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Genetic study for epistatic gene effects for major yield contributing traits against drought in rice

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Abstract

The study subjected to estimate gene effects and inheritance of quantitative traits of rice with Generation Mean Analysis (GMA). Segregation analysis and estimation of genetic parameters under epistatic model indicated partial dominance and importance of additive effects in the inheritance of drought tolerance, respectively. In present study, absence of epistasis by scaling tests was recorded only for plant height in cross NDR-359 x P0 1564, grains per panicle in cross DSL- 63-8 x NDR- 359, test weight in cross Sarjoo-52 x P0 359, harvest-index in cross NDR-359 x P0 1564 and spikelets per panicle in cross Sarjoo-52 x P0 359 and NDR-359 x P0 1564 in irrigated condition and days to 50 per cent flowering in cross P0 359 x Sonam and harvest-index in cross NDR-359 x P0 1564 in drought condition. In remaining cases, existence of epistasis was observed in either one or both conditions by one or both types of scaling tests. The presence of complementary epistasis in cross P0 359 x Sonam and P0 1564 x Sarjoo-52 would make progress through selection procedures exploiting additive gene actions faster while existence of duplicate epistasis in cross NDR-359 x P0 1564 would have reverse impact. The non-additive gene effects in NDR-359 x P0 1564 for grain yield plant⁻¹ may also be utilized for facilitating development of pureline cultivars by involving population improvement methods. Our study concluded that for a large number of traits in six crosses, dominance gene effects and epistatic interactions were significant under drought and irrigated conditions implying that utilization of heterosis through hybrid varieties will act as a budding choice.

Keywords: Drought, Epistasis, Generation mean analysis, Metric traits

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INTRODUCTION

To fulfill the requirement of the food demand, it is essential to boost up production of rice either by escalating the yield per unit area or cultivated areas under this crop. However, there is very less possibility of increasing the land under cultivation in respect to the current scenario. Emerging importance of drought tolerant rice varieties has recently gained attraction by the breeders as studies on the genetics of drought tolerance in rice have been limited (Singh *et al.*, 2015). The proposed study was undertaken to understand genetic architecture of drought tolerance score by partitioning genetic means and also by segregation analysis (Pantuwan *et al.*, 2002). The experimental findings will be helpful in designing breeding work to develop modern rice varieties with higher ability to cope with drought stress at reproductive stage (Majumdar *et al.*, 1990). Yield is

mainly dependent upon interaction between yield associated traits and environment. This is the reason behind difficulties occurring to improve yield through breeding considering that yield is not only the main factor rather yield contributing traits are also equally important for selection while improving the grain yield (Misra *et al.*, 1994). Generation mean analysis is as important technique for estimation of allelic and non allelic interactions. Considering this, it has greater advantage of estimating crosses between additive itself, dominance itself and between additive and dominance (Viana, 2000; Singh and Singh, 1992). This research paper aims to emphasize gene effects and genetic variability in different crosses of rice.

MATERIALS AND METHODS

The experimental material comprised of parents (P₁ and P₂), F₁, F₂, B₁ and B₂ generations of six

crosses, viz., P0 359 x Sonam, IR-74409-730-08 x Saita, NDR-359 x P0 1564, Sarjoo-52 x P0 359, P0 1564 x Sarjoo-52 and DSL-63-8 x NDR-359. The eight diverse genotypes of rice were sown in crossing nursery during wet season, 2013 and desired six cross combinations (F₁'s) were made. The hybrid seeds (F₁'s) of three crosses were raised along with respective eight parents in dry season nursery, 2013 at Central Rice Research Institute (CRRRI), Cuttack, Orissa, for making the backcrosses (B₁ and B₂) with both the parents of each cross and obtained the F₂ generations from the respective self-fertilized seeds of F₁'s.

The six generations each of crosses were evaluated under irrigated and drought conditions by laying out two separate trials in Compact Family Block Design (Singh and Singh, 1992) with three replications during wet season. The families (crosses) were randomized among the main plots of a replication, while the progenies (generations) were randomized between the sub-plots with in a family main plot. The rows of three meter length were used for making sub-plots of two rows for P₁, P₂ and F₁ generations while for B₁ and B₂ generations four rows have been used. Furthermore, for F₂ generations six rows of each cross were included. The row to row and plant to plant were 20 x 15 cm.

Management of water stress: In case of assured irrigated condition (E₁), the experimental field was left uncovered to receive natural rainfall. In addition to this, experimental plots were irrigated using well laid channels for supplying tube well water, as and when required, to maintain appropriate moisture levels as recommended for irrigated rice. In case of drought condition (E₂), the experiment field was covered by constructing temporary shelter at a height of 10-12 fetes using polythene sheets to exclude any possibility of natural rainfall falling in the experimental plots. Care was taken to check the inflow or seepage of water from the adjoining areas by making adequate bunds with plastic sheet (at the depth of 2.5 meter) around the experiment in drought condition. The flowering stage drought was created by withholding the irrigation on week before panicle exertion. Plants were exposed to drought for two weeks (60-80 K Pa.). Drought was released by irrigation. Recovery was measured at 10th days after release of drought. The seeds of all the generations of six crosses were directly sown in case of both the trials. The crop was raised as per recommended package and practices.

Observation and evaluation: Days to 50 per cent flowering (DFF): Number of days from the date of seeding to 50 per cent panicle emergence was recorded on the individual row basis; Size of flag leaf excluding sheath (cm²): The area of primary flag leaf was recorded at maturity by measuring the largest length and highest breadth and

multiplying the value by factor (0.75); Plant height (cm): Plant height was recorded in centimeters using measuring scale from (ground to main tip of plant) without considering awns at maturity stage; Panicle bearing tillers plant⁻¹: Number of panicle bearing tillers was recorded by counting panicle bearing tillers of a plant; Panicle length (cm): Length of main panicle was recorded in centimeters from the base to the tip of the panicle excluding awns for a plant. Grains panicle⁻¹: It was counted on the basis of filled grains present in the panicle of main shoot of each randomly selected plant at maturity; Spikelets panicle⁻¹: Total numbers of fertile and sterile spikelets present in the panicle of main shoot of a plant were counted; Test weight: Weight of grains (in grams) of randomly selected plants were chosen for representing the sample consisting of 1000 grains; Biological yield plant⁻¹ (g): Each randomly selected plant (biomass excluding root) was sun-dried and dry matter was weighed in grams to estimate the biological yield per plant; Grain yield plant⁻¹ (g): Fertile grains (as unfertile grains removed during cleaning) of each randomly selected plant were hand threshed and sun-dried and then weighed in grams and Harvest-index (%): The ratio of grain yield (g) to biological yield (g) of plant was considered as harvest-index and expressed in percentage. Tagging of five randomly sampled plants entry⁻¹ replication⁻¹ for the non-segregating (parents and F₁s) and ten randomly sampled plants entry⁻¹ replication⁻¹ for the segregating (F₂s, B₁s and B₂s) were performed prior and later on observations were recorded as per the tagging. The data were subjected to analysis of variance for Compact Family Block Design (Singh and Singh, 1994). The simple scaling tests (Hayman & Mather, 1955) were applied prior to the use of six parameter models (Jinks and Jones, 1958) for the estimation of various genetic components.

RESULTS AND DISCUSSION

Analysis of variance: ANOVA revealed that six cross families differed significantly for all the traits in irrigated and drought conditions except for spikelet fertility in E₁. This implies that families/crosses involved under present study had extensive range in variations in number of traits in both conditions except a few exceptions.

ANOVA showed significant differences among the progenies between generation and crosses for all the crosses and traits under both environments, except for spikelet fertility and harvest-index in all the six crosses in E₁ and spikelet fertility in cross III and VI and harvest-index in cross I, II, IV, V and VI in E₂. The present study needs further validation due to ample amount of variations existing in the tested materials.

Simple scaling tests: Significant values for the A, B, C and D (scaling tests) for characters under

Table 1. Place of origin and salient features of parents of rice.

S.N.	Name of parents	Centre	Salient features
1	P0 359	T.N.A.&U., Tamil Nadu	Introgressed line (Bold seeded, DT)
2	P0 1564	T.N.A.&U., Tamil Nadu	Introgressed line (Bold seeded, DT)
3	DSL-63-8	IRRI, Philippines	Double Haploid line (Medium height, DT)
4	IR-74409-730-08	IRRI, Philippines	Double Haploid line (Medium height, DT)
5	Sarjoo-52	N.D.U.A.&T., Faizabad	Late maturity, long bold grains, resistant to BLB
6	NDR-359	N.D.U.A.&T., Faizabad	Late maturity, tolerant to blast and BLB
7	Sonam	Local cultivar	Late maturity, susceptible to drought
8	Saita	Local cultivar	Highly susceptible to drought, susceptible to BLB

Table 2. Summary of results of simple and joint scaling tests for sixteen traits in six crosses in irrigated and drought conditions.

Characters	E	Cross I (Sarjoo-52 x P0 359)		Cross II (P0 359 x Sonam)		Cross III (NDR-359 x P0 1564)		Cross IV (P0 1564 x Sarjoo-52)		Cross V (IR-74409-730 -08 x Saita)		Cross VI (DSL- 63-8 x NDR- 359)	
		S	J	S	J	S	J	S	J	S	J	S	J
		Days to 50 per cent Flowering	E ₁	E	E	E	E	--	E	--	E	E	--
Size of Flag Leaf (cm)	E ₂	E	E	--	--	E	E	E	E	E	E	E	E
Plant Height (cm)	E ₁	E	E	E	E	E	E	E	E	E	E	E	E
Panicle Bearing Tillers Plant ⁻¹	E ₂	E	E	E	E	E	E	E	E	E	E	E	E
Panicle Length (cm)	E ₁	E	E	E	E	E	E	E	E	E	E	E	E
Grains Panicle ⁻¹	E ₂	E	E	E	E	E	E	E	E	E	E	E	E
Spikelet's Panicle ⁻¹	E ₁	E	E	E	E	E	E	E	E	E	E	E	E
Spikelet Fertility (%)	E ₂	E	E	E	E	E	E	E	E	E	E	E	E
Test Weight (g)	E ₁	--	--	E	E	E	E	E	E	E	E	E	E
Grain Yield Plant ⁻¹ (g)	E ₂	E	E	E	E	E	E	E	E	E	E	E	E
Biological Yield Plant ⁻¹ (g)	E ₁	E	E	E	E	E	E	E	E	E	E	E	E
Harvest Index (%)	E ₂	E	E	E	E	E	E	E	E	E	E	E	E

S = Simple scaling test; J=Joint scaling test; E=Presence of epistasis; --=Absence of epistasis

study in a cross showed incidence of epistasis and insufficiency of AD model (Table 1). For DFF simple scaling tests detected the presence of epistasis in all the six crosses in both conditions except in cross III and IV in E₁. In case of SFL, the presence of epistasis was revealed in all the six crosses in E₁ and E₂. While epistasis observed or PH in all the six crosses in E₁ and E₂ except absence epistasis observed for cross II and III in E₁. In case of PL and G/P, simple scaling tests detected existence of epistasis in all the six crosses in E₁ and E₂ except lack of epistasis recorded for cross DSL- 63-8 x NDR- 359 in E₁. The presence of epistasis was also revealed for S/P in all the crosses in E₁ and E₂ except absence of epistasis in cross I and VI in E₁. For SF, presence of epistasis was noted in E₁ and E₂ for all the crosses except absence of epistasis in cross II and V and in cross I in E₂. In case of TW, GY/P and BY/P, simple scaling tests detected presence of epistasis in all the six crosses in E₁ and E₂ condition except

absence of epistasis found in cross I for TW in E₁. For HI, presence of epistasis was revealed in E₁ and E₂ except lack of epistasis noted in cross I and II and cross III in E₁ and in cross VI in E₂.

These results for all the characters and crosses in term of simple scaling tests in both water regimes revealed the significance of epistatic interactions for above said traits. The absence of epistasis in E₁ and E₂ was recorded only for PH in cross III, G/P in cross VI, TW in cross I, HI in cross III and S/P in cross I and VI in E₁ and DFF in cross II and HI in cross VI in E₂. In this way, the study showed the value of epistasis in-heritance in major traits. Earlier Saravanan *et al.* (2006) and Singh *et al.* (2007) had also reported similar results. Ten crosses indicated presence of epistasis while it is lacking in simple scaling test.

Gene effects: The present study was undertaken to use P₁, P₂, F₁, F₂, B₁ and B₂ generations of each of the six crosses in order to obtain information about epistasis in E₁ and E₂ presented

Table 3. Summary of gene effects for sixteen traits in six crosses under irrigated and drought conditions.

Characters	E	Cross I	Cross II	Cross III	Cross IV	Cross V	Cross VI
Days to 50 per cent Flowering	E ₁	dhil, D	jl	d	d	j	hil, D
	E ₂	dl	d	djl	hijl, D	dhijl, D	hijl, D
Size of Flag Leaf (cm)	E ₁	hil, D	dhil, D	dhi	jl	hij	dhil, D
	E ₂	dijl	dil	hijl, D	hijl, D	hil, D	hil, D
Plant Height (cm)	E ₁	dhij	dh	d	dhijl, D	dj	dhil, D
	E ₂	dhi	j	dhjl, C	jl	hj	Dhij
Panicle Bearing Tillers Plant ⁻¹	E ₁	dj	ijl	--	d	hij	hijl, D
	E ₂	dh	hl, C	jl	j	jl	dhijl, D
Panicle Length (cm)	E ₁	hil, D	dhi	hijl, D	dl	hij	Dhi
	E ₂	j	dhil, D	d	hijl, D	hijl, D	J
Grains Panicle ⁻¹	E ₁	jl	dhijl, D	dhijl, D	dj	hil, D	Dh
	E ₂	dhjl, C	hil, D	dhjl, C	dhj	hil, D	Dh
Spikelet's Panicle ⁻¹	E ₁	d	dhijl, D	dhijl, D	hi	hil, D	Dh
	E ₂	hj	j	dhij	dhij	dhijl, D	Hi
Spikelet Fertility (%)	E ₁	l	dh	hi	dhijl, D	h	--
	E ₂	d	hijl, D	hil, D	ij	dijl	Dij
Test Weight (g)	E ₁	d	dh	--	dhij	dhl, D	Dhij
	E ₂	j	hij	hi	hijl, D	hijl, D	Hij
Grain Yield Plant ⁻¹ (g)	E ₁	dh	dh	hj	dl	dl	Hi
	E ₂	dhi	dhil, D	hijl, D	dhjl, C	hijl, D	D, il
Biological Yield Plant ⁻¹ (g)	E ₁	dhj	dhij	hij	dl	dl	Hi
	E ₂	dl	dhil, D	dhil, D	jl	dhijl, C	ljl
Harvest Index (%)	E ₁	--	d	--	d	--	--
	E ₂	dh	d	hijl, D	hij	Dhil, C	D

-- = Value was not considerable to low and non-significant value

in Table 2 to 3.

Days to 50 per cent flowering (DFF): In case of DFF in E₁, the (d) was significant in Cross I, III and IV, while (h) was significant in cross I and VI. Among the epistatic interactions, significance of (i) in cross I and VI; (j) in cross II and V and (l) in cross I, II and cross VI was observed. Duplicate epistasis was noted for cross I and VI. The above results suggested that exploitation of fixable (d) effects can be aimed in further generations. In E₂, significant estimates of all the five gene effects with duplicate epistasis were observed in cross IV, V and VI except non-significance of (d) in cross IV and VI. The significance (i) was recorded in cross I, II and III along with significance of (j) in cross III and (l) in cross I and III. The significance of (d) in cross I, II and III with non-significant (h) and significant (j) in cross II and (l) in cross I and III sowed that these three crosses are likely to exhibit improvement mainly through selection methods by exploitation of fixable (d). The significance of all the five gene effects in cross V with duplicate epistasis suggested that exploitation of (d) and (h) may be fruitful in improving early flowering. Koli *et al.* (2014) reported role of (d) and (h) gene action for days to 50 per cent flowering.

Size of flag leaf excluding sheath (SFL): In E₁, cross II, III and VI showed significance of (d) and dominance (h) gene effects and additive x additive (i) interactions along with (l) and duplicate epistasis in cross II and VI. Thus, improvement of SFL in cross II, III and VI would require handling of segregating population for exploiting gene actions.

However, presence of duplicate epistasis in cross II and VI would be difficult due to fixable variance. The significance of gene effects (h), (i) and (l) in cross I, (j) and (l) in cross IV and (h), (i) and (j) in cross V with duplicate epistasis in cross I indicated that these three crosses should be subjected to exploitation of (h) gene actions for getting desirable changes in SFL for E₁. In E₂, the (d) along with (i), (j) and (l) interactions were significant in cross I and II with exception of (j) in cross II. Thus, significance of fixable (d) and partially fixable (i) epistasis in cross I and II indicates exploitation of these two crosses mainly through breeding procedure aimed at using fixable components of genetic variance for improving this character. In case of cross III, IV, V and VI, the significance of (h), (i), (l) and duplicate epistasis along with (j) interactions in cross III and IV hinted that these four crosses should be subjected to breeding methods aimed at exploitation of non-fixable non-additive gene actions.

Plant height (PH): In E₁, the (d) and (h) were significant in cross I, II, IV and VI along with significant estimates of (i) and (j) in cross I, (i), (j) and (l) in cross IV and (i) and (l) in cross VI which suggested that exploitation of (d) and (h) gene actions may be recommended for changing the plant structure in their advance generations. However, presence of duplicate epistasis in cross IV and VI would render progress through selection slower. The significance of only additive genetic variance (d) in cross III and with exception of significance (j) in cross V indicated that manipulation of PH

would be feasible through use of selection procedures exploiting fixable additive effects. In the E_2 , the (d) and (h) gene effects were significant in cross I, III and VI along with significance of (i) in cross I and VI, (j) in cross III and VI and (l) in cross III. The presence of complementary epistasis in cross III would be beneficial for gain through selection procedures. Similar findings for PH were reported with predominance of additive gene effects by Koli *et al.* (2014) while preponderance of non-additive gene action was observed by Muthuvijayaragavan and Murugan (2017).

Ear bearing tillers plant⁻¹ (EBT): In E_1 , cross I and IV showed significant (d) and (j) interaction. The significance of (i), (j) and (l) in cross II, (h), (i) and (j) in cross (v) and (h), (i), (j) and (l) in cross VI suggested that application of breeding methods meant for utilizing non-additive gene actions would be fruitful in manipulating this character in E_1 . Presence of duplicate epistasis in cross VI would be hindrance in the way of selection procedures in applied. In E_2 , all the estimates (d, h, i, j, l) along with duplicate type of epistasis were observed in cross VI. The significance of (d) and (h) gene effects in cross I suggested possibility of attaining improvement for this trait in later generations of this cross by exploiting (d) and (h). The significance of (h) and (i) in cross II, (j) and (i) in cross III and V and only (j) in cross IV revealed importance of non-fixable and non-additive gene actions. Madhukar *et al.* (2018) reported importance of additive and non-additive gene action for EBT.

Panicle length (PL): In E_1 , the (d) and (h) with (i) interactions were significant in cross II and VI while additive gene effects with (l) interactions were importance in cross IV. The significance of (h), (i), (j) and (l) in cross I, (h), (i), (j) and (l) in cross III and (h), (i) and (j) in cross V, suggested that these three crosses should be subjected to breeding producers aimed at using non-additive gene actions. The presence of duplicate epistasis in cross I and III would be cause further hindrance in success of selection producers. In E_2 , the significance of (d), (h), (i) and (l) with duplicate epistasis was found in cross II. The significance of (h), (i), (j) and (l) with duplicate epistasis in cross IV and V and only (j) epistatic component in cross I and VI, revealed importance of only non-additive gene actions in inheritance of PL in these four crosses. The existence of duplicate epistasis in cross II, IV and V would be further block in gaining good response to selection. Perraju and Sharma (1999) reported that PL was under control of non-additive gene effects, while Muthuvijayaragavan and Murugan (2017) found role of additive genetic variance only.

Grains panicle⁻¹ (G/P): In E_1 , estimates of all the five gene effects along with duplicate epistasis were found to be important for grains per panicle

in cross II and III, while significance of (d) and (j) in cross IV and (d) and (h) in cross VI was observed. Thus, these four crosses, namely, cross II, III, IV and VI, exhibiting importance of additive as well as non-additive gene actions, may be handled in further generations by breeding methods. The significance of (h), (i), and (l) along with duplicate epistasis in cross V and (j) and (l) in cross I. The presence of duplicate epistasis in cross II, III and V is likely to reduce the effectiveness of selection procedures in E_1 . In E_2 , the importance of (d), (h), (j) and (l) gene effects along with complementary epistasis was recorded in cross I and III while importance of (d) and (h) in cross VI and (d), (h) and (j) in cross IV was also noted. In case of cross II and IV, only non-additive components of genetic variance (h, l, j) along with duplicate epistasis were significant which suggested that breeding methods aimed at exploitation of non-additive gene actions would be useful while presence of duplicate epistasis would be hindrance for selection procedures. Kour *et al.* (2019) observed predominance of non-additive gene action, whereas preponderance of additive gene action was found by Madhukar *et al.* (2018) for grains panicle⁻¹.

Spikelets panicle⁻¹ (S/P): In E_1 , all (d, h, i, j, l) along with duplicate epistasis were found important in cross II and III while (d) and (h) gene effects, assumed importance in cross VI for S/P. Cross I may be recommended for exploitation through utilization of additive gene action as only additive (d) gene effect was significant in its case. The significance of (h) gene effect and (i) interaction effect in cross IV and V in addition to importance of (l) and duplicate epistasis in cross V revealed possibility of improving S/P through exploitation of non-additive components of genetic variance predominant in them. However, presence of duplicate type of epistasis in cross II, III and V would cause hindrance in achieving improvement through selection procedures. In case of E_2 , the (d), (h), (i) and (j) components of genetic variance were significant in cross III, IV and V while (l) and duplicate epistasis were also important in cross V. Due to presence of duplicate epistasis, selection intensity must be slow to exploit additive gene action. The significance of (h) and (j) parameters in cross I, (h) and (i) in cross VI and only (j) in cross II, representing non-additive genetic components, revealed usefulness of breeding methods based on utilization of non-additive gene actions in E_2 .

Test weight (TW): For TW in E_1 , the (d), (h), (i), and (j) gene effects were significant in cross IV, V and VI with exception of (j) component in case of cross V while only (d) and (h) gene effects were significant in cross II. The importance of (d) and (h) of genetic variance recorded for TW in cross II, IV, V and VI advocated handling of further generations by breeding procedures. The lack of suffi-

cient genetic variation for test-weight in cross III revealed by non-significance of all the five estimates of gene effects indicated little scope of improvement for E_1 . In E_2 , (d) gene effect was found non-significant in all the six crosses for test-weight. Cross II, III, IV, V and VI had significant estimates of (h), (i) and (j) parameters except non-significant (j) noted for cross III. The significance of (l) component was also observed in cross IV and V while only (j) interactions assumed importance in case of cross I. Thus, significance of one or more components of non-additive genetic variance in all the crosses for TW in E_2 advocated for use of breeding methods thriving on non-additive gene actions for improving TW. The existence of duplicate epistasis in cross IV and V would be detrimental in utilization of additive gene actions which are already un-important. Importance of additive as well as non-additive gene effects with greater role of additive component in inheritance of TW was recorded by Rao *et al.* (2017) reported greater role of non-additive gene effects.

Biological yield plant⁻¹ (BY/P): In E_1 , the significance of parameters (d), (h), (i) and (j) in cross II, (d), (h) and (j) in cross I and (d) and (l) in cross IV and V was recorded. Significance of (h), (i) and (j) in cross III and (h) and (i) in cross VI, revealed key function of breeding depend on utilization of non-additive gene actions in later generations of these crosses. In E_2 , the five parameters (d, h, i, j, l) were noteworthy in cross II, III and V except non-significant (j) in case of cross II and III. In case of cross I, (d) gene effects with (l) interactions were significant. In cross V, occurrence of complementary epistasis will cause increase in improvement in selection procedures whereas in duplicate epistasis reverse might be seen. The significance of parameters, (j) and (l) in cross IV and (i), (j) and (l) in cross VI, representing mainly non-additive components of genetic variance, indicates usefulness mainly of breeding procedures exploiting non-additive gene action for enhancement of BY/P in advance generations. Savitha and Kumari (2015) also reported significant role of additive and non-additive gene action with predominance of non-additive component for BY/P.

Harvest index (HI): For HI in E_1 , only (d) gene effect was significant in cross II and IV indicating thereby exclusive role of breeding methods utilizing additive gene action in later generations of these crosses for enhancing the better partitioning of photosynthates. The non-significance of all the five parameters in cross I, III, V and VI indicated apparent lack of variation for this trait, perhaps due to absence of requisite genetic diversity among their parents. In E_2 , the significance of parameters (d), (h), (i) and (l) in cross V and (d) and (h) in cross I indicated that the later generations of these crosses can be handled through

breeding methods meant for utilizing additive and/or not additive gene actions for deriving desirable segregates for HI. Only (d) gene effect was significant in cross II and VI which showed exclusive role of breeding methods meant for exploiting (d) for enhancing HI. In case of cross III (h, i, j, l) and cross IV (h, i, l), only non-additive components of genetic variance were important indicating the need for application of breeding methods utilizing non-additive gene actions. The presence of complementary epistasis in cross V and duplicate epistasis in cross III would help and harm, respectively, in the exploitation of additive gene actions. Savitha and Kumari (2015) found importance of additive and non-additive gene effects with greater role of non-additive component of genetic variance for HI.

Grain yield plant⁻¹ (GY/P): For GY/P in E_1 , (d) and (h) were significant in cross I and II while (d) gene effect with (l) interactions was significant in cross IV and V. This indicated that the later generations of cross I, II, IV and V may be subjected to breeding methods for isolating genotypes with higher grain yield potential in their advance generations. The significance of only non-additive components of genetic variances were in cross III (h, j) and cross VI (h, i), suggested exclusive role of breeding methods for improving grain yield in later generations of these crosses in E_1 . In E_2 , (d) and (h) gene effects were significant along with (i) in cross I, (i) and (l) in cross II and (j) and (l) in cross IV. In case of cross VI, (d) gene effect with (i) and (l) interactions assumed importance. In case of cross III and V, (h), (i), (j) and (l) parameters with duplicate epistasis assumed significance. However, presence of duplicate epistasis in cross III and V would make exploitation of partially fixable additive gene action represented by (i) interactions difficult. Koli *et al.* (2014) reported that GY/P was conditioned by (d) while, Perraju and Sarma (1999) found GY/P under control of (h). Importance of (d) and (h) with predominance of non-additive gene effects was observed for GYP⁻¹ by Muthuvijayaragavan and Murugan (2017).

Conclusion

Reaction towards selection is complicated when traits show epistasis. Digenic epistatic model represents the variation in the generation variants and improvement in this situation is fairly challengeable versus additive-dominance model. Majority of dominance effect in traits causes more complexity than additive impact. Cross between additive x additive were more crucial than dominant x dominant. In this study, single complementary epistasis has been seen. This paves way to higher probability of success in breeding as this situation is further congruent as compared to dominant x dominant effects and/or duplicates epistasis.

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