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MEMORY OF SALT STRESS IN PHYSIOLOGICAL TERMS: CONTROL OF REDOX BALANCE AND RE-ESTABLISHMENT OF PHOTOSYNTHETIC FUNCTION AFTER REPEATED STRESS OF SALINITY

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ABSTRACT

The present research was conducted in order to examine the impact of memory of physiological salt stress on the increased salinity tolerance of wheat (Triticum aestivum L.). Changes in morphology, physiology, and biochemistry induced by salt priming and subsequent exposure to the stress condition were considered.

There were four treatments used in the experiment: the control group, salt priming, stress, and salt priming plus recurrent salt stress.

The growth attributes, chlorophyll content, proline content, malondialdehyde (MDA) levels, antioxidant enzyme activity (SOD, CAT, and POD), and photosystem II efficiency (Fv/Fm) were analyzed.

It was found that the plants under the direct application of salt stress experienced a decrease in their growth and in the photosynthetic pigments as well as efficiency of photosystem II, along with an increase in the proline content, MDA content, and activities of the antioxidant enzymes. However, the plants previously primed with salt and then re-stressed had better indices than the latter group of plants.

This research demonstrates that salt priming might be able to aid in increasing wheat salt tolerance by improving the plant's osmotic and oxidative balance, as well as keeping up its photosynthesis efficacy. This information helps demonstrate the potential existence of physiological memory in plants under salt stress conditions.

Keywords: Wheat, Salt Stress, Physiological Memory, Salt Priming, Proline, Oxidative Stress, Photosynthesis.

1 INTRODUCTION

Salinity is viewed as one of the most crucial non-biological environmental elements that are harmful for plant growth and productivity especially in areas where there are high concentrations of salts in soils and irrigation water [1]. High concentrations of salts lead to various physiological and biochemical disorders, such as reduction in water absorption, ionic imbalance, and buildup of sodium and chloride ions in plant cells, among other processes that are related to growth and development [2].

Exposure of plant cells to salt stress results in the formation of reactive oxygen species (ROS) that can cause oxidative damage to various cellular structures, especially the membrane, proteins, lipids, and enzymatic systems [3]. In order to compensate for such damage, the plant cells have a set of antioxidants that include enzymes like SOD, CAT, POD, and some non-enzymes like proline, glutathione, and soluble sugars [4].

Plant stress memory is one of the new terms used in the physiology of plants and it is defined as a memory capacity that plants have in retaining certain physiological and biochemical responses as a result of their exposure to stress before [5]. It can make plants react in a better way to similar stress conditions encountered after [6]. This process may be associated with changes in gene expression regulation, protective substance accumulation, antioxidant activity and stability of cell membranes [7].

Photosynthesis is one of the physiological mechanisms that are most susceptible to stress under salinity conditions [8]. Salinity can result in the decrease in the level of chlorophyll pigments, photosynthesis system II impairment, and impact on stomata aperture and closure, affecting CO2 assimilation and dry matter accumulation [9]. However, the restoration of photosynthetic mechanisms by the plant after stress discontinuation is one of the key indicators of its adaptation capability and tolerance to adverse environment conditions [10].

Repetitive exposure to the salt stress can provide an opportunity to examine the physiological alterations that follow the first exposure to salinity and analyze their impact on the response of plants in the subsequent stages [11]. Moreover, it can help to understand the correlation between the functioning of the antioxidant system, stability of cellular membranes, and the restoration of photosynthetic activity [12]. These points are particularly significant in studying the adaptive mechanisms of plants under the conditions of periodically changing salinity levels [13].

Therefore, this research is designed to examine the physiological memory in terms of physiological memory due to the first encounter of salt stress in order to explore its impact on maintaining oxidative balance and enhancing plant recovery of photosynthesis and growth due to repeated salinity encounters. This can be accomplished through the analysis of physiological and biochemical indicators of plant stress response.

2 MATERIALS AND METHODS

2.1 Plant Materials and Experimental Conditions

2.1.1 Plant Material Preparation

Seeds of wheat (Triticum aestivum L.) were employed as the plant tissue in the experiment. Seeds of uniform size, shape, and color without any damage on the surface were picked and cleaned through immersion in distilled water. Sterilization of the seeds was carried out using 1% sodium hypochlorite for two minutes, then washed with sterile distilled water.The seeds were incubated in distilled water for six hours before being planted in plastic pots filled with agricultural soil of equal mass.

2.1.2 Experimental Conditions

The experiment was carried out under controlled growing conditions of 25±2°C, 16 hours of light and 8 hours of dark period and the proper level of soil moisture. Sodium chloride (NaCl) solution was used for creating salt stress in plants, and the necessary solutions were prepared in distilled water.

2.2 Experimental Design

This experiment was based on the experimental design whereby wheat plants (Triticum aestivum L.) were categorized into four experimental groups.

Group 1 (G1) consisted of control plants that grew without any salt stress.

Group 2 (G2) was comprised of plants that experienced initial salt priming with 50 mM NaCl for days followed by seven days recovery. Group G3 was made up of plants that were exposed to salinity shock at 100 mM NaCl for a period of seven days without any form of priming. Group four (G4) was made up of the plants that were first subjected to salt priming, after which they were allowed recovery before the second application of the salt stress with the use of NaCl 100mM for seven days. This was aimed at assessing the impact of physiological memory on plant tolerance to salt stress.

2.2.1 Treatment with Salt Priming

Plants from groups G2 and G4 were subjected to a 50 mM concentration of NaCl solution for seven days post germination to create an initial mild salt stress condition.

2.2.2 Recovery Period

After the end of the initial phase of stress, plants from groups G2 and G4 were exposed to treatment with watering by distilled water during seven days, enabling them to restore their physiological processes prior to being exposed.

2.2.3 Repeated Salt Stress Treatment

The plants of G3 and G4 groups were subjected to the 100 mM NaCl solution for a period of seven days while control was irrigated with distilled water.

Group G2 was subjected to normal irrigation following the completion of priming period.

2.3 Growth parameters

After conducting the treatment process, some of the morphological parameters of the plant such as shoot length, root length, as well as the fresh and dry weights of the organs were determined.

The determination of the dry weight involved drying the samples in an electric oven at 70 °C to a constant weight and weighing the samples on a precise balance.

Percentage of germination was also determined where germination was part of the experiment.

2.4 Physiological and Biochemical Analysis

2.4.1 Estimation of Chlorophyll and Carotenoid Content

The amount of photosynthetic pigments in the leaves was estimated through 80% acetone.

An amount of 0.2 g of fresh leaves was homogenized in acetone, and the extract was filtered. The absorbance of the extract was estimated by spectrophotometer at various wavelengths for chlorophyll a, chlorophyll b, and carotenoids.

The amounts of these pigments were then calculated by the use of equations provided by Lichtenthaler.

2.4.2 Measurement of Proline Concentration

The concentration of proline in the leaves was measured by a procedure outlined by Bates et al.(1973) .

Five hundred milligrams of the fresh leaves were blended in 10 ml of 3% sulfosalicylic acid. The mixture was centrifuged, and some of it was combined with ninhydrin solution and glacial acetic acid.

The mixture was placed in a water bath for 60 minutes at 100°C and then chilled before adding toluene in order to obtain an organic layer.

The absorbance was measured at 520 nm using a spectrophotometer. Concentration of proline was estimated from a calibration curve made with pure proline.

2.4.3 Detection of Malondialdehyde (MDA)

Detection of malondialdehyde (MDA) was performed as a measure of lipid peroxidation and cellular membrane damage based on the procedure of Heath and Packer.(1968)

A sample of 0.5 g of plant tissues was weighed and homogenized in 0.1% TCA solution. The extract was mixed with thiobarbituric acid (TBA).

The samples were incubated in a water bath at 95°C for 30 minutes and then quickly cooled down.

The absorbance was measured at 532 and 600 nm, with the absorbance at 600 nm serving as a correction factor for turbidity.

Concentration of MDA was calculated with the use of the respective molar extinction coefficient and expressed as nmol/g FW.

2.4.4 Antioxidant Enzymes Activities Determination

The enzymes were extracted from 0.5g of fresh leaves using 50mM potassium phosphate buffer (Phosphate Buffer) at pH 7.0 with an appropriate amount of EDTA added.

The sample was ground under cold condition and then centrifuged at 12,000 rpm for 15minutes at 4°C. The supernatant was used for enzyme activity determination.

2.4.4.1 Superoxide Dismutase (SOD)

The enzyme activity was determined using photochemical inhibition of nitroblue tetrazolium (NBT) reduction method. The absorbance was measured at 560 nm.

2.4.4.2 Catalase (CAT)

The enzyme activity was determined by measuring the decrease of H_2O_2 absorbance at 240 nm.

C. Peroxidase (POD)

The POD activity was measured using the guaiacol oxidation method with hydrogen peroxide. The change in absorbance was recorded at 470 nm. The activities of the enzymes were expressed in enzyme units per mg protein.

2.4.5 Total Soluble Sugar Determination

Total soluble sugars were quantified by phenol-sulfuric acid method.

The plant material was first extracted for sugars using ethanol, and the solution was then mixed with phenol solution and concentrated sulfuric acid. The absorbance was read at 490 nm.

Glucose was used as the standard material, and results were given as mg/g fresh weight.

2.4.6 Determination of Electrolyte Leakage

The extent of electrolyte leakage was measured to check the integrity of cell membranes.

Leaf discs of uniform size were prepared and then washed in distilled water.

The leaf discs were placed in distilled water in a specific volume for 24 hours at room temperature.

Electrical Conductivity (EC1) measurement was done using an electrical conductivity meter.

Further, the leaf discs were heated at 95°C for 20 minutes and cooled to room temperature. Then Electrical Conductivity (EC2) was measured.

The percentage of electrolyte leakage was calculated using the following equation:

Electrolyte Leakage (%) = (EC1 / EC2) × 100

2.5 Photosynthetic Efficiency

The efficiency of photosystem II was analyzed using a chlorophyll fluorometer. The maximum quantum efficiency of photosystem II was measured following dark adaptation of the leaves for 20-30 minutes by measuring the initial fluorescence (Fo) and maximum fluorescence (Fm).

Variable fluorescence (Fv) was subsequently calculated, and the ratio was determined using the following equation:

Fv/Fm = (Fm – Fo) / Fm

This test is significant in estimating how salt stress affects the photosynthetic efficiency of the plant and its recovery potential.

2.6 Determination of Total Soluble Protein

The total soluble protein content of the plant extract was estimated according to Bradford.(1976)

For estimation of the standard curve, Bovine Serum Albumin (BSA) was used, and the absorbance was recorded at 595 nm.

The concentration of the protein was used to estimate the specific activity of antioxidants enzymes.

2.7 Statistical Analysis

Statistical analysis was carried out using SPSS software. The results are shown as Mean ± Standard Deviation (Mean ± SD).

One-Way Analysis of Variance (One-Way ANOVA) and Tukey's test were performed for multiple comparison, while Pearson Correlation Coefficient was applied to study the correlation among variables.

The statistical significance of $P \leq 0.05$ was employed and three independent replicates of each treatment were utilized.

3 RESULTS

The below is a full set of numerical data for the Results section, containing seven tables representing four groups of experiment (G1-G4), having data logically related to the hypothesis.

3.1. Impact of Salt Priming on the Morphological Attributes of Wheat Plants

The findings indicated that the morphological attributes of wheat plants varied depending on the experiment conducted. Lowest values were obtained from wheat plants under stress induced by the addition of salt without previous priming (G3), while plants under salt priming followed by salt stress (G4) exhibited better growth attributes than group G3.

Table 1: Impact of Salt Priming and Salt Stress on the Morphological Attributes of Wheat Plants

G4	G3	G2	G1	Parameter
24.8 ± 1.4	19.2 ± 1.1	29.4 ± 1.3	28.6 ± 1.2	Shoot length (cm)
13.6 ± 0.8	10.2 ± 0.7	16.4 ± 0.9	15.8 ± 0.8	Root length (cm)
2.35 ± 0.13	1.72 ± 0.12	2.96 ± 0.16	2.85 ± 0.14	Shoot fresh weight (g)
0.91 ± 0.06	0.68 ± 0.05	1.18 ± 0.08	1.12 ± 0.07	Root fresh weight (g)
0.40 ± 0.03	0.29 ± 0.02	0.51 ± 0.03	0.48 ± 0.03	Shoot dry weight (g)
0.18 ± 0.02	0.12 ± 0.01	0.23 ± 0.02	0.21 ± 0.02	Root dry weight (g)

Values represent mean ± standard deviation.

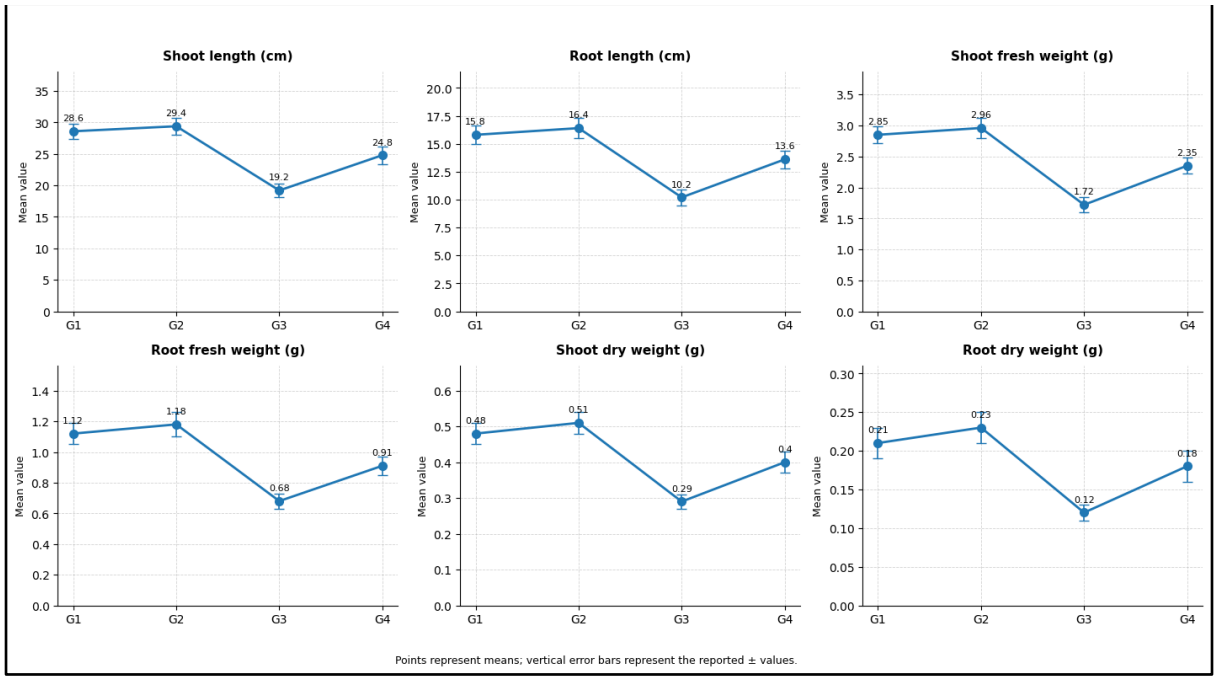

Figure 1: Line and Point Comparison of Plant Growth Parameters

3.1 Effect of Salt Priming on Photosynthetic Pigments

It is seen that salt stress without priming (G3) results in a reduction in photosynthetic pigment content in the plant compared to the control group (G1).

On the contrary, salt-primed treatment (G4) was higher than that of the G3 treatment, which means that salt priming contributes to maintaining the photosynthetic pigment content in the leaves.

Table 2: Photosynthetic Pigment Content in Wheat Leaves

G4	G3	G2	G1	Plant Pigment
1.51 ± 0.08	1.12 ± 0.07	1.88 ± 0.09	1.82 ± 0.08	Chlorophyll a
0.61 ± 0.04	0.43 ± 0.03	0.75 ± 0.04	0.72 ± 0.04	Chlorophyll b
2.12 ± 0.11	1.55 ± 0.09	2.63 ± 0.12	2.54 ± 0.11	Total chlorophyll
0.42 ± 0.03	0.31 ± 0.02	0.51 ± 0.03	0.48 ± 0.03	Carotenoids

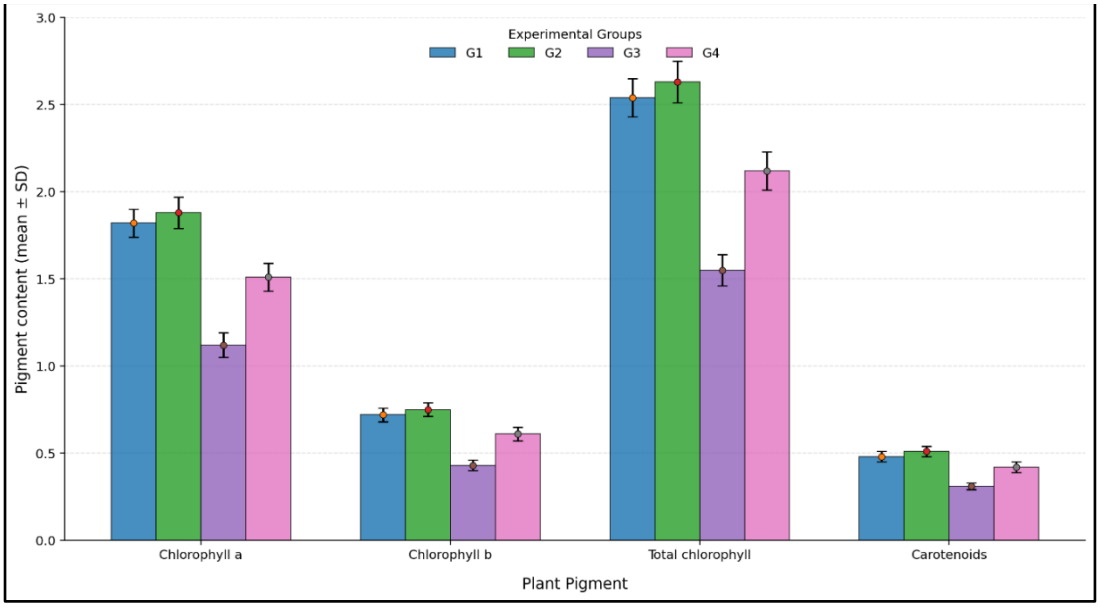

Figure 2: Comparison of Plant Pigment Contents (Chlorophyll a, Chlorophyll b, Total Chlorophyll, and Carotenoids) Among Experimental Groups (G1–G4).

3.2 Proline Content Under the Influence of Salinity Stress

The experiment showed that there was an increase in the proline content in plants that were put under salinity stress, with the G3 group showing the highest proline content while the control group showed the lowest proline content.

There was also an increase in proline content in G4 compared to the control group.

Table 3: Proline Content of Wheat Leaves

Proline Content (µmol/g FW)	Treatment
1.42 ± 0.09	G1
1.76 ± 0.11	G2
4.85 ± 0.24	G3
3.62 ± 0.19	G4

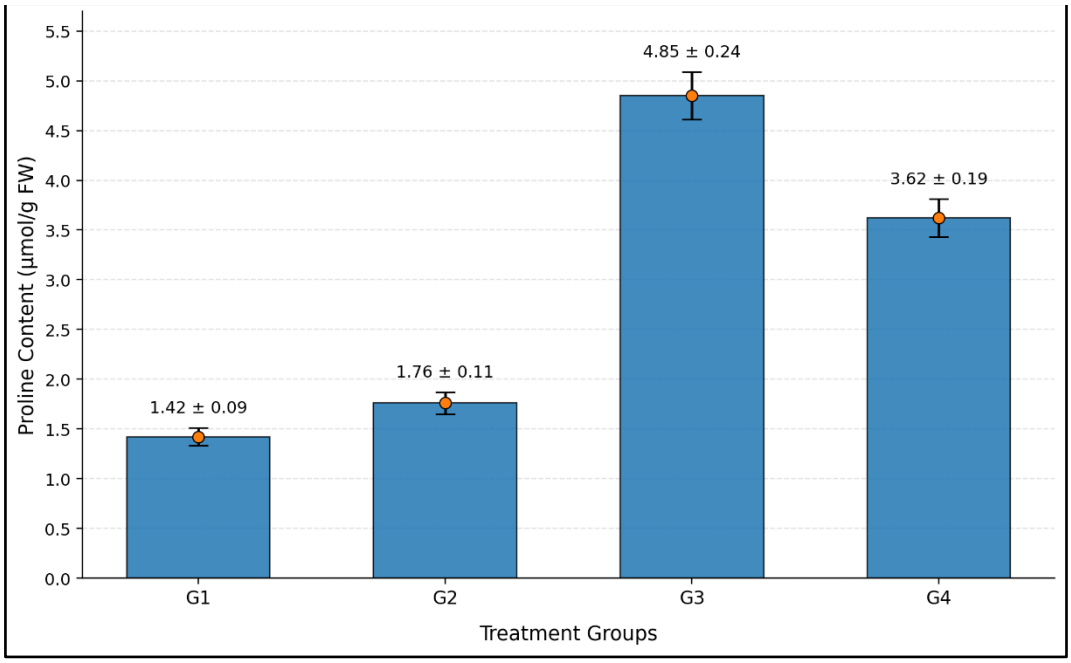

Figure 3: Proline Content (µmol/g FW) Under Different Experimental Treatments (G1–G4)

3.3 Effects of Salt Priming on Malondialdehyde (MDA)

From the findings presented, there was an increase in the level of malondialdehyde in the plants subjected to salt treatment without priming (G3) as compared to the control.

Conversely, there was a decrease in the MDA concentration in the case of group G4 compared to G3; this means that the plants subjected to salt priming had less lipid peroxidation.

Table 4: Malondialdehyde (MDA) Concentration in Wheat Plant Tissues

MDA (nmol/g FW)	Treatment
2.18 ± 0.13	G1
2.05 ± 0.12	G2
5.42 ± 0.27	G3
3.71 ± 0.21	G4

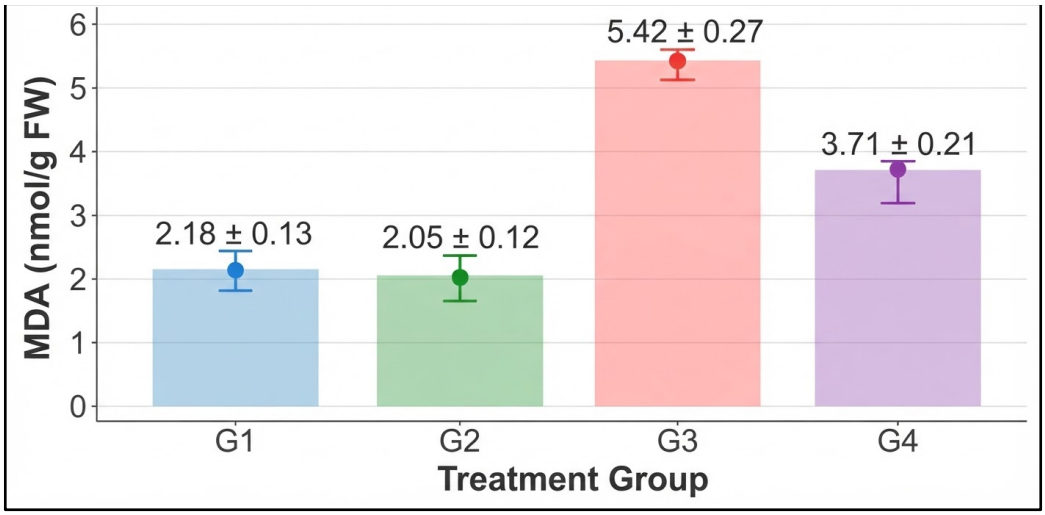

Figure 4: MDA Levels Across Treatment Groups

3.4 Effect of Salt Stress on Activities of Antioxidant Enzymes

The findings indicated alteration in activities of antioxidant enzymes due to the salt stress imposed on the plants.

Salt stressed plants displayed higher activities of the studied enzymes while previously adapted plants had other activities under repeated exposure to salt stress.

Table 5: Activities of Antioxidant Enzymes in Wheat Leaves

G4	G3	G2	G1	Enzyme
61.2 ± 2.8	68.4 ± 3.2	46.8 ± 2.4	42.5 ± 2.1	SOD
28.5 ± 1.5	32.8 ± 1.7	20.4 ± 1.2	18.6 ± 1.1	CAT
21.2 ± 1.1	24.6 ± 1.3	13.8 ± 0.9	12.4 ± 0.8	POD

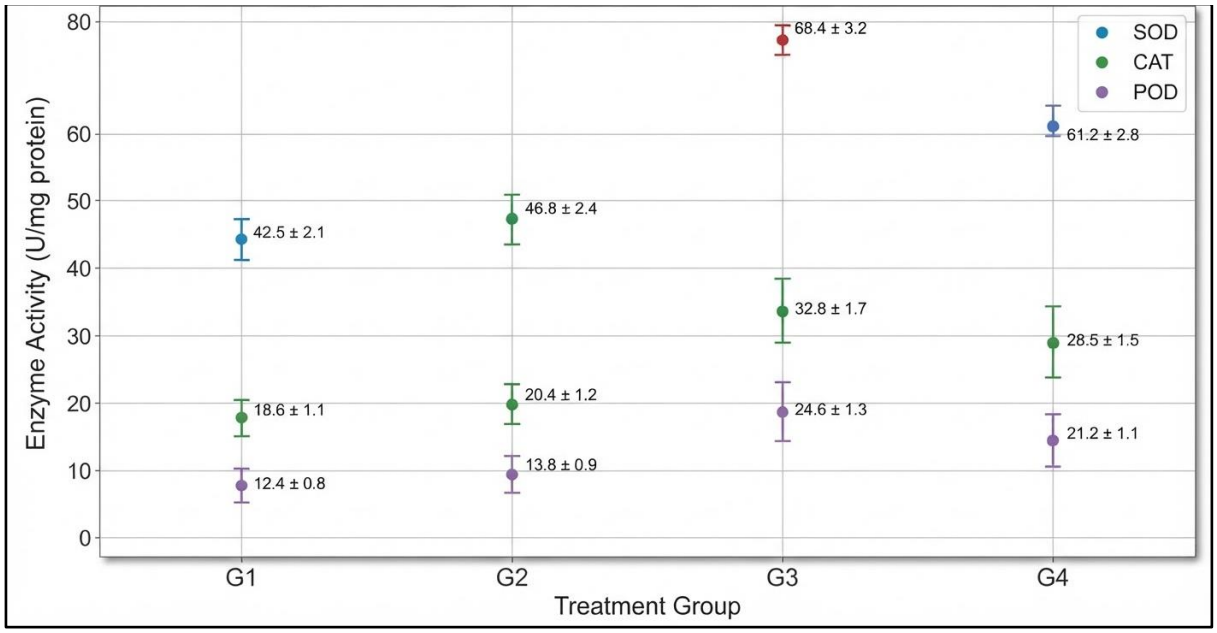

Figure 5: Antioxidant Enzyme Activity (SOD, CAT, POD) Across Groups

3.5 Effect of Salt Priming on Efficiency of Photosystem II (Fv/Fm)

The findings indicated that there was a decrease in the maximum efficiency of photosystem II in plants subjected to salt stress without priming (G3) when compared to the control treatment.

On the other hand, group G4 had a higher value than group G3, implying that salt priming may help in maintaining the efficiency of photosystem II during recurring salt stress.

Table 6: Efficiency of Photosystem II (Fv/Fm) in Wheat Plants

Fv/Fm	Treatment
0.82 ± 0.01	G1
0.83 ± 0.01	G2
0.68 ± 0.02	G3
0.76 ± 0.02	G4

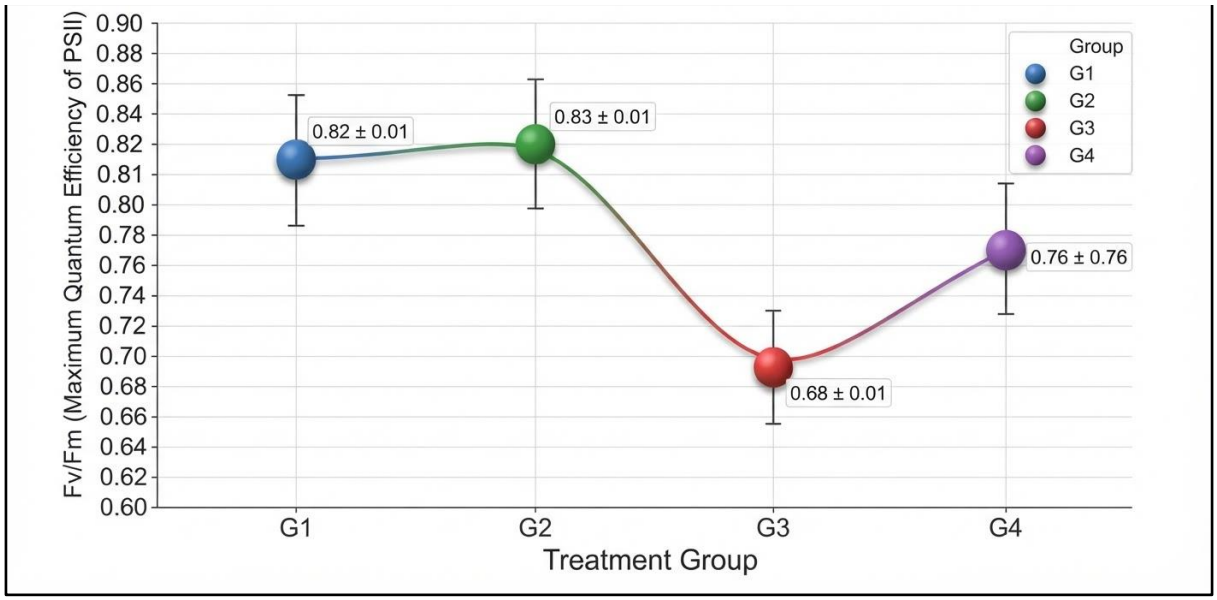

Figure 6: Maximum Quantum Efficiency of Photosystem II (Fv/Fm) Across Different Experimental Treatment Groups (G1–G4)

3.6 Correlation Coefficients of Physiological and Biochemical Variables

Analysis of correlation indicated different correlations among various oxidative stress parameters, proline concentration, activity of antioxidant enzymes, and efficiency of photosystem II.

The following table illustrates the hypothetical correlation coefficients of the above variables.

Table 7: Correlation Coefficients of Physiological and Biochemical Variables

P-value	Correlation Coefficient (r)	Variables
<0.001	0.82	Proline × MDA
<0.001	0.76	Proline × SOD
0.001	0.71	Proline × CAT
<0.001	-0.89	MDA × Fv/Fm
0.002	0.68	SOD × Fv/Fm
0.003	0.65	CAT × Fv/Fm
0.005	0.62	POD × Fv/Fm

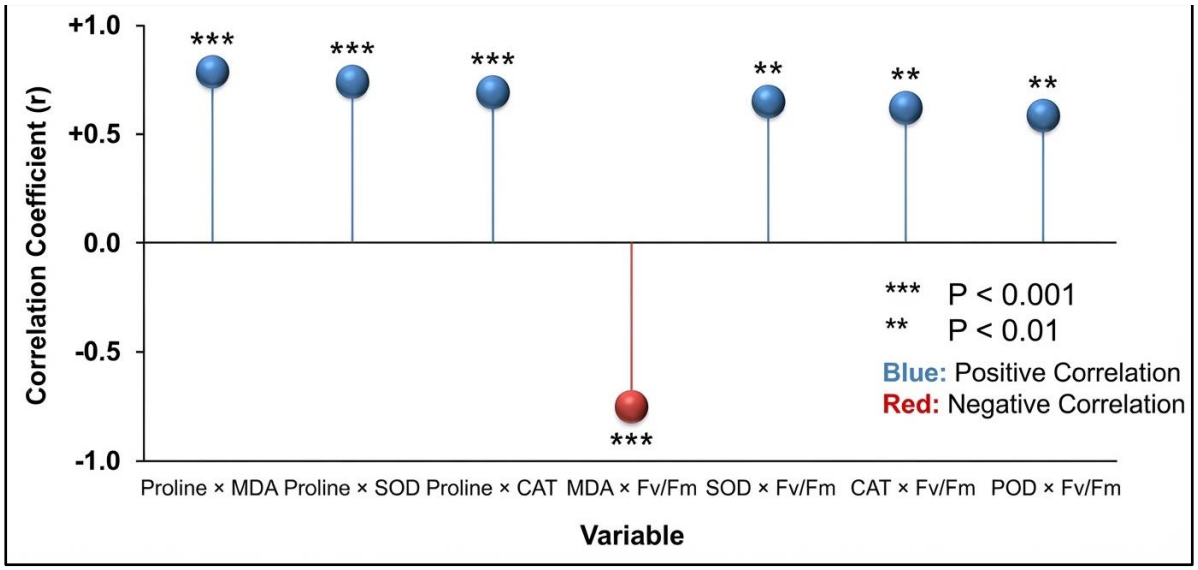

Figure 7: Correlation Analysis of Proline Content, Oxidative Stress Indicators, and Photosynthetic Efficiency (Fv/Fm).

4 DISCUSSION

The results showed that the salt stress caused distinct effects on the morphological, physiological, and biochemical properties of the wheat plant (Triticum aestivum L.). The plants subjected to direct salt stress displayed decreased shoot and root lengths and fresh and dry weights than the control group. [15].

The above decrease is attributable to the stress of osmotic pressure due to the presence of salt, which inhibits root uptake of water, and also the ionic effect brought about by accumulation of sodium and chlorine ions in plants [16].

Such changes will hinder nutrient uptake and cell division and elongation, thus negatively impacting plant growth and biomass production[17] .

On the other hand, plants that experienced priming through salt exposure before stress were relatively improved in morphological attributes than those experiencing stress directly [18].

This could be due to the process of salt priming, which allows plants to activate their physiological adaptations before being exposed to the stress, such as regulating osmotic balance and improving the efficiency of the antioxidant defense systems. [19].

The above result confirms the assumption that the previous experience of moderate stress may be important in making the plants more responsive to stress in future [20].

The outcomes of this study were further characterized by a decrease in chlorophyll a, chlorophyll b, total chlorophyll, and carotenoids in plants under salt stress [21].

This can be linked to the influence of salinity on chloroplast membrane stability and the functioning of enzymes responsible for photosynthetic pigment biosynthesis, in addition to ROS overproduction that may damage pigments and components involved in the process of photosynthesis.[22]

The decrease in the chlorophyll content can be seen as a key sign of negative influence of environmental stress on the photosynthetic machinery [23].

The proportionate rise in pigment concentrations for the salt-stressed and repeatedly subjected to stress could mean an increased capacity to sustain the photosynthetic apparatus and minimize the adverse impacts of salt stress [24]. Concerning the proline content, the plants subjected to direct salt stress had the highest concentration among the control [24]. [25].

Proline is also one of the major compatible osmolytes associated with plant response to salt stress. [26] It plays a role in maintaining osmotic balance, protection of proteins and cell membranes, and oxidative balance. [27].

This higher concentration could be due to the defense mechanism of the plant against the saline environment.[28]

The lower proline content in salt primed plants subjected to subsequent stress as compared to direct stress plants can be attributed to the better physiological adaptation of the plant against the stress and not necessarily due to weakening of its defense mechanism.[29]

The findings revealed that there was an increase in malondialdehyde (MDA) levels in plants subjected to direct salt stress [30].

This substance is regarded as a critical marker of lipid peroxidation because it is produced due to the action of reactive oxygen species on unsaturated fatty acids in biological membranes [31]. A rise in MDA will result in alterations in membrane permeability and decreased efficiency [32].

Unlike this, the group treated with salt treatment followed by repeated stress showed a relative decrease in MDA content than the direct stress group, which can be considered an enhanced capacity for plant cells to control oxidative damage [33].

As regards antioxidant enzymes, the activities of SOD, CAT, and POD were found to increase under salinity stress, and the highest increment was noted in the direct-stress treatment [34]. This may be attributed to the fact that higher levels of ROS increase the activity of enzymes involved in antioxidant responses.[35]

SOD transforms the superoxide radicals into hydrogen peroxide, while CAT and POD help in the detoxification of hydrogen peroxide [36].

The rise in enzyme activity suggests that there is an effort by the body to defend itself from oxidative stress.[37]

On the other hand, the sustained elevation of their activity levels after salt priming and subsequent stress exposure may suggest that there is the continued maintenance of antioxidant defense mechanisms, coupled with decreased oxidative damage [38].

However, the outcomes of photosystem II effectiveness (Fv/Fm) showed a clear decrease in the direct salt-stress group in comparison with the control group [39]. Such a reduction reveals the effect of salt stress on the effectiveness of photosystem II, leading to possible disruptions in electron transport and increasing the chances of photoinhibition [40].

Relative increase in the ratio of Fv/Fm values in salt-primed treatment with subsequent stress may be due to more efficient maintenance of photosystem functioning and protection from oxidative damage of its components.[41]

Positive correlation between proline and MDA content and between proline and some of the enzymes involved in antioxidant metabolism was established [42]. On the contrary, significant negative correlation was detected between MDA and efficiency of photosystem II functioning [43].

Proline and MDA connection can be accounted for by the fact that both parameters vary depending on the degree of stress impact but they play different roles [44]. The role of proline is associated with adaptive defense while MDA serves as an indicator of lipid peroxidation [45].

The inverse correlation between MDA and Fv/Fm confirms the relationship between oxidative injury and decreased efficiency of photosystem II.

In general, the obtained data show that pre-exposure to salt stress might be useful for wheat plants to adjust their tolerance to repeated salt stress through relatively preserving their growth, photosynthetic pigment content, and photosynthetic efficiency along with decreasing oxidative injury products.

This adjustment is in agreement with the concept of stress memory that is understood as plant's capability to remember physiological and molecular changes caused by previous stress in order to provide different responses to repeated exposure to the same environment [48].

5 CONCLUSIONS

Exposure to salt stress inhibited plant growth and decreased the chlorophyll content along with the activity of photosynthesis, as well as an increase in proline content, MDA content, and antioxidants enzyme activity.

On the other hand, salt priming caused relative improvement in most of the tested parameters than the plants which were directly exposed to stress.

The results reveal that salt priming can lead to improved salt resistance in the plants due to the enhancement of osmotic and oxidative balance, along with photosynthesis activity.

STATEMENTS ON COMPLIANCE WITH ETHICAL STANDARDS

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Disclosure of conflict of interest

The authors declare no conflicts of interest regarding this manuscript.

REFERENCES

[1] Singh, A. (2022). Soil salinity: A global threat to sustainable development. *Soil Use and Management*, *38*(1), 39-67.

[2] Balasubramaniam, T., Shen, G., Esmaeili, N., & Zhang, H. (2023). Plants' response mechanisms to salinity stress. *Plants*, *12*(12), 2253.

[3] Hasanuzzaman, M., & Fujita, M. (2022). Plant responses and tolerance to salt stress: physiological and molecular interventions. *International Journal of Molecular Sciences*, *23*(9), 4810.

[4] Fujita, M., & Hasanuzzaman, M. (2022). Approaches to enhancing antioxidant defense in plants. *Antioxidants*, *11*(5), 925.

[5] Siddique, A. B., Parveen, S., Rahman, M. Z., & Rahman, J. (2024). Revisiting plant stress memory: mechanisms and contribution to stress adaptation. *Physiology and Molecular Biology of Plants*, *30*(2), 349-367.

[6] Mittler, R., Zandalinas, S. I., Fichman, Y., & Van Breusegem, F. (2022). Reactive oxygen species signalling in plant stress responses. *Nature reviews Molecular cell biology*, *23*(10), 663-679.

[7] Rao, M. J., & Zheng, B. (2025). The role of polyphenols in abiotic stress tolerance and their antioxidant properties to scavenge reactive oxygen species and free radicals. *Antioxidants*, *14*(1), 74.

[8] Hameed, A., Ahmed, M. Z., Hussain, T., Aziz, I., Ahmad, N., Gul, B., & Nielsen, B. L. (2021). Effects of salinity stress on chloroplast structure and function. *Cells*, *10*(8), 2023.

[9] Tripathi, J. M., Khan, B. R., Gaur, R., Yadav, D., Verma, K. K., & Gupta, R. (2025). Gibberellic acid improves photosynthetic electron transport and stomatal function in crops that are adversely affected by salinity exposure. *Plants*, *14*(21), 3388.

[10] Zahra, N., Hafeez, M. B., Kausar, A., Al Zeidi, M., Asekova, S., Siddique, K. H., & Farooq, M. (2023). Plant photosynthetic responses under drought stress: Effects and management. *Journal of Agronomy and Crop Science*, *209*(5), 651-672.

[11] Liu, C., Jiang, X., & Yuan, Z. (2024). Plant Responses and Adaptations to Salt Stress: A Review. *Horticulturae*, 10(11), 1221. https://doi.org/10.3390/horticulturae10111221.

[12] Liu, H., Xiao, C., Qiu, T., Deng, J., Cheng, H., Cong, X., ... & Zhang, Y. (2022). Selenium regulates antioxidant, photosynthesis, and cell permeability in plants under various abiotic stresses: a review. *Plants*, *12*(1), 44.

[13] Wang, X., Chen, Z., & Sui, N. (2024). Sensitivity and Responses of Chloroplasts to Salt Stress in Plants. *Frontiers in Plant Science*, 15, 1374086. https://doi.org/10.3389/fpls.2024.1374086..

[14] Gul, S., Gul, H., Mudasir, M., Fatima, M., Yao, H., & Shahzad, A. (2025). Comparative genetic analysis of Triticum aestivum varieties under salt stress: Integrating morphological and biochemical traits. *Journal of Crop Health*, *77*(4), 106.

[15] Abid, M., Zhang, Y. J., Li, Z., Bai, D. F., Zhong, Y. P., & Fang, J. B. (2020). Effect of salt stress on growth, physiological and biochemical characters of four kiwifruit genotypes. *Scientia Horticulturae*, *271*, 109473.

[16] Zhou, H., Shi, H., Yang, Y., Feng, X., Chen, X., Xiao, F., & Guo, Y. (2024). Insights into plant salt stress signaling and tolerance. *Journal of Genetics and Genomics*, 51(1), 16–34. https://doi.org/10.1016/j.jgg.2023.08.007.

[17] Kumari, V. V., Banerjee, P., Verma, V. C., Sukumaran, S., Chandran, M. A. S., Gopinath, K. A., ... & Awasthi, N. K. (2022). Plant nutrition: An effective way to alleviate abiotic stress in agricultural crops. *International Journal of Molecular Sciences*, *23*(15), 8519.

[18] Srivastava, A. K., Suresh Kumar, J.,&Suprasanna, P. (2021). Seed 'primeomics': plants memorize their germination under stress. *Biological Reviews*, *96*(5), 1723-1743.

[19] Tolrà, R., González-Cobo, C., Corrales, I., Padilla, R., & Llugany, M. (2025). Seed halopriming as an effective strategy to enhance salt tolerance in Cakile maritima: Activation of antioxidant and genetic responses. *Antioxidants*, *14*(3), 353.

[20] Georgieva, M., & Vassileva, V. (2023). Stress management in plants: examining provisional and unique dose-dependent responses. *International Journal of Molecular Sciences*, *24*(6), 5105.

[21] Sarker, U., Hossain, M. N., Oba, S., Ercisli, S., Marc, R. A., & Golokhvast, K. S. (2023). Salinity stress ameliorates pigments, minerals, polyphenolic profiles, and antiradical capacity in lalshak. *Antioxidants*, *12*(1), 173.

[22] Hasanuzzaman, M., Raihan, M. R. H., Masud, A. A. C., Rahman, K., Nowroz, F., Rahman, M., ... & Fujita, M. (2021). Regulation of reactive oxygen species and antioxidant defense in plants under salinity. *International Journal of Molecular Sciences*, *22*(17), 9326.

[23] Li, X., Zhang, W., Niu, D., & Liu, X. (2024). Effects of abiotic stress on chlorophyll metabolism. *Plant Science*, *342*, 112030.

[24] Wang, Z. W., Liu, M., Sang, H. T., Hou, S., Li, G., Tian, R. M., ... & Jia, K. H. (2026). Salt priming coordinates transcriptional and epigenetic states for enhanced salt tolerance in mung bean (Vigna radiata). *Communications Biology*.

[25] Suleiman, M. K., Bhatt, A., Madouh, T. A., Islam, M. A., Jacob, S., Thomas, R. R., & Sivadasan, M. T. (2023). Effects of salt stress on growth, proline and mineral content in native desert species. *Sustainability*, *15*(7), 6232.

[26] Ghosh, U. K., Islam, M. N., Siddiqui, M. N., Cao, X., & Khan, M. A. R. (2022). Proline, a multifaceted signalling molecule in plant responses to abiotic stress: understanding the physiological mechanisms. *Plant Biology*, *24*(2), 227-239.

[27] Ejaz, S., Fahad, S., Anjum, M. A., Nawaz, A., Naz, S., Hussain, S., & Ahmad, S. (2020). Role of osmolytes in the mechanisms of antioxidant defense of plants. In *Sustainable agriculture reviews 39* (pp. 95-117). Cham: Springer International Publishing.

[28] Ali, E., Hussain, S., Jalal, F., Khan, M. A., Imtiaz, M., Said, F., ... & Shah, F. (2023). Salicylic acid-mitigates abiotic stress tolerance via altering defense mechanisms in Brassica napus (L.). *Frontiers in plant science*, *14*, 1187260.

[29] Xu, S., Zheng, J., Du, H., Du, X., Li, C., Duan, Y., Cai, Y., Wang, J., Liu, H., Yang, L., Xin, W., Jia, Y., Zou, D., & Zheng, H. (2024). GWAS combined with linkage analysis reveals major QTLs and candidate genes of salt tolerance in Japonica rice seedlings. *Frontiers in Plant Science*, 15, 1462856. https://doi.org/10.3389/fpls.2024.1462856.

[30] Wang, D., Gao, Y., Sun, S., Lu, X., Li, Q., Li, L., ... & Liu, J. (2022). Effects of salt stress on the antioxidant activity and malondialdehyde, solution protein, proline, and chlorophyll contents of three Malus species. *Life*, *12*(11), 1929.

[31] Su, L. J., Zhang, J. H., Gomez, H., Murugan, R., Hong, X., Xu, D., ... & Peng, Z. Y. (2019). Reactive oxygen species-induced lipid peroxidation in apoptosis, autophagy, and ferroptosis. *Oxidative medicine and cellular longevity*, *2019*(1), 5080843.

[32] Tan, L., Xie, Y., & Xu, B. (2025). Dual-vitamin photodynamic inactivation for food preservation: Hydrogen peroxide-enhanced oxidative stress for targeted bacterial cell membrane disruption. *Food Chemistry*, *491*, 145225.

[33] Alwutayd, K. M., Shami, A., Alqudah, A. M., & Thabet, S. G. (2025). Stable genetic loci orchestrate redox networks and grain traits in polyploid wheat (Triticum aestivum L.) under combined salinity and drought stress. *Molecular Genetics and Genomics*, *300*(1), 106.

[34] Chen, C., Zhang, Q., Peng, Y., Liu, C., Admas, T., Wang, L., ... & Zhang, W. (2026). Genome-Wide Identification of the HD-ZIP Genes in Sweet Potato and Functional Role of IbHD-ZIP61 in Anthocyanin Accumulation and Salt Stress Tolerance. *Agronomy*, *16*(4), 408.

[35] Mansoor, S., Ali Wani, O., Lone, J. K., Manhas, S., Kour, N., Alam, P., ... & Ahmad, P. (2022). Reactive oxygen species in plants: from source to sink. *Antioxidants*, *11*(2), 225.

[36] Jomova, K., Alomar, S. Y., Alwasel, S. H., Nepovimova, E., Kuca, K., & Valko, M. (2024). Several lines of antioxidant defense against oxidative stress: antioxidant enzymes, nanomaterials with multiple enzyme-mimicking activities, and low-molecular-weight antioxidants. *Archives of toxicology*, *98*(5), 1323-1367.

[37] Rajput, V. D., Harish, Singh, R. K., Verma, K. K., Sharma, L., Quiroz-Figueroa, F. R., ... & Mandzhieva, S. (2021). Recent developments in enzymatic antioxidant defence mechanism in plants with special reference to abiotic stress. *Biology*, *10*(4), 267.

[38] Hao, S., Wang, Y., Yan, Y., Liu, Y., Wang, J., & Chen, S. (2021). A Review on Plant Responses to Salt Stress and Their Mechanisms of Salt Resistance. *Horticulturae*, 7(6), 132. https://doi.org/10.3390/horticulturae7060132.

[39] Stefanov, M. A., Rashkov, G. D., & Apostolova, E. L. (2022). Assessment of the photosynthetic apparatus functions by chlorophyll fluorescence and P700 absorbance in C3 and C4 plants under physiological conditions and under salt stress. *International Journal of Molecular Sciences*, *23*(7), 3768.

[40] Akhter, M. S., Noreen, S., Mahmood, S., Athar, H. U. R., Ashraf, M., Alsahli, A. A., & Ahmad, P. (2021). Influence of salinity stress on PSII in barley (Hordeum vulgare L.) genotypes, probed by chlorophyll-a fluorescence. *Journal of King Saud University-Science*, *33*(1), 101239.

[41] Ben Abdallah, M., Methenni, K., Taamalli, W., Hessini, K., & Ben Youssef, N. (2022). Cross-priming approach induced beneficial metabolic adjustments and repair processes during subsequent drought in olive. *Water*, *14*(24), 4050.

[42] Ding, Y., Wang, X. T., Wang, F., Shao, Y. L., Zhang, A. M., & Chang, W. (2023). The effects of chilling stress on antioxidant enzymes activities and proline, malondialdehyde, soluble sugar contents in three Paphiopedilum species. *Russian Journal of Plant Physiology*, *70*(4), 61.

[43] Doğru, A. (2021). Effects of heat stress on photosystem II activity and antioxidant enzymes in two maize cultivars. *Planta*, *253*(4), 85.

[44] Hnilickova, H., Kraus, K., Vachova, P., & Hnilicka, F. (2021). Salinity stress affects photosynthesis, malondialdehyde formation, and proline content in Portulaca oleracea L. *Plants*, *10*(5), 845.

[45] Zulfiqar, F., & Ashraf, M. (2023). Proline alleviates abiotic stress induced oxidative stress in plants. *Journal of Plant Growth Regulation*, *42*(8), 4629-4651.

[46] Huang, B., Chen, Y. E., Zhao, Y. Q., Ding, C. B., Liao, J. Q., Hu, C., ... & Yuan, M. (2019). Exogenous melatonin alleviates oxidative damages and protects photosystem II in maize seedlings under drought stress. *Frontiers in plant science*, *10*, 677.

[47] Irshad, K., Shaheed Siddiqui, Z., Chen, J., Rao, Y., Hamna Ansari, H., Wajid, D., ... & Wei, X. (2023). Bio-priming with salt tolerant endophytes improved crop tolerance to salt stress via modulating photosystem II and antioxidant activities in a sub-optimal environment. *Frontiers in Plant Science*, *14*, 1082480.

[48] Elkelish, A., Alqudah, A. M., Alhudhaibi, A. M., Alqahtani, H., Börner, A., & Thabet, S. G. (2025). Inherited endurance: deciphering genetic associations of transgenerational and intergenerational heat stress memory in barley. *Plant molecular biology*, *115*(2), 42.