

Enhancing salinity tolerance in rice using *Saccharomyces cerevisiae* inoculation: physiological and yield responses across diverse genotypes

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Abstract: Salinity stress is a major environmental constraint limiting crop productivity worldwide. The application of beneficial microorganisms is an effective strategy to improve plant tolerance to abiotic stresses. This study evaluated the role of *Saccharomyces cerevisiae* inoculation in enhancing physiological performance, oxidative stress tolerance, and yield of rice genotypes under saline-water irrigation. A lysimeter experiment was conducted during the 2024 and 2025 seasons. Five rice genotypes were exposed to saline water (6 000 ppm) with and without inoculation. Gas exchange, water status, oxidative stress markers, antioxidant enzyme activities, and yield-related traits were assessed. The results showed that inoculation significantly enhanced CO₂ assimilation (12.27%), stomatal conductance (15.71%), transpiration rate (8.78%), and relative water content (16.36%) across both seasons. Furthermore, inoculation significantly reduced malondialdehyde (MDA) by 19.75% and hydrogen peroxide (H₂O₂) by 23.72%. While superoxide dismutase activity (SOD) increased by 35.32% and catalase activity (CAT) by 20.63%. Grain yield per plant improved by 18.91% and biological yield by 12.84%, accompanied by a reduction in grain sterility (14.47%). The assessed genotypes exhibited significant variation across all parameters studied. IRRI-165 and Giza-179 exhibited superior performance and responsiveness. Giza-182 and Sakha-104 displayed intermediate levels, while Giza-177 was the most sensitive genotype. Multivariate analyses confirmed strong positive associations between inoculation and genotypic performance. Whereas genotypic performance was negatively associated with oxidative stress markers. These results suggest that *S. cerevisiae* inoculation improves rice performance under salinity stress. The enhancement may contribute to the integration of physiolo-

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gical and biochemical mechanisms. Therefore, combining microbial inoculation with tolerant genotypes provides a sustainable strategy to improve rice productivity in salt-affected environments.

Keywords: antioxidant defence; osmotic stress; heatmap and hierarchical clustering; microbial biostimulant; multivariate analysis; oxidative damage; principal component analysis biplot

Salinity stress is one of the most severe abiotic constraints limiting agricultural productivity worldwide (Llanes 2026). A substantial proportion of cultivated land is affected by salinity (Rahman et al. 2026). The projections suggest further expansion due to climate change and unsustainable agricultural practices (Rosa 2022). Rice (*Oryza sativa* L.) is a staple food crop for more than half of the global population (Tagliapietra et al. 2024). It is vulnerable to salinity stress, especially during early vegetative and reproductive stages (Awaad et al. 2025). Exposure to high salt concentrations leads to osmotic stress, ion toxicity, and nutrient imbalance (ElSherbiny et al. 2026). Osmotic stress reduces water uptake, decreases cell turgor, and causes stomatal closure (Wang et al. 2023). Consequently, it restricts CO₂ diffusion and lowers photosynthetic efficiency (Zuo et al. 2024). Ionic toxicity results in the accumulation of sodium and chloride ions in plant tissues (Selem et al. 2022). Furthermore, salinity stress enhances the generation of reactive oxygen species (ROS) (ElSayed et al. 2022). This induces oxidative damage to cellular membranes, proteins, and nucleic acids (Tavu and Redillas 2025). At the same time, plants possess antioxidant defence systems, including enzymatic components such as superoxide dismutase and catalase (Desoky et al. 2021b). These mechanisms are often insufficient to mitigate excessive ROS accumulation under severe stress conditions.

Several agronomic strategies have been explored to mitigate the adverse effects of salinity (Desoky et al. 2021a). The use of plant growth-promoting microorganisms is an environmentally sustainable approach (Mourouzidou et al. 2023). These microorganisms enhance plant tolerance to abiotic stress through multiple mechanisms (Munir et al. 2022). They contribute to better osmotic adjustment, activation of antioxidant defence systems, and maintenance of cellular homeostasis (Zandi and Schnug 2022). *Saccharomyces cerevisiae* is considered a promising biostimulant (Nazzal et al. 2025). It can produce a wide range of bioactive compounds (Doolam et al. 2025). These compounds play critical roles in promot-

ing plant growth and stress adaptation. In addition, *S. cerevisiae* enhances photosynthetic activity, water relations, and antioxidant enzyme activities, subsequently reducing oxidative damage under adverse environmental conditions (Lu et al. 2021).

Rice genotypes differ significantly in their ability to regulate ion transport, maintain osmotic balance, and activate antioxidant defence systems (Kumar et al. 2024). These differences influence their tolerance to salinity and their responsiveness to microbial inoculation (Ghosh et al. 2025). Exploring the response of diverse rice genotypes to inoculation treatments is essential for optimising the use of biostimulants under salinity stress. Integrating microbial inoculation with salt-tolerant genotypes is a promising strategy to improve crop productivity in saline environments. Although *Saccharomyces cerevisiae* has been recognised as a promising biostimulant for improving plant performance under abiotic stress, its effects on different rice genotypes under controlled saline irrigation conditions remain insufficiently characterised. In particular, limited information is available on whether the physiological, oxidative, and yield responses to inoculation are consistent across genetically distinct rice materials exposed to salinity over multiple growing seasons. Therefore, it evaluated the genotype-dependent responses of five rice genotypes to *S. cerevisiae* inoculation under saline irrigation, integrating measurements of gas exchange, water status, oxidative stress markers, antioxidant enzyme activities, and yield traits over two seasons. Accordingly, the present study aimed to determine the effect of *Saccharomyces cerevisiae* inoculation on the physiological performance, oxidative stress status, antioxidant defence system, and yield attributes of five rice genotypes grown under saline irrigation conditions. In addition, the study aimed to assess the extent of genotypic variation in response to inoculation and to identify the most responsive genotypes under salinity stress. Multivariate analyses were also employed to clarify the relationships among inoculation treatment, genotypic performance, and the measured physiological and agronomic traits.

Table 1. Soil physical and chemical properties of the used soil in lysimeters

Season	Sand	Silt	Clay	pH	EC (dS/m)	OC (%)	N	P	Ca ²⁺	Mg ²⁺	K ⁺	Na ⁺	HCO ₃ ⁻ Cl ⁻ SO ₄ ²⁻		
													(meq/L)		
2024	12.6	32.3	55.1	8.20	2.30	0.93	650	18.80	8.40	5.10	1.15	12.30	8.70	18.80	2.85
2025	12.9	32.2	54.9	8.09	2.95	0.88	520	14.20	10.04	7.42	1.40	14.10	9.40	19.34	3.22

EC – electrical conductivity; OC – organic carbon

MATERIAL AND METHODS

Experimental design and plant materials. This experiment was conducted in the lysimeters at the Sakha Research Station, Kafr El-Sheikh, Egypt, during the 2024 and 2025 seasons. Five rice genotypes were used: Giza-177, Giza-179, Giza-182, Sakha-104, and IRRI-165. The genotypes were provided by the Rice Research Department, Kafr El-Sheikh, Egypt. The experiment was arranged in a factorial randomised complete block design (RCBD) with genotype and inoculation as the two main factors, using three replications.

Lysimeter conditions and salinity management. The experiment was conducted under artificially saline conditions in lysimeters. Each lysimeter container had dimensions of 2 m in length, 1 m in width, and 1 m in depth. The containers were filled with soil, leaving a 10 cm gap at the top to ensure proper drainage and avoid overflow during irrigation. Before planting, soil samples were collected from the 0–30 cm soil layer using an auger and analysed for physical and chemical properties. The experimental soil was

classified as a clayey soil according to the USDA textural classification system. The particle-size distributions of 55.1% clay, 32.3% silt, and 12.6% sand in 2024, and 54.9% clay, 32.2% silt, and 12.9% sand in 2025. According to the FAO World Reference Base classification, the soil is classified as a Vertisol. Soil pH was slightly alkaline, while electrical conductivity was 2.30 dS/m in 2024 and 2.95 dS/m in 2025. Organic carbon content was 0.93% and 0.88% in 2024 and 2025, respectively. Available nitrogen was 650 ppm in 2024 and 520 ppm in 2025, whereas available phosphorus was 18.80 ppm and 14.20 ppm in the same seasons, respectively. The detailed soil chemical characteristics are presented in Table 1. Meteorological data for the 2024 and 2025 growing seasons, including mean air temperature, relative humidity, and precipitation, were obtained from the meteorological station at Sakha Agricultural Research Station. Detailed weather data are presented in Table 2. Drainage, irrigation, and salinity were precisely managed throughout the experiment. To establish an artificial salinity level of 6 000 ppm, calcium chloride (CaCl₂) and sodium chloride (NaCl) were used in

Table 2. Monthly weather conditions during the 2024 and 2025 seasons

Month	Temperature (°C)		Precipitation (mm)	Humidity (%)
	min	max		
Season 2024				
May	16.69	33.59	0.00	47.64
June	22.05	40.88	0.23	49.47
July	24.17	38.70	0.00	50.26
August	21.66	39.77	0.02	52.67
September	22.72	37.09	0.00	54.07
Season 2025				
May	17.32	34.75	0.23	44.75
June	19.68	37.66	0.34	51.90
July	22.53	40.26	0.12	48.71
August	23.67	39.14	0.00	50.72
September	21.29	35.66	2.38	58.57

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a 1:2 ratio to salinise the water artificially (6 000 ppm). The lysimeters were drained one day before each four-day irrigation cycle. The electrical conductivity (EC) of the drainage water was measured for each lysimeter plot. Salinity levels were readjusted to maintain constant salinity throughout the season. All treatments were evaluated under saline irrigation, while no non-saline control was included.

Twenty-five-day-old seedlings were transplanted into 2 m rows for each variety. After transplanting, each lysimeter contained 50 plants, spaced 15 × 15 cm apart. The plots were irrigated with saline water starting 15 days after transplanting and continued until maturity.

Two strains were used: *Saccharomyces cerevisiae* NCAIMY-00216 and *Saccharomyces cerevisiae* NCAIMY-0262. These strains were provided by the National Collection of Agricultural and Industrial Microorganisms (NCAIM), Hungary. The strains were cultured in a medium containing 3 g/L yeast extract, 3 g/L malt extract, 5 g/L peptone, 10 g/L glucose, and 20 g/L agar at 30 °C and 200 rpm for 48 h (Surussawadee et al. 2015). Inocula were prepared using a peat-based carrier, with 15 mL of 10⁸ CFU (colony forming unit)/mL culture per 30 g of sterilised carrier. The two strains were mixed before application and used as a combined inocula treatment. Inoculation was applied 10 days after transplanting at a rate of 0.40 g inoculum per lysimeter (2 m²). The combined inocula were applied by placing the peat-based inocula directly around the roots in each lysimeter. The non-inoculated control received the same sterilised peat carrier, applied in the same manner as the inoculated treatment. According to the lysimeter area (2 m²), phosphorus fertiliser was applied 3.17 g P per lysimeter in the form of single superphosphate (15% P₂O₅). Immediately after application, the lysimeters were irrigated and lightly levelled. Nitrogen fertiliser was applied at a rate of 165 kg N/ha, equivalent to 33 g N per lysimeter, as urea (46.5% N). The nitrogen dose was split into two applications, with two-thirds applied before transplanting and the remaining one-third applied 30 days after transplanting. Throughout the growing season, irrigation was applied every four days using saline water. Lysimeters were drained 1 day before each irrigation event, and the electrical conductivity of drainage water was monitored regularly to maintain the target salinity level. Weeds were controlled manually when necessary, and plants were monitored regularly for pests and diseases. No severe pest or disease infestations were observed during the experimental period.

Physiological traits. Carbon dioxide (CO₂) rates, stomatal conductance, transpiration rate and relative water content (RWC%) were recorded. A portable steady-state porometer (LICOR, LI-1600, Lincoln, USA) was used to assess leaf-level CO₂ and H₂O exchange. Leaf diffusive resistance (LDR) was calculated using the following equation:

$$\text{LDR} = (\text{DR}_{\text{ad}} \times \text{DR}_{\text{ab}}) / (\text{DR}_{\text{ad}} + \text{DR}_{\text{ab}})$$

where: DR_{ad} and DR_{ab} – diffusive resistance of the adaxial and abaxial surfaces, respectively (Schulze and Hall 1982).

Stomatal conductance and leaf transpiration rate (μmol/m²/s) were measured on the fully expanded flag leaf. RWC was determined according to the method described by Weatherley (1950). Malondialdehyde and thiobarbituric acid reactive substances were evaluated at the panicle initiation stage following Du and Bramlage (1992). Approximately 0.5 g of leaf tissue was ground in liquid nitrogen. Then it was mixed with a hydro-acetone buffer (4:1 v/v). Subsequently, 0.65% thiobarbituric acid and 0.01% butylated hydroxytoluene were added. After incubation at 95 °C, the homogenate was centrifuged at 10 000 × g for 15 min, and the supernatant was analysed at 532 nm and 600 nm.

Leaf hydrogen peroxide (H₂O₂) content was measured colourimetrically following Viljevac Vuletić et al. (2019). Five representative leaves (0.5 g) were homogenised using liquid nitrogen and trichloroacetic acid (TCA: 0.1%). The homogenised sample was centrifuged at 3 000 rpm for 20 min. The extract (1 mL) was mixed with 10 mmol K-phosphate buffer (pH 7.0, 1.0 mL) and potassium iodide (2 mol, 1 mL). The absorbance of the mixture was recorded at 390 nm using a spectrophotometer. A standard curve was generated under the same conditions, and H₂O₂ content was expressed as μmol g/FW (fresh weight).

Enzymatic antioxidants were extracted from fresh leaf tissue by freezing 1 g samples in liquid nitrogen to minimise proteolytic activity, followed by homogenisation in 5 mL of ice-cold extraction buffer containing 0.1 mol/L phosphate buffer (pH 7.0), 0.5 mmol/L EDTA, and 2% (w/v) polyvinylpyrrolidone (PVP). The homogenate was centrifuged at 10 000 × g for 20 min, and the supernatant was collected as the crude enzyme extract (Gegenheimer 1990). Superoxide dismutase (SOD; EC 1.15.1.1) activity was determined by its ability to inhibit the photochemical reduction of nitroblue tetrazolium (NBT) (Flohé and Otting 1984). The reaction mixture contained enzyme extract, 50 mmol/L potassium phosphate

buffer, 13 mmol/L methionine, 0.075 mmol/L NBT, 0.10 mmol/L EDTA, and 0.002 mmol/L riboflavin. The tubes were exposed to light for 15 min, and the formation of blue formazan was measured spectrophotometrically at 550 nm against a blank lacking enzyme extract. SOD activity was expressed as U/mg protein. Catalase (CAT; EC 1.11.1.6) activity was measured according to Aebi (1974) by monitoring the decomposition of hydrogen peroxide. The reaction mixture contained enzyme extract and 0.2 mmol/L H₂O₂ in 10 mmol/L potassium phosphate buffer (pH 7.0), and the decrease in absorbance was recorded at 240 nm. CAT activity was expressed as U/mg protein.

Agronomical traits. Agronomic traits were evaluated using 10 randomly selected plants from each replication. The number of panicles per plant was recorded. Additionally, ten panicles were collected from the inner rows to estimate panicle length (cm), panicle weight (g), and the number of filled/unfilled grains per panicle and primary branches per panicle. Thousand-grain weight (g), grain yield per plant (g) (PGY), and biological yield per plant (g) were determined.

Statistical analysis. Data were analysed using analysis of variance (ANOVA). The two growing seasons were analysed separately to assess treatment effects within each season. Mean separation was conducted using the least significant difference (LSD) test at $P < 0.05$. Main effects of inoculation and genotype, and their interaction, were tested, with significance defined at $P < 0.05$ and high significance at $P < 0.01$. Non-significant effects ($P > 0.05$) are denoted as "ns." Data are presented as the mean \pm standard error of three replicates. Multivariate statistical analyses, including heatmap and principal component analysis (PCA), were performed using R software version 4.2.0 (Vienna, Austria).

RESULTS

Gas exchange and water status parameters. The physiological responses of 5 rice genotypes to inoculation with *Saccharomyces cerevisiae* strains under saline water stress were evaluated. The inoculation significantly improved gas exchange and water status parameters compared to the non-inoculated control across both the 2024 and 2025 growing seasons (Table 3). In 2024, inoculated plants showed a 11.95% increase in leaf CO₂ assimilation rate, a 14.66% increase in stomatal conductance, an 8.73% increase in transpiration rate, and a 15.86% increase

in relative water content. Similarly, in 2025, the inoculated plants exhibited significant increases in the aforementioned parameters of 12.59, 16.75, 8.82, and 16.86%, in the same order. This indicates a strong positive effect of inoculation under salinity stress. Furthermore, significant genotypic differences were observed for gas exchange and water status parameters. In 2024, IRRI-165 recorded the highest values for CO₂ assimilation rate (22.23 $\mu\text{mol}/\text{m}^2/\text{s}$), stomatal conductance (0.722 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$), transpiration rate (40.36 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$), and relative water content (64.28%). Giza-179 also showed superior performance in several traits. Conversely, Giza-177 consistently recorded the lowest values across most parameters. In 2025, the same trend persisted, with IRRI-165 and Giza-179 outperforming other genotypes. While Giza-177 remained the least performing genotype. The interaction between inoculation and rice genotypes across both seasons is illustrated in Figure 1. The response of assessed genotypes varied to inoculation under salinity stress. IRRI-165 showed the highest increase under inoculation in both seasons, followed by Giza-179. In contrast, Giza-177 recorded the lowest gas exchange and water status parameters under both inoculated and non-inoculated conditions. The interaction results indicate that the beneficial effects of *Saccharomyces cerevisiae* inoculation on gas exchange and water status are genotype-dependent under salinity stress.

Oxidative stress markers and enzymatic antioxidant activities. Inoculation with *Saccharomyces cerevisiae* strains significantly reduced the accumulation of oxidative stress markers compared with non-inoculated controls. Malondialdehyde content (MDA) decreased by 20.12% in 2024 and 19.38% in 2025 using inoculation compared to non-inoculated controls (Table 4). Similarly, hydrogen peroxide (H₂O₂) levels were significantly lower in inoculated plants than in non-inoculated plants, by 22.69% in 2024 and 24.75% in 2025. Moreover, the inoculation significantly enhanced antioxidant defence mechanisms. The activity of superoxide dismutase increased by 35.16% in 2024 and 35.48% in 2025. Catalase activity also showed significant improvements of 19.94% in 2024 and 21.31% in 2025. The evaluated genotypes exhibited significant variations in oxidative stress markers and antioxidant enzymes. In 2024, IRRI-165 recorded the lowest MDA (19.51 $\mu\text{mol}/\text{g FW}$) and H₂O₂ (14.59 $\mu\text{mol}/\text{g FW}$) values. It recorded the highest SOD (34.40 U/mg protein) and CAT (34.73 U/mg protein) activities. Giza-179 also showed relatively

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Table 3. Effect of inoculation with *Saccharomyces cerevisiae* strains compared with control without inoculation on leaf CO₂ assimilation rate, stomatal conductance, transpiration rate, and relative water content of five rice genotypes under saline water stress across two growing seasons (2024–2025)

Studied factor	Leaf CO ₂ assimilation rate (μmol/m ² /s)	Stomatal conductance (μmol CO ₂ /m ² /s)	Transpiration rate	Relative water content (%)
Season 2024				
Inoculation				
Non-inoculated	18.01 ± 2.35 ^B	0.587 ± 0.01 ^B	34.57 ± 3.09 ^B	53.60 ± 3.22 ^B
Inoculated	20.16 ± 2.72 ^A	0.673 ± 0.03 ^A	37.59 ± 2.29 ^A	62.10 ± 2.36 ^A
Genotype				
Giza-177	15.30 ± 1.10 ^d	0.468 ± 0.05 ^d	30.11 ± 2.63 ^e	50.13 ± 4.06 ^e
Giza-179	21.10 ± 1.23 ^b	0.695 ± 0.07 ^a	38.36 ± 1.46 ^b	61.07 ± 4.82 ^b
Giza-182	18.34 ± 0.92 ^c	0.612 ± 0.06 ^c	35.27 ± 1.14 ^d	55.03 ± 4.46 ^d
IRRI-165	22.23 ± 1.76 ^a	0.722 ± 0.04 ^a	40.36 ± 2.26 ^a	64.28 ± 4.96 ^a
Sakha-104	18.45 ± 1.18 ^c	0.652 ± 0.05 ^b	36.32 ± 1.30 ^c	58.73 ± 5.05 ^c
ANOVA	<i>df</i>	mean squares and significance		
Inoculation (YI)	1	34.73**	0.055**	68.34**
Genotype (G)	4	43.81**	0.067**	89.85**
YI × G	4	0.614*	0.002 ^{ns}	2.115**
Season 2025				
Inoculation				
Non-inoculated	17.34 ± 1.61 ^B	0.553 ± 0.10 ^B	33.77 ± 2.29 ^B	52.29 ± 3.35 ^B
Inoculated	19.52 ± 2.18 ^A	0.645 ± 0.01 ^A	36.75 ± 3.18 ^A	61.10 ± 4.17 ^A
Genotype				
Giza-177	14.43 ± 1.37 ^d	0.443 ± 0.04 ^e	28.35 ± 1.95 ^e	47.91 ± 4.17 ^e
Giza-179	20.32 ± 1.27 ^b	0.683 ± 0.08 ^b	38.07 ± 1.46 ^b	60.66 ± 5.16 ^b
Giza-182	17.47 ± 0.81 ^c	0.547 ± 0.06 ^d	34.13 ± 1.66 ^d	53.78 ± 4.76 ^d
IRRI-165	21.97 ± 1.72 ^a	0.730 ± 0.03 ^a	40.30 ± 2.10 ^a	64.05 ± 4.86 ^a
Sakha-104	17.98 ± 1.20 ^c	0.592 ± 0.07 ^c	35.47 ± 1.42 ^c	57.07 ± 5.33 ^c
ANOVA	<i>df</i>	mean squares and significance		
Inoculation	1	35.77**	0.067**	70.84**
Genotype	4	49.80**	0.052**	123.5**
YI × G	4	0.670*	0.001*	1.930**

Data are expressed as means ± standard error (SE). Means with different letters are significantly different according to the least significant differences test ($P < 0.05$). The uppercase red letters belong to inoculation, while the lowercase blue letters belong to the assessed rice genotypes. *df* – degree of freedom; ns – not significant; * $P < 0.05$; ** $P < 0.01$

low oxidative damage and high antioxidant activity. In contrast, Giza-177 exhibited the highest MDA (33.16 μmol/g FW) and H₂O₂ (22.95 μmol/g FW) contents. In 2025, IRRI-165 maintained superior performance, and Giza-177 showed the poorest response. The interaction between inoculation and genotype was significant for oxidative stress indicators. Inoculation significantly reduced MDA and H₂O₂ levels across all five rice genotypes com-

pared to the non-inoculated control (Figure 2). The inoculation effectively mitigates salinity-induced oxidative damage to membranes. The magnitude of the effect varied among the assessed genotypes. Giza-179 and IRRI-165 showed significant decreases in MDA and H₂O₂ in response to the inoculation treatment. Giza-182 and Sakha-104 demonstrated intermediate MDA levels. Giza-177 showed the highest MDA and H₂O₂ levels under both conditions but

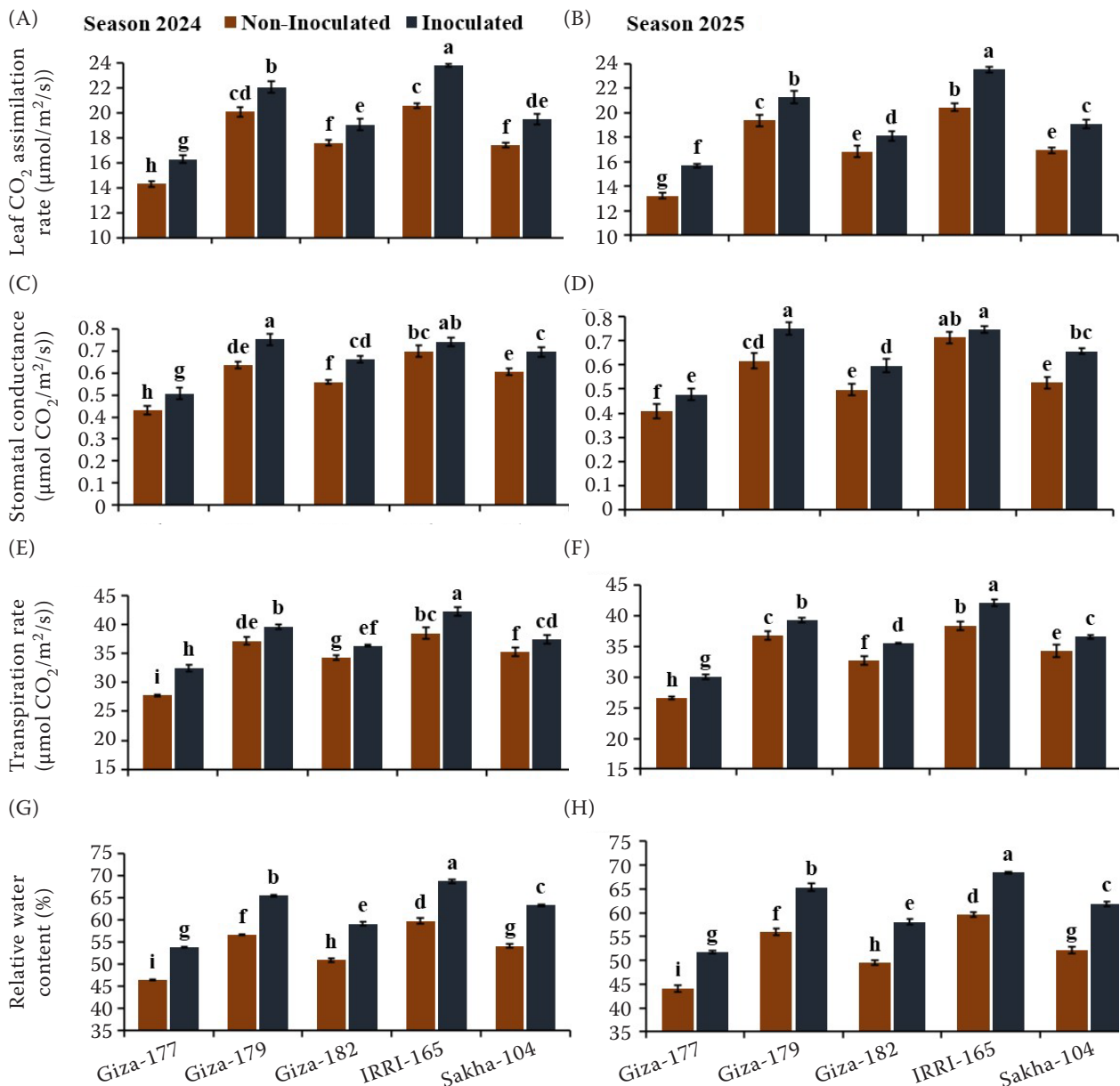


Figure 1. The influence of inoculation with *Saccharomyces cerevisiae* strains compared to untreated control on gas exchange and water status parameters of five rice genotypes under saline conditions across the 2024 and 2025 seasons. Error bars represent the standard error, and different letters indicate significant differences among genotype-by-treatment combinations

exhibited a significant reduction upon inoculation. Moreover, the inoculation increased activities of superoxide dismutase (SOD) and catalase (CAT) across all genotypes (Figure 2). IRRI-165 exhibited the greatest enhancement in SOD and CAT activities under inoculation, followed by Giza-179.

Yield traits. The effect of *Saccharomyces cerevisiae* inoculation on panicle traits under salinity stress is presented in Table 5. Inoculation significantly im-

proved the number of panicles per plant, branches per panicle, panicle length, and panicle weight compared with the non-inoculated control in both seasons. In 2024, inoculated plants showed increases of 8.42% in the number of panicles per plant, 7.90% in the number of branches per panicle, 7.64% in panicle length, and 10.35% in panicle weight compared to non-inoculated plants. Similarly, in 2025, inoculation increased these traits by 8.06, 9.86, 7.66, and 12.04%,

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Table 4. Effect of inoculation with *Saccharomyces cerevisiae* strains compared with control without inoculation on malondialdehyde (MDA), superoxide dismutase activity (SOD), catalase activity (CAT) and hydrogen peroxide (H₂O₂) of five rice genotypes under salinity stress across two growing seasons (2024–2025)

Studied factor	MDA		H ₂ O ₂	SOD		CAT
	(μmol/g FW)			(U/mg protein)		
Season 2024						
Inoculation						
Non-inoculated		29.25 ± 2.31 ^A	20.65 ± 3.64 ^A	23.56 ± 3.14 ^B		25.26 ± 1.87 ^B
Inoculated		23.37 ± 1.83 ^B	15.97 ± 2.80 ^B	31.85 ± 1.50 ^A		30.29 ± 2.30 ^A
Genotype						
Giza-177		33.16 ± 2.25 ^a	22.95 ± 2.75 ^a	21.07 ± 1.65 ^e		22.03 ± 1.70 ^e
Giza-179		20.56 ± 3.39 ^d	15.17 ± 2.26 ^d	31.57 ± 1.93 ^b		30.65 ± 2.92 ^b
Giza-182		30.54 ± 2.38 ^b	20.21 ± 1.85 ^b	24.78 ± 2.03 ^d		24.67 ± 2.11 ^d
IRRI-165		19.51 ± 1.21 ^e	14.59 ± 2.28 ^d	34.40 ± 2.51 ^a		34.73 ± 1.37 ^a
Sakha-104		27.79 ± 2.24 ^c	18.64 ± 1.92 ^c	26.69 ± 2.70 ^c		26.79 ± 2.94 ^c
ANOVA	<i>df</i>	mean squares and significance				
Inoculation (YI)	1	259.7**	164.6**	514.7**		190.3**
Genotype (G)	4	219.3**	73.41**	170.1**		150.2**
YI × G	4	5.433**	2.842**	16.70**		5.510**
Season 2025						
Inoculation						
Non-inoculated		30.89 ± 2.25 ^A	19.72 ± 1.68 ^A	22.99 ± 4.12 ^B		24.38 ± 3.28 ^B
Inoculated		24.90 ± 3.61 ^B	14.84 ± 2.07 ^B	31.15 ± 3.71 ^A		29.59 ± 2.64 ^A
Genotype						
Giza-177		36.03 ± 2.51 ^a	21.68 ± 2.78 ^a	20.09 ± 1.84 ^e		21.57 ± 1.66 ^e
Giza-179		21.70 ± 2.65 ^d	14.59 ± 2.34 ^d	31.01 ± 2.07 ^b		30.09 ± 2.93 ^b
Giza-182		32.38 ± 1.35 ^b	18.83 ± 3.64 ^b	24.01 ± 1.56 ^d		23.12 ± 2.38 ^d
IRRI-165		20.03 ± 1.30 ^e	14.17 ± 2.16 ^d	34.35 ± 2.41 ^a		34.49 ± 2.37 ^a
Sakha-104		29.32 ± 2.76 ^c	17.14 ± 2.65 ^c	25.88 ± 1.56 ^c		25.66 ± 1.16 ^c
ANOVA	<i>df</i>	mean squares and significance				
Inoculation	1	176.18**	194.97**	499.1**		202.6**
Genotype	4	258.51**	53.41**	192.1**		168.0**
YI × G	4	9.16**	1.77**	12.87**		5.079**

Data are expressed as means ± standard error (SE). Means with different letters are significantly different according to the least significant differences test ($P < 0.05$). The uppercase red letters belong to inoculation, while the lowercase blue letters belong to the assessed rice genotypes. *df* – degree of freedom; ns – not significant; ** $P < 0.01$; FW – fresh weight

respectively. These increments indicate that inoculation enhanced reproductive and yield formation in rice under salinity stress. Significant differences among genotypes were observed for all studied traits. In 2024, IRRI-165 recorded the highest number of panicles per plant (16.30), number of branches per panicle (11.38), panicle length (18.83 cm), and panicle weight (2.37 g). Also, Giza-179 showed superior panicle performance. In 2025, IRRI-165

and Giza-179 produced the highest values for most traits. The interaction between inoculation and rice genotypes for yield-related traits is illustrated in Figure 3. The results showed a positive response to inoculation in both seasons, with varying magnitudes among genotypes. Inoculation increased panicle traits across all genotypes in both seasons. The highest values were recorded in IRRI-165 under inoculated conditions, followed by Giza-179. The

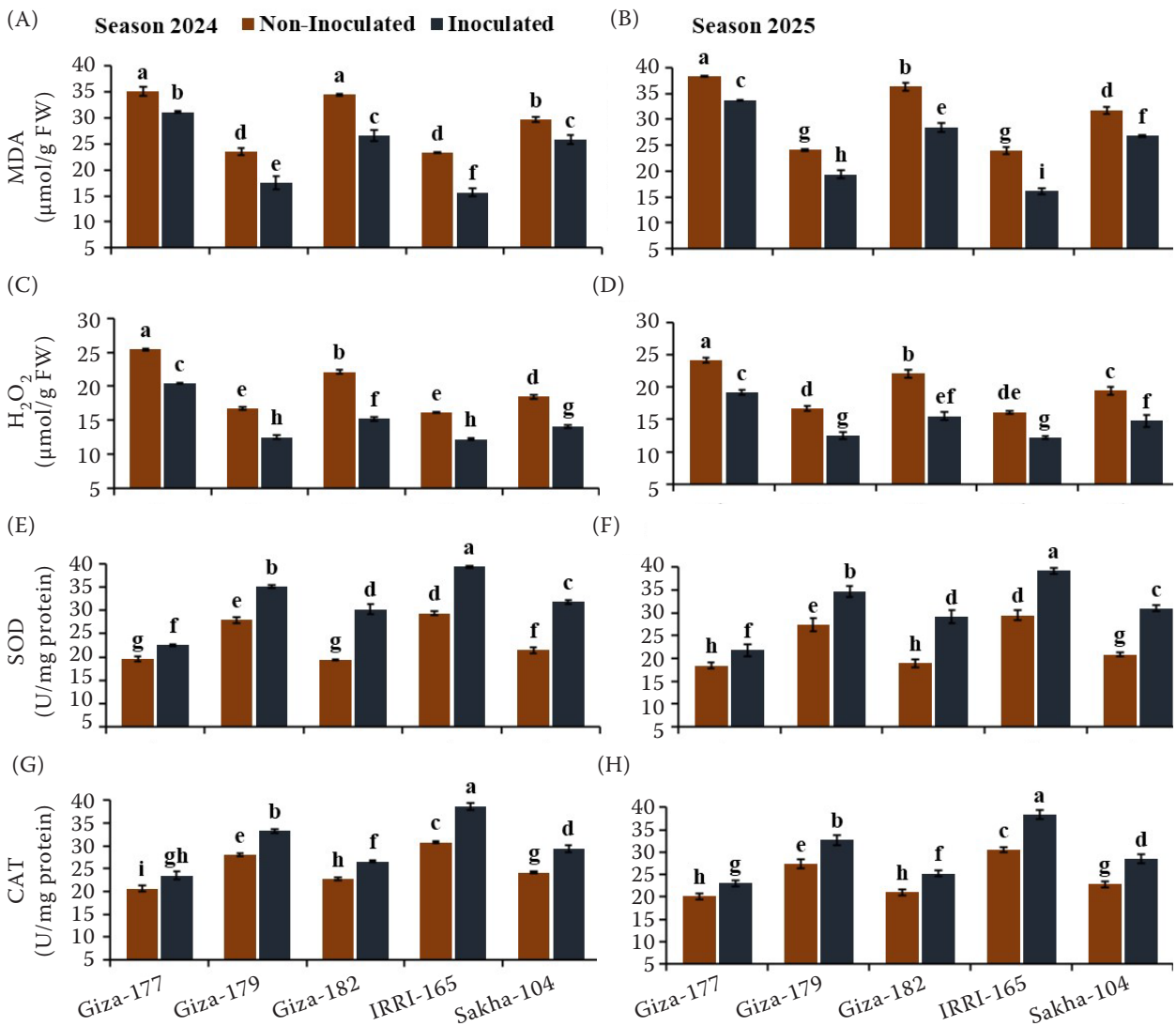


Figure 2. The influence of inoculation with *Saccharomyces cerevisiae* strains compared to untreated control on oxidative stress markers and enzymatic antioxidant activities of five rice genotypes under saline conditions across the 2024 and 2025 seasons. Error bars represent the standard error, and different letters indicate significant differences among genotype and treatment combinations; FW – fresh weight

relative improvement from inoculation was evident across all genotypes, but was more pronounced in high-yielding genotypes. These results suggest that the beneficial effects of *Saccharomyces cerevisiae* inoculation on yield formation are influenced by the genetic background of rice genotypes.

The effect of *Saccharomyces cerevisiae* inoculation on grain yield and its related components under salinity stress is presented in Table 6. Inoculation significantly improved the number of filled grains per panicle, thousand-grain weight, grain yield per plant, and biological yield per plant. While it reduced the number of unfilled grains per panicle in

both seasons. In 2024, inoculated plants showed an increase of 7.83% in the number of filled grains per panicle, 6.06% in thousand grain weight, 17.61% in grain yield per plant, and 12.84% in biological yield per plant compared with non-inoculated plants. Meanwhile, the number of unfilled grains per panicle decreased by 19.38%. In 2025, inoculation increased filled grains per panicle by 10.26%, thousand grain weight by 3.70%, grain yield per plant by 20.28%, and biological yield per plant by 12.84%. Whereas unfilled grains decreased by 9.56%. These results suggest the positive effect of inoculation on yield traits under salinity stress. Significant genotypic variation was

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Table 5. Effect of inoculation with *Saccharomyces cerevisiae* strains compared with control without inoculation on the number of panicles per plant, the number of branches per panicle, panicle length and panicle weight of five rice genotypes under salinity stress across two growing seasons (2024–2025)

Studied factor		Number of panicles per plant	Number of branches per panicle	Panicle length (cm)	Panicle weight (g)
Season 2024					
Inoculation					
Non-inoculated		13.47 ± 1.17 ^B	10.13 ± 1.30 ^A	17.10 ± 1.13 ^B	1.93 ± 0.16 ^B
Inoculated		14.53 ± 1.55 ^A	10.93 ± 1.16 ^A	18.41 ± 1.07 ^A	2.13 ± 0.17 ^A
Genotype					
Giza-177		11.13 ± 0.82 ^c	9.00 ± 0.63 ^c	16.45 ± 0.98 ^c	1.72 ± 0.09 ^c
Giza-179		15.63 ± 1.64 ^a	11.33 ± 1.02 ^a	18.02 ± 1.15 ^{ab}	2.02 ± 0.11 ^b
Giza-182		13.30 ± 1.03 ^b	10.17 ± 0.47 ^b	18.02 ± 1.41 ^{ab}	1.95 ± 0.14 ^b
IRRI-165		16.30 ± 0.49 ^a	11.83 ± 0.71 ^a	18.83 ± 1.28 ^a	2.37 ± 0.10 ^a
Sakha-104		13.63 ± 1.34 ^b	10.33 ± 1.29 ^b	17.45 ± 0.53 ^{bc}	2.12 ± 0.07 ^b
ANOVA	<i>df</i>	mean squares and significance			
Inoculation (YI)	1	8.530*	4.80 ^{ns}	12.81*	0.300**
Genotype (G)	4	25.20**	7.28*	4.64**	0.338**
YI × G	4	0.03 ^{ns}	1.22*	0.37 ^{ns}	0.002 ^{ns}
Season 2025					
Inoculation					
Non-inoculated		12.40 ± 2.04 ^B	9.47 ± 1.05 ^B	15.83 ± 1.07 ^B	1.83 ± 0.29 ^B
Inoculated		13.40 ± 2.17 ^A	10.40 ± 1.12 ^A	17.04 ± 0.96 ^A	2.05 ± 0.31 ^A
Genotype					
Giza-177		9.83 ± 0.75 ^c	8.50 ± 0.74 ^c	15.23 ± 0.71 ^c	1.50 ± 0.09 ^d
Giza-179		15.00 ± 0.63 ^a	10.83 ± 1.16 ^a	16.67 ± 1.02 ^{ab}	1.90 ± 0.16 ^{bc}
Giza-182		12.17 ± 1.18 ^b	9.50 ± 0.94 ^{bc}	16.67 ± 1.13 ^{ab}	1.85 ± 0.13 ^c
IRRI-165		15.00 ± 1.05 ^a	11.17 ± 0.47 ^a	17.45 ± 1.21 ^a	2.40 ± 0.08 ^a
Sakha-104		12.50 ± 1.13 ^b	9.67 ± 1.16 ^b	16.15 ± 0.58 ^{bc}	2.03 ± 0.10 ^b
ANOVA	<i>df</i>	mean squares and significance			
Inoculation	1	7.50*	6.533*	11.04*	0.363**
Genotype	4	28.38**	6.967**	3.99**	0.635**
YI × G	4	0.083 ^{ns}	1.37 ^{ns}	0.351 ^{ns}	0.096 ^{ns}

Data are expressed as means ± standard error (SE). Means with different letters are significantly different according to the least significant differences test ($P < 0.05$). The uppercase red letters belong to inoculation, while the lowercase blue letters belong to the assessed rice genotypes. *df* – degree of freedom; ns – not significant; * $P < 0.05$; ** $P < 0.01$

observed for all yield traits. In 2024, IRRI-165 recorded the highest number of filled grains per panicle (97.17), thousand grain weight (20.97 g), grain yield per plant (36.17 g), and biological yield per plant (75.07 g). Additionally, it recorded the lowest number of unfilled grains per panicle (27.50). Giza-179, followed by Sakha-104 and Giza-182, also exhibited relatively high performance across most traits. While Giza-177 recorded the lowest performance. In 2025, IRRI-165 maintained superior performance

across all yield attributes. The interaction between inoculation and rice genotypes for grain yield traits is illustrated in Figure 4. The data indicate significant improvement in inoculated plants across both seasons. Inoculation increased yield and its related components in all genotypes during both seasons. IRRI-165 recorded the highest values under inoculated conditions, followed by Giza-179 and Giza-182. The relative increase due to inoculation was more pronounced in high-performing genotypes. Across

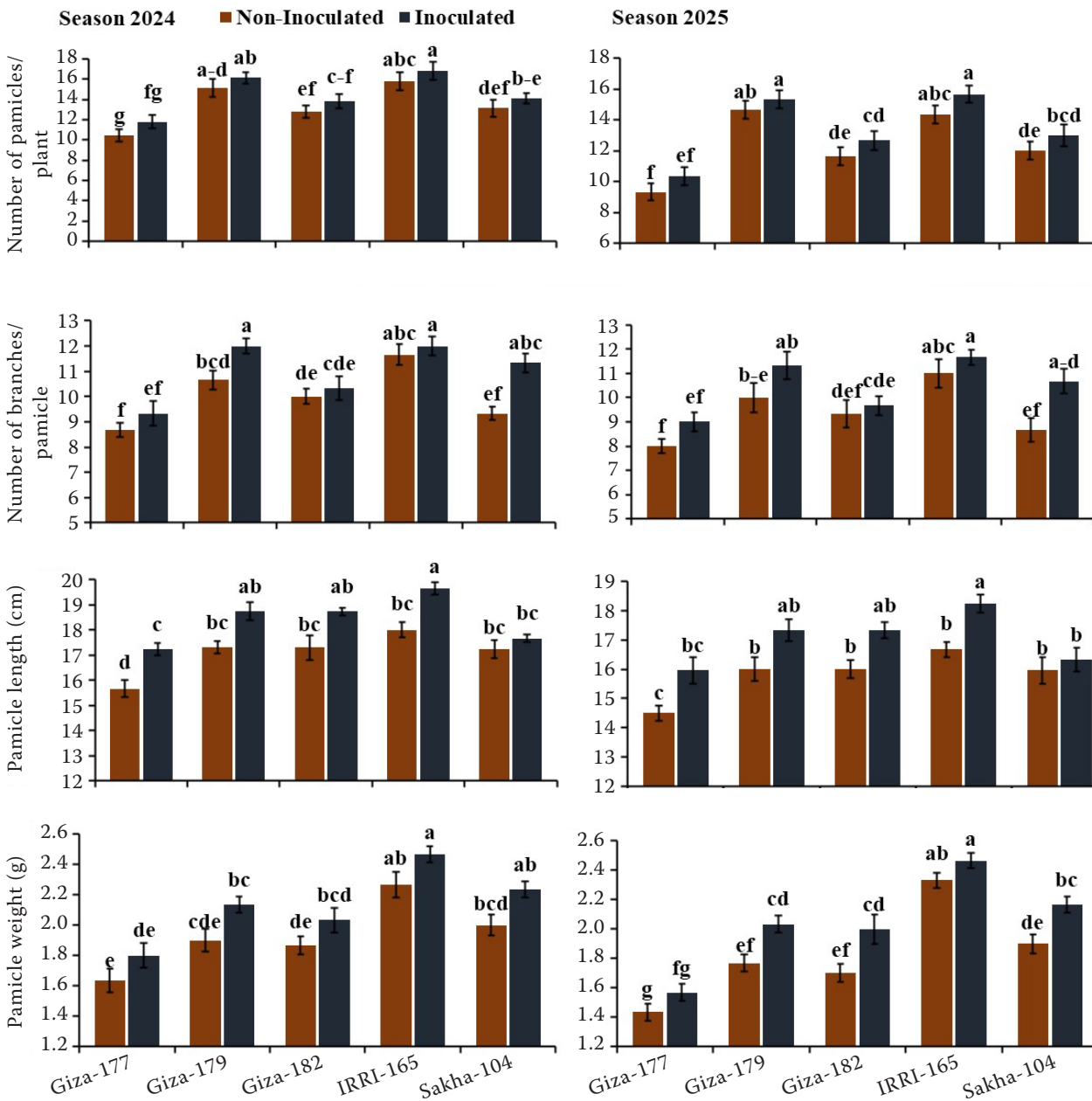


Figure 3. The influence of inoculation with *Saccharomyces cerevisiae* strains compared to untreated control on panicle traits of five rice genotypes under saline conditions across seasons of 2024 and 2025. Error bars represent the standard error, and different letters indicate significant differences among genotype by treatment combinations

both seasons, the interaction results suggest that inoculation with *Saccharomyces cerevisiae* enhanced yield and its components under salinity stress.

Multivariate analysis and clustering pattern. The heatmap and hierarchical clustering analysis (Figure 5) illustrate the response pattern of rice genotypes to *Saccharomyces cerevisiae* inoculation under salinity stress across measured physiological and yield-related traits. A clear separation was observed between the

inoculated and non-inoculated treatments. Inoculated genotypes were grouped and characterised by higher values of positive performance traits. These traits were represented by blue colouration and improved plant performance under inoculation. In contrast, non-inoculated treatments formed a distinct cluster. These treatments were associated with higher levels of oxidative stress markers as indicated by red colouration. This pattern reflects increased oxida-

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Table 6. Effect of inoculation with *Saccharomyces cerevisiae* NCAIM Y. 00216 and *Saccharomyces cerevisiae* NCAIM Y. 0262 compared with control without inoculation on thousand grain weight, grain yield per plant, and biological yield per plant of five rice genotypes under salinity stress across two growing seasons (2024–2025)

Studied factor		Number of filled grains per panicle	Number of unfilled grains per panicle	Thousand grain weight (g)	Grain yield per plant (g)	Biological yield per plant (g)
Season 2024						
Inoculation						
Non-inoculated		85.20 ± 5.34 ^B	38.87 ± 4.21 ^A	18.75 ± 1.11 ^B	24.33 ± 3.63 ^B	60.53 ± 4.38 ^B
Inoculated		91.87 ± 4.46 ^A	31.33 ± 3.58 ^B	19.42 ± 1.04 ^A	28.60 ± 2.92 ^A	68.30 ± 4.26 ^A
Genotype						
Giza-177		68.50 ± 4.97 ^d	47.33 ± 6.19 ^a	19.03 ± 0.33 ^b	16.83 ± 1.72 ^e	53.03 ± 4.15 ^c
Giza-179		95.00 ± 3.20 ^{ab}	29.67 ± 4.27 ^c	19.05 ± 0.47 ^b	29.83 ± 2.35 ^b	64.83 ± 3.21 ^b
Giza-182		91.83 ± 2.07 ^{bc}	34.67 ± 5.65 ^b	18.05 ± 0.39 ^c	23.17 ± 2.14 ^d	75.23 ± 2.84 ^a
IRRI-165		97.17 ± 4.26 ^a	27.50 ± 1.87 ^d	20.97 ± 0.44 ^a	36.17 ± 2.62 ^a	75.07 ± 4.43 ^a
Sakha-104		90.17 ± 3.31 ^c	36.33 ± 3.98 ^b	18.33 ± 0.28 ^c	26.33 ± 2.15 ^c	53.90 ± 3.95 ^c
ANOVA	<i>df</i>	mean squares and significance				
Inoculation (YI)	1	333.3**	425.6**	3.33**	136.5*	453.2**
Genotype (G)	4	796.9**	357.9**	7.77**	313.7**	706.2**
YI × G	4	24.17 ^{ns}	13.97*	0.014 ^{ns}	2.20 ^{ns}	7.95 ^{ns}
Season 2025						
Inoculation						
Non-inoculated		81.93 ± 5.45 ^B	37.67 ± 3.82 ^A	18.63 ± 1.09 ^B	22.95 ± 3.78 ^B	58.20 ± 4.92 ^B
Inoculated		89.93 ± 5.90 ^A	32.07 ± 4.15 ^B	19.32 ± 1.26 ^A	27.60 ± 4.07 ^A	65.67 ± 5.04 ^A
Genotype						
Giza-177		64.00 ± 4.22 ^d	47.17 ± 2.46 ^a	18.90 ± 1.17 ^b	14.53 ± 1.49 ^e	51.00 ± 3.13 ^c
Giza-179		92.17 ± 4.13 ^b	29.33 ± 3.14 ^d	18.95 ± 0.52 ^b	29.00 ± 2.13 ^b	62.33 ± 2.26 ^b
Giza-182		88.33 ± 2.71 ^c	33.33 ± 1.97 ^c	17.95 ± 1.16 ^d	22.17 ± 2.05 ^d	72.33 ± 4.76 ^a
IRRI-165		97.33 ± 2.94 ^a	29.00 ± 0.89 ^d	20.85 ± 0.81 ^a	35.67 ± 3.41 ^a	72.17 ± 3.33 ^a
Sakha-104		85.00 ± 3.94 ^c	40.50 ± 2.07 ^b	18.22 ± 1.19 ^c	25.00 ± 3.02 ^c	51.83 ± 3.07 ^c
ANOVA	<i>df</i>	mean squares and significance				
Inoculation	1	520.8**	97.20**	3.605**	162.4*	418.1**
Genotype	4	982.4**	368.2**	7.721**	370.5**	651.9**
YI × G	4	22.83*	33.95**	0.045 ^{ns}	4.370 ^{ns}	5.380 ^{ns}

Data are expressed as means ± standard error. Means with different letters are significantly different according to the least significant differences test ($P < 0.05$). The uppercase red letters belong to inoculation, and the lowercase blue letters belong to the assessed rice genotypes. *df* – degree of freedom; ns – not significant; * $P < 0.05$; ** $P < 0.01$

tive damage under salinity stress in the absence of inoculation treatment. Specifically, IRRI-165 under inoculated conditions (Inoc-IR165) formed a distinct cluster. It was characterised by the highest positive trait values and the lowest oxidative stress indicators. This confirms its superior tolerance and responsiveness. Giza-179 under inoculation (Inoc-G179) showed a similar clustering pattern, indicating high performance. Intermediate clustering patterns were observed for Giza-182 and Sakha-104. The inoculated

treatments showed moderate improvements compared to their corresponding controls. While Giza-177 under non-inoculated conditions (Non-G177) was presented in a separate cluster. It was associated with elevated oxidative stress markers and reduced physiological and yield performance. The clustering also indicates strong negative relationships between oxidative stress markers (MDA and H_2O_2) and physiological and yield traits. The heatmap confirms that inoculation with *Saccharomyces cerevisiae* enhanced

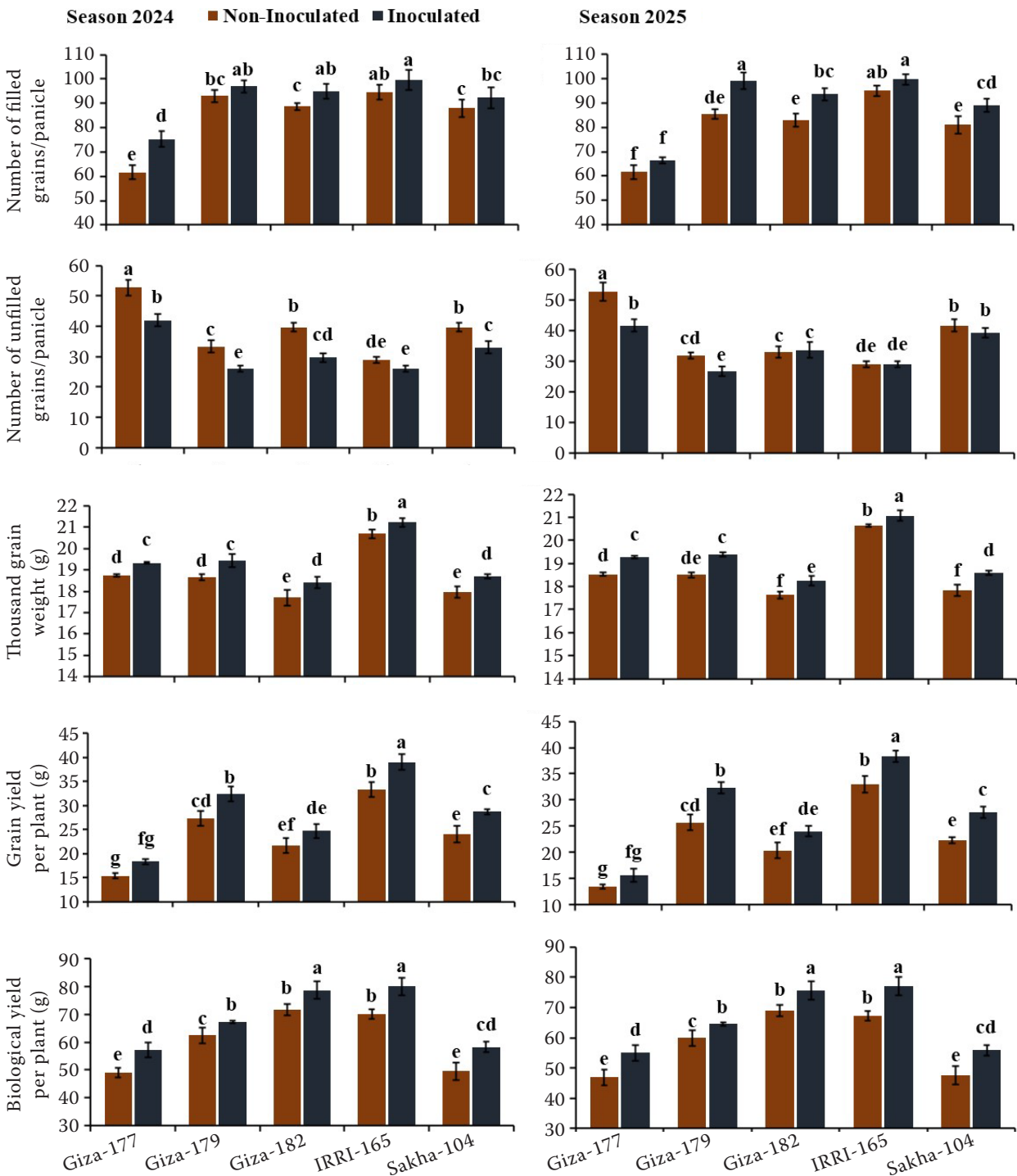


Figure 4. The influence of inoculation with *Saccharomyces cerevisiae* strains compared to untreated control on grain yield-related traits of five rice genotypes under saline conditions across the 2024 and 2025 seasons. Error bars represent the standard error, and different letters indicate significant differences among genotype-by-treatment combinations

physiological efficiency, antioxidant capacity, and yield performance while reducing oxidative stress.

The principal component analysis (PC) biplot (Figure 6) revealed clear differentiation among

treatments and genotypes based on the measured physiological and yield-related traits. The first two principal components explained 90.79% of the total variation, with PC1 accounting for 84.95% and

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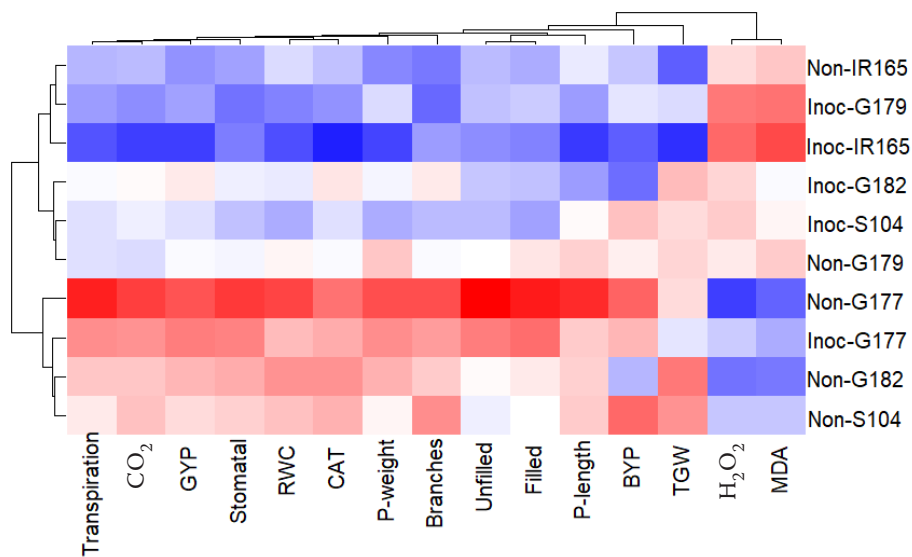


Figure 5. Heatmap and hierarchical clustering of physiological and yield-related traits of five rice genotypes under *Saccharomyces cerevisiae* inoculation and non-inoculated conditions under salinity stress conditions. Inoc – inoculated with *Saccharomyces cerevisiae* strains; Non – non-inoculated control; G177 – Giza-177; G179 – Giza-179; G182 – Giza-182; IR165 – IRR1-165; S104 – Sakha-104. Transpiration – transpiration rate; CO₂ – CO₂ assimilation rate; GYP – grain yield per plant; stomatal – stomatal conductance; RWC – relative water content; CAT – catalase activity; P-weight – panicle weight; branches – number of branches per panicle; unfilled – number of unfilled grains per panicle; filled – number of filled grains per panicle; P-length – panicle length; BYP – biological yield per plant; TGW – thousand grain weight; H₂O₂ – hydrogen peroxide; MDA – malondialdehyde

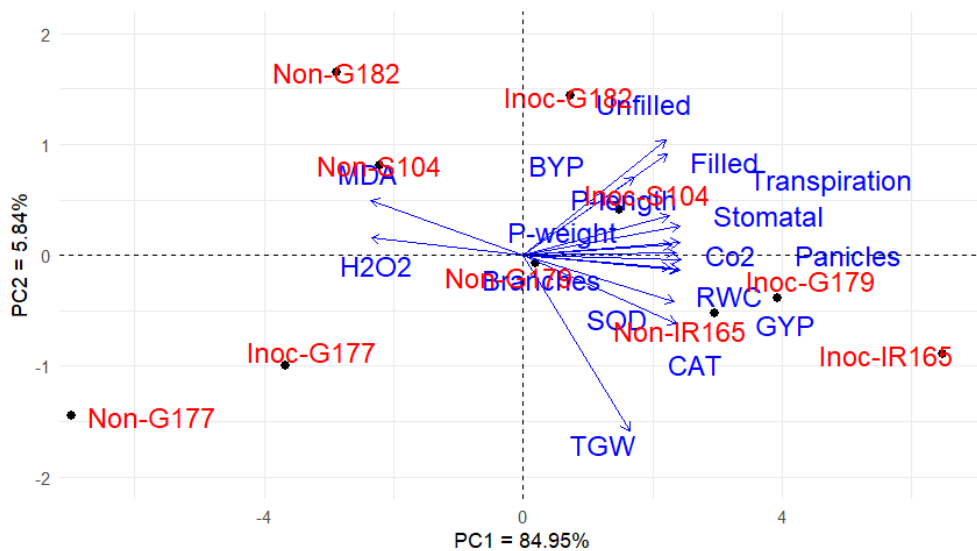


Figure 6. Principal component analysis biplot of relationships among physiological and yield traits and the distribution of rice genotypes under inoculated and non-inoculated conditions in salinity stress. Inoc – inoculated with *Saccharomyces cerevisiae* strains; Non – non-inoculated control; G177 – Giza-177; G179 – Giza-179; G182 – Giza-182; IR165 – IRR1-165; S104 – Sakha-104; Transpiration – transpiration rate; CO₂ – CO₂ assimilation rate; GYP – grain yield per plant; stomatal – stomatal conductance; RWC – relative water content; SOD – superoxide dismutase activity; CAT – catalase activity; P-weight – panicle weight; branches – number of branches per panicle; unfilled – number of unfilled grains per panicle; filled – number of filled grains per panicle; P-length – panicle length; BYP – biological yield per plant; TGW – thousand grain weight; H₂O₂ – hydrogen peroxide; MDA – malondialdehyde

PC2 contributing 5.84%. This indicates that most of the variability among treatments was captured along PC1. Along this axis, the inoculated genotypes were positioned on the positive side and oriented toward higher stomatal conductance, transpiration rate, intercellular CO₂ concentration, RWC, antioxidant enzyme activity (CAT and SOD), thousand grain weight (TGW), grain yield per plant (GYP), number of panicles and branches, and filled grains, reflecting an overall improvement in physiological status and yield formation under salinity. In contrast, non-inoculated treatments were shifted toward the negative side of PC1 and clustered near the vectors for H₂O₂ and MDA, indicating a close association with oxidative damage and inferior agronomic performance. Among the inoculated genotypes, IRRI-165 (Inoc-IR165) occupied the extreme positive region of PC1 in the lower-right quadrant, closely aligned with GYP, TGW, CAT, and RWC, highlighting it as the most responsive genotype to inoculation under saline conditions. Inoculated Giza-179 (Inoc-G179) also plotted on the positive side of PC1, in proximity to panicle number, stomatal conductance and transpiration rate, indicating a favourable combination of gas-exchange traits and reproductive output. The non-inoculated IRRI-165 and Giza-179 remained on the positive side of PC1 but closer to the origin, suggesting intermediate performance compared with their inoculated counterparts. By contrast, Giza-177 under non-inoculated conditions (Non-G177) was displaced toward the far negative side of PC1 and negative PC2, clearly separated from the remaining genotypes and associated with high oxidative stress and poor yield-related attributes, while Non-G182 and Non-S104 were located in the upper-left quadrant and more strongly related to MDA and H₂O₂.

DISCUSSION

Salinity imposes osmotic and ionic stress that disrupts water uptake, impairs stomatal regulation, and reduces photosynthetic efficiency. The present study demonstrated that inoculation with *Saccharomyces cerevisiae* enhances rice performance under salinity stress through integrated physiological and agronomic adjustments. The increases in CO₂ assimilation, stomatal conductance, and transpiration rate under inoculation indicate a partial restoration of stomatal functionality and gas exchange processes. Thereby sustaining photosynthetic carbon fixation under saline conditions. The improvement in relative water

content further supports the role of inoculation in enhancing plant water status. Moreover, mitigating oxidative stress is an important mechanism underlying the improved performance of inoculated plants. Salinity stress commonly induces excessive accumulation of ROS. This leads to lipid peroxidation, membrane damage, and metabolic dysfunction. The significant reduction in MDA and H₂O₂ levels observed in this study indicates that the inoculation effectively limited oxidative damage and preserved membrane stability. This effect was associated with a significant increase in antioxidant enzyme activities of SOD and CAT. These enzymes play critical roles in ROS scavenging. The upregulation of these enzymes suggests that inoculation enhanced the efficiency of the enzymatic antioxidant defence system. Consequently, maintaining cellular redox homeostasis under stress conditions is crucial. Inoculation significantly improved panicle number, branching, panicle length, and panicle weight. This reflects enhanced vegetative vigour and reproductive development in the inoculated plants. These improvements translated into higher grain fill rates, increased thousand-grain weight, and greater grain and biological yields. The reduction in unfilled grains further indicates improved reproductive success during grain filling. The improved yield performance observed under inoculation suggests that enhanced physiological efficiency and reduced oxidative damage enabled better allocation of assimilates toward reproductive sinks. The present results suggest that inoculation with *Saccharomyces cerevisiae* improved rice performance under saline irrigation through its association with more favourable physiological and biochemical status. Inoculated plants showed higher gas exchange and relative water content, together with lower accumulation of MDA and H₂O₂ and increased activities of SOD and CAT, indicating reduced oxidative stress and a stronger antioxidant response. These coordinated changes were accompanied by improved panicle development, grain filling, and yield, suggesting that improved water relations and oxidative balance may have contributed to the superior performance of inoculated plants under salinity stress.

The results obtained are consistent with previous studies demonstrating the role of plant growth-promoting microorganisms in alleviating salinity stress across different crops. Lu et al. (2021), Abdulfatah and Naji (2023), and Ehtaiwesh and Abuiflayjah (2024) reported that the application of *Saccharomyces cerevisiae* improves plant growth and physiological

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performance under saline conditions. They elucidated that *Saccharomyces cerevisiae* enhances water status, photosynthetic efficiency, and metabolic activity. The reduction in oxidative stress markers and the enhancement of antioxidant enzymes are also supported by Lu et al. (2021), Babaousmail et al. (2022), Alzandi and Naguib (2022), and Ehtaiwesh (2023). Moreover, the improvement in yield-related traits is consistent with the findings of Sadak and Dawood (2023) and Ehtaiwesh and Abuiflayjah (2024). They demonstrated that the plant growth-promoting microbe *Saccharomyces cerevisiae* enhances reproductive development and yield under stress conditions.

The assessed genotypes displayed significant variations in stress tolerance and responsiveness to microbial inoculation. Inoculated IRRI-165 exhibited superior performance across all evaluated parameters under salinity stress. This indicates strong tolerance to salinity combined with a high capacity to benefit from the inoculation treatment. This genotype showed lower oxidative stress levels, higher antioxidant activity, and greater improvements in physiological and yield traits. Giza-179 also exhibited relatively high performance, while Giza-182 and Sakha-104 displayed intermediate levels. Otherwise, Giza-177 showed limited responsiveness to inoculation. It maintained higher oxidative stress levels and lower productivity under both treatments. Consequently, inoculation effectiveness is greater in genotypes with higher adaptive capacity. The interaction analysis further confirms that the response to inoculation is genotype-dependent. Transpiration rate, oxidative stress markers, and grain-filling components showed interaction effects. This indicates that these processes are more sensitive to the combined effects of genotype and microbial treatment. In contrast, some yield traits showed more stable responses across genotypes. Differences among genotypes in salinity tolerance and responsiveness to microbial inoculation are attributed to variations in physiological adaptability, antioxidant capacity, and nutrient uptake efficiency. The observed genotypic variation in response to inoculation is also consistent with Mahreen et al. (2023) and Guigard et al. (2023). They demonstrated that plant–microbe interactions are strongly genotype-dependent.

Saccharomyces cerevisiae inoculation did not affect all rice genotypes equally. The magnitude of the response varied substantially with genetic background. IRRI-165 and Giza-179 consistently exhibited the greatest improvements in gas exchange, water status,

antioxidant enzyme activity, and yield-related traits. Whereas Giza-177 remained the least responsive across both seasons. This pattern suggests that the effectiveness of inoculation is closely linked to the inherent adaptive capacity of each genotype under saline conditions.

The multivariate analyses provide an integrated perspective on trait relationships and treatment effects (Omar et al. 2022, Mansour et al. 2023). The heatmap clustering clearly separated inoculated treatments from non-inoculated ones. The inoculated plants were associated with higher physiological efficiency, stronger antioxidant activity, and improved yield traits. Conversely, non-inoculated treatments were associated with elevated oxidative stress indicators. The PCA results further reinforced this pattern by showing strong alignment of inoculated genotypes with positive performance traits along the principal axis. While non-inoculated genotypes clustered with stress-related variables. The strong negative association between oxidative stress markers and productivity traits demonstrates the role of oxidative balance in determining plant performance under salinity stress. The findings suggest that inoculation represents an effective strategy for improving rice performance under salinity stress. However, the genotypic responses suggest that optimal benefits can be achieved by combining microbial inoculation with the salt-tolerant genotypes. This integrated approach has practical implications for sustainable rice production in salt-affected environments.

The observed improvements were associated with a broader physiological shift in the plant response to salinity. The stronger performance of inoculated genotypes suggests that inoculation maintained a more favourable internal water status, supported gas exchange, and enhanced antioxidant defence, thereby limiting oxidative damage under stress conditions. In contrast, the poorer performance of non-inoculated plants, particularly the close association with H_2O_2 and MDA, indicates that salinity stress intensified membrane injury and metabolic disturbance in the absence of inoculation. The distinct separation of IRRI-165 and Giza-179 under inoculation also suggests genotype-dependent responsiveness, with inoculation potentially improving stress tolerance by reinforcing traits linked to carbon assimilation, reproductive development, and grain filling.

Finally, it can be concluded that inoculating rice with *Saccharomyces cerevisiae* is an effective strategy for enhancing rice performance under salinity

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stress. The inoculation improved gas exchange parameters and plant water status. In addition, it reduced oxidative damage by lowering MDA and H₂O₂ levels. While significantly enhanced antioxidant enzyme activities of SOD and CAT were observed. These improvements reflect better physiological performance under saline conditions. The physiological enhancements were directly translated into improved yield performance. This was evidenced by increases in panicle traits, grain filling, grain yield, and biological yield, and a reduction in the number of unfilled grains. The results also revealed clear genotypic variation in response to salinity and inoculation IRR1-165 and Giza-179 exhibited superior tolerance and responsiveness. The interaction analysis and multivariate approaches confirmed that the inoculation effectiveness is genotype-dependent. Greater benefits observed in more tolerant genotypes. Overall, *S. cerevisiae* inoculation enhances salinity tolerance by improving physiological efficiency, strengthening antioxidant defence, and optimising yield formation. These findings suggest the potential of combining microbial inoculation with salt-tolerant genotypes for improving rice productivity in salt-affected environments.

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