RESEARCH

Post-Flowering Drought Tolerance Using Managed Stress Trials, Adjustment to Flowering, and Mini Core Collection in Sorghum

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ABSTRACT

Sorghum [*Sorghum bicolor* (L.) Moench] crop in the semiarid tropics often suffers from post-flowering drought stress, which causes substantial losses in grain yield and stover quality. This research was aimed at studying the yield response of sorghum mini core accessions to post-flowering drought stress to identify drought-tolerant sources for sorghum improvement. Mini core accessions were grouped based on days to 50% flowering (extra early, early, medium, late, and extra late) and evaluated in two post-rainy seasons under managed drought stress and optimally irrigated conditions. Drought tolerance index (DTI), as a standard residual after removing the known contributory effects of flowering time and grain yield under optimum irrigation (yield potential) from the grain yield under drought, was used to segregate the genotypic responses to drought stress. The residual (or restricted) maximum likelihood analysis of data revealed significant genotypic variance (σ^2_g) for days to 50% flowering, grain yield, and DTI (except in the extra late flowering group), in both the seasons and significant genotype × environment interactions for DTI in extra early to late flowering groups. On the basis of DTI, seven accessions, i.e., 'IS 14779', 'IS 23891', 'IS 31714', 'IS 4515', 'IS 5094', 'IS 9108', and 'IS 15466', were identified as drought tolerant and five accessions were sensitive to drought in both of the post-rainy seasons. The tolerant accessions belonging to *durra, caudatum*, or *durra-caudatum* races were of diverse geographical origins, and most yielded at par with or greater than the extensively grown cultivar 'IS 33844'. These accessions can be employed to investigate the physiological and molecular basis of drought adaptation and to breed for drought tolerance in sorghum.

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Abbreviations: BLUP, best linear unbiased predictor; DAP, days after planting; DTI, drought tolerance index; REML, residual (or restricted) maximum likelihood.

SORGHUM [*Sorghum bicolor* (L.) Moench] is a dryland C_4 multipurpose crop with high photosynthetic efficiency, mostly grown for food, feed, and fuel. Sorghum is the fifth most important cereal after maize (*Zea mays* L.), rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), and barley (*Hordeum vulgare* L.). Annual average contribution of sorghum to the global cereal production (2.519 billion Mg) during 2009 to 2013 was 58.7 million Mg, with Africa, the Americas, Asia, and Oceania contributing 24.3, 21.6, 9.8, and 2.1 million Mg, respectively (http://www.faostat.fao.org; data accessed on 30 Nov. 2015). The major sorghum-producing countries are Nigeria, Ethiopia, former Sudan, Burkina Faso, Mali, Cameroon, and Niger in Africa; the United States, Mexico, Argentina, and Brazil in the Americas; India and China in Asia; and Australia in Oceania.

Worldwide, sorghum is largely grown during the rainy season in the semiarid tropical regions of Africa and Asia, which is often characterized by increasing moisture stress that causes plant stress as the season progresses (Assefa et al., 2010). Sorghum is more drought-tolerant than any other cereal crop and 80% of sorghum production in the world is under dryland conditions (Assefa et al., 2010). Nevertheless, the crop suffers large grain yield and biomass losses caused by drought (Craufurd and Peacock, 1993; Assefa et al., 2010; Dwivedi et al., 2010; Tari et al., 2013). Post-flowering drought stress is the most critical constraint, causing substantial losses to grain and stover yields in cereals, including sorghum,

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worldwide (Assefa et al., 2010; Dwivedi et al., 2010; Tari et al., 2013). Post-rainy season sorghum is widely grown on stored-receding soil moisture after the cessation of rains on shallow- and medium-deep soils in a vast area of the Deccan Plateau, India (Prabhakar and Reddy, 2014). With meager or no in-season rains, the crop often suffers progressively increasing water deficit as the season advances and as the crop approaches maturity (Kholová et al., 2013). Drought stress at the vegetative stage reportedly reduces yield by >36%, whereas stress at the reproductive stage reduces yield by >55% (Assefa et al., 2010).

In India, sorghum is the fourth most important food crop and is grown in two distinct sorghum-growing seasons: *kharif* (rainy season, June–October) and *rabi* (post-rainy season, October–January) (Reddy et al., 2012). The annual average sorghum production during the 2009–2010 to 2013–2014 period was 6.10 million Mg from 6.68 million ha, and 52% (3.16 million Mg) of it came during the post-rainy season from the crop grown on 3.9 million ha in the Deccan Plateau of India (http://eands.dacnet.nic.in/APY_96_To_06.htm; accessed on 2 Dec. 2015). The average yield of the post-rainy season crop was lower (0.79 Mg ha^{-1}) than that of the rainy-season crop (1.10 Mg ha^{-1}) (http://eands.dacnet.nic.in/APY_96_To_06.htm; accessed on 2 Dec. 2015). With the help of crop simulation models using available historical weather data and relevant crop management practices, the entire *rabi* sorghum belt of India had been characterized into different zones that varied in the type and intensity of drought stress. This belt included areas with most severe drought occurring in 25% of the seasons where stress began before flowering, resulting in the failure of grain production (Kholová et al., 2013). The grains produced during the post-rainy season are primarily used for human consumption, whereas stover is used as livestock feed in India. The post-rainy season produce is highly valued for its pearly white, lustrous, and bold grains, as well as for good stover quality. Thus, post-rainy season sorghum plays an important role in ensuring food and fodder security to millions of rural families in India (Rao et al., 2010).

Drought stress in sorghum adversely affects both physiological and yield traits, such as stay-green, chlorophyll content, canopy temperature, water extraction, transpiration efficiency, grain yield, seed numbers, seed weight, and harvest index (Sivakumar et al., 1979; Harris et al., 2007; DeLacy et al., 2010; Mutava et al., 2011; Vadez et al., 2011; Kapanigowda et al., 2013). Additionally, the crop also suffers from drought-associated root and stalk rots, leading to severe crop lodging apart from loss of stover, seed quality, and productivity (Borrell et al., 2000). Vadez et al. (2011) evaluated a part of sorghum reference set accessions (149) under well-watered (control) and drought-stressed conditions. The study revealed a large range of variation for grain yield (0.23–36.76 g plant^{-1} under drought stress and 2.06–82.83 g plant^{-1} under well-watered conditions), harvest index (0.05–0.52 under drought stress and 0.02–0.53 under well-watered conditions), transpiration efficiency (3.21–6.09 g kg^{-1} under drought stress and 2.95–5.59 g kg^{-1} under well-watered conditions), and total water extraction (10,600–15,200 g plant^{-1} under drought stress and 10,500–42,300 g plant^{-1} under well-watered conditions). Overall, about 50% reduction in mean grain yield (mean grain yield: 20.59 g plant^{-1} under drought stress and 41.97 g plant^{-1} under well-watered conditions) under post-flowering drought stress was noticed as compared with well-watered conditions (Vadez et al., 2011).

As the absolute grain yields can fluctuate and be unreliable owing to environmental influences, there is a need for appropriate indices that are free from known contributory effects of flowering time and grain yield under optimum irrigation (yield potential) from the grain yield under drought that would allow researchers to evaluate the drought response of sorghum, specifically under the post-rainy season's receding soil moisture environments (Sinclair and Muchow, 2001; Hammer et al., 2009). A large number of drought tolerance measures have been used, e.g., stress tolerance index, mean productivity, geometric mean productivity, stress susceptibility index, tolerance index, yield index, and yield stability index for each genotype based on grain yield under drought stress and irrigated conditions, as seen in recent studies to evaluate drought tolerance of sorghum in Eritrea and Brazil (Menezes et al., 2014; Abraha et al., 2015). None of these indices considers adjustment of yield under drought for all the known major influences and presents the positive residuals as a measure of intrinsic potential for drought tolerance. Therefore, the current work explores the appropriateness of such indices for a precise evaluation of drought tolerance in sorghum.

Yield under drought can be explained by traits that are fully independent of the response of genotypes to the drought environment. Crop duration in sorghum plays a critical role and contributes to genotype × environment interactions (Vadez et al., 2011; Upadhyaya et al., 2014a). Under post-rainy season conditions, differences in crop duration and yield potential are the two influential factors that contribute to grain yield under drought stress, and the residual after removal of these effects has been shown to provide a reliable measure of stress tolerance per se (Bidinger et al., 1987; Saxena, 1987, 2003; Krishnamurthy et al., 2010). Therefore, while selecting germplasm for drought tolerance, it is important to properly separate attributes that are inherent to a given line (constitutive traits) from those that only reflect a genotype's response to stress (adaptive traits). Here, we used drought tolerance index (DTI) (Bidinger et al., 1987), a standard residual after removal of the known contributory effects of drought escape (flowering time) and yield potential from the grain yield under drought stress, to segregate the genotypic responses to drought stress. In the past, DTI has been successfully employed to assess the drought response in pearl millet [*Pennisetum glaucum* (L.) R. Br.] and chickpea (*Cicer arietinum* L.) under terminal drought conditions (Bidinger et al., 1987; Saxena, 1987, 2003; Krishnamurthy et al., 2010). This exercise had also revealed that there were several processes, such as seed setting and seed filling, that explained differences in DTI under drought-stressed conditions.

Mini core collections representing diversity of the entire collection of a given species conserved in a genebank are ideal genetic resources for identifying new sources of variations for agronomically desirable traits (Upadhyaya et al., 2013, 2014b). In this study, we evaluated sorghum mini core collection (Upadhyaya et al., 2009) accessions (242) for two post-rainy seasons under managed-stress trials (irrigated and drought-stressed conditions) for sorghum response to post-flowering drought stress to identify drought-tolerant accessions that can be used to investigate the physiological and molecular basis of drought adaptation and to breed for drought tolerance in sorghum.

MATERIALS AND METHODS

Description of Materials

The material for evaluation included 242 accessions of sorghum mini core collection from 57 countries (Upadhyaya et al., 2009) and three controls. The mini core collection accessions included both the five basic sorghum races (*caudatum* 16.1%, *durra* 12.4%, *guinea* 12%, *kafir* 8.7%, and *bicolor* 8.3%) and 10 intermediate races (*caudatum-bicolor* 12.4%; *guinea-caudatum* 11.2%; *durra-caudatum* 7.9%; *durra-bicolor* and *kafir-caudatum* each 2.9%; *kafir-durra* 1.7%; *guinea-kafir* 1.2%; and *guinea-bicolor*, *guinea-durra,* and *kafir-bicolor* each 0.8%) (Upadhyaya et al., 2009). The controls included in this study were: 'IS 2205', 'IS 18758', and 'IS 33844'; among these, IS 33844 is the most popular sorghum cultivar grown under receding soil moisture conditions during the post-rainy season in India, whereas IS 18758 is cultivated in Burkina Faso and Burundi (Upadhyaya et al., 2014a). IS 33844 has exceptionally high plasticity to perform well under diverse environmental conditions, is tolerant to terminal drought, and possesses excellent grain quality attributes (Upadhyaya et al., 2016). IS 2205, a *durra-bicolor* landrace from India, is resistant to shoot fly [*Atherigona soccata* (Rondani)] and stem borer [*Chilo partellus* (Swinhoe)].

Experimental Details

The experiment was conducted at Patancheru (17.53° N, 78.27° E, and 545 m above sea level), India, in precision fields on Vertisol Kasireddipally series isohypothermic Typic Pellustert (El-Swaify et al., 1985) during two post-rainy seasons, 2010–2011 and 2011–2012. Accessions were planted in a split-plot design in three replications using drought stress and control (optimally irrigated) treatments as the main plot and genotypes as the subplots in five maturity groups (extra early, flowered $\leq$60 d after planting [DAP]; early, flowered 61–70 DAP; medium, flowered 71–80 DAP; late, flowered 81–90 DAP; and extra late, flowered >90 DAP) based on days to 50% flowering observations recorded during the 2009–2010 post-rainy season at Patancheru. This duration grouping became necessary, as grain yield of a genotype under terminal drought was consistently confounded by the flowering time (Bidinger et al., 1987). The experimental fields in both years were kept fallow during the rainy seasons. The precision fields at the ICRISAT center have uniform fertility and have irrigation facilities with a gentle slope of 0.5%. The experimental materials were planted in the second week of October each year. Plot size was one 4-m long row, with 75 cm between plots and an interplant spacing of 10 cm. Seeds were sown at a uniform depth of 2 to 3 cm using a tractor-mounted four-cone planter, and crop-specific agronomic practices, including plant protection measures, were followed. Ammonium phosphate was applied at the rate of 150 kg ha^{-1} as a basal dose, whereas urea was applied at the rate of 100 kg ha^{-1} as topdressing 3 wk after planting. A ridge and furrow system of cultivation was adopted, and each time, the experimental plots received about 7 cm irrigation water. Observations on days to 50% flowering were recorded as the day when 50% or more of the plants had reached anthesis in a plot, whereas grain yield (g plant^{-1}) was recorded from panicles (including tillers) of five representative plants of each accession at harvest maturity.

Environmental Conditions at Patancheru

The minimum and maximum temperatures of the crop-growing period across 2 yr were similar; minimum temperature ranged from 4.5 to 24.2°C (average 16°C) during 2010–2011 and 5.6 to 24.2°C (average 15.8°C) during 2011–2012, whereas maximum temperature ranged from 21.8 to 37.7°C (average 31.2°C) during 2010–2011 and 25.0 to 39.3°C (average 32.2°C) during 2011–2012 (Table 1). The cumulative rainfall during the 2010–2011 crop season was 23.9 mm, of which about 16 mm occurred during the vegetative growth stage in all the flowering groups; 0.4 and 0.6 mm at dough (hard) stage in early and late flowering groups, respectively; and 0.4, 0.2, and 7.5 mm at flowering, at dough (hard), and at maturity stages, respectively, in the extra late flowering group. In the 2011–2012 post-rainy season, total rainfall during the crop season was 30.5 mm, of which 23.6 mm occurred at vegetative stage across all five groups, whereas the extra late flowering group received additional 6.9 mm at the maturity stage. The average day length was 11.64 (range 11.08–12.75) h yr^{-1}.

Drought Stress Imposition

Crop plants are more sensitive to drought stress at flowering. To simulate drought-stressed condition and to stress the plants at flowering, irrigation was stopped at 25 DAP in extra early, 37 DAP in early, 47 DAP in medium, 57 DAP in late, and 66 DAP in extra late flowering groups. The optimally irrigated plots (control) received six irrigations in total, whereas the plots with limited irrigation (water-stressed conditions) received one irrigation in extra early, two in early, three in medium, four in late, and five in extra late flowering groups before the onset of drought-stress treatment.

Statistical Analysis

Data were analyzed using residual (or restricted) maximum likelihood (REML) (Patterson and Thompson, 1971) in

Table 1. Environmental conditions (temperature and rainfall) during evaluation of sorghum mini core collection evaluated in the 2010–2011 and 2011–2012 post-rainy seasons at Patancheru, India.

Season/crop growth stage	Temperature Minimum	Temperature Maximum	Rainfall (flowering group)
	°C	°C	mm
Post-rainy 2010–2011	04.5–24.2	21.8–37.7	23.9
Vegetative stage	13.5–16.2	27.9–28.6	16 (across all flowering groups)
Flowering stage	10.6–17.3	27.5–31.0	0.4 (extra late)
Dough stage	10.8–18.5	29.3–35.2	0.4 (early); 0.6 (late); 0.2 (extra late)
Maturity stage	15.5–21.5	31.2–36.1	7.5 (extra late)
Post-rainy 2011–2012	05.6–24.2	25.0–39.3	30.5
Vegetative stage	15.0–16.1	30.2–30.7	23.6 (across all flowering groups)
Flowering stage	10.6–15.2	29.2–30.3	
Dough stage	13.8–16.0	30.0–32.7	
Maturity stage	13.7–18.2	29.5–36.6	6.9 (extra late)

GenStat 14.1 software (VSN International, 2013). The replication-wise values of each accession for days to 50% flowering, grain yield, and DTI in each maturity group in each year were used for statistical analysis. Genotypes were considered random, since mini core accessions were selected randomly from core collection (Grenier et al., 2001), which represented the entire collection of sorghum conserved in the ICRISAT genebank (Upadhyaya et al., 2009). In combined analysis, genotypes were considered random and drought and season as fixed. Variance components attributable to genotypes (σ^2_g), replication (σ^2_r), genotype × environment (σ^2_{ge}), genotype × drought (σ^2_{gd}), genotype × drought × environment (σ^2_{gde}), error (σ^2_e), and their SE were determined. Significance of variance components was tested against their respective SEs and that of environment, drought, and their interactions using Wald (1943) statistics. Best linear unbiased predictors (BLUPs) for the genotypes were calculated. Means were compared using the Newman–Keuls procedure (Newman, 1939; Keuls, 1952). Regression coefficient analysis was performed for each flowering group in both seasons to study the effect of (i) flowering time on grain yield under drought condition and (ii) grain yield under irrigated condition (grain yield potential) with the grain yield under drought condition.

Previous work has shown that the residual after removing the effects of drought escape (early flowering) and yield potential (optimally irrigated yield) of a genotype gave a good indication of the true drought tolerance of the genotype (Bidinger et al., 1987; Saxena, 1987, 2003; Vadez et al., 2007; Krishnamurthy et al., 2010). The mean grain yield of accessions under drought stress had shown significant dependency on the time to flowering (even within each flowering group) and yield potential (grain yield under irrigated conditions). Therefore, DTI were calculated using the BLUPs derived from REML analysis of individual year × soil water treatment × flowering group interaction. The residuals were calculated using the multiple regression approach (Bidinger et al., 1987). Briefly, this approach considers grain yield under drought stress condition (Y_s) as a function of yield potential (Y_p), days to 50% flowering (F), and DTI, such that the yield of a genotype can be expressed as follows:

$$Y_{si} = a + bY_p + cF_i + \mathrm{DTI}_i + E$$

where E is random error with zero mean and unit variance, a is the intercept, b is the slope value of yield potential, and c is the slope value of days to 50% flowering. Standard residual, which is the DTI, was calculated as the difference between the actual and estimated yields under stress divided by the standard error of the estimated yield (σ). For this multiple regression, days to 50% flowering (F_i) under drought stress and grain yield potential (Y_p), defined as the average grain yield under irrigated conditions, for an individual accession were considered.

RESULTS AND DISCUSSION

Variance Components, Mean and Range

The REML analysis of individual season data revealed significant genotypic variance (σ^2_g) for days to 50% flowering and grain yield under irrigated and drought-stressed conditions, and for DTI in the extra early, early, medium and late flowering groups (Table 2). In extra late group, σ^2_g for days to 50% flowering was significant under irrigated and drought-stressed conditions in both years. For grain yield, σ^2_g in the 2010–2011 season was significant under irrigated and drought-stressed conditions, whereas in the 2011–2012 season, σ^2_g was significant only under the drought-stressed condition. The REML analysis of combined data indicated significant σ^2_g for days to 50% flowering and grain yield in all the five flowering groups. These results indicated the presence of adequate diversity for days to 50% flowering and grain yield in the sorghum mini core collection. The significant interaction between genotype and season (σ^2_{ge}) was observed for days to 50% flowering in all five flowering groups and for DTI in all flowering groups, except in extra late flowering group (data not shown), indicating the differential influence of environment on genotypic expression with respect to days to 50% flowering. Wald statistics revealed significant effects of drought on days to 50% flowering and grain yield in extra early to medium flowering groups and grain yield in late flowering group, of environment on days to 50% flowering and grain yield in all flowering groups, and of drought × environment interaction on days to 50% flowering in early and late flowering groups and grain yield in extra early to late flowering groups (data not shown). As the drought × environment interaction effects for flowering and grain yield were significant and the DTI was the

Table 2. Estimates of genotypic variance (σ^2_g), mean, and range for days to 50% flowering, grain yield, and drought tolerance index (DTI) in the mini core collection of sorghum germplasm evaluated during the 2010–2011 and 2011–2012 post-rainy seasons grown under drought stressed and optimally irrigated conditions at Patancheru, India.

	2010–2011					2011–2012				
		Days to 50% flowering		Grain yield			Days to 50% flowering		Grain yield	
Flowering group	DTI	Drought	Irrigated	Drought	Irrigated	DTI	Drought	Irrigated	Drought	Irrigated
		——— d ———		—— g plant^{-1} ——			——— d ———		—— g plant^{-1} ——	
Extra early flowering group (<60 d to 50% flowering, 36 entries including controls)										
Trial mean	0	61.8a†	62.3a	15.7a	17.4a	0	63.5a	64.6a	18.4b	26.4a
Range of predicted means	–1.3–1.1	47.5–82.8	48.2–80.8	4.2–32.1	5.2–32.9	–1.26–1.31	49.1–86.5	51.2–78.2	9.1–32.4	13.6–74.5
SEd	0.19	1.07	1.10	2.89	2.14	0.14	1.08	1.18	2.03	3.23
σ^2_g	0.45**	54.3**	53.4**	38.6**	53.0**	0.6 **	76.7**	53.7**	37.9**	150.8**
Early flowering group (>61–70 d to 50% flowering, 85 entries including controls)										
Trial mean	0	66.0a	66.3a	20.3a	20.7a	0	70.9a	68.9a	18.4b	25.8a
Range of predicted means	–1.5–3.3	51.1–82.8	47.4–83.9	7.7–41.5	8.6–40.9	–1.5–1.8	57.6–91.6	55.3–83.6	8.3–34.8	11.7–55.4
SEd of treatment means	0.1	1.17	0.98	2.84	2.31	0.09	1.24	1.32	3.77	2.97
σ^2_g	0.6**	22.8**	20.7**	51.9**	51.8**	0.7**	45.4**	37.1**	92.2*	85.9*
Medium flowering group (>71–80 d to 50% flowering, 91 entries including controls)										
Trial mean	0	73.8a	72.2b	21.4b	23.4a	0	78.9a	78.1a	20.9b	28.1a
Range of predicted means	–1.9–2.3	65.0–82.3	64.5–83.1	2.21–40.3	2.22–38.0	–2.4–1.6	66.3–105.1	65.6–115.6	5.9–38.2	7.2–51.2
SEd	0.09	1.21	1.04	3.16	2.71	0.09	1.69	1.91	3.97	6.87
σ^2_g	0.6**	19.9**	21.9**	53.7**	60.9**	0.6**	45.9**	48.6**	58.6**	98.7**
Late flowering group (>81–90 d to 50% flowering, 34 entries including controls)										
Trial mean	0	81.9a	81.5a	19.5a	21.0a	0	87.5a	88.6a	21.4b	26.7a
Range of predicted means	–1.5–1.5	69.3–93.4	68.6–94.1	4.9–36.4	6.2–38.5	–1.6–2.2	72.2–110.4	71.2–109.1	3.1–48.7	8.1–57.9
SEd	0.19	1.05	1.03	3.03	2.62	0.12	1.61	1.35	3.62	5.13
σ^2_g	0.5**	27.4**	25.8**	63.5**	61.8**	0.8**	82.2**	77.5**	88.6**	131.4**
Extra late flowering group (>91 d to 50% flowering, 11 entries including controls)										
Trial mean	0	84.9a	86.4a	16.3a	19.6a	0	93.9a	95.9a	24.9a	28.5a
Range of predicted means	–0.7–0.5	68.1–105.8	68.1–108.6	5.7–34.5	4.2–38.1	–0.9–1.1	71.5–111.9	69.7–131.6	11.2–45.5	11.1–44.2
SEd	0.38	1.58	0.86	3	2.7	0.3	4.46	1.31	4.59	7.39
σ^2_g	0.3	100.5*	109.47*	92.2*	85.9*	0.6	188.7*	280.3*	140.1*	106

* Significant at the 0.05 probability level; ** significant at the 0.01 probability level.

† Means were tested by Newman–Keuls test (Newman, 1939; Keuls, 1952); means followed by different letters differ significantly at *P* = 0.05.

residual yield after removal of the influences of flowering time and yield potential, we considered results of both years separately for assessing variation for days to 50% flowering and grain yield under drought and irrigated conditions, and for identification of drought-tolerant accessions.

Mean days to 50% flowering in both the years was not significantly different between irrigated and drought-stressed conditions in all flowering groups, except in medium flowering group in the 2010–2011 season (Table 2). These results showed that accessions in each flowering group were under optimum growing conditions (i.e., with adequate soil moisture) until days to 50% flowering across flowering groups. In the 2010–2011 season, days to 50% flowering was significantly delayed by about 2 d and grain yield was reduced by 8.5% under drought-stressed conditions in the medium flowering group. Grain yield was reduced up to 17% in the 2010–2011 season and up to 30% in the 2011–2012 season, indicating that drought stress had significant effect on grain yield. The narrow range of variation for days to 50% flowering was noted in all five groups between irrigated and drought-stressed conditions in both the years (Table 2). The variation range for grain yield under irrigated and drought-stressed conditions was similar in extra early, early, and extra late flowering groups (five- to nine-fold of the least-yielding accession), whereas a large range of variation was noted in the medium flowering group (17–18-fold) during the 2010–2011 season and in the late flowering group (7–16-fold) during the 2011–2012 season.

Relationship of Flowering Time and Potential Yield with Drought Yield

Flowering time is an important consideration in sorghum breeding, as it affects adaptation and yield potential and the adaptation to a broad range of growing conditions, mainly in response to the photoperiod (Chantereau et al., 2001). Therefore, drought stress was applied to every accession close to their flowering time, but as the accessions varied widely in phenology, all the accessions were grouped into five groups, with a maximum of 10-d interval in flowering time. In spite of grouping the germplasm based on prior knowledge of flowering, the accessions within each group still showed some deviation in flowering time (Table 2). Flowering time as a mean of drought escape and yield potential together has been known to contribute to yield variation under drought, and elimination of these effects was suggested while estimating any drought response indices and to arrive at the intrinsic drought tolerance (Bidinger et al., 1987). To test the operation of any such contribution, the flowering time under drought-stressed conditions and the yield potential (grain yield under irrigated conditions) were regressed separately against grain yield under drought-stressed conditions. There were significant associations of these two characteristics with grain yield under drought stress. Under drought stress, grain yield increased with increasing flowering duration, largely in extra early and, to some extent, in early flowering groups. In later groups, it started to decrease with increasing flowering time (Fig. 1). Therefore, it is desirable to have a duration of about 50 to 70 d to 50% flowering so that genotypes can escape or manage to produce higher grain yield than that of accessions that take >70 d to 50% flowering under post-flowering drought stress. Similar trends on flowering time and grain yield were also observed under irrigated conditions. Positive associations between grain yield under drought and irrigated conditions were noticed in all flowering groups (Fig. 2), indicating that high grain-yielding accessions tended to produce high yields under drought condition but with reduced yield relative to irrigated condition (up to 30% grain yield reduction in the 2011–2012 season and up to 17% during the 2010–2011 season; drought stress in the 2011–2012 season was more severe than in 2010–2011). Therefore, it was necessary to adopt the regression approach for removing the effects of flowering time and grain yield potential and consider the standard residuals as the measure of drought-response.

Variability for Drought Tolerance Index, Grain Yield, and Flowering Time

Large variations in days to 50% flowering, grain yield, and DTI were detected in all groups, thereby providing an opportunity for selection of sources for drought tolerance. The DTI was used as a measure of drought response, with positive and negative values of DTI indicating drought tolerance and susceptibility, respectively. Because of highly significant σ^2_{ge} for DTI, BLUPs based on combined analysis tend to give misleading values, particularly for those accessions that had mostly negative DTI in one season but positive DTI in another season. This was mainly attributable to difference in drought intensity between years. Drought intensity during 2011–2012 was more severe than in the 2010–2011 post-rainy season. Therefore, we considered BLUP of accessions for both years separately to identify stable drought-tolerant accessions.

As the accessional range of DTI variation was large, twice the LSD of DTI was used to segregate and group drought response of accessions in each of the flowering groups. In the 2010–2011 season, 38 accessions (three in extra early, 13 in early, 20 in medium, and two in late flowering groups) were found to be tolerant to drought, whereas in the 2011–2012 season, 62 accessions (five in extra early, 24 in early, 23 in medium, and 10 in late flowering groups) were tolerant to drought. The drought-susceptible accessions were 45 (two in extra early, 16 in early, 25 in medium, and two in late flowering groups) in the 2010–2011, and 72 accessions (nine in extra early, 29 in early, 24 in medium, and 10 in late flowering groups) in the 2011–2012 season (data not shown). Among these drought-tolerant and susceptible accessions, those with significantly positive or negative DTI close to 1 (or >1) in both the seasons were regarded as stable tolerant or susceptible ones. Drought-tolerant accessions with DTI value greater than +1 numbered 16 in the 2010–2011 and 22 in the 2011–2012, whereas those having DTI lower than −1 (termed as susceptible) numbered 15 and 24 in the 2010–2011 and 2011–2012 seasons, respectively (data not shown). Of these, 'IS 14779' in the extra early flowering group, 'IS 23891' and 'IS 31714' in the early flowering group, and 'IS 4515', 'IS 5094', 'IS 9108', and 'IS 15466' in the medium flowering group were found to be stable for drought tolerance in both of the seasons, whereas stable drought-susceptible accessions were 'IS 1004', 'IS 26046', and 'IS 30536' in the early flowering group and 'IS 26617' and 'IS 29239' in the medium flowering group (Table 3). In the 2010–2011 season, DTI of the stable drought-tolerant accessions ranged from +0.926 to +1.417, whereas in the 2011–2012 season, it varied from +0.981 to +1.820. Likewise, in the susceptible group, DTI ranged from −1.670 to −1.030 in the 2010–2011 season and from −1.381 to −0.921 in the 2011–2012 season (Table 3). No stable drought-tolerant or susceptible accessions were identified in late and extra late flowering groups, as the tested number of accessions was quite small, with a limited range of performance.

Stable drought-tolerant accessions were compared with the control IS 33844, which was the most consistent for high grain yield (irrigated conditions, 27–51 g plant^{-1}; drought-stressed conditions, 22–33 g plant^{-1}). However, it showed variable DTI response in different flowering groups (Table 3). Such variability is acceptable, since the DTI of an individual accession depends on its performance relative to its comparators within the group and thus is used in a particular test, and DTI values are valid only within the group of accessions. If a large number of tested genotypes are highly drought tolerant, then the DTI of IS 33844 would register a more negative value and vice versa. However, the accession that has greater DTI over the control has a good value for utilization.

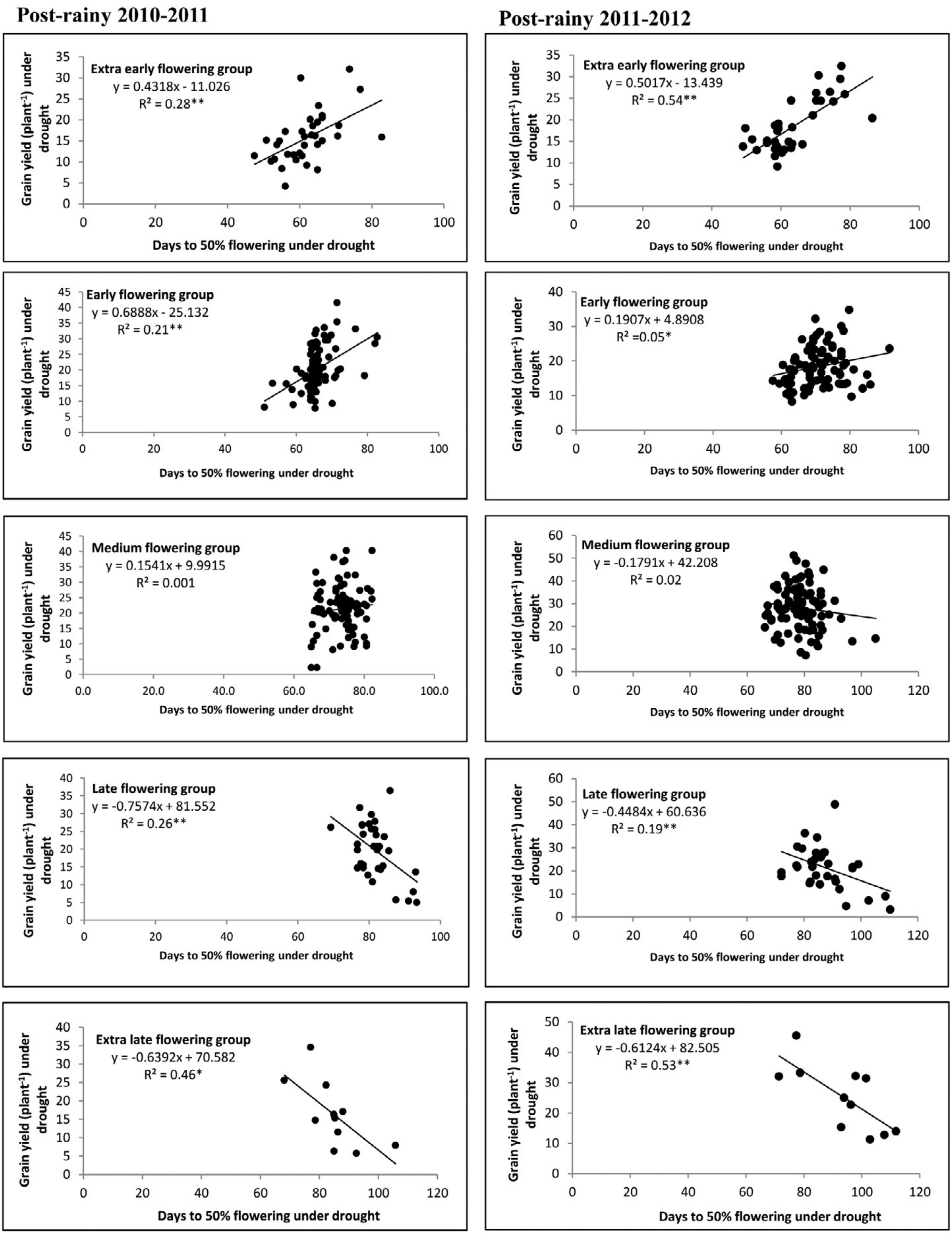

Fig. 1. Relationship of grain yield with days to 50% flowering under drought in the five flowering groups of sorghum mini core accessions grown under drought-stressed and optimally irrigated conditions during the 2010–2011 and 2011–2012 post-rainy seasons, Patancheru, India.

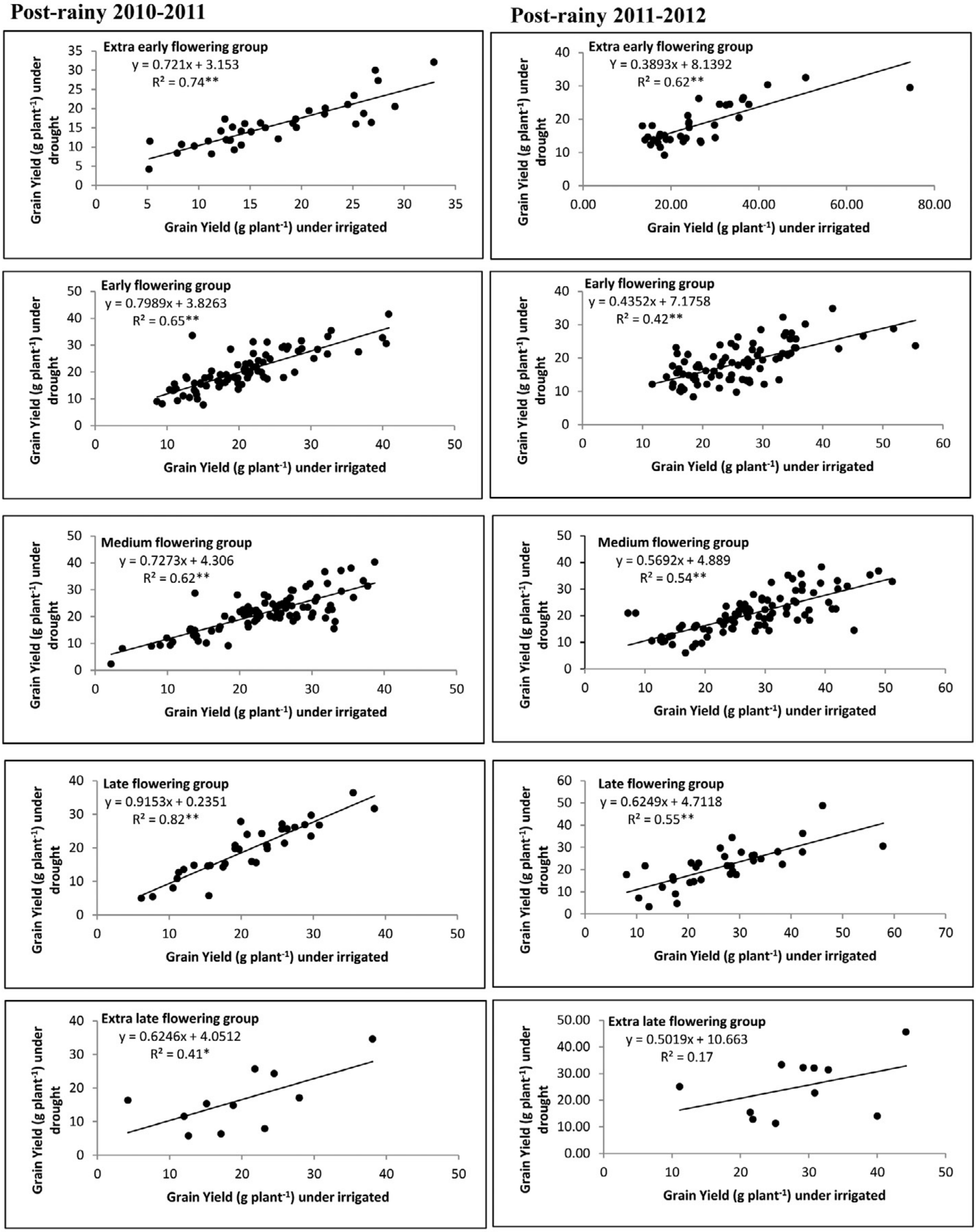

Fig. 2. Relationship of grain yield potential (grain yield under irrigation) with grain yield under drought in the five flowering groups of sorghum mini core accessions grown under both drought-stressed and optimally irrigated conditions, 2010–2011 and 2011–2012 post-rainy season, Patancheru, India.

Table 3. Selected drought tolerant and sensitive accessions of sorghum based on drought tolerance index (DTI) estimated from sorghum mini core collection evaluated under drought stress and optimally irrigated conditions during 2010-2011 and 2011-2012 post-rainy seasons at Patancheru, India.

			2010–2011					2011–2012				
				Days to 50% flowering		Grain yield			Days to 50% flowering		Grain yield	
Accession	Race	Origin	DTI	Drought	Irrigated	Drought	Irrigated	DTI	Drought	Irrigated	Drought	Irrigated
				d		g plant^{-1}			d		g plant^{-1}	
Extra early flowering group												
Tolerant												
IS 14779	*Caudatum*	Cameroon	1.019	60.7	61.3	17.2	12.6	0.981	63.0	65.3	24.4	31.1
Control												
IS 18758	*Guinea-caudatum*	Ethiopia	–0.545	70.9	69.6	18.6	26.1	1.235	70.9	72.2	30.3	42.1
IS 2205	*Durra-bicolor*	India	–0.644	82.8	80.8	15.9	25.3	0.349	78.6	78.2	25.9	36.4
IS 33844	*Durra*	India	1.044	76.8	77.2	27.3	27.5	0.922	77.6	78.2	32.5	50.7
Trial Mean			0	61.83	62.34	15.56	17.37	0	63.53	64.60	18.43	26.43
LSD			0.372	2.14	2.20	5.78	4.28	0.290	2.16	2.36	4.06	6.46
Early flowering group												
Tolerant												
IS 23891	*Durra*	Yemen	0.926	71.5	69.6	41.5	40.9	1.785	79.8	80.7	34.8	41.7
IS 31714	*Durra-caudatum*	Yemen	1.417	67.9	65.7	31.0	24.0	1.820	70.0	63.8	32.2	33.4
Sensitive												
IS 1004	*Durra*	India	–1.538	82.8	83.9	30.5	40.5	–1.270	91.6	83.0	23.6	55.5
IS 26046	*Guinea*	Mali	–1.330	79.3	68.9	18.1	23.4	–1.381	80.5	82.3	9.7	25.6
IS 30536	*Caudatum-bicolor*	Republic of Korea	–1.030	64.1	64.7	13.4	19.9	–1.264	63.5	65.4	10.9	22.8
Control												
IS 18758	*Guinea-caudatum*	Ethiopia	0.782	68.9	68.6	29.5	26.3	0.380	71.7	68.3	22.3	29.6
IS 2205	*Durra-bicolor*	India	1.078	82.2	82.0	28.4	18.9	–0.036	78.9	77.1	19.4	30.0
IS 33844	*Durra*	India	0.324	76.7	76.1	33.1	32.4	1.267	77.6	77.8	30.1	37.1
Trial Mean			0	66.04	66.32	20.33	20.64	0	70.89	68.92	18.36	25.80
LSD			0.189	2.34	1.96	5.68	4.62	0.170	2.48	2.64	7.54	5.94
Medium flowering group												
Tolerant												
IS 4515	*Durra*	India	1.326	74.6	73.6	37.0	34.1	1.437	74.8	75.7	32.3	31.1
IS 5094	*Durra*	India	1.015	78.8	77.5	27.3	23.9	1.491	76.4	74.7	35.5	36.0
IS 9108	*Caudatum*	Kenya	1.124	72.1	68.1	28.0	23.4	1.571	73.4	73.1	35.1	33.8
IS 15466	*Caudatum*	Cameroon	1.308	75.0	79.8	40.3	38.7	1.481	82.3	82.6	33.8	34.6
Sensitive												
IS 26617	*Caudatum-bicolor*	Madagascar	–1.364	77.2	82.4	9.1	18.4	–0.921	82.0	85.2	8.1	18.0
IS 29239	*Kafir*	Swaziland	–1.670	80.7	76.9	18.0	33.2	–1.171	66.3	65.6	9.6	19.5
Control												
IS 18758	*Guinea-caudatum*	Ethiopia	0.845	68.2	67.8	29.8	27.2	0.093	73.4	69.2	21.7	27.5
IS 2205	*Durra-bicolor*	India	0.544	82.3	82.1	24.5	24.6	0.628	77.4	78.7	25.8	29.5
IS 33844	*Durra*	India	–0.860	78.5	76.6	22.5	32.8	–0.403	76.4	77.3	32.7	51.2
Trial Mean			0	73.76	72.17	21.00	23.40	0	78.87	78.41	20.46	27.99
LSD			0.183	2.42	2.08	6.32	5.42	0.183	3.38	3.82	7.94	13.74

Large variations in grain yield under drought-stressed conditions were observed among select drought-tolerant and drought-susceptible accessions (Table 3). Accession IS 14779 under drought stress in extra early flowering yielded 63 to 75% of the grain yield of IS 33844, whereas in early flowering group, IS 23891 and IS 31714 yielded 116 to 125% and 94 to 107% of IS 33844, respectively. In the 2010–2011 season, IS 4515, IS 5094, IS 9108, and IS 15466 in the medium flowering group under drought stress produced 121 to 179% of the grain yield of IS 33844, whereas these accessions under similar conditions during the 2011–2012 season showed up to 108% of the yield of IS 33844. The greater grain yield advantage of IS 23891 in the early flowering group and of IS 4515, IS 5094, IS 9108, and IS 15466 in the medium flowering group in the 2010–2011 season, as compared with IS 33844, was likely because the crop was affected less as the drought stress was low to moderate in magnitude. However, these accessions in the 2011–2012 season produced grain yield of 99 to 116% of IS 33844. IS 1004 among the drought-susceptible accessions yielded 78 to 92% of IS 33844 under drought-stressed conditions in both seasons, whereas other accessions, in relation to IS 33844, could produce 40 to 80% in the 2010–2011 and 25 to 36% in the 2011–2012 seasons. All of these changes in yield variation can be seen as the end result of several functional processes of the accessions properly matching their reproductive duration with soil water availability, leading to better seed set and grain fill.

Response of Races and Intermediate Races for Drought Stress

Sorghum's diversity is reported to be structured according to geographic regions and races within the region (Morris et al., 2013; Wang et al., 2013). The current study also confirmed that response to drought, to a large extent, can depend on races and intermediate races or geographical regions of origin. The seven identified stable drought-tolerant accessions are either of *durra* (IS 23891, IS 4515, and IS 5094), *caudatum* (IS 14779, IS 9108, and IS 15466), or an intermediate race between these two, *durra-caudatum* (IS 31714). Of the seven, two each were from India (IS 4515 and IS 5094), Yemen (IS 23891 and IS 31714), and Cameroon (IS 14779 and IS 15466) and one was from Kenya (IS 9108). The races *durra* and *caudatum* had been found to possess high transpiration efficiency and, therefore, high drought tolerance (Vadez et al., 2011). In addition, the environmental conditions in which these landraces have evolved could have been the key for their superiority. Frequency of occurrence of drought tolerance in accessions was the highest in *durra* and *caudatum* races, whereas drought sensitivity was highest in *caudatum-bicolor*, *guinea*, and *guinea-caudatum* races (data not shown). Among the five stable sensitive accessions selected, two were from *caudatum-bicolor*, and one each was from *guinea*, *kafir*, and *durra*. Therefore, future evaluations of sorghum germplasm aiming to identify superior drought-tolerant accessions need to concentrate on *durra* and *caudatum* races first for quicker and greater success rates.

Drought-Tolerant Sources for Sorghum Improvement

Drought tolerance is a complex mechanism involving different pathways, and drought-tolerant genotypes use various strategies to cope with drought stress (Blum, 2011; Fracasso et al., 2016). The strategies and mechanisms can vary depending on the genotype; therefore, further studies on the genetic and physiological mechanisms involved in a selected set of accessions can provide the pool of strategies that can be pyramided for developing the best drought-adapted cultivars or breeding lines. The tolerant accessions identified in this study mostly yielded at par with, or greater than, the control cultivar IS 33844, a released high-yielding sorghum cultivar mostly grown under receding soil moisture conditions during post-rainy seasons in India. A few drought-tolerant accessions reported here were also found to be resistant to certain pests and diseases; for example, IS 4515 and IS 5094 were tolerant to shoot fly and stem borer (http://www.icrisat.org/what-we-do/crops/sorghum/Project1/pfirst.asp); IS 5094 and IS 31714 were resistant to downy mildew [*Peronosclerospora sorghi* (W. Weston & Uppal) C.G. Shaw] (Radwan et al., 2011; Sharma et al., 2010); and IS 30536 to grain mold (Sharma et al., 2010) and IS 9108 to leaf blight [*Setosphaeria turcica* (Pass.) K.J. Leonard & Suggs)] (Sharma et al., 2012). Germplasm collections at ICRISAT are available under the terms and conditions of the Standard Materials Transfer Agreement of the International Treaty on Plant Genetic Resources for Food and Agriculture (http://10.3.1.36:8080/what-we-do/crops/SMTA.pdf).

CONCLUSION

Sorghum mini core collection showed a significantly large variation in response to drought stress with a maximum grain yield reduction of up to 30%. This study has demonstrated that estimation of DTI is essential as a selection measure, as the time to flowering and the yield potential can heavily influence grain yield under drought. There were large variations in DTI of the sorghum mini core collection accessions. Accessions IS 4515, IS 5094, IS 9108, IS 14779, IS 15466, IS 23891, and IS 31714 were identified as highly stable in drought tolerance. These drought-tolerant sources are also expected to have much wider adaptability because they were selected based on a DTI, which is free from the effects of yield potential and flowering time, and can be employed to investigate the physiological and molecular basis of drought adaptation and in breeding for drought tolerance in sorghum. The races d*urra* and *caudatum* yielded a high frequency of drought-tolerant accessions, and future drought tolerance screening programs need to concentrate more on these two races. The tolerant accessions identified were diverse in origin and variable in grain yield under drought stress, yielding at par with or greater than IS 33844, the high-yielding and post-rainy season adapted sorghum cultivar in India.

Conflict of Interest

The authors declare there to be no conflict of interest.

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