

Genetic Options for Drought Management in Sorghum

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Sorghum is one of the most important food and feed crops in the arid and semi-arid tropics of the world. Sorghum being C₄ species with higher photosynthetic capacity, and greater nitrogen and water use efficiency, is relatively more drought tolerant compared to other cereals such as maize, making it, the logical cereal to support the world, predicted to have 25% of its population experiencing severe water scarcity by 2025. Enhancement of its genetic resistance to drought stress would stabilize productivity trends and contribute to sustainable production systems in drought-prone environments. Although a population of drought stresses are experienced by the crop in drought-prone environments, depending on the stage of the crop and timing, duration and severity of drought stress, four growth stages in sorghum have been considered as most vulnerable-germination and seedling emergence, mid-season, preflowering and post-flowering. The responses of sorghum to moisture stress at these four growth stages have been well characterized and genetic variation in these responses has been observed and found to be heritable. Considering that large genotypic differences are observed, if the water-stress is confined to one stage, and the differences are masked if it occurs at more than one stage, the screening techniques have been developed to identify drought-resistant genotypes at each of the growth stages, separately. Of the several mechanisms to circumvent drought stress in sorghum, drought escape (related to maturity duration), drought avoidance (maintenance of high leaf water potential) and drought tolerance (related to osmotic potential) are considered as most important and have been well characterized. Stay green trait, known to confer post-flowering resistance in sorghum has been very well exploited to enhance postflowering drought tolerance in sorghum. Though several other physiological traits are identified, they do not sufficiently relate to the field response to merit selection based on them and also the screening techniques developed based on them are not cost-effective. At ICRISAT, growth stage-specific breeding for drought resistance which involves alternate seasons of screening in specific drought and yield potential environment is used to breed sorghum which can yield well in high yield potential areas/seasons as well as in seasons/years of drought at specified growth stage. As the

progress in enhancing drought resistance levels in sorghum through conventional approaches are limited by the quantitative inheritance of drought resistance and yield coupled with complexity of timing, severity and duration of drought, biotechnology appears to offer promising tools such as marker-assisted selection (MAS) for genetic enhancement of drought resistance in sorghum. Four stable and major Quantitative Trait Loci (QTLs) have been identified for stay green trait and are being introgressed through MAS into elite agronomic background at ICRISAT.

INTRODUCTION

Sorghum (*Sorghum bicolor* (L.) Moench) is characteristically grown in the semi-arid tropics (SAT) of south Asia and the Sahelian-Sudanian zone of Africa that are characterized by high temperatures, high radiation, high evaporative demand, unreliable and irregular rainfall and soils of poor structure, low fertility, and low water holding capacity. The production of sorghum is affected by several biotic and abiotic constraints. Among the abiotic yield constraints (water, temperature and nutritional stresses), water will likely be the primary yield constraint throughout the SAT in the coming years (Ryan and Spencer 2001). Most of the reduction in yield due to abiotic stresses is primarily attributed to water stress (Kramer and Boyer 1995). Sorghum uniquely adapts to extremes of abiotic stresses making this crop the logical grain to support the poor world of the predicted to have 25% of its population experiencing severe water scarcity by 2025. Sorghum, being C₄ plant species, is better adapted to stress environments, especially soil moisture stress than C₃ plants. For a given rate of transpiration, photosynthesis is greater in C₄ than in C₃ plants (Blum 1988). This advantage is translated into a greater plant or crop water-use efficiency (Begg and Turner 1976). Its rich genetic diversity for stress tolerance makes it an excellent crop model and choice for studying the genetic and physiological mechanisms of drought tolerance.

DROUGHT AND DROUGHT RESISTANCE

Drought is recognized as a condition where the water requirement of the plants, at different crop growth stages exceeds the available water by more than 50% in the root zone because of inadequate precipitation (excluding other soil problems such as excessive concentration of aluminium, Na⁺, clay etc.), leading to perceptible reduction in normal growth parameters. In agricultural context of SAT, drought tolerance is defined as stability of crop yield under a specific target drought stress environment. Turner (1979) defines drought resistance as the ability of a genotype to yield satisfactorily in areas subjected to periodic water deficits. Although sorghum is more drought tolerant compared to other cereals such as maize (Nagy *et al.* 1995), improving drought resistance in sorghum would further increase and stabilize grain production in low rainfall and harsh environmental regions of the world and contribute to food security to millions of poor depending on it.

MECHANISMS OF DROUGHT RESISTANCE

The complete exploitation of genetic diversity for genetic improvement of crops for stress tolerance requires identification of mechanisms that ameliorate internal stresses and those

that minimize drought injury (Steponkus *et al.* 1980). The mechanisms of drought resistance can be described as escape, avoidance and tolerance (Levitt 1972; Blum 1979; Ludlow 1993). While early maturity is a well-known "drought-escape" mechanism through which the crop matures before experiencing water-stress and is often associated with reduced yield potential, other two are physiological responses to water-stress. Early sorghum genotypes compared to late ones have lower evapotranspiration rates due to smaller leaf area and smaller root density (Blum 1979). Dehydration avoidance is defined as the plant's ability to retain a relatively higher level of hydration i.e., maintenance of higher turgor or water potential under conditions of atmospheric water stress. Drought tolerance refers to physiological and/or biochemical adaptations that enable plant tissues to withstand water deficits (Clark and Durley 1981) or the ability of leaf cell membranes to function under stress or adapt to low tissue water potential (osmotic adjustment) (Blum 1979). Given sufficient time, plants subjected to water stress may avoid dehydration through the control of leaf water potential and or adapt to low tissue water potential. While Wood *et al.*, (1996) have reported that increased levels of glycine betaine and proline levels in leaves are known to contribute to drought tolerance, Abu *et al.* (2002) have identified significant association of micronutrients, K and Fe in grains with drought tolerance in sorghum. They have also noticed decreased concentration of Fe with maturity in tolerant genotypes, while it increased with maturity in susceptible genotypes.

SCREENING TECHNIQUES FOR DROUGHT RESISTANCE

Moisture stress is known to cause significant reduction in grain yield depending on the stage of the crop and frequency, duration and severity of moisture stress. Thus, in reality, a population of moisture stress situations will be experienced by crop grown in drought prone environments. However, four growth stages are recognized as most vulnerable to moisture stress, based on the findings of ICRISAT and US sorghum breeding programs (Reddy 1985).

These are 1) Germination and seedling emergence, 2) early seedling stage (from seedling emergence to panicle initiation), 3) Mid-season (from panicle differentiation to flowering) and 4) Post-flowering (from flowering to grain filling stage). The responses of sorghum to moisture stress at these four growth stages have been well characterized and genetic variation in these responses has been observed and found to be heritable (Reddy 1985; Mkhabela 1996). Considering that large genotypic differences are observed, if the water-stress is confined to one stage and differences are masked if it occurs at more than one stage (Garrity *et al.* 1982), it is suggested that the screening techniques should aim to identify genotypes for responses of the crop at each of the growth stages, separately (Reddy 1985).

Several effective and reliable screening techniques have been developed at ICRISAT, Australia and USA to identify resistant/tolerant sources from the germplasm and breeding lines based on either the plant responses at these growth stages or physiological mechanism of drought tolerance. Besides these, empirical screening techniques have also been reported. These techniques are reviewed and discussed below.

A. GROWTH STAGE-SPECIFIC SCREENING TECHNIQUES

ICRISAT, during late 1970s and early 1980s developed reliable screening techniques to identify resistant sources for various growth stages at which genotypic differences to drought stress occur and the same are described below.

1. **Screening for coleoptile and mesocotyl lengths:** Longer mesocotyl and seedling emergence from deep planting and from high surface soil temperatures, and recovery from drought at seedling stage are considered important for crop establishment. It is established that initial selection for coleoptile length (the trait associated with germination under deep sowing, which is desirable to capitalize initial rains) of test lines at 5 days after planting in germination boxes followed by selection in raised brick tanks using charcoal and heavy kaolin to simulate higher or less than normal temperatures, respectively in 12 cm planting depth based on plant counts (as a reflection of mesocotyl length) is highly effective in identifying lines with long mesocotyl length that is necessary for emergence in deep-sowing areas such as Africa.
2. **Screening for seedling emergence under high surface soil temperature:** Selection of breeding lines in the sandy soil-filled brick tanks spread uniformly with charcoal powder @125 gm-2 (which induce high temperature) based on the seedling emergence counts at 6th day after planting was effective in identification of lines with high seedling emergence under high surface soil temperature that is prevalent in Africa during sowing season.
3. **Screening for recovery from seedling drought:** It was established that selection of breeding lines for recovery from severe seedling drought induced after germination for 24 days followed by termination of drought in the 29th day after planting in PVC vases based on recovery scales, number of plants recovered/vase and number of green leaves/vase was effective to screen for recovery from seedling drought.
4. **Screening for recovery from mid-season drought:** Selection of breeding lines under natural field conditions for plant recovery from mid-season drought induced for 35 days after initial nonstress growth period of 21 days after planting followed by termination of drought was effective to screen for plant recovery from mid-season drought stress.
5. **Screening for terminal drought stress tolerance:** Selection of breeding lines for stay-green trait-a proven trait known to confer terminal drought (typically experienced by post rainy season sorghums in India) tolerance was useful for screening for terminal drought tolerance. The differences for stay-green trait can be maximized when the materials at post-flowering stage are exposed to moisture stress.

Since 1975, attempts have been made at ICRISA T to evolve simple and direct empirical screening methods to evaluate large number of germplasm accessions and breeding lines for drought tolerance i) drought during panicle development stage (mid season stress/pre-flowering stress) and ii) receding soil moisture conditions in Vertisols (post-flowering stress). While, sandy soil or shallow soil sites are best suited for pre-flowering evaluation, heavier and deeper soils are best for evaluating post-flowering stress (Rosenow *et al.*, 1997).

To screen for mid-season stress, which represents the midseason drought pattern of the rainy season in many parts of SAT, mild moisture stress is not sufficient for the expression of the genotypic differences. Efforts at ICRISAT indicated that although severe stress during summer caused larger deviation from predicted yield, it provided an opportunity to tentatively identify a number of genotypes that might have different responses to stress. Yields were monitored in a field situation at an appropriate location with controlled irrigation facilities in a rain free season. Curtailing irrigations three weeks after sowing in sandy soils, for over 45 days is considered to provide required level of drought stress (Reddy 1985).

The second pattern experienced in post rainy season (*rabi*) crops in India is similar to that experienced by 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). Comparison of yields on shallow Vertisols or on partially saturated deep Vertisols with yields with an irrigated control has been advocated to screen genotypes for drought resistance in receding moisture conditions. Yield potential and terminal drought resistance was monitored under field condition by choosing appropriate time of sowing to ensure that crop experienced terminal drought stress. Since it is usually accompanied by charcoal rot (*Macrophomina phaseolina*), stay-greeness and lodging along with yield should be considered in selection criteria (Reddy 1985).

Line source (LS) sprinkler irrigation technique was developed at ICRISA T for screening sorghum genotypes for drought resistance. Each side of the LS formed one replication. The field was uniformly irrigated (using perfo-spray) until the crop reached boot stage and the LS was used at 50, 61 and 77 days after sowing to create a gradient of soil moisture (stress). The amount of water received across the plot was measured in catch cans placed at crop height. The LS was also used to study the effect of soil moisture stress on charcoal rot incidence (Seetharama *et al.*, 1982). The rows of plants farthest from the LS showed disease earlier than those nearest. This was apparent for each of the 3 parameters of disease spread: percentage of soft stalks; number of nodes crossed and the length of fungal spread (Seetharama *et al.*, 1987).

B. PHYSIOLOGICAL MECHANISMS-BASED SCREENING TECHNIQUES

1. **Water potential:** As leaf is directly involved in the production of assimilates for growth and yield, leaf-water potential is the common immediate measure of plant water stress. At ICRISA T, leaf firing was found to be a simple phenotypic trait that allows large populations to be screened (Andrews *et al.* 1983). Leaf rolling is an established symptom of wilting in cereals (Jones 1979) and delayed leaf rolling under drought stress is being used as one component of a selection index for drought resistance in sorghum (Rosenow *et al.*, 1983). Greater leaf rolling was indicative of reduced leaf water potential in different sorghum genotypes (Blum *et al.*, 1989). However, Flower *et al.* (1990) concluded that while drought resistant sorghum varieties had better osmotic adjustment and consequently less leaf rolling under stress as compared with susceptible varieties, these responses did not influence growth under very dry and hot conditions. Evidently, the magnitude of genotypic variation for leaf rolling varies with the type of drought stress, its severity and duration. Under

relatively mild stress, delayed leaf rolling may be associated with sustained plant growth and production. However, under severe drought and heat stress conditions, greater leaf rolling may be associated with better chances for regrowth upon recovery (Blum *et al.* 1992). While, Gaosegelwe and Kirkham (1990) suggested that water potential, rather than stomatal resistance, might be used as an easy and fast way to screen for drought-sensitive genotypes, Voigt *et al.* (1983) suggested that sorghum lines, which can maintain higher rates of CO₂ uptake under stress environments should be considered as valuable drought tolerant germplasm for use in breeding programs. Stricevic and Mastrorilli (1992) and Stricevic and Caki (1997) showed a pre-dawn leaf water potential of -0.5 MPa as the threshold value for scheduling irrigation, as physiological processes were significantly decreased below this value, indicating that genotypes showing better yield performance at this level of leaf water potential as drought tolerant.

2. **Osmotic adjustment:** Under water-limiting conditions, the genotypes water with high osmotic adjustment (OA) produced larger maximum leaf area and had better leaf retention during grain filling. Based on this, Tangpremsri *et al.* (1995) concluded that the adverse effect of water stress could be reduced by selecting sorghum genotypes with high OA. Studies on osmotic adjustment have been accelerated by the use of pressure chamber method and analysis of pressure volume graphs to measure water, osmotic and turgor potentials (Tyree and Hammel 1972). Thermo couple psychrometry have also aided in measurement of water and osmotic potentials (Parsons 1982).

At Purdue University of USA, specific nurseries have been used in dry environments, such as Mexico, to screen for pre-and post-flowering drought response (Rosenow *et al.* 1997). In Sudan, nurseries in the past (Ejeta 1987) have been designed to specifically evaluate for either pre- or post-flowering drought stress. In the public breeding program in Queensland, Australia, breeding progenies are routinely evaluated in regular field breeding nurseries for premature leaf and plant senescence at or near physiological maturity.

C. EMPIRICAL SCREENING METHOD

Osmanzai (1994) has proposed an empirical drought susceptibility index (DSI) to screen the genotypes for drought tolerance under field conditions.

$$DSI = [1 - Y / YP] / D$$

Where,

DSI = Drought susceptibility index; D = Drought-stress intensity; Y = Yield in stress
YP = Yield in irrigated conditions; D = 1-[Y / YP]

Y = Mean yield of all genotypes under stress conditions

YP = Mean yield of all genotypes in irrigated conditions.

The DSI estimates indicate reduction in yield of a genotype under drought stress-free conditions relative to mean reduction in yield under drought stress. Also, the sum of ratios of yield of a particular genotype in stress (rain fed) and the ratio of yield in relieved stress

(irrigated) provides information on mean relative performance (MRP). The higher the MRP, the better the performance under stress.

$$MRP = [Y / Y + YP / YP]$$

The usefulness of these indices, DSI and MRP is illustrated in Table 1.

TABLE 1: Agronomic performance of sorghum hybrids and cultivars under two soil moisture regimes at Matapos and Kadoma (Zimbabwe) and Kasinthula (Malawi) during 1991/1992

Hybrids/cultivars	Number	Yield reduction (%)	Drought susceptibility index ¹	MRP ²
Hybrids	12	62	0.98	2.47
Improved cultivars	11	63	1.00	1.83
Local landraces	5	69	1.09	1.76

¹Estimation of the reduction in yield by drought stress for genotypes relative to the mean reduction in yield by drought stress

²Mean Relative Performance (MRP) - the sum of the ratios of yield of genotypes in stress (rainfed) and yield in relieved stress (irrigated).

$$MRP = [(Stress\ yield/Stress\ mean\ yield) + (Relative\ stress\ yield/Relieved\ mean\ stress\ yield)]$$

BREEDING APPROACHES

A. Rationale

Ability of genotype to yield reasonably high in specified drought stress environments is considered as drought resistance from plant breeding point of view, which is different from ecological point of view (low but stable yielding). This follows that drought resistant lines should have good plasticity in the sense that such lines should manifest high yield potential, if drought stress is relieved or better environment is provided.

Four approaches of breeding for drought tolerance/resistance have been proposed. The first is to breed for high yields under optimal conditions i.e., to breed for yield potential and then to assume that this will provide a yield advantage under sub optimal conditions. The second is to breed for maximum yield in the target environment. The third approach is to select in the F₅ and F₆ generations for yield and yield components under optimal environmental conditions and selection of duplicate samples under stress conditions (Blum 1979; Blum 1983). The fourth breeding approach aims to establish that a single drought resistance character incorporated into existing yield breeding program will benefit yield. Yield improvement in wheat under stress conditions due to hydraulic root resistance (Richards and Passioura 1981 a, b) and high endogenous levels of abscissic acid (Quarrie, 1985) have been reported. Physiological response traits such as higher maximum green leaf area, delayed onset of leaf senescence, and reduced rate of leaf senescence should be sought to improve sorghum yield under terminal drought situation (Hammer and Muchow 1994).

At ICRISAT, a combination of two breeding approaches, i.e. breeding for traits conferring growth stage-specific drought tolerance and breeding for yield, with pedigree selection is followed. It consists of selection of breeding materials for specific traits such as emergence under crust, seedling drought recovery, and grain yield under drought prone and yield

potential areas for early stage drought, for drought recovery and for grain yield under drought-prone and yield potential areas alternatively for midseason drought; and for stay green and non-lodging and grain yield under drought prone and yield potential areas alternatively for terminal drought (Reddy 1986). Testing for drought resistance under mild stress will be adequate as the rankings of genotypes for potential and drought yields were similar, since the drought resistant lines selected under mild stress will have high yield potential in non-stress environments. These findings were in very well agreement with the theoretical considerations (Rosielle and Hamblin 1981) showing that if there is some scope for selection under a particular stress environment such as mild-stress that is referred here and genetic variance is high compared to that under non-stress, drought tolerance might be improved without a concomitant yield decrease in non-stress environment.

B. Genetic mechanisms and cultivar options

It has been established in many studies that F_1 hybrids had superior stability (or buffering capacity) across variable environments, as compared to varieties in sorghum in both rainy (Table 2) and post rainy seasons (Table 3) in India.

TABLE 2: Comparative performance of sorghum hybrids over improved varieties/landrace cultivars during rainy season

Years of testing	Yield (kg ha ⁻¹)		% increase over variety/local	Reference
	Hybrid	Variety		
1985-90	3665 (07)	3189(04)	14.9	Murty 1992
1993	3404 (09)	3142 (09)	8.3	
1994	3561 (10)	3003 (10)	18.5	
1995	3913 (17)	3036 (12)	28.9	
1996	3567 (06)	3280 (05)	8.8	

Figures in parentheses denote the number of hybrids/varieties tested.

TABLE 3: Comparative performance of sorghum hybrids over improved varieties/ landrace cultivars during postrainy season

Years of testing	Yield (kg ha ⁻¹)		% increase over variety/local	Reference
	Hybrid	Variety		
1996	2.8 (04)	2.2 (04)	28.4	Rana <i>et al.</i> 1997
2000	4.9 (16)	4.1 (03)	18.6	SPSHT ¹ 2000 PR ²
2001	4.8 (13)	4.7 (02)	1.8	SPSHT 2001 PR
2002	4.2 (10)	3.9 (01)	7.4	SPSHT 2002 PR

Figures in parentheses denote the number of hybrids/varieties tested

¹Seed Producers Sorghum Hybrid Trial conducted at several seed producers' experimental plots and ICRISAT

²Postrainy season.

For a given growth duration and biochemical photosynthetic efficiency, the total photosynthetic product of a crop species is finite and hence increased performance of hybrids compared to their parents is due to greater growth rates and greater total biomass production and increased partitioning of larger part of this biomass into grain (Blum 1966; Blum *et al.* 1977; Gibson and Schertz, 1977) with or without an apparent increase

in leaf photosynthetic rates (Sinha and Khanna, 1975). This advantage of the hybrid is often associated with reduced growth duration (Quinby, 1974). As the heterozygote may contain more than one gene product as against the homozygote, it becomes biochemically diversified and this biochemical diversification allows better adaptation to diverse environments (Srivastava 1981). Bhale *et al.* (1982) found that some sorghum hybrids showed heterosis for proline accumulation (known to confer drought tolerance) under moisture stress. Blum *et al.* (1992) and Osmanzai (1994) have shown that hybrids perform better than varieties under moisture conditions and recover faster when moisture stress is released. Evaluation of 12 single-cross sorghum hybrids along with their parents and two local varieties in Kenya under drought stress ranging from non stress to extreme stress (pre-flowering and terminal) revealed mean hybrid superiority over mid parent values by 54% and by 12% over local varieties for grain yield (Hausmann *et al.* 1998). Rao and Renu Khanna (1990) have also reported superiority of sorghum hybrids over their parents for leaf area and dry matter production under both pre-flowering and post-flowering drought stress. Greater performance of hybrids than their parents/varieties under several other abiotic stresses has also been reported by many researchers. For example, seedling germination and emergence was higher in sorghum x Sudan grass hybrids (Blum 1969) and sorghum hybrids (Pinthus and Rosenblum 1961) under suboptimal temperatures. Kannan (1981) found that two sorghum hybrids showed fewer iron-deficiency symptoms than their parents when grown in an iron-deficient nutrient culture and recovered better than the parental lines when stress was released. Besides these, hybrid superiority over their parents/varieties under drought-related abiotic stresses such as soil salinity toxicity (Jiqing Peng *et al.* 1994) and aluminium toxicity (ICRISAT, 2000) has been reported.

These results suggest that wider adaptability of hybrids is due to their relative resistance to wide range of abiotic stresses including soil moisture stress-related factors and therefore breeding for hybrid cultivars is a better option than varieties while improving sorghum grain productivity in water limited environments. Further, for increasing the grain yield within the limits 'of the available water supply, the choice of female parent for hybrid production should be made for both leaf area and photosynthetic rate and the selection of pollinators should be made for maximum seed number per panicle (Krieg, 1988). The improvement of *per se* performance and combining ability of parents for agronomic traits including grain yield under drought stress should be given strategic importance, considering that parental *per se* performance and general combining ability in sorghum is strongly correlated with hybrid performance (Quinby and Karper 1946; Murthy 1991; Murthy 1992; Bhavsar and Borikar, 2002). It is well established in sorghum breeding that good varieties make good parents for hybrids, because heterosis results primarily from additive gene action (Kambal and Webster 1965; Miller and Kebede 1981). Importance of the improvement in parental lines to increase the hybrid performance has been shown by Doggett (1988). He claimed that about one-half of the yield increase could be ascribed to better parents.

C. Selection among land races and breeding material

Landraces are valuable genetic resources for environmental stress resistance as they have evolved under natural selection pressure over several years. Drought tolerance of landrace

sorghum selection, M 35-1, a highly popular post-rainy season adapted cultivar in India, has been repeatedly demonstrated (Seetharama *et al.* 1982; Shackel and Hall 1983).

At ICRISAT, germplasm lines and breeding lines, tolerant to specific drought environments have been identified. Promising lines with resistance to seedling emergence under crust and high temperature identified are: IS 4405, IS 4663, IS 17595 and IS 1037 (ICRISAT 1982, ICRISAT 1986) and the improved lines developed for good seedling emergence included two A/B-lines (VZMI-B and 2077B) and eight R-lines (IS 2877, IS 1045, D 38061, D 38093, D 38060, ICSV 88050, ICSV 88065 and Spy 354). Nearly 1300 germplasm lines and 332 breeding lines were screened at ICRISAT for early- and mid-season drought stresses. The most promising of these are: early season and terminal drought: E 36-1, DJ 1195, DKV 17, DKV 3, DKV 4, IS 12611, IS 69628, and DKV 18. Mid-season stress: DKV 1, DKV 3, DKV 7, DJ 1195, ICSV 378, ICSV 572, ICSV 272, ICSV 273 and ICSV 295. The A/B-lines identified at ICRISAT with tolerance to early seedling drought include ICSBs 3, 6, 11, 37, 54 and 88001; the lines tolerant to midseason drought include ICSBs 58 and 196 and those with tolerant to terminal drought include ICSB 17 (Deb and Bantilan 1998).

Thirty six lines (13 pure lines, 12 A/B-lines and 11 R-lines) with a stay-green score ranging from 1 to 2 on a scale of 1 to 5; (where 1 = more green and 5 = least green) and a plant agronomic score ranging from 1 to 3 (on a scale of 1 to 5; where 1 = very good and 5 = poor) have been selected (Reddy *et al.* 2004). Further details on the characteristics of these lines can be obtained from ICRISAT web page:

<http://www.ICRISAT.ORG/Text/research/grep/homepage/sorghum/breeding/main.htm>.

BREEDING FOR DROUGHT ESCAPE

Early maturity constitutes an important attribute of drought escape. The relative yield advantage of early genotypes especially under late-season moisture stress has been reported by Saeed and Francis (1983) and Saeed *et al.* (1984). In the Indian Peninsula, the replacement of traditional long duration varieties (130- to 180- days) with early hybrids and varieties of 100 - 110 days duration, which mature before the end of rains or before soil moisture is depleted, has resulted in a remarkable increase in sorghum production (Rao *et al.* 1979). Selection for improved productivity under conditions of water stress resulted in a genetic shift towards early flowering (Blum 1980). Most of these studies have also confirmed the positive association between the long growth duration and yield potential, under potential conditions. It is therefore evident that while exploiting drought escape as a solution, some of the potential yield must be sacrificed in return for improved stability under stress (Blum 1988). The reduced yield potential in early genotypes may be compensated to some extent by increasing plant density (Blum 1970). Under terminal water stress during the post-rainy season, early maturity sorghum genotype produce equal grain but less dry matter than late cultivars.

Some early-maturing A-/B-lines that have the potential in the development of early-maturing hybrids, which can escape drought, have been identified at ICRISAT, which include ICSA/B 615, 628, 629, 630, 634 and 635. While drought escape is desirable method of reducing losses due to water stress, it may not be a feasible method in many

areas of the world because of uncertainty in onset and cessation of rainfall (Dalton 1967). Therefore, genetic resistance to water stress ensures limited yield losses to water stress.

PHYSIOLOGICAL RESPONSE TRAITS-BASED BREEDING FOR DROUGHT RESISTANCE

Although several physiological traits such as heat tolerance, desiccation tolerance, osmotic adjustments, rooting depth and epicuticular wax (Downes 1972; Levitt 1972; Sullivan 1972; Sullivan and Ross 1979; Turner 1979; Jordan and Monk 1980; Kramer 1980; Jordan and Sullivan 1982; Peacock and Sivakumar 1987; Krieg 1993; Ludlow 1993) are known to contribute to drought resistance and several screening techniques for drought resistance have been reported based on these (Christiansen and Lewis 1982; Garrity *et al.* 1982; Seetharama *et al.* 1982; Blum 1983; Jordan *et al.* 1983; Blum 1987; Ejeta 1987), little if any progress using specific physiological traits has been documented, partly because of poor understanding of these physiological mechanisms involved in drought tolerance (Bonhert *et al.* 1995). It appears that individual physiological traits identified to date are not sufficiently related to overall drought response or field performance to merit selection based on them (Rosenow *et al.* 1997). However, some important physiological responses such as leaf water potential (related to drought avoidance) and osmotic adjustment (related to drought tolerance) have been exploited to breed for increased yield potential under water stress and are discussed here.

A. Osmotic adjustment (OA)

Osmotic adjustment is recognized both as a drought avoiding and drought-tolerance trait.

1. **Drought avoidance:** Drought avoiding plants possess a variety of morphological and physiological adaptations to maintain favorable water status, either by maintaining an efficient water supply to above ground organs or conserving water during periods of soil water deficit (Clark and Durley 1981).

The role of osmotic adjustment and stomatal activity in dehydration avoidance was found to vary with plant development in sorghum (Ackerson *et al.* 1980). Before flowering, dehydration avoidance was maintained largely by stomatal response to leaf-water potential, while after flowering, osmoregulation and turgor maintenance were important. This could be partly responsible for the different classification of drought resistance before and after flowering in sorghum (Rosenow *et al.* 1983). The most evident control of leaf water potential is at the root system. A normal sorghum plant sustained growth with only the tips of several root axes immersed in a nutrient solution while the rest of the root system was suspended for weeks in the air. Thus, deep root penetration is a distinct and effective component of drought resistance (Jordan and Miller 1980; Meyers *et al.* 1984). Leaf water potentials will be affected by root length density, root axial resistance and root radial resistance. Small root resistances and a large root-length density would contribute to the maintenance of a higher leaf-water potential. Blum and Arkin (1984) have shown that root-length density increased with reduced soil moisture at certain soil depths.

2. **Drought tolerance:** Prolonged periods of water stress, a characteristic of SAT, are more likely to cause low tissue water potential. Plants recover from stress after rains

(heat and desiccation tolerance) or adapt to low tissue water potential (Osmotic adjustment). Sullivan and Ross (1979) have cited several reports in which heat tolerance test were used to select for drought resistance in sorghum. Summer was an appropriate environment to test for resistance needed in rainy season. Three hundred and sixty four advanced selections from the drought resistance-breeding project were evaluated in replicated trails at Sangareddy (20 km west of ICRISAT center) during hot summer (April- May) of 1980 when the maximum daily temperature varied between 35° C and 43° C. Many entries showing resistance to leaf firing were also agronomically good. Good correlations between scores for leaf firing and ability to recover was reported (Seetharama *et al.* 1982).

Variation in OA among the sorghum genotypes was found to range from null to 1.7 Mpa (Blum and Sullivan 1986). Basnayake *et al.* (1995) reported that two independent major genes (OA I and OA 2), with some minor effects control OA in sorghum. Landraces from dry habitats have greater capacity for OA (Blum and Sullivan 1986). Diurnal and seasonal OA to water stress have been noted in sorghum (Jones and Turner 1979). OA has direct positive effect on yield under moisture stress (Ludlow *et al.* 1990; Santamaria *et al.* 1990) and is largely ascribed to increase in root size, root length density and soil moisture extraction (Tangpremsri *et al.* 1991a, Tangpremsri *et al.* 1991b). At ICRISAT, genotypic differences have been detected in pre dawn osmotic potentials even under mild stress. Postrainy season cultivars such as M 35 -1 and CSH 8 have a greater capacity to decrease their osmotic potential under stress than the rainy season cultivar CSH 6 (Seetharama *et al.* 1982). However, breeding programs have been slow to adopt this trait.

GROWTH STAGE-SPECIFIC BREEDING FOR DROUGHT RESISTANCE

A. Crop establishment

The conditions for seedling establishment are hardly ideal in the semi-arid tropics with soil surface crust and drying surface layers caused due to absence of subsequent rain after initial planting rain. A hot dry seedbed environment during crop establishment is very likely with soil surface temperature often greater than 55°C (Gupta 1986; Hoogmoed and Klaij 1990; Peacock *et al.*, 1993). Seedling death can occur at one of the three defined stages in crop establishment: (i) germination, (ii) seedling emergence and (iii) post-emergence.

1. **Germination:** Many factors, both management and environment affect the germinability of seeds. Germinability has also long been known to be affected by environmental conditions experienced by the mother plant during grain filling (Clark *et al.* 1967). Sorghum seeds developing on plants subjected to drought stress showed a high level of germination earlier in the maturation period as compared to control seeds (Benech-Amold *et al.* 1991). Screening the sorghum lines for emergence in alfisols is done with limited soil moisture during hot dry summer season and under differential irrigation (5 to 30 mm) using line source sprinkler system. Seedling emergence % is noted at 5 days after sowing (DAS). Useful variability (10 to 50%) was noticed in 166 sorghum genotypes screened.

2. **Emergence:** Diminishing soil water availability after germination greatly affects seedling growth and survival. Sorghum cultivars exhibit genotypic differences in their ability to both emerge at low soil moisture conditions (Soman 1990) and subsequently grow (O'Neill and Diaby 1987). One strategy for maintaining adequate moisture in the seed and root zone for a longer time period is deeper sowing of the seed which result in longer mesocotyl length, reducing the effect of sowing depth on shoot meristem depth (Soman and Seetharama 1992; Harris 1996). Genotypic differences in mesocotyl growth rates have been shown in sorghum (Radford and Henzell 1990). They also found significant genotypic differences for seedling growth rate and response to temperature.
3. **Post-emergence/seedling survival:** Sustained seedling growth following emergence depends not only on the physiological processes for germination and emergence, but also on the capacity of the seedling to elongate, produce leaves and become autotrophic. Post-emergence seedling death due to abiotic stress under field conditions is primarily caused by the prevalent high soil surface temperatures, at least in the first ten days following sowing, and only after that does water deficit start to take effect (Stomph 1990; Peacock *et al.* 1993).

B. Early-stage drought (occurring form germination to panicle initiation)

Though this stage is also recognized as sensitive to drought, efforts to breed for tolerance to early-stage drought stress have been scanty.

C. Pre-flowering drought stress

The pre-flowering response is expressed when plants are stressed during panicle differentiation prior to flowering. Symptoms of mid season or pre-flowering drought stress susceptibility include: leaf rolling; uncharacteristic leaf erectness; leaf bleaching; leaf tip and margin burn; delayed flowering; poor panicle exertion; panicle blasting and floret abortion; and reduced panicle size. Tolerance to pre-flowering drought stress is indicated by the alternative condition in each instance. Since the panicle is directly affected, severe pre-flowering stress can result in drastic reductions in grain yield, At ICRISAT, a large number of progenies were screened for pre flowering or mid season stress recovery and the ones with high recovery were selected further for grain yield alternatively under mid season drought and yield potential environments in India. Some of the most promising lines are DJ 1195, ICSV 213, ICSV 221 and ICSV 210. When these lines were tested in drought prone environments in Africa, they found to have greater stability and grain and biomass yield than other varieties that were developed for favorable environments (ICRISA T 1982; ICRISA T 1986; ICRISA T 1987).

D. Post-flowering drought stress

Post-flowering stress is expressed when moisture stress occurs during the grain filling stage especially during the later portion of grain fill. Symptoms of post-flowering drought stress susceptibility include pre-mature plant (leaf and stem) death or plant senescence, stalk collapse and lodging, and charcoal rot (*Macrophomina phaseolina*), along with a significant reduction in seed size, particularly at the base of the panicle. Tolerance is indicated when plants remain green and fill grain normally. Such green stalks also have

good resistance to stalk lodging and to charcoal rot. Such cultivars are referred to as having 'stay green' trait.

Stay green trait governed by recessive allele not only slows down senescence, but also arrests the decline in protein content of the aging leaves "(Humphrey's 1994). While, Walulu *et al.* (1994) have concluded that the stay green trait in B 35 is influenced by a major gene that exhibits varied levels of dominant gene action depending on the environment in which evaluations are made, its inheritance in Q 141, which is derived from B 35 appeared to be polygenic (Henzell *et al.* 1992). It is also known to contribute to terminal drought and charcoal rot resistance (Rosenow and Clark 1995, Garud *et al.* 2002). Stay green trait is now considered as an important post-flowering drought resistance trait (Rosenow *et al.* 1997). Genotypes possessing the stay green trait maintain a greater green leaf area under post-flowering drought than their senescent counterparts (Rosenow *et al.* 1977). Contrary to earlier reports that the leaves can remain green due to a lack of assimilate demand because the plants have small panicles under post-flowering drought (Henzell and Gillerion 1973, Rosenow *et al.* 1983), recent studies have shown that they stay green not only because of small sink demand, but also due to higher leaf nitrogen status (Borrell and Douglas 1997; Borrell *et al.*, 1999) and transpiration efficiency (Borrell *et al.*, 2000b), resulting in maintenance of photo synthetic capacity and ultimately, higher grain yield and lodging resistance (Borrell *et al.* 2000a). Greater green leaf-area duration during grain filling appears to be a product of different combinations of three distinct factors: green leaf area at flowering, time of onset of senescence, and subsequent rate of senescence (Van Oosterom *et al.* 1996; Borrell *et al.* 2000a). Further, all the three factors appear to be inherited independently (Van Oosterom *et al.* 1996), and thus sources expressing these components can be combined easily in breeding programs (Borrell *et al.* 2000a).

Sorghum hybrids containing the stay green trait have been found to yield significantly more under water-limited conditions compared with hybrids not possessing this trait (Rosenow *et al.* 1983; Henzell *et al.*, 1992; Borrell and Douglas 1996). Stay green hybrids have been shown to produce significantly greater total biomass after anthesis, retain greater stem carbohydrate reserves, maintain greater grain growth rates, and have significantly greater yields under terminal drought stress than related but senescent hybrids (Henzell *et al.* 1997; Borrell *et al.* 1999; Borrell *et al.* 2000b). Excellent sources of resistance to both pre and post-flowering drought have been identified. High levels of both the types of resistance are generally not found in the same genotype. However, some genotypes possess good levels of resistance to both types (Rosenow *et al.* 1997). Breeding for terminal drought resistance utilizing stay green trait has been extensively done in Australia. The stay green trait from IS 12555 (SC 35) has been successfully used in Australia to develop post-flowering drought stress resistance and lodging resistance in parental lines and commercial hybrids (Henzell *et al.* 1992b; Henzell and Hare 1996).

Conventional breeding for stay green has been primarily based on two sources for this trait, B 35 and KS 19 (Mahalakshmi and Bidinger, 2002). KS 19 is a selection from a cross of short Kaura, an improved landrace cultivar from northern Nigeria, with combine Kafir 60 (Henzell *et al.* 1984). B 35 (P 1534133) was selected from a converted (dwarf, height, early flowering) version of IS 12555, an Ethiopian landrace (Rosenow *et al.* 1983, Rosenow *et al.* 1997). KS 19 has been commercially used primarily in the breeding program of Queensland Department of Primary Industries (QDPI) while B 35 is widely

used in both public and private sector breeding programs in USA (Mahalakshmi and Bidinger 2002). The partially converted (B 35) and fully converted (SC 35C-14E) versions of IS 12555 (Rosenow *et al.* 1983) have provided the major and best sources of the trait used in QDPI program (Henzell *et al.* 1997). QL 41 was the key line developed, and was derived from the cross QL 33 x B 35 (Henzell *et al.* 1992 a). It has a high level of expression of stay-green and crosses of it with QL 38 and QL 39 (sorghum midge resistant lines) formed the basis of the female stay-green and midge resistant gene pool in the QDPI programs, although Jess progress has been made in developing such germplasm in the male population (Henzell *et al.* 1997). Hybrids involving non-senescent lines QL40 and QL41 showed the least stalk rot incidence and severity, particularly with natural exposure, and performed better than commercial hybrids Texas 671 and E 57 (Dodman *et al.* 1992).

While most commercial sorghum hybrids in USA possess good tolerance to pre-flowering drought stress, only a few have good post-flowering resistance (Nguyen *et al.* 1997). In spite of the availability of simply inherited stay-green trait associated with terminal drought tolerance, progress in enhancing post-flowering drought resistance is slow (Rosenow *et al.* 1997). This is because, the expression of this trait is strongly influenced by environmental factors and limited number of sources of stay green that are currently in use in sorghum breeding programs (Mahalakshmi and Bidinger, 2002).

The stay-green trait expresses best in environments in which crop is dependent on stored soil moisture, but where this is sufficient to meet only a part of the transpiration demand. Sufficient expression of trait for selection is thus dependent upon the occurrence of a prolonged period of drought stress of sufficient severity during the grain filling period to accelerate nominal leaf senescence, but not of sufficient magnitude to cause premature death of the plants (Mahalakshmi and Bidinger 2002). Because of this precise requirement for the trait expression, field environments do not offer ideal conditions for selection and therefore, identification of QTLs conferring stay green trait and the molecular markers tightly linked to these QTLs will provide powerful tools to enhance drought resistance (Crasta *et al.* 1999; Xu *et al.* 2000; Mahalakshmi and Bidinger 2002). Recent identification of several (e.g. IS 22380, QL 27, QL 10, E 36 x R 16 8/1) tropically adapted lines with stay-green expression equivalent to those of the best temperate lines B 35 and KS 19 (Mahalakshmi and Bidinger 2002) is further expected to hasten the process of mapping QTLs and their subsequent introgression into agronomically elite lines.

BIOTECHNOLOGY-ASSISTED BREEDING FOR DROUGHT RESISTANCE

The direct selection for drought tolerance components using conventional approaches has been slow and difficult (Ejeta *et al.* 2000) largely due to its quantitative inheritance coupled with unpredictable timing duration and severity of drought. Controlled by many genes and dependent on a population of drought situations, drought tolerance is one of the more difficult traits to study and manage genetically. Hence, use of molecular markers and QTL analysis based on carefully managed replicated tests has the potential to alleviate the problems associated with inconsistent and unpredictable onset of moisture stress or the confounding effect of other related stresses such as heat (Ejeta *et al.* 2000).

Many researchers (Tuinsta *et al.* 1996; Tuinsta *et al.* 1997; Tuinsta *et al.* 1998; Crasta *et al.* 1999; Subūdhi *et al.* 2000; Tao *et al.* 2000; Xu *et al.* 2000; Ejeta *et al.* 2000; Kebede *et al.* 2001; Coulibaly 2002) have identified QTLs associated with pre- and post-flowering drought tolerance in sorghum. The molecular genetic analysis of QTLs influencing stay green trait, an important post flowering drought resistance (Tao *et al.* 2000; Xu *et al.* 2000; Haussmann *et al.*, 2002) resulted in the identification of upto four QTLs. Subudhi *et al.* (2000) confirmed an the four QTLs (Stg -1, -2, -3, -4) that were identified earlier by Xu *et al.* 2000 by evaluating Recombinant in bred line (RIL) populations derived from B35 x Tx700 in two locations for two years. Similarly, comparisons of stay green QTL locations with earlier reports indicated that three of the four stay green QTLs showed consistency across different genetic backgrounds and environments. They concluded that Stg-2 QTL region is expected to increase our understanding of stay green trait leading to either marker-assisted introgression of this QTL into elite agronomic background or map based cloning to genetically engineer this locus into improved cultivars.

Although it has been possible to identify several regions of the sorghum genome that condition the expression of drought tolerance, it provided little information concerning the expression of individual QTL. Therefore, analysis of near-isogenic lines (NILs) that differ at QTL of interest can be an effective approach for the detailed mapping and characterizing the individual QTL (Ejeta *et al.* 2000).

Tuinستا *et al.* (1998) developed a procedure for developing NILs for any region of the genome that can be analyzed with molecular or other genetic factors. This analyzed with molecular markers to identify heterogeneous inbred families that are isogenic at most loci in the genome form NILs that differ in marker linked to QTL of interest. Tuinsta *et al.* (1996) used these NILs to test the phenotypic effects of three different genomic regions associated with various measures of agronomic performance in drought and/or non-drought environments. In most cases, NILs contrasting for a specific locus differed in phenotype as predicted by QTL analysis. NILs contrasting at QTL marker tM5/75 indicated large differences in yield across a range of environments. Further analysis indicated that differences in agronomic performance might be associated with a drought-tolerance mechanism that also influences heat tolerance. NILs contrasting at QTL marker tH19/50 also differed in yield under drought and non-drought conditions. The analysis of these NILs indicated that these differences might be influenced by a' drought-tolerance mechanism that conditions plant water stress and expression of stay green. NILs contrasting at QTL marker t329/232 differed in yield and seed weight. These differences appear to be the result of two QTLs that are closely linked in repulsion phase.

At ICRISAT, QTLs for stay green trait have been mapped by phenotyping RILs from two-*Striga* resistance mapping populations having agronomically elite, *Striga* susceptible, stay green parent E 36-1. Results have indicated that this source has several QTLs for stay green trait that were not detected in previous studies based on sources B 35 and SC 5. Across the three available stay green sources (B 35, SC 56 and E 36-1) for which QTLs have been mapped to date, QTLs have been identified on all 10 sorghum linkage groups. ICRISAT has initiated marker-assisted backcross program to introgress QTLs for the stay green trait from sources B 35 and E 36-1 into a diverse range of farmer-accepted sorghum cultivars adapted to diverse agro-ecologies in tropical Asia, Africa and Latin America (ICRISAT 2005).

SUMMARY

Sorghum being C_4 species is relatively more drought tolerant compared to other cereals such as maize and consequently has rich diversity for stress tolerance. Further enhancement of its resistance to drought stress would stabilize productivity trends and contribute to sustainable production systems in drought-prone environments. Responses to drought stress depend on the growth stage at which drought stress occurs. Four growth stages have been considered as most vulnerable to drought stress in sorghum - (1) germination and seedling emergence, (2) midseason, (3) pre-flowering and (4) post-flowering. Of the several mechanisms to circumvent drought stress in sorghum, drought escape, drought avoidance and drought tolerance are considered as most important and have been well characterized. Genetic differences for responses to drought stress at each of the four growth stages exist and breeding programs have exploited drought escape, drought avoidance and drought tolerance mechanisms to elevate drought tolerance in sorghum. Stay green trait, known to confer post-flowering resistance in sorghum has been very well exploited to enhance post-flowering drought tolerance in sorghum. At ICRISAT, growth stage-specific breeding for drought resistance which involves alternate seasons of screening in specific drought and yield potential environment is used to breed sorghum which can yield well in high yield potential areas/seasons as well as in seasons/years of drought at specified growth stage. Though several physiological traits are identified, they do not sufficiently relate to the field responses to merit selection based on them and also the screening techniques developed based on them are not cost-effective. Since hybrids exhibited relatively better performance than varieties for grain productivity under water limited environments, hybrid cultivar -development (including their parents) should be given a strategic importance for enhancing sorghum production in water-limited environments. As the progress in enhancing drought resistance levels in sorghum utilizing conventional approaches are limited by the quantitative inheritance of yield and drought resistance coupled with complexity of timing, severity and duration of drought, biotechnology appears to offer a better scope for genetic enhancement of drought resistance in sorghum. Four stable and major Quantitative trait loci (QTLs) have been identified for stay green trait and are being introgressed through marker assisted-selection into elite agronomic background at ICRISAT.

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