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Studies on the genetic basis of heterosis, inbreeding depression, heritability and genetic advance through generation mean analysis for yield and its attributing traits in rice (*Oryza sativa* L.)

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Abstract
The current study began in *rabi*-2019 at the Main Rice Research Centre, intending to determine the genetic parameters of three crosses, including heterosis, inbreeding depression, heritability, and genetic advance, using generation mean analysis (each of which has P_1, P_2, F_1, F_2, BC_1, and BC_2 generations) in a Compact Family Block Design (CFBD) with three replications. For the majority of the characteristics, very substantial and positive relative heterosis, heterobeltiosis, standard heterosis, and inbreeding depression were seen in all crosses. The best heterotic cross for grain yield per plant was cross I (IET-24336 × IET-26375), which showed significant heterosis in the desired direction for days to flowering, days to maturity, productive tiller per plant, grains per panicle, panicle length, 100-grain weight, grain yield per plant, straw yield per plant, grain length, protein content, and amylose content For the majority of the traits in all three crosses, high to moderate heritability (narrow-sense) values were found, along with moderate to high genetic advance. As a result, traits with high heritability and high genetic advance can be further improved by adopting selections in subsequent generations.

Keywords: generation mean analysis, compact family block design, heterosis, inbreeding depression, heritability, genetic advance

Introduction
Rice (*Oryza sativa* L.) is a princess among the cereals and the most important cereal and food crop, second only to wheat in terms of annual production for human consumption globally. Asia is considered the 'rice bowl' of the world, producing and consuming more than 90 % of world rice. India ranks first position in the area and second position in production.

Hybrid varieties are an essential strategy for fulfilling the demands of an ever-increasing population. Hybrid rice is a cost-effective way to boost the production potential of cultivars. In F_1 hybrid rice, heterosis in yield contributing characteristics led to yield enhancement (Vanaja and Babu, 2004) [22]. In terms of yield and other qualities, the heterosis reflects the F_1 hybrid's superiority or inferiority over its parents. Inbreeding depression, on the other hand, refers to the loss or decline in vigour, fertility, and yield caused by inbreeding. Both positive and negative heterosis are advantageous in crop growth, depending on the breeding aims and nature of the traits. The magnitude of heterosis aids in the identification of suitable cross combinations for use in a conventional breeding program to provide a wide range of diversity in segregating generations. Knowledge of heterosis and the level of inbreeding depression in following generations is critical for getting the most out of heterosis by using the right breeding methods.

Heritability expresses the relative amount of the heritable portion of the variation. Only the genetic component of variation is essential in crop development since it is the only one that is passed down from generation to generation. As a result, heritability estimates acted as a valuable reference for the breeder. However, when combined with genetic advance, it is more effective in predicting the impact of selecting the best individuals.

Materials and Methods
In this study, six generations, *viz.,* P_1, P_2, F_1, F_2, BC_1, and BC_2 of three crosses were generated from six parental genotypes (IET-26375, IET-27170, IET-25470, IET-25477, IET-24336 and IET-25453) of rice selected based on protein content were utilized to investigate the genetics of fourteen traits, as shown in Table 1.

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The crossing program was initiated during *rabi*-2019 to produce three F_1 hybrids (IET-24336 × IET-26375, IET-25470 × IET-25453, and IET-27170 × IET-25477) among six selected genotypes while backcrossing and selfing of F_1 were done in *kharif*-2020 to obtain BC_1, BC_2 and F_2 seeds of respective crosses. The experimental material consisted of six generations of each of the three single crosses grown in Compact Family Block Design with three replications at Navsari Agricultural University's Main Rice Research Centre during *kharif*-2021. Each replication was split into three compact blocks. Six generations were then assigned to each plot inside a block at random. Each plot had one row of each parent and F_1 generation, two rows of the back cross generation, and twenty rows of the F_2 generation of each cross. The distance between and within rows was 45 cm and 10 cm, respectively. Per replication, ten competitive plants were randomly chosen from each P_1, P_2, and F_1, two hundred plants from F_2, and twenty plants from each of the BC_1 and BC_2 generations, and observations were made on an individual plant basis for fourteen distinct characteristics, *viz.,* days to flowering, days to maturity, plant height, productive tillers per plant, grains per panicle, panicle length (cm), 100-grain weight (g), grain yield per plant (g), straw yield per plant (g), grain length (mm), grain breadth (mm), Length/Breadth ratio, protein content (%) and amylose content (%).

Table 1: Details of parental lines used in hybridization program

Sr. No.	Parent	Pedigree	Source
1.	IET-26375	IR 68144-2B-2-2-3-1-120 × IR-64	
2.	IET-27170	Moro × IR 94046-31	
3.	IET-25470	IR 91181-96-1-1-1-2	M.R.R.C., N.A.U., Navsari
4	IET-25477	Lalmati × IR 681444B-13-2-1-1	
5	IET-24336	BPT 5204 × MTU 1010	
6	IET-25453	ARC 10075 × Naveen	

Heterosis was estimated as per cent increase or decrease in the mean value of F_1 hybrid over the mid-parent, *i.e.,* relative heterosis (Briggle, 1963), over the better parent, *i.e.,* heterobeltiosis (Fonseca and Patterson, 1968) and standard check, *i.e.,* standard heterosis (Meredith and Bridge, 1972) for each character.

$$\text{Relative heterosis (\%)} = \frac{\overline{F_1} - \overline{MP}}{\overline{MP}} \times 100$$

$$\text{Heterobeltiosis (\%)} = \frac{\overline{F_1} - \overline{BP}}{\overline{BP}} \times 100$$

$$\text{Standard heterosis (\%)} = \frac{\overline{F_1} - \overline{SC}}{\overline{SC}} \times 100$$

Where,

$\overline{F_1}$ = Mean performance of the F_1 hybrid

$\overline{MP}$ = Mean value of the parents (P_1 and P_2) of a hybrid
$\overline{BP}$ = Mean value of better parent
$\overline{SC}$ = Mean value of the standard check

The following formulas were used to calculate inbreeding depression:

$$\text{ID (\%)} = \frac{\overline{F_1} - \overline{F_2}}{\overline{F_2}} \times 100$$

As stated by Warner (1952) [25], the narrow-sense heritability was estimated as follows::

$$h^2_{(n)}(\%) = \frac{\widehat{\sigma}^2_A}{\widehat{\sigma}^2_P} \times 100$$

Where,

$h^2_{(n)}$ = Heritability in a narrow sense
$\widehat{\sigma}^2_A$ = Additive genotypic variance (d)
$\widehat{\sigma}^2_P$ = Phenotypic variance

After a single generation of selection, the expected genetic advance represents the change in a population mean towards the superior side under selection pressure. It was computed using the approach proposed by Johnson *et al.* (1955) [10].

$$\text{Expected genetic advance} = k \cdot h^2_{(ns)} \cdot \widehat{\sigma}_P$$

Where,

$h^2_{(ns)}$ = Heritability in a narrow-sense
$\widehat{\sigma}_P$ = Phenotypic standard deviation
k = Selection differential
(k = 2.06 at 5 per cent selection pressure intensity as suggested by Allar

Result and discussion
Analysis of variance and *Per se* performance
The analysis of variance between generations within each family indicated significant differences among six-generation means for all the characters studied in all the three crosses except panicle length and length/breadth ratio in cross I (IET-24336 × IET-26375) (Table 2). Hence, further genetic analysis of heterosis, inbreeding depression, heritability, and the genetic advance was done. The results obtained on these aspects for different characters studied in three crosses of rice, *viz.,* cross I (IET-24336 × IET-26375), cross II (IET-25470 × IET-25453), and cross III (IET-27170 × IET 25477) hereafter referred to as cross I, cross II, and cross III, are presented and discussed in the following paragraphs.

Variation among the generation's mean was highly significant for days to flowering, days to maturity, plant height, grains per panicle, grain yield, straw yield, grain length, protein content, and amylose content (cross I, cross II, cross III), productive tillers per plant (cross I, cross II), panicle length, length/breadth ratio (cross II, cross III), 100-grain weight (cross II) and grain breadth (cross I) in all the three crosses.

Moreover, a significant difference was recorded among the generations for productive tillers per plant (cross III), 100-grain weight (cross I, cross III), and grain breadth (cross II, cross III). While a non-significant difference was observed between generations in cross I for panicle length and length/breadth ratio (Table 2).

For most of the traits studied, the mean sum of squares exhibited substantial variations across generations in all crosses, suggesting high variability in the experimental material. Significant variation in the expression of many traits under investigation might be attributable to more diversity between parents, resulting in high variability across

generations and less environmental effect on the expression of these traits.

Based on *per se* performance (Table 3), F_1s fell outside the parent range, indicating the presence of overdominance in cross I for days to maturity and protein content; cross II for plant height, productive tillers per plant, and amylose content; cross III for protein content. The mean performance of F_1s was observed at par with one of the parents, indicating the presence of complete dominance in cross I for plant height, productive tillers per plant, grain yield per plant, straw yield per plant, and grain length; cross II for days to maturity, 100-grain weight, and grain length; cross III for days to maturity. The presence of partial dominance was observed in cross II for protein content. The presence of no dominance was confirmed by at par value of F_1s with a mid-parental value which was observed in cross I for the characters, *viz.,* days to flowering, grains per panicle, panicle length, 100-grain weight, grain breadth, length/breadth ratio, and amylose content; cross II for days to flowering, grain per panicle, panicle length, grain yield per plant, straw yield per plant, grain breadth and length/breadth ratio; cross III for all the characters except protein content and days to maturity.

F_2s were found to be at par with F_1s in all the crosses for days to maturity and plant height, while at par for days to flowering in cross I showing the absence of inbreeding depression. The significantly lower value of F_2s confirmed the further presence of inbreeding depression as compared to respective F_1s in cross I for panicle length, 100-grain weight, and protein content; cross II for productive tillers per plant, panicle length, grain length, and protein content; cross III for panicle length, grain yield per plant and protein content. Moreover, at par mean value of F_2s as compared to respective F_1s was recorded for grains per panicle, straw yield per plant, grain breadth, length/breadth ratio, and amylose content in all three crosses; grain yield per plant in cross I and cross II; productive tillers per plant and grain length in cross I and cross III; 100-grain weight in cross II and cross III. While the significantly lower mean value of F_2s compared to respective F_1s was recorded for days to flowering in cross II and cross III, revealing the presence of desirable transgressive segregants as for days to flowering, significantly lower mean values are desirable.

BC_1 generation was found to be significantly higher in magnitude than the female parent or/and F_1s in cross I for days to maturity, straw yield per plant, grain length, and grain breadth; cross II for grains per panicle, 100-grain weight, grain yield per plant, straw yield per plant and amylose content; cross III for grains per panicle, grain yield per plant, panicle length, straw yield per plant, grain breadth, grain length and protein content, which demonstrated that the genes underlying the characteristic under investigation were present in respective parents and that a backcross selection technique would be useful for future development. While significantly lower in magnitude in cross I for panicle length, protein content, and amylose content; cross II for plant height, days to maturity, grain length, panicle length, and protein content; cross III for plant height, days to flowering, panicle length and amylose content. Due to the accumulation of divergent alleles, their F_1s may have done better than their parents, indicating the existence of epistatic gene interaction.

BC_2 generations were found to be significantly higher than the male parent or/and F_1s in cross I for days to maturity, plant height, days to flowering, grain yield per plant, and straw yield per plant; cross II for days to maturity, productive tillers per plant, days to flowering, 100-grain weight, straw yield per plant, grain breadth, grain yield per plant, protein content and amylose content; cross III for days to maturity, grain yield per plant, plant height, straw yield per plant, length/breadth ratio, grain length, protein content, and amylose content. This demonstrated that genes for the characteristic under research were present in respective parents and that a backcross selection technique would be efficient for future development. While significantly lower in magnitude in cross I for grains per panicle, productive tillers per plant, straw yield per plant, protein content, and amylose content; cross II for panicle length, grain length, productive tillers per plant, and length/breadth ratio; cross III for grains per panicle and panicle length.

Based on *per se* performance for grain yield per plant, the best cross was cross I, which also performed well for plant height, days to flowering, grains per panicle, productive tillers per plant, panicle length, 100-grain weight, grain length, straw yield per plant and protein content.

Table 2: Analysis of variance (mean sum of squares) for six generations in three crosses of rice for different characters.

Traits	Cross I (IET-24336 × IET-26375)			Cross II (IET-25470 × IET-25453)			Cross III (IET-27170 × IET-25477)		
	Replications	Generations	Error	Replications	Generations	Error	Replications	Generations	Error
df	2	5	10	2	5	10	2	5	10
Days to flowering	2.39	29.08**	3.59	4.41	17.12**	1.25	0.73	22.20**	1.76
Days to maturity	5.27	32.90**	3.98	6.7	35.47**	2.96	1.07	24.48**	3.08
Plant height (cm)	10.58	54.41**	9.78	2.42	76.49**	7.55	4.25	49.65**	6.93
Productive tillers per plant	0.37	11.32**	0.8	0.86	8.22**	0.58	0.04	3.03*	0.58
Grains per panicle	208.04	918.64**	64.7	10.15	141.17**	29.15	4.72	304.16**	23.81
Panicle length (cm)	5.53	11.35	4.1551	0.35	5.24**	0.6	0.92	13.20**	0.49
100-grain weight (g)	0.01	0.05*	0.01	0.01	0.06**	0.01	0.01	0.06*	0.01
Grain yield per plant (g)	0.12	14.01**	1.57	0.95	11.71**	1.6	1	7.39**	1.29
Straw yield per plant (g)	1.48	44.48**	1.56	0.72	29.95**	2.53	1.36	20.50**	2.03
Grain length (mm)	0.17	2.10**	0.17	0.04	1.29**	0.04	0.02	1.62**	0.1
Grain breadth (mm)	0.01	0.17**	0.02	0.01	0.20*	0.05	0.01	0.21*	0.06
Length/Breadth ratio	0.11	0.09	0.1	0	0.75**	0.13	0.02	0.53**	0.09
Protein content (%)	0.063	1.90**	0.09	0.11	5.60**	0.05	0.02	1.93**	0.06
Amylose content (%)	0.15	4.27**	0.6	0.16	7.61**	0.53	1.18	10.16**	0.56

* and **, significant at 5 % and 1 %, respectively

Table 3: Mean performance of different generations of three crosses for grain yield and its component traits in rice

Treatment	Days to flowering	Days to maturity	Plant height (cm)	Productive tillers per plant	Grains per panicle	Panicle length (cm)	100-grain weight (g)	Grain yield per plant (g)	Straw yield per plant (g)	Grain length (mm)	Grain breadth (mm)	Length/ Breadth ratio	Protein content (%)	Amylose content (%)
Cross I (IET-24336 × IET-26375)														
P₁ (IET-24336)	90.97 ± 0.51	120.97 ± 0.72	111.83 ± 1.23	12.63 ± 0.25	195.90 ± 4.37	23.36 ± 0.63	2.59 ± 0.06	19.06 ± 0.30	29.70 ± 0.62	7.89 ± 0.05	2.10 ± 0.03	3.78 ± 0.06	9.73 ± 0.08	24.28 ± 0.18
P₂ (IET-26375)	96.33 ± 0.44	126.47 ± 0.62	106.20 ± 1.07	10.60 ± 0.29	155.57 ± 2.95	25.59 ± 0.51	2.78 ± 0.06	15.25 ± 0.23	20.70 ± 0.47	9.76 ± 0.09	2.63 ± 0.04	3.74 ± 0.07	8.96 ± 0.06	23.60 ± 0.17
F₁ (P₁ × P₂)	90.27 ± 0.63	117.30 ± 0.80	116.73 ± 1.17	14.57 ± 0.29	187.73 ± 2.93	27.95 ± 0.51	2.84 ± 0.05	20.77 ± 0.24	28.65 ± 0.36	10.23 ± 0.07	2.60 ± 0.04	3.54 ± 0.06	11.20 ± 0.09	23.23 ± 0.14
F₂	88.48 ± 0.20	118.64 ± 0.20	112.64 ± 0.53	14.30 ± 0.10	186.44 ± 1.63	23.77 ± 0.21	2.60 ± 0.02	18.98 ± 0.15	27.78 ± 0.25	9.53 ± 0.04	2.47 ± 0.02	3.49 ± 0.03	9.98 ± 0.05	23.91 ± 0.07
BC₁ (F₁ × P₁)	91.83 ± 0.53	122.67 ± 0.57	111.30 ± 1.46	13.60 ± 0.30	192.38 ± 3.35	23.83 ± 0.46	2.73 ± 0.05	20.73 ± 0.38	31.40 ± 0.58	9.93 ± 0.08	2.51 ± 0.03	4.00 ± 0.07	10.24 ± 0.08	22.14 ± 0.17
BC₂ (F₁ × P₂)	95.68 ± 0.51	123.15 ± 0.60	118.13 ± 1.28	9.93 ± 0.21	159.32 ± 3.89	27.19 ± 0.50	2.90 ± 0.05	20.90 ± 0.33	24.85 ± 0.57	9.85 ± 0.07	2.80 ± 0.04	3.92 ± 0.07	9.23 ± 0.10	21.13 ± 0.18
CD	3.45	3.62	5.69	1.63	14.63	3.70	0.20	2.28	2.27	0.76	0.27	0.59	0.54	1.41
Cross II (IET-25470 × IET-25453)														
P₁ (IET-25470)	89.03 ± 0.60	120.30 ± 0.74	120.43 ± 0.66	11.17 ± 0.20	125.40 ± 2.32	24.02 ± 0.23	1.98 ± 0.05	18.98 ± 0.39	25.80 ± 0.54	8.11 ± 0.05	2.68 ± 0.03	3.04 ± 0.04	10.53 ± 0.08	20.52 ± 0.17
P₂ (IET-25453)	93.23 ± 0.50	125.70 ± 0.70	127.37 ± 0.79	8.37 ± 0.18	116.83 ± 2.16	22.57 ± 0.22	2.10 ± 0.04	14.92 ± 0.29	19.38 ± 0.48	9.38 ± 0.07	2.09 ± 0.03	4.52 ± 0.07	6.86 ± 0.07	22.62 ± 0.21
F₁ (P₁ × P₂)	90.70 ± 0.47	119.00 ± 0.74	133.67 ± 0.70	13.03 ± 0.23	126.20 ± 1.61	24.03 ± 0.19	2.22 ± 0.03	16.90 ± 0.29	24.66 ± 0.38	9.70 ± 0.06	2.74 ± 0.04	3.57 ± 0.06	9.99 ± 0.07	24.34 ± 0.16
F₂	88.44 ± 0.25	119.61 ± 0.27	130.02 ± 0.44	11.27 ± 0.10	130.85 ± 0.87	20.43 ± 0.10	2.15 ± 0.02	17.11 ± 0.14	24.62 ± 0.23	9.21 ± 0.03	2.69 ± 0.02	3.49 ± 0.02	8.40 ± 0.04	24.30 ± 0.08
BC₁ (F₁ × P₁)	88.30 ± 0.68	117.13 ± 0.74	122.70 ± 0.79	12.15 ± 0.31	135.90 ± 2.62	22.63 ± 0.25	2.33 ± 0.05	20.72 ± 0.37	29.18 ± 0.58	8.19 ± 0.05	2.45 ± 0.04	3.39 ± 0.06	9.92 ± 0.07	23.76 ± 0.19
BC₂ (F₁ × P₂)	93.63 ± 0.58	124.97 ± 0.65	130.68 ± 1.10	9.90 ± 0.16	120.58 ± 1.79	22.50 ± 0.27	2.36 ± 0.05	17.58 ± 0.37	25.37 ± 0.50	9.17 ± 0.06	2.75 ± 0.04	3.37 ± 0.06	9.77 ± 0.12	24.80 ± 0.22
CD	2.03	3.13	4.99	1.39	9.82	1.40	0.17	2.30	2.90	0.38	0.40	0.65	0.40	1.32
Cross III (IET-27170 × IET-25477)														
P₁ (IET-27170)	87.50 ± 0.51	118.73 ± 0.61	112.10 ± 0.69	8.47 ± 0.13	111.43 ± 1.45	20.25 ± 0.20	1.93 ± 0.04	13.83 ± 0.33	18.31 ± 0.34	7.78 ± 0.06	2.21 ± 0.04	3.54 ± 0.05	6.85 ± 0.07	25.27 ± 0.15
P₂ (IET-25477)	92.10 ± 0.56	124.23 ± 0.66	122.93 ± 1.07	10.67 ± 0.19	140.67 ± 2.38	25.40 ± 0.18	1.59 ± 0.04	15.85 ± 0.31	19.64 ± 0.35	8.41 ± 0.06	2.79 ± 0.04	3.03 ± 0.06	7.30 ± 0.06	19.79 ± 0.15
F₁ (P₁ × P₂)	92.07 ± 0.42	117.10 ± 0.50	119.07 ± 0.82	9.07 ± 0.16	118.13 ± 1.66	23.81 ± 0.19	1.88 ± 0.03	16.74 ± 0.26	21.06 ± 0.43	8.33 ± 0.06	2.91 ± 0.04	2.87 ± 0.04	8.04 ± 0.06	22.79 ± 0.17
F₂	89.63 ± 0.19	116.63 ± 0.21	118.60 ± 0.41	8.35 ± 0.07	116.74 ± 0.73	20.29 ± 0.08	1.97 ± 0.02	14.65 ± 0.12	21.49 ± 0.18	8.01 ± 0.03	2.80 ± 0.01	2.90 ± 0.02	7.28 ± 0.03	21.74 ± 0.07
BC₁ (F₁ × P₁)	87.30 ± 0.49	118.80 ± 0.61	112.93 ± 1.01	8.73 ± 0.21	120.20 ± 1.55	21.95 ± 0.24	1.91 ± 0.05	16.84 ± 0.32	23.74 ± 0.49	9.07 ± 0.06	2.84 ± 0.04	3.22 ± 0.04	8.69 ± 0.07	23.02 ± 0.23
BC₂ (F₁ × P₂)	93.97 ± 48	121.32 ± 0.52	117.67 ± 0.96	10.40 ± 0.20	123.20 ± 2.48	23.77 ± 0.22	1.72 ± 0.05	18.12 ± 0.28	25.43 ± 0.42	9.76 ± 0.07	2.53 ± 0.05	3.95 ± 0.09	8.77 ± 0.09	21.44 ± 0.24
CD	2.41	3.19	4.79	1.39	8.77	1.27	0.23	2.06	2.59	0.58	0.45	0.53	0.46	1.36
Check (GR-15)														
GR-15	95.97 ± 0.38	127.83 ± 0.36	124.20 ± 0.66	12.03 ± 0.26	215.50 ± 1.28	27.12 ± 0.17	2.40 ± 0.03	20.59 ± 0.39	27.40 ± 0.79	9.61 ± 0.05	2.69 ± 0.02	3.58 ± 0.03	7.67 ± 0.07	24.14 ± 0.21

Heterosis and inbreeding depression

For a successful heterosis breeding program in rice, there must be adequate proof of the existence of a major heterotic impact in the hybrids, as well as the production of hybrid seed on a commercial scale being economically possible. Future breeding initiatives will be guided by heterosis and heterobeltiosis, which may be used to identify potential cross combinations.

In cross I, the considerable relative heterosis in the intended direction was observed for days to maturity, productive tillers per plant, days to flowering, grains per panicle, 100-grain weight, panicle length, grain yield per plant, grain length, straw yield per plant and protein content. Substantial heterobeltiosis in the anticipated direction was observed for productive tillers per plant, days to maturity, panicle length, grain length, grain yield per plant, and protein content. Significant standard heterosis in the desired direction was observed for days to maturity, productive tillers per plant, plant height, days to flowering, 100-grain weight, grain length, and protein content. All the traits exhibited positively

significant inbreeding depression except in productive tillers per plant, days to maturity, straw yield per plant, grains per panicle, and length/breadth ratio indicates the more chances of getting desired transgressive segregants. Positive inbreeding depression in days to flowering and plant height is desired as early flowering, and dwarf stature is anticipated in rice (Table 4).

The substantial relative heterosis in the intended direction was detected in cross II for days to maturity, grains per panicle, productive tillers per plant, 100-grain weight, straw yield per plant, panicle length, grain length, and amylose content. Substantial heterobeltiosis in the intended direction was found for productive tillers per plant, 100-grain weight, protein content, grain length, and amylose content. Substantial standard heterosis in the intended direction was found for days to maturity, productive tillers per plant, days to flowering, and protein content. Substantial and negative inbreeding depression observed for grains per panicle increases the likelihood of obtaining desired transgressive segregants. While, substantial positive inbreeding depression

was observed for panicle length, grain length, 100-grain weight, productive tillers per plant, and protein content. Significant positive inbreeding depression for days to flowering and plant height is desired. The results suggested that the selection of desired recombinants can be made in cross II (Table 4).

In cross III, the characters, *viz.,* days to maturity, panicle length, 100-grain weight, grain yield per plant, grain length, straw yield per plant, and protein content expressed substantial relative heterosis in the intended direction. The traits, *viz.,* days to maturity, and protein content depicted substantial heterobeltiosis in the intended direction, while all other characteristics showed heterobeltiosis in the undesired direction. Significant standard heterosis in the intended direction was observed for days to flowering, plant height, days to maturity, grain breadth, and protein content. Significant negative inbreeding depression was observed for 100-grain weight, which indicates the chances of getting transgressive segregants for 100-grain weight. Positive inbreeding depression for days to flowering is desired as early flowering rice varieties are anticipated in rice (Table 4).

The results of the present study for heterosis and inbreeding depression are in accordance with the results of Panwar and Ali (2010) [14], Soni and Sharma (2011) [21], Vennila *et al.* (2011) [24], Ghara *et al.* (2014) [9,] Venkanna *et al.* (2014) [12], Anis *et al.* (2016) [2], Borah *et al.* (2017) [5], Rumanti *et al.* (2017) [16], Lingaiah (2019) [12] and Singh and Patel (2021) [20] for different characteristics.

Heritability and Genetic Advance

Grain yield per plant and its components were found to have high, moderate, and low estimates of narrow-sense heritability. All three crosses recorded a high narrow-sense heritability in grain yield per plant. Crosses with high to moderate narrow-sense heritability for grain yield per plant also showed high to moderate yield contributing trait estimations (Table 5). As far as protein content and amylose content is concerned, general estimates of narrow-sense heritability were high, moderate to low, but equitable results were observed for high to moderate. The higher heritability estimates indicate that these traits were comparatively less affected by environment, and their phenotype is a good reflection of genotype, and thus had paramount importance in selecting a superior genotype based on the phenotypic performance of these matric traits, but in the case of lower heritability, pedigree or progeny tests can be used to improve it.

The degree of genetic advance for most characteristics was high to moderate (Table 5). In terms of grain yield per plant, all three crosses showed a significant genetic advance. However, a low genetic advance was recorded for the traits, *viz.,* days to flowering (cross I and III), days to maturity (cross I and III), productive tiller per plant (cross III), panicle length (cross III), and grain breadth (cross III).

High to moderate heritability (narrow-sense) estimates coupled with moderate to high genetic advance was observed for most of the characters in all three crosses as illustrated in figure 1. Heritability and a high genetic advance were most likely due to additive gene effects. As a result, traits with high heritability and a high genetic advance may be improved even further by adopting selections in subsequent generations.

The results of the present investigation for heritability and genetic advance are in accordance with the results of Gangashetty *et al.* (2013) [8], Sathya and Jebaraj (2013) [18], Anyanwu Chinyere and Obi (2014) [3], Sadimantra *et al.* (2014), Venkatesan *et al.* (2017) [23], Bagudam *et al.* (2018) [4], Patel *et al.* (2019) [15], Singh and Patel (2020) [19], Kumari and Parmar (2020) [11] for different traits.

Table 4: Estimates of relative heterosis (RH %), heterobeltiosis (HB %), standard heterosis (SH %) and inbreeding depression (ID %) for different traits in three crosses of rice

Particulars	Days to flowering		Days to maturity		Plant height (cm)		Productive tillers per plant		Grains per panicle		Panicle length (cm)		100 grain weight (g)	
	Estimates	SE	Estimates	SE	Estimates	SE	Estimates	SE	Estimates	SE	Estimates	SE	Estimates	SE
Cross I (IET-24336 × IET-26375)														
RH %	−3.61**	± 0.71	−5.19**	± 0.93	7.08**	± 1.43	25.40**	± 0.34	6.83**	± 3.94	14.18**	± 0.65	5.93*	± 0.06
HB %	−0.77	± 0.81	−3.03**	± 1.01	9.92**	± 1.70	15.30**	± 0.38	−4.17	± 5.26	9.21**	± 0.72	2.14	± 0.08
SH %	−5.94**	± 0.73	−8.24**	± 0.88	−6.02**	± 1.35	21.08**	± 0.39	−12.89**	± 3.20	3.07	± 0.54	18.45**	± 0.06
ID %	1.99**	± 0.66	−1.14	± 0.82	3.51**	± 1.29	1.83	± 0.30	0.69	± 3.35	14.95**	± 0.55	8.73**	± 0.06
Cross II (IET-25470 × IET-25453)														
RH %	−0.48	± 0.61	−3.25**	± 0.90	7.88**	± 0.87	33.45**	± 0.27	4.20*	± 2.26	3.16**	± 0.25	8.71**	± 0.04
HB %	1.87*	± 0.76	−1.08	± 1.05	10.99**	± 0.96	16.72**	± 0.31	0.64	± 2.82	0.06	± 0.30	5.70**	± 0.04
SH %	−5.49**	± 0.60	−6.91**	± 0.83	7.62**	± 0.96	8.28**	± 0.35	−41.44**	± 2.06	−11.38**	± 0.26	−7.41**	± 0.04
ID %	2.49**	± 0.53	−0.51	± 0.79	2.73**	± 0.82	13.56**	± 0.25	−3.69*	± 1.83	14.99**	± 0.22	2.99*	± 0.03
Cross III (IET-27170 × IET-25477)														
RH %	2.52**	± 0.57	−3.61**	± 0.67	1.32	± 1.04	−5.23*	± 0.20	−6.28**	± 2.16	4.33**	± 0.24	7.05**	± 0.04
HB %	5.22**	± 0.66	−1.38*	± 0.79	6.22**	± 1.07	−15.00**	± 0.25	−16.02**	± 2.90	−6.26**	± 0.26	−2.28	± 0.05
SH %	−4.06**	± 0.57	−8.40**	± 0.62	−4.13**	± 1.05	−24.63**	± 0.31	−45.18**	± 2.10	−12.19**	± 0.26	−21.59**	± 0.04
ID %	2.64**	± 0.47	0.41	± 0.54	0.39	± 0.91	7.90**	± 0.17	1.18	± 1.81	14.81**	± 0.21	−4.44*	± 0.04

* and **, significant at 5 % and 1 %, respectively

Table 4: Contd…

Particulars	Grain yield per plant (g)		Straw yield per plant (g)		Grain length (mm)		Grain breadth (mm)		Length/Breadth ratio		Protein content (%)		Amylose content (%)	
	Estimates	SE	Estimates	SE	Estimates	SE	Estimates	SE	Estimates	SE	Estimates	SE	Estimates	SE
Cross I (IET-24336 × IET-26375)														
RH %	21.07**	± 0.31	13.70**	± 0.53	15.94**	± 0.08	10.11**	± 0.05	−5.72**	± 0.07	19.84**	± 0.10	−2.95**	± 0.19
HB %	8.96**	± 0.38	−3.52	± 0.72	4.83**	± 0.11	−0.90	± 0.05	−6.20**	± 0.08	15.15**	± 0.12	−4.33**	± 0.23
SH %	0.88	± 0.46	4.55	± 0.87	6.41**	± 0.08	−3.23*	± 0.04	−1.07	± 0.06	46.01**	± 0.11	−3.76**	± 0.25
ID %	8.61**	± 0.29	3.03	± 0.44	6.83**	± 0.08	5.12**	± 0.04	1.49	± 0.06	10.88**	± 0.10	−2.90**	± 0.16
Cross II (IET-25470 × IET-25453)														
RH %	−0.26	± 0.38	9.15**	± 0.53	10.97**	± 0.07	14.88**	± 0.05	−5.49**	± 0.08	−5.11**	± 0.11	12.87**	± 0.21

HB %	−10.93**	± 0.49	−4.41	± 0.66	3.47**	± 0.09	2.17	± 0.05	−20.98**	± 0.09	14.91**	± 0.09	7.65**	± 0.26
SH %	−17.91**	± 0.49	−10.01**	± 0.88	0.90	± 0.07	1.99	± 0.04	−0.23	± 0.07	30.24**	± 0.10	0.84	± 0.26
ID %	−1.24	± 0.33	0.15	± 0.44	5.11**	± 0.06	1.77	± 0.04	2.17	± 0.07	15.91**	± 0.08	0.17	± 0.18
Cross III (IET-27170 × IET-25477)														
RH %	12.83**	± 0.34	10.95**	± 0.50	2.90**	± 0.07	16.51**	± 0.05	−12.70**	± 0.06	13.70**	± 0.07	−9.83**	± 0.23
HB %	−5.63*	± 0.41	−7.19*	± 0.56	−0.98	± 0.08	4.27	± 0.06	−19.00**	± 0.07	10.23**	± 0.08	1.15	± 0.20
SH %	−18.69**	± 0.47	−23.15**	± 0.90	−13.35**	± 0.07	8.31**	± 0.05	−19.80**	± 0.05	4.81**	± 0.09	−5.58**	± 0.27
ID %	12.50**	± 0.28	−2.07	± 0.47	3.82**	± 0.06	3.94*	± 0.04	−1.17	± 0.04	9.56**	± 0.07	4.59**	± 0.18

* and **, significant at 5 % and 1 %, respectively

Table 5: Estimates of heritability and genetic advance for different traits in three crosses of rice

Particulars	Estimates (%)						
	Days to flowering	Days to maturity	Plant height (cm)	Productive tillers per plant	Grains per panicle	Panicle length (cm)	100 grain weight (g)
Cross I (IET-24336 × IET-26375)							
Heritability (ns) %	61.57	26.87	64.77	55.19	100.70	97.56	96.21
Genetic advance %	6.64	2.23	15.30	21.16	46.09	41.15	40.22
Cross II (IET-25470 × IET-25453)							
Heritability (ns) %	75.98	62.41	103.05	67.89	65.41	63.44	47.95
Genetic advance %	10.74	6.92	17.77	29.88	22.70	13.88	20.16
Cross III (IET-27170 × IET-25477)							
Heritability (ns) %	74.43	57.00	84.39	6.65	39.11	44.68	79.95
Genetic advance %	8.06	5.10	14.89	2.40	11.81	8.37	45.27
	Grain yield per plant (g)	Straw yield per plant (g)	Grain length (mm)	Grain breadth (mm)	Length/ Breadth ratio	Protein content (%)	Amylose content (%)
Cross I (IET-24336 × IET-26375)							
Heritability (ns) %	91.39	98.25	122.48	86.05	105.35	128.56	90.40
Genetic advance %	36.88	46.48	25.41	26.72	42.83	31.11	14.73
Cross II (IET-25470 × IET-25453)							
Heritability (ns) %	61.52	86.54	117.44	70.11	83.91	87.53	74.68
Genetic advance %	24.63	40.04	18.92	20.77	29.20	19.58	13.22
Cross III (IET-27170 × IET-25477)							
Heritability (ns) %	74.51	64.11	92.87	12.30	–	87.59	–
Genetic advance %	28.22	26.26	15.27	3.19	–	19.16	–
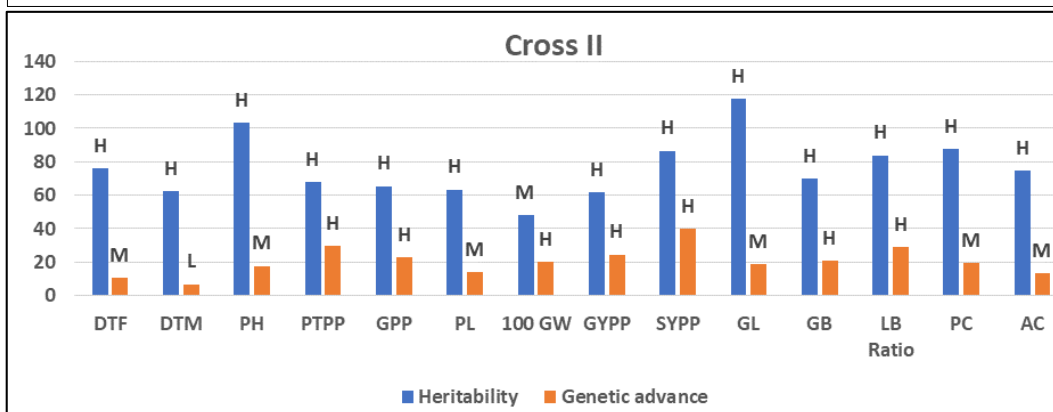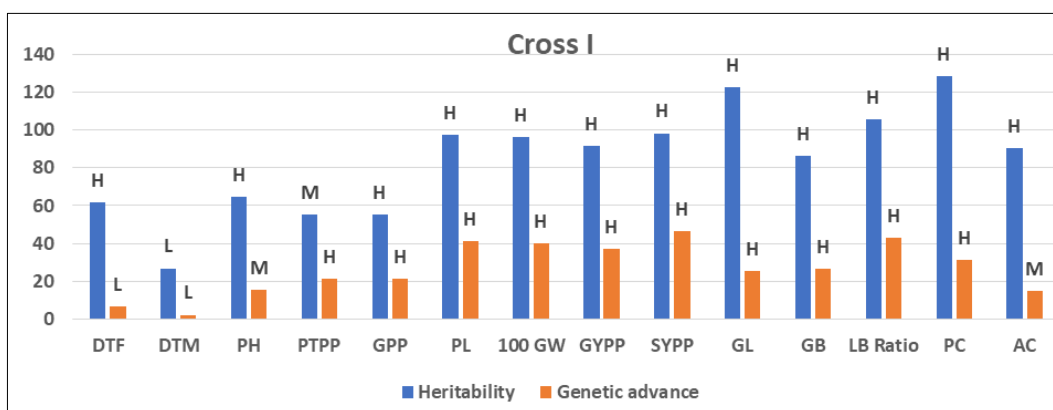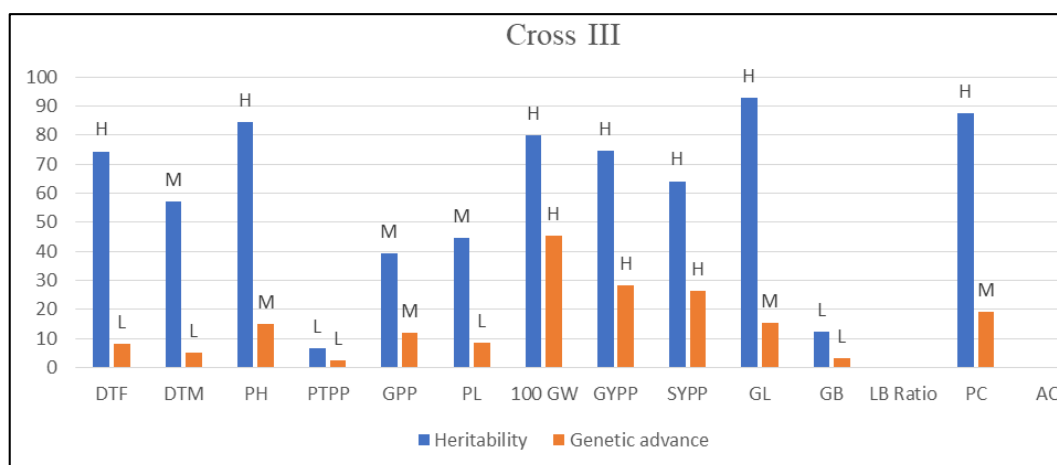
DTF: Days to flowering, DTM: Days to maturity, PH: Plant height, PTPP: Productive tillers per plant, GPP: Grains per panicle, PL: Panicle length, 100 GW: 100-Grain weight, GYPP: Grain yield per plant, SYPP: Straw yield per plant, GL: Grain length, GB: Grain breadth, LB Ratio: Length/Breadth ratio, PC: Protein content, AC: Amylose content.
H = High heritability/genetic advance M = Moderate heritability/genetic advance
L = Low heritability/genetic advance

Fig 1: Graphical representation of comparative heritability and genetic advance for fourteen characteristics in rice

Conclusions
For the majority of the characteristics, very substantial and positive relative heterosis, heterobeltiosis, standard heterosis, and inbreeding depression were seen in all crosses. Significant heterosis over mid-parent and better parent, as well as positive inbreeding depression, may be ascribed to a significant contribution from dominance (h) and additive × additive (i) gene effects, where selection will be effective only in later generations. The best heterotic cross for grain yield per plant was cross I (IET-24336 IET-26375), which showed significant heterosis in the desired direction for days to flowering, days to maturity, productive tiller per plant, grains per panicle, panicle length, 100-grain weight, grain yield per plant, straw yield per plant, grain length, protein content, and amylose content. So, heterosis breeding in cross I would be a more feasible technique for higher grain yield. Characters with high heritability and a high genetic advance may be improved even further by making selections in subsequent generations.

Acknowledgements

Conflict of Interest
Conflict of interest none declared.

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