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Assessing the performance of hybrids developed using iso-cytoplasmic restorers and identification of promising combiners in rice

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Abstract

Iso-cytoplasmic restorers (ICRs) are valuable sources of fertility restoration for three line rice hybrids derived from wild-abortive cytosterile (WA-CMS) lines. They carry a full complement of fertility restorer (*Rf*) genes and sterile cytoplasm. We have test-crossed a set of 25 ICRs with four WA-CMS lines namely, IR 79156A, IR 58025A, Pusa 6A and RTN 12A following a line x tester mating design. Significant estimates of general and specific combining ability for agro-morphological traits revealed the involvement of both additive and non-additive gene effects. The combining ability estimates implied that some of the restorers were good general combiners for traits such as plant height, number of tillers per plant, panicle length, spikelet fertility, grain weight and yield per plant. Four promising ICRs namely, PRR317, PRR354, PRR381 and PRR390 with high general combining ability for yield across different environments were identified based on their hybrid performance. Additionally, location-specific ICRs, namely PRR300 and PRR396 for timely sown conditions of New Delhi, PRR348 for Pusa and Karnal, and Pusa 307 for Karnal and late sown conditions of New Delhi environments were identified. The restorers identified in the current study demonstrates ICRs as potential source for restorer development and can lead to the development of heterotic hybrids.

Key words: Combining ability, heterosis, iso-cytoplasmic restorers, line x tester analysis, rice

Introduction

Among the most important crops, rice adorns a primary position accounting 47% of cereal production in India. It also plays a vital role as the staple cereal for more than 60% of the country's population, there by sustaining food security. Grown in about 44 million hectares, the highest area occupied by any crop in the country, rice productivity is crucial in shaping the socioeconomic sustainability of India. However, the current productivity level of 36.95 q/ha on average, which is significantly lower than the global average of 47.26q/ha (FAO, 2016), remains a perturbing challenge in productivity improvement. On the contrary, neighbouring China produces 211.1 million tonnes from only 30.44 million hectares with a productivity of 69.32 q/ha. High rice productivity of China, which is almost double than that of India, has been primarily attributed to the wide-scale adoption of hybrid rice. Therefore, hybrid rice can offer a great potential in building the livelihood security in India, which will not only improve rice grain production but also can bring in a significant impact on social and economic growth in the country. Hybrid rice introduced in India in the late 1980s was mainly based on the most widely used wild-abortive cytoplasmic male sterility (WA-CMS) system. Subsequent research efforts in hybrid development for the last two decades have resulted in the commercial release of 102 hybrids (Shidenur et al. 2019), of which 35 are from public sector institutions and 67 are from private sector research companies. Inspite of these efforts, the adoption of hybrids has been slower in India, with merely 2.8 million ha, which represents only 6.4% of the total rice area.The slow adoption by farmers can be attributed to several factors

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such as high seed cost, marginal yield benefit and inability to recycle the seeds, being the prominent reasons. Therefore, there is an imminent need to improve hybrid seed production and hybrid yield to address the issue of marginal adoption. Parental line improvement plays a vital role in the development of hybrids with better acceptability.

Restorer diversification is a continuous process in three line hybrid breeding in rice involving WA-CMS systems. Conventionally, restorers (R lines) are identified from the cultivated germplasm based on test crosses by assessing fertility restoration potential and agronomic performance of hybrids. Therefore, the restorers may possess different cytoplasm (alloplasmic) other than the WA cytoplasm conferring male sterility. In such cases, differential fertility restoration may be observed in hybrids between the potential restorers and WA-CMS plant due to nucleo-cytoplasmic interactions between fertility restorer (*Rf*) genes and the WA cytoplasm (Hu et al. 2016). Severe interactions, therefore, can significantly reduce the possibility of identifying potential restorers from a large set of testcrosses made. Since the whole process of testcross based screening is cumbersome and expensive, a low restorer turnover may be deterrent to hybrid rice breeding (Waters et al. 2015). Alternatively, iso-cytoplasmic restorers (ICR) are stable restorer lines derived from a maternal stock that carries the same cytoplasm and are usually derived from segregating populations from an elite hybrid (Kumar et al. 2019). They may be different in nuclear genomes. These ICRs provides the advantage of minimising background interactions between the cytoplasm and *Rf* genes, resulting in higher fertility levels in the hybrids. In the WA-CMS system, because of the presence of WA cytoplasm among the ICRs, hybrids can attain the same level of spikelet fertility (>85%) as that of the restorer parent (Dan et al. 2014). Since ICRs are derivatives of elite hybrids, they are expected to possess the best gene combinations for better combining ability. Therefore, in the restorer diversification programs, ICRs with better combining ability, yield heterosis and broader genetic base can be classified into distinct heterotic pools (Kumar et al. 2019).

Combining ability is a robust estimate for establishing parental value while producing superior hybrids and hybrid derivatives. It is useful in identifying the potential parents and heterotic crosses, while providing an insight into nature and relative magnitude of gene actions (Peng and Virmani, 1990). Among the available mating designs to estimate both general and specific combining abilities (GCA and SCA), diallel (Griffing, 1956) and line x tester (Kempthorne, 1956) are the most reliable. Line x tester mating design has been widely used due to its ability to accommodate more genotypes in the testing program as compared to diallel mating design.

Till date, no systematic studies have been undertaken to assess the potential of ICR lines and identify promising restorers for utilisation in hybrid rice breeding. We, in our earlier studies, had developed a set of 390 ICRs from 25 commercial hybrids by systematic pedigree-based screening (Kumar et al. 2017a), of which 25 ICRs were validated for high restoration potential and stable performance (Kumar et al. 2017b). This study aims at determining the combining ability of these selected ICR lines for assessing their potential in hybrid development.

Materials and methods

A set of 100 testcrosses were developed by crossing 25 superior ICR lines with four WA-CMS lines namely, IR 79156A, IR 58025A, Pusa 6A and RTN 12A in a line x tester mating design. The hybridisation was carried out during *Kharif* 2014 and 2015 in ICAR-IARI, New Delhi and during *Rabi* 2014-15 at RBGRC, ICAR-IARI, Aduthurai, Tamil Nadu. The ICRs were initially identified from a segregating population of 390 restorer lines derived from 25 elite commercial hybrids (Kumar et al. 2017a) based on WA-CMS system, that were further screened for their fertility restoration potential (Kumar et al. 2017b). Finally, a set of 25 ICRs, one best performing restorer line derived from each of the 25 hybrid progenies were selected and used for developing testcrosses (Table 1). The testcross hybrids were evaluated for agronomic and yield performances under a multilocation experiment following standard agronomic practices.

The testcross hybrids were evaluated at three locations namely, New Delhi, Karnal (Haryana) and Pusa (Bihar) in augmented design along with their male and female parents and ten standard checks with four replications. At Delhi, the evaluation was conducted under two sowing times, early and late sowing. For each tester, the corresponding isogenic maintainer line was used as a parental check. Transplanting of 21-days-old seedlings was done with one seedling per hill at a spacing of 20x15 cm, and observations were recorded on agro-morphological traits, pollen, and

Table 1. List of parental lines and checks used in the experiment

Iso-cytoplasmic restorers (Lines)		CMS lines (Testers)	Checks
ICR No.	Hybrid parent		
PRR300	DRRH 2	IR 79156A	KRH 2
PRR307	DRRH 3	IR 58025A	HRI 174
PRR311	PSD 3	Pusa 6A	US 312
PRR314	PRH 10	RTN 12A	PA 6129
PRR317	CORH 3		US 312
PRR323	Sahyadri 1		PA 6444
PRR326	Sahyadri 2		PHB 71
PRR329	Sahyadri 3		PRH 10
PRR334	Sahyadri 4		IR 64
PRR337	GK 5003*		MTU 1010
PRR342	US 312*		
PRR347	NK 5251*		
PRR348	INDAM 200-017*		
PRR354	DRH 775*		
PRR358	PA 6129*		
PRR363	PA 6201*		
PRR367	PA 6444*		
PRR368	PHB 71*		
PRR372	Indira Sona		
PRR376	Suruchi 5401*		
PRR381	JRH 8		
PRR386	JKRH 401*		
PRR390	PAC 835*		
PRR395	PAC 837*		
PRR396	KRH 2		

*Indicates hybrids from private sector companies

spikelet fertility. Data were recorded on five healthy plants for each of the hybrids. The agro-morphological features observed were days to 50% flowering, plant height, panicle length, tiller number, grains per panicle, pollen fertility (%), spikelet fertility (%), test weight, yield per plant, kernel dimensions before cooking, kernel dimensions after cooking and kernel elongation ratio (KER). Post harvest measurements were also recorded from the same five plants selected earlier. The data on yield per plant of the testcross hybrids, their respective parents and the checks were used for calculating heterosis over both the parents, mid-parent and standard checks.

Data analysis

The analysis of variance (ANOVA) for the quantitative data obtained from the ICR lines and hybrids was analysed using SAS 9.3 software (SAS Institute Inc., Cary, NC, USA). Only those traits which showed significant variation among the test entries were used for further analyses. Combining ability was estimated using line x tester analysis as per the standards given by Kempthorne (1957) and implemented in the software, Windostat 8.0. To investigate the genotype-by-environment interaction of the test hybrids and parental lines, a GGE biplot analysis (Yan and Kang, 2003) was performed using the R-package, GGEBiplotGUI (Frutos et al. 2014). Estimates of yield heterosis were computed using standard formulae (Hallauer et al. 2010).

Results and discussion

Performance of the parental lines and their hybrids at different locations

ANOVA revealed significant genotypic differences for all the traits studied (Table 2). The variation due to the environment was significant for most of the traits except for filled grains per panicle, the weight of 1000 grains and pollen fertility. The non-significant differences for pollen fertility further validates the effectiveness of these ICRs for restoration of fertility in the testcross hybrids. While partitioning the genotypic variation, in general, parents showed significant variation for filled grains per panicle and pollen fertility, which was also reflected in the hybrids for all the traits. Parent x hybrid component of variation showed remarkable differences for most of the traits except for panicle length, pollen fertility, and days to 50% flowering. Analysing the parental variations, it was seen that testers had no apparent variation for any of the traits, while lines showed recognisable variations for all the traits. Variations due to the interaction effect of parents with environments, lines with environments, and testers with environments were also non-discernible for all the traits, although environment x hybrids showed significant variation for panicle length alone. The variance for environment x genotype was substantial for grain yield per plant, suggesting varying adaptability of specific hybrids to each environment. In general, hybrids showed more consistency in their performance over environments as compared to their parents. Among the parents, the interaction effects of lines and testers had significant variation for all the traits, that indicated the presence

Table 2. Analysis of variance and estimates of genetic variance among 100 F_1 hybrids and their parents across different locations

Components of variation	PH	NT	PL	FG	SF	TSW	PF	DFF	PY
Environment	4968.7**	234.2**	238.8**	244.5	1918.0**	7.3	613.5	801.6	2524.3**
Treatment	783.4**	130.6**	49.3**	4101.8**	658.1**	124.6**	1258.1**	858.4**	296.0**
Parent	403.9	7.2	18.0	3624.0**	267.4	51.9	1730.0**	349.0	78.3
Parent x cross	5971.2**	3577.3**	49.1	68727.8**	1493.3*	704.3**	85.0	199.6	7265.3**
Cross	838.4**	130.7**	58.2**	3584.1**	760.1**	139.3**	1136.5**	1009.2**	287.2**
Line (L)	1348.2*	355.0**	99.3**	3927.4**	1370.9**	191.9*	1612.7**	1965.7**	607.3**
Line (L) x tester (T)	692.3**	57.0**	46.1**	3568.4**	574.2**	121.9**	980.1**	714.3**	191.2**
Env x Treatment	225.6	54.5**	19.2	1684.2	171.0	32.3	415.4	242.5	104.8**
Env x Cross	297.0	284.1	62.7**	23.8	1569.1	205.4	39.6	408.1	273.8
σ^2_L	4.9	3.7	0.5	-118.4	15.4	2.1	5.6	27.3	4.4
σ^2_T	-1.9	0.2	-0.1	-9.2	-0.9	0.2	1.6	-1.4	-0.7
σ^2_{GCA}	-1.0	0.7**	-0.0	-24.3	1.3	0.5	2.1	2.5	-0.0
σ^2_{SCA}	66.0**	4.7**	3.9**	373.7**	55.1**	10.2**	84.5**	66.6**	17.7**
σ^2_a	-2.0	1.4	-0.1	-48.6	2.6	1.0	4.2	5.1	-0.0
σ^2_d	66.0	4.7	3.9	373.7	55.1	10.2	84.5	66.6	17.7
σ^2_a/σ^2_d	-0.0	0.3	-0.0	-0.1	0.1	0.1	0.1	0.1	0.0
Degree of dominance	5.8	1.8	8.7	2.8	4.6	3.2	4.5	3.6	35.5
σ^2_P	46.0	11.8	2.2	178.0	28.9	7.6	51.3	50.7	21.0
Heritability (NS) %	-4.3	12.0	-2.3	-27.3	9.1	13.2	8.3	10.0	-0.1
Genetic advance 5%	-0.6	0.9	-0.1	-7.5	1.0	0.8	1.2	1.5	-0.0
Contribution (L) %	39.0	65.9	41.4	26.6	43.7	33.4	34.4	28.4	51.3
Contribution (T) %	1.0	2.4	0.9	1.0	1.3	3.0	2.9	8.3	0.3
Contribution (LxT) %	60.1	31.8	57.7	72.4	54.9	63.7	62.7	63.3	48.4

PH = Plant height in cm; NT = Number of tillers per plant; PL = Panicle length in cm; FG = Number of filled grains per panicle; SF = Spikelet fertility percentage; TW = Test weight in g; PF = Pollen fertility percentage; DFF = Days to fifty percent flowering; PY = Yield per plant in g; L = line; T = Tester; LxT = Line x tester; σ^2P = Phenotypic variance; a = Additive; d = Dominance; GCA = General combining ability; SCA = Specific Combining Ability; NS = Narrow sense; Env = Environment

*,** Significant as $p<0.05$. #The components of variation for Tester, Env x Parents, Env x Line, and Env x Tester have shown non-significant variation as $p>0.05$

of both additive and non-additive gene actions. Importance of non-additive genes for expression of yield and its components have been reported earlier by several workers (Dalvi and Patel, 2009; Saidaiah et al. 2010; Selvaraj et al. 2011). Although grown under different environments, the scale of environmental variance indicated that genetic expression of traits was moderate, and the genotypes had better stability across environments. However, there was significant genotype x environment interaction (GEI) for grain yield per plant that qualified for the analysis for stability. Compared to the testers, the ICR lines used as the male parent were found to possess maximum variation for all the traits, indicating that the progenitor of these lines, the commercial hybrids, had sufficient genetic variance to be inherited to their progenies. It has already been established that the hybrid progenitors used in this study originated from a diverse group of restorers (Kumar et al. 2017a). This information is pertinent in CMS based hybrids because the male sterile lines possess limited variability and therefore, the use of genetically diverse restorers is essential in developing successful commercial hybrids in rice. The significance of parents x crosses component of variation for all the traits, except for panicle length and the number of panicles per plant, could indicate that considerable heterosis existed for these traits, which could be valuable in hybrid rice development,

particularly for improving grain yield. The above observation is supported by earlier findings of Jayasudha and Sharma (2009) and Rahimi et al. (2010), in which they reported a significant difference among parents x crosses and an excellent correlation to heterosis.

Agronomic performance of the lines and hybrids (Supplementary Table 1) indicated the presence of significant genetic variability for the improvement of all the traits. The traits that are recognised as the yield contributing as well as adaptation-related are essential parameters to look for in hybrid rice development to obtain a successful widely adapted hybrid. Average plant height among the testcross hybrids ranged between 61.5 cm (IR58025A/PRR307) and 108.9 cm (Pusa6A/PRR348) as against the cumulative mean plant height of 89.3 cm. For the number of tillers per plant, the lowest number of tillers was produced by Pusa6A/PRR342 (9.5), while hybrids from the cross IR79156A/PRR300 produced as many as 22.2 tillers on average. Hybrids derived from restorer parents, namely, PRR334 (20.2) followed by PRR323 (18.9) and PRR396 (17.8) exhibited better tillering pattern. Length of the panicles among the hybrids ranged between 15.1 cm (IR58025A/PRR307, Pusa6A/PRR368) and 28.3 cm (IR79156A/PRR347). Among the ICR lines, PRR347, PRR381, and PRR390 had produced hybrids with longer panicles on average, respectively 26.9 cm, 26.7 cm and 26.2 cm. Filled grains per panicle is one of the important yield components to realise higher plant yield in hybrids primarily when CMS system is used for their development. Therefore, successful hybrids should possess high number of filled grains per panicle indicated by high spikelet fertility. In this study, hybrids of the cross, IR58025A/PRR337 had the lowest number of filled grains per panicle (54.5), as against Pusa6A/PRR381 with high grain number (176.6). The ICRs, namely PRR381, PRR396 and PRR300 were found to be superior restorers that resulted in hybrids with a higher number of filled grains per panicle. Similarly, the lowest spikelet fertility of 30.8% was observed in the hybrid IR58025A/PRR334, while 83.0% fertile spikelets were produced in the hybrid, IR79156A/PRR342. Spikelet fertility determines the potential seed output of the hybrids and hence is recognised as an esential trait in hybrid seed production. Typically, more than 80% of spikelet fertility is considered as a benchmark for the selection of potential hybrid combinations (Virmani et al. 1997). Weight of 1000 grains is measured as a yield component in rice because it reflects the grain filling and the grain compactness, two main factors that can lead to higher yield. ICRs with better average grain weight included PRR367 (15.6 g) followed by PRR323 (23.8 g) with a mean of 18.7 g among all the genotypes. Among the hybrids, IR58025A/PRR323 had grain weight of 24.9 g per 1000 grains, which was the highest recorded in the experiment. The lowest grain weight of 9.7 g per 1000 grains was recorded in the hybrid Pusa 6A/PRR386. Among the ICRs, PRR381 (85.5%), followed by PRR396 (80.9%) and PRR323 (82.5%) recorded the highest average pollen fertility among the hybrids, and PRR311 recorded the lowest (56.0%). The range for days to fifty percent flowering was from 62.5 (Pusa6A/PRR342) to 105.1 (RTN12A/PRR329) among the hybrids. For grain yield per plant, the best performance was observed in the hybrid from the cross, IR79156A/PRR381 (40.06 g) followed by hybrid of IR79156A/PRR396 (38.89 g). The lowest single plant yield was recorded in the hybrid, IR58025A/PRR311 (15.05 g). The average yield among the testcross hybrids indicated that restorer parents, PRR390 (34.24 g), PRR381 (33.67 g), PRR396 (32.93 g), PRR348 (32.82 g) and PRR300 (29.94 g) were promising across locations.The genotypic variances due to the lines and the testers had no significant difference implying a strong influence of environment among the test materials, which is not unexpected because one of the locations (Pusa, Bihar) used in the study was geographically apart from the other two sites, New Delhi and Karnal.

Combining ability of iso-cytoplasmic restorers

Line x tester is fundamentally an extension of the topcross design wherein several testers are used instead of one tester in the topcross (Kempthorne, 1957). Generally, this design involves hybridisation between lines (*f*, female) and testers (*m*, male) in one to one fashion generating *f* x *m* = *fm* hybrids (Sharma, 2006). The testers used in the line x tester analysis are generally elite lines with a broad genetic base, in terms of agronomic performance. However, in the present case, we have used the male sterile lines as testers (female) as they could not be used as males owing to their pollen sterility. Alternately, the ICR lines were used as lines (males) resulting in the development of 100 testcross hybrids. Further, any reciprocal difference among the lines and testers was not expected due to the presence of same cytoplasm in both the parents.

The general combining ability (GCA) estimates

also showed non-significant differences for all the traits except for the number of tillers implying a preponderance of non-additive gene action, which was further evident from the high variance of specific combining ability (SCA) effects. However, the lower GCA variance was not indicative of poor GCA, but uniform GCA effects among the ICR lines. A comparison of GCA estimates of the lines indicated that several of them had high positive GCA for grain yield (Fig. 1), with restorers such as PRR323, PRR381, and PRR390 showing positive GCA in all four environments. Similarly, there are nine top ICRs that showed positive GCA in at least three environments. PRR354 (12.73), PRR396 (11.81), PRR300 (10.52) for early sown conditions of Delhi (DEL-E), PRR342 (8.82) and PRR317 (8.65) for late sown conditions of Delhi (DEL-L), PRR348 (8.34), PRR390 (7.99) and PRR342 (6.97) for Pusa, Bihar (PUS) along with PRR348 (7.72) and PRR368 (6.90) for Karnal (KAR) have shown highest GCA effects (Supplementary Table 2). Higher values of positive GCA is indicative of the presence of additive gene action, and the estimates of high positive SCA effect are useful in determining the potential of a particular cross combination in the exploitation of heterosis. When restorer lines have significant positive GCA together with high SCA with several of the testers, it signifies additional presence of non-additive gene effects in trait control. In practical terms, this will translate into potential restorers that can be widely used in hybrid development as well as for improvement of restorers. The role of additive and non-additive traits in hybrid rice development was also reported by Borgohain and Sarma (1998) and Hong et al. (2002). Generally, high x high, low x high and high x low general combiner parents produced good specific cross combinations. Under such situations, additive x additive, dominance x additive, and additive x dominance type of gene action were found to act in trait expression, respectively. Whereas, in some cases, high x high general combiners could produce inferior hybrids, if there is a preponderance of epistatic gene action in the non-additive component (Bagheri and Jelodar, 2010). Such epistatic interactions for several traits have been reported in rice (Sarkar et al. 2002).

The high SCA is suggestive of the usefulness of the ICRs in hybrid breeding because a line with relatively high SCA under several hybrid combinations can produce good hybrids by crossing with specific CMS lines. High SCA is often associated with dominance which is the major component of the non-additive gene action. Higher dominance can be directly translated into high heterosis for the target trait. The potential value of high SCA effects in hybrid breeding has also been discussed by Ramalingam (1997). In the present case, the variance due to dominance was higher than the variation due to additivity, which was further substantiated by the low magnitude of σ^2_a/σ^2_d ratio. The estimates of narrow-sense heritability also reflected a similar trend, indicating an accumulation of dominance genes in parental populations (Table 2). By multiparent quantitative trait loci (QTL) mapping in maize for several agronomic traits, Larièpe et al. (2012) have demonstrated an overdominance expression by the assembly of favourable heterotic QTLs that scales down the differences in heterozygous genotypes. They hypothesised that most of these loci are proximal to the centromeric region and thus undergo relatively less recombination, thereby conserving the heterotic loci in coupling phase.

The SCA variance of hybrids for grain yield per plant indicated a consistent trend across testers and changing pattern across the lines (Supplementary Table 2). Hybrids with positive SCA was less under DEL-E than other three environments. Among the ICRs, the consistency in positive SCA expression was more in DEL-L, KAR, and PUS locations. When crossed with IR79156A, two ICRs, PRR311 and PRR381 showed positive SCA for grain yield in three situations, DEL-L, PUS, and KAR, while PRR334 and PRR390 showed positive SCA under DEL-E, DEL-L and KAR environments. PRR334 registered positive SCA in DEL-E, PUS, and KAR. When hybrids were derived with IR58025A, the restorers, PRR323 and PRR342 had shown positive SCA in all four environments, whereas, PRR300 and PRR317 exhibited the same only in three situations, except for DEL-E.SCA estimated for hybrid combinations derived from Pusa6A showed consistency of positive SCA when crossed with restorers PRR337, PRR348, and PRR367. Two of the hybrid combinations from RTN12A obtained by crossing with PRR311 and PRR334 had positive SCA for grain yield in all four environments. Among the remaining hybrids derived from RTN12A, hybrids derived with PRR358, PRR368, PRR386, and PRR395 showed positive SCA in three environments each. PRR334, PRR342, and PRR358 produced the highest number (eight) of positive SCA combinations across four environments. Several crosses having high SCA effects for grain yield per plant in rice were reported by several researchers (Mehla et al. 2000; Sarker et al. 2002; Sharma et al. 2005).

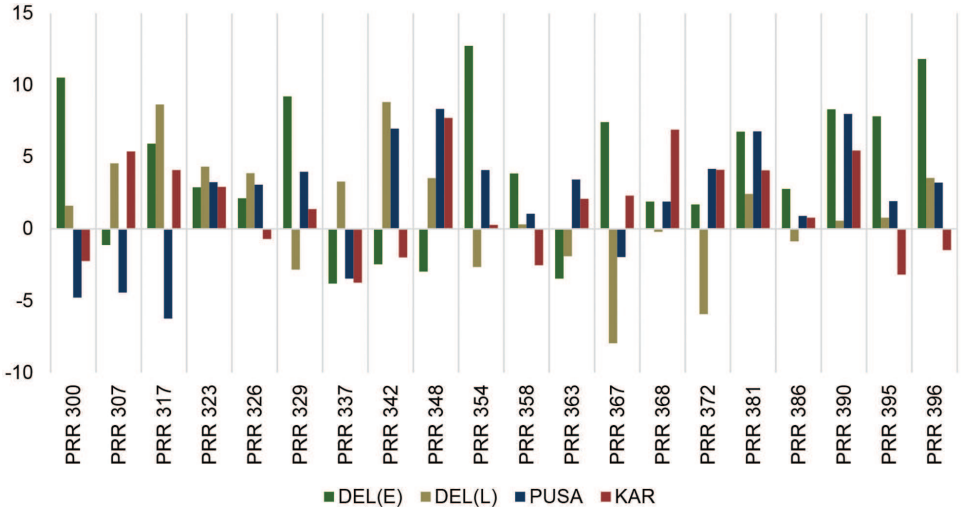

Fig. 1. General combining abilities of top twenty iso-cytoplasmic restorer lines at three locations for grain yield per plant (g). Only three ICR lines showed positive GCA in all four environments

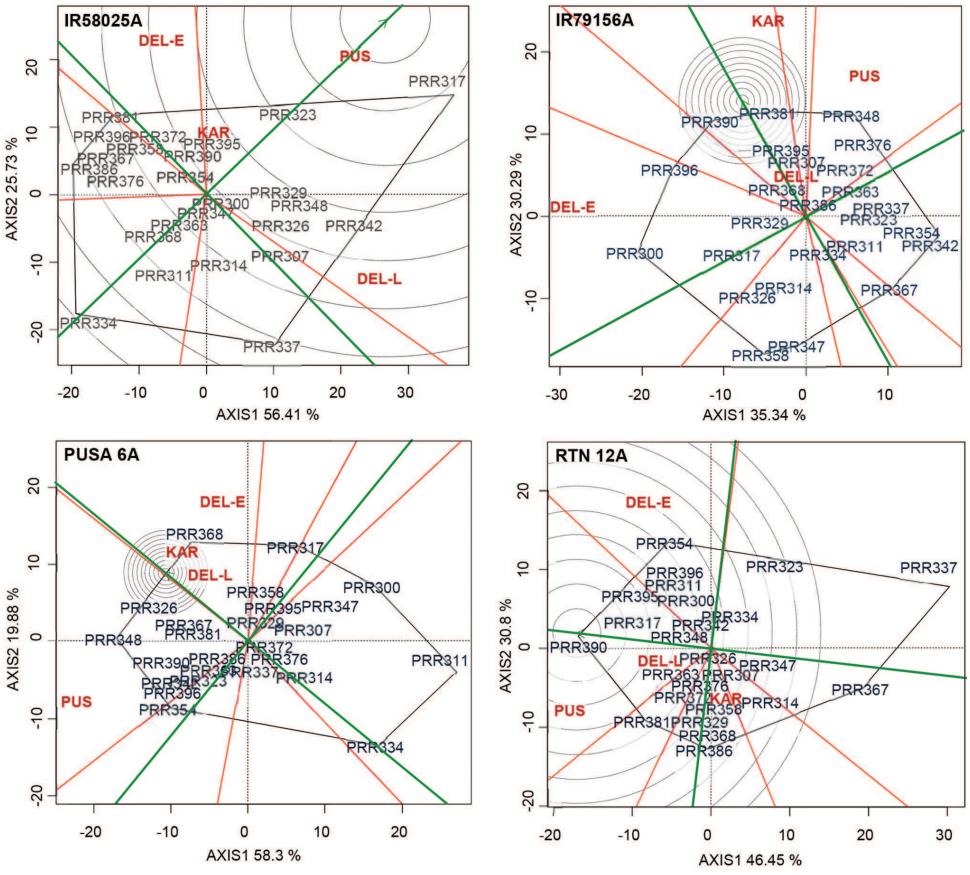

Fig. 2. GGE biplots of hybrids developed by the iso-cytoplasmic restorer lines with for male-sterile parents grown under four environments in three locations. The hybrids are identified by their respective restorer parents in the biplots

The proportional contribution of lines, testers and their interaction to the total variance showed that the ICR lines played a prominent role towards the trait expression, which is indicated by the high contributory values of the lines for all the traits. However, significant contribution of the line x tester component observed in the present study suggested higher SCA variance effects. These results are in partial agreement with the findings of Rashid et al. (2007) in Basmati rice, wherein significant maternal influence (lines) was reported for some of the agronomic traits, but not for line x tester combinations. Sanghera and Hussain (2012) while investigating the combining abilities of WA-CMS based parental combinations of rice hybrids, reported a predominance of line x tester contribution to the total variance leading to higher estimated SCA and realised heterosis in hybrids. In our study also, the significantly higher contribution of lines and lines x testers is indicative of the potential of ICR lines in the development of superior hybrids, possibly contributed by the diverse nature of parental materials.

Heterotic expression for yield

The degree of heterosis differed with crosses and traits. Parel et al. (1994) in upland rice observed a varying degree of heterosis for yield and its related traits. Whereas, Watanesk (1993) and Rao et al. (1996) found high heterosis for grain yield and its

components. In our study, under New Delhi conditions, DEL-E and DEL-L, hybrids generated from IR 79156A and IR 58025A, were highly heterotic for yield per plant (Table 3). Under DEL-E environment, the restorers, PRR396 followed by PRR300 produced hybrids with higher heterosis when crossed to IR 79156A, and in DEL-L, PRR342, PRR337, PRR307 produced superior hybrids with IR 58025A. Hybrids generated using Pusa 6A and RTN 12A had better yield performance under PUS environment, wherein the best restorers were PRR390 and PRR381 for RTN 12A and PRR348 for Pusa6A. At KAR environment, PRR307 and PRR348 were the best restorers for IR 79156A, PRR368 for Pusa 6A and PRR314 for RTN 12A, and produced superior cross combinations with high grain yield. Based on the hybrid performance, specific male sterile lines and ICR combinations could be suggested for each location to maximize heterosis. A comparison of the observed heterosis and the GCA of their parents revealed that most of the heterotic combinations were generated from the crosses between parents with high and low GCA, suggesting a role of both additive and dominant gene action in realising heterosis. Correspondence between *per se* performance and GCA effects for most of the traits in rice has been observed by Rosamma and Vijaykumar (2005) and Sharma et al. (2005).

Grain and cooking quality of ICR derived hybrids

Grain quality is one of the most critical parameters determining consumer acceptance of rice varieties/ hybrids. Grain quality is often ignored in the rice breeding programmes, because the major focus lies on higher yield, and there is an apparent negative association of several grain quality parameters with yield (Veni et al. 2013; Xu et al. 2015). Not withstanding, grain quality plays a significant role in the success of a rice hybrid. The crosses derived from ICR lines were compared with their parents and hybrid checks for grain and cooking quality (Table 4). The range for hulling percentage was between 66.2% and 87.2%, while that of milling and head rice recovery was 63.9-82.1% and 54.0-75.8%, respectively. Kernel length and breadth before cooking ranged from 4.3 to 6.7 mm and 1.3 to 2.1 mm, respectively. Kernel elongation ratio showed a moderate variation ranging between 1.4 and 2.7. The mean performances for ICR lines along with their parents and hybrid checks were compared. For hulling percentage, crosses derived from ICRs (82.0%) were found to be superior to the hybrid checks (81.8%). Hybrid checks and crosses derived from ICRs had shown comparable performance for milling percentage (76.1 and 76.0, respectively). Head rice recovery among the hybrids and checks was similar to each other with the former having 68.2% recovery, and the latter having 67.1%. Further, the hybrids developed in the present study were found to be better in hulling, milling and head rice recovery percentage over respective parents, and similar or better than the checks used. ICR derived hybrids were found to possess longer milled kernels measuring up to 5.2 mm on average (range 4.3-6.3 mm) with a kernel breadth of 1.6 mm, as against 1.7 mm recorded in the hybrid checks, demonstrating that the hybrids derived using the ICRs were predominantly of slender grain type with a range of 1.3 to 1.8 mm. However, no significant variation was observed for cooked kernel length between hybrids, parents and checks on average, although some of the hybrids and ICR had maximum cooked kernel length exceeding 10.0 mm which was below 10.0 mm for the checks. Elongation ratio for the check hybrids was the highest (2.41) followed by maintainers of the CMS lines (1.78), ICRs (1.65) and testcross hybrids (1.59).

Genotype by environment interaction for grain yield

GGE biplot analysis (Yan and Kang, 2003) weighs the genotypic performance by combining genotypic (G) and genotype x environment (GE) effects. In practice, G and GE effects are inseparable and hence partitioning them into two different components may render them biologically meaningless (Yan et al. 2000). GGE biplot analysis thus uses an environment centered data in which the environment (E) main effects are removed. The transformed data is then decomposed to obtain principal components (PC) that displayed the G+GE effects in the spatial spread between the first two PC axes, accumulating maximum variation. Analysis of the grain yield data in the present study was done separately based on the hybrid performance derived from a particular CMS line (Fig. 2). In the first case, the hybrids derived from IR58025A showed that the first two PC axes explained a cumulative variation of 82.1%, with the first axis accounting for 56.4% and the second axis 25.7%. For those hybrids derived from IR 79156A, the cumulative variation encompassed by the first two PCs was 65.6% with individual component explaining 35.3% and 30.3% respectively for PC1 and PC2. Total variation explained by the first two PCs in case of hybrid derivatives from Pusa 6A was 78.2% with PC1 accounting for 58.3% of the variation followed by the PC2 explaining 20.0% of the variation. A total variation of 77.3% was explained by PC1 and PC2 for the hybrids derived

Table 3. Estimation of heterosis for yield per plant

Environment	Hybrid	Mean	R line	Mid-parent	B line	KRH2	HRI 174	US 312	PA 6129	US 314	PA 6444	PRH 10	PHB 71	IR 64	1010 MTU
Del (E)	IR 79156A/PRR396	52.22	155.98	129.54	108.05	68.94	67.53	82.91	52.24	79.02	80.19	45.62	61.92	128.33	88.86
	IR 79156A/PRR300	50.46	75.57	87.44	101.04	63.25	61.89	76.74	47.11	72.99	74.12	40.71	56.47	120.64	82.50
	RTN 12A/PRR354	43.54	148.37	137.60	127.72	40.86	39.69	52.50	26.94	49.26	50.24	21.42	35.01	90.38	57.47
	IR 79156A/PRR390	41.78	6.36	29.79	66.45	35.17	34.04	46.34	21.81	43.23	44.17	16.51	29.55	82.68	51.10
	IR 58025A/PRR381	41.34	118.50	98.89	82.52	33.74	32.63	44.80	20.52	41.72	42.65	15.28	28.19	80.76	49.51
	IR 58025A/PRR396	41.30	102.45	91.87	82.34	33.61	32.50	44.66	20.41	41.58	42.51	15.17	28.06	80.59	49.37
	IR 58025A/PRR386	40.09	108.37	91.41	77.00	29.70	28.62	40.42	16.88	37.44	38.34	11.80	24.31	75.30	44.99
	IR 79156A/PRR317	39.01	92.83	72.12	55.42	26.21	25.15	36.64	13.73	33.73	34.61	8.78	20.96	70.57	41.08
	RTN 12A/PRR396	38.82	90.29	96.46	103.03	25.59	24.54	35.97	13.18	33.08	33.95	8.25	20.37	69.74	40.40
Del (L)	IR 58025A/PRR342	52.29	252.60	229.39	209.04	66.85	88.30	111.53	75.06	76.12	133.13	80.37	90.35	58.12	119.89
	IR 58025A/PRR337	48.51	96.48	133.17	186.70	54.79	74.68	96.24	62.40	63.39	116.27	67.33	76.59	46.69	103.99
	IR 58025A/PRR307	46.76	70.04	110.54	176.36	49.20	68.38	89.16	56.55	57.49	108.47	61.30	70.22	41.40	96.64
	IR 58025A/PRR317	46.71	114.56	141.46	176.06	49.04	68.20	88.96	56.38	57.33	108.25	61.12	70.04	41.25	96.43
	IR 79156A/PRR381	43.04	46.25	88.52	165.19	37.33	54.99	74.11	44.09	44.96	91.89	48.46	56.68	30.15	80.99
	IR 79156A/PRR342	42.74	188.20	175.21	163.34	36.38	53.91	72.90	43.09	43.95	90.55	47.43	55.59	29.24	79.73
	IR 58025A/PRR326	39.92	88.39	109.50	135.93	27.38	43.75	61.49	33.65	34.46	77.98	37.70	45.32	20.71	67.87
	RTN 12A/PRR376	38.37	40.19	54.34	71.68	22.43	38.17	55.22	28.46	29.24	71.07	32.36	39.68	16.03	61.35
	IR 79156A/PRR323	37.17	61.12	89.16	129.02	18.60	33.85	50.36	24.44	25.19	65.72	28.22	35.31	12.40	56.31
Pusa, Bihar	RTN 12A/PRR390	58.44	59.72	63.97	68.46	14.41	22.82	44.73	25.41	57.56	37.90	39.71	38.98	89.86	63.93
	Pusa 6A/PRR348	54.84	58.54	74.98	95.23	7.36	15.26	35.81	17.68	47.86	29.40	31.10	30.42	78.17	53.83
	RTN 12A/PRR381	54.44	0.83	22.78	56.93	6.58	14.42	34.82	16.82	46.78	28.46	30.15	29.46	76.87	52.71
	Pusa 6A/PRR354	54.24	132.89	111.13	93.09	6.19	14.00	34.32	16.39	46.24	27.98	29.67	28.99	76.22	52.15
	Pusa 6A/PRR342	53.14	35.25	57.73	89.18	4.03	11.69	31.60	14.03	43.27	25.39	27.04	26.37	72.64	49.06
	IR 79156A/PRR376	52.93	62.91	65.72	68.62	3.62	11.24	31.08	13.58	42.71	24.89	26.54	25.87	71.96	48.47
	Pusa 6A/PRR390	52.24	42.77	61.53	85.97	2.27	9.79	29.37	12.10	40.85	23.27	24.89	24.23	69.72	46.54
	IR 58025A/PRR317	51.53	50.72	58.12	66.28	0.88	8.30	27.61	10.58	38.93	21.59	23.19	22.54	67.41	44.54
	Pusa 6A/PRR326	51.14	27.88	50.24	82.06	0.12	7.48	26.65	9.74	37.88	20.67	22.26	21.62	66.15	43.45
Karnal	IR 79156A/PRR307	41.36	111.13	178.24	307.89	69.79	63.41	51.89	-4.31	-22.94	-26.21	-4.31	-20.77	21.22	-19.48
	IR 79156A/PRR348	40.53	32.28	98.77	299.70	66.38	60.13	48.84	-3.12	-21.98	-25.29	-3.12	-19.78	22.72	-18.48
	Pusa 6A/PRR368	39.93	88.88	92.85	96.99	63.92	57.76	46.64	3.08	-16.99	-20.51	3.08	-14.65	30.58	-13.26
	IR 79156A/PRR390	38.33	51.26	116.07	278.01	57.35	51.44	40.76	-17.69	-33.72	-36.53	-17.69	-31.85	4.26	-30.74
	RTN 12A/PRR314	36.40	111.14	76.74	51.98	49.43	43.82	33.68	17.41	-5.45	-9.47	17.41	-2.79	48.73	-1.21
	Pusa 6A/PRR348	34.26	11.81	34.59	69.02	40.64	35.36	25.82	-35.71	-48.23	-50.43	-35.71	-46.77	-18.56	-45.91
	Pusa 6A/PRR317	31.71	41.63	48.66	56.44	30.17	25.29	16.45	5.91	-14.71	-18.33	5.91	-12.30	34.17	-10.88
	RTN 12A/PRR368	31.40	48.53	39.28	31.11	28.90	24.06	15.31	0.41	-19.14	-22.57	0.41	-16.86	27.20	-15.51
	Pusa 6A/PRR326	31.31	52.81	53.63	54.46	28.53	23.71	14.98	-136.95	-129.75	-128.49	-136.95	-130.59	-146.80	-131.09

Table 4. Comparison of hybrids with their parental lines and elite rice hybrids for grain and cooking quality

Variable	Genotypes	HP	MP	HRR	KLBC (mm)	KLAC (mm)	KBBC (mm)	KBAC (mm)	ER
Mean	Hybrids	81.99	76.01	67.14	5.33	8.46	1.62	2.31	1.59
	MS parent	78.38	73.60	63.53	5.00	8.87	1.47	2.25	1.78
	Restorer parent	80.87	75.41	65.37	5.23	8.62	1.63	2.39	1.65
	Checks	81.71	76.06	68.21	5.00	8.55	1.72	1.66	2.41
Min	Hybrids	66.22	63.94	54.00	4.27	6.93	1.27	2.00	1.38
	MS parent	75.71	72.55	59.88	4.87	8.20	1.33	2.20	1.58
	Restorer parent	76.48	70.07	55.75	4.40	6.73	1.33	2.00	1.41
	Checks	78.94	73.82	64.84	4.53	7.93	1.62	1.60	2.13
Max	Hybrids	85.21	81.63	75.80	6.33	10.13	1.80	3.73	1.97
	MS parent	81.99	74.87	67.02	5.20	9.73	1.67	2.27	2.00
	Restorer parent	87.12	82.15	70.00	6.67	11.33	2.00	3.07	2.13
	Checks	85.39	79.35	71.82	6.07	9.80	2.09	1.67	2.73
CV	Hybrids	4.61	4.81	6.23	8.42	8.41	6.15	11.18	7.87
	MS parent	3.45	1.36	4.69	2.88	7.93	9.82	1.48	10.16
	Restorer parent	3.55	2.98	4.96	11.24	12.96	9.73	12.35	10.09
	Checks	2.95	2.61	3.93	9.45	8.08	9.00	1.42	10.19

Where, HP = hulling percentage, MP = milling percentage, HRR = head rice recovery percentage, KLBC (mm) = kernel length before cooking, KLAC (mm) = kernel length after cooking, KBBC (mm) = kernel breadth before cooking, KBAC (mm) = kernel breadth after cooking, ER = elongation ratio

from RTN 12A, with the former accounting for 46.5% and the latter for 30.8%.

The convex hull was formed by connecting the vortex genotypes in each biplot by a straight line, in such a way that all the remaining genotypes are encompassed in the hull. The convex hulls of the hybrids based on the extreme performance indicated different shapes of polygons in each set of hybrids derived from the CMS parents. Presence of several sided polygons indicates substantial variations among the hybrids in each case, leading to the possibility of identifying distinct environments and environment-specific adaptation of genotypes. In such cases, identification of grouped environments (mega-environments) is rather typical. In the case of hybrids derived from IR58025A, where the complex hull was five faced, one mega-environments was detected, comprising of PUS, KAR, and DEL-L, while for IR 79156A derived hybrids, a nine-faced polygon was observed with a mega-environment containing KAR and DEL-L. A seven-sided convex hull was derived from Pusa 6A derived hybrids that included a mega-environment comprised of DEL-E, DEL-L and KAR, while the hybrids developed from RTN 12A, had a six-sided polygon, with one mega-environment containing PUS and DEL-L environments.

Environment-specific hybrids identified by which-won-where pattern analysis

The which-won-where pattern in the GGE biplot is a vital display that identifies specific and widely adapted genotypes in the study. When IR 58025A was used as a female parent, the testcross hybrid with PRR317 was located at the top of the polygon. This hybrid is expected to perform well under DEL-L, PUS and KAR environments. Testcross hybrid with PRR317 was the highest yielder, followed by that from PRR323. PRR381 followed by PRR372 were top-performing restorers that produced the best combinations under DEL-E conditions. Hybrids derived from PRR334 was the poorest among those derived from IR58025A. Hybrids generated using IR 79156A as the female parent, indicated that those derived from PRR381 and PRR390 were among the best performers, and suitable for DEL-L and KAR conditions. Hybrids developed from PRR348, and PRR376 had better adaptation to PUS conditions, while PRR317 and PRR300 produced specifically adapted hybrids for DEL-E conditions. Among the Pusa 6A derived hybrids, those from

PRR368 were found specifically adapted to DEL-E, DEL-L and KAR followed by those derived from PRR358. Pusa 6A/PRR348 was the best-suited hybrid for PUS conditions. PRR390, PRR317 and PRR395 produced superior hybrids with RTN 12A, that were widely adapted to PUS and DEL-L situations. RTN 12A/ PRR354 was more suited to DEL-E environment alone. The hybrids that are best and poor performers are located at the extremes from the biplot origin and were found to show specific adaption to a particular environment.

Identification of high ranking hybrids based on the average environment

The average environment axis is a line drawn through the average environment coordinate (AEC), which indicates yield ranking and stability of the genotypes. The line running perpendicular to AEC showed yield stability (Lakew et al. 2014). Thus, ICRs producing better hybrids with IR 58025A were in the order of PRR317>PRR323>PRR395, among which, PRR323 was the restorer that produced hybrids with better stability. In case of restorers that produced high yielding hybrids with IR 79156A, PRR381 stood at the prominent position followed by PRR390, PRR395 and PRR307. Except for PRR390, these restorers showed high average stability. PRR368, PRR326, PRR367 and PRR381 produced better ranking test cross hybrids with the average environment, and none of these showed excellent stability when crossed with Pusa 6A. No stable hybrid with average stability was produced with RTN 12A when crossed with ICRs such as PRR390, PRR317 and PRR348. Differential performance of ICR derived hybrids under different environments, however, is not large enough to categorise best and inferior hybrids, because several of them are found distributed closer to biplot origin, indicating non-specific adaptation and yield stability. This could be due to the contribution of maximum heterotic variance from the ICR lines, that are derived from elite commercial hybrids. Since these hybrids are sourced from diverse parental groups, the ICRs used in the present study display a wide array of genetic variation, which may be helpful in defining their heterotic affinity.

A more significant extent of variability and preponderance of non-additive variances observed among the ICRs indicated an ample scope in hybrid rice breeding. Four promising ICRs namely, PRR317, PRR354, PRR381 and PRR390 were identified based on the performance of testcross hybrids. This amounts to a proportion of 16% from 25 ICRs selected arbitrally from an initial pool of ICRs originally developed. The turnover is highly encouraging, and can be translated into several more if entire ICR population is subjected to simailr analyses. Further, inclusion of more number of hybrids in ICR development may be fruitful in identifying several restorers in future. The selected genotypes can be utilised in further breeding programme for enhancing the level of heterosis in rice. Restorer lines with sound GCA effects can be hybridised for generation of promising transgressive segregants in the segregating generations which can be further utilised as commercial varieties.

Authors' contribution

Conceptualization of research (AKS, GKS); Designing of the experiments (AKS, GKS, AK); Contribution of experimental materials (AKS, AK, PKB); Execution of field/lab experiments and data collection (AK, GKS, VJS, PKB, RS, MN); Analysis of data and interpretation (AK, GKS, PKB, AKS, KKV); Preparation of manuscript (AK, GKS, KKV, PKB, AKS, RKE, HB).

Declaration

The authors declare no conflict of interest.

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Supplementary Table S1. Mean performance of test crosses throughout different locations

Parent	Plant height (cm)					Tillers/plant					Panicle length (cm)				
	IR 79156A	IR 58025A	Pusa 6A	RTN 12A	F_1 mean	IR 79156A	IR 58025A	Pusa 6A	RTN 12A	F_1 mean	IR 79156A	IR 58025A	Pusa 6A	RTN 12A	F_1 mean
PRR300	85.6	85.7	89.2	83.8	86.1	22.2	15.7	14.0	17.2	17.3	25.6	24.6	24.4	25.3	25.0
PRR307	89.1	61.5	86.5	84.7	80.5	17.9	16.2	14.2	15.5	16.0	25.9	15.1	23.3	23.6	22.0
PRR311	93.9	63.0	84.3	90.4	82.9	20.3	15.1	13.4	18.1	16.7	26.9	16.1	24.5	27.0	23.6
PRR314	88.7	92.9	89.7	85.1	89.1	20.1	14.8	14.1	14.8	16.0	27.0	26.5	26.1	26.2	26.5
PRR317	95.1	99.0	73.8	63.3	82.8	20.2	20.1	11.3	12.9	16.1	26.1	25.2	17.6	17.7	21.7
PRR323	94.3	102.7	96.6	88.4	95.5	18.2	20.9	16.2	20.2	18.9	25.3	25.5	23.6	24.6	24.7
PRR326	83.0	84.1	70.8	88.5	81.6	19.5	19.3	13.1	17.4	17.3	26.1	25.7	17.3	25.3	23.6
PRR329	97.3	71.6	96.4	87.7	88.2	21.5	11.9	17.8	17.9	17.3	25.0	17.3	24.2	22.9	22.3
PRR334	88.7	83.8	82.1	87.4	85.5	19.8	23.4	20.4	17.1	20.2	25.7	25.0	23.9	26.1	25.2
PRR337	97.9	69.2	93.7	85.1	86.5	16.4	10.4	17.7	17.7	15.6	26.5	15.8	23.5	23.9	22.4
PRR342	91.5	92.0	68.8	91.7	86.0	14.7	21.7	9.5	15.9	15.5	27.4	25.7	16.8	24.6	23.6
PRR347	83.8	91.2	92.5	90.1	89.4	21.7	17.2	17.5	13.7	17.5	28.3	26.8	26.4	26.2	26.9
PRR348	106.0	106.1	108.9	99.2	105.1	15.4	16.3	14.7	13.5	15.0	26.5	26.3	25.7	24.8	25.8
PRR354	79.1	104.0	103.1	103.7	97.5	11.9	17.6	17.2	16.2	15.7	19.0	26.3	25.0	25.3	23.9
PRR358	64.3	91.6	93.2	92.8	85.5	10.5	14.9	18.2	14.2	14.5	18.9	26.1	24.9	26.1	24.0
PRR363	100.5	94.1	68.7	97.1	90.1	19.5	18.8	12.9	15.3	16.6	27.6	23.0	15.9	25.0	22.9
PRR367	70.6	90.1	90.5	93.2	86.1	10.3	16.9	21.3	15.1	15.9	17.4	25.0	24.6	24.0	22.7
PRR368	90.7	89.1	67.7	90.0	84.4	19.7	14.7	10.7	16.2	15.3	27.9	24.9	15.1	25.0	23.2
PRR372	96.4	96.3	97.0	96.8	96.6	16.8	16.3	15.7	17.0	16.4	27.5	25.5	25.2	25.5	25.9
PRR376	90.2	91.7	94.6	93.3	92.5	16.9	14.9	16.2	16.5	16.1	25.8	24.5	24.3	24.5	24.8
PRR381	92.8	98.4	100.9	96.0	97.0	20.3	14.6	14.6	15.1	16.1	27.5	26.4	27.1	25.7	26.7
PRR386	86.7	86.8	64.0	94.5	83.0	21.3	14.7	12.6	15.7	16.1	25.1	25.4	16.5	25.9	23.2
PRR390	100.1	100.1	101.2	101.3	100.7	19.1	15.1	16.9	18.9	17.5	26.4	25.4	26.5	26.5	26.2
PRR395	65.1	85.7	91.5	89.4	82.9	13.9	13.6	18.5	19.5	16.4	18.9	25.3	25.4	25.1	23.7
PRR396	98.0	92.4	96.2	97.5	96.0	18.8	14.6	17.1	20.5	17.8	26.1	23.9	25.4	26.6	25.5
Mean	89.2	88.9	88.1	90.8	89.3	17.9	16.4	15.4	16.5	16.5	25.2	23.9	22.9	24.9	24.2

Parent	Filled grains per panicle					Spikelet fertility (%)					1000 grain weight (g)				
	IR 79156A	IR 58025A	Pusa 6A	RTN 12A	F_1 mean	IR 79156A	IR 58025A	Pusa 6A	RTN 12A	F_1 mean	IR 79156A	IR 58025A	Pusa 6A	RTN 12A	F_1 mean
PRR300	161.2	130.6	137.5	147.6	144.2	78.3	76.6	75.2	76.3	76.6	18.1	16.2	17.6	14.4	16.6
PRR307	138.1	85.2	143.3	153.8	130.1	63.3	54.9	70.6	68.6	64.3	21.9	13.1	19.5	16.1	17.6
PRR311	110.8	60.4	87.9	163.5	105.7	70.6	38.0	56.8	76.1	60.4	20.1	11.5	20.1	18.7	17.6
PRR314	118.1	132.2	139.7	158.7	137.2	71.4	74.8	68.7	80.2	73.8	17.6	17.9	17.3	19.0	18.0
PRR317	96.2	118.9	96.5	98.7	102.6	69.8	72.5	45.4	41.5	57.3	23.2	20.9	13.6	13.9	17.9
PRR323	110.6	114.3	91.9	100.2	104.3	71.3	75.4	57.9	53.9	64.6	24.7	24.9	22.8	22.6	23.8
PRR326	112.7	117.8	109.2	137.9	119.4	80.8	73.2	55.8	71.3	70.3	19.4	18.1	12.6	22.9	18.2
PRR329	106.0	100.3	90.2	104.2	100.2	66.5	53.7	65.2	66.8	63.0	23.8	11.6	19.1	21.3	19.0
PRR334	76.4	54.5	73.9	134.6	84.9	44.9	30.8	43.8	69.5	47.2	20.2	16.1	20.3	19.0	18.9
PRR337	130.6	95.6	138.7	97.2	115.5	73.2	45.9	66.7	42.5	57.1	21.2	13.3	21.8	18.3	18.6
PRR342	170.4	148.9	99.7	139.7	139.7	83.0	74.4	54.7	72.3	71.1	18.7	18.9	10.8	18.8	16.8
PRR347	116.7	132.1	117.4	135.1	125.3	62.2	69.2	59.6	67.6	64.7	21.8	18.3	16.8	19.2	19.0
PRR348	114.1	123.9	157.9	125.9	130.4	76.8	68.3	71.1	73.0	72.3	21.6	21.3	22.5	21.3	21.7
PRR354	79.3	128.5	134.4	140.6	120.7	53.5	68.6	65.2	62.3	62.4	12.1	20.4	21.9	20.7	18.8
PRR358	90.2	115.9	112.8	136.1	113.7	51.1	65.4	68.2	72.2	64.2	13.6	21.5	22.9	22.4	20.1
PRR363	134.1	130.1	94.5	149.1	126.9	71.5	67.3	49.0	75.7	65.9	16.0	18.1	12.6	19.6	16.6
PRR367	74.6	136.7	145.4	157.5	128.5	53.6	81.8	74.7	73.8	71.0	10.5	16.5	18.5	17.1	15.6
PRR368	134.4	108.0	83.2	139.6	116.3	79.8	63.9	49.2	72.3	66.3	20.1	18.9	14.2	17.4	17.6
PRR372	125.6	118.5	109.7	108.6	115.6	76.3	62.6	67.3	57.0	65.8	22.0	21.5	21.3	20.7	21.4
PRR376	128.8	126.3	137.2	142.0	133.6	62.3	61.2	62.0	66.6	63.0	18.6	18.3	17.2	18.7	18.2
PRR381	145.5	161.5	176.6	170.2	163.4	80.8	70.9	76.5	72.9	75.3	22.6	17.8	18.9	20.8	20.0
PRR386	106.0	109.5	94.3	134.0	111.0	74.9	63.2	51.8	72.4	65.6	14.8	18.4	9.7	20.3	15.8
PRR390	107.9	115.5	122.4	140.2	121.5	75.0	74.5	74.6	74.3	74.6	22.3	22.2	20.6	22.5	21.9
PRR395	85.4	136.3	120.3	100.1	110.5	55.9	80.7	73.1	68.3	69.5	12.9	20.5	19.8	24.0	19.3
PRR396	153.6	169.3	167.0	159.4	162.3	76.1	80.3	76.5	75.8	77.2	17.3	16.1	18.1	17.9	17.3
Mean	117.1	118.8	119.3	135.0	122.5	68.9	65.9	63.2	68.1	66.5	19.0	18.1	18.0	19.5	18.7

Parent	Pollen fertility (%)					Days to 50% flowering					Yield per plant(g)				
	IR 79156A	IR 58025A	Pusa 6A	RTN 12A	F_1 mean	IR 79156A	IR 58025A	Pusa 6A	RTN 12A	F_1 mean	IR 79156A	IR 58025A	Pusa 6A	RTN 12A	F_1 mean
PRR300	87.2	79.6	86.8	45.8	74.9	86.3	88.8	88.1	87.4	87.7	33.56	30.55	25.14	30.5	29.94
PRR307	59.7	59.0	84.3	65.6	67.2	94.3	73.5	99.4	80.4	86.9	32.00	22.95	26.5	30.5	27.98
PRR311	45.3	52.1	59.3	67.4	56.0	97.6	74.0	98.6	101.6	93.0	27.93	15.05	16.99	33.78	23.44
PRR314	86.0	90.7	87.4	79.2	85.8	86.3	89.1	88.6	98.4	90.6	26.89	23.82	24.43	32.02	26.79
PRR317	84.6	89.3	64.8	53.7	73.1	97.6	99.6	72.4	71.2	85.2	31.82	37.81	20.36	24.22	28.55
PRR323	77.7	83.5	84.6	84.2	82.5	90.8	96.8	95.4	99.1	95.5	30.71	37.55	29.93	29.84	32.01
PRR326	76.5	64.3	63.0	86.1	72.5	83.8	85.8	64.7	87.9	80.6	29.54	30.86	23.96	28.97	28.33
PRR329	86.4	64.1	87.3	58.0	73.9	96.6	75.3	100.4	105.1	94.3	31.32	20.82	28.68	28.41	27.31
PRR334	63.1	22.3	70.6	86.4	60.6	95.6	99.3	99.1	99.4	98.4	27.88	17.10	18.28	29.58	23.21
PRR337	63.2	38.5	82.8	50.9	58.9	93.6	72.0	98.9	98.6	90.8	30.44	17.53	28.57	19.37	23.98
PRR342	86.4	87.0	58.5	89.1	80.3	87.6	88.3	62.5	90.9	82.3	29.52	36.10	21.02	30.82	29.36
PRR347	79.2	61.1	74.7	79.3	73.6	84.6	86.3	86.9	91.1	87.2	24.93	27.00	26.83	26.73	26.37
PRR348	67.2	68.0	79.4	74.6	72.3	96.3	97.6	99.1	98.9	98.0	33.14	30.91	35.99	31.24	32.82
PRR354	61.5	87.5	85.9	79.8	78.7	71.0	100.6	96.9	99.1	91.9	17.96	30.23	29.96	32.88	27.76
PRR358	61.7	91.2	67.1	90.9	77.7	59.5	89.9	71.9	95.9	79.3	17.52	27.82	30.81	29.04	26.30
PRR363	78.8	81.2	63.5	88.7	78.0	94.6	94.9	66.2	97.1	88.2	30.88	25.91	19.59	30.15	26.63
PRR367	60.6	86.7	85.9	87.3	80.1	66.0	88.1	94.6	95.1	86.0	16.57	25.68	32.51	24.29	24.76
PRR368	69.0	67.6	59.8	83.9	70.1	84.3	91.6	67.0	98.4	85.3	33.50	23.73	24.43	32.00	28.42
PRR372	83.5	77.1	79.4	71.6	77.9	96.6	100.6	99.1	102.4	99.7	33.39	27.95	27.01	30.35	29.67
PRR376	64.3	82.8	84.1	69.2	75.1	91.0	100.6	99.6	97.2	97.1	33.81	24.07	26.75	31.29	28.98
PRR381	80.8	85.9	87.6	87.5	85.5	85.1	85.4	89.6	94.9	88.7	40.06	29.49	31.81	33.33	33.67
PRR386	74.3	57.3	49.8	80.8	65.6	89.8	90.9	65.7	96.9	85.8	32.12	25.12	19.70	31.45	27.10
PRR390	82.7	87.8	85.3	88.0	85.9	89.8	93.1	88.1	93.4	91.1	37.75	30.83	31.69	36.7	34.24
PRR395	59.2	65.2	88.2	40.7	63.3	67.5	68.6	92.6	89.9	79.7	23.25	31.33	28.49	33.97	29.26
PRR396	83.1	83.2	70.5	86.6	80.9	86.3	84.6	88.4	89.6	87.2	38.89	27.63	31.19	34.03	32.93
Mean	72.9	72.5	75.6	75.0	74.0	86.9	88.6	86.9	94.4	89.2	29.81	27.11	26.42	30.22	28.39

Supplementary Table S2. Combining Ability (CA) effects of parents for yield per plant

Parent	GCA and SCA effects for plant yield (Delhi-Early)						GCA and SCA effects for plant yield (Delhi-late)						
	IR 79156A	IR 58025A	Pusa 6A	RTN 12A	GCA_{Line}	σ^2_{GCA}	σ^2_{SCA}	IR 79156A	IR 58025A	Pusa 6A	RTN 12A	GCA_{Line}	σ^2_{GCA}	σ^2_{SCA}
PRR300	7.95	-9.12	-3.71	-2.26	10.52	110.67	165.25	-2.36	3.55	1.73	-6.59	1.61	2.59	64.59
PRR307	-4.07	-2.65	0.26	-0.67	-1.13	1.28	24.10	-1.60	13.49	-5.41	-10.14	4.56	20.79	316.63
PRR311	-5.85	-8.19	-4.78	11.68	-2.05	4.20	260.57	0.29	-1.29	-7.91	5.25	-1.29	1.66	91.88
PRR314	3.52	-8.28	-0.54	-1.85	-1.95	3.80	84.66	-4.61	3.05	-1.90	-0.20	-2.00	4.00	34.20
PRR317	1.09	-6.90	0.01		5.93	35.16	48.80	-4.88	9.34	-5.70	-2.43	8.65	74.82	149.44
PRR323	-10.65	6.07	-7.97	5.41	2.89	8.35	243.06	1.38	3.87	-2.01	-6.90	4.33	18.75	68.53
PRR326	3.91	-5.04		-3.66	2.12	4.49	54.09	-2.33	7.34	-1.37	-7.30	3.87	14.98	114.47
PRR329	-5.17	-18.70	-1.49	-18.54	9.21	84.82	722.37	0.04		-2.48	1.88	-2.83	8.01	9.69
PRR334	3.71	-6.94	-11.08	7.17	-5.09	25.91	236.10	-2.84	-4.70	-0.06	3.93	-5.92	35.05	45.60
PRR337	-2.09	-7.51	3.30	-0.83	-3.81	14.52	72.35	-3.86	16.50	-5.75	-10.55	3.29	10.82	431.51
PRR342	-12.77	1.79		6.20	-2.47	6.10	204.72	2.46	14.75	-8.94	-11.94	8.82	77.79	446.10
PRR347	-0.87	-1.72	1.02	-5.58	1.05	1.10	35.89	-6.03	-0.46	7.02	-4.20	1.12	1.25	103.49
PRR348	-5.57	-7.77	-1.02	7.23	-2.97	8.82	144.71	-4.05	1.53	5.51	-6.66	3.53	12.46	93.46
PRR354	-26.19	-8.59	-14.55	1.91	12.73	162.05	975.05		2.12	0.35	-0.29	-2.65	7.02	4.70
PRR358	0.43	0.21	4.38	-12.15	3.85	14.82	167.04	-0.47	-11.95	5.91	2.85	0.31	0.10	186.07
PRR363	-3.08	-3.46		1.76	-3.46	11.97	24.56	1.98	-2.35	-0.05	-3.24	-1.91	3.65	19.94
PRR367	-16.47	-4.29	-4.30	-17.06	7.42	55.06	599.20		-7.00	8.82	0.36	-7.96	63.36	126.92
PRR368	4.25	-3.35		-5.68	-0.57	0.32	61.55	-1.78	-6.84	4.95	0.01	-0.21	0.04	74.46
PRR372	-1.81	2.80	-1.47	-6.66	1.69	2.86	57.63	0.63	-4.89	-3.03	3.63	-5.93	35.16	46.67
PRR376	-2.35	1.65	-2.47	-3.98	-0.97	0.94	30.19	-3.17	-14.70	1.86	12.35	0.00	0.00	382.12
PRR381	-0.03	8.00	-3.49	-11.62	6.76	45.70	211.21	9.16	-12.72	-0.83	0.73	2.43	5.90	246.93
PRR386	-1.37	10.73		-14.14	2.78	7.73	316.95	-1.70	-10.35	-1.25	9.63	-0.87	0.76	204.31
PRR390	1.49	-0.83	-7.15	-0.64	8.31	69.06	54.44	1.33	-2.66	-5.54	3.21	0.56	0.31	49.84
PRR395	-6.84	-1.27	-0.38	1.36	7.83	61.31	50.39	-1.23	-2.53	-4.43	4.53	0.77	0.59	48.06
PRR396	8.42	2.90	-16.57	-1.90	11.81	139.48	357.48	-2.78	-11.78	4.66	6.24	3.54	12.53	207.15
GCA_{Tester}	4.42	-0.98	2.35	1.34				5.85	3.11	-5.71	0.41			
σ^2_{GCA}	19.54	0.96	5.52	1.80				34.22	9.67	32.60	0.17			
σ^2_{SCA}	1611.48	1172.31	834.10	1584.45				257.96	1785.87	559.90	963.06			

Test of significance of GCA effects: (Line 3.1297 at 5% and 4.1203 at 1%, tester 1.2519 at 5% and 1.6481 at 1% level of importance), Test of significance of SCA effects: (6.2594 at 5% and 8.2407 at 1% level of significance)

Combining Ability (CA) effects of parents for yield per plant

Parent	GCA & SCA Effects for plant yield (Bihar)						GCA & SCA Effects for plant yield (Karnal)							
	IR 79156A	IR 58025A	Pusa 6A	RTN 12A	GCA_{Line}	σ^2_{GCA}	σ^2_{SCA}	IR 58025A	IR 6A	Pusa 12A	RTN	GCA_{Line}	σ^2_{GCA}	σ^2_{SCA}
PRR300	-5.87	3.76	-11.96	9.47	-4.78	22.85	281.32	4.10	5.33	-6.10	-6.11	-2.24	5.02	119.76
PRR307	-8.12	0.31	-4.11	7.32	-4.43	19.62	136.51	12.09		-4.62	-1.28	5.38	28.94	169.15
PRR311	3.35	-0.12	-16.24	8.40	-8.51	72.42	345.53	4.86		-2.36	3.70	-4.43	19.62	42.88
PRR314	-5.60	2.83	-3.29	1.45	-2.46	6.05	52.30	-3.58	-8.41	-4.57	13.76	-1.08	1.17	293.77
PRR317	-2.01	22.42		10.43	-6.24	38.94	615.48	-4.68	0.38	3.62	-2.10	4.09	16.73	39.56
PRR323	-2.20	9.73	2.71	-14.85	3.24	10.50	327.38	-4.38	3.57	-1.90	-0.07	2.91	8.47	35.54
PRR326	-11.22	1.81	6.39	-1.58	3.07	9.42	172.49	-5.88	-2.61	8.01	-2.31	-0.70	0.49	110.88
PRR329	-8.62	8.21	-5.01	0.82	3.97	15.76	167.48	1.98	3.37	-3.51	-4.63	1.37	1.88	49.03
PRR334	6.78	-12.69	-5.31	6.62	-7.93	62.88	279.03	0.36	0.95	-4.12	0.01	-2.88	8.29	18.01
PRR337	12.11		6.85	-26.75	-3.46	11.97	909.14	-2.00	-3.81	2.10	0.93	-3.74	13.99	23.79
PRR342	-4.02	1.21	4.49	-6.28	6.97	48.58	77.22	-4.26	1.76	-1.86	1.58	-1.99	3.96	27.20
PRR347	-4.40	5.73	-6.79	0.85	-5.16	26.63	99.02	-5.16	0.02	-0.26	2.62	-6.18	38.19	33.56
PRR348	-8.70	4.93	4.81	-5.65	8.34	69.56	155.05	8.91	-5.25	2.53	-8.99	7.72	59.60	194.17
PRR354	-3.95	-6.12	8.46	-3.00	4.09	16.73	133.63	0.01	5.50	-4.37	-3.93	0.27	0.07	64.79
PRR358		-1.76	-3.63	0.24	1.05	1.10	16.33	-9.87	8.53	-1.61	0.17	-2.53	6.40	172.80
PRR363	-3.45	-5.84	1.03	3.66	3.43	11.76	60.46	2.61	1.55	-2.84	-4.12	2.09	4.37	34.25
PRR367	2.50	-2.36	8.01	-12.75	-1.96	3.84	238.54	-12.41	3.00	2.20	4.43	2.31	5.34	187.47
PRR368	1.05	-6.71	-1.44	2.50	1.89	3.57	54.45	-2.86	-9.75	9.03	0.79	6.90	47.61	185.41
PRR372	7.58	-4.38	-7.11	-0.68	4.17	17.39	127.66	-2.20	0.64	0.10	-1.32	4.11	16.89	7.00
PRR376	12.33	-5.43	-6.96	-4.53	2.62	6.86	250.48	1.84	-0.07	-2.21	-2.34	-0.38	0.14	13.75
PRR381	4.10	-11.59	-1.02	3.91	6.78	45.97	167.47	1.63	0.68	-2.96	-2.13	4.07	16.56	16.42
PRR386	4.45	-13.81	2.96	1.80	0.89	0.79	222.52	-1.80	-3.22	-0.31	2.55	0.77	0.59	20.21
PRR390	-8.45	-5.41	2.56	6.70	7.99	63.84	152.11	8.98	-3.66	-0.94	-7.16	5.45	29.70	146.19
PRR395	-1.87	4.37	-6.06	-1.03	1.92	3.69	60.38		3.87	1.99	1.32	-3.18	10.11	20.68
PRR396	6.63	-11.23	5.74	-5.73	3.22	10.37	235.85	0.88	-0.02	-1.67	-1.99	-1.48	2.19	7.52
GCA_{Tester}	-0.56	-3.19	3.14	5.21				0.96	-0.02	1.07	0.78			
σ^2_{GCA}	0.31	10.18	9.86	27.14				0.92	0.00	1.14	0.61			
σ^2_{SCA}	1055.69	1583.35	1009.35	1689.43				769.24	425.37	347.04	492.15			

Test of significance of GCA effects: (Line 3.1297 at 5% and 4.1203 at 1%, tester 1.2519 at 5% and 1.6481 at 1% level of significance), Test of significance of SCA effects: (6.2594 at 5% and 8.2407 at 1% level of significance)