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RESEARCH ARTICLE

Insights into the genetic basis of yield and its components in rice (*Oryza sativa* L.) through generation mean analysis

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Abstract

Generation mean analysis conducted was to recognize the inheritance patterns of yield-related traits in rice populations developed from crosses between salinity-tolerant (*Saltol 1* QTL) and phosphorus (P) starvation-tolerant (*Pup1* QTL) backcross inbred lines. The study involved four crosses: BIL33 × C16-1-2-8, BIL752 × D5-1-3-2-1, BIL1094 × C16-1-2-8 and BIL1102 × D5-1-3-2-1, aimed at developing multiple stress-tolerant versions of CR 1009 Sub1 and ADT 37 varieties. Six generations - Pt_1, Pt_2, F_1, F_2, BC_1F and BC_2F were evaluated for thirteen quantitative traits during *Kharif* 2023-2024 at Agricultural College and Research Institute, TNAU, Madurai. Scaling tests revealed significant epistatic interactions for most traits across crosses. Grain yield showed complementary epistasis with significant interaction effects in all crosses, while traits like plant height and flag leaf characteristics displayed varying patterns of gene action. The existence of both additive and non-additive gene effects raises the possibility that selection may be postponed to future generations. The study advises maintaining larger populations during the initial generations and applying pedigree selection from the F_4 generation onward to achieve effective trait enhancement. These findings provide valuable insights for developing breeding strategies to pyramid salinity and phosphorus starvation tolerance in rice varieties.

Keywords

genetic effects; low P tolerance; salinity tolerance; scaling test

Introduction

Rice (*Oryza sativa* L.) is a vital staple crop, significantly contributing to global food security. It is especially important in Asia, where it supplies over 60 % of the daily calorie consumption (1). However, the sustainability of rice production is under threat from numerous abiotic stresses, with phosphorus deficiency and soil salinity standing out as key factors limiting rice productivity on a global scale. These stresses are particularly severe in rainfed lowland ecosystems, where they often co-occur, leading to substantial yield losses (2).

The development of climate-resilient rice varieties has become increasingly important in the context of changing environmental conditions. While varieties like CR 1009 Sub1 and ADT 37 have shown promising adaptability, their tolerance to phosphorus starvation and salinity stress remains limited. Gaining insights into genetic determinants of yield and related traits is vital for the development of improved varieties with tolerance to multiple stresses. Introgression of beneficial alleles from stress-tolerant donors into elite varieties requires a comprehensive understanding of the gene actions controlling key agronomic traits.

Generation mean analysis (GMA) is an effective approach in quantitative genetics that helps dissect the genetic makeup of complex traits by breaking down genetic effects into additive {d}, dominance {h} and interaction components, including additive × additive {i}, additive × dominance {j} and dominance × dominance {l} (3). The degree and direction of these genetic effects determine inheritance patterns and guide selection strategies in breeding programs. The six-parameter model, incorporating both main effects and digenic interactions, enables estimation of gene effects through weighted least squares regression analysis of generation means. This understanding is indispensable in designing operative breeding approaches and predicting breeding progress.

The present investigation aims to interpret the form and degree of gene actions controlling yield and allied traits in four crosses developed between backcross inbred lines possessing tolerance to phosphorus starvation and salinity stress. The study employs generation mean analysis using six basic generations - Pt_1, Pt_2, F_1, F_2, BC_1F and BC_2F to estimate the comparative relevance of additive, dominance and epistatic effects. This information will be valuable in formulating efficient breeding strategies for evolving rice varieties with boosted tolerance to multiple abiotic stresses while maintaining high yield potential.

Materials and Methods

The current study was conducted at the Agricultural College and Research Institute of Tamil Nadu Agricultural University in Madurai from the *Kharif* season of 2023 - 2024. The studied material was derived from the cross of rice genotypes BIL 33, BIL 752, BIL 1094, BIL 1102, D5-1-3-2-1 and C16-1-2-8. The female parents (P_1), BIL 33 and BIL 752 is the improved ADT 37 variety while BIL 1102 and BIL 1094 is the improved CR 1009 *Sub*1 variety and all the four BILs were introgressed with *Saltol* 1 QTL for salinity tolerance (4) D5-1-3-2-1 and C16-1-2-8 used as male parent (P_2) were the improved version of CR 1009 *Sub*1 introgressed with *Pup*1 QTL for low phosphorus tolerance. The breeding program was initiated to develop multiple stress tolerant versions of CR 1009 *Sub 1* and ADT 37 with enhanced tolerance to low phosphorus and salinity condition.

Six generations *viz.*, Pt_1, Pt_2, F_1, F_2 , BC_1F and BC_2F developed from the crosses, cross I- BIL33 x C16-1-2-8, cross II - BIL752 x D5-1-3-2-1, cross III - BIL1094 x C16-1-2-8 and cross IV - BIL1102 x D5-1-3-2-1 were evaluated in this study. The hybridization between the female and male parents began in *Kharif* 2023 for the development of F_1s. F_1s were grown in *Rabi* 2023 and real F_1s were identified using four gene-specific markers (K46-1 and K29-3 for Pup 1, RM 3412 for Saltol 1 and ART 5 for Sub 1) and progressed to F_2 by selfing. True F_1 was also backcrossed to the parents Pt_1 and Pt_2 to generate BC_1F and BC_2F plants, respectively. The experimental material *viz.*, parents (Pt_1 and Pt_2), F_1, F_2, BC_1F and BC_2F was laid in a randomized complete block design with three replications during *Kharif*, 2024. Data were collected on ten plants in the case of parents (Pt_1 and Pt_2) and F_1's, 150 F_2 plants and 20 plants of BC_1F and BC_2F per replication. The average values of phenotypic traits were measured on randomly selected plants from each entry in the segregating populations for 12 quantitative traits namely, DFP - days to 50 percent flowering, PLH - plant height in cm, NuPTP - number of productive tillers per plant, PaLh - panicle length in cm, FLLh - flag leaf length in cm, FLWh - flag leaf width in cm, FLAr - flag leaf area in cm, NuFGPP - number of filled grains per panicle, ToGPP- total number of grains per panicle, SFP - spikelet fertility (%), HSWt - hundred seed weight in g and GYPt - single plant yield in g/ plant.

Generation mean analysis was carried out in two stages, using the methodologies provided by Hayman and Jinks and Jones (3)and (5). The first stage of testing for epistasis by scaling test was performed by Mather (6). The significance of any of these four scales suggested the existence of epistasis. Following that, an analysis was conducted to assess gene effects and variances and determine the nature of epistasis present. The gene effects - m, d and h and their interactions - i, j and l were estimated using a six-parameter model in accordance with the guidelines (3). The six genetic parameters, mean (m), additive gene effects (d), dominance gene effects (h) and three types of non-allelic gene interactions, additive x additive (i), additive x dominance (j) and dominance x dominance (l) were estimated using the mean values of Pt_1 , Pt_2 , F_1 , F_2 , BC_1F and BC_2F populations as follows :

$[m] = \frac{1}{2} P_1 + \frac{1}{2} P_2 + 4F_2 - 2B_1 - 2B_2$

$[d] = \frac{1}{2} P_1 - \frac{1}{2} P_2$

$[h] = 6B_1 + 6B_2 - 8F_2 - F_1 - 3/2\ P_1 - 3/2\ P_2$

$[i] = 2B_1 + 2B_2 - 4F_2$

$[j] = 2B_1 - P_1 - 2B_2 + P_2$

$[l] = P_1 + P_2 + 2F_1 + 4F_2 - 4B_1 - 4B_2$

Statistical analyses were performed by employing TNAUSTAT software (7).

Results

The estimates of the scaling test and epistatic parameters obtained in each of the four crosses for the twelve characters are furnished below (Table 1).

DFP

The results of the scaling test indicated that all the scales for cross II, A and D in cross I and for cross III, A, B and D, were significant. This confirmed the existence of inter-allelic interaction. The mean (m) was shown to have positive significance for all four crosses. Negative and significant additive (d) component was noted in case of cross I, II and IV whereas the dominance (h) effect had positive significance in crosses I, III and IV. The interactions (i), (j) and (j) were observed significantly in the crosses I and IV. Cross II and III showed significant dominance (do) x dominance (do) - (l) and additive (ad) x dominance (do) - (j). Cross II demonstrated complementary epistasis through the same sign of (h) and (l), while three crosses (I, III and IV) exhibited duplicate interaction

Table 1. Estimates of scaling test and genetic factors for yield and yield components in four crosses

Traits	Crosses	Scales				Gene effects						Epistasis
		A	B	C	D	(m)	(d)	(h)	(i)	(j)	(l)	
DFP	BIL33 x C16 -1-2-8	3.100*	-0.500	-1.806	-2.203*	111.873*	-1.650*	3.956*	4.406*	1.800*	-7.006*	D
	BIL752 x D5 -1-3-2-1	-4.800*	-11.400*	-16.166*	0.016*	108.233*	-2.150*	0.6167	-0.033	3.300*	16.233*	C
	BIL1094 x C16-1-2-8	5.300*	1.200	4.486*	-1.0067	117.746*	0.900	6.563*	2.0133	2.050*	-8.513*	D
	BIL1102 x D5-1-3-2-1	-2.500*	6.100*	0.953	-1.323*	117.113*	-3.150*	6.497*	2.647*	-4.300*	-6.247*	D
PLH	BIL33 x C16 -1-2-8	-121.310*	-76.139*	-130.362*	33.804*	104.752*	-2.300	-16.613*	-67.608*	-22.846*	265.578*	D
	BIL752 x D5 -1-3-2-1	-89.140*	-73.590*	-151.126*	5.802*	99.976*	-11.250*	54.361*	-11.605*	-7.775*	174.335*	C
	BIL1094 x C16-1-2-8	-65.100*	-36.060*	-91.461*	4.849*	92.125*	-3.200	11.901*	-9.699*	-14.520*	110.859*	D
	BIL1102 x D5-1-3-2-1	-58.750*	-23.510*	-70.656*	5.802*	99.976*	-11.250*	-5.885	-11.605*	-17.620*	93.865*	C
NuPTP	BIL33 x C16 -1-2-8	-30.800*	-26.800*	-75.333*	-8.867*	9.367	-0.100*	47.733*	17.733*	-2.000*	39.867*	C
	BIL752 x D5 -1-3-2-1	-27.000*	-18.200*	-50.927*	-2.863*	9.793*	-2.650*	24.077*	5.727*	-4.400*	39.473*	C
	BIL1094 x C16-1-2-8	-43.300*	-45.800*	-73.493*	7.803*	15.227*	2.250*	25.993*	-15.607*	1.25	104.707*	C
	BIL1102 x D5-1-3-2-1	-2.000*	-11.000*	-35.727*	-11.363*	9.793*	3.150	31.877*	22.727*	4.500*	-9.727*	D
PaLh	BIL33 x C16 -1-2-8	-9.581*	-1.255	-0.965	4.936*	-23.985*	-0.445*	-12.948*	-9.871*	-4.163*	20.707*	D
	BIL752 x D5 -1-3-2-1	-11.421*	-2.801*	-16.591*	-1.185*	23.153*	-0.611	5.456*	2.369*	-4.310*	11.853*	C
	BIL1094 x C16-1-2-8	6.793*	1.174	11.924*	1.978*	23.357*	4.085*	-4.506*	-3.957*	2.810*	-4.010*	C
	BIL1102 x D5-1-3-2-1	0.980	3.350*	1.917*	-1.206*	23.159*	-0.325	1.853	2.413*	-1.185*	-6.743*	D
FLLh	BIL33 x C16 -1-2-8	5.770*	-6.251*	6.666*	3.573*	21.717*	0.410	-4.847*	-7.147*	6.011*	7.628*	D
	BIL752 x D5 -1-3-2-1	-13.477*	-28.969*	-36.459*	2.993*	23.369*	-1.924	9.528*	-5.987*	7.746*	48.433*	C
	BIL1094 x C16-1-2-8	-5.957*	-11.884*	-14.860*	1.491	21.180*	1.821	-4.373	-2.981	2.963*	20.822*	D
	BIL1102 x D5-1-3-2-1	-5.460*	-9.450*	-9.735*	2.587*	23.369*	-1.400	-15.780*	-5.175*	1.995*	20.085*	D
FLWh	BIL33 x C16 -1-2-8	-0.030	-0.190*	0.216*	0.218*	1.354*	0.130*	-0.036	-0.436*	0.080*	0.650*	D
	BIL752 x D5 -1-3-2-1	-0.240*	0.210*	-0.535*	-0.253*	1.239*	-0.330*	0.980*	0.505*	-0.225*	-0.475*	D
	BIL1094 x C16-1-2-8	-0.060	-0.270*	-1.119*	-0.395*	0.933*	0.020	1.044*	0.789*	0.105*	-0.459*	D
	BIL1102 x D5-1-3-2-1	0.110	0.520*	0.076	-0.277*	1.234*	-0.185*	0.524*	0.554*	-0.205*	-1.184*	D

FLAr	**BIL33 x C16-1-2-8**	5.786*	-10.888*	13.511*	9.307*	29.495*	3.141*	-7.408*	-18.613*	8.337*	23.715*	D
	BIL752 x D5-1-3-2-1	-30.165*	-37.314*	-70.850*	-1.685	29.212*	-9.875*	38.819*	3.371	3.575	64.108*	C
	BIL1094 x C16 -1-2-8	-9.464*	-20.367*	-39.814*	-4.992*	20.187*	2.025*	14.539*	9.983*	5.452*	19.848*	C
	BIL1102 x D5-1-3-2-1	-19.323*	-13.630*	-24.995*	3.979*	29.105*	2.043	3.755	-7.959*	-2.847*	40.912*	C
NuFGPP	**BIL33 x C16-1-2-8**	-136.000*	-56.500*	-154.580*	18.960*	120.580*	17.000*	-60.170*	-37.920*	-39.750*	230.420*	D
	BIL752 x D5-1-3-2-1	32.400*	-34.300*	-87.667*	-42.883*	132.433*	21.150*	123.867*	85.767*	33.350*	-83.867*	D
	BIL1094 x C16 -1-2-8	13.600*	6.900	-140.153*	-80.327*	90.587*	27.200*	151.403*	160.653*	3.350	-181.153*	D
	BIL1102 x D5-1-3-2-1	-169.000*	-124.300*	-382.720*	-44.710*	98.120*	33.850*	90.420*	89.420*	-22.350*	203.880*	C
ToGPP	**BIL33 x C16-1-2-8**	-123.900*	-31.600*	-122.147*	16.677*	141.113*	8.750*	-48.653*	-33.353*	-46.150*	188.853*	D
	BIL752 x D5-1-3-2-1	46.900*	-31.300*	-23.513	-19.557*	161.347*	24.650*	84.663*	39.113*	39.100*	-54.713*	D
	BIL1094 x C16 -1-2-8	19.800*	5.000	-70.847*	-47.823*	120.913*	28.150*	85.397*	95.647*	7.400*	-120.447*	D
	BIL1102 x D5-1-3-2-1	-170.900*	-103.100*	-310.247*	-18.123*	125.413*	22.050*	33.497	36.247*	-33.900*	237.753*	C
SFP	**BIL33 x C16-1-2-8**	-12.941*	-21.938*	-31.077*	1.901	84.388*	7.338*	-7.708*	-3.802	4.499*	38.681*	D
	BIL752 x D5-1-3-2-1	-6.627*	-3.225	-43.176*	-16.662*	81.724*	-0.766	30.825*	33.324*	-1.701	-46.940	D
	BIL1094 x C16 -1-2-8	-2.740	2.098	-59.245*	-29.301*	75.663*	1.128	59.235*	58.603*	-2.419	-57.961*	D
	BIL1102 x D5-1-3-2-1	-3.500*	-21.500*	-71.013*	-23.007*	77.547*	10.700*	48.213*	46.013*	9.000*	-21.013*	D
HSWt	**BIL33 x C16-1-2-8**	2.032*	0.112	1.017*	-0.563*	2.056*	0.494*	1.005*	1.127*	0.960*	-3.271*	D
	BIL752 x D5-1-3-2-1	-0.343*	-0.074	-0.113*	0.078*	1.974*	-0.099*	-0.593*	-0.157*	-0.209*	0.426*	D
	BIL1094 x C16 -1-2-8	1.098*	0.121	1.027*	-0.096	2.048*	0.374*	0.431*	0.192	0.489*	-1.411*	D
	BIL1102 x D5-1-3-2-1	-0.687*	0.034	-0.882*	-0.115*	1.964*	0.073	-0.489*	0.229*	-0.361*	0.424*	D
GYPt	**BIL33 x C16-1-2-8**	-91.867*	-84.874*	-202.446*	-12.853*	22.997*	5.565*	100.202	25.705*	-3.497	151.036*	C
	BIL752 x D5-1-3-2-1	-79.499*	-62.948*	-170.295*	-13.924*	26.278*	-4.674	86.187*	27.848*	-8.276*	114.599*	C
	BIL1094 x C16 -1-2-8	-76.430*	-102.149*	-196.225*	-8.823*	27.613*	18.140*	115.415*	17.646*	12.860*	160.933*	C
	BIL1102 x D5-1-3-2-1	-81.122*	-70.114*	-223.682*	-36.223*	20.343*	19.565*	85.165*	72.446*	-5.504*	78.790*	C

- significance @ 0.05% ; C- complementary epistasis; D – duplicate epistasis
- DFP- days to 50 per cent flowering; PLH- plant height; NuPTP - number of productive tillers per plant; PaLh - panicle length; FLLh- flag leaf length; FLWh - flag leaf width; FLAr- flag leaf area; NuFGPP- number of filled grains per panicle; ToGPP- total number of grains per panicle; SFP- spikelet fertility percentage; HSWt - hundred seed weight and GYPt - grain yield per plant.

due to the different signs of (h) and (l).

PLH

Estimates of the scaling test revealed that all the scales were significant for four cross combinations suggested the presence of epistatic interaction. This extended the study to analyse the interaction effect. The mid parental impact (m) was determined to be significant and positive for each of the four crosses. In cross I and III, do (h), ad x ad (i), ad x do (j) and do x do (l) showed significance. All the parameters were significant in the cross II. Significance of ad (d), ad x ad (i), ad x do (j) and do x do (l) was detected for Cross IV. Regarding the signs, cross I and III showed contradicting signs of (h) and (l), but cross II and IV showed the same indications. This suggested that PLH is inherited with both complimentary and duplicate epistasis.

NuPTP

A, B, C and D scales displayed significance in all the crosses. For this trait, all the cross combinations registered positive and significant mid parent effect (m). Significant ad (d) and do (h) component was displayed for all crosses. All interaction effects were significant in cross I, II and IV. Except for ad x do (j) component, significance was recorded for ad x ad (i) and do x do (l) in cross III. Duplicate epistasis (opposite sign of (h) and (l)) was exhibited by cross IV and remaining crosses exhibited complementary epistasis (same sign of (h) and (l)).

PaLh

PaLh exhibited significant A and D scales in cross I, all scales for cross II, A, C and D scales in cross III and B, C and D scales for cross II. A significant mid parent effect (m) was observed for four crosses. In cross III, ad effect (d) was positive and significant and the remaining crosses had a non-significant effect. Among the four crosses, do effect (h) was positive and significant for cross II and negative significant for crosses I and III whereas it was positive and non-significant for cross IV. The components ad x ad (i), ad x do (j) and do x do (l) enumerated significance in all crosses. The complementary and duplicate epistasis nature of the interaction was verified by the symbols of the (h) and (l) components, which were in the same order in Cross II and III and the opposite direction in Cross I and IV.

FLLh

Significant A, B, C and D scales of the crosses I, II and IV and scales A, B and C in the cross III were noted. The (m) effects were positive and significant in all crosses. Significant do (h) effect and non-significant ad effect (d) were noted for this trait in all the crosses. The significance of ad x ad (i), ad x do (j) and do x do (l) were detected for the cross I, II and IV and the components ad x do (j) and do x do (l) for cross III. Complementary interaction in cross II and duplicate interaction in another three crosses were detected.

FLWh

The significance of all four scales was revealed by the cross II. In case of Cross I and III, B, C and D scales and B and D scales in fourth cross were found to be significant. It designated the inter-allelic interaction in the trait inheritance. All crosses showed that mid parent effect was significantly positive. Ad x ad (i) components were positive and significant for cross II, III and IV and negative significant for cross I. The (j) component exhibited positive and significance in cross I and III while negative significant effect was exhibited by the cross II and IV. Fully non-fixable component (l) displayed positive significance in cross I and remaining crosses showed negative significance. Duplicate epistasis (all four crossings) was involved in the inheritance of the trait FLWh from the signs of the (h) and (l) components.

FLAr

In scaling test, all scales were substantial in cross I, III and IV, though scale A, B and C showed significance in cross II indicated the existence of interaction effect. Mid parent effect (m) showed significance in all crosses. All the crosses except cross IV showed significant ad (d) and do effect (h). The (i), (j) and (l) component were significant in cross I, III and IV while only (l) components were significant in cross II. From the signs of the (h) and (l) components, it was found that the complementary (cross II, III and IV) and duplicate (cross I) type epistasis were involved in the inheritance of this character.

NuFGPP

The scaling test showed the significance of all scales in the crosses I, II and IV and scales A, C and D in cross III suggested the importance of epistatic gene action in the inheritance of this trait. Positive and significant ad (d) and do (h) effect was documented in all crosses except cross I where positive significant ad (d) effect and negative significant do (h) effect was noted. In crosses II and III, positive significant (i) and (j) and negative significant (l) were recognized. Positive significant (l) and negative significant (i) and (j) was noted in cross I. The cross IV showed positive significant (i) and (l) components and negative significant (j) components. Cross IV revealed complementary epistasis and other three crosses displayed duplicate epistasis.

ToGPP

All scales in cross I and IV, scales A, B and D for cross II and scales A, C and D in cross III were noticed to be significant. Ad (d) and do (h) effect were distinguished as positive and significant in the crosses II and III whereas positive significant (d) effect and negative significant (h) effect was documented in cross I. Significance of all interaction components was observed for four crosses. The sign of do (*h*) and do × do *(l)* gene effects in Cross I, II and III were same and opposite in cross IV which specifies the presence of duplicate and complementary epitasis.

SFP

According to the results of the scaling test, the scales A, B and C in cross I, A, C and D in cross II, C and D in cross III and all the scales in cross IV were significant, indicating the existence of non-allelic gene interactions. Do (h) effect showed positive significance in the crosses II and III. Regarding cross I, the positive significance of ad (d) effect and negative significance of do (h) effect were disclosed. Positive and significant ad (d) and do (h) effect was observed in the cross IV. The estimations of do (h) and do × do (l) interaction impact demonstrated the existence of duplicate gene interaction in the inheritance of SFP.

HSWt

In crossings I, II and IV, the scales A, C and D were significant; in cross III, the scales A and C were also significant. In cross II, the ad (d) impact was substantial and negative, while in all other crosses, it was significant and positive. There was positive significance in crosses I and III and negative significance in crosses II and IV for the do (h) impact. The components (j) and (l) in cross III, as well as all the interaction components (i, j and l) in crosses I, II and IV were significant. The presence of a duplicate kind of gene interaction for this character was suggested by the indications of (h) and (l) pointing in the opposite way.

GYPt

In the entire cross combinations, all the scales analyzed were articulated to be significantly designate the existence of inter-allelic interaction in this trait inheritance. The mid-parent (m) effect was significant for all the crosses. In crosses III and IV, ad (d) and do (h) effect were positive and significant. Ad (d) effect was positive and significant for the cross I and do (h) effect was positive and significant for cross II. Ad x ad (i), ad x do (j) and do x do (l) effects were significant for the crosses II, III and IV and ad x ad (i) and do x do (l) for cross I. Complementary gene interaction (same sign of (h) and (l)) were involved in inheritance of GYPt.

Discussion

Understanding the relative importance of additive and non-additive gene action involved in the phenotypes is essential for the success of any plant breeding project that aims to improve various quantitative traits. To better understand the nature of gene activity that controls the inheritance of yield and its individual components, generation mean analysis was employed. GM's mean effect (m), additive effect (d), dominance effect (h), additive x additive (i), additive x dominance (j) and dominance x dominance (l) are its most notable advantages. As a result, two major categories of non-allelic interactions may be identified. The presence of the same sign in the first (h) and (l) suggests that interactions are mostly complementary, whereas the opposite sign in the second (h) and (l) indicates that interactions are primarily duplicates (5). In this study, generation means analysis using a six-parameter model was used to divide the genetic variation into additive, dominance and epistasis in four crosses (cross I- BIL33 x C16-1-2-8, cross II- BIL752 x D5-1-3-2-1, cross III- BIL1094 x C16-1-2-8 and cross IV- BIL1102 x D5-1-3-2-1), which aids in the formulation of an efficient breeding program. Twelve traits were compiled from segregating and non-segregating generations and gene action was computed; the findings are being discussed below.

Scaling test

Scaling test determine the appropriateness of the basic additive dominance model. Individual scaling tests, A, B, C and D of (6) employed determine the existence of epistasis from the data of different generations in all four crosses. The research assists in developing appropriate breeding techniques based on the targeted attribute. The scaling test results for the quantitative characteristics analysed changed considerably across all four crossings, confirming the existence of interallelic interaction among the genes implicated in trait inheritance. A and B tests demonstrate the incidence of all sorts of non-allelic gene interactions. The significance of C scale indicates dominance x dominance (l) interaction. The substantial D scale disclose additive x additive gene connections, whereas the significant C and D scales imply additive x additive and dominance x dominance gene interactions, respectively. The scaling test across characteristics reveals intricate patterns of epistatic interactions in the analysed crosses. PLH showed significance for all four scales - A, B, C, D in four crosses, indicating strong epistatic effects, while NuPTP demonstrated uniform significance across all scales and crosses, suggesting consistent non-allelic interactions. PaLh displayed varying patterns, with cross II showing significance for all scales, while other crosses showed partial scale significance, indicating cross-specific epistatic effects. Flag leaf characteristics showed comprehensive significance patterns - FLLh had all scales significant in crosses I, II and IV, with three scales significant in cross III; FLWh showed all scales significant in cross II and partial significance in other crosses; and FLAr demonstrated significance for all scales in crosses I, III and IV and with three scales significance for cross II. For grain-related traits, NuFGPP showed all scales significant in crosses I, II and IV, with three scales significant in cross III; ToGPP had complete scale significance in crosses I and IV, with partial significance in crosses II and III. SFP demonstrated varying significance patterns across crosses, while HSWt consistently showed significance for scales A, C and D in most crosses. Notably, GYPt exhibited significance for all scales across all crosses, indicating comprehensive epistatic interactions in yield inheritance. These scaling test results provide crucial indication for the presence and extent of non-allelic interactions across traits, with some traits showing consistent epistatic effects across crosses (like NuPTP and GYPt), while others demonstrate cross-specific patterns of interaction (like PaLh and flag leaf characteristics). This understanding of the scaling test results forms the foundation for interpreting gene actions and developing appropriate breeding strategies for trait improvement. The varying patterns of scale significance across traits and crosses suggest that breeding approaches may need to be trait-specific and, in some cases, cross-specific to effectively utilize the genetic interactions present.

Genetic components of yield & yield attributing traits estimated through six parameter model

The generation mean analysis revealed complex inheritance patterns through significant scaling tests, indicating strong epistatic interactions particularly in cross II which showed significance for all scales. The genetic architecture of DFP was characterized by consistent positive mean (m) effects across crosses, negative significant additive effects (d) of crosses I, II and IV and positive significance of dominance effects (h) in crosses I, III and IV suggesting additive and non-additive gene actions are important for trait expression. The presence of significant interaction components along with predominant duplicate epistasis in three crosses indicates complex gene interactions controlling the trait. This genetic architecture suggests that conventional selection methods alone might not be effective. The recommended breeding strategies include delayed selection to later generations (F_5 or F_6) to allow beneficial gene combinations to stabilize, maintaining larger populations in early generations to capture desirable recombinants, implementing a modified bulk-pedigree method with selection initiated in F4 and considering population improvement through recurrent selection to accumulate favourable alleles. Cross II, showing complementary epistasis, may be more promising for obtaining superior segregants and could be prioritized in the breeding program.

PLH showed significant mid-parental effects across all crosses, with complex epistatic interactions manifested through both duplicate (crosses I & III) and complementary (crosses II & IV) epistasis. The existence of significant additive, dominance and its interaction effects suggests that height is controlled by multiple genes with intricate interactions. This genetic architecture necessitates delayed selection strategies, preferably using modified pedigree method with selection initiated in F_4 or F_5 generations. The presence of both types of epistasis (complementary and duplicate) indicates that different crosses might require different breeding approaches to maximize genetic gain.

NuPTP exhibited significant additive and dominance effects across all crosses, accompanied by epistatic interactions. The predominance of complementary epistasis in three crosses suggests good potential for obtaining transgressive segregants. The significant interaction components indicate that selection in early generations might not be successful. A breeding strategy combining recurrent selection with periodic intercrossing would be appropriate to accumulate favourable alleles while maintaining beneficial epistatic combinations.

PaLh demonstrated varying patterns of gene action, with dominance effects being significant for the crosses I, II and III. Complementary (crosses II & III) and duplicate (crosses I & IV) epistasis, along with significant interaction effects, suggests complex inheritance. The non-significant additive effects in most crosses indicate that simple selection procedures might not be effective. Population improvement methods with emphasis on specific combining ability would be more appropriate for improving this trait.

FLLh showed strong dominance effects across all crosses with non-significant additive effects. The prevalence of duplicate epistasis in three crosses suggests potential difficulties in achieving rapid genetic gain. Given this genetic architecture, reciprocal recurrent selection would be more effective than pure line selection. The significant epistatic interactions indicate the need for maintaining larger populations in early generations to capture desirable recombinants.

FLWh demonstrated significant epistatic interactions with predominant duplicate epistasis across all crosses. The significance of interaction components with negative dominance × dominance effects suggest complex inheritance. This genetic pattern calls for delayed selection procedures with larger population sizes in early generations to allow beneficial combinations to express and fix.

FLAr showed mixed inheritance patterns with three crosses exhibiting complementary epistasis and one showing duplicate epistasis. The significant additive and dominance effects in most crosses, combined with epistatic interactions, suggest the importance of additive and non-additive gene actions. A combination of pedigree breeding with periodic recurrent selection would be appropriate to improve this trait.

NuFGPP displayed significant epistatic interactions across all crosses, with three crosses showing duplicate epistasis and one showing complementary epistasis. The presence of both additive and dominance effects suggests that hybrid breeding approaches might be effective. The complex inheritance pattern indicated delaying of selection to later generations when gene combinations become more stable.

ToGPP demonstrated significant epistatic interactions with mixed patterns of complementary and duplicate epistasis. The presence of significant additive and dominance effects in maximum crosses suggests good potential for improvement through both selection and hybridization approaches. A modified bulk method followed by pedigree selection would be appropriate.

SFP showed complex inheritance patterns with varying epistatic interactions across crosses. The genetic components analysis revealed interesting patterns - crosses II and III showed positive significant dominance effects, while cross I displayed positive significant additive effects with negative significant dominance effects. Cross IV demonstrated both positive and significant additive and dominance effects. Notably, the presence of duplicate nature of gene interaction suggests that improvement of this trait might be challenging through conventional breeding approaches. The complex genetic architecture indicates that breeding strategies should focus on delayed selection in later generations, preferably F_5 or F_6, to allow for the fixation of favourable gene combinations. Population improvement methods like recurrent selection could be effective in accumulating beneficial alleles while breaking unfavourable linkages.

HSWt showed an interesting pattern of additive effects - negative significance in cross II but positive significance in all other crosses. The dominance effects varied across crosses, with positive significance of crosses I and III and negative significance of crosses II and IV. All interaction components were significant for the crosses I, II and IV, though cross III showed significance only for j and l components. The presence of duplicate type gene interaction suggests that selection for this trait could be postponed to later generations. The significance of additive effects in most crosses indicate that pedigree breeding could be effective, but the presence of substantial epistasis suggested maintaining of larger populations in early generations would be beneficial. A modified bulk-pedigree approach, with selection initiated in F4 generation and intensive selection in later generations, would be appropriate. Additionally, the varying patterns of gene effects across crosses suggest that cross-specific breeding strategies might be needed for optimal improvement of HSWt

GYPt showed complementary epistasis with significant interaction effects across crosses. The presence of additive effects alongside epistatic interactions suggests good potential for improvement through careful breeding approaches. The recommended strategy would include maintaining larger populations in early generations, followed by pedigree selection from F_4 onwards. The complementary nature of gene interactions indicates potential for obtaining superior recombinants through systematic breeding efforts.

The results of this investigation aligned with the findings of (8) for PLH and PaLh and (8,9) for FLLh and FLWh, (10) for SFP, (11) for GYPt and NuFGPP, (12) for ToGPP, (13) for HSWt, (14) for DFP and NuPTP.

Conclusion

The generation mean analysis revealed complex inheritance patterns for yield and component traits in rice populations developed for multiple stress tolerance, with significant epistatic interactions demonstrated through scaling tests. Grain yield consistently showed complementary epistasis across all crosses, while other traits displayed varying patterns of both additive and non-additive gene action. The significant interaction effects suggest postponing of selection to later generations when gene combinations become more stable, along with maintaining larger populations in early generations to capture desirable recombinants. Based on the findings, a modified pedigree method with delayed selection is recommended for traits showing duplicate epistasis, while population improvement methods like recurrent selection would be more effective for traits with complementary epistasis. These insights provide crucial guidance for developing breeding strategies to successfully incorporate salinity and phosphorus starvation tolerance into CR 1009 Sub1 and ADT 37 varieties while maintaining or improving yield-related traits.

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Authors' contributions

The collaborative research effort involved a diverse team with distinct roles. RCG generated the experimental material, initiated the study's concept and data collection, while NA and MG designed the research and experimental framework, provided project supervision and manuscript review. RPG, SMP, PSP and RA provided predominant research guidance and final manuscript approval, collectively ensuring a comprehensive and rigorous scientific investigation.

Compliance with ethical standards

Conflict of interest: Authors declare no conflict of interests

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