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Generation Mean Analysis Reveals the Inheritance of Yield and its Components in Wide Compatible Elite *indica* Rice Restorer Line

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Abstract

The experiment was conducted during *rabi* (December-2021 to April-2022) at ICAR–National Rice Research Institute (NRRI), Cuttack, Odisha, India to unravel the genetic architecture underlying yield and its associated traits, generation mean analysis was conducted on six generations (P_1, P_2, F_1, F_2, B_1 and B_2) derived from a cross between two elite rice restorer lines, CR 1033 and CR 22-1-5-1. Results from the scaling tests indicated the presence of epistatic interactions across all studied traits, necessitating the application of a six-parameter model to dissect the generation means into additive, dominance, and interaction components. The inheritance of all evaluated traits was governed by a complex interplay of additive, dominance, and epistatic gene actions, with non-additive variance consistently surpassing additive or fixable variance components. For the majority of traits, dominance effects (h) emerged as the most influential gene effects, while (dominance×dominance) interactions (l) represented the predominant epistatic effects. Interestingly, several traits—including days to 50% flowering, days to maturity, plant height, grains panicle^{-1}, yield plant^{-1}, grain length, grain width, and the grain length-to-width ratio—displayed opposing signs for dominance effects (h) and (dominance×dominance) interactions (l), suggesting the involvement of duplicate epistasis in their genetic control. Consequently, selection for these traits may be more effective in later generations. Furthermore, bi-parental mating among superior segregants may help disrupt unfavorable linkages and facilitate the accumulation of desirable alleles. Traits such as plant height, grain width, and the grain length-to-width ratio exhibited significant negative heterobeltiosis, largely due to the subpar performance of F_1 hybrids relative to their parents.

Keywords: Wide-compatibility, generation mean analysis, scaling test, gene action

1. Introduction

Rice is a staple cereal crop cultivated and consumed across all inhabited continents, with Asia accounting for nearly 90% of global production and consumption. In this region, rice is not merely a dietary staple but a critical pillar of food security (Khush, 2005). Nutritionally, rice serves as an excellent source of carbohydrates-the body's primary energy supply-while also providing modest amounts of protein and fat (Huang, 2024). As the global population continues to expand, the importance of rice as a fundamental food source will only intensify (Fukagawa and Ziska, 2019). However, the twin challenges of rapid population growth and accelerating urbanization-which steadily encroach upon arable land-have created an urgent need to enhance rice productivity on diminishing cultivated areas (Kumar et al., 2023). In this context, genetic improvement of rice parental lines and the advancement of hybrid rice technology emerge as the most promising strategies for breeders aiming to sustainably increase yields (Nanda et al., 2024). Despite possessing the largest area under rice cultivation worldwide, India continues to lag behind China in total rice production, primarily due to lower productivity and the limited adoption of hybrid rice varieties (Das et al., 2022a). Moreover, as the yielding potential of high-performing intraspecific (*indica*×*indica*) hybrids in India shows signs of plateauing, it has become imperative for breeders to seek new sources of genetic diversity (Dan

et al., 2014). One particularly promising direction lies in the development of inter-subspecific hybrids-specifically crosses between the *indica* and *japonica* subspecies-which are known to exhibit significantly higher heterotic potential (Ikehashi and Araki, 1984).

Despite their promising yield potential, the widespread commercial use of *indica*×*japonica* hybrids have been hindered by partial hybrid sterility (Sakthivel et al., 2024), which arises post-zygotically (Sundaram et al., 2010). This sterility is governed by a tri-allelic system at the S5 locus on chromosome 6, known as the wide compatibility (WC) system (Yang et al., 2012). The system comprises three alleles: the S5-i (*indica*), S5-j (*japonica*), and the S5-n (neutral) allele (Chen et al., 2008). Crosses between S5-i and S5-j alleles typically result in partial sterility, whereas the presence of the S5-n allele-either in combination with S5-i or S5-j-leads to complete fertility in hybrids (Sundaram et al., 2010). Therefore, wide-compatible varieties (WCVs) harboring the S5-n allele serve as effective genetic bridges to facilitate *indica-japonica* hybridization (Kallugudi et al., 2022).

In designing effective breeding strategies, it is essential for breeders to comprehend both the nature and magnitude of gene action governing yield and its component traits (Naing et al., 2024). Generation mean analysis serves as a robust and straightforward biometrical approach for unraveling the genetic architecture of complex quantitative traits, including yield (Lenka et al., 2021). This method enables the estimation of key genetic parameters-mean (m), additive (d), and dominance (h) effects-as well as epistatic interactions such as additive×additive (i), additive×dominance (j), and dominance×dominance (l) effects, utilizing first-order statistical values like the mean data of different generations under study (Mather and Jinks, 1971). Such insights are vital for the selection of superior parental lines and for enhancing selection efficiency among segregating progenies with diverse genetic potential (Pujar et al., 2022). The six-parameter model of generation mean analysis remains one of the most comprehensive frameworks for capturing the full spectrum of gene interactions, particularly epistasis, thus making it an indispensable tool for achieving precise and sustainable genetic improvement (Yadav et al., 2017). In this context, the present study was undertaken to investigate the nature of gene action controlling yield and its associated traits through generation mean analysis in a cross between two elite rice restorer lines.

2. Materials and Methods

The present investigation was carried out during *Rabi* (December–2021 to April–2022) at the ICAR-National Rice Research Institute (NRRI), Cuttack, Odisha, India utilizing two elite restorer lines with proven combining ability (Table 1). A cross between these lines was made during the rabi (December-2020 to April-2021) to generate the F_1 (first filial) generation. Subsequently, the F_2 (second filial) generation and two backcross generations-B_1 (F_1×P_1) and B_2 (F_1×P_2)-

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

Sl. No.	Genotypes	Properties
1.	CR 1033	an *indica* line having *Rf*3 and *Rf*4 genes but lacking WC gene
2.	CR 22-1-5-1	an *indica*×*japonica*–derivative line possessing *Rf*3, *Rf*4, and WC gene

were developed during *kharif* (June-2021 to October-2021). All six generations-P_1 (Parent 1), P_2 (Parent 2), F_1, F_2, B_1, and B_2-were evaluated during the *rabi* season of 2022 in a Compact Family Block Design with three replications, following standard agronomic practices recommended for rice cultivation. Phenotypic 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 plant^{-1} (ETPP), panicle length (PL), grains panicle^{-1} (GPP), chaffs panicle^{-1} (CPP), spikelet fertility percentage (SF %), test weight (TW), yield plant^{-1} (YPP), grain length (GL), grain width (GW), and grain length-to-width ratio (GL/W ratio). For data collection, 20 plants were randomly selected from each replication of the non-segregating generations (P_1, P_2 and F_1), 30 plants from the backcross generations (B_1 and B_2), and 40 plants from each replication of the segregating F_2 generation. The mean and variance values for each trait, averaged across replications, were subjected to four scaling tests (A, B, C and D) as outlined by Mather (1949) to determine the adequacy of the additive-dominance model. When the absence of epistatic interactions was confirmed, gene effects were estimated using the three-parameter model proposed by Jinks and Jones (1958). However, in the presence of epistasis, the six-parameter model developed by Hayman (1958) was employed to partition the generation means into main gene effects and epistatic interaction effects.

Scaling Tests formulas as devised by (Mather 1949):

$A=2\bar{B}_1+\bar{P}_1-\bar{F}_1$ $\quad V_A=4V_{\bar{B}1}+V_{\bar{P}1}+V_{\bar{F}1}$

$B=2\bar{B}_2-\bar{P}_2-\bar{F}_1$ $\quad V_B=4V_{\bar{B}2}+V_{\bar{P}2}+V_{\bar{F}1}$

$C=4\bar{F}_2-2\bar{F}_1-\bar{P}_1-\bar{P}_2$ $\quad V_C=16V_{\bar{F}2}+4V_{\bar{F}1}+V_{\bar{P}1}+V_{\bar{P}2}$

$D=2\bar{F}_2-\bar{B}_1-\bar{B}_2$ $\quad V_D=4V_{\bar{F}2}+V_{\bar{B}1}+V_{\bar{B}2}$

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

$S.E._A=(V_A)^{1/2}$ $\quad t_A=A/S.E._A$

$S.E._B=(V_B)^{1/2}$ $\quad t_B=B/S.E._B$

$S.E._C=(V_C)^{1/2}$ $\quad t_C=C/S.E._C$

$S.E._D=(V_D)^{1/2}$ $\quad t_D=D/S.E._D$

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 variance 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.

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

$m=\bar{F}_2$

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

$h=\bar{F}_1-4\bar{F}_2-(½)\bar{P}_1-(½)\bar{P}_2+2\bar{B}_1+2\bar{B}_2$

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

$j=\bar{B}_1-(½)\bar{P}_1+(½)\bar{P}_2-\bar{B}_2$

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

Where,

m=mean effect

d=additive effect

h=dominance effect

i=additive×additive type of gene interaction

j=additive×dominance type of gene interaction

l=dominance×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:

$V_m=V_{\bar{F}2}$

$V_d=V_{\bar{B}1}+V_{\bar{B}2}$

$V_h=V_{\bar{F}1}+16V_{\bar{F}2}+(1/4)V_{\bar{P}1}+(1/4)V_{\bar{P}2}+4V_{\bar{B}1}+4V_{\bar{B}2}$

$V_i=4V_{\bar{B}1}+4V_{\bar{B}2}+16V_{\bar{F}2}$

$V_l=V_{\bar{P}1}+V_{\bar{P}2}+4V_{\bar{F}1}+16V_{\bar{F}2}+16V_{\bar{B}1}+16V_{\bar{B}2}$

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:

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

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

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

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

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

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

Heterosis Formulas:

Mid-Parent Heterosis (MPH %) $=\dfrac{(\bar{F}_1-\overline{MP})}{\overline{MP}}\times100$

(Singh and Chaudhary 1985)

Better-Parent Heterosis (BPH %) $=\dfrac{(\bar{F}_1-\overline{BP})}{\overline{BP}}\times100$

(Singh and Chaudhary, 1985)

Residual Heterosis over mid-parent (RHM %) $=\dfrac{(\bar{F}_2-\overline{MP})}{\overline{MP}}\times100$

Inbreeding depression (ID%) $=\dfrac{\bar{F}_1-\bar{F}}{\bar{F}_1}\times100$ (Kempthorne, 1957

Potence Ratio $=\dfrac{(\bar{F}_1-\overline{MP})}{0.5\times(\bar{P}_2-\bar{P}_1)}\times100$ (Smith, 1952)

Standard errors were calculated using the formulae discussed in (Soehendi and Srinives, 2005)

S.E. (M.P.H.) $=\{V_{\bar{F}1}+((V_{\bar{P}1}+V_{\bar{P}2})/4)\}^{1/2}$ $\quad t\ (M.P.H.)=\dfrac{(\bar{F}_1-\overline{MP})}{S.E.\ (M.P.H.)}$

S.E. (B.P.H.) $=(V_{\bar{F}1}+\overline{BP})^{1/2}$ $\quad t\ (B.P.H.)=\dfrac{(\bar{F}_1-\overline{BP})}{S.E.\ (B.P.H.)}$

S.E. (R.H.M.) $=\{V_{\bar{F}2}+((V_{\bar{P}1}+V_{\bar{P}2})/4)\}^{1/2}$ $\quad t\ (R.H.M.)=\dfrac{(\bar{F}_2-\overline{MP})}{S.E.\ (R.H.M.)}$

S.E. (I.D.) $=\{V_{\bar{F}1}+V_{\bar{F}2}\}^{1/2}$ $\quad t\ (I.D.)=\dfrac{(\bar{F}_1-\bar{F}_2)}{S.E.\ (I.D.)}$

Where, $V_{\bar{F}1}$, $V_{\bar{F}2}$, $V_{\bar{P}1}$, and $V_{\bar{P}2}$ are the mean variances of the sample mean of respective generation and $\overline{MP}$, $\overline{BP}$ F_1, F_2, P_1, and P_2 are the sample mean of mid-parent, better-parent, F_1, F_2, P_1, and P_2 respectively.

3. Results and Discussion

The adequacy of the additive-dominance genetic model was assessed using four standard scaling tests (A, B, C, and D). The results (Table 2) revealed that at least one of the scaling tests was significant for each trait evaluated in the cross CR 1033×CR 22-1-5-1, indicating the presence of epistatic interactions influencing the inheritance of these traits. These findings are in agreement with earlier reports by Sakr et al. (2024), Arsode et al. (2022), and Revathi (2015), who also observed epistatic effects in similar genetic studies. To further dissect the genetic architecture, mean and variance data for all traits were analyzed using the six-parameter model of generation mean analysis, which allows for the estimation of both primary gene effects and their interactions. Partitioning of the generation means into six genetic components (Table 3) showed that the mean effect (m) was significant and positive across nearly all traits. The magnitude of this effect consistently exceeded that of other genetic components, suggesting considerable variability among the generations and confirming the quantitative nature of trait inheritance. These findings are consistent with previous research by Arsode et al. (2022), Ganapati et al. (2020), and Collado et al. (2019).

For both days to 50% flowering (DFF) and days to maturity (DM), all genetic and interaction effects were significant. Notably, the additive×additive (i) interaction exhibited the highest magnitude for DFF (12.30**), while dominance×dominance (l) interaction was most pronounced for DM (-16.10**). The negative value of the (l) component in both traits points to the presence of ambidirectional dominance between the parents. Furthermore, the opposing signs of the dominance (h) and dominance×dominance (l) components suggest the operation of duplicate epistasis in controlling these traits. This complexity in gene action implies that early selection may be ineffective, and that genetic gain for DFF and DM would be better achieved through intermating among segregating populations followed by recurrent selection in later generations. Similar findings for DFF and DM were also reported by Arsode et al. (2022), Gobu et al. (2021), and Ganapati et al. (2020).

For plant height (PH), all gene effects except the dominance× additive interaction (j) were significant. Among these,

Table 2: Scaling test of fifteen quantitative traits

Traits	Scaling tests			
	A±SeA	B±SeB	C±SeC	D±SeD
DFF	-2.70**±0.84	-0.55±0.82	-15.55**±1.61	-6.15**±0.84
DM	-1.00±0.90	2.10*±1.04	-13.90**±1.49	-7.5**±0.84
PH	11.10**±3.00	7.88*±3.87	4.10±6.50	-7.44*±3.24
FLL	7.45**±2.25	2.45±2.11	13.55**±4.99	1.83 ±2.48
FLW	0.02±0.08	-0.26**±0.08	0.29*±0.15	0.27**±0.08
NETPP	-0.45±0.50	-2.05**±0.52	-2.90**±1.14	-0.2±0.59
PL	1.74±1.17	2.88**±0.69	9.51**±2.94	2.45±1.51
NGPP	16.15±23.34	-25.70*±12.77	-131.55**±30.79	-61**±19.00
NCPP	45.85±23.97	72.35**±13.20	96.50**±34.01	-10.85±21.09
SF%	-7.44±4.43	-20.83**±3.19	-33.15**±8.80	-2.44±4.93
TW	0.07±0.08	-0.21*±0.10	-0.47*±0.20	-0.17±0.10
GYPP	3.12*±1.40	-1.01±1.32	-6.30**±2.26	-4.20**±1.22
GL	-0.586*±0.299	0.568**±0.198	-1.619**±0.488	-0.80**±0.25
GW	-0.158**±0.049	-0.005±0.067	0.356*±0.162	0.26**±0.08
GL/W ratio	-0.011±0.134	0.248*±0.115	-1.174**±0.232	-0.71**±0.13

**: Significant at p=0.01; *: Significant at p=0.05; DFF: Days to fifty percent flowering; DM: Days to maturity; PH: Plant height; FLL: Flag leaf length; FLW: Flag leaf width; ETPP: Effective tillers plant^{-1}; PL: Panicle length; GPP: Grains panicle^{-1}; CPP: Chaff panicle^{-1}; SF%: Spikelet fertility %; TW: Test-weight; YPP: Yield plant^{-1}; GL: Grain length; GW: Grain width; GL/W ratio: Grain length-width ratio

the dominance×dominance interaction (l) showed the greatest influence (-33.86), followed by additive×additive (i), dominance (h), and additive (d) effects. The substantial negative (l) value again reflects ambidirectional dominance between the parents, while the positive and significant (i) value (14.88*) highlights the presence of favorable additive alleles. The opposite directions of (h) and (l) further corroborate the presence of duplicate epistasis in the inheritance of this trait. These observations echo the findings of Sharma et al. (2024), Gobu et al. (2021), and Lingaiah et al. (2020). The predominance of interaction effects and epistasis underscores the importance of delaying selection for plant height until advanced generations. Recurrent selection following intermating among superior segregants would likely enhance genetic gain.

In the case of flag leaf length (FLL), only the dominance×additive interaction (j) was found to be significant (5.00*), whereas for flag leaf width (FLW), the additive×additive (i) effect (-0.53**), dominance (h) effect (-0.45**), and dominance×additive (j) interaction (0.27**) were all significant. The negative sign of the dominance component (h) for FLW suggests that the parental line CR 22-1-5-1 contributed more prominently to the expression of this trait. These results are consistent with those reported by Arsode et al. (2022), Das et al. (2022), and Revathi (2015).

Regarding effective tillers plant^{-1} (ETPP), only the dominance ×additive interaction component (j) showed significance (1.60**), indicating a limited but specific form of gene interaction influencing this trait. Similarly, for panicle length (PL), only the dominance effect (h) was significant (-6.33**), with its negative value again pointing to CR 22-1-5-1 as the primary contributor to this trait's expression. These results align with previous findings by Gobu et al. (2021), Ganapati et al. (2020), and Gajanan (2015), supporting the notion that dominance effects play a critical role in the inheritance of these traits.

For grains panicle^{-1} (GPP), all genetic components-except the dominance×additive interaction (j)-were found to be statistically significant. Among them, the additive×additive interaction (i) demonstrated the highest magnitude (122.00**), followed by dominance×dominance interaction (l) (-112.45**), dominance (h) (109.63**), and additive (d) (42.40**). The large and positive value of the additive×additive effect underscores a strong synergistic association of favorable alleles within the parental lines, indicating their potential as good combiners. Moreover, the opposing signs of the dominance (h) and dominance×dominance (l) components provide strong evidence for the presence of duplicate epistasis in the genetic control of this trait. These results corroborate the findings of Kathiresan et al. (2024), Kumar et al. (2024), and Lingaiah et al. (2020). The negative value of the dominance×dominance interaction (l) indicates the occurrence of ambidirectional

dominance between the parents. This genetic complexity, characterized by substantial non-additive interactions and duplicate epistasis, suggests that selection for GPP should be deferred to later generations. Instead, adopting population improvement strategies through intermating and recurrent selection would be more effective for accumulating favorable alleles and developing superior genotypes with enhanced panicle grain number.

In the case of chaffs panicle^{-1} (CPP), only the dominance ×dominance interaction (l) was significant (-139.90**), highlighting the predominant role of epistatic interactions in its inheritance. For spikelet fertility percentage (SF%), both the dominance×dominance (l) (23.40*) and dominance×additive (j) (13.39**) components were found to be significant. These findings suggest that non-additive gene action plays a crucial role in the expression of these traits. The observed patterns of gene action for CPP and SF% imply that breeding strategies focusing on heterosis exploitation-particularly through hybrid development-may be more effective for their improvement. These results are consistent with those reported by Nofal and Gaballah (2024), Kathiresan et al. (2024), and Gobu et al. (2021), further validating the significance of non-additive effects in shaping these traits.

For test weight (TW), all genetic components-except for the additive×additive (i) and dominance×dominance (l) interactions-were found to be significant. Among these, the dominance effect (h) exhibited the highest magnitude (0.43*), followed by the dominance×additive interaction (j) (0.28**) and the additive effect (d) (0.21**). These results underscore the importance of non-additive gene action in the inheritance of this trait, suggesting that breeding strategies capitalizing on heterosis may prove particularly effective. These findings are consistent with earlier reports by Kathiresan et al. (2024), Sreelakshmi and Babu (2022).

In the case of yield plant^{-1} (YPP), all genetic components were highly significant. The dominance×dominance interaction (l) registered the highest magnitude (-10.51**), followed by the dominance effect (h) (9.03**), additive×additive interaction (i) (8.41**), dominance×additive interaction (j) (4.13*), and additive effect (d) (3.28**). The high and positive magnitude of the additive×additive interaction (i) indicates a strong accumulation of favorable alleles within the parental lines. However, the negative value of the dominance×dominance interaction (l) reveals the presence of ambidirectional dominance, while the opposing signs of (h) and (l) indicate duplicate epistasis. This complex genetic architecture suggests that early selection may not yield significant gains; instead, delayed selection in advanced generations is advisable. A breeding approach involving biparental mating among elite segregants, followed by recurrent selection, could facilitate the identification and isolation of superior recombinants. These findings are in agreement with those of Kathiresan et al. (2024), Kumar et al. (2024), and Sreelakshmi and Babu (2022).

For grain length (GL), all genetic components were significant, with the additive×additive interaction (i) showing the highest magnitude (1.6**), followed by the dominance×dominance interaction (l) (-1.58), dominance effect (h) (1.37**), dominance×additive interaction (j) (-1.15**), and additive effect (d) (-0.66**). The negative sign of the (l) component signifies ambidirectional dominance between the parental lines. The contrasting signs of the dominance (h) and dominance×dominance (l) effects provide compelling evidence of duplicate epistasis. This genetic complexity indicates that early-generation selection would be ineffective for improving grain length. Instead, breeding strategies such as biparental mating or reciprocal recurrent selection would be more effective in harnessing the latent variability. The negative additive effect (d) further suggests a major contribution from the male parent, CR 22-1-5-1, to the trait's expression. These observations are corroborated by Sharma et al. (2024), Kour et al. (2019), and Ramli et al. (2016).

For grain width (GW), all genetic components were significant. The dominance×dominance interaction (l) had the highest magnitude (0.68**), followed by the dominance effect (h) (-0.56**), additive×additive interaction (i) (-0.52**), dominance×additive interaction (j) (-0.15**), and additive effect (d) (-0.1*). The opposing signs of the dominance (h) and dominance×dominance (l) components once again point to the presence of duplicate epistasis in the inheritance of this trait. The negative value of (h) further highlights the contribution of CR 22-1-5-1 in donating dominant alleles for grain width. To effectively exploit this genetic potential, selection should be deferred to later generations within a pedigree breeding framework. These insights align with previous findings by Sharma et al. (2024) and Kamara et al. (2017).

Finally, for the grain length-width ratio, all genetic components-except for the dominance×additive interaction (j)-were significant. The dominance×dominance interaction (l) recorded the highest magnitude (-1.65**), followed by additive×additive interaction (i) (1.41**), dominance effect (h) (1.35**), and additive effect (d) (-0.39**). The negative sign of the (l) component reflects ambidirectional dominance, while the contrasting signs of (h) and (l) confirm the involvement of duplicate epistasis. These findings imply that early selection would not be effective, and emphasize the value of advanced-generation selection strategies. Furthermore, the negative additive effect (d) underlines the significant genetic contribution of CR 22-1-5-1 in the expression of this trait. Similar patterns have been documented by Kour et al. (2019), supporting the reliability of these results.

Estimates of mid-parent heterosis (%), better-parent heterosis (%), residual heterosis over mid-parent (%), inbreeding depression (%), and potence ratio for yield and its component traits are summarized in Table 3. Mid-parent heterosis, also known as relative heterosis, was found to be significantly negative for several traits, including days to fifty percent

Table 3: Genetic effects of fifteen quantitative traits

Traits	m±Sem	d±Sed	h±Seh	i±Sei	j±Sej	l±Sel	Epistasis type
DFF	105.35**±0.34	1.15*±0.49	7.23**±1.73	12.30**±1.68	-2.15*±1.06	-9.05*±4.54	Duplicate
DM	131.30**±0.30	1.20*±0.59	10.05**±1.74	15.00**±1.69	-3.10**±1.25	-16.10**±4.66	Duplicate
PH	108.05**±1.30	4.16**±1.94	13.83*±6.78	14.88*±6.49	3.22±4.20	-33.86**±10.05	Duplicate
FLL	41.05**±1.09	-0.38±1.19	-3.37±5.10	-3.65±4.95	5.00*±2.70	-6.25±7.29	-
FLW	2.03**±0.03	0.00±0.05	-0.45**±0.16	-0.53**±0.15	0.27**±0.10	0.77±4.01	-
NETPP	6.35**±0.25	0.40±0.30	1.05±1.21	0.40±1.18	1.60**±0.65	2.10±4.25	-
PL	30.54**±0.70	0.45±0.57	-6.33*±3.05	-4.89±3.02	-1.15±1.26	0.27±5.10	-
NGPP	226.80**±7.22	42.40**±12.36	109.63**±38.38	122.00**±38.01	41.85±26.27	-112.45**±40.11	Duplicate
NCPP	70.60**±8.21	5.75±13.24	22.55±42.41	21.70±42.18	-26.50±26.80	-139.90**±43.94	-
SF%	76.87**±2.11	2.49±2.56	3.49±9.95	4.87±9.87	13.39**±5.22	23.40*±11.49	-
TW	2.04**±0.04	0.21**±0.05	0.43*±0.21	0.33±0.21	0.28**±0.11	-0.20±4.01	-
GYPP	25.12**±0.46	3.28**±0.80	9.03**±2.53	8.41**±2.44	4.13*±1.78	-10.51*±5.17	Duplicate
GL	8.353**±0.10	-0.655**±0.14	1.370**±0.516	1.601**±0.499	-1.153**±0.325	-1.583*±0.750	Duplicate
GW	2.491**±0.04	0.071*±0.04	-0.555**±0.170	-0.518**±0.168	-0.153*±0.078	0.680**±0.215	Duplicate
GL/W ratio	3.364**±0.05	-0.392**±0.07	1.348**±0.260	1.411**±0.255	-0.259±0.171	-1.648**±0.376	Duplicate

**: Significant at p=0.01; *: Significant at p=0.05; [Days to fifty percent flowering (DFF); DFF: Days to fifty percent flowering; DM: Days to maturity; PH: Plant height; FLL: Flag leaf length; FLW: Flag leaf width; ETPP: Effective tillers plant^{-1}; PL: Panicle length; GPP: Grains panicle^{-1}; CPP: Chaff panicle^{-1}; SF%: Spikelet fertility %; TW: Test-weight; YPP: Yield plant^{-1}; GL: Grain length; GW: Grain width; GL/W ratio: Grain length-width ratio

flowering, days to maturity, panicle length, and grains panicle^{-1}, suggesting that the F_1 hybrids matured earlier or were inferior in these traits compared to the mid-parent average. In contrast, significantly positive mid-parent heterosis was observed for effective tillers plant^{-1} and test weight, reflecting hybrid vigor in these yield-contributing attributes. Better-parent heterosis, or heterobeltiosis, also showed a predominantly negative and significant trend for days to fifty percent flowering, days to maturity, flag leaf length, panicle length, grains panicle^{-1}, and spikelet fertility percentage. This negative heterobeltiosis indicates that the F_1 hybrids underperformed compared to the better-performing parent for these traits. However, significantly positive heterobeltiosis was recorded for chaffs panicle^{-1}, grain width, and grain length-width ratio, reflecting transgressive segregation or heterotic effects favoring these parameters. Among the traits, effective tillers plant^{-1} exhibited the highest mid-parent heterosis (9.63**), while chaffs panicle^{-1} showed the most pronounced heterobeltiosis. These results are in agreement with earlier studies by Nuruzzaman et al. (2002), Ganapati et al. (2020), and Gajanan (2015), who reported similar trends in heterosis expression.

Residual heterosis over the mid-parent—which measures hybrid performance beyond the average heterotic effect—was significantly negative for days to fifty percent flowering, days to maturity, grains panicle^{-1}, spikelet fertility percentage, yield plant^{-1}, grain length, and grain length-width ratio. In contrast, traits such as flag leaf length, flag leaf width, panicle length, and chaffs panicle^{-1} exhibited significantly positive residual heterosis, indicating additive gains in hybrid performance for these characteristics. Inbreeding depression (%) was notably high and significant for a suite of yield-related traits including effective tillers plant^{-1}, panicle length, grains panicle^{-1}, chaffs panicle^{-1}, spikelet fertility percentage, test weight, yield plant^{-1}, and grain length-width ratio. Among these, chaffs panicle^{-1} displayed the highest residual heterosis over the mid-parent (53.31**) and the most severe inbreeding depression (-50.53**), highlighting its sensitivity to inbreeding and the strong advantage of heterozygosity for this trait. These patterns are consistent with the observations made by Ganapati et al. (2020), Alam et al. (2004), and Nuruzzaman et al. (2002).

To assess the nature and degree of dominance, potence ratios were calculated. A potence ratio greater than +1-indicative of overdominance in favor of the better parent-was observed for days to fifty percent flowering, days to maturity, effective tillers plant^{-1}, and panicle length. Interestingly, test weight and grain length exhibited a potence ratio greater than -1, signifying overdominance leaning toward the inferior parent in the cross. The remaining traits had potence ratios between -1 and +1, suggesting partial dominance, whether in a positive or negative direction. These findings are aligned with those reported in cotton by EL-Refaey and EL-Razek (2013) and in maize by Collado et al. (2019).

4. Conclusion

Non-additive genetic effects, particularly dominance (h), outweighed additive effects (d) across traits, highlighting considerable gene dispersion between parents. Opposite signs of dominance and dominance×dominance effects indicated duplicate epistasis, rendering early-generation selection ineffective. Biparental mating among superior segregants is recommended to promote favorable allele recombination and improve later-stage selection. Furthermore, significant negative heterobeltiosis and potence ratios between -1 and +1 reinforced the need for carefully structured mating systems and delayed selection strategies in breeding programs targeting these complex traits.

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