

## Dissecting genetic variability and character associations of physiological, biochemical, agronomic, and yield traits in rice genotypes under salinity stress

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**Abstract:** Salinity stress poses an increasing threat to global rice production, particularly under climate change. Enhancing salinity tolerance is crucial to sustain rice production and food security. This study aimed to assess genetic variation among rice parental genotypes and their derived crosses under salinity stress by evaluating physiological, biochemical, agronomic, and yield-related traits. Seven diverse rice genotypes were used to develop 21 crosses using a half-diallel mating design in the summer of 2023. The parental genotypes and their derived crosses were evaluated in the summer of 2024 under controlled greenhouse lysimeter conditions. Salinity stress was induced by irrigation with water containing 10.60 dS/m, and soil salinity was maintained at 9.60 dS/m through controlled irrigation and drainage. Twenty key traits were studied, including phenological and agronomic attributes, yield traits, and physiological and biochemical markers such as relative water content, leaf CO<sub>2</sub> assimilation, proline accumulation, malondialdehyde content, and antioxidant enzyme activities, to assess salinity tolerance in rice genotypes. The results demonstrated highly significant variation among the evaluated parental genotypes and their derived crosses across physiological, biochemical, agronomic, and yield-related traits, indicating considerable genetic variability in the studied plant materials. The genotypes C9, R8, and R6 were identified as superior combiners contributing favourable alleles for salinity tolerance. Eleven promising F<sub>1</sub> crosses exhibited enhanced growth, improved antioxidant enzyme activities, osmotic adjustment, reduced oxidative damage, and higher grain yield under salinity stress. Exploiting these plant materials can improve the development of novel rice genotypes tolerant of salt-affected environments, addressing the current challenges posed by climate change. Strong associations were observed among physiological, biochemical, agronomic, and yield-related traits, indicating an integrated network of responses that collectively contribute to enhanced salinity tolerance in rice.

**Keywords:** *Oryza sativa* L.; rice breeding; nutrition; diallel analysis; lysimeter experiment; physiological parameters; agronomic performance; sustainable rice production

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Rice (*Oryza sativa* L.) is one of the most important staple food crops worldwide (Rezvi et al. 2023). It plays a critical role in food security, as billions of people depend on rice as a primary source of calories and nutrients (Verma et al. 2021). The global cultivated area is around 168 million hectares and produces around 800 million tons (FAOSTAT 2023). However, the sustainability of rice production faces increasing challenges from environmental stresses, including salinity, particularly in arid and semi-arid regions and coastal agricultural areas (ElShamey et al. 2022, Sackey et al. 2025).

Salinity is an abiotic stressor that constrains plant growth and development and reduces final grain yield (Mansour et al. 2021). It disrupts water uptake by lowering osmotic potential, leading to physiological drought even when water is available (Selem et al. 2022). This osmotic stress causes reduced cell expansion, impaired photosynthesis, stunted growth, and decreased biomass accumulation (ElSayed et al. 2022). In addition, excessive sodium and chloride ions lead to ion toxicity, causing nutrient imbalances (Desoky et al. 2021). Ion toxicity disrupts metabolic processes, damages cellular membranes, and causes oxidative stress by generating reactive oxygen species (Rao et al. 2025). Salinity also impairs reproductive development by reducing panicle numbers, decreasing the number of filled grains per panicle, and lowering fertility rates (Mheni et al. 2024). These adverse effects necessitate efforts to develop new salt-tolerant rice varieties capable of maintaining productivity in saline environments, which are further exacerbated by climate change (Anwar et al. 2025).

Improving salt tolerance in rice is difficult due to the complex interactions among multiple physiological, biochemical, and agronomic traits, each controlled by polygenic inheritance (Moustafa et al. 2021, Saleem et al. 2025). The adaptive strategies in

rice include osmotic adjustment and enhancement of antioxidative defence systems to mitigate reactive oxygen species-induced cellular damage (Talaat et al. 2023). Effective breeding for salt tolerance requires generating novel genetic variability and accurate phenotypic evaluation under controlled salinity stress conditions (Hu and Schmidhalter 2023). This approach facilitates combining favourable alleles from diverse parental genotypes to develop resilient rice cultivars that sustain productivity (Gracia et al. 2012, Salem et al. 2020). Besides, enables comprehensive exploration of critical physiological and biochemical pathways and associated yield-related traits.

Diallel mating designs remain a valuable tool for estimating combining abilities and detecting heterosis (Sakran et al. 2022, Heiba et al. 2023). Hence, identification of superior parental genotypes and crosses for breeding programs (Kamara et al. 2021, Galal et al. 2023). This study aimed to evaluate genetic variability and combining abilities for a range of physiological, biochemical, agronomic, and yield-related traits in diverse rice genotypes and their crosses under controlled salinity stress using lysimeter conditions. The results aim to provide actionable insights and germplasm resources to enhance breeding efforts to improve rice productivity in salt-affected environments amid ongoing climate adversity.

## MATERIAL AND METHODS

### Experimental site and plant materials

This study was conducted at the Rice Research and Training Centre (RRTC) in Sakha, Kafr El Sheikh Governorate, Egypt, during the summer seasons of 2023 and 2024. Seven diverse rice genotypes comprising three local and four exotic genotypes were used as parental genotypes (Table 1). The three lo-

Table 1. Name, pedigree, subspecies, and origin of the parental genotypes used in the study

No	Code	Name	Pedigree	Subspecies	Origin
1	Z1	GZ-11332-2-2-2	GZ8455-9-1-1-2/SKC23819-192-2-2-2-1-1-2-2-1-2/HUA565	Japonica	Egypt
2	G8	Giza-183	Giza 178/SKC23893	Indica/Japonica	Egypt
3	S4	Sakha-104	GZ4096-8-1/GZ4100-9	Japonica	Egypt
4	R6	AR-061-20-2-3-2-2-3	Introduced from Africa RC	Indica/Japonica	Africa RC
5	R7	AR-278-28-2-2-1-3	Introduced from Africa RC	Indica/Japonica	Africa RC
6	R8	AR-278-41-1-1-6-3	Introduced from Africa RC	Indica/Japonica	Africa RC
7	C9	CSR-90	IR 10206-29-2-1/SUAKOKO	Indica	India

/ – sequential crosses between the listed parental genotypes; Africa RC – Africa Rice Centre

cal genotypes were obtained from the Agricultural Research Centre in Egypt, three from the Africa Rice Centre (ARC), and one from the Central Soil Salinity Research Institute (CSSRI), India (Table 1). Giza-183 and Sakha-104 are high-yielding Egyptian rice varieties developed to mitigate the effects of climate change, such as drought and salinity, and to provide high-quality grains. The other parental genotypes were homozygous advanced breeding lines. A half diallel mating design (7 × 7) was implemented during the summer of 2023. The emasculation was performed using hot water (43 °C for 10 min), followed by manual pollination. For each cross, 20 panicles per parental combination were emasculated. Pollination was carried out the following morning using fresh pollen from the designated male parent. The crossing resulted in 21 F<sub>1</sub> crosses among the seven parental genotypes.

#### Salinity conditions and experimental design.

The experiment was carried out in the summer of 2024 under salinity stress using greenhouse lysimeter beds (1 m × 2 m) filled with layered soil (60 cm clay, 20 cm sand, 20 cm gravel). Salinity was artificially induced at EC = 10.6 dS/m in irrigation water using NaCl and CaCl<sub>2</sub> (2:1 ratio). Soil salinity was stabilised at 9.60 dS/m with controlled irrigation and drainage. A randomised complete block design with three replicates was applied; each replicate contained three 1-m rows per genotype, spaced 15 × 15 cm apart.

**Data collection.** Data were collected on twenty traits representing rice response to salinity stress. Relative water content (RWC) was calculated using the following formula.  $RWC (\%) = [(fresh\ weight - dry\ weight) / (turgid\ weight - dry\ weight)] \times 100$  (Barrs and Weatherley 1962). Leaf CO<sub>2</sub> assimilation rate was measured using gas samples analysed by a gas chromatograph equipped with a flame ionisation detector (GC-8A, Shimadzu Corporation, Kyoto, Japan). Lipid peroxidation was estimated by determining malondialdehyde (MDA) content using the method described by Hodges et al. (1999). Proline concentration was quantified spectrophotometrically according to the method of Bates et al. (1973). Catalase (CAT) activity was determined using the method of Aebi (1984). Ascorbate peroxidase (APX) activity was determined following the method described by Fielding and Hall (1978). Superoxide dismutase (SOD) activity was assayed according to the procedure described by Giannopolitis and Ries (1977). Days to heading was recorded as the number of days from sowing to when 50% of plants in a row showed

fully emerged panicles. Plant height was measured from the soil surface to the tip of the tallest panicle at maturity. The number of panicles per plant was counted manually on 20 plants selected from the middle row of each plot. Panicle length was measured from the base to the tip of the panicle. Panicle weight was determined by weighing the harvested panicles after air-drying. Filled and unfilled grains per panicle were counted using visual examination. Fertility percentage was calculated as the ratio of filled grains to total grains. The number of branches per panicle was counted. The grain weight was recorded by weighing 1 000 grains from dried samples. Grain yield per plant was measured by threshing, cleaning, and weighing grains from each plant. Biological yield was the total aboveground biomass dry weight. The harvest index was computed as the ratio of grain yield to biological yield.

**Statistical analysis.** The collected data were subjected to statistical analyses to determine the significance of genotypic variation and combining abilities. Analysis of variance (ANOVA) was performed using a randomised complete block design (RCBD) model. General and specific combining abilities were estimated using the Griffing method (Griffing 1956). Multivariate statistical analyses, including cluster analysis, principal component analysis, and heatmaps, were performed in R version 4.2.0 using the packages ggplot2, factoextra, and FactoMineR (Boston, USA). A correlation matrix was generated using the corrplot package.

## RESULTS

**Analysis of variance.** The analysis of variance presented in Table 2 displays highly significant genetic variability for all studied physiological, biochemical, agronomic, and yield traits. The significant differences observed among genotypes, crosses, and parental genotypes indicate considerable genetic variability in the studied plant materials. The detected significant differences between parental genotypes and crosses indicate the effectiveness of the applied crossing scheme in generating new genetic combinations with enhanced traits. The developed crosses produced highly significant mean squares for all traits, reflecting hybrid vigour and the capacity to exploit heterosis for yield and salinity tolerance. Main effects due to parental genotypes were also significant for most traits, indicating inherent genetic diversity among the parental genotypes. The partitioning of variance

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Table 2. Mean squares of analysis of variance for physiological, biochemical, agronomic and yield traits of parental rice genotypes and their developed crosses evaluated under salinity conditions

Source of variation	df	RWC	CO <sub>2</sub>	MDA	PRO	APX	SOD	CAT
Genotypes	27	40.82**	18.28**	10.95**	0.1024**	2.44**	7.36**	7.47**
Crosses (Cr)	20	40.63**	16.15**	12.49**	0.1047**	1.51**	8.31**	8.74**
Parents (P)	6	38.71**	17.38**	5.41**	0.0979**	2.82**	4.89**	4.13**
PvsCr	1	57.41**	66.48**	13.41**	0.0830**	18.94**	3.38**	2.09**
GCA	6	44.40**	16.69**	6.97**	0.0934**	1.49**	3.34**	4.62**
SCA	21	4.81**	3.07**	2.70**	0.0172**	0.62**	2.20**	1.88**
Error	54	0.99	0.21	0.43	0.0011	0.12	0.07	0.09
		DTH	PLH	NPP	PLT	PWE	NBP	FER
Genotypes	27	117.41**	536.48**	13.91**	17.01**	0.71**	19.64**	137.22**
Crosses	20	106.35**	499.45**	11.96**	19.33**	0.60**	15.91**	148.61**
Parents	6	47.54**	220.71**	9.76**	9.08**	1.18**	34.97**	44.78**
PvsCr	1	757.81**	3 171.57**	77.78**	18.35**	0.27**	2.29 <sup>ns</sup>	464.12**
GCA	6	57.09**	191.39**	9.47**	5.31**	0.48**	18.79**	61.26**
SCA	21	34.01**	175.24**	3.26**	5.77**	0.17**	3.05**	41.30**
Error	54	0.67	6.37	0.23	0.68	0.01	0.27	0.32
		FGP	UGP	TGW	GYP	BYP	HRI	
Genotypes	27	1 138.34**	505.75**	10.54**	104.12**	530.67**	32.67**	
Crosses	20	1 106.12**	510.76**	10.46**	84.88**	422.22**	33.74**	
Parents	6	1410.08**	214.11**	11.28**	114.44**	373.65**	29.28**	
PvsCr	1	152.44**	2 155.43**	7.65**	426.92**	3641.92**	31.72*	
GCA	6	1 010.28**	203.71**	9.67**	83.10**	319.95**	19.55**	
SCA	21	199.21**	158.55**	1.75**	20.88**	136.02**	8.42**	
Error	54	6.26	1.29	0.04	1.02	3.42	1.99	

PvsCr – parents versus crosses; df – degrees of freedom. Statistical significance levels are indicated using \* $P < 0.05$  and \*\* $P < 0.01$ . RWC – relative water content; CO<sub>2</sub> – leaf CO<sub>2</sub> assimilation rate; PRO – proline content; MDA – malondialdehyde; APX – ascorbate peroxidase; SOD – superoxide dismutase; CAT – catalase; DTH – days to heading; PLH – plant height; NPP – number of panicle/plant; PLT – panicle length; PWE – panicle weight; NBP – number of branches/panicle; FER – fertility percentage; FGP – filled grains/panicle; UGP – unfilled grains/panicle; TGW – thousand grain weight; GYP – grain yield per plant; BYP – biological yield per plant; HRI – harvest index

indicated that both general combining ability (GCA) and specific combining ability (SCA) contributed significantly to trait variance. Significant differences were observed for GCA and SCA across traits, suggesting the importance of additive and non-additive genetic effects to salt tolerance.

### Mean performance

**Physiological and biochemical parameters.** The studied physiological and biochemical traits in rice parental genotypes and their derived crosses under salinity stress are presented in Table 3. Relative water content is an important indicator of plant water status

under salinity. It ranged from 68.44% to 81.73% in all evaluated genotypes. The highest RWC were assigned for R8 × C9, Z1 × C9, G8 × C9, R7 × C9, R6 × C9, and C9. Measurements of leaf CO<sub>2</sub> assimilation rate ranged from 15.95 to 25.01 μmol/m<sup>2</sup>/s, reflecting differences in photosynthetic performance in the evaluated genotypes. The highest photosynthetic capacity was recorded by S4 × C9, Z1 × C9, R6 × R8, G8 × C9, R8 × C9, and R7 × C9. Malondialdehyde content, a marker of lipid peroxidation and oxidative damage, ranged from 14.57 to 22.82 μmol/g FW (fresh weight), indicating differential levels of damage. The lowest values were observed by G8 × C9, G8 × R7, S4 × C9, R7 × C9, G8 × R6, and Z1 × C9 compared to

Table 3. Physiological and biochemical responses of rice parental genotypes and their derived crosses under salinity stress

Genotype	RWC (%)	CO <sub>2</sub> (μmol/m <sup>2</sup> /s)	MDA (μmol/g FW)	PRO (μmol/g DW)	APX	SOD	CAT
					(unit g/protein)		
Z1	68.44	15.95	22.06	1.49	4.97	12.28	13.88
G8	73.50	18.97	19.78	1.54	5.64	15.44	15.06
S4	70.20	19.20	20.38	1.66	6.00	12.78	14.54
R6	75.24	21.63	19.02	1.64	6.35	14.34	16.10
R7	77.50	22.23	19.34	1.74	7.02	15.00	14.33
R8	74.47	20.65	18.67	1.90	7.58	14.10	14.42
C9	78.22	22.99	17.90	1.98	7.44	15.57	17.20
Z1 × G8	71.30	17.59	22.12	1.64	6.79	12.97	14.83
Z1 × S4	69.17	19.59	22.82	1.46	6.42	13.43	15.43
Z1 × R6	77.37	21.25	19.15	1.82	7.48	13.09	14.53
Z1 × R7	76.60	20.93	18.59	1.87	7.39	11.98	13.33
Z1 × R8	78.03	22.93	18.83	1.75	7.09	13.11	15.01
Z1 × C9	80.53	24.97	17.87	1.70	7.57	12.84	13.88
G8 × S4	69.47	16.89	22.24	1.48	7.35	15.78	11.86
G8 × R6	73.25	21.59	17.82	1.62	7.28	12.54	14.45
G8 × R7	74.02	20.97	15.72	1.70	7.65	11.12	14.36
G8 × R8	75.32	23.30	18.21	1.65	7.99	13.42	14.51
G8 × C9	80.42	24.63	14.57	1.91	8.16	10.75	18.47
S4 × R6	72.01	21.59	18.20	1.84	7.58	13.30	17.16
S4 × R7	72.78	20.30	18.93	1.80	7.58	12.90	17.97
S4 × R8	74.08	22.63	19.15	1.91	6.91	14.80	15.01
S4 × C9	76.84	25.01	15.98	1.97	7.35	15.24	18.83
R6 × R7	75.56	23.30	19.41	1.57	5.71	13.85	15.46
R6 × R8	76.33	24.67	19.69	1.57	8.55	14.07	15.66
R6 × C9	79.96	23.63	19.09	1.95	8.61	15.41	17.27
R7 × R8	77.66	23.92	18.01	2.04	8.36	14.22	14.87
R7 × C9	80.39	24.01	16.68	2.11	7.91	16.65	15.33
R8 × C9	81.73	24.26	19.00	2.02	8.28	17.29	16.00
LSD <sub>0.01</sub>	2.820	1.30	1.86	0.10	1.00	0.74	0.83
LSD <sub>0.05</sub>	3.750	1.73	2.48	0.13	1.33	0.99	1.11

RWC – relative water content; CO<sub>2</sub> – leaf CO<sub>2</sub> assimilation rate; MDA – malondialdehyde; PRO – proline content; APX – ascorbate peroxidase; SOD – superoxide dismutase; CAT – catalase; FW – fresh weight; DW – dry weight

the other genotypes, reflecting differential oxidative stress levels. Proline accumulation, as an osmoprotectant, varied between 1.46 and 2.11 μmol/g DW (dry weight). PRO was significantly higher in several genotypes, in particular R7 × C9, R7 × R8, R8 × C9, C9, S4 × C9, and R6 × C9, compared to the other genotypes. Antioxidant enzyme activities, including ascorbate peroxidase, superoxide dismutase, and catalase, were significantly higher in crosses than in parental genotypes, indicating an enhanced an-

tioxidative defence mechanism in response to salinity stress. The activities of APX, SOD and CAT ranged from 4.97 to 8.61, 10.75 to 17.29, and 11.86 to 18.83 units g/protein, respectively. The highest APX activity was produced by R6 × C9, R6 × R8, R7 × R8, R8 × C9, G8 × C9, and G8 × R8. The uppermost SOD activity was displayed by R8 × C9, R7 × C9, G8 × S4, C9, G8, and R6 × C9. The greatest CAT activity was recorded by S4 × C9, G8 × C9, S4 × R7, R6 × C9, C9, and S4 × R6.

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**Agronomic traits.** Considerable variation was observed among the rice parental genotypes and their crosses for agronomic traits under salinity stress, indicating that substantial genetic diversity could be utilised for breeding salt-tolerant cultivars. Days to heading (DTH) ranged from 84.33 to 108.00 days, reflecting variation in development rate under stress conditions (Table 4). The genotypes G8, R6 × R7, Z1, R7 × R8, R6, and R7 displayed the earliest heading under salinity stress. While the genotypes S4 × C9, R8 × C9, S4 × R6, S4 × R8, R6 × C9, and G8 × R6

exhibited the latest heading. Plant height (PLH) also showed wide variation from 75.33 to 122.67 cm, suggesting heterosis effects on vegetative growth. The genotypes Z1, G8, Z1 × G8, G8 × S4, S4, and Z1 × R7 had the shortest stature. The highest plant height values were assigned for G8 × R8, G8 × C9, G8 × R7, G8 × R6, R8 × C9, and Z1 × C9. The number of panicles per plant (NPP) varied from 9.67 to 18.33, with crosses surpassing parental genotypes. It was greatest in the crosses S4 × C9, S4 × R7, G8 × C9, G8 × C9, S4 × R8, and S4 × R8. Panicle length (PLT)

Table 4. Agronomic traits of rice parental genotypes and their derived crosses evaluated under salinity stress conditions

Genotype	DTH (day)	PLH (cm)	NPP	PLT (cm)	PWE (g)	NBP
Z1	86.67	75.33	9.67	20.83	2.27	7.67
G8	84.33	76.33	12.33	20.17	2.59	11.00
S4	95.00	86.00	12.33	21.50	2.55	10.33
R6	89.00	93.67	11.67	25.00	3.71	14.67
R7	90.33	90.33	11.00	21.33	3.38	15.67
R8	91.00	91.67	10.67	23.67	3.90	15.67
C9	95.00	97.67	15.33	21.00	3.14	16.67
Z1 × G8	98.33	84.00	11.00	23.00	3.18	9.67
Z1 × S4	98.00	88.33	10.33	24.33	2.98	11.33
Z1 × R6	99.67	89.00	13.33	20.33	3.49	11.00
Z1 × R7	94.67	86.33	13.67	23.00	3.51	14.00
Z1 × R8	92.00	109.3	12.00	26.00	3.72	13.00
Z1 × C9	96.00	110.7	14.00	22.50	3.63	11.33
G8 × S4	92.67	85.67	11.67	18.83	2.58	8.00
G8 × R6	100.0	116.0	13.33	25.33	3.18	16.00
G8 × R7	92.00	120.0	14.67	25.00	3.48	15.67
G8 × R8	98.67	122.7	13.00	24.83	3.95	16.00
G8 × C9	91.00	122.3	16.33	27.83	3.71	10.33
S4 × R6	105.0	103.3	16.33	20.17	2.88	12.33
S4 × R7	94.67	103.7	17.00	19.83	2.74	11.33
S4 × R8	103.0	91.33	15.67	19.00	2.88	12.33
S4 × C9	108.0	100.0	18.33	22.00	2.38	10.67
R6 × R7	86.00	95.67	14.00	26.67	2.66	15.33
R6 × R8	95.00	95.67	14.00	23.83	3.14	15.67
R6 × C9	101.0	88.33	15.67	21.00	2.74	11.33
R7 × R8	87.00	94.67	13.33	21.67	3.71	15.00
R7 × C9	100.0	109.7	14.67	23.67	3.57	13.00
R8 × C9	107.0	114.3	13.33	24.33	3.28	13.67
<i>LSD</i> <sub>0.01</sub>	2.33	7.15	1.36	2.34	0.26	1.48
<i>LSD</i> <sub>0.05</sub>	3.10	9.53	1.81	3.12	0.35	1.98

DTH – days to heading; PLH – plant height; NPP – number of panicles/plant; PLT – panicle length; PWE – panicle weight; NBP – number of branches/panicle

showed significant variation from 18.83 to 27.83 cm. The uppermost length was displayed by G8 × C9, R6 × R7, Z1 × R8, G8 × R6, and R6. Panicle weight (PWE) extended from 2.27 to 3.95 g. The heaviest panicle weights were recorded by G8 × R8, R8, Z1 × R8, R6, R6, and R6. The number of branches per panicle (NBP) varied from 7.67 to 16.67 g. The highest branch number was produced by C9, G8 × R6, G8 × R6, R7, and R7.

**Yield traits.** Studied yield-attributed traits demonstrated diverse genotypic responses to salinity stress (Table 5). Fertility percentage (FER) spanned from

66.01% and 89.90% with some genotypes showing higher fertility associated with better reproductive success under stress conditions. The genotypes G8 × R7, C9, R6, G8 × R6, G8 × C9, and R7 × R8 exhibited the highest fertility percentage. Filled grains per panicle (FGP) ranged from 101.67 to 166.67 grains. The best-performing genotypes were G8 × R8, R6 × R8, R8, R6 × C9, R6, and R7 × R8. The number of unfilled grains per panicle (UGP) varied from 15.67 to 63.00. The genotypes with the fewest unfilled grains, indicating better grain-filling efficiency, were C9, G8 × R7, G8 × R6, R6, G8, and G8 × C9. Thousand-grain weight

Table 5. Yield traits of rice parental genotypes and their derived crosses evaluated under salinity stress conditions

Genotype	FER (%)	FGP	UGP	TGW (g)	GYP (g)	BYP (g)	HRI (%)
Z1	81.12	101.67	23.67	25.23	22.67	57.00	39.97
G8	85.53	116.33	19.67	21.87	29.33	62.67	46.80
S4	83.08	127.67	26.00	25.23	26.00	66.67	39.03
R6	89.15	159.00	19.33	19.83	35.33	76.00	46.47
R7	82.24	137.33	29.67	23.17	31.67	73.00	43.47
R8	79.82	162.00	41.00	21.83	36.33	79.33	45.83
C9	89.65	135.67	15.67	22.83	40.33	90.33	44.70
Z1 × G8	76.46	113.67	35.00	24.33	26.67	59.33	45.07
Z1 × S4	76.35	112.00	34.67	22.33	26.00	58.67	44.37
Z1 × R6	78.03	139.00	39.00	23.00	36.33	89.67	40.53
Z1 × R7	74.79	128.67	43.33	24.73	34.33	80.33	42.77
Z1 × R8	77.90	142.33	40.33	24.00	39.00	89.33	43.70
Z1 × C9	85.20	138.00	24.00	26.00	42.67	90.00	47.43
G8 × S4	81.30	104.33	24.00	22.67	25.33	78.67	32.23
G8 × R6	88.95	142.33	17.67	21.67	38.67	90.67	42.67
G8 × R7	89.90	151.33	17.00	21.87	37.00	81.67	45.37
G8 × R8	80.36	166.67	40.67	21.43	38.33	85.67	44.83
G8 × C9	88.46	156.00	20.33	21.53	44.33	98.00	45.23
S4 × R6	69.48	129.67	57.00	21.80	38.33	93.33	41.10
S4 × R7	72.81	112.33	42.00	21.70	35.33	93.33	37.87
S4 × R8	66.39	108.67	55.00	23.17	36.67	93.67	39.20
S4 × C9	74.14	145.33	50.67	20.00	43.33	104.0	41.77
R6 × R7	66.01	122.33	63.00	18.83	38.00	97.00	39.20
R6 × R8	84.34	164.67	30.67	18.33	39.00	93.00	41.93
R6 × C9	82.75	159.67	33.33	20.00	34.00	76.33	44.53
R7 × R8	87.71	157.00	22.00	21.90	39.00	91.33	42.67
R7 × C9	79.71	145.33	37.00	22.90	42.67	103.33	41.30
R8 × C9	76.72	145.00	44.00	23.17	39.33	87.00	45.23
<i>LSD</i> <sub>0.01</sub>	1.60	7.10	3.22	0.58	2.86	5.31	4.21
<i>LSD</i> <sub>0.05</sub>	2.13	9.45	4.29	0.77	3.81	7.07	5.60

FER – fertility percentage; FGP – filled grains/panicle; UGP – unfilled grains/panicle; TGW – thousand grain weight; GYP – grain yield per plant; BYP – biological yield per plant; HRI – harvest index

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(TGW) significantly varied between 18.33 to 26.0 g, demonstrating genotypic variability in grain size and density. The genotypes with the heaviest grains were Z1 × C9, Z1, Z1 × R7, Z1 × G8, and Z1 × R8. Grain yield per plant (GYP) showed substantial differences from 22.67 to 44.33 g. The highest yielding genotypes were G8 × C9, S4 × C9, Z1 × C9, Z1 × C9, C9, and R8 × C9. Biological yield per plant (BYP), representing total plant biomass, varied significantly under salinity stress, ranging from 57.00 to 104.0 g. The genotypes with the greatest biomass production were S4 × C9, R7 × C9, G8 × C9, R6 × R7, S4 × R8, and S4 × R6. Finally, the harvest index (HRI), which measures the efficiency of converting biomass into grain, showed a range from 32.23% to 47.43%. The most efficient genotypes were Z1 × C9, G8, R6, R8, G8 × R7, and G8 × C9.

### Hierarchical cluster analysis

The performed dendrogram explores the genetic relationships among rice parental genotypes and their derived crosses under salinity stress (Figure 1). It separated the genotypes into five main groups, each clustering genotypes with similar physiological, biochemical, and agronomic responses. The green group contained six crosses: G8 × C9, G8 × R6, G8 × R7, Z1 × C9, Z1 × R8, and G8 × R8, which exhibited elevated beneficial physiological responses and enhanced antioxidant capacity under salinity stress. In addition, these crosses displayed higher agronomic parameters and superior performance under salinity stress. The orange group consisted of six genotypes: R7 × C9, R8 × C9, C9, R7 × R8, R6 × R8, and R6 × C9. These genotypes also displayed high performance for salinity tolerance traits and higher yield parameters. The black group contained seven

genotypes: Z1 × R6, Z1 × R7, R6, R7, and R8, which displayed high- to intermediate-level physiological and agronomic performance under salinity stress. The red cluster grouped five crosses: R6 × R7, S4 × C9, S4 × R8, S4 × R6, and S4 × R6, displayed low-intermediate levels of physiological and agronomic performance. The blue group included three parental genotypes: G8, Z1, and S4, and their direct crosses, G8 × S4, Z1 × G8, and Z1 × S4, exhibited relatively lower values for all evaluated traits.

Furthermore, a hierarchical clustered heatmap was utilised to visually summarise the variation and patterns in physiological, biochemical, and agronomic traits among rice genotypes and their crosses under salinity stress (Figure 2). The figure effectively separated genotypes into distinct clusters, reflecting their collective trait profiles. Genotypes and crosses exhibiting superior performance under salinity stress, as indicated by blue colour for beneficial parameters (Figure 2). The genotypes R8 × C9, R7 × C9, C9, R7 × R8, R6 × C9, R6 × R8, G8 × R8, Z1 × R8, G8 × R6, G8 × R7, Z1 × C9, and R8 × C9 displayed blue colour for physiological, agronomic, and yield traits. Moreover, these genotypes showed lower MDA values in red under salinity stress, suggesting reduced stress impact and better cellular protection. In contrast, parental genotypes Z1, S4, and G8, and their crosses Z1 × S4, Z1 × G8, and G8 × S4, clustered separately, with primarily red colour for most physiological and agronomic traits and blue colour for MDA, indicating reduced performance and high sensitivity under salinity conditions. Trait clustering revealed strong correlations among harvest index, panicle length (PL), and filled grains per panicle (FGP), which were grouped with yield traits. At the same time, stress-sensitivity indicators UFGP and MDA clustered together.

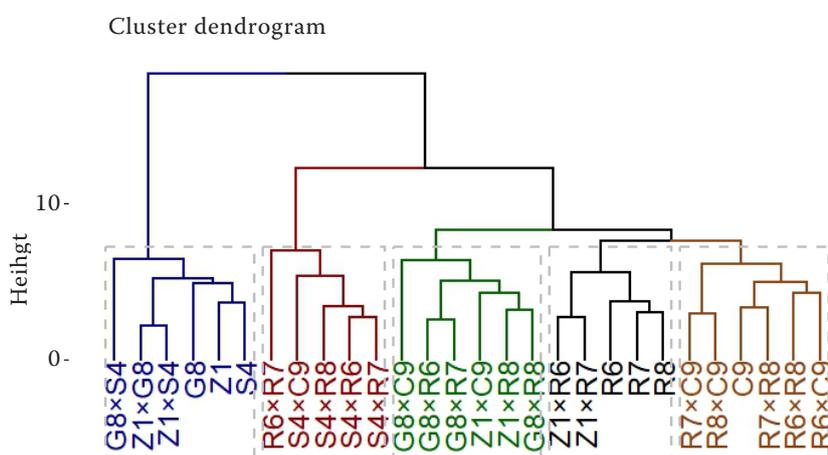


Figure 1. Hierarchical cluster dendrogram of twenty-eight rice genotypes, including seven parental genotypes and their derived twenty-one crosses, based on physiological, biochemical, and agronomic traits under salinity stress

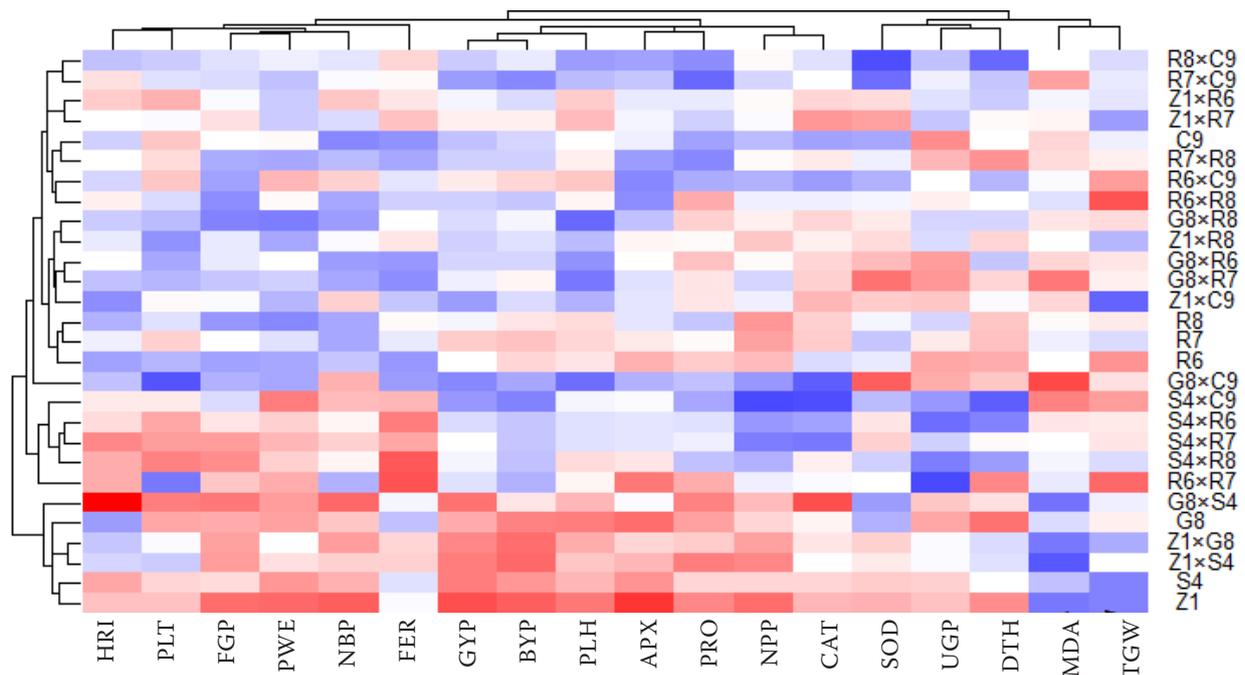


Figure 2. Hierarchical clustered heatmap of physiological, biochemical, and agronomic traits in rice genotypes and their derived crosses under salinity stress. Blue colour indicates high values, and red colour indicates low values for the studied traits. Traits are abbreviated as follows: RWC – relative water content; CO<sub>2</sub> – leaf CO<sub>2</sub> assimilation rate; PRO – proline content; MDA – malondialdehyde; APX – ascorbate peroxidase; SOD – superoxide dismutase; CAT – catalase; DTH – days to heading; PLH – plant height; NPP – number of panicles/plant; PLT – panicle length; PWE – panicle weight; NBP – number of branches/panicle; FER – fertility percentage; FGP – filled grains/panicle; UGP – unfilled grains/panicle; TGW – thousand grain weight; GYP – grain yield per plant; BYP – biological yield per plant; HRI – harvest index

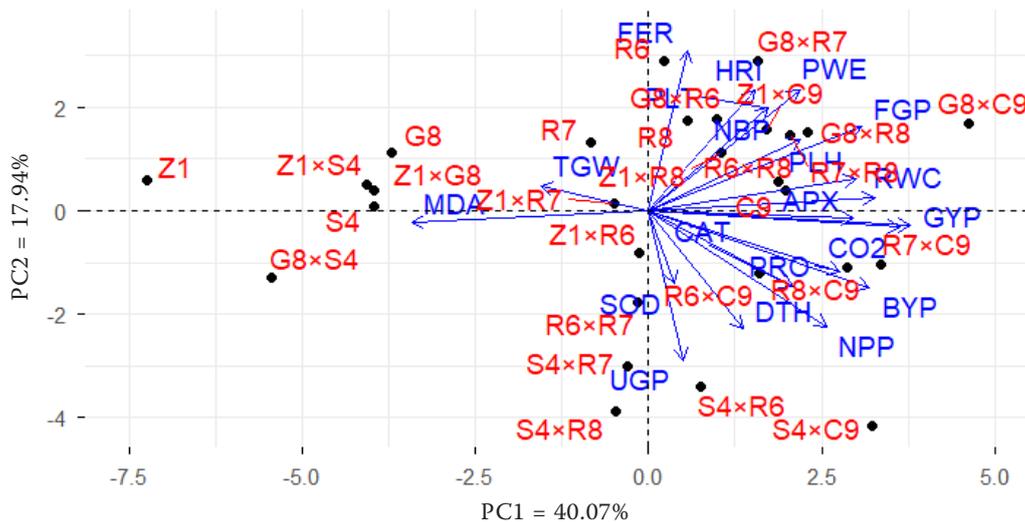


Figure 3. Principal component analysis biplot of physiological, biochemical and agronomic traits in rice genotypes and their derived crosses under salinity stress. Traits are abbreviated as follows: RWC – relative water content; CO<sub>2</sub> – leaf CO<sub>2</sub> assimilation rate; PRO – proline content; MDA – malondialdehyde; APX – ascorbate peroxidase; SOD – superoxide dismutase; CAT – catalase; DTH – days to heading; PLH – plant height; NPP – number of panicles/plant; PLT – panicle length; PWE – panicle weight; NBP – number of branches/panicle; FER – fertility percentage; FGP – filled grains/panicle; UGP – unfilled grains/panicle; TGW – thousand grain weight; GYP – grain yield per plant; BYP – biological yield per plant; HRI – harvest index

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### Principal component analysis

Principal component analysis (PCA) was applied to examine relationships among the evaluated rice genotypes under salinity stress and to identify patterns in the physiological, biochemical, and agronomic traits (Figure 3). The first principal component (PC1) accounted for 40.07% of the total variance, while the second principal component (PC2) explained 17.94%. The biplot positioned the parental genotypes and crosses based on their performance. The genotypes Z1, S4, G8, Z1 × S4, G8 × S4, and Z1 × G8 were positioned on the negative side of PC1. These genotypes were located opposite to beneficial physiological and yield traits, indicating lower performance under salinity stress. Furthermore, these low-performing genotypes were associated with MDA, which negatively loaded on PC1. Otherwise, the genotypes G8 × C9, G8 × R7, Z1 × C9, G8 × R6, G8 × R8, R7 × R8, R6 × R8, C9, R7 × C9, R8 × C9, and R6 × C9 were located on the positive side of PC1. Moreover, the traits contributed positively to PC1, such as grain yield per plant (GYP), biological yield per plant (BYP), relative water content (RWC), proline content (PRO), and major antioxidant enzyme activities (APX, SOD, CAT), were associated with these genotypes positioned on the positive axis, indicating their potential for salinity tolerance improvement. In addition, these traits are important selection indicators for enhanced salinity tolerance. PC biplot indicates considerable diversity in trait performance between the assessed genotypes under salinity conditions. It effectively discriminated high-performing crosses and identified essential measurements that could be utilised for selection under saline conditions.

### Phenotypic correlation matrix

The phenotypic correlation presented in Figure 4 presents the relationships among the studied physiological, biochemical, agronomic, and yield traits of rice genotypes under salinity stress. The figure reveals that several important traits display strong and significant correlations, reflected by blue (positive) and red (negative) colour gradations. GYP, BYP, RWC, TGW, and HRI were positively and significantly intercorrelated with each other and with major agronomic and physiological traits, indicating that selection for these traits can improve salinity tolerance. Conversely, MDA displayed significant

negative correlations with most agronomic traits, indicating its value as a selection criterion for reduced oxidative damage in salt-stressed plants. Moreover, antioxidant enzyme activities, including SOD, CAT, and APX, exhibited strong positive associations with RWC, PRO, and CO<sub>2</sub> assimilation. In addition, relationships among growth traits such as PLH, PLT, and FGP emphasised their importance for high performance under adverse conditions.

### General combining ability effects for parental genotypes

The analysis of general combining ability (GCA) revealed substantial differences among rice parental genotypes for the studied physiological and biochemical parameters under salinity stress (Figure 5). The parent C9 demonstrated the highest and significant positive GCA effects for RWC, CO<sub>2</sub> assimilation, PRO, APX, SOD, and CAT, indicating its superior ability to provide favourable alleles for salinity tolerance (Figure 5). Furthermore, it contributed to significantly reduced MDA levels, indicating enhanced cellular protection against oxidative damage. The parental genotypes R8, R7, and R6 could also be considered strong combiners for physiological parameters, with positive GCA effects for most of the studied parameters, supporting their utility in breeding for salinity tolerance. Conversely, Z1, G8, and S4 showed negative GCA effects on most physiological parameters, suggesting limited potential to improve salinity tolerance.

Figure 6 displays significant differences in GCA among parental genotypes for the studied agronomic traits. Parental genotypes Z1, G8, and R7 exhibited significant negative effects, indicating early heading under salinity stress. While S4 and C9 exhibited significant positive GCA effects for days to heading, indicating delayed heading and maturity. Z1 and S4 contributed to reduced plant stature, while the highest positive GCA effects were recorded for C9, R8, and G8, indicating their strong contribution to increased vegetative growth under salinity. C9 and S4 could be excellent general combiners for NPP, while Z1 showed the highest significant negative effect, limiting this trait. R6 and R8 had the strongest positive effects for PLT, while S4 negatively impacted this trait. R8 and R7 provided moderate positive GCA values for PWE, suggesting their importance for seed setting and grain production. The highest positive GCA effects for the NBP were assigned for R8, R7, and R6, which are

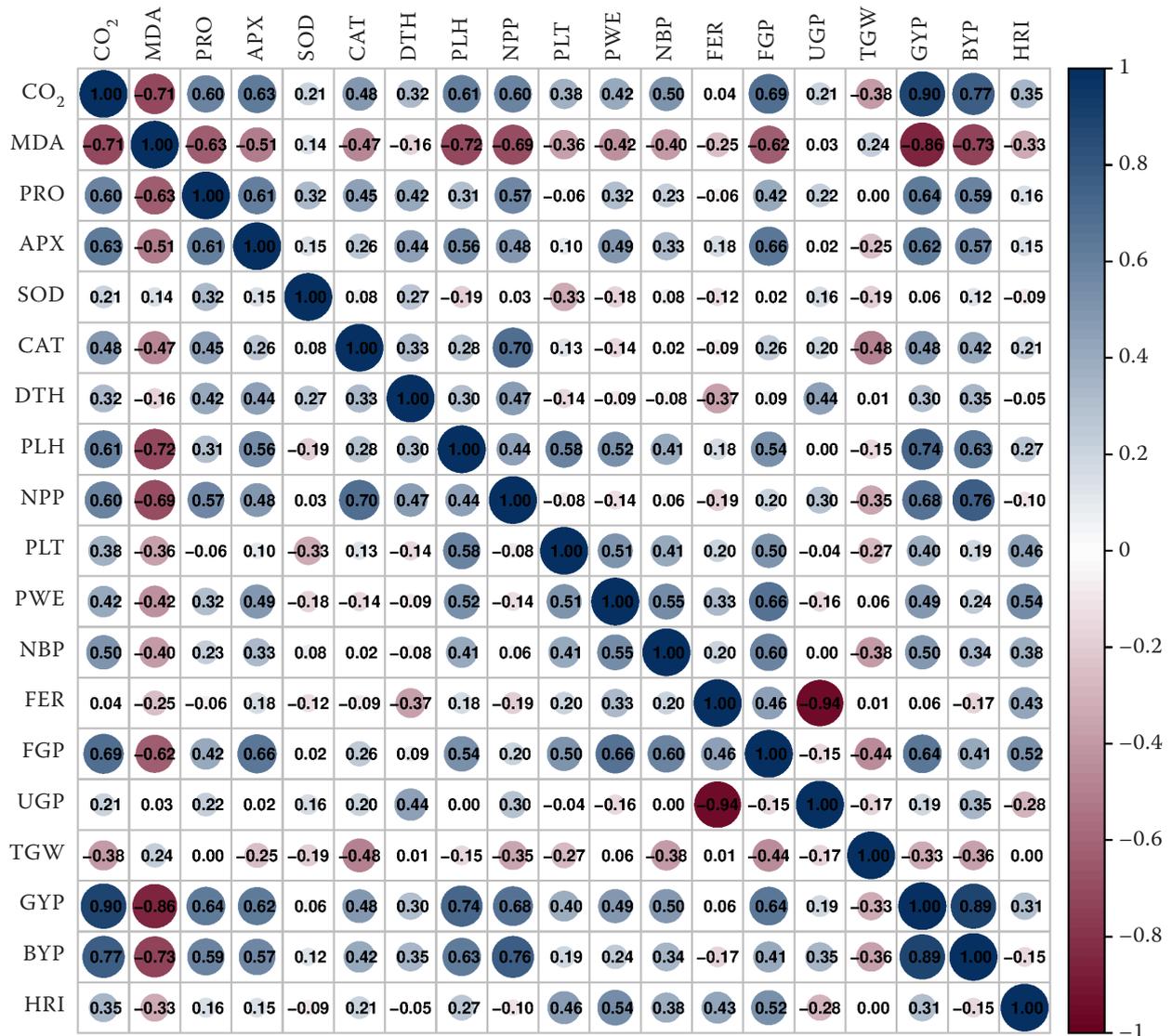


Figure 4. Phenotypic correlation matrix among physiological, biochemical, agronomic, and yield traits of rice genotypes under salinity stress. Blue circles indicate positive phenotypic correlations and red indicate negative correlations between trait pairs. The intensity of the colour and the size of the circles reflect the strength of the correlation (from -1 to +1). The numeric values within the cells represent Pearson correlation coefficients for each trait pair. Traits are abbreviated as follows: RWC – relative water content; CO<sub>2</sub> – leaf CO<sub>2</sub> assimilation rate; PRO – proline content; MDA – malondialdehyde; APX – ascorbate peroxidase; SOD – superoxide dismutase; CAT – catalase; DTH – days to heading; PLH – plant height; NPP – number of panicles/plant; PLT – panicle length; PWE – panicle weight; NBP – number of branches/panicle; FER – fertility percentage; FGP – filled grains/panicle; UGP – unfilled grains/panicle; TGW – thousand grain weight; GYP – grain yield per plant; BYP – biological yield per plant; HRI – harvest index

valuable for increasing reproductive sink size and yield potential. In contrast, Z1, G8, and S4 displayed strong negative values, limiting branching under stress.

The GCA effects for parental genotypes for yield traits under salinity stress demonstrate substantial genetic variation (Figure 7). The parent C9 exhibited the highest significant positive GCA for FER and FGP,

indicating it is a strong donor for grain set under saline conditions. R6 also displayed positive GCA effects for these traits. In contrast, Z1 and S4 had substantial negative GCA effects for fertility and grain filling, indicating limited usefulness for improving these components under stress. G8 and C9 showed strong beneficial effects in reducing unfilled grains,

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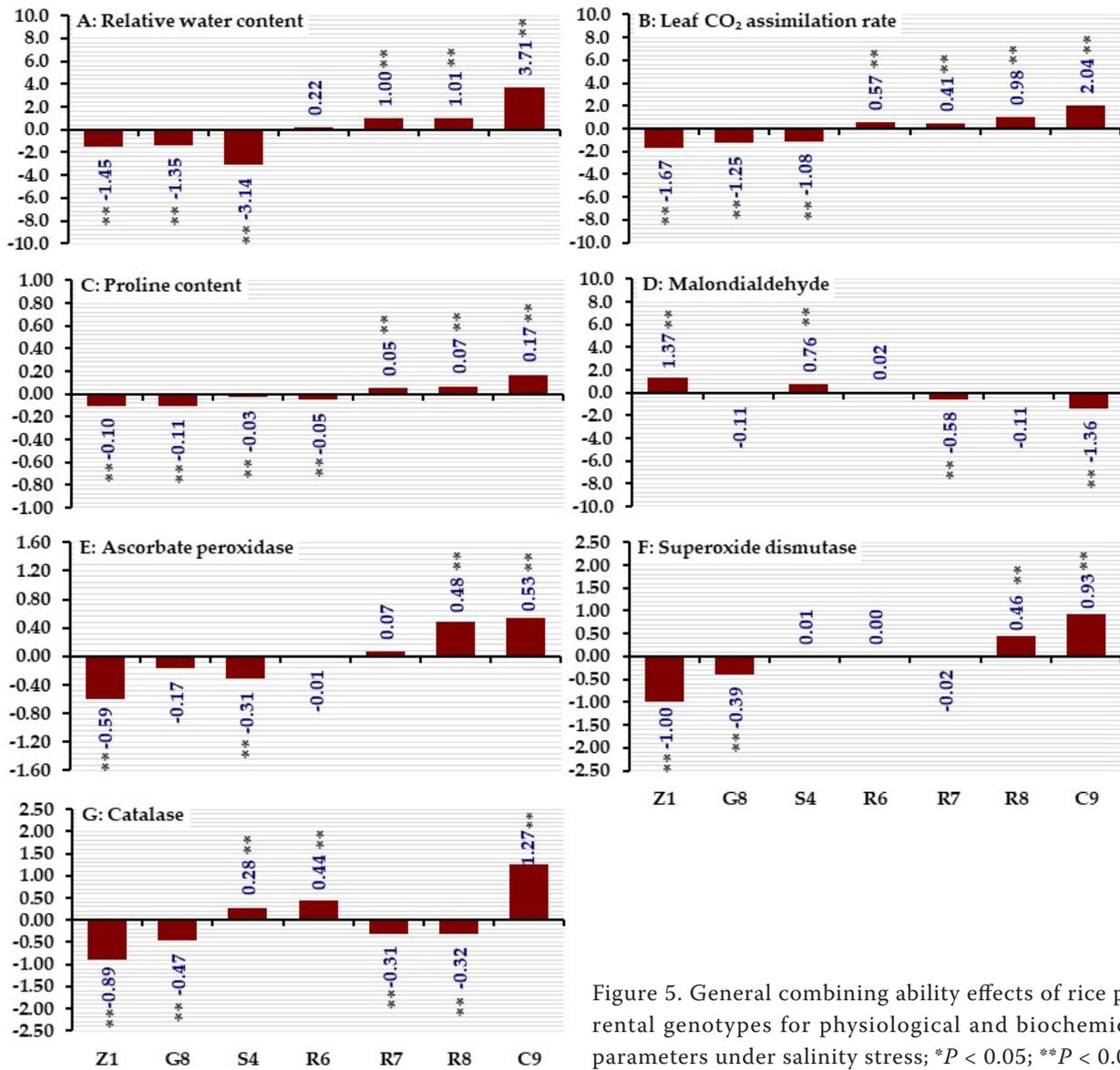


Figure 5. General combining ability effects of rice parental genotypes for physiological and biochemical parameters under salinity stress; \* $P < 0.05$ ; \*\* $P < 0.01$

while S4 and R8 showed positive GCA, which was associated with increased sterility. C9 showed the uppermost positive GCA effects for grain yield per plant and biological yield, confirming its pivotal role in providing favourable alleles and yield potential under salinity tolerance. R8 and R6 also demonstrated positive contributions, making them valuable sources for yield improvement. Otherwise, Z1, G8, and S4 were associated with the negative effects on grain yield. The superior biological yield of C9 under salinity stress indicates its overall adaptation efficiency, followed by R6, R7, and R8. In contrast, Z1, G8, and S4 had a strongly negative GCA for biological yield. The uppermost harvest index of C9 under salinity stress further indicates its efficiency in assimilate

partitioning, while S4 had a strongly negative GCA for harvest index.

### Specific combining ability effects for derived crosses

The assessment of specific combining ability (SCA) effects revealed several crosses with significant positive SCA for physiological, biochemical, agronomic, and yield traits under salinity stress. The crosses Z1 × R6, Z1 × R7, Z1 × R8, Z1 × C9, G8 × C9, and R8 × C9 exhibited significant positive SCA effects on RWC, indicating their potential to improve water status under salinity stress (Table 6). Likewise, Z1 × R8, Z1 × C9, G8 × R8, G8 × C9, S4 × C9, and R6 × R8

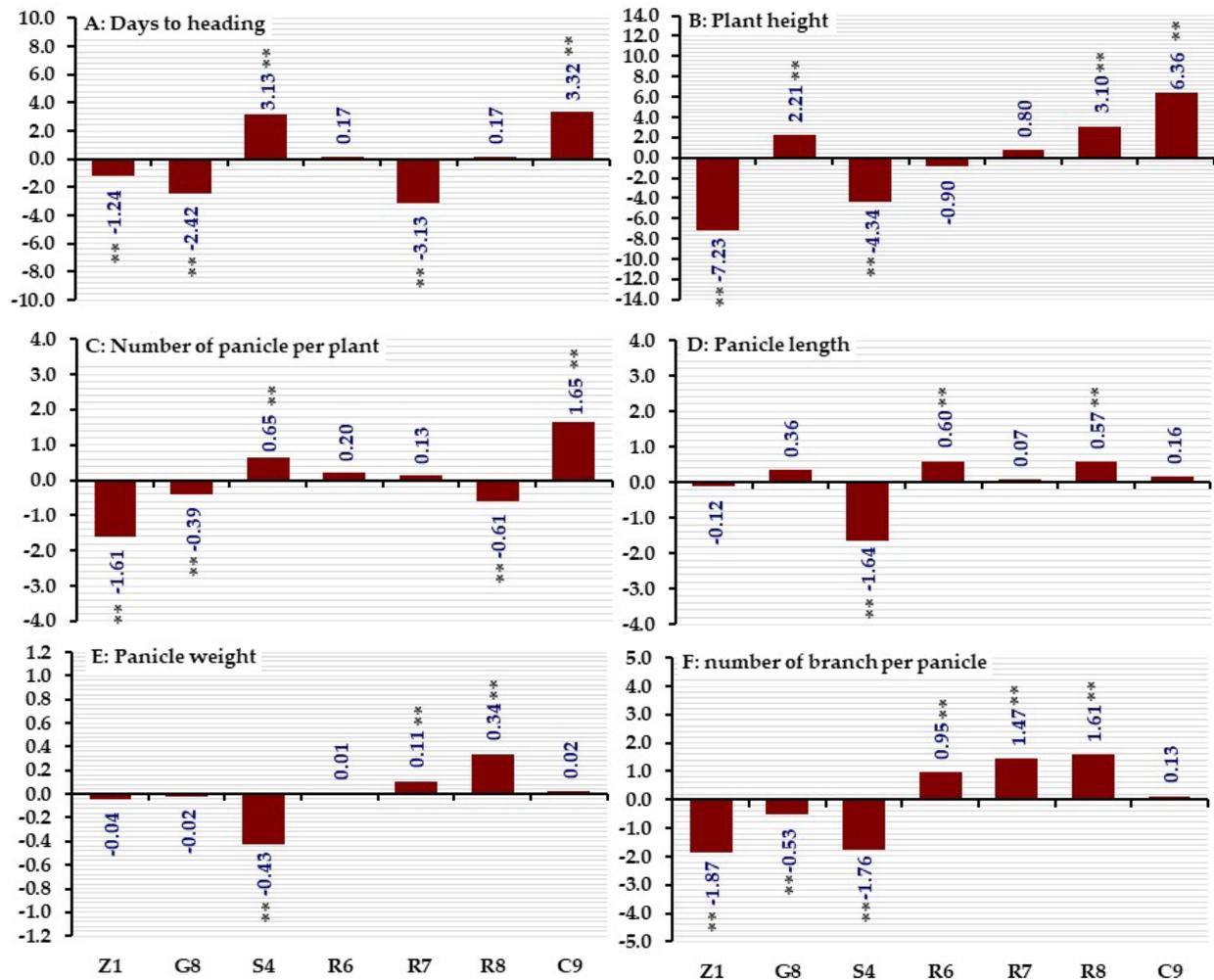


Figure 6. General combining ability effects of rice parental genotypes for agronomic traits under salinity stress. \*\* $P < 0.01$

showed positive SCA for  $\text{CO}_2$  and enhanced photosynthetic capacity. The crosses  $\text{R6} \times \text{C9}$ ,  $\text{R7} \times \text{R8}$ , and  $\text{R7} \times \text{C9}$  exhibited significant positive SCA effects for PRO. The crosses  $\text{Z1} \times \text{R6}$ ,  $\text{Z1} \times \text{R7}$ ,  $\text{Z1} \times \text{R8}$ ,  $\text{Z1} \times \text{C9}$ ,  $\text{G8} \times \text{R7}$ ,  $\text{G8} \times \text{C9}$ ,  $\text{S4} \times \text{R6}$ , and  $\text{S4} \times \text{C9}$  showed significant negative SCA effects on MDA, indicating reduced oxidative damage. The crosses  $\text{Z1} \times \text{R6}$  and  $\text{Z1} \times \text{R7}$ ,  $\text{G8} \times \text{S4}$ ,  $\text{G8} \times \text{C9}$ ,  $\text{S4} \times \text{R6}$ ,  $\text{R6} \times \text{R8}$ , and  $\text{R6} \times \text{C9}$  showed significant positive SCA effects for APX, suggesting enhanced enzymatic antioxidative defence. SOD activity was significantly positively influenced by crosses  $\text{Z1} \times \text{G8}$ ,  $\text{Z1} \times \text{S4}$ ,  $\text{G8} \times \text{S4}$ ,  $\text{S4} \times \text{C9}$ , and  $\text{S4} \times \text{R8}$ . CAT activity had significant positive SCA effects in crosses  $\text{Z1} \times \text{G8}$ ,  $\text{Z1} \times \text{S4}$ ,  $\text{Z1} \times \text{R8}$ ,  $\text{G8} \times \text{C9}$ ,  $\text{S4} \times \text{R6}$ ,  $\text{S4} \times \text{R7}$ , and  $\text{S4} \times \text{C9}$ .

Agronomic traits also displayed significant SCA effects (Table 7). Variation in DTH indicates genetic diversity in stress-induced maturity timing. It had significant negative SCA effects in  $\text{Z1} \times \text{R8}$ ,  $\text{Z1} \times \text{C9}$ ,

$\text{G8} \times \text{S4}$ ,  $\text{G8} \times \text{C9}$ ,  $\text{R6} \times \text{R7}$ ,  $\text{G8} \times \text{R6}$ ,  $\text{G8} \times \text{R7}$ , and  $\text{R7} \times \text{R8}$  (Table 7). While  $\text{Z1} \times \text{G8}$ ,  $\text{Z1} \times \text{R6}$ ,  $\text{Z1} \times \text{R7}$ ,  $\text{G8} \times \text{R6}$ ,  $\text{G8} \times \text{R7}$ ,  $\text{G8} \times \text{R8}$ ,  $\text{S4} \times \text{R6}$ ,  $\text{S4} \times \text{R8}$ ,  $\text{S4} \times \text{C9}$ ,  $\text{R7} \times \text{C9}$ , and  $\text{R8} \times \text{C9}$  recorded significant positive SCA effects for DTH. Significant positive and negative SCA effects on PH reflected genetic influences on vegetative growth. The crosses  $\text{Z1} \times \text{G8}$ ,  $\text{Z1} \times \text{R7}$ ,  $\text{G8} \times \text{S4}$ ,  $\text{S4} \times \text{R8}$ ,  $\text{R6} \times \text{R7}$ ,  $\text{R6} \times \text{R8}$ ,  $\text{R6} \times \text{C9}$ , and  $\text{R7} \times \text{R8}$  possessed significant negative SCA effects for PH. While  $\text{Z1} \times \text{R8}$ ,  $\text{Z1} \times \text{C9}$ ,  $\text{G8} \times \text{R6}$ ,  $\text{G8} \times \text{R7}$ ,  $\text{G8} \times \text{R8}$ ,  $\text{G8} \times \text{C9}$ ,  $\text{S4} \times \text{R6}$ ,  $\text{S4} \times \text{R7}$ ,  $\text{R7} \times \text{C9}$ , and  $\text{R8} \times \text{C9}$  recorded significant positive SCA effects for PH. NPP exhibited significant positive effects in  $\text{Z1} \times \text{R6}$ ,  $\text{Z1} \times \text{R7}$ ,  $\text{G8} \times \text{R7}$ ,  $\text{G8} \times \text{C9}$ ,  $\text{S4} \times \text{R6}$ ,  $\text{S4} \times \text{R7}$ ,  $\text{S4} \times \text{R8}$ ,  $\text{S4} \times \text{C9}$ , and  $\text{R6} \times \text{R8}$ . PLT enhanced SCA in  $\text{Z1} \times \text{S4}$ ,  $\text{Z1} \times \text{R8}$ ,  $\text{G8} \times \text{R6}$ ,  $\text{G8} \times \text{R7}$ ,  $\text{G8} \times \text{C9}$ , and  $\text{R6} \times \text{R7}$ . PWE recorded significant positive SCA effects in  $\text{Z1} \times \text{S4}$ ,  $\text{Z1} \times \text{R6}$ ,  $\text{Z1} \times \text{R7}$ ,  $\text{Z1} \times \text{R8}$ ,  $\text{Z1} \times \text{C9}$ ,  $\text{G8} \times \text{R7}$ ,  $\text{G8} \times \text{R8}$ ,  $\text{G8} \times \text{C9}$ , and  $\text{R7} \times \text{C9}$ . NBP was positively in-

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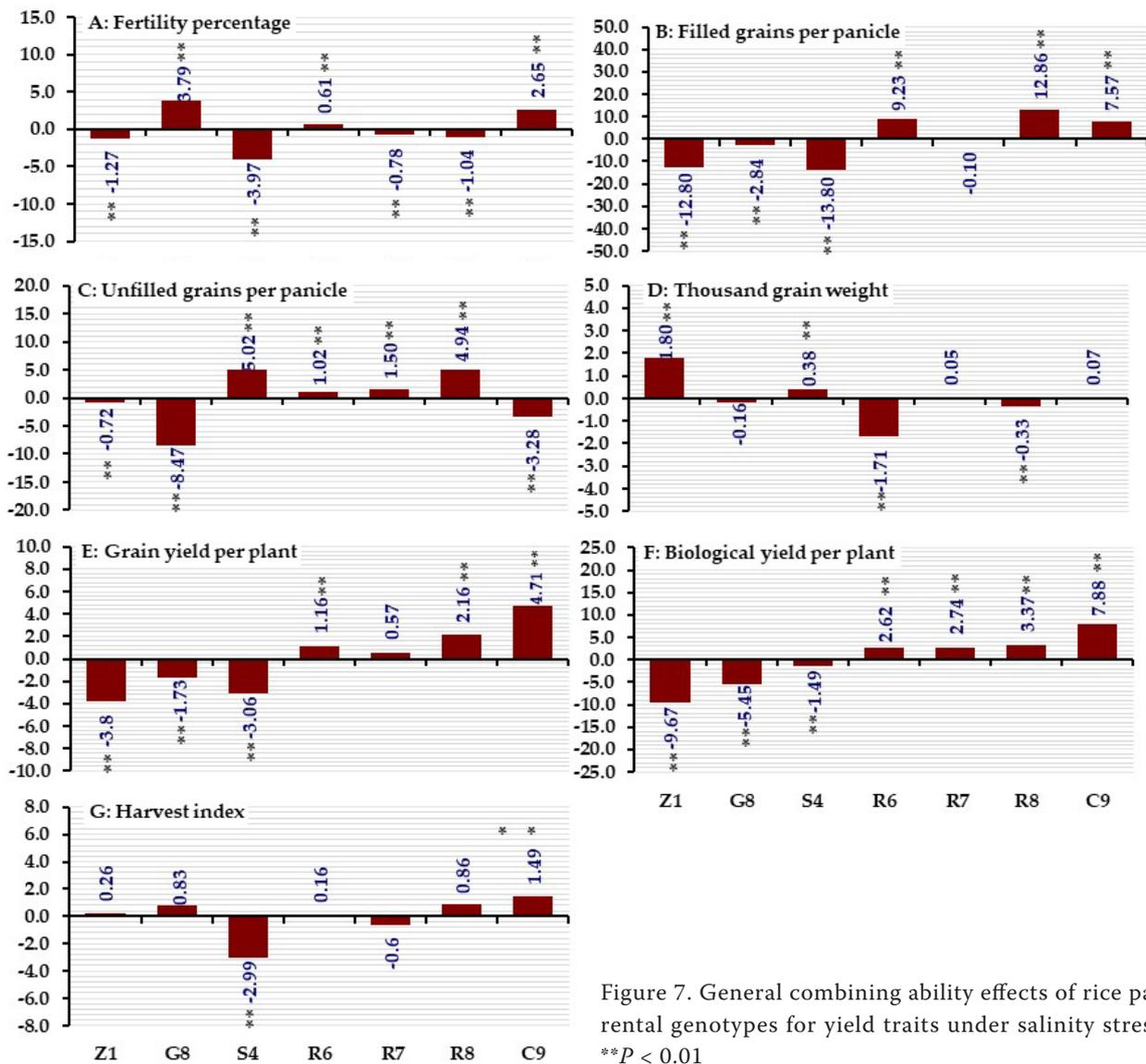


Figure 7. General combining ability effects of rice parental genotypes for yield traits under salinity stress \*\* $P < 0.01$

fluenced in Z1 × S4, Z1 × R7, G8 × R6, G8 × R7, and G8 × R8. Regarding yield traits, FER showed positive SCA effects in crosses Z1 × S4, Z1 × C9, G8 × S4, G8 × R6, G8 × R7, G8 × C9, R6 × R8, and R7 × R8 (Table 8). FGP is crucial for grain yield, had significant positive SCA in Z1 × R6, Z1 × R7, Z1 × R8, Z1 × C9, G8 × R7, G8 × R8, G8 × C9, S4 × C9, R6 × R8, R6 × C9, and R7 × R8. Whereas UGP had significant negative SCA in crosses Z1 × S4, Z1 × C9, G8 × S4, G8 × R6, G8 × R7, R6 × R8, R7 × R8 indicating better grain filling efficiency. Thousand-grain weight was positively influenced by the crosses Z1 × G8, Z1 × R6, Z1 × R7, Z1 × C9, G8 × R6, S4 × R6, S4 × R8, R7 × C9, and R8 × C9. GYP showed strong positive SCA effects in the crosses Z1 × R6, Z1 × R8, Z1 × C9, G8 × R6, G8 × R7, G8 × R8, G8 × C9, S4 × R6, S4 × R7, S4 × R8,

and S4 × C, indicating their potential under salinity stress. The crosses Z1 × R6, Z1 × R8, Z1 × C9, G8 × R6, G8 × C9, S4 × R6, S4 × R7, S4 × R8, S4 × C9, R6 × R7, R7 × C9 exhibited significant positive effects for BYP. Finally, HRI was positively affected in crosses Z1 × S4, Z1 × C9, and G8 × R7.

## DISCUSSION

Soil salinisation increasingly threatens rice production by expanding the severity of salt-affected lands under current climate change. Therefore, generating and assessing genetic variation in key physiological and agronomic traits is essential for identifying superior combiners and developing novel rice genotypes with enhanced salinity tolerance and yield potential.

Table 6. Specific combining ability effects of the derived crosses for physiological and biochemical traits under salinity stress

Cross	RWC	CO <sub>2</sub>	PRO	MDA	APX	SOD	CAT
Z1 × G8	-1.26	-1.26**	0.09**	1.97**	0.30	0.49*	0.83**
Z1 × S4	-1.62*	0.57	-0.17**	1.79**	0.08	0.55**	0.69**
Z1 × R6	3.24**	0.58	0.21**	-1.14*	0.83**	0.22	-0.36
Z1 × R7	1.68*	0.41	0.15**	-1.10*	0.66*	-0.87**	-0.82**
Z1 × R8	3.10**	1.84**	0.01	-1.33*	-0.05	-0.22	0.88**
Z1 × C9	2.91**	2.83**	-0.13**	-1.04*	0.39	-0.97**	-1.84**
G8 × S4	-1.41	-2.54**	-0.13**	2.68**	0.58*	2.29**	-3.30**
G8 × R6	-0.99	0.50	0.02	-1.00	0.21	-0.94**	-0.87**
G8 × R7	-1.00	0.03	0.001	-2.49**	0.50	-2.33**	-0.21
G8 × R8	0.29	1.80**	-0.07**	-0.47	0.42	-0.52*	-0.05
G8 × C9	2.69**	2.08**	0.09**	-2.87**	0.55*	-3.66**	2.32**
S4 × R6	-0.45	0.34	0.16**	-1.48**	0.65*	-0.57**	1.09**
S4 × R7	-0.46	-0.80*	0.02	-0.16	0.57*	-0.95**	2.65**
S4 × R8	0.83	0.96**	0.11**	-0.41	-0.51	0.46*	-0.30
S4 × C9	0.90	2.28**	0.07**	-2.33**	-0.12	0.43*	1.93**
R6 × R7	-1.04	0.55	-0.19**	1.06*	-1.60**	0.01	-0.01
R6 × R8	-0.28	1.35**	-0.22**	0.87	0.83**	-0.26	0.19
R6 × C9	0.66	-0.74*	0.07**	1.52**	0.85**	0.61**	0.22
R7 × R8	0.27	0.75*	0.15**	-0.20	0.56*	-0.09	0.16
R7 × C9	0.31	-0.21	0.12**	-0.29	0.06	1.88**	-0.97**
R8 × C9	1.64*	-0.53	0.02	1.57**	0.02	2.03**	-0.29
SE <sub>(Sij)</sub>	0.76	0.35	0.03	0.50	0.27	0.20	0.22
LSD <sub>0.05</sub>	1.52	0.70	0.05	1.01	0.54	0.40	0.45
LSD <sub>0.01</sub>	2.03	0.93	0.07	1.34	0.72	0.53	0.60

RWC – relative water content; CO<sub>2</sub> – leaf CO<sub>2</sub> assimilation rate; PRO – proline content; MDA – malondialdehyde; APX – ascorbate peroxidase; SOD – superoxide dismutase; CAT – catalase; \**P* < 0.05; \*\**P* < 0.01

The present study explored genetic variability in rice parental genotypes and their derived crosses under salinity stress across physiological, biochemical, agronomic, and yield-related traits. The results revealed considerable genetic variability among the evaluated parental genotypes and their crosses under salinity stress, as evidenced by the analysis of variance results. The detected genetic variability among the parental genotypes and their derived crosses is important for breeding salt-tolerant rice cultivars and selection of superior allelic combinations, as reported in studies of Bimpong et al. (2016), Chattopadhyay et al. (2015), Elias et al. (2020), Kulsum et al. (2022), and Valarmathi et al. (2019).

The parental genotype C9 could be considered the most valuable general combiner for most studied traits. It exhibited consistently strong positive GCA effects across physiological, biochemical, agronomic, and yield traits, including RWC, photosynthetic

capacity, antioxidant enzyme activities, fertility percentage, and grain yield. This indicates that C9 has vigorous potential to enhance salinity tolerance and yield potential under stress conditions. Other parental genotypes, such as R8 and R6, also demonstrated significant positive GCA effects as important donors. Identification of parental genotypes with strong positive GCA for multiple adaptive traits, such as C9, R8, and R6 with enhanced photosynthetic capacity, osmotic adjustment, antioxidant activity, and yield traits, is important for developing high-yielding, salt-tolerant rice cultivars. This aligns with global breeding efforts that emphasise the use of elite donors combined with hybridisation to exploit genetic effects on salinity tolerance (Solis et al. 2020, Chapagain et al. 2022, Sun et al. 2025, Wang et al. 2024).

The crosses G8 × C9, G8 × R7, Z1 × C9, G8 × R6, G8 × R8, R7 × R8, R6 × R8, C9, R7 × C9, R8 × C9, and

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Table 7. Specific combining ability effects of the derived crosses for agronomic traits under salinity stress

Cross	DTH	PH	NPP	PLT	PWE	NBP
Z1 × G8	6.60**	-8.91**	-0.52	0.02	0.06	-0.74
Z1 × S4	0.71	1.98	-2.22**	3.35**	0.27**	2.15**
Z1 × R6	5.34**	-0.80	1.22**	-2.89**	0.34**	-0.89*
Z1 × R7	3.64**	-5.17**	1.63**	0.31	0.26**	1.59**
Z1 × R8	-2.32**	15.54**	0.70	2.81**	0.24**	0.44
Z1 × C9	-1.47*	13.61**	0.44	-0.28	0.47**	0.26
G8 × S4	-3.44**	-10.13**	-2.11**	-2.63**	-0.15*	-2.52**
G8 × R6	6.86**	16.76**	0.00	1.63*	0.01	2.78**
G8 × R7	2.16**	19.06**	1.41**	1.83**	0.21**	1.93**
G8 × R8	5.53**	19.43**	0.48	1.17	0.45**	2.11**
G8 × C9	-5.29**	15.83**	1.56**	4.57**	0.53**	-2.07**
S4 × R6	6.31**	10.65**	1.96**	-1.54*	0.12	0.33
S4 × R7	-0.73	9.28**	2.70**	-1.33*	-0.12	-1.19**
S4 × R8	4.31**	-5.35**	2.11**	-2.67**	-0.21**	-0.33
S4 × C9	6.16**	0.06	2.52**	0.74	-0.39**	-0.52
R6 × R7	-6.44**	-2.17	0.15	3.26**	-0.64**	0.11
R6 × R8	-0.73	-4.46*	0.89*	-0.07	-0.39**	0.30
R6 × C9	2.12**	-15.06**	0.30	-2.50**	-0.47**	-2.56**
R7 × R8	-5.44**	-7.17**	0.30	-1.70**	0.08	-0.89*
R7 × C9	4.42**	4.57*	-0.63	0.70	0.26**	-1.41**
R8 × C9	8.12**	6.94**	-1.22**	0.87	-0.26**	-0.89*
SE <sub>(Sij)</sub>	0.63	1.93	0.37	0.63	0.07	0.40
LSD <sub>0.05</sub>	1.26	3.86	0.73	1.27	0.14	0.80
LSD <sub>0.01</sub>	1.67	5.15	0.98	1.69	0.19	1.07

DTH – days to heading; PLH – plant height; NPP – number of panicles/plant; PLT – panicle length; PWE – panicle weight; NBP – number of branches/panicle; \* $P < 0.05$ ; \*\* $P < 0.01$

R6 × C9 exhibited enhanced performance and positive SCA for RWC, CO<sub>2</sub> assimilation, and proline accumulation, which reflects improved photosynthetic capacity and osmotic adjustment under salinity. Also, these crosses exhibited enhanced antioxidant enzyme activities of APX, SOD, and CAT, which are crucial for mitigating cellular damage under salinity stress. Besides, the observed lower MDA levels confirm reduced membrane damage and enhanced cellular stability. Furthermore, these crosses outperformed the parental genotypes and the other crosses in plant height, panicle number, and grain yield components under saline conditions. Besides, these crosses exhibited the highest yield traits, including fertility percentage, filled grain number, grain weight, grain yield per plant, and biological yield under salinity stress. Similarly, Hossen et al. (2022) compared morpho-physiological responses and stress tolerance

mechanisms in diverse rice genotypes. The results indicated that superior tolerance was associated with enhanced osmotic adjustment and antioxidant defence. Under stress, all genotypes showed reduced water status, biomass, and pigments, along with elevated hydrogen peroxide, electrolyte leakage, MDA, and methylglyoxal levels, indicating oxidative damage. However, tolerant genotypes maintained a lower Na<sup>+</sup>/K<sup>+</sup> ratio and higher proline accumulation, as well as elevated activities of ascorbate-glutathione, monodehydroascorbate reductase, dehydroascorbate reductase, and glutathione peroxidase. Also, the tolerant genotypes exhibited robust glyoxalase system activity for methylglyoxal detoxification. These mechanisms align with the present findings that superior F1 crosses exhibit higher physiological performance and better yield under salinity stress. This suggests that heterotic combinations can en-

Table 8. Specific combining ability effects of the derived crosses for yield traits under salinity stress

Cross	FER	FGP	UGP	TGW	GYP	BYP	HRI
Z1 × G8	-6.36**	-7.22**	10.42**	0.36*	-3.37**	-9.09**	1.29
Z1 × S4	1.29**	2.15	-3.40**	-2.18**	-2.70**	-13.72**	4.41**
Z1 × R6	-1.60**	6.04**	4.94**	0.58**	3.41**	13.17**	-2.56*
Z1 × R7	-3.46**	5.04**	8.79**	0.65**	2.00*	3.72*	0.42
Z1 × R8	-0.09	5.74**	2.34**	0.20	5.07**	12.09**	-0.10
Z1 × C9	3.51**	6.70**	-5.77**	1.80**	6.19**	8.24**	3.00**
G8 × S4	1.19**	-15.52**	-6.32**	0.11	-5.44**	2.06	-8.30**
G8 × R6	4.25**	-0.63	-8.66**	1.20**	3.67**	9.94**	-1.01
G8 × R7	6.59**	17.70**	-9.81**	-0.26	2.59**	0.83	2.45*
G8 × R8	-2.69**	20.07**	10.42**	-0.41**	2.33**	4.20**	0.45
G8 × C9	1.72**	14.70**	-1.69	-0.71**	5.78**	12.02**	0.22
S4 × R6	-7.45**	-2.26	17.19**	0.79**	4.67**	8.65**	1.25
S4 × R7	-2.74**	-10.26**	1.71	-0.97**	2.26**	8.54**	-1.23
S4 × R8	-8.90**	-26.89**	11.27**	0.78**	2.00*	8.24**	-1.36
S4 × C9	-4.84**	15.07**	15.16**	-2.78**	6.11**	14.06**	0.58
R6 × R7	-14.13**	-23.37**	26.71**	-1.75**	0.70	8.09**	-3.04**
R6 × R8	4.47**	6.00**	-9.06**	-1.96**	0.11	3.46*	-1.77
R6 × C9	-0.81	6.30**	1.82*	-0.69**	-7.44**	-17.72**	0.20
R7 × R8	9.22**	7.67**	-18.21**	-0.05	0.70	1.69	-0.28
R7 × C9	-2.47**	1.30	5.01**	0.55**	1.81*	9.17**	-2.28*
R8 × C9	-5.19**	-12.00**	8.56**	1.10**	-3.11**	-7.80**	0.20
SE <sub>(Sij)</sub>	0.43	1.91	0.87	0.16	0.77	1.41	1.08
LSD <sub>0.05</sub>	0.86	3.83	1.74	0.31	1.55	2.83	2.16
LSD <sub>0.01</sub>	1.15	5.10	2.32	0.41	2.06	3.77	2.88

FER – fertility percentage; FGP – filled grains/panicle; UGP – unfilled grains/panicle; TGW – thousand grain weight; GYP – grain yield per plant; BYP – biological yield per plant; HRI – harvest index; \* $P < 0.05$ ; \*\* $P < 0.01$

hance ion homeostasis, proline-mediated osmotic adjustment, and reactive oxygen species scavenging capacity. Consequently, these identified crosses represent promising candidates for incorporation into breeding programs under saline environments to optimise tolerance and rice productivity.

Cluster and heatmap analyses explore the genetic relationships and phenotypic diversity among the evaluated parental genotypes and their crosses (Omar et al. 2022, Mansour et al. 2023). The hierarchical cluster dendrogram grouped genotypes into different clusters based on physiological, biochemical, agronomic, and yield traits. The superior genotypes G8 × C9, G8 × R6, G8 × R7, Z1 × C9, Z1 × R8, G8 × R8, R7 × C9, R8 × C9, C9, R7 × R8, R6 × R8, and R6 × C9, exhibited enhanced salinity tolerance and yield performance. The heatmap further visually presented these genotypes with higher relative water content, antioxidant enzyme activities, and grain yield, and lower

MDA level. Likewise, Emon et al. (2015), Khanam et al. (2023), Lokeshkumar et al. (2023), and Rasel et al. (2020) applied multivariate analyses to explore the presence of genetic diversity and provide practical guidance for selecting elite genotypes for breeding programs in salt-affected environments.

The PCA biplot effectively separated genotypes based on their performance in the studied traits, including RWC, antioxidant enzyme activities (APX, SOD, CAT), and grain yield. The correlation matrix further elucidated strong positive associations among physiological traits and yield components, indicating the integrated nature of salinity tolerance. Conversely, stress indicators, such as MDA, displayed significant negative correlations with yield and physiological performance, emphasising their role as markers of oxidative damage. These traits provide a selection framework to enhance the efficiency of breeding programs focused on developing

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salt-tolerant rice varieties, as elucidated by Amanat et al. (2022), Krishnamurthy et al. (2016), Xu et al. (2024), and Zhang et al. (2025).

Gene action plays an important role in the inheritance of salinity tolerance traits in rice, thereby affecting the effectiveness of breeding strategies (Kumar et al. 2024). The results revealed significant contributions from both additive and non-additive gene effects, as evidenced by GCA and SCA estimates. Additive gene action, reflected in GCA, is crucial for the stable transmission of favourable alleles from superior parental genotypes such as C9, R8, and R6, which are valuable for breeding programs aimed at salinity tolerance. Moreover, significant SCA effects indicate the importance of the dominance effect in enhancing hybrid vigour as observed in the high-performing crosses G8 × C9, G8 × R7, Z1 × C9, G8 × R6, G8 × R8, R7 × R8, R6 × R8, C9, R7 × C9, R8 × C9, and R6 × C9. Understanding these gene actions is essential for optimising parental selection, hybrid development, and the accumulation of beneficial alleles to develop rice cultivars with enhanced tolerance to salinity (Pabuayon et al. 2021, Zhang et al. 2024).

In conclusion, this study demonstrated the importance of genetic variability in rice for improving salinity tolerance under the increasing threat of soil salinisation intensified by climate change. Considerable genetic diversity was identified among rice parental genotypes and their derived crosses through evaluation of physiological, biochemical, agronomic, and yield-related traits. The analysis revealed parental genotypes such as C9, R8, and R6 as superior combiners, providing valuable alleles for enhanced salinity tolerance and rice productivity under salinity stress. The crosses G8 × C9, G8 × R7, Z1 × C9, G8 × R6, G8 × R8, R7 × R8, R6 × R8, C9, R7 × C9, R8 × C9, and R6 × C9 exhibited improved performance under salinity stress. The exploitation of these genetic resources in breeding programs offers promising materials for developing high-yielding rice genotypes capable of sustaining productivity under climate-driven salinity challenges. Strong positive associations among physiological resilience parameters, such as antioxidant enzyme activities and relative water content, with key yield components demonstrate the integrated response mechanisms underlying salinity tolerance in rice. In contrast, negative correlations with stress indicator MDA indicate its utility as a marker of oxidative damage. Employing these traits enhances the selection efficiency for salinity tolerance. Both additive and

non-additive gene actions significantly contribute to the inheritance of salinity tolerance traits, with additive effects being crucial for trait transmission from superior parental genotypes, and non-additive effects enhancing hybrid vigour in crosses. Understanding the balance between these gene actions is essential for optimising breeding strategies to effectively combine favourable alleles, thereby enhancing the development of salt-tolerant rice cultivars.

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