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INSIGHTS ON GENE BEHAVIOUR GOVERNING YIELD AND YIELD-CONTRIBUTING TRAITS IN RICE UNDER NON-SALINE AND SALINE ENVIRONMENTS

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ABSTRACT

Understanding the genetics of yield-contributing traits under salinity is essential for developing high-yielding, salt-tolerant rice cultivars. The present research investigated the gene action of yield and its component traits in direct and reciprocal crosses of Pusa 44, a high-yielding variety and Kalarata 1-24, a salt-tolerant landrace. Six basic generations viz., P_1 , P_2 , F_1 , F_2 , B_1 and B_2 were evaluated under non-saline and saline conditions using generation mean analysis. Analysis of variance revealed substantial genetic variability for most traits across both environments. The scaling and joint scaling test indicated the inadequacy of the additive-dominance model, suggesting the involvement of epistatic interactions. Six-parameter generation mean analysis revealed significant additive and dominance gene effects for most of the traits; however, dominance effects generally exceeded additive effects in magnitude, indicating the predominance of non-additive gene action. Significant additive effects for plant height, productive tillers, panicle length, thousand-grain weight, and single-plant yield under saline conditions suggest improving these traits through selection. Positive dominance $\times$ dominance interactions predominated over additive $\times$ additive interactions for most traits, highlighting the greater contribution of non-fixable gene effects to trait expression. In addition, the prevalence of duplicate epistasis for most traits indicates that direct selection in early segregating generations may be ineffective. Gene action varied between direct and reciprocal crosses and between non-saline and saline environments, demonstrating the influence of cross direction and genotype $\times$ environment interactions on the inheritance of yield-related traits. These findings emphasise that breeding strategies should be tailored to the genetic architecture expressed under specific environments and support the use of population improvement approaches, including biparental mating or recurrent selection followed by pedigree breeding in advanced generations, for enhancing grain yield under both non-saline and saline conditions.

Key words : Salinity tolerance, Gene action, Digenic epistasis, Genotype $\times$ environment interaction, Yield traits.

Introduction

Rice (*Oryza sativa* L.) is a major cereal crop and serves as the primary food source for over half of the world's population, contributing significantly to global food and nutritional security. Nearly 90% of the world's rice is produced and consumed in Asia, where rice is a major source of calories, employment, and livelihood for millions of people (FAO, 2024). The global population is projected

to approach 9.7 billion by 2050, necessitating an estimated 25–30% more rice production to meet future food requirements (FAO, 2017). However, sustaining rice productivity has become increasingly difficult due to climate change and the rapid expansion of abiotic stresses, among which soil salinity is one of the most severe constraints limiting rice production worldwide (Mheni *et al.*, 2024). Around 1.4 billion hectares of the world's land

area is affected by salinity, including nearly 10% of irrigated and rainfed croplands. Climate change and unsustainable land and water management are expected to put an additional one billion hectares at risk, further threatening global food security (FAO, 2024). In India, approximately 7 million hectares are currently affected by salinity, and the extent of salt-affected soils is projected to increase to about 16.2 million hectares by 2050 (Liu *et al.*, 2020). Rice is highly sensitive to salinity, particularly during the seedling and reproductive stages (Ganie *et al.*, 2019) and salinity disrupts plant growth through osmotic stress, ion toxicity, nutrient imbalance, oxidative damage, and impaired photosynthesis, resulting in reduced tillering, spikelet fertility, grain filling, and grain yield (Das *et al.*, 2015). Due to the increasing impact of salinity on rice production, breeding rice varieties that combine salinity tolerance with high and stable yield potential has become an urgent priority for ensuring food security in salt-affected ecosystems (Pruthi *et al.*, 2023). As grain yield under saline environments is a complex quantitative trait governed by multiple genes and strong genotype $\times$ environment interactions, developing high-yielding salt-tolerant rice cultivars remains a major objective of rice improvement programmes (Mheni *et al.*, 2024).

A comprehensive understanding of the genetic architecture underlying economically important traits is essential for crop breeding programme. Estimation of additive, dominance, and epistatic gene effects enables breeders to formulate efficient breeding strategies for crop improvement (Hayman, 1960). Despite the availability of several salt-tolerant donor lines and molecular markers associated with salinity tolerance, information on how the genetic control of yield and yield-related traits differs between saline and non-saline environments is still limited. Understanding these differences is essential for identifying traits and crosses governed by favourable additive gene effects that can be effectively fixed through selection under saline conditions, rather than relying on gene action estimated under normal conditions. Generation mean analysis, based on the means and variances of P_1 , P_2 , F_1 , F_2 , B_1 , B_2 , provides a simple yet powerful biometrical approach to partition genetic variation into additive (d), dominance (h) and digenic epistatic components, while also testing the adequacy of the simple additive–dominance model through scaling tests. In addition to valuable information on the nature of gene action governing quantitative traits, it helps in identifying suitable breeding methods for their improvement (Hayman, 1960; Mather and Jinks, 1982). Furthermore, the expression of gene action may differ between favourable and stress environments because

salinity activates distinct physiological and molecular pathways that alter the inheritance of complex traits (Ganie *et al.*, 2019). Therefore, investigating the gene action governing yield and yield-related traits under both non-saline and saline conditions through generation mean analysis is essential for developing environment-specific breeding strategies and accelerating the development of salinity-tolerant, high-yielding rice cultivars.

Materials and Methods

Experimental material

The experimental cross comprises both direct (Cross A) and reciprocal (Cross B) crosses, made between the high-yielding salt-sensitive rice variety Pusa 44 and an *indica* salt-tolerant landrace, Kalarata 1-24 at Agricultural Research farm, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi in *Kharif* 2022 and *Kharif* 2023. In *Kharif* 2023, F_1 of both cross A and B were selfed and backcrossed with respective parents, viz., in cross A, F_1 was crossed to Pusa 44 to produce B_1 and with Kalarata 1-24 to produce B_2 , while in cross B, F_1 was crossed with Kalarata 1-24 to produce B_1 and with Pusa 44 to produce B_2 .

Experimental layout and field condition

In *Kharif* 2024, all six populations P_1 , P_2 , F_1 , F_2 , B_1 , and B_2 of both crosses (Cross A and B) were planted in a compact family block design with three replications under saline and non-saline conditions at Pandit Jawaharlal Nehru College of Agriculture and Research Institute, Karaikal, Puducherry, India. The saline field was irrigated with saline water of 6 dSm⁻¹ from 10 days before the booting stage and maintained till maturity (IRRI, 2021). The non-saline field was maintained with fresh water of EC of ~ 0.5 dSm⁻¹ throughout the growth period. The field salinity level was regularly monitored at periodic intervals using piezometers installed at multiple locations across the experimental area, and the stress level of the field was adjusted by irrigating with fresh water whenever EC exceeded 6 dS/m and by adding NaCl or saline water whenever the EC levels declined.

Observations recorded

Observations were recorded in 10 plants in stable population like P_1 , P_2 and F_1 and in segregating populations 30 plants were observed for B_1 and B_2 and 100 plants in F_2 in all the three replications in both cross A and B. Morphological and yield contributing traits such as days to flowering (DAF), plant height (PHT), number of productive tillers (PTL), panicle length (PNL), spikelet sterility percentage (SS%), thousand grain weight (TGW) and single plant yield (SPY) were recorded.

Statistical analysis

Analysis of variance

The analysis of variance (ANOVA) encompassing all the traits was conducted using R software (version 4.2.3) in accordance with the methodology delineated by Panse and Sukhatme (1985).

Generation mean analysis

The presence of epistatic gene interactions was initially assessed using the scaling tests (A, B, C, and D) proposed by Mather (1949). To further evaluate the suitability of the additive–dominance (A–D) model, Cavalli's (1952) joint scaling test, as described by Mather and Jinks (1982), was performed using the means of the six generations. The goodness of fit of the A–D model was determined by comparing the observed and expected generation means through a chi-square (χ^2) test. A non-significant χ^2 value indicated that the additive–dominance model adequately explained the inheritance of the trait, whereas a significant χ^2 value suggested the involvement of non-allelic interactions and the inadequacy of the model. For traits exhibiting an inadequate fit, generation mean analysis was extended by fitting the six-parameter models proposed by Hayman (1958). These models were used to estimate the mean effect (m), additive (d) and dominance (h) gene effects, together with the epistatic components, namely additive $\times$ additive (i), additive $\times$ dominance (j), and dominance $\times$ dominance (l). The significance of the estimated genetic parameters was tested using the *t*-test.

Results and Discussion

A comprehensive understanding of the genetic basis of yield contributing traits under salinity in rice is critical for the development of resilient cultivars, as it facilitates the selection of appropriate breeding methodologies and genetic improvement strategies. Generation mean analysis is a powerful and very effective biometrical approach for elucidating the genetic basis of quantitative traits by estimating the relative contributions of additive, dominance and epistatic gene effects.

Analysis of variance

Analysis of variance for six generations revealed significant generation mean squares for most of the traits in both crosses under non saline and saline conditions, except days to flowering and thousand grain weight in cross A under saline conditions (Table 1). These results indicate the substantial genetic diversity in the expression of yield-contributing traits generated through crosses between genetically contrasting parents.

Table 1 : Analysis of variance of six generations for yield and yield-contributing traits in rice under non-saline and saline conditions.

Traits	DAF		PHT		PTL		PNL		SS %		TGW		SPY	
	Cross A	Cross B	Cross A	Cross B	Cross A	Cross B	Cross A	Cross B	Cross A	Cross B	Cross A	Cross B	Cross A	Cross B
Non saline	1177.60**	1189.70**	7122.00**	11107.00**	1312.60**	1568.30**	28.72**	44.08**	306.72**	355.70**	0.25**	0.30**	1083.40**	1171.30**
Saline	171.73	420.10**	5293.00**	5921.00**	940.00**	971.20**	50.75**	94.83**	2595.90**	5147.00**	0.06	0.32**	3551.00**	1613.80**

* and ** represent significance at 5% and 1%, respectively.

Scaling test

Scaling test revealed that all the studied traits exhibited at least one significant scale among the four scales, except days to flowering under non saline condition and thousand grain weight under saline condition in cross A (Table 2). Since the joint scaling test provides a more robust assessment than individual scaling tests, particularly for correlated quantitative traits (Singh, 1984), the adequacy of the additive–dominance (A–D) model was evaluated using this approach. The joint scaling test revealed that the mean (m), additive (d), and dominance (h) components were significant for all the traits studied under both saline and non-saline conditions (Table 3). However, the significant χ^2 values obtained for both crosses indicated that the additive–dominance model did not adequately account for the observed variation in generation means. The poor fit of the model suggests the involvement of non-allelic gene interactions (epistasis) and/or genotype $\times$ environment interactions (GEI), as also reported by Supritha *et al.* (2025). Consequently, the inadequacy of the A–D model necessitated the application of the six-parameter generation mean model to estimate both the main genetic effects and epistatic interactions governing the inheritance of these traits.

Gene effects and interactions

Six-parameter generation mean analysis based on the digenic epistasis model revealed significant mean (m) effects for all the studied traits under both non-saline and

saline conditions, except plant height in Cross A under non-saline conditions, days to flowering and spikelet sterility percentage in Cross B under saline conditions, and single plant yield in both crosses under saline conditions (Table 4). The significant variation among generation means for most traits in both crosses under contrasting environments indicates the presence of substantial genetic variability for yield and its component traits among the parental lines and their derived generations. Significant additive (d) and dominance (h) gene effects were detected for several traits in both crosses across the two environments. Significant additive effects were observed for plant height, number of productive tillers, panicle length, thousand grain weight, and single plant yield in both crosses under saline conditions, indicating the potential of these parental lines for developing high-yielding, salinity-tolerant rice cultivars. Their utilization in hybridization programmes is expected to facilitate the development of transgressive segregants with enhanced yield potential and salinity tolerance. In contrast, additive effects were non-significant for days to flowering and single plant yield in Cross B, and number of productive tillers, panicle length, and single plant yield in Cross A under non-saline conditions, as well as for days to flowering and spikelet sterility percentage in both crosses under saline conditions. Negative dominance (h) effects were recorded for all the studied traits except plant height in both crosses under both environments,

Table 2 : Estimates of scaling tests (A, B, C, and D) for yield and yield-contributing traits in rice under non-saline and saline conditions.

Traits	Cross	A		B		C		D	
		Non saline	Saline	Non saline	Saline	Non saline	Saline	Non saline	Saline
DAF	Cross A	-1.60**	4.40	-8.50**	8.80**	8.82	10.32*	9.46	-1.44
DAF	Cross B	-1.20	6.40	6.90	5.40*	-7.14	18.88**	-6.42	3.54
PHT	Cross A	-0.30	4.30	9.50*	3.20	24.36**	25.74*	7.58	9.12
PHT	Cross B	3.40	-20.50**	-17.50**	-6.60*	45.30**	19.94*	29.70**	23.52**
PTL	Cross A	5.20	0.40	3.70	1.90**	34.82**	25.58**	12.96**	11.64
PTL	Cross B	10.30**	2.70	1.40	-0.50	38.30**	26.36**	13.30**	12.08**
PNL	Cross A	0.80	-0.39	0.44	-1.47*	4.76**	4.46**	1.76*	3.16**
PNL	Cross B	2.94*	-1.32	-0.20	1.98**	5.77**	8.26**	1.52	3.80**
SS%	Cross A	-0.53	-13.51**	1.42	6.85	11.48**	-31.18**	5.29**	-12.26*
SS%	Cross B	-5.41**	24.61**	4.39**	-1.63	12.28**	-45.16**	6.65**	-34.07**
TGW	Cross A	-0.08	0.04	-0.14*	-0.01	0.27**	0.11	0.24**	0.04
TGW	Cross B	-0.14*	0.01	-0.01	0.29**	0.35**	0.50**	0.25**	0.10*
SPY	Cross A	-15.95**	9.87**	-11.78	11.34**	1.89**	59.07**	14.81**	18.93**
SPY	Cross B	-13.00**	7.94**	-10.51**	25.24**	-33.33**	40.61**	-4.91	3.71

Table 3 : Estimates of mean (m), additive (d), dominance (h), and χ^2 values from the joint scaling test for yield and yield-contributing traits in two rice crosses under non-saline and saline conditions.

Traits	Cross	m		d		h		χ^2 value	
		Non saline	Saline	Non saline	Saline	Non saline	Saline	Non saline	Saline
DAF	Cross A	98.13*	90.33*	4.56*	2.81*	10.67*	-3.07**	128.44**	25.70**
DAF	Cross B	100.63*	90.01**	-2.86**	-3.74*	3.72*	-2.56*	156.37**	22.58**
PHT	Cross A	113.75*	99.75*	-21.83**	-19.99**	-1.29**	1.26**	172.54**	398.83**
PHT	Cross B	113.80*	98.88**	27.78*	21.67**	-0.59**	3.39**	168.85**	325.44**
PTL	Cross A	21.34*	8.67*	1.38*	-2.59**	-2.16**	1.57*	38.55**	81.10**
PT	Cross B	21.07*	10.10**	0.24**	2.28**	-2.34**	0.54*	68.95**	68.95**
PNL	Cross A	21.88*	16.84*	-0.20**	-1.14*	-0.21**	1.00*	13.29*	52.59**
PL	Cross B	22.09*	17.89**	0.60*	0.62**	-0.04**	-0.25*	25.86**	105.76**
SS%	Cross A	9.30*	42.60*	-1.56**	13.61**	1.55*	8.11**	62.88**	187.93**
SS	Cross B	9.53*	57.23**	-0.54**	-7.74*	1.91*	-13.04	92.12**	324.47**
TGW	Cross A	2.05*	1.87*	-0.01**	-0.03**	0.10*	0.03**	19.69**	28.55**
TGW	Cross B	2.07*	1.93**	-0.02**	-0.03*	0.08*	-0.07*	21.04**	64.08**
SPY	Cross A	25.63*	15.31*	-1.81**	-6.08**	13.40*	-5.09**	23.49**	80.18**
SPY	Cross B	25.40*	18.71**	-0.24**	0.46*	11.44*	-11.82*	57.11**	281.93**

spikelet sterility percentage in both crosses under saline conditions, and single plant yield in Cross B under non-saline conditions. The predominance of negative dominance effects suggests that dominance generally contributed to a reduction in the expression of these traits. Similar observations have been reported by Sreelakshmi and Babu (2019), Singh and Patel (2020), and Patel *et al.* (2020). Across both crosses and under both saline and non-saline conditions, the estimated dominance effect (h) was greater than the additive effect (d) for all the traits studied, indicating the predominant role of dominance gene action in their inheritance. The predominance of non-additive gene effects suggests that direct selection in early segregating generations may not be effective, as favourable alleles can be masked by dominance and epistatic interactions. In such a situation, the pedigree breeding method would be more effective in later generations where favourable alleles become fixed and present in a homozygous condition. These findings are consistent with the reports of Singh and Patel (2020), Patel *et al.* (2020), and Gobu *et al.* (2021). Gamble (1962) proposed that large dominance effects are often associated with significant epistatic interactions. In agreement with this hypothesis, the high estimates of dominance (h) observed for several yield-contributing traits in the present study suggest that epistasis also played an important role in their genetic control across the respective crosses.

The additive $\times$ additive (i) gene effects were significant and negative for most of the studied traits, except spikelet sterility percentage in Cross B under saline conditions. This suggests the dispersion of favourable alleles between the parental lines and indicates that fixation of additive effects in subsequent generations may lead to a reduction in the expression of these traits. In contrast, the dominance $\times$ dominance (l) interaction was significantly positive for most traits, indicating its enhancing influence on trait expression. The predominance of positive dominance $\times$ dominance (l) epistasis over additive $\times$ additive (i) interactions suggests that non-fixable gene effects play a major role in the inheritance of these traits. Similar findings for yield and yield-contributing traits were reported by Gobu *et al.* (2021) and Kumar *et al.* (2025) under both stress and non-stress environments, while Singh and Patel (2020), Patel *et al.* (2020), Das *et al.* (2022), and Duppala *et al.* (2023) reported comparable results under non-stress conditions. Therefore, breeding approaches such as biparental mating, recurrent selection, and population improvement would be more rewarding than conventional selection methods for exploiting the available genetic variability. Significant negative additive $\times$ dominance (j) interactions were observed for plant height and thousand grain weight in Cross A and days to flowering in Cross B under both non-saline and saline conditions; spikelet sterility percentage in Cross A and single plant yield in

Table 4 : Estimates of mean (m), additive (d), dominance (h), additive $\times$ additive (i), additive $\times$ dominance (j), and dominance $\times$ dominance (l) gene effects for yield and yield-contributing traits in two rice crosses under non-saline and saline conditions.

Traits	Cross	m		d		h		i		j		l		Epistasis	
		Non saline	Saline	Non saline	Saline	Non saline	Saline	Non saline	Saline	Non saline	Saline	Non saline	Saline	Non saline	Saline
DAF	Cross A	149.35**	89.60*	3.25*	0.10	-87.09**	-27.94**	-32.52**	-9.52	0.50	13.00**	63.02**	14.92*	D	D
DAF	Cross B	159.40**	87.30	-3.90	-1.20	-77.42**	-40.76*	-19.76*	-17.08**	-16.40**	-7.00*	62.96**	20.28*	D	D
PHT	Cross A	116.70	112.90*	-12.30**	-8.50**	-56.92	-74.98	-24.76	-31.24	-64.30**	-61.20**	29.96	43.24	-	-
PHT	Cross B	110.85*	106.10**	15.35**	5.60**	-80.35	-38.08	-45.40	-25.64	62.10**	58.80*	38.50	20.64	-	-
PTL	Cross A	22.80*	21.65**	1.00	-1.35*	-79.24**	-71.41**	-35.72**	-31.28**	6.00*	-7.30**	41.52**	40.98**	D	D
PT	Cross B	26.45*	19.95*	1.75*	1.65*	-92.85**	-69.97*	-40.60**	-31.16*	-3.20	4.50*	49.90**	39.46*	D	D
PNL	Cross A	22.86*	19.66*	-0.01	-0.19**	-12.40**	-11.89**	-5.36**	-5.80**	-0.63	-4.29**	6.88**	6.88**	D	D
PL	Cross B	25.56*	20.34**	0.81**	-0.40*	-19.12**	-21.31*	-7.47**	-9.58*	-0.35	3.67*	11.39**	11.89*	D	D
SS%	Cross A	22.28**	77.59*	-1.48**	0.62	-43.80**	21.55	-17.69**	17.10	-7.77**	39.86**	27.44**	0.72	D	-
SS	Cross B	20.59**	75.04	-1.28**	1.38	-41.99**	44.61	-17.88**	36.40**	9.02**	-39.27*	25.76**	-11.77	D	-
TGW	Cross A	2.43*	2.21*	0.00**	0.01**	-0.99**	-0.66**	-0.46**	-0.22**	-0.20**	-0.17**	0.63**	0.47**	D	D
TGW	Cross B	2.44*	2.19**	-0.02**	-0.06*	-1.19**	-1.62*	-0.54**	-0.62*	0.02**	0.18*	0.74**	0.95*	D	D
SPY	Cross A	72.06**	6.87	-1.21	-2.43*	-55.59**	-117.34**	-24.23**	-53.92**	-12.63*	-7.76	43.87**	56.90**	D	D
SPY	Cross B	78.29**	11.01	-0.60	-2.24*	3.90	-91.37*	8.59	-36.07*	-11.30**	28.35*	16.76	45.86*	-	D

both crosses under non-saline conditions; and number of productive tillers, panicle length in Cross A and spikelet sterility percentage in Cross B under saline conditions. These interactions indicate the involvement of increasing and decreasing alleles at interacting loci, reflecting the contrasting genetic constitution of the parental lines used to develop the respective crosses (Owusu *et al.*, 2022). In all the studied traits except plant height in both crosses under both environments, spikelet sterility percentage in both crosses under saline conditions, and single plant yield in Cross B under non-saline conditions, the dominance (h) and dominance $\times$ dominance (l) effects exhibited opposite signs, indicating the predominance of duplicate epistasis. This type of gene interaction suggests that alleles with similar effects are dispersed among the interacting loci, thereby limiting the effectiveness of selection. Similar patterns have been reported by Rao *et al.* (2017), Sreelakshmi and Babu (2019), Singh and Patel (2020), Ganapathi *et al.* (2020), Gobu *et al.* (2021), Duppala *et al.* (2023), Pravin Kumar *et al.* (2025) and Patel *et al.* (2025) for yield and yield-contributing traits. The prevalence of duplicate epistasis may impede genetic improvement by reducing the efficiency of fixing superior genotypes because of the antagonistic effects of interacting genes.

The gene action governing most of the studied traits, except thousand grain weight, varied between the direct and reciprocal crosses as well as between non-saline and saline environments, reflecting the complex genetic architecture of these traits and the influence of cross direction and genotype $\times$ environment interactions on their expression. This observation is consistent with the findings of Omrani *et al.* (2022), who reported that the genetic control of agronomic and physiological traits differs between normal and saline environments. Collectively, these findings indicate that breeding strategies should be tailored to the genetic architecture expressed under each environment, as variations in gene action between non-saline and saline conditions suggest the activation of distinct sets of

genes in response to salinity stress. Such environment-dependent genetic regulation highlights the importance of developing environment-specific breeding strategies for the effective genetic improvement of salinity tolerance in rice. The predominance of dominance and duplicate-type digenic epistasis for most yield-contributing traits in both the direct and reciprocal crosses, together with the pronounced influence of genotype $\times$ environment interactions on gene action, suggests that population improvement approaches, such as biparental mating, recurrent selection, or intermating among selected segregants in the early generations followed by pedigree selection in advanced generations, would be more effective than direct selection in early segregating generations for improving yield potential under both non-saline and saline conditions.

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