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RESEARCH ARTICLE

Trait performance of F_1 and F_2 generations of rice (*Oryza sativa* L.) in relation to heterosis and inbreeding depression under saline soils

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Abstract

The extent of heterobeltiosis and economic heterosis of 24 F_1s and inbreeding depression in 24 F_2 generations, along with the parents, were raised in saline soils and estimated for ten characters under this study. Heterotic effects of 24 F_1s revealed high and significant positive heterosis for grain yield in the cross combinations KPS 10640 × KPS 2874, KPS 10631 × KPS 2874, KPS 10642 × KPS 2874, KPS 10640 × RNR11718 and KPS 10633 × RNR11718, according to the results of better parent heterosis. The results of economic heterosis showed and high and significant positive heterosis for grain yield in the cross combinations KPS 10628 × CSR23, KPS 10640 × CSR23, KPS 10633 × RNR 11718, KPS 10651 × CSR36 and KPS 10640 × RNR11718. The range of inbreeding depression for grain yield was 4.09 % (KPS 10631 × CSR 23) to 42.45 % (KPS 10640 × RNR 11718). Twenty-one of the twenty-four crossings showed a substantial and positive inbreeding depression in F_2 for grain yield. Not withstanding their grain yield, these F_1s exhibited notable heterosis and inbreeding depression for a few key yield-contributing traits. This study showed that non-additive gene action is present in the inheritance of grain yield plant^{-1}, along with several other yield-contributing traits and in the development of cultivars that can withstand salinity for long-term production.

Keywords: grain yield; heterosis; inbreeding depression; rice; salinity

Introduction

Rice belongs to the family of Gramineae and more than three billion people globally rely as one of their major foods, providing 20 % of the worlds' nutritional energy supply. The growth and productivity of rice plants are affected by a number of abiotic stressors, including drought, salinity, flooding, temperature extremes and heavy metal stress. Among these, soil salinity is causing yield losses of up to 30 %–50 % per year, which is having a significant global influence on rice production and yield (1). During the seedling and reproductive stages, it is highly sensitive because it is a glycophyte. Changes in plant physiological processes affect its growth, development and yield, especially during pollination and fertilisation (2). These alterations cause rice to delay the heading stage, which further reduces other components of yield (3). Reclamation procedures can be used to decrease soil salinity, although they may increase production costs. So, producing high-yielding cultivars, usually F_1 hybrids, with outstanding stress tolerance potential is vital. To develop a cultivar that would be appropriate for each environment and every consumer choice, however, is not possible. As a result, locally selected hybrids with desirable yield traits are developed to achieve high seed yield. This adaptability is mainly attained through heterosis breeding (4).

Heterosis, also known as hybrid vigour, is a natural phenomenon in which the hybrid progeny of genetically diverse lines performs better (or inferior) than the better parent (heterobeltiosis) or over check cultivar (Economic/standard heterosis) (5). The biochemical and physiological idea of heterosis was proposed by scholars several decades ago (6). However, new developments in molecular genetics have demonstrated that heterosis is solely genetic in origin (7). In order to identify heterotic hybrids and suitable parents, heterosis breeding entails evaluating elite parents and the F_1 generation (8).

Genetic diversity among individuals can change in two opposite directions, increasing and decreasing, leading to heterosis and inbreeding depression (9). Inbreeding depression (ID), which is the opposite of heterosis and refers to the decrease in inbred vigour brought on by inbreeding, differs based on the species (10). Non-additive gene action is responsible for both inbreeding depression and heterosis (11). Even though inbreeding produces subpar outcomes, it is nevertheless a useful technique in crop breeding and is practically necessary to create a superior genotype. Determining the efficacy of selection is aided by knowledge about the kind and severity of ID (12). Therefore, the goal of the current study was to quantify the degree of heterosis in different crosses in order to create improved F_1 hybrids and the level of inbreeding depression in the F_2 generation, which would subsequently be used in future crop development programs.

Materials and Methods

Experimental material

Prior screening studies were used to select the salinity-tolerant parental lines and E.C. 4 dS/m and pH 9.2 were used to assess their yield performance under salinity conditions. By using six lines and four testers in accordance with the line × tester approach, a total of twenty-four test crosses were created (13). During *Rabi* 2019–2020, the hybrids, testers and lines (Table 1) were assessed at the Agricultural Research Station, Kampasagar in Nalgonda, alongside check varieties. Using a randomised complete block design (RCBD) with three replications, the experiment was conducted in *Kharif* 2021, under E.C. 4 dS/m salt stress conditions, while adhering to the proper management procedures. Seedlings that were 25 days old were transplanted onto the experiment field, spaced 20 × 15 cm apart.

Observations recorded

On a plot-by-plot basis, mortality percentage, days to 50 % flowering and yield parameters and contributing characteristics were recorded. In accordance with IRRI-SES 2013, visual scoring of salt injury was also documented during the reproductive stage (Table 2). The following data were recorded: spikelet sterility (S %), 1000 grain weight (TW), plant height (PH), panicle length (PL), number of productive tillers (NPT), number of grains panicle^{-1} (NGP), number of unfilled grains panicle^{-1} (UFG), mortality percentage (M %) and days to 50 % flowering (DFF) and seed yield (SY). Ten randomly selected plants were observed in each entry and the mean value was calculated. In this study, the heterosis of F_1s in percentage over better parent, economic heterosis and inbreeding depression of F_2s over F_1s for twelve traits were analysed and the findings are shown in Table 3-12.

Statistical analysis

The mean over replications for each hybrid was computed for each trait to estimate the heterosis. The following formula was used to determine the superiority of the hybrid from the superior parent (HB). SH was stated as a percentage rise or reduction observed in F_1 over standard checks. ID was calcuted as per the formula in Equation 1-3.

$$\text{Heterobeltiosis (\%)} = \frac{\overline{F_1} - \overline{BP}}{BP} \times 100 \qquad \text{(Eqn. 1)}$$

where, BP = In the respectable cross combination, the average performance of the superior parent, F_1 = Mean hybrid performance

$$\text{Standard heterosis (\%)} = \frac{\overline{F_1} - \text{Mean of check}}{\text{Mean of check}} \times 100 \qquad \text{(Eqn. 2)}$$

$$\text{Inbreeding depression (\%)} = \frac{F1 - F2}{F1} \text{ X } 100 \qquad \text{(Eqn. 3)}$$

where F_1 is the mean hybrid performance, F_2 is the mean of the F_2 population for a characteristic and ID (%) is the inbreeding depression. By comparing the computed value of "t" with the tabulated value of "t" at the 0.05 and 0.01 levels of probability of error, the Student t-test was used to determine the significance of the estimations of heterosis, heterobeltiosis and inbreeding depression.

Results

The magnitude of better parent heterosis for mortality percentage ranged from -80.78 (KPS 10651 × KPS 2874) to 27.13 (KPS 10628 × CSR 36) and useful heterosis ranged from -52.96 (KPS 10651 × KPS 2874) to 145.54 (KPS 10640 × KPS 2874). Out of 24 crosses, KPS 10651 × KPS 2874, KPS 10642 × KPS 2874, KPS 10642 × RNR 11718 and KPS 10651 × RNR 11718 showed significant negative heterosis. The cross combinations KPS 10631 × CSR 23, KPS 10631 × KPS 2874, KPS 10631 × RNR 11718, KPS 10633 × CSR 36 and KPS 10631 × CSR 36 show low inbreeding depression. In respect of days to 50 % flowering, better parent heterosis ranged from -10.03 (KPS 10642 × KPS 2874) to 3.16 (KPS 10640 × RNR 11718) and economic heterosis ranged from -16.56 (KPS 10640 × KPS 2874) to -5.31 (KPS 10628 × CSR 23). The negative significant hybrids were KPS 10633 × RNR 11718, KPS 10642 × KPS 2874, KPS 10640 × KPS 2874, KPS 10628 × RNR 11718 and KPS 10642 × CSR 23. The cross combinations KPS 10640 × CSR 23, KPS 10628 × CSR 23 and KPS 10628 × CSR 36 show low inbreeding depression.

Table 1. List of lines, testers and check utilised for heterosis studies

S. No.	Material lines	Characteristics
1.	KPS 10628	Advanced breeding line
2.	KPS 10631	Advanced breeding line
3.	KPS 10633	Advanced breeding line
4.	KPS 10640	Advanced breeding line
5.	KPS 10642	Advanced breeding line
6.	KPS 10651	Advanced breeding line
	Testers	
7.	CSR 23	Alkalinity and salinity-tolerant
8.	CSR 36	Alkalinity tolerant
9.	KPS 2874	Local yield check
10.	RNR 11718	Local alkalinity and salinity
	Check	
11.	FL 478	Salinity check

Table 2. Scoring of damage for salt injury in field conditions in the rice standard evaluation system scale (IRRI-SES 2013)

Score	Growth scale	Salinity-induced reaction
1	Normal growth, no leaf symptoms	Highly tolerant
3	Nearly normal growth, but the leaf tips of a few leaves are whitish and rolled	Tolerant
5	Growth severely retarded, most leaves rolled, only a few are elongating	Moderately tolerant
7	Complete cessation of growth, most leaves are dry, some plants are drying	Susceptible
9	Almost all plants are dead or drying	Highly susceptible

Table 3. Heterobeltiosis (BP %), economic heterosis (SH %) and inbreeding depression (ID %) for mortality percentage in twenty-four crosses in rice

Hybrid	Mortality percentage		
Heterosis	HB	SH	ID
KPS 10628 × CSR 23	26.19**	139.24**	12.25*
KPS 10628 × CSR 36	27.13**	141.02**	8.54
KPS 10628 × KPS 2874	-16.66**	57.99**	-7.01
KPS 10628 × RNR 11718	-36.53**	20.33*	-4.06
KPS 10631 × CSR 23	-9.32**	114.99**	0.87
KPS 10631 × CSR 36	-1.79	132.86**	5.18
KPS 10631 × KPS 2874	-0.65	135.55**	1.63
KPS 10631 × RNR 11718	1.76	141.27**	2.40
KPS 10633 × CSR 23	-1.44	102.87**	6.47
KPS 10633 × CSR 36	3.99	114.05**	2.62
KPS 10633 × KPS 2874	-28.31**	47.57**	-1.11
KPS 10633 × RNR 11718	-61.77**	-21.30**	-52.76**
KPS 10640 × CSR 23	-4.53	127.80**	38.04**
KPS 10640 × CSR 36	-70.63**	-29.91**	-62.47**
KPS 10640 × KPS 2874	2.91	145.54**	26.30**
KPS 10640 × RNR 11718	-67.99**	-23.63**	-58.26**
KPS 10642 × CSR 23	9.94*	123.94**	51.75**
KPS 10642 × CSR 36	-71.88**	-42.72**	-66.17**
KPS 10642 × KPS 2874	-72.94**	-44.88**	-68.85**
KPS 10642 × RNR 11718	-72.16**	-43.30**	-65.75**
KPS 10651 × CSR 23	-26.15**	80.71**	7.51
KPS 10651 × CSR 36	-23.41**	87.42**	-1.27
KPS 10651 × KPS 2874	-80.78 **	-52.96 **	-76.18 **
KPS 10651 × RNR 11718	-71.85**	-31.11**	-62.96**

*Significant at 5 % level; ** Significant at 1 % level; HB: Heterobeltiosis; SH: Standard heterosis; ID: Inbreeding depression.

Table 4. Heterobeltiosis (BP %), economic heterosis (SH %) and inbreeding depression (ID %) for days to 50 % flowering in twenty-four crosses in rice

Hybrid	Days to 50 % Flowering		
Heterosis	HB	SH	ID
KPS 10628 × CSR 23	-2.57	-5.31	0.84
KPS 10628 × CSR 36	-2.89	-5.63	1.85
KPS 10628 × KPS 2874	-8.04**	-10.63**	-1.61
KPS 10628 × RNR 11718	-8.68**	-11.25**	-4.70
KPS 10631 × CSR 23	-4.53	-14.38**	-1.08
KPS 10631 × CSR 36	-3.48	-13.44**	-2.64
KPS 10631 × KPS 2874	-7.12*	-14.38**	-5.84
KPS 10631 × RNR 11718	-3.14	-13.13**	-2.80
KPS 10633 × CSR 23	-8.50**	-15.94**	-4.10
KPS 10633 × CSR 36	0.34	-7.81**	2.43
KPS 10633 × KPS 2874	-5.42	-12.81**	-5.26
KPS 10633 × RNR 11718	-10.20**	-17.50**	-8.81
KPS 10640 × CSR 23	2.14	-10.63**	0.57
KPS 10640 × CSR 36	-2.84	-14.38 **	-2.49
KPS 10640 × KPS 2874	-9.49**	-16.56**	-7.13
KPS 10640 × RNR 11718	3.16	-8.13**	4.07
KPS 10642 × CSR 23	-8.36**	-14.38**	-3.18
KPS 10642 × CSR 36	-7.36*	-13.44 **	-4.65
KPS 10642 × KPS 2874	-10.03**	-15.94**	-6.43
KPS 10642 × RNR 11718	-2.68	-9.06**	-0.34
KPS 10651 × CSR 23	-4.86	-14.38**	-1.26
KPS 10651 × CSR 36	-7.29*	-16.56**	-4.32
KPS 10651 × KPS 2874	-1.69	-9.38**	-0.51
KPS 10651 × RNR 11718	-5.56	-15.00**	-2.06

*Significant at 5 % level; ** Significant at 1 % level; HB: Heterobeltiosis; SH: Standard Heterosis; ID: Inbreeding depression.

Table 5. Heterobeltiosis (BP %), economic heterosis (SH %) and inbreeding depression (ID %) for plant height in twenty-four crosses in rice

Hybrid	Plant height (cm)		
Heterosis	HB	SH	ID
KPS 10628 × CSR 23	0.14	-8.61*	7.81*
KPS 10628 × CSR 36	-6.31	-14.49**	0.11
KPS 10628 × KPS 2874	-24.93**	-28.63**	-23.40**
KPS 10628 × RNR 11718	-4.45	-12.80**	-4.25
KPS 10631 × CSR 23	-5.71	-17.60**	-0.52
KPS 10631 × CSR 36	-8.97*	-20.44**	-4.69
KPS 10631 × KPS 2874	-18.78**	-22.78**	-15.36**
KPS 10631 × RNR 11718	-4.05	-12.80**	-2.17
KPS 10633 × CSR 23	2.83	-13.92**	6.28
KPS 10633 × CSR 36	-1.76	-17.76**	0.74
KPS 10633 × KPS 2874	-15.68**	-19.84**	-10.32**
KPS 10633 × RNR 11718	10.84**	0.73	15.39**
KPS 10640 × CSR 23	4.77	-4.51	12.73**
KPS 10640 × CSR 36	-21.45**	-28.41**	-16.12**

KPS 10640 × KPS 2874	-25.10**	-28.79**	-23.52**
KPS 10640 × RNR 11718	16.57**	6.23	16.73**
KPS 10642 × CSR 23	8.42*	-0.32	17.12**
KPS 10642 × CSR 36	16.11**	6.75	24.49**
KPS 10642 × KPS 2874	-22.01**	-25.85**	-20.70**
KPS 10642 × RNR 11718	-16.91**	-23.61**	-16.43**
KPS 10651 × CSR 23	-4.26	-15.10**	1.71
KPS 10651 × CSR 36	-1.66	-12.80**	3.67
KPS 10651 × KPS 2874	-6.09	-10.72**	-2.82
KPS 10651 × RNR 11718	-2.36	-11.26**	-1.16

*Significant at 5 % level; ** Significant at 1 % level; HB: Heterobeltiosis; SH: Standard heterosis; ID: Inbreeding depression.

Table 6. Heterobeltiosis (BP %), economic heterosis (SH %) and inbreeding depression (ID %) for the number of productive tillers/m^2 in twenty -four crosses in rice

Hybrid	Number of productive tillers/m^2		
Heterosis	HB	SH	ID
KPS 10628 × CSR 23	57.83**	51.07**	56.05**
KPS 10628 × CSR 36	43.24*	29.66	36.71*
KPS 10628 × KPS 2874	84.39**	69.72**	80.39**
KPS 10628 × RNR 11718	42.86*	46.79*	55.34**
KPS 10631 × CSR 23	36.14	33.64	37.85*
KPS 10631 × CSR 36	11.84	9.79	16.37
KPS 10631 × KPS 2874	32.09	29.66	36.33*
KPS 10631 × RNR 11718	5.65	8.56	8.07
KPS 10633 × CSR 23	47.28*	40.98*	33.92**
KPS 10633 × CSR 36	68.58**	52.60**	71.48**
KPS 10633 × KPS 2874	116.94**	99.69**	102.49**
KPS 10633 × RNR 11718	52.98**	57.19**	55.27**
KPS 10640 × CSR 23	57.83**	51.07**	61.44**
KPS 10640 × CSR 36	119.73**	100.92**	120.84**
KPS 10640 × KPS 2874	32.89	22.32	33.33
KPS 10640 × RNR 11718	113.99**	119.88**	126.46**
KPS 10642 × CSR 23	72.20**	64.83**	79.97**
KPS 10642 × CSR 36	109.46**	89.60**	113.06**
KPS 10642 × KPS 2874	72.43**	58.72**	76.83**
KPS 10642 × RNR 11718	69.94**	74.62**	83.60**
KPS 10651 × CSR 23	48.88*	42.51*	52.54**
KPS 10651 × CSR 36	65.10**	50.46**	65.66**
KPS 10651 × KPS 2874	101.33**	85.32**	102.34**
KPS 10651 × RNR 11718	78.87**	83.79**	89.59**

*Significant at 5 % level; ** Significant at 1 % level; HB: Heterobeltiosis; SH: Standard heterosis; ID: Inbreeding depression.

Table 7. Heterobeltiosis (BP %), economic heterosis (SH %) and inbreeding depression (ID %) for panicle length in twenty-four crosses in rice

Hybrid	Panicle length (cm)		
Heterosis	HB	SH	ID
KPS 10628 × CSR 23	12.39	5.69	14.04
KPS 10628 × CSR 36	20.46*	13.28	21.95*
KPS 10628 × KPS 2874	6.77	0.41	13.30
KPS 10628 × RNR 11718	3.46	-2.71	6.06
KPS 10631 × CSR 23	3.71	-5.28	8.71
KPS 10631 × CSR 36	5.47	-3.25	10.78
KPS 10631 × KPS 2874	35.34**	12.60	35.56**
KPS 10631 × RNR 11718	14.24	2.17	18.55*
KPS 10633 × CSR 23	-3.48	-2.30	1.48
KPS 10633 × CSR 36	-9.37	-8.27	-4.92
KPS 10633 × KPS 2874	-1.20	0.00	8.45
KPS 10633 × RNR 11718	-5.76	-4.61	0.07
KPS 10640 × CSR 23	6.97	-2.30	9.99
KPS 10640 × CSR 36	-0.15	-8.40	2.89
KPS 10640 × KPS 2874	9.58	-5.42	11.59
KPS 10640 × RNR 11718	7.12	-4.20	9.02
KPS 10642 × CSR 23	5.92	-2.98	6.07
KPS 10642 × CSR 36	-7.39	-15.04	-7.32
KPS 10642 × KPS 2874	-6.21	-14.09	-1.71
KPS 10642 × RNR 11718	13.91	4.34	15.27
KPS 10651 × CSR 23	-2.82	-11.25	1.55
KPS 10651 × CSR 36	-4.28	-12.20	0.23
KPS 10651 × KPS 2874	9.74	-8.40	9.92
KPS 10651 × RNR 11718	12.27	0.41	16.14

*Significant at 5 % level; ** Significant at 1 % level; HB: Heterobeltiosis; SH: Standard heterosis; ID: Inbreeding depression.

Table 8. Heterobeltiosis (BP %), economic heterosis (SH %) and inbreeding depression (ID %) for the total number of grains/panicle in twenty-four crosses in rice

Hybrid	Total number of grains/panicle		
Heterosis	HB	SH	ID
KPS 10628 × CSR 23	8.05	34.55**	10.52
KPS 10628 × CSR 36	3.71	30.76**	4.36
KPS 10628 × KPS 2874	46.14**	85.56**	47.56**
KPS 10628 × RNR 11718	52.59**	90.01**	55.37**
KPS 10631 × CSR 23	4.31	24.08*	5.19
KPS 10631 × CSR 36	10.25	39.00**	14.39
KPS 10631 × KPS 2874	-13.68	9.60	-10.14
KPS 10631 × RNR 11718	24.86*	49.92**	26.50**
KPS 10633 × CSR 23	28.84**	53.26**	35.17**
KPS 10633 × CSR 36	22.26*	54.15**	31.81**
KPS 10633 × KPS 2874	57.02**	99.37**	69.83**
KPS 10633 × RNR 11718	71.06**	105.38**	80.25 **
KPS 10640 × CSR 23	55.27**	90.23**	57.56**
KPS 10640 × CSR 36	76.33**	122.31**	78.85**
KPS 10640 × KPS 2874	37.89**	75.09**	40.36**
KPS 10640 × RNR 11718	62.73**	99.37**	64.37**
KPS 10642 × CSR 23	3.71	30.76**	6.73
KPS 10642 × CSR 36	57.24**	98.25**	57.24**
KPS 10642 × KPS 2874	2.98	30.76**	3.35
KPS 10642 × RNR 11718	41.87**	78.87**	45.34**
KPS 10651 × CSR 23	-16.09	3.36	-14.63
KPS 10651 × CSR 36	31.27**	65.51**	32.80**
KPS 10651 × KPS 2874	84.91**	134.79**	87.71**
KPS 10651 × RNR 11718	66.37**	104.94**	68.50**

*Significant at 5 % level; ** Significant at 1 % level; HB: Heterobeltiosis; SH: Standard heterosis; ID: Inbreeding depression.

Table 9. Heterobeltiosis (BP %), economic heterosis (SH %) and inbreeding depression (ID %) for unfilled grains/panicle in twenty-four crosses in rice

Hybrid	Unfilled grains/panicle		
Heterosis	HB	SH	ID
KPS 10628 × CSR 23	-44.91*	-0.74	-44.74*
KPS 10628 × CSR 36	-51.15**	-8.30	-50.15**
KPS 10628 × KPS 2874	-44.86*	10.04	-42.05*
KPS 10628 × RNR 11718	-63.04**	-26.64	-61.25**
KPS 10631 × CSR 23	-47.70*	-1.82	-46.47**
KPS 10631 × CSR 36	-56.32**	-18.01	-56.32**
KPS 10631 × KPS 2874	-75.14**	-50.37	-74.37**
KPS 10631 × RNR 11718	-79.89**	-60.08	-79.33**
KPS 10633 × CSR 23	-87.61**	-68.71	-85.50**
KPS 10633 × CSR 36	-79.06**	-47.14	-75.98**
KPS 10633 × KPS 2874	-60.26**	0.33	-55.61**
KPS 10633 × RNR 11718	-69.66**	-23.40	-66.03**
KPS 10640 × CSR 23	18.07	111.46 **	28.95
KPS 10640 × CSR 36	-8.05	72.62 *	0.56
KPS 10640 × KPS 2874	-27.57	44.57	-17.03
KPS 10640 × RNR 11718	-28.26	42.41	-18.01
KPS 10642 × CSR 23	-21.69	40.25	-11.56
KPS 10642 × CSR 36	-26.44	38.09	-15.23
KPS 10642 × KPS 2874	-29.19	41.33	-16.29
KPS 10642 × RNR 11718	-67.39**	-35.27	-61.54**
KPS 10651 × CSR 23	-76.15**	-43.90	-72.92**
KPS 10651 × CSR 36	-24.77	76.93*	-16.33
KPS 10651 × KPS 2874	-50.00**	17.60	-45.91**
KPS 10651 × RNR 11718	-66.06**	-20.16	-63.18 **

*Significant at 5 % level; ** Significant at 1 % level; HB: Heterobeltiosis; SH: Standard heterosis; ID: Inbreeding depression.

Table 10. Heterobeltiosis (BP %), economic heterosis (SH %) and inbreeding depression (ID %) for sterility percentage in twenty-four crosses in rice

Hybrid	Sterility percentage		
Heterosis	HB	SH	ID
KPS 10628 × CSR 23	-51.06**	-25.23	-49.78**
KPS 10628 × CSR 36	-53.46**	-30.56	-52.80**
KPS 10628 × KPS 2874	-62.33**	-41.05	-70.90**
KPS 10628 × RNR 11718	-76.90**	-61.72*	-75.36**
KPS 10631 × CSR 23	-51.47**	-20.06	-49.64**
KPS 10631 × CSR 36	-64.71**	-41.86	-72.96**
KPS 10631 × KPS 2874	-72.25**	-54.30	-71.54**
KPS 10631 × RNR 11718	-83.72**	-73.03*	-83.68**
KPS 10633 × CSR 23	-91.13**	-79.01 **	-89.22**
KPS 10633 × CSR 36	-85.33**	-65.28 *	-92.01**
KPS 10633 × KPS 2874	-78.79**	-49.77	-74.46**
KPS 10633 × RNR 11718	-84.17**	-62.53 *	-81.38**
KPS 10640 × CSR 23	-26.85	11.76	-18.49

KPS 10640 × CSR 36	-7.67	-6.52	-5.94
KPS 10640 × KPS 2874	0.47	-1.24	0.87
KPS 10640 × RNR 11718	-0.96	-3.42	-0.80
KPS 10642 × CSR 23	-8.20	-9.63	-5.44
KPS 10642 × CSR 36	8.13	9.47	12.89**
KPS 10642 × KPS 2874	5.21	3.42	8.29
KPS 10642 × RNR 11718	-12.94*	-15.37**	-10.87*
KPS 10651 × CSR 23	-7.41	-8.85	-6.08
KPS 10651 × CSR 36	-6.29	-5.12	-3.63
KPS 10651 × KPS 2874	-1.26	-2.95	0.00
KPS 10651 × RNR 11718	7.99	4.97	8.86

*Significant at 5 % level; ** Significant at 1 % level; HB: Heterobeltiosis; SH: Standard heterosis; ID: Inbreeding depression.

Table 11. Heterobeltiosis (BP %), economic heterosis (SH %) and inbreeding depression (ID %) for 1000 grain weight in twenty-four crosses in rice

Hybrid	1000 grain weight		
Heterosis	HB	SH	ID
KPS 10628 × CSR 23	-8.04	-9.47	-3.56
KPS 10628 × CSR 36	-2.76	-1.55	3.34
KPS 10628 × KPS 2874	-1.42	-3.11	3.31
KPS 10628 × RNR 11718	6.87	3.88	11.41*
KPS 10631 × CSR 23	1.88	1.09	2.28
KPS 10631 × CSR 36	-1.84	-0.62	-0.85
KPS 10631 × KPS 2874	0.01	-0.78	0.47
KPS 10631 × RNR 11718	1.72	0.93	2.77
KPS 10633 × CSR 23	8.52	6.83	9.29
KPS 10633 × CSR 36	-6.29	-5.12	-4.31
KPS 10633 × KPS 2874	7.42	5.59	8.11
KPS 10633 × RNR 11718	-6.07	-8.70	-6.00
KPS 10640 × CSR 23	-10.25	-11.65*	-9.83*
KPS 10640 × CSR 36	-7.67	-6.52	-5.94
KPS 10640 × KPS 2874	0.47	-1.24	0.87
KPS 10640 × RNR 11718	-0.96	-3.42	-0.80
KPS 10642 × CSR 23	-8.20	-9.63	-5.44
KPS 10642 × CSR 36	8.13	9.47	12.89**
KPS 10642 × KPS 2874	5.21	3.42	8.29
KPS 10642 × RNR 11718	-12.94*	-15.37**	-10.87*
KPS 10651 × CSR 23	-7.41	-8.85	-6.08
KPS 10651 × CSR 36	-6.29	-5.12	-3.63
KPS 10651 × KPS 2874	-1.26	-2.95	0.00
KPS 10651 × RNR 11718	7.99	4.97	8.86

*Significant at 5 % level; ** Significant at 1 % level; HB: Heterobeltiosis; SH: Standard heterosis; ID: Inbreeding depression.

Table 12. Heterobeltiosis (BP %), economic heterosis (SH %) and inbreeding depression (ID %) for seed yield per plant in twenty-four crosses in rice

Hybrid	Seed yield per plant		
Heterosis	HB	SH	ID
KPS 10628 × CSR 23	10.07	114.25**	14.13*
KPS 10628 × CSR 36	20.65*	99.11**	6.18*
KPS 10628 × KPS 2874	32.10**	98.89**	27.81**
KPS 10628 × RNR 11718	28.40**	93.32**	28.40**
KPS 10631 × CSR 23	-12.59	70.16**	4.09
KPS 10631 × CSR 36	19.30*	96.88**	12.43**
KPS 10631 × KPS 2874	40.32**	93.76**	43.33**
KPS 10631 × RNR 11718	0.30	51.00**	6.77
KPS 10633 × CSR 23	0.57	95.77**	18.15*
KPS 10633 × CSR 36	6.21	75.28**	16.16*
KPS 10633 × KPS 2874	26.13*	74.16**	26.74**
KPS 10633 × RNR 11718	36.39**	105.35**	22.95**
KPS 10640 × CSR 23	7.78	109.80**	28.16**
KPS 10640 × CSR 36	19.03*	96.44**	21.94**
KPS 10640 × KPS 2874	44.52**	99.55**	27.37**
KPS 10640 × RNR 11718	34.02**	101.78**	42.45**
KPS 10642 × CSR 23	1.37	97.33**	17.35*
KPS 10642 × CSR 36	14.44	88.86**	23.17**
KPS 10642 × KPS 2874	38.84**	96.66**	30.61**
KPS 10642 × RNR 11718	28.70**	93.76**	32.62**
KPS 10651 × CSR 23	-1.14	92.43**	1.46
KPS 10651 × CSR 36	22.54**	102.23**	20.65**
KPS 10651 × KPS 2874	33.13**	92.43**	26.17**
KPS 10651 × RNR 11718	20.56*	81.51**	23.02**

*Significant at 5 % level; ** Significant at 1 % level; HB: Heterobeltiosis; SH: Standard heterosis; ID: Inbreeding depression.

Heterobeltiosis for plant height ranged between -24.93 (KPS 10628 × KPS 2874) to 16.57 (KPS 10640 × RNR 11718) and economic heterosis ranged from -28.79 (KPS 10640 × KPS 2874) to 6.75 (KPS 10642 × CSR 36). Heterosis over better/superior parent for panicle length ranged from -9.37 (KPS 10633 × CSR 36) to 35.34 (KPS 10631 × KPS 2874) and useful heterosis ranged from -15.04 (KPS 10642 × CSR 36) to 13.28 (KPS 10628 × CSR 36). Out of 24 crosses, KPS 10631 × KPS 2874 and KPS 10628 × CSR 36 resulted in more panicle length than the better parent. The cross combinations KPS 10628 × CSR 36, KPS 10633 × CSR 36, KPS 10651 × CSR 23 and KPS 10651 × CSR 36 resulted in low inbreeding depression. The better parent values for number of productive tillers/m^2 were 5.65 (KPS 10631 × RNR 11718) to 119.73 (KPS 10640 × CSR 36) and economic heterosis ranged from 8.56 (KPS 10631 × RNR 11718) to 119.88 (KPS 10640 × RNR 11718). Out of 24 crosses, KPS 10640 × CSR 36, KPS 10633× KPS 2874, KPS 10640 × RNR 11718 and KPS 10642 × CSR 36 had higher ranks for desirable heterosis. The cross combinations KPS 10631 × RNR 11718, KPS 10631 × CSR 36, KPS 10640 × KPS 2874 and KPS 10633 × CSR 23 showed low inbreeding depression.

The heterosis over better/superior parent for the total number of grains per panicle ranged from -16.09 (KPS 10651 × CSR 23) to 84.91 (KPS 10651 × KPS 2874) and economic heterosis ranged from 3.36 (KPS 10651 × CSR 23) to 134.79 (KPS 10651 × KPS 2874). Out of 24 crosses, KPS 10651 × KPS 2874, KPS 10640 × CSR 36, KPS 10633 × RNR 11718 and KPS 10651 × RNR 11718 resulted in more grains than the better parent. The cross combinations KPS 10642 × KPS 2874, KPS 10628 × CSR 36, KPS 10631 × CSR 23 and KPS 10642 × CSR 23 resulted in low inbreeding depression. The heterobeltiosis for unfilled grains panicle^{-1} ranged from -87.61 (KPS 10633 × CSR 23) to 18.07 (KPS 10640 × CSR 23) and heterosis over the check ranged from -68.71 (KPS 10633 × CSR 23) to 111.46 (KPS 10640 × CSR 23). The cross KPS 10640 × CSR 36 exhibits very low inbreeding depression for this character. The range of estimates over better parent for sterility percentage was -91.13 (KPS 10633 × CSR 23) to -26.85 (KPS 10640 × CSR 23) and economic heterosis ranged from -79.01 (KPS 10633 × CSR 23) to 11.76 (KPS 10640 × CSR 23).

The better parent heterosis for 1000 grain weight started with a range from -12.94 (KPS 10642 × RNR 11718) to 8.13 (KPS 10642 × CSR 36) and economic heterosis ranged from -15.37 (KPS 10642 × RNR 11718) to 9.47 (KPS 10642 × CSR 36). Out of 24 crosses, KPS 10633 × CSR 23, KPS 10642 × CSR 36 and KPS 10651 × RNR 11718 had high values for desirable heterosis. The cross KPS 10651 × KPS 2874 exhibited no inbreeding depression for this character. The heterobeltiosis for seed yield ranged between -12.59 (KPS 10631 × CSR 23) to 44.52 (KPS 10640 × KPS 2874) and economic heterosis ranged from 51.00 (KPS 10631 × RNR 11718) to 114.25 (KPS 10628 × CSR 23). The cross combinations KPS 10628 × CSR 23, KPS 10640 × CSR 23, KPS 10633 × RNR 11718, KPS 10651 × CSR 36 and KPS 10640 × RNR 11718 showed a high value of economic heterosis. The crosses KPS 10651 × CSR 23 and KPS 10631 × CSR 23 exhibited low inbreeding depression. The cross combinations KPS 10631 × KPS 2874, KPS 10642 × RNR 11718, KPS 10642 × KPS 2874 and KPS 10628 × RNR 11718 showed high inbreeding depression.

Discussion

When F_1 hybrids outperform their better/superior parent (heterobeltiosis), the degree of heterosis is measured. The viability of producing hybrid seeds on a commercial scale determines the potential for utilising hybrid vigour. In a traditional crop improvement program, heterobeltiosis is a measure of the amount of transgressive segregants since the superiority of hybrids aids in identifying prospective cross combinations that have the ability to yield the highest level of transgressive segregants. In the current investigation, heterosis is reported over a better/superior parent (heterobeltiosis) and over a check (economic/standard heterosis) (Table 3).

The negative heterosis expressed by several crosses for characters such as mortality percentage, plant height, days to 50 % flowering, number of un-filled grains panicle^{-1}, sterility percentage, while positive heterosis for characters number of productive tillers/m^2, panicle length, total number of grains panicle^{-1}, 1000 grain weight and seed yield plant^{-1}, suggested that hybrids were superior to the parents for these traits and heterotic effects were in the desired direction. Negative heterosis for mortality % is desirable because hybrids showing less % of mortality than the parents have an added advantage to increase yield via other attributes and are more tolerant to stress conditions. Most of the crosses recorded negative heterosis with significant values. These combinations suggest a high probability of finding the low percentage of mortality under stress. Plants with negative heterosis are desirable for breeding short-durational, early-maturity hybrids and varieties. Some hybrids show positive heterosis; this may be due to genetic and epigenetic reprogramming of genes in specific hybrids as a result of combining two genetic components. The crosses expressed significant negative heterosis over better parent and economic parent in F_1, also showed favourable inbreeding depression in their F_2s, indicating earliness. Hence, selection for earliness in all these crosses would be effective in F_2 and subsequent generations (14-16).

Hybrids with negative or dwarf-semi dwarf stature were desired. The crosses expressed significant negative heterosis over better parent and economic parent in F_1, also showed favourable inbreeding depression in their F_2s, indicating dwarfness. Hence, selection for dwarfness in all these crosses would be effective in F_2 and subsequent generations. The importance of negative significant heterosis for plant height to develop dwarf plant types, in contrast to positive significant heterosis for plant height (17-19). Length of the panicle directly increases the yield, which is a desirable trait. Out of all the crosses, only two crosses have shown significance over better parents (20-22). Nineteen crosses have shown positive significant difference over better/superior parents for the trait number of productive tillers and eighteen were found significant over the check (23-24). The most important characteristic was a greater number of grains in the panicle, which adds economic weight to the crop. Significance for this trait over the better parent was shown by sixteen crosses and 22 crosses over the check. The presence of unfilled grain is not a desirable character. It should be negligible or low in number. The number of crosses that have shown significance over a better parent was sixteen.

Sterility percentage is less; the reproducing ability of the panicle is more, which is the most important yield trait, directly influencing the increase in yield. The number of crosses that showed negative heterobeltiosis was twenty-one and 7 crosses showed high economic heterosis (25-26). 1000-grain weight is an indicator of the end product, i.e. grain yield (26-29). High heterosis accompanied by low or no inbreeding depression indicates the predominance of additive gene action in the expression of such traits. Seed yield per plant is the ultimate product of hybrids. And the number of crosses that have shown a significant positive difference over better/superior parents was fifteen and 24 crosses over the check (26, 30). Overall, significant heterosis, heterobeltiosis and standard heterosis for seed yield plant^{-1} and other related characteristics indicated that there was a lot of genetic variation among the testers, lines and crosses. Additionally, the unidirectional distribution of allelic constitution contributed to the desired heterosis in the current material. This study highlights the potential of heterosis breeding for achieving higher yields and improving crop productivity. The results suggest that heterosis breeding can be a useful strategy for crop improvement programs. In this study, certain cross combinations showed good heterosis in terms of the number of productive tillers, filled grains per panicle and the panicle length. Additionally, some cross combinations had the highest economic heterosis for seed yield per plant. Future breeding projects may employ the cross combinations to maintain the particular rice gene pool by improving transgressive segregants and increasing grain yield. In general, these results offer a significant understanding of the use of heterosis breeding to address the challenges of food security and sustainable agriculture.

One crucial factor for crop breeding programs is inbreeding depression. Self-pollinated crop species, such as rice, exhibit less inbreeding depression because of their low genetic load. Large-effect harmful gene mutations should be eliminated via natural selection and/or plant breeding. Consequently, it is believed that the inbreeding depression seen in this study is not caused by homozygous harmful allele expression, as is the case with cross-pollinated crops. Table 3-12 displays the cross-wise and character outcomes of inbreeding depression. The degree of inbreeding depression differed among crosses, suggesting that the genetic makeup of the crosses had an impact.

Both heterosis and low to moderate levels of inbreeding were seen in the current investigation. Low inbreeding depression and highly significant and positive heterosis are preferred. There was a positive inbreeding depression identified in KPS 10631 × RNR 11718, KPS 10633 × CSR 36 and KPS 10628 × CSR 36 for mortality percentage and KPS 10640 × CSR 23 and KPS 10640 × RNR 11718 for days to first flowering, showing the likelihood of obtaining the desired segregants in the generations that are segregating. Similarly, a markedly positive ID was also noted for plant height in cross KPS 10628 × CSR 23 and KPS 10640 × CSR 23. Significant inbreeding depression was seen in both positive and negative directions for plant height (14-16). In case of sterility percentage and unfilled grains per panicle, significant negative inbreeding depression was seen in the majority of the crosses. It indicates that these crossings have high seed setting and a high chance of surviving under stress conditions may be due to additive gene action. Twenty-one crossings showed positive and significant inbreeding depression in F_2 for the number of productive tillers/plant and seed yield per plant. In almost all the crosses, high heterosis for grain yield and yield-associated characters followed by inbreeding depression in F_2 was observed, suggesting the presence of non-additive (dominant) gene action in controlling the heterosis for seed yield per plant (26, 30).

Crossing the desired segregants in a biparental mating pattern in F_2 and subsequent generations to produce selected plant types in progenies, hence preventing inbreeding depression. The existence of undesired inbreeding depression and greater estimates of different heterotic effects in a positive direction indicated that heterosis breeding would be extremely valuable for increasing rice grain production in salinity-prone environments. According to the current research, the salinity tolerance genes should be present in the parents involved in the crossing programme. Both additive and non-additive gene actions control tolerance expression, indicating that heterosis breeding is an ideal method for enhancing tolerance in rice genotypes.

Conclusion

The current study suggests that parents participating in the crossing program should have genes for salinity tolerance. Heterosis breeding is the best way to increase tolerance in rice genotypes because both additive and non-additive gene activities regulate tolerance expression. Desired segregants should be crossed in a bi-parental mating way to produce preferred plant types in the offspring to prevent inbreeding depression in F_2 and subsequent generations. The existence of unwanted inbreeding depression and greater estimates of various heterotic effects in a positive direction indicated that heterosis breeding would be extremely beneficial for increasing rice seed yield.

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Authors' contributions

PHB carried out the experiment, took observations and analysed the data and writing the original draft. GSP guided the research by formulating the research concept and approved the final manuscript. KS contributed by developing the ideas, reviewed the manuscript. RMS contributed by imposing the experiment, helped in editing, summarizing, revising and approved the final manuscript. CHDR helped in summarizing, editing and revising the manuscript. All authors read and approved the final version of the manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

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