

Mitigation of salt stress in *Phaseolus vulgaris* L. by dopamine: Effects on growth, physiological parameters and antioxidant activity

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ABSTRACT

Salinity, is one of the most important problems of the world's soils, has negative effects on germination and seedling growth, therefore reducing the yield of plants. This study investigated the effects of salt stress and dopamine (DA) treatments on plant growth, physiological parameters and nutritional elements of bean (*Phaseolus vulgaris* L.) through a pot experiment under greenhouse conditions. In this study, five different levels of DA: D-0 (0 μ M), D-50 (50 μ M), D-100 (100 μ M), D-150 (150 μ M), D-200 (200 μ M) and three different doses of NaCl: S-0 (0 mM), S-50 (50 mM), S-100 (100 mM) were employed. The effects of salinity and DA on growth, physiological and biochemical properties of bean seedlings were statistically significant. Plant height, stem diameter, leaf area, shoot fresh weight (FW), shoot dry weight (DW), root FW and root DW of bean seedlings treated with 50 mM and 100 mM NaCl were lower than control (0 mM NaCl). However, exogenous DA treatments improved the growth parameters of bean seedlings in both 50-mM and 150-mM salt stress compared with control. 100 mM NaCl stress led to decrease in plant height (45.59%), stem diameter (14.33%), leaf area (62.81%), shoot FW (61.21%), shoot DW (46.70%), root FW (43.47%), root DW (45.33%) and CRV (49.44%) compared with control. Treatment with 100 μ M exogenous DA at 100 mM NaCl increased plant FW by 129.30%, plant DW by 20.95%, root FW by 66.67%, root DW by 70.73% and CRV by 25.71%, compared with the control (0 mM NaCl). These findings suggest that

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DA may be used to decrease the effect of salt stress by inducing the systemic tolerance of plants. Thus, understanding the role of DA in salt tolerance introduces new possibilities to use this compound for agricultural purposes.

Keywords: dopamine, *Phaseolus vulgaris*, plant growth, salt stress

INTRODUCTION

The natural environment for plants is composed of abiotic and biotic stresses (Cramer et al., 2011). Abiotic stress conditions cause extensive losses in agricultural production worldwide. Stress conditions such as drought, salinity or heat have been the subject of intense research (Dos Santos et al., 2022). Environmental stresses can inhibit seed germination, delay growth, promote senescence and even lead to plant death (Li et al., 2019).

High salinity is one of the most widespread abiotic stress factors that severely restricts crop productivity (Yadav et al., 2020; Iftikhar et al., 2024). It is reported that about 7% of the Earth's land and 20% of the total arable area are affected by high salt contents (Rasool et al., 2013). High soil salinity is a severe and growing problem, and it is preventing the achievement of sustainable agriculture (Vijayan et al., 2008; Roy et al., 2014). Soil salinity can hinder plant growth in two primary ways. First, the salt in the soil water makes it harder for plants to absorb the necessary water, slowing their growth. This is known as the osmotic or water-deficit effect of salinity. Second, excessive salt absorbed by the plant through its transpiration stream can damage cells in the leaves, further impeding growth. This is referred to as the salt-specific or ion-excess effect (Carillo et al., 2011; Haghsheenas et al., 2024). Salinity can cause a decrease in leaf water potential, ionic imbalance and cell damage in plants, as well as causing increased accumulation of reactive oxygen species (ROS), negatively affecting protein synthesis, enzymatic activities and photosynthesis (Ait-El-Mokhtar et al., 2019; Hayat et al., 2024).

Phytohormones play an important role in alleviating abiotic stresses in plants by facilitating growth, development, nutrient distribution and source-sink relationships. Some important phytohormones that alleviate salinity stress in plants include abscisic acid (ABA), gibberellins (GA3), brassinosteroids (BRs), ethylene (ET), jasmonic acid (JA) and nitric oxide (NO). All these phytohormones show diversity in their modes of action under salt tolerance. Due to the prominent role of growth regulators in plants, there is a demand for novel PGR to facilitate the increasing demand for biochemical developmental processes (Verma et al., 2022). Dopamine (DA) is an important catecholamine neurotransmitter in the nervous system (Wang et al., 2018). It is common in animals and plants where it plays a variety of important roles, including in stress responses (Gao et al., 2020). Although widely found in animals, it was first recognized in plants as an antioxidant with greater anti-oxidative capacity than

catechin, glutathione and flavonoids (Kulma and Szopa, 2007). It has a strong reducing capacity, allowing it to scavenge free radicals and maintain a dynamic balance of ROS. Therefore, it plays a vital role in the regulation of intercellular ion osmosis and chloroplast photophosphorylation (Kanazawa and Sakakibara, 2000). There is a relationship between DA and plant stress resistance, and studies have shown that DA can improve plant adaptation to adverse conditions (Liu et al., 2020; Jiao et al., 2021; Yildirim et al., 2024).

Legumes are rich in proteins and are very important components of human and animal nutrition because of their protein content and converting the free nitrogen of the air into a form that plants can benefit from (Jukanti et al., 2012). Plants in this group are the most sensitive to salt among cultivated plants. The increase in salt concentration in the soil causes an increase in osmotic pressure, making it difficult for the plant to take water from the soil. As a result, the structure of the soil deteriorates, and plant growth slows down or may even stop. Bean (*Phaseolus vulgaris* L.) is an important legume providing a major protein source for the human worldwide. The mature dry seed and fresh pods are often consumed as vegetables, and the rest of the plants are used as animal fodder (Berber and Yaşar, 2011). Bean has been reported to be a very sensitive crop to salinity conditions (Garcia et al., 2019).

The time-consuming and very expensive methods of reclaiming the areas with salinity problems reveal the necessity of alternative applications. It is possible to eliminate soil salinity by some methods, which causes significant losses in agricultural production. Irrigation with water of high salt content, washing the soil, establishing a good drainage system and applying some chemicals to the soil are among the measures that can be taken. The limited measures and the difficulty of implementation, the long-term effects and the expensiveness limit their use. Along with these measures, the emergence of salt stress-tolerant varieties and their breeding offer more permanent and effective solutions in crops (Singh et al., 2021). However, it takes a long time to develop resistance genotypes against salinity stress. To mitigate the negative impacts of salt stress, some hormones and plant growth regulators, including DA, have been used (Oral et al., 2020; Dadasoglu et al., 2021, 2022; Yildirim et al., 2022; Ahammed and Li, 2023).

Several studies have been conducted to determine the effect of DA against stress in plants (Liu et al., 2020). However, to our knowledge, no study has been

found on the effects of DA in bean plants exposed to salt stress. Therefore, this research was conducted to reveal the effects of DA against salt stress on plant growth, physiological and biochemical characteristics of bean plants.

MATERIALS AND METHODS

Plant material and experiment design

The experiment was conducted in semi-controlled greenhouse conditions. Greenhouse temperature and humidity conditions were controlled via a sensor set to a range from an average temperature of 24°C ($\pm 2^\circ\text{C}$) during the day to 18°C ($\pm 2^\circ\text{C}$) during the night. Humidity was maintained at around 50% ($\pm 5\%$). The average photosynthetically available radiation measured at noon ranged from $952 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ to $1255 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Bean (*P. vulgaris* L. cv 'Hinis') plants, which is a very sensitive cultivar, were maintained under natural light conditions. We have changed the positions of the pots every 2 days.

DA treatments

DA hydrochloride (Sigma Aldrich, St. Louis, MO, USA) was initially dissolved, and concentrations of D-0 (0 μM), D-50 (50 μM), D-100 (100 μM), D-150 (150 μM) and D-200 (200 μM) were made up with distilled water containing 0.02% Tween 20 (polyoxyethylenesorbitan monolaurate; Sigma Chemicals, UK) as a surfactant. Ten days after emerging seedlings, when they reached about 20 cm above ground, the plants were foliar treated with DA at five levels: 0 (control), 50, 100, 150 and 200 μM . The concentrations were determined based on the findings of Li et al. (2015) and Liang et al. (2018). The foliar DA treatments were repeated four times at 3 days interval. Solutions of DA (25 mL) were applied to plants during late afternoon to avoid the sun effect using a handheld sprayer 10 days after emergence. To avoid interferences with different moisture levels, a control spray treatment consisting of 0.02% Tween 20 in distilled water was applied to those treatments not receiving DA at a given time. Lower leaf surface was sprayed until becoming wet as well as the upper surface because it was reported that absorption by the lower leaf surface was rapid and effective (Hull et al., 1975).

Salinity treatments

Salinity treatments were initiated the day after DA treatments. The irrigation water was applied at three levels of NaCl (0, 50 and 100 mM), and their electrical conductivities were measured as 0.54, 5.23 and 7.61 dS $\cdot \text{m}^{-1}$ in the rhizosphere area in the pot, respectively. Plants were irrigated with a half-strength Hoagland solution with 1-week intervals four times. A 100 mL treatment solution was applied to the pots. Seeds were planted in 2 L pots filled with perlite. A total of 225 plants were used with three replications and five plants per replication in the study.

Determination of growth parameters

The pot study was terminated on the 45th day from seed sowing to determine the plant growth parameters, including root and shoot fresh weights (FWs), root and shoot dry weights (DWs) (70°C for 48 hr), plant height, stem diameter and leaf area. Leaf area was quantified with a leaf area meter (LI-3100, LICOR, Lincoln, NE, USA).

Chlorophyll reading values-CRV (SPAD)

A chlorophyll meter (SPAD-502, Konica Minolta Sensing, Inc., Sakai, Japan) was used to determine the chlorophyll content in the leaves of the bean. The measurements were carried out at 10 different spots on leaves of each pot, and then the average was used for analyses (Dadasoglu et al., 2022).

Lipid peroxidation (measurement of malondialdehyde) and hydrogen peroxide (H_2O_2)

Lipid peroxidation was defined by the content of malondialdehyde (MDA). Thiobarbituric acid-reactive substances were measured as MDA, a degraded product of the lipid. The concentration of MDA was determined from the absorbance, by using an extinction coefficient of $155 \text{ mmol} \cdot \text{L}^{-1} \cdot \text{cm}^{-1}$ (Ekinci et al., 2021).

H_2O_2 was determined according to Velikova et al. (2000). Leaf tissues (200 mg) were homogenized in 2 mL of 0.1% (w/v) trichloroacetic acid (TCA) solution on ice. The homogenate was centrifuged at $12000 \times g$ for 15 min, and 0.4 mL of the supernatant was added to 0.4 mL of 10 mmol $\cdot \text{L}^{-1}$ potassium phosphate buffer, pH 7.0 and 0.8 mL of 1 mol $\cdot \text{L}^{-1}$ KI. The absorbance of the supernatant was measured at 390 nm. The content of H_2O_2 was calculated by comparing with a standard calibration curve previously made using different concentrations of H_2O_2 .

Measurement of electrolyte leakage

For the measurement of electrolyte leakage (EL), 10 leaf discs (10 mm in diameter) from the young fully expanded leaves from two plants per replicate were placed in 50-mL glass vials and rinsed with distilled water to remove the electrolytes released during leaf disc excision. Vials were then filled with 30 mL of distilled water and allowed to stand in the dark for 24 hr at room temperature. Electrical conductivity (EC1) of the bathing solution was determined at the end of the incubation period. Vials were heated in a temperature-controlled water bath at 95°C for 20 min and then cooled to room temperature and the (EC2) was again measured. EL was calculated as a percentage of EC1/EC2 (Shi et al., 2006).

Leaf relative water content

Leaf relative water content (LRWC) was measured according to Yildirim et al. (2015). Three young fully expanded leaves were first removed from the stem and

immediately weighed to determine the FW. Leaves, then, were floated in distilled water inside a closed Petri dish to determine the turgid weight (TW). At the end of the imbibition periods when a steady state was achieved, leaves were placed in an oven at 70°C for 48 hr to obtain DW. Values of FW, TW and DW were used to determine leaf LRWC (%) using the following equation: $LRWC = [(FW - DW) / (TW - DW)] \times 100$.

Mineral analysis

To determine the mineral concentrations in bean leaves from each plot, samples were oven-dried at 68°C for 48 hr and ground. K and Na were determined after wet digestion of dried and ground subsamples using a HNO₃–H₂O₂ acid mixture (2:3 v/v) with three steps in a microwave (Bergof Speedwave Microwave Digestion Equipment MWS-2) Berghof Products + Instruments GmbH (Germany) (Mertens, 2005a). Tissue K and Na were determined with an inductively coupled plasma spectrophotometer (Optima 2100 DV; Perkin-Elmer, Shelton, CT, USA) (Mertens, 2005b).

Assay of proline

A 50 mg frozen leaf sample was powdered with liquid nitrogen and extracted with a pestle and mortar with 4.5 mL of 5-sulfosalicylic acid 3% in an ice bath. The homogenates were filtered with a filter paper (#2). Two mL of filtrate were reacted with 2 mL acid-ninhydrin and 2 mL of glacial acetic acid in a test tube for 1 hr at 100°C. The reaction terminated in an ice bath. The filtrates were used for the analysis. Proline concentration was assayed spectrophotometrically at 520 nm (Bates et al., 1973).

Assay of antioxidant enzyme activity

Superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT) activities were measured according to the method (Angelini et al., 1990; Abedi and Pakniyat, 2010). One milligram of leaf material was ground in 6 mL of ice-cold 50 mM potassium phosphate buffer (pH 7.0) containing 2 mM sodium EDTA and 1% (w/v) polyvinyl-pyrrolidone (PVP). The resulting homogenate was centrifuged at 10000 × g (4°C) for 10 min. The extracted tissue samples were either stored at –78°C or immediately used to analyse SOD and CAT activity. Soluble protein content was quantified using a Coomassie blue dye-binding assay with bovine serum albumin (BSA) as the standard. SOD activity was measured by assessing its ability to inhibit the photochemical reduction of nitro-blue tetrazolium (NBT) in the presence of riboflavin

and light. One unit of SOD activity was defined as the amount of enzyme required to inhibit 50% of the NBT reduction rate, determined by monitoring absorbance at 560 nm. CAT activity was assayed by measuring the decrease in absorbance at 240 nm, reflecting the decomposition of H₂O₂.

Hormone analysis

Extraction and purification processes were executed as described by Kuraishi et al. (1991) and Battal and Tileklioğlu (2001). The detection of salicylic acid (SA), indole acetic acid (IAA) and ABA was performed using a UV detector at 265 nm (Turan et al., 2014).

Statistical analyses

The experimental design was a completely randomized factorial experiment with three replications. The data obtained were analysed by using SPSS 25 (IBM, NY, USA). A two-way MANOVA was performed to test the main effects of NaCl and DA, as well as their interactions on growth and physiological parameters. The differences among the means were compared using Duncan multiple range tests ($p < 0.05$).

RESULTS

Growth parameters

Under salt stress, the growth and development of bean seedlings were remarkably inhibited. Table 1 shows the analysis of variance for the effects of salt × DA and interactions of the growth parameters of bean. Variance analysis showed that growth parameters of bean were affected significantly by salt and DA treatment (Table 1). 100 mM NaCl stress led to decrease in plant height (45.59%), stem diameter (14.33%), leaf area (62.81%), shoot FW (61.21%), shoot DW (46.70%), root FW (43.47%), root DW (45.33%) and CRV (49.44%) compared with control. Exogenous DA applications on plant growth under salinity stress were found to be statistically significant ($p < 0.001$). Results showed that 150 µM exogenous DA treatment increased plant height by 2.12%–15.37%, stem diameter by 15.99%–16.72%, leaf area 18.64%–104.17%, at 50 mM and 100 mM NaCl, compared with the control (0 mM NaCl), respectively. At 50 mM NaCl, treatment with 150 µM exogenous DA increased plant FW by 25.06%, plant DW by 36.81%, root FW by 25.00%, root DW by 39.62% and CRV by 25.51%. On the contrary, 100 µM exogenous DA treatment increased plant FW by 129.30%, plant DW by

Table 1. Analysis of variance for the effects of salt DA and interactions of growth parameters of bean.

Source	Plant height	Stem diameter	Leaf area	Shoot FW	Shoot DW	Root FW	Root DW
Salt	***	***	***	***	***	***	***
DA	***	***	***	***	***	***	***
Salt × dopamine	***	***	***	***	***	***	***

***Significant at $p < 0.001$.

DA, dopamine; DW, dry weight; FW, fresh weight.

Table 2. Analysis of variance for the effects of salt DA and interactions of H₂O₂, MDA, LRWC, CRV, EL, proline, enzyme, hormone and mineral contents of bean.

Source	H ₂ O ₂	MDA	LRWC	CRV	EL	Proline	CAT	POD	SOD	IAA	ABA	SA	K	Ca	Na
Salt	***	***	***	***	***	***	***	***	***	NS	***	***	***	***	***
DA	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
Salt × DA	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***

***Non-significant or significant at $p < 0.001$, respectively.

ABA, abscisic acid; CAT, catalase; DA, dopamine; EL, electrolyte leakage; IAA, indole acetic acid; LRWC, leaf relative water content; MDA, malondialdehyde; NS, non-significant; POD, peroxidase; SA, salicylic acid; SOD, superoxide dismutase.

20.95%, root FW by 66.67%, root DW by 70.73%, CRV by 25.71% at 100 mM NaCl, compared with the control (0 mM NaCl) (Tables 3 and 4).

Physiological parameters

The interactive effects of salinity and DA on physiological parameters of bean are shown in Table 2. The statistical analysis indicates that physiological parameters were significantly affected in bean with respect to all salinity and DA levels. Salt stress statistically ($p < 0.001$) affected EL and LRWC compared with the non-salt-treated plants. LRWC decreased by 45.33% while EL increased by 150.00% under 100 mM NaCl compared with control (Table 4). The value of EL decreased with 150 μ M DA in both 50 mM and 100 mM NaCl salinity stress condition. The best results were achieved when 150 μ M DA was applied under salt stress.

A considerable increase in H₂O₂ and MDA content was observed under 100 mM NaCl as compared with non-stressed conditions. A significant interaction effect of salinity × DA was recorded on H₂O₂ and MDA; however, exogenous DA treatment significantly lowered H₂O₂ and MDA content by 34%–83%, 85%–90% in bean seedlings as compared with the control plants under saline conditions (respectively 50 mM and 100 mM NaCl) (Table 4).

Salinity stress conditions significantly increased the activity of antioxidant enzymes. At the same time, DA application caused an extra increase in antioxidant enzyme content in bean seedlings (Figure 1).

It was observed that the amount of proline was increased depending on the salt stress level. DA applications further increased the proline content under salt stress. 100 μ M DA led to further increase in proline content 346% and 177% under 50 mM and 100 mM NaCl (Figure 2).

Table 2 shows analysis of variance for the effects of salt × DA and interactions of biochemical parameters of bean. Variance analysis showed that biochemical parameters of bean were affected significantly by salt and DA treatment (Table 1). It was observed that IAA decreased with the increase in salt content. The application of 150 μ M DA increased by 76% compared with the control group. The best results were obtained by 150 μ M DA (46% increase) and by 50 μ M DA (1100% increase), respectively, with 50 mM and 100 mM of NaCl application (Figure 2). ABA content of bean seedlings

significantly increased with salinity stress. However, the DA amendment into soil declined the content of ABA bean seedlings by a ratio of 48% under salinity stress conditions (Figure 2). SA content decreased as salt concentration increased, but DA applications increased at this rate (Figure 2).

K⁺/Na⁺ ratio was significantly affected by salinity treatments (Figure 2). It was observed that the K⁺/Na⁺ ratio decreased with the increase in the salt content. DA amendment elevated the ratio of K⁺/Na⁺ in bean seedlings too (Figure 2).

DISCUSSION

Salinity, which is one of the factors limiting crop production, is increasing its pressure on agricultural lands day by day (Carillo et al., 2011). In this study, the morphological, physiological and biochemical effects of exogenous DA applications in bean plants under moderate and high salinity stress were investigated. Salinity adversely affects the growth and yield of several crop plants. However, the interaction of DA with several crops in saline conditions reduces the extent of poor growth and thus helps plants to survive in adverse conditions. Our results suggest that DA promote better growth of plants under salt treatment. The growth traits were improved by DA application. In the interaction between salinity and DA, it is important to note that, under high salinity stress of 100 mM, the rate of 100 μ M and 150 μ M DA recorded the highest increase in plant growth parameters.

The results obtained from the study showed that salt stress negatively affected plant growth parameters and significantly reduced plant height, stem diameter, leaf area, shoot FW, shoot DW and root fresh and DWs to the control (non-salinity) (Table 3). Bean has been reported to be a very sensitive crop to salinity conditions (Garcia et al., 2019). One of the first observed effects of salt stress is a decrease in the growth rate of plants. Salt stress inhibits plant growth by preventing the uptake of some plant nutrients and the continuity of photosynthesis and causing metabolic toxicity (Ran et al., 2021). Salt-stressed plants had lower CRV than unstressed plants (Table 4). The amount of photosynthetic pigment generally decreases in plants under salt stress. Earlier researches have indicated that salt stress reduces the chlorophyll content in plants (Shams and Yildirim,

Table 3. Effect of DA on growth parameters of bean plants under salt stress.

NaCl (mM)	DA (μ M)	Plant height (cm)	Stem diameter (mm)	Leaf area ($\text{cm}^2 \cdot \text{plant}^{-1}$)	Shoot FW ($\text{g} \cdot \text{plant}^{-1}$)	Shoot DW ($\text{g} \cdot \text{plant}^{-1}$)	Root FW ($\text{g} \cdot \text{plant}^{-1}$)	Root DW ($\text{g} \cdot \text{plant}^{-1}$)
0	0	57.75 $\pm$ 3.3 a	3.35 $\pm$ 0.05 b	315.76 $\pm$ 14.09 c	9.59 $\pm$ 0.05 cd	1.97 $\pm$ 0.04 d	3.29 $\pm$ 0.03 e	0.75 $\pm$ 0.04 de
	50	57.75 $\pm$ 1.4 a	3.31 $\pm$ 0.18 bc	343.75 $\pm$ 8.76 a	11.54 $\pm$ 0.39 a	2.21 $\pm$ 0.03 b	3.62 $\pm$ 0.07 b	0.86 $\pm$ 0.04 c
	100	56.25 $\pm$ 0.5 ab	3.66 $\pm$ 0.18 a	315.75 $\pm$ 2.95 c	9.95 $\pm$ 0.08 c	2.11 $\pm$ 0.04 c	3.82 $\pm$ 0.02 a	0.81 $\pm$ 0.03 cd
	150	50.42 $\pm$ 1.8 c	3.57 $\pm$ 0.06 a	321.37 $\pm$ 15.23 bc	11.42 $\pm$ 0.07 a	2.89 $\pm$ 0.09 a	3.87 $\pm$ 0.06 a	1.00 $\pm$ 0.08 a
	200	56.25 $\pm$ 1.3 ab	3.65 $\pm$ 0.09 a	330.82 $\pm$ 10.44 ab	10.92 $\pm$ 0.23 b	2.12 $\pm$ 0.12 c	3.65 $\pm$ 0.08 b	0.92 $\pm$ 0.04 b
50	0	55.08 $\pm$ 1.7 ab	3.19 $\pm$ 0.06 c	261.28 $\pm$ 1.92 f	8.94 $\pm$ 0.17 e	1.44 $\pm$ 0.03 g	2.69 $\pm$ 0.05 g	0.53 $\pm$ 0.02 i
	50	54.50 $\pm$ 1.3 b	3.28 $\pm$ 0.01 bc	306.73 $\pm$ 6.70 cd	9.89 $\pm$ 0.20 c	1.69 $\pm$ 0.02 e	3.32 $\pm$ 0.05 de	0.65 $\pm$ 0.04 fg
	100	54.50 $\pm$ 1.0 b	3.32 $\pm$ 0.03 bc	282.48 $\pm$ 2.23 e	9.25 $\pm$ 0.27 de	1.59 $\pm$ 0.02 f	3.51 $\pm$ 0.04 c	0.63 $\pm$ 0.01 gh
	150	56.25 $\pm$ 0.8 ab	3.70 $\pm$ 0.09 a	309.99 $\pm$ 4.54 c	11.18 $\pm$ 0.16 ab	1.97 $\pm$ 0.06 d	3.37 $\pm$ 0.04 de	0.74 $\pm$ 0.04 e
	200	53.83 $\pm$ 1.5 b	3.31 $\pm$ 0.05 bc	294.12 $\pm$ 13.87 de	9.73 $\pm$ 0.55 c	1.56 $\pm$ 0.03 f	3.41 $\pm$ 0.03 cd	0.68 $\pm$ 0.03 fg
100	0	31.42 $\pm$ 1.3 e	2.87 $\pm$ 0.07 e	117.44 $\pm$ 6.80 k	3.72 $\pm$ 0.08 i	1.05 $\pm$ 0.08 j	1.86 $\pm$ 0.08 i	0.41 $\pm$ 0.02 j
	50	30.67 $\pm$ 0.9 e	2.92 $\pm$ 0.02 de	138.71 $\pm$ 3.11 j	3.85 $\pm$ 0.04 i	1.15 $\pm$ 0.05 i	2.69 $\pm$ 0.06 g	0.55 $\pm$ 0.01 i
	100	30.08 $\pm$ 1.0 e	3.34 $\pm$ 0.04 b	169.25 $\pm$ 1.53 h	8.53 $\pm$ 0.30 f	1.27 $\pm$ 0.03 h	3.10 $\pm$ 0.05 f	0.70 $\pm$ 0.02 ef
	150	36.25 $\pm$ 1.0 d	3.35 $\pm$ 0.11 b	239.78 $\pm$ 3.71 g	5.96 $\pm$ 0.18 g	1.23 $\pm$ 0.04 hi	2.52 $\pm$ 0.12 h	0.58 $\pm$ 0.03 hi
	200	31.25 $\pm$ 0.3 e	3.03 $\pm$ 0.05 d	153.23 $\pm$ 5.03 i	5.10 $\pm$ 0.13 h	1.24 $\pm$ 0.03 hi	3.03 $\pm$ 0.07 f	0.64 $\pm$ 0.01 fh

Different letters in the same column indicate significant difference ($p \leq 0.05$) among the treatments.

DA, dopamine; DW, dry weight; FW, fresh weight.

Table 4. Effect of DA on EL, CRV (SPAD), LRWC, H₂O₂ and MDA of bean plants under salt stress.

NaCl (mM)	DA (μM)	EL (%)	CRV (SPAD)	LRWC (%)	H ₂ O ₂ (mmol · kg ⁻¹)	MDA (mmol · kg ⁻¹)
0	0	24.65 ± 1.44 g	36.93 ± 0.78 ab	81.80 ± 1.96 ab	0.54 ± 0.09 gh	7.92 ± 0.37 fg
	50	22.88 ± 2.01 g	35.73 ± 1.47 b	82.95 ± 3.01 ab	0.51 ± 0.03 gh	6.33 ± 0.83 g
	100	21.99 ± 2.63 g	35.87 ± 1.87 b	85.18 ± 0.86 a	0.46 ± 0.06 h	7.23 ± 1.06 fg
	150	23.01 ± 1.16 g	38.23 ± 0.23 a	85.52 ± 2.94 a	0.55 ± 0.06 gh	6.95 ± 1.54 fg
	200	22.82 ± 1.27 g	37.77 ± 1.51 a	80.47 ± 3.52 b	0.66 ± 0.08 gh	8.06 ± 0.56 fg
50	0	52.90 ± 0.97 b	23.48 ± 0.62 e	69.62 ± 1.38 ef	2.38 ± 0.17 c	60.08 ± 14.91 c
	50	42.34 ± 1.88 d	28.50 ± 1.23 c	74.76 ± 4.25 cd	0.81 ± 0.07 f-h	9.33 ± 2.16 fg
	100	43.54 ± 0.73 d	24.63 ± 0.31 de	72.85 ± 2.31 ce	1.12 ± 0.30 e-h	23.45 ± 5.62 de
	150	34.55 ± 1.21 f	29.47 ± 0.87 c	75.42 ± 1.74 c	1.03 ± 0.20 e-h	15.93 ± 0.89 e-g
	200	38.52 ± 1.74 e	25.77 ± 0.58 d	70.89 ± 2.51 de	1.26 ± 0.11 e-g	27.88 ± 0.93 d
100	0	61.99 ± 0.61 a	18.67 ± 0.59 g	44.72 ± 2.27 i	8.59 ± 1.45 a	165.86 ± 7.86 a
	50	54.59 ± 3.48 b	23.23 ± 0.81 e	59.30 ± 0.83 h	1.43 ± 0.11 d-f	16.50 ± 0.53 ef
	100	49.32 ± 0.40 c	23.47 ± 1.52 e	66.12 ± 0.99 fg	2.05 ± 0.24 cd	102.83 ± 0.76 b
	150	44.70 ± 0.72 d	22.70 ± 1.35 ef	66.58 ± 1.41 fg	1.69 ± 0.06 c-e	28.21 ± 2.39 d
	200	48.80 ± 2.21 c	21.00 ± 0.75 f	64.00 ± 0.96 g	4.03 ± 0.31 b	108.47 ± 6.95 b

Different letters in the same column indicate significant difference ($p \leq 0.05$) among the treatments.

DA, dopamine; EL, electrolyte leakage; LRWC, leaf relative water content; MDA, malondialdehyde.

2021; Wang et al., 2022; Assouguem et al., 2024). Taibi et al. (2016) suggested that the decrease in the amount of photosynthetic pigment in plants under salt stress is an indicator of oxidative stress and that chlorophyllase, a proteolytic enzyme, is activated by salt stress and breaks down the pigments. According to the results obtained from the study, salt stress decreased LRWC values (Table 4). Plants with more water in their tissues in saline conditions are considered more tolerant to salinity. It was determined that as the salt concentration applied to the plants increased, the water potential and osmotic potential had more negative values (Cocozza et al., 2013). This study pointed out that salinity stress elevated EL, H₂O₂ and MDA content of bean plants (Table 2). Similarly, previous studies showed salinity caused an increase in EL, H₂O₂ and MDA content in various crops (Chen et al., 2020; Zahedi et al., 2021). It is thought that EL increases due to the deterioration of the cell membrane under salt stress. MDA, the end product of lipid peroxidation, is one of the important biomarkers of oxidative damage. Abiotic stresses cause the formation of superoxide (O₂⁻) and H₂O₂ as a result of redox reactions (Martinez et al., 2016; Dadasoglu et al., 2022).

At different salinity levels, DA had a positive effect on the growth and physiological parameters. In terms of the interaction between salinity and DA, the exogenous treatments of DA alleviated the negative effects of salinity stress on the plant growth, physiological and biochemical characteristics of bean plants. DA-treated bean seedlings had higher plant height, leaf area, plant FW, plant DW, root FW and root DW than non-treated plants in both non-saline and saline conditions (Table 3). Furthermore, DA improved CRV (SPAD) and LRWC values of bean plants under salinity stress (Table 4). This

molecule helped to regulate chlorophyll concentrations and stomatal behaviour, while also altering the uptake, transport, partitioning and resorption of nutrients within the whole plant (Liang et al., 2018). We propose that this LRWC efficiency, regulatory role of DA has a positive influence on salt tolerance and offers new opportunities for its use in agriculture, especially in regions that are challenged by such stress conditions in the field. DA has been reported to enhance the photosynthetic activity in plants under salt stress. In addition, exogenous DA treatments enhance water-use efficiency (Liu et al., 2020). DA applications decreased the increased MDA and H₂O₂ levels caused by salt stress (Table 4). DA-treated bean plants had higher antioxidant enzyme activity in both saline and unsalted conditions than non-DA-treated bean plants (Figure 1). DA, a water-soluble antioxidant, has been reported to be involved in plants' tolerance to abiotic stresses, modulating various metabolic processes in plant cells, such as oxygen scavenging processes, plant sugar metabolism and photophosphorylation of chloroplasts. It has been reported that DA applications to plants exposed to abiotic stress factors such as salinity promote the functioning of the antioxidant defence mechanism, strengthen the plant body, have positive effects such as photosynthesis and water use efficiency, and increase the resistance of plants to stress factors by reducing lipid peroxidation and membrane permeability in plants under stress (Ahammed and Li, 2023).

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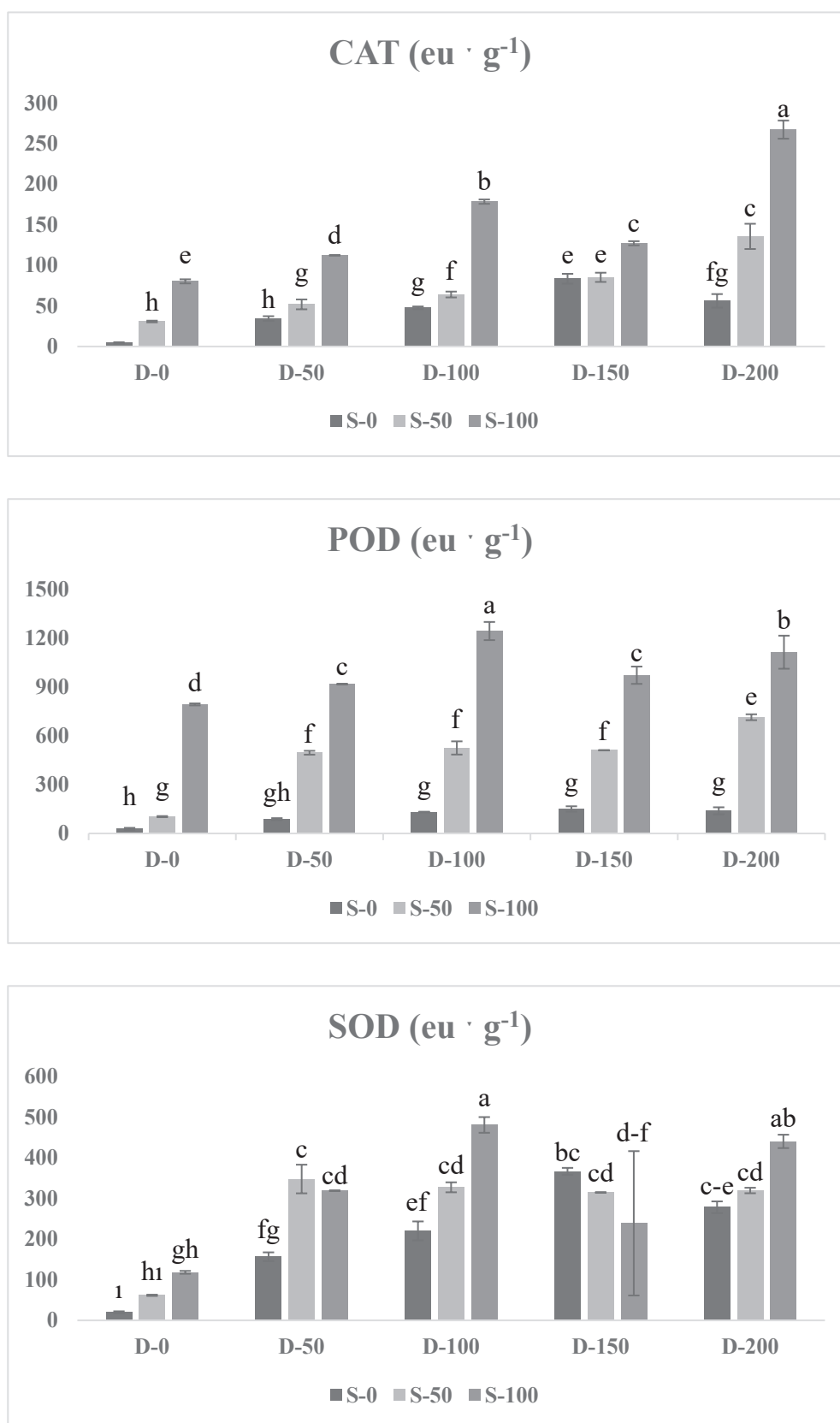


Figure 1. Effects of DA on activities of CAT, POD and SOD in leaves of bean plants under salt stress. Data presented are the means $\pm$ SD. Different letters indicate significant difference ($p \leq 0.05$) among the treatments. CAT, catalase; DA, dopamine; POD, peroxidase; SOD, superoxide dismutase.

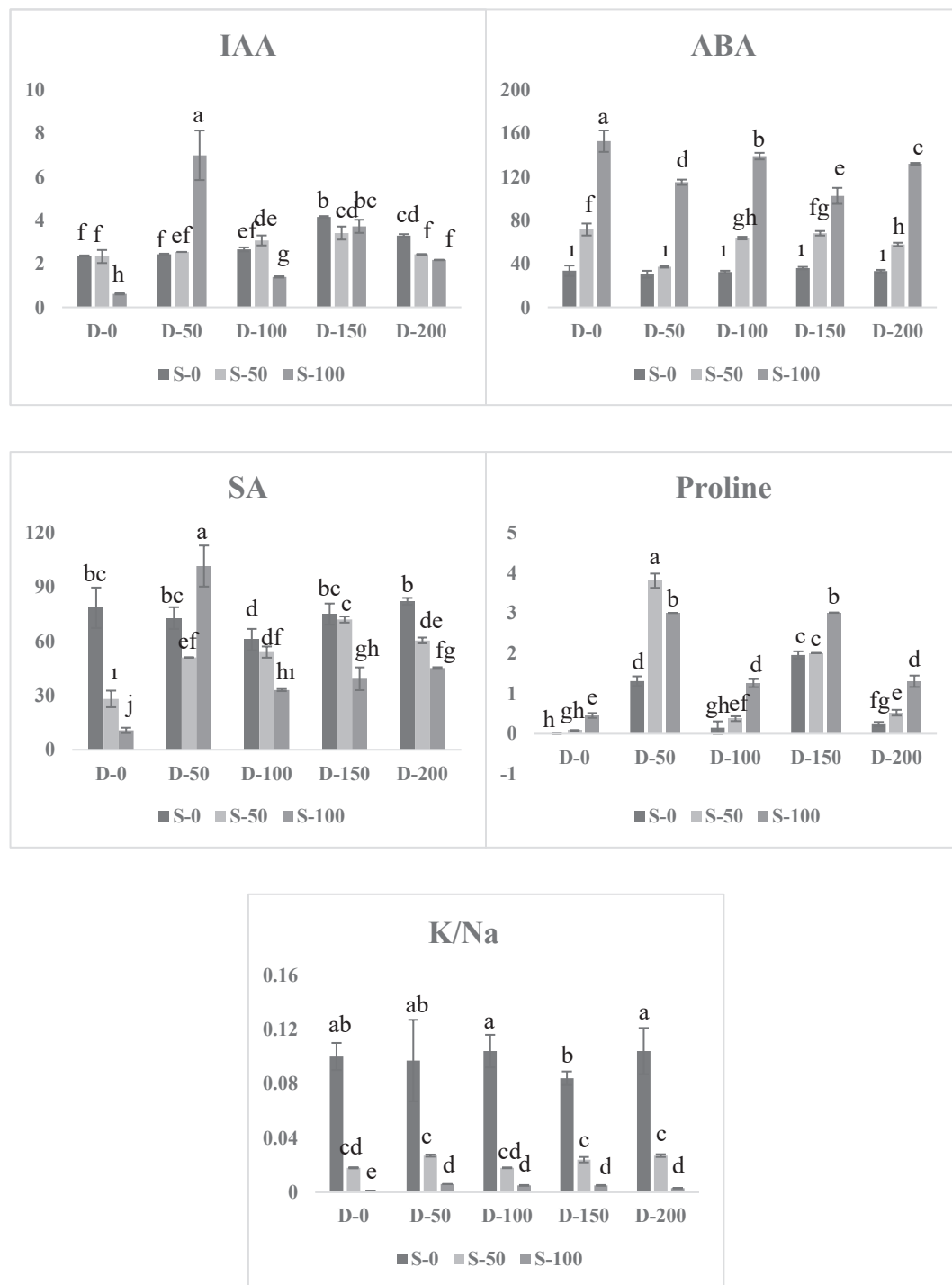


Figure 2. Effects of DA on IAA, ABA, SA and proline content and K/Na ratio in leaves of bean plants under salt stress. Data presented are the means $\pm$ SD. Different letters on the bars indicate significant difference ($p \leq 0.05$) between the treatments. ABA, abscisic acid; DA, dopamine; IAA, indole acetic acid; SA, salicylic acid.

the resistance of plants to stress factors by reducing lipid peroxidation and membrane permeability in plants under stress (Ahammed and Li, 2023). Similarly, Abdulmajeed et al. (2022) signified that DA had remarkable anti-stress effects, which could help regulate plant self-defence systems, reflecting satisfactory plant growth and productivity in bean under cadmium stress. The findings of this study revealed that salt stressed bean plants had more SOD, POD and CAT activity (Figure 2).

When the plant is exposed to any abiotic stress such as salinity, its sensitivity to stress conditions increases and the H_2O_2 level changes. Reducing the ROS level is achieved by antioxidant enzymes such as SOD, POD and CAT (Dadasoglu et al., 2021). Exogenous DA treatments enhance antioxidant activity (SOD, POD, CAT) and reduce the production of H_2O_2 of crops under salinity conditions. Akcay et al. (2024) determined exogenous DA treatments lowered EL under drought stress, MDA

levels under salinity stress in tomato seedlings. When plants face stressful conditions, DA can have some surprising benefits. Studies show it can increase their rate of photosynthesis, allowing them to capture more sunlight for energy. Additionally, DA helps plants to use water more efficiently and strengthens their antioxidant defences (Akçay et al., 2024).

DA also has been shown to modulate the photosynthetic oxygen reduction process. The ameliorative impact of DA on plants under salinity conditions can be attributed to its function as an oxygen reduction factor, allowing oxygen reduction to participate in energy conversion during photosynthesis. Thus, DA may have an ameliorative impact in plants under salinity conditions by preventing oxidative stress-induced tissue damage. This may also be due to DA oxidation leading to the production of melanin, an effective free radical scavenger. This study is in concordance with Li et al. (2015) who determined DA treatments could enhance SOD, CAT and POD activities and suppress H_2O_2 in apple plants under salinity conditions. Just like vitamin C and catechin, DA and its by-product, melanin, act as powerful antioxidants within plants. They directly eliminate harmful molecules called ROS that can damage cells. When these ROS appear, DA transforms into a red pigment called dopachrome, signalling the stressed area. Dopachrome then gets further oxidized into the familiar black pigment, melanin (Roshchina, 2022). In this study, it was determined salt stressed plants had much more proline content than non-stressed plants (Figure 2). Proline accumulation is a common phenomenon in many monocot and dicot plant species under salt stress (Elrys et al., 2020). In this study, DA treatments had positive impact on proline content in bean under salinity stress (Figure 2). Positive impact of DA on plant growth and physiological parameters in stressful conditions can be directly or indirectly attributed to the role of DA in nutrient uptake and root system architecture, photosynthetic capacity and pigments, stomatal regulation, N fixation and photophosphorylation (Farouk et al., 2023).

Salinity conditions had significant impacts on the hormone content of seedlings. Our findings demonstrated that salt stress resulted in decreased IAA and SA content in bean seedlings (Figure 2). However, salt-stressed seedlings had more ABA content than the non-stressed ones. ABA, known as a stress hormone, accumulates in significant amounts in plants under stress conditions and helps the plant survive (Waśkiewicz et al., 2013; Yu et al., 2020). Samancıoğlu et al. (2016) reported that drought stress elevated ABA content but reduced IAA and GA in cabbage plants. Our study findings are in concordance with those of Kazan (2013), who found that the IAA concentration decreases and the ABA amount increases in potatoes, rice and tomatoes under salt stress. Plant hormones are active members of signalling compounds involved in the induction of stress responses in plants (Kaya et al., 2009). Moreover, DA treatments caused elevated IAA

and SA content while decreasing ABA content of bean plants. DA is coordinated with phytohormone activity to regulate growth and enable plants to fine-tune their stress responses (Kulma and Szopa, 2007).

Salinity stress decreased the K/Na^+ ratio compared with the control treatment (Figure 2). With the increase of Na^+ concentration in the rhizosphere region, while Na^+ entry into the plant stem cell increases, the uptake of K^+ into the cell decreases, and accordingly, the K/Na^+ balance of the plant stem cell is disturbed. This is because Na^+ competes with K^+ for areas where K^+ will bind (Ahmad et al., 2015). Along with the fact that excess salt decreases the water potential in the cell in plants, it also disrupts the ion balance in the cell, negatively affecting plant growth (Hao et al., 2021). K/Na values increased with DA treatments in salinity conditions (Figure 2). Na and K content can be used as a good indicator of tolerance to salinity stress in plants. DA treatments could reduce Na^+ uptake by plants while keeping of K^+ content. In fact, earlier researches determined that DA treatments could enhance the water-use efficiency in salt stressed plants. High water use efficiency can decrease salt uptake by plants and prevent water shortage. It has been suggested that plant cells under salt stress may lower the concentration of Na^+ in the cells by expelling them or compartmentalizing them into vacuoles, thus decreasing the negative effect of the salt stress (Liu et al., 2020).

CONCLUSIONS

Salinity has an important role in plant production. High concentrations of salinity can cause toxic effects for plants. To our knowledge, this is the first study to reveal the effects of DA treatments on plant growth of bean during seedling under NaCl stress. This study shows that DA may be used to decrease the effect of salt stress by inducing the systemic tolerance of plants. In conclusion, DA mitigates NaCl stress by regulating antioxidant enzymes activity, plant nutrient and phytohormones content in bean. Further studies should be conducted under field conditions at large scale. Moreover, economic analysis should be made to determine availability.

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AUTHOR CONTRIBUTIONS

E.D. and E.Y. conceived and designed the experiments. E.D. and E.Y. performed the experiments. M.T., S.E. and

D.S. analyze data and prepare graph. E.Y., S.E., D.S., A.A. and M.M.A. prepared first draft of manuscript and revised; E.Y., A.E., A.A.A., G.M.A., Q.M.A., M.M.A. and E.D. revised and finalize the manuscript.

CONFLICT OF INTEREST

There is no conflict of interest among the authors.

REFERENCES

- ABDULMAJEED, A. M., ALHARBI, B. M., ALHARBY, H. F., ABUALRESH, A. M., BADAWEY, G. A., SEMIDA, W. M., AND RADY, M. M. (2022). Simultaneous action of silymarin and dopamine enhances defense mechanisms related to antioxidants, polyamine metabolic enzymes, and tolerance to cadmium stress in *Phaseolus vulgaris*. *Plants*, 11(22), 3069, <https://doi.org/10.3390/plants11223069>.
- ABEDI, T., AND PAKNIYAT, H. (2010). Antioxidant enzymes changes in response to drought stress in ten cultivars of oilseed rape (*Brassica napus* L.). *Czech Journal of Genetic and Plant Breeding*, 46, 27–34, <https://doi.org/10.17221/67/2009-CJGPB>.
- AHAMMED, G. J., AND LI, X. (2023). Dopamine-induced abiotic stress tolerance in horticultural plants. *Scientia Horticulturae*, 307, 111506, <https://doi.org/10.1016/j.scienta.2022.111506>.
- AHMAD, P., HASHEM, A., ABDALLAH, E. F., ALQARAWI, A. A., JOHN, R., EGAMBERDIEVA, D., AND GUCEL, S. (2015). Role of *Trichoderma harzianum* in mitigating NaCl stress in Indian mustard (*Brassica juncea* L.) through antioxidative defense system. *Frontiers in Plant Science*, 6, 868, <https://doi.org/10.3389/fpls.2015.00868>.
- AIT-EL-MOKHTAR, M., LAOUANE, R. B., ANLI, M., BOUTASKNIT, A., WAHBI, S., AND MEDDICH, A. (2019). Use of mycorrhizal fungi in improving tolerance of the date palm (*Phoenix dactylifera* L.) seedlings to salt stress. *Scientia Horticulturae*, 253, 429–438, <https://doi.org/10.1016/j.scienta.2019.04.066>.
- AKCAY, U. C., GENÇAY, R., AND KOC, F. Z. (2024). Effect of dopamine and progesterone on the physiological and molecular responses of tomato seedlings to drought and salt stress. *Cogent Food & Agriculture*, 10(1), 2321308, <https://doi.org/10.1080/23311932.2024.2321308>.
- ANGELINI, R., MANES, F., AND FEDERICO, R. (1990). Spatial and functional correlation between diamine-oxidase and peroxidase activities and their dependence upon de-etiolation and wounding in chickpea stems. *Planta*, 182, 89–96, <https://doi.org/10.1007/BF00239989>.
- ASSOUGUEM, A., LAHLALI, R., JOUTEL, A. B., KARA, M., BARI, A., ABERKANI, K., KAUR, S., MOKRINI, F., AND LAZRAQ, A. (2024). Assessing *Panonychus ulmi* (Acari: Tetranychidae) infestations and their key predators on *Malus domestica* Borkh in varied ecological settings. *Agronomy*, 14(3), 457, <https://doi.org/10.3390/agronomy14030457>.
- BATES, L. S., WALDREN, R. A., AND TEARE, I. D. (1973). Rapid determination of free proline for water-stress studies. *Plant and Soil*, 39, 205–207, <https://doi.org/10.1007/BF00018060>.
- BATTAL, P., AND TILEKLIOĞLU, B. (2001). The effects of different mineral nutrients on the levels of cytokinins in maize (*Zea mays* L.). *Turkish Journal of Botany*, 25, 123–130.
- BERBER, I., AND YAŞAR, F. (2011). Characterization of bean (*Phaseolus vulgaris* L.) cultivars grown in Turkey by SDS-PAGE of seed proteins. *Pakistan Journal of Botany*, 43(2), 1085–1090.
- CARILLO, P., ANNUNZIATA, M. G., PONTECORVO, G., FUGGI, A., AND WOODROW, P. (2011). Salinity stress and salt tolerance. In A. Shanker and B. Venkateswarlu (Eds), *Abiotic Stress in Plants - Mechanisms and Adaptations* (pp. 21–38). InTech, <https://doi.org/10.5772/22331>.
- CHEN, L., LIU, L., LU, B., MA, T., JIANG, D., LI, J., ZHANG, K., SUN, H., ZHANG, Y., BAI, Z., AND LI, C. (2020). Exogenous melatonin promotes seed germination and osmotic regulation under salt stress in cotton (*Gossypium hirsutum* L.). *PloS ONE*, 15, 0228241, <https://doi.org/10.1371/journal.pone.0228241>.
- COCOZZA, C., PULVENTO, C., LAVINI, A., RICCARDI, M., D'ANDRIA, R., AND TOGNETTI, R. (2013). Effects of increasing salinity stress and decreasing water availability on ecophysiological traits of quinoa (*Chenopodium quinoa* Wild.) grown in a Mediterranean-type agroecosystem. *Journal of Agronomy and Crop Science*, 199, 229–240, <https://doi.org/10.1111/jac.12012>.
- CRAMER, G. R., URANO, K., DELROT, S., PEZZOTTI, M., AND SHINOZAKI, K. (2011). Effects of abiotic stress on plants: A systems biology perspective. *BMC Plant Biology*, 11, 163, <https://doi.org/10.1186/1471-2229-11-163>.
- DADASOGLU, E., EKINCI, M., KUL, R., SHAMS, M., TURAN, M., AND YILDIRIM, E. (2021). Nitric oxide enhances salt tolerance through regulating antioxidant enzyme activity and nutrient uptake in pea. *Legume Research*, 44, 41–45, <https://doi.org/10.18805/LR-540>.
- DADASOGLU, E., TURAN, M., EKINCI, M., ARGIN, S., AND YILDIRIM, E. (2022). Alleviation mechanism of melatonin in chickpea (*Cicer arietinum* L.) under the salt stress conditions. *Horticulturae*, 8, 1066, <https://doi.org/10.3390/horticulturae8110666>.
- DOS SANTOS, T. B., RIBAS, A. F., DE SOUZA, S. G. H., BUDZINSKI, I. G. F., AND DOMINGUES, D. S. (2022). Physiological responses to drought, salinity, and heat stress in plants: A review. *Stresses*, 2(1), 113–135, <https://doi.org/10.3390/stresses2010009>.
- EKINCI, M., KOCAMAN, A., ARGIN, S., TURAN, M., AND DADASOGLU, F. (2021). Rhizobacteria alleviate the adverse effects of salt stress on seedling growth of *Capsicum annuum* L. by modulating the antioxidant

- enzyme activity and mineral uptake. *Taiwania*, 66, 287–297, <https://doi.org/10.6165/tai.2021.66.287>.
- ELRYS, A. S., ABDO, A. I., ABDEL-HAMED, E. M., AND DESOKY, E. S. M. (2020). Integrative application of licorice root extract or lipoic acid with fulvic acid improves wheat production and defenses under salt stress conditions. *Ecotoxicology and Environmental Safety*, 190, 110–144, <https://doi.org/10.1016/j.ecoenv.2019.110144>.
- FAROUK, S., EL-HADY, M. A. A., EL-SHERPINY, M. A., HASSAN, M. M., ALAMER, K. H., AL-ROBAI, S. A., AND EL-BAUOME, H. A. (2023). Effect of dopamine on growth, some biochemical attributes, and the yield of crisp head lettuce under nitrogen deficiency. *Horticulturae*, 9(8), 945, <https://doi.org/10.3390/horticulturae9080945>.
- GAO, T., LIU, X., SHAN, L., WU, Q., LIU, Y., ZHANG, Z., MA, F., AND LI, C. (2020). Dopamine and arbuscular mycorrhizal fungi act synergistically to promote apple growth under salt stress. *Environmental and Experimental Botany*, 178, 104–159, <https://doi.org/10.1016/j.envexpbot.2020.104159>.
- GARCIA, C. L., DATTAMUDI, S., CHANDA, S., AND JAYACHANDRAN, K. (2019). Effect of salinity stress and microbial inoculations on glomalin production and plant growth parameters of snap bean (*Phaseolus vulgaris*). *Agronomy*, 9, 545, <https://doi.org/10.3390/agronomy9090545>.
- HAGHSHEENAS, M., VANDELLEN, S. H., AND NAZARIDELJOU, M. J. (2024). Effects of nutrient solution strength, PGPB, and mycorrhizal inoculation on growth, yield, and quality of strawberry. *Turkish Journal of Agriculture and Forestry*, 48(3), 390–401, <https://doi.org/10.55730/1300-011X.3189>.
- HAO, S., WANG, Y., YAN, Y., LIU, Y., WANG, J., AND CHEN, S. (2021). A review on plant responses to salt stress and their mechanisms of salt resistance. *Horticulturae*, 7, 132, <https://doi.org/10.3390/horticulturae7060132>.
- HAYAT, F., KHAN, U., ZEESHAN, M., ALI, Q., NAWAZ, M. A., AHMED, N., ERCISLI, S., KANDHAN, K., AL-ZAYADNEH, W., SULIEMAN, S., SHETIWI, M., AND ALYAFEI, M. (2024). Mechanistic understanding of hormone regulation of abiotic stresses in horticultural plants: A review. *Turkish Journal of Agriculture and Forestry*, 48(6), 825–840, <https://doi.org/10.55730/1300-011X.3224>.
- HULL, H. M., MORTON, H. L., AND WHARRIE, J. R. (1975). Environmental influence on cuticle development and resultant foliar penetration. *The Botanical Reviews*, 41, 421–451, <https://doi.org/10.1007/BF02860832>.
- IFTIKHAR, N., PERVEEN, S., ALI, B., SALEEM, M. H., AND AL-SADOON, M. (2024). Physiological and biochemical responses of maize (*Zea mays* L.) cultivars under salinity stress. *Turkish Journal of Agriculture and Forestry*, 48(3), 332–343, <https://doi.org/10.55730/1300-011X.3185>.
- JIAO, C., LAN, G., SUN, Y., WANG, G., AND SUN, Y. (2021). Dopamine alleviates chilling stress in watermelon seedlings via modulation of proline content, antioxidant enzyme activity, and polyamine metabolism. *Journal of Plant Growth Regulation*, 40, 277–292, <https://doi.org/10.1007/s00344-020-10096-2>.
- JUKANTI, A. K., GAUR, P. M., GOWDA, C. L. L., AND CHIBBAR, R. N. (2012). Nutritional quality and health benefits of chickpea (*Cicer arietinum* L.): A review. *The British Journal of Nutrition*, 108, 11–26, <https://doi.org/10.1017/S0007114512000797>.
- KANAZAWA, K., AND SAKAKIBARA, H. (2000). High content of dopamine, a strong antioxidant, in cavendish banana. *Journal of Agricultural and Food Chemistry*, 48, 844–848, <https://doi.org/10.1021/jf9909860>.
- KAYA, C., TUNA, A. L., AND YOKAŞ, I. (2009). The role of plant hormones in plants under salinity stress. In M. Ashraf, M. Ozturk and H. Athar (Eds), *Salinity and Water Stress. Tasks for Vegetation Sciences*, vol. 44. (pp. 45–50). Dordrecht: Springer, https://doi.org/10.1007/978-1-4020-9065-3_5.
- KAZAN, K. (2013). Auxin and the integration of environmental signals into plant root development. *Annals of Botany*, 112(9), 1655–1665, <https://doi.org/10.1093/aob/mct229>.
- KULMA, A., AND SZOPA, J. (2007). Catecholamines are active compounds in plants. *Plant Science*, 172, 433–440, <https://doi.org/10.1016/j.plantsci.2006.10.013>.
- KURAISHI, S., TASAKI, K., SAKURA, N., AND SADATOKU, K. (1991). Changes in levels of cytokinins in etiolated squash seedlings after illumination. *Plant and Cell Physiology*, 32, 585–591, <https://doi.org/10.1093/oxfordjournals.pcp.a078120>.
- LIANG, B., GAO, T., ZHAO, Q., MA, C., CHEN, Q., WEI, Z., LI, C., AND MA, F. (2018). Effects of exogenous dopamine on the uptake, transport, and resorption of apple ionome under moderate drought. *Frontiers in Plant Science*, 9, 755, <https://doi.org/10.3389/fpls.2018.00755>.
- LI, C., SUN, X., CHANG, C., JIA, D., WEI, Z., LI, C., AND MA, F. (2015). Dopamine alleviates salt-induced stress in *Malus hupehensis*. *Physiologia Plantarum*, 153, 584–602, <https://doi.org/10.1111/ppl.12264>.
- LI, J., LIU, J., ZHU, T., ZHAO, C., LI, L., AND CHEN, M. (2019). The role of melatonin in salt stress responses. *International Journal of Molecular Sciences*, 20, 1735, <https://doi.org/10.3390/ijms20071735>.
- LIU, Q., GAO, T., LIU, W., LIU, Y., ZHAO, Y., LIU, Y., LI, W., DING, K., MA, F., AND LI, C. (2020). Functions of dopamine in plants: A review. *Plant Signaling and Behavior*, 15, 1827782, <https://doi.org/10.1080/15592324.2020.1827782>.
- MARTINEZ, V., MESTRE, T. C., RUBIO, F., GIRONES-VILAPLANA, A., MORENO, D. A., MITTLER, R., AND RIVERO, R. M. (2016). Accumulation of flavonols over hydroxycinnamic acids favors oxidative damage protection under abiotic stress. *Frontiers in Plant Science*, 7, 838, <https://doi.org/10.3389/fpls.2016.00838>.

- MERTENS, D. (2005a). "AOAC Official Method" 922.02. Plants preparation of laboratory sample. In W. Horwitz and G. W. Latimer (Eds), *Official Methods of Analysis* (18th ed., Chap. 3, pp. 1–2). Gaithersburg, MD, USA: AOAC-International.
- MERTENS, D. (2005b). "AOAC Official Method" 975.03. Metal in plants and pet foods. In W. Horwitz and G. W. Latimer (Eds), *Official methods of analysis* (Chap. 3, pp. 3–4). Gaithersburg, MD, USA: AOAC-International.
- ORAL, E., TUNÇTÜRK, R., TUNÇTÜRK, M., AND KULAZ, H. (2020). Effect of silicium on reducing salt (NaCl) stress in beans (*Phaseolus vulgaris* L.). *Kahramanmaraş Sutcu Imam University Journal of Agriculture and Nature*, 23, 1616–1625, <https://doi.org/10.18016/ksutarimdogavi.702302>.
- RAN, X., WANG, X., GAO, X., LIANG, H., LIU, B., AND HUANG, X. (2021). Effects of salt stress on the photosynthetic physiology and mineral ion absorption and distribution in white willow (*Salix alba* L.). *PloS ONE*, 16, 0260086, <https://doi.org/10.1371/journal.pone.0260086>.
- RASOOL, S., AHMAD, A., SIDDIQI, T. O., AND AHMAD, P. (2013). Changes in growth, lipid peroxidation and some key antioxidant enzymes in chickpea genotypes under salt stress. *Acta Physiologia Plantarum*, 35, 1039–1050, <https://doi.org/10.1007/s11738-012-1142-4>.
- ROSHCHINA, V. V. (2022). Biogenic amines in plant cell at normal and stress: probes for dopamine and histamine. In T. Aftab and M. Naeem (Eds), *Emerging Plant Growth Regulators in Agriculture* (pp. 357–376). Academic Press.
- ROY, S. J., NEGRÃO, S., AND TESTER, M. (2014). Salt resistant crop plants. *Current Opinion in Biotechnology*, 26, 115–124, <https://doi.org/10.1016/j.cobio.2013.12.004>.
- SAMANCIOGLU, A., YILDIRIM, E., TURAN, M., KOTAN, R., SAHIN, U., AND KUL, R. (2016). Amelioration of drought stress adverse effect and mediating biochemical content of cabbage seedlings by plant growth promoting rhizobacteria. *International Journal of Agriculture and Biology*, 18, 5, <https://doi.org/10.17957/IJAB/15.0195>.
- SHAMS, M., AND YILDIRIM, E. (2021). Variations in response of CaPAO and CaATG8c genes, hormone, photosynthesis and antioxidative system in pepper genotypes under salinity stress. *Scientia Horticulturae*, 282, 110041, <https://doi.org/10.1016/j.scienta.2021.110041>.
- SHI, Q., BAO, Z., ZHU, Z., YING, Q., AND QIAN, Q. (2006). Effects of different treatments of salicylic acid on heat tolerance, chlorophyll fluorescence, and antioxidant enzyme activity in seedlings of *Cucumis sativa* L. *Plant Growth Regulation*, 48, 127–135, <https://doi.org/10.1007/s10725-005-5482-6>.
- SINGH, M., NARA, U., KUMAR, A., CHOUDHARY, A., SINGH, H., AND THAPA, S. (2021). Salinity tolerance mechanisms and their breeding implications. *Journal of Genetic Engineering and Biotechnology*, 19(1), 173, <https://doi.org/10.1186/s43141-021-00274-4>.
- TAIBI, K., TAIBI, F., ABDERRAHIM, L. A., ENNAJAH, A., BELKHODJA, M., AND MULET, J. M. (2016). Effect of salt stress on growth, chlorophyll content, lipid peroxidation and antioxidant defense systems in *Phaseolus vulgaris* L. *South African Journal of Botany*, 105, 306–312, <https://doi.org/10.1016/j.sajb.2016.03.011>.
- TURAN, M., EKINCI, M., YILDIRIM, E., GÜNEŞ, A., KARAGÖZ, K., KOTAN, R., AND DURSUN, A. (2014). Plant growth-promoting rhizobacteria improved growth, nutrient, and hormone content of cabbage (*Brassica oleracea*) seedlings. *Turkish Journal of Agriculture and Forestry*, 38, 327–333, <https://doi.org/10.3906/tar-1308-62>.
- VELIKOVA, V., YORDANOV, I., AND EDREVA, A. J. P. S. (2000). Oxidative stress and some antioxidant systems in acid rain-treated bean plants: Protective role of exogenous polyamines. *Plant Science*, 151, 59–66, [https://doi.org/10.1016/S0168-9452\(99\)00197-1](https://doi.org/10.1016/S0168-9452(99)00197-1).
- VERMA, T., BHARDWAJ, S., SINGH, J., KAPOOR, D., AND PRASAD, R. (2022). Triacntanol as a versatile plant growth regulator in overcoming negative effects of salt stress. *Journal of Agriculture and Food Research*, 10, 100351, <https://doi.org/10.1016/j.jafr.2022.100351>.
- VIJAYAN, K., CHAKRABORTI, S. P., SHYAMA, P., ERCISLI, S., AND GHOSH, P. D. (2008). NaCl induced morpho-biochemical and anatomical changes in mulberry (*Morus* spp.). *Plant Growth Regulation*, 56(1), 61–69, <https://doi.org/10.1007/s10725-008-9284-5>.
- WANG, C., WEI, L., ZHANG, J., HU, D., GAO, R., LIU, Y., FENG, L., GONG, W., AND LIAO, W. (2023). Nitric oxide enhances salt tolerance in tomato seedlings by regulating endogenous S-nitrosylation levels. *Journal of Plant Growth Regulation*, 42, 275–293, <https://doi.org/10.1007/s00344-021-10546-5>.
- WANG, S., CHE, T., LEVIT, A., SHOICHET, B. K., AND WACKER, D. (2018). Structure of the D₂ dopamine receptor bound to the atypical antipsychotic drug risperidone. *Nature*, 555, 269–273, <https://doi.org/10.1038/nature25758>.
- WAŚKIEWICZ, A., BESZTERDA, M., AND GOLIŃSKI, P. (2013). ABA: Role in plant signaling under salt stress. In P. Ahmad, M. M. Azooz and M. N. V. Prasad (Eds), *Salt Stress in Plants: Signaling, Omics and Adaptations* (pp. 175–196). New York, NY, USA: Springer.
- YADAV, S., MODI, P., DAVE, A., VIJAPURA, A., PATEL, D., AND PATEL, M. (2020). Effect of abiotic stress on crops. In M. Hasanuzzaman, M. C. M. T. Filho, M. Fujita and T. A. R. Nogueira (Eds), *Sustainable Crop Production*. IntechOpen, <https://doi.org/10.5772/intechopen.88434>.
- YILDIRIM, E., EKINCI, M., AND TURAN, M. (2022). Biochar mitigates salt stress by regulating nutrient uptake

- and antioxidant activity, alleviating the oxidative stress and abscisic acid content in cabbage seedlings. *Turkish Journal of Agriculture and Forestry*, 46, 28–37, <https://doi.org/10.3906/tar-2104-81>.
- YILDIRIM, E., EKINCI, M., TURAN, M., DURSUN, A., KUL, R., AND PARLAKOVA, F. (2015). Roles of glycine betaine in mitigating deleterious effect of salt stress on lettuce (*Lactuca sativa* L.). *Archives of Agronomy and Soil Science*, 61, 1673–1689, <https://doi.org/10.1080/03650340.2015.1030611>.
- YILDIRIM, E., EKINCI, M., TURAN, M., YUCE, M., ORS, S., ARAZ, O., TORUN, U., AND ARGIN, S. (2024). Exogenous dopamine mitigates the effects of salinity stress in tomato seedlings by alleviating the oxidative stress and regulating phytohormones. *Acta Physiologiae Plantarum*, 46(5), 59, <https://doi.org/10.1007/s11738-024-03656-6>.
- YU, Z., DUAN, X., LUO, L., DAI, S., DING, Z., AND XIA, G. (2020). How plant hormones mediate salt stress responses. *Trends in Plant Science*, 25, 1117–1130, <https://doi.org/10.1016/j.tplants.2020.06.008>.
- ZAHEDI, S. M., HOSSEINI, M. S., FAHADI HOVEIZEH, N., GHOLAMI, R., ABDELRAHMAN, M., AND TRAN, L. S. P. (2021). Exogenous melatonin mitigates salinity-induced damage in olive seedlings by modulating ion homeostasis, antioxidant defense, and phytohormone balance. *Physiologia Plantarum*, 173, 1682–1694, <https://doi.org/10.1111/ppl.13589>.

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