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COMBINING ABILITY AND HETEROTIC STUDIES IN AROMATIC RICE THROUGH LINE BY TESTER ANALYSIS

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SUMMARY

Estimating combining ability helps to evaluate genotypes and determine the nature and degree of gene activities. This study aimed to identify the best parental genotypes and superior hybrids of aromatic rice using a line × tester mating design. Five CMS (cytoplasmic male sterility) lines and four testers of local and exotic origins of aromatic rice were studied in this experiment. The unweighted pair group method with arithmetic mean (UPGMA) cluster analysis revealed genetic variability among the studied CMS and restorer lines. The analysis of variance showed that parental lines, testers, and their line by testers populations had enough genetic variability. Five out of 20 hybrids found positive heterosis for grain yield, and the hybrid BRRI1A × BUdhan2R had the maximum heterosis. In terms of the agronomic traits evaluated, specific combining ability (SCA) effects were higher than general combining ability (GCA) effects. Genotypes IR58025A, BRRI1A, and BUdhan2R were identified as superior parents based on their performances for yield traits and GCA effects in the desired direction. IR58025A × BUdhan2R and BRRI1A × BUdhan2R were chosen as promising genotypes due to their highest grain yield, heterosis, and desirable SCA. Low ratios of σ^2gca/σ^2sca and $(\sigma^2D/\sigma^2A)^{1/2}$, and low to high estimations of narrow-sense heritability indicated that both additive and non-additive gene effects predominated in the inheritance of the studied traits. Pearson's correlation showed that among the 10 studied traits, grain yield plant^{-1} was highly significant and positively correlated with flag leaf area, spikelet fertility (%), and filled grains panicle^{-1}, as well as, significant and negatively correlated with days to flowering and days to maturity. Superior parental genotypes and hybrids that have been identified can be employed as donor parents to improve the grain yield in aromatic rice.

Keywords: Aromatic rice, heterosis, line by tester analysis, GCA and SCA, cluster analysis, correlation

Key findings: Given the heterotic effects, the hybrids had better mean performance for the evaluated traits than their parental lines and testers. The parental genotypes, IR58025A, BRRI1A lines, and the BUdhan2R tester, were identified as appropriate for hybridization. IR58025A × BUdhan2R and BRRI1A × BUdhan2R were also the best crosses due to higher grain yield, heterosis, and combining abilities. These parents and hybrid combinations could be deployed in an aromatic rice hybridization program.

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INTRODUCTION

Rice is more than simply a staple food for Bangladeshi people because it is closely linked to their culture, politics, and economics. Rice provides two-thirds of the country's overall calorie need and half of its protein intake (Hassan, 2021). Bangladesh has made incredible progress in expanding rice production, and it is expected to reach 36.0 million tons by 2020 (USDA, 2020). The Bangladesh government figured out that rice production peaked at 10.59 million tons in 1971 and reached 37.4 million tons by 2020 (Hassan, 2021).

Rice genotypes are categorized as aromatic and non-aromatic according to their aroma (Nadiger and Kasturiba, 2015). The aroma of aromatic rice is measured by the amount of 2-acetyl-1-pyrroline, which fluctuates depending on hereditary and environmental factors (Nadaf *et al.,* 2006). Bangladesh produces a wide range of high-quality aromatic and non-aromatic rice cultivars for daily consumption. Local aromatic rice cultivars like Kataribhog, Kataktara, Kalijira, Chinigura, Sakkorkhora, and Nizershail are some good types grown for regular consumption. In Bangladesh, aromatic rice is culturally and economically important and is in high demand at home and abroad (Kabir *et al.,* 2020).

Moreover, aromatic cultivars are frequently more costly than non-aromatic types (BRRI, 2017). With its high price, farmers are more interested in growing aromatic rice. As a result, it is necessary to accelerate the adoption of aromatic rice to meet domestic and global demands (Trang and Napasintuwong, 2016). On the other hand, Bangladesh produces 1.8 million mt of aromatic rice each year, and the major portion of total aromatic rice is produced during the rainy season, while some are also grown during the dry season (Parvez, 2021). Local rice cultivars can produce 1.40–2.23 mt/ha of aromatic rice, whereas high-yielding genotypes generate 3.35–6.13 mt/ha (BRRI, 2019).

Several biotic and abiotic factors have contributed to aromatic rice's low productivity and yield. So, varietal improvement and genetic analysis of yield components are effective mechanisms for combating low productivity (Suvi *et al.,* 2021). Heterosis is a method of enhancing rice production and productivity, and heterotic hybrids can meet the global food demand (Bano and Singh, 2019). However, producing good F_1s or segregants does not always necessitate parents with high mean performance for grain yield and other traits (Nirmaladevi *et al*., 2015; Veeresha *et al.,* 2015). Among numerous genetic methods, hybrid rice technology appears to be the most practical and easily adaptable strategy for breaking the yield barrier of inbred rice varieties (Bagati *et al*., 2016; Thorat *et al.,* 2017). Hybrid rice varieties provide a 15%–20% yield advantage over traditional high-yielding rice varieties cultivated under identical conditions (Virmani, 1996). Rice is a self-pollinated crop, hence developing and producing F_1 hybrid varieties necessitates adopting an efficient male sterility technique. The availability of stable cytoplasmic male sterility (CMS) lines, maintainers, identifying restorers, evaluating parental lines, and converting potential maintainer lines into CMS lines are all essential components of a successful hybrid rice breeding program (Sanghera and Hussain, 2012). Besides, identifying good parental lines for developing hybrid combinations is the most important factor in effective hybrid rice technology. As a result, rice breeders are constantly faced with difficulty selecting potential parental lines.

To solve this difficulty, the combining ability is used to explore the potential of certain parental lines to pass genetic information down to their offspring, which helps in selecting better parents for effective breeding (Aly, 2013; Bhati *et al*., 2015; Kahani *et al*., 2018). Among the various combining ability analysis techniques, line × tester analysis (Gaballah *et al.,* 2021) has been frequently utilized in both self and cross-pollinated crops to evaluate general and specific combing abilities of particular characteristics, as well as, to identify desirable parents and crosses (Rai *et al.,* 2019). The general combining ability (GCA) measures the parents' average performance that demonstrates additive gene action (Sprague and Tatum, 1942). The specific combining ability (SCA) estimates the performance of hybrid combinations and indicates non-additive gene action related to dominance, overdominance, and epistatic effects (Latha *et* *al.,* 2013; Su *et al.,* 2017). The one-to-one pattern of the line × tester mating design prioritizes the crossing between lines and testers, resulting in hybrids (Sharma, 2006). We may use this strategy to identify suitable parents based on the GCA and desirable hybrids based on estimated SCA. In light of this, the recent study was conducted to examine combining abilities to select good parents and superior hybrid combinations.

MATERIALS AND METHODS

During the 2014–2015 growing season, five rice CMS lines (IR58025A, IR62829A, BRRI1A, GAN46A, and IR68888A) and four restorer lines (BUdhan2R, ChiniguraR, KataribhogR, and SakkorkhoraR) used as pollen or male parents were crossed in a line × tester mating design developed by Kempthorne (1957), resulted in the creation of 20 F_1 hybrids. The 20 F_1 hybrids and their nine parents were planted in the research field of Bangabandhu Sheikh Mujibur Rahman Agricultural University, Gazipur, Bangladesh, during the 2015–2016 growing season. The experiment was laid out in a randomized complete block design with three replications. In each replication, parents and F_1 hybrids were sown in two rows of 1 m length, with a spacing of 20 cm between rows and 5 cm between plants. After 25 days, old seedlings were transplanted with a single seedling per hill. To ensure a good yield, recommended cultural measures were followed. Nitrogen and phosphorous fertilizers were applied @ 130 and 60 kg/ha. To record grain yield and related component attributes, isogenic maintainer (B) lines were grown in place of CMS (A) lines. The grain yield and other yield-related traits, such as, flag leaf area (cm^2), plant height (cm), days to flowering, days to maturity, effective tillers per plant, panicle length (cm), spikelet fertility (%), number of filled grains per panicle, 1000-grain weight (gm), and grain yield per plant (gm), were recorded according to the standard evaluation system (IRRI, 1996).

Statistical analysis

A UPGMA method of hierarchical clustering was used to estimate the parental diversity based on their yield component traits (Esteves, 2018). The collected data for plant characters were analyzed using the analysis of variance (Steel and Torrie, 1980). Analysis of line by tester mating design was performed by open-source R-statistical software version 3.0.1 using the 'agricolae' package per the standard method given by Kempthorne (1957). The Pearson's phenotypic correlation coefficients were calculated for studied traits using STAR 2.0.1 software (https://sourceforge.net/projects/linnix/). The percentage increase of F_1 over the mean parental value for a given characteristic was calculated as percent heterosis (Virmani *et al.,* 1997). According to Griffiths *et al.* (2000), both broad-sense heritability (H^2) and narrow-sense heritability (h^2) were measured for the studied characters.

RESULTS AND DISCUSSION

Genetic variability among lines, testers, and hybrids

Analysis of variance for genotypes crosses and line vs tester interactions showed highly significant differences in combining ability for all studied traits. The parents had a wide genetic variation for all the traits, except the effective tillers plant^{-1}. In terms of parent vs. cross interactions, highly significant ($p \leq 0.01$) variations were observed among the studied traits, except for filled grains panicle^{-1} and grain yield plant^{-1} (Table 1). Additionally, variance due to lines was not found significant for flag leaf area, plant height, panicle length, and grain yield plant^{-1}. Similarly, variance due to testers was found significant for all traits under the study, except the effective tillers plant^{-1}, panicle length, and the filled grains panicle^{-1}. The studied genotypes displayed a wide range of genetic variability among themselves for all the 10 traits. The prevalence of additive variance was corroborated by the relevance of variation owing to lines and testers, but significant differences for line × tester among all the characteristics were found, demonstrating the importance of both additive and non-additive kinds of gene action among parents (Kumar *et al.,* 2015; Thorat *et al.,* 2017).

Additive effects are critical for fixing the characteristics and identifying better parents early (Islam *et al.,* 2015). However, due to segregation, dominance effects are not identifiable. Therefore, late selection of genotypes for future breeding research to improve new aromatic rice genotypes could be beneficial (Ashfaq *et al.,* 2012; Kahani and Hittalmani, 2016). On the other hand, Singh *et al.* (2021) suggested that heterosis breeding is an effective method for improving such characteristics governed by dominant gene

Table 1. Analysis of variance based on mean squares and genetic components through line by tester analysis in aromatic rice.

Source	d.f.	FLA	PH	DF	DM	ET	PL (cm)	SF (%)	FGP	1000 gwt	GYP
Replications	2	9.36	0.72	4.59	1.69	7.17	8.84	5.83	54.39	1.20	3.80
Genotypes	28	193.41**	712.09**	322.42**	332.48**	5.96**	8.30**	34.67**	725.42**	31.63**	28.22**
Parents	8	310.79**	1448.50**	570.90**	566.68**	1.95	8.52**	8.25*	729.33**	52.64**	5.37**
Parent vs. Crosses	1	349.59**	4245.70**	1791.71**	1611.14**	28.15**	25.14**	327.60**	65.66	155.20**	0.90
Crosses	19	135.77**	216.04**	140.47**	166.57**	6.48**	7.32**	30.38**	758.49**	16.28**	39.28**
Lines	4	74.44	95.64	205.03**	248.23**	15.06*	11.27	43.50*	1767.43**	17.63*	44.27
Testers	3	550.84**	691.31*	510.68**	600.95**	4.84	6.92	89.35**	1111.53	57.84**	88.28*
Lines × Testers	12	52.44**	137.35**	26.39**	30.76**	4.03**	6.11**	11.27**	333.92**	5.44**	25.37**
Error	56	13.79	4.91	3.71	3.99	1.29	1.07	3.63	50.97	1.61	1.91

****:** Significant at 1% level and ***:** Significant at 5% level. FLA = Flag leaf area (cm^2), PH = Plant height (cm), DF = Days to flowering, DM = Days to maturity, ET = Effective tillers plant^{-1}, PL = Panicle length (cm), SF = Spikelet fertility (%), FGP = Filled grains panicle^{-1}, 1000 gwt = 1000-grain weight (g), GYP = Grain yield plant^{-1} (g).

Table 2. Mean performance of lines, testers, and F_1 hybrids for various traits in aromatic rice.

Name of Accession	FLA	PH	DF	DM	ET	PL	SF (%)	FGP	1000 gwt	GYP
Lines										
IR58025A	44.55	101.00	87.00	117.00	10.67	28.00	93.33	119.00	15.33	12.00
IR62829A	34.88	102.33	86.67	116.67	11.00	27.83	92.00	119.00	18.00	9.00
BRRI1A	30.73	86.00	74.00	104.00	11.00	23.67	94.00	112.00	19.33	11.33
GAN46A	54.64	103.67	86.33	117.33	10.00	27.17	91.00	118.33	17.67	10.67
IR68888A	32.08	87.67	77.33	107.33	11.00	25.00	92.33	113.67	17.33	11.00
Testers										
BUdhan2R	51.30	118.67	92.67	122.33	11.00	28.83	94.67	123.67	22.50	13.67
ChiniguraR	31.17	135.33	108.00	138.00	9.67	26.50	90.67	150.33	9.43	12.67
KataribhogR	24.30	137.33	108.00	138.00	9.33	27.83	90.00	140.33	14.33	12.00
SakkorkhoraR	37.50	145.00	111.67	141.67	9.00	27.50	94.00	151.67	10.33	12.33
F1 Hybrids										
IR58025A × BUdhan2R	53.68	110.00	86.33	113.33	9.67	29.00	93.67	149.67	22.00	20.33
IR58025A × ChiniguraR	30.81	136.33	100.00	128.00	7.33	23.67	90.33	131.33	16.67	14.33
IR58025A × KataribhogR	32.27	134.67	101.00	131.00	7.67	25.33	88.67	122.33	18.33	11.33
IR58025A × SakkorkhoraR	34.37	136.33	100.00	129.67	7.67	24.67	90.33	127.67	16.00	10.00
IR62829A × BUdhan2R	40.85	117.67	98.00	127.67	7.33	24.67	90.33	123.33	18.33	12.00
IR62829A × ChiniguraR	30.57	124.00	98.00	128.00	7.00	24.00	87.00	129.33	16.67	10.67
IR62829A × KataribhogR	31.81	125.33	103.33	133.33	8.00	25.00	85.33	126.33	18.00	11.33
IR62829A × SakkorkhoraR	28.41	127.00	104.33	134.33	9.00	25.00	88.00	123.33	18.00	10.00
BRRI1A × BUdhan2R	47.78	119.00	87.67	116.00	11.67	29.00	96.67	183.00	24.00	23.00
BRRI1A × ChiniguraR	31.19	138.67	107.33	137.33	11.00	28.00	85.67	118.33	17.67	11.00
BRRI1A × KataribhogR	32.89	139.00	109.00	138.67	11.00	28.17	87.00	104.33	19.33	10.33
BRRI1A × SakkorkhoraR	28.75	134.33	105.67	135.67	10.33	26.00	88.33	137.00	18.67	10.33
GAN46A × BUdhan2R	36.08	111.00	99.00	128.33	9.00	25.00	87.00	122.33	25.00	12.00
GAN46A × ChiniguraR	31.19	138.67	107.33	137.33	11.00	28.00	85.67	118.33	17.67	11.00
GAN46A × KataribhogR	32.89	139.00	109.00	138.67	11.00	28.17	87.00	104.33	19.33	10.33
GAN46A × SakkorkhoraR	32.01	135.33	108.33	138.33	11.00	25.67	88.33	124.67	20.00	11.00
IR68888A × BUdhan2R	34.91	132.00	97.33	127.33	11.00	26.00	90.33	130.67	19.67	10.00
IR68888A × ChiniguraR	29.54	129.67	108.67	138.33	8.67	25.33	86.33	118.67	18.00	7.33
IR68888A × KataribhogR	30.32	127.00	107.67	137.67	8.67	25.00	81.67	115.00	17.00	10.67
IR68888A × SakkorkhoraR	29.63	127.00	113.67	143.67	8.33	25.00	86.33	126.33	18.00	10.00
CV (%)	10.63	1.80	1.94	1.55	12.03	3.94	2.13	5.54	7.03	11.74
Hsd (0.05)	11.92	7.11	6.18	6.41	3.65	3.32	6.11	22.91	4.07	4.44

FLA = Flag leaf area (cm^2), PH = Plant height (cm), DF = Days to flowering, DM = Days to maturity, ET = Effective tillers plant^{-1}, PL = Panicle length (cm), SF = Spikelet fertility (%), FGP = Filled grains panicle^{-1}, 1000 gwt = 1000-grain weight (g), GYP = Grain yield plant^{-1} (g).

action. Abdullah *et al.* (2020) demonstrated that dominant genes influence grain yield and its characteristics. Both additive and dominant gene actions are important for grain yield and yield contributing traits (Hijam *et al.*, 2019).

Mean performance of parents and hybrids

The performance for all studied traits of all 29 genotypes (five lines, four testers, and 20 hybrids) was assessed and calculated individually (Table 2). Maximum flag leaf area was obtained from GAN46A (line), BUdhan2R (tester), and the combination of IR58025A × BUdhan2R. The combination was higher than the average parental value. In the studied traits, the lower mean value of plant height (dwarf plants), days to flowering (early flowering), and days to maturity (early maturity) were desirable. It was recorded that the IR58025A line, BUdhan2R tester, and their combination (IR58025A × BUdhan2R) showed a lower mean value for plant height, days to flowering, and days to maturity. However, the hybrid's mean performance was higher than the average parental means of lines and testers. In terms of effective tillers plant^{-1}, it was seen that lines used in the experiment generally had similar values, and BUdhan2R had the highest mean value among testers.

The BRRI1A × BUdhan2R showed the highest mean value of effective tillers plant^{-1}, which exceeded their parental value. Among lines, the maximum panicle length was obtained from IR58025A and the minimum from BRRI1A, and in the tester. BUdhan2R showed the maximum panicle length. However, maximum panicle length was observed in two combinations (IR58025A × BUdhan2R and BRRI1A × BUdhan2R), indicating the tester BUdhan2R had a dominant effect on lines. The highest spikelet fertility (%) values were observed for parents BRRI1A (line), BUdhan2R (tester), and cross BRRI1A × BUdhan2R; whereas, the lowest value was observed for IR68888A × KataribhogR. Concerning filled grains panicle^{-1}, the highest value was found for the cross BRRI1A × BUdhan2R and parents IR58025A, IR62829A, and SakkorkhoraR. However, the lowest value was observed for genotypes BRRI1A × KataribhogR, GAN46A × KataribhogR, BRRI1A, and BUdhan2R. Meantime, the maximum 1000-grain weight was found for crosses, GAN46A × BUdhan2R and BRRI1A × BUdhan2R, compared with IR58025A × SakkorkhoraR, IR58025A × ChiniguraR, and IR62829A × ChiniguraR.

The highest grain yield was obtained from cross BRRI1A × BUdhan2R (23 g/plant) and parents, IR58025A (12 g/plant) and BUdhan2R (13.67 g/plant). However, the lowest mean values were observed with genotypes IR68888A × ChiniguraR (7.33 g/plant). In this study, the days to flowering are a critical attribute that must be explored in each generation, as well as, days to maturity and panicle length, which must be chosen in the early segregating generation (Ganapati *et al.,* 2020). The findings validated the studies of Chen *et al.* (2019) for plant height, panicle length, 1000-grain weight, and grain yield plant^{-1}, Liu *et al.* (2016) for the effective tillers plant^{-1}, and Xiang *et al.* (2016) for flag leaf area, plant height, spikelet fertility (%), filled grains panicle^{-1}, and grain yield plant^{-1}.

Phylogenetic analysis of parental lines and testers

The dendrogram comprises three main clusters (Cluster-I, Cluster-II, and Cluster-III). Cluster-I contains two CMS lines (IR68888A and BRRI1A), while Cluster-III contains three restorer lines (KataribhogR, SakkorkhoraR, and ChiniguraR) (Figure 1). However, in Cluster-II, a restorer line (BUdhan2R) was separated from the rest of the aromatic restorer lines and showed a strong affinity for the CMS lines IR58025A and IR62829A. Based on their phylogeny, it was suggested that genotypes with similar phylogenies were placed together in the same cluster. The UPGMA cluster analysis revealed a strong diversity difference between this study's CMS and restorer lines. This wide diversity could lead to the development of heterotic hybrid rice (Xie *et al.,* 2014; Wang *et al.,* 2018).

Heterosis

The nature and magnitude of percent heterosis were measured for all 20 crosses to determine gene activity and utilize heterosis for high grain yield and its related traits (Table 3). Negative heterosis was preferred for plant height, days to flowering, and days to maturity, whereas positive heterosis was preferred for the rest of the traits. Heterosis for grain yield was positive, ranging from 5.88%–84.00% for five out of 20 hybrids. Among them, two-hybrid combinations, i.e. BRRI1A × BUdhan2R and IR58025A × BUdhan2R, had heterosis for yields of 84.00% and 58.44%, with corresponding actual yield levels of 23.00 and 20.33 g/plant, respectively. The hybrid combination BRRI1A × BUdhan2R showed the highest positive heterosis for spikelet fertility (%), filled grains panicle^{-1},

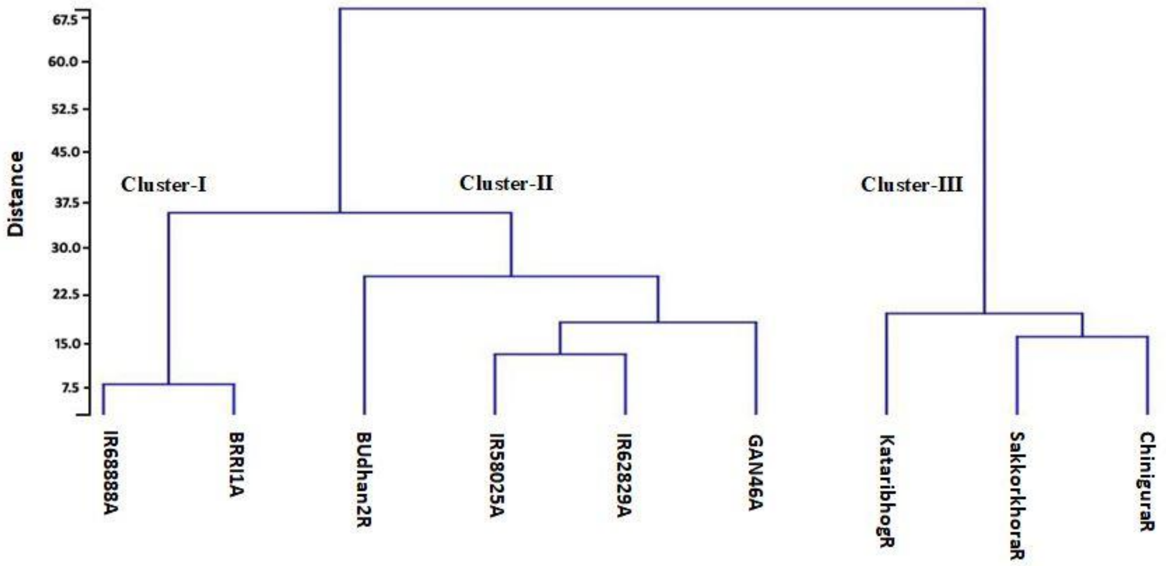


Figure 1. Dendrogram of aromatic rice parental lines and testers based on their morphological and yield component traits.

Table 3. Heterosis in F_1 hybrids for morphological and yield related traits in aromatic rice.

Crosses	FLA	PH	DF	DM	ET	PL	SF (%)	FGP	1000 gwt	GYP
IR58025A × BUdhan2R	12.00	0.15	-3.90	-5.29	-10.77	2.05	-0.35	23.35	-6685.16	58.44
IR58025A × ChiniguraR	-18.63	15.37	2.56	0.39	-27.87	-13.15	-1.81	-2.48	36.63	16.22
IR58025A × KataribhogR	-6.27	13.01	3.59	2.75	-23.33	-9.25	-3.27	-5.66	72.81	-5.56
IR58025A × SakkorkhoraR	-16.23	10.84	0.67	0.26	-22.03	-11.11	-3.56	-5.67	59.19	-17.81
IR62829A × BUdhan2R	-5.19	6.49	9.29	6.83	-33.33	-12.94	-3.21	1.65	-151.28	5.88
IR62829A × ChiniguraR	-7.44	4.35	0.68	0.52	-32.26	-11.66	-4.74	-3.96	-16.53	-1.54
IR62829A × KataribhogR	7.49	4.59	6.16	4.71	-21.31	-10.18	-6.23	-2.57	-58.72	7.94
IR62829A × SakkorkhoraR	-21.50	2.70	5.21	4.00	-10.00	-9.64	-5.38	-8.87	64.93	-6.25
BRRI1A × BUdhan2R	16.50	16.29	5.20	2.50	6.06	10.48	2.47	55.30	2135.87	84.00
BRRI1A × ChiniguraR	0.76	25.30	17.95	13.50	6.45	11.63	-7.22	-9.78	35.51	-8.33
BRRI1A × KataribhogR	19.53	24.48	19.78	14.60	8.20	9.39	-5.43	-17.31	218.41	-11.43
BRRI1A × SakkorkhoraR	-15.74	16.31	13.82	10.45	3.33	1.63	-6.03	3.92	-165.01	-12.68
GAN46A × BUdhan2R	-31.90	-0.15	10.61	7.09	-14.29	-12.28	-6.28	1.10	-117.54	-1.37
GAN46A × ChiniguraR	-27.31	16.04	10.46	7.57	11.86	2.44	-5.69	-11.91	109.40	-5.71
GAN46A × KataribhogR	-16.67	15.35	12.18	8.62	13.79	0.60	-3.87	-19.33	399.82	-8.82
GAN46A × SakkorkhoraR	-30.53	8.85	9.43	6.82	15.79	-7.78	-4.50	-7.65	69.93	-4.35
IR68888A × BUdhan2R	-16.27	27.95	14.51	10.89	0.00	-3.41	-3.39	10.11	-398.58	-18.92
IR68888A × ChiniguraR	-6.60	16.29	17.27	12.77	-16.13	-1.62	-5.65	-10.10	78.89	-38.03
IR68888A × KataribhogR	7.53	12.89	16.19	12.23	-14.75	-5.36	-10.42	-9.45	-9.32	-7.25
IR68888A × SakkorkhoraR	-14.83	9.17	20.28	15.39	-16.67	-4.76	-7.33	-4.77	-34.91	-14.29

1000-grain weight, and the positive heterosis for the rest of the studied traits.

Similarly, IR58025A × BUdhan2R exhibited the lowest negative heterosis for days to flowering and days to maturity, and also had positive heterosis for flag leaf area, panicle length, and filled grains panicle^{-1} (Table 3). Regardless, the highest heterosis was obtained in crosses, BRRI1A × KataribhogR, GAN46A × SakkorkhoraR, and BRRI1A × ChiniguraR, for flag leaf area, effective tillers plant^{-1}, panicle length, but the lowest for plant height was in the cross, GAN46A × BUdhan2R (Table 3). Percent heterosis was also estimated by Gramaje *et al.* (2020) for plant height, effective tillers plant^{-1}, panicle length, 1000-grain weight, grain length, grain width, and grain yield plant^{-1}. Chen *et al.* (2019) stated that heterosis was caused by non-additive gene action, and crosses of *indica* × *japonica* had greater heterosis than crosses of *indica* × *indica*, *japonica* × *japonica*, and *japonica* × *indica*. Similarly, Gokulakrishnan and Kumar (2013) discovered that the cross combinations, IR58025A × ASD19, IR62829A × ASD16, and PUSA3A × IR42, had a high heterosis percentage and were potential for grain yield.

Estimation of combining ability

The combining ability analysis was driven by significant differences in genotypes for all the evaluated characteristics (Table 1). The general combining ability (GCA) identifies better parents, whereas the specific combining ability (SCA) aids in the identification of favorable hybrid combinations that may eventually result in hybrid development (Shiva *et al.,* 2013). Negative GCA and SCA effects were desired in plant height, days to flowering, and days to maturity, while positive GCA and SCA effects were desired in other studied traits.

General combining ability effects

The GCA effects of lines and testers for various traits were studied to find the most suitable parent for future hybrid development. When the GCA effects of 10 traits were examined, IR58025A exhibited highly significant GCA for the flag leaf area, days to flowering, days to maturity, and grain yield plant^{-1} (Table 4). Besides, BRRI1A also showed significant GCA effects for days to flowering, days to maturity, effective tillers plant^{-1}, and grain yield plant^{-1}, respectively. As a result, these two lines were chosen as the best general combiners for each characteristic. Similarly, IR62829A was identified as a good general combiner for plant height and days to flowering, and the line GAN46A for the effective tillers plant^{-1}. However, none of the lines showed significant and positive GCA effects for panicle length, spikelet fertility (%), filled grains panicle^{-1}, and 1000-grain weight.

Among four testers, BUdhan2R was identified as a good combiner for the flag leaf area, plant height, days to flowering, days to maturity, effective tillers plant^{-1}, and grain yield plant^{-1}. Consequently, this tester was deemed the best general combiner for the studied characteristics. On the contrary, ChiniguraR, KataribhogR, and SakkorkhoraR had no significant and desired GCA effects for the investigated traits. Good general combiners have been identified for the flag leaf area (Sanghera *et al.,* 2012), plant height (Xiang *et al.,* 2016), days to 50% flowering (Shukla and Pandey, 2008), days to maturity, effective tillers plant^{-1} (Sao and Motiramani, 2006), and grain yield plant^{-1} (Huang *et al.,* 2015; Gramaje *et al.,* 2020), as observed in the studies.

Specific combining ability effects

The SCA effects are essential for identifying certain cross combinations (hybrids) regarding selecting specific traits. The recent research showed that no single cross combination had positive SCA values for all the studied traits (Table 5). This finding agrees with those reported in previous studies (Huang *et al.,* 2015; Yuga *et al.,* 2018). Among 20 crosses, only two (IR54025A × BUdhan2R, BRRI1A × BUdhan2R) had positive and significant SCA effects on the flag leaf area. Likewise, a significant and negative SCA effect in the desired direction for plant height was found in five crosses, viz., IR54025A × BUdhan2R, BRRI1A × ChiniguraR, GAN46A × BUdhan2R, IR68888A × KataribhogR, and IR68888A × SakkorkhoraR. For days to flowering, adverse significant desired SCA effects were observed in IR62829A × ChiniguraR, BRRI1A × BUdhan2R, and IR68888A × KataribhogR. Similarly, IR54025A × BUdhan2R, IR62829A × ChiniguraR, BRRI1A × BUdhan2R, and IR68888A × KataribhogR crosses possessed significant SCA effects in a negative direction.

No positive significant SCA effects were found among 20 cross combinations for effective tillers plant^{-1}, panicle length, spikelet fertility (%), filled grains panicle^{-1}, and 1000-grain weight (Table 5). In the case of grain yield, IR54025A × BUdhan2R, BRRI1A × BUdhan2R, IR68888A × KataribhogR, and IR68888A × SakkorkhoraR crosses had

Table 4. General combining ability effects of parental lines and testers for various traits in aromatic rice.

Parents	FLA	PH	DF	DM	ET	PL	SF (%)	FGP	1000 gwt	GYP
Lines										
IR58025A	4.21**	1.23	-5.4**	-6.283**	-0.98**	-0.21	2.50	3.32	-0.67	2.15**
IR62829A	-0.67	-4.60**	-1.3*	-0.95*	-1.23**	-1.21	-0.58	-3.85	-1.17	-0.85*
BRRI1A	-0.53	-0.35	-1.6**	-1.617**	0.68*	1.13	1.42	19.32	1.00	1.82**
GAN46A	-0.53	2.90**	3.7**	3.883**	1.43**	0.83	-1.25	-12.02	1.58	-0.77
IR68888A	-2.47**	0.82	-	4.967**	0.10	-0.54	-2.08	-6.77	-0.75	-2.35**
S.E.(g_i)line	1.07	0.64	0.56	0.58	0.33	0.30	0.55	2.06	0.37	0.40
S.E.(g_i – g_j) line	1.52	0.91	0.79	0.82	0.46	0.42	0.78	2.91	0.52	0.56
Testers										
BUdhan2R	9.08**	-10.167**	-8.6**	-9.25**	0.67**	0.86	3.35	12.37	2.88	3.62**
ChiniguraR	-3.32**	2.967**	1.2*	1.15*	-0.67**	-0.48	-0.98	-3.23	-1.52	-1.05**
KataribhogR	-2.82**	3.3**	3.2**	3.55**	-0.20	0.23	-2.38	-7.50	-0.58	-0.98**
SakkorkhoraR	-2.94**	3.9**	4.2**	4.55**	0.20	-0.61	0.02	-1.63	-0.78	-1.58**
S.E.(g_t) tester	0.96	0.57	0.50	0.52	0.29	0.27	0.49	1.84	0.33	0.36
S.E. (g_i – g_j) tester	1.36	0.81	0.70	0.73	0.41	0.38	0.70	2.61	0.46	0.50

*, **: Indicates significant at 5% and 1% level of probability respectively, *S.E.(g_i)* = Standard error (*gca* effect for lines), *S.E.(g_i – g_j) line* = Standard error (between *gca* effect of two lines), *S.E.(g_t)* = Standard error (*gca* effect for tester), *S.E. (g_i – g_j)* = Standard error (between *gca* effect of two testers).

Table 5. Specific combining ability effects of F_1 hybrids for various traits in aromatic rice.

F_1 Hybrids	FLA	PH	DF	DM	ET	PL	SF (%)	FGP	1000 gwt	GYP
IR58025A × BUdhan2R	6.81**	-9.17**	-1.95	-2.92*	0.92	2.48	-0.43	4.55	0.87	2.72**
IR58025A × ChiniguraR	-3.65	4.03**	1.98	1.35	-0.08	-1.53	0.57	1.82	-0.07	1.38
IR58025A × KataribhogR	-2.69	2.03	0.98	1.95	-0.22	-0.56	0.30	-2.92	0.67	-1.68*
IR58025A × SakkorkhoraR	-0.47	3.10*	-1.02	-0.38	-0.62	-0.39	-0.43	-3.45	-1.47	-2.42**
IR62829A × BUdhan2R	-1.14	4.33**	5.63**	6.08**	-1.17	-0.86	-0.68	-14.62	-2.30	-2.62**
IR62829A × ChiniguraR	0.98	-2.47	-4.10**	-3.98**	-0.17	-0.19	0.32	6.98	0.43	0.72
IR62829A × KataribhogR	1.72	-1.47	-0.77	-1.05	0.37	0.11	0.05	8.25	0.83	1.32
IR62829A × SakkorkhoraR	-1.56	-0.40	-0.77	-1.05	0.97	0.94	0.32	-0.62	1.03	0.58
BRRI1A × BUdhan2R	5.66*	1.42	-4.37**	-4.92**	1.25	1.14	3.65	21.88	1.20	5.72**
BRRI1A × ChiniguraR	-0.57	-4.05**	1.23	1.68	-1.08	-0.53	-1.68	-12.18	-0.40	-1.95*
BRRI1A × KataribhogR	-3.73	-0.05	2.23*	2.28	-0.55	-0.23	-0.62	0.42	-0.33	-2.02*
BRRI1A × SakkorkhoraR	-1.35	2.68*	0.90	0.95	0.38	-0.39	-1.35	-10.12	-0.47	-1.75*
GAN46A × BUdhan2R	-6.05**	-9.83**	1.63	1.92	-2.17**	-2.57	-3.35	-7.45	1.62	-2.70**
GAN46A × ChiniguraR	1.47	4.70**	0.23	0.52	1.17	1.77	-0.35	4.15	-1.32	0.97
GAN46A × KataribhogR	2.67	4.70**	-0.10	-0.55	0.70	1.23	2.38	-5.58	-0.58	0.23
GAN46A × SakkorkhoraR	1.91	0.43	-1.77	-1.88	0.30	-0.43	1.32	8.88	0.28	1.50
IR68888A × BUdhan2R	-5.28*	13.25**	-0.95	-0.17	1.17	-0.19	0.82	-4.37	-1.38	-3.12**
IR68888A × ChiniguraR	1.77	-2.22	0.65	0.43	0.17	0.48	1.15	-0.77	1.35	-1.12
IR68888A × KataribhogR	2.04	-5.22**	-2.35*	-2.63*	-0.30	-0.56	-2.12	-0.17	-0.58	2.15**
IR68888A × SakkorkhoraR	1.48	-5.82**	2.65*	2.37*	-1.03	0.28	0.15	5.30	0.62	2.08*
S.E.(s_{ij})	2.14	1.28	1.11	1.15	0.66	0.60	1.10	4.12	0.73	0.80
S.E.(s_{ij}- s_{kl}) *tester*	3.03	1.81	1.57	1.63	0.93	0.84	1.55	5.83	1.03	1.13

*, **: Indicates significance at 5% and 1% level of probability, respectively, *S.E.*(s_{ij}) = Standard error (*sca* effects for crosses), *S.E.*(s_{ij}- s_{kl}) = Standard error (between SCA effects of two crosses).

positive and significant SCA effects. These four crosses were good specific combiners for grain yield. Our findings revealed that two hybrid combinations, IR58025A × BUdhan2R, and BRRI1A × BUdhan2R, had at least one parent with a good GCA and had a highly significant SCA for numerous characteristics. This is because the positive alleles of the parents interact with their genes (Chen *et al.,* 2019; Zaid *et al.,* 2019).

The other two hybrid combinations (IR68888A × KataribhogR and IR68888A × SakkorkhoraR) had parents with poor or negative GCA effects and had considerably higher SCA in desirable traits (Table 5). This is due to genetic interaction between the positive and negative alleles of the parents (Singh *et al.,* 2019; Chen *et al.,* 2019; Zaid *et al.,* 2019). Similarly, Dorosti and Monajjem (2014) found that hybrid IR62829A × IR57301-158-1R had a highly significant and positive SCA effect for grain yield plant^{-1} when the parents had low × high GCA effects. The best SCA combination for grain yield per plant was IR68888A × Sepidroud, which had a low × low GCA. According to the study, GCA only identifies better parents; hence, discarding parents with low GCA will be unwise. However, Virmani (1997) reported that it is usually preferable to find superior hybrid combinations based on significant SCA effects and heterosis values.

Estimation of genetic components

The variances due to GCA, SCA, additive genetic variance, dominance genetic variance, the average degree of dominance, and broad and narrow-sense heritability are provided in Table 6. The results showed that variances of SCA were higher than GCA variances, and the ratio of GCA/SCA variances was smaller than unity for all the studied traits, indicating the inheritance of corresponding traits was dominated by the non-additive gene effect. Moreover, the degree of dominance scores was greater than unity (>1), indicating that all of the characters were dominant. As shown in the studies, dominant gene action was identified for days to 50% flowering, effective tillers plant^{-1}, and biological yield (Verma and Srivastawa, 2004), panicle length and 1000-grain weight (Li *et al.,* 2010), plant height (Mirarab and Ahmadikhah, 2010), maturity period, effective tillers plant^{-1}, panicle length, spikelet fertility, and test weight (Gramaje *et al.,* 2020) and days to 50% flowering, 1000-grain weight, effective tillers plant^{-1} and panicle length (Gunasekaran *et al.,* 2020). Ganapati *et al.* (2020) also reported dominant effects for the plant height, filled grain panicle^{-1}, grains panicle^{-1} and yield hill^{-1}, yield tiller^{-1}, and 1000-grain weight.

In this study, broad-sense heritability (H^2) ranged from 78.00% (effective tillers plant^{-1}) to 99.00% (plant height, days to flowering, and days to maturity), whereas narrow-sense heritability (h^2) ranged from 2.48% (plant length) to 38.05% (days to maturity) as shown in Table 6. According to Burton *et al.* (1952), broad-sense heritability is classified as low (below 50%), medium (50%–70%), and high (above 70%). Our results estimated that the H^2 values were high for all the traits studied, indicating that the traits less influenced the environment in their expression. Robinson (1966) categorized the estimation of narrow-sense heritability into three groups: high (> 30%), medium (10%–30%), and low (< 10%). However, most traits had low h^2 values, indicating that traits were primarily influenced by non-additive gene action (dominance gene action) and that heterosis breeding is beneficial. Yet, high values of h^2 were observed for days to flowering and days to maturity, indicating that the additive gene effect governed these two traits. Similar findings were reported by Bano and Singh (2019).

The proportional contribution of genotypes

The proportional contribution of lines, testers, and their line × tester interaction for various studied traits are provided in Table 7. The findings showed that testers contributed more to the expression of the six traits, such as, flag leaf area, plant height, days to flowering, days to maturity, spikelet fertility (%), and 1000-grain weight, indicating these characteristics had a high paternal influence. Similarly, the lines contributed more in the filled grains panicle^{-1} (49.06%) and the effective tillers plant^{-1} (48.94%), representing that these traits have a predominant influence. The contribution of line × tester interaction was high for two traits, viz., panicle length, and grain yield plant^{-1}, ranging from 39.25% to 52.69%, whereas low percent contribution was observed in days to maturity (11.66%). These results were following Rashid *et al*. (2007), Akter *et al.* (2010), and Fellahi *et al.* (2013).

Table 6. Genetic components for various traits through line × tester analysis in aromatic rice.

Genetic components	FLA (cm^2)	PH (cm)	DF	DM	ET	PL (cm)	SF (%)	FGP	1000 gwt	GYP
σ^2gca	2.43	2.3	3.33	3.96	0.07	0.04	0.56	12.39	0.32	0.41
σ^2sca	70.7	101.06	81.22	96.44	2.23	2.34	14.8	340	8.45	16.91
σ^2gca/σ^2sca	0.03	0.02	0.04	0.04	0.03	0.02	0.04	0.04	0.04	0.02
σ^2A	4.86	4.59	6.66	7.93	0.14	0.07	1.12	24.78	0.63	0.81
σ^2D	12.88	44.15	7.56	8.92	0.91	1.68	2.55	94.32	1.28	7.82
$(\sigma^2D/\ \sigma^2A)^{1/2}$	1.63	3.10	1.07	1.06	2.55	4.90	1.51	1.95	1.43	3.11
H^2	93.00	99.00	99.00	99.00	78.00	87.00	90.00	93.00	95.00	93.00
h^2	15.41	8.56	37.14	38.05	5.98	2.48	15.34	14.57	17.90	7.69

σ^2gca = Variance of general combining ability (GCA), σ^2sca = Variance of specific combining ability (SCA), σ^2A = Additive genetic variance, σ^2D = Dominance genetic variance, $(\sigma^2D/\sigma^2A)^{1/2}$ = Average degree of dominance, H^2 = Broad-sense heritability, h^2 = Narrow-sense heritability, FLA = Flag leaf area (cm^2), PH = Plant height (cm), DF = Days to flowering, DM = Days to maturity, ET = Effective tillers plant^{-1}, PL = Panicle length (cm), SF = Spikelet fertility (%), FGP = Filled grains panicle^{-1}, 1000 gwt = 1000-grain weight (g), GYP = Grain yield plant^{-1} (g)

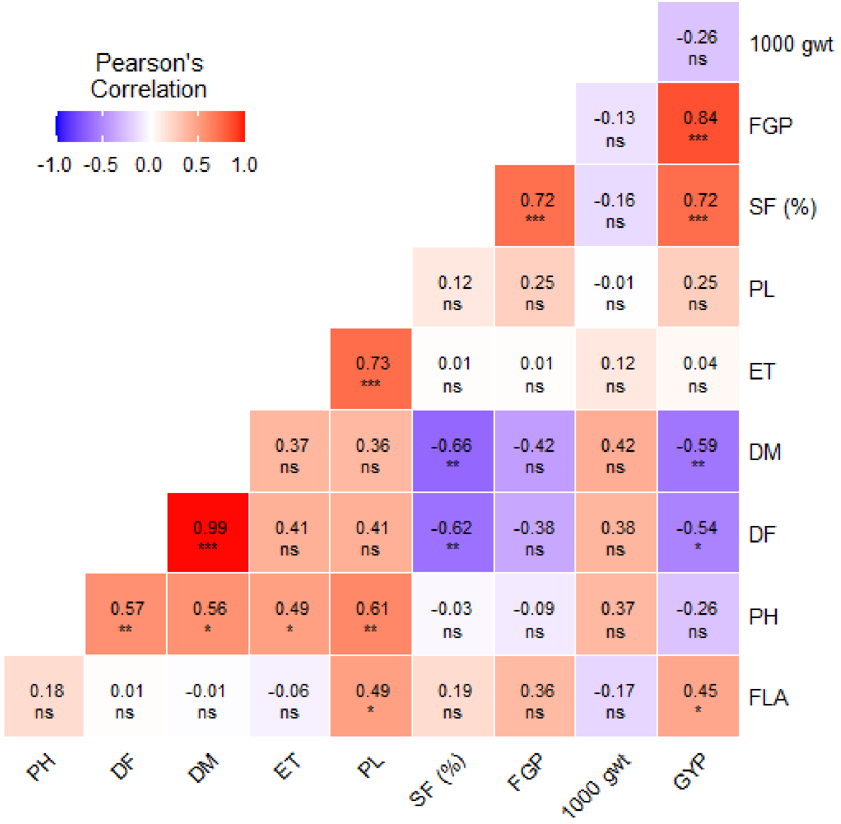
Table 7. The proportional contribution of lines, testers, and their line × tester interactions in aromatic rice.

Characters	Contribution (%)		
	Lines	Testers	Lines × Testers
Flag leaf area (cm^2)	11.54	64.06	24.40
Plant height (cm)	9.32	50.53	40.15
Days to flowering	30.73	57.40	11.87
Days to maturity	31.37	56.96	11.66
Effective tillers plant^{-1}	48.94	11.81	39.25
Panicle length (cm)	32.40	14.91	52.69
Spikelet fertility (%)	30.14	46.44	23.42
Filled grains panicle^{-1}	49.06	23.14	27.80
1000-grain weight (g)	22.80	56.11	21.09
Grain yield plant^{-1} (g)	23.73	35.49	40.79

Phenotypic correlation

To establish a selection procedure, it is necessary to investigate the relationship between the studied traits and their association with grain yield. According to Pearson's correlation, grain yield plant^{-1} showed the highly significant positive correlation with spikelet fertility (%) and filled grains panicle^{-1}, significant positive with flag leaf area; and significant negative with days to flowering and days to maturity, indicating genotypes that mature early produce lower grain yields (Figure 2). Qamar *et al.* (2005) reported a positive and non-significant correlation between spikelet fertility (%) and grain yield plant^{-1}. Islam *et al.* (2016) showed a positive and significant correlation between filled grains panicle^{-1} and grain yield plant^{-1}. However, Majumder *et al.* (2013) observed a negative and significant correlation between flag leaf area and grain yield plant^{-1} at the phenotypic level for 20 aromatic rice genotypes. The negative correlation of grain yield plant^{-1} with days to flowering and days to maturity was also noticed by many researchers (Lakshmi *et al.,* 2017; Gayathri and Padmalatha, 2018).

On the other hand, Sarkar *et al.* (2014) and Venkata Lakshmi *et al.* (2014) observed a positive correlation between grain yield plant^{-1} with days to flowering and days to maturity. This inconsistency may be attributed to genotype or environmental effects. Spikelet fertility (%) revealed a significant and positive correlation with filled grains panicle^{-1}, as well as, a negative and significant correlation with days to flowering and days to maturity. Plant height showed a positive and significant correlation with panicle length, effective tillers plant^{-1}, days to flowering, and days to maturity. Islam *et al.* (2016) reported a positive and significant correlation of plant height with panicle length, days to flowering, and days to maturity, as well as. Akhi *et al.* (2016), reported a highly significant positive correlation between plant height and effective tillers plant^{-1}. Days to flowering revealed a positive and highly significant correlation with days to maturity. Qamar *et al.* (2005) also discovered highly significant and positive



ns p >= 0.05; * p < 0.05; ** p < 0.01; and *** p < 0.001

Figure 2. Phenotypic correlation among the independent and dependent traits in aromatic rice. FLA = Flag leaf area (cm^2), PH = Plant height (cm), DF = Days to flowering, DM = Days to maturity, ET = Effective tillers plant^{-1}, PL = Panicle length (cm), SF = Spikelet fertility (%), FGP = Filled grains panicle^{-1}, 1000 gwt =1000-grain weight (g), GYP = Grain yield per plant (g).

relationships between days to flowering and days to maturity in aromatic rice at both the phenotypic and genotypic levels, indicating that genotypes that flower vigorously mature earlier. However, this characteristic exhibited a negative and highly significant correlation with grain yield plant^{-1}, which is consistent with the recent findings. In the study, panicle length exhibited a positive and significant correlation with flag leaf area, plant height, and effective tillers plant^{-1} (Figure 2). Chhangte and Devi (2019) also found a significant and positive correlation of panicle length with plant height and effective tillers plant^{-1}.

CONCLUSIONS

The necessity of both the GCA and the SCA for discovering the genetic linkages among yield and yield-related traits was emphasized in this study. Three parents, viz., IR58025A, BRRI1A, and BUdhan2R, were good combiners for most of the desired traits depending on mean performance, gene action, combining ability, and heterosis of the parental genotypes. On the other hand, IR58025A × BUdhan2R and BRRI1A × BUdhan2R were recorded to be the best crosses for yield contributing characteristics and grain yield. Thus, these populations will contribute to developing potential aromatic hybrid rice cultivars and increase aromatic rice production in Bangladesh.

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