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The Ameliorate Effects of Azelaic Acid on Salt Stress Tolerance in *Glycine max* L.

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ABSTRACT

Background: Azelaic acid (AzA) is recognized as an inducer of systemic acquired resistance under biotic stress; however, its role in plant cell wall regulation and reactive oxygen species (ROS) metabolism under abiotic stress remains unclear. This study investigated the physiological, biochemical, enzymatic and molecular responses of soybean plants treated with AzA under salinity stress.

Methods: In this experimental study conducted in 2024 at the Sinop University Plant Physiology Laboratory, 10-day-old soybean (*Glycine max* L.) plants were treated with AzA (12 and 24 ppm) and 250 mM NaCl. After 10 days, physiological parameters including growth, water status, chlorophyll content and electrolyte leakage were evaluated. Biochemical analyses included ROS content, hydroxyl radical scavenging capacity and proline accumulation. Antioxidant enzymes (SOD, CAT, POX, APX, GR, GST, DHAR and MDHAR), cell wall-related enzymes (PAL and PME) and expression levels of XTH3, EXPA2 and WAK4 genes were also analyzed.

Result: AzA treatment alleviated salt-induced oxidative damage in soybean plants. It improved biomass, photosynthetic performance, membrane stability and ROS scavenging capacity under salinity stress. AzA also regulated antioxidant defense systems and enhanced PAL and PME activities associated with cell wall metabolism. Molecular analyses showed significant changes in XTH3, EXPA2 and WAK4 gene expressions in AzA-treated plants under salinity conditions. AzA plays an important role in improving salinity tolerance in soybean by regulating oxidative stress responses, antioxidant defense mechanisms and cell wall-related pathways. These findings provide new insights into the molecular and physiological mechanisms of AzA-mediated stress tolerance in plants.

Key words: Cell wall, Salinity, Soybean, Systemic acquired resistance.

INTRODUCTION

Azelaic acid (AzA) is a saturated C9 dicarboxylic acid involved in systemic acquired resistance (SAR). During pathogen attack, AzA biosynthesis stimulates the release of free fatty acids from membrane lipids, which contribute to AzA production (Yu *et al.*, 2013). Plant cell walls are dynamic structures that can be remodeled during growth and stress conditions (Tenhaken, 2014; Rani and Sharma, 2017). Their architecture plays an essential role in stress perception, signal transduction and tolerance mechanisms.

Soybean (*Glycine max* L.) is one of the most important crops worldwide because of its high oil and protein content (Ren *et al.*, 2018). However, soybean is relatively sensitive to salinity stress, which significantly reduces growth and productivity (Nadeem *et al.*, 2019). Therefore, understanding the physiological and molecular responses of soybean under salinity stress is important for improving stress tolerance.

This study investigated the effects of AzA application on soybean leaves under salinity stress. Physiological parameters, ROS regulation, antioxidant enzyme activities, cell wall-related enzymes and stress-related gene expressions were evaluated to determine the role of AzA in salinity tolerance. Different concentrations of AzA were applied under salt stress conditions and their effects were compared. The results showed that AzA treatment alleviated salt-induced oxidative damage by enhancing ROS scavenging capacity and regulating antioxidant defense mechanisms. In addition, AzA induced cell wall-related enzyme activities and altered the expression of stress-responsive genes associated with cell wall remodeling. These findings suggest that AzA plays an important role in improving salinity tolerance in soybean through physiological, biochemical and molecular regulation mechanisms.

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MATERIALS AND METHODS

Soybean (*Glycine max* L.) ATAEM seeds were obtained from the Black Sea Agricultural Research Institute (Samsun,

Türkiye). Seeds were surface sterilized with 1% hypochloric acid for 10 min, rinsed with distilled water and germinated in darkness for 5 days at 22°C. Germinated seeds were transferred to plastic pots containing a soil:clay:clay-loam mixture (2:1:1, pH 6.5). Seedlings were grown in a controlled growth chamber at 25°C under a 16 h light/8 h dark photoperiod with a light intensity of 350 µmol m^{-2} s^{-1} and irrigated with Hoagland nutrient solution for 10 days (Hoagland and Arnon, 1950).

Azelaic acid (AzA; Sigma Chemical Co.) and salinity concentrations were selected according to preliminary experiments. The experimental design consisted of six groups: Control (C), 12 ppm AzA (A1), 24 ppm AzA (A2), 250 mM NaCl (S), NaCl+12 ppm AzA (S+A1) and NaCl+24 ppm AzA (S+A2). Treatments were applied through the Hoagland solution *via* roots and plants were harvested on the 10th day. AzA was dissolved in 5 mM MES buffer before addition to the nutrient solution. Plants were irrigated daily with 20 mL solution per plant. Experiments were conducted randomly with three biological replicates and harvested samples were stored at -80°C for further analyses.

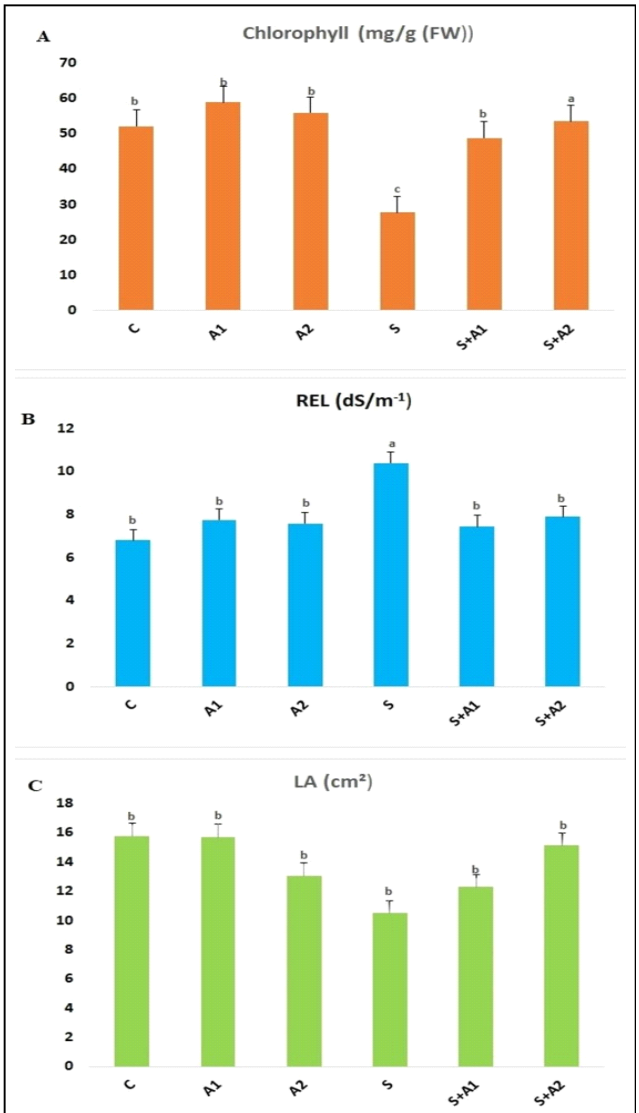
Physiological analyses included relative water content (Smart and Bingham, 1974), chlorophyll content (Lichtenthaler and Buschmann, 1987), relative electrolyte leakage (Singh *et al.*, 2008) and leaf area measurements using a CI-201 portable leaf area meter. Oxidative stress and antioxidant responses were evaluated through measurements of superoxide radical (Ke and Sun, 2004), hydroxyl radical scavenging activity (Kim *et al.*, 1997), malondialdehyde (MDA; Madhava Rao and Stresty 2000), hydrogen peroxide (H_2O_2; Velikova *et al.*, 2000) and proline (Claussen, 2005) content according to previously described methods.

Antioxidant enzyme activities including superoxide dismutase (SOD; Fridovich 1971), catalase (CAT; Bergmeyer 1970), ascorbate peroxidase (APX; Nakano and Asada, 1981), glutathione reductase (GR; Foyer and Halliwell, 1976), glutathione-S-transferase (GST; Habig *et al.*, 1974), peroxidase (POX) (Herzog and Fahimi, 1973)., dehydroascorbate reductase (DHAR) (Nakano and Asada 1981) and monodehydroascorbate reductase (MDHAR) (Hossain and Asada, 1984) were determined spectrophotometrically using established protocols. In addition, pectin methylesterase (PME) (Hagermann and Austin, 1986) and phenylalanine ammonia lyase (PAL) (Pascholati *et al.*, 1986) activities were analyzed as cell wall-related enzymes.

Gene expression analyses of *GmXTH1*, *GmEXPA2* and *GmWAK4* were performed by RT-qPCR. Total RNA was isolated using the QIAGEN RNeasy Plant Mini Kit and reverse-transcribed into cDNA. RT-qPCR reactions were carried out using SYBR Green chemistry with soybean actin 1 as the internal control. Statistical analyses were conducted using IBM SPSS Statistics 26. Since data were not normally distributed, the Kruskal-Wallis H test followed by Bonferroni post-hoc test was applied. Statistical significance was accepted at $p<0.05$.

RESULTS AND DISCUSSION

In the present study, chlorophyll content was increased slightly by 76% and 92.7% under Salt+AzA_1 and S+AzA_2 treatments, respectively (Fig 1). REL was decreased by 28.4% and 24% under S+AzA_1 and S+AzA_2 compared to salt alone, indicating improved membrane stability. O_2 content was increased under all stress treatments; however, S+AzA applications reduced it by 45.3% and 48.1% compared to salt alone. Under non-stress conditions, AzA_1 caused a slight 1.7-fold increase in superoxide levels relative to control.



Control (C), AzA_1; 12 ppm (A1), AzA_2; 24 ppm (A_2), NaCl 250 mM (S), NaCl+AzA_1 (S+A_1), NaCl+AzA_2 (S+A_2). Columns, marked with different letters represent groups with significantly different values ($P<0.05$). Data represent mean±SD (n= 3).

Fig 1: The effects of AzA on A) chlorophyll (CHL), B) leaf area (LA) and C) relative electrolyte leakage (REL) under the salt stress in soybean leaves.

MDA content was decreased by 23.6% under S+AzA_1 and by 31.9% under S+AzA_2 compared with salt treatment, although these changes were not significant. H_2O_2 levels were significantly affected by AzA treatments, increasing by 40% with AzA_1 and 58.18% with AzA_2. Proline content was increased up to 2.2 and 2.3-fold under S+AzA_2 compared to salt alone. Superoxide dismutase (SOD) activity was increased by 64.4% with AzA_1 compared to control.

Phenylalanine ammonia lyase enzyme activity was increased under S+AzA treatments by 33% (AzA_1) and 39.6% (AzA_2) compared to salt alone (Fig 4). *GmXTH3* expression showed 3.5-fold and 1-fold increases under AzA treatments, while S+AzA treatments resulted in 1.85-fold and 1.2-fold increases.

In the present study, salinity significantly reduced root length, whereas other growth parameters showed only slight and non-significant decreases (Table 1). This reduction may be associated with impaired sugar metabolism and disruption of water balance under salt stress. In addition, salt stress induces stomatal closure, limiting stomatal conductance and reducing photosynthetic carbon assimilation (Dhansu, 2026). The decline in photosynthetic activity subsequently decreases sucrose production and alters carbohydrate metabolism in plants (Ahmad, 2017; Yılmaz and Kulaz, 2019).

Under non-stress conditions, both AzA concentrations affected root length, however, AzA_1 was more effective than AzA_2 in promoting root elongation compared with the control. These findings suggest that increasing AzA concentration may suppress root growth. Similar results were reported by Alvarez-Rodriguez *et al.* (2024), who demonstrated that AzA competes with auxin for binding sites in Arabidopsis roots. Therefore, AzA may influence auxin regulation in soybean roots, resulting in changes in root development.

According to the results, obtained under stress conditions, an increase in the length of roots/shoots under only one conditions occurred (15.2%) was under S+AzA_1 application in terms of root length (Table 1). These results indicate that under stress conditions, AzA might alleviate growth parameters in soybean plants by maintaining water uptake. Similarly, (Cetinkaya *et al.*, 2025) presented that AzA priming treatment enhances water uptake by increasing the accumulation of organic matter in barley.

According to the literature, Rodrigues *et al.* (2023) reported that soybean plants sprayed with 1 mM AzA exhibited improved photosynthetic performance under pathogen effect. In this work, this important improvement in chlorophyll content could be attributed to the action of AzA on photosynthesis mechanisms in soybean leaves. AzA may protect soybean leaves from stress-induced chlorosis *via* a reduction in Na^+ entry to roots as determined by Haghighi and Sheibanirad (2018). Decreased leaf growth may depend on decreased photosynthetic activity under stress conditions, while AzA appears to restore this activity. Based on the data obtained from his study, it can be said that the applied AzA concentrations generally affected biochemical results by decreasing ROS, increasing proline and chlorophyll levels and decreasing MDA levels, more than physiological parameters. The increase in H_2O_2 levels stimulates some enzyme activities, while in some cases, it can be interpreted as indicating the presence of stress. Furthermore, the decrease in MDA levels caused by AzA application is supported by the decrease in REL and the increase in LA.

As mentioned above, AzA treatment with salt led to an increase in LA (Fig 1). Based on these findings, it appears that G3P treatment maintains ion homeostasis via the addition of Na^+ and other minerals to *Pistachio vera* as Raoufi *et al.* (2020) reported.

When the REL was examined, an increase in this content under stress conditions (salt 3.66-fold) compared to that in the control group (Fig 1) was detected. A similar trend was observed in soybean leaves under conditions of salinity, which was showed by Ayvacı *et al.* (2023). It is thought that stress application damaged the membrane structure and led to an increase in this content. On the other hand, AzA treatment caused a decrease in the REL, which was disrupted by membrane damage caused by stress treatment. In parallel with our findings, Bubier (2004) observed that overexpression of *EARLI1* in Arabidopsis transgenic plants produced a reduction in electrolyte leakage under freezing-induced damage. In this way, AzA could inhibit oxidative damage by producing a decrease in REL and its content.

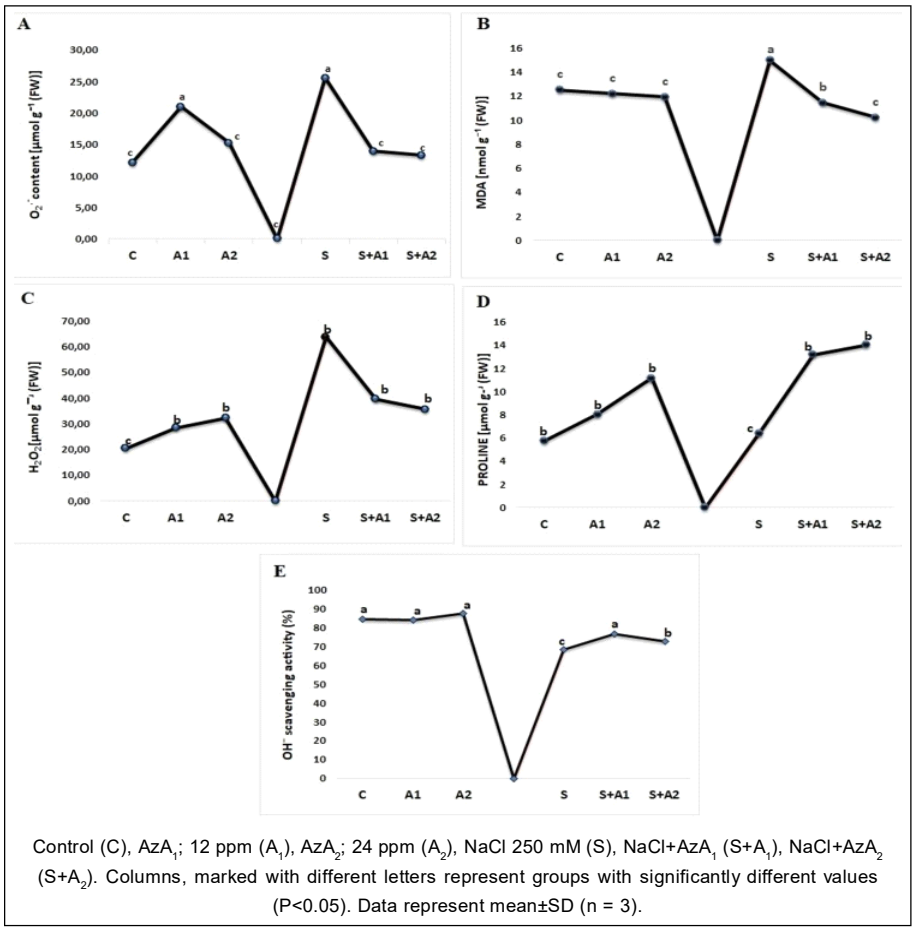
Under normal conditions, only 12 ppm AzA led to an increase in the superoxide radical content compared to that in the control group. Stress induces oxidative damage

Table 1: The effects of AzA on lengths, fresh and dry weights, relative water content (RWC) under the salt stress in soybean leaves.

	Length (cm)		Fresh weight (gr)		Dry weight (gr)		RWC (%)
	Root	Shoot	Root	Shoot	Root	Shoot	Leave
C	18.4±1.15^c	34.0±1.00	0.27±0.03	1.63±0.63	0.020±0.03	0.21±0.0	85.30±3.62
A1	25.2±4.04^a	30.6±4.04	0.22±0.07	1.30±0.04	0.014±0.01	0.16±0.0	81.98±6.89
A2	21.2±1.10^b	32.8±1.53	0.25±0.05	1.76±0.46	0.018±0.05	0.17±0.0	86.00±5.83
S	15.61±2.08	28.8±3.06^b	0.11±0.05	1.17±0.21	0.010±0.00	0.14±0.06	79.55±4.11
S+A1	17.8±2.69	30.6±2.89^a	0.19±0.06	1.30±0.10	0.014±0.00	0.15±0.02	82.26±3.01
S+A2	20.2±2.54	27.2±2.52	0.20±0.03	1.40±0.24	0.015±0.01	0.20±0.11	86.97±6.06

by ROS accumulation in plants (Singh and Dhal, 2023) and this situation could damage cell components (Mansoor *et al*., 2023). In this study, as shown in Fig 2, AzA treatment produced a decrease in superoxide radical content under different stress conditions, but this reduction was greatest under salt stress. In this study, AzA inhibited stress-induced oxidative damage by facilitating a decrease in the superoxide radical content. Moreover, variable results with respect to AzA treatment under stress and treatment days were found. It was recently showed that AzA and hexanoic acid treatments led to a reduction in superoxide radical and hydrogen peroxide contents in soybean plants under biotic stress (Rodrigues *et al*., 2023). In this regard, this study is the first to show that AzA can protect soybean leaves from abiotic stress-triggered oxidative damage.

In this work, salt stress increased the proline content (11.3%) compared to that in the control group (Fig 2). Under non stress conditions, this finding can be explained by the results from the previous report by Pitzschke *et al.* (2016) who reported that the *AZI1* protein is a glycoprotein that is rich in hydroxyproline. Therefore, the results of the present study suggest that exogenous AzA produced an increase in proline content in soybean leaves. This finding shows that AzA has a two-way effect on proline by either inducing or producing a decrease in proline. S+AzA$_1$ induced proline. In this work, it can be argued that AzA could act as an antioxidant to eliminate ROS without a requirement for proline accumulation. These results positively correlated with superoxide radical, MDA and REL contents under AzA. Salt treatment caused an increase in SOD enzyme activity (by 2.1-fold) when compared with that in the control groups. SOD activity also negatively correlated with REL and MDA, while it positively correlated with LA, CHL content and hydroxyl radical scavenging capability (Fig 3). In the present study, in addition to having an antioxidant role, AzA scavenged radicals by facilitating an increase in SOD enzyme activity in soybean leaves under abiotic stress. Beside this, hexanoic acid treatment induced SOD enzyme activity and did not cause changes in APX enzyme activity under (*A. solani)* treatment in tomato plants (Rabiei *et al*., 2022). Lastly, Haghpanah *et al.* (2024) showed that 1 mM Aza induced POX and CAT activities during the initial stages of the same infection. Overall, in the present study, AzA1,2 protected soybean leaves by acting as an antioxidant without

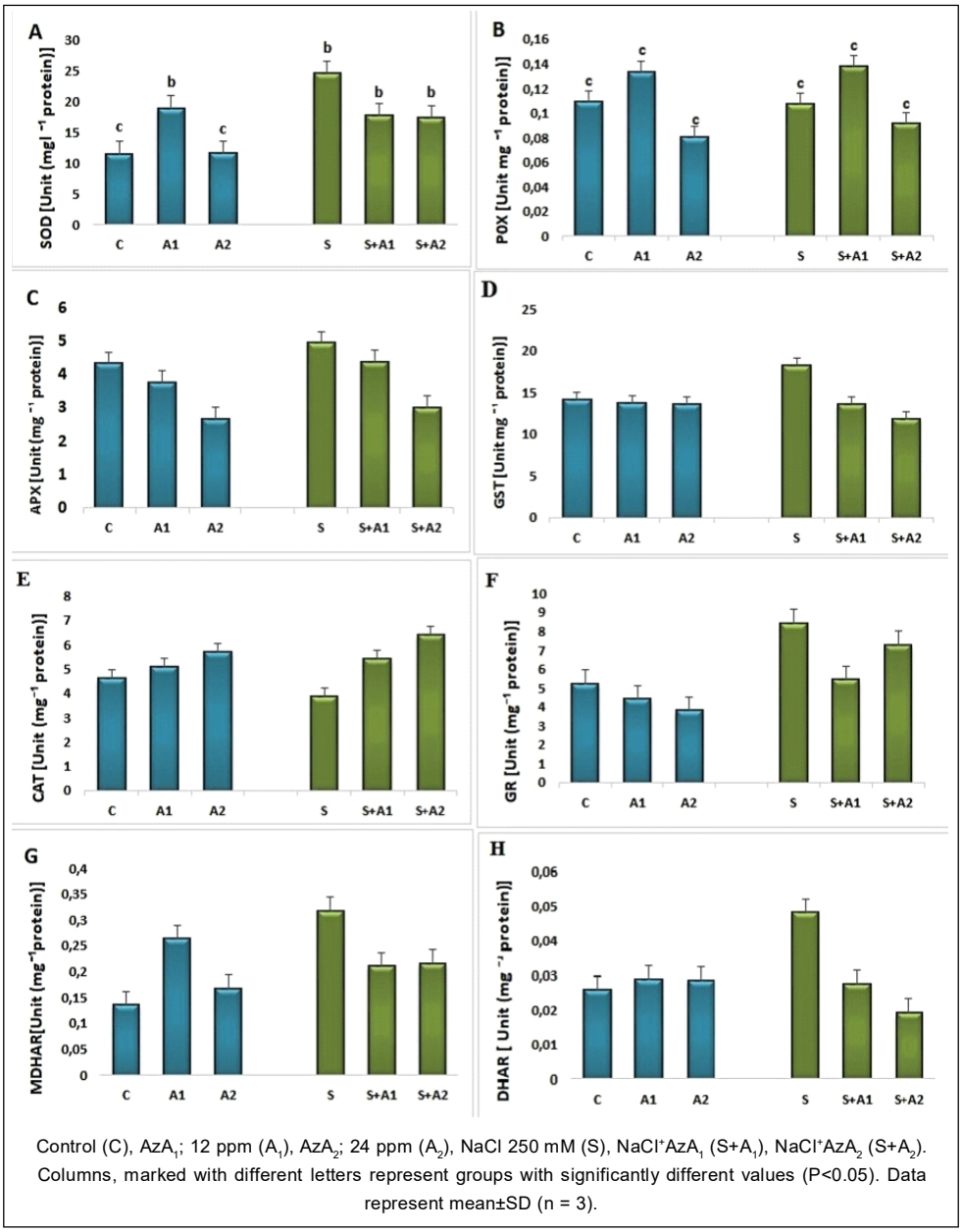


Control (C), AzA$_1$; 12 ppm (A$_1$), AzA$_2$; 24 ppm (A$_2$), NaCl 250 mM (S), NaCl+AzA$_1$ (S+A$_1$), NaCl+AzA$_2$ (S+A$_2$). Columns, marked with different letters represent groups with significantly different values (P<0.05). Data represent mean±SD (n = 3).

Fig 2: The effects of AzA on A) Superoxide anion radicle (O_2.-), B) Malondialdehyde (MDA), C) Hydrogen peroxide (H_2O_2), D) Proline; E) OH.- scavening capacity under the salt stress in soybean leaves.

induction of all antioxidant enzymes (except SOD). In addition, AzA concentration and duration of stress are very important. To our knowledge, this is the first study of the effect of AzA on antioxidant enzymes under abiotic stress. Moreover, different effects of AzA on PAL enzyme activities in all treatments were detected. Specifically, under saline conditions, while AzA1 led to a induction in PAL enzyme activity. Similarly, it was reported that AzA increases lignin formation in (*S. lycopersicum)* under biotic stress by inducing PAL enzyme activity (Haghpanah *et al.*, 2024) (Fig 4). AzA may have led to a reduction in the activity of this enzyme during the first days of stress. Therefore, AzA may also act as an opposite defense system by facilitating a reduction/induction in activities, which are altered under stress conditions.

The increase in Chl, LA, PAL activity, the increase in OH radical scavenging capacity, the decrease in MDA, PME, REL and the increase in SOD enzyme activity with XTH and EXP genes, which are cell wall-related genes, can be interpreted as the stimulatory effect of applied AzA on cell



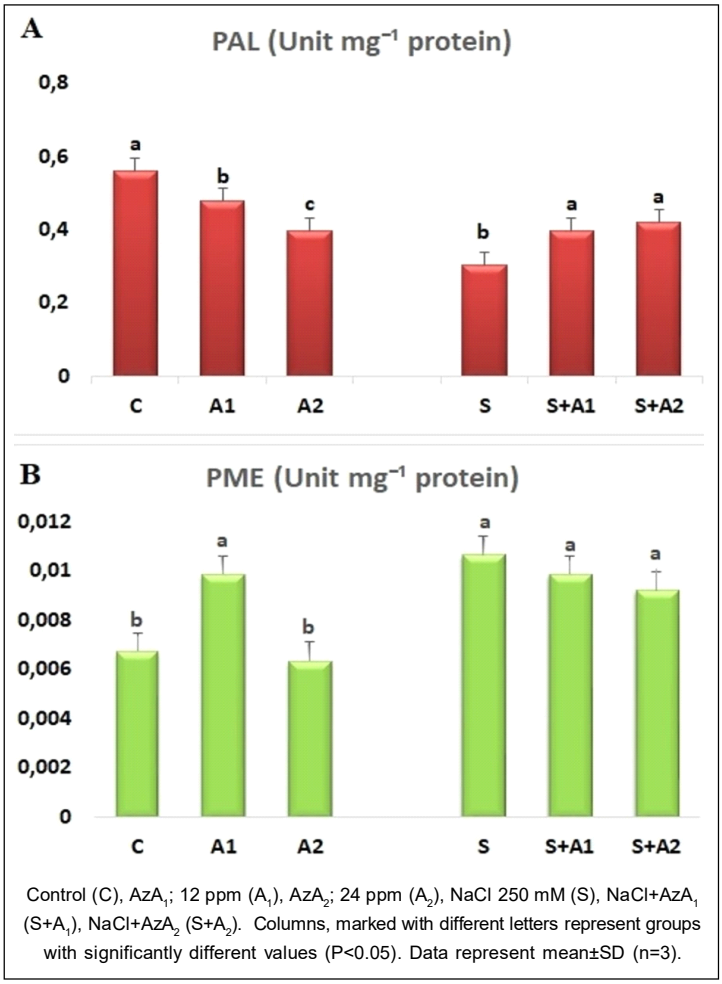
Control (C), AzA_1; 12 ppm (A_1), AzA_2; 24 ppm (A_2), NaCl 250 mM (S), $NaCl^+AzA_1$ ($S+A_1$), $NaCl^+AzA_2$ ($S+A_2$). Columns, marked with different letters represent groups with significantly different values ($P<0.05$). Data represent mean±SD (n = 3).

Fig 3: The effects of AzA on A) Superoxide dismutase (SOD), B) Peroxidase (POX) C) Ascorbate peroxidase (APX), D) Glutathione S-Transferase (GST E) Catalase (CAT), F) Glutathione reductase (GR), G) Monodehydroascorbate reductase (MDHAR) activity, H) Dehydroascorbate reductase (DHAR) activity under the salt stress in soybean leaves.

wall stability under salt stress conditions, providing protection. In the present study, Salt induced PME activity in soybean leaves. Similarly, Pal *et al.* (2016) showed that the expression of *SlPME* genes was upregulated under drought stress in *S. lycopersicum*. In addition, under stress treatments, AzA1 treatment led to a notable inhibition in the activity of the PME enzyme (Fig 4). As emphasized before, AzA can maintain cell wall homeostasis by regulating membrane integrity and solute exchange. XTH plays a role in regulating cell wall structure and morphology but also plays a crucial role in plant adaptation to external stress (Ishida and Yokoyama, 2022). In the present study, the *GmXTH3* gene expression was increased by 3.94-fold and 9.15-fold after exposure to the because of the capability of AzA to trigger cell growth in leaves by inducing XTHs.

GmWAK4 (soybean wall associated kinase) gene expression was downregulated in the salt treatment group when compared with the control group (Fig 5). These results are in agreement with the findings of *XTH* gene expression and decreased oxidative damage in response to AzA treatment. Similarly, in soybean, *GmWAK1* gene expression changed in response to salicylic acid and produced a decrease in oxidative damage under pathogen stress (Zhao *et al.*, 2023). This finding suggests that AzA could maintain Na^+ accumulation in soybean leaves as reported by (Meco *et al.*, 2020), who detected *WAK1* genes in tomato.

TaEXPB23 (wheat expansin gene) is involved in the regulation of salt stress tolerance in wheat (Yang *et al.*, 2012). In parallel with these previous reports, *GmEXPA2* gene expression induced by 2.7-fold after S+AzA1 application compared to that with salt application. The results reveal that these results were accompanied by up-regulation of other genes whose expression was similar to that determined in this study (*GmXTH3* and *GmEXPA2)* under the same treatment (S+AzA_2, S+AzA_1) as shown in Fig 5. Overall, AzA has positive effects on cell wall-related genes and PME activity and ameliorates these effects, which is correlated with a reduction in MDA and maintenance of ion homeostasis in soybean leaves to protect against stress-induced damage.



Control (C), AzA_1; 12 ppm (A_1), AzA_2; 24 ppm (A_2), NaCl 250 mM (S), NaCl+AzA_1 (S+A_1), NaCl+AzA_2 (S+A_2). Columns, marked with different letters represent groups with significantly different values ($P<0.05$). Data represent mean±SD (n=3).

Fig 4: The effects of AzA on A) Phenylalanine ammonia lyase (PAL) activity B) Pectin methylesterase (PME) activity.

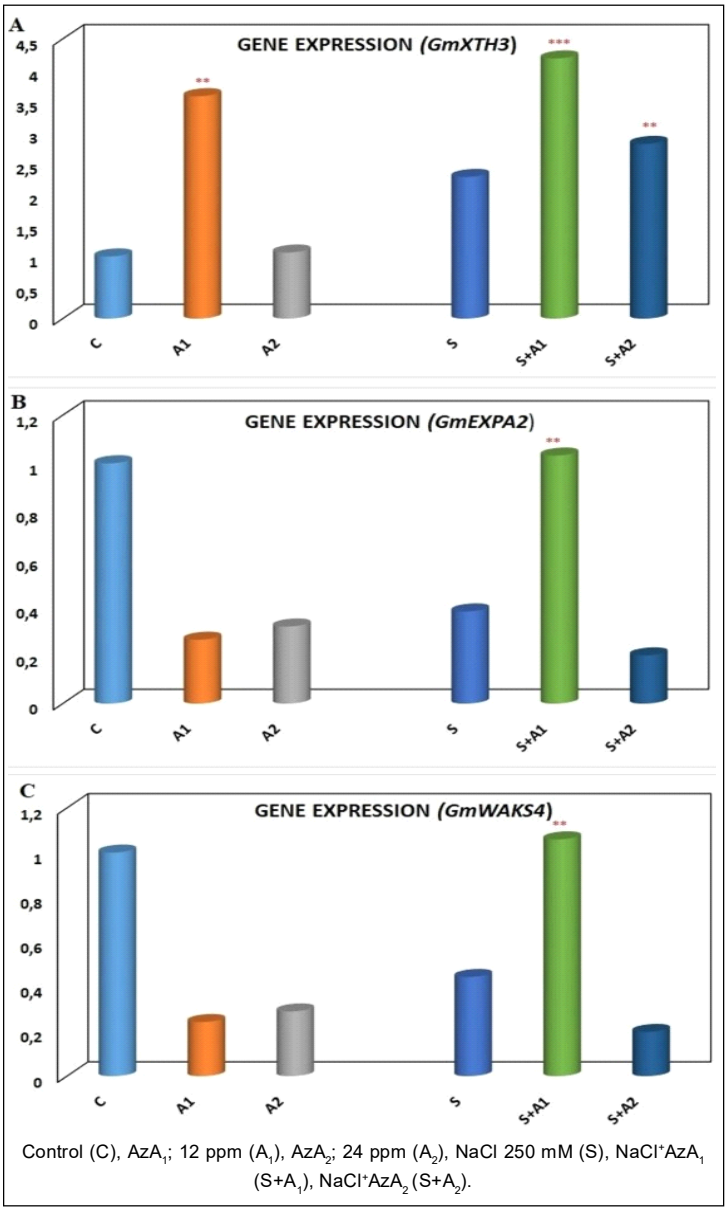


Fig 5: The effects of AzA on gene expression analyses of A) *GmXTH1,* B) *GmEXPA2*, C) *GmWALK4* under the salt stress in soybean leaves.

CONCLUSION

AzA protected soybean leaves from salt stress by regulating physiological, biochemical and molecular processes and acting as an antioxidant to reduce ROS accumulation. It also enhanced membrane stability by maintaining ion homeostasis and upregulating cell wall-related genes. Since this study was conducted under climate chamber conditions at the seedling stage, further studies under greenhouse and field conditions with different doses are needed to confirm AzA's potential for improving crop yield and stress tolerance.

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Disclaimers

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Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this article. No funding or sponsorship influenced the design of the study, data collection, analysis, decision to publish, or preparation of the manuscript.

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