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ORIGINAL ARTICLE

Exogenous dopamine mitigates the effects of salinity stress in tomato seedlings by alleviating the oxidative stress and regulating phytohormones

Ertan Yildirim[1] · **Melek Ekinci**[1] · **Metin Turan**[2] · **Merve Yuce**[1] · **Selda Ors**[3] · **Oğuzhan Araz**[1] · **Umit Torun**[1] · **Sanem Argin**[2]

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Abstract

Salt stress is a worldwide major threat to agricultural production. The aim was to investigate the effects of exogenous dopamine (DA) treatments on physiological, morphological and biochemical characteristics of tomato seedlings under salinity stress. Salt stress was created using a 100 mM NaCl solution. Dopamine solutions (0, 50, 100 and 200 μM) were applied with 7-day intervals. Salt stress significantly suppressed plant growth and DA treatments alleviated the negative effects of salt stress on the growth of tomato seedlings. 100 μM DA treatment increased plant and root dry weights, plant stem diameter, plant height and, leaf area by 286.84%, 150.00%, 108.37%, 160.89%, and 158.28%, respectively, compared to the control. Under salinity LRWC, SPAD, chl-a, chl-b, and total chlorophyll contents decreased; membrane permeability (MP), H_2O_2, MDA, proline and sucrose contents, CAT, POD and SOD activities increased. Under salt stress, when 100 μM DA was applied, LRWC, SPAD, chl-a, chl-b, and total chlorophyll contents of plants increased by 13.64%, 18.62%, 43.08%, 64.90%, and 50.00%, while MP reduced by 21.08% compared to the control. When 200 μM DA was applied under salt stress, H_2O_2, MDA, proline and sucrose contents, and CAT, POD and SOD activities were reduced by 31.86%, 18.66%, 56.00%, 38.24%, 11.16%, 17.81% and 10.80%, respectively, compared to non-DA-treated plants. Exogenous application of DA increased IAA content, decreased ABA content and increased ratio of K^+/Na^+ and Ca^{2+}/Na^+ under salt stress as well. In conclusion, exogenous dopamine treatments effectively prevent cellular damage in tomato seedlings and improve plant tolerance to salt stress.

Keywords Dopamine · Oxidative stress · Physiology · Plant growth · Salt stress · Tomato

Introduction

Salinity is a worldwide problem decreasing the production of most crops and disturbing the ecological balance (Shrivastava and Kumar 2015). Worldwide, approximately 45 million hectares of soil are affected by salinization due to over-irrigation, and 1.5 million hectares of land become unusable every year due to salinity on soil (Munns and Tester 2008).

The direct effect of salt stress on plants is the inhibition of the growth and development due to osmotic stress, ion imbalance and toxicity (Parida and Das 2005). The external osmotic stress resulted from the increase in the amount of salt in the root rhizosphere also causes a decrease in the amount of usable water and this phenomenon is called "physiological drought" (Tuteja 2007). Moreover, there are indirect (secondary) effects of salinity, which involve the production of toxic compounds and structural breakdown in the plant as a result of the stress factors. Synthesis of reactive oxygen species (ROS) that impair DNA, protein, membrane functions and chlorophyll; restriction of photosynthesis; metabolic toxicity; restriction of K^+ uptake are the indirect effects caused by salinity which result in cell and tissue malfunction and even death of

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✉ Ertan Yildirim
ertanyil@atauni.edu.tr

[1] Department of Horticulture, Faculty of Agriculture, Atatürk University, Erzurum, Turkey

[2] Department of Agricultural Trade and Management, Faculty of Economy and Administrative Sciences, Yeditepe University, Istanbul, Turkey

[3] Department of Agricultural Structure and Irrigation, Faculty of Agriculture, Atatürk University, Erzurum, Turkey

plant cells (Botella et al. 2005). Effects of salt stress on plants vary with the type of the plant, the type and concentration of the salt, and the exposure time. In saline environments, plants give very different responses depending on the genotypic differences (Dajic 2006).

Tomato is among the most produced and consumed vegetables in the world. Tomato production is very concentrated in semiarid regions, where saline waters are frequently used for irrigation and salinity problems are most severe. Tomato is a crop that is moderately sensitive to salinity. Breeding new salt-tolerant crop varieties is one strategy to alleviate the adverse impacts of salinity on crop production, but success has been limited (Flowers 2004). Breeding salt-tolerant plants can be very difficult and complex due to the interaction of environmental conditions and many genes (Murillo-Amador et al. 2006). Another approach is to use hormones (serotonin, melatonin, dopamine etc.) to reduce the negative effects of salinity stress (Liu et al. 2018). Despite the promising effects of dopamine on salt stress, the amount of studies is scarce. Dopamine is a type of catecholamine synthesized in humans, plants and animals. The molecular formula of dopamine is $C_8H_{11}NO_2$ and its molecular weight is 153.18 (Wang et al. 2018). Catecholamines are a group of biogenic amines with a 3,4-dihydroxy-substituted phenyl ring and their synthesis is regulated by stress conditions in plants (Kulma and Szopa 2007). Dopamine affects plant growth and development by interacting with phytohormones. Dopamine plays an important role in the intracellular regulation of ion permeability and photophosphorylation of chloroplasts due to its reducing power, which ends with the scavenging of free radicals. (Kulma and Szopa 2007). Researches suggest that catecholamines are involved in plant stress response by increasing resistance to pathogen infection, chilling damage, and salt stress (Dufeu et al. 2003; Li et al. 2015; Skirycz et al. 2005). Dopamine can support the growth of plants under various stressful environments (Jiao et al. 2019). More recent studies have shown that dopamine can improve tolerance to drought, salt stress, and nutrient deficiency in plants (Liang et al. 2017, 2018). Moreover, dopamine can enhance the ability of plants to resist biological stressors. To the authors' best knowledge, this is the first study investigating the effects of exogenous dopamine treatments on tomato seedlings under salinity stress. We hypothesized that exogenous dopamine applications could reduce the negative effects of salinity stress in tomato seedlings. Thus, this study focused to evaluate the potential of dopamine in enhancing the physiological and biochemical attributes of salt stress tolerance in tomato during seedling.

Material and method

Plant material and growth conditions

Tomato plants (*Solanum lycopersicon* L cv H2274) were grown in the greenhouse of Atatürk University, Erzurum under ambient light, at 20–35 °C, and with a relative humidity of 50–75%. To eliminate the position effect, containers were rotated weekly. Standard horticultural practices were followed for disease and pest control.

Tomato seeds were sown into multi-celled plastic trays containing peat. When the seedlings had two true leaves, they were transplanted to the pots (12.5 diameter, 12.5 depth) containing soil:sand:peat medium in the ratio of 2:1:1 (v:v:v). The experimental layout was completely randomized. Some physical and chemical properties of the medium were as follows: Sandy loam texture (26.4% clay, 35.2% silt, and 40.2% sand); the pH (7.1); electrical conductivity (EC) (0.10 dS m^{-1}); organic matter (2.76%); NH_4 –N (1.95 mg kg^{-1}); NO_3-N (0.95 mg kg^{-1}); P (3.1 mg kg^{-1}); K (2.70 cmolc kg^{-1}); Ca (18.00 cmolc kg^{-1}); Mg (2.10 cmolc kg^{-1}); Na (0.20 cmolc kg^{-1}); Fe (4.20 mg kg^{-1}); Mn (0.55 mg kg^{-1}); Zn (0.30 mg kg^{-1}); Cu (0.68 mg kg^{-1}); B (0.75 mg kg^{-1}); and $CaCO_3$ (2.4%).

Dopamine and salinity treatments

Dopamine (Dopamine hydrochloride, Sigma Aldrich, St. Louis, MO, USA) solutions of 0, 50, 100 and 200 µM (pH 6.0–6.5) were prepared with distilled water containing 0.02% Tween 20 (polyoxyethylene sorbitan monolaurate, Sigma Chemicals, UK). Dopamine concentrations were determined according to the studies of Li et al. (2015), Liang et al. (2018) and Ahmad et al. (2021). Dopamine solutions were applied during late afternoon hours with 7-day intervals using a hand-held sprayer when the seedlings had four complete true leaves. In order to avoid interferences with different moisture levels, a control spray treatment consisting of 0.02% Tween 20 in deionized water was applied to the treatments not receiving DA at a given time. During spraying, care has been taken to ensure that both surfaces of the leaves are completely wet. Before transplanting seedlings, soil moisture was fixed to 90% of the field capacity and pots were irrigated twice a week during the study. A portable moisture meter (HH2 Moisture Meter, WET Sensor, Delta-T Devices, Cambridge, England) was used to measure the field capacity.

Salt treatments were applied two days after transplantation. Salinity concentration was determined according to Wu et al. (2011). The first two irrigations were made with 25 mM and 50 mM NaCl solutions (Sodium chloride 99.99

Suprapur®. CAS No. 7647–14-5, EC Number 231–598-3) to avoid osmotic shock. A 100 mM NaCl solution was used for the rest of the irrigations. Half-strength Hoagland solution was given once a week with saline solutions. The electrical conductivities (EC) of soils were determined with a portable EC meter (HH2 Moisture Meter, WET Sensor, Delta-T Devices, Cambridge, England). EC of non-saline and saline soils were measured as 1.54 dS m^{-1} and 5.68 dS m^{-1}, respectively.

Measurements and analysis

Growth parameters

The study was terminated 40 days after the seedling transplantation. Plant height, stem diameter, leaf area, seedling dry weight and root dry weight were determined. For dry weight measurements, the plant material was dried at 70 °C for 48 h. The leaf area was determined by using a leaf area meter (CI-202 Portable Laser Leaf Area Meter by CID Bio-Science, USA).

Chlorophyll reading values

The amount of chlorophyll was determined by the method defined by Lichtenthaler and Buschmann (2001). The equations below were used to calculate the amounts of chlorophyll a, chlorophyll b and total chlorophyll in fresh weight (mg g^{-1}). Where V is the extraction volume and W is the sample weight:

$$\text{Chlorophyll a}\left(\text{mg g}^{-1}\right) = (12.7 * 663\ \text{nm}) - (2.69 * 645\ \text{nm}) * V/W * 10000$$

$$\text{Chlorophyll b}\left(\text{mg g}^{-1}\right) = (22.91 * 645\ \text{nm}) - (4.68 * 663\ \text{nm}) * V/W * 10000$$

$$\text{Total chlorophyll}\left(\text{mg g}^{-1}\right) = \text{chlorophyll a} + \text{chlorophyll b}$$

Physiological properties

Leaf relative water content (LRWC) was determined by the method of Smart and Bingham (1974). The leaf discs (1 cm in diameter) were cut from randomly selected plants (5 discs for each replicate), and were immediately weighed for fresh weight determination (FW). Then, leaf discs were placed in distilled water for 5 h to determine the turgor weights. Finally, discs were oven dried at 72 ℃ for 48 h and weighed for dry weight (DW) determination. Tissue water content was calculated according to the following equation (Arora et al. 1998):

$$\text{LRWC}\ (\%) = \left[(\text{FW} - \text{DW})/(\text{TW} - \text{DW})\right] \times 100.$$

Biochemical properties

Superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) activities were determined based on the method given by Sahin et al. (2018). Leaf materials (1 mg) were ground in 6 ml of ice cold 50 mM potassium phosphate buffer solution (pH 7.0) containing 2 mM sodium EDTA and 1% (w/v) polyvinyl–polypirrolidone (PVP). The homogenates were centrifuged at 10,000 × g at 4 °C for 10 min. The tissue extracts were used for analyses of enzyme activity. SOD, CAT and POD activities were spectrophotometrically measured at 560 nm, 240 nm and 436 nm, respectively.

Proline contents were determined according to the slightly modified method of Bates et al. (1973) by using the absorbance values at 528 nm. The amount of H_2O_2 in the leaves was quantified as described by Loreto and Velikova (2001) at 390 nm. Malondialdehyde (MDA) content was measured with the method by Heath and Packer (1968). The concentration of MDA was determined from the absorbance curve, by using an extinction coefficient of 155 mM^{-1} cm^{-1}. The amount of sucrose was determined in the spectrophotometer at 620 nm according to Wu et al. (2011)

Hormone analysis

Extraction and purification of samples for hormone analysis were performed as described by Kuraishi et al. (1991) and Battal and Tileklioglu (2001). Indole acetic acid (IAA) and abscisic acid (ABA) were detected at 265 nm using a UV detector (Turan et al. 2014).

Ion content

Plant and root samples were subjected to combustion in nitric acid-hydrogen peroxide (2: 3) acid solutions in a microwave wet combustion unit resistant to 40 bar pressure (Speedwave MWS-2 Berghof products + Instruments Harresstr.1. 72,800 Enien, Germany) prior to mineral element analyses to determine K, Ca, and Na contents spectrophotometrically (Optima 2100 DV, ICP/OES; Perkin-Elmer, Shelton, CT) according to Mertens (2005a) and Mertens (2005b).

Statistical analysis

The study was conducted in three replications, 5 pots in each repeat as according to the completely randomized design (CRD), and was analysed in a 2 × 4 factorial experiment design (SPSS 18 program (IBM, NY, USA) were used for data analyse. Differences between means of analysis of variance (ANOVA) were identified by Duncan multiple comparison test (SPSS 2010).

Results

Salinity treatments (100 mM NaCl) significantly suppressed plant growth, causing a diminution in plant height by 46.66%, plant dry weight by 70.67%, root dry weight by 60.00%, stem diameter by 41.11%, and leaf area by 55.53%, compared to control treatment (no salt) (Figs. 1, 2, 3, 4 and 5). The dopamine (DA) treatments alleviated the decrease in tomato seedlings growth under salinity.100 µM DA treatment increased plant dry weight, root dry weight, plant height, plant stem diameter and leaf area by 286.84%, 150.00%, 108.37%, 160.89%, and 158.28%, respectively, compared to non-DA treatment under salt stress. Dopamine positive effect on salt tolerance of tomato seedlings were found statistically significant, and the most effective dose levels were 112 µM for plant dry weight, 110 µM for root dry weight, 104 µM for plant height, 129 µM for plant stem diameter and 108 µM for leaf area according to the regression analysis (Figs. 1, 2, 3, 4 and 5).

Salt stress statistically affected membrane permeability (MP), chlorophyll reading value (SPAD), LRWC, chl-a, chl-b, and total chlorophyll contents compared to the control treatment (Table 1). While MP increased by 128.86%, LRWC, SPAD, chl-a, chl-b, and total chlorophyll contents decreased by 23.74%, 20.20%, 34.34%, 40.78% and 36.62%, respectively, under 100 mM NaCl compared to control. The favourable results were obtained from 100 µM DA dose under salt stress: MP reduced by 21.08%, while LRWC, SPAD, chl-a, chl-b, and total chlorophyll contents of plants increased by 13.64%, 18.62%, 43.08%, 64.90%, and 50.00% compared to non-DA treated plants (Table 1).

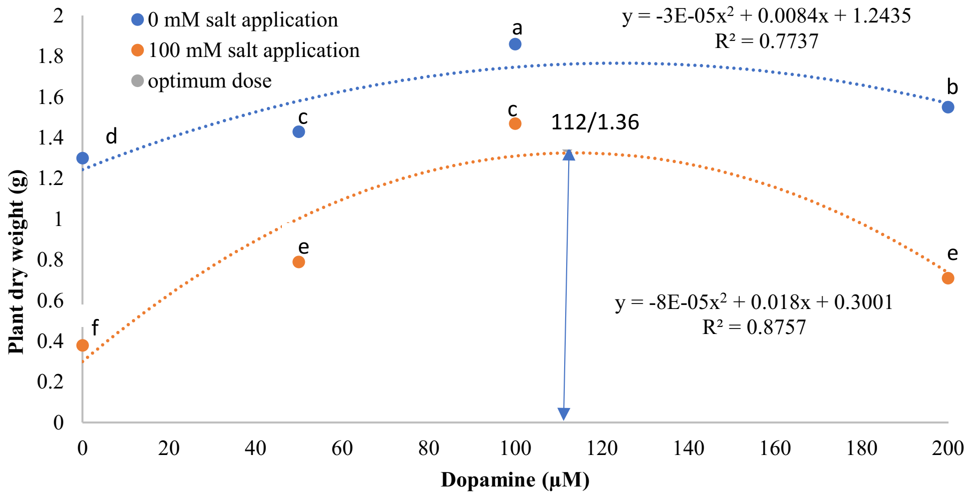

Fig. 1 Effects of dopamine application on plant dry weight of tomato seedlings under salt stress

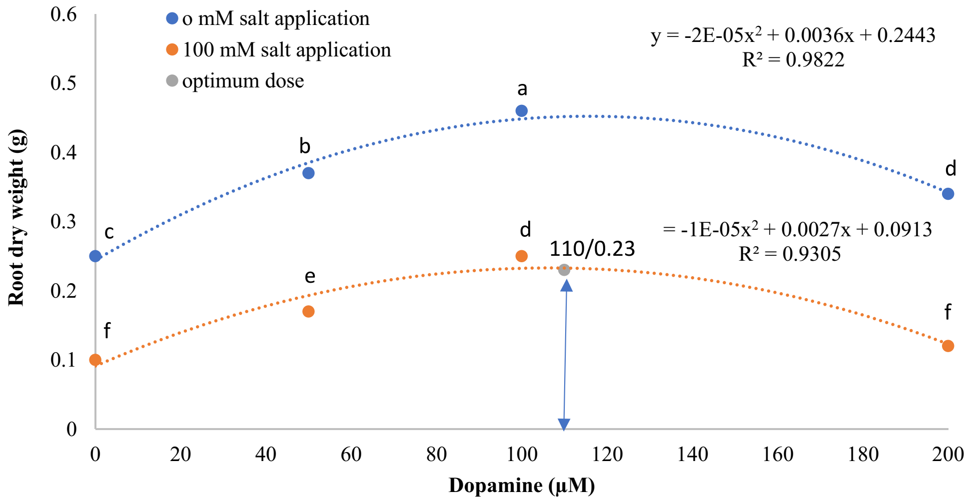

Fig. 2 Effects of dopamine application on root dry weight of tomato seedlings under salt stress

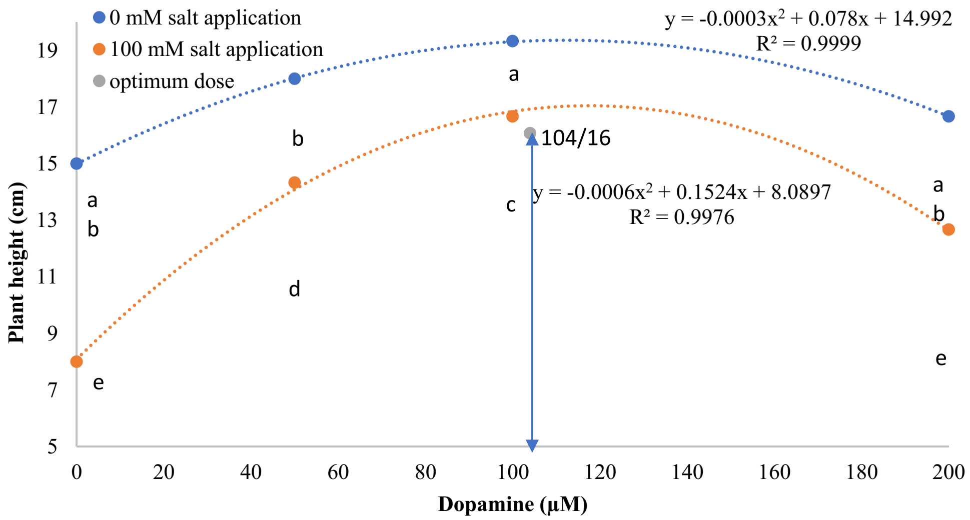

Fig. 3 Effects of dopamine application on plant height of tomato seedlings under salt stress

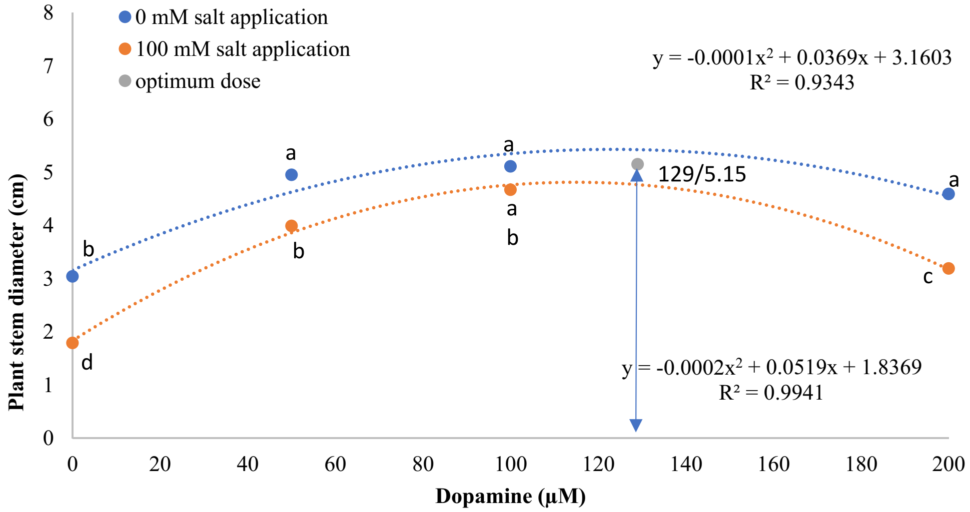

Fig. 4 Effects of dopamine application on stem diameter of tomato seedlings under salt stress

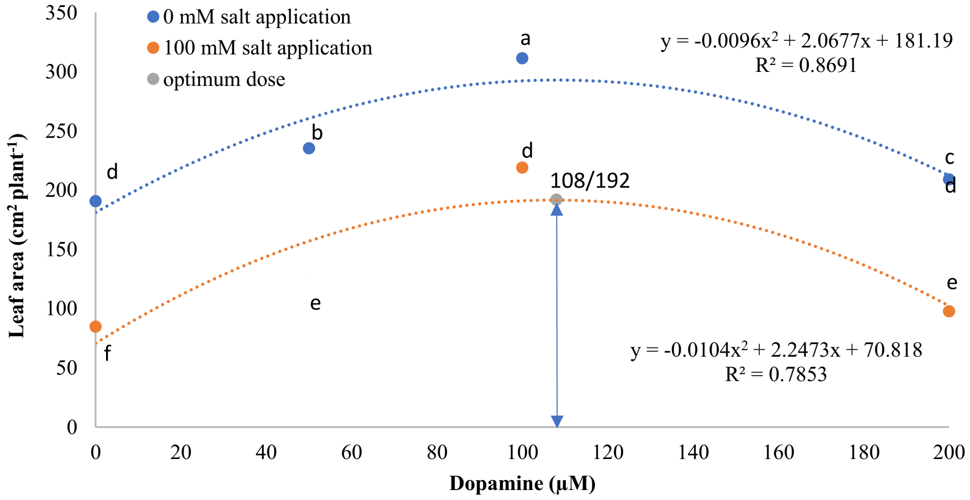

Fig. 5 Effects of dopamine application on leaf area of tomato seedlings under salt stress

Table 1 Effects of dopamine application on membrane permeability (MP), leaf relative water content (LRWC), chlorophyll reading value (SPAD), chlorophyll a, chlorophyll b, and total chlorophyll contents of tomato seedlings under salt stress

Salt	Dopamine Treatment	MP (%)	LRWC (%)	Chlorophyll reading value (SPAD)	Chlorophyll a (mg g^{-1})	Chlorophyll b (mg g^{-1})	Chlorophyll total (mg g^{-1})
0 mM	0 µM	28.03 ± 1.98 d	71.61 ± 2.91 b	50.00 ± 3.10 ab	4.95 ± 0.09 b	2.55 ± 0.04 bc	7.51 ± 0.12 bc
	50 µM	21.99 ± 2.33 e	72.42 ± 3.90 b	51.63 ± 2.85 a	5.45 ± 0.18 a	3.12 ± 0.25 a	8.57 ± 0.43 a
	100 µM	19.64 ± 2.10 e	72.89 ± 2.53 b	51.10 ± 1.14 a	4.84 ± 0.12 bc	2.72 ± 0.14 b	7.56 ± 0.11 b
	200 µM	23.86 ± 3.09 e	78.43 ± 2.23 a	52.77 ± 1.40 a	5.36 ± 0.19 a	3.05 ± 0.08 a	8.42 ± 0.24 a
100 mM	0 µM	64.15 ± 1.59 a	54.61 ± 0.96 e	39.90 ± 0.62 e	3.25 ± 0.07 f	1.51 ± 0.06 f	4.76 ± 0.15 e
	50 µM	59.05 ± 1.95 b	59.59 ± 1.31 cd	44.23 ± 0.55 d	4.34 ± 0.10 d	2.31 ± 0.10 de	6.65 ± 0.18 d
	100 µM	50.63 ± 2.40 c	62.06 ± 1.53 c	47.33 ± 0.31 bc	4.65 ± 0,06 c	2.49 ± 0.04 cd	7.14 ± 0.02 c
	200 µM	56.39 ± 3.04 b	56.83 ± 0.28 de	45.53 ± 0.80 cd	4.09 ± 0,11 e	2.23 ± 0.09 e	6.32 ± 0.20 d
Mean Treatments	0 µM	46.09 ± 19.85 A	63.11 ± 9.51 B	44.95 ± 5.88 B	4.10 ± 0.94 C	2.03 ± 0.57 B	6.13 ± 1.51 B
	50 µM	40.52 ± 20.38 B	66.01 ± 8.64 A	47.93 ± 4.45 A	4.90 ± 0.62 A	2.71 ± 0.48 A	7.61 ± 1.09 A
	100 µM	35.14 ± 17.09 C	67.47 ± 6.22 A	49.22 ± 2.19 A	4.75 ± 0.13 AB	2.61 ± 0.16 A	7.35 ± 0.24 A
	200 µM	40.13 ± 18.02 B	67.63 ± 11.92 A	49.15 ± 4.09 A	4.73 ± 0.71 B	2.64 ± 0.46 A	7.37 ± 1.16 A
Mean Salt	0 mM	23.38 ± 3.81 B	73.84 ± 3.78 A	51.38 ± 2.21 A	5.15 ± 0.30 A	2.86 ± 0.28 A	8.01 ± 0.55 A
	100 mM	57.56 ± 5.46 A	58.27 ± 3.09 B	44.25 ± 2.90 B	4.08 ± 0.11 B	2.14 ± 0.39 B	6.22 ± 0.94 B

Data represent the average of three replicates (± SD). Different letters in each column indicate a significant difference at $P \leq 0.001$

Under salt stress, H_2O_2, MDA, proline and sucrose contents, as well as CAT, POD and SOD activities increased by 40.20%, 32.89%, 108.33%, 48.27%, 19.10%, 19.52% and 18.85%, respectively, compared to the control treatment with non-stressed plants. When 200 µM DA was applied under saline conditions, H_2O_2, MDA, proline and sucrose contents, and CAT, POD and SOD activities were reduced by 31.86%, 18.66%, 56.00%, 38.24%, 11.16%, 17.81% and 10.80%, respectively, compared to the non-DA-treatment (Table 2).

IAA content of tomato seedlings under saline conditions decreased by 91.89% whereas ABA content increased by 66.70% as compared to the contents of non-stressed plants (Fig. 6 and 7). Application of 100 µM exogenous DA increased IAA content by 36.75% and decreased ABA content by 36.86% compared to the non-DA treated plants under salt stress. Most effective doses of DA for IAA and ABA were determined as 115 µM, and 117 µM, respectively according to the regression analysis.

Ratio of Ca^{2+}/Na^+ and K^+/Na^+ were significantly altered by salt and DA treatments (Table 3). Under salt stress, the ratio of Ca^{2+}/Na^+ and K^+/Na^+ in plants decreased by 78.83% and 77.43%, respectively compared to the control treatments.

Table 2 Effects of dopamine application on H_2O_2, MDA, proline and sucrose content, and CAT, POD and SOD activity of tomato seedlings under salt stress

Salt	Dopamine Treatment	H_2O_2 (mmol kg^{-1})	MDA (mmol kg^{-1})	Proline (mmol kg^{-1})	Sucrose (%)	CAT (eu g $leaf^{-1}$)	POD (eu g $leaf^{-1}$)	SOD (eu g $leaf^{-1}$)
0 mM	0 µM	35.57 ± 1.29 bc	15.84 ± 0.49 de	0.24 ± 0.02 de	2.61 ± 0.04 d	414 ± 26.16 bcd	20,774 ± 347.99 ef	1745 ± 40.32 cd
	50 µM	36.24 ± 0.51 b	15.05 ± 0.70 e	0.33 ± 0.02 b	2.56 ± 0.17 de	409 ± 26.72 cd	20,067 ± 719.92 f	1689 ± 57.72 cd
	100 µM	31.59 ± 1.22 ef	15.31 ± 0.53 de	0.24 ± 0.01 de	2.93 ± 0.16 c	419 ± 14.24 bcd	26,821 ± 959.41 c	1845 ± 23.79 b
	200 µM	30.96 ± 1.29 f	15.87 ± 0.39 de	0.22 ± 0,01 e	2.42 ± 0.07 de	401 ± 2.76 d	28,865 ± 1571.28 b	1772 ± 40.08 bc
100 mM	0 µM	49.87 ± 0.86 a	21.05 ± 0.90 a	0.50 ± 0.04 a	3.87 ± 0.05 a	493 ± 7.97 a	24,828 ± 339.62 d	2074 ± 24.07 a
	50 µM	33.23 ± 0.41 de	16.26 ± 0.23 cd	0.28 ± 0.01 c	3.22 ± 0.13 b	444 ± 15.95 b	21,815 ± 914.87 e	1675 ± 58.0 d
	100 µM	36.50 ± 1.29 b	18.15 ± 0.25 b	0.26 ± 0.01 cd	3.32 ± 0.10 b	444 ± 6.28 b	31,152 ± 330.15 a	1771 ± 59.60 bc
	200 µM	33.98 ± 0.62 cd	17.12 ± 0.06 c	0.22 ± 0.02 e	2.39 ± 0.06 e	438 ± 11.70 bc	20,405 ± 561.12 ef	1850 ± 44.90 b
Mean Treatments	0 µM	42.72 ± 7.90 A	18.45 ± 2.92 A	0.37 ± 0.14 A	3.24 ± 0.69 A	454 ± 46.66 A	22,801 ± 2241.81 C	1910 ± 182.17 A
	50 µM	34.73 ± 1.70 B	15.66 ± 0.81 C	0.30 ± 0.03 B	2.89 ± 0.38 B	424 ± 25.89 B	20,941 ± 1207.04 D	1682 ± 52.73 C
	100 µM	34.04 ± 2.91 B	16.73 ± 1.60 B	0.25 ± 0.02 C	3.13 ± 0.24 A	431 ± 16.87 B	28,986 ± 2457.74 A	1808 ± 57.47 B
	200 µM	32.47 ± 1.88C	16.50 ± 0.72 B	0.22 ± 0.01 D	2.40 ± 0.06 C	420 ± 21.92 B	24,635 ± 4752.33 B	1811 ± 57.33 B
Mean Salt	0 mM	33.59 ± 2.62 B	15.52 ± 0.59 B	0.26 ± 0.05 B	2.63 ± 0.22 B	411 ± 18.41 B	24,132 ± 4049.01 ns	1763 ± 68.73 B
	100 mM	38.39 ± 7.07 A	18.14 ± 1.92 A	0.31 ± 0.12 A	3.20 ± 0.56 A	454 ± 25.67 A	24,550 ± 4345.76	1842 ± 159.37 A

Data represent the average of three replicates (± SD). Different letters in each column indicate a significant difference at $P \leq 0.001$

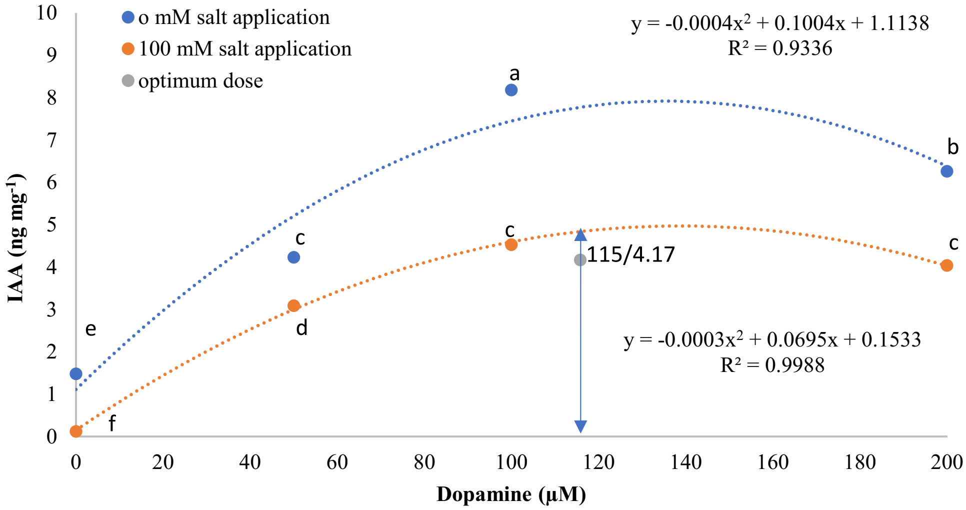

Fig. 6 Effects of dopamine application on IAA content of tomato seedlings under salt stress

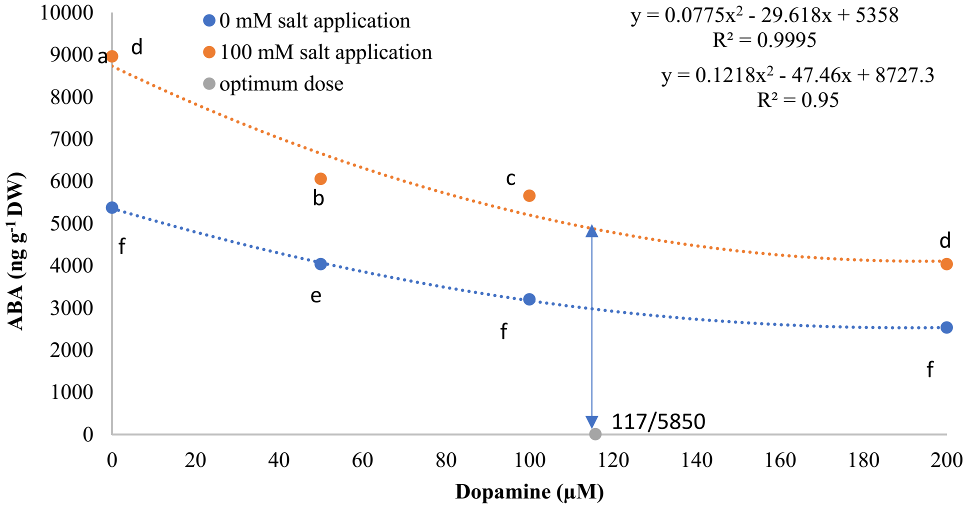

Fig. 7 Effects of dopamine application on ABA content of tomato seedlings under salt stress

However, exogenous DA applications increased K^+/Na^+ and Ca^{2+}/Na^+ ratios under salt stress conditions.

Discussion

As expected, the results of the study showed that salinity negatively affected the growth characteristics of tomato seedlings (Figs. 1, 2, 3, 4 and 5). Salinity in the root zone restricts plant development and morphology by negatively altering various features of biochemistry and physiology of plants (Shams et al. 2019, 2020; Dadasoglu et al. 2021; Shams and Yildirim 2021; Ekinci et. al. 2021). However, our results showed that application of dopamine effectively alleviated the aforementioned negative effects of salt stress on plant growth and morphology. Application of dopamine significantly increased plant dry weight, root dry weight, plant height, plant stem diameter and leaf area under salt stress. Lan et al. (2020) also stated that exogenous dopamine significantly increased plant height, stem diameter, dry weight and fresh weight under nitrate stress, and they reported that 100–150 µM dopamine was the most effective dose. Since salinity is an as osmotic stress creator, the LRWC was reduced (Table 1) and as a result of that, a decrease was observed in the ratios of dry and fresh matter in leaves and roots due to the osmotic adjustment in the plant.

As given in Table 1, salt stress decreased the chlorophyll content of tomato seedlings. Stressed plant minimizes or closes its stomata to prevent water loss, however, this precaution restricts the nutrient uptake and CO_2 entrance to the leaf cells. Decreased carbon dioxide and water content together with insufficient nutrient uptake cause a sharp decline in the photosynthesis. According to Marschner (2012), deficiencies of Fe^{2+} and Mg^{2+} reduce chlorophyll synthesis under these conditions. Generally, chlorophyll a and b contents decrease with salt stress as a result of the damage in the chlorophyll membranes. It can be suggested

Table 3 Effects of dopamine application on K^+/Na^+ and Ca^{2+}/Na^+ ratios under salt stress

Salt	Dopamine Treatment	K^+/Na^+ (mg kg^{-1})	Ca^{2+}/Na^+ (mg kg^{-1})
0 mM	0 µM	119.67 ± 4.04 a	80.33 ± 3.40 b
	50 µM	123.33 ± 2.08 a	83.00 ± 1.73 b
	100 µM	107.00 ± 7.21 b	65.33 ± 4.93 c
	200 µM	119.33 ± 5.86 a	95.00 ± 5.57 a
100 mM	0 µM	27.00 ± 1.00 d	17.00 ± 1.01 e
	50 µM	47.67 ± 4.10 c	34.00 ± 1.70d
	100 µM	52.00 ± 5.00 c	33.00 ± 1.37 d
	200 µM	52.00 ± 4.36 c	36.33 ± 2.52 d
Mean Treatments	0 µM	73.33 ± 50.82 C	48.67 ± 34.78 C
	50 µM	85.50 ± 41.54 A	58.50 ± 26.88 B
	100 µM	79.50 ± 30.46 B	49.17 ± 17.99 C
	200 µM	85.67 ± 37.17 A	65.67 ± 32.37 A
Mean Salt	0 mM	117.33 ± 7.81 A	80.92 ± 11.63 A
	100 mM	44.67 ± 11.11 B	30.08 ± 8.12 B

Data represent the average of three replicates (± SD). Different letters in each column indicate a significant difference at $P \leq 0.001$

that this deterioration is observed in pigments as a result of weakening of the protein-pigment-lipid complex caused by salt or increased chlorophyllase enzyme activity (Suriyan and Chalermpol 2009). Table 1 show that exogenous DA treatments increased the chlorophyll content of tomato seedlings under salt stress, which indicates the role of DA in protecting protein- pigment–complexes. Similar to our results, Abdelkader et al. (2012) also suggested that exogenous DA treatments enhanced photosynthetic activities of salt stressed rice plants.

Intensive accumulation of Na^+ and Cl^- ions in the plants growing under salt stress causes nutritional imbalance, thus nutrient deficiency. Moreover, this accumulation also increases synthesis of ROS which results in DNA damage, reduced protein and chlorophyll syntheses as well as membrane function impairment (Botella et al. 2005; Hu and Schmidhalter 2005; Hong et al. 2009). As it can be seen in Table 2, salt stress increased H_2O_2 and MDA contents of tomato seedlings. H_2O_2 is known as a strong oxidant that is produced under abiotic stress and MDA is the major reactive aldehyde. Under salinity conditions lipid composition in the cell membrane may change or irregularities in the hydrolysis of phospholipids may occur. The elevated levels of H_2O_2 due to the oxidative damage in the cell membranes cause an increase in the MDA content, which makes cell membranes more permeable (Table 1). In accordance with our results, Gao et al. (2020a) also reported that exogenous dopamine mitigated the oxidative stress caused by salt stress-induced (200 mM NaCl) excessive accumulation of ROS in *Malus domestica* growth. Our results showed that exogenous DA application reduced the MP, H_2O_2 and MDA contents of tomato seedlings under saline conditions (Table 1 and Table 2). Similarly, Li et al. (2015) reported that DA treatments lowered H_2O_2 content of Malus seedlings under salt stress and Liang et al. (2018) found that DA is effective in scavenging free radicals.

Table 2 shows saline conditions increased the proline and sucrose contents of tomato seedlings since plants tend to accumulate proline and sucrose to improve their salt tolerance (Kishor et al. 2005; Hasegawa et al. 2000). On the other hand, DA treatment reduced proline and sucrose accumulation. Similarly, Abdelkader et al. (2012) found that DA caused a decline in proline content in rice under salt stress conditions. On the other hand, Ahmad et al., (2021) reported an increase proline content due to hydrocarbon toxicity and exogenous DA application caused a further increase. The maximum POD, SOD, and CAT activities in tomato seedlings were observed under saline conditions (Table 2). Since dopamine is known as a powerful antioxidant that can lessen ROS damage, a reduction was observed in antioxidant enzyme activity in tomato seedlings under salinity stress with DA treatment (Table 2). Gao et al. (2020b) has suggested that dopamine regulates antioxidant enzyme activity by activating Ca^{2+} signalling pathway through increased expression of CaM/CML genes. This mechanism might be the underlying reason of the reduction in antioxidant enzyme activity since calcium uptake is increased in tomato seedlings with dopamine application.

Figures 6 and 7 show that under salt stress IAA content decreased and ABA content increased. However, after a critical application concentration of DA, hormone content of tomato seedlings was stabilized under salt stress. Since DA regulated the ion balance, the phytohormones reached the regular levels despite the salt stress. Similar findings on the change of phytohormone levels with DA treatment were reported by Abdelkader et al. (2012), and Dai et al. (1993).

K^+/Na^+ and Ca^{2+}/Na^+ ratios were decreased under salt stress; however, application of DA elevated these ratios (Table 3). Salinity induced a nutrition disorder via its physiological effects on nutrient availability, competitive uptake, transport or partitioning within the cell, which influence the plant performance and productivity. Many studies stated that exogenous application of DA increased K^+ content and decreased Na^+ accumulation in the above-ground parts of different plants grown in saline soil (Li et al. 2015). This can be also an explanation of increased LRWC with dopamine application since K^+/Na^+ ratio is enhanced as an effect of dopamine, which regulated by osmotic potential. Since the balance between Na^+ and K^+ is crucial for salt tolerance, this remediation effect of DA on tomato seedlings becomes more critical. Previous studies also stated that dopamine alleviates the salt stress not only by influencing antioxidant defences but also by other processes of ion homeostasis (Li et al. 2015; Lan et al. 2021; Ahammed and Li 2023). On the other hand, the specific ionic and molecular mechanisms of DA in the control of ion transport modulation and intracellular ionic homeostasis in salt-stressed plants are not completely known.

Conclusions

Salt stress is a major threat to agricultural production. The data suggest that dopamine application can ameliorate the detrimental effects of salinity on plant growth due to its potent antioxidant capacity and positive effect on plants' water use efficiency. Our results showed that the exogenous DA treatment improved plant growth significantly under salt stress, especially with doses over 100 µM DA. We have also shown that DA regulates ion transport, sugar mechanism and phytohormones which reduce the negative impacts of salt stress on tomato seedlings. In conclusion, under saline conditions, exogenous dopamine treatments effectively provide protection against cellular and macromolecular damage in tomato seedlings and improve plant tolerance to salt stress.

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Data availability No data was used for the research described in the article.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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