



Unveiling the role of cadaverine in mitigating salinity and/or Bisphenol A toxicity in tomato plants and reduced Bisphenol A accumulation in tomato roots

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ABSTRACT

Mitigating the co-existence of environmental stresses on crop plants necessitates the development of integrated, eco-friendly, and sustainable approaches to alleviate plant stress responses. This study represents the first attempt to mitigate the toxic impact of prevalent pollutant (salinity) and an emergent plastic manufacturing pollutants (bisphenol A, BPA) using the polyamine (cadaverine). Tomato plants, treated with or without cadaverine, were subjected to NaCl salinity (120 mM), BPA (375 mg kg⁻¹ soil), and their combinations compared to non-stressed control plants examining morphological, physiological, metabolic, and molecular responses. After 10 days of transplanting, tomato plants under combined stress were unable to survive without cadaverine application. However, cadaverine spraying mitigated the damaging effects of both single and combined stresses under short- and long-term exposure, enabling stressed plants to endure the conditions and complete their life cycles. Cadaverine efficiently restrained the reduction in chlorophylls, carotenoids, and cytosolutes under applied stresses compared to the stressed plants. Cadaverine also increased α -tocopherol content (by 171 and 53 %) and enhanced the activity of polyphenol oxidase (by 26 and 32 %), glutathione s-transferases (by 18 and 39 %), superoxide dismutase (by 23 and 46 %), and phenylalanine ammonia-lyase (by 9 and 25 %), under BPA and salinity stress, respectively. Thus, cadaverine ameliorated the oxidative and nitrosative burst induced by BPA or salinity, respectively by declining hydroxyl radical (by 28 % and 20 %), superoxide anion (by 73 % and 74 %), nitric oxide (by 60 and 65 %), lipid peroxidation (by 35 % and 54 %), and lipoxygenase activity (by 74 and 68 %). Moreover, cadaverine enhanced the expression of defence-related genes, including polyphenol oxidase, tubulin, and thaumatin-like protein, and reduced the uptake of BPA in the tomato's roots while promoting its metabolism in leaves and fruits. This ensured the safety of the harvested fruits. By mitigating stress, improving plant resilience, and limiting pollutant accumulation, cadaverine presents significant potential for sustainable agricultural practices and food safety. These findings offer valuable insights into the role of cadaverine in managing abiotic stress and safeguarding crop health in environmentally challenging conditions.

1. Introduction

Occurrences of abiotic stress significantly reduce the growth and yield of numerous crops worldwide, including tomatoes

(Sánchez-Bermúdez and Pernas, 2022). Abiotic stress, such as light, drought, heat, cold, nutrient deficiencies and excess salt or toxic metal levels or emerging contaminants in the soil, cause anatomical alterations, osmotic pressure, oxidative stress, ionic stress, and nutritional

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stress on tomatoes. Thus, these stresses disturb tomato metabolic homeostasis and impact various physiological processes in their development (Egea et al., 2022). The tomato plant, *Lycopersicon esculentum* Mill., is one of the most important vegetable crops, ranking among the top three in this category. However, it is highly susceptible to various biotic and abiotic stressors, resulting in substantial economic losses (Abekoon et al., 2024). While the impacts of individual environmental stress on crops have been well-documented, their simultaneous occurrence is more common in natural environments, requiring more attention on uncovering their interactions. Growing interest about the detrimental impacts of plastics (BPA) on ecosystems and organisms, coupled with the exacerbating impact of saline soils on plants due to climate change, underscore the importance of investigating the combined effects of BPA and other abiotic stressors rather than individual studying of BPA.

Bisphenol A (BPA), scientifically designated as 4, 4'-isopropylidenediphenol or 2,2-bis(4 hydroxyphenyl) propane), is a rising environmental concern related to anthropogenic activities. It has been reported that global BPA production has steadily increased and is expected to reach 7.1 million tons by 2027 (Abraham and Chakraborty, 2020), causing detrimental consequences for humans, animals, and plants (Xiao et al., 2020). The release of BPA into the environment occurs along with plastic products through wastewater treatment plant effluents linked to the utilization of BPA in the resins of epoxy or polycarbonate as well as wastewater irrigation and industrial discharges (Zaborowska et al., 2023). It was exhibited that BPA can interfere with the physiological activities of animals and humans, especially those associated with the reproductive and endocrine systems (Delbès et al., 2022). However, there is a lack of extensive research on the phytotoxic impacts of BPA on land-based plant species, and the mechanism via which BPA harms plants remains unclear (Surendran et al., 2023).

Germination, photosynthetic pigments, levels of free radicals, free-radical scavengers enzyme contents, karyokinesis, and cell division are just a few of the physiological and biochemical aspects that have been altered by high levels of BPA, and they have the potential to severely impact the biomass of maize plants (Hussain et al., 2023). It was documented that plants can uptake BPA, translocate to the upper parts, and break it down through their metabolic processes (Ahammed et al., 2020). However, the toxicity of BPA needs to be more comprehensive, especially regarding possible plant defence mechanisms against BPA toxicity. Thus, further research is required to understand the effects that BPA can have on plants.

Salinity stress, a widespread and highly detrimental abiotic stress, poses a complex challenge to crop plants by adversely affecting their metabolic, molecular and physiological systems. Salinity stress decreased plants biomass by directly reducing photosynthetic efficiency, causing osmotic and ionic stress, and increasing photorespiration (Jahan et al., 2023). These results produced oxygen radicals that severely impacted critical biological molecules like genetic materials, proteins, and cellular membranes (Dawood et al., 2022b). Furthermore, saltiness's adverse impacts on crops are attributed to an imbalance in nutrient absorption, hormonal imbalance, and the reduction of major defence-related enzymes or genes in plants (Sofy et al., 2022; Jahan et al., 2023). Hence, addressing the impact of changing climatic conditions, including single or combined salt or BPA stresses, necessitates identifying sustainable solutions for crop adaptation.

Plant tolerance to abiotic stress is a multifaceted phenomenon, and extensive research endeavors have concentrated on elucidating the tolerance mechanisms in tomato plants (Guo et al., 2022). Employing regulators of plant growth is recognized as a potential approach to enhance tolerance to abiotic stress (Oyebamiji et al., 2024). Polyamines have emerged as novel category of biostimulants known to promote plant growth and influence multiple biological processes, including the transcriptome, enzyme production, and the division and differentiation of cells (Dunn and Becerra-Rivera, 2023). Polyamines, including diamine, triamine, and tetramine (putrescine, spermidine, and spermine) are widely acknowledged as plant growth regulators.

The polyamine cadaverine is a diamine that functions as a growth regulator through a distinct biosynthetic pathway. Although differing in structure from putrescine, cadaverine shares a similar mode of action with putrescine (Rajpal and Tomar, 2020). Cadaverine accumulated in multiple crop's tissues due to living and non-living factors (Amini et al., 2023; Gibbs et al., 2021). Reports suggest that plants may absorb cadaverine from their surroundings and utilize it for subsequent metabolic and signaling processes. For instance, Wu et al. (2021) observed that spongy mesophyll absorbed fluorescent cadaverine and translocated into the conducting system through the transmembrane pathway. Like other polyamines, cadaverine has been involved in stress response, such as enhancing seed development and growth parameters (Ozmen et al., 2023). Cadaverine induces multifaceted functions by being a precursor for polyamides, facilitating water absorption, promoting cell survival under stress conditions, and serving as a protective agent for cells deprived of orthophosphate under an oxygen-deprived environment (Ma et al., 2017). Furthermore, cadaverine enhances the ability to tolerate stress conditions, facilitates cellular defence, and increases resistance to insects and other organic and inorganic contaminants (Ozmen et al., 2023).

Significant gaps still need to be understood in plant responses to cadaverine. Despite the existence of numerous studies that improved the detrimental effects of BPA or salinity stress, there is a lack of comprehensive investigations exploring their response to cadaverine application, especially when both stresses co-exist. Thus, this research seeks to i) investigate the differential effects of single or combined stress of NaCl salinity and BPA on tomato plants and their physiological and biochemical responses to cadaverine, ii) elucidate the mechanistic role of cadaverine in mitigating osmotic and oxidative stress caused by these stressors, iii) understand the capacity of cadaverine to induce stress related genes expression under individual and combined stresses, iv) ensure the safety of harvested tomato fruits by using HPLC to monitor the translocation and metabolism of BPA from roots to fruits. To the best of our knowledge, this study is the first to demonstrate the phytotoxicological consequences of common and emergent pollutants, salinity and/or BPA, while uncovering the potential of cadaverine spraying as an eco-friendly and sustainable protective agent. Thus, this study provides basic information for future studies on crop acclimatization under environmental changes and provides practical insights for improving agriculture sustainability.

2. Material and methods

2.1. Soil preparation

In 2022, a pot experiment was conducted at the City of Scientific Research and Technological Application greenhouse, Borg El-Arab, Alexandria, Egypt. The experiment was done under natural temperature, humidity, and light conditions. The pots were lined with a plastic bag filled with 3 kg of soil (1 clay: 2 sandy, w: w). The physical and chemical characteristics of the prepared soils were determined (Table 1). Four sets of pots were prepared: i) saline-treated pots

Table 1

The pH value, total soluble salts (TSS%), organic matter content (OM) mg g⁻¹ dry soil, concentrations of Na, Ca, Mg, Cl, HCO₃⁻, and N (mg g⁻¹ dry soil), K, Cu, Fe, Mn, Ni, Pb, and Zn (µg g⁻¹ dry soil) in the studied soil. Values are means ± SE.

pH	TSS	OM	Na	Ca	Mg	Cl	HCO ₃ ⁻
8.26	0.77	7.72 ±	0.096	0.25	0.38	0.5 ±	2.37 ±
	± 0.02	0.13	± 0.01	± 0.02	± 0.03	0.03	0.17
0.15							
K	Cu	Fe	Mn	Ni	Pb	Zn	N
4.41	2.98	50.04	6.62 ±	0.32	1.19	2.91	0.15 ±
	± 0.12	± 6.95	1.20	± 0.06	± 0.06	± 0.42	0.01
0.01							

(received 120 mM NaCl salinity), ii) BPA-treated pots (received 375 mg kg⁻¹ BPA), iii) mixed soil from salinity and BPA, iv) and control pots (no contamination applied). All the treatments were applied one week before transplanting tomatoes to ascertain their interaction with the soil environment. The salinity and BPA levels were chosen based on previous studies (Abdelmoneim et al., 2023, 2024).

2.2. Plant materials, experimental setup, and cadaverine spraying

The 45-day-old seedlings of tomato hybrid T-186 were transplanted into ready-arranged pots (4 plants per pot). Thus, there were four groups of pots. The pots of each group were classified into two categories: one set sprayed with cadaverine (+Cad) at a concentration of 1.09 mM (selected previously based on a preliminary experiment), 5 mL/plant, and the other set sprayed with distilled water (- Cad). Five pots per treatment were prepared.

Foliar cadaverine application was applied within intervals of 72 h till the harvesting time (30 days). The water content of the soil was kept around the field capacity throughout the experiment until harvesting. The pots received a Hoagland solution once a week to provide plants with the required micro- and macro-nutrients needed to continue their growth to yield production (Hoagland and Arnon, 1938). A schematic representation of the experimental design was presented in Fig. 1. The spraying with cadaverine stopped with the onset of flowering (30 days), and some pots were left for tomatoes' fruit formation and ripening that were harvested for BPA determination after (120 days from transplanting).

2.3. Plant sampling and biochemical analyses

Tomato plants were harvested three times: A) Short-duration, after 10 days of transplanting, the plants under different treatments were collected for fresh and dry weight as well as pigmentation and total protein estimations; B) Long-duration, after 30 days of transplantation, tomatoes under T1 or/and T2 sprayed with/without cadaverine were

collected for phenological, physiological, and gene expression studies; C) After 120 days, the ripened tomato fruits were collected for BPA determination.

2.3.1. Determination of growth parameters of tomato plants and primary metabolites

After harvesting, the immediate weights of the shoots and roots were registered, and then the shoots and roots were placed in a well-ventilated oven at 70 °C for 2 days to estimate their dry weight. The pigment fractions (chlorophyll a (Chl a), chlorophyll b (Chl b), and total carotenoids (TC)) were estimated using the spectrophotometric method suggested by Lichtenthaler (1987). Briefly, the fresh tomato leaves were suspended in test tubes with screw caps containing 10 ml of ethanol 60 %, then heated in a water bath at 70 °C until decolorization. The absorbance reading was determined at 452, 644, and 663 nm using a UV-visible spectrophotometer (EMC-NANO-UV, Germany). The content of photosynthetic pigments was determined according to the following equations:

$$\text{Chl a} = (13.36 \times A_{663}) - (5.19 \times A_{644}) \mu\text{g/ml}$$

$$\text{Chl b} = (27.49 \times A_{644}) - (8.12 \times A_{663}) \mu\text{g/ml}$$

$$\text{TC} = ((1000 \times A_{452}) - ((2.13 \times \text{Chl a}) - (97.64 \times \text{Chl b}))) / 209 \mu\text{g/ml}$$

The fresh tomato leaves were ground using liquid nitrogen and then homogenized in a potassium phosphate buffer with a pH of 7.8 for osmolyte estimation. Soluble carbohydrates were quantified using the anthrone sulfuric acid (Fales, 1951; Schlegel, 1956). Leaf extract (ml) was mixed with anthrone reagent, then boiled in a water bath for 7 min, cooling, and the absorbance of the developed color was monitored at 620 nm. Soluble proteins were determined according to the method of Lowry et al. (1951). Lowry C was added to the leaf extract and left for 10 min; diluted Folin reagent (1:2 v/v) was added and mixed well, and then the absorbance of the blue color was determined at 750 nm after 30 min. Free amino acids were analyzed by ninhydrin assays (Lee and Takahashi, 1966). Stannous chloride reagent was added to plant extract,

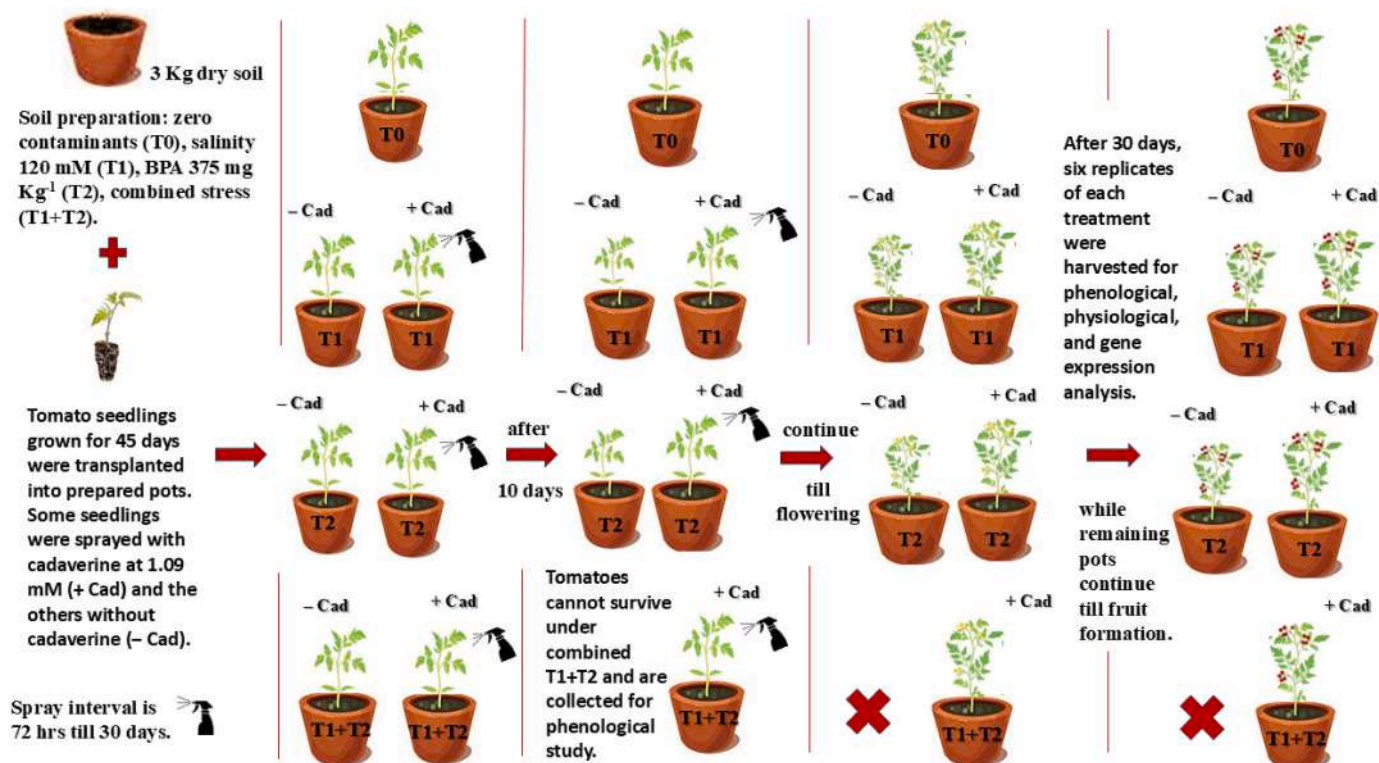


Fig. 1. Soil contamination, cadaverine treatment, and experimental design.

which boiled in a water bath for 20 min, then diluent reagent was applied and mixed well, then the absorbance of the developed purple color was recorded at 570 nm. The ninhydrin reagent method determined the leaf's proline contents (Bates et al., 1973). The supernatant of sulfosalicylic acid extract of tomato leaves was combined with a mixture of (ninhydrin and glacial acetic acid) for 45 min under 95 °C using a water bath. Following the cooling process, toluene was subsequently introduced and well-shaken. The reading of the extracted proline was monitored at 520 nm.

2.3.2. Determination of oxidative agents and nitric oxide content

The levels of free radicals in tomato leaves were measured using the established methods (Halliwell, 1977; Halliwell et al., 1987; Mukherjee and Choudhuri, 1983). For H₂O₂, leaves were homogenized in cold acetone and centrifuged; then, the supernatant was combined with a sulfuric acid-titanium dioxide reagent to measure the resulting color at 420 nm. To determine the concentration of O₂^{•-}, the fresh leaves were homogenized in a potassium phosphate buffer. After centrifugation, the supernatant was combined with hydroxylamine hydrochloride and naphthylamine. The optical density of the chromophores was measured at 520 nm. For OH[•], the fresh leaves were suspended in potassium phosphate buffer containing 2-deoxy-D-ribose at 37 °C for 2 h. A mixture of glacial acetic acid and 2-thiobarbituric acid dissolved in sodium hydroxide was added to the suspending solution, which was then boiled for 10 min. After centrifugation, the absorbance of the developed color was read at 532 nm. The content of nitric oxide (NO) was determined in the leaves of tomato plants using the kit procedure (CAT. No. NO 2533) purchased from a Biodiagnostic company in Giza, Egypt. The absorbance was read at 540 nm. Sulphanilamide was added to the enzyme extract and left for 5 min, N-(1-naphthyl)-ethylenediamine was added, mixed well, and left to stand for 5 min.

2.3.3. Determination of membrane damage biomarkers

The Lipid peroxidation product, malondialdehyde MDA, content was determined on leaves at 534 nm using the MDA detection kit (CAT. No. MD 2529), which was purchased from Biodiagnostic Company, Giza, Egypt. The sample was mixed well with chromogen (thiobarbituric acid, detergent, and stabilizer) and heated in a boiling water bath for 30 min. The lipoxygenase (EC. 1.13.11.12, linoleate: oxygen 13-oxidoreductase) activity was estimated by using linoleic acid as substrate according to Axelrod et al. (1981). The reaction mixture comprised 10 µL of plant extract, 20 µL of 10 mM sodium linoleate, and 1000 µL of 50 mM sodium phosphate buffer at a pH of 6.5. After 2 min, the activity was quantified at a wavelength of 234 nm. The enzyme activity was determined using the molar extinction coefficient 25.000 M⁻¹ cm⁻¹.

2.3.4. Determination of secondary metabolites and non-enzymatic free-radical scavengers

The methods previously outlined were used to estimate the flavonoid and anthocyanin contents (Krizek et al., 1998; Zou et al., 2004). The flavonoid content was estimated by using a methanolic extract of leaf tissues. The methanolic extract was combined with NaOH for 5 min, followed by NaNO₂ for 6 min, and then AlCl₃ was added, and the mixture was incubated for 6 min. The resulting mixture was then diluted to a final volume of 5 mL using distilled water. The color's intensity was quantified at 510 nm using a UV-Visible Spectrophotometer, EMC-NANO-UV, Germany. The anthocyanin content was detected by grinding fresh tissues in acidified methanol. The supernatant was kept in the dark for 5 hrs at a temperature of 5 °C. Subsequently, the concentration of anthocyanins was estimated at a wavelength of 550 nm. The content of free phenolic compounds was quantified following the method of Kofalvi and Nassuth (1995). The Folin-Ciocalteu reagent and sodium carbonate solution were applied to the methanolic extract of fresh leaves, and then the absorbance was read at 720 nm. The content of free phenolic compounds was calculated using a calibration curve of gallic acid.

The ascorbic acid (AsA) was determined using the methods described before (Jagota and Dani, 1982). The fresh tissues were grounded in a 5 % trichloroacetic acid (TCA) solution. Subsequently, 10 % trichloroacetic acid was added to the resulting clear supernatant. Finally, a diluted solution of Folin-Ciocalteu reagent was introduced, and the intensity of the blue color was estimated at 760 nm. The reduced glutathione (GSH) level was measured at 405 nm using the GSH detection kit (CAT. No. GR 2511) from the Biodiagnostic company in Giza, Egypt. The enzyme extract was mixed with trichloroacetic acid and centrifuged at 3000 rpm for 15 min. After that, the supernatant was well mixed with buffer and 5, 5' dithiobis (2-nitrobenzoic acid). The level of α-tocopherol was determined using the previously published method (Kivçak and Mert, 2001). The fresh tissues were homogenized using chloroform. Following centrifugation, the supernatant was treated with a dipyrindyl reagent. Subsequently, ferric chloride was introduced, and the resulting color development was monitored for 50 s at a wavelength of 522 nm.

2.3.5. Determination of the enzymatic activity of anti-free radicals

Plant samples were ground in liquid nitrogen, followed by the addition of extraction buffer (potassium phosphate buffer with a pH of 7.8, supplemented with EDTA 0.1 mM and polyvinylpyrrolidone (PVP) 0.9 mM). The homogenate was centrifuged at 11,500 rpm for 30 min at 4 °C and used for various enzymatic activity using a NanoDrop spectrophotometer (model 2000c, Thermo Scientific, USA).

The activity of guaiacol peroxidase (GP, EC 1.11.1.7) was estimated by adding the enzyme extract to a mixture of guaiacol, hydrogen peroxide, and potassium phosphate buffer, then recording the increasing absorbance at 470 nm (Fielding and Hall, 1978). The activity of glutathione-S-transferases (GSTs, EC 2.5. 1.18) was determined by adding enzyme extract to a mixture of potassium phosphate buffer, GSH, and 1-chloro-2,4-dinitrobenzene at 340 nm (Habig et al., 1974). The quantification of superoxide dismutase (SOD, EC 1.15.1.1) activity was performed by mixing the enzyme extract with epinephrine using a sodium carbonate buffer. The resulting increase in absorbance was measured at a wavelength of 480 nm (Misra and Fridovich, 1972). The activity of ascorbate peroxidase (APX, EC 1.11.1.11) was assessed by mixing the enzyme extract with a potassium phosphate buffer in the presence of EDTA, H₂O₂, and ascorbate and measuring the absorbance at 290 nm (Tahjib-Ul-Arif et al., 2019). The activity of glutathione peroxidase (GPX, EC 4.3.1.5) was quantified at 340 nm using a commercial kit (CAT. No. GP 2524, Biodiagnostic company, Giza, Egypt). The reaction mixture was buffer, NADPH, enzyme extract, and H₂O₂. Polyphenol oxidase activity (PPO, EC 1.10.3.1) was assessed by adding enzyme extract to potassium phosphate buffer and catechol, and the reaction was carried out for 5 min at 25 °C. Subsequently, a solution of diluted H₂SO₄ was added to terminate the reaction, and then the absorbance was measured at 495 nm (Kumar and Pa, 1982). The L-phenylalanine ammonia-lyase (PAL, EC 4.3.1.5) activity was estimated in a reaction mixture of the enzyme extract with borate buffer and phenylalanine. Hydrochloric acid terminated the reaction, and the absorbance was done at 290 nm (Havir and Hanson, 1968).

2.3.6. Extraction and determination of the content of residual bisphenol A by HPLC analysis

Bisphenol A was extracted as previously described (Ferrara et al., 2006). Dried material (0.1 g) from soil, roots, leaves, and fruits were suspended in pure methanol and mechanically shaken for 4 h. After centrifuging, a rotary evaporator evaporated the supernatant at 40 °C. The residue was dissolved in a mixture of acetonitrile and water (70:30), and the mixture was filtered using 0.45 µm Millipore™ filters and then examined by high-performance liquid chromatography (HPLC). The HPLC system consisted of a Spectra System™ pump (LC-20AR, Shimadzu, Japan) paired with a SIL-10AP injection valve. The sample was connected to a Shim-pack PREP-ODS chromatographic column with dimensions (250 mm × 20 mm) No 2025D41. The mobile phase comprises 30 % water and 70 % acetonitrile. BPA had a retention duration of

3 min at a flow rate of 0.8 mL min⁻¹. A UV detector quantified Bisphenol A concentration at 228 nm. The quantification analysis of BPA was conducted with a Spectra System SPD-M40 diode array detector from Shimadzu, made in Japan, utilizing an external standard.

2.3.7. Relative gene expression of peroxidase (POD), polyphenol oxidase (PPO), thaumatin-like proteins (TLPs), and tubulin (TUB) using quantitative RT-PCR (qRT-PCR)

2.3.7.1. cDNA conversion from extracted RNA of tomato foliar. 100 mg of tomato leaves were ground by TRIzol LS reagent for RNA extract (33). The concentration and purity of the extracted RNA were assessed by employing the A260/A280 ratio using a NanoDrop spectrophotometer (model 2000c, Thermo Scientific, USA). One g of RNA, treated with DNase I, was employed to generate cDNA using an oligo (dT) primer following the previous procedures (34). Then, the ultimate cDNA was preserved in a deep freeze (-20 °C).

2.3.7.2. Transcriptome analysis of tomato' leaves. The qRT-PCR assessed the expression levels of four specific genes in tomato leaves: POD, PPO, TLPs, and TUB. The β -actin gene was used as a reference gene for all experimental conditions, serving as a housekeeping gene. The primer nucleotide sequences utilized in this work are presented in Table 2. The assessment of β -actin expression was conducted across all treatment modalities, yielding no statistically significant alterations. The qPCR reactions for each biological treatment were performed individually using a SYBR Green Mix (Thermo Fisher, CA, USA) and a Rotor-Gene 6000 real-time thermocycler (QIAGEN, Germantown, MD, USA). The approach utilized for the polymerase chain reaction (PCR) reaction mixture and reaction conditions followed the procedures described in a previous study (Hafez et al., 2013). The RQ for each gene of interest was estimated by the following equation: $2^{-\Delta\Delta CT}$ (Livak and Schmittgen, 2001).

2.4. Statistical analysis

In the greenhouse of the City of Scientific Research and Technological Applications in New Borg El-Arab City, Alexandrina, Egypt, the pots were placed randomly on the ground, following the natural conditions. The collected data were analyzed using the SPSS 21 software, employing normality plots with tests and one-way ANOVA. The data was analyzed using Tukey's honest significant differences (H.S.D.) test at a significance level of $p < 0.05$, and the symbol "a" denotes the lowest mean. Each treatment was replicated three times.

3. Experimental results

3.1. The role of cadaverine in mitigating the growth of tomato plants grown under single or combined stress of salinity and bisphenol A

For a short-duration experiment (10 days of transplanting), the

Table 2

The nucleotides sequence of the primers that were used in this study.

Primer and Gene Name	Abbreviation	Direction	Nucleotide Sequence 5'-3'
Peroxidase	POD	Forward	GCTTTGTCAGGGGTTGTG AT
		Reverse	TGCATCTCTAGCAACCAA CG
Polyphenol oxidase	PPO	Forward	CATGCTCTTGATGAGGC GTA
		Reverse	CCATCTATGGAACGGGAAGA
Thaumatim-like proteins	TLPs	Forward	CATGTCTCTCCACAGAGTAC
		Reverse	ATATAATCCCATTTCTGCTTATG
Tubulin	TUB	Forward	AGGATGCTACAGCCGATGAG
		Reverse	GCCGAAGAACTGACGAGAATC
β -actin	β -actin	Forward	TGGCATACAAAGACAGGACAGCCT
		Reverse	ACTCAATCCCAAGGCCAACAGAGA

application of salinity (T1), BPA(T2), and their mixture (T1+T2) significantly attenuated the growth of tomato plants (Table 3). In this regard, shoot fresh weight (SFW) was significantly decreased by 58 %, 61 %, and 85 %, and root fresh weight (RFW) declined by 32 %, 25 %, and 59 % for T1, T2, and T1 + T2 without cadaverine application (-Cad) as opposed to the control group (T0), respectively. However, spraying the stressed tomato plants with cadaverine (+Cad) significantly enhanced the SFW at T1, T2, and T1 + T2 by 8, 51, 200 %, and RFW by 10 %, 53 %, and 3 % compared to their corresponding stressed plants T1, T2 and T1 + T2, respectively.

According to Fig. 2 A, B, and C, the photosynthetic pigments adversely affected by single or combined stresses where a significant reduction in the contents of chl a (45, 30, and 88 %), chl b (63, 56, and 64 %), and carotenoids (48 %, 37 %, and 74 %) for T1, T2, and T1 + T2, respectively, compared to non-contaminated plants (Supplementary Table 1). In contrast, the application of cadaverine notably restricted the reduction of photosynthetic pigments, with enhancement percentages of (20 %, 52 %, and 258 %) for Chl a, (73 %, 50 %, and 49 %) for Chl b, and (31 %, 56 %, and 84 %) for carotenoids for T1, T2, and T1 + T2 compared to non-cadaverine sprayed plants (Fig. 2 A, B, and C). As an essential primary metabolite, total proteins (TP) were significantly decreased in tomatoes' leaves, regardless of the stress applied, with a maximal decline of 39 % at T2 treatment compared to the control plant; however, cadaverine alleviated the reduction of proteins significantly for combined stress (Fig. 2D).

After 10 days of transplanting and adding cadaverine, the plants experienced a combined stress of salinity and BPA, which could not endure the stress applied. These plants depleted and died at this time, while the single stresses completed their life cycle, showing adverse impacts on plant growth criteria. Interestingly, the combined stressed plants that received cadaverine completed their life cycle until the crop yield.

In the long-duration experiment (30 days post-transplanting), as depicted in Table 3, exposure to salinity or BPA led to a significant reduction of SFW (54 % and 30 %), RFW (18 % and 12 %), SDW (70 % and 44 %), and RDW (59 % and 8 %) compared to non-stressed plants. Interestingly, the tomato plants subjected to combined stress exhibited permanent wilting without any signs of vitality. The exogenous spraying of cadaverine potentially prevented the death of tomato plants grown under combined salinity and BPA stresses and promoted the development of plants subjected to single stressors. The data in Table 3 demonstrated a substantial increase in the fresh weights (34 % and 38 %) and dry weights (44 % and 42 %) of shoots under T1 and T2, respectively. However, the root growth was not affected by cadaverine application, except for RFW of BPA (157 % compared to stressed plants only).

The concentrations of chl a (27 % and 37 %), chl b (42 % and 45 %), and TC (23 % and 33 %) significantly declined under salinity or BPA compared to plants that are not experiencing stress (Fig. 3A, B, and C). However, when tomato plants were exposed to salt stress and sprayed with cadaverine, chlorophyll a, b, and TC levels significantly increased. Specifically, there were detected increases of 125 %, 144 %, and 62 % in chl a, chl b, and TC, respectively, as opposed to the corresponding treatments that did not receive cadaverine application (Fig. 3A, B, and C). Nevertheless, cadaverine did not significantly affect the photosynthetic pigments of tomatoes under BPA treatments. The pigment content of combined stressed plants under cadaverine application is like that of BPA-stressed plants. At the same time, the growth is close like that of salinity-stressed plants, revealing the complex nature of combined stress behavior or response to cadaverine (Supplementary Table 2).

3.2. The role of cadaverine in mitigating primary metabolites of tomato plants grown under single or combined stress of salinity and bisphenol A

Applying saline or BPA stresses resulted in a considerable reduction in the contents of SC, SP, and TP compared to the control plants. In this

Table 3

The fresh and dry weight of shoots and roots of tomato plants grown under salinity or/and bisphenol A sprayed with cadaverine (+ Cad) or without cadaverine (- Cad) after 10 or 30 days of spraying. T0: control; T1: salinity (120 mM); T2: bisphenol A (375 mg kg⁻¹); T1 +T2: the combination of salinity and bisphenol A. Values are means ± SE. Mean values with different letters are significantly different at P ≤ 0.05, according to Tukey's test. * and ** = significant difference at P ≤ 0.05 and P ≤ 0.01 confidence level, respectively.

Treatments		Biomass					
		After 10 days		After 30 days			
		SFW	RFW	SFW	RFW	SDW	RDW
T0	- Cad	8.55 ^c ±0.72	1.37 ^{bc} ±0.03	21.44 ^c ±2.52	2.95 ^b ± 0.18	4.27 ^d ± 0.14	1.08 ^b ± 0.10
T1	- Cad	3.57 ^b ± 0.28	0.93 ^{ab} ± 0.11	09.90 ^a ±0.21	2.42 ^b ± 0.22	1.26 ^a ±0.08	0.44 ^a ±0.04
	+ Cad	3.88 ^b ± 0.11	1.02 ^{ab} ± 0.09	13.29 ^a ±1.03	2.87 ^b ± 0.09	1.82 ^{ab} ± 0.04	0.47 ^a ±0.06
T2	- Cad	3.33 ^b ± 0.27	1.03 ^{ab} ± 0.14	15.06 ^{ab} ± 1.4	2.59 ^b ± 0.10	2.38 ^b ± 0.29	0.99 ^b ± 0.10
	+ Cad	5.03 ^b ± 0.33	1.58 ^a ±0.17	20.84 ^{bc} ±0.21	7.59 ^c ±0.24	3.38 ^c ±0.14	1.17 ^b ± 0.11
T1 + T2	- Cad	1.24 ^a ±0.15	0.56 ^a ±0.08	x	x	x	x
	+ Cad	3.75 ^c ±0.25	0.54 ^a ±0.04	9.42 ^a ±0.38	1.23 ^a ±0.24	1.13 ^a ±0.09	0.20 ^a ±0.04
F value		39.55**	12.75**	16.98**	136.04**	66.60**	26.05**

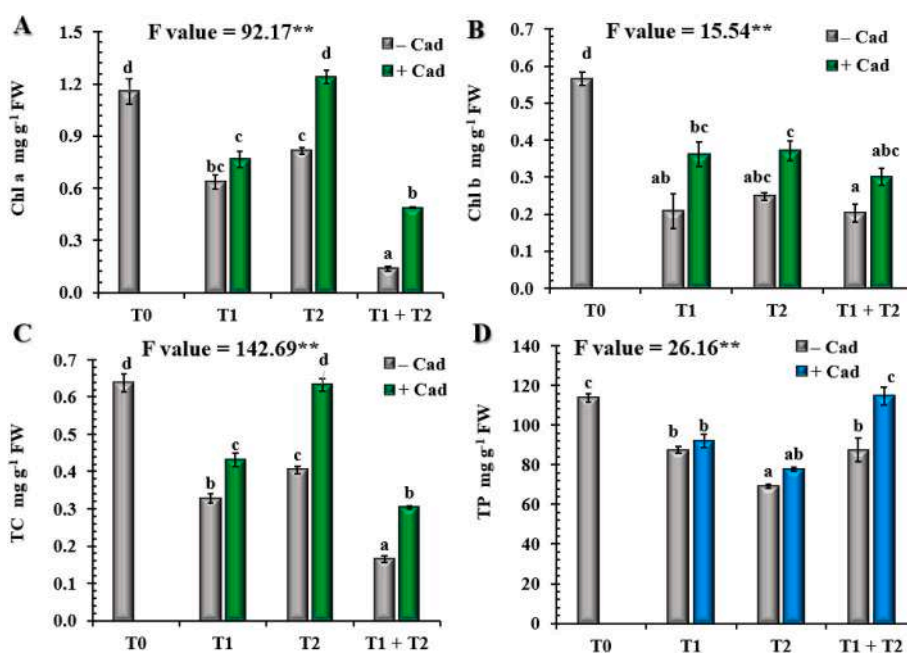


Fig. 2. Photosynthetic pigments **A:** chlorophyll a (Chl a), **B:** chlorophyll b (Chl b), **C:** total carotenoids (TC), and **D:** total protein (TP) of tomatoes' leaves grown under salinity or/and bisphenol A sprayed with cadaverine (+ Cad) or without cadaverine (- Cad) after 10 days of spraying. T0: control; T1: salinity (120 mM); T2: bisphenol A (375 mg kg⁻¹); T1 +T2: the combination of salinity and bisphenol A. Mean values with different letters are significantly different at P ≤ 0.05, according to Tukey's test. * and ** = Significant difference at P ≤ 0.05 and P ≤ 0.01 confidence level, respectively.

regard, the percent reduction of SC was (54 and 33 %), (51 % and 13 %) for SP, as well as (52 % and 42 %) for TP under T1 and T2, respectively, compared to control. In contrast, the FAA had a non-significant response under the applied stresses. Nevertheless, the content of SP, SC, and FAA were not significantly impacted by the introduction of cadaverine in comparison to the corresponding stressed only (Fig. 4A–C, and D) except for significant accumulation of SP by 40 % under BPA treatment and TP by 90 % under salinity stress (Fig. 4B–and C). On the contrary, TP levels under saline or BPA treatments were increased by the spraying with cadaverine when compared to the respective stressed plants (Fig. 4B). The contents of SC, SP, TP, and FAA were maintained with reasonable values between both single stresses because of the interaction effect of cadaverine and combined stress (Supplementary Table 2).

The proline content is solely influenced by saltness, exhibiting a significant rise of 138 % compared to non-treated plants. Nevertheless, the application of cadaverine spray resulted in a substantial 61 % decrease in proline levels in plants exposed to salt stress, as compared to the corresponding stressed plants that did not receive cadaverine treatment. Interestingly, combined stressed plants receiving cadaverine

showed a highly significant accumulation of proline by 140 % compared to control plants (Fig. 4E and Supplementary Table 2).

3.3. The role of cadaverine in reducing free radicals and membrane damage biomarkers of tomato plants grown under single or combined stress of salinity and bisphenol A

According to Fig. 5A, it was demonstrated that there was a notable rise in H₂O₂ levels in plants subjected to BPA stress treatments by 52 % when compared to control plants, without a significant effect of salinity on H₂O₂ content. Nevertheless, when crops exposed to BPA were treated with cadaverine, it led to a significant reduction of H₂O₂ without a significant effect on H₂O₂ levels of salinity-stressed plants that received cadaverine in comparison with their plants experiencing stress. The content of H₂O₂ was comparable to that of control plants for combining stressed plants sprayed with cadaverine. Unlike H₂O₂, the levels of OH[•] and O₂^{•-} were significantly doubled in plants subjected to single treatment in comparison to the control group. The percentage increases were (242 and 535 %) for OH[•] and (300 and 346 %) for O₂^{•-} under salinity or

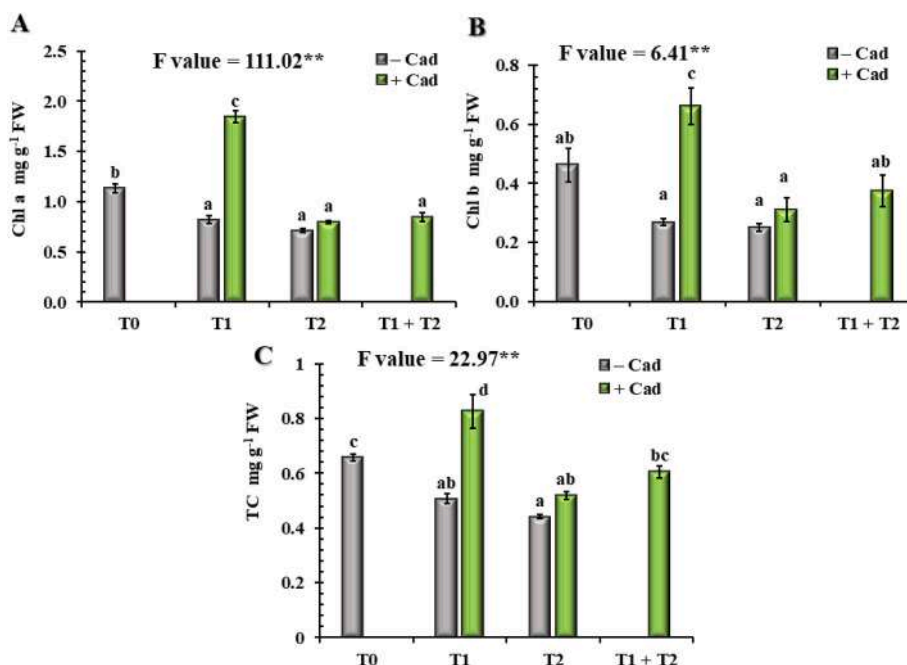


Fig. 3. Photosynthetic pigments **A:** chlorophyll *a* (Chl *a*), **B:** chlorophyll *b* (Chl *b*), and **C:** total carotenoids (TC) of tomatoes' leaves grown under salinity or/and bisphenol A sprayed with cadaverine (+ Cad) or without cadaverine (- Cad) after 30 days of spraying. T0: control; T1: salinity (120 mM NaCl); T2: bisphenol A (375 mg kg⁻¹); T1 +T2: the combination of salinity and bisphenol A. Mean values with different letters are significantly different at $P \leq 0.05$, according to Tukey's test. * and ** = Significant difference at $P \leq 0.05$ and $P \leq 0.01$ confidence level, respectively.

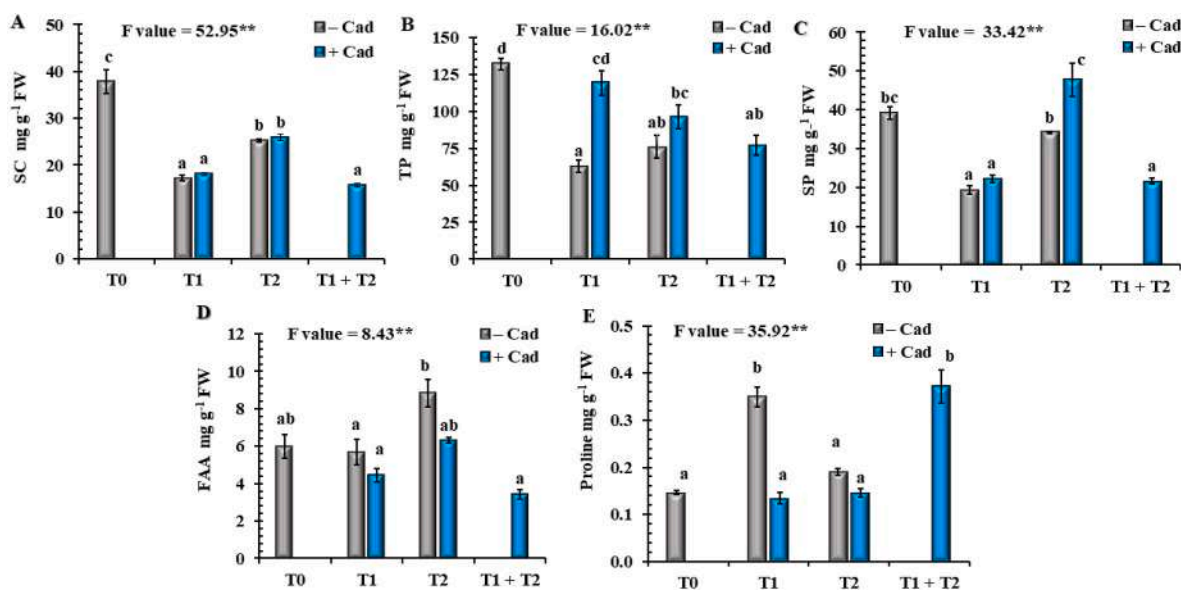


Fig. 4. The primary metabolites **A:** soluble carbohydrates (SC), **B:** Total protein (TP), **C:** soluble protein (SP), **D:** free amino acids (FAA), and **E:** Proline of tomatoes' leaves grown under salinity or/and bisphenol A sprayed with cadaverine (+ Cad) or without cadaverine (- Cad) after 30 days of spraying. T0: control; T1: salinity (120 mM NaCl); T2: bisphenol A (375 mg kg⁻¹); T1 +T2: the combination of salinity and bisphenol A. Mean values with different letters are significantly different at $P \leq 0.05$, according to Tukey's test. * and ** = Significant difference at $P \leq 0.05$ and $P \leq 0.01$ confidence level, respectively.

BPA, respectively, compared to control. However, when plants were sprayed with cadaverine, the levels of OH^\bullet and $\text{O}_2^{\bullet-}$ significantly reduced compared to the crops under stress (Fig. 5B–and C). Interestingly, the interactive effect of cadaverine maintained the values of OH^\bullet and $\text{O}_2^{\bullet-}$ in tomatoes' leaves under combined stresses less than single-stressed plants but still greater than non-treated plants (Supplementary Table 3).

For reactive nitrogen species, the levels of NO content exhibited a considerable increase in T1 and T2 plants when compared to T0 plants, with a percentage increase of 73 and 300 % for saline and BPA stress,

respectively, as opposed to a non-contaminated group (Supplementary Table 3). However, spraying single stressed plants with cadaverine resulted in a significant decline in NO content compared to their stressed plants without alleviation (Fig. 5D). The foliar content of NO was comparable to control in plants that experienced combined stress and cadaverine spraying.

The membrane damage biomarkers of tomato plants are affected immensely by NaCl or BPA in the soil (Supplementary Table 3). Regarding this matter, the activity of lipoxygenase and the

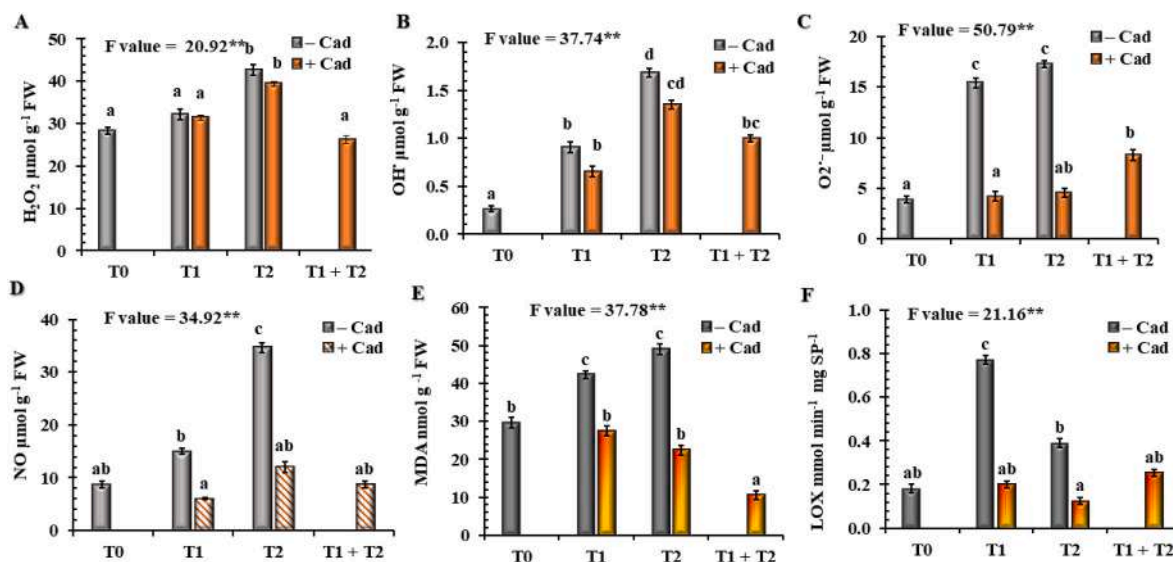


Fig. 5. Content of reactive oxygen species, oxidative, and membrane damage marker where **A:** hydrogen peroxide (H₂O₂), **B:** hydroxyl radical (OH[•]), **C:** superoxide anion (O₂^{•-}), **D:** nitric oxide (NO), **E:** malondialdehyde (MDA), and **F:** lipoxygenase enzyme (LOX) of tomatoes' leaves grown under salinity or/and bisphenol A sprayed with cadaverine (+ Cad) or without cadaverine (- Cad) after 30 days of spraying. T0: control; T1: salinity (120 mM NaCl); T2: bisphenol A (375 mg kg⁻¹); T1 +T2: the combination of salinity and bisphenol A. Mean values with different letters are significantly different at P ≤ 0.05, according to Tukey's test. * and ** = Significant difference at P ≤ 0.05 and P ≤ 0.01 confidence level, respectively.

concentration of malondialdehyde in tomato leaves considerably increased compared to plants grown in soil without contamination. Compared with the control, the level of MDA increased by 42 and 65 %, whilst the activity of LOX accumulated by 323 and 114 % for saline or BPA, respectively. Nevertheless, spraying salinity- or BPA-stressed plants with cadaverine declined the content of MDA significantly (by 35 and 55 %) and the activity of LOX (by 75 and 70 %) compared to corresponding treatments without cadaverine. Interestingly, under a mixture of salinity and BPA, cadaverine potentially maintained the level of MDA lower than control plants while keeping the activity of LOX comparable to the control plants (Fig. 5E and F).

3.4. The role of cadaverine in regulating secondary metabolites and non-enzymatic anti-free radicals in tomato plants treated with single or combined levels of salinity and bisphenol A

As shown in Fig. 6A, B, and C, free phenolic compounds and anthocyanin were significantly increased under single stressors compared to control. Compared to non-stressed plants, the percent accumulation was (13 and 95 %) for free phenolic compounds and (18 and 13 %) for anthocyanins, with significant values only for BPA-treated plants. Flavonoid content increased significantly under BPA by 93 %, with a non-significant reduction under saltiness as opposed to non-contaminated plants (Supplementary Table 4). Conversely, spraying tomatoes grown under salinity or BPA by cadaverine decreased the

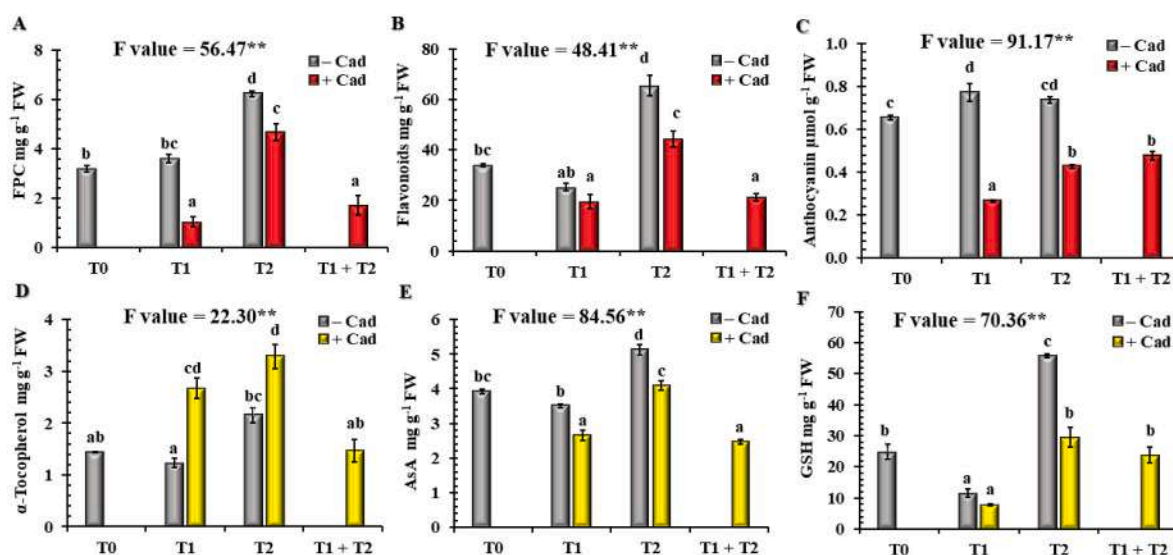


Fig. 6. Content of secondary metabolites **A:** free phenolic compounds (FPC), **B:** flavonoids, and **C:** Anthocyanin and the non-enzymatic antioxidants; **A:** α-tocopherol, **B:** ascorbic acid (AsA), and **C:** reduced glutathione (GSH) of tomatoes' leaves grown under salinity or/and bisphenol A sprayed with cadaverine (+ Cad) or without cadaverine (- Cad) after 30 days of spraying. T0: control; T1: salinity (120 mM NaCl); T2: bisphenol A (375 mg kg⁻¹); T1 +T2: the combination of salinity and bisphenol A. Mean values with different letters are significantly different at P ≤ 0.05, according to Tukey's test. * and ** = Significant difference at P ≤ 0.05 and P ≤ 0.01 confidence level, respectively.

levels of secondary metabolites compared to their corresponding stressed plants. Although the combined stressed plants without cadaverine died, the values of free phenolics, flavonoids, and anthocyanins in tomato leaves grown under combined stresses were lower than those of the control when cadaverine was applied.

In Fig. 6, plants that experienced BPA stress showed a notable rise in α -tocopherol levels (by 50 %) and a non-significant decline under salt stress as opposed to non-stressed plants. Contrary to plants grown under salinity or BPA, cadaverine significantly raised the α -tocopherol content of plants experiencing salinity or BPA stress by 117 % and 52 %, respectively. Furthermore, the foliar spraying of cadaverine kept the α -tocopherol levels like those in the control group in plants exposed to mixed stress (Supplementary Table 4).

The non-enzymatic antioxidants were differentially affected by the applied treatments (Supplementary Table 4). BPA induced a notable increment in the concentrations of AsA and GSH of 31 % and 125 %, respectively, when compared to non-stressed plants. In contrast, salinity stress reduced the values of AsA and GSH by 10 and 55 %, respectively, in comparison with control plants. However, the application of cadaverine resulted in a further reduction of ascorbic acid and reduced glutathione levels in crops treated with T1 or T2 compared to T0 (Fig. 6E and F). The combined stressed plants that received cadaverine kept the values of GSH around the control values, while the content of AsA was lower than the control plants.

3.5. The role of cadaverine in ameliorating the antioxidant enzymes of tomato crops transplanted under a single or combined stress of salinity and bisphenol A

In Fig. 7A, B, C, E, and G, a significant increment in the activities of PPO (by 88 and 48 %), GP (by 61 and 88 %), GPX (by 200 % and 100 %), PAL (by 59 % and 57 %), and SOD (by 393 and 94 %) was noticed in tomato plants exposed to salt or BPA stress, respectively, as opposed to zero-contaminant plants. However, the APX activity showed a

significant rise of 349 % for BPA-stressed plants without a substantial effect of salinity on APX activity compared to non-stressed plants (Fig. 7D). Unlike APX activity, GST activity showed a considerable increasing trend of 115 % under salinity stress, without a significant increase recorded for BPA-stressed plants (Fig. 7F and supplementary Table 5).

The exogenous application of cadaverine exhibited various impacts on the activity of anti-free radical enzymes in herbs exposed to stress conditions. In this regard, cadaverine induced a further increase in PPO (by 26 % and 35 %), PAL (by 9 % and 25 %), GST (by 18 % and 39 %), and SOD (by 23 % and 46 %) activities under salinity or BPA, respectively, as opposed to compared to non-alleviated stressed plants (Fig. 7A–E, F, and G). However, cadaverine reduced the activities of APX and GPX of BPA- and salinity-treated plants compared to the corresponding stressed plants but kept their activities around the control values. Also, the application of cadaverine retarded the activity of GP, which was lower than the single stressed as well as the control plants. For combined stress, the co-application of cadaverine and combined stressed plants significantly enhanced the activities of PPO, GP, GST, and SOD to be more than that in the non-treated group. Moreover, under the same treatment, cadaverine kept the activities of PAL, GPX, and APX around the control values (Fig. 7B, C, and D and supplementary Table 5).

3.6. The effect of cadaverine on BPA accumulation in soils, roots, leaves, and tomato fruits

In the soils collected after 30 days, the information displayed in Table 4 indicated that the soil concentration of BPA decreased by 92 % compared to the initial level. The interactive effect of BPA and cadaverine reduced BPA content in soil from 375 mg kg⁻¹ to 40 mg/kg. In tomato plants grown under a single BPA stress, BPA was accumulated in tomato roots exposed to BPA stress. In contrast, when BPA-stressed plants were sprayed with cadaverine, more BPA accumulation was observed than BPA-stressed plants without cadaverine. Interestingly,

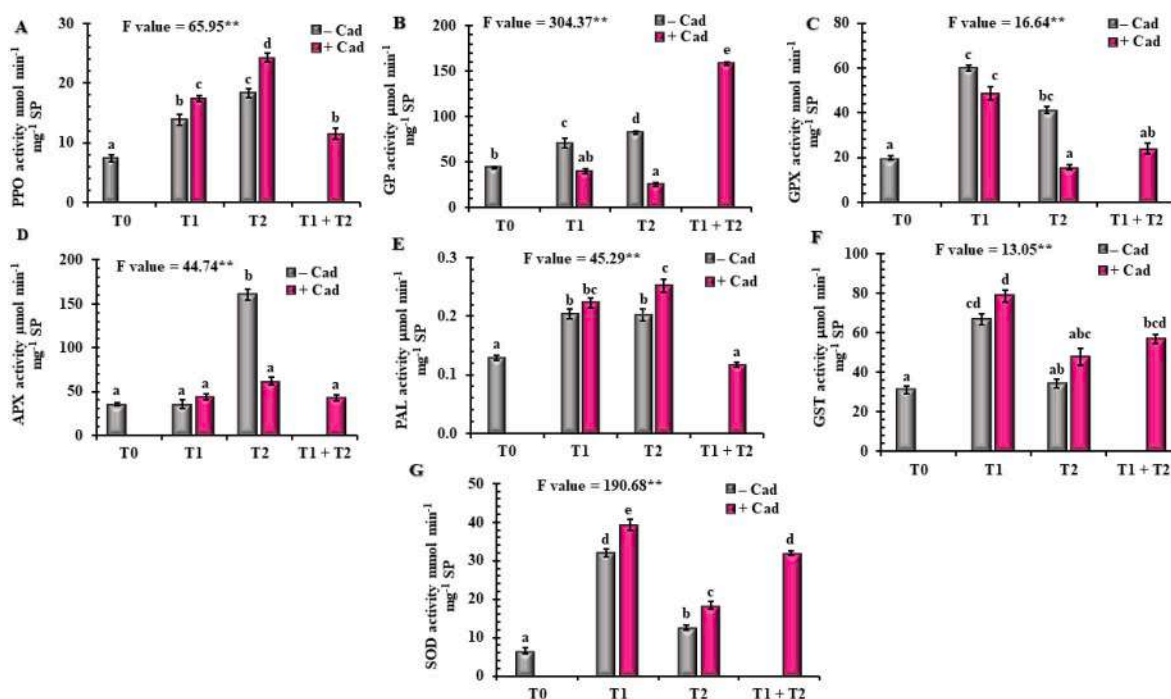


Fig. 7. The activity of antioxidant enzymes; A: polyphenol oxidase (PPO), B: Guaiacol peroxidase (GP), C: glutathione peroxidase (GPX), D: ascorbate peroxidase (APX), E: L-phenylalanine ammonia-lyase (PAL), F: glutathione s-transferases (GST), and G: superoxide dismutase (SOD) of tomatoes' leaves grown under salinity or/and bisphenol A sprayed with cadaverine (+ Cad) or without cadaverine (- Cad) after 30 days of spraying. T0: control; T1: salinity (120 mM NaCl); T2: bisphenol A (375 mg kg⁻¹); T1 +T2: the combination of salinity and bisphenol A. Mean values with different letters are significantly different at $P \leq 0.05$, according to Tukey's test. * and ** = Significant difference at $P \leq 0.05$ and $P \leq 0.01$ confidence level, respectively.

Table 4

Calculated amount of bisphenol A in soils (mg g^{-1} dry soil), roots, leaves, and fruits (mg g^{-1} DW) of tomato plants grown under salinity or/and bisphenol A sprayed with cadaverine (+ Cad) or without cadaverine (- Cad) after 30 or 120 days of spraying. T2: bisphenol A (375 mg kg^{-1}); T1 +T2: the combination of salinity (120 mM NaCl) and bisphenol A. Values are means \pm SE. * and ** = Significant difference at $P \leq 0.05$ and $P \leq 0.01$ confidence level, respectively.

Treatments	BPA content mg g^{-1} dry soil				
	Soil	Root	Leaf	Tomato	
T2	(- Cad)	0.03 ± 0.03	0.36 ± 0.02	ND	ND
	(+Cad)	0.04 ± 0.03	1.25 ± 0.62	ND	ND
T1 + T2	(+Cad)	ND	ND	ND	ND
F value	1.96	33.53**	-	-	

with or without cadaverine, leaves and fruits of tomato plants exposed to BPA, the level of BPA was below the detection limit. Similarly, tomato plants grown under mixed stresses treated with cadaverine, the BPA residual in the soil, roots, leaves, and fruits were also not detected by HPLC analysis.

3.7. The expression of antioxidants and defense-related genes of tomato' leaves grown under single or combined stress of salinity and bisphenol A

The PPO relative expression (RQ) dramatically increased in plants subjected to BPA-induced stress as opposed to the non-contaminated group. However, the rise in the RQ of PPO under salinity stress is insignificant. Also, cadaverine further increased the RQ of PPO under BPA or salinity stresses compared to the stressed plants. The triple effect of cadaverine-BPA-salinity stress maintained the RQ of PPO around the control. However, the RQ of POD was dramatically reduced in plants subjected to salinity stress relative to plants devoid of pollutants, without a significant effect of BPA on the RQ of POD. Foliar spraying of cadaverine to stressed plants had no impact on the RQ of POD compared to the corresponding stressed plants (Fig. 8B). The RQ of POD remained around the control in plants and experienced mixed stress and cadaverine (Supplementary Table 6).

The expression of TUB genes showed a non-significant reduction of salinity or BPA compared to non-stressed plants. The use of cadaverine

enhanced the relative expression of TUB for single or combined stressed plants as opposed to single stressed and non-treated group (Fig. 8C). Fig. 8D shows that the presence of salinity led to a notable increase in the expression of TLPs, relative to the reference plants. However, the presence of BPA significantly influences the expression of TLPs in stressed plants. However, compared to non-ameliorated stressed plants, the RQ of TLPs was raised by cadaverine under single stress. In addition, the triple effect of cadaverine-BPA-salinity also enhanced the RQ of TLPs to be higher than the control plants (Fig. 8D and supplementary Table 6).

4. Discussion

Soil salinization has impacted agricultural soils for hundreds to thousands of years, and the main reasons for this are human activities like irrigation, inadequate land utilization, and excessive fertilization. In addition, salt stress intensified in soils by water scarcity and continuous agricultural land degradation leads to substantial decreases in productivity, especially in regions that receive rainfall less than 500 mm a year (Balasubramaniam et al., 2023). More recently, BPA has been introduced into farmland through irrigation with wastewater. The germination and enlargement of plants are influenced adversely by both abiotic and biotic stresses, resulting in physiological irregularities and endangering global food security. Thus, the current study investigates the use of cadaverine to mitigate the impacts of both existing and newly identified pollutants singly or in combination with tomato plants. The NaCl or BPA stresses severely impacted tomatoes' biomass, but salinity had the most drastic effect. When both stressors were combined, the growth of tomatoes was at its lowest during the first 10 days of post-transplanting. Following prolonged exposure of plants to BPA and salinity, wilting occurred, ultimately resulting in their inability to survive, leading to eventual death. These findings might be connected to the suppression of energy production, which resulted in reduced growth of tomato plants. This energy is mainly derived from photosynthesis, which affects plant development and growth. Plants exposed to single or mixed stress exhibited a decline in photosynthetic pigments, according to the present study. The impact was more pronounced under combined stress, as indicated at 10 days (Figs. 2 and 3). This decrease can be ascribed to the susceptibility of chlorophyll to both organic contaminants and salinization of soils (Bourgeade et al., 2021; Singh et al., 2022;

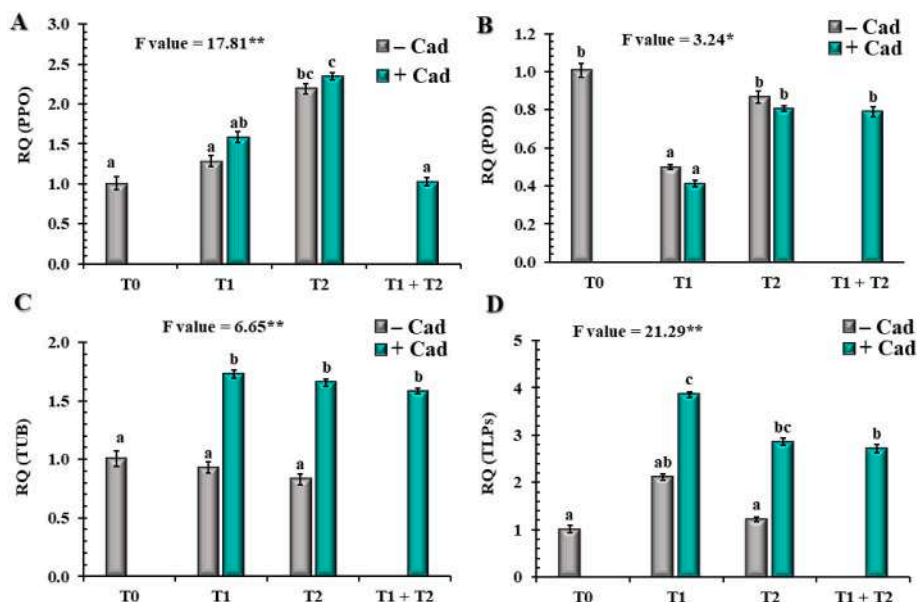


Fig. 8. Relative quantitative expression analysis (RQ) of four genes. A: polyphenol oxidase (PPO), B: Peroxidase (POD), C: tubulin (TUB), and D: thaumatin-like proteins (TLPs) of tomatoes' leaves grown under salinity or/and bisphenol A sprayed with cadaverine (+ Cad) or without cadaverine (- Cad) after 30 days of spraying. T0: control; T1: salinity (120 mM NaCl); T2: bisphenol A (375 mg kg^{-1}); T1 +T2: the combination of salinity and bisphenol A. Mean values with different letters are significantly different at $P \leq 0.05$, according to Tukey's test. * and ** = Significant difference at $P \leq 0.05$ and $P \leq 0.01$ confidence level, respectively.

Jahan et al., 2023). Li et al. (2018) reported that prolonged irrigation of cucumber with BPA reduced the pigmentation level of leaves. It was explained that BPA suppresses chlorophyll production by lowering the chlorophyll precursors 5-aminolevulinic acid (ALA) and protoporphyrin IX (PPIX). In addition, BPA suppresses the conversion of ALA to iron PPIX, which is a crucial stage in chlorophyll biosynthesis (Jiao et al., 2015; Hu et al., 2024). However, in salty environments, the decrease in chlorophyll levels can occur due to the inhibition of chl *a* and *b* synthesis, disruption of the production of light-absorbing compounds, and degradation of the green pigment caused by photooxidation (Qin et al., 2020; Wang et al., 2024), as well as inducing chlorophyll-degrading enzymes, such as chlorophyllase (Li et al., 2022). Thus, in the present study, the plants could no longer adapt to these stressful conditions, and death resulted from prolonged exposure to mixed stresses.

However, using cadaverine stimulated the growth parameters of seedlings experiencing single stress and enabled crops facing several co-stresses to continue growing under those conditions until yield production. As a group of plant growth regulators, when cadaverine was applied exogenously on tomato plants, herein significantly ameliorated the detrimental effects of saltiness on growth attributes. Additionally, it served as a novel chemical agent for mitigating the impact of BPA and preventing the death of tomatoes subjected to salinity and BPA stress for an extended period. Regarding this polyamine, Gibbs et al. (2021) found that cadaverine regulates biotin production, which modulates primary root growth in plants. These roles are an unanticipated activity of cadaverine. Furthermore, PAs regulates various physiological processes such as DNA duplication, transcription of genetic information, converting genetic information into proteins, cell multiplication, regulation of enzyme function, maintaining the stability of nucleic acids, and cellular membrane functions (Nehela and Killiny, 2020).

In this investigation, cadaverine application fundamentally ameliorated the applied stresses through chlorophyll restoration, especially at the early stages (10 days post-transplanting) of stress imposition. This restoration enhanced energy availability, enabling stressed plants, particularly those exposed to BPA and combined stresses, to exhibit improved growth compared to plants subjected to BPA stress alone. The findings of Zhou et al. (2024) align with our results, demonstrating that cadaverine enhances the biomass of lettuce plants by improving photosynthetic properties in both saline and control groups. Cadaverine regulates several proteins related to photosystems I (PSI) and II (PSII), thereby enhancing light energy absorption and strengthening the structural integrity of PSII.

Plant growth and development is primarily dependent on soluble sugar and proteins, which are essential components of plant structure and function. This study revealed that under salt stress conditions, the reduced growth of tomato was positively correlated with the highest decrease in photosynthetic pigments and osmolyte contents (soluble sugars and proteins). In contrast, BPA stress stimulated amino acids without significant effect on proteins, revealing less osmotic stress in these plants. These osmotic imbalances elucidated the severity conditions of combined stress combinations, which ultimately lead to depletion and death. Similar reductions in soluble proteins and soluble carbohydrates have been reported under the effect of BPA (Sun et al., 2019b) and salt stress (Attia et al., 2021).

Although cadaverine enhanced the pigments of stressed plants during prolonged exposure, osmolyte levels remained unchanged, except for a significant increase in soluble proteins in plants stressed by BPA. Cadaverine notably stimulated a highly significant accumulation of total proteins under stress conditions, indicating that it promoted the synthesis of insoluble proteins at the expense of amino acids and soluble proteins, hence stabilizing protoplasmic colloids. Thus, total protein contents, which play a critical role in regulatory and defense mechanisms, enabled plants to respond to environmental stressors such as BPA, high salinity, or their combination. Notably, the response of stressed plants sprayed with cadaverine closely mirrored that of plants subjected to salinized plants treated with cadaverine. In addition, PAs are known

to regulate the cellular of nitrogen and carbon balance. Due to their high nitrogen content, PAs are reported to serve as a nitrogen source for amino acid synthesis and chlorophyll production (Tan et al., 2022). Supporting this interpretation, cadaverine has been shown to increase total protein content in barely seedlings under stress conditions (Ozmen et al., 2023).

Plants typically respond to stress by retaining compatible osmolytes like proline, which help maintain cell membranes integrity, stabilize enzymes and proteins, and regulate osmotic pressure. These osmolytes can accumulate at high concentrations in the cytoplasm without damaging cellular components (Sofy et al., 2022). In this study, proline was observed to be exclusively accumulated under salt stress and combined stress conditions treated with cadaverine. Consistent with these findings, *Portulaca oleracea* L., showed elevated proline levels under salinity stress (Hnilickova et al., 2021). Similarly, Balci et al. (2023) noticed increased proline concentration in *Triticum aestivum* under nitrate and cadaverine treatments. Thus, cadaverine up-regulated osmotic pressure, enhanced water absorption, improved relative water content, and promoted tissue hydration.

The generation of ROS is a common initial reaction of plants to various stressors, whether individual or combined (Sheteiwy et al., 2023; Dawood et al., 2025). The overproduction of ROS, driven by overstimulation of PSII, suppression of carbon absorption, and overproduction of the respiratory chain, harms the photosynthetic machinery (Sheteiwy et al., 2022). The current study demonstrated that BPA or salinity raised oxidative markers, such as H₂O₂, O₂^{•-}, and OH[•] beyond the antioxidant scavenging capacity of tomato plants, although salinity did not trigger H₂O₂ production, revealing stress-specific responses. The excessive accumulation of ROS disrupts chloroplasts and thylakoid membranes, inhibiting plant growth under salinity (Dawood et al., 2023) or high BPA concentrations (Liang et al., 2022), especially in the absence of sufficient non-enzymatic antioxidants (Pinto et al., 2003). ROS generation also occurs via high-energy electron transfer from the citric acid cycle or anaerobic metabolism to O₂, leading to O₂^{•-} formation (Vranová et al., 2002).

However, the spraying of cadaverine reduced the levels of free radicals in stressed plants, demonstrating its role in mitigating the oxidative stress biomarkers. This aligns with Farooq et al. (2009), who stated that PAs hinder the activity of metal ions like Fe and Cu involved in ROS generation, thereby indirectly lowering ROS levels. Concomitant to this study, cadaverine phosphate prevented the oxygen radical's accumulation in lettuce under nitrate stress (Zhou et al., 2024). In this study, cadaverine-treated tomato plants under combined stress exhibited reduced oxidative stress and recorded ROS levels comparable to single-stressed plants treated with cadaverine. These findings elucidate the potential role of cadaverine in attenuating oxidative stress, enabling highly stressed plants to sustain growth and complete their life cycle, unlike untreated stressed plants, which succumb prematurely.

As a crucial signalling molecule, NO levels increased in stressed plants; however, cadaverine mitigated the elevated NO levels in single and combined stressed plants, restoring them to control values. The rise in NO under stress conditions is indicative of stress, and cadaverine effectively counteracted this response. Thus, stressed plants did not experience only oxidative but also nitrosative stress, which accentuated the influence of various stressors on tomato plant development in the presence of salt or BPA. Reports showed similar reductions in NO levels in stressed plants when exposed to other protective agents (Abdelrhim et al., 2024).

Under BPA or salinity level, the accumulation of free radicals induces redox imbalance and disrupts cellular membrane permeability. This study demonstrated a significant increase in membrane lipid peroxidation and LOX activity in plants exposed to salt or BPA. Elevated malondialdehyde (MDA) levels under salinity stress are consistent with previous findings (Sheteiwy et al., 2022; Sofy et al., 2022). Similarly, BPA stress increased the levels of MDA and H₂O₂ in *Azolla filiculoides* (Sarkar et al., 2022) and cucumbers (Ahammed et al., 2020),

corroborating our findings. However, applying cadaverine decreased lipoxygenase activity and lipid peroxidation levels, ameliorating oxidative damage under single or combined stress. This observation aligns with previous research that demonstrated showing cadaverine decreased MDA levels in *Hordeum vulgare* plantlets under stress (Ozmen et al., 2023). Polyamines, including cadaverine, can act as radical scavengers and antioxidants, preventing redox imbalance and lipid peroxidation by regulating the Fenton reaction (Stewart et al., 2018). Quenching free radicals is a potential strategy to enhance plant tolerance to stressors. Antioxidant enzyme activities were evaluated in tomato plants exposed to BPA or salinity stress. In this aspect, the activities of SOD and peroxidases (APX, GP, and GPX), key ROS-scavenging enzymes, were significantly upregulated in response to oxidative stress. The availability of substrates, such as superoxide anions ($O_2^{\cdot-}$) for SOD and hydrogen peroxide (H_2O_2) for APX, GP, and GPX, likely explains these enzymatic activation (Younes et al., 2024). Notably, BPA stress specifically induced SOD, GP, and APX activity to combat H_2O_2 and $O_2^{\cdot-}$, while salinity stress primarily activated SOD against $O_2^{\cdot-}$, with no significant impact on H_2O_2 levels. In addition, glutathione-dependent enzymes like GPX and GST play a pivotal role in mitigating oxidative damage. While salinity stress increased GPX and GST activities, BPA primarily enhanced GST, revealing distinct oxidative stress mechanisms under these stressors (Dawood et al., 2022a). These findings illustrate the differential antioxidant responses of tomato plants under BPA and salinity stress and the role of cadaverine in alleviating oxidative damage.

Ascorbate and reduced glutathione function as redox buffering agents, maintaining the cellular redox state balance and protecting the integrity of the plasma membrane. Elevated levels of ascorbate and glutathione, as substrates for APX and GPX, are linked to the direct reduction of oxygen radicals (Dawood and Azooz, 2020). In this work, salinity stress had no significant effect on APX activity although it caused a slight decrease in GSH and AsA content. However, BPA stress increased AsA, α -tocopherol, and GSH levels, suggesting a stronger antioxidant response under BPA stress compared to salinity. Such response suggests that the tomato plants are in a state of emergency, trying to deal with the sudden increase in oxidative burst caused by BPA. Therefore BPA-treated plants exhibited less growth retardation than those under salinity stress due to their enhanced antioxidant defense system.

Apart from enzymatic antioxidants, secondary metabolites like phenolics, flavonoids, and anthocyanins play a crucial role in combating ROS. In the present study, BPA, as a phenolics compound itself, significantly increased the estimated secondary metabolites in tomatoes' leaves. In contrast, anthocyanin was raised dramatically under salinity stress. These differential responses to the stresses applied indicated complex detoxification mechanisms triggered by the applied stresses. In this regard, under stress conditions, flavonoid production is activated as the activity of anti-ROS enzymes decreases (Liu et al., 2019). According to earlier studies, the presence of BPA led to a rise in the levels of unbound phenolic compounds and flavonoids in the onion's roots (Vujčić Bok et al., 2023). In this study, BPA significantly increased phenolics and flavonoids in tomato leaves, whereas salinity stress primarily elevated anthocyanin levels. These findings suggest distinct detoxification mechanisms triggered by BPA and salinity. Flavonoids, for instance, are activated when anti-ROS enzyme activities decrease, as recorded by Liu et al. (2019). BPA stress has been linked to increased unbound phenolics and flavonoids in onions (Vujčić Bok et al., 2023), while salinity stress promotes anthocyanin synthesis, which aids in ROS scavenging (Morales et al., 2020; Naing and Kim, 2021). Despite these positive responses, the excessive ROS under BPA or salinity stress exceeded the plants' antioxidant capacity by antioxidants or secondary metabolites, leading to lipid peroxidation and oxidative damage.

Interestingly, cadaverine application significantly mitigated oxidative stress, reducing ROS and lipid peroxidation levels. Polyamines like cadaverine help maintain protein and cellular functions under stress by enhancing antioxidant activities (Seo et al., 2019). Thus, the singly

stressed plants treated with cadaverine mainly maintained the values of antioxidants and secondary metabolites around the control, which sufficed with enhancing the α -tocopherol, SOD, GST, PPO, and PAL activity higher than the stressed plants. Cadaverine-treated plants-maintained antioxidant and secondary metabolite levels comparable to control plants while showing elevated α -tocopherol, SOD, GST, PPO, and PAL activities. This suggests cadaverine stimulates stress-specific protective mechanisms rather than directly alleviating stress. For instance, α -tocopherol production, enhanced under stress, reduces ROS and prevents lipid peroxidation in thylakoid membranes (Ghosh et al., 2022) and *Vigna angularis* after spermidine application (Ahanger et al., 2020). Consequently, these studies may give an explanation on decreasing superoxide anion and hydroxyl radical for the stressed plants by cadaverine in this study. It is well-established that boosting SOD activity improves plants' ability to withstand environmental stress (Zhou et al., 2019). Similarly, cadaverine has been shown to increase SOD activity, improving stress tolerance for plants treated with cadaverine, mitigating oxidative damage (Zhou et al., 2024; Ozmen et al., 2023). Additionally, cadaverine reduced phenolic and anthocyanin levels in stressed plants, as observed in *Rosa hybrida* (Yousefi et al., 2021). This antioxidative role is crucial in countering salt-induced damage by scavenging toxic oxygen radicals, as demonstrated in sea fig under salinity stress (Kuznetsov et al., 2007). Furthermore, cadaverine alleviated nitrate toxicity in wheat by enhancing GO, SOD, GST activity (Balci et al., 2023). Thus, the ability of cadaverine to enhance antioxidative enzyme activities and regulate secondary metabolites underscores its potential as a protective agent against abiotic stresses like salinity and BPA.

In line with this, Cadaverine stimulated phenylalanine ammonia-lyase (PAL) and polyphenol oxidase (PPO) activities under single or combined stress conditions. PAL activity, linked to stress adaptation, was also shown to promote in *Achillea millefolium* treated with putrescine application (Behdarvand Askar et al., 2020) and in garlic under high salinity (Astaneh et al., 2018). Similarly, PPO and PAL activities increased in salinity-stressed guava treated with putrescine (Ghalati et al., 2020). Similarly, when Indian mustard plants were sprayed with cadaverine grown under salt stress, their enzymes and metabolites further increased (Tomar et al., 2013). These findings suggest that Cadaverine enhances tomato plant resilience under salinity or BPA stress by activating key antioxidants like α -tocopherol, SOD, GST, PAL, and PPO.

HPLC analysis revealed that tomato plants could accumulate BPA in their roots, with higher levels under Cadaverine and BPA combination. This aligns with Ferrara et al. (2006), who reported BPA accumulation in roots without complete detoxification. However, BPA levels in leaves and fruits were below detection limits, likely due to efficient shoot detoxification or transformation into by-products through hydroxylation and glycosylation. These processes produce BPA derivatives, such as mono- and di-O- β -D-glucopyranosides and quinones, which lack estrogenic activity but may still have harmful impacts.

Furthermore, the co-application of salinity and BPA under cadaverine treatment promoted the breakdown of PBA in roots, reducing the toxicity of pollutants on tomato plants. This supports earlier studies where GSH metabolism and GST enzyme induced BPA detoxification through glutathionylation (Kanwar et al., 2020; Sun et al., 2019a). PAs, like Cadaverine, promote enhancing transcriptome modulation, detoxification, and xenobiotic compartmentalization in vacuoles (Spormann et al., 2021) aligns with its stress-alleviating effects in this study.

The ability to tolerate high levels of abiotic stress is directly linked to the existence of antioxidant enzymes like POD and PPO, which were significantly influenced by Cadaverine. BPA increased PPO activity and relative gene expression, with further stimulation by Cadaverine, consistent with findings by Azzam et al. (2021). PPO activity may serve as an adaptive mechanism to delay senescence and enhance stress defenses. Additionally, polyamines like spermine, spermidine, and putrescine have been shown to stimulate PPO activity under stress (Tait et al., 2019). Plant peroxidases play an essential role in the regulation of

growth through lignification, cell wall modification, and auxin breakdown, and are biochemical markers for various stresses (Azzam et al., 2021). Although BPA and salinity triggered GP activity, RQ levels significantly decreased with or without cadaverine suggesting gene downregulation as part of a stress response. Similar discrepancies between POD activity and mRNA expression have been reported (Wang et al., 2020). Similarly, there is no clear correlation between the activity of peroxidases and the transcriptome of mRNA (Dunand et al., 2003). However, the downregulation of POD genes in response to cadaverine and the applied stressors could be ascribed to enhancing the resilience of tomatoes via susceptible reaction.

Thaumatin-like proteins (TLPs) play vital roles in plant defense, development and growth (Wang et al., 2022). Although salinity and BPA had minimal impacts on TLP expression, Cad enhanced TLP gene expression, hence enhancing plant development and inducing stress resilience. Similar protective and developmental roles of TLPs were observed by Sharma et al. (2022). In addition, He et al. (2021) stated that the genetically modified *Brassica oleracea* showed remarkable resistance to salinity and aridity factors through enhancing TLP transcriptome.

Also, the present study includes the TUB gene, which encodes the protein α -tubulin. Cadaverine enhanced RQ of TUB for plants exposed to salinity and/or BPA stress, hence enhancing microtubule formations. TUB encodes α -tubulin, essential for cell structure, division, and vesicle transport (Ma and Han, 2020). Increased TUB expression under Cad treatment correlates with improved microtubule organization, supporting stress adaptation (Chen et al., 2022; Lytvyn et al., 2013). Microtubules also mediate mechanical stress and osmotic responses, highlighting their role in cellular resilience (Sallee and Feldman, 2021). The upregulation of specific stress-response genes is a hallmark of plant resilience under diverse and challenging conditions. However, resistance to salinity or BPA stress, as well as cadaverine activation, is unlikely to be controlled solely by a single gene sequence or translational level. Instead, it underscores the complex crosstalk of multiple genetic, biochemical, and physiological mechanisms.

Overall, Cad-induced upregulation of stress-response genes and activation of antioxidant systems reveals its efficacy to induce tomato plant resilience to salinity or/and BPA stress. This multifaceted adaptation involves enzyme activation, secondary metabolite modulation, and detoxification mechanisms.

5. Conclusion

The study revealed distinct defense mechanisms in tomatoes under salinity and BPA stress. Under salinity stress, metabolites like proline and anthocyanin, alongside antioxidants such as PPO, GPX, PAL, GST, and SOD, played key roles in cellular stress responses. Conversely, tomatoes responded to BPA stress by accumulating free phenolics, flavonoids, AsA, GSH, and α -tocopherol, while showing increased activity of PPO, GP, GPX, and APX, as well as upregulated PPO transcripts. Cadaverine exhibited a unique mechanism in mitigating stress caused by salinity and/or BPA. It promoted the synthesis of α -tocopherol, elevated the activity of PPO, PAL, GST, and SOD, and enhanced the expression of PPO, TUB, and TLP genes. However, the combination of salinity and BPA was detrimental on tomato plants, which cannot survive more than 10 days under these conditions. Under combined stress conditions, cadaverine enabled tomato plants to survive until fruiting stage via maintaining metabolite levels near control values while boosting the activity of PPO, GP, GST, and SOD enzymes and increasing TUB and TLP gene expression compared to untreated controls. These findings suggest that cadaverine effectively enhances crop tolerance to abiotic stresses from salinity and BPA while reducing BPA accumulation in tomato roots. Future research could investigate the uncover the hormonal responses under combined stress and cadaverine as well as the controlling genes. Including more omics approaches to give more information on cadaverine's precise role in stress response networks. Furthermore,

cadaverine can be applied for its ameliorating effects on other stresses beyond single or combined effects of BPA and salinity and focusing on the secondary metabolites and genetic basis of such improvements to ensure its efficacy to broad-spectrum stressors. Additionally, analyzing BPA by-products in plant tissues is crucial to determine their potential toxicity. Studying soil microbiota under salinity and BPA stress may also provide insights into whether microorganisms contribute to accelerating BPA decomposition in such environments. Also, broader application of cadaverine in ameliorating other single or combined stresses beyond salinity and BPA should be conducted to ensure its efficacy to broad-spectrum stressors.

CRedit authorship contribution statement

Mahmoud S. Abdelmoneim: Conceptualization, Methodology, providing chemicals, practical work, Formal analysis, Investigation, Writing – review & editing. **Mona F.A. Dawood:** Supervision, Conceptualization, Methodology, Writing – review & editing. **Elsayed E. Hafez:** Supervision, Conceptualization, Writing – review & editing, Methodology, providing reagents and devices. **Sherif F. Hammad:** Supervision, providing chemicals and devices, Writing – review & editing. **Mohamed A. Ghazy:** Supervision, Writing – review & editing.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix ASupplementary data

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Data availability

Data will be made available on request.

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