially those that influence soil water extraction patterns. At ICRISAT, significant genotypic differences in response to drought at the seedling stage were found in both the germplasm and breeders' elite lines, as measured by scoring for wilting, recovery, and survival after stress. Many lines resistant to drought at the seedling stage were observed to have light-green leaves with a glossy surface. The susceptible lines generally had dark-green leaves (Maiti 1980). Currently, more germplasm is being screened for wide-scale applicability in the breeding program.

In addition, nutrient uptake, metabolism under stress, and mineral toxicity need more intensive study. Sorghum production problems such as higher incidence of *Striga*, charcoal rot, and root lodging are closely associated with drought.

Modeling

Crop weather models are useful in quantifying the response of factors, singly or in combination, on crop growth and development. If sufficiently accurate and properly used (Passioura 1973), these models are powerful research tools in designing alternate strategies, either in plant structure or in management. Fortunately, some models of varying complexity are already available to sorghum workers: PLANTGRO (R. J. Hanks, Utah State University, Logan, pers. comm.), SORGF (Arkin et al 1976), and the model by Hodges et al (1979). Simulation models for individual plant responses, such as leaf water potential, also are available (Takami and Yukimura 1979).

The use of agroclimatic analogues in the transfer of technology using models of known areas is well established (Nix 1980). But it must be noted that the usefulness of the models will not be thoroughly appreciated until they are placed in the hands of physiologists, breeders, agronomists, soil scientists, and engineers.

Exchange of germplasm and training

Despite locational specificity, exchange of genetic material can take place if a reasonable correspondence between sites is established (House 1980). Germplasm and breeding material can be exchanged most usefully between similar adaptation zones (especially after reaping the initial benefits of introduced exotics) on different continents. Material received from corresponding sites can be further improved according to local needs, to suit specific patterns of drought and for other traits concerned with productivity such as disease or pest resistance.

With the help of empirically established correspondence between sites and with further refinement by using models, the basic idea regarding the adaptability of a cultivar to a site can be transferred.

One of the more appropriate ways to deal with locational and temporal specificity throughout the sorghum-growing regions is by encouraging the formation of interdisciplinary teams to work in regional and national programs. Since its inception, ICRISAT has recognized the need to train more sorghum workers to tackle such problems as drought to enable them to find an appropriate solution to the kind of drought prevalent in their own countries.

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