



Journal of Experimental Biology and Agricultural Sciences

<http://www.jebas.org>

ISSN No. 2320 – 8694

Gene action of yield and its contributing traits in wide-compatible elite rice (*Oryza sativa* L.) restorer lines

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Received – September 06, 2024; Revision – December 10, 2024; Accepted – December 27, 2024

Available Online – January 15, 2025

DOI: [http://dx.doi.org/10.18006/2024.12\(6\).850.859](http://dx.doi.org/10.18006/2024.12(6).850.859)

KEYWORDS

Wide compatibility

Generation mean analysis

Scaling test

Gene action

Genetic effects

ABSTRACT

Profiling the genetic architecture of quantitative traits, such as yield and its contributing factors, is essential for successful breeding programs. Understanding the genetic components of variation is key to maximizing genetic gains with precision in crop improvement programs. This study evaluated the genetics of yield and its contributing/attribution traits through generation mean analysis in six generations (P1, P2, F1, F2, B1, and B2) of crosses involving elite rice restorer lines. Results from the scaling tests indicated that epistatic interactions were present for all traits examined, except for effective tillers per plant in crosses I (CR 22-153-1 x Lemont) and II (CR 22-153-1 x CR 22-1-5-1). The six-parameter analysis showed a combination of additive, dominance, and epistatic gene effects, although their contributions varied. In both crosses, the additive or fixable variance was consistently lower than the non-additive variance for most yield-related traits. Among the genetic effects, the dominance effect and the dominance × dominance effect were significantly higher for most traits in both crosses. However, the values of these effects often exhibited opposite signs for different traits, underscoring the importance of duplicate epistasis in the inheritance and expression of these traits. The predominance of dominance, interaction effects, and duplicate epistasis across all studied traits and crosses limits the potential for early generation selection. Nevertheless, bi-parental matings between superior segregants may help disrupt undesirable linkages and produce favorable segregants with an accumulation of positive alleles for trait development.

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Peer review under responsibility of Journal of Experimental Biology and Agricultural Sciences.

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1 Introduction

Rice is a crucial cereal crop that is grown and consumed on every inhabited continent. It serves as a staple food in Asia, where 90% of its production and consumption occurs (Kumar et al. 2023). However, as the global population continues to grow and arable land decreases due to rapid urbanization, there is an urgent need to increase rice production on the limited land available. Enhancing rice yields through genetic improvements is the most feasible solution for rice breeders to meet this demand. Although India has the largest area of rice cultivation in the world, it still lags behind China in terms of production due to lower productivity and the slow adoption of hybrid varieties (Das et al. 2022a). Since high-yielding intraspecific rice varieties and hybrids of the *indica* × *indica* type have reached a yield plateau in India, breeders must seek new sources of genetic variability, such as inter-subspecific hybrids (*indica* × *japonica*), to boost productivity (Revathi 2015). Studies demonstrate that *indica* × *japonica* hybrids exhibit high heterotic potential (Ikehashi and Araki 1984), but their commercial production is limited by partial hybrid sterility, a post-zygotic issue (Sundaram et al. 2010). This sterility is controlled by a tri-allelic system, known as the wide compatibility (WC) system, located at the S5 locus on chromosome 6. The system includes three alleles: 'S5i' *indica* allele, 'S5j' *japonica* allele, and 'S5n' neutral allele (Chen et al. 2008). The interaction between the S5i and S5j alleles leads to partial hybrid sterility in *indica* × *japonica* hybrids. However, when 'S5n' allele interacts with either the S5i or S5j allele, it produces fully fertile embryos (Sundaram et al. 2010). Therefore, wide-compatible varieties (WCVs) that carry 'S5n' allele (WC gene) can act as a bridge to facilitate *indica-japonica* hybridization (Kallugudi et al. 2022). When developing a breeding strategy, breeders need to understand the type and extent of gene action that influences yield-contributing traits and overall yield. Generation mean analysis is the most commonly used, straightforward, and reliable biometrical method for studying gene action in quantitative traits such as yield and its associated characters or traits (Lenka et al. 2021). First-degree statistics are used to estimate mean (m), additive (d), dominance (h), and epistatic gene effects, including additive × additive (i), additive × dominance (j), and dominance × dominance (l) effects (Mather and Jinks 1971). Understanding the nature and extent of gene action for yield and its contributing traits is crucial for selecting superior parents and evaluating the effectiveness of selection among progeny with varying genetic values (Kumar et al. 2019). The six-parameter model (Hayman 1958) of generation mean analysis is the only biometrical approach that can estimate the nature and magnitude of all types of epistatic gene effects (i, j, and l), which is essential for accurately maximizing genetic gain. The objective of this study was to use generation mean analysis to assess gene action on yield and associated traits in two distinct crosses between elite restorer lines of rice.

2 Materials and Methods

This study involved two crosses: CR 22-153-1 × Lemont and CR 22-153-1 × CR 22-1-5-1. These were developed using three elite restorer lines (Table 1), selected for their superior combining ability. The experiment took place during the Rabi season of 2022-23 at the ICAR-National Rice Research Institute in Cuttack. A Compact Family Block Design was employed, where six generations were grown: Parent 1 (P1), Parent 2 (P2), the first filial generation (F1), the second filial generation (F2), and backcross generations B1 and B2. Each generation was cultivated in three replications following a standard package of agricultural practices. Observations were recorded for fifteen quantitative traits: days to 50% flowering (DFF), days to maturity (DM), plant height (PH), flag leaf length (FLL), flag leaf width (FLW), effective tillers per plant (ETPP), panicle length (PL), grains per panicle (GPP), chaff per panicle (CPP), spikelet fertility percentage (SF%), test weight (TW), yield per plant (YPP), grain length (GL), grain breadth (GB), and the grain length-breadth ratio (GL/B ratio). For observations, 20 plants from both parental and F1 populations, 30 plants from the backcross (BC) generations, and 40 plants from the F2 population were randomly selected. To evaluate the adequacy of the additive-dominance model, the mean and variance of all six generations across replications were analyzed using the scaling tests (A, B, C, and D) proposed by Mather (1949). When epistatic interactions were detected, Hayman's six-parameter model (1958) was used to estimate gene effects and their interactions. In the absence of epistasis, the three-parameter model (Jinks and Jones 1958) was employed to assess gene effects alone. Scaling Tests formulas as devised by (Mather 1949):

$$\begin{aligned} A &= 2\bar{B}_1 + \bar{P}_1 - \bar{F}_1 & V_A &= 4V_{B_1} + V_{P_1} + V_{F_1} \\ B &= 2\bar{B}_2 - \bar{P}_2 - \bar{F}_1 & V_B &= 4V_{B_2} + V_{P_2} + V_{F_1} \\ C &= 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2 & V_C &= 16V_{F_2} + 4V_{F_1} + V_{P_1} + V_{P_2} \\ D &= 2\bar{F}_2 - \bar{B}_1 - \bar{B}_2 & V_D &= 4V_{F_2} + V_{B_1} + V_{B_2} \end{aligned}$$

Standard errors and 't'-values of the above scales are calculated as follows:

$$\begin{aligned} \text{S.E.}_A &= (V_A)^{1/2} & t_A &= A / \text{S.E.}_A \\ \text{S.E.}_B &= (V_B)^{1/2} & t_B &= B / \text{S.E.}_B \\ \text{S.E.}_C &= (V_C)^{1/2} & t_C &= C / \text{S.E.}_C \\ \text{S.E.}_D &= (V_D)^{1/2} & t_D &= D / \text{S.E.}_D \end{aligned}$$

Where A, B, C, and D are the scales and $\bar{P}_1, \bar{P}_2, \bar{F}_1, \bar{F}_2, \bar{B}_1,$ and \bar{B}_2 are generated means of the trait. $V_A, V_B, V_C,$ and V_D are the corresponding variances of the scales and $V_{\bar{P}_1}, V_{\bar{P}_2}, V_{\bar{F}_1}, V_{\bar{F}_2}, V_{\bar{B}_1},$ and $V_{\bar{B}_2}$ are the variance of the sample means of respective generation.

Table 1 List of the elite restorer lines used in the study

S. N.	Parent genotype	Important feature
1	CR 22-153-1	Interspecific (<i>indica x japonica</i>) elite restorer –carrying fertility restorer genes, <i>Rf3</i> and <i>Rf4</i> but lacking <i>wc</i> gene
2	CR 22-1-5-1	Interspecific (<i>indica x japonica</i>) elite restorer possessing, <i>Rf3</i> , <i>Rf4</i> , and <i>WC</i> gene
3	Lemont	A <i>japonica</i> variety possessing <i>Rf3</i> , <i>Rf4</i> , and <i>WC</i> gene

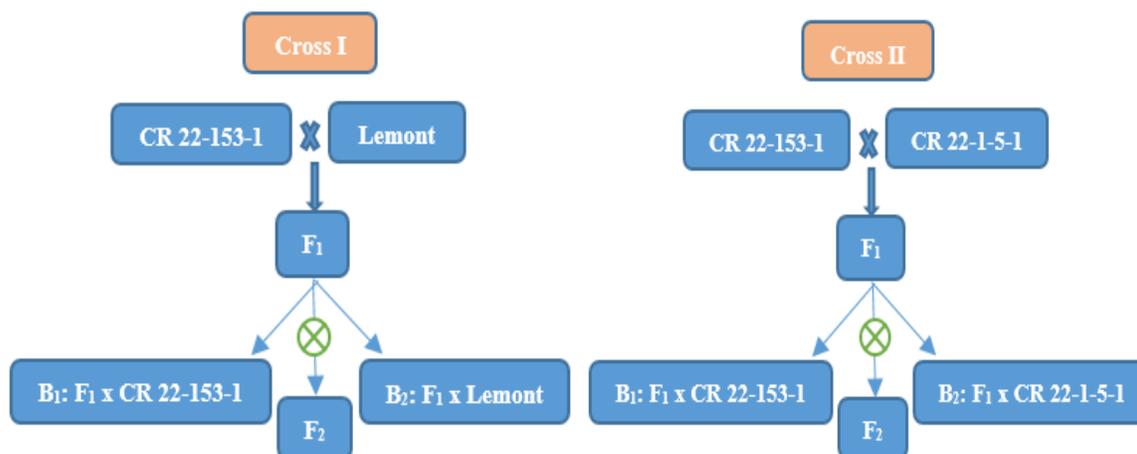


Figure 1 Two crosses made between the elite restorer lines

Estimation of the gene effects using the six-parameter model suggested by Hayman (1958) and Jinks and Jones (1958):

$$m = \bar{F}_2$$

$$d = \bar{B}_1 - \bar{B}_2$$

$$h = \bar{F}_1 - 4\bar{F}_2 - (\frac{1}{2})\bar{P}_1 - (\frac{1}{2})\bar{P}_2 + 2\bar{B}_1 + 2\bar{B}_2$$

$$i = 2\bar{B}_1 + 2\bar{B}_2 - 4\bar{F}_2$$

$$j = \bar{B}_1 - (\frac{1}{2})\bar{P}_1 + (\frac{1}{2})\bar{P}_2 - \bar{B}_2$$

$$l = \bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 + 4\bar{F}_2 - 4\bar{B}_1 - 4\bar{B}_2$$

Where,

m = mean effect

d = additive effect

h = dominance effect

i = additive \times additive type of gene interaction

j = additive \times dominance type of gene interaction

l = dominance \times dominance type of gene interaction

\bar{P}_1 , \bar{P}_2 , \bar{F}_1 , \bar{F}_2 , \bar{B}_1 , and \bar{B}_2 are the mean values of different generations.

Variances of the above gene effects are:

$$V_m = V_{\bar{F}_2}$$

$$V_d = V_{\bar{B}_1} + V_{\bar{B}_2}$$

$$V_h = V_{\bar{F}_1} + 16V_{\bar{F}_2} + (\frac{1}{4})V_{\bar{P}_1} + (\frac{1}{4})V_{\bar{P}_2} + 4V_{\bar{B}_1} + 4V_{\bar{B}_2}$$

$$V_i = 4V_{\bar{B}_1} + 4V_{\bar{B}_2} + 16V_{\bar{F}_2}$$

$$V_j = V_{\bar{B}_1} + (\frac{1}{4})V_{\bar{P}_1} + (\frac{1}{4})V_{\bar{P}_2} + V_{\bar{B}_2}$$

$$V_l = V_{\bar{P}_1} + V_{\bar{P}_2} + 4V_{\bar{F}_1} + 16V_{\bar{F}_2} + 16V_{\bar{B}_1} + 16V_{\bar{B}_2}$$

Where, $V_{\bar{P}_1}$, $V_{\bar{P}_2}$, $V_{\bar{F}_1}$, $V_{\bar{F}_2}$, $V_{\bar{B}_1}$, and $V_{\bar{B}_2}$ are the mean variances of the sample mean of the respective generation

Standard errors and 't'-values for the above gene effects are calculated as follows:

$$S.E. m = (V_m)^{1/2} \quad t_m = m / S.E. m$$

$$S.E. d = (V_d)^{1/2} \quad t_d = d / S.E. d$$

$$S.E. h = (V_h)^{1/2} \quad t_h = h / S.E. h$$

$$S.E. i = (V_i)^{1/2} \quad t_i = i / S.E. i$$

$$S.E. j = (V_j)^{1/2} \quad t_j = j / S.E. j$$

$$S.E. l = (V_l)^{1/2} \quad t_l = l / S.E. l$$

3 Results and Discussion

The suitability of the additive-dominance model for estimating genetic components was evaluated using the A, B, C, and D scales. The results from both crosses showed significance for at least one

of the scales for nearly every trait examined, except for the effective tillers per plant in Cross I (CR 22-153-1 x Lemont) and Cross II (CR 22-153-1 x CR 22-1-5-1). The scaling test results (Table 2) indicated significant epistatic interactions for nearly all traits, rendering the additive-dominance model ineffective for

Table 2 Scaling test of fifteen quantitative traits for Cross-I and Cross-II

Traits	Cross	A ± SeA	B ± SeB	C ± SeC	D ± SeD
DFF	I	-7.60±0.82**	0.9±0.95	-3.40±1.46*	1.65±0.77*
	II	2.00±1.02*	4.25±1.07**	-12.25±2.00**	-9.25±0.82**
DM	I	-7.15±1.08**	0.2±1.06	-3.35±1.63*	1.8±0.90*
	II	2.55±1.11*	5.55±1.07**	-10.00±2.16**	-9.05±0.94**
PH	I	6.50±3.08*	0.23±3.06	-11.26±5.45*	-8.99±2.84**
	II	2.05±3.34	4.2±3.30	-11.85±6.00*	-9.05±2.98**
FLL	I	-18.70±2.41**	-1.35±1.64	-27.55±2.81**	-3.75±1.64*
	II	4.71±2.13*	4.15±1.93*	-7.20±3.40*	-8.03±1.61**
FLW	I	-0.30±0.10**	-0.18±0.09*	-1.09±0.15**	-0.31±0.07**
	II	-0.19±0.09*	-0.20±0.08*	-0.65±0.13**	-0.13±0.06*
ETPP	I	-0.6±0.53	-1.15±0.62	-2.25±1.31	-0.25±0.65
	II	0.5±0.45	0.05±0.50	-0.25±1.13	-0.4±0.55
PL	I	-4.20±1.25**	-5.39±0.70**	-10.27±1.20**	-0.34±0.82
	II	4.39±1.03**	2.38±1.20*	0.7±2.19	-3.03±1.24**
GPP	I	-48.50±18.37**	-17.85±16.08	-305.85 ± 22.66**	-119.75±10.42**
	II	65.50±29.86*	-23.1±24.59	-133.40±66.74*	-87.9±36.98**
CPP	I	6.25±22.01	43.70±14.13**	-33.55±13.74*	-41.75±13.20**
	II	59.15±19.84**	121.85±15.82**	289.20±43.47**	54.1±23.64*
SF%	I	-3.54±4.51	-14.45±4.43**	-17.40±4.10**	0.3±3.45
	II	-8.26±3.74*	-29.66±3.17**	-65.61±7.14**	-13.84±3.92**
TW	I	0.1±0.07	0.26±0.08**	0.29±0.18	0.02±0.09
	II	0.20±0.08**	-0.14±0.07*	-0.26±0.13*	-0.16±0.07*
YPP	I	-2.07±1.37	3.26±0.96**	-11.05±1.78**	-6.12±0.82**
	II	4.24±1.51**	-1.51±1.11	-8.20±3.45*	-5.47±1.70**
GL	I	0.775±0.227**	0.571±0.236*	1.296±0.429**	-0.025±0.23
	II	-0.05±0.160	0.748±0.315*	-0.392±0.511	-0.54±0.27*
GB	I	-0.191±0.068**	0.221±0.054**	-0.314± 0.116**	-0.17±0.06**
	II	0.276±0.100**	-0.256±0.129*	0.758±0.174**	0.37±0.11**
G. L/B ratio	I	0.522±0.135**	-0.143±0.100	0.867±0.239**	0.24±0.13*
	II	-0.341±0.103**	0.872±0.338**	-1.149±0.341**	-0.84±0.23**

** -Significant at $P = 0.01$, * - Significant at $P = 0.05$, days to fifty percent flowering (DFF), days to maturity (DM), plant height (PH), flag leaf length (FLL), flag leaf width (FLW), effective tillers per plant (ETPP), panicle length (PL), grains per panicle (GPP), chaff per panicle (CPP), spikelet fertility % (SF%), test-weight (TW), yield per plant (YPP), grain length (GL), breadth (GB), and grain length-breadth ratio (G L/B ratio),

assessing all the genetic components. To comprehensively evaluate all genetic components, the six-parameter model of generation mean analysis was used to analyze the mean and variance data for each trait in both crosses, with the exception of effective tillers per plant. For this specific trait, a three-parameter model was applied to estimate only the gene effects in both crosses. These findings are consistent with previous studies (Gobu et al. 2021; Arsode et al. 2022; Sharma et al. 2024). The breakdown of the generation mean into six distinct genetic components revealed that the mean effect (m) had a significant positive influence, with a greater magnitude than other genetic effects for nearly every trait in both crosses tested (Table 3). This suggests that these traits exhibited significant variation across generations and were quantitatively inherited. However, in Cross I, the magnitude of the genetic components (h and i) surpassed the mean effect for grains per plant (GPP), while the components (l, h, and i) exceeded the mean effect for chaffs per plant (CPP). Similar results were reported by Das et al. (2022b) and Ganapati et al. (2020).

Our findings indicated that all gene and interaction effects were significant for days to fifty percent flowering (DFF) in both crosses. Among the genetic components measured, the magnitude of 'h' (-13.0**) was highest in Cross I, whereas 'l' (-24.75**) was highest in Cross II. This suggests that the nature and magnitude of the interaction components are specific to each cross. The significant values of 'h' and 'l' with opposing signs in both crosses indicate the presence of duplicate epistasis in the inheritance and expression of this trait. The stronger dominance effect, combined with duplicate epistasis, suggests that plant selection should be postponed to later generations, with the intermating of segregants followed by recurrent selection to enhance the trait. Similar findings have been reported in previous studies (Lingaiyah et al. 2020; Das et al. 2022a; Sakr et al. 2024). The negative dominance gene effect 'h' in Cross I (-13.0**) indicates that Lemont contributed more to the expression of the trait. Both crosses exhibited significant genetic effects for days to maturity (DM). Among all genetic components, the 'l' (-26.2**) component had the highest value in Cross II, while 'h' (-13.78**) was the highest in Cross I. The negative values for 'l' indicated ambidirectional dominance between the parents. Both 'h' and 'l' showed significant values with opposite signs in both crosses, further suggesting the presence of duplicate epistasis in the inheritance and expression of the trait. Similar results were reported by Gobu et al. (2021), Sreelakshmi and Babu (2022), and Arsode et al. (2022). The presence of a strong dominance effect and duplicate epistasis limited the potential for early generation selection. The negative dominance gene effect 'h' in Cross I (-13.78**) indicates that Lemont contributed dominant genes for the expression of DM.

All genetic components, except for 'j', were significant for plant height (PH) in both crosses, with 'l' demonstrating the highest value. Plant height exhibited ambidirectional dominance between

the parents, as indicated by the negative values for 'l' in both Cross-I (-24.71**) and Cross-II (-24.35**). The positive and high values of 'i' in both Cross-I (17.98**) and Cross-II (18.1**) suggested a strong association of alleles in the parents. The opposite signs for 'h' and 'l' in both crosses indicated the presence of duplicate epistasis in the inheritance and expression of the trait. These findings align with those reported by Solanke et al. (2019), Kumar et al. (2024), and Nofal and Gaballah (2024). The dominance of interaction effects, coupled with duplicate epistasis, suggests that selection should be postponed until more advanced generations. The negative values for the additive gene effects 'd' in both Cross-I (-3.5*) and Cross-II (-4.25*) indicated significant contributions from Lemont and CR 22-1-5-1 to the expression of the trait in their respective crosses.

For flag leaf length (FLL), the magnitude of all genetic components was substantial in Cross-I, while all components except 'j' were significant in Cross-II. The 'j' component (-17.35**) had the largest magnitude among all components in Cross-I, while 'l' (-24.92**) showed the highest value in Cross-II. In Cross-I, both 'h' and 'l' had identical signs (both positive), indicating complementary epistasis. However, in Cross-II, they had opposing signs, suggesting duplicate epistasis in the inheritance and expression of the trait. These findings highlight the complexities involved in the trait's inheritance and expression, as well as the influence of the cross combination on improvement. These results are consistent with those of Arsode et al. (2022), Kathiresan et al. (2024), and Sakr et al. (2024). The negative value of the additive gene effect 'd' in Cross-I (-2.75*) suggests that Lemont is the major contributor to the expression of this trait.

For flag leaf width (FLW), the genetic components 'd', 'h', and 'i' were significant in both Crosses-I and II, with 'h' showing the highest magnitude in both cases. The additive genetic components ('d' and 'i') were positive, and their sum exceeded the non-additive dominance component 'h' in both crosses. This suggests that selection should be postponed to later generations until the epistatic effect is reduced. Similar observations for flag leaf width were reported by Kumar et al. (2024), Kathiresan et al. (2024), and Gobu et al. (2021).

For effective tillers per plant (ETPP), the non-significant values for all four scales necessitated the use of the three-parameter model to estimate gene effects in both crosses. In both crosses, only the dominance gene effect 'd' showed a significant value, indicating the involvement of additive gene action in the inheritance and expression of the trait. Similar findings for effective tillers per plant were reported by Gajanan (2015) and Ganapati et al. (2020). Simple selection in early generations or a pedigree breeding strategy would be effective in exploiting the additive gene action present in this trait. However, such results are likely to occur only in specific crosses, as observed in this experiment. The negative additive effect 'd' in

Table 3 Genetic effects of fifteen quantitative traits for Cross I and II

Trait	Cross	$m \pm \text{Sem}$	$d \pm \text{Sed}$	$h \pm \text{Seh}$	$i \pm \text{Sei}$	$j \pm \text{Sej}$	$l \pm \text{Sel}$	Epistasis Type
DFF	I	105.90±0.29**	2.05±0.51**	-13.00±1.61**	-3.30±1.55*	-8.50±1.13**	10.00±4.57*	Duplicate
	II	109.05±0.33**	3.05±0.49**	15.28±1.80**	18.50±1.63**	-2.25±1.07*	-24.75±4.72**	Duplicate
DM	I	132.45±0.32**	3.30±0.64**	-13.78±1.88**	-3.60±1.81*	-7.35±1.39**	10.55±4.71*	Duplicate
	II	135.75±0.39**	3.75±0.53**	14.40±2.03**	18.10±1.88**	-3.00±1.18**	-26.20±4.81**	Duplicate
PH	I	97.26±1.11**	-3.50±1.76*	16.44±5.89**	17.98±5.67**	6.27±3.93	-24.71±8.26**	Duplicate
	II	99.70±1.17**	-4.25±1.86*	19.78±6.26**	18.10±5.97**	-2.15±4.02	-24.35±8.94**	Duplicate
FLL	I	33.00±0.54**	-2.75±1.24*	7.13±3.40*	7.50±3.28*	-17.35±2.75**	12.55±5.66*	Complementary
	II	41.00±0.59**	2.63±1.09**	16.16±3.45**	16.06±3.22**	0.56±2.42	-24.92±6.04**	Duplicate
FLW	I	1.79±0.03**	0.13±0.05*	0.73±0.15**	0.61±0.14**	-0.13±0.11	-0.13±4.00	-
	II	2.01±0.02**	0.10 ±0.05*	0.32±0.14*	0.26±0.13*	0±0.11	0.13±4.00	-
ETPP	I	6.63±1.32**	-1.02±0.16*	-0.97±30.42	-	-	-	No Epistasis
	II	5.83±1.10**	-0.53±0.15**	1.73±30.23	-	-	-	No Epistasis
PL	I	26.41±0.24**	1.61±0.66**	3.32±1.68*	0.67±1.64	1.19±1.38	8.93±4.38*	Complementary
	II	28.14±0.50**	1.41±0.72*	5.46±2.51*	6.06±2.48**	2.01±1.49	-12.82±5.09**	Duplicate
GPP	I	191.85±2.31**	55.15±9.34**	206.28±23.27**	239.50±20.84**	-30.65±20.37	-173.15±34.23**	Duplicate
	II	281.45±16.12**	99.80±18.12**	205.60±74.46**	175.80±73.96*	88.60±37.17*	-218.20±82.26**	Duplicate

Trait	Cross	$m \pm \text{Sem}$	$d \pm \text{Sed}$	$h \pm \text{Seh}$	$i \pm \text{Sei}$	$j \pm \text{Sej}$	$l \pm \text{Sel}$	Epistasis Type
CPP	I	51.95±2.36**	29.55±12.33*	64.03±26.88*	83.50±26.41**	-37.45±25.68	-133.45±32.46**	Duplicate
	II	138.30±10.34**	14.3±11.48	-121.60±47.76**	-108.20±47.29*	-62.70±24.09**	-72.8±53.33	-
SF%	I	78.77±0.83**	-2.34±3.01	-0.34±6.99	-0.59±6.89	10.91±6.15*	18.58±10.51	-
	II	67.31±1.63**	3.27±2.17	29.87±7.97**	27.69±7.83**	21.40±4.53**	10.24±10.07	-
TW	I	1.98±0.04**	0.17±0.05**	-0.05±0.19	-0.04±0.19	-0.26±0.10**	-0.21±4.01	-
	II	2.08±0.03**	0.25±0.04**	0.37±0.15**	0.32±0.14*	0.34±0.10**	-0.37±4.00	-
YPP	I	22.15±0.28**	2.20±0.59**	11.55±1.78**	12.25±1.64**	-5.32±1.51**	-13.44±4.64**	Duplicate
	II	25.79±0.78**	5.36±0.69**	11.30±3.48**	10.93±3.40**	5.75±1.68**	-13.66±5.58**	Duplicate
GL	I	8.450±0.091**	0.284±0.135*	0.981±0.466*	0.05±0.452	0.204±0.298	-1.396±0.689*	Duplicate
	II	8.400±0.115**	-0.954±0.149**	1.290±0.559*	1.089±0.547*	-0.798±0.331**	-1.786±0.786**	Duplicate
GB	I	2.322±0.026**	0.209±0.037**	0.430±0.131**	0.344±0.128**	-0.412±0.083**	-0.373±0.189*	Duplicate
	II	2.700±0.040**	0.516±0.077**	-0.761±0.226**	-0.738±0.22**	0.532±0.160**	0.719±0.354*	Duplicate
G. L/B ratio	I	3.647±0.053**	-0.179±0.071**	-0.314±0.263	-0.488±0.257	0.664±0.157**	0.109±0.372	-
	II	3.131±0.079**	-1.166±0.169**	1.731±0.468**	1.679±0.464**	-1.213±0.348**	-2.210±0.757**	Duplicate

** -Significant at $P = 0.01$, * - Significant at $P = 0.05$, days to fifty percent flowering (DFF), days to maturity (DM), plant height (PH), flag leaf length (FLL), flag leaf width (FLW), effective tillers per plant (ETPP), panicle length (PL), grains per panicle (GPP), chaff per panicle (CPP), spikelet fertility % (SF%), test-weight (TW), yield per plant (YPP), grain length (GL), breadth (GB), and grain length-breadth ratio (G L/B ratio)

Cross-I (-1.02*) and Cross-II (-0.53**) indicated that Lemont and CR 22-1-5-1 made significant contributions to the expression of the trait in their respective crosses.

For panicle length (PL), all genetic components except for 'j' were significant in cross II, while 'i' and 'j' were insignificant in cross I. In cross I, the largest value was for 'l' (8.93*), followed by 'h' (3.32*) and 'd' (1.61**). In cross II, 'l' had the highest value (-12.82**), followed by 'i' (6.06**), 'h' (5.46**), and 'd' (1.41*). The magnitudes of both 'h' and 'l' in cross I had similar signs, indicating complementary interactions. In contrast, in cross II, they had opposite signs, suggesting the presence of duplicate interactions in the inheritance and expression of the trait. This highlights the complexities involved in trait inheritance and expression, as well as the influence of cross-combinations on trait improvement. Similar findings regarding panicle length have been reported by Sahoo et al. (2022), Kathiresan et al. (2024), and Sakr et al. (2024). Cross I has the potential to benefit from heterosis breeding due to the significant dominance effects present. The negative value of 'l' in cross II indicates ambidirectional dominance, which, along with duplicate epistasis, limits the potential for early-generation selection to enhance this trait.

In terms of grains per panicle (GPP), all genetic components were significant in cross II, while all except 'j' were significant in cross I. In cross I, 'i' had the highest value (239.5**), followed by 'h' (206.28**), 'l' (-173.15**), and 'd' (55.15**). In cross II, 'l' had the highest value (-218.2**), followed by 'h' (205.6**), 'i' (175.8*), 'd' (99.8**), and 'j' (88.6*). The positive and high magnitude of 'i' indicates a strong association of alleles in the parents. The influence of duplicate epistasis on the inheritance and expression of this trait was evident from the opposing signs of 'h' and 'l'. Similar results have been found in previous research (Arsode et al. 2022; Kumar et al. 2024; Kathiresan et al. 2024). The negative signs for 'l' in both crosses indicate ambidirectional dominance between the parents, which, together with duplicate epistasis, reduces the potential for early generation selection to improve the trait. The majority of the genetic components displayed nearly equal magnitudes, suggesting that population improvement could lead to the development of superior lines carrying several desirable genes.

In terms of chaff per panicle (CPP), the significant genetic components identified in cross I included 'd', 'h', 'i', and 'l'. Meanwhile, in Cross II, the significant components were 'h', 'i', and 'j'. Cross I recorded the largest magnitude for the genetic component 'l' (-133.45**), whereas Cross II showed the largest magnitude for 'h' (-121.6**). The contrasting signs for 'h' and 'l' in cross I suggest that there are duplicate interactions involved in the inheritance and expression of this trait. Similar findings for CPP have been reported by Ganapati et al. (2020), Gobu et al. (2021), and Sreelakshmi and Babu (2022).

For test weight (TW), all genetic components except for 'l' were significant in Cross II, while only 'd' and 'j' were significant in Cross I. In Cross II, the largest magnitude was observed for 'h' (0.37**), while in Cross I, the largest magnitude was recorded for 'j' (-0.26**). These results are consistent with previous studies (Solanke et al. 2019; Gobu et al. 2021; Kathiresan et al. 2024).

When examining yield per plant (YPP), all genetic components were significant in both crosses. In Cross I, the highest magnitude was recorded for 'l' (-13.44**), followed by 'i' (12.25**), 'h' (11.55**), 'j' (-5.32**), and 'd' (2.2**). In Cross II, the highest magnitude was also for 'l' (-13.66**), followed by 'h' (11.30**), 'i' (10.93**), 'j' (5.75**), and 'd' (5.36**). The negative values for 'l' indicate ambidirectional dominance, while the substantial positive dominance gene effect for 'h' and the highly significant negative dominance \times dominance effect for 'l' suggest duplicate epistasis in the inheritance and expression of this trait. These results align with the findings of Arsode et al. (2022), Sakr et al. (2024), Kumar et al. (2024), and Nofal and Gaballah (2024) regarding per plant yield. These observations suggest that selection may be delayed until the dominance and epistatic effects dissipate in advanced generations. Additionally, biparental mating of superior segregants, along with recurrent selection, might be effective in producing desirable segregants.

In the case of grain length (GL), all genetic components were found to be significant in Cross II. However, in Cross I, all the components except for 'i' and 'j' were significant. The highest value for the parameter 'l' was observed in both crosses, measuring -1.4* in Cross I and -1.79** in Cross II. Grain length demonstrated ambidirectional dominance, as indicated by the negative value of 'l'. The contrasting signs of 'h' and 'l' in both crosses suggested duplicate interactions in how the trait is inherited and expressed. Consequently, it is advisable to defer selection to advanced generations. Strategies such as biparental matings or recurrent selection could be employed to obtain desirable early segregants. Similar findings were reported by Sharma et al. (2024) and Kour et al. (2019). Furthermore, the negative value of the additive gene effect 'd' in Cross II (-0.95**) indicated that the genotype CR 22-1-5-1 played a significant role in the expression of this trait.

For grain breadth (GB), all genetic components were significant in both crosses. Among these, the highest values were observed for 'h', with measurements of 0.43** in Cross I and -0.76** in Cross II. The contrasting signs of 'h' and 'l' in both crosses suggested the presence of duplicate-type interactions in the trait's inheritance and expression. Non-allelic interactions with duplicate-type epistasis can be effectively utilized in pedigree breeding by delaying selection until advanced generations. These results align with the findings reported by Sharma et al. (2024) and Kamara et al. (2017).

Additionally, the negative dominance effect 'h' in Cross II suggested that the genotype CR 22-1-5-1 harbors dominant genes influencing trait expression.

Regarding the grain length-breadth ratio (GL/B ratio), all genetic components were significant in Cross II, while only 'd' and 'j' were significant in Cross I. The highest magnitude was recorded for 'l' in Cross II at -2.21** and for 'j' in Cross I at 0.66**. In Cross II, the contrasting signs of 'h' and 'l' indicated the presence of duplicate-type interactions for the inheritance and expression of this trait. These findings are consistent with those of Kour et al. (2019). The negative values for the additive gene effect 'd' in both crosses suggested that the male parent significantly contributed to the expression of the trait in their respective crosses.

Conclusion

The analysis of yield and its contributing traits in both crosses indicated that a combination of additive, dominance, and epistatic gene effects influenced most traits. Generally, non-additive effects outweighed additive ones, except for effective tillers per plant and flag leaf width, where additive effects were significant. The dominance effect ('h') was greater than the additive effect ('d') for most traits, suggesting substantial genetic variation between the parental lines. The dominance \times dominance ('l') effect was the strongest interaction, followed by additive \times additive ('i') and additive \times dominance ('j') effects. These interactions often showed opposing directions, indicating the presence of duplicate epistasis, which can reduce the effectiveness of early-generation selection. Notably, dominance \times dominance interactions had the highest frequency of negative values. Contrasting signs in interactions for traits such as days to fifty percent flowering (DFF), days to maturity (DM), plant height (PH), grain per plant (GPP), yield per plant (YPP), grain length (GL), grain breadth (GB), and grain length to breadth ratio (GL/B) suggested that there are dispersed alleles in the interacting loci. These findings highlight the significance of dominance and interaction effects in the genetic control of yield-related traits. It is recommended to use biparental mating of superior segregants to break undesirable linkages and concentrate favorable alleles for improved yield.

Conflict of interest

The authors declare that they have no conflict of interest.

Funding

The authors did not receive funding from any organization for the submitted work.

Ethical Clearance

No ethical clearance required for this study.

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