

Genetic Analysis of Heterotic Crosses in Rice (*Oryza sativa L.*) under Rainfed Ecosystem

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Abstract

An experiment consisting of fifteen testers, three lines and their forty five crosses was conducted at crop research farm of Birsa Agriculture University, Kanke, Ranchi, Jharkhand during *kharif* season. Each parent and F₁s were sown in five rows plot of 5.0×1.0 m² spaced at 20×15 cm² between rows and plants respectively. The experiment was laid out in Randomized Complete Block Design replicated thrice. All the recommended packages of practices were adopted to raise a good crop except irrigations as crop was irrigated through rains itself. The observations were recorded on five randomly selected plants from each of parents and F₁ crosses on fifteen yield and yield attributing traits. Heterosis over mid parent for yield and its components was calculated as usual procedure. Cross combinations namely; BAU-274-92×IR-36 gave significantly positive heterosis to the tune of 31.39% followed by BR-8×IR-36 (27.57%) and BR-8×BD-202 (27%) and BAU-211-90×IR-36 (27.44%), BAU-211×BD-202 (25.83%) and BAU-269-92×IR-36 (25.97%) for grain yield plant⁻¹. The gca status of the parents involved revealed high×high, high×low and low×low combinations means involvement of both additive and non additive gene effects. The combinations can be further improved through simple selection procedures (additive×additive) or after advancing the generations through transgression effects.

1. Introduction

Rice is the basic staple for most of the people. More than 90% of rice is produced and consumed in Asia only. In the early 1960's high yielding variety played a central role in the success of green revolution and enhance Asian rice production by more than triple in the past four plus decades from 200 mt (paddy equivalent) in the early 1960 s to more than 600 mt in 2010. This has been possible with the introduction of modern varieties along with assured irrigation facility, subsidised inputs etc. According to the United Nations 2010 population projection there is addition of 700 billion people in next 30 years. 5 billion people will be added by 2035 and 5.15 billion by 2050 in Asia alone. On the basis of per capita consumption trends of Asia in last two decades, total consumption is expected to grow at the rate of population growth or may even exceeds as per the recent uptrend in three countries (China, India, and Indonesia) continue. The global consumption will probably rise from 439 mt (milled rice) in 2010 to 555 mt in 2035 (FAO, 2012).

In the early period of green revolution (first three decades)

witness higher productivity growth of more than 2% annually, that intended farmers to bring additional area into rice production. The current area under rice cultivation is all time high at around 160 mha compared with 120 mha in the early 1960 s. Further area expansion under rice cultivation cannot be possible for most of the rice growing countries. To meet the growing global needs, yield growth will have to be maintained at 1.2-1.5% to about 2020 and 1.0-1.2% annually beyond 2020 without any possibility of area expansion. Thus a combination of both productivity growth and increasing cropping intensity through adoption of high yielding short duration variety is needed. To achieve this goal exploitation of the heterosis or hybrid vigour could be the better option. Heterosis is the superiority of the F₁s over both the parents. Vanaja and Babu (2004) has also mentioned that yield increase in rice was due to favourable heterosis in flag leaf area, number of spikelets panicle⁻¹ and number of grains panicle⁻¹. There is need to study various morphological traits to get better level of heterosis in different combination of genotypes. Therefore, increasing its productivity is of high importance in breeding programs.



Reduced plant height, moderate tillering, large and compact panicles, increased kernel number per panicle, increased thousand kernel weight and higher yield are the most important characters of rice that has to be improved in breeding programs (Mackill and Lei, 1997; Miller et al., 1993; Nemoto et al., 1995; Paterson et al., 2005; Wayne and Dilday, 2003). Since some rice hybrids show heterosis, it subsequently results to production in terms of yields which is 15 to 30% higher than inbred varieties (Yuan, 1994; Fujimura et al., 1996), and finding a better cross combination is of high importance. Most of the improved varieties hybrids utilize this phenomenon of hybrid vigour (Singh et al., 1999). Line \times tester analysis is used to evaluate the general and specific combining ability of various lines and to estimate gene effects and it is useful in deciding the relative ability of female and male lines to produce desirable hybrid combinations (Kempthorne, 1957).

2. Material and Methods

The genetic material was comprised of fifteen diverse testers of rice as female crossed with three established lines as male. A total of 45 crosses were made during *kharif* 2011 (June-December) at Crop Research station of Birsa agricultural University, Kanke, Ranchi. The method of analysis used was line \times tester (Kempthorne, 1957). All the forty five F_1 hybrids along with eighteen parents were evaluated for heterosis over MP and BP in randomized block design in three replications in the next 2012 (June-December). The plot size was kept 5 \times 1

m^2 and spacing was 20 \times 15 cm 2 . Recommended agronomic practices were followed for raising good crop except irrigation pattern. The crop was grown solely on rain water even in extreme weather condition. Five randomly selected plants plot $^{-1}$ from parents and F_1 plant population were tagged for recording observation on days to panicle emergence, plant height, total number of leaves plant $^{-1}$, flag leaf area, total number of tillers plant $^{-1}$, total number of ear bearing tillers plant $^{-1}$, panicle length, number of grains panicle $^{-1}$, spikelet fertility (%), grain yield plant $^{-1}$, days to maturity and harvest index (%). Relative heterosis and heterobeltiosis were calculated. Heterosis was estimated from mean values according to Fehr (1987) and t-test was performed.

3. Results and Discussion

The analysis of variance (Table 1a&1b) with sixty-three entries including parents and crosses in a line \times tester design revealed significant varietal differences for all the fifteen quantitative characters. Both the parents as well as crosses were found to be significantly different for all the characters studied except panicle length. The differences among parents versus crosses were also highly significant for all the characters except the characters number of effective tillers plant $^{-1}$ and panicle length. The similar results were also obtained by Reddy and De in 1996.

The general combining ability variance ($\sigma^2 gca$) was reported significant for all the characters except for panicle length,

Table 1a: Analysis of variance of 15 quantitative characters in rice (m.s.s.)

Sources of variation	D.F.	Days of panicle emergence	Plant height	Days to maturity	Total no. of leaves plant $^{-1}$	Flag leaf area	Total no. tillers plant $^{-1}$	No. of effective tillers plant $^{-1}$	Panicle length
Replication	2	0.323	9.255	1.180	51.176	7.310	2.589	0.009	2.550
Genotypes	62	370.324**	555.484**	391.845**	441.550**	175.339**	20.928**	15.899**	12.864*
Parents	17	456.646**	671.628**	447.882**	355.326*	181.732**	15.373*	7.790*	10.670
Crosses	44	391.085**	506.830**	355.328**	459.239**	136.409**	22.231**	19.043**	13.812
P vs C	1	1157.57**	721.812**	1045.945**	1129.067*	1779.582**	58.039**	15.435**	8.453
Error	124	1.721	52.897	1.594	169.508	6.719	7.460	4.537	9.462
CV %		1.542	9.073	1.079	20.194	14.526	18.635	17.375	14.514

Table 1b: Analysis of variance of 15 quantitative characters in rice (m.s.s.)

Sources of variation	D.F.	No. of grains panicle $^{-1}$	Spikelet fertility (%)	Grain yield panicle $^{-1}$	1000 grain weight	Biological yield	Grain yield plant $^{-1}$	Harvest index
Replication	2	170.110	25.857	0.016	0.043	7.429	1.762	3.300
Genotypes	62	1653.026**	385.754**	0.461**	11.688**	67.575**	21.616**	81.730**
Parents	17	1484.923**	116.656**	0.425*	9.092**	41.793**	11.897**	31.275**
Crosses	44	1446.639**	462.895**	0.467**	10.009**	78.346**	25.260**	94.098**
P vs C	1	10010.524**	1566.219**	0.826*	129.700**	31.959*	26.522**	395.301**
Error	124	156.293	35.301	0.200	0.701	7.767	1.211	2.975
CV %		14.574	7.961	25.522	4.012	7.557	8.118	4.712

*significant at ($p=0.05$); **significant at ($p=0.01$)

number of grains panicle⁻¹, spikelet fertility, grain yield panicle⁻¹, 1000 grain weight and harvest index [Table 2a & 2b]. The variances due to specific combining ability (σ^2_{sca}) were also found significant for all the characters except the panicle length. The sca variance was higher than the corresponding gca variance for each character. The relative proportion σ^2_{gca} and σ^2_{sca} revealed that specific combining ability was higher for all the traits indicating the preponderance of non-additive gene action for these traits. These results are in general agreement with the findings of Saidaiah et al. (2010), Pratap et al. (2013) and Thakare et al. (2013).

The estimate of heterosis and heterobeltiosis of cross combinations for each character in desired direction are presented in table 3a,b,c,d & e. The crosses viz., BAU-274-92×IR-36, BR-8×IR-36, BR-8×BD-202, BAU-211-90×IR-36, BAU-211-90×BD-202 and BAU-269-92×IR-36 had shown desirable positive heterosis for grain yield as well as other yield related characters like biological yield, 1000 grains weight, total number of effective tillers plant⁻¹, days of panicle emergence and days to maturity. These crosses also exhibited significant heterosis for grain yield panicle⁻¹ except BAU-211-90×BD-202 and BAU-269-92×IR-36 (Ali and Khan, 1995; Rao et al., 1996; Yolanda and Das, 1996; Singh and Haque, 1999; Vishwakarma et al., 1999). With regard to plant height, the three hybrids i.e., BR-8 BD-202, BAU-274-92×BD-202 and BAU-198-90×IR-64 had desirable relative negative heterosis. The crosses i.e. BAU-198-90×IR-64 and BR-8×BD-202 had also shown desirable negative heterobeltiosis indicating the scope for breeding superior hybrids with desirable plant height. In

the same way the crosses BAU-269-92×IR-36, and BAU-295-93×IR-36 had shown desirable significant relative heterosis for days to maturity and Mashuri×IR-36 and BAU-295-93×IR-36 exhibited significant heterobeltiosis showing further scope for developing early varieties. Similar results were obtained by scientists Ali and Khan (1995), Pandey et al. (1995), Rao et al. (1996), Yolanda and Das (1996), Singh and Haque (1999) and Vishwakarma et al. (1999). A considerable amount of relative heterosis was found only in BAU-205-90×BD-202, BAU-211-90×IR-36 and BR-8×BD-202 for total number of leaves plant⁻¹ whereas single cross BAU-29-93×IR-36 exhibited significant heterobeltiosis. The significant relative heterosis was observed maximum in BAU-294-93×IR-64 followed by IR-36-2×IR-64 for flag leaf whereas IR-36-2×IR-64 had shown highest magnitude of heterosis over better parent. This is in accordance with other studies of Julfiqar and Tepora (1992), Xiong et al. (1996) and Singh and Haque (1999). Significant high heterosis was observed in BAU-211-90×BD-202 followed by BAU-211-90×IR-36 over mid parent for the character total number of tillers plant⁻¹. The crosses BAU-270-92×BD-202 and BR-8×BD-202 had shown desirable heterosis over better parent. This has also been reported by Ali and Khan (1995) and Reddy and Nerker (1995). The cross BAU-274-92×IR-36 had shown maximum heterosis over both mid and better parent for grain yield panicle⁻¹ followed by Mahshuri×IR-36 whereas BAU-198-90×IR-36 exhibited only significant higher relative heterosis. Similar results were also observed in previous studies conducted by other workers (Ali and Khan, 1995; Pandey et al., 1995 and Quin et al., 1995). The desirable relative

Table 2a: Estimates of variance components and combining ability variances for all the 15 quantitative characters studied in rice

Characters	Days of panicle emergence	Plant height	Days to maturity	Total no. of leaves plant ⁻¹	Flag leaf area	Total no. tillers plant ⁻¹	No. of effective tillers plant ⁻¹	Panicle length
σ^2_f	43.389**	78.676**	55.081**	51.275*	16.463**	2.545*	2.916**	0.067
σ^2_m	4.365	2.135	4.233**	-6.674	15.645**	-0.265	-0.111	-0.122
σ^2_{fm}	194.696**	224.265**	188.899**	156.548**	50.546**	8.023**	6.382**	4.408
σ^2_{gca}	1.375*	2.492**	1.697**	1.666**	0.127*	0.082*	0.097*	-0.010
σ^2_{sca}	54.899**	74.755**	62.966**	52.183**	16.849**	2.674**	2.127**	1.469
$\sigma^2_{gca}/\sigma^2_{sca}$	0.021	0.033	0.027	0.032	0.008	0.031	0.045	-0.007

Table 2b: Estimates of variance components and combining ability variances for all the 15 quantitative characters studied in rice

Characters	No. of grains panicle ⁻¹	Spikelet fertility (%)	Grain yield panicle ⁻¹	1000 grain weight	Biological yield	Grain yield plant ⁻¹	Harvest index
σ^2_f	-23.689	-8.517	0.050*	0.952*	10.673**	4.525**	9.352*
σ^2_m	26.954	11.828	0.001	0.004	-0.562	-0.047	-0.302
σ^2_{fm}	1303.048**	427.789*	0.122*	6.575**	41.164**	11.187**	64.960**
σ^2_{gca}	-3.255	-1.155	0.001	0.026	0.347*	0.152*	0.270
σ^2_{sca}	434.349*	142.596**	0.041*	2.192**	13.721**	3.729**	21.653**
$\sigma^2_{gca}/\sigma^2_{sca}$	-0.007	-0.008	0.035	0.012	0.025	0.041	0.012

*significant at (p=0.05); **significant at (p=0.01)



Table 3a: Estimates of heterosis (%) over mid parent (mp) and better parent

Crosses	Days of panicle emergence		Plant height (cm)		Days to maturity	
	over mp	over bp	over mp	over bp	over mp	over bp
BAU 198-90×IR-36	-12.580**	-23.190**	33.798	47.654	-6.165**	-13.810**
BAU 198-90×BD-202	-10.190**	-20.590**	5.527	10.284	-5.405**	-13.220**
BAU 198-90×IR-64	-5.979**	-17.390**	-21.093**	-17.590**	-11.410**	-19.620**
Mashuri×IR-36	-22.710**	-30.430**	-9.837	-0.423	-13.680**	-20.920**
Mashuri×BD-202	4.052**	-6.960**	-5.998	-1.840	7.018**	-1.840
Mashuri×IR-64	0.483	-9.570**	-18.568*	-14.892	7.311**	-0.460
BAU 270-92×IR-36	1.205	-8.700**	-3.642	4.495	0.148	-6.360**
BAU 270-92×BD-202	-6.478**	-15.080**	6.304	34.893	-3.540**	-9.920**
BAU 270-92×IR-64	7.229**	-3.260*	1.829	16.894	5.677**	-2.420
BAU 274-92×IR-36	8.350**	1.090	6.154	21.192	6.017**	2.210
BAU 274-92×BD-202	-7.241**	-12.870**	-21.437	5.604	-8.441**	-11.850**
BAU 274-92×IR-64	-16.12**	-21.740**	-13.729	4.506	-13.560**	-17.740**
BAU 291-93×IR-36	7.634**	2.170	11.450	25.998	1.420	-1.380
BAU 291-93×BD-202	-13.080**	-16.910**	-10.101	19.525	-4.397**	-7.160**
BAU 291-93×IR-64	-11.070**	-15.580**	41.700	69.903	-6.723**	-10.480**
BAU 294-93×IR-36	-7.353**	-8.700**	-12.083	1.459	-4.709**	-4.980**
BAU 294-93×BD-202	-7.778**	-8.460**	-12.357	-12.071	-6.224**	-6.610**
BAU 294-93×IR-64	-20.590**	-21.740**	-11.292	-3.318	-16.940**	-18.280**
BAU 295-93×IR-36	-25.930**	-27.840**	-0.230	7.864	-17.430**	-19.790**
BAU 295-93×BD-202	-17.940**	-20.620**	-5.975	18.898	-11.110**	-13.540**
BAU 295-93×IR-64	-22.750**	-24.740**	-1.738	12.437	-13.760**	-15.100**
BAU 213-92×IR-36	-21.550**	-23.450**	-12.827	-11.046	-14.320**	-16.140**
BAU 213-92×BD-202	14.230**	10.690**	-17.399*	-2.141	11.470**	9.260**
BAU 213-92×IR-64	6.007**	3.440*	-15.833*	-9.354	8.000**	7.140**
BAU 200-90×IR-36	-13.860**	-20.910**	8.872	31.493	-11.420**	-18.850**
BAU 200-90×BD-202	-11.300**	-19.090**	-1.777	40.574	-5.013**	-12.870**
BAU 200-90×IR-64	-13.860**	-20.910**	-1.508	26.529	-8.798**	-15.400**
BAU 205-90×IR-36	1.840	-9.780**	6.581	6.677	3.428**	-4.150**
BAU 205-90×BD-202	15.050**	2.570	-12.145	1.631	8.929**	0.830
BAU 205-90×IR-64	11.660**	-1.090	-7.256	-2.297	10.430**	1.080
BR-8×IR-36	-20.210**	-21.880**	-18.227*	-14.795	-8.540**	-8.790**
BR-8×BD-202	-18.570**	-20.830**	-24.848**	-16.805*	-5.365**	-5.490**
BR-8×IR-64	-22.340**	-23.960**	-18.455*	-17.515*	-8.967**	-9.950**
IR-36-2×IR-36	-1.124	-4.350**	1.707	23.101	-2.145	-4.950**
IR-36-2×BD-202	3.019*	0.360	4.786	50.322	0.669	-2.080
IR-36-2×IR-64	-6.742**	-9.780**	36.574	75.842	-6.085**	-7.550**
BAU 211-90×IR-36	19.050**	8.700**	-4.972	-3.938	9.091**	4.420**
BAU 211-90×BD-202	20.000**	10.290**	-1.119	15.904	10.090**	5.230**
BAU 211-90×IR-64	1.190	-7.610**	-4.426	1.919	-0.996	-6.450**
BAU 269-92×IR-36	-23.400**	-25.000**	38.708	49.310	-18.160**	-19.680**
BAU 269-92×BD-202	-20.710**	-22.920**	22.727	54.438	-10.960**	-12.500**
BAU 269-92×IR-64	-23.400**	-25.000**	27.792	45.562	-16.580**	-17.020**
BAU 275-92×IR-36	-7.778**	-9.780**	17.545	21.220	-12.930**	-14.210**
BAU 275-92×BD-202	-4.851**	-6.250**	9.353	22.383	-5.163**	-6.430**

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BAU 275-92×IR-64	-11.110**	-13.040**	14.184	16.667	-15.170**	-15.280**
SEm±	0.930	1.070	5.140	5.940	0.890	1.030
CD ($p=0.05$)	2.570	2.970	14.250	16.460	2.470	2.860
CD ($p=0.01$)	3.380	3.900	18.730	21.630	3.250	3.750

*significant at ($p=0.05$); **significant at ($p=0.01$)

Table 3b: Estimates of heterosis (%) over mid parent (mp) and better parent

Crosses	Total number of leaves plant ⁻¹		Flag leaf area		Total number of tillers plant ⁻¹	
	over mp	over bp	over mp	over bp	over mp	over bp
BAU 198-90×IR-36	-14.561	-17.240	-63.540	-71.124	-14.286	-16.092
BAU 198-90×BD-202	8.840	-0.086	-70.385	-71.901	10.675**	1.580
BAU 198-90×IR-64	-23.344	-29.472	-45.444	-55.140	-22.284	-27.974
Mashuri×IR-36	6.673	-4.920	-80.593	-81.068	10.448**	-0.766
Mashuri×BD-202	6.131	6.085	-63.459	-69.222	7.434**	7.203*
Mashuri×IR-64	-13.787	-26.654	-21.746	-23.639	-12.974	-25.623
BAU 270-92×IR-36	-11.776	-18.515	-24.742	-37.459	-8.299	-15.326
BAU 270-92×BD-202	16.832	-14.620	-81.086	-81.244	17.209**	14.053**
BAU 270-92×IR-64	-2.165	-3.985	-39.325	-47.496	2.724	-9.882
BAU 274-92×IR-36	2.734	5.527	-18.859	-26.691	5.055	-8.429
BAU 274-92×BD-202	-32.181	-53.692	-68.828	-71.844	-32.506	-34.913
BAU 274-92×IR-64	-13.462	-19.704	-15.729	-20.339	-12.936	-27.633
BAU 291-93×IR-36	7.965	32.335*	-14.314	-30.413	8.119**	4.598
BAU 291-93×BD-202	-36.259	51.331	-36.362	-37.651	-37.307	-41.779
BAU 291-93×IR-64	-19.282	-17.835	13.494**	-4.157	-10.987	-18.416
BAU 294-93×IR-36	-34.541	-33.241	-40.758	-57.804	-34.008	-37.548
BAU 294-93×BD-202	-32.753	-49.960	-10.978	-43.189	-27.149	-30.886
BAU 294-93×IR-64	-31.940	-32.195	80.065**	24.567**	-30.418	-37.532
BAU 295-93×IR-36	-48.434	-41.764	-19.104	-28.159	-47.490	-47.893
BAU 295-93×BD-202	-20.231	-36.936	-20.419	-40.111	-19.313	-26.834
BAU 295-93×IR-64	-27.199	-23.698	35.338**	15.167**	-26.182	-30.705
BAU 213-92×IR-36	-16.126	-28.333	-77.264	-78.945	-16.592	-28.736
BAU 213-92×BD-202	1.456	-33.661	-56.401	-66.111	6.091*	0.024
BAU 213-92×IR-64	-13.662	-22.678	-14.311	-24.134	-13.389	-29.339
BAU 200-90×IR-36	-34.249	-19.514	-45.348	-46.089	-29.762	-32.184
BAU 200-90×BD-202	-12.088	-32.975	-36.985	-48.544	-13.717	-19.753
BAU 200-90×IR-64	-33.222	-32.110	10.230**	3.618	-31.343	-37.191
BAU 205-90×IR-36	-7.633	0.278	23.388**	18.289	-3.178	-5.440
BAU 205-90×BD-202	32.536*	5.488	-60.008	-68.067	14.286**	0.767
BAU 205-90×IR-64	-12.938	-8.699	-21.673	-28.340	-8.642	-11.589
BR-8×IR-36	8.092*	-5.643	-44.784	-54.210	1.856	-5.364
BR-8×BD-202	28.139	-12.944	-34.093	-34.467	17.321**	13.418**
BR-8×IR-64	1.241	-6.449	-3.190	-16.414	-2.901	-14.320
IR-36-2×IR-36	-24.989	-10.294	11.745**	0.000	-23.517	-28.352
IR-36-2×BD-202	5.333	-21.779	4.712	-20.733	6.178*	1.754
IR-36-2×IR-64	-4.656	-5.175	63.456**	40.105**	-4.415	-15.003
BAU 211-90×IR-36	35.481**	21.504	-27.225	-29.064	22.467**	6.513*
BAU 211-90×BD-202	-12.106	-12.106	-64.013	-70.889	26.368**	11.404**
BAU 211-90×IR-64	-29.917	-35.509	-42.311	-46.382	-30.041	-41.970

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BAU 269-92×IR-36	-8.156	23.983	-45.180	-45.423	-2.174	-7.216
BAU 269-92×BD-202	-23.053	-34.537	-60.473	-67.489	-21.600	-32.646
BAU 269-92×IR-64	-24.648	-24.613	-37.409	-40.646	-23.288	-23.536
BAU 275-92×IR-36	-24.987	-44.051	-53.414	-64.942	-26.622	-37.165
BAU 275-92×BD-202	-4.935	-38.383	-44.809	-50.983	-9.367	-14.334
BAU 275-92×IR-64	-35.213	-42.391	-5.553	-26.453	-36.117	-47.773
SEm±	9.210	10.630	1.830	2.120	1.930	2.230
CD ($p=0.05$)	25.510	29.460	5.080	5.870	5.350	6.180
CD ($p=0.01$)	33.530	38.720	6.680	7.710	7.030	8.120

*significant at ($p=0.05$); **significant at ($p=0.01$)

Table 3c: Estimates of heterosis (%) over mid parent (mp) and better parent (bp) for different quantitative characters

Crosses	Total number of effective tillers plant ⁻¹		Panicle length		No. of grains panicle ⁻¹	
	over mp	over bp	over mp	over bp	over mp	over bp
BAU 198-90×IR-36	-11.164	-13.426	24.292**	16.807**	-6.624	-24.083
BAU 198-90×BD-202	11.227**	3.877	3.874	1.401	-21.240	-29.942
BAU 198-90×IR-64	-26.484	-31.020	-7.765	-18.487	-23.045	-37.052
Mashuri×IR-36	10.026**	-0.926	-16.618	-26.098	-22.681	-24.456
Mashuri×BD-202	9.972**	6.336**	-6.180	-13.695	-25.128	-30.837
Mashuri×IR-64	-2.956	-15.596	-14.551	-28.682	-3.365	-5.118
BAU 270-92×IR-36	-7.463	-13.889	0.761	-3.470	-0.260	-14.809
BAU 270-92×BD-202	21.978**	19.355	-7.467	-7.845	-28.559	-19.433
BAU 270-92×IR-64	9.308**	-1.885	-3.404	-13.094	-9.249	-13.463
BAU 274-92×IR-36	7.013**	-4.630	-0.625	-2.304	-7.562	-17.970
BAU 274-92×BD-202	-36.599	-39.394	-4.805	-6.737	-88.017	-86.909
BAU 274-92×IR-64	-14.428	-26.307	8.333**	-0.154	-35.340	-38.596
BAU 291-93×IR-36	9.880**	5.556*	-3.135	-4.630	-29.270	-38.214
BAU 291-93×BD-202	-32.626	-36.197	-6.024	-8.208	-71.812	-70.889
BAU 291-93×IR-64	-5.556	-12.596	32.776**	22.531**	50.205**	64.017**
BAU 294-93×IR-36	-36.232	-38.889	2.229	0.611	-15.560	-36.495
BAU 294-93×BD-202	-34.043	-37.374	6.116*	2.089	-18.487	-15.312
BAU 294-93×IR-64	-33.643	-38.732	14.286**	5.313	0.037	-5.843
BAU 295-93×IR-36	-45.199	-45.833	-2.857	-7.815	-14.880	-34.165
BAU 295-93×BD-202	-25.450	-31.296	-1.449	-9.974	-14.504	-8.943
BAU 295-93×IR-64	-39.640	-42.588	2.342	-10.944	-26.316	-28.694
BAU 213-92×IR-36	-11.172	-24.537	38.538**	33.014**	2.009	-31.004
BAU 213-92×BD-202	4.559*	-5.234	-7.006	-14.092	-4.510	-9.621
BAU 213-92×IR-64	-8.333	-24.593	8.897**	-4.045	-2.031	-16.994
BAU 200-90×IR-36	-20.000	-25.000	2.694	-2.711	-9.155	-35.330
BAU 200-90×BD-202	-12.262	-14.815	4.194	-4.942	-14.305	-15.176
BAU 200-90×IR-64	-32.701	-39.160	6.137*	-7.808	-0.077	-10.937
BAU 205-90×IR-36	-2.059	-3.146	7.143*	5.263	15.058	-12.701
BAU 205-90×BD-202	15.789**	4.549**	-3.738	-9.091	-39.566	-36.721
BAU 205-90×IR-64	-3.524	-6.170	6.944**	-3.418	-8.373	-23.720
BR-8×IR-36	6.203**	-0.926	-9.360	-11.694	-11.190	-23.405
BR-8×BD-202	28.219**	25.100**	-7.402	-13.504	-22.713	-19.194
BR-8×IR-64	5.238*	-5.313	8.260**	-3.418	-17.332	-10.868
IR-36-2×IR-36	-15.869	-22.685	3.183	-1.754	-7.066	-20.854

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IR-36-2×BD-202	14.763**	13.499**	-1.445	-9.679	-32.166	-21.274
IR-36-2×IR-64	5.797**	-6.170	20.646**	5.632	-55.074	-52.165
BAU 211-90×IR-36	29.947**	12.500**	2.640	-0.797	-39.712	-39.712
BAU 211-90×BD-202	27.381**	17.906**	0.316	-6.737	-29.472	-29.472
BAU 211-90×IR-64	-25.831	-37.875	11.307**	-1.223	-18.372	-30.277
BAU 269-92×IR-36	7.551**	6.359**	12.539**	10.802**	-23.889	-44.426
BAU 269-92×BD-202	-16.792	-24.870	10.241**	7.679*	-40.161	-39.431
BAU 269-92×IR-64	-21.145	-23.308	2.341	-5.556	-12.801	-20.297
BAU 275-92×IR-36	-22.581	-33.333	-8.006	-9.274	-20.898	-42.318
BAU 275-92×BD-202	-7.784	-15.152	1.357	-1.147	-39.286	-38.618
BAU 275-92×IR-64	-34.190	-45.159	3.183	-4.629	-11.857	-35.164
SEm±	1.510	1.740	2.180	2.510	8.840	10.210
CD ($p=0.05$)	4.170	4.820	6.030	6.960	24.500	28.290
CD ($p=0.01$)	5.490	6.330	7.920	9.150	32.200	37.180

*significant at ($p=0.05$); **significant at ($p=0.01$)

Table 3d: estimates of heterosis (%) over mid parent (mp) and better parent

Crosses	Spikelet fertility (%)		Grain yield panicle ⁻¹		1000 grain weight	
	over mp	over bp	over mp	over bp	over mp	over bp
BAU 198-90×IR-36	0.967	-3.605	47.019**	20.920**	14.555**	12.463**
BAU 198-90×BD-202	-3.548	-8.738	14.695**	2.910**	4.923**	0.462**
BAU 198-90×IR-64	-1.015	-3.745	3.823**	-1.753	11.142**	3.912**
Mashuri×IR-36	-1.799	-2.142	58.799	45.865**	12.456**	10.029**
Mashuri×BD-202	-0.394	-0.984	40.678**	17.374**	13.324**	8.148**
Mashuri×IR-64	-4.884	-6.986	25.366**	0.180	3.042**	-3.971
BAU 270-92×IR-36	-2.319	-6.091	-29.686	-40.684	11.397**	10.159**
BAU 270-92×BD-202	-8.143	-12.485	35.185**	24.786**	12.875**	8.842**
BAU 270-92×IR-64	-1.634	-3.665	12.358**	9.573**	-9.588	-14.886
BAU 274-92×IR-36	1.575	0.190	64.507**	46.366**	15.212**	9.266**
BAU 274-92×BD-202	-78.650	-79.136	-34.745	-47.071	-9.775	-16.466
BAU 274-92×IR-64	-13.727	-14.176	36.806**	6.486**	13.853**	3.018**
BAU 291-93×IR-36	-35.923	-19.026	28.585**	3.994**	11.637**	6.329**
BAU 291-93×BD-202	-56.982	-58.943	-34.729	-42.550	-4.283	-11.014
BAU 291-93×IR-64	10.366	8.282	-1.408	-8.602	3.298**	-6.154
BAU 294-93×IR-36	-2.476	-2.862	-23.391	-34.896	-9.898	-10.110
BAU 294-93×BD-202	-0.188	-0.738	-30.970	-35.764	-6.193	-8.765
BAU 294-93×IR-64	-13.434	-15.386	-28.685	-29.861	0.232**	-4.850
BAU 295-93×IR-36	2.837	-5.615	-24.095	-35.273	2.999**	-1.347
BAU 295-93×BD-202	2.099	-5.493	-24.906	-29.806	6.056	-0.863
BAU 295-93×IR-64	-22.411	-13.002	-31.668	-32.451	-5.029	-13.260
BAU 213-92×IR-36	-10.805	-12.961	-5.137	-15.400	-2.647	-5.096
BAU 213-92×BD-202	-17.510	-18.767	-12.103	-13.645	1.288	-3.681
BAU 213-92×IR-64	-10.393	-14.156	-7.016	-10.450	-8.937	-15.429
BAU 200-90×IR-36	-11.095	-15.947	-17.093	-29.688	7.861**	5.597**
BAU 200-90×BD-202	5.197	0.335	-17.757	-23.611	10.637**	10.151**
BAU 200-90×IR-64	-2.293	-9.256	-1.326	-3.125	4.066*	1.070
BAU 205-90×IR-36	7.987	2.487	3.339**	-20.325	-0.830	-2.061
BAU 205-90×BD-202	-6.640	-10.608	3.981**	-13.279	-11.948	-15.203

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BAU 205-90×IR-64	-0.440	-7.186	-13.777	-24.526	-9.038	-14.476
BR-8×IR-36	-5.285	-8.138	6.572**	-10.374	3.866**	3.774**
BR-8×BD-202	-1.013	-4.866	2.957**	-5.272	7.182**	4.590**
BR-8×IR-64	-8.807	-9.885	3.237	0.340	-13.277	-17.407
IR-36-2×IR-36	-6.672	-9.059	-9.323	-25.243	18.710**	14.963**
IR-36-2×BD-202	-12.576	-15.588	5.216**	-5.340	20.427**	13.786**
IR-36-2×IR-64	-30.847	-31.342	6.053**	0.647	-5.160	-12.469
BAU 211-90×IR-36	3.430	-1.843	33.954**	14.109**	16.866**	11.214**
BAU 211-90×BD-202	-5.099	-9.138	-18.980	-24.339	18.614**	10.182**
BAU 211-90×IR-64	-11.005	-17.139	25.893**	24.339**	1.445	-7.912
BAU 269-92×IR-36	-16.630	-17.133	-4.981	-22.741	13.896**	3.083**
BAU 269-92×BD-202	-12.042	-6.427	-16.095	-25.701	2.081*	-9.689
BAU 269-92×IR-64	-6.140	-8.443	-28.214	-33.022	-5.458	-18.154
BAU 275-92×IR-36	-3.890	-8.589	-25.624	-40.969	21.204**	5.891**
BAU 275-92×BD-202	-15.180	-18.610	-36.627	-45.374	28.000**	9.427**
BAU 275-92×IR-64	-1.965	-8.415	-38.138	-43.906	20.262**	0.703
SEm±	4.200	4.850	0.320	0.360	0.590	0.680
CD ($p=0.05$)	11.640	13.440	0.880	1.010	1.640	1.890
CD ($p=0.01$)	15.300	17.670	1.150	1.330	2.160	2.490

*significant at ($p=0.05$); **significant at ($p=0.01$)

Table 3e: Estimates of heterosis (%) over mid parent (mp) and better parent (bp) for different quantitative characters

Crosses	Biological yield		Grain yield plant ⁻¹		Harvest index	
	over mp	over bp	over mp	over bp	over mp	over bp
BAU 198-90×IR-36	19.708**	11.486**	17.066**	7.368**	-1.893	-7.543
BAU 198-90×BD-202	15.680**	6.256	7.052**	-0.199	-7.166	-10.053
BAU 198-90×IR-64	-9.852	-13.104	-17.876	-16.473	-9.104	-10.983
Mashuri×IR-36	7.853**	-1.590	11.312**	7.088**	2.412	-5.396
Mashuri×BD-202	-4.728	-14.235	2.030*	0.000	6.090**	-4.531
Mashuri×IR-64	-18.857	-20.053	-24.152	-30.669	-6.586	-19.704
BAU 270-92×IR-36	12.883**	11.158**	12.100**	3.842**	-0.468	-7.215
BAU 270-92×BD-202	24.906**	21.204**	25.354**	18.131**	0.719	-3.500
BAU 270-92×IR-64	24.083**	13.263**	16.507**	13.687**	-5.960	-6.826
BAU 274-92×IR-36	16.005**	8.018*	31.387**	35.166**	12.665**	6.096**
BAU 274-92×BD-202	34.277**	23.317**	-48.285	-42.798	-61.618	-64.811
BAU 274-92×IR-64	-14.036	-17.130	-15.596	-22.900	-1.680	-13.990
BAU 291-93×IR-36	50.564**	39.850**	24.654**	12.674**	-25.803	-28.664
BAU 291-93×BD-202	1.026	-7.447	-36.631	-41.761	-37.062	-37.749
BAU 291-93×IR-64	-5.989	-9.137	-9.533	-9.294	-4.614	-8.465
BAU 294-93×IR-36	-7.583	-13.731	-29.956	-35.599	-23.875	-25.536
BAU 294-93×BD-202	-4.053	-11.669	-32.625	-36.986	-29.517	-29.997
BAU 294-93×IR-64	-17.834	-20.981	-36.797	-38.031	-22.980	-27.334
BAU 295-93×IR-36	-16.775	-22.549	-38.712	-46.571	-32.958	-34.484
BAU 295-93×BD-202	-14.276	-21.318	-25.483	-33.923	-12.925	-13.427
BAU 295-93×IR-64	-29.455	-31.947	-39.890	-40.899	-13.982	-18.764
BAU 213-92×IR-36	4.280	1.336	3.295**	2.989*	-1.057	-2.024
BAU 213-92×BD-202	11.195**	9.071**	4.134**	6.923**	-5.883	-7.650
BAU 213-92×IR-64	-6.287	-17.765	-16.305	-25.463	-10.051	-16.103

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BAU 200-90×IR-36	-9.251	-14.546	-9.904	-14.921	2.165	0.133
BAU 200-90×BD-202	5.450	-2.083	-4.231	-7.961	-6.592	-10.977
BAU 200-90×IR-64	-9.036	-13.313	-20.306	-23.653	-10.083	-18.411
BAU 205-90×IR-36	1.062	-13.049	3.116**	-23.077	2.755	-1.098
BAU 205-90×BD-202	8.475**	-7.829	15.531**	-12.506	7.164**	6.114**
BAU 205-90×IR-64	-5.236	-9.950	-9.882	-20.199	-5.364	-9.277
BR-8×IR-36	21.679**	19.547**	27.573**	17.773**	4.730**	2.343
BR-8×BD-202	27.637**	23.575**	27.144**	19.518**	-0.021	-0.602
BR-8×IR-64	16.884**	8.871**	9.089**	2.034	-6.400	-11.607
IR-36-2×IR-36	6.849*	0.899	8.517**	0.365	3.860*	3.110
IR-36-2×BD-202	19.403**	11.182**	18.412**	11.493**	-0.697	-4.172
IR-36-2×IR-64	24.021**	20.039**	2.477*	-3.254	-16.802	-23.613
BAU 211-90×IR-36	33.117**	31.392**	25.829**	23.802**	-5.807	-7.868
BAU 211-90×BD-202	31.299**	27.702**	24.670**	25.014**	-4.694	-9.347
BAU 211-90×IR-64	0.610	-6.685	-23.262	-31.096	-23.079	-30.334
BAU 269-92×IR-36	16.675**	6.896*	25.966**	12.178**	8.422**	5.163**
BAU 269-92×BD-202	5.785*	-4.386	-1.063	-10.426	-5.999	-6.179
BAU 269-92×IR-64	-8.677	-8.778	-16.561	-15.823	-8.458	-12.900
BAU 275-92×IR-36	-2.282	-13.564	-26.218	-46.293	-24.110	-26.272
BAU 275-92×BD-202	-1.117	-13.661	28.157	-46.870	-25.117	-25.136
BAU 275-92×IR-64	-11.784	-13.508	-38.456	-46.395	-30.262	-33.762
SEm±	1.970	2.280	0.780	0.900	1.220	1.410
CD ($p=0.05$)	5.460	6.310	2.160	2.490	3.380	3.900
CD ($p=0.01$)	7.180	8.290	2.830	3.270	4.440	5.130

*significant at ($p=0.05$); **significant at ($p=0.01$)

heterosis for test weight was found in BAU-275-92×IR-36 and BAU-275-92×BD-202 and desirable heterobeltiosis was shown by the cross i.e. IR-36-2×IR-36, IR-36-2×BD-202 and BAU 198-90×IR-36. Similar results were obtained by Julfiquar and Tepora (1992) and Reddy and Nerker (1995). Significant heterosis over mid parent was found in BAU-211-90×BD-202, BAU-211-90×IR-36, BR-8×BD-202 whereas over better parent BAU-270-92×BD-202 exhibited better heterosis for the character total number to tillers plant⁻¹. The significant heterosis over mid parent was exhibited by BAU-211-90×IR-36 and BR-8×BD-202 and over better parent was shown by BR-8×BD-202 and BAU-270-92×BD-202 for total number of effective tillers plant⁻¹ which can be further exploited. Similar are the results of works of many other scientists (Pandey et al., 1995; Reddy and Nerker, 1995 and Singh and Haque, 1999). For panicle length significant heterosis over mid parents and better parents in desired magnitude was found in BAU-213-92×IR-36 and BAU-291-93×IR-64 which is in accordance with other studies (Julfiquar and Tepora, 1992 and Pandey et al., 1995). The cross BAU-291-93×IR-36 and BAU-211-90×IR-36 had shown marked heterosis over both mid parent and better parent for biological yield which is similar to the findings of Quin et al. (1995). For the character number of grains panicle⁻¹, single cross i.e. BAU-29-93×IR-64 had shown

significant relative heterosis and heterobeltiosis similar to the studies of Dong et al. (1995) and Rao et al. (1996). None of the crosses exhibited significant heterosis for spikelet fertility. This result was also obtained by Rao et al. (1996). The crosses i.e. BAU-274-92×IR-36 followed by BAU-269-92×IR-36 and BAU-205-90×BD-202 had shown significant heterosis over mid parent for harvest index and the crosses i.e. BAU-205-90×BD-202, BAU-274-92×IR-36 and BAU-269-92×IR-36 exhibited better heterosis over better parent. Similar information was also gathered by Vishwakarma et al. (1999), Jelodar et al. (2010), Mirarab et al. (2011), Vennila et al. (2011) and Zhou et al. (2014).

The inheritance of yield and most of the yield contributing characters is polygenic in nature which shows continuous variation. The choice of appropriate breeding procedure depends on the type of gene action involved in the expression of these characters (Table 4) in a genetic population. Study of the nature gene action involved reveals that the sca variances are higher than gca variances for all the characters thus showing the preponderance of non-additive gene action (dominance and epistasis) and therefore, heterosis breeding may be rewarding.

There is continuous discussion on the validity of the causes that

Table 4: Best crosses with their sca effects in relation to per se performance

Characters	Best hybrids on the basis of per se performance	Best specific combiners	No. of grains panicle ⁻¹	BAU -291-93×IR-64	Mashuri×IR-36 IR-36-2×BD-202
Days of panicle emergence	Mashuri×IR -36 BAU-295-93×IR-36 BAU-295-93×IR-64 BAU-269 -92×IR-36 BAU-269-92×IR-64	Mashuri×IR-36 BAU 270-92×BD-202 BAU 291-93×IR-64 BAU 213-92×IR-36 BAU 211-90×IR-64	Grain yield panicle ⁻¹	BAU-198-90×IR-36 Mashuri×IR-36 BAU-274-92×IR-36 BAU-274-92×IR-64 BAU-211-90×IR-36 BAU-211-90×IR-64	BAU-198-90×IR-36 Mashuri×IR-36 BAU-274-92×IR-36 BAU-274-92×IR-64 BAU-211-90×IR-36 BAU-211-90×IR-64
Plant height (Cm)	BAU-198-90×IR-64 Mashuri×IR-64 BAU-274 -92×BD -202 BR-8×BD-202 BR-8×IR -64	BAU 198-90×IR-64 BAU 274-92×IR-64 BAU 295-93×BD-202 BR-8×IR-36 BR-8×BD-202	1000 grain weight	BAU-198-90×IR-36 BAU-270-92×IR-36 IR-36-2×IR-36 IR-36-2×BD-202 BAU-211-90×BD-202 BAU-275-92×IR-36 BAU-275-92×IR-202 BAU-275-92×IR-64	BAU 294-93×IR-64 BAU 200-90×BD-202 BAU 200-90×IR-64 IR-36-2×IR-36 IR-36-2×IR-64
Days to maturity	BAU-198-90×IR-64 Mashuri×IR-36 BAU-294-93×IR-64 BAU-295-93×IR-36 BAU-200-90×IR-36 BAU-269-92×IR-36 BAU-269-92×IR-64 BAU-275-92×IR-64	BAU 213-92×IR-36 BAU 270-92×BD-202 BAU 294-93×IR-64 BAU 274-92×IR-64 BAU 274-92×BD-202 Mashuri×IR-36 BAU 211-90×IR-64	Biological yield	BAU-274 -92×BD-202 BAU-291-93×IR-36 BR-8×BD-202 BAU-211-90×IR-36 BAU-211-90×BD-202	Mashuri×BD-202 BAU 295-93×IR-36 BR-8×IR-64 BAU 269-92×IR-64
Total number of leaves plant ⁻¹	BAU-205-90×BD-202 BAU-211-90×IR-36 BAU-291-93×IR-36		Grain yield plant ⁻¹	BAU-274-92×IR-36 BR-8×IR-36 BR-8×BD-202 BAU-211-90×IR-36 BAU-211-90×BD-202 BAU-269-92×IR-36	Mashuri×IR-36 Mashuri×BD-202 BAU 291-93×BD-202 BAU 205-90×IR-36 BR-8×IR-64
Flag leaf area	BAU-291-93×IR-64 BAU-294-93×IR-64 BAU-295-93×IR-64 BAU-205-90×IR-36 IR-36-2×IR-64	BAU 198-90×IR-64 Mashuri×IR-36 BAU 274-92×IR-36 IR-36-2×IR-64	Harvest index	Mashuri×IR-36 BAU-274-92×IR-36 BAU-205-90×BD-202 BR-8×IR-36 BAU-269-92×IR-36	Mashuri×IR-36 BAU 294-93×BD-202 BAU 213-92×IR-36 BAU 200-90×IR-36 BAU 205-90×IR-36 IR-36-2×IR-36 IR-36-2×BD-202
Total number of tillers plant ⁻¹	BAU-270-92×BD-202 BAU-205-90×BD-202 BR-8×BD-202 BAU-211-90×IR-36 BAU-211-90×BD-202				
Total number of effective tillers plant ⁻¹	BAU-270-92×BD-202 BAU-205-90×BD-202 BR-8×BD-202 IR-36-2×BD-202 BAU-211 -90×IR-36 BAU-211-90×BD-202 BAU-198-90×IR-36 BAU-291-93×IR-64 BAU-213-92×IR-36 IR-36-2×IR-64				

are responsible for heterosis. Over the time depending on the specific study and the crop, epistasis has been identified as part of the control of heterosis, mainly in rice. This was especially true for complex characters such as yield. For example, Yu et al. (1997) found in rice that dominance and overdominance had little effect on heterosis for yield and its components, while epistasis was found to have a major effect in this respect. Epistasis was found to be important in rice heterosis also in the control of simpler traits such as heading date and plant height (Yu et al., 2002). In their theoretical framework for the resolution of epistasis, dominance, and overdominance effects on heterosis, Melchinger et al. (2007) referred to the epistasis effect by the term ‘augmented dominance effect’. Birchler et al.



(2010) tended to conclude that where the effect of these three gene actions is considered, the relative role of each might be related to the trait in question.

4. Conclusion

BAU-274-92×IR-36 gave significantly high positive heterosis followed by BR-8×IR-36, BR-8×BD-202, BAU-211-90×IR-36, BAU-211×BD-202 and BAU-269-92×IR-36 for grain yield plant-1. The gca status of the parents revealed that high×high, high×low and low×low combinations shows involvement of both additive and non-additive gene effects. These cross combinations can be further improved through simple selection procedures (high×high). Other combinations with high×low gca can be further improved through transgression. The combinations with low×low gca can be utilized for hybrid development through CGMS system.

5. Future Thrust

The crosses viz. BAU-274-92×IR-36, BR-8×BD-202, BAU-211-90×IR-36, BAU-211×BD-202, and BAU-269-92×IR-36 can be more beneficial in future if handled carefully and intensive selection pressure can be applied to isolate transgressive segregants and/or can be utilised for development of high yielding hybrids if combined with suitable CGMS lines suitable for (drought/rainfed) environment.

6. References

- Ali, S.S., Khan, M.G., 1995. Studies for heterosis and combining ability in rice. Pakistan Journal of Scientific and Industrial Research 38(5-6), 200-204.
- Birchler, J.A., Yao, H., Chudalayandi, S., Vaiman, D., Veitia, R.A., 2010. Heterosis. The Plant Cell 22, 2105-2112.
- Dong Xu, Z., Fenghao, D., Zhen, Z., Zhang, Xue Quing, Y., 1995. Heterosis of hybrid rice combined with indica photoperiod temperature sensitive genitive male sterile line M25 with marker. Acta Agricultural Zhejiangensis 7(4), 232 -325.
- FAO, 2012. World Agriculture towards 2030/2050: The 2012 Revision. Available from <http://www.fao.org/docrep/016/ap106e/ap106e.pdf>
- Fehr, W.R., 1987. Heterosis In: Principles of cultivar development: Theory and Techniques (Vol. 1). Macmillan Publishing Company, New York, pp 115.
- Fujimura, T., Akagi, H., Oka, M., Nakamura, A., Sawada, R., (1996). Establishment of a rice protoplast culture and application of an asymmetric protoplast fusion technique to hybrid rice breeding. Plant Tissue Cult. Lett. 13, 243-247.
- Jelodar, N.B., 2010. Heterosis and combining ability analysis for yield and related-yield traits in hybrid rice. International Journal of Biology 2(2), 222- 231.
- Julfiquar, A.W., Tepora, N.M., 1992. Heterosis in some quantitative characters in F1 hybrid rice (*Oryza sativa* L.). CLSU Scientific Journal of Philippines 12(2), 30-36.
- Kamphorne, O., 1957. An introduction to Genetic Statistics. John Wiley and Sons. Inc., New York, Chapman and Hall, London.
- Mackill, D.J., Lei, X.M., (1997). Genetic variation for traits related to temperate adaptation of rice cultivars. Crop Sci. 37, 1340-1346.
- Melchinger, A.E., Utz, H.F., Piepho, H.P., Zeng, Z.B., Schon, C.C., 2007. The role of epistasis in the manifestation of heterosis: a systemsoriented approach. Genetics 177, 1815-1825.
- Miller, B.C., Foin, T.C., Hill, J.E., (1993). CARICE: a rice model for scheduling and evaluating management actions. Agron. J. 85, 938-947.
- Mirarab, M., Asadollah, A., Mohamad, H.P., 2011. Study on combining ability, heterosis and genetic parameters of yield traits in rice. African Journal of Biotechnology 10(59), 12512-12519.
- Nemoto, K., Morita, S., Baba, T., (1995). Shoot and root development in rice related to the phyllochron. Crop Sci. 35, 24-29.
- Pandey, M.P., Singh, J.P., Singh, H., 1995. Heterosis breeding for grain yield and other agronomic characters in rice (*Oryza sativa* L.). Indian Journal of Genetics 55(4), 438-455.
- Paterson, A.H., Freeling, M., Sasaki, T., (2005). Grains of knowledge: genomics of model cereals. Genome Res. 15, 1643-1650.
- Pratap, N., Shekhar, R., Singh, P.K., Soni, S.K., 2013. Combining ability, gene action and heterosis using CMS lines in hybrids rice (*Oryza sativa* L.). The Bioscan 8(4), 1521-1528.
- Quin, Y., Quan, L.Y., Zhang, S.Z., Yulan, W., Wang, Y.B., Zhang, G.Q., 1995. Analysis of heterosis combining ability and path coefficients in japonica rice hybrid. Acta Agriculture Scanghai 11(4), 23-27.
- Rao, A.M., Ramesh, S., Kulkarni, R.S., Savithramma, D.L., Madhusudan, K., 1996. Heterosis and combining ability in rice. Crop Improvement 23(1), 23-56.
- Reddy, C.D.R., Nerkar, Y.S., 1995. Heterosis and inbreeding depression in upland rice crosses. Indian Journal of Genetics 55(4), 389-393.
- Reddy, J.N., De, R.N., 1996. Genetic variability in lowland rice. Madras Agricultural Journal 83(4), 269-270.
- Saidaiah, P., Sudheer K.S., Ramesha, M. S., 2010. Combining ability studies for development of new hybrids in rice over environments. Journal of Agricultural Science 2(2), 225-233.
- Singh, M., Maurya, D.M., 1999. Heterosis and inbreeding



- depression in rice for yield and yield components using CMS system. *Oryza*, 36(1), 24-27.
- Singh, S.K., Haque, M.F., 1999. Heterosis for yield and components in rice (*Oryza sativa L.*). Indian Journal of Genetics 52(2), 237-238.
- Thakare, I.S., Patel, A.L., Mehta, A.M., 2013. Line×Tester analysis using CMS system in rice (*Oryza sativa L.*). The Bioscan 8(4), 1379-1381.
- Vanaja, T., Babu, L.C., 2004. Heterosis for yield and yield components in rice (*Oryza sativa L.*). Journal of Tropical Agriculture 42(1/2), 43-44.
- Vennila, S., Anbuselvam, Y., Palaniraja, K., 2011. Heterosis studies for yield and its components in rice (*Oryza sativa L.*). International Journal of Recent Scientific Research 2(9), 261-262.
- Vishwakarma, D.N., Maurya, D.M., Verma, G.P., Vishwakarma, S.R., 1999. Heterosis for yield components in rice hybrids (*Oryza sativa L.*). Indian Journal of Agricultural Sciences 69(7), 530.
- Wayne, S.C., Dilday, R.H., (2003). Rice: Origin, History, Technology, and Production. Wiley Series in Crop Science, John Wiley&Sons, Inc. p. 324.
- Xiong, L.W., Yi, L., Tingchai, Y., 1996. The heterotic effects on dry matter production and grain yield formation in hybrid rice. Journal of Fujian Agricultural University 25(3), 260-265.
- Yolanda, J.L., Das, L.D.V., 1996. Heterosis in hybrid rice. Madras Agricultural Journal 83(2), 115-117.
- Yuan, L.P., 1994. Increasing yield potential in rice by exploitation of heterosis. In: Virmani SS (ed) Hybrid rice technology. New developments and future prospects. IRRI, Manila, Philippines, p. 1-6.
- Yu, S.B., Li, J.X., Xu, C.G., Tan, Y.F., Gao, Y.J., Li, X.H., Zhang, Q., Saghai Maroof, M.A., 1997. Importance of epistasis as the genetic basis of heterosis in an elite rice hybrid. Proceedings of the National Academy of Sciences, USA 94, 9226-9231.
- Yu, S.B., Li, J.X., Xu, C.G., Tan, Y.F., Li, X.H., Zhang, Q., 2002. Identification of quantitative trait loci and epistatic interactions for plant height and heading date in rice. Theoretical and Applied Genetics 104, 619-625.
- Zhou, G., Chen, Y., Yao, W., Zhang, C., Xie, W., Hua1, J., Xing, Y., Xiao, J., Zhang, Q., 2014. Genetic composition of yield heterosis in an elite rice hybrid. PNAS 109(39), 15847-15852.

