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Research Article

Study of genetic architecture of grain yield and quality traits through generation mean analysis in rice (*Oryza sativa* L.)

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Abstract
A perusal of gene effects in generation mean analysis for three crosses *viz.,* BPT 5204 x IR 36, BPT 5204 x NLR 34449 and RNR 2465 x IR 64 revealed the presence of a significant proportion of epistatic effects besides the major components *viz*., additive (d) and dominance (h) gene effects for important yield and quality attributes. Partitioning of variance indicating that the mean values (m) for gene effects were highly significant in all the three crosses for most of the traits, the results of dominance (h) and dominance × dominance (l) type interactions revealed that duplicate type of epistasis was prevalent for most of the traits in all the six crosses except in RNR 2465 x IR 64 for the number of filled grains per panicle; BPT 5204 x NLR 34449 for kernel breadth and kernel elongation ratio and BPT 5204 x IR 36 for harvest index where, complementary gene action played a vital role in the inheritance of the traits. Therefore, improvement of these traits appears to overwhelmed with difficulties as simple selection techniques will not be able to fix superior lines in the early segregating generations. Postponement of selection for superior lines to later generations in pedigree breeding will be effective. However, one or two cycles of recurrent selection followed by pedigree breeding will be effective and useful to utilize both additive and non-additive gene effects. The predominance of dominance and epistatic interactions in all the crosses for quality traits indicates that selection would be more effective if the dominance and epistatic effects are first reduced by a few generations of selfing.

Keywords: Rice, generation mean analysis, gene action

INTRODUCTION

The detection and estimation of epistasis in the inheritance of various quantitative traits are of utmost important to understand the genetic cause of heterosis with greater reliability and to frame an efficient breeding plan leading to rapid improvement. Generation mean analysis (Hayman, 1958) has been considered to be one of the best methods for estimating the different components of genetic variance and testing the presence or absence of epistasis using the scaling test, which measures epistasis accurately whether it is complimentary (Additive × Additive) or duplicate (Additive × Dominance and Dominance × Dominance) at the digenic level. In this method, a set of segregating and non-segregating generations belonging to common ancestry is subjected to analysis simultaneously for extracting a comprehensive picture of gene action controlling the trait. In view of this the present study was formulated to study the gene action in three selected crosses in rice for its grain yield and quality traits.

MATERIALS AND METHODS

The present investigation was carried out at Agricultural Research Station, Nellore, ANGRAU, Andhra Pradesh during the four consecutive seasons of 2014, 2015, 2016 and 2017 *rabi* seasons, respectively. The material comprising of six generations (P1, P2, F_1, F_2, BC_1 and BC_2) of the three crosses *viz*., BPT 5204 x NLR 34449, BPT 5204 x IR 36 and RNR 2465 x IR 64. All the material was planted in a randomized block design with three replications having 75 plants of each P1 and P2; 50 plants of F_1, 100 plants of BC_1 and BC_2 and 200 plants of F_2 population per replication. All the crop management practices were followed as per the recommendations from time to time to obtain a healthy crop. The crop was planted with a spacing of 20 x 15 cm and data were recorded for 23 yield and quality traits *viz*., days to 50% flowering, days to maturity, plant height, panicle length, the number of ear bearing tillers per plant, the number of filled grains per panicle, the number of unfilled grains per panicle, test weight, harvest index, SPAD Chlorophyll Meter Reading (SCMR) and grain yield and quality traits *viz*., kernel length, kernel breadth, kernel L/B ratio, hulling percent, milling percent, head rice recovery, water uptake, volume expansion ratio, kernel elongation ratio, gel consistency, alkali spreading value and amylose content.

Statistical analysis

The analysis of variance (ANOVA) was carried out through Statistics10. To confirm the data adequacy, Mather's (1949) scaling test (A, B, C, and D) was performed for confirmation of additive-dominance model reported by Singh and Chaudhary (1985).

$$A = P1 + F_1 - 2BC_1 = ½([i]-[j]+[l])$$
$$B = P2 + F_1 - 2BC_2 = ½([i]+[i]+[l])$$
$$C = P1 + P2 + 2F_1 - 4F_2 = 2(i) + (l)$$
$$D = 2F_2 - BC_1 - BC_2$$

Estimates of various gene effects, allelic interaction, and their test of significance were computed by a six parameter model of Hayman (1958) and Jinks and Jones (1958) by the following equations:

m = Mean = F_2

d = Additive effect = $BC_1 - BC_2$

h = Dominance effect = $2BC_1 + 2BC_2 + F_1 - 4F_2 - (1/2)P_1 - 1/2\ P_2$

i = Additive x Additive genetic interaction = $2BC_1 + 2BC_2 - 4F_2$

j = Additive x Dominance genetic interaction = $2BC_1 - P_1 - 2BC_2 + P_2$

l= Dominance x Dominance genetic interaction = $P1 + P2 + 2F_1 + 4F_2 - 4BC_1 - 4BC_2$

RESULTS AND DISCUSSION

With a view to study the nature and mode of gene action of yield, quality and its component traits generation mean analysis was carried out utilizing mean data of six basic generations *viz*., P1, P2, F_1, F_2, BC_1 and BC_2 of three crosses *viz*., BPT 5204 x IR 36, BPT 5204 x NLR 34449, and RNR 2465 x IR 64. The three crosses were selected based on the grain yield performance of F_1 hybrids. The significance of A and B scales indicates the presence of all the three types of non- allelic interactions *viz*., additive x additive (i), additive x dominance (j) and dominance x dominance (l). The significance of C scale suggests d x d (l) type interaction. The significance of D scale reveals additive x additive (i) type gene interaction and significance of both C and D scales indicates additive x dominance (j) and dominance x dominance (l) type of gene interactions. The significance of any one of the scaling tests indicates inadequacy of simple additive – dominance model.

In the present investigation, the calculated values of A, B, C and D scaling tests were highly significant for all the hybrids under study except for kernel L/B ratio in the cross BPT 5204 x NLR 34449, suggesting that the simple additive – dominance model is inadequate. The data were subjected to further analysis using six parameter model as suggested by Hayman (1958).

The mean performance of six generations with respect to yield and its associated traits along with SE and the estimates of individual scaling tests (A, B, C and D) and genetic effects *viz*., a (d), d (h), a x a (i), a x d (j) and d x d (l) were presented in **Tables 1& 2**

The performance of F_1 hybrid was superior to both the parents in case of ear bearing tillers per plant, panicle length, harvest index, grain yield, water uptake and head rice recovery, in all the three crosses studied. Whereas SCMR, filled grains per panicle, volume expansion ratio, kernel elongation ratio in two crosses *viz*., BPT 5204 x NLR 34449 and RNR 2465 x IR 64 and test weight, kernel length in BPT 5204 x NLR 34449 milling percent in BPT 5204 x IR 36, kernel L/B in RNR 2464 x IR 64. F_1 values were intermediate for test weight in both the crosses *viz*., BPT 5204 x IR 36, RNR 2465 x IR 64. Filled grains per panicle, SCMR, kernel L/B, milling percent in BPT 5204 x NLR 34449, days to 50% flowering, days to maturity, panicle length, unfilled grains per panicle, kernel L/B ratio, hulling percent in BPT 5204 x IR 36 and kernel length in RNR 2465 x IR 64 also recorded intermediate values of F_1 to both of the parents involved in the cross.

The mean values of the traits *viz*., ear bearing tillers per plant, grain yield, harvest index, SCMR, head rice recovery, gel consistency, alkali spreading value, water uptake recorded high values for F_1 generation than the F_2 generation. Low plant height and less number of ill filled grains per panicle were the desirable traits and these traits exhibited lower values in F_1generation. The superiority of F_1 over the parental mean values denotes the over dominance whereas the inferior performance of F_1 over parental mean is due to selection of parents with contrast traits. The results indicated that high degree of inbreeding depression for many of the characters and revealed that non additive gene action plays an important role which includes both epistasis gene action plays an important role which includes both epistasis as well as dominance interactions.

Table 1. Estimates of generation means and standard errors

Cross	P_1	P_2	F_1	F_2	BC_1	BC_2
Days to 50% flowering						
BPT 5204 x NLR 34449	92.900±0.416	91.050±0.583	88.600±0.438	111.500±0.506	98.900±0.286	94.525±0.330
BPT 5204 x IR 36	103.050±0.569	91.000±0.528	102.000±0.562	78.483±0.343	94.975±0.259	92.950±0.386
RNR 2465 x IR 64	96.950±0.380	91.050±0.344	87.950±0.495	81.500±0.360	93.900±0.512	100.475±0.312
Days to maturity						
BPT 5204 x NLR 34449	124.950+0.690	123.100+0.721	120.150+0.595	146.017+0.655	131.000+0.523	127.925+0.350
BPT 5204 x IR 36	135.550+0.806	123.000+0.692	134.600+0.638	115.433+0.425	127.950+0.369	125.475+0.440
RNR 2465 x IR 64	128.900+0.492	122.900+0.518	119.600+0.596	116.533+0.387	126.525+0.529	135.025+0.429
Plant height						
BPT 5204 x NLR 34449	73.110+0.321	68.900+0.507	76.900+0.464	102.517+0.926	75.900+1.072	70.800+1.050
BPT 5204 x IR 36	73.110+0.321	73.500+0.484	66.850+0.572	101.100+0.754	67.425+1.432	75.300+1.240
RNR 2465 x IR 64	77.950+0.531	71.750+0.602	82.900+1.194	109.100+0.941	76.225+1.584	70.650+1.327
Number of ear bearing tillers per plant						
BPT 5204 x NLR 34449	12.200±0.468	12.650±0.310	18.300±0.539	11.800±0.327	22.815±0.324	21.718±0.258
BPT 5204 x IR 36	12.200±0.468	12.850±0.406	17.550±0.573	12.400±0.315	16.515±0.513	16.410±0.395
RNR 2465 x IR 64	14.200±0.427	11.560±0.421	18.050±0.456	9.433±0.225	21.400±0.536	20.150±0.526
Panicle length						
BPT 5204 x NLR 34449	17.200+0.321	18.900+0.390	21.320+0.508	21.383+0.361	22.525+0.320	21.725+0.548
BPT 5204 x IR 36	17.200+0.321	21.400+0.351	19.825+0.779	20.867+0.319	20.612+0.235	23.830+0.402
RNR 2465 x IR 64	22.050+0.387	19.950+0.399	23.030+0.641	21.783+0.345	20.445+0.520	22.315+0.496
Number of filled grains per panicle						
BPT 5204 x NLR 34449	180.100+14.168	157.900+9.605	178.500+38.155	149.185+10.983	178.700+7.805	163.100+9.868
BPT 5204 x IR 36	180.100+3.764	132.500+2.209	191.500+6.080	143.133+5.464	130.875+2.475	109.625+1.348
RNR 2465 x IR 64	165.900+4.053	118.050+1.512	170.000+4.992	156.233+3.214	233.500+6.001	161.025+2.843
Number of un filled grains per panicle						
BPT 5204 x NLR 34449	18.500+1.374	18.500+0.773	15.100+1.281	23.417+0.788	21.205+1.130	22.200+0.909
BPT 5204 x IR 36	18.500+1.374	13.900+0.628	17.200+1.311	27.917+1.472	8.100+0.320	21.525+1.301
RNR 2465 x IR 64	16.100+1.256	13.800+0.702	15.050+0.783	23.200+1.278	27.625+1.228	14.600+0.544
Test weight						
BPT 5204 x NLR 34449	13.352+0.082	14.799+0.177	16.265+0.093	21.756+0.281	15.802+0.149	13.267+0.146
BPT 5204 x IR 36	13.352+0.082	20.940+0.240	15.210+0.156	12.161+0.224	17.848+0.413	19.130+0.298
RNR 2465 x IR 64	15.765+0.079	25.020+0.291	16.816+0.161	16.614+0.194	15.092+0.225	18.080+0.226
Harvest index						
BPT 5204 x NLR 34449	46.985+1.144	57.350+0.870	68.050+0.916	50.352+0.773	59.853+0.963	64.190+1.059
BPT 5204 x IR 36	46.985+1.144	56.645+1.051	69.500+0.869	46.280+1.202	59.625+1.017	45.188+0.733
RNR 2465 x IR 64	53.710+0.712	54.370+0.731	67.100+1.341	56.845+0.589	67.650+0.926	63.565+0.830
SCMR						
BPT 5204 x NLR 34449	42.375+0.591	47.460+0.551	46.029+0.555	34.770+0.413	48.695+0.538	49.425+0.446
BPT 5204 x IR 36	42.375+0.591	45.690+0.355	45.700+0.758	40.073+0.426	48.102+0.685	48.270+0.896
RNR 2465 x IR 64	43.410+0.602	42.900+0.422	48.317+0.830	39.431+0.429	50.050+0.725	50.138+0.652
Grain yield						
BPT 5204 x NLR 34449	26.925+0.964	28.170+1.072	50.978+2.015	37.543+1.278	60.882+1.549	45.154+0.987
BPT 5204 x IR 36	26.925+0.964	32.365+1.495	55.450+2.413	25.200+1.110	35.430+1.151	37.990+1.006
RNR 2465 x IR 64	36.650+1.040	30.483+1.017	52.525+1.834	26.718+0.621	68.192+1.516	57.675+1.606

Table 1. Continued..

			Kernal length			
BPT 5204 x NLR 34449	5.600+0.054	5.585+0.041	5.905+0.070	5.888+0.046	5.750+0.052	6.200+0.051
BPT 5204 x IR 36	5.600+0.054	6.930+0.046	5.320+0.107	6.380+0.063	6.400+0.079	6.802+0.060
RNR 2465 x IR 64	5.985+0.049	7.090+0.054	6.300+0.081	5.660+0.047	5.900+0.041	6.400+0.067
			Kernal breadth			
BPT 5204 x NLR 34449	1.900+0.032	1.910+0.035	1.765+0.051	1.937+0.028	1.850+0.030	1.952+0.028
BPT 5204 x IR 36	1.900+0.032	1.910+0.025	1.755+0.039	2.007+0.044	1.818+0.037	1.877+0.041
RNR 2465 x IR 64	1.975+0.035	2.275+0.045	1.950+0.043	2.003+0.036	1.772+0.031	2.052+0.028
			Kernal L/B ratio			
BPT 5204 x NLR 34449	2.958+0.042	3.640+0.048	3.046+0.061	3.257+0.068	3.595+0.110	3.696+0.092
BPT 5204 x IR 36	2.958+0.042	3.640+0.048	3.046+0.061	3.257+0.068	3.595+0.110	3.696+0.092
RNR 2465 x IR 64	3.055+0.066	3.150+0.081	3.252+0.064	2.883+0.060	3.373+0.069	3.139+0.052
			Hulling per cent			
BPT 5204 x NLR 34449	74.870+0.795	74.400+0.550	74.000+0.465	72.275+0.237	72.250+0.301	63.700+0.416
BPT 5204 x IR 36	74.870+0.795	75.500+0.803	75.300+0.411	75.760+0.219	76.825+0.306	75.300+0.394
RNR 2465 x IR 64	73.400+0.550	77.125+0.473	77.550+0.456	74.850+0.330	76.250+0.417	76.675+0.311
			Milling per cent			
BPT 5204 x NLR 34449	67.150+0.678	67.400+0.419	67.250+0.528	61.900+0.261	66.713+0.342	54.525+0.386
BPT 5204 x IR 36	67.150+0.678	67.600+0.650	68.700+0.363	65.100+0.383	68.650+0.400	69.725+0.324
RNR 2465 x IR 64	67.650+0.525	70.365+0.660	66.600+0.499	68.775+0.355	71.000+0.479	69.725+0.304
			Head rice Recovery			
BPT 5204 x NLR 34449	52.335+0.549	54.500+0.489	58.500+0.526	50.162+0.489	55.025+0.481	45.600+0.361
BPT 5204 x IR 36	52.335+0.549	57.700+0.775	61.500+0.709	50.850+0.359	53.330+0.701	49.751+0.456
RNR 2465 x IR 64	43.400+0.617	58.600+0.622	62.400+0.613	55.810+0.391	58.455+0.545	56.575+0.558
			Water uptake			
BPT 5204 x NLR 34449	170.350+2.528	188.000+1.373	262.150+6.428	254.483+3.578	222.075+3.537	171.625+2.734
BPT 5204 x IR 36	170.350+2.528	239.000+1.806	356.000+7.000	229.600+4.357	164.525+3.445	185.625+3.992
RNR 2465 x IR 64	233.450+3.471	179.450+4.722	297.750+6.691	232.617+4.164	216.175+4.168	188.625+.648
			Volume expansion ratio			
BPT 5204 x NLR 34449	4.140+0.048	4.375+0.068	3.855+0.088	4.624+0.079	3.435+0.102	3.547+0.066
BPT 5204 x IR 36	4.140+0.048	3.475+0.051	4.500+0.082	4.927+0.061	2.565+0.039	3.320+0.099
RNR 2465 x IR 64	3.440+0.035	4.295+0.055	5.515+0.116	4.835+0.067	3.927+0.108	5.738+0.107
			Kernal elongation ratio			
BPT 5204 x NLR 34449	1.619±0.020	1.570±0.034	1.472±0.027	1.252±0.012	1.371±0.018	1.403±0.013
BPT 5204 x IR 36	1.619±0.020	1.588±0.007	1.929±0.057	1.277±0.014	1.284±0.015	1.276±0.015
RNR 2465 x IR 64	1.485±0.017	1.570±0.028	1.696±0.040	1.376±0.013	1.365±0.020	1.357±0.017
			Gel consistancy			
BPT 5204 x NLR 34449	49.800+0.427	56.500+0.626	48.050+2.197	33.683+1.448	52.050+1.670	21.525+1.293
BPT 5204 x IR 36	49.800+0.427	62.000+0.637	42.650+1.748	21.533+0.847	50.150+1.164	36.600+0.819
RNR 2465 x IR 64	45.000+1.177	44.000+0.669	29.300+1.451	26.667+1.078	34.250+1.178	39.500+1.305
			Alkali spreading value			
BPT 5204 x NLR 34449	5.200+0.117	4.050+0.153	2.100+0.161	4.500+0.191	3.550+0.182	3.500+0.186
BPT 5204 x IR 36	5.200+0.117	5.000+0.145	3.030+0.097	2.567+0.135	2.525+0.164	2.025+0.121
RNR 2465 x IR 64	4.700+0.164	4.145+0.043	4.500+0.267	2.100+0.125	3.000+0.172	2.550+0.168
			Amylose content			
BPT 5204 x NLR 34449	23.090+0.158	26.035+0.561	19.561+0.553	20.839+0.258	24.905+0.266	24.493+0.259
BPT 5204 x IR 36	23.090+0.158	24.620+0.380	19.305+0.406	20.295+0.345	24.535+0.434	23.452+0.315
RNR 2465 x IR 64	24.590+0.213	24.475+0.306	19.700+0.370	21.562+0.208	19.785+0.250	24.160+0.340

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Table 2. Scaling tests and estimates of gene effects

Cross	A	B	C	D	m	d	h	L (dxd)	I (axa)	J (axd)
					Days to 50% flowering					
BPT 5204 x NLR 34449	16.30**	9.40**	84.85**	29.57**	151.12**	0.92*	-95.97**	33.45**	-59.15**	3.45
BPT 5204 x IR 36	-15.10**	-7.10**	-84.12**	-30.96**	35.11**	6.03**	106.61**	-39.72**	61.92**	-4.00
RNR 2465 x IR 64	2.90*	21.95**	-37.90**	-31.38**	31.25**	2.95**	144.30**	-87.60**	62.75**	-9.52
					Days to maturity					
BPT 5204 x NLR 34449	16.90**	12.60**	95.72**	33.11**	190.24**	0.92	-106.81**	36.71**	-66.21**	2.15
BPT 5204 x IR 36	-14.25**	-6.65**	-66.02**	-22.56**	84.16**	6.28**	74.66**	-24.22**	45.12**	-3.80
RNR 2465 x IR 64	4.55**	27.55**	-24.87**	-28.48**	68.93**	3.00**	139.73**	-89.07**	56.97**	-11.50
					Plant height					
BPT 5204 x NLR 34449	1.79	-4.20	114.26**	58.33**	187.67**	2.10**	-229.85**	119.08**	-116.67**	2.99
BPT 5204 x IR 36	-5.11	10.25**	124.09**	59.47**	192.25**	-0.19	-239.21**	113.81**	-118.95**	-7.68
RNR 2465 x IR 64	-8.40*	-13.35**	120.90**	71.33**	217.50**	3.10**	-299.00**	164.40**	-142.65**	2.47
					Number of ear bearing tillers per plant					
BPT 5204 x NLR 34449	15.13**	12.49**	-14.25**	-20.93**	-29.44**	-0.22	117.22**	-69.48**	41.87**	1.32
BPT 5204 x IR 36	3.28*	2.42*	-10.55**	-8.13**	-3.73*	-0.33	43.23**	-21.95**	16.25**	0.43
RNR 2465 x IR 64	10.55**	10.69**	-24.13**	-22.68**	-32.49**	1.32**	117.14**	-66.61**	45.37**	-0.07
					Panicle length					
BPT 5204 x NLR 34449	6.53**	3.23*	6.79**	-1.48	15.08**	-0.85**	18.96**	-12.73**	2.97	1.65
BPT 5204 x IR 36	4.20**	6.44**	5.22*	-2.71**	13.88**	-2.10**	22.00**	-16.05**	5.42**	-1.12
RNR 2465 x IR 64	-4.19**	1.65	-0.93	0.81	22.61**	1.05**	-3.74	4.15	-1.61	-2.92
					Number of filled grains per panicle					
BPT 5204 x NLR 34449	-1.20	-10.20	-98.26**	-43.43**	82.14**	11.10**	171.82**	-75.46**	86.86**	4.49
BPT 5204 x IR 36	-109.85**	-104.75**	-123.07**	45.77**	247.83**	23.80**	-362.47**	306.13**	-91.53**	-2.55
RNR 2465 x IR 64	131.10**	34.00**	0.98	-82.06**	-22.14	23.92**	521.36**	-329.22**	164.12**	48.55
					Number of un filled grains per panicle					
BPT 5204 x NLR 34449	8.81**	10.80**	26.47**	3.43	25.36**	-	2.50	-12.75	-6.86	-1.00
BPT 5204 x IR 36	-19.50**	11.95**	44.87**	26.21**	68.62**	2.30**	-111.38**	59.97**	-52.42**	-15.72
RNR 2465 x IR 64	24.10**	0.35	32.80**	4.18	23.30**	1.15	7.85	-16.10*	-8.35	11.88
					Test weight					
BPT 5204 x NLR 34449	8.81**	10.80**	26.47**	3.43	25.36**		2.50	-12.75	-6.86	-1.00
BPT 5204 x IR 36	7.13**	2.11**	-16.07**	-12.66**	-8.17**	-3.79**	57.93**	-34.56**	25.31**	2.51
RNR 2465 x IR 64	-2.40**	-5.68**	-7.96**	0.06	20.51**	-4.63**	-11.87**	8.18**	-0.11	1.64
					Harvest index					
BPT 5204 x NLR 34449	4.67	2.98	-39.03**	-23.34**	5.49	-5.18**	116.89**	-54.33**	46.68**	0.85
BPT 5204 x IR 36	2.76	-35.77**	-57.51**	-12.25**	27.31**	-4.83**	33.69**	8.50	24.50**	19.27
RNR 2465 x IR 64	14.49**	5.66*	-14.90**	-17.53**	18.99**	-0.33	103.31**	-55.20**	35.05**	4.41
					SCMR					
BPT 5204 x NLR 34449	8.99**	5.36**	-42.81**	-28.58**	-12.24**	-2.54**	129.78**	-71.51**	57.16**	1.81
BPT 5204 x IR 36	8.13**	5.15*	-19.17**	-16.23**	11.58**	-1.66**	79.85**	-45.73**	32.45**	1.49
RNR 2465 x IR 64	8.37**	9.06**	-25.22**	-21.33**	0.50	0.25	107.90**	-60.08**	42.65**	-0.34
					Grain yield					
BPT 5204 x NLR 34449	43.86**	11.16**	-6.88	-30.95**	-34.35**	-0.62	202.25**	-116.92**	61.90**	16.35
BPT 5204 x IR 36	-11.51**	-11.83**	-69.39**	-23.02**	-16.40**	-2.72**	94.54**	-22.69*	46.04**	0.16
RNR 2465 x IR 64	47.21**	32.34**	-65.31**	-72.43**	-111.30**	3.08**	388.24**	-224.42**	144.86**	7.43

Table 2. Continued..

					Kernal length					
BPT 5204 x NLR 34449	0.00	0.91**	0.56*	-0.17	5.25**	0.01	1.91**	-1.25**	0.35	-0.46
BPT 5204 x IR 36	1.88**	1.35**	2.35**	-0.44**	5.38**	-0.66**	4.06**	-4.12**	0.89**	0.26
RNR 2465 x IR 64	-0.49**	-0.59**	-3.03**	-0.98**	4.58**	-0.55**	2.61**	-0.88*	1.96**	0.05
					Kernal breadth					
BPT 5204 x NLR 34449	0.03	0.23**	0.41*	0.07	2.05**	0.00	-0.16	-0.12	-0.14	-0.10
BPT 5204 x IR 36	-0.02	0.09	0.71**	0.32**	2.54**	0.00	-1.35**	0.56	-0.63**	-0.05
RNR 2465 x IR 64	-0.38**	-0.12	-0.14	0.18*	2.49**	-0.15**	-1.40**	0.86**	-0.36*	-0.13
					Kernal L/B ratio					
BPT 5204 x NLR 34449	-0.08	0.05	-0.38	-0.17	2.60**	0.01	1.12	-0.32	0.35	-0.07
BPT 5204 x IR 36	1.19**	0.71**	0.34	-0.78**	1.74**	-0.34**	4.75**	-3.45**	1.56**	0.24
RNR 2465 x IR 64	0.44**	-0.12	-1.18**	-0.75**	1.61**	-0.05	3.45**	-1.81**	1.49**	0.28
					Hulling per cent					
BPT 5204 x NLR 34449	-4.37**	-21.00**	-8.17**	8.60**	91.83**	0.23	-60.41**	42.57**	-17.20**	8.31
BPT 5204 x IR 36	3.48**	-0.20	2.07	-0.60	73.98**	-0.32	5.81	-4.49	1.21	1.84
RNR 2465 x IR 64	1.55	-1.32	-6.23**	-3.23**	68.81**	-1.86**	15.41**	-6.68*	6.45**	1.44
					Milling per cent					
BPT 5204 x NLR 34449	-0.97	-25.60**	-21.45**	2.56**	72.40**	-0.13	-36.85**	31.70**	-5.13**	12.31
BPT 5204 x IR 36	1.45	3.15**	-11.75**	-8.18**	51.02**	-0.22	38.63**	-20.95**	16.35**	-0.85
RNR 2465 x IR 64	7.75**	2.49*	3.89*	-3.17**	62.66**	-1.36**	20.53**	-16.58**	6.35**	2.63
					Head rice recovery					
BPT 5204 x NLR 34449	-0.78	-21.80**	-23.18**	-0.30	52.82**	-1.08**	-16.30**	21.98**	0.60	10.51
BPT 5204 x IR 36	-7.17**	-19.70**	-29.63**	-1.38	52.25**	-2.68**	-14.86*	24.11**	2.76	6.26
RNR 2465 x IR 64	11.11**	-7.85**	-3.56	-3.41**	44.18**	-7.60**	28.30**	-10.08**	6.82**	9.48
					Water uptake					
BPT 5204 x NLR 34449	11.65	-106.90**	135.28**	115.27**	409.71**	-8.82**	-473.34**	325.78**	-230.53**	59.27
BPT 5204 x IR 36	-197.30**	-223.75**	-202.95**	109.05**	422.78**	-34.32**	-705.93**	639.15**	-218.10**	13.22
RNR 2465 x IR 64	-98.85**	-99.95**	-77.93**	60.43**	327.32**	27.00**	-349.23**	319.67**	-120.87**	0.55
					Volume expansion ratio					
BPT 5204 x NLR 34449	-1.12**	-1.13**	2.27**	2.27**	8.79**	-0.12**	-11.73**	6.79**	-4.53**	0.00
BPT 5204 x IR 36	-3.51**	-1.33**	3.09**	3.97**	11.74**	0.33**	-20.03**	12.78**	-7.94**	-1.09
RNR 2465 x IR 64	-1.10**	1.67**	0.57	0.01	3.88**	-0.43**	2.19*	-0.56	-0.01	-1.38
					Kernal elongation ratio					
BPT 5204 x NLR 34449	-0.35**	-0.24**	-1.13**	-0.27**	1.05**	0.02	0.38*	0.04	0.54**	-0.06
BPT 5204 x IR 36	-0.98**	-0.97**	-1.96**	-0.01	1.59**	0.02	-1.60**	1.93**	0.01	-0.01
RNR 2465 x IR 64	-0.45**	-0.55**	-0.94**	0.03	1.58**	-0.04*	-0.95**	1.06**	-0.06	0.05
					Gel consistancy					
BPT 5204 x NLR 34449	6.25	-61.50**	-67.67**	-6.21	40.73**	-3.35**	-35.52*	42.83**	12.42	33.88
BPT 5204 x IR 36	7.85**	-31.45**	-110.97**	-43.68**	-31.47**	-6.10**	137.88**	-63.77**	87.37**	19.65
RNR 2465 x IR 64	-5.80	5.70	-40.93**	-20.42**	3.67	0.50	66.37**	-40.73**	40.83**	-5.75
					Alkali spreading value					
BPT 5204 x NLR 34449	-0.20	0.85	4.55**	1.95**	8.52**	0.57**	-9.67**	3.25*	-3.90**	-0.52
BPT 5204 x IR 36	-3.18**	-3.98**	-5.99**	0.58	6.27**	0.10	-11.56**	8.33**	-1.17	0.40
RNR 2465 x IR 64	-3.20**	-3.54**	-9.44**	-1.35**	1.72*	0.28**	-1.27	4.04**	2.70**	0.17
					Amylose content					
BPT 5204 x NLR 34449	7.16**	3.39**	-4.89**	-7.72**	9.12**	-1.47**	36.43**	-25.99**	15.44**	1.88
BPT 5204 x IR 36	6.68**	2.98**	-5.14**	-7.40**	9.06**	-0.76**	34.69**	-24.45**	14.79**	1.85
RNR 2465 x IR 64	-4.72**	4.15**	-2.22	-0.82	22.89**	0.06	-2.12	-1.07	1.64	-4.43

* & * * significant at 5% and 1% level, respectively

Among yield and its attributes, the additive gene component was significant in all the three crosses except unfilled grains, test weight, ear bearing tillers per plant and grain yield in BPT 5204 x NLR 34449, plant height, ear bearing tillers per plant in BPT 5204 x IR 36, unfilled grains per panicle and harvest index in RNR 2465 x IR 64 indicating the importance of additive gene effects in the expression of the traits and simple selection would be useful for improvement of these traits. The positive sign of additive gene effects (d) indicates that the high yielding parent (P1) showed more number of genes for increasing the yield and its attributing traits whereas the negative sign for h revealed that the dominance gene action was due to the male parent (P2) of the respective cross combination. Murugan and Ganesan (2006) also observed the predominant role of additive component for productive tillers per plant and panicle length in rice, whereas Sanjeev *et al.* (2005) observed predominant additive gene action for the traits days to 50% flowering and test weight in rice. With respect to the quality traits additive gene component was significant for most of the traits except for kernel breadth, kernel L/B ratio, hulling percent, milling percent, kernel elongation ratio in the cross BPT 5204 x NLR 34449, kernel breadth, hulling per cent, milling percent, kernel elongation ratio, alkali spreading ratio in BPT 5204 x IR 36 and in kernel L/B, amylose content in RNR 2465 x IR 64. Yadav *et al.* (2013) reported similar results for alkali spreading value and volume expansion in rice. Rao and Senapathi (2011) reported additive type gene action for kernel breadth, kernel L/B ratio and Ramli *et al.* (2015) for kernel length and milling percent in rice.

Dominance component (h) was significant in all the three crosses for most of the traits except unfilled grains per panicle, test weight, kernel breadth, kernel L/B, gel consistency in BPT 5204 x NLR 34449, plant height, ear bearing tillers per plant, kernel breadth, hulling percent, milling percent, kernel elongation ratio, alkali spreading value in BPT 5204 x IR 36 and unfilled grains per panicle, harvest index, kernel L/B, amylose content in RNR 2465 x NLR 145. In general higher magnitude of negative dominance gene effects were recorded for 14 traits in BPT 5204 x NLR 34449, 11 traits in BPT 5204 x IR 36 and for eight traits in RNR 2465 x IR 64. The negative dominance effects of the genes indicated the dominance of decrease alleles in the inheritance of the characters studied **(Table 3).** Hence, selection would be effective only at later generations for the traits. Murugan and Ganesan (2006) and Patil *et al.* (2006) observed dominance gene action for grain yield in rice. Verma *et al*. (2006) reported similar results for grain yield the number of tiller per plant, grains per panicle and test weight. Gnanamalar and Vivekanandan (2013) reported dominance gene action for hulling percent, head rice recovery, kernel length and kernel breadth.

Among the interaction effects additive x additive (i) type of epistatic interaction was significant for many of the traits in all the three crosses except panicle length, unfilled grains per panicle, test weight, kernel breadth kernel L/B ratio, head rice recovery in BPT 5204 x NLR 34449, hulling percent, head rice recovery, kernel elongation ratio and alkali spreading value in BPT 5204 x IR 36 and panicle length, unfilled grains per panicle, test weight, volume expansion ratio, kernel elongation ratio and amylose content in RNR 2465 x IR 64 in the cross combinations where negative sign appears indicated that little scope of improvement through the simple pedigree method of selection. These results were in conformity with Roy and Senapathi (2011) for kernel breadth, kernel L/B ratio, kernel elongation ratio and linear elongation ratio in rice. Yadav *et al.* (2013) observed the additive x additive gene effects for the number of ear bearing tillers per plant and the number of grains per panicle in rice.

Table 3. Summary of generation means

Generation	BPT 5204 x NLR 34449	BPT 5204 x IR 36	RNR 2465 x IR 64
F_1> P1/P2	PH, EBTS, PL, TW, HI, GY	EBTS, FG/P, HI, SCMR, GY	PH, EBTS, PL, FG/P, HI, SCMR, GY
	KL, HRR, WU	M%,HRR, WU, VER, KER	KL/B, H%, HRR,WU, VER, KER
F_1 intermediate	FG/P, SCMR	DFF, DM, PL, UFG/P, TW	TW
	KL/B, M%	KL/B, H%	KL
F_1>F_2	EBTS, FG/P, HI, SCMR, GY	DFF,DM, EBTS, FG/P, TW, HI, SCMR, GY	DFF, DM, EBTS, PL, FG/P, HI, SCMR, GY
	H%, M%, HRR, WU, VER, GC	M%, HRR, WU, KER, GC, ASV	KL, KL/B, H%, HRR, WU, VER, VER, GC,ASV
F_1=F_2	KL		
BC_1>BC_2	DFF, DM, PH, PL, FG/P, TW, GY	DFF, DM, FG/P, HI	DFF, PH, EBTS, FG/P, UFG/P, HI, GY
	H%, M%, HRR, WU, ASV, AC	H%, HRR, KER, ASV, AC	KL/B, M%, HRR, WU, KER, ASV
BC_1=BC_2	EBTS	SCMR	SCMR
			H%

Table 4. Depiction of positive/negative signs with clear depiction of significance or non significance of the traits in respective crosses

S.No	Character	BPT 5204 x NLR 34449				BPT 5204 x IR 36				RNR 2465 x IR 64			
		d	h	i	L	d	h	i	L	d	h	i	L
1	Days to 50% flowering	+*	-*	-*	+*	+*	+*	+*	-*	+*	+*	+*	-*
2	Days to maturity	+	-*	-*	+*	+*	+*	+*	-*	+*	+*	+*	-*
3	Plant height	+*	-*	-*	+*	-	-*	-*	+*	+*	-*	-*	+*
4	Panicle length	-*	+*	+	-*	-*	+*	+*	-*	+*	+*	-	-
5	Ear bearing tillers per plant	-	+*	+*	-*	-	+*	+*	-*	+*	+*	+*	-*
6	Filled grains per panicle	+*	+*	+*	-*	+*	-*	-*	+*	+*	+*	+*	-*
7	Unfilled grains per plant	-	+	-	-	+*	-*	-*	+*	+	+	-	-*
8	Test weight	-	+	-	-	-*	+*	+*	-*	-*	-*	-	+*
9	Harvest index	-*	+*	+*	-*	-*	+*	+*	+	-	+*	+*	-*
10	SCMR	-*	+*	+*	-*	-*	+*	+*	-*	+	+*	+*	-*
11	Grain yield	-	+*	+*	-*	-*	+*	+*	-*	+*	+*	+*	-*
12	Kernel length	+	+*	+	-*	-*	+*	+*	-*	-*	+*	+*	+*
13	Kernel breadth	-	-	-	-	-	-*	-*	+	-*	-*	-*	-*
14	Kernel L/B ratio	+	+	+	-	-*	+*	+*	+*	-*	+*	+*	-*
15	Hulling per cent	+	-*	-*	+*	-	+	+	-	-*	+*	+*	-*
16	Milling per cent	-	-*	-*	+*	-	+*	+*	-*	-*	+*	+*	-*
17	Head rice recovery	-*	-*	+	+*	-*	-*	-*	+*	-*	+*	+*	-*
18	Volume expansion ratio	-*	-*	-*	+*	+*	-*	-*	+*	-*	-*	-	-
19	Kernel elongation ratio	+	+*	+*	+	+	-*	-*	+*	-*	+*	-	+*
20	Water uptake	-*	-*	-*	+*	-*	-*	-*	+*	+*	+*	-*	+*
21	Gel consistency	-*	-*	+	+*	-*	+*	+*	-*	-*	-*	+*	-*
22	Alkali spreading value	+*	-*	-*	+*	+	-*	-*	+*	+*	+	+*	+*
23	Amylose content	-*	+*	+*	-*	-*	+*	+*	-*+	+	+	+	-

+: Positive; - :Negative; *: Significant

The additive x dominance type of gene interaction was non-significant in all the traits in all the three cross combinations studied (**Table 4**). The dominance x dominance gene action was significant for majority of the traits in all the three crosses studied except unfilled grains per panicle, test weight, kernel length, kernel breadth, head rice recovery, gel consistency in the cross BPT 5204 x NLR 34449, hulling percent, head rice recovery, kernel elongation ratio, alkali spreading value in BPT 5204 x IR 36 and panicle length, unfilled grains per panicle, test weight, volume expansion ratio, kernel elongation ratio, amylose content in the cross RNR 2465x IR 64 indicating that the epistatic gene action i.e., dominance x dominance gene action also plays a predominant role in the inheritance of characters along with additive x additive type of gene action. But, the magnitude of epistasis could be biased by the presence of linkages *viz*., (i) and (l). Hence, biparental mating and reciprocal recurrent selection in early generations are suggested to break the linkages in the repulsion phase followed by selection and isolation of pure lines in later generations may be the better strategy than the pedigree breeding method alone.

The results from the present study revealed that the dominance x dominance (l) and dominance (h) type interactions revealed the existence of a duplicate type of epistasis for almost of all the traits in all the three crosses except kernel breadth, kernel elongation ratio in BPT 5204 x NLR 34449, harvest index, kernel L/B in BPT 5204 x IR36 and amylose content in RNR 2465 x IR 64, where complementary gene action played a vital role in the inheritance of the traits. It leads to limit the pace of progression through selection. Hence, it would be suggested that a few cycles of recurrent selection followed by the pedigree method would be effective by mating of selected plants in early generations; it would be effective to utilize different types of gene effects and also to maintain better heterozygosity. Similar results were already reported by Ashish (2015) for productive tillers per plant and test weight, Kacharabhai *et al.* (2015) for total grains per panicle and grain yield, Subbulakshmi *et al.* (2016) for test weight, hulling percent, milling percent, amylose content and Gnanamalar and Vivekanandan (2013) for hulling percent, head rice recovery, kernel length, kernel breadth, kernel L/B ratio in rice with different cross combinations. The predominance of dominance and epistatic interactions in all the three crosses studied for yield and quality traits indicates that selection would be more effective if the dominance and epistatic effects are first reduced by a few generations of selfing.

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