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ARAŞTIRMA MAKALESİ **RESEARCH PAPER**

Improvement of the Antioxidant Mechanism by Exogenous H_2O_2 in Two genotypes of Eggplant (*Solanum melongena* L.) Under Salt Stress [*]

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Abstract: Salinity is an increasing environmental problem that directly affects crop production. Foliar application of H_2O_2 stimulates the abiotic stress tolerance of plants is an important process. As an effective signaling molecule, H_2O_2 can reduce the deleterious effects of salt stress in plants. Application of exogenous H_2O_2 and H_2O_2 synthase inhibitor (DPI) to the eggplant genotypes Mardin (salt-tolerant) and Artvin (salt-sensitive) showed differential tolerance to salinity. We investigated the possible involvement of MDA and H_2O_2 content and activities of Catalase and Superoxide dismutase in these eggplant genotypes by foliar applications to seedlings of H_2O_2 and DPI 48 hours before exposure to moderate salinity. Salt application increased the amount of MDA in both genotypes, this increase was more pronounced in the salt-sensitive Artvin genotype. Externally applied H_2O_2 increased the MDA amount more in Artvin genotype. The application of H_2O_2 synthesis inhibitor DPI caused a significant increase in the amount of MDA. Salt application increased CAT enzyme activity in both genotypes. It has been observed that H_2O_2 applied by foliar spraying also increased CAT enzyme activity. Salt application caused an increase in SOD activity in both genotypes. This increase is more evident in the Mardin genotype. In both genotypes, SOD activity decreased in Artvin genotype and increased in Mardin genotype in H_2O_2 applied group. This study shows that the salt-tolerant Mardin genotype is more affected by exogenously applied H_2O_2 and DPI than the salt-sensitive Artvin genotype.

Keywords: Diphenyleneiodonium, eggplant, foliar application, hydrogen peroxide, NaCl salinity.

Dıştan Uygulanan H_2O_2'in Tuz Stresi Altındaki iki Patlıcan Genotipinde (*Solanum melongena* L.) Antioksidan Mekanizmasını İyileştirmesi

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Öz: Tuzluluk, bitkisel üretimi doğrudan etkileyen bir çevre sorunudur. H_2O_2'nin yapraktan uygulanması, bitkilerin abiyotik stres toleransını uyaran önemli bir süreçtir. Etkili bir sinyal molekülü olarak H_2O_2, bitkilerde tuz stresinin zararlı etkilerini azaltabilir. Bu çalışmada, Mardin (tuza dayanıklı) ve Artvin (tuza duyarlı) patlıcan genotiplerine dıştan uygulanan H_2O_2 ve H_2O_2 sentaz inhibitörü (DPI) uygulamasının olası etkileri araştırılmıştır. Patlıcan fidelerinin yapraklarına 48 saat boyunca H_2O_2 ve DPI uygulamalarının orta derecede tuzluluğa maruz kalan bu patlıcan genotiplerinde MDA ve H_2O_2 içeriği ile Katalaz ve Süperoksit dismutaz aktivitelerinin olası katılımı araştırılmıştır. Tuz uygulaması, her iki genotipte de MDA miktarını artırmıştır, bu artış tuza duyarlı Artvin genotipinde daha belirgin olmuştur. Dışarıdan uygulanan H_2O_2, Artvin genotipinde MDA miktarını daha fazla artırmıştır. H_2O_2 sentez inhibitörü DPI uygulaması ise, MDA miktarında önemli bir artışa neden olmuştur. Tuz uygulaması, her iki genotipte de CAT enzim aktivitesini artırmıştır. Yapraktan püskürtme yoluyla uygulanan H_2O_2' nin de CAT enzim aktivitesini arttırdığı görülmüştür. Tuz uygulaması, iki genotipte de SOD aktivitesinde artışa neden olmuştur. Bu artış Mardin genotipinde daha belirgindir. Her iki genotipte de H_2O_2 uygulanan grupta SOD aktivitesi Artvin genotipinde azalırken Mardin genotipinde artmıştır. Bu çalışma, tuza dayanıklı Mardin genotipinin, tuza duyarlı Artvin genotipine göre dıştan uygulanan H_2O_2 ve DPI' dan daha fazla etkilendiğini göstermektedir.

Anahtar kelimeler: Difenileniyodonyum, hidrojen peroksit, NaCl tuzluluğu, patlıcan, yapraktan uygulama.

[*] *This article is derived from Corresponding Author's PhD thesis.*

INTRODUCTION

Salinity is one of the most important environmental constraints affecting crop productivity and threatening food security around the world (Mbarki et al., 2020). Soils affected by soluble salts account for 30% of the irrigated area and 6% of the total world area (Parihar et al., 2015). Soil salinization threatens crop production, but many crops are not salt-tolerant (Bhatnagar-Mathur et al., 2008).

Salt stress stimulates osmotic, ionic, and oxidative stresses that prevent normal cell growth and division (Munns & Tester, 2008; Flowers & Colmer, 2008). Oxidative stress significantly increases the level of Reactive Oxygen Species (ROS) in the cell (Tanou et al., 2009b; Ahmad & Umar, 2011). All these effects can lead to plant death by causing metabolic disorders, including nutrient imbalance, enzymatic inhibition, membrane damage, and inhibit photosynthesis (Mahajan & Tuteja, 2005; Hasanuzzaman & Fujita, 2012). Eggplant, one of the most important crops in Turkey, belonging to the Solanaceae family, is moderately sensitive to saline conditions. The Mediterranean basin, including Turkey, is the second center of diversification of this species. For this reason, there is great genetic variability in eggplant in Turkey (Yaşar, 2013).

Solving soil salinity problems is a very expensive and time-consuming task. For this reason, it would be beneficial to improve the salt tolerance of crop plants to increase the yield. For this purpose, it is important to determine the dosage and form of exogenous administration of stress-relieving or stress-reducing substances. In this regard, osmoprotectants, plant hormones, and antioxidants applied externally to the plant can increase plant productivity. Several studies have shown that one of the most important signaling molecules, hydrogen peroxide, can effectively increase yield by reducing salt damage in plants (de Azevedo Neto et al., 2005; Fedina et al., 2009; Gao et al., 2010; Gondim et al., 2012; Güler & Pehlivan, 2016).

H_2O_2, which is involved in several biochemical and physiological processes, is an important messenger molecule in plants under stress. However, not all mechanisms have been thoroughly investigated (Zhang et al., 2007; Sathiyaraj et al., 2014). H_2O_2 is a dual-acting signaling molecule with a dose-dependent function in plant metabolism. Through Fenton reactions, H_2O_2 is converted to the hydroxyl radical, which then exerts a variety of toxic effects in different compartments of the cell. In the cell, this reaction causes lipid peroxidation, protein degradation/alteration, and DNA damage (Fridovich, 1986). Different species of ROS, especially H_2O_2, are important signaling molecules that are produced and controlled in plant cells. H_2O_2 is a dual molecule that acts as a signal molecule at low concentrations and damages the plant at high concentrations (Gechev et al., 2002; Quan et al., 2008). Experiments at low H_2O_2 concentrations where plants are exposed to abiotic stress show that H_2O_2 positively affects plant growth and development.

The aim of the present study was to determine the effects of foliar application of H_2O_2 or the H_2O_2 synthase inhibitor *Diphenyleneiodonium* (DPI) on malondialdehyde (MDA) and H_2O_2 levels and antioxidant responses in salt-tolerant and –sensitive eggplant seedlings when exposed to moderate salinity.

MATERIAL AND METHOD

Plant Material and Growth Conditions: In this study, two eggplant genotypes named Artvin (salt-resistant) and Mardin (salt-tolerant) (Yaşar, 2003) which were previously known to be salt-tolerant were used as plant material. Seeds of the two eggplant genotypes (*Solanum melongena* L.) were surface sterilized in 1% (v/v) NaOCl and rinsed with distilled water. Then, the sterilized seeds were germinated in the Petri dishes with filter paper and irrigated with water only for 2 days in the dark. Then the seeds were planted in pots with 2:1 peat/perlite (Table 1).

Table 1. The composition of the peat used in the experiment.

Composition	Chemical properties
Black peat (%) 30	Cu (mg kg^{-1}) 16.7
White peat (%)70	Total N (mg/L) 210
pH 6.0	P_2O_5 (mg/L) 240
Salt (dS m^{-1}) 0.4	K_2O (mg/L) 270
Field capacity (%) 80.0	S (mg/L) 150
Wilting point (%) 15.0	

Irrigation was continued using ½ strength of Hoagland's nutrient solution (Hoagland & Arnon, 1938) until full development of the fourth true leaf. All studies, including germination and growth stages, were conducted under controlled conditions in the "Digi-Tech Growth Chamber PG34-3" climate chamber. The temperature was 25 ºC and the relative humidity was 60-70%.

Treatment Groups: Eggplant seedlings were sprayed with H_2O_2 and DPI every 6 hours for 48 hours. After the completion of chemical applications, salt treatment was started by adding 100 mM NaCl to the irrigation solution. In this experiment, we formed six treatment groups. (1) Control (irrigated with Hoagland only), (2) NaCl (irrigated with 100Mm NaCl for 10 days), (3) 0.5 mM H_2O_2 (sprayed with H_2O_2), (4) 0.5 mM H_2O_2+NaCl (sprayed with H_2O_2 and then exposed to the salinity of 100Mm NaCl), (5) 0.2 mM DPI (sprayed with DPI), (6) 0.2 mM DPI+NaCl (sprayed with DPI and then exposed to the salinity of 100Mm NaCl). The pre-treatments were applied according to Zhang et al. (2007).

Plant Analysis: In this study, the amount of malondialdehyde (MDA) (Lutts et al., 1996) internal

amount of H_2O_2 (Velikova et al., 2000), and antioxidant enzyme activities superoxide dismutase (SOD) and Catalase (CAT) were investigated in eggplant seedlings of the Artvin and Mardin genotypes (Giannopolitis & Ries, 1977; Cakmak & Marschner, 1992).

The amount of MDA and H_2O_2 was analyzed in fresh leaves.

Superoxide dismutase (SOD) activity (EC 1.15.1.1) was measured by reducing NBT (nitroblue tetrazolium chloride) with O_2^- under the light as described by Giannopolitis and Ries (1977).

Catalase (CAT) activity (EC 1. 11.1.6) was determined from the H_2O_2 fragmentation rate at 240 nm (E = 39.4 mM cm^{-1}) as described by Cakmak and Marschner (1992).

Statistical Analyzes: The experiment was a completely randomized design with three repetitions. All data obtained were analyzed using the GraphPad Prism 8.0 program. Data from the two genotypes were analyzed separately, and the significance of changes within each genotype was examined using analysis of variance (two-way ANOVA). Control for the significance of differences between applications was assessed by Tukey's multiple comparison test ($P < 0.05$). The means of all replicates were evaluated with the t-test so that the difference between the means of the varieties was checked.

RESULTS

Changes of Lipid Peroxidation (Malondialdehyde= MDA) Inner H_2O_2 Content in Response to Pretreatments: The difference between genotypes (t = 9.029) in response to the application in the amount of MDA content was found to be significant at the $p < 0.05$ level (Figure 1a, 1b). Salt stress-induced lipid peroxidation in plant cells, so the amount of MDA increased in both genotypes compared to the control group. This increase corresponds to 83.1% in the salt-sensitive Artvin genotype and 62% in the salt-tolerant Mardin genotype.

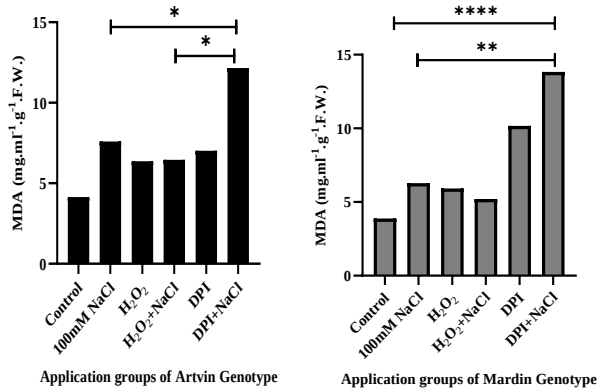

Figure 1. Effects of pretreatments with NaCl, H_2O_2, and DPI on MDA content in (a) Artvin genotype and (b) Mardin genotype.

The increase in MDA content when 100 mM NaCl was applied was reduced by 15% in the Artvin genotype and 6% in the Mardin genotype by H_2O_2 pretreatment. There is no significant difference between H_2O_2 and H_2O_2+NaCl application in the two genotypes. DPI application resulted in an increase in the amount of MDA in both genotypes compared with the control group. These changes in the form of decrease and increase were more evident in the salt-tolerant Mardin genotype compared with the Artvin genotype. The MDA concentration reached the highest value in all application groups when DPI+salt was applied (Figure 1a, 1b).

The internal H_2O_2 content increased in both genotypes in the 100 mM NaCl treatment group compared to the control group. Upon H_2O_2 application, the amount of H_2O_2 decreased by 46.4% in the Artvin genotype and 27.1% in the Mardin genotype compared to the salt-only treatment group (Figure 2a, 2b).

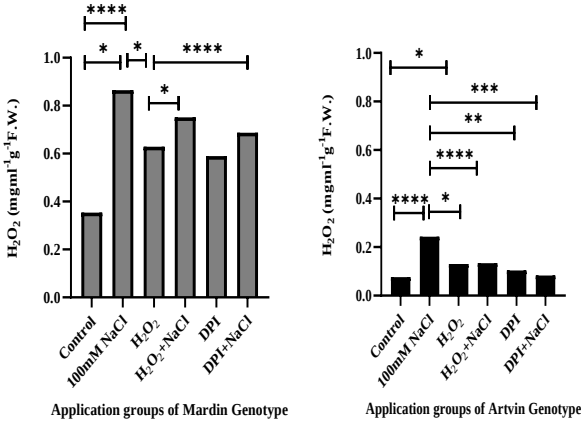

Figure 2. Effects of NaCl, H_2O_2, and DPI pretreatments on H_2O_2 amount in (a) Artvin genotype and (b) Mardin genotype.

DPI application increased the amount of H_2O_2 in both genotypes compared with the control group. In the Mardin genotype, DPI+salt application group, the internal H_2O_2 content increased compared to the DPI-only treated group, and there was no change in the Artvin genotype.

Changes in Enzyme Activities in Response to Pretreatments: The present study showed that salt stress stimulated the antioxidant enzyme activities (SOD and CAT) in both eggplant genotypes. The present study shows that salt-induced stress stimulates the activity of antioxidant enzymes (SOD and CAT) in both eggplant genotypes.

Salt stress caused a significant increase in CAT enzyme activity compared to the control ($p < 0.05$). The CAT activity upon H_2O_2 application increased in both genotypes compared to control and salt-treated groups.

In the group combining exogenous H_2O_2 with 100 mM salt treatment, CAT activity decreased in the Artvin genotype compared to H_2O_2 (Figure 3a, 3b). 100 mM NaCl

stress caused an increase in CAT activity in both genotypes; this increase was 78.6% in the Artvin genotype and 19.8% in the Mardin genotype. CAT activity in H_2O_2 - treated plants increased in both genotypes compared to the control group. Comparing the application of 100 mM NaCl and H_2O_2 +100 mM NaCl, CAT activity decreased in the Artvin genotype (19.82%) and increased in Mardin genotype (55.4%). Compared to the group treated with 100 mM salt, DPI application caused a decrease of 52.6% in the Artvin genotype and 40.72% in the Mardin genotype.

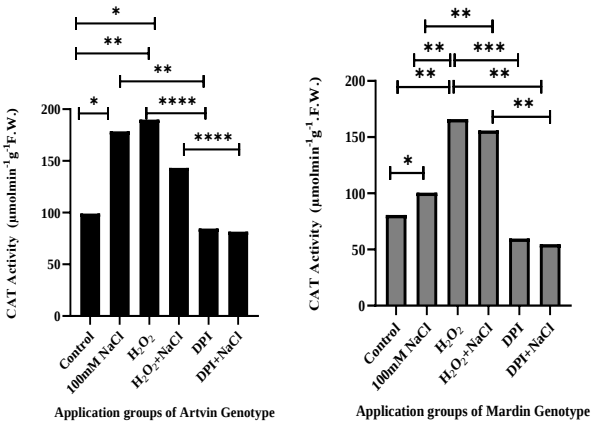

Figure 3. Effects of NaCl, H_2O_2, and DPI pretreatments on CAT activity in (a) Artvin genotype and (b) Mardin genotype.

When the results on SOD activity were examined, it was found that externally applied H_2O_2 and DPI did not significantly alter SOD activity in the Artvin genotype. For the Mardin genotype, the changes in MDA levels were significant ($p < 0.005$). The application of 100mM NaCl increased the SOD activity of the Mardin genotype (16.1%) and the application of H_2O_2 caused an increase of 28.3% compared to the control group, the application of DPI decreased the SOD activity by 26.4% compared to the control group. Compared to the application of 100mM NaCl, the application of DPI+salt caused a 44.8% decrease in SOD activity (Figure 4a, 4b).

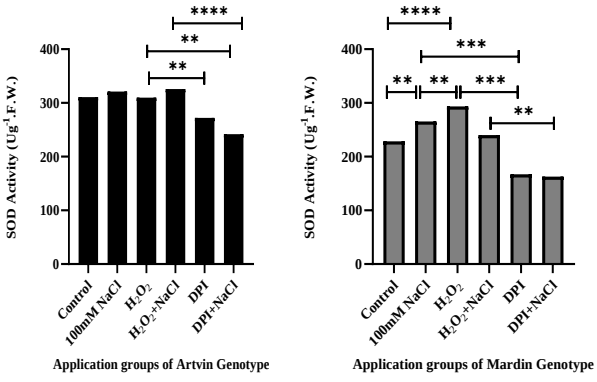

Figure 4. Effects of NaCl, H_2O_2, and DPI pretreatments on the activity of SOD in (a) Artvin genotype and (b) Mardin genotype.

DISCUSSION

Salinity inhibits plant growth and development by interfering with photosynthesis, protein synthesis, and energy metabolism. Therefore, soil salinity limits production efficiency (Parida et al., 2004). Salt stress causes osmotic stress, ion toxicity, nutritional disorders, oxidative stress, alterations in metabolic processes, membrane disorders, reduction in cell division, and genotoxicity (Zhu, 2004; Munns et al., 2006). Plants generally overcome salt stress in two ways: the ability to resist salt stress or enhance this ability and adapt to stressful conditions.

Malondialdehyde (MDA) is one of the cells' final products of polyunsaturated fatty acids peroxidation. An increase in free radicals causes the overproduction of MDA. Malondialdehyde level is commonly known as a marker of oxidative stress and the antioxidant status in stressed plants. Lipid peroxidation reflects membrane damage induced by salt stress (Zhao et al., 2006).

Salt and osmotic stress from salinity inhibit the plant photosystem, resulting in excessive production of ROS (Hasanuzzaman et al., 2017). It is known that the increased amount of ROS in the cell increases the amount of MDA (Malondialdehyde) by causing lipid peroxidation (Mishra & Choudhuri, 1999). In our study, salt application caused an increase in the amount of MDA in both eggplant genotypes compared to the control group (Figure 1). It was again found that in the salt-sensitive Artvin genotype, the membrane lipids were more damaged by the negative effect of salt and the amount of MDA was higher. While the amount of MDA in plants treated with H_2O_2 alone increased in both genotypes compared to the control group, it was observed that the amount of MDA was lower compared to salt application alone. The beneficial effect of H_2O_2 in reducing the negative effects of salt stress was observed more clearly in the Artvin genotype. Although H_2O_2 also had a protective effect in the salt-tolerant Mardin genotype. In the groups in which H_2O_2 synthesis was inhibited only by the application of DPI (H_2O_2 synthesis inhibitor), the increase in the amount of MDA together with salt stress was quite high compared with the group in which only salt was applied. This confirms the protective role of H_2O_2 in the cell. S In two genotypes, MDA concentration reached the highest value with the DPI+salt applied group. Both H_2O_2 synthesis inhibitor and salt stress applications create "combined stress" in the plant, which causes serious increases in the amount of MDA. Similar to our results, externally applied H_2O_2 in mung bean (Saleh, 2007), wheat (Li et al., 2008), *Panax ginseng* (Sathiyaraj et al., 2017) barley (Kim et al., 2005), and maize (Chen & Li, 2002) was reported to prevent the increase in MDA amount by reducing electrolyte leakage, which increases during stress. In cucumber (Hasanuzzaman et al., 2017)

soybean (Güler & Pehlivan, 2016), and canola (Gao et al., 2010) the application of H_2O_2 did not change the amount of MDA.

H_2O_2 is a signaling molecule that triggers numerous defense responses in plants that enhanced resistance to various abiotic and biotic stress factors. Various environmental stresses, such as soil salinity, lead to a temporary increase in the amount of H_2O_2 in plant cells. In addition to ionic and osmotic stress, salt stress causes the accumulation of ROS, which lead to oxidative damage to macromolecules, resulting in delayed growth and even plant death. H_2O_2, which belongs to ROS, is a compound that increases in the cell during stress, and it has become a key modulator of stress signal transduction pathways in recent years. Salt stress is known to increase internal H_2O_2 levels in plants (Yaşar, 2003). In our study, the internal H_2O_2 amount was significantly increased in the only salt group treated with 100 mM NaCl compared with the control group in both genotypes (Figure 2). This shows us that plants get oxidative stress. In the group treated with H_2O_2 only, it was found that the internal H_2O_2 amount decreased significantly in both genotypes. In the groups treated with the H_2O_2 synthesis inhibitor DPI together with salt, the internal H_2O_2 amount decreased in both genotypes compared with the Salt application group; however, this decrease was more significant in the Artvin genotype. Similar to our results, Fedina et al. (2010) emphasized that the internal H_2O_2 amount decreased in *Hordeum vulgare* seedlings exposed to 150 mM NaCl for 7 days after H_2O_2 pre-application compared with the group in which only salt was applied.

Several studies have reported that the activity of CAT either increases (Furtana Baysal et al., 2010) does not change (Nohar et al., 2015), or decreases (Hasanuzzaman & Fujita, 2012) in plants grown under salt stress conditions. In our study, it was found that the activity of CAT increased in plants treated with H_2O_2 alone compared to the group treated with salt alone. This increase was higher and more significant in the Mardin genotype. Similar to our study, it was reported by de Azevedo Neto et al. (de Azavedo Neto et al., 2005) and Gechev et al. (2002) that H_2O_2 applied via the leaf increased CAT activity in maize and tobacco. In another study, it was reported that the increase in CAT enzyme activity in maize plants treated with H_2O_2 occurs through a complex mechanism that includes CAT gene regulation (Guler and Pehlivan, 2016). In addition, CAT was reported by Mhamdi et al. (2010) to have a higher affinity for H_2O_2 in contrast to other enzymes that intercept H_2O_2. In addition, researchers reported that CAT transcripts increased in H_2O_2 -treated plants (Mhamdi et al., 2010; Ashraf, 2009). In plants treated with the H_2O_2 synthesis inhibitor DPI, the activity of CAT significantly decreased in both genotypes compared to the salt-only treated group, while it increased in the DPI and salt-treated groups (Figure 3).

The increase in cellular ROS levels caused by salinity can negatively affect plant growth and development and lead to plant death. Highly reactive ROS cause significant damage to lipids, proteins, DNA, and some other metabolites (Ashraf, 2009). Elimination of salinity-induced oxidative damage is achieved by promoting the synthesis of antioxidant enzymes (CAT, SOD, APX, GR) (Neill et al., 2002). In our study, salt stress significantly increased the activities of SOD and CAT in both genotypes. The SOD enzyme is an efficient antioxidant enzyme whose main activity is the conversion of O_2^- reagent to H_2O_2 and O_2 (Fridovich, 1986). In our study, the SOD enzyme activity in plants treated with 100 mM NaCl showed no significant increase in the salt-sensitive Artvin genotype, while it increased significantly in the tolerant Mardin genotype. In plants treated with H_2O_2, the activity of SOD increased in both genotypes compared to the control and salt-only treated groups. When the group treated with H_2O_2 and salt was compared with the group treated with H_2O_2 only, it was observed that the activity of SOD increased in the Artvin genotype but decreased in the Mardin genotype, but these increases and decreases were not significant (Figure 4). In the plants treated with the H_2O_2 synthesis inhibitor DPI, the activity of SOD significantly decreased in both genotypes compared to the salt-only treated group, while the activity of SOD significantly increased in the genotype Artvin and not significantly in the genotype Mardin in the DPI+salt treated group. As for the activity of CAT and SOD, the effects of the pretreatments are more evident in the salt-tolerant Mardin genotype.

CONCLUSION

H_2O_2 is a dual and important signaling molecule in plant cells.

In our research, the role of H_2O_2, which is present in the cell and acts as a secondary messenger, in signal transduction and their relationship with each other has also been demonstrated by the use of inhibitors under salt stress conditions. The results of our study show that H_2O_2 pretreatment reduced the salt stress-induced increase in internal MDA and H_2O_2 levels in both genotypes. This decrease was found to be significant only in the salt-tolerant Mardin genotype. Regarding the activity of CAT and SOD, the effects of the pretreatments were more pronounced in the salt-tolerant Mardin genotype.

CONFLICTS OF INTEREST

No conflict of interest was declared by the authors.

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