

Genetics of post-flowering drought tolerance traits in post-rainy sorghum [*Sorghum bicolor* (L.) Moench]

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Abstract

Post-rainy sorghum (*Sorghum bicolor* L. Moench) is mostly cultivated under receding soil moisture leading to post-flowering moisture stress. Gene effects governing six moisture stress tolerance attributing traits were studied in nine generations of a cross between drought susceptible parent, SPV 1587 and drought tolerant parent, Phule Maulee under natural receding soil moisture regime during winter season of 2006-07 under randomized block design with three replications. Phule Maulee recorded higher relative leaf water content, chlorophyll stability index and grain yield per plant. Stomata frequencies were less on both surfaces in the drought tolerant parent. Heterosis and preponderance of duplicate epistasis (particularly dominance \times dominance) were recorded for all the traits. This suggested the potential for hybrid breeding for drought tolerance in sorghum. Transgressive segregants were recorded for all the traits. Presence of significant dominance \times dominance epistatic interactions suggests that selection for drought tolerance should be avoided in early generations and practiced in the advanced generations.

Key words : Genetics, gene effects, drought tolerance, epistasis, sorghum

Introduction

Sorghum (*Sorghum bicolor* L. Moench) is the fifth most important grain crop in the world after wheat, maize, rice and barley. It is predominantly cultivated in semi-arid tropics (SAT) and its grain is main food source in many developing countries. Besides food, it is also used for animal feed, fuel, syrup, alcoholic beverages and ethanol. Sorghum is grown both during the rainy as well as post-rainy seasons in India, mostly as rain

fed crop. In India, this crop is cultivated in 8.33 m ha, of which 3.66 m ha is cultivated during rainy season and remaining during post-rainy season with a total annual production of 7.39 m t. Though the productivity of post-rainy sorghum (784 kg/ha) is lower than the rainy season sorghum (10.23 kg/ha), the produce is predominantly consumed as food, while the rainy season sorghum grain is utilized mainly for non-food purposes.

Among various abiotic stresses affecting field crops, moisture stress assumes great importance across the world, which has become more relevant particularly under changing climatic scenario [1]. As sorghum is predominantly cultivated as rain fed crop, it suffers from moisture stress. Particularly, the post-rainy sorghum is grown under receding moisture condition leading to post-flowering drought in major parts of India. Though generally sorghum is a drought tolerant crop as compared to other field crops, drought stress at pre- or post-flowering stage significantly decreases grain yield [2]. For pre-flowering drought tolerance leaf photosynthetic rates, greater canopy temperature depression, improved panicle exertion and increased pollen viability play an important role [3]. Rooting depth, stay-greenness, increased seed filling rate, longer seed filling duration among others contribute towards post-flowering drought tolerance [4].

Genetic enhancement for drought tolerance has a special significance particularly for post-rainy sorghum improvement. Genetic diversity among the germplasm plays a very important role in any breeding program. Genetic diversity in sorghum has been

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evaluated using both morphological and molecular markers or in combination [5]. However, studies on diversity for physiological traits related to biotic stresses are scanty. In recent past Mutava *et al.* [2] made a comprehensive study on the diversity in grain sorghum for physiological traits with reference to moisture stress. They have reported wide variability for physiological and yield traits, like chlorophyll content, leaf temperature, grain numbers and grain weight per panicle etc., which were more stable among caudatum accessions under stress conditions as compared to other races. Knowledge on the genetics of drought tolerance traits is of paramount importance in designing the breeding methods with enhanced selection effectiveness.

Generation mean analysis (GMA) has been employed by several researchers to study genetic effects affecting various trait expressions in many crops including sorghum [6-9]. It is relatively simple and reliable tool, in which first order statistics are used for estimating the genetic effects. Gene actions involved in inheritance of yield and other traits have been studied in sorghum using GMA, which identified complex inheritance of the traits involving higher order gene interactions [10, 11]. Though post-flowering drought is one of the major production constraint across SAT, genetics of traits attributing to drought tolerance is lacking in sorghum. The present work was carried out with an objective to study the genetics of various traits attributing to drought tolerance in sorghum under rain fed conditions using GMA.

Materials and methods

Experimental material

In the current investigation, a drought susceptible line, SPV 1587, and a drought tolerant variety, Phule Maulee were used. SPV 1587 is a derivative from a cross between RSLG 117 and IS 2312, while Phule Maulee is a selection from local land race of Maharashtra, India. In subsequent text SPV 1587 and Phule Maulee will be referred to as P_1 and P_2 , respectively. The parents were crossed during the post-rainy season, 2004-05 to obtain F_1 . The F_1 were selfed as well as backcrossed to P_1 and P_2 during post rainy season, 2005-2006 to obtain F_2 and backcrosses (B_1 and B_2), respectively. During 2006 rainy season the B_1 , B_2 and F_2 were selfed to generate B_1F_2 , B_2F_2 and F_3 progenies. All the populations were evaluated together during post-rainy season, 2006-07 in randomized block design with three replications. Non-segregating

generations, viz., P_1 , P_2 and F_1 were grown in single row of 4.5 m length in each replication, whereas segregating generations, viz., F_2 , B_1 , B_2 , F_3 , B_1F_2 and B_2F_2 were grown in six rows with row length of 4.5 m accommodating about 30 plants per row. Recommended crop management practices were followed for good plant stand evaluation for post flowering drought tolerance were carried out under rainfed conditions in the experimental field of Mahatma Phule Krishi Vidyapeeth at Rahuri, India.

Observations recorded

To study the moisture regime of the experimental plots, soil moisture levels at every plot representing different generations across all the three replications were recorded at 15 and 30 cm depth at 30 days interval starting from sowing to harvesting. Gravimetric method was carried out to determine soil moisture content. Observations on important drought tolerant traits such as relative leaf water content (RLWC), chlorophyll stability index (CSI), stomatal frequencies at adaxial and abaxial surface (no./mm²), panicle length (cm) and grain yield per plant (g) were recorded. RLWC was determined according to the modified method of Barrs and Weatherly [12] at 50% flowering stage and was expressed in percent. The CSI was computed using the methodology proposed by Arnon [13] at soft dough stage. Observations were recorded on ten competitive randomly selected plants from each replication totaling to 30 plants in non-segregating generations (P_1 , P_2 and F_1) and 25 plants per replication adding up to 75 plants in segregating generations (F_2 , F_3 , B_1 , B_2 , B_1F_2 , and B_2F_2).

Statistical analysis

To test the significance of treatment differences among the parents and their generations the data for all the characters were analyzed using randomized block design. The mean values for each generation were computed for all the traits. Adequacy of additive dominance model was tested by scaling tests of Mather [14] and joint scaling test of Cavalli [15]. Parameters of generation means (m : mean, d : additive, h : dominance, i : additive x additive, j : additive x dominance, l : dominance x dominance) were calculated as described elsewhere [16].

Results and discussion

In the present investigation, nine sorghum populations were evaluated under receding soil moisture during post-rainy season to estimate the genetics of six

drought tolerance attributing traits using GMA. The mean gravimetric soil moisture content at 15 and 30 cm depth at 30 days interval from sowing date till harvest over all generations are presented in Table 1. Significant differences in terms of soil moisture content at both the depths were recorded at all the growth stages. Adequate soil moisture (~25%) was available at the time of sowing leading to satisfactory germination and initial growth. The difference in soil moisture at the time of sowing till 30 days after sowing (DAS) was very less due to rainfall at regular intervals during the period. The mean soil moisture contents at the time of sowing (27.88% at 15 cm and 24.35% at 30 cm), 30 DAS (23.54% at 15 cm and 21.41% at 30 cm) and 60 DAS (18.53% at 15 cm and 15.81% at 30 cm) were sufficient to support optimum crop growth. However, the depleted moisture levels (8.03% and 9.02 % at harvesting at 15 and 30 cm depth, respectively) indicated that crop experienced severe moisture stress. In crops like sorghum and maize roots are mostly concentrated in the upper layer of soil (0-30 cm) [17] and moisture content at this region was just near to the permanent wilting point at physiological maturity and at that stage crop experienced severe drought.

Analysis of variance indicated highly significant differences for all the six traits under study. The mean performances of nine populations, P₁, P₂, F₁, F₂, F₃, B₁, B₂, B₁F₂ and B₂F₂ for various traits are presented in Table 2. Results on scaling tests and joint scaling tests, and best fit model for various traits are presented in Tables 3 and 4, respectively. Accordingly, the

character-wise findings on various genetic components are discussed below:

Relative leaf water content (RLWC)

RLWC is one of the important physiological factors related to moisture stress [18]. The drought susceptible parent, P₁ had lower RLWC (73.66 ± 0.44) compared to the resistant parent (78.91 ± 0.52). Higher RLWC in resistant parent indicated its moisture stress tolerance. The F₁ showed significantly higher RLWC, indicating heterosis for the trait. All subsequent generations showed inbreeding depression for the trait with B₁ and B₂ mean being closer to their respective recurrent parent. Significance of A, B and C scaling tests and joint scaling test suggested presence of non-allelic interactions for RLWC inheritance. Predominance of additive [*d*] and dominance x dominance [*l*] type of gene actions were found governing RLWC, with [*l*] type contributing towards desirable direction.

Chlorophyll stability index (CSI)

Like RLWC, higher CSI also plays important role in drought tolerance [19]. CSI was higher in P₂ and the F₁ showed partial dominance for higher CSI content (Table 2). Stability of chlorophyll corresponds to better performance of the genotypes under stress conditions. Inbreeding depression was significant in all the subsequent generations. All the four scaling tests as well as joint scaling test were significant. This indicated that simple additive-dominance model was not effective for CSI content inheritance. Prevalence of

Table 1. Soil moisture content (%) at 15 and 30 cm depth at different growth stages in various generations

Soil depth (cm)	At sowing		30 DAS		60 DAS		At harvesting	
	15 cm	30 cm	15 cm	30 cm	15 cm	30 cm	15 cm	30 cm
P ₁	26.31	23.49	21.98	22.43	19.27	16.43	8.54	8.91
P ₂	26.30	23.67	22.25	21.17	17.75	16.07	8.69	9.83
F ₁	22.70	24.89	24.44	21.24	19.87	15.34	8.42	8.36
F ₂	29.27	25.75	26.44	22.62	20.27	16.71	7.66	10.69
B ₁	28.49	25.19	25.47	21.05	19.94	15.36	8.32	8.80
B ₂	25.59	21.74	22.13	19.47	18.25	13.76	8.41	7.93
F ₃	28.22	25.58	23.22	22.73	17.88	17.19	7.03	9.56
B ₁ F ₂	26.25	24.38	22.63	21.35	16.31	15.45	7.57	8.71
B ₂ F ₂	27.44	24.49	23.28	20.62	17.26	15.97	7.64	8.40
Mean	27.88	24.35	23.54	21.41	18.53	15.81	8.03	9.02
LSD at 5%	1.42	1.29	1.37	1.53	1.63	2.01	1.51	1.54

Table 2. Mean performances of different generations of SPV1587 x Phule Maulee cross for various traits associated with drought tolerance in sorghum

Generation	RLWC	CSI	Ad St freq	Ab St freq	PL (cm)	PGY (g)
P ₁	73.66 ± 0.44	0.312 ± 0.00	130.67 ± 1.13	148.90 ± 1.48	30.24 ± 0.24	66.51 ± 0.97
P ₂	78.91 ± 0.52	0.341 ± 0.00	120.13 ± 1.82	131.23 ± 1.70	29.54 ± 0.21	70.42 ± 0.96
F ₁	80.18 ± 0.55	0.332 ± 0.00	131.07 ± 1.32	144.50 ± 2.17	31.40 ± 0.26	75.39 ± 1.07
F ₂	76.99 ± 0.40 (-3.98)	0.329 ± 0.00 (-0.90)	132.47 ± 0.89 (1.07)	150.92 ± 1.30 (4.44)	30.52 ± 0.14 (-2.80)	70.94 ± 0.63 (-5.90)
B ₁	75.46 ± 0.28 (-5.89)	0.317 ± 0.00 (-4.52)	136.25 ± 1.81 (3.95)	154.03 ± 0.93 (6.60)	29.27 ± 0.15 (-6.78)	65.51 ± 0.78 (-13.11)
B ₂	77.05 ± 0.32 (-3.90)	0.311 ± 0.00 (-6.33)	130.97 ± 0.70 (-0.08)	151.03 ± 1.01 (4.52)	29.26 ± 0.16 (-6.82)	66.15 ± 0.60 (-12.26)
F ₃	74.86 ± 0.38 (-6.64)	0.29 ± 0.00 (-13.55)	133.11 ± 0.89 (1.56)	156.72 ± 0.97 (8.46)	29.07 ± 0.13 (-7.42)	60.94 ± 0.84 (-19.17)
B ₁ F ₂	73.47 ± 0.40 (-8.37)	0.309 ± 0.00 (-6.93)	132.48 ± 0.69 (1.08)	152.51 ± 1.16 (5.54)	27.61 ± 0.16 (-12.07)	58.96 ± 0.78 (-21.79)
B ₂ F ₂	69.51 ± 0.34 (-13.31)	0.298 ± 0.00 (-10.24)	136.07 ± 0.85 (3.81)	153.65 ± 0.91 (6.33)	27.14 ± 0.15 (-13.57)	56.33 ± 0.64 (-25.28)

RLWC: Relative leaf water content; CSI: Chlorophyll stability index; Ad St freq: Adaxial stomatal frequency; Ab St freq: Abaxial stomatal frequency; PL: Panicle length; PGY: Plant grain yield; Values in parenthesis indicate the inbreeding depression

dominance gene action and all the three epistatic interactions with additive x additive [*l*] and dominance x dominance [*l*] towards desirable direction was observed. As difference between the parents for the trait was less (0.031) none of the effects were very high. The [*h*] and [*l*] components possessed opposite sign, indicating presence of duplicate epistasis.

Stomata frequency

Stomata frequencies play a very vital role in leaf water potential balance of plant [20]. Stomata frequencies were lower in both adaxial and abaxial surfaces in drought tolerant parent (P₂). Lower stomata density in turn helps the genotypes to prevent water losses, thus contributing towards drought tolerance [20, 21]. Abaxial stomata frequency showed dominance for higher stomata number, while adaxial frequency expressed

co-dominance. Interestingly, in none of the advanced generations stomata number showed inbreeding depression. Significant scaling and joint scaling tests clearly indicated prevalence of non-additive interactions governing stomata number inheritance. Additive [*d*] and dominance [*h*] gene actions increased stomata number, while dominance x dominance [*l*] interaction contributed towards reducing the stomata number inheritance. For abaxial stomata number inheritance in addition to [*l*] type of interaction additive x additive [*l*] was also effective. The [*l*] type interaction effect acted in undesirable direction as it leads to increase in stomata number. For stomata count inheritance again duplicate epistatic interactions were recorded. [*l*] type gene interaction was towards desirable direction as it reduces the number.

Table 3. Estimation of scaling test for detecting non-allelic interactions for eight characters of sorghum

Scaling test	RLWC	CSI	Ad St freq	Ab St freq	PL (cm)	PGY (g)
A	-2.92**	-0.019**	10.77**	14.65**	-3.10**	-11.41**
B	-4.78**	-0.034**	10.74**	19.92**	-2.42**	-14.04**
C	-4.97*	0.015**	16.93**	21.54**	-2.49**	-7.22*
D	1.46	0.022**	-7.29**	-6.21*	2.51**	9.12**
χ^2 joint scaling	312.25**	201.31**	28.06**	12.37**	295.79**	301.53**

Table 4. Estimation of gene effects, estimates of predominant gene action and gene interaction effects for traits associated with drought tolerance in sorghum

Character	Genetic parameters					Gene action	Type of epistasis	Main favorable interaction effects
	<i>m</i>	<i>d</i>	<i>h</i>	<i>i</i>	<i>l</i>			
RLWC	76.98**	-1.59**	-	-	10.84**	Add	-	Dom x Dom
CSI	0.32**	-	-0.05**	-0.04**	0.02**	Dom	Duplicate	Add x Dom, Dom x Dom
Ad St freq	132.46**	5.27**	10.25**	-	-26.10**	Add, Dom	-	Dom x Dom
Ab St freq	152.92**	4.22**	10.36**	12.42*	-46.40**	Add, Dom	Duplicate	Dom x Dom
PL (cm)	30.52**	1.92**	-3.52**	-5.03**	10.55**	Add, Dom	Duplicate	Dom x Dom
PGY (g)	70.38**	-3.64**	-10.77**	-18.23**	43.69**	Add, Dom	Duplicate	Dom x Dom

*, **, Significant at 5 and 1 percent, respectively. Add = Additive, Dom = Dominance

Panicle length

Panicle length though is not directly associated with drought tolerance, its length may influence the grain yield. In our study the drought susceptible parent, SPV 1587 had marginally higher panicle length as compared to the tolerant parent, Phule Maulee. In fact, under well watered situation the susceptible parent had longer panicle than the resistant one (data not shown). The F_1 showed longer panicle length than either of the parents. Advanced generations recorded inbreeding depression ranging from -2.8% to -13.57%. Scaling test and joint scaling test results indicated presence of non-allelic interactions governing panicle length inheritance. Additive [*d*], dominance [*h*], additive x additive [*l*] and dominance x dominance [*l*] interactions were found to be significant for inheritance of panicle length inheritance. However, out of these [*d*] and [*l*] acted in favourable direction. [*d*] and [*h*] gene action was observed to act on opposite direction. Duplicate epistasis found to be effective to govern this trait inheritance as well.

Grain yield per plant

Whatever may be the anatomical and/or physiological differences between genotypes, drought tolerance is ultimately reflected in terms of grain yield under stress condition [22]. P_2 recorded higher plant yield as against P_1 , under moisture stress. Significant better parent heterosis was recorded in F_1 , while advanced generations recorded inbreeding depression ranging from -5.9% to -25.28%. Like other traits both scaling tests indicated existence of non-allelic interaction governing grain yield inheritance with both additive and dominance gene actions towards undesirable direction along with [*l*] type of interaction. [*l*] and [*l*] type of interactions influenced plant grain yield inheritance in favourable direction. Duplicate type of epistatic interactions governed the trait inheritance.

Heterosis over better parent was recorded for majority of the traits except CSI and abaxial stomatal count (Table 2). Thus, the hybrid performed better under drought situation. Inbreeding depression was high for all the traits except for stomata frequencies on both surfaces. This may be attributed to the fact that additive [*d*], dominance [*h*] and additive x additive [*l*] interactions for stomata number inheritance act on opposite direction to that of dominance x dominance interactions [*l*] and upon inbreeding they may cancel effects of each other leading to no inbreeding depression.

To the best of our knowledge, there are no studies on inheritance of drought tolerance traits in sorghum using generation means. We have observed that epistatic interactions, predominantly duplicate epistasis, were effective for all the traits. Existence of duplicate epistatic effects governing water stress tolerance related traits has been reported in wheat [23]. Dominance x dominance [*l*] interactions were the most common and favoured interaction for all the traits. Ahmadi *et al.* [24] suggested importance of [*l*] type of interaction over other epistatic effects in governing drought related traits in wheat. However, Rao and Singh [25] observed combination of duplicate and complementary epistatic interaction governing drought related traits in maize. Kumar and Sharma [26] reported predominance of additive gene effects for RLWC inheritance in wheat

under water stress. However, they found that both additive-dominance model and digenic epistatic model were predominantly ineffective to explain the variation for most of the traits related to drought tolerance. Most of the reports suggested preponderance of epistatic interactions governing drought tolerance. However, additive-dominance gene action governing drought tolerance in wheat has been reported by Golabadi *et al.* [27].

Generation mean analysis assumes unidirectional distribution of genes between two parents [28]. However, detection of epistatic interactions contradicts this assumption. We have observed overlapping distribution in backcross generations, which is indicative of existence of epistatic interaction [7]. Such interactions make the partitioning of genetic variance in the segregating generations into additive or dominance components extremely biased. As we have observed mostly [I] type interactions towards favourable direction, conclusion derived from the study will not be biased. Preponderance of epistatic interactions (particularly dominance x dominance interactions) for all the drought tolerance related traits suggests the potential for hybrid breeding for drought tolerance in sorghum. However, till now hybrids have not been able to make much dent during post-rainy sorghum. This is mainly due to consumer preferences for grain types. In this regard, hybrid breeding for moisture stress tolerance may be practiced but while selecting materials care will have to be taken on grain traits as well. Among the parents in our study, Phule Mailee is a well accepted post-rainy sorghum variety, while SPV 1587 also has adapted well post rainy season conditions. The hybrid between them has higher yield under depleting moisture regime. However, it needs to be tested on wider scale to decide its superiority. Lines derived from these potentially be identified as drought tolerant. In majority of cases the additive effect was low or towards unfavourable directions. Hence, derivation of superior lines from such crosses may not be feasible. However, as we recorded transgressive segregants for majority of traits, it is likely that the parents retained different alleles for the traits. Therefore, superior lines may be derived upon advancing the generations letting new combination of alleles to arise. Predominant epistatic effects may retard the selection process in the earlier generations. Hence, as suggested by Audilakshmi *et al.* [7] in presence of high epistatic interactions selection for drought tolerance should be avoided in early generations and practiced in later generations.

It must be kept in mind that gene effects, as estimated in our study are often cross specific. Hence, similar study needs to be extended on more crosses involving different resistant and tolerant lines.

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