



## Genetic Effects and Combining Ability for Agronomic and Yield Traits Clustered with Biochemical Profiling of Rice (*Oryza sativa* L.) under Optimal and Water Deficit Conditions

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### Abstract

In order to evaluate the combining ability and genetic effects for morpho-physiological and yield parameters in rice under well-watered and drought situations, this study was conducted in Sakha, Kafr El-Sheikh, Egypt, during the summers of 2022 and 2023. Seven rice accessions were intercrossed in a  $7 \times 7$  half-diallel scheme, generating a total of 21  $F_1$  hybrids during summer 2022. In 2023, parents and  $F_1$  hybrids were evaluated in a RCBD under control watering (every 4 days) and water-deficit stress (every twelve days). Significant variations observed among the genotypes and their components revealed substantial genetic diversity. Hybrids; GZ 179  $\times$  IET-1444 and IET-1444  $\times$  HR-5824 exhibited the highest mean performance for most traits under both conditions. For every variable, ANOVA revealed highly significant G.C.A and S.C.A impacts. Additive effects dominated for earliness and 1000-grain weight, whereas non-additive effects controlled traits *viz.*, chlorophyll content, yield/plant<sup>1</sup>, and harvest index, indicating that effective selection and hybridization are crucial in rice adjustment. GZ 179, Sakha 107, and IET-1444 were the best general combiners, whereas GZ 179  $\times$  IET-1444, GZ 179  $\times$  HR-5824, and IET-1444  $\times$  HR-5824 were superior specific combinations at both environments. Under drought, antioxidant enzyme activities, proline, and phenolic contents increased, while Malondialdehyde (MDA) and R.O.S radical levels decreased, indicating enhanced stress tolerance. Cluster analysis grouped genotypes by drought response, identifying tolerant rice entries with strong biochemical defense and stable yield performance.

**Key words:** Rice, Drought, Combining ability, Gene effect, Biochemical response.

### Introduction

Over half of the world's population depends on rice for their food security, making it one of the most significant staple crops in the world. The cultivated area in 2023 season reached approximately 1.77 million fed., an increase of 40.9% compared to 1.32 million fed. in the previous season. Production rose from 4.38 to 6.20 million tons of paddy rice (a 41.5% increase), and average national yield improved by 12.2%, from 8.76 to 9.98 t/ha, largely due to the efforts of national rice improvement programs (FAOSTAT, 2023).

Sustaining rice production in Egypt faces critical challenges due to limited arable land and declining water resources. The country relies almost entirely on the River Nile for irrigation, but increasing demand and potential reductions in water inflow following the construction of the Ethiopian Renaissance Dam have intensified water scarcity (Abo-Yousef *et al.*, 2023; El-Agoury *et al.*, 2023). Consequently, the Egyptian government has imposed

restrictions on rice cultivation to conserve water, highlighting the critical necessity to enhance rice productivity under limited watering and drought conditions.

As a semi-aquatic crop, rice is highly sensitive to drought, leading to global yield reductions of approximately 25% over the past two decades (El-Gammaal *et al.*, 2023). Water deficit impairs plant growth, reduces chlorophyll content and photosynthetic efficiency, and severely decreases yield. Therefore, it is crucial to use both conventional and molecular breeding techniques to create high-yielding, drought-tolerant cultivars (El-Badawy *et al.*, 2022). Drought stress affects several agronomic traits including short stature, flag leaf area, SPAD chlorophyll content, panicles number, 1000-grain weight, and harvest index while increasing sterility percentage, necessitating a deeper understanding of morpho-physiological and biochemical responses (Shehab *et al.*, 2023 and Daher *et al.*, 2024).

Understanding how related qualities are genetically controlled and selecting parental

combinations with superior general (GCA) and specific combining ability (SCA) are necessary to improve drought tolerance (Griffing, 1956). Yield and stress-related features are greatly influenced by both additive and non-additive gene activities (Sakran *et al.*, 2022; El-Agoury *et al.*, 2023).

Excessive reactive oxygen species (ROS) under drought stress result in oxidative damage, however antioxidant enzymes including peroxidase, catalase, and superoxide dismutase are essential for protection (Das *et al.*, 2024). Drought-tolerant genotypes typically exhibit enhanced antioxidant activity, increased proline and phenolic contents, and reduced lipid peroxidation (El-Badawy *et al.*, 2022).

The purpose of this study is to (1) assess how well seven rice genotypes and twenty-one F<sub>1</sub> hybrids function in both normal and water-deficit environments, (2) assess combining effects and gene action, and (3) analyze biochemical and physiological responses using clustered heatmap analysis to identify superior drought-tolerant genotypes.

## Materials and Methods

Seven rice genotypes were selected to represent a broad range of variation in phenological, morphophysiological, yield, and drought tolerance traits. The set included 4 local Egyptian varieties and 3 exotic entries. All parental line grains were gained from the Rice Research and Training Center's (RRTC) genetic stock in Sakha, Egypt. Their origins, types, pedigrees, and labels are listed in Table (1).

In 2022 season, seeds of parents were sown two times at 10-day intervals to synchronize flowering and facilitate hybridization. Thirty day old seedlings were transplanted in two rows of 5 m length (20 × 20 cm spacing) for each parent. Crosses were made among the parents in a 7 × 7 half-diallel mating design (excluding reciprocals), producing 21 F<sub>1</sub> hybrids using the hot-water emasculation method of Jodon (1938), modified by Butany (1961).

In the 2023 summer season, the parents and their F<sub>1</sub> hybrids were evaluated in Sakha, Kafr El-Sheikh, Egypt under two irrigation regimes: well-watered (irrigation every four days) and water-deficit (irrigation every twelve days). The experiment followed a randomized complete block design (RCBD) with 3 replications. Each genotype was planted in three rows per replicate (5 m × 20 cm spacing). Drought stress was imposed two weeks after transplanting using flush irrigation (no standing water). Water use was monitored with counters, showing total water consumption of 6,460 m<sup>3</sup>/fed under normal irrigation and 4650 m<sup>3</sup>/fed under stress (Table 2). Agronomic and management practices followed RRTC (2024) recommendations. Climatic data (Table 3), showing typical conditions for rice cultivation, with moderate humidity and high

temperatures that occasionally induced mild heat stress.

Following IRRI (2024) criteria, observations were taken on ten randomly chosen plants per genotype each replication for the following essential traits: days until 50% initial flowering, chlorophyll content (SPAD reading), one thousand kernel weight (g), grain yield plant<sup>-1</sup> (g) and harvest index (%). For biochemical tests, fresh flag leaf samples were gathered throughout the flowering period. After homogenizing the samples in 50 mM phosphate buffer (pH 7.8), the supernatant was kept at 80°C after the samples were centrifuged for 15 minutes at 4°C at 15,000 rpm. According to Yagi (1998), Bates *et al.* (1973), Shahidi, and Naczk (1995), respectively, the Folin–Denis method was used to quantify the levels of lipid peroxidation (MDA), free proline concentration, and total soluble phenols. Superoxide radicals (O<sub>2</sub><sup>·</sup>), hydroxyl radicals (OH<sup>·</sup>), and other reactive oxygen species (ROS) and hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) were determined following, Alexieva *et al.* (2001), and Loreto and Velikova (2001). Antioxidant enzymes: As per Putter (1974) and Nakano and Asada (1987), the activities of peroxidase (POX), superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) were measured.

Collected data were analyzed according to Steel and Torrie (1980). Homogeneity of error variances was tested before performing combined analysis across irrigation treatments (Gomez and Gomez, 1984). According Griffing (1956), which developed the diallel Method 2, Model 1, which was used to estimate general (GCA) and specific (SCA) combining ability. The relative significance of additive and non-additive gene effects was assessed using the GCA/SCA ratio (Singh and Chaudhary, 1979). A clustered heatmap using standardized Z-scores and hierarchical clustering visualized trait variation, identifying rice genotypes that are sensitive and drought-tolerant.

## Results and Discussion

Analyses of mean square for all evaluated features are depicted in Table (4). The mean squares (MS) due to environments (E) were highly significant for all traits, indicating strong environmental influence. Mean values recorded under normal irrigation were consistently higher than those obtained under drought conditions (Table 5). This decline under moisture stress is expected, as water deficit severely constrains rice growth by reducing photosystem II (PSII) activity, transpiration rate (Tr), internal CO<sub>2</sub> concentration (Ci), water usage efficiency (WUE), stomatal conductance (Gs), and net photosynthetic rate (Pn). Significant yield losses result from the considerable reduction of the membrane stability index (MSI) and relative water content (RWC). These results align with previous

findings by Huanhe *et al.*, (2024); Jarin *et al.*, (2024), Aryan *et al.*, (2025) and Zhou *et al.*, (2025).

For all traits at both and across irrigation regimes, M.S. resulting from genotypes and their partitions (parents, crosses, and parents vs. crosses) were also very significant. These results confirm the existence of substantial genetic variability among the tested materials, suggesting the presence of valuable allelic diversity that can be exploited in selection and hybridization programs. The observed genetic variation agrees with the findings of Shehab *et al.*, (2023) and Channa *et al.*, (2025).

Significant MS for parents vs. crosses were detected under both environments, confirming the existence of considerable heterosis. Similar patterns of heterotic expression have been reported by, Shukla *et al.*, (2020); Arunkumar and Narayanan (2024) and Gaballah *et al.*, (2025).

Genotypes and its partitioning  $\times$  environment interactions MS were significant for most traits, except parent's  $\times$  E and parents vs. crosses  $\times$  E for days to 50% initial heading, and for (SPAD) chlorophyll content and one thousand-grain weight (g). This indicates that genotype ranking varied between irrigation environments, reflecting differential responses to water stress. Similar interactions were reported by Kushawaha *et al.*, (2022); Al-Daej (2023); Zayed *et al.*, (2023) and Alkhader *et al.*, (2025). For harvest index (%), the Cr.  $\times$  E and Par vs. Cr  $\times$  E interactions were non-significant, suggesting stable cross performance under both water regimes, corroborating previous findings by Dianga *et al.*, (2020) and El-Refaee *et al.*, (2021).

Overall, these findings demonstrate that crossing tolerant and high-yielding parents without taking environmental interactions into account is not enough to create drought-resistant and high-production rice lines (El-Gammaal *et al.*, 2023).

Mean performance of the 7 parents and 21  $F_1$  hybrids for earliness, morpho-physiological, and yield traits under both and across irrigation treatments are depicted in Table (5). In general, drought stress significantly reduced all measured traits compared with normal irrigation, consistent with previous reports (Sakran *et al.*, 2020 and 2022). Water deficit accelerated heading in most genotypes, reflecting an escape mechanism to avoid prolonged drought. Parent Giza 179 (P3) exhibited the shortest duration to 50% flowering under normal and combined analysis (90.33 and 88.00 days), while Sakha 107 (P5) showed the earliest flowering under drought (85.67 days). The hybrids Giza 179  $\times$  Sakha 107 and Sakha 106  $\times$  Giza 179 recorded the earliest flowering across environments (87.00–84.33 days and 89.00–86.00 days, respectively). Early maturing, high yielding genotypes are desirable in drought-prone areas, as they enhance resource use efficiency and climate resilience. For chlorophyll content (SPAD), the highest parental means were recorded

by Sakha 107 under normal conditions (43.17%) and Sakha 106 under drought (38.08%). Among hybrids, Giza 179  $\times$  HR 5824 exhibited the highest chlorophyll content (46.21%, 39.86%, and 43.04% under normal, drought, and combined conditions, respectively), followed by IET 1444  $\times$  HR 5824 and Sakha 106  $\times$  Sakha 107.

Regarding 1000-grain weight, Sakha 107 (P5) recorded the best parental performance (28.10, 25.39, and 26.74 g), respectively. The hybrid Giza 179  $\times$  IET 1444 produced the highest 1000-grain weight under well-watered conditions (29.48 g), whereas Giza 179  $\times$  HR 5824 had the highest under drought and combined environments (26.90 and 28.17 g). Concerning grain yield (g) per plant, Sakha 101 (P1) under well-irrigation along with Giza 179 (P3) under drought recorded the highest parental yields (46.00 and 38.42 g). The cross Giza 179  $\times$  IET 1444 outperformed all others across environments (57.63, 45.51, and 51.57 g), indicating superior hybrid vigor. Harvest index (%) was highest in Giza 179 (48.24%, 40.50%, and 44.37%) and Sakha 101 (46.46%, 38.78%, and 42.62%), respectively. The hybrid Giza 179  $\times$  IET 1444 also exhibited the highest harvest index across environments (50.54%, 45.78%, and 48.16%), respectively. Under water deficit, the reproductive stage was the most critical for yield loss, as drought stress during flowering reduced fertilization and spikelet fertility (Yang *et al.*, 2024). Despite this, several hybrids showed resilience, reflecting superior physiological adaptability and heterosis.

In summary, the crosses Giza 179  $\times$  IET 1444, Giza 179  $\times$  HR 5824, IET 1444  $\times$  HR 5824, Sakha 101  $\times$  Sakha 107, and Sakha 101  $\times$  Sakha 106 demonstrated superior mean performance across environments and are promising candidates for developing drought-resilient, high-yielding rice hybrids.

ANOVA for general (GCA) and specific (SCA) combining ability effects revealed significant mean squares for all traits under both and across irrigation conditions (Table 4). This suggests that both additive and non-additive gene actions are important in trait expression.

The GCA variance exceeded SCA variance for earliness and 1000-grain weight under both irrigation treatments, indicating a predominance of additive genetic control. Conversely, SCA variance was greater for chlorophyll content, grain yield per plant, and harvest index, suggesting the importance of dominance effects in these features. These outcomes underscore the value of selecting superior parents for hybridization to exploit heterosis in non-additive traits, while additive traits can be improved through selection. Both GCA and SCA  $\times$  environment interactions were significant, except for SCA  $\times$  E in chlorophyll content, but of smaller magnitude than the main effects, indicating moderate environmental influence. The greater sensitivity of GCA  $\times$  E

compared to SCA  $\times$  E suggests that additive gene effects are more influenced by drought stress. These outcomes are align with those of Bayoumi *et al.*, (2022), Sakran *et al.*, (2022), and Gaballah *et al.*, (2025), confirming that additive effects largely control earliness and grain weight, whereas non-additive effects predominate in yield-related and physiological traits.

Notably, the ratio of SCA  $\times$  E/SCA in the most studied characters, was lower than GCA  $\times$  E/GCA; except; days to (50%) heading, and one thousand kernel weight (g) characters. This result indicated that additive effects were more influenced by water deficit stress than non-additive genetic effects for these traits. This conclusion is in well agreement with those reported by EL-Refaee *et al.*, (2021); El-Naem *et al.*, (2024) and Gaballah *et al.*, (2025).

General combining ability (GCA) analysis is fundamental for identifying superior parents that can be effectively utilized in rice breeding programs. High positive GCA values ( $\hat{g}_i$ ) are desirable for most studied traits, except for heading date (days), plant height, and spikelet sterility, where significant negative estimates are more beneficial from a breeder's perspective.

The GCA effects ( $\hat{g}_i$ ) for each rice parent across different agronomic traits under both and across irrigation treatments are presented in Figures. (1-5). Results revealed substantial genetic variability among parents, reflecting their diverse genetic potential and adaptability across environments.

The most notable and desired negative GCA impacts were observed for days to 50% flowering in the parent Sakha 107 (P5) under well-watered conditions (-3.54) and Giza 179 (P3) under both water stress (-3.54) and combined analysis (-3.50). These results suggest that they may help produce progeny that blossom early. A beneficial characteristic for avoiding heat stress and terminal drought, two major variables affecting rice productivity, is earliness. The variety IET 1444 showed highly significant positive GCA effects (1.27, 0.74, and 1.00 under normal, water-deficit, and combined conditions, respectively) in terms of chlorophyll content (SPAD values), demonstrating its superior combining ability to maintain chlorophyll concentration under stress.

For 1000-grain weight, Giza 179 (P3) exhibited the most desirable and highly significant GCA effects across all environments (0.81, 0.79, and 0.80 under control, drought, and combined analyses, respectively), confirming its value as a parent for grain weight improvement.

Concerning, grain yield/plant<sup>-1</sup>, Giza 179 (P3) again expressed the highest positive and significant GCA effects (1.06, 1.63, and 1.35 under normal, drought, and combined analyses, respectively), suggesting that this parent is the best general combiner for yield potential under both water regimes.

For harvest index (%), the variety Sakha 106 exhibited the highest significant GCA effects under all conditions (1.93, 2.08, and 2.00 under normal, drought, and combined environments, respectively), implying its strong genetic contribution to efficient assimilate partitioning.

Giza 179 (P3) and IET 1444 (P4) as superior general combiners for yield improvement due to their favorable additive gene effects across multiple traits. In contrast, Sakha 107 (P5) and PL-7 7-8-4 (P6) exhibited predominantly negative GCA effects, indicating limited potential in yield improvement. Future breeding efforts should focus on incorporating high-GCA parents such as Giza 179 and IET 1444 into hybrid rice development programs to enhance both productivity and drought resilience. Multiple crosses involving these parents, followed by selection in segregating generations, are expected to yield superior genotypes. These outcomes are consistent with previous reports by Zayed *et al.* (2023), El-Naem *et al.* (2024), and Gaballah *et al.* (2025).

SCA effects ( $\hat{s}_{ij}$ ) for the F<sub>1</sub> hybrid combinations under both and across the mention environments are presented in Table (6). High positive SCA values are desirable for most traits, whereas negative estimates are preferred for heading date to promote earliness. Significant SCA effects arise mainly from dominance and epistatic interactions between the parental alleles, reflecting the potential of non-additive genetic components to exploit heterosis.

For days to 50% flowering, 10, 8, and 6 out of 21 hybrids showed desirable significant and negative S. C. A. effects under well-watering, water deficit, and across them, respectively. The most profitable crosses for this trait were Giza 179  $\times$  Sakha 107 (-5.54 under normal and -4.94 at across environments) and GZ. 179  $\times$  IET 1444 (-7.34 under drought), indicating their ability to produce early-flowering hybrids.

Eight, nine, and eight hybrids showed notable positive SCA impacts in terms of chlorophyll content (SPAD) in normal, drought, and combined over them, respectively. The cross Giza 179  $\times$  HR 5824 showed great promise for preserving chlorophyll stability under moisture stress, recording the largest SCA effects (4.96, 5.15, and 5.06 across the corresponding conditions). Under normal, drought, and combined analyses, four, three, and three crosses, respectively, showed positive and significant SCA impacts for 1000-grain weight. The cross Giza 179  $\times$  HR 5824 again displayed the most desirable SCA effects (2.51, 3.01, and 2.76), confirming its superiority for grain weight stability under variable irrigation.

Under normal, drought, and mixed conditions, respectively, nine, eight, and eight crosses demonstrated substantial favorable SCA impacts in terms of grain yield/plant<sup>-1</sup>. The cross Giza 179  $\times$

IET 1444 was the greatest hybrid combination for increasing output across environments, as evidenced by its highest SCA estimations (14.49, 8.57, and 11.53).

For harvest index (%), nine, seven, and eight hybrids expressed highly favorable and substantial SCA impacts under good-watering, drought, and mixed circumstance, respectively. Giza 179 × IET 1444 was the most attractive cross for this feature, with SCA effects of 9.79, 11.21, and 10.44\*\* under the corresponding circumstances.

Overall, the hybrids Giza 179 × IET 1444, Giza 179 × HR 5824, and IET 1444 × HR 5824 were identified as the most promising combinations, exhibiting superior SCA effects across multiple traits and environments. These crosses are of high breeding value for developing high-yielding, drought-tolerant rice cultivars.

Under water shortage stress conditions, several key biochemical markers associated with plant defense mechanisms were evaluated, including lipid peroxidation (MDA), free proline, soluble phenols, and reactive oxygen species (ROS) such as superoxide ( $O_2^-$ ), hydroxyl radicals ( $OH^-$ ), and hydrogen peroxide ( $H_2O_2$ ). Peroxidase (POX), superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) were among the antioxidant enzyme activities that were evaluated in relation to the various irrigation treatments. In order to combat oxidative damage, the results (Figures 6-8) demonstrated that drought stress raised the generation of ROS and, in turn, the activity of antioxidant enzymes. Furthermore, soluble phenols and free proline accumulated more when there was a water deficit, although MDA levels dropped when drought stress was present.

ROS production across different rice genotypes under normal and water-deficit conditions was assessed at the heading stage, as illustrated in Fig. (6). Water stress disrupts cellular homeostasis, inducing oxidative stress and increasing ROS levels, which negatively affect  $CO_2$  assimilation, photosynthesis, and electron transport (Evamoni *et al.*, 2023; Tavu & Redillas, 2025; Zhang *et al.*, 2024; Zhou *et al.*, 2025). Elevated hydroxyl radicals ( $OH^-$ ) contribute to lipid peroxidation, leading to chlorophyll degradation, membrane damage, protein denaturation, and ultimately cell death (Xie *et al.*, 2019). Excessive ROS also inactivate essential enzymes and reduce membrane stability index (MSI) (She *et al.*, 2024). However, tolerant genotypes demonstrated better oxidative stress management by maintaining redox homeostasis and accumulating higher levels of antioxidant enzymes (Chandio *et al.*, 2023; Abd-Allah *et al.*, 2025). Specifically, levels of superoxide ( $O_2^-$ ), hydroxyl radicals ( $OH^-$ ), and hydrogen peroxide ( $H_2O_2$ ) significantly increased ( $p < 0.05$ ) under drought across all genotypes. Notably, parental lines such as Giza 179, IET 1444, and Sakha 107, along with their hybrids (e.g., Giza 179 × IET

1444; Sakha 106 × Sakha 107; IET 1444 × HR 5824), exhibited the lowest and most favorable ROS profiles under both irrigation regimes, indicating superior oxidative stress tolerance. These findings confirmed and align with previous reports that higher production of ROS radicals reduce the efficiency of rice plant cell and showed susceptibility under water shortage treatment (Alafari *et al.* (2024); She *et al.*, 2024 and Zhou *et al.*, (2025).

Malondialdehyde (MDA) serves as a key indicator of lipid peroxidation and membrane damage caused by drought-induced oxidative stress. In contrast, the accumulation of free proline and total soluble phenols (TSP) plays a crucial role in enhancing drought tolerance by maintaining cell turgor, osmotic balance, and supporting antioxidant defenses (Bhandari *et al.*, 2023). In the present study, significant variations were observed among rice genotypes for MDA, proline, and phenol contents under both well-watered and drought-stress conditions. Under water-deficit stress, MDA levels generally declined, while free proline and soluble phenol concentrations increased markedly. Genotypes such as IET 1444, Giza 179, and Sakha 107, along with their hybrids (IET 1444 × HR 5824, Giza 179 × IET 1444, and Sakha 101 × Sakha 107), exhibited the lowest MDA accumulation and the highest levels of proline and phenols, indicating superior membrane stability and oxidative stress tolerance (Fig. 7). These findings are consistent with earlier reports showing that reduced MDA content is associated with improved membrane integrity, lower oxidative injury, and enhanced photosynthetic efficiency under drought conditions (Ghidan & Khedr, 2021; Abo-Youssef *et al.*, 2023). Conversely, elevated MDA levels correlated with poor stress tolerance and impaired cellular function (Aslam *et al.*, 2022; Freeg *et al.*, 2022).

Enhanced accumulation of leaf free proline and phenolic compounds in water stress-tolerant genotypes contributes to osmotic adjustment, ROS detoxification, and protein synthesis under water scarcity (Singh *et al.*, 2020). These metabolites are widely regarded as reliable biochemical markers of drought tolerance. In contrast, drought-sensitive genotypes accumulated less proline and phenols, reflecting weaker defense responses. The observed increase in TSP among tolerant genotypes highlights the activation of secondary metabolic pathways that strengthen antioxidant defense, osmotic regulation, and stress signaling further confirming their role in drought resilience (Abd-Allah *et al.*, 2025).

The activities of key antioxidant enzymes; e.g., Peroxidase (POX), Superoxide Dismutase (SOD), Catalase (CAT), and Ascorbate Peroxidase (APX) were also assessed in both parental and hybrid rice genotypes under normal and drought conditions at the flowering stage (Fig. 8). A significant increase in enzymatic activity was observed under drought stress, underscoring their vital role in mitigating

oxidative damage through ROS scavenging. Genotypes with higher enzyme activity maintained better redox homeostasis and cellular stability. Specifically, IET 1444, Giza 179, and Sakha 107, along with their hybrids (Giza 179 × IET 1444, IET 1444 × HR 5824, and Giza 179 × HR 5824), consistently recorded the highest POX, SOD, CAT, and APX activities, confirming their strong antioxidant defense and superior drought tolerance. Conversely, genotypes exhibiting lower enzyme activities were more vulnerable to oxidative stress, reinforcing the direct relationship between antioxidant capacity and drought resilience. These findings are in agreement with earlier studies emphasizing the role of enhanced antioxidant enzyme activity in safeguarding rice plants from oxidative damage under drought stress (She *et al.* 2024; Zhang *et al.* 2024 and Zhou *et al.*, 2025).

#### Clustered Heatmap:

Drought tolerance among 28 rice genotypes was evaluated under well-watered and drought conditions using morpho-physiological, yield, and

biochemical traits, including chlorophyll content, grain yield (GY), harvest index (HI), ROS indicators, antioxidant enzymes (SOD, CAT, APX, POX), and osmoprotectants (LFP, SPC). Hierarchical clustering and heatmap analysis revealed two major clusters and three sub-clusters, reflecting wide genetic and physiological diversity. Antioxidant enzymes grouped together, indicating their coordinated role in ROS detoxification, while yield-related traits (GY, TGW, HI) clustered separately, linking productivity with stress adaptation as depicted in Fig. (9).

Under drought stress, tolerant genotypes such as P4, P3 × P4, P3 × P7, and P3 exhibited strong antioxidant activity and high yield, while P1, P6, and P7 were more susceptible. The color gradients clearly showed trait upregulation or downregulation under stress. Overall, drought tolerance was closely associated with integrated antioxidant defense and yield stability, highlighting key genotypes for breeding resilient rice varieties (El-Refaee *et al.*, 2021 and Gaballah *et al.*, 2025).

**Table 1.** Included genotypes' names, type, origin and pedigree.

NO.	Genotypes	Type	Origin	Pedigree
1	Sakha 101 (P1)	Japonica	Egypt	(Giza 176 / Milyang 79)
2	Sakha 106 (P2)	Japonica	Egypt	(Giza 177 / Hexi 30)
3	Giza 179 (P3)	Indica / Japonica	Egypt	(Giza 1368-S-5-4 /Giza 6296-12-1-2)
4	IET 1444 (P4)	Indica	India	(TN1/CO29)
5	Sakha 107 (P5)	Japonica	Egypt	(Giza 177/BL1)
6	HR 5824 (P6)	Indica	IRRI	(Akiyudaka x Suweon 310)
7	PL-77-8-4 (P7)	Japonica	IRRI	Unknown

**Table 2.** Total amount of water used/fed for a few rice entries in both standard and water stress.

Water used during:	Continues Irrigation/m <sup>3</sup>	Water stress Conditions (m <sup>3</sup> )
Land preparation	1465	1465
Growth period	4995	3185
Total water used / fed.	6460	4650

**Table 3.** Provides Sakha Station's monthly air temperature and relative humidity data for the rice seasons of 2023 and 2024.

Months	2023 summer season.				2024 summer season.			
	Air Temp. (°C)		RH (%)		Air Temp. (°C)		RH (%)	
	Min	Max	Min	Max	Min	Max	Min	Max
May	22.46	34.21	45.49	71.10	25.53	32.06	45.27	76.51
June	26.07	36.62	46.49	75.50	29.47	39.78	50.92	80.01
July	28.57	40.93	56.39	81.49	33.33	46.16	56.79	84.93
August	25.38	41.92	56.05	83.92	29.83	45.94	62.38	86.58
September	24.68	39.29	51.50	83.14	26.57	40.79	50.22	85.41
October	21.45	32.16	62.64	74.32	23.70	28.74	62.52	72.80

Rainfall was zero (mm/day) in 2023 and 2024 seasons.

**Table 4.** Days to 50% initial flowering, (SPAD) chlorophyll content, thousand-grain weight (g), grain yield/plant (g), and harvest index (%) mean squares of half-diallel analysis for both and across water regime conditions:

S.O.V.	DF	Days to 50% flowering			Chlorophyll content			1000- grain weight (g)			Grain yield / plant (g)			Harvest index (%)			
	Single	Comb.	N	D	Comb.	N	D	Comb.	N	D	Comb.	N	D	Comb.	N	D	Comb.
<b>Environment</b>		1			2191.1**			1795.9**			519.97**			1897.46**			1600.5**
Reps/ E	2	4	3.05	2.51	2.78	35.53	28.62	21.71	13.54	5.64	9.59	4.48	17.58	11.03	13.69	16.01	14.85
Genotypes (G)	27	27	70.47**	69.52**	123.77**	24.23**	26.21**	48.07**	6.72**	7.14**	12.29**	111.29**	64.84**	160.62**	144.95**	133.59**	272.73**
Parents (P)	6	6	181.4**	144.04**	303.87**	10.12**	14.48**	22.53**	8.85**	5.91**	13.73**	13.77**	21.6**	26.55**	85.30**	33.15**	106.71**
Crosses (Cr)	20	20	40.12**	49.13**	73.93**	28.37**	28.63**	54.52**	6.10**	7.75**	12.45**	145.32**	78.55**	208.63**	156.38**	159.14**	311.27**
Par. vs. Cr.	1	1	11.96**	30.06**	39.97**	25.91**	48.19**	72.39**	6.43**	5.26**	4.53**	15.79**	50.21**	14.84**	274.06**	225.04**	497.90**
Genotypes x E		27			16.22**			2.36			1.56			15.52**			5.85**
Parents x E		6			21.57**			2.06			1.02			8.82**			11.74**
Crosses x E		20			15.32**			2.48			1.40			15.24**			4.25
Par. vs. Cr. x E		1			2.05			1.71			8.16**			61.15**			1.21
<b>Error</b>	54	108	4.50	2.95	3.87	2.45	2.87	2.66	1.24	1.37	1.31	4.25	3.90	4.07	2.63	3.76	3.20
$\delta^2$ GCA	6	6	90.32**	68.31**	152.98**	6.30**	3.18**	8.75**	4.72**	3.17**	6.62**	7.94**	12.01**	15.47**	31.29**	20.12**	49.36**
$\delta^2$ SCA	21	21	4.41**	10.28**	9.33**	8.58**	10.32**	18.10**	1.53**	2.15**	3.38**	45.43**	24.36**	64.42**	53.18**	51.50**	102.78**
$\delta^2$ GCA x E		6			16.22**			2.36**			1.56**			15.52**			5.80**
$\delta^2$ SCA x E		21			5.65**			1.73**			1.27**			4.49**			2.05**
<b>Error term</b>	54	108	1.6	0.98	1.29	0.82	0.96	0.89	0.41	0.46	0.44	1.42	1.30	1.36	0.88	1.25	1.07
GCA/SCA			20.54	6.65	16.39	0.73	0.31	0.48	3.09	1.47	1.96	1.47	1.96	0.24	0.59	0.39	0.48
GCA x E/GCA					0.1060			0.2698			0.0301			0.9933			0.1176
SCA x E/SCA					0.6049			0.0405			0.0130			0.0696			0.0199

Where; \* and \*\* symbols refer to significant and highly significant at the 0.05 and 0.01 probability levels, respectively.

**Table 5.** Average genotype performance for all predicted attributes under normal watering (N), water deficit stress (D), as well as the sum of both (C).

Traits Genotypes	Days to 50% flowering			Chlorophyll content			1000- grain weight (g)			Grain yield / plant (g)			Harvest index (%)		
	N	D	Comb.	N	D	Comb.	N	D	Comb.	N	D	Comb.	N	D	Comb.
Sakha 101 (P1)	105.67	92.00	98.67	40.20	33.29	36.75	27.73	23.44	25.59	46.00	32.82	39.41	46.46	38.78	42.62
Sakha 106 (P2)	94.00	89.00	91.67	42.63	38.08	40.36	27.82	25.35	26.60	40.60	30.91	35.76	44.04	38.51	41.28
Giza 179 (P3)	90.33	86.00	88.00	39.22	31.74	35.48	27.63	24.33	25.98	44.22	38.42	41.32	48.24	40.50	44.37
IET 1444 (P4)	110.67	106.33	108.33	41.58	34.69	38.14	23.84	21.43	22.64	42.33	35.16	38.75	44.43	37.50	40.97
Sakha 107 (P5)	91.00	85.67	88.33	43.17	34.93	39.05	28.10	25.39	26.74	42.39	34.71	38.55	40.53	35.84	38.19
PL -77-8-4 (P6)	96.00	91.33	93.67	42.03	34.42	38.23	26.43	24.04	25.23	41.56	31.43	36.49	36.50	33.40	34.95
HR 5824 (P7)	102.33	91.33	97.00	38.23	31.70	34.97	24.60	22.88	23.74	39.70	31.66	35.68	35.50	29.92	32.71
Sakha 101 x Sakha 106	97.33	84.67	91.00	43.94	38.37	41.15	29.30	24.00	26.65	47.77	35.14	41.46	44.37	36.99	40.68
Sakha 101 x Giza 179	98.67	91.67	95.00	44.16	36.35	40.25	27.67	21.69	24.68	37.58	31.66	34.62	36.68	30.54	33.61
Sakha 101 x IET 1444	106.33	95.67	102.00	44.77	39.20	41.98	26.50	22.72	24.61	34.83	32.33	33.58	33.60	30.02	31.81
Sakha 101 x Sakha 107	95.67	87.33	91.67	42.67	37.71	40.19	27.66	22.87	25.26	48.39	39.59	43.99	45.62	34.91	40.26
Sakha 101 x PL -77-8-4	98.67	90.00	94.33	38.23	33.64	35.94	27.53	22.87	25.20	43.85	32.30	38.08	39.50	36.29	37.90
Sakha 101 x HR 5824	98.00	91.67	94.67	38.23	32.70	35.47	25.91	20.94	23.42	36.04	31.02	33.53	32.30	27.63	29.97
Sakha 106 x Giza 179	89.00	82.67	86.00	43.91	38.00	40.96	27.20	23.16	25.18	35.21	32.26	33.74	30.26	25.17	27.71
Sakha 106 x IET 1444	102.00	92.00	97.00	40.23	31.39	35.81	26.80	22.81	24.80	36.72	30.30	33.51	38.57	33.26	35.91
Sakha 106 x Sakha 107	91.00	87.67	90.33	45.23	39.54	42.39	28.33	23.82	26.08	45.33	40.13	42.73	48.33	41.86	45.10
Sakha 106 x PL -77-8-4	96.67	94.00	95.33	36.15	28.90	32.52	27.67	24.47	26.07	43.67	38.99	41.33	48.45	41.90	45.18
Sakha 106 x HR 5824	93.67	88.33	91.00	38.17	32.62	35.39	26.76	23.55	25.16	36.47	32.09	34.28	34.49	27.80	31.15
Giza 179 x IET 1444	101.33	85.00	93.00	44.73	38.99	41.86	29.48	25.84	27.65	57.63	45.51	51.57	50.54	45.78	48.16
Giza 179 x Sakha 107	87.00	81.67	84.33	38.16	31.92	35.04	28.70	25.78	27.22	38.69	32.59	35.64	34.42	27.50	30.96
Giza 179 x PL -77-8-4	97.67	92.00	94.67	42.13	34.99	38.56	26.10	23.54	24.82	36.67	32.53	34.60	30.58	22.13	26.36
Giza 179 x HR 5824	97.00	91.67	94.33	46.21	39.86	43.04	29.42	26.90	28.17	48.53	42.67	45.60	47.43	42.93	45.18
IET 1444 x Sakha 107	102.33	94.67	98.67	44.23	35.23	39.73	26.40	23.53	24.97	38.40	34.26	36.33	32.30	25.16	28.73
IET 1444 x PL -77-8-4	101.33	93.00	97.33	43.91	38.45	41.18	26.63	23.34	24.99	30.90	26.41	28.66	28.70	23.63	26.16
IET 1444 x HR 5824	103.67	97.00	100.67	46.13	37.44	41.79	26.84	24.39	25.61	53.90	43.75	48.82	45.57	39.88	42.73
Sakha 107 x PL -77-8-4	96.67	86.00	91.67	44.83	37.19	41.01	27.00	23.58	25.29	45.50	41.73	43.62	40.44	35.24	37.84
Sakha 107 x HR 5824	94.00	90.33	93.33	42.53	36.57	39.55	26.83	23.26	25.05	36.80	32.50	34.65	32.39	25.24	28.82
PL -77-8-4 x HR 5824	96.00	91.63	93.67	41.23	35.09	38.16	23.10	19.57	21.33	36.46	32.74	34.60	30.57	24.10	27.34
Mean of all Genotypes	98.00	90.67	94.33	41.95	35.46	38.75	27.07	23.55	25.31	40.65	36.84	39.25	39.39	33.23	36.31
L. S. D. 5%	1.93	3.07	1.80	1.20	2.85	1.53	1.04	1.91	1.08	1.38	2.79	1.54	1.40	3.17	1.71
L. S. D. 1%	2.57	4.09	2.38	1.59	3.79	2.03	1.39	2.55	1.43	1.83	3.71	2.04	1.86	4.21	2.27

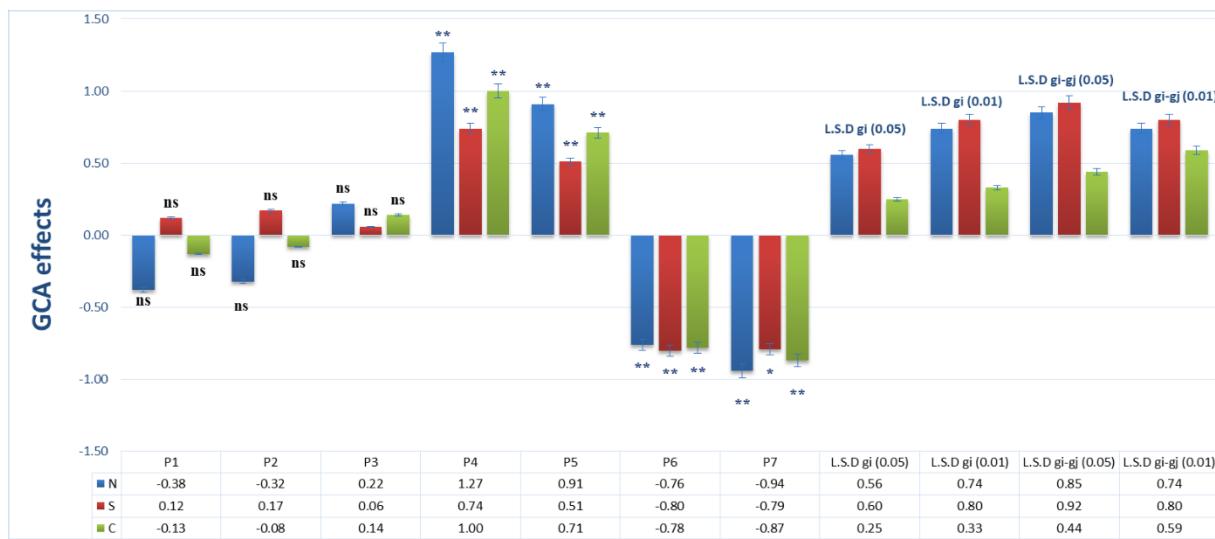
**Table 6.** Assessment of ( $\hat{S}_{ij}$ ) SCA impacts for all studied traits under both and across environments:

Hybrids	Traits			Days to 50% flowering			Chlorophyll content			1000- grain weight (g)			Grain yield / plant (g)			Harvest index (%)		
	N	D	Comb.	N	D	Comb.	N	D	Comb.	N	D	Comb.	N	D	Comb.	N	D	Comb.
Sakha 101 x Sakha 106	-0.32	-4.85**	-2.59**	2.66**	2.64**	2.65**	1.27**	0.70	0.99	6.07**	2.48**	4.28**	1.98**	0.84	1.41			
Sakha 101 x Giza 179	1.97	2.76**	2.37	2.34**	0.73	1.53	-0.59	-1.94**	-1.27**	-5.94**	-3.59**	-4.77**	-5.55**	-4.11**	-4.83**			
Sakha 101 x IET 1444	-1.94**	1.00	-0.97	1.90*	2.91**	2.41*	-0.26	0.22	-0.02	-8.05**	-1.67	-4.86**	-7.47**	-4.82**	-6.14**			
Sakha 101 x Sakha 107	-1.39**	0.33	-0.53	0.16	1.65	0.90	-0.30	-0.54	-0.42	5.41**	4.77**	5.09**	5.23**	1.31	3.27**			
Sakha 101 x PL -77-8-4	-1.35**	-1.58	-1.47	-2.60**	-1.11	-1.86	0.70	0.36	0.53	2.84**	-0.26	1.29	1.70*	3.97**	2.84*			
Sakha 101 x HR 5824	-2.89**	1.34	-0.79	-2.42**	-2.06*	-2.24*	-0.60	-1.45*	-1.03	-5.80**	-2.72**	-4.26**	-5.77**	-4.39**	-5.08**			
Sakha 106 x Giza 179	-2.91**	-2.91**	-2.9**	2.04*	2.34*	2.19*	-1.25**	-1.65**	-1.45**	-6.74**	-3.33**	-5.04**	-12.83**	-10.72**	-11.78**			
Sakha 106 x IET 1444	1.01	-1.95**	-0.47	-2.69**	-4.94**	-3.82**	-0.15	-0.88	-0.51	-4.60**	-4.05**	-4.32**	-3.13**	-2.82**	-2.98*			
Sakha 106 x Sakha 107	-0.47	0.92	0.23	2.67**	3.43**	3.05**	0.18	-0.77	-0.29	3.92**	4.97**	4.44**	7.08**	7.03**	7.05**			
Sakha 106 x PL -77-8-4	1.80	4.02**	3.41**	-4.74**	-5.90**	-5.32**	0.66	0.78	0.72	4.23**	6.08**	5.16**	9.67**	8.34**	9.06**			
Sakha 106 x HR 5824	-2.10**	-1.29	-1.70	-2.55**	-2.19*	-2.37*	0.06	-0.02	0.02	-3.80**	-1.98	-2.89**	-4.45**	-5.46**	-4.96**			
Giza 179 x IET 1444	1.08	-7.34**	-3.13**	1.27	2.76**	2.02	2.28**	1.76**	2.02**	14.49**	8.57**	11.53**	9.79**	11.21**	10.44**			
Giza 179 x Sakha 107	-5.54**	-4.33**	-4.94**	-4.94**	-4.08**	-4.51**	0.32	0.92	0.62	-4.54**	-5.17**	-4.86**	-6.67**	-5.84**	-6.26**			
Giza 179 x PL -77-8-4	3.74**	4.40**	4.07**	0.71	0.76	0.73	-1.15	-0.48	-0.81	-4.59**	-2.97**	-3.78**	-7.92**	-9.93**	-8.92**			
Giza 179 x HR 5824	2.18	1.46	1.82	4.96**	5.15**	5.06**	2.51**	3.01**	2.76**	6.44**	6.01**	6.22**	8.66**	11.16**	9.91**			
IET 1444 x Sakha 107	2.28	1.57	1.92	0.08	-1.44	-0.68	-0.48	-0.26	-0.37	-4.20**	-2.26**	-3.23*	-7.40**	-8.36**	-7.88**			
IET 1444 x PL -77-8-4	-2.26**	-2.48**	-2.37**	1.44	3.09**	2.26*	0.89	0.45	0.67	-9.73**	-7.84**	-8.79**	-8.41**	-8.62**	-8.52**			
IET 1444 x HR 5824	-2.02**	1.01	-0.50	3.83**	2.06*	2.95**	1.40**	1.62**	1.51**	12.44**	8.32**	10.38**	8.18**	7.93**	8.05**			
Sakha 107 x PL -77-8-4	2.81**	-1.86*	0.47	2.71**	2.06*	2.39*	0.06	-0.22	-0.08	4.78**	6.66**	5.72**	3.77**	4.23**	4.00**			
Sakha 107 x HR 5824	1.16	1.16	1.16	0.59	1.42	1.00	0.20	-0.41	-0.11	-4.75**	-3.74**	-4.24**	-4.56**	-5.47**	-5.01**			
PL -77-8-4 x HR 5824	-2.25**	-1.55**	-1.90**	-0.7	-0.08	-0.39	-2.4**	-3.20**	-2.80**	-3.12**	1.09	-1.02	-3.78**	-5.34**	-4.56**			
L.S.D (Sij) 0.05	2.33	1.67	2.43	1.62	1.76	2.03	1.16	1.21	1.42	2.14	2.04	2.51	1.68	2.01	2.22			
L.S.D (Sij) 0.01	3.10	2.22	3.3	2.16	2.34	2.75	1.54	1.62	1.93	2.84	2.72	3.41	2.23	2.67	3.02			
L.S.D (Sij-Sik) 0.05	3.46	2.48	2.09	2.41	2.61	1.74	1.72	1.80	1.22	3.17	3.04	2.15	2.50	2.99	1.91			
L.S.D (Sij-Sik) 0.01	4.60	3.30	2.83	3.20	3.47	2.36	2.28	2.40	1.66	4.22	4.04	2.92	3.32	3.97	2.59			
L.S.D (Sij-Skl) 0.05	3.26	2.46	0.75	2.25	2.44	0.61	1.61	1.69	0.43	2.97	2.84	0.76	2.33	2.79	0.67			
L.S.D (Sij-Skl) 0.01	4.34	3.27	1.05	3.00	3.25	0.83	2.14	2.25	0.58	3.95	3.78	1.03	3.11	3.72	0.91			

Where; Significant and highly significant at the 0.05 and 0.01 probability levels, respectively, are indicated by the symbols \* and \*\*.



**Fig. 1.** Calculations of GCA effects ( $\hat{g}_i$ ) for days to 50% flowering attribute under study in both and across environments:



**Fig. 2.** Calculations of GCA effects ( $\hat{g}_i$ ) for chlorophyll content attribute under study in both and across environments:



**Fig. (3):** Calculations of GCA effects ( $\hat{g}_i$ ) for 1000-grains weight attribute under study in both and across environments:

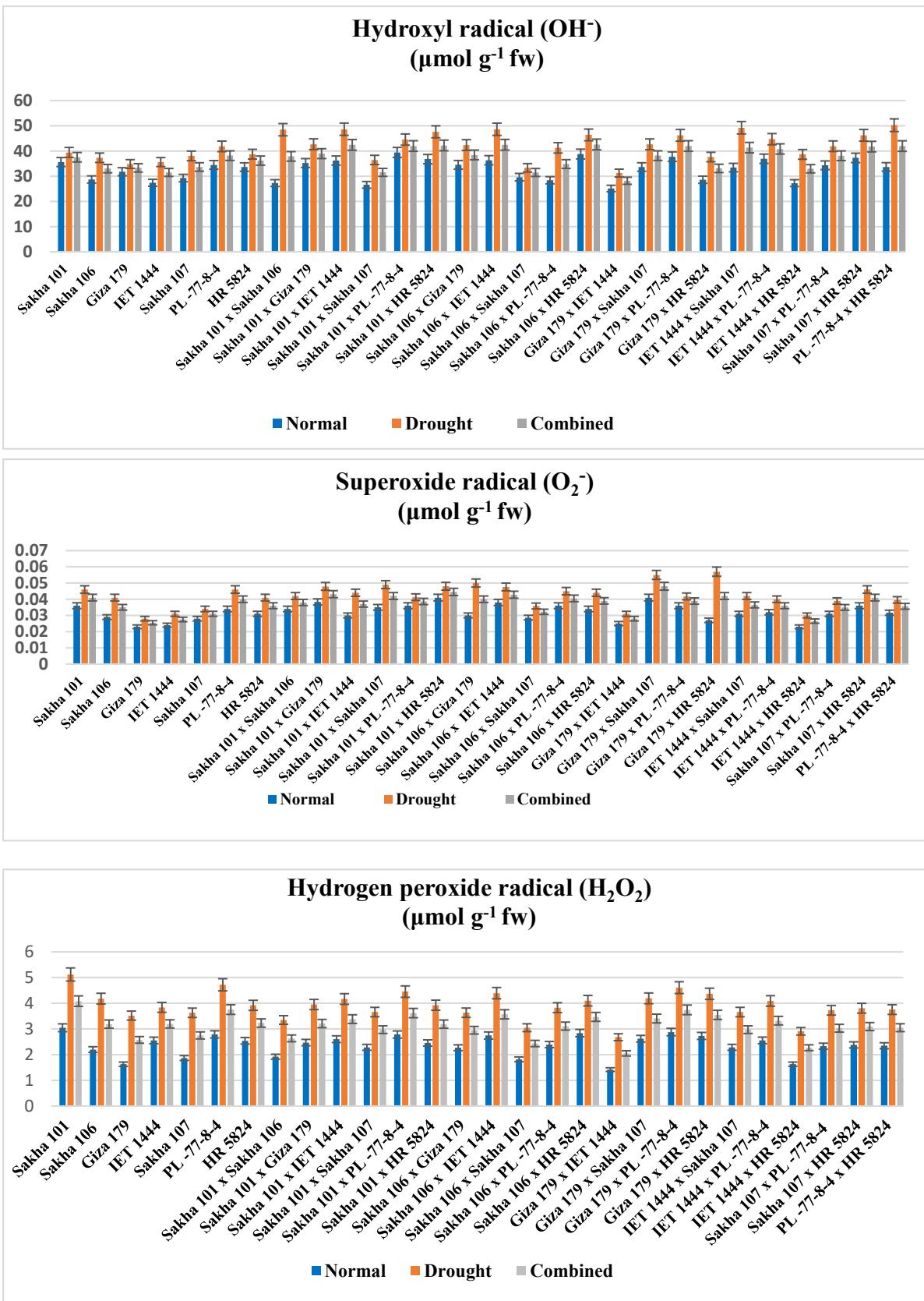


**Fig. (4):** Calculations of GCA effects ( $\hat{g}_i$ ) for grain yield/plant $^{-1}$  attribute under study in both and across environments:

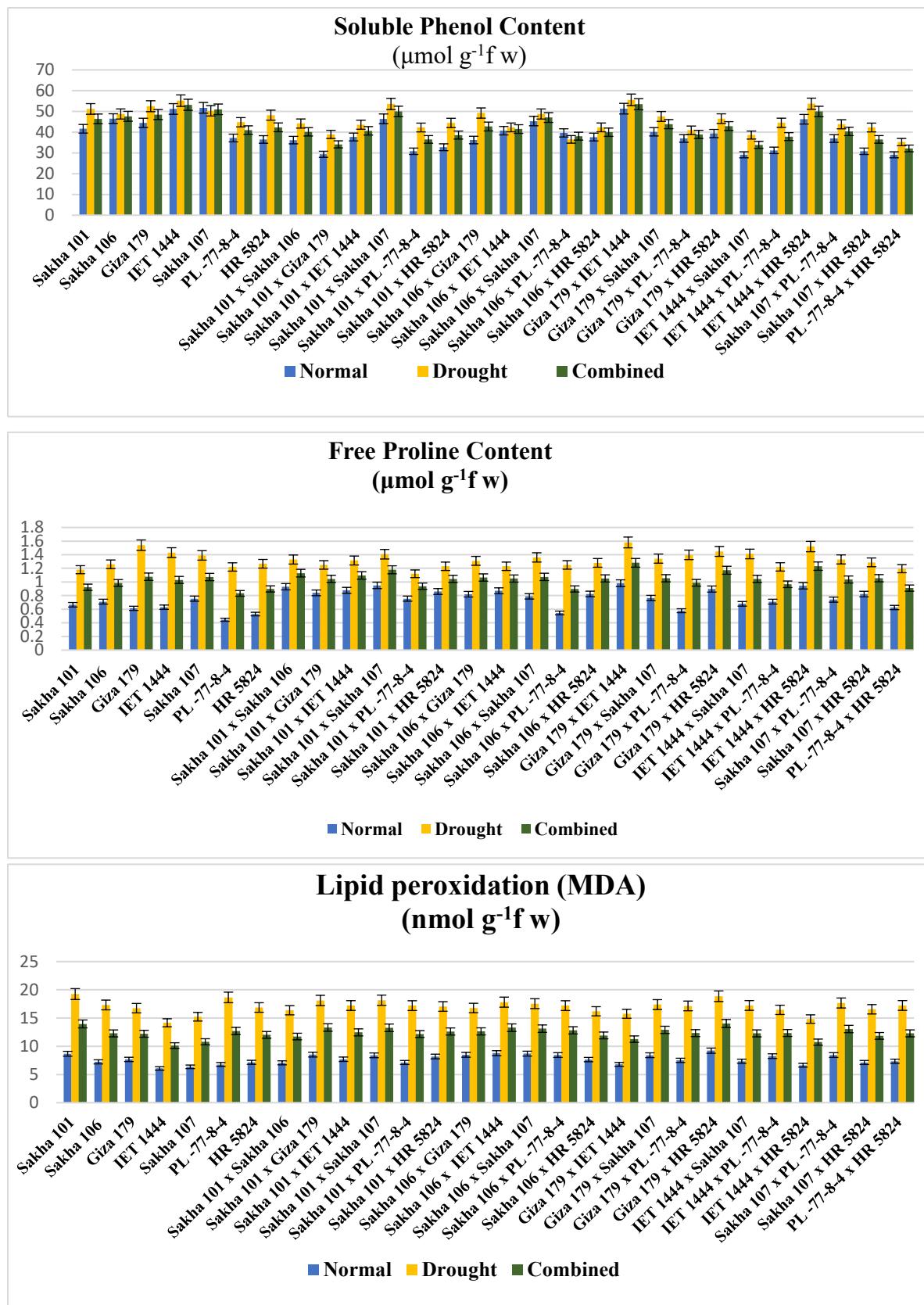


**Fig. (5):** Calculations of GCA effects ( $\hat{g}_i$ ) for harvest index (%) attribute under study in both and across environments:

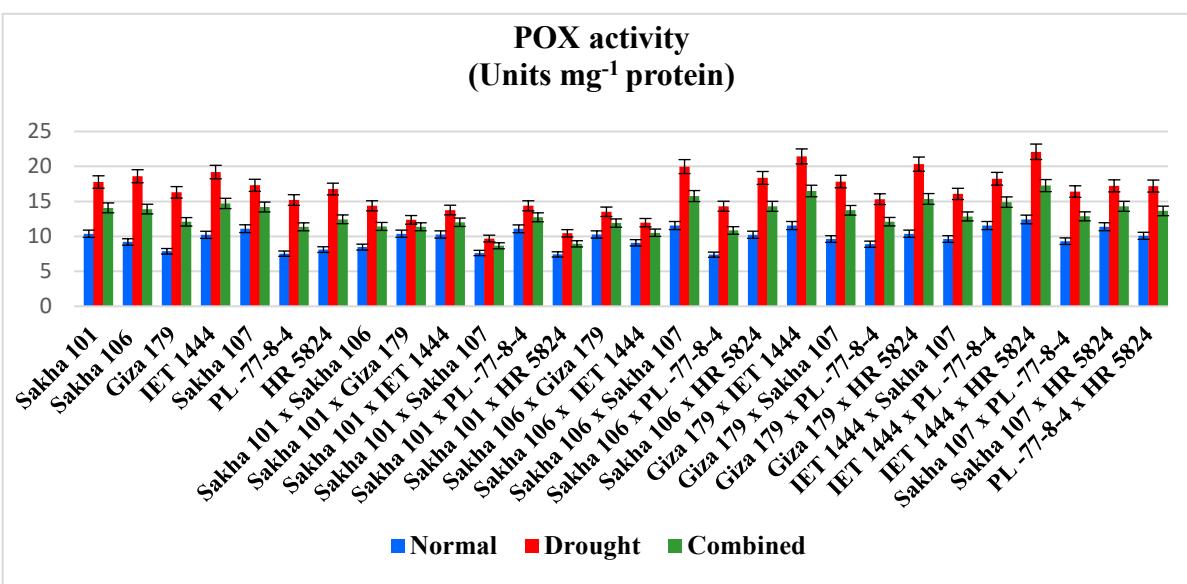
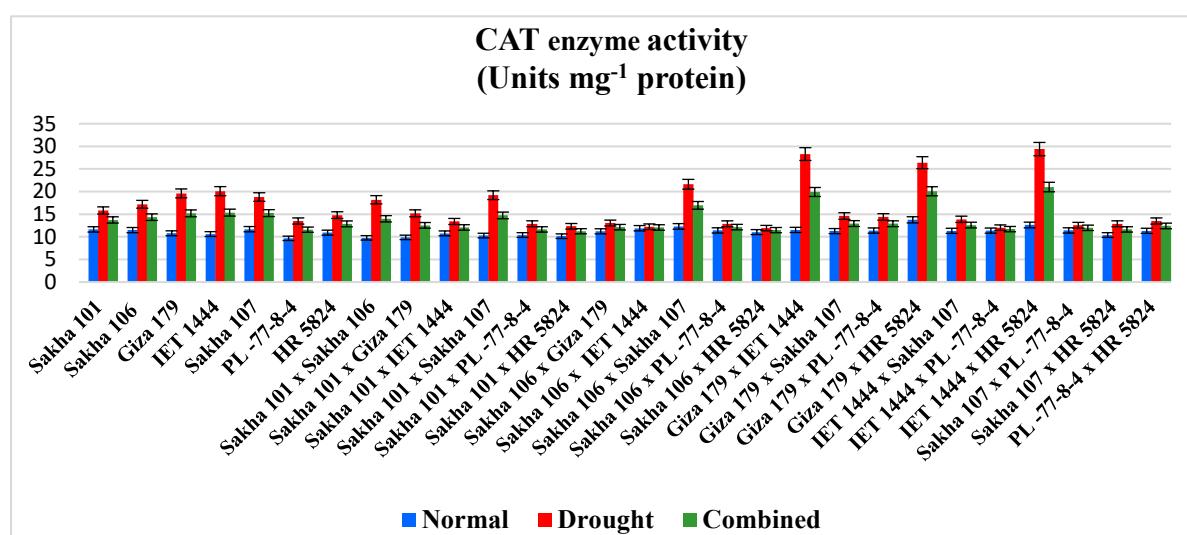
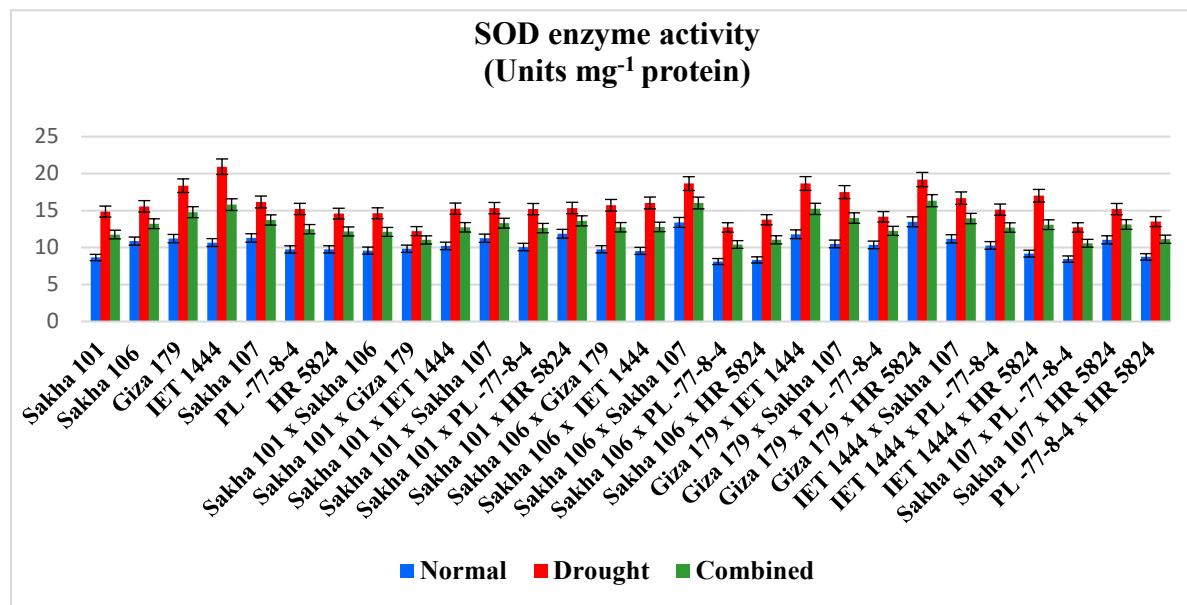
**Where:** highly significant, significant and non-significant at the 0.05 and 0.01 probability levels, respectively, are indicated by the symbols \*\*, \* and ns.

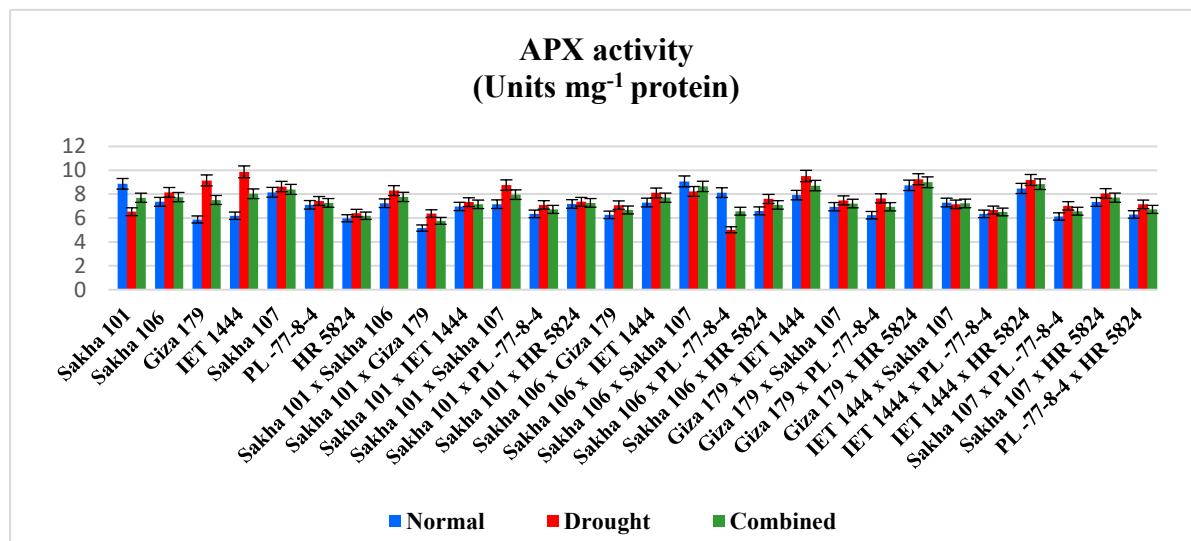


**Fig. 6.** Variations in the hydrogen peroxide ( $\text{H}_2\text{O}_2$ ), hydroxyl ( $\text{OH}^-$ ), and superoxide ( $\text{O}_2^-$ ) radicals of several rice entries during both well-watering and water regime conditions, as well as combined studies.

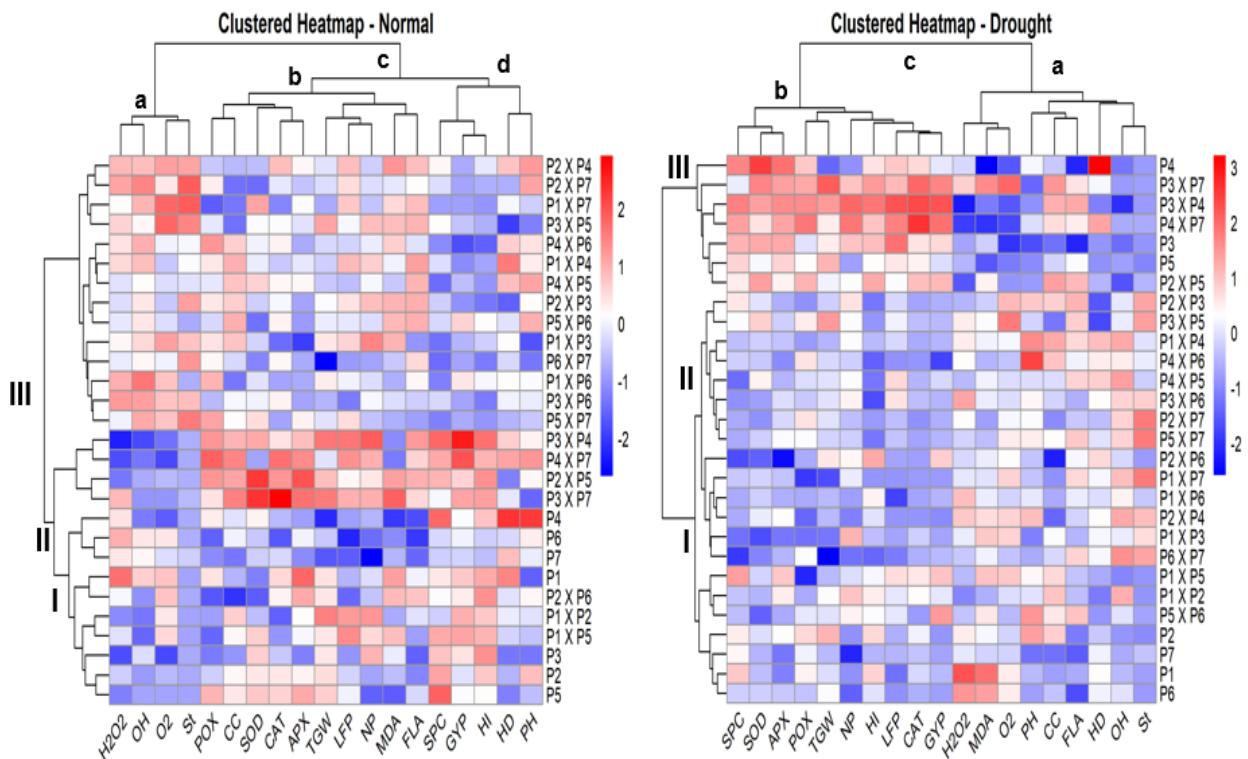


**Fig. 7.** Malondialdehyde (MDA) content, free proline accumulation and soluble phenol content of rice leaves under normal and water stress conditions as well as combined analyses.





**Fig. 8.** Antioxidant activities in rice leaves of different rice entries under control irrigation and water shortage conditions as well as combined across them.



**Fig. 9.** Heat map and hierarchical clustering analysis on agronomic, physiological, yield and related variables as well as bio-chemical response of 28 rice accessions under both good watering and water deficiency conditions.

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