Journal of Elementology ISSN 1644-2296

Altuntaş, Ö., Dasgan, H., Akhoundnejad, Y., Kusvuran, S. and Yanardağ, I. (2025)
'Effects of mycorrhiza and silicon on the alleviation of salt damage
in salt-sensitive and salt-tolerant pepper genotypes',
Journal of Elementology, 30(2), 255-269,
available: https://doi.org/10.5601/jelem.2025.30.1.3473

RECEIVED: 4 January 2025
ACCEPTED: 22 May 2025

ORIGINAL PAPER

Effects of mycorrhiza and silicon on the alleviation of salt damage in salt-sensitive and salt-tolerant pepper genotypes

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Abstract

Salinity is a detrimental abiotic stress that occurs in arid and semi-arid environmental conditions. Salinity adversely affects the growth, yield, and quality of plants. Some plants are sensitive to salt stress, while others are more resistant owing to the tolerance mechanisms induced by physiological, biochemical, and molecular responses. The present study was conducted to investigate the effects of mycorrhizal colonization (*Glomus clarum*) and silicon (Si) under different salinity levels on the activity of antioxidant enzymes, such as super oxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione oxidase (GPX) and lipid peroxidation (MDA), of salinity sensitive (cv. Demre) and tolerant (cv. Karaisali) pepper cultivars. Three diffe-rent salt doses (0 mM NaCl, 75 mM NaCl, 150 mM NaCl), with AM and 2 mM K_2SiO_3, were applied into 4-L vermiculite-containing pots with pepper plants. The antioxidant enzyme activities increased following the increasing salt doses. All antioxidant enzymes were observed to display differences in their activity in the two pepper genotypes that differed in salt sensitivity. Catalase, ascorbate peroxidase, and glutathione reductase activities were higher in the salt-sensitive pepper genotype. Si and mycorrhiza treatment improved the defense mechanisms in peppers, and attenuated the oxidative damage in cellular functional molecules caused by the overproduction of reactive oxygen species (ROS) under salt stress. Therefore, mycorrhiza and silicon applications, resulting in increased salt tolerance, can be used in areas with salinity problems.

Keywords: *Capsicum annuum,* silicon, mycorrhiza, salinity stress, antioxidative enzymes, abiotic stress

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* No funding source.

INTRODUCTION

Salinity is a major abiotic stress that negatively impacts crop productivity and quality (Hirt and Shinozaki 2003). It is projected that salinization will lead to a loss of 30% of cultivable land within the next 25 years and up to 50% within 40 years (Ruiz-Lozano et al. 2012). Salt stress symptoms vary by plant species and manifest as numerous morphological, physiological, molecular, and cellular disturbances. These include reduced photosynthesis, ion toxicity, oxidative stress, and nutrient imbalances (Manivannan et al. 2016, Hegazi, El-Shraiy 2017).

In response to abiotic stress, plants adopt various strategies to maintain growth and productivity. These adaptations involve changes in morphology (growth plasticity), as well as physiological and biochemical modifications (Fahad et al. 2015). Salt stress in particular induces excessive accumulation of reactive oxygen species (ROS), such as superoxide radicals (O_2^-), hydroxyl radicals ($\cdot$OH), singlet oxygen ($^1O_2$), and hydrogen peroxide (H_2O_2), which collectively cause oxidative damage to cells (Khoshgoftarmanesh et al. 2014). To counteract this, plants rely on antioxidant defense systems comprising both non-enzymatic antioxidants (e.g., ascorbic acid, glutathione, carotenoids) and enzymatic antioxidants e.g., superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR) – Fahad et al. (2015), Hegazi, El-Shraiy (2017).

Hydrogen peroxide (H_2O_2), a particularly harmful ROS, is detoxified by catalase (CAT) and peroxidases into water and oxygen (Zhu et al. 2004). APX, GPX, and CAT enzymes each scavenge H_2O_2 through distinct mechanisms, with APX utilizing the ascorbate-glutathione cycle – a regeneration system involving ascorbate and glutathione (Sofo et al. 2015). In this cycle, oxidized ascorbate is reduced by glutathione (GSH), which in turn is regenerated from its oxidized form (GSSG) by GR using NADPH (Yasar et al. 2006, Kusvuran et al. 2007). Plants with high levels of these antioxidants, whether constitutive or stress-induced, demonstrate greater resistance to oxidative damage (Turkan et al. 2005, Kusvuran et al. 2013).

Silicon (Si), although not classified as an essential nutrient, is widely recognized for its beneficial effects in enhancing plant resilience to environmental stressors (Coskun et al. 2016). Si contributes to stress mitigation through structural support and by triggering metabolic responses that include enhanced antioxidant activity (Luyckx et al. 2017). Under salt stress, Si application has been shown to improve plant growth and reduce ROS levels by increasing CAT and APX enzyme activities, thus reducing oxidative damage and malondialdehyde (MDA) levels (Manivannan et al. 2016, Kim et al. 2017).

Arbuscular mycorrhizal (AM) fungi, such as *Glomus clarum*, naturally occur in most soils and colonize the roots of numerous plant species. These symbiotic fungi promote plant growth and productivity by enhancing the uptake of essential nutrients, particularly phosphorus, and by modulating plant hormonal responses (Jansa et al. 2019, Diagne et al. 2020, Song et al. 2020). AM fungi also contribute to improved photosynthesis, osmotic balance, and resistance to environmental stressors. Mycorrhizal inoculation can further reduce the need for fertilizers by increasing nutrient use efficiency (Xie et al. 2022). This study aims to investigate the effects of mycorrhizal inoculation with *Glomus clarum* and silicon application on mitigating salt stress and to explore their relationship with antioxidant enzyme activity in salt-sensitive and salt-tolerant pepper (*Capsicum* spp.) genotypes.

MATERIALS AND METHOD

Experimental design

Two different local pepper genotypes, of which the salt sensitivity had been determined in previous studies (Altuntas et al. 2016), were used in this study. The Karaisali genotype was salt stress-tolerant, while Demre was a salt stress-sensitive genotype (Figure 1). Mycorrhizal inoculum of *Glomus clarum* was obtained from Cukurova University, Agriculture Faculty, and silicon (K_2SiO_3) fertilizer was purchased from Merck company (Sigma-Aldrich, 792640). The study was carried out in climate chambers adjusted to 16 h light at 24°C and 8 h dark at 20°C. The relative humidity was about 60-65% and the photosynthetic photon flux density was about 300 μmol m^{-2} s^{-1} at plant height. The pepper seeds were sown to a 1/2 peat + 1/2 perlite mixture using vials. Three seedlings at 45 days were planted in 4-L vermiculite-containing pots. The seedlings were irrigated with ½ Morgan and Lennard (2000) nutrition solutions. The layout of the experiment was a randomized block design with three replicates and three plants in each repetition. Silicon (K_2SiO_3) and salt (NaCl) were only added in the silicon and salt treatments (NaCl) – Figure 2.

Fig. 1. Effect of mycorrhiza on the root growth of the varieties Karasali and Demre under salt stress (75 and 150 mM)

Fig. 2. Effect of mycorrhiza on root development under salt stress

Salt, silicon, and mycorrhizal inoculation treatments

Following 15 days of growth in the pots, the seedlings were subjected to salt stress with different NaCl doses (0, 75, 150 mM). The applied amount of water in the study was calculated according to the drained water/applied water ratio, which was approximately 30%. The seedlings were initially irrigated with water containing 50 mM salt to avoid osmotic salt shock, and the salt dose was gradually increased until reaching 150 mM. In addition to the salt, 2 mM K_2SiO_3 was applied. A hundred spores per plant of vermiculite based inoculum of *Glomus clarum* were placed in a pot, before transferring seedlings, to facilitate fungal colonization of plant roots.

Lipid peroxide content

Lipid peroxidation was determined in terms of the malondialdehyde (MDA) content using the thiobarbituric acid (TBA) reaction proposed by Madhava and Sresty (2000). A total of 0.5 g leaf samples was homogenized with TCA (trichloroacetic-11 acid) and centrifuged at 10 000 rpm for 5 min. A mixture of TBA- (2-thiobarbituric acid) and TCA- (trichloroacetic acid) was added to the supernatant. The mixture was kept at 95°C for 30 min and centrifuged at 10000 rpm for 15 min. The enzymatic activity was measured by the absorbance changes between 532 and 600 nm. The MDA content was calculated using the molar extinction coefficient of MDA (155 mM^{-1} cm^{-1}).

Enzyme analyses and preparation for the extraction

About 0.5 g of fresh leaf sample was homogenized with 0.1 mM NaEDTA-containing 50 mM phosphate buffer (pH 7.6) using liquid nitrogen (5 ml). Then, the samples were centrifuged at 15 000 rpm and +4°C for 15 min. The supernatants were used in the enzyme and protein analyses. The catalase enzymatic activity was determined using the degradation of H_2O_2 (E=39.4 mM cm^{-1}) (Cakmak, Marschner 1992). The ascorbic peroxidase activity was measured using the ascorbic oxidation rate

(E=2.8 mM cm^{-1}) method proposed by Nakano and Asada (1981). The glutathione reductase activity was measured using the NADPH oxidation (E=6.2 mM cm^{-1}) method proposed by Foyer and Halliwell (1976).

Statistical analyses

The data were first tested for normality using the Kolmogorov-Smirnov test. When data did not fit normal distribution, non-parametric Kruskal-Wallis tests were performed, and if the assayed data were significant, a multiple comparison *Z*-values test was performed using the DunnTest function in Sigma plot 14.0 software. Mean comparisons were performed with one-way analysis of variance (ANOVA) followed by post-hoc tests, Tukey's honestly significant difference (HSD) tests for all-pair comparisons, and Dunnett's comparisons for the control system, and terms were considered significant at $P<0.05$ by SPSS 26.0 software.

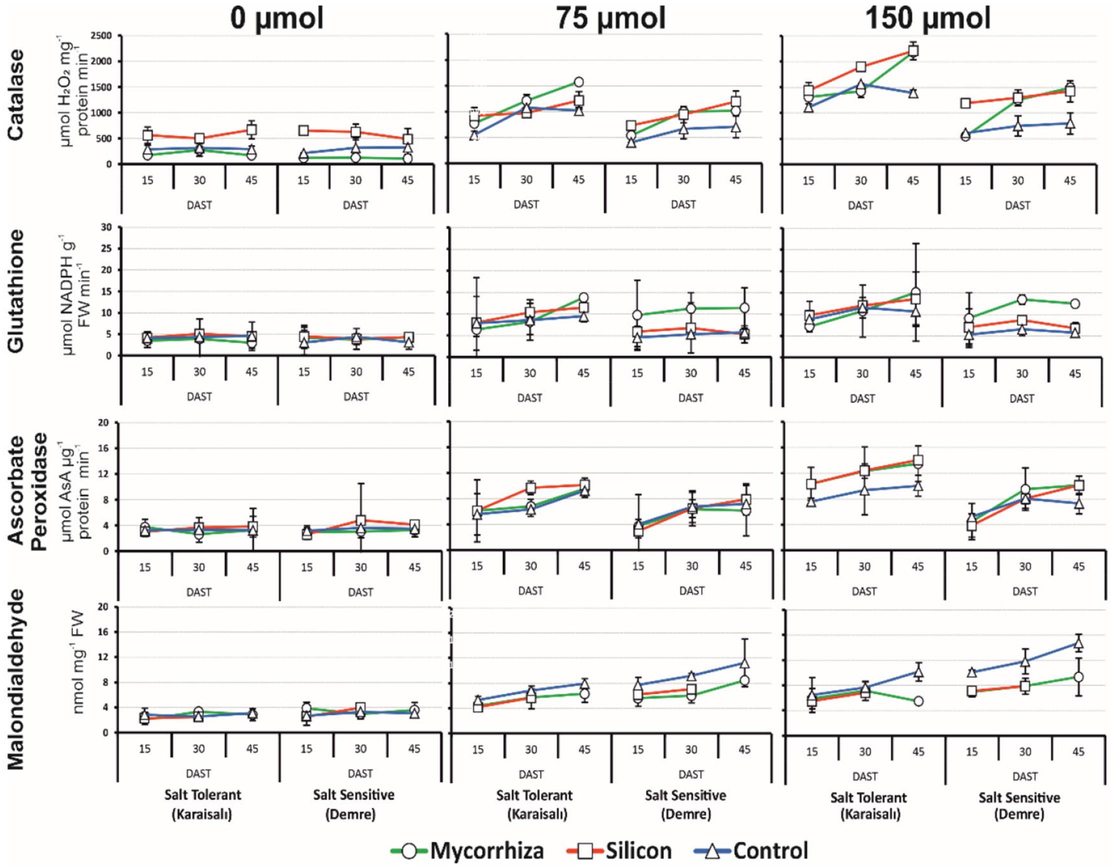
RESULTS AND DİSCUSSİON

The effects of silicon (Si) and arbuscular mycorrhizal fungi (AMF) on salt stress in both salt-sensitive and salt-tolerant pepper genotypes were investigated, with a focus on enzyme activity. The results showed that all treatments significantly increased enzyme activities under both 75 mM and 150 mM NaCl salinity levels. According to enzyme analyses conducted at 15, 30, and 45 days after salt treatment (DAST), the highest catalase (CAT) activity was observed in the salt-tolerant Karaisali cultivar treated with Si and AMF under 150 mM NaCl, reaching 2206.43 and 2178.0 μmol min^{-1} mg^{-1} FW, respectively.

CAT activity increased under 75 mM NaCl and peaked in both Karaisali and Demre cultivars at 150 mM NaCl (Figure 3). Notably, CAT activity in plants treated with Si or AMF was significantly higher than in untreated controls. In the salt-sensitive Demre cultivar under 150 mM NaCl, CAT activity reached 1489.0 μmol min^{-1} mg^{-1} FW with AMF, 1421.3 with Si, and only 800.41 in the control group.

By 45 DAST, both Si and AMF treatments had markedly increased CAT activity compared to the control. These treatments activated CAT at similarly high levels, with a more pronounced effect in the salt-tolerant Karaisali genotype, suggesting an enhanced protective response to salt stress. This aligns with findings by Zhi et al. (2010), who reported significantly higher CAT activity in AM symbiotic tomato plants compared to non-AM plants under both salt stress and control conditions.

Ascorbate peroxidase (APX) activity was affected by the Si and AMF treatments, NaCl doses (75 and 150 mM NaCl), and duration of the stress conditions (30 and 45 DAST). The APX increased with increasing salt stress



Source of Variation	F	P
Plant	33.32	<0.001
Time	14.21	<0.001
Salt dose	115.14	<0.001
Plant x Time	0.35	0.709
Plant x Salt dose	10.79	<0.001
Time x Salt dose	3.04	<0.05
Plant x Time x Salt dose	0.08	0.988

Source of Variation	F	P
Plant	17.49	<0.001
Time	4.41	<0.05
Salt dose	45.57	<0.001
Plant x Time	1.50	0.225
Plant x Salt dose	3.18	<0.05
Time x Salt dose	1.06	0.38
Plant x Time x Salt dose	0.32	0.863

Source of Variation	F	P
Plant	29.96	<0.001
Time	23.87	<0.001
Salt dose	114.73	<0.001
Plant x Time	1.82	0.166
Plant x Salt dose	10.88	<0.001
Time x Salt dose	4.45	<0.01
Plant x Time x Salt dose	0.25	0.912

Source of Variation	F	P
Plant	43,593	<0.001
Time	13,849	<0.001
Salt dose	139,208	<0.001
Plant x Time	0.73	0.483
Plant x Salt dose	7,084	<0.001
Time x Salt dose	2,021	0.094
Plant x Time x Salt dose	0.38	0.824

Fig. 3. Effects of nutrient solutions containing different salt doses on some enzyme activities of the Karasali and Demre pepper cultivars

compared to the control. After 45 days of treatment, the highest APX activity was 14.05 µmol min^{-1} mg^{-1} FW in the Si-treated and 13.49 in the AMF inoculated Karaisali cultivar at 150 mM NaCl treatment. Compared to the control plants, the APX activity was 103.20 and 134.07% higher in the AMF inoculated Karaisali cultivar, and 85.85 and 138.67% higher in the AMF inoculated Demre cultivar at 75 and 150 mM NaCl treatments, respectively.

Plant cells contain an array of protection mechanisms and repair systems, which are controlled by various enzymatic and non-enzymatic antioxidant defense systems. Enzymatic antioxidant defense systems include CAT, APX, POX, SOD, MDHAR, DHAR and GR (Latef, Chaoxing 2011, Sen 2012). Some enzymes regulate the intracellular H_2O_2 content, which is the most important component of catalase and peroxidase enzymes (Mhamdi et al. 2010). Catalase catalyzes the reduction of H_2O_2 to water using either an iron or manganese cofactor, and they can also remove organic H_2O_2 to oxidize toxins, such as phenols, formic acid, and hydroperoxides (Moron, Castilla--Cortázar 2012, Riaz et al. 2018).

Ascorbate is used in the ascorbate-glutathione cycle as a specific electron donor, especially in the chloroplast. Therefore, ascorbate is crucially important as a catalyst in the conversion of H_2O_2 into H_2O and a primary H_2O_2 detoxifying system in plant cells under abiotic stress conditions (Sofo et al. 2015). In this study, APX activity was increased with stress treatment in all the applications. However, this increase was significant in AM-applied plants compared to non-AM plants. Under 75 mmol salt stress, neither Si nor AMF applications had a statistically significant effect on the APX enzyme activity compared to the control group (P>0.05). In contrast, at 150 mmol salt stress, both Si and AMF treatments significantly increased APX activity. These results suggest that the salt-sensitive pepper variety (Demre) exhibits evident salt damage due to its limited capacity to produce APX enzyme under stress conditions. Although both Si and AMF application triggered better performance than the control groups, it was observed to be at a very low level compared to the salt-tolerant variety (Karaisali). Rennenberg (1980) and Manivannan et al. (2016) stated that Si increases the activity of APX in plants, similar to our results. Also, He et al. (2007) indicated that higher APX and POD activity in AM tomato may be associated with the enhanced plant growth and salt tolerance under salt and saltless condition.

Salt stress increased the glutathione reductase (GR) activity in both pepper genotypes. The GR activity in Si-treated plants at 75 and 150 mM NaCl treatments reached 11.48 (an increase of 121.2%) and 13.56 (an increase of 127.0%) µmol min^{-1} mg^{-1} FW in the Karaisali cultivar (tolerant) 30 and 45 DAST, respectively. Also, AMF-treated plants at 75 and 150 mM NaCl treatments reached 13.78 (an increase of 145.5%) and 15.11 (an increase of 145.6%) µmol min^{-1} mg^{-1} FW in the Karaisali cultivar (tolerant) 30 and 45 DAST, respectively. Under the same conditions, the GR activity in the Si-treated plants of the Demre cultivar (sensitive) was 5.27

(a decrease of 92.6%) and 6.76 (an increase of 116.9%) μmol min^{-1} mg^{-1} FW and, it was 11.38 (an increase of 199.8%) and 12.48 (an increase of 216.0%) μmol min^{-1} mg^{-1} FW in AMF inoculated plants.

The glutathione level increases with increasing GR activity in plants, which, then, improves salt tolerance in plants. It was clearly determined that Si and AMF applications under salt stress had a high level of effect on all antioxidant enzymes and there were similarities in both applications. However, it was determined that AMF application on GR enzyme activity was more significant than Si and control, and this salience was much more prominent in the salt sensitive Demre genotype. Zhu et al. (2004) reported that Si applications under salt stress increased the GR enzyme activity in cucumber plant, similar to our study. The activity of APX and GR and the content of AsA and GSH increased due to AMF in salt-affected *C. sativus* (Abd_Allah et al. 2015, Hashem et al. 2015) and *Capsicum annuum* (Cekic et al. 2012).

Silicon (Si) protects plants from oxidative stress under saline conditions by enhancing antioxidant enzyme activity, which helps scavenge reactive oxygen species (ROS). This is considered the primary mechanism by which Si mitigates salt-induced damage (Manivannan et al. 2016). The findings recorded in this study are consistent with those reported for different plant species under different stress conditions (El-Banna, Abdelaal 2018, Wang et al. 2016). Arbuscular mycorrhizal symbiosis may have stimulated productivity by reducing the ROS production under saline conditions, as indicated by an increase in enzyme activities (such as CAT and POX) – Talaat, Shawky (2011). Moreover, the authors showed that since the cell membrane damage was lower in AM symbiosis compared to non-AM plants and SOD, APX and POD activity was contributed to protect plant from salinity injury, the induced SOD, APX and POD activity in AM symbiosis may be an important mechanism to improve salt resistance of AM plants (Munns 2005, Langenfeld-Heyse et al. 2007).

The results of enzyme activity can be attributed to silicon and AMF affecting membrane stability and selective permeability, ultimately increasing electrolyte leakage (El-Banna, Abdelaal, 2018). The salinity stress increases free oxygen radicals, such as hydroxyl radicals (OH), hydrogen peroxide (H_2O_2), singlet oxygen (O_2), alkoxyl radical (RO) and superoxide radical (SOR), in plant cells, thus causing oxidative stress (Sharma et al. 2013). The oxidation due to ROS limits the normal metabolism of cells and destroys the DNA, proteins, lipids, and other macromolecules of cells (Perez-Lopez et al. 2009, Gill, Tuteja 2010, Wang et al. 2012, Ahanger et al. 2020). These free radicals lead to irreversible damage to lipids and proteins. Lipid peroxidation through ROS is an essential mechanism of salt toxicity in higher plants, and destroys the integrity of the cell membranes, and eventually, cell death occurs (Dolatabadian et al. 2008, Kusvuran et al. 2013, Coskun et al. 2016). The application of silicon improves the ROS-scavenging ability of plants by regulating the activity of antioxidant enzymes (Kim et al. 2017).

The MDA accumulation in pepper leaves was determined under different levels of salinity and the results revealed a significant increase in MDA level under salt stress between 30 and 45 days after the stress treatment (DAST). The highest MDA levels (11.81 and 14.23 µmol g^{-1} FW) were recorded in the control treatment with the Demre genotype following the 150 mM NaCl treatments at 30 and 45 DAST, respectively (Figure 3). Similarly, the activity was lower with Si and AM treatment when compared with control in the Karaisalı genotype. The MDA content which is an indicator of stress in plants and an end-product of lipid peroxidation reflects the effects of stress on membranes, which are the primary targets of stress. The increase in the MDA content under abiotic stress conditions showed that the stress triggered lipid peroxidation in the cell membrane through ROS (Moussa, Aziz 2008, Qiu et al. 2014, Qing et al. 2015). Previous studies have shown that MDA levels increased especially in stress-sensitive genotypes. This increase in MDA content was attributed to the formation of ROS. The differences in MDA content between genotypes can be associated with the differences in the ROS scavenging abilities of genotypes, and the ability of genotypes to protect themselves against oxidative stress (Rosales et al. 2012, Li et al. 2013, Mansori et al. 2015). The MDA content in pepper leaves increased with an increase in salt stress, and Si and AMF application reduced MDA accumulation significantly when compared to non-Si plants. Moreover, these determined changes indicated that a decrease in lipid peroxidation content with Si and AMF application compared to control groups was demonstrated in the salt-sensitive genotype (Demre). Similar to the results obtained in this study, Si application significantly decreased the MDA concentration, the end-product of lipid peroxidation in maize (Moussa 2006), and grapevine rootstock (Soylemezoglu et al. 2009). Coskun et al. (2016) suggested that silicon (Si) may contribute to maintaining membrane integrity and reducing permeability under stress conditions. Similarly, Huang et al. (2010) reported that arbuscular mycorrhizal fungi (AMF) inoculation significantly decreased superoxide (O_2^-) and malondialdehyde (MDA) contents in tomato leaves. This indicates that AMF can mitigate the adverse effects of salinity and play a crucial role in supporting tomato growth. Saline conditions increase osmotic pressure, which restricts water uptake and leads to ionic imbalance, as well as oxidative, ionic, and osmotic stresses (Soundararajan et al. 2017).The K ions in the K_2SiO_3 fertilizer applied with the presence of excessive salt (NaCl) in the vermiculite substrate quickly react with sodium, causing the formation of Na_2SiO_3. The formation of Na-silicate prevents salt damage to the plants. Increased photosynthetic activity, K/Na ratio, enzymatic activity, and concentration of the soluble materials in the xylem are the indicators of positive influence of silicon application under salt stress conditions (Matichenkov, Bocharnikova 2001). Although dry weight and chlorophyll content of plants were negatively affected by salt stress, the

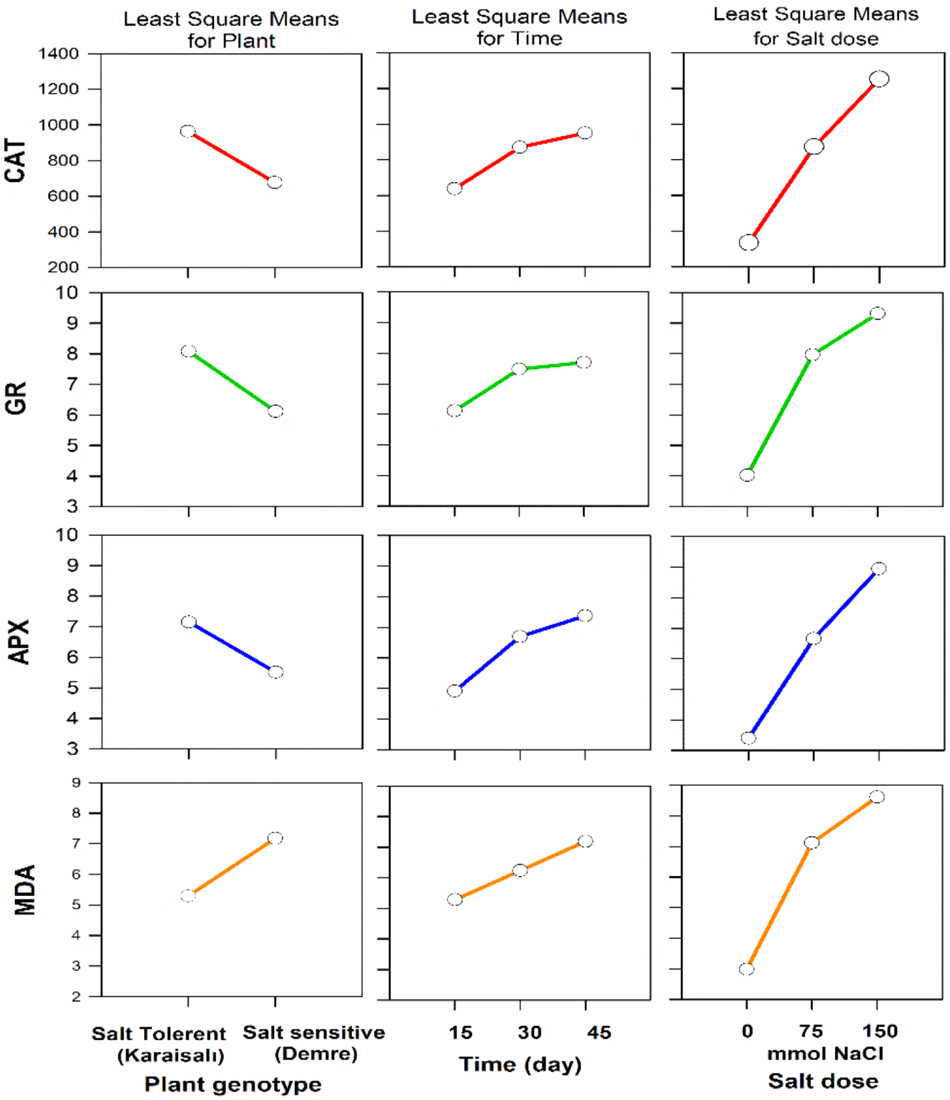


Figure 4. Mean effects of nutrient solutions containing different salt doses on some enzyme activities of the Karasali and Demre pepper cultivars tested with the least mean squares analysis.

application of sodium silicate – Na_2SiO_3 (0.25-0.50 mM Si) to the nutrient solution of wheat plants grown under salt stress (100 mM NaCl) increased proline content and reduced membrane permeability (Tuna et al. 2008).

Following the observations of biochemical analyses, we found that AM colonization and silicon treatments enhanced the plant growth and ability of antioxidant defence enzymes to act under different salt stress levels in pepper. AMF and Si might alleviate the growth limitations imposed by saline conditions. Our results showed that salt stress caused damage in the pepper genotypes. However, this damage was lesser following the AMF and Si applications, where the plants used antioxidative response mechanisms more effectively and had significantly increased levels of enzyme activity.

The study data showed that all salt doses, treatments, time, and pepper genotypes, as well as the interaction of pepper genotype and salt dose were statistically significant in the response of all antioxidant enzymes. As a result of the least square mean analysis on antioxidant enzymes, plant genotype, time and salt doses, it was determined that the antioxidant enzyme production was high in the salt-resistant pepper genotype (Karaisali) and the MDA production was low, while the antioxidant enzyme production was lower in the sensitive genotype (Demre) – Figure 4. This means that the defence mechanism (derived from antioxidant enzymes) is stronger in salt-resistant varieties, and the low production of MDA means that salt stress tolerates the damage to the cell. In terms of sampling time, antioxidant enzyme production increased in order to reduce the effect of salt damage to the cell as time progressed, and MDA production continued to increase as the cell was damaged. When the effects of salt doses on enzyme activities were evaluated, the plant defense mechanism did not occur in the control groups, and the MDA content was very low because there was no antioxidant enzyme production and cell damage. However, with increasing salt doses, it is seen that the plant gets defensive and increases the production of antioxidant enzymes, and similarly, the MDA content increases due to cell damage.

CONCLUSION

Salt stress can seriously damage plant growth, reduce quality and yield; therefore, it is necessary to reduce/mitigate oxidative stress under salt stress conditions in order to maintain crop production in saline soils. Peppers were inoculated with arbuscular mycorrhizal fungi and treated with silicon (Silicon and AMF) to evaluate the effect of salt on enzymatic activity in salt stress sensitive and resistant pepper genotypes. The results showed that the application of silicon and AMF increased the salt tolerance of pepper plants. However, it was determined that antioxidant enzyme production was high in the salt-resistant pepper genotype (Karaisali), MDA production was low due to defence mechanism (derived from antioxidant enzymes). In addition, it was observed that the MDA content was very low in the control groups, since stress condition did not occur and there was no antioxidant enzyme production and cell damage. The positive effects of silicon and AMF on plants consist of its enhanced antioxidant defence capability, which alleviates oxidative damage caused by the overproduction of reactive oxygen species under conditions of salt stress.

Future studies could investigate the effects of different silicon and AMF-containing fertilizers on the enzymatic activities and physiological parameters of other plants under abiotic or biotic stress conditions and evaluate in detail the response of plants to silicon and AMF application.

Author contributions

Ö.A. – conceptualization, H.Y.D. – writing, İ.H.Y. – review & editing, Ş.K. – funding acquisition, Ö.A., Y.A. – methodology, Ö.A., Y.A., H.Y.D., Ş.K., İ.H.Y. – visualization, writing - original draft preparation. All authors have read and agreed to the published version of the manuscript.

Conflicts of interest

The authors have no conflicts of interest to declare

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