PREDICTION OF COMBINING ABILITY AND HETEROSIS IN THE SELECTED PARENTS AND HYBRIDS IN RICE (*Oryza Sativa*.L)

Prediksi Daya Gabung dan Heterosis Tetua Terseleksi dan Hibrida pada Padi (Oryza Sativa.L)

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ABSTRAK

Seleksi tetua berdasarkan nilai daya gabungnya merupakan salah satu pendekatan yang efektif untuk perakitan padi hibrida. Empat galur CMS dan 4 galur R disilangkan menggunakan metode persilangan lini x tester menghasilkan 16 F1 hibrida. Sebanyak 8 galur tetua dan 16 hibrida ditanam dengan rancangan acak kelompok lengkap diulang 3 kali di KP Kuningan dan Muara BB Padi selama tahun 2012-2013. Hasilnya menunjukkan nilai daya gabung umum (DGU) yang signifikan terdapat pada karakter jumlah gabah isi per malai, bobot 1000 butir, dan umur 50% berbunga. Nilai daya gabung khusus (DGK) signifikan terdapat pada karakter tinggi tanaman dan hasil gabah. Tetua dengan nilai DGU terbaik GMJ12A (galur A) dan CRS703 (galur R) dan berpotensi menghasilkan F₁ hibrida hasil tinggi. Diantara F₁ hibrida, GMJ6A/CRS707 dan GMJ12A/CRS707 menunjukkan nilai DGK positif tertinggi untuk hasil gabah.

Kata kunci: DGK, DGU, heterosis, lini x tester, padi hibrida

ABSTRACT

Selection of parents based on their combining ability is an effective approach in hybrid breeding. Four CMS and four restorer lines were crossed in line x tester mating design to obtain $16 F_1$ hybrids rice. The 8 parental lines and 16 hybrids rice were planted in randomized complete block design with three replications at Kuningan and Muara field station of ICRR during 2012-2013. The results revealed that mean squares for GCA were significant for number of fertile spikelet per panicle, a thousand-grains weight, and 50% days of flowering. Mean squares for SCA were significant for plant height and grain yield. Parental lines exhibited the highest GCA effects for GMJ12A (line) and CRS703 (tester) for grain yield trait and revealed good potential to be used as parents for hybrid rice. Among all the crosses, GMJ6A/CRS707 and GMJ12A/CRS707 showed the greatest positive SCA effects for grain yield and had heterosis over better parent and midparent.

Key words: GCA, heterosis, hybrid rice, line x tester, SCA

INTRODUCTION

Breeding program based on selection of hybrids require expected level of heterosis as well as the specific combining ability. In breeding high yielding varieties of crop plants, the breeders often face with the problems of selecting parents and crosses. Before initiating any crop improvement program, it is necessary to understand the genetic nature of the parents. The selection of parents on the basis of their mean performance does not necessarily lead to desired results (Rai and Asati, 2011; Satya and Jebaraj, 2013). Combining ability analysis help breeders in choosing suitable genotypes as parents for hybridization and superior cross combinations through general combining ability (GCA) and specific combining ability (SCA) studies.

The line×tester analysis provides information about GCA of parents and SCA effects of hybrids. The GCA is the result of additive gene effects, while the SCA is the result of non-allelic interactions (Jinks, 1954). The estimates of combining ability are useful to predict the relative performance of different lines in hybrid combinations. The information on the nature and magnitude of gene action is important in understanding the genetic potential of population and deciding the breeding procedure to be adopted in a given population (Saidaiah et al., 2010). Amongst a large array of biometrical procedures for relative estimation of genetic components, line × tester is an efficient procedure as it allows the inclusion of a large number of lines and provides reliable estimates of combining ability and gene action governing a complex trait in crop plants i.e. maize (Chandel and Mankotia, 2014), barley (Patial et al., 2016), sorgum (Tariq et al., 2014), and rice (Latha et al., 2013;)Sathya and Jebaraj, 2015).

Hybrid rice technology exploits the phenomenon of hybrid vigor (heterosis) to increase the yield potential of rice varieties with reported yield advantage of 15– 20% over inbred commercial high-yielding varieties (Xangsayasane *et al.*, 2010). Heterosis estimates, for different morphological and yield related characters, are attributed to both additive and non additive gene actions. Dar *et al.* (2014) reported high contribution of general combining ability for genetic control of hybrid rice characters. Raju *et al.* (2014) and Dorosti and Monajjem (2014) identified the best specific and general combiners that were efficient for breeding grain yield in hybrid rice. The objective of present study was to determine estimates of combining ability for selected parental lines (GCA and SCA) and to evaluate the heterosis of yield hybrid rice compared to their parents.

MATERIALS AND METHODS

Four stable CMS lines i.e. GMJ6A, GMJ7A, GMJ12A, and GMJ13A and 4 restorer lines i.e. CRS703, CRS707, CRS735, and CRS757 were selected as parental lines and testers respectively. To determine GCA and SCA, the CMS lines GMJ6A, GMJ7A, GMJ12A, and GMJ13A as lines were crossed with 4 restorer lines as testers i.e. CRS703, CRS707, CRS735, and CRS757 to generate 16 hybrid combinations in line \times tester mating design (Kempthorne, 1957).

The hybrids were evaluated along with parents in a Randomized Complete Block Design with three replications during dry season, 2013 at Kuningan and Muara field station of Indonesian Center for Rice Research (ICRR) under irrigated conditions. Twenty-one days old seedlings were transplanted with 25 cm x 25 cm spacing and 1-2 seedlings per plant. Standard agronomic and irrigation management practices were adopted for proper growth and development of the hybrids and their parents.

The maintainer of CMS lines were raised for recording the grain yield and related component traits. The grain yield (GY) was measured. The other yield related traits: 50% Days of flowering (DFF); Plant Height (PH); Number of productive tillers per plant (NPH); Number of fertile spikelets per panicle (NFP); and a Thousand grains weight (TGW) were all measured according to the standard evaluation system (IRRI, 1996).

Data were subjected to analysis of variance following Randomized Complete Block Design. Analyses of variance were conducted for all the traits measured, using individual plot data for each environment separately. Prior to combined data analysis across locations Bartlett's test for grain yield was conducted to test homogeneity of variance (Gomez and Gomez, 1984). Based on the test result, data from two locations were analyzed for all traits combined using Statistical Tool for Agricultural Research (STAR) from IRRI. Line x tester analyses of variance was performed to estimate general combining ability (GCA) and specific combining ability (SCA), assuming the following statistical model (Singh and Chaudhary, 1979):

$Y_{hijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + R_h + \varepsilon_{hijk}$

where Y_{hijk} = the observation of the k-th genotype in a plot in h replication of the i-th male parent (tester) and

the j-th female parent (line); μ = the general mean; α_i = the effect of the i-th male parent; β_i = the effect of j-th female parent; $(\alpha\beta)_{ij}$ = the interaction of male and female parents; R_h = the effect of h-th replication and ε_{hijk} = the environment effect and remainder of the genetic effect between hybrids combination. The structure of analysis variance combining ability analysis was showed at Table 1.

The GCA and SCA were determined by the following formula (Singh and Chaudhary, 1979):

$$GCA_{(Lines)} = \frac{Yi.}{tr} + \frac{Y...}{1tr}$$

$$GCA_{(Testers)} = \frac{Y.j}{tr} + \frac{Y...}{1tr}$$

$$SCA_{(ij)} = \frac{Yij}{r} - \frac{Yi..}{rt} - \frac{Y.j.}{r1} + \frac{Y...}{1tr}$$

The genetic components was estimated according to Singh and Chaudary (1979) as follow:

Cov H.S (line) = (Ml - Ml x t) / rtCov H.S.(tester) = (Mt - Ml x t) / rlCov H.S.(average) = 1/r (2lt - l - t) [(l-1) (M1) + (t-1)](Mt) / 1 + t - 2 - Mlxt $\sigma^2 \text{ GCA} = \text{Cov H.S}$ $\sigma^2 SCA = M_{lxt} - M_e / r$ Proportion contribution of lines, testers, and interaction

lines x testers

Contribution of Lines = $SS(1) \times 100 / SS(Crosses)$

Contribution of Testers = $SS(t) \times 100 / SS(Crosses)$ Contribution of $(1 \text{ x t}) = SS(1 \text{ x t}) \times 100 / SS(Crosses)$ Where,

Yi..= Total of the ith line, Y.j.= Total of the jth tester, Y... = Grand total

r, l and t = number of replications, lines and testers, respectively.

 M_{lxt} = linextester mean square, M_e =error mean square $\sigma^2 A = \sigma^2 GCA$ varians Aditif; $\sigma^2 D = \sigma^2 SCA =$ varians Dominan

Mid-parent heterosis (MPH) was determined as percentage increase of the F₁ over the mean parental value, otherwise Heterobeltiosis was determined as percentage increase of the F_1 over the best parent value for a given trait (Virmani et al.,. 1997) i.e.:

Heterobeltiosis
$$= \frac{F1 \text{ hybrid -Best parent}}{Best parent} X 100\%$$

Mid Parent $= \frac{F1 \text{ hybrid -Mean of two parent}}{Mean of two parent} X 100\%$

RESULTS AND DISCUSSION

Mean of two parent

Genetic variability among parents and hybrids

Analysis of variances for all the studied traits, i.e., 50% days of flowering, plant height, number of productive tillers per plant, number of fertile spikelets per panicle,

Table 1. Anova for combining ability over environments (Singh and Chaudary, 1979)

Source of variation	Df	Mean Square (MS)	F values
Environment (E)	e-1		
Genotypes (G)	(g-1)	MS _g	MS_g/Ms_e
Parents (P)	(p-1)	MS _p	MS_p/Ms_e
P x C	1	MS _{pxc}	$\mathrm{MS}_{\mathrm{pxc}}/\mathrm{MS}_{\mathrm{e}}$
Crosses (C)	(c-1)	MS _c	MS_{e}/MS_{e}
Lines (L)	(l-1)	MS ₁	MS_{l}/MS_{lxt}
Testers (T)	(t-1)	MS_t	MS_t/MS_{lxt}
LxT	(l-1)(t-1)	MS _{lxt}	MS_{lxt}/MS_{e}
C x E	(c-1)/(e-1)	MS _{cxe}	$\mathrm{MS}_{\mathrm{cxe}}/\mathrm{MS}_{\mathrm{lxtxe}}$
LxE	(l-1)/(e-1)	MS _{lxe}	$\mathrm{MS}_{\mathrm{lxe}}/\mathrm{Ms}_{\mathrm{lxtxe}}$
ТхЕ	(t-1)/(e-1)	MS _{txe}	$\mathrm{MS}_{\mathrm{txe}}/\mathrm{Ms}_{\mathrm{lxtxe}}$
L x T x E	(l-1)(t-1)/(e-1)	MS _{lxtxe}	$\mathrm{MS}_{\mathrm{lxtxe}}/\mathrm{M}_{\mathrm{e}}$
Pooled Error	e(g-1)(r-1)	MS _e	

a thousand grains weight, and grain yield combined over both environments are presented in Table 2. Results revealed that environments mean squares were highly significant for all the studied traits. Mean squares due to crosses, lines (L) and testers (T) were significant for all studied traits except lines for number of productive tiller per plant, number of fertile spikelet per panicle, and a thousand grain weight; testers for number of fertile spikelet per panicle. Variance due to interaction effects of lines and testers were significant for plant height and grain yield. The significant variance of L × T interaction indicated the importance of specific combing ability.

Test crosses evaluation is used to determine the relative potential of parental lines in a hybrid breeding program. The mean squares due to testers were of a larger magnitude than those of lines and $L \times T$ interaction for all the characters except plant height indicating greater diversity among the testers than the lines. Mean squares due to $L \times T$ interactions were significant for plant height and grain yield suggested that inbred lines may have different combining ability patterns and performed differently in crosses depending on type of tester used.

Similar results were reported earlier in maize (Chandel and Mankotia, 2014).

The interactions between crosses and environment was significant for grain yield indicating that test crosses presented differential performance in the testing environments. The L × E was not significant for all studied traits but the T × E interactions were significant for number of productive tiller per plant, number of fertile spikelet per panicle, and grain yield indicated that inbred lines performed differently as reflected in their respective test crosses from one environment to another. The interactions for L × T × E were significant only for plant height and grain yield. These findings indicated that these are different ranks of interaction of inbred lines (parental) in their test crosses from one environment to another that appeared in grain yield.

Agronomic performance of parents and hybrids

Mean performance of test crosses for all the studied traits combined over the environments are presented in Table 3. Mean comparison of grain yield and its component traits using LSD analysis revealed that only 5

Table 2. Analysis of variance for combining ability effects of different hybrid rice characters.

5		0	5		2		
Source of variation	Df	DFF	PH	NPH	NFP	TGW	GY
Environment (E)	1	43.3	259.5	230.5	71725.8	1503.8	5812117.4
Genotypes (G)	23	223**	212.6**	9.4*	1314.2*	37.4**	562371**
Parents (P)	7	152.1**	562.9**	2.4	183.2	82.4**	416709.2**
P x C	1	718.8**	52.9**	34.9**	15883.6**	117.8**	173068**
Crosses (C)	15	223**	59.7**	11	870.8	11.1*	656300**
Lines (L)	3	282.5**	71.4**	6.5	224.6	11.7	484069.4**
Testers (T)	3	519.4**	68.8**	21.7*	1450.7	28.3*	1588452.8**
L x T	9	104.4	52.8**	8.9	892.8	5.1	402992.6**
C x E	15	107.9	26	9.9	784.1	3.8	445033.3**
L x E	3	128.8	10.1	5.5	28.1	6	141902.8
ТхЕ	3	184.8	28.9	17	2319.2*	4.7	1383508.3**
LxTxE	9	75.2	30.3	9.1	524.5	2.7	233251.9*
Pooled Error	92	49.84	11.92	4.64	590.08	3.36	120911.6

Note: DFF: 50% days of flowering, PH: plant height (cm), NPH: number of productive tillers per plant, NFP: number of fertile spikelets per panicle, TGW: a thousand-grains weight (g), and GY: grain yield (g/plot). ^{ns}, * and **: non-significant and significant effect at 0.05 and 0.01 probability, E: Environment, G; Genotypes, P: parents, C: crosses, L: lines, and T:testers.

hybrid rice i.e. GMJ6A/CRS703 (1350 g/plot), GMJ12A/ CRS703 (1358.3 g/plot), GMJ13A/CRS703 (1100 g/ plot), GMJ6A/CRS707 (1083.3 g/plot), and GMJ12A/ CRS707 (1183.3 g/plot were significantly superior to overall mean (845.3 g/plot) well adapted to the moderate and high land conditions of Muara and Kuningan, West Java. Further, as many as three hybrids performed significantly better than the parents for grain yield. However, all of testers in this study recorded a good performance for most of the traits including the grain yield except CRS735. Among the female parent lines, GMJ12A gave the highest mean grain yield 1266.7 g/ plot.

Table 3. Means of the measured c	haracters for 8 parental line	es and their 16 F1 hybrids
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Genotypes	DFF	PH	NPH	NFS	TGW	GY	
Lines							
GMJ6A	100ab	92.7j	14.1bcd	86def	23.4g	738.3d-i	
GMJ7A	100ab	104fgh	15.1bcd	84.1def	20.7h	466.7ij	
GMJ12A	101ab	98i	13.3d	77.6ef	25.9f	1266.7ab	
GMJ13A	87e	90.9j	13.6d	76f	28.3cde	666.7ghi	
Testers							
CRS703	101ab	112.3bc	13.7d	84.8def	30.2abcd	1033.3a-f	
CRS707	102a	116.7a	13.7d	88def	29.1cde	1083.3а-е	
CRS735	94abcd	113ab	14.7bcd	75.6f	28def	833.3c-h	
CRS757	97abcd	107.6def	13.8d	89.6c-f	32ab	1066.7a-f	
Lines x Testers							
GMJ6A/CRS703	101ab	106.4defg	14.6bcd	104.1a-f	29.3cde	1350a	
GMJ7A/CRS703	97abcd	110bcd	15bcd	107.1a-e	28.3cde	950b-g	
GMJ12A/CRS703	98abc	108.2cde	13.4d	124.9ab	29.6cde	1358.3a	
GMJ13A/CRS703	94abcd	100hi	14.4bcd	128.8a	30.3abcd	1100abcd	
GMJ6A/CRS707	97abcd	108.8cde	14.4bcd	120.2abc	28.3cde	1083.3а-е	
GMJ7A/CRS707	97abcd	108.4cde	16.7ab	98.8a-f	27.5ef	703.3f-i	
GMJ12A/CRS707	98abc	107.9def	14.7bcd	104.1a-f	29.7bcde	1183.3abc	
GMJ13A/CRS707	89de	103gh	18.4a	82.5ef	27.7ef	250j	
GMJ6A/CRS735	89de	104fgh	15.3bcd	114.1abcd	29.4cde	666.7ghi	
GMJ7A/CRS735	91cde	107.7def	15.7bcd	98.8a-f	27.4ef	550hij	
GMJ12A/CRS735	92bcde	107.3def	15bcd	97.2b-f	28.5cde	833.3c-h	
GMJ13A/CRS735	74f	106.3defg	16.5abc	104.7а-е	27.6ef	506.7hij	
GMJ6A/CRS757	92bcde	103.9fgh	14cd	92.2c-f	29.4cde	388.3ij	
GMJ7A/CRS757	93bcde	105efg	13.4d	97.8b-f	30.6abc	733.3e-i	
GMJ12A/CRS757	93bcde	98.7i	15.6bcd	99.1a-f	32.5a	610ghij	
GMJ13A/CRS757	95bcde	105.1efg	13.4d	105.3a-f	29.7bcde	866.7c-h	
Overall mean	95	105.2	14.7	97.6	28.5	845.3	
LSD _{0.05}	8.84	4.12	2.66	30.29	2.38	363.37	

Note: DFF: 50% days of flowering, PH: plant height (cm), NPH: number of productive tillers per plant, NFP: number of fertile spikelets per panicle, TGW: a thousand-grains weight (g), and GY: grain yield (g/plot). Means within each column followed by the same letter are not significantly different from each other based on the 0.05 probability level of LSD.

General combining ability analysis

The GCA effects for 4 A lines and the 4 testers combined over both environments are shown in Table 4. For maturity and plant height negative GCA effects are desirable (Sen and Singh, 2011). Minimum plant height is required to protect the plant from lodging. The results exhibited that the parental lines CRS735 and GMJ13A gave negative values of GCA effects for 50% days of flowering and CRS757, GMJ12A, and GMJ13A had a negative GCA effects for plant height. The parental lines could be reduced plant height and lesser days for maturity. None of parental lines showed good general combining ability for number of productive tiller per plant, number of fertile spikelet per panicle, and a thousand -grains weight. Furthermore, GMJ6A showed positive GCA effects for grain yield. In addition, the obtained results in the same table showed that CRS735 was the best general combiner for 50% days of flowering, whereas the CRS757 was the best combiner for plant height. The best combiner for grain yield was GMJ12A.

Specific combining ability analysis

SCA effect is an index to determine the usefulness of a particular cross combination in the exploitation of heterosis. Since yield is a complex trait having low heritability, per se, selection for it is generally ambiguous and leads to unpredictable results. While selecting the best specific combination for yield, it would be important to give due weightage to yield related traits. Crosses with significant SCA for different traits in the desirable direction are listed in Table 5. The best SCA effects were obtained in GMJ13A/CRS735 for 50% days of flowering, GMJ12A/CRS757 for plant height, GMJ6A/ CRS707 for number of fertile spikelet per panicle, and GMJ13A/CRS757 for grain yield.

Proportion contribution and gene action

Genetic variance components for all the studied traits over the environments and their interaction with environments are shown in Table 6. It was evident from the finding that testers played very important role for 50% days of flowering, number of productive tillers per plant, number of fertile spikelets per panicle, a thousand grains weight, and grain yield. It was indicated dominance of rertorer lines as male parent influence for the traits. Lines were more important but their contribution was not too high, revealed low influence of maternal effect for all traits. The contribution of maternal and paternal interaction (line x tester) was low to high for all the traits under study. These results were confirmity with Akhter *et al.* (2010) and Hasan *et al.* (2014).

Genotypes	DFF	PH	NPH	NPH NSP TGW		GY
Testers						
CRS703	1.40	0.16	-0.23	3.75	0.09	1.40
CRS707	0.69	0.45	0.34	-1.19	-0.27	0.69
CRS735	-2.18	0.22	0.20	-0.43	-0.29	-2.18
CRS757	0.09	-0.83	-0.31	-2.12	0.47	0.09
SE (gi) testers	2.28	1.12	0.69	7.84	0.59	112.23
SE (gi-gj)	5.19	1.24	0.48	61.46	0.35	12594.96
Lines						
GMJ6A	0.51	0.04	-0.15	0.89	-0.01	17.08
GMJ7A	0.52	0.71	0.06	-1.45	-0.21	-28.89
GMJ12A	0.68	-0.05	-0.13	0.46	0.33	58.47
GMJ13A	-1.71	-0.70	0.22	0.11	-0.10	-46.67
SE (gi) lines	2.28	1.12	0.69	7.84	0.59	112.23
SE (gi-gj)	5.19	1.24	0.48	61.46	0.35	12594.96

Table 4. General combining ability effects for yield characters in parental of hybrid rice

Note: DFF: 50% days of flowering, PH: plant height (cm), NPH: number of productive tillers per plant, NFP: number of fertile spikelets per panicle, TGW: a thousand-grains weight (g), and GY: grain yield (g/plot).

1	0 7		2			
Genotypes	DFF	РН	NPH	NSP	TGW	GY
GMJ6A/CRS703	0.63	0.03	0.23	-4.93	-0.01	36.39
GMJ7A/CRS703	-0.55	0.58	0.17	-1.58	-0.15	-50.97
GMJ12A/CRS703	-0.54	0.74	-0.20	2.44	-0.25	-2.22
GMJ13A/CRS703	0.46	-1.35	-0.19	4.07	0.41	16.81
GMJ6A/CRS707	0.06	0.56	-0.40	5.39	0.00	75.69
GMJ7A/CRS707	0.21	-0.25	0.17	0.58	-0.04	-5.00
GMJ12A/CRS707	0.17	0.34	-0.33	0.45	0.15	67.64
GMJ13A/CRS707	-0.44	-0.65	0.56	-6.42	-0.11	-138.33
GMJ6A/CRS735	0.16	-0.80	0.05	2.57	0.38	-7.92
GMJ7A/CRS735	0.98	-0.24	-0.04	-0.19	-0.05	-0.83
GMJ12A/CRS735	1.27	0.37	-0.09	-2.61	-0.22	6.25
GMJ13A/CRS735	-2.40	0.68	0.08	0.23	-0.11	2.50
GMJ6A/CRS757	-0.84	0.21	0.13	-3.02	-0.38	-104.17
GMJ7A/CRS757	-0.64	-0.10	-0.30	1.19	0.24	56.81
GMJ12A/CRS757	-0.90	-1.44	0.62	-0.29	0.32	-71.67
GMJ13A/CRS757	2.38	1.33	-0.45	2.13	-0.19	19.03
S.E. (SCA effects)	4.56	2.23	1.39	15.68	1.18	224.45
S.E. (Sij - Skl)	6.44	3.16	1.96	22.17	1.66	317.43

Table 5. Specific combining ability effects for characters in hybrids rice

Note: DFF: 50% days of flowering, PH: plant height (cm), NPH: number of productive tillers per plant, NFP: number of fertile spikelets per panicle, TGW: a thousand-grains weight (g), and GY: grain yield (g/plot).

in rice								
Characters	Lina	Tester	Interaction	Variance estimates and their ratio				
Characters	Line	Tester	LxT	σ ² GCA	$\sigma^2 SCA$	$\sigma^2 GCA/\sigma^2 SCA$		
Days 50% flowering	25.34	46.58	28.08	14.53	14.03	1.04		
Plant height	23.91	0.01	53.05	1.82	12.62	0.14		
Number of productive tiller								
per plant	11.93	39.52	48.55	0.4	1.03	0.39		
Number of fertile spikelet								
per panicle	5.16	33.32	61.52	16.3	51.75	0.32		
A thousand grain weight	21.15	51.2	27.65	0.73	0.31	2.32		
Grain yield	14.75	48.41	36.84	34781.87	83951.02	0.41		

Table 6. Proportional contribution of lines, testers and their interactions to total variance in a set of line × tester crosses in rice.

Results revealed that estimates of general combining ability variance components, σ^2 GCA was larger than σ^2 SCA for 50% days of flowering and a thousandgrain weight These results indicated preponderance of additive gene action than non-additive gene action in the inheritance of these traits, whereas σ^2 SCA was higher than σ^2 GCA for plant height, number productive tiller per plant, number fertile spikelet per panicle, and grain yield indicated that non-additive gene action was important than additive gene action in the inheritance of these traits. Hence, for exploiting heterosis, selection of superior plants, in terms of yield and associated traits should be postponed to later generation, where these traits can be improved by making selections among the recombinants within the segregating populations. These findings are consistent with that of Pratap et al. (2013), and Dhasarathan et al. (2015) who reported the predominance of non-additive gene action for most of the traits studied by them and also matches with that of Dar *et al.* (2014) who also reported the predominance of SCA variance over GCA variance.

Heterosis

For exploitation of hybrid rice breeding it is important to determine the level of heterosis. Percent heterosis for grain yield and yield related traits was calculated over mid parent and better parent (heterobeltiosis). The estimates of mid-parent and over better parent heterosis revealed at Table 7. All of hybrids showed negative mid-parent heterosis and heterobeltiosis, it indicated most of hybrid having maturity less than their parents. Five hybrids recorded positive mid-parents heterosis values for grain

Table 7. Mid-parent heterosis and heterobeltiosis of 16 F₁ hybrid rice

The density with a	D	FF	Р	Н	NF	РН	NS	SP	TG	W	G	Y
Hybrid fice	MP	HT	MP	HT	MP	HT	MP	HT	MP	HT	MP	HT
GMJ6A/CRS703	0.2	-0.3	3.8	14.7	5.0	3.4	21.9	21.0	9.5	-97.2	52.4	30.6
GMJ7A/CRS703	-3.5	-3.8	1.8	5.8	4.3	-0.5	26.9	26.3	11.3	-97.3	26.7	-8.1
GMJ12A/CRS703	-3.1	-3.3	2.9	10.4	-1.0	-2.6	53.9	47.3	5.6	-97.7	18.1	7.2
GMJ13A/CRS703	-0.6	-7.4	-1.5	10.1	6.1	5.4	60.2	51.9	3.7	-97.1	29.4	6.5
GMJ6A/CRS707	-4.3	-5.1	3.9	17.4	3.8	2.1	38.2	36.6	7.7	-97.4	18.9	0.0
GMJ7A/CRS707	-3.9	-4.6	-1.8	4.2	16.3	10.8	14.8	12.3	10.7	-97.5	-9.3	-35.1
GMJ12A/CRS707	-3.7	-4.2	0.5	10.1	8.8	7.1	25.7	18.3	8.2	-97.7	0.7	-6.6
GMJ13A/CRS707	-6.4	-13.1	-0.8	13.3	35.2	34.2	0.6	-6.3	-3.6	-97.4	-71.4	-76.9
GMJ6A/CRS735	-8.8	-11.5	1.2	12.2	6.4	4.2	41.2	32.6	14.2	-96.5	-15.2	-20.0
GMJ7A/CRS735	-6.3	-9.0	-0.7	3.6	5.1	3.9	23.7	17.4	12.8	-96.7	-15.4	-34.0
GMJ12A/CRS735	-5.1	-8.6	1.7	9.5	6.9	1.8	26.9	25.3	6.0	-97.7	-20.6	-34.2
GMJ13A/CRS735	-18.1	-21.1	4.3	16.9	17.0	12.5	38.1	37.8	-2.0	-96.7	-32.4	-39.2
GMJ6A/CRS757	-6.3	-7.7	3.8	12.1	0.7	-0.5	5.1	2.9	5.9	-97.2	-57.0	-63.6
GMJ7A/CRS757	-5.7	-7.0	-0.7	1.0	-7.4	-11.4	12.7	9.2	16.2	-97.1	-4.4	-31.3
GMJ12A/CRS757	-6.2	-8.3	-3.9	0.7	15.1	12.9	18.6	10.6	12.1	-97.4	-47.7	-51.8
GMJ13A/CRS757	3.5	-1.7	5.9	15.6	-1.8	-2.8	27.2	17.6	-1.7	-97.2	0.0	-18.7

Note: DFF: 50% days of flowering, PH: plant height (cm), NPH: number of productive tillers per plant, NFP: number of fertile spikelets per panicle, TGW: a thousand-grains weight (g), and GY: grain yield (g/plot). MP: mid-parents heterosis, HT: heterobeltiosis

yield i.e. GMJ6A/CRS703, GMJ7A/CRS703, GMJ12A/ CRS703, GMJ13A/CRS703, and GMJ6A/CRS707. However, only three hybrids showed heterobeltiosis values for grain yield higher than their best parent.

CONCLUSIONS

The high GCA effects of the parents showed that GMJ12A and CRS703 have the potential to be used in breeding programs for high yield of hybrid rice. The F_1 hybrids GMJ6A/CRS707 and GMJ12A/CRS707 proved to be good specific combiners for grain yield.

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REFERENCES

- Akhter, A., M.J. Hasan, H. Begum, M.U. Kulsum, and M.K. Hossain. 2010. Combining ability analysis in rice (Oryza sativa L.). Bangladesh J. Pl. Breed Genet. 23(2):07-13.Available from: https://www.banglajol. info/index.php/BJPBG/article/view/9319/6871. http://dx.doi.org/10.3329/bjpbg.v23i2.9319.
- Chandel, U. and B.S. Mankotia. 2014. Combining ability in local and cimmyt inbred lines of maize (Zea mays l.) for grain yield and yield components using line × tester analysis. SABRAO Journal of Breeding and Genetics 46 (2): 256-264.
- Dar, S.H., A.G. Rather, M.A. Ahanger, N.R. Sofi, and S. Talib. 2014. Gene action and combining ability studies for yield and component traits in rice (Oryza sativa L.): A Review. Journal of Plant and Pest Science 1(3): 110-127.
- Dhasarathan, C. Babu, and K. Iyanar. 2015. Combining ability and gene action studies for yield and quality traits in baby corn (Zea mays L.). SABRAO Journal of Breeding and Genetics 47(1): 60-69.
- Dorosti, H. and S. Monajjem. 2014. Gene action and combining ability for grain yield and yield related traits in rice (Oryza sativa L.). The Journal of Agricultural Sciences 9(3): 100-108.

- Gomez, K.A. and A.A. Gomez. 1984. Statistical Procedures for Agricultural Research, 2nd Edition. New York: John Wiley and Sons.
- Hasan, M.J, M.U. Kulsum, and M.M. Rahman. 2014. Combining ability of different yield related characters in rice. SAARC J. Agric. 12(2): 143-153.
- IRRI. 1996. Standard Evaluation System. Manila, Philippines. Manila, Philippines: IRRI.
- Jinks, J.L. 1954. Analysis of continuous variation in diallel cross of Nicotiana rustica varieties. Genet. 39: 767-788.
- Latha, S., D. Sharma, and G.S. Sanghera. 2013. Combining ability and heterosis for grain yield and its component traits in rice (Oryza sativa L.). Notulae Scientia Biologicae. 5(1): 90-97.
- Kempthorne, O. 1957. An Introduction to Genetic Studies. New York, USA: John Willey and Sons Inc.
- Patial, M., D. Pal, and J. Kumar. 2016. Combining ability and gene action studies for grain yield and its component traits in barley (Hordeum vulgare L.). SABRAO Journal of Breeding and Genetics 48 (1): 90-96.
- Pratap, N., P.K. Singh, R. Shekhar, S.K. Sonil, and A.K. Mall. 2013. Genetic variability, character association and diversity analyses for economic traits in rice (Oryza sativa L.). SAARC J Agriculture 10(2): 83-94.
- Raju, C.D., S.S. Kumar, C.S. Raju, and A. Srijan. 2014. Combining ability studies in the selected parents and hybrids in rice (Oryza sativa L.). Int J Pure and Applied Bioscience 2(4): 271-279.
- Rai, N. and B.S. Asati. 2011. Combining ability and gene action studies for fruit yield and yield contributing traits in brinjal. Indian J. Hort. 68(2): 212-215.
- Saidaiah, P., S.S. Kumar, and M.S. Ramesha. 2010. Combining Ability Studies for Development of New Hybrids in Rice over Environments. Journal of Agricultural Science. 2 (2): 225-233.
- Sathya, R., and S. Jebaraj. 2015. Evaluation of aerobic hybrid analysis of combining ability in three line hybrids in Rice (Oryza sativa L.) under aerobic conditions. African Journal of Agricultural Research. 10(18): 1971-1981.
- Sen, C. and R.P. Singh. 2011. Study on heterosis in Boro x high yielding rice hybrids. Int J Pl Breed and Genet. 5(2): 141-149.

- Singh R.K. and B.D. Chaudhary.1979. Biometrical method in quantitative genetic analysis. New Delhi: Kalyani Publ.
- Tariq, A.S., Z. Akram, G. Shabbir, K.S. Khan, T. Mahmood, and M.S. Iqball. 2014. Heterosis and combining ability evaluation for quality traits in forage sorghum (Sorghum bicolor L.). SABRAO Journal of Breeding and Genetics 46 (2): 174-182.
- Virmani, S.S., B.C. Virakhtamath, C.L. Casal, R.S. Toledo, M.T. Lopez, and J.O. Manalo. 1997. Hybrid Rice Breeding Manual. IRRI. Manila. Philippines.
- Xangsayasane, P., F. Xie, J.E. Hernandez, T.H. Borromeo. 2010. Hybrid rice heterosis and genetic diversity of IRRI and Lao rice. Field Crops Research 117:18–23.