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Generation Mean Analysis for quantitative traits in the population of AKDRMS 21-54 x YH3 cross of rice (*Oryza sativa* L.)

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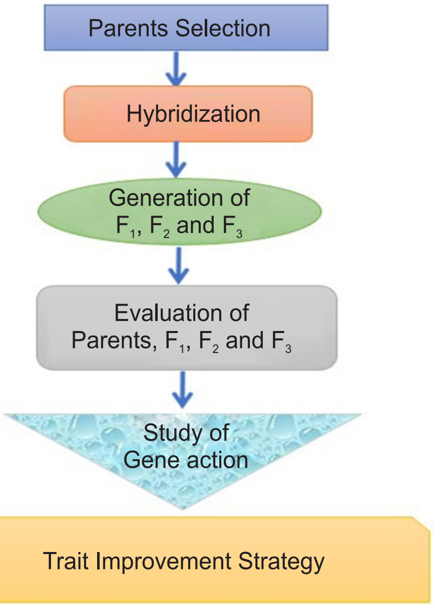
Abstract

Aim: To study the genetic components of inheritance for 12 quantitative traits which leads into genetic improvement by identification of gene actions for yield and yield related traits.

Methodology: Twelve quantitative traits for yield and yield attributing traits were studied at Agricultural College, Bapatla during *Rabi* 2021-22 deploying Hayman's five parameter model generation mean analysis in estimating the gene effects in the population (P_1, P_2, F_1, F_2 and F_3) generated from the cross AKDRMS 21-54 x YH3. Estimated mean effects affirm the existence of significant variation in the traits studied. Significance of either one or both, scales C or D inferred the existence of epistatic interaction for the traits studied. Digenic non-allelic interaction model explained the gene action of the traits studied in the present investigation.

Results: The generation mean for all the traits showed the importance of both additive and dominance type of gene effects. Among the epistatic gene effects, the additive x additive gene interaction was reported predominant for shoot length, plant height, flag leaf length, spikelet fertility and flag test weight. The gene interaction is associated with homozygosity, therefore, pedigree method of breeding may be adopted for isolation of desirable lines, while for all other traits, along with grain yield per plant, dominance x dominance gene interaction was found to be pre-dominant. The gene interaction is not fixable, hence, population improvement approaches, would be effective.

Interpretation: Dominance x dominance gene interaction was predominant for grain yield per plant and majority of yield component traits studied coupled with duplicate epistasis, infers to takeup population improvement approaches, such as bi-parental mating and recurrent selection, followed by isolation of purelines in later generations for competent improvement.



Key words: Epistasis, Five parameter model, Generation Mean Analysis, Quantitative traits, Rice

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Introduction

Rice (*Oryza sativa* L.) the prominent and primitive cereal crop feeding the mankind from ancient times has pivotal role in ensuring global food security. Rice is accountable for feeding 50 per cent of world's population, *i.e.* 7.8 billion people across the globe, but the anticipated global population would reach up to 9.8 billion by 2050. However, Asia, the global rice bowl would loose 5 million ha rice cultivable land by 2050 due to accommodation of growing population (Samal *et al.,* 2021). Consistent efforts from scientists have been achieved, leading to sustainable food supply to the ever-growing population by overcoming the imposed climate changes (Wakweya, 2023). As the land frontiers for many countries have been exhausted, and more land is being diverted for non-agricultural purposes, the growth in many countries has to come from an increase in productivity (Wang, 2022). Plant Genetics is the foundation to understand and utilise the hidden yield potential of crops, ultimately ensuring global security. However, the yield has reached a plateau in many growing regions and it is time to break the yield ceiling in those areas to feed the growing population in the years to come (Ronald, 2011). Hybridization between two parents helps in breaking the yield plateau by integrating the beneficial traits scattered across the parents (Kumar *et al.,* 2017).

The ability to develop successful crop breeding techniques depends on our knowledge of the genetics of inheritance and the mode of gene action, hence, the current investigation was done to study the genetic architecture for yield related traits. Yield is a complex quantitative trait which is under genetic control of many yield attributing traits. Complete knowledge on the kind and nature of genetic variations for yield related traits in plant population are prominence to plant breeders (Duppala *et al.,* 2022). The preference of breeding techniques for genetic advancement of a crop builds upon gene effects and gene interactions effecting the traits of interest. Generation mean analysis is one of the finest techniques for understanding and estimating the gene effects, along with identification of magnitude and mode of epistasis, unlike diallel mating and line x tester analysis where only the presence or absence of epistasis is revealed. among the different genetic analysis tools available to plant breeders (Bano *et al.,* 2017). In the present study, the overview of the components of genetic variation, additive (*d*), dominance (*h*) and epistatic contributions additive × additive (i) and dominance × dominance (l) were estimated by portioning the population means of parents, F_1, F_2 and F_3 of AKDRMS 21-54 x YH3 cross combination. Interacting and non-interacting traits were sorted out with the help of scaling test (Mather, 1949). The scales deviating from zero proved that the additive-dominance model was inadequate by indicating the occurrence of non-allelic interaction.

Materials and Methods

The present study was carried out during *Kharif* season 2019 to *Rabi* 2021-22 at the Agricultural College Farm, Agricultural College, Bapatla, Acharya N G Ranga Agricultural University, Guntur. The experimental material was generated from the cross between the rice genotypes, namely, AKDRMS 21-54 and YH3. The female parent, AKDRMS 21-54 is improved Akshayadhan through the introgression of *Xa21* and Pi54 genes for bacterial leaf blight and blast tolerance, while the male parent, YH3 is improved MTU 1121 (Sri Druthi), a high yielding and popular Rabi rice variety developed in Acharya NG Ranga Agricultural University, by the incorporation of tolerance to low soil phosphorus, through introgression of pup1 gene.

Five generations (P_1, P_2, F_1, F_2 and F_3) developed from the cross, AKDRMS 21-54 x Yh3 (Fig. 1) were evaluated during *Rabi* 2019-20. The crossing was initiated during *Kharif* 2019, between the female parent AKDRMS 21-54 and male parent YH3 the development of F_1's. True F_1's were identified with the help of gene-specific markers and advanced to F_2 during *Rabi* 2019-20 by selfing. F_2 plants, homozygous and positive for the target traits, were advanced to F_3 generations through selfing. The experiment was laid in a randomized complete block design with six replications during *Rabi* 2021-22. The parental lines and F_1's, were planted in 2 rows whereas F_2's and F_3's were planted in 4 rows, each of 4m length at a spacing of 25 cm x 10 cm. Data were recorded on 10 plants in case of parents and F_1's 50 plants of F_2's and F_3's per replication. The mean values of phenotypic traits were assessed on randomly selected plants from each individual entry in the segregating generations for 12 quantitative traits namely, days to 50 per cent flowering (days), shoot length (cm), plant height (cm), productive tillers per plant, flag leaf length (cm), flag leaf width (cm), panicle length (cm), filled grains per panicle, total grains per panicle, spikelet fertility (%), test weight (g) and grain yield per plant (g). Further five parameter model was used to estimate the gene effects (*m, d* and *h*) and their interactions (*i* and *l*) following the protocols (Hayman, 1958) and (Jinks and Jones, 1958).

The five genetic parameters *viz*., mean (*m*), additive gene effects (*d*), dominance gene effects (*h*) and two types of non-allelic gene interactions *viz*., additive x additive (*i*) and dominance x dominance (*l*) were estimated as follows :

$$[m] = \overline{F}_2$$
$$[d] = 1/2\overline{P}_1 - 1/2\,\overline{P}_2$$
$$[h] = 1/6(4\overline{F}_1 + 12\overline{F}_2 - 16\overline{F}_3)$$
$$[i] = \overline{P}_1 - \overline{F}_2 + (1/2)(\overline{P}_1 - \overline{P}_2 + h) - 1/4l$$
$$[l] = 1/3(16\overline{F}_3 - 24\overline{F}_2 + 8\overline{F}_1)$$

where $\overline{P}_1$, $\overline{P}_2$, $\overline{F}_1$, $\overline{F}_2$ and $\overline{F}_3$ are meal values of P_1, P_2 , F_1, F_2 and F_3 generations, respectively.

Results and Discussion

The mean performances of five generation materials namely, P_1, P_2, F_1, F_2, and F_3 for 12 characters studied are presented in Table 1. The estimated means as a result of gene effects along with gene interactions had significant variability, reflecting the possibility of transgressive segregants for all the 12 quantitative traits studied from the cross AKDRMS 21-54 x Yh3.

Table 1: Estimates of generation means and standard errors of AKDRMS 21-54 x YH3 for yield and yield components

Characters	P1	P2	F1	F2	F3
	Mean ± SEm	Mean ± SEm	Mean ± SEm	Mean ± SEm	Mean ± Sem
Days to 50 per cent flowering	83.5±0.45	89.5±0.28	78.67±0.66	88.55±0.87	89.66±0.8
Shoot length	93.97±1.08	82.49±0.55	88.5±0.87	88.64±0.66	89.44±0.74
Plant height	123.67±1.45	103.95±0.69	115.97±1.37	116.94±0.88	120.33±0.96
Productive tillers per plant	15.03±0.39	11.3±0.47	16.48±0.59	11±0.26	11.89±0.23
Flag leaf length	26.38±0.52	30.52±0.68	33.74±0.71	31.29±0.54	26.83±0.42
Flag leaf width	1.18±0.04	1.62±0.03	1.41±0.03	1.5±0.02	1.42±0.01
Panicle length	24.47±0.4	29.02±0.47	27.71±0.44	28.42±0.24	27.87±0.27
Filled grains per panicle	138.83±4.96	240.92±7.31	239.97±8.59	244.99±4.8	216.46±3.79
Total grains per panicle	164.6±6.26	260.85±7.86	257.82±9.25	269.15±5.36	246.52±4.14
Spikelet fertility	85.44±1.3	92.33±0.31	93.09±0.36	91.11±0.29	87.88±0.46
Test weight	20.75±0.68	25.3±0.62	27.86±0.63	25.42±0.52	24.02±0.32
Grain yield per plant	22.85±1.39	30.50±1.53	37.68±3.09	33.79±1.07	31.13±0.7

Table 2: Estimates of genetic factors for yield and yield components in AKDRMS 21-54 x YH3

Characters	Scaling test		Estimation of Genetic factors					Epistasis
	C	D	[m]	[d]	[h]	[i]	[l]	
Days to 50 per cent flowering	23.88**	8.55*	88.55**±0.87	3.00**±0.26	-9.55**±2.78	4.28±2.68	-20.44*±8.35	Complementary
Shoot length	1.11	4.00*	88.64**±0.66	-5.74**±0.61	-2.21±2.45	-13.97**±2.38	3.86±7.01	Duplicate
Plant height	8.22	19.8**	116.94**±0.88	-9.86**±0.8	-9.68**±3.24	-31.54**±3.17	15.44±9.43	Duplicate
Productive tillers per plant	-15.3**	-0.79	11.00**±0.26	-1.86**±0.31	1.29±0.9	-5.75**±1.05	19.35**±2.91	Complementary
Flag leaf length	-4.22	-1.15*	31.29**±0.54	4.57**±0.43	2.85±1.64	9.21**±1.83	4.09±5.26	Complementary
Flag leaf width	0.37**	-0.13	1.50**±0.02	0.22**±0.02	0.15**±0.06	0.58**±0.07	-0.67**±0.18	Duplicate
Panicle length	4.76**	1.16	28.42**±0.24	2.27**±0.31	0.98±0.92	4.57**±1.02	-4.80*±2.7	Duplicate
Filled grains per panicle	120.29**	-3.91	244.99**±4.8	51.04**±4.42	72.75**±15.07	124.74**±17.41	-165.60** ±49.05	Duplicate
Total grains per panicle	135.52**	22.34	269.15**±5.36	48.13**±5.02	52.78**±16.58	103.94**±19.17	-150.90** ±54.14	Duplicate
Spikelet fertility	0.51	-8.48**	91.12**±0.29	3.44**±0.67	9.95**±1.37	12.63**±1.36	-11.99**±3.47	Duplicate
Test weight	-0.1	-0.82*	25.42**±0.52	2.28**±0.46	5.35**±1.4	5.08**±1.67	-0.95±4.77	Duplicate
Grain yield per plant	-45.45**	-9.18*	39.84**±1.07	4.08**±1.03	22.94**±3.51	6.7**±4.17	48.36**±12.47	Complementary

* and ** Significant at 5 % and 1 % levels of probability, respectively

Among the parents, YH3 (P_2) showed higher *per se* performance than AKDRMS 21-54 (P_1) for the traits days to 50 per cent flowering (89.5 days), flag leaf length (30.52 cm), flag leaf width (1.62 cm), panicle length (29.02 cm), filled grains per panicle (240.92), total grains per panicle (260.85), spikelet fertility (92.33), test weight (25.30 g) and grain yield per plant (30.50).

However, AKDRMS 21-54 (P_1) has higher shoot length (93.97 cm), plant height (123.67 cm) and productive tillers per plant (15.03) in comparison with YH3 (P_2). Kumar and Singh (2018), had also reported similar variation among parents for grain yield, yield components and quality traits, earlier, in their studies on 'Generation Mean analysis for yield and quality traits in F_2 and backcross generations of rice'. Hybrids (F_1) recorded superior performance than parents for yield and yield contributing traits like productive tillers per plant (16.48), flag leaf length (33.74 cm), spikelet fertility (93.09), test weight (27.86 g) and grain yield per plant (37.68 g) inferring the presence of dominant gene effects and gene interactions for the above traits (Sreelakshmi and Babu, 2019). Compared to both parents, F_1 hybrids bloomed and reached maturity earlier, which is desirable for further selections. In contrast, declined performance was noticed for the characters like shoot length (88.50 cm), plant height (115.97 cm), flag leaf width (1.41 cm), panicle length (27.71 cm), filled grains per panicle (239.97) and total grains per panicle (257.82) in F_1 hybrids. Ghritlahre *et al.* (2018) had reported similar decline in F_1

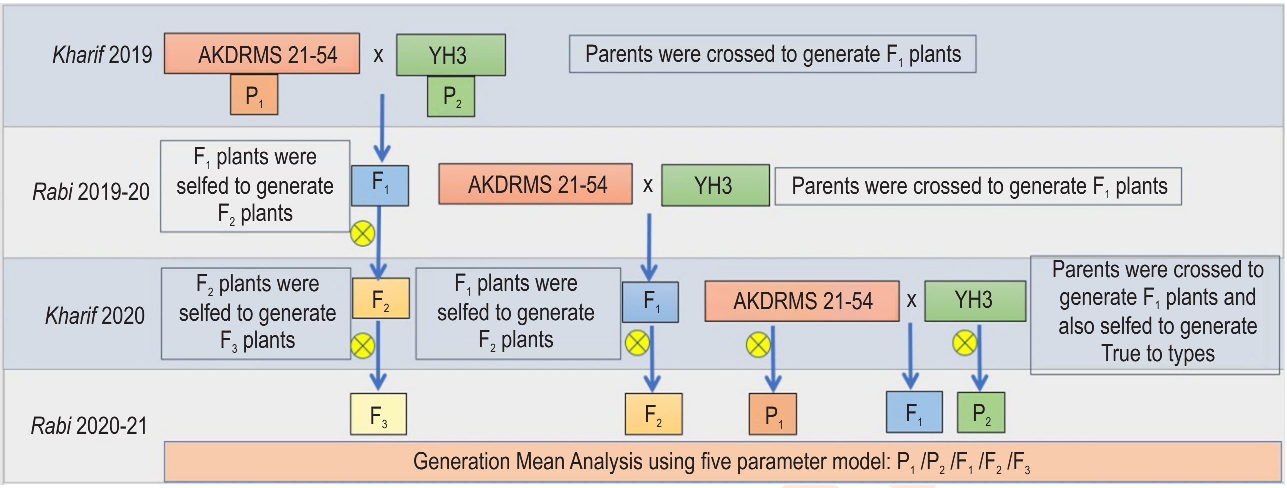

Fig. 1: Generation of experimental material for generation mean analysis.

performance over the better parent for days to flowering and seeds per panicle, earlier, in their studies on "Generation mean analysis for sheath blight disease resistance and yield related traits in rice". Segregating generation (F$_2$) exhibited higher number of filled grains per panicle (244.99) and total grains per panicle (269.15) than parents and hybrids, indicating the presence of transgressive segregants for the trait. However, shoot length, plant height, productive tillers per plant, flag leaf length, flag leaf width, panicle length, spikelet fertility, test weight and grain yield per plant of segregating generations (F$_2$ and F$_3$) were observed to be intermediate to the parents.

The declined performance of segregating generations maybe due to residual inbreeding depression due to the presence of recessive lethal alleles for these traits. Singh *et al.* (2015), had also reported inbreeding depression for grain yield per plant as the reason for declined yields in the segregating generations due to inbreeding depression, earlier in their studies on "Genetic architecture, heterosis and inbreeding depression for yield and associated physiological traits in rice under drought conditions". The YH3 parent (P$_2$) had recorded higher grain yield per plant compared to AKDRMS 21-54. The grain yield F$_1$ generation was higher than that of the parents due to heterosis for the trait, but yields of the two segregating populations (F$_2$ and F$_3$) was lower than that of the F1 generation due to existence of inbreeding depression for the trait. Significant deviation of observed generation means from the expected generation means may be due to the existence of non-allelic interactions among the traits studied, as reported by Makwana *et al.* (2018) in their studies on "Inferences on magnitude and nature of gene effects for morpho-physiological traits in rice".

The results of scaling tests to estimate the adequacy of simple additive dominance model are presented in Table 2. The days to 50 per cent flowering (23.88**; 8.55*) and grain yield per plant (-45.45**; -9.18*) were significant for both C and D scales, indicating the presence of both additive x additive and dominant x dominant gene interactions, while shoot length (4.00*), plant height (19.80**), flag leaf length (-1.15*), spikelet fertility (-8.48**) and test weight (-0.82*) were significant for scale D suggesting the preponderance of dominance × dominance gene interactions. Further, productive tillers per plant (-15.30**), flag leaf width (0.37**), panicle length (4.76**), filled grains per panicle (120.29**) and total grains per panicle (135.52**) displayed positively significant for scale C infers the preponderance of additive x additive gene interactions. Either one or both C and D scales were found significant for the traits of the cross AKDRMS 21-54 x YH3, revealing the inadequacy of simple additive-dominance model indicating digenic interactions owned to non-allelic interactions. Ghritlahre *et al.* (2018) attributed it to the occurrence of digenic, non-allelic interactions.

Digenic non-allelic interaction model with five parameters namely, *m, d, h, i* and *l* demonstrated that the epistatic interaction model was found to be sufficient to explain the gene activity in the traits examined in the present study. The estimates of gene effects like mean (*m*), additive (*d*), dominance (*h*), additive x additive (*i*) and dominance × dominance (l) for all the quantitative traits studied were presented in Table 2; Fig. 2 - 3. The generation mean analysis for most of the characters exhibited the importance of both additive and dominance type of gene effects along with the epistatic gene interactions. Days to 50 per cent flowering (-9.55**; -20.44*) had significant dominance effect (*h*) and dominance × dominance (*l*) interaction effects in negative direction. Further, shoot length (-5.74**; -13.97**) and plant height (-9.86**; -31.54**) had significant additive (*d*) effect and additive x additive (*i*) effects in negative direction indicating the diminishing effect on expression of the above traits which are highly desirable in plant breeding programmes.

In contrast, the flag leaf length (4.57**; 9.21**) had significant additive (*d*) effect and additive x additive (*i*) effects in

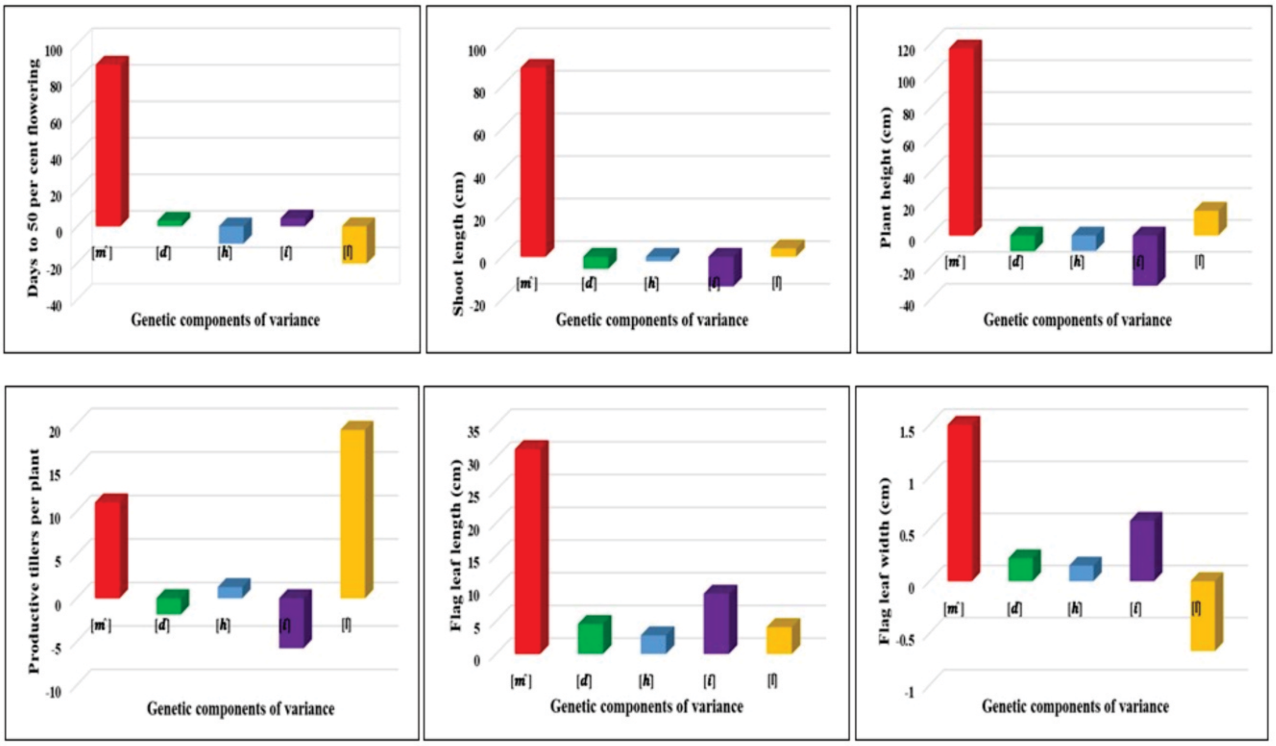

Fig. 2: Genetic components of AKDRMS 21-54 x YH3 cross for morphological traits.

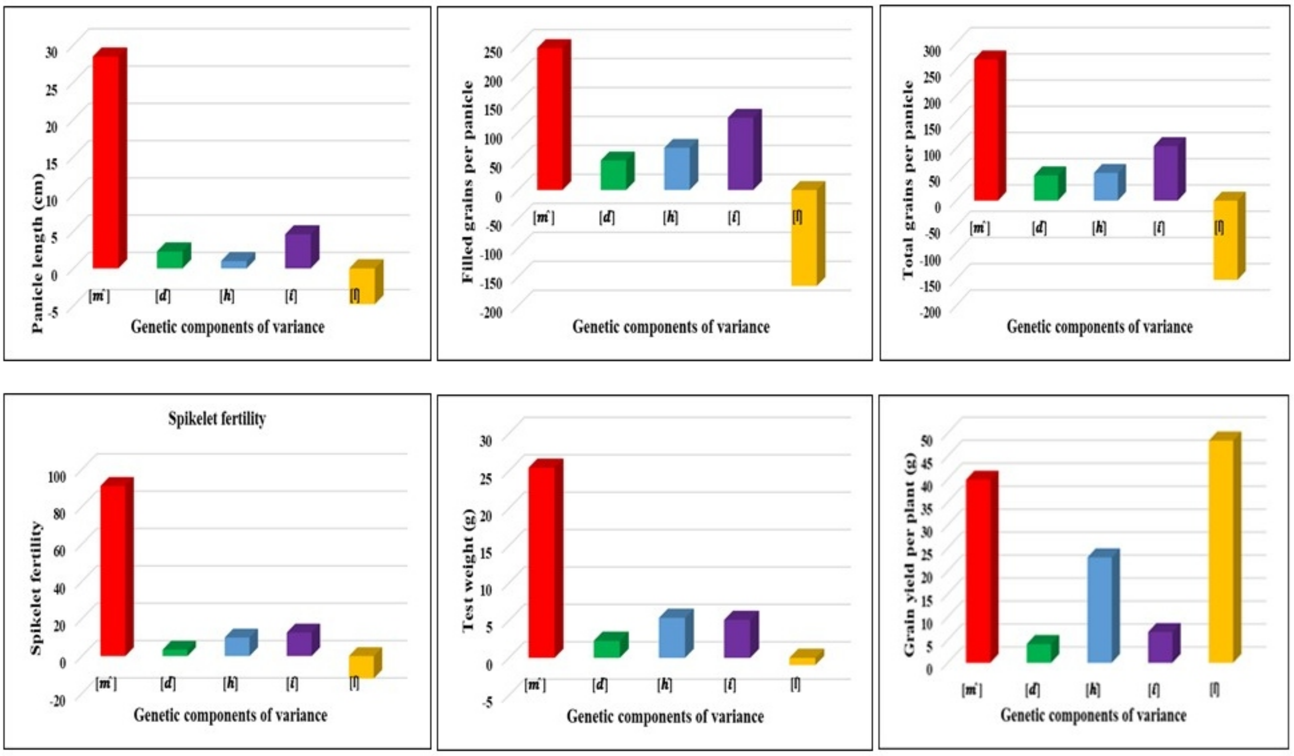

Fig. 3: Genetic components of AKDRMS 21-54 x YH3 cross for grain yield and yield component traits.

positive direction indicating the enhancing effect which helps in increasing the photosynthetic area. However, the grain yield per plant had significant dominance effect (h) and dominance × dominance (l) interaction effects in positive direction which is highly desirable for effecting early selections (Sreedhar *et al.*, 2005). The additive x additive gene interaction was predominant for shoot length (-13.97**), plant height (-31.54**), flag leaf length (9.21**), spikelet fertility (12.63**) and test weight (5.08**). The gene interaction is correspondent to homozygosity therefore, selection for these traits will be higher effective in early generations and breeding procedures, such as pedigree method of breeding may be adopted for isolation of desirable lines. However, in the traits days to 50 per cent flowering (-20.44**), productive tillers per plant (19.35**), flag leaf width (-0.67**), panicle length (-4.80*), filled grains per panicle (-165.60**) and total grains per panicle (-150.90**) along with grain yield per plant (48.36**), dominance x dominance gene interaction was found to be pre-dominant.

The gene interaction is not fixable and hence, population improvement approaches, such as bi-parental mating and recurrent selection, followed by isolation of purelines in later generations would be effective. The dominance (*h*) and dominance × dominance (*l*) gene effects displayed opposite signs for the traits *viz.,* shoot length (-2.21; 3.86), plant height (-9.68; 15.44), flag leaf width (0.15; -0.67), panicle length (0.98; -4.80), filled grains per panicle (72.75; -165.60), total grains per panicle (52.78; -150.90), spikelet fertility (9.95; -11.99) and test weight (5.35; -0.95) indicating duplicate epistasis. In contrast, days to 50 per cent flowering (-9.55; -20.44), productive tillers per plant (1.29; 19.35), flag leaf length (2.85; 4.09) and grain yield per plant (22.94; 48.36) reported same sign for (h) and (l), indicating complementary epistasis. Preponderance of dominance × dominance (*l*) gene effects along with complementary epistasis of inheritance was noticed in days to 50 per cent flowering (Savitha and Kumari, 2015), productive tillers per plant (Palaniraja, 2017) and grain yield per plant (Singh and Patel, 2020), similar to the results of earlier workers, indicating the need for adoption of an early generation selection in bi-parental mating for the traits. However, flag leaf length (Jondhale *et al.*, 2018) had exhibited preponderance of additive x additive (*i*) gene effects along with complementary epistasis, similar to earlier reports, indicating the importance of selection of transgressive segregants in early generations for these traits. In contrast, preponderance of additive x additive (*i*) gene effects along with duplicate epistasis were shown by, shoot length (Subbulakshmi *et al.,* 2016), plant height (Ganapathi *et al*., 2020), spikelet fertility (Kumari *et al.*, 2020) and test weight (Sand and Lal, 2014), in line with earlier findings, for which selection of transgressive segregants in later generations is advisable. However, flag leaf width (Divya *et al.*, 2014), panicle length (Kacharabhai, 2015), filled grains per panicle (Bano *et al.,* 2017) and total grains per panicle (Subbulakshmi *et al.*, 2016) exhibited preponderance of dominance × dominance (l) gene effects along with duplicate epistasis, in agreement with the results of earlier workers, for which Population improvement approach would be effective.

When there are numerous pairs of interacting genes, the classification of gene interactions depends on the estimations of the dominance and dominant dominance effects, as well as their magnitudes and signs (Jinks and Jones, 1958). The parent with the greatest concentration of genes for the trait is indicated by the sign corresponding to the estimates of (d) and (h) (Falconer, 1964). The positive sign for (d) was observed in the traits, days to 50 per cent flowering (3.00), flag leaf length (4.57), flag leaf width (0.22), panicle length (2.27), filled grains per panicle (51.04), total grains per panicle (48.13), spikelet fertility (3.44), test weight (2.28) and grain yield per plant (4.08), indicating that AKDRMS 21-54 contributed positively to these traits, as compared to YH3. Further, the negative sign for (h) was observed in the traits, days to 50 per cent flowering (-9.55), shoot length (-2.21) and plant height (-9.68) indicating that the dominance due to male parent YH3 as observed earlier by (Ghritlahre *et al.,* 2018).

The study revealed additive x additive gene action for shoot length, plant height, flag leaf length, spikelet fertility and test weight and hence, the effectiveness of selection for these traits in early generations and usefulness of pedigree method of breeding for isolation of desirable lines, while for all other traits, including grain yield per plant, dominance x dominance gene interaction was found to be pre-dominant. Therefore, population improvement approaches, such as bi-parental mating and recurrent selection, followed by isolation of purelines in later generations would be effective.

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Authors contribution: M.K. Duppala: Carried out entire research work and drafted the manuscript; **T. Srinivas:** Formulated the research work and evaluated the manuscript: **Y. Suneetha:** Examined the entire crossing programme and evaluated the manuscript; **G. Suresh:** Helped in lay out of the experiment, data collection and evaluation.

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