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Research Article

The genetic control of sink size traits in pearl millet: from generation means and triple test cross analyses

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Abstract
Sink size traits are the major determinates of grain yield in pearl millet. The genetic architecture of three sink size component traits (panicle length, panicle girth and grain size) were studied using generation means and triple test cross analyses. The plant materials for genetic analysis consisted of two crosses for the generation means, and one cross for triple test cross (TTC) analysis for each of three traits. The genetic populations were developed during the 2005-06 and the field experiments were conducted during the 2006 rainy season and 2007 summer season. Scaling and joint scaling tests revealed that a simplistic additive-dominance model did not adequately explain the observed variation for all the three sink size traits in both seasons, providing an evidence for the presence of epistasis. The six-parameter model and the TTC analyses revealed significance of both additive and dominance gene effects for cross 1 of panicle length, panicle girth and grain size. However, cross 2 of panicle length and panicle girth revealed only additive effect, and of grain size showed the presence of both additive and dominance gene effects. All three types of interactions (additive x additive, additive x dominance and dominance x dominance) were found to be significant in cross 1 of all the traits across seasons using generation means analysis. However, TTC analysis revealed the presence of all types of epistasis for panicle length and panicle girth, and for grain size it revealed the presence of additive x dominance and dominance x dominance (j + l) epistasis. In cross 2, additive x additive (i) interaction alone was significant for panicle length and panicle girth, whereas for grain size, dominance x dominance (l) followed by additive x dominance (j) contributed significantly across the seasons. Breeding strategies for the improvement of sink size traits are discussed based on genetic information obtained.

Key words
Pearl millet, sink size traits, gene action, generation means and triple test cross

Introduction

Pearl millet is a major cereal crop grown in the semi-arid regions of Asia and Africa. It is cultivated on about 26 million ha in Asia and Africa. Of this, more than 40% of the area is in Asia, where India is a major producer of this crop with about 10 million ha and an average productivity of 870 kg ha^{-1} (Agricultural statistics, 2006). The increasing trend in the reduction of pearl millet cropping area would require a further increase in grain yield potential to meet the growing demands for pearl millet grain. Grain yield is a function of total dry matter and harvest index. Therefore, enhancing the total dry matter, harvest index or both can increase grain yield. The harvest index could be increased through improving the sink size capacity. In many correlation studies, traits such as panicle length, panicle girth and grain size are identified as important sink size components since these traits have shown direct positive correlation with grain yield (Jindla and Gill, 1984; Maman *et al.,* 2004). However, the poor sink capacity with low harvest index (15 - 20%) is a basic problem of the pearl millet species itself (Yagya and Bainiwal, 2001), causing this crop to produce low grain yields. Therefore, in pearl millet, emphasis needs to be given to increase sink size component traits to achieve further advance in productivity.

The ICRISAT Genetic Resources Unit at Patancheru has assembled pearl millet germplasm accessions from different countries that provides wide variability for panicle length (5-114 cm), panicle girth (13 - 55 mm) and 1000-grain mass (4-21 g). Knowledge about genetic factors responsible for the inheritance of sink size characters, for which there is a great genetic variability in the germplasm collections, is essential for any applied breeding programme. Despite five decades of research about the type of gene action, there is still debate about the type of gene action predominating for important traits. Almost all the previous pearl millet studies have been conducted using parental material not as diverse as those now available with pearl millet research programme at ICRISAT, which were included in the present study to understand the genetic control of sink size traits.

The genetical study based on the means of basic generations, is a simple method for estimating the gene effects for a polygeneic trait and has been used in many crop species. The greatest merit of generation means analysis lies in its ability to estimate the epistatic effects (Mather and Jinks, 1982). However, it has its own limitations and assumptions. Triple test cross is another powerful method of genetic analysis, which provides unbiased test for epistasis. In addition, it also estimates the additive and dominance components of variation with high accuracy when epistasis is

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absent (Kearsey and Jinks, 1968). The present study was made to understand the genetic control of sink size traits in pearl millet through generation means and triple test cross analyses using diverse parental lines, and to suggest a breeding strategy to improve these traits in the applied breeding programmes.

Materials and methods

Plant materials and development of genetic populations: For studying the genetic control of sink size traits, three groups of parental lines (panicle length, panicle girth and grain size) were selected from the trait-specific breeding lines during 2005 rainy season. The pedigree of selected parental lines in each group and cross combinations subjected to generation means analysis (GMA) and triple test cross (TTC) studies are presented in table 1. To develop the basic genetic populations (P_1, P_2, F_1, F_2, BC_1 and BC_2) for generation means analysis, the parental lines in each group were sown in 4 m four-row plots in a crossing block during post-rainy season of 2005-06. The crosses were made between lines with low trait value as seed parent and lines with high trait value as pollen parent in all the trait-specific groups. The seeds of parental lines and their F_1's of each group were planted under greenhouse condition. In each trait-specific group, the F_1's were selfed to generate the F_2 seeds and also backcrossed with their female and male parent to generate BC_1 and BC_2 seeds, respectively during May-June 2006. For generating TTC families, the parental lines and the F_1s of selected cross from each of the trait-specific groups were sown in 4 m two-row plots at three staggered sowing with one-week interval to synchronize with the flowering period of the F_2 population, which was planted in 4 m 10 row-plot during 2006 rainy season. Sixty individual F_2 plants were tagged and selfed to collect pollen. Pollens collected from individual F_2 plants were used for crossing to their respective parents (P_1 and P_2) and F_1 to produce three types of families L_{1i} (P_1 x F_{2i}), L_{2i} (P_2 x F_{2i}), and L_{3i} (F_1 x F_{2i}) in each of the trait-specific groups.

Field experiments and phenotypic observations: The trials were conducted on ICRISAT farm, Patancheru during the 2006 rainy and 2007 summer seasons. Generation means trials were evaluated in both the seasons, six generations (P_1, P_2, F_1, F_2, BC_1 and BC_1) of the two crosses from each of the trait-specific groups were planted in a randomized complete block design with three blocks. In each block, parents and their F_1s, backcrosses (BC_1s and BC_2s) and F_2s were raised in 2, 6 and 20 row plots, respectively. The TTC families of each trait-specific group were evaluated along with the generation means trial as one experiment in a randomized complete block design with three replications during 2007 summer season. This trial consisted of 180 TTC families (60 each of L_{1i}, L_{2i} and L_{3i}) for each trait specific groups, which were planted in single-row plots. In both season trials, the rows were 4 m long and 60 cm apart, and the seeds were hand dibbled at a spacing of 20 cm in each row. Seeds were treated with fungicide before sowing to protect from soil borne pathogens. Standard cultural practices were followed to raise a successful crop. Phenotypic observations on panicle length, panicle girth and grain size were recorded in their respective trait-specific crosses. For generation means analysis, observations were recorded on 20 individual plants each in parents and their F_1s, 100 plants each in backcrosses (BC_1 and BC_2) and 350 plants in F_2 population from each block for a cross. For the TTC analysis, observations were recorded on 10 competitive plants from each of the 180 TTC families in each replication.

Generation means analysis: The basic generations data obtained from the each of the trait-specific groups were subjected to scaling test for examine the adequacy of a simple additive-dominance model. The scaling test for A, B and C scales were calculated as per the method suggested by Mather (1949). Joint scaling test of Cavalli (1952) was also performed to estimate the three parameters mid-parental value (m), dominance (h) and additive (d) gene effects following the least square method (Mather and Jinks, 1971). Adequacy of three-parameter model was tested using chi-square test for goodness of fit at 3 (n–3) degrees of freedom, where n is the number of generation from which the three parameters were estimated. In case of inadequacy of three-parameter model revealed through the scaling or join scaling test, equations formulated by Hayman (1958) were utilized to obtain six parameters, the average effect (m), additive effect (d), dominance effect (h), additive x additive interaction (i), additive x dominance (j) interaction and dominance x dominance (l) interaction.

Triple test cross analysis: Triple test cross (TTC) analysis has been carried out using the model proposed by Kearsey and Jinks (1968). The test of significance of the difference [(L_{1i} + L_{2i} – $2L_{3i}$) where, i = F_2 individuals] provides information about the presence or absence of epistasis. Therefore, L_{1i} + L_{2i} – $2L_{3i}$ for each line (F_2 individuals) and each replication was first computed and then tested. The total epistasis for 'n' (n = 60) degree of freedom was calculated as uncorrected genotype (F_2 individuals) sums of square based on the total of these components over the replications.

$$\text{Total epistasis} = \frac{\sum_{i=1}^{60} (\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i})^2}{n}$$

The total epistasis was partitioned into two components. The correction factor (c.f) measures

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mainly the epistasis of additive x additive (i) type with one degree of freedom.

$$[i] \text{ epistasis (c.f)} = \frac{\left[\sum_{i=1}^{60}(\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i})\right]^2}{n}$$

The corrected genotypes sum of squares is a measure of the combined additive x dominance and dominance x dominance (j + l) epistasis with n – 1 degrees of freedom.

$$[j+l] \quad \text{epistasis} = \frac{\sum_{i=1}^{60}(\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i})^2}{n} - \frac{\left[\sum_{i=1}^{60}(\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i})\right]^2}{n}$$

On the assumption of no epistasis, an additive-dominance model was also fitted for the observed data as outlined by Kearsey and Jinks (1968).

Results and discussion

The mean values among the parents for panicle length, panicle girth and grain size of the two crosses studied differed significantly in both the seasons (Table 2). However, the difference was larger in parental lines of cross 1 in all the trait-specific groups. The means of F_1, F_2 and backcross generations also differed substantially from one another. The F_1s mean of panicle length in both the crosses were lower than the mid-parental values, suggesting apparently the presence of partial dominance of genes with small panicle (P_1) over those with longer panicle (P_2). The presence of partial dominance of genes with thick panicle and large grain size over those of thin panicle and small grain size was inferred, as their F_1 means in both the crosses were higher than the mid-parental values. The means of six generations were subjected for scaling and joint scaling test indicating that a simple additive-dominance or three-parameter model was not sufficient to explain the total genetic variation for all the three traits in both the crosses across the seasons (Table 3). The lack of fit of additive-dominance model reveals the presence of non-allelic interactions for these traits, and thus warranted the use of six-parameter model.

The six-parameter model in the estimation of various genetic components for panicle length revealed that the additive effect was highly significant in both the crosses across the seasons (Table 4). Although the dominance effect for panicle length was found to be significant in cross 1 in both the seasons, but it was non-significant in cross 2. The significant effects of both additive and dominance components for panicle length in cross 1 was similar to the reports of Singh and Sagar (2001). For panicle girth and grain size also both the additive and dominance gene effects were found to be highly significant in both the crosses across the seasons. The importance of both additive and dominance gene effects for panicle girth was also reported by Singh *et al.* (2000). TTC analysis of variances for sums and differences indicated significance of their mean squares for all the three traits, which also provide evidence for the presence of both additive and dominance gene effects in the genetic control of these traits (Table 5).

The magnitude of additive component was found to be higher than dominance for all the three traits in the generation means analysis, indicating the relative importance of additive gene effects. The preponderance of additive gene effects for panicle length was also reported by Singh *et al.* (2000). This suggests the presence of partial degree of dominance and additive x additive (i) epistasis for these traits. Presence of partial dominance for this trait was confirmed, as the estimates were less than unity in both the crosses across the seasons. The results of TTC analysis however, revealed the presence of overdominance for the traits panicle length and grain size, and partial dominance for panicle girth. Estimates of additive and dominance genetic effects may not be free from bias, since both the generation means and TTC analyses signified the presence of epistatic interactions. If the genes of like effect are not completely associated in the parents, it is possible that additive gene effects are underestimated as a result of the canceling out of additive (d), additive x additive (i) and additive x dominance (j) effects, however dominance (h) effects are not influenced by the distribution of the alleles in the parents (Mather and Jinks, 1982). The significant dominant component and negative significant correlation between sums and differences from TTC suggests that dominant alleles are predominantly unidirectional among parents, and the dominant alleles more frequently carry the increasing effect for panicle length and panicle girth. Whereas for grain size, ambidirectional distribution of dominant and recessive allele among the parents, and increasing effects of dominance allele have on grain size were inferred from the significant dominance component and negative non-significant correlation coefficient between sums and differences.

All the three types of digeneic interaction effects were highly significant for panicle length and grain size of cross 1 in both the seasons, and for panicle girth, additive x additive and dominance x dominance interactions were found to be the most important component, being significant in both the seasons (Table 4). However, the magnitude of dominance x dominance interaction was greater than other interactions for all the traits in cross 1. The test of epistasis through TTC analysis for

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cross 1 of panicle length and panicle girth also revealed the presence of additive x additive (i) and additive x dominance and dominance x dominance (j + l) epistasis, whereas for grain size, the additive x dominance and dominance x dominance (j + l) epistasis was significant while the fixable component additive x additive epistasis was non-significant (Table 5). Chand *et al.* (1973) also reported the significance of both additive x dominance and dominance x dominance interactions for grain size.

In cross 2 of trait-specific groups, additive x additive interaction was found to be significant for panicle length and panicle girth in both the seasons (Table 4). The additive x dominance interaction was also found to be significant for panicle girth in cross 2 during 2007 summer season. The dominance x dominance interaction for panicle length and panicle girth of cross 2 was non-significant across the seasons. The lack of dominance x dominance component for panicle length and panicle girth of cross 2 may be accounted to the selection pressure which results in fixation of additive x additive component in the parental lines, as evidenced from comparatively lesser contrast between the parental lines of cross 2 than cross 1. However for grain size in cross 2, the interaction components dominance x dominance followed by additive x dominance contributed significantly towards their inheritance. Large significant dominance component of interaction for grain size in both the crosses and for panicle length in cross 1 is a recognizable pattern underlying genetic parameters for fitness traits that might be the result of directional selection. Willis and Orr (1993) opined that when a number of loci are controlled by dominant or overdominant loci for a trait, intense directional selection and to some extent stabilizing selection will not erode as much additive variance as it would if the trait were controlled purely by additive effects, and an additional expectation is that duplicate epistasis should also arise in directionally selected traits. Opposite sign of dominance (negative) and dominance x dominance (positive) components for grain size in both the crosses and for panicle length of cross 1 in both the seasons confirms the expectation of duplicate interaction for these traits. Duplicate type of epistasis for grain size and panicle length was reported by Sheoran *et al.* (2000). However, panicle length of cross 2 and panicle girth of both the crosses revealed complementary epistasis as both (h) and (l) components were in same direction (positive). Presence of complementary epistasis for panicle girth was reported by Sheoran *et al.* (2000).

In general, panicle length, panicle girth and grain size of cross 1 was found to have all the six genetic components at significant levels (Table 4). Previous studies have not reported the significance of all the six-genetic components for a trait in any single cross. This may be because the parental lines did not represent extreme contrast in earlier studies, which in turn represents the dispersal of like genes between the parental lines. The dispersal of alleles among the parental lines may cause the canceling out of some genetic effects, resulting in the under estimation of additive (d), additive x additive (i) and additive x dominance (j) interactions. Further, panicle length and panicle girth of cross 2 showed significant largely for additive and additive x additive genetic components. The attribution of other genetic components might be because the parental lines utilized in this cross may have been subjected to optimizing selection, and hence are expected to have a predominantly additive architecture with less pronounced dominance components (Gilchrist and Partridge, 2001).

The results of generation means and TTC analyses in the present study had a general agreement to each other to a large extent (Table 4 and 5). TTC analysis revealed the importance of epistasis, particularly additive x additive epistasis was significant for panicle length and panicle girth, and additive x dominance and dominance x dominance (j + l) epistasis along with additive and dominance components were significant in the genetic control of panicle length, panicle girth and grain size. The results of generation mean analysis also confirmed the above interpretation, except for additive x additive interaction for grain size that was also found to be significant in generation means, however its magnitude was lower than additive x dominance and dominance x dominance interactions. A general agreement between the results of TTC and generation means analyses observed in the present study was similar to the findings of Nanda *et al.* (1990) while studying the inheritance of quantitative traits in bread wheat.

Any selection scheme that exploits high degree of heterozygosity and heterogeneity, additive effects are of primary importance, while those that exploit homozygosity, dominance and epistatic effects may also be of importance. In the present study, additive genetic effects and additive x additive interactions were found to be of prime importance for panicle length of cross 2 and panicle girth of both the crosses. Dominance effects were also observed, but were lower in magnitude than the additive effects. Under such conditions, mass selection can be effective, but S_1 or S_2 selection is likely to be more effective. The presence of non-additive effects for these traits suggests that mass selection would be less effective. Selections based on progeny performance using an inbred tester are of particular interest to breeders to hasten additive genetic variances. Selection among S_1 or S_2 progenies is attractive on theoretical grounds because, in the absence of overdominance, it is

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expected to be appreciably more effective than testcross method for changing population gene frequencies (Wright, 1980). In pearl millet, Dutt and Bainiwal (2005) reported that S_1 progeny selection method appears to be superior to either of half sib or full sib methods of progeny selection in exposing the hidden variability.

Epistatic interactions, particularly dominance x dominance and additive x additive interaction were found to be the important genetic components for panicle length of cross 1 and grain size of both the crosses. Along with epistatic interactions, additive and dominance gene effects were also found to be significant for these traits. Hence, the successful breeding method for these traits would be the one that can capitalize on epistatic as well as additive and dominance genetic variation.

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Table 1. Pedigree of selected parental lines of trait specific groups and crosses subjected for generation means and triple test cross analysis

Group	Trait / Cross	Pedigree of parental lines			Crosses subjected	
		Female parent		Male Parent	GMA	TTC
1	**Panicle length**					
	Cross 1	(ICMB 89111 x IPC 1466)-21-1-3-6-B-5	x	(((SRC II C3 S1-19-3-2xHHVBC)-5-3-1)x(IP19626-4-1-3))-B-7-1-1	✓	✓
	Cross 2	[81B x SRL 53-1) x 843B]-30-2-B	x	ICMV-IS 94206-7x(SRC II C3 S1-1-1-2x HHVBC)-1-3-3))-B-10-1-1	✓	
2	**Panicle girth**					
	Cross 1	(96111Bx4017-3-3-B)-4-5-4-1-1-1-1-B-3	x	HHVBC HS-10-1-2-1-1-1-1	✓	✓
	Cross 2	NCD2 BC7F14- 12-1--3-5-5	x	HHVDBC dwarf HS-249-1-2-1-B-3	✓	
3	**Grain size**					
	Cross 1	(81Bx4025-3-2-B)-11-5-2-2-B-2	x	HHVBC II D2 HS-302-3-1-6-8-2-6-2-B	✓	✓
	Cross 2	(ICMB 96555 x IP 10437)-8xICMB 97444)-6-4-1-1	x	MC 94 C2 -S1-3-1-3-3-1-2-4-B	✓	

GMA- Generation mean analysis; TTC- Triple test cross

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Table 2. Mean performance of parents, F_1, F_2 and backcross generations for sink size traits

Cross / Season	Generation	Population size	Sink Size Traits		
			Panicle length	Panicle girth	Grain size
Cross 1					
Rainy 2006	P_1	60	16.45 ±0.13	17.94 ±0.23	4.40 ±0.07
	P_2	60	67.19 ±0.22	49.04 ±0.25	13.14 ±0.09
	F_1	60	36.74 ±0.18	35.14 ±0.25	8.32 ±0.10
	F_2	1050	35.26 ±0.31	29.71 ±0.21	7.89 ±0.08
	BC_1	300	25.42 ±0.28	22.68 ±0.29	6.27 ±0.09
	BC_2	300	42.73 ±0.55	38.63 ±0.37	8.98 ±0.07
Summer 2007	P_1	60	17.51 ±0.12	18.52 ±0.22	5.03 ±0.08
	P_2	60	66.45 ±0.24	48.32 ±0.18	13.52 ±0.09
	F_1	60	39.09 ±0.19	34.88 ±0.16	8.73 ±0.12
	F_2	1050	35.80 ±0.31	28.65 ±0.21	8.62 ±0.07
	BC_1	300	26.08 ±0.28	22.66 ±0.27	6.82 ±0.09
	BC_2	300	41.89 ±0.55	37.29 ±0.37	9.83 ±0.10
Cross 2					
Rainy 2006	P_1	60	16.29 ±0.17	14.40 ±0.17	5.22 ±0.08
	P_2	60	46.81 ±0.23	41.37 ±0.28	13.78 ±0.11
	F_1	60	29.60 ±0.21	26.67 ±0.21	8.59 ±0.04
	F_2	1050	28.67 ±0.22	24.30 ±0.17	8.46 ±0.07
	BC_1	300	21.67 ±0.29	18.93 ±0.18	7.01 ±0.09
	BC_2	300	37.46 ±0.33	32.23 ±0.28	9.62 ±0.10
Summer 2007	P_1	60	17.37 ±0.18	15.63 ±0.14	5.88 ±0.07
	P_2	60	44.48 ±0.23	40.06 ±0.27	14.85 ±0.10
	F_1	60	30.49 ±0.22	27.32 ±0.23	9.68 ±0.04
	F_2	1050	28.48 ±0.23	24.51 ±0.17	9.45 ±0.08
	BC_1	300	22.43 ±0.29	19.08 ±0.17	7.38 ±0.08
	BC_2	300	35.94 ±0.31	32.54 ±0.28	11.25 ±0.12

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Table 3. Scaling and joint scaling test for sink size traits

Season /	Panicle length		Panicle girth		Grain size	
Parameter	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2
Scaling test						
Rainy 2006						
A	-2.35 ** ± 0.60	-2.55 ** ± 0.64	-7.71 ** ± 0.67	-3.20 ** ± 0.45	-0.19 ± 0.22	0.22 ± 0.20
B	-18.47 ** ± 1.14	-1.49 * ± 0.73	-6.92 ** ± 0.82	-3.58 ** ± 0.66	-3.49 ** ± 0.19	-3.12 ** ± 0.24
C	-16.09 ** ± 1.30	-7.62 ** ± 1.02	-18.43 ** ± 1.05	-11.91 ** ± 0.86	-2.62 ** ± 0.39	-2.36 ** ± 0.33
Summer 2007						
A	-4.44 ** ± 0.60	-2.99 ** ± 0.65	-8.09 ** ± 0.61	-4.78 ** ± 0.43	-0.11 ± 0.24	-0.80 ** ± 0.19
B	-21.74 ** ± 1.13	-3.09 ** ± 0.70	-8.63 ** ± 0.78	-2.30 ** ± 0.66	-2.58 ** ± 0.25	-2.03 ** ± 0.25
C	-18.94 ** ± 1.33	-8.89 ** ± 1.06	-22.02 ** ± 0.94	-12.28 ** ± 0.87	-1.53 ** ± 0.39	-2.27 ** ± 0.35
Joint scaling test						
Rainy 2006						
m	41.19 ** ± 0.12	31.20 ** ± 0.13	32.19 ** ± 0.16	26.93 ** ± 0.14	8.41 ** ± 0.05	9.07 ** ± 0.06
(d)	-24.93 ** ± 0.12	-15.21 ** ± 0.14	-15.62 ** ± 0.16	-13.16 ** ± 0.14	-3.92 ** ± 0.05	-3.87 ** ± 0.06
(h)	-5.50 ** ± 0.21	-2.44 ** ± 0.25	0.18 ± 0.29	-1.88 ** ± 0.25	-0.96 ** ± 0.11	-0.57 ** ± 0.07
χ^2 value	389.38 **	63.47 **	377.44 **	204.38 **	340.66 **	194.60 **
Summer 2007						
m	41.15 ** ± 0.13	30.45 ** ± 0.14	32.00 ** ± 0.13	27.11 ** ± 0.14	9.11 ** ± 0.06	10.07 ** ± 0.05
(d)	-23.89 ** ± 0.13	-13.47 ** ± 0.14	-15.25 ** ± 0.13	-12.11 ** ± 0.14	-4.02 ** ± 0.06	-4.36 ** ± 0.06
(h)	-3.57 ** ± 0.22	-1.02 ** ± 0.25	1.18 ** ± 0.21	-1.97 ** ± 0.25	-0.90 ** ± 0.12	-0.51 ** ± 0.07
χ^2 value	557.11 **	86.94 **	706.48 **	248.35 **	114.16 **	103.91 **

*, ** Significance at 5 and 1 per cent level, respectively

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Table 4. Estimates of the genetic components using six-parameter model for sink size traits

Season /	Panicle length		Panicle girth		Grain size	
Parameter	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2
Rainy 2006						
m	35.26 ** ± 0.31	28.67 ** ± 0.22	29.71 ** ± 0.21	24.30 ** ± 0.17	7.89 ** ± 0.08	8.46 ** ± 0.07
(d)	-17.32 ** ± 0.62	-15.79 ** ± 0.44	-15.95 ** ± 0.47	-13.30 ** ± 0.33	-2.72 ** ± 0.11	-2.61 ** ± 0.14
(h)	-9.81 ** ± 1.76	1.62 ± 1.27	5.45 ** ± 1.31	3.92 ** ± 0.99	-1.52 ** ± 0.41	-1.47 ** ± 0.41
(i)	-4.72 ** ± 1.75	3.57 ** ± 1.24	3.79 ** ± 1.27	5.13 ** ± 0.95	-1.07 ** ± 0.39	-0.55 ± 0.40
(j)	8.06 ** ± 0.63	-0.53 ± 0.46	-0.40 ± 0.50	0.19 ± 0.37	1.65 ** ± 0.13	1.67 ** ± 0.16
(l)	25.54 ** ± 2.80	0.48 ± 2.03	10.84 ** ± 2.15	1.65 ± 1.58	4.75 ** ± 0.60	3.46 ** ± 0.65
$(h/d)^{1/2}$	0.75	0.32	0.58	0.54	0.75	0.75
Summer 2007						
m	35.80 ** ± 0.31	28.48 ** ± 0.23	28.65 ** ± 0.21	24.51 ** ± 0.17	8.62 ** ± 0.07	9.45 ** ± 0.08
(d)	-15.82 ** ± 0.61	-13.51 ** ± 0.43	-14.63 ** ± 0.46	-13.46 ** ± 0.33	-3.01 ** ± 0.14	-3.87 ** ± 0.14
(h)	-10.13 ** ± 1.76	2.37 ± 1.28	6.77 ** ± 1.27	4.67 ** ± 0.98	-1.71 ** ± 0.42	-1.25 ** ± 0.43
(i)	-7.24 ** ± 1.75	2.81 * ± 1.25	5.31 ** ± 1.25	5.20 ** ± 0.95	-1.15 ** ± 0.39	-0.56 * ± 0.43
(j)	8.65 ** ± 0.63	0.05 ± 0.45	0.27 ± 0.48	-1.24 ** ± 0.36	1.23 ** ± 0.15	0.61 ** ± 0.16
(l)	33.42 ** ± 2.79	3.27 ± 2.01	11.40 ** ± 2.07	1.88 ± 1.57	3.84 ** ± 0.67	3.39 ** ± 0.67
$(h/d)^{1/2}$	0.80	0.42	0.68	0.59	0.75	0.57

*, ** Significance at 5 and 1 per cent level, respectively

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Table 5. Triple test cross analysis for sink size traits

Traits / Source	DF	Panicle length	Panicle girth	Grain size
		MS	MS	MS
ANOVA for testing epistatic model ($L_{1i} + L_{2i} - 2L_{3i}$)				
[i] type epistasis	1	53.93 **	127.67**	5.21
[j+l] type epistasis	59	223.94 **	149.20**	21.68**
Total epistasis	60	221.11 **	148.84**	21.40**
[i] x block	2	1.40 **	0.51	1.55
[j+l] x block	118	4.47	3.30	2.01
Total epistasis x block	120	4.42	3.25	2.01
ANOVA for testing additive model ($L_{1i} + L_{2i}$)				
Replication	2	0.32	0.48	1.57
Lines (sums)	59	279.82**	119.06**	7.97**
Error	118	1.11	1.01	0.57
ANOVA for testing dominance model ($L_{1i} - L_{2i}$)				
Replication	2	3.04	2.03	1.74
Lines (differences)	59	349.98**	102.28**	9.93**
Error	118	1.13	0.74	0.67
Genetic components				
Additive component (D)		371.62	157.40	9.87
Dominance component (H)		465.14	135.39	12.34
Degree of dominance		1.12	0.93	1.12
Direction of dominance (r)		-0.59**	-0.67**	-0.09