

# Genetic Enhancement for Drought Tolerance in Sorghum

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## I. INTRODUCTION

Sorghum (*Sorghum bicolor* (L.) Moench) is a predominant food and fodder crop grown in the semiarid tropical (SAT) regions 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 low fertility and low water-holding capacity. Sorghum production is affected by a range of biotic and abiotic yield constraints (drought, temperature, and nutritional stresses). Among these, drought 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 attributed primarily to drought (Kramer and Boyer 1995). Sorghum, being C4 plant species, is better adapted to stress environments, especially soil moisture stress, compared to maize (Nagy et al. 1995). As such, it is the logical crop to support the poor of the world, 25% of whom are expected to experience severe water scarcity by 2025 (Ryan and Spencer 2001). Genetic enhancement of sorghum for drought tolerance is a cost-effective approach to further increase its productivity, stabilize production, and contribute to food security. This chapter reviews and discusses various mechanisms, screening techniques, inheritance and efforts to breed sorghum for drought tolerance and output.

## II. BREEDING FOR DROUGHT TOLERANCE

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 aluminum (Al), sodium ( $\text{Na}^+$ ), chloride ( $\text{Cl}^-$ ), or clay), leading to perceptible reduction in crop growth and economic yield. Drought tolerance refers to physiological or biochemical adaptations that enable plant tissues to withstand water deficits (Clarke and Durley 1981) or the ability of plant tissues to function under stress or adapt to low tissue water potential (i.e., osmotic adjustment) (Blum 1979a). From a crop production point of view, drought tolerance is defined as stability of crop yield under a specific target drought stress environment, resulting from the operation of drought tolerance mechanisms. Turner (1979) defines crop drought tolerance as the ability of a genotype to yield satisfactorily in areas subjected to periodic water deficits. However, to be agronomically useful, a drought-tolerant cultivar should also have a good yield potential under favorable moisture conditions, since it is difficult to predict drought in time and space.

The effective exploitation of genetic diversity in drought tolerance requires unraveling the mechanisms that ameliorate internal stresses and those that minimize drought injury (Steponkus et al. 1980). The

mechanisms of drought tolerance in sorghum can be described as escape, avoidance, and tolerance (Levitt 1972; Blum 1979b; Ludlow 1993). Early maturity is a well-known "drought-escape" mechanism through which the crop completes its life cycle before the onset of severe moisture deficits and is often associated with reduced yield potential; other two mechanisms are physiological responses to water stress (Blum et al. 1992). Short-duration sorghums have lower evapotranspiration rates due to smaller leaf area and smaller root density compared to those of long-duration types (Blum 1979b) as well as reduced seasonal transpiration due to a shorter life cycle. Avoidance is defined as the plant's ability to maintain a relatively higher level of hydration (i.e., maintenance of higher turgor or leaf-water potential [LWP] under conditions of soil or atmospheric moisture stress). Given sufficient time, plants subjected to moisture stress may avoid dehydration by maintaining higher LWP or adapt to low tissue water potential (osmotic adjustment). Sorghum avoids low LWP by one or more mechanisms, such as a change in rooting pattern, an increased root growth, or an adjustment in leaf area (Seetharama et al. 1982). Leaf area adjustment has been suggested as one of the most powerful mechanisms of drought avoidance in sorghum (Passioura 1976). Apart from these physiological adaptations, certain biochemical compounds and micronutrients are known to confer drought tolerance in sorghum. Increased levels of glycine betaine and proline levels are reported to contribute to drought tolerance in sorghum (Wood et al. 1996). Abu et al. (2002) have identified significant association of grain micronutrients (potassium and iron) with drought tolerance in sorghum.

Ability of the genotype to yield reasonably high in specified drought stress environments is considered drought tolerance. As already mentioned, it is desirable that drought-tolerant lines have the ability to manifest high yield potential, if drought stress is relieved or a better environment is provided. Strategies for genetic enhancement of crop plants for drought tolerance have been widely discussed (Hurd 1976; Blum 1979b; Sharma and Saxena 1979; Townley-Smith and Hurd 1979; Reddy et al. 1980; Saxena and O'Toole 2002; Luigi et al. 2008; Blum et al. 1992; Wang et al. 2005). It has been postulated that drought tolerance can be improved without sacrificing substantial yield (Muchow et al 1996).

Four basic approaches to the breeding for drought tolerance 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 suboptimal conditions). The second is to breed for maximum yield by empirical selection in the field in the target drought-prone environment. The success of this

approach depends entirely on how variable the target environment is. It works well in the Indian post-rainy season environment, which is very predictable, but not in the rainy season environment, which is highly unpredictable. The third approach is to incorporate the selected physiological and morphological mechanisms conferring drought tolerance into traditional breeding programs. For example, Blum (1979b, 1983) has recommended selection in the  $F_5$  and  $F_6$  generations for yield and yield components under optimal production conditions and simultaneous selection of duplicate samples under moisture-stress conditions. The fourth breeding approach involves identifying a key trait that confers drought tolerance at specific growth stages and its introgression into the high-yielding background. This method was established and followed at the International Crops Research Institute for Semi-Arid Tropics (ICRISAT, Patancheru, India (17°30'N, 78°16'E, altitude 545 m); Reddy 1986). This method involves pedigree selection of breeding materials for specific traits, such as (1) longer mesocotyl length for emergence under crust, and grain yield under drought-prone and yield potential areas for early seedling stage drought; (2) for grain yield under drought-prone and yield potential areas alternatively for midseason drought; and (3) for stay-green and nonlodging and grain yield under drought-prone and yield potential areas alternatively for terminal drought. Crosses were made between high-yielding adapted lines, and lines were selected for high yields under drought or with one or more drought-related traits. Selections from  $F_2$  onward were made by evaluating the segregating material in alternate generations under specified drought (early, midseason, and terminal stage) and in yield potential environments. The  $F_5/F_6$  pure lines were evaluated for drought yield, potential yield, and for specific drought-related traits. Testing for yield under mild stress was adequate, as the rankings of genotypes for potential and drought yields were similar, since the drought-tolerant lines selected under mild stress had high yield potential in nonstress environments. These practical investigations agree well with those of Rosielle and Hamblin (1981), who indicated general increase in mean yield in both stress and stress-free environments if selection is practiced for mean productivity (i.e., average yield in stress and stress-free environments). Fischer and Maurer (1978) proposed an empirical drought susceptibility index (DSI) to screen the genotypes for drought tolerance under field conditions. This index is calculated as shown:

$$DSI = Y[1 - \bar{Y}/\overline{YP}]/D$$

where

$Y$  = Yield in stress conditions

$YP$  = Yield in irrigated conditions

$\bar{Y}$  = Mean yield of all genotypes under stress conditions

$\overline{YP}$  = Mean yield of all genotypes in irrigated conditions

$D$  = Drought-stress intensity ( $D = 1 - [\bar{Y}/\overline{YP}]$ )

The DSI estimates indicate reduction in yield of a genotype under drought stress conditions relative to mean reduction in yield of all genotypes 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), which is calculated as

$$\text{MRP} = [Y/\bar{Y} + YP/\overline{YP}].$$

The higher the MRP, better the performance under stress.

Osmanzai (1994b) demonstrated the usefulness of DSI and MRP indices for screening and evaluating the sorghum cultivars for drought tolerance (Table 3.1). This index, however, has a weakness in that it identifies both drought-escaping and drought-tolerant genotypes as "tolerant."

**Table 3.1.** 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 Y index <sup>z</sup>	Mean relative performance (MRP) <sup>y</sup>
Hybrids	12	62	0.98	2.47
Improved cultivars	11	63	1.00	1.83
Local landraces	5	69	1.09	1.76

<sup>z</sup>Estimation of the reduction in yield by drought stress for genotypes relative to the mean reduction in yield by drought stress

<sup>y</sup>Mean relative performance (MRP) = the sum of the ratios of yield of genotypes in stress (rainfed) and yield in relieved stress (irrigated).

Source: Osmanzai (1994b).

### III. SELECTION AMONG CULTIVARS AND LANDRACES

#### A. Cultivar Options

The greater grain yield of hybrids, compared to the improved and landrace cultivars in drought-prone environments, has been demonstrated on a number of occasions. For example, sorghum hybrids showed superior performance across variable environments, as compared to cultivars in both rainy (Table 3.2) and post-rainy seasons (Table 3.3) in India (Patil 2007; Reddy et al. 2007).

As growing conditions become stressed, the yields of both hybrids and cultivars decline, but the yield difference between hybrids and cultivars becomes larger by about 30%, favoring the hybrids (House et al. 1997). Blum et al. (1992) and Osmanzai (1994a) showed that hybrids performed better than cultivars under moisture-stress conditions and recover faster when moisture stress was relaxed. Evaluation of 12

**Table 3.2.** Comparative performance of sorghum hybrids over improved varieties/landrace cultivars during rainy season in India.

Year of testing	Grain yield (T HA <sup>-1</sup> )		Increase over cultivar or local check (%)	Reference
	Hybrid	Cultivar		
1985-90	3.7 (07)	3.2 (04)	14.9	Murty (1992)
1993	3.4 (09)	3.1 (09)	8.3	—
1994	3.6 (10)	3.0 (10)	18.5	—
1995	3.9 (17)	3.0 (12)	28.9	—
1996	3.6 (06)	3.3 (05)	8.8	Rana et al. (1997)

Figures in parentheses denote the number of hybrids or cultivars tested.

**Table 3.3.** Comparative performance of sorghum hybrids over improved varieties/landrace cultivars during post-rainy season in India.

Year of testing	Grain yield (T HA <sup>-1</sup> )		Increase over cultivar or local check (%)	Reference
	Hybrid <sup>z</sup>	Cultivar		
1996	2.8 (4)	2.2 (04)	28.4	Rana et al. (1997)
2000	4.9 (16)	4.1 (03)	18.6	SPSHT <sup>y</sup> 2000
2001	4.8 (13)	4.7 (02)	1.8	SPSHT 2001
2002	4.2 (10)	3.9 (01)	7.4	SPSHT 2002

<sup>z</sup>Figures in parentheses denote the number of hybrids/cultivars tested.

<sup>y</sup>Seed Producers Sorghum Hybrid Trial conducted at several seed producers' experimental plots and ICRISAT, Patancheru, India.

single-cross sorghum hybrids along with their parents and two local cultivars in Kenya under varying levels of drought stress, ranging from nonstress to extreme stress (preflowering and terminal), revealed mean hybrid superiority over midparent values by 54% and by 12% over local cultivars for grain yield (Hausmann et al. 1998). The single-cross hybrids were consistently superior to their parents with an average heterosis of 54% across eight frequently drought-prone environments in the semiarid Makueni district of Kenya (Hausmann et al. 2000). Rao and Khanna (1999) have also reported superiority of sorghum hybrids over their parents for leaf area and dry-matter production under both preflowering and postflowering drought stress.

Greater performance of hybrids than their parents or cultivars under drought stress or related abiotic stresses was also reported. Field research based on a limited number of genotypes (Peng et al. 1994; Azhar et al. 1998) indicated that hybrids have better salinity-stress (which mimics drought stress) tolerance than their parental lines or pure-line cultivars. It has been established in many studies that  $F_1$  hybrids had superior stability (or buffering capacity) across variable environments as compared to homozygotes in sorghum (Blum 1988).

For a given growth duration and biochemical photosynthetic efficiency, the total photosynthetic product of a crop species is finite. Hence increased performance of hybrids from their parents is due to greater growth rates and greater total biomass production and higher harvest index (Blum 1966; Blum et al. 1977b; Gibson and Schertz 1977) with or without an apparent increase in leaf photosynthetic rates (Sinha and Khanna 1975). The advantages of the hybrids are often associated with reduced crop growth duration (Quinby 1974). As the heterozygote may contain more than one gene product than the homozygote, it becomes biochemically diversified. 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. All these evidences suggest that the wider adaptability of hybrids is due to their relative tolerance to a wide range of abiotic stresses including soil moisture stress and related factors. Therefore, breeding for hybrid cultivars is a better option than open-pollinated (OP) cultivars for improving sorghum grain yield in water-scarce environments. Furthermore, to increase the grain yield within the limits of the available water supply, female parents for hybrid production should be chosen based on both leaf area and photosynthetic rate. Pollinators should be selected for maximum seed number per panicle (Krieg 1988). The improvement of performance per

se and combining ability of parents for agronomic traits and grain yield under drought stress should be given strategic importance, considering that parental performance per se and general combining ability (GCA) in sorghum is strongly correlated with hybrid performance (Quinby and Karper 1946; Murty 1991; Murty 1992; Bhavsar and Borikar 2002). It is well established in sorghum breeding that good OP cultivars make good parents for hybrids, because heterosis results primarily from additive gene action (Kambal and Webster 1965; Miller and Kebede 1981). Doggett (1988) showed the importance of the parental improvement to increase the hybrid performance and claimed that about 50% of the sorghum grain yield increase could be ascribed to better parents.

### B. Selection among Landraces 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, which is a highly popular post-rainy season adapted cultivar in India, has been repeatedly demonstrated (Seetharama et al. 1982; Shackel and Hall 1983). Blum and Sullivan (1986) evaluated 13 sorghum landraces (six from Mali and seven from Sudan) that evolved along geographical gradients of rainfall for drought tolerance under hydroponics conditions. The experiment was carried out in a growth chamber and water stress was induced by adding polyethylene glycol-800 to the nutrient solution with a solute water potential of 0.5 MPa compared to a control solution at 0.03 MPa. The result indicated that drought tolerance in terms of relatively less growth inhibition under stress was higher in races from dry regions than in those from humid regions. Germplasm lines and breeding lines tolerant to drought at specific growth stages have been identified at ICRISAT (Table 3.4).

**Table 3.4.** Sorghum germplasm and breeding lines tolerant to drought at specific growth stages, ICRISAT, Patancheru, India.

Growth stage	Tolerant sources/ improved lines
Seedling emergence	IS 4405, IS 4663, IS 17595 and IS 1037, VZM1-B and 2077 B, IS 2877, IS 1045, D 38061, D 38093, D 38060, ICSV 88050, ICSV 88065 and SPV 354
Early seedling	ICSB 3, ICSB 6, ICSB 11 and ICSB 37, ICSB 54 and ICSB 88001
Midseason	DKV 1, DKV 3, DKV 7, DJ 1195, ICSV 272, ICSV 273, ICSV 295, ICSV 378, ICSV 572, ICSB 58 and ICSB 196
Terminal drought	E 36-1, DJ 1195, DKV 3, DKV 4, DKV 17, DKV 18, ICSB 17

Source: ICRISAT (1982), Reddy et al. (2004).



#### IV. BREEDING FOR DROUGHT ESCAPE

In regions where end-of-season drought stress is common, such as those in Indian peninsula in rainy and post-rainy season environments, the most effective way to reduce losses due to drought is through the development of early-maturing genotypes to enable them escape end-of-season drought (Blum 1979b; Turner 1979). 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 OP cultivars (130 to 180 days) with early hybrids and OP cultivars of 100- to 110-day duration, which mature before the end of rains or before soil moisture is depleted, has resulted in a remarkable increase in rainy season sorghum production (Rao et al. 1979). However, early-maturing cultivars have become highly prone to grain molds, as the grain-filling and maturation periods normally coincide with continuous rains. Breeding sorghum for grain mold resistance for rainy season adaptation is therefore one of the major objectives of most sorghum improvement programs globally. Under terminal drought typically experienced by post-rainy season sorghums in India, early-maturing improved sorghum cultivars, such as CSH 1 (100 days and 4 t ha<sup>-1</sup>), CSH 6 (95 days and 3.2 t ha<sup>-1</sup>), and NK 300 (88 days and 4 t ha<sup>-1</sup>), produced better grain yields than long-duration cultivars, such as M 35-1 (105 days 1.9 t ha<sup>-1</sup>) and SPV 86 (108 days and 3 t ha<sup>-1</sup>) (Seetharama et al. 1982).

Sorghum production in the Great Plains of the United States is based on the development of early-maturing genotypes that escaped late-season stress by maturing before soil moisture reserves are exhausted (Smith and Frederiksen 2001). Sorghum improvement programs at ICRISAT and elsewhere are most successful in exploiting a "drought-escape" mechanism and have bred specific maturity cultivars that match the available soil moisture. Selection for enhanced grain yield under conditions of moisture 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 in high-potential environments. It is therefore evident that while exploiting drought escape as a solution, some of the potential grain yield must be sacrificed in return for improved stability under moisture stress (Blum, pers. comm.). The reduced yield potential in early genotypes may be compensated for to some extent by increasing plant density (Blum 1970). Under terminal water stress during the post-rainy season, short-duration sorghum genotypes produce equal grain but less dry matter than late cultivars.

Some early-maturing A/B lines that facilitate development of early-maturing hybrids, which can escape drought, have been identified at ICRISAT: for example, ICSA/B-615, 628, 629, 630, 634, and 635.

Drought escape is, however, not drought tolerance per se. Therefore, breeding for early maturity may not be always associated with higher yield in regions with erratic rainfall pattern. Concerted breeding for tolerance to a given pattern of drought in a target region is the best way to improve grain yield under moisture-limited conditions. Successful breeding for tolerance to a particular drought requires the availability of large-scale, cost-effective screening techniques, which can facilitate efficient discrimination of genotypes for drought tolerance. However, responses of genotypes to drought stress are complex. Moisture stress is known to cause differing degrees of reduction in grain yield, depending on the stage of the crop and frequency, duration, and severity of moisture stress. Nevertheless, four growth stages are recognized as most vulnerable to moisture stress (Reddy 1985; Rooney 2004):

1. Germination and seedling emergence
2. Early seedling stage (from seedling emergence to panicle initiation)
3. Midseason (from panicle differentiation to flowering [preflowering])
4. Postflowering (from flowering to grain-filling stage)

The responses of sorghum to moisture stress at these four growth stages have been well characterized. Genetic variation for drought tolerance at these growth stages has been observed and found to be heritable (Reddy 1985; Mkhabela 1996). Repeatable genotypic differences in drought response are observed, if the moisture stress is confined to one stage, but differences are masked if it occurs at more than one stage (Garrity et al. 1982). It is therefore suggested that screening techniques aim to discriminate genotypes for drought tolerance at each of the growth stages separately (Reddy 1985). Sandy soil or shallow soil sites are best suited for preflowering field evaluation of stress response; heavier and deeper soils are best for evaluating postflowering drought stress (Rosenow et al. 1997c). Several effective and reliable screening techniques were developed during the late 1970s and early 1980s at ICRISAT, India and in the United States and Australia, and drought-tolerant sources at different growth stages, from the germplasm and breeding lines, were identified. This approach led to several attempts to breed sorghum for

drought tolerance based on either the plant responses at these growth stages or physiological response traits conferring drought tolerance. These techniques are discussed in the next two sections.

## V. GROWTH STAGE-SPECIFIC SCREENING TECHNIQUES

### A. Germination and Seedling Emergence

The condition ideal for seedling survival is hardly present in the SAT, especially those of sub-Saharan Africa. A hot dry seedbed environment with soil surface temperature often greater than 55°C during crop establishment due to absence of subsequent rain after initial planting rain is a common occurrence in most regions of SAT (Gupta 1986; Hoogmoed and Klaij 1990; Peacock et al. 1993). Seedling death can occur at one of three defined stages—germination, emergence, and postemergence—during crop establishment. Under such situations, longer mesocotyl and ability of seedling emergence from deep planting (where soil moisture is greater) and from soils with high surface temperatures and tolerance to, or recovery from, drought at the seedling stage are considered important for crop establishment. Experience at ICRISAT showed that initial selection for coleoptile length (the trait associated with germination under deep sowing, which is desirable to capitalize on initial rains) of test lines 5 days after planting in germination boxes followed by selection in raised brick tanks using charcoal and heavy kaoline (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. Useful genetic variation was noted for seedling emergence (10–50%) at 5 days after sowing among 166 sorghum genotypes grown in alfisols with limited soil moisture during a hot dry summer season and under differential irrigation (5–30 mm) using a line-source sprinkler system (Seetharama et al. 1982).

Diminishing soil water availability after germination due to dry spells after initial rains during sowing greatly affects seedling growth and survival. Selection of breeding lines in the sandy soil-filled brick tanks spread uniformly with charcoal powder at 125 gm<sup>-2</sup> (which induces high soil surface temperatures) based on the seedling emergence counts 6 days after planting was effective in identification of lines with high seedling emergence under the high surface soil

temperature that is prevalent in Africa during the sowing season (Reddy 1985). Significant cultivar differences for seedling emergence at low soil moisture conditions (Soman 1990) and subsequent growing ability have been reported in sorghum (O'Neill and Diaby 1987).

### **B. Postemergence and Early-Seedling Stage**

Sustained seedling growth following emergence depends on the capacity of the seedling to elongate, produce leaves, and become autotrophic. Postemergence seedling death due to moisture stress under field conditions is primarily caused by the prevalent high soil surface temperatures, at least in the first 10 days following sowing, and only after that does water deficit start to take effect (Stomph 1990; Peacock et al. 1993). Selection of sorghum 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 polyvinyl chloride (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 (Reddy 1985). Wenzel (1991) reported that additive effects controlled variation for seedling drought tolerance and that the trait was highly heritable. However, the relative magnitude of genotypic variation is far lower than that of soil temperature variation.

### **C. Midseason and Preflowering Stage**

The preflowering response is expressed when plants are stressed during panicle differentiation prior to flowering. Symptoms of mid-season or preflowering drought stress susceptibility include leaf rolling, uncharacteristic leaf erectness, leaf bleaching, leaf tip and margin burn (leaf firing), delayed flowering, poor panicle exertion, panicle blasting and floret abortion, and reduced panicle size (Seetharama et al. 1982; Rosenow et al. 1997a,b,c). Tolerance to preflowering drought stress is indicated by the alternative condition in each instance. Since the panicle is directly affected, severe preflowering stress can result in drastic reductions in grain yield. For screening for midseason stress, which represents the midseason drought pattern of the rainy season in many parts SAT, mild moisture stress is not sufficient for the expression of the genotypic differences for responses to moisture stress. Curtailing irrigation 3 weeks after sowing for over 45 days in a rain-free season was found to provide the required

level of drought stress for effective screening for preflowering drought stress (Reddy 1985). Specific nurseries were used in dry environments in Sudan (Ejeta 1987) and in Mexico (Rosenow et al. 1997a) to screen sorghum genotypes for preflowering drought stress. Excellent sources of tolerance to preflowering drought have been identified (Rosenow et al. 1997a,b,c). These sources of tolerance have been utilized by researchers to develop inbred lines, hybrids, and cultivars that have good levels of preflowering drought tolerance (Rooney 2004).

At ICRISAT, India a large number of progenies were screened for tolerance to preflowering drought stress. Those with better tolerance were selected further for grain yield alternatively under midseason 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 sub-Saharan Africa, they showed greater stability for grain and biomass yields than other cultivars that were developed for favorable environments (ICRISAT 1982, 1986, 1987). Selection of sorghum breeding lines for grain yield in field conditions under midseason drought (induced for 35 days), after initial nonstress growth period of 21 days after planting, was effective to identify promising lines for midseason drought stress tolerance.

In replicated trials at Sangareddy (20 km west of ICRISAT, Patancheru, India), 364 advanced selections from the drought tolerance breeding project were evaluated during the hot summer (April–May) of 1980, when the maximum daily temperature varied between 35°C and 43°C. Many entries showing tolerance to leaf firing were also agronomically good. Good correlations between scores for leaf firing and ability to recover were reported (Seetharama et al. 1982).

Little effort was made to breed sorghum specifically for drought tolerance at specific growth stages, particularly at germination and emergence, and early-seedling stages and relate it to whole-plant tolerance to drought. The earlier efforts for genetic enhancement of sorghum for preflowering drought tolerance in the United States and ICRISAT, Patancheru helped in identification of improved sorghum lines for drought tolerance (Reddy et al. 2004).

#### **D. Terminal and Postflowering Stage**

**1. Screening Techniques.** Postflowering stress is due to inadequate soil moisture during the grain-filling stage, especially during the later portion of grain filling. Postrainy season sorghum in India typically experiences such postflowering stress. It is similar to that experienced

by crops grown under receding soil moisture conditions in the West Asian region (Israel and Yemen) as well as parts of West Africa (Lake Chad area in Nigeria and in Mali). Symptoms of postflowering drought stress susceptibility include premature plant (leaf and stem) death or plant senescence, stalk collapse and lodging, and charcoal rot (caused by *Macrophomina phaseolina*), along with a significant reduction in grain 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 tolerance to stalk lodging and to charcoal rot (Rosenow and Clark 1995; Garud et al. 2002). The cultivars that remain green under postflowering drought are referred to as having the "stay green" trait. Selection of breeding lines for the stay-green trait was useful for screening for terminal drought tolerance. The stay-green trait is expressed only when the materials at postflowering stage are exposed to severe moisture stress.

Comparison of yield on shallow vertisols or on partially saturated deep vertisols with an irrigated control has been advocated to screen genotypes for terminal drought tolerance in receding moisture conditions. Effective screening for terminal drought tolerance can be carried out under field conditions by choosing the appropriate time of sowing to ensure that the crop experiences terminal drought stress.

The line source (LS) sprinkler irrigation technique developed at Utah State University was followed at ICRISAT for screening sorghum genotypes for terminal drought tolerance. Each side of the LS formed one replication. The field was uniformly irrigated until the crop reached boot stage, and the LS were 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. 1987). The rows of plants farthest from the LS showed disease earlier than those nearest. This was apparent for each of the three parameters of disease spread: percentage of soft stalks, number of nodes crossed, and the length of fungal spread (Seetharama et al. 1987). Specific nurseries were used in dry environments in Sudan (Ejeta 1987) and in Mexico (Rosenow et al. 1997c) to screen sorghum genotypes for postflowering drought tolerance. In the sorghum improvement program of University of Queensland (Australia), breeding progenies are routinely evaluated in regular field screening nurseries for premature leaf and plant senescence at or near physiological grain maturity (Borell et al. 2000a, 2000b).

**2. Breeding.** Unlike the situation at other stages, considerable progress has been made for genetic enhancement of sorghum for drought tolerance at the postflowering stage. Stay-green trait is now considered as an important postflowering drought tolerance trait (Rosenow et al. 1997c). Genotypes possessing the stay-green trait maintain a greater green leaf area during grain filling and extend photosynthesis in upper canopy leaves after physiological grain maturity under postflowering drought compared to their senescent counterparts (Rosenow et al. 1977). Earlier reports indicated that the leaves remain green due to a lack of assimilate demand because the plants have small panicles under postflowering drought (Henzell and Gillerion 1973; Rosenow et al. 1983a). However, recent studies have shown that they are stay green not only because of their small sink demand but also due to their higher leaf nitrogen status (Borrell and Douglas 1997; Borrell et al. 1999; Borrell and Hammer 2000). Although small sink demand enables plants to maintain photosynthetic capacity and ultimately result in higher grain yield and lodging resistance (Borrell et al. 2000a), higher leaf nitrogen status retards the decline in protein content of the aging leaves (Humphreys 1994) and higher transpiration efficiency (Borrell et al. 2000b). The stay-green sorghums accumulate more soluble sugars in stems than do senescent counterparts, both during and after grain filling (Duncan et al. 1981; McBee et al. 1983). The higher concentration of stem sugars improves the digestible energy content of the stover (Vietor et al. 1989). Stay-green genotypes are less susceptible to lodging, more resistant to charcoal rot, and retain higher levels of stem carbohydrates than non-stay-green genotypes (Mahalakshmi and Bidinger 2002).

*Inheritance of Stay Green.* 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 where evaluations are made. Its control in Q 141, which is derived from B 35, appeared to be however multigenic (Henzell et al. 1992). 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). All the three factors appear to be inherited independently (Van Oosterom et al. 1996), and thus sources expressing these components can be combined in breeding programs (Borrell et al. 2000a). This is supported by the identification of multiple quantitative trait loci (QTL) affecting the trait (Harris et al. 2006).

*Stay Green, Grain Yield, and Size.* Stay green and grain yield were positively associated in a range of studies conducted in both Australia (Borrell et al. 2000a) and India (Borrell et al. 1999), highlighting the value of retaining green leaf area under terminal drought. Grain yield is the product of grain number and grain size (completeness of grain filling). Grain number is generally the main determinant of differences in grain yield, and this has also been observed in sorghum grown under terminal drought stress in southern India (Borrell et al. 1999). Grain size is a secondary yield determinant and is often negatively associated with grain number under nonstress conditions. Grain size was correlated with relative rate of leaf senescence during grain filling such that reducing rate of leaf senescence from 3% to 1% loss of leaf area per day resulted in doubling grain size from about 15 to 30 mg (Borrell et al. 1999). Hence, the stay-green trait can potentially increase grain yield by improving grain number and grain filling ability.

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. 1983b; 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).

Conventional breeding for the stay-green trait has been based primarily on two sources for this trait, B 35 and KS 19 in programs in Australia and the United States (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 (PI 534133) was selected from a converted (dwarf, early-flowering) version of IS 12555, an Ethiopian landrace (Rosenow et al. 1977c, 1983a). The stay-green trait from IS 12555 (as SC 35) has been successfully used by Queensland Department of Primary Industries (QDPI) program in Australia to develop postflowering drought stress tolerance and lodging resistance in parental lines and commercial hybrids (Henzell et al. 1992b; Henzell and Hare 1996). KS 19 has been used commercially primarily in the breeding program of QDPI, while B 35 is widely used in both public and private sector breeding programs in United States (Mahalakshmi and Bidinger 2002). The partially converted (B 35) and fully converted (SC 35C-14E) versions of IS 12555 (Rosenow et al. 1983b) have provided the major and best sources of the trait used in the QDPI program (Henzell et al. 1997).



QL 41 was the key line developed, and was derived from the cross QL 33 × B 35 (Henzell et al. 1992 a). It has a high level of expression of stay-green. 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 at QDPI), although less progress has been made in developing such germplasm in the restorer program (Henzell et al. 1997). Hybrids involving nonsenescent lines QL 40 and QL 41 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).

In most sorghum improvement programs globally, E 36-1 and B 35 have been extensively used for developing hybrid seed parents (B-lines) and pollen parents (R-lines) and cultivars. E 36-1 is a widely adapted *zera-zera* germplasm line from Ethiopia. Several stay-green hybrid seed parents were developed prior to 2000 following a trait-based breeding approach at ICRISAT (Reddy et al. 2005). These seed parents were evaluated for stay-green and grain yield potential during the 2003 post-rainy season at ICRISAT in Patancheru. Some of these seed parents are better than the stay-green source, E 36-1, for stay green and grain yield under terminal drought (Table 3.5). The grain size of

**Table 3.5.** Performance of selected ICRISAT-bred sorghum stay-green B-lines (ICRISAT, Patancheru, 2003 post-rainy season).

Stay-green lines	Days to 50% flowering	Plant height (M)	Stay green score <sup>z</sup>	Grain yield (T HA <sup>-1</sup> )	100-grain weight (G)
ICSB 375	71	1.7	2.0	3.5	3.14
ICSB 405	72	1.2	1.5	3.0	3.27
ICSB 675	72	1.0	2.5	3.1	3.28
ICSB 676	73	0.9	1.5	3.4	3.00
ICSB 677	72	1.1	2.5	3.3	3.28
<b>Controls</b>					
296B <sup>y</sup>	76	1.1	2.5	2.6	3.01
E 36-1 (Stay green control)	65	1.5	2.0	2.8	3.71
Mean	73	1.4	2.6	3.5	3.12
SE±	0.87	0.05	0.43	0.36	0.17
LSD (5%)	2.68	0.15	1.30	1.10	0.53
CV (%)	1.68	5.31	23.57	14.26	7.58

<sup>z</sup>Stay green score taken on a 1 to 5 scale at harvest, where 1 => 75% green; 2 = 51–75%; 3 = 26–50%; 4 = 10–25%; and 5 =< 10% green.

<sup>y</sup>Hybrid seed parent of several popular and released or marketed hybrids in India.

these B-lines is significantly better than 296B, the hybrid seed parent (known for its large grain) of several popular and released/ marketed sorghum hybrids in India. Since 2000, several improved stay-green R-lines and cultivars were developed. Some of these R-lines and cultivars are significantly better than E-36-1 for grain yield with comparable stay greenness and grain size under terminal drought (Table 3.6). These hybrid parents have good potential for developing stay-green hybrids.

Although most U.S/ commercial sorghum hybrids possess good tolerance to preflowering drought stress, only a few have good postflowering drought tolerance (Nguyen et al. 1997). Despite the availability of simply inherited stay-green trait associated with terminal drought tolerance, progress in enhancing postflowering drought tolerance is slow (Rosenow et al. 1997c). This is because the expression of stay-green trait is dependent on the occurrence of a prolonged period of drought stress of sufficient severity during the grain-filling period to accelerate normal leaf senescence, but not of sufficient magnitude to

**Table 3.6.** Performance (mean of two years) of selected ICRISAT-bred sorghum stay-green cultivars and R-lines (ICRISAT, Patancheru, 2003 post-rainy season).

Cultivars/ R-lines	Days to 50% flowering	Plant height (M)	Stay green score <sup>z</sup>	Grain yield (T HA <sup>-1</sup> )	100-grain weight (G)
ICSV 21001	77	1.6	1.5	3.4	3.45
ICSR 21004	77	1.5	2.5	4.1	3.67
ICSR 21005	76	1.5	2.5	4.9	3.69
ICSR 21006	77	1.5	2.5	5.4	3.63
ICSR 21009	71	1.6	2.0	3.6	3.61
ICSR 21010	73	1.5	2.5	3.8	3.34
ICSV 21012	73	1.7	2.5	4.4	3.26
ICSV 21013	71	1.5	2.0	3.5	3.48
<b>Controls</b>					
E 36-1 (stay green control)	65	1.5	2.0	2.8	3.71
M 35-1 <sup>y</sup>	69	2.2	3.0	3.6	3.45
R 16 <sup>y</sup>	67	1.8	2.5	3.3	3.08
Mean	73	1.4	2.6	3.5	3.12
SE±	0.87	0.05	0.43	0.36	0.17
LSD (%)	2.68	0.15	1.30	1.10	0.53
CV (%)	1.68	5.31	23.57	14.26	7.58

<sup>z</sup>Stay green score taken on a scale 1 to 5 at harvest, where 1 => 75% green, 2 = 51–75%, 3 = 26–50%, 4 = 10–25%, and 5 =< 10% green.

<sup>y</sup>Popular post-rainy season cultivars released in India

cause premature death of the plants. Only a limited number of sources are currently in use in sorghum breeding programs (Mahalakshmi and Bidinger 2002). Because of this precise requirement for the trait expression, natural field environments do not offer ideal conditions for selection. QTL for stay-green trait and the molecular markers tightly linked to these QTL have been identified and are serving as powerful tools to enhance terminal drought tolerance in sorghum (details are discussed in the Section IX).

## **VI. PHYSIOLOGICAL RESPONSE TRAITS FOR DROUGHT TOLERANCE**

Several physiological traits such as leaf water potential (LWP), osmotic adjustment (OA), heat tolerance, desiccation tolerance, rooting depth, and epicular 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 tolerance. Screening techniques and genetic variability based on some of these traits (LWP and OA) have been reported (Christiansen and Lewis 1982; Garrity et al. 1982; Seetharama et al. 1982; Blum 1983; Jordan et al. 1983; Blum 1987; Ejeta 1987) and are discussed in the next sections.

### **A. Leaf Water Potential (LWP)**

The physiological adaptations effective in improving tolerance to moisture stress were found to vary with plant growth stage in sorghum (Ackerson et al. 1980). Before flowering, plants avoid dehydration largely by maintaining higher LWP; after flowering, plants avoid dehydration by maintaining higher turgor at a given level of moisture stress. This activity could be partly responsible for the different classification of drought tolerance before and after flowering in sorghum (Rosenow et al. 1983a). The most evident control of LWP is at the root system. Small root resistances and a large root-length density would contribute to the maintenance of a higher LWP. The root-length density increased with reduced soil moisture only at certain soil depths (Blum and Arkin 1984). Genotypic differences in sorghum root growth have been noted under moisture stress (Blum et al. 1977b,c). Blum (1979a) has shown that early-maturing sorghum genotypes not only escape drought but also avoid it because of reduced transpiration as a result of increased root length accompanied by reduced leaf area (high

**Table 3.7.** Genotypic differences in expansion rates of culm (leaf + stem; Ter) and of leaf (Ler) under control and moisture-stress during the panicle development stage in sorghum (ICRISAT, Patancheru, India).

Genotype	Ter <sup>z</sup> (MM H <sup>-1</sup> )		Reduction (%)	Ler <sup>z</sup> (MM H <sup>-1</sup> )		Reduction (%)
	Control	Stress		Control	Stress	
CSV 15	2.42	1.42	41.3	2.18	1.23	43.6
V 302	2.37	1.53	35.4	1.76	1.11	36.9
CSH 8	2.09	1.79	14.4	1.74	1.47	15.5
M 35-1	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
CS 3541	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	2.2	23.3	2.06	1.65	19.9
Mean	2.61	1.89	27.19	1.86	1.37	26.51
Se±	0.22	0.16	4.10	0.13	0.11	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

<sup>z</sup>Data for period 1600 hrs on 31 January 1981 to 1530 hrs on 2 February 1981.

Source: Seetharama et al. (1982)

root length to leaf area ratio). Because of high sensitivity of leaf area expansion to changes in turgor, several researchers (Hsiao and Acevedo 1974; Boyer and McPherson 1975) suggested the use of leaf area expansion as the criterion for screening the genotypes for drought tolerance. Large differences for leaf expansion rates among sorghum cultivars and hybrids have been observed in Patancheru. The cultivars CSV 5 and V 302, which were sensitive to drought, showed more reduction in leaf expansion than M 35-1 or CSH 8 (known to be drought tolerant) (Table 3.7).

At ICRISAT, 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 tolerance (avoidance) in sorghum (Rosenow et al. 1983a). Greater leaf rolling was indicative of reduced LWP in different sorghum genotypes (Blum et al. 1989). Gaosegelwe and Kirkham (1990) suggested that LWP could be used as an easy and fast way to screen sorghum genotypes for drought avoidance. 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 recovery when moisture stress is relieved (Blum et al. 1992). Stricevic and Mastrorilli (1992) and Stricevic and Caki (1997) showed a predawn LWP of  $-0.5$  MPa as

the threshold value for scheduling irrigation. Physiological processes were significantly decreased below this value, which suggests that those genotypes that maintain predawn LWP above this level can be considered as drought tolerant. However, breeding programs are slow to adopt this trait for selection.

### **B. Osmotic Adjustment (OA)**

Prolonged periods of water stress, a characteristic of SAT, cause low tissue water potential and tolerant plants adapt to low tissue water potential (OA). The genotypes with high OA retain higher turgor at a given level of plant water deficit and produce higher leaf area and subsequently support carbon assimilation. 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. However, Flower et al. (1990) concluded that while drought tolerant sorghum cultivars had better OA and consequently less leaf rolling under stress compared with susceptible cultivars, these responses did not influence growth under very dry and hot conditions. Studies on OA 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). Thermocouple psychrometry has also aided in measurement of water and osmotic potentials (Parsons 1982).

Variation in osmotic adjustment (OA) among sorghum genotypes was found to range from nil to 1.7 Mpa (Blum and Sullivan 1986). Landraces from dry habitats compared to those from humid regions 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,b). At ICRISAT, genotypic differences have been detected in predawn osmotic potentials even under mild stress. Post-rainy 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). Two independent major genes (*OA 1* and *OA 2*), have been reported to control the inheritance of OA in sorghum (Basnayake et al. 1995). Little if any progress in breeding for drought tolerance using either OA or any of the other physiological traits has been documented in sorghum, partly because of poor understanding of the traits conferring drought tolerance (Bonhert et al. 1995), and lack of

procedures to impose reproducible stresses and rapid methods to measure these traits (Santamaria et al. 1990). It appears that individual physiological traits identified to date are not sufficiently related to overall drought tolerance under field conditions to merit selection based on them (Rosenow et al. 1997c).

## VII. MARKER-ASSISTED BREEDING FOR DROUGHT TOLERANCE

The direct selection for drought tolerance components using conventional breeding approaches has been slow and difficult (Ejeta et al. 2000), largely due to unpredictable timing, duration, and severity of drought occurrence under natural conditions and difficulty of establishing screening environments. The use of molecular markers and QTL analysis based on carefully managed replicated tests therefore 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, 1997, 1998; Crasta et al. 1999; Ejeta et al. 2000; Subudhi et al. 2000; Tao et al. 2000; Xu et al. 2000; Kebede et al. 2001; Coulibaly 2002; Sanchez et al. 2002) identified QTL associated with pre- and postflowering drought tolerance in sorghum. Tuinsta et al. (1996) found six distinct genomic regions that were associated with preflowering drought tolerance in sorghum in recombinant inbred lines (RIL) derived from the cross Tx7078  $\times$  B 35. These loci accounted for approximately 40% of the total phenotypic variation for yield under preflowering drought and were detectable across a range of environments. Kebede et al. (2001) reported four QTL that confer preflowering drought tolerance in sorghum RIL derived from the cross SC 56  $\times$  Tx7000. However, these QTL were not consistent across the environments. Kebede et al. (2001) also noted a strong association between preflowering drought tolerance and days to 50% flowering.

The molecular genetic analysis of QTL influencing the stay-green trait, which is an important postflowering drought tolerance character (Tao et al. 2000; Xu et al. 2000; Haussmann et al. 2002), resulted in the identification of up to four QTL located on linkage groups B, G, and I. Subudhi et al. (2000) confirmed all four QTL (*Stg* -1, -2, -3, -4) that were identified earlier by Xu et al. (2000) by evaluating RIL populations derived from B35  $\times$  Tx700 in two locations for two years. Similarly, comparisons of stay-green QTL across locations with earlier reports

indicated that three of the four stay-green QTL showed consistency across different genetic backgrounds and environments. They concluded that *Stg-2* is expected to increase the understanding of the 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. The efficient map-based cloning requires the availability of a high-resolution integrated genetic and physical map, large segregating populations, and accurate phenotyping (Mullet et al. 2001). The construction of an integrated sorghum genome map is well under way ([http://www.cropscience.org.au/icsc2004/poster/3/2/1/965\\_borrellak.htm](http://www.cropscience.org.au/icsc2004/poster/3/2/1/965_borrellak.htm) verified 15 October 2008). Significantly, one of the markers linked to stay-green QTL located on linkage group B is a PCR-based SSR marker. This type of marker is “user friendly” and therefore can readily be used in breeding programs (<http://www.cimmyt.org/english/docs/proceedings/molecApproaches/pdfs/physiologBasis.pdf> verified 15 October 2008).

QTL for stay-green trait have been mapped by phenotyping RIL from two-*Striga* tolerance mapping populations having agronomically elite, *Striga* susceptible, stay-green parent E 36-1. Results have indicated that this source has several QTL for the stay-green trait that were not detected in previous research using as sources B 35 and SC 5. Across the three available stay-green sources (B 35, SC 56 and E 36-1) for which QTL have been mapped to date, QTL have been identified on all 10 sorghum linkage groups (Reddy et al. 2006).

Although it has been possible to identify several regions of the sorghum genome that condition the expression of drought tolerance, little information is available on the expression of individual QTL. Therefore, analysis of near-isogenic lines (NIL) that differ at QTL of interest can be an effective approach for the detailed mapping and characterizing the individual QTL (Ejeta et al. 2000). Tuinsta et al. (1998) developed a procedure for developing NIL for any region of the genome that can be analyzed with molecular or other genetic factors to identify heterogeneous inbred families that are isogenic at most loci in the genome from NIL that differ in marker linked to QTL of interest. Tuinsta et al. (1996) used these NIL to test the phenotypic effects of three different genomic regions associated with various measures of agronomic performance in drought and/or nondrought environments. In most cases, NIL contrasting for a specific locus differed in phenotype, as predicted by QTL analysis. NIL 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. NIL contrasting at QTL marker *tH19/50* also differed in yield under drought and nondrought conditions. The analysis of these NIL indicated that these differences might be influenced by a drought-tolerance mechanism that conditions plant water stress and expression of stay green. NIL contrasting at QTL marker *t329/232* differed in yield and seed weight. These differences appear to be the result of two QTL that are closely linked in repulsion phase.

Molecular marker-assisted backcross (MABC) introgression of the stay-green QTL from B 35 and E 36-1 donors into R 16 (a popular post-rainy season cultivar in India); ISIAP Dorado (a popular cultivar across Latin America); and IRAT 204, ICSV 111 and S 35— a selection from ICSV 111 (all popular cultivars in several African countries) is under way to develop improved sorghum lines for drought tolerance (ICRISAT 2005). At present, the derivatives are in advanced backcross generations. The identification of several (e.g., IS 22380, QL 27, QL 10, E 36 × 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 QTL and their subsequent introgression into agronomically elite lines.

Among the other biotechnological methods, it was reported that increase of glycinebetamine (GB) synthesis improved drought tolerance in cotton (Sulian et al. 2007) and efforts were also made in sorghum (Yang et al. 2003) to study the variability for GB in 240 genotypes at post-flowering stage. The total quaternary ammonium compound (QAC) levels in the betain fraction of the flag leaves were found to range from as low as  $0.1 \mu\text{mol g}^{-1}$  fresh weight (FW) to as much as  $33 \mu\text{mol g}^{-1}$  FW indicating high variability. Transgenic sorghums for drought tolerance are at infancy.

## VIII. OUTLOOK

Sorghum is one of the most important food-fodder-feed crops in the SAT worldwide. Sorghum with greater water use efficiency is relatively more drought tolerant than maize, making it a logical cereal to support the tropics. Genetic enhancement of sorghum for drought tolerance would stabilize productivity trends and contribute to sustainable production systems in drought-prone environments. The extent of grain yield losses due to drought stress depends on the stage of the crop and the timing, duration, and severity of drought stress. However, four growth stages in sorghum have been considered as most



vulnerable: germination and seedling emergence, postemergence or early seedling stage, midseason or preflowering, and terminal or postflowering stages. Sorghum responses to moisture stress at these four growth stages have been characterized. Variation in these responses has been observed and found to be heritable. Genotypic differences are observed, for drought tolerance through appropriate screening techniques for each of the growth stages, separately (Reddy 1986; Blum et al. 1989; Muchow et al. 1996; Hausman et al. 1998; Borrell et al. 200a,b; Harris et al. 2007). Of the several mechanisms to circumvent drought stress in sorghum, drought escape (related to maturity duration), drought avoidance (maintenance of higher LWP), and drought tolerance (related to OA) are considered as most important and have been characterized. However, LWP and OA do not relate to the field response well enough to merit selection based on them; in addition, the screening techniques developed based on them are not cost effective. Stay-green trait, which is known to confer postflowering drought tolerance, has been exploited to enhance postflowering drought tolerance in sorghum.

In most sorghum improvement programs including that at ICRISAT, growth stage-specific breeding for drought tolerance (which involves screening in specific drought and yield potential environments) is used to breed sorghum that can yield well in high-yield-potential environments as well as in drought-prone environments at specified growth stages. Since hybrids exhibited relatively better performance than OP cultivars for grain yield under water-limited environments, hybrid cultivar development (including their parents) should be given strategic importance for enhancing sorghum production in water-scarce environments. The progress in enhancing drought tolerance in sorghum through conventional approaches is limited by the quantitative inheritance of drought tolerance and yield coupled with complexity of timing, and severity and duration of drought. Biotechnology appears to offer promising tools, such as marker-assisted selection, for genetic enhancement of drought tolerance in sorghum. Four stable and major QTL were identified for stay-green trait and are being introgressed through MAS into elite agronomic backgrounds at ICRISAT, QDPI, Purdue University, and Texas A&M University in the USA.

The integration of sorghum genetic map developed from QTL information with the physical map will greatly facilitate the map-based cloning and precise dissection of complex trait like drought in sorghum. Sorghum is a drought tolerant crop with compact genome size ( $2n = 20$ ) can be an excellent model for identifying genes involved in drought tolerance to facilitate their use in other crops.

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