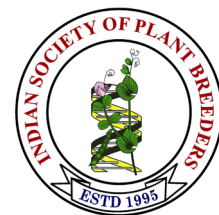


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Research Article

Estimation of genetic components and assessing heterosis association with molecular markers in half diallel derived rice hybrids developed with landraces of NE India

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Abstract

Combining ability and heterosis were estimated in 45 rice hybrids generated by mating 10 parents, comprising both land races and advance breeding lines, in half diallel fashion. Hayman's graphical analysis showed that all the twelve morphological traits studied had significant positive dominance variance. Narrow sense heritability was high for Days to fifty percentage flowering, Plant height, Panicle length and Test weight (> 30 %), and low for Grain yield per plant. According to the VrWr graph, traits like GYPP, PL, PH, TN and plot yield showed partial dominance, whereas traits like Blast disease index showed overdominance. A significant improvement over check was observed for heterosis and the crosses Mynri x CAUS103, Joha x CAUS107, CAUS 126 x CAUS107 and CAUS103 x CP, exhibited significantly positive standard heterosis for GYPP (>80 %) and PY (>100 %). Genetic distance based on fourteen markers revealed significant positive association with mid parent and better parent heterosis for Spikelet's per plant, Filled grains per plant, Harvest index, Grain yield per plant, Panicle number and Plot yield. Therefore, it is evident that crosses with larger genetic distance between the parents gave hybrids with higher heterosis.

Keywords: Landraces, Hayman's graphical analysis, Heterosis, Genetic distance

INTRODUCTION

Rice is the staple food crop of majority of the world's population and is grown in 154 million hectares and yields 470 million tonnes of milled rice. More than 90% of rice is produced and consumed in Asia (Sarwar *et al.*, 2022). Global rice demand is expected to rise from 490 million tonnes in 2020 to 555 million tonnes in 2035 (Seck *et al.*, 2012). Among the cereals, rice is a rich source of carbohydrates and continues to gain popularity in African and American continents where coarse cereals were grown traditionally. Since 1965, All India Crop Improvement Project (AICRIP) had released

1436 varieties including 127 rice hybrids (Roy *et al.*, 2023). But still the average national productivity of rice lies around 2.8 tonnes/hectare which is lower than other rice growing countries. Recently, India curbed the export on non-basmati rice to reduce its price and to meet the local demands. Also, the human population is galloping and rice production has been in plateau for many years. Hence, developing a suitable high yielding variety is a pre requisite. The use of hybrid rice in China and other countries had shown great potential by increasing the rice yield in the last three decades. They exploited the

heterosis of specific hybrid combinations and utilized male sterility to produce hybrid seeds for cultivation in large scale. This technology is also employed in India by many private companies and the results were promising. During 2019-20, rice was grown in 3.2 million hectares in North East India producing 7.12 million tonnes, but the rice requirement was 7.5 million tonnes during 2022 and is expected to reach 8.3 million tonnes by 2035 (10.5% increase) (Laitonjam *et al.*, 2022). The landraces in the North East region, for example Jwain and Mynri in Meghalaya are preferred for their grain quality characteristics. There is a scope to improve these landraces in terms of yield, plant architecture, nutrient use efficiency and blast resistance, while maintaining their preferred grain quality. In rice it has been observed that heterozygosity at a locus increases the heterotic effects due to the additive/ partial dominance/ overdominance nature of each allele that all together function by allelic dosage effects. A better understanding of heterosis will change the crop breeding approaches and help in meeting malnutrition and food insecurity (Huang *et al.*, 2016). Among the different approaches to assess combining ability and heterosis, diallel analysis is widely used (Ariharasutharsan *et al.*, 2022). Many researchers have used the molecular genetic distance obtained from cluster analysis of parents and associated it with heterosis values of offspring's to identify the diverse genomic regions that could potentially causes heterosis (Huang *et al.*, 2016, Rahman *et al.*, 2022, Salem *et al.*, 2022). For studying the genetic diversity and relationship among organisms, SSR (Simple Sequence Repeat) markers are effective tools due to their transferability and high polymorphism. SSR markers play an important role in identifying the genetic variation in germplasm, the genetic relationship among species, heterosis and for diversity analysis (Jin *et al.*, 2010). Using suitable markers will help us identify the ideal haplotype required to combat the biotic and abiotic stresses specific for each region.

Therefore, the study was carried out using the half diallel derived 45 rice F_1 s to estimate mid parent, better parent and standard heterosis. Seven SSR markers and seven gene specific markers including four yield related markers were used to study the diversity among the parents to associate it with heterosis values of the offsprings and to assess the correlation between heterosis and genetic distance.

MATERIALS AND METHODS

Development of F_1 hybrids : The experiments were carried out in College of Post Graduate Studies in Agricultural Sciences, Central Agricultural University, (CAU, Imphal), Meghalaya. Ten parents were selected based on various characteristics for initiating the hybridization programme (Table 1). Crosses were performed as per half diallel analysis in all possible combinations excluding the reciprocal crosses to derive 45 F_1 hybrids. The F_1 seeds were grown in nursery and 21 old seedlings were transplanted into main field during *khari*f, 2020. Ten F_1

seedlings of each cross were planted in a single row of length 1.5 m, with a spacing of 20 x 15 in a randomized block design with three replications along with CAUR1 as standard check. Observations were recorded on randomly selected five plants per genotype per replication, excluding the border plants. The agro-morphological traits like Days to fifty percentage flowering (DTFF), Plant height (PH), Panicle number (PN), Panicle length (PL), Spikelet's per plant (SP), Filled grains per plant (FGP), Spikelet fertility (SF), Test weight (TW, 1000 seed weight), Grain yield per plant (GYPP) and Harvest Index (HI), were recorded as per the standard evaluation system of IRRI, (2014). Plot yield (PY) was the sum total yield of eight plants measured in grams. Blast affected spikelet per plant (DSPP) was measured by counting whitish grey to black colour unfilled and partially filled spikelet as they were considered to be affected by rice blast disease. From this Blast disease index is calculated in percentage as, $(BDI) = (DSPP/SP) \times 100$

DNA extraction and polymerase chain reaction (PCR): DNA extraction was done using Cetyl Trimethyl Ammonium Bromide (CTAB) method (Doyle and Doyle, 1987) and the final DNA concentration was 200ng/ μ l in 1X TE buffer and was stored at -20°C. PCR tube of 100 μ l capacity was filled with 1 μ l DNA sample, 1 μ l PCR buffer, 0.7 μ l of 25mM $MgCl_2$, 1.2 μ l of 10mM primers (forward + reverse), 0.5 μ l of 5U Taq polymerase and 5.45 μ l of nuclease free water. The PCR was carried out in a Bio-rad thermocycler with the following steps. I) initial denaturation at 95 °C for 5 minutes, II) denaturation at 95 °C for 30 seconds, III) annealing at different T_m (depending on the marker) for 30 seconds, IV) extension at 72 °C for 45minutes V) steps II to IV are repeated for 34 times, VI) final elongation at 72 °C for 5 minutes, VII) hold at 4 °C for 10 minutes. The samples after PCR cycles were run in 2.5% agarose gel with a reference of 100bp ladder in electrophoresis setup. After completion of the run, the gel was viewed in gel documentation unit and saved for scoring polymorphism. Scoring was done based on the size of the allele amplified. The 15 markers used in this study were given can be seen in Fig.1

Hayman's diallel analysis and heterosis analysis: The Hayman's (1954) graphical approach of diallel analysis was carried out to get information of genetic components from the VrWr graph. The analysis was performed in AGD-R v.5.1 software. Variances and covariances of parents and offspring's were calculated and its significance was tested. First variance components like additive genetic variance (D), dominance variance (H_1), proportion of + and - genes in parents (H_2), environmental variance (E), mean of covariance of additive and dominance effects over array (F), dominance effect (h^2) were calculated. From the variance components, other ratios like mean degree of dominance $[(H_1/D)]^{1/2}$; proportion of genes with positive and negative effects in the parents ($H_2/4H_1$); proportion of dominant and recessive genes in the parents $(\frac{K_2}{K_1})$ coefficient of correlation (r) between the parental

Table 1. Characteristics of the ten parents used in the crossing programme

S.No. Parents	Parentage	Collected location	Special characteristics	Undesirable traits	
1	Jwain	Landrace	Meghalaya	Lengthy panicles	Tall stature
2	Mynri	Landrace	Meghalaya	Bold grains	Blast Susceptible
3	Kala Joha	Landrace	Assam	Aromatic, small, and black grain	Blast Susceptible
4	Blm	Landrace	Orissa	Early flowering and has <i>Pi9</i> gene	Tall, bold grains
5	CAUS123	Kasalath x Shahsarang	CPGS	Early flowering	-
6	CAUS126	Kasalath x Boro paddy	CPGS	Wide adaptable	-
7	CAUS103	Shahsarang x Mynri	CPGS	Better grain quality	-
8	CAUS107	Shahsarang x CAUR1	CPGS	High yielding	-
9	Kasalath	Landrace	West Bengal	Slender grain with <i>PSTOL1</i> gene	Poor yielding
10	Chakhao poireiton (CP)	Landrace	Manipur	Purple aromatic rice	Blast Susceptible

CPGS- College of post graduate studies in agricultural sciences, Meghalaya

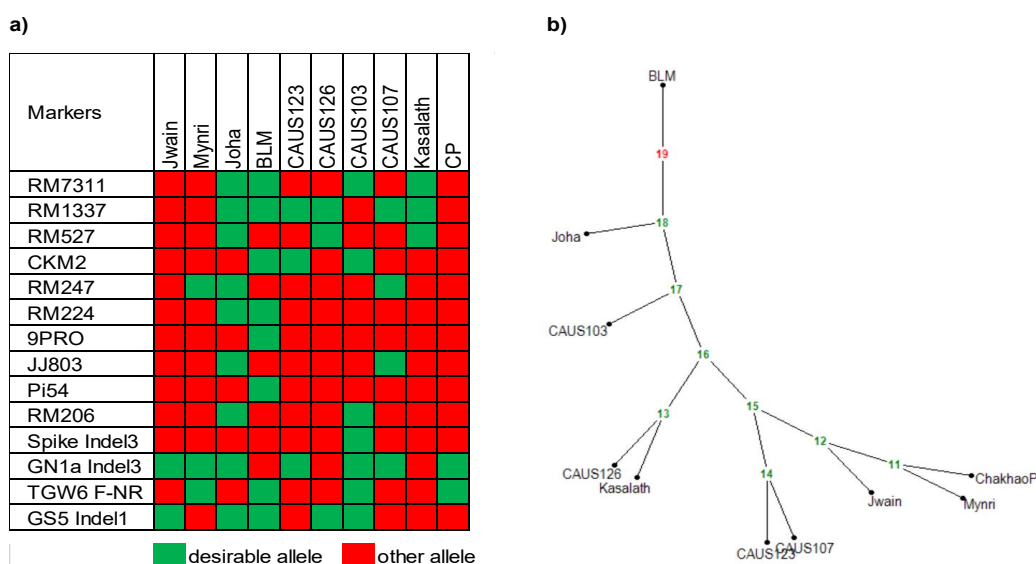


Fig. 1 Heat map showing allelic status (a) and cluster diagram (b) based on molecular markers for the studied ten parents

order of dominance ($Wr+Vr$) and parental measurement $Yr(r)$; prediction for measurement of completely dominant and recessive parents (r^2); the number of groups of genes for which the trait that exhibit dominance) (h^2/H_2); heritability in broad sense (h^2_{bs}); heritability in narrow-sense (h^2_{ns}) were calculated as per Singh and Chaudhary, 1979. The mid parent, better parent and standard heterosis were estimated as per Mather and Jinks (1982) and their significance was checked based on least significant values (LSD) as per Salem *et al.* (2022).

Cluster analysis and association study: The molecular marker-based polymorphism observed for the parental lines were scored and the corresponding genetic distance was obtained. Genetic distance (GD) was calculated using the dissimilarity index as,

$$d_{ij} = 1 - \frac{1}{L} \sum_{i=1}^L \frac{m_i}{\pi}$$

where, ' d_{ij} ' is the dissimilarity between units i and j ; ' L ' is the number of loci; ' π ' is ploidy; ' m_i ' is the number of matching alleles for locus i . Cluster tree was constructed using hierarchical clustering by UPGMA (unweighted pair group method with arithmetic mean) method. All the above analyses were performed in Darwin v.6.0.21 software (Perrier *et al.*, 2003). Pearson correlation (r) was calculated between the genetic distance and all the three heterosis values, and significance was checked at 0.05 % levels (Singh and Chaudhary, 1979)

RESULTS AND DISCUSSION

Among many mating designs, half-diallel analysis is preferred by breeders, because it includes crosses in all possible combinations excluding reciprocal crosses.

Hayman's graphical approach (Hayman, 1954) is generally used to investigate various genetic components, heritability and to draw VrWr graph to know the gene action.

Hayman's graphical approach for estimating genetic components: The analysis of variance revealed significant difference between genotypes ($p < 0.01$) for all the traits studied (Table 2). Different genetic components and ratios obtained from Hayman's diallel analysis (Table 3) indicated that all the observed traits had significant ($p < 0.05$) and positive dominance variance (H_1) whereas traits like DTFF, PH, PL, SF, TW, HI, BDI had significant ($p < 0.05$) and positive additive variance (D). Environmental variance (E) was low and non-significant for PH and TW. The presence of significant D and low E for PH and TW shows that these traits can be directly selected in early generations. All the other traits registered higher dominance variance which was similar to the findings of El-malky and Al-daej, 2018. Proportion of positive and negative genes (H_2) and dominance effects (h^2), which is the sum of all the heterozygous loci among the parents were significant for all the traits. All the traits had dominance gene action at certain levels which could be exploited through heterosis breeding. Mean of covariance of additive and dominance effects (Fr) over the arrays (F) was significant for PL, TW and BDI. The F value was positive for all the traits denoting the presence of dominant alleles in parents. Similar results were obtained by Chamundeswari *et al.* (2016) and Gunasekaran *et al.* (2020). The average degree of dominance (H_1/D)^{1/2} values revealed, partial dominance for DTFF, PH, PL and TW (Table 3), while all the other traits showed over dominance. Knowing the degree of dominance will help us predict the segregation pattern in the subsequent generations which will help us in selection. Positive and negative alleles ($H_2/4H_1$) were symmetrically distributed in parents for traits like PN and SP (close to 0.25). The ratio of dominant and recessive genes in the parents (Kd/Kr) showed that, dominant and recessive genes are equal in parents for the traits DTFF and PH, similar results were seen in the study of Bassuony and Zsembeli, 2021, while for all the other traits more dominant genes were present in any one of their parents (>1). The correlation coefficient (r) was negative for all the traits except BDI and it showed parents contained mostly dominant genes. The prediction

for measurement of complete dominant parent (r^2) were high for the traits viz., PH, PL, GYPP and BDI (>0.5). High prediction values shows that the dominant parents were highly efficient in inheriting these traits. Number of gene groups (h^2/H_2) which control the character and exhibit dominance were two for DTFF, TW and four for BDI, PH and PY respectively. Less than one gene group was observed for SP, whereas HI showed one gene group and more than six gene groups were observed for all the other traits. Knowing the number of gene groups will also aid in understanding the trait and thereby selecting suitable genotypes as parents. Heritability in broad sense (h^2_{bs}) was high for DTFF, PH, TW and HI (>0.6) whereas heritability in narrow sense (h^2_{ns}) was high for DTFF, PH, PL and TW (>0.3). Low h^2_{ns} for GYPP shows it was governed by non-additive gene action. Similar low narrow sense heritability was obtained for all the above traits by Gunasekaran *et al.* (2020). The trait BDI showed moderate h^2_{bs} and h^2_{ns} whereas, GYPP showed moderate h^2_{bs} and low h^2_{ns} .

Graphical estimations and prediction from VrWr graph: Occurrence of parents on the regression line towards the origin indicates, high number of dominant genes in them and if they were placed away from origin, it denotes the presence of higher recessive genes (Hayman, 1954). Almost all landraces had dominant genes for all the traits (Fig. 2). CAUS103 and Kasalath had recessive genes for most traits and other advanced breeding lines had equal distributions. Based on the information of dominant and recessive genes in parents for various traits, it is assumed that hybrids developed by crossing Jwain or CP with CAUS123 will have plants with dominant genes for all the traits recorded. The significant deviation of regression coefficient (b) from zero ($H_0: b=0$) or non-significant deviation from unity ($H_0: b=1$) and non-significant t^2 values were crucial to fulfil all the Hayman's assumptions (Jaiswal, 2019). The uniformity of Vr and Wr indicated that all the assumptions of Hayman's analysis were fulfilled. Significant deviation of 'b' from zero and non-significant deviation of 'b' from unity was observed for BDI (Table 3). In the VrWr graphs, the regression line was observed to pass slightly below the origin for the trait BDI indicating over dominance. For the traits GYPP, PY, PL, PH and TN the regression line passes above the origin and cuts the parabola indicating partial dominance.

Table 2. Analysis of variance for 12 traits of rice assessed by Hayman's diallel approach

Source of variation	Degree of freedom	Mean sum of square											
		DTFF	PN	PH	PL	SP	FG	BDI	GYPP	HI	SF	TW	PY
Replication	2	1.8	1	9.6	1.5	22768.6	5598	1.5	10.3	24.3	1.9	0.2	68.8
Genotypes	54	92 **	6.1 **	665.7 **	9.5 **	109587.2 **	57662.4 **	3.7 **	42.1 **	698 **	146.7 **	23.3 **	7345.5 **
Error	108	35	5.2	361.8	4	92846.9	41469.8	0.5	34.4	312	155.6	15.2	2995.2

Days to fifty percentage flowering (DTFF), Plant height (PH), Panicle number (PN), Panicle length (PL), Spikelet's per plant (SP), Filled grains per plant (FGP), Spikelet fertility (SF), Test weight (TW, 1000 seed weight), Grain yield per plant (GYPP), Harvest Index (HI), Plot yield (PY), blast disease index (BDI); * Significance at 5% level; ** significance at 1% level

Table 3. Genetic components of variation obtained from Hayman’s diallel method

	DTFF	PH	PN	PL	SP	FG	SF	TW	GYPP	HI	PY	BDI
t ²	19.8*	0.03	17.5*	0.03	25*	17*	4.4	0.04	21*	1.7	6.8*	1.98
H ₀ :b=0	12.4*	5.8*	0.7	5.7*	0.3	1.2	1.2	1.3	1.8	4.2*	1	11*
H ₀ :b=1	5.5*	0.5	8.6*	0.8	10.4*	8.1*	4.6*	2	8.5*	2.3	5.6*	1.85
E	2.5*	18	2.5*	1.7*	44421.7*	16618.4*	61.9*	0.3	14.1*	22.8	1291.4*	0.2*
D	78.7*	588.5*	0.6	6.1*	11336.5	4383.2	34.9*	32.2*	3.1	298*	285.2	3.3*
F	4	4.2	1.5	0.6*	26156.8	10113.3	52.4	10.9*	7.1	54.5	658.1	4.6*
H ₁	33.4**	479**	4.4**	1.7**	81887.4**	60438.6**	226.4**	20.4**	47.5**	406.8**	6200.5**	4.1**
H ₂	22.1**	424**	4.3**	2.1**	79140.1**	50754.7**	210.1**	15.3**	43.8**	280.3**	4885**	2.4**
h ²	46*	1745.1*	27.5*	22*	607023*	325878.4*	69.9*	33.8*	301.9*	275*	20262.6*	9.4*
(H ₁ /D) ^{1/2}	0.65	0.9	2.62	0.54	2.69	3.71	2.55	0.8	3.93	1.17	4.66	1.12
(H ₂ /4H ₁)	0.17	0.22	0.24	0.3	0.24	0.21	0.23	0.19	0.23	0.17	0.2	0.14
Kd/Kr	1.08	1.01	2.57	1.21	2.5	1.9	1.84	1.54	1.83	1.17	1.66	4.39
r	-0.25	-0.83	-0.31	-0.74	-0.43	-0.19	-0.34	-0.63	-0.82	-0.29	-0.13	0.93
r ²	0.06	0.69	0.09	0.54	0.18	0.03	0.12	0.4	0.66	0.08	0.02	0.86
h ² _{H2}	2.08	4.12	6.44	10.37	7.67	6.42	0.33	2.21	6.9	0.98	4.15	4
h ² _{bs}	0.95	0.96	0.22	0.64	0.24	0.47	0.46	0.98	0.43	0.92	0.57	0.58
h ² _{ns}	0.85	0.72	0.01	0.53	0.02	0.14	0.18	0.76	0.07	0.7	0.21	0.22

* Significance at 5% level; ** significance at 1% level

Days to fifty percentage flowering (DTFF), Plant height (PH), Panicle number (PN), Panicle length (PL), Spikelet’s per plant (SP), Filled grains per plant (FGP), Spikelet fertility (SF), Test weight (TW, 1000 seed weight), Grain yield per plant (GYPP), Harvest Index (HI), Plot yield (PY), Blast disease index (BDI)

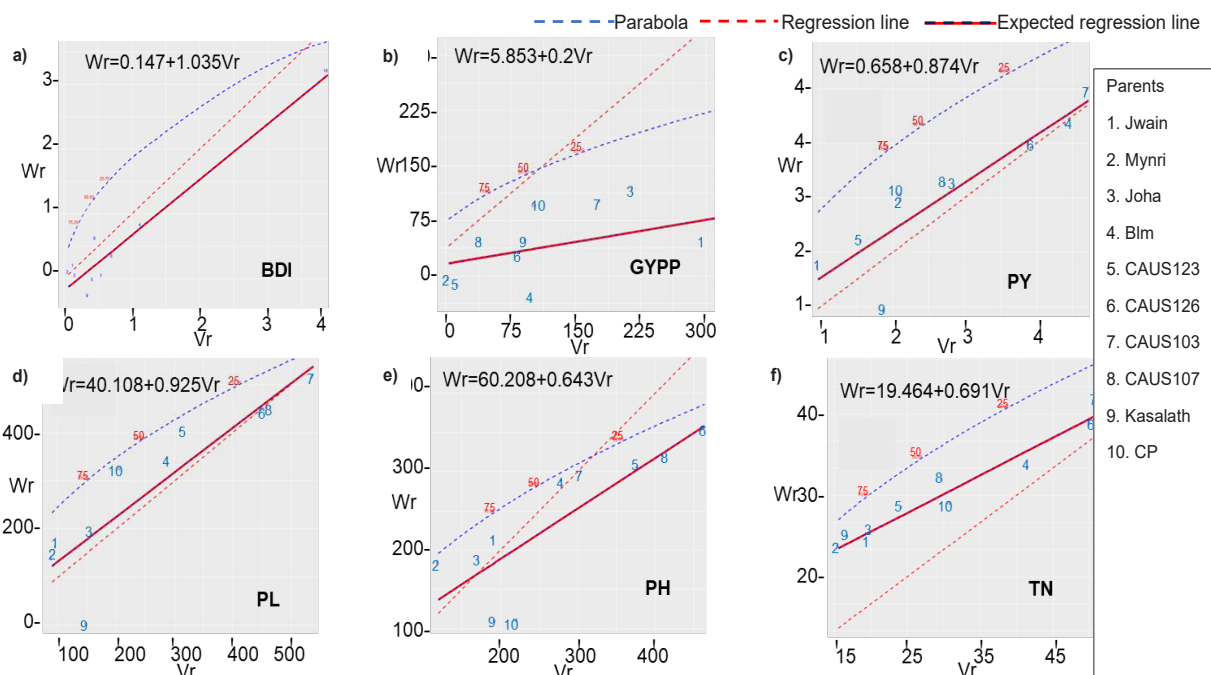


Fig.2. VrWr graph showing various levels of dominance for different traits

a) Blast disease index, b) Grain yield per plant, c) Plot yield d) Panicle length, e) Plant height, f) Tiller number

Heterosis estimation: Among the 45 F_1 hybrids studied, the cross Jwain x CP had significant negative mid parent (-13.18 %) and better parent (-16.53 %) heterosis for DTFF at $p < 0.01$. While, for PN the cross, CAUS126 x CP showed significant positive mid parent and standard heterosis. Overall thirty crosses showed significantly higher standard heterosis values over the check variety (>29 %) for PN. The crosses Mynri x Joha and Mynri x CAUS123 had significantly negative mid parent and better parent heterosis for PH (> -20%). For PL the cross combination CAUS123 x CAUS107 had significantly positive mid parent heterosis (14.29 %). Joha had higher number of SP and FG and the cross involving it, Joha x CP had significantly higher mid parent and better parent heterosis for SP and FG. Also, Joha x CAUS103 had significantly positive mid parent and standard parent heterosis for FG. Kasalath crosses with CAUS103, CAUS107 and Joha x CAUS107 had high significant negative mid and better heterosis for BDI. For GYPP the crosses Joha x CAUS103 had significantly higher mid parent and standard parent heterosis (>80%). Standard heterosis is preferred by breeders over the other two heterosis estimation (Vadivel *et al.*, 2018). Mynri crosses with CAUS123, CAUS126, CAUS107, CAUS103; Joha crosses with CAUS103, CAUS107; CAUS126 x CAUS107, CAUS103 x CAUS107 and CAUS103 x CP were the crosses that had significantly positive standard heterosis (> 80 %) for GYPP. Joha cross with Blm and CAUS103 had significantly positive mid parent and better parent heterosis for PY. Mynri crosses with Blm, CAUS123, CAUS103, Joha x CAUS107, CAUS126 x CAUS107 and CAUS103 x CP had significantly higher standard heterosis (>100 %) for PY. Usually, heterosis for grain yield is expected to be 20- 40% above the standard checks but we observed standard heterosis around 80-100%, it may be due to the poor performance of CAUR1. There were also reports for 80-120% heterosis in rice F_2 s (Virmani *et al.*, 1982, Saini *et al.*, 1974), suggesting that we cannot ignore the heterosis obtained.

Molecular marker-based clustering and association study to predict hybrids: A total of 14 markers were studied for their allelic status among the parents and all the markers amplified in all the parents. A heatmap showing the polymorphism among the parents is shown in **Fig. 1a** and the information regarding genetic distance of each parent is furnished in **Fig. 1b**. Genetic distance was calculated for the allelic data using dissimilarity index and cluster tree was constructed for the parents. Blm had the highest genetic distance from CP, whereas Kasalath was genetically like CAUS123 and CAUS126. This is expected because the parents CAUS123 and CAUS126 were selected from cross involving Kasalath as one of the parents. It is generally known that increase in genetic distance increases heterosis. Manonmani and Khan (2004) have reported that parents with more genetic distance produce good heterotic hybrids. Association study for the genetic distance of the parents and the heterosis values of the progenies are presented in **Table 4**. Initially six random rice SSR (RM) markers (**Fig. 1a**) were used for association studies and it showed a non-significant relationship between genetic distance and heterosis. But when the number of markers was increased by including four polymorphic yield related and four gene based markers, significant positive association was observed for SP, FG, HI and GYPP for mid parent and better parent heterosis. Traits like PN and PY showed significant positive association for standard parent and better parent heterosis respectively. This was similar to the findings of Rahman *et al.* (2022). There was no correlation between marker distance and standard heterosis for traits like DTFF, PH, PL, BDI, SF and negative correlation was observed for TW and HI. Salem *et al.* (2022), have reported no correlation between genetic distance and mid parent heterosis, whereas Huang *et al.* (2016) and Rahman *et al.* (2022) reported significant positive correlation for mid-parent, better parent, as well as standard parent heterosis. In the present study significant positive correlation was observed between genetic distance and

Table 4. Correlation coefficient between genetic distance and heterosis for 12 traits

Traits	Mid parent heterosis	Better parent heterosis	Standard heterosis
DTFF	-0.12	-0.03	0
PN	0.17	0.25	0.38 **
PH	-0.01	0.03	0.07
PL	0.11	0.1	-0.13
SP	0.45 **	0.43 **	0.22
FG	0.37 **	0.33 *	0.11
BDI	0.03	0.01	0.10
GYPP	0.41 **	0.35 **	-0.01
HI	0.34 *	0.32 *	-0.36 **
SF	0.09	0.24	-0.13
TW	0.13	0.12	-0.3 *
PY	0.22	0.26 *	

* Significance at 5% level; ** significance at 1% level

mid parent, better parent heterosis for majority of the yield related traits. Thus, the use of molecular markers, especially yield related markers, can help in predicting the heterosis by just studying the molecular diversity of the parental lines. Mynri crosses with CAUS 103, CAUS123, CAUS126, CAUS107 and Joha crosses with CAUS 103, CAUS107 and CAUS103 x CP were some of the important crosses with significant positive heterosis showing that higher genetic distance between the parents was crucial to obtain maximum heterosis. Therefore, these crosses exhibiting higher heterosis could be evaluated for their suitability for Meghalaya conditions and hill region of NE India.

The average degree of dominance values revealed, partial dominance for DTFF, PH, PL and TW, whereas all the other traits showed over dominance. Knowing the dominance nature will help to predict the segregation pattern. The crosses Mynri x CAUS103, Joha x CAUS107, CAUS 126 x CAUS107 and CAUS103 x CP had significant positive standard heterosis values for GYPP (>80 %) and PY (>150 %). The association of genetic distance with mid parent and better parent heterosis in this study indicates that, genetic distance between the parents identified based on yield related molecular markers could aid in early prediction of heterosis.

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