



Physiological mechanism by which exogenous salicylic acid alleviates salt stress injury in *Osmanthus fragrans* seedlings

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Abstract

Salicylic acid (SA) mitigates salt stress in plants, yet its combined effects with salinity on *Osmanthus fragrans* remain unstudied. *O. fragrans* is a key Chinese ornamental tree, whose growth and use are restricted by salinization. Therefore, we aimed to evaluate the effect of SA application on *O. fragrans* under salt stress. *O. fragrans* seedlings were subjected to NaCl, SA, and NaCl+SA treatments, and their physiological and growth responses to salt stress were examined. Under NaCl, plant height, leaf mass per area, photosynthetic rate, and pigments of *O. fragrans* decreased by 29.5, 20.6, 42.2, and 29.2%, respectively. Notably, the SA application alleviated these effects by enhancing photosynthesis and the activities of antioxidant enzymes, improving photosynthetic pigments, and the contents of compatible solutes. The findings provide important insights into physiological mechanisms underlying SA-mediated salt tolerance, and provide a practical basis for the application of SA in improving the growth of *O. fragrans* in saline soils.

Keywords: chlorophyll; gas exchange; osmoregulation; plant biomass; superoxide dismutase.

Introduction

Soil salinity is a significant global environmental factor that limits the growth of various plant species and crop productivity (Yang and Guo 2018). Approximately 20% of the world's irrigated agricultural land is adversely affected by soil salinization (Qadir *et al.* 2014). Expanding soil salinization drives extensive research on plant salt responses to guide cultivation practices (Ashraf and Orooj 2006, Flowers and Colmer 2008).

Osmanthus fragrans (Thunb.) Lour. has been cultivated in China for over 2,500 years (Zang and Xiang 2004). This evergreen shrub originates from Southwest China and is now extensively grown across the Yangtze River Basin (Zang and Xiang 2004, Wang *et al.* 2006). *O. fragrans* is a kind of noteworthy horticultural plant belonging to the Oleaceae family. Its essential oil ranks among the finest natural fragrances and is exclusively applied in high-end perfumes and cosmetics (Mar and Pripdeevech 2016). In addition, its flowers are commonly processed

Highlights

- Exogenous salicylic acid (SA) enhances photosynthesis and promotes plant growth
- Exogenous SA increased the activities of superoxide dismutase and catalase
- The application of SA helps manage *Osmanthus fragrans* in areas with salinized soil

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Abbreviations: APX – ascorbate peroxidase; Car – carotenoids; CAT – catalase; Chl *a(b)* – chlorophyll *a(b)*; C_i – intercellular CO₂ concentration; DM – dry mass; *E* – transpiration rate; FM – fresh mass; g_s – stomatal conductance; LDMC – leaf dry mass content; LMA – leaf mass per area; MDA – malondialdehyde content; P_N – net photosynthetic rate; POD – guaiacol peroxidase; ROS – reactive oxygen species; RWC – relative water content; SA – salicylic acid; SOD – superoxide dismutase; SS – soluble sugar; TM – turgid fresh mass; WUE – water-use efficiency ($= P_N/E$); ψ_w – water potential.

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into food additives and daily foods, such as scented tea, wine, preserves, pastries, and various dishes (Xin *et al.* 2013, Wei *et al.* 2020). Soil salinization has become a major obstacle to agricultural and forestry development across China. The total area of saline soil in China is approximately 3.6×10^7 ha, accounting for 4.88% of the country's total available land base (Li *et al.* 2014a). NaCl is one of the major abiotic stresses restraining *O. fragrans* growth and productivity (Yang *et al.* 2018). Accordingly, exploring practical measures to relieve salt stress damage on *O. fragrans* is of great practical significance.

Plant damage caused by salinity originates from osmotic stress, ionic toxicity, and secondary oxidative damage (Munns and Tester 2008). The decline in soil solution water potential under saline conditions first causes osmotic stress. Afterwards, high salt contents in the cytoplasm lead to ionic imbalance and toxicity. Increased reactive oxygen species (ROS) generated by salt-related oxidative stress will ultimately cause cell death. Salt stress has detrimental impacts on plant development and growth at both the physiological and biochemical levels (Oueslati *et al.* 2010). Plant response mechanisms to salinity are complex; they include photosynthetic regulation to maintain high photosynthetic efficiency, active oxygen scavenging to reduce oxidative damage, and the regulation of osmotic balance under the osmotic stress caused by high salinity (Guo *et al.* 2022). Plants maintain a dynamic balance between the generation and elimination of ROS under natural growth conditions. However, salt stress disrupts this equilibrium and triggers excessive ROS accumulation. Excessive accumulation of ROS can damage DNA, inactivate enzymes, and cause lipid peroxidation (Pang *et al.* 2011, Esan *et al.* 2017). One of the most negative effects of oxidative damage is the peroxidation of membrane lipids, which results in the production of malondialdehyde (MDA) (Lu *et al.* 2021). To mitigate the harm from oxidative stress, plants eliminate ROS through two primary pathways: enzymatic and nonenzymatic systems (Mittler 2002, Roussos *et al.* 2013). The antioxidant enzymes involve superoxide dismutases (SOD, EC 1.15.1.1), guaiacol peroxidase (POD, EC 1.11.1.7), catalases (CAT, EC 1.11.1.6), and ascorbate peroxidase (APX, EC 1.11.1.11), which can scavenge free radicals and neutralize ROS (Rattan *et al.* 2020). The nonenzymatic mechanisms involve the synthesis of compatible solutes, such as glycine betaine, proline, soluble protein, and sugar. The accumulation of these substances under stress triggers the plant antioxidant system and raises leaf relative water content (RWC), thereby shielding the photosynthetic apparatus from oxidative injury (Matysik *et al.* 2002, Guo *et al.* 2017).

According to the responding mechanisms in plants, the amplification defense system in plants can alleviate the salt stress injury to plant growth. Recent research has demonstrated that exogenous phytohormones, including salicylic acid (SA), can enhance plant salt tolerance. As an endogenous phenolic regulator in plants, SA modulates multiple physiological and biochemical processes and exerts beneficial effects on plant tolerance to

both abiotic and biotic stresses (Durner and Klessig 1996, Ghassemi-Golezani and Farhangi-Abri 2018). SA induced changes in plants such as the promotion of immunity (Pokotylo *et al.* 2021), antioxidant systems activities (Lu *et al.* 2021, Saleem *et al.* 2021), osmoregulation (Munsif *et al.* 2022), and phytochemical metabolism (Kováčik *et al.* 2009, Quaglia *et al.* 2022). At present, there are studies focusing on the color and fragrance of *O. fragrans* (Han *et al.* 2015, Fu *et al.* 2019). Also, there are reports on its stress resistance to drought, low temperatures, and heavy metal stress (Liao *et al.* 2018, Qian *et al.* 2018, Li *et al.* 2020). However, whether exogenous SA can alleviate salt stress injury in *O. fragrans*, and the physiological mechanisms of exogenous SA to alleviate salt stress injury in *O. fragrans* are still unknown. In this study, seedlings of *O. fragrans* were subjected to NaCl, SA, and NaCl+SA treatments, and their physiological and growth responses to the salt stress were examined. This study aimed to determine the stress injury caused by NaCl and the defense system employed by measuring gas-exchange characteristics, photosynthetic pigments, the enzymatic antioxidant system, membrane injury, water status, and compatible solutes. We hypothesized that exogenous SA could alleviate salt stress injury in *O. fragrans* seedlings by improving photosynthetic performance, regulating ROS homeostasis, and increasing antioxidant enzyme activities. Accordingly, the findings of this study could clarify the physiological responses of *O. fragrans* to salt stress and provide references for its rational cultivation and utilization in salinized regions.

Materials and methods

Seed collection and germination: Seeds of *O. fragrans* were collected from Xi'an University, located in Shaanxi province in China (34°13.35'N, 108°54.47'E), in May 2020. Seeds were kept in moist sand at 4°C for pre-germination preservation. Before the start of the experiment, the seeds were surface-sterilized with 0.52% sodium hypochlorite solution for 1 min and rinsed three times with distilled water to avoid fungal infection. Then the seeds were placed on three fold filter paper on 30 Petri dishes (100 mm diameter and 15 mm height, 10 seeds per dish) and kept at a photon flux density of 350–400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ with 12/12-h photoperiod at a temperature of 25/18°C (day/night) in a phytotron (PQX 330H, Ningbo Life Technology Co., Zhejiang, China) in May 2021. Seeds started germinating 15 d after sowing.

Experimental design: *O. fragrans* seedlings were transplanted into 80 plastic pots (10 cm diameter and 15 cm height) filled with cleaned sand, and all pots were placed in a sunlit greenhouse. The seedlings were irrigated with Hoagland solution every three days to ensure an adequate water supply. The temperature was maintained at 25/18°C (day/night) by three air conditioners, and the relative humidity was kept at *ca.* 50%. The daytime photosynthetic photon flux density averaged 654 $\mu\text{mol m}^{-2} \text{s}^{-1}$. When the seedlings had six leaves of a uniform size, the pots were divided into four 20-pot groups. Four groups were exposed

to four treatments for two weeks, including control (CK), 100 mmol(NaCl) L⁻¹ (NaCl), 0.5 mmol(SA) L⁻¹ (SA), and 100 mmol(NaCl) L⁻¹ plus 0.5 mmol(SA) L⁻¹ (NaCl+SA). The plants received regular irrigation with the Hoagland solution that was modified solely by varying NaCl and SA contents. During the whole experimental period, pots were arranged in a randomized complete block design and rotated twice weekly to mitigate the impact of placement differences. All the experiments were repeated six times. *O. fragrans* seedlings were sampled and measured using the methods described below.

Gas exchange: After two weeks of treatment, measurements of net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), and intercellular CO₂ concentration (C_i) on fully expanded leaves were taken on the same day using Li-6400 portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska, USA) at PPFD about 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$, provided by an external halogen lamp. The ambient temperature in the measuring cuvette was maintained at 25°C with a relative humidity of about 65%. CO₂ cartridge was used to maintain CO₂ concentration of 360 $\mu\text{mol mol}^{-1}$ during measurements. Three measurements were carried out in one plant. Steady-state values from each leaf were recorded after a 200-s equilibration period. Leaf water-use efficiency (WUE) was calculated as follows: $\text{WUE} = P_N/E$.

Plant height, mass, leaf area, and LMA: Plant heights were measured after gas-exchange measurements. Plants were separated into root and shoot. All separated samples were placed in perforated paper bags at 80°C for 48 h and then weighed for the dry mass (DM) with a SE202F electronic balance (Ohaus Corp., Parsippany, NJ, US). The second fully expanded leaves (2nd leaf from the shoot top) of *O. fragrans* were sampled randomly from six plants in each group. Leaf area was measured using a flatbed scanner connected to a personal computer running image analysis software. All leaf samples were placed in perforated paper bags separately and oven-dried at 80°C for 24 h, then weighed for dry mass. Leaf mass per area (LMA) denotes leaf dry mass per area (Cornelissen *et al.* 2003).

Leaf photosynthetic pigment: Photosynthetic pigments were extracted by 95% ethanol. The absorbance values of photosynthetic pigments were measured at wavelengths of 470, 649, and 664 nm (752S UV-Vis spectrophotometer, Shanghai Lengguang Technology Co., Ltd., Shanghai, China). Chlorophyll (Chl) and carotenoid contents were calculated using the formulas revised by Lichtenthaler (1987), and the results were expressed as milligrams of pigment per gram of fresh leaf mass.

Soluble protein and antioxidant enzymes: Leaf tissue of 0.5 g was extracted in 10 ml of 100 mmol L⁻¹ potassium phosphate buffer (pH = 6.8) for antioxidant enzymes assay. The homogenate was centrifuged at 12,000 $\times g$ for 25 min at 4°C, and the supernatant fraction was used as the extract for protein and antioxidant enzyme determinations.

The amount of soluble protein was measured by the method of Bradford (1976), taking bovine serum albumin as the standard protein (Bradford 1976). SOD (EC 1.15.1.1) activity was measured according to the method of Giannopolitis and Ries (1977). The SOD activity depended on its ability to prevent the photochemical reduction of nitro blue tetrazolium (NBT). POD (EC 1.11.1.7) activity was estimated by the method of Chance and Maehly (1955). The CAT (EC 1.11.1.6) activity was determined by detecting the consumption of H₂O₂ by the method of Aebi (1984). APX (EC 1.11.1.11) activity was measured according to Nakano and Asada (1981). SOD, POD, CAT, and APX activities were assayed on a 752S UV-Vis spectrophotometer (Shanghai Lengguang Technology Co., Ltd., Shanghai, China). All enzyme activities were calculated as activity units per milligram total soluble protein per minute, with unit definitions consistent with the corresponding assay methodologies: SOD (50% inhibition of NBT photochemical reduction per minute), POD (0.01 absorbance increase per minute), CAT (1 μmol of H₂O₂ decomposed per minute), APX (0.01 absorbance decrease per minute).

Leaf MDA, H₂O₂, RWC, and ψ_w : Malondialdehyde (MDA) was measured by the method of thiobarbituric acid reaction (Kosugi and Kikugawa 1985). H₂O₂ content was determined by using a spectrophotometer (UV755B, Shandong Olabo Instrument Co., Ltd., China) (Velikova *et al.* 2000). The 2nd fully expanded leaves were sampled at about 09:00 h, and then weighed immediately to obtain fresh mass (FM) in the field. Leaves were sealed in distilled water-filled plastic bags and soaked overnight for full hydration. Their turgid mass (TM) was measured the following day. Afterwards, samples were transferred to perforated paper bags and dried at 80°C for 24 h to obtain dry mass (DM). Leaf relative water content (RWC) was calculated using the formula: $\text{RWC} = (\text{FM} - \text{DM}) / (\text{TM} - \text{DM})$ (Barrs and Weatherley 1962). Leaf ψ_w was detected on freshly cut leaves using a dewpoint water potential meter (Wescor Inc., Logan, Utah).

Proline, glycine betaine, and soluble sugar contents: Dry leaves were ground using a mortar and pestle to pass through a 100-mesh screen. The ground dry leaf sample was used to determine proline content according to the acid-ninhydrin method (Bates *et al.* 1973). The glycine betaine was determined by the method of reverse-phase ion-pair HPLC (Chen *et al.* 2000). The soluble sugars were measured using the anthrone-sulfuric acid method (Ebell 1969).

Statistical analysis: All results were presented as the means $\pm$ standard errors (SE). Analysis of variance (ANOVA) was performed on data of plant height, biomass, leaf area, LMA, gas-exchange parameters (P_N , E , g_s , C_i , and WUE), photosynthetic pigment, antioxidant enzymes, MDA, H₂O₂, RWC, ψ_w , proline, soluble sugar, and protein content, and glycine betaine content to determine divergence in the four treatments with Tukey's HSD multiple comparison test. A difference was considered

significant if $p < 0.05$. All statistical analyses on the data were performed using SPSS 17.0 (SPSS for Windows, Chicago, IL, USA), and all figures were processed by Origin 10.0 (OriginLab Corporation, USA).

Results

Plant height, leaf area, and leaf mass per area (LMA): Compared with CK, NaCl treatment significantly decreased plant height, leaf area and LMA by 29.5, 22.5, and 20.6%, respectively (Fig. 1A–C). The 0.5 mmol(SA) L⁻¹ treatment did not significantly affect plant height, leaf area, and LMA. Interestingly, compared with NaCl treatment, NaCl+SA treatment significantly enhanced plant height by 47.9%, and increased plant leaf area and LMA by 14.7 and 18.5%, indicating that addition of SA promoted *O. fragrans* growth under salt stress.

Shoot and root biomass: SA treatment did not significantly affect plant shoot, root, and total biomass (Fig. 1D–F). In contrast, NaCl stress reduced plant shoot, root, and total biomass in both NaCl and NaCl+SA treatments. However, NaCl-induced negative effects on shoot and total biomass were significantly diminished in the NaCl+SA treatment (Fig. 1D,F). Shoot and total biomass in NaCl+SA treatment significantly increased 35.9 and 28.0% compared with those in NaCl treatment, respectively.

Gas exchange: SA treatment did not significantly affect P_N , E , and g_s (Fig. 2A–C). Compared with CK, P_N and

g_s decreased significantly by 42.2 and 42.0% following NaCl exposure (Fig. 2A,C). Nevertheless, NaCl-induced negative effects on P_N and g_s were significantly alleviated in the NaCl+SA treatment. Compared with CK, NaCl+SA treatment reduced P_N by 16.0% and increased g_s by 0.9%, respectively. E decreased significantly in the NaCl and NaCl+SA treatment (Fig. 2B). C_i of *O. fragrans* was reduced 26.2, 25.2, and 25.0% in the NaCl, SA, and NaCl+SA treatments compared with CK, respectively (Fig. 2D). NaCl and SA treatment did not significantly affect WUE (Table 1). However, WUE significantly increased 38.0% in the NaCl+SA treatment compared with CK.

Photosynthetic pigments: SA treatment exerted no significant influence on the contents of Chl *a* and total Chl (Fig. 3A,D). A significant reduction of 28.8% in Chl *a* and 29.2% in Chl (*a+b*) contents was observed in *O. fragrans* subjected to NaCl relative to CK. Notably, the combined NaCl and SA treatment caused a marked rise in Chl *a* and total Chl contents by 38.4 and 29.2% compared to NaCl treatment alone. Chl *b* contents were reduced 30.3, 16.9, and 24.3% in the NaCl, SA, and NaCl+SA treatments compared with CK, respectively (Fig. 3B). NaCl and SA treatments did not significantly affect the Chl *a/b* ratio (Fig. 3C). But the Chl *a/b* ratio increased significantly by 30.7% in the NaCl+SA treatment compared with NaCl treatment. There was no significant difference in the carotenoid (Car) content between the different

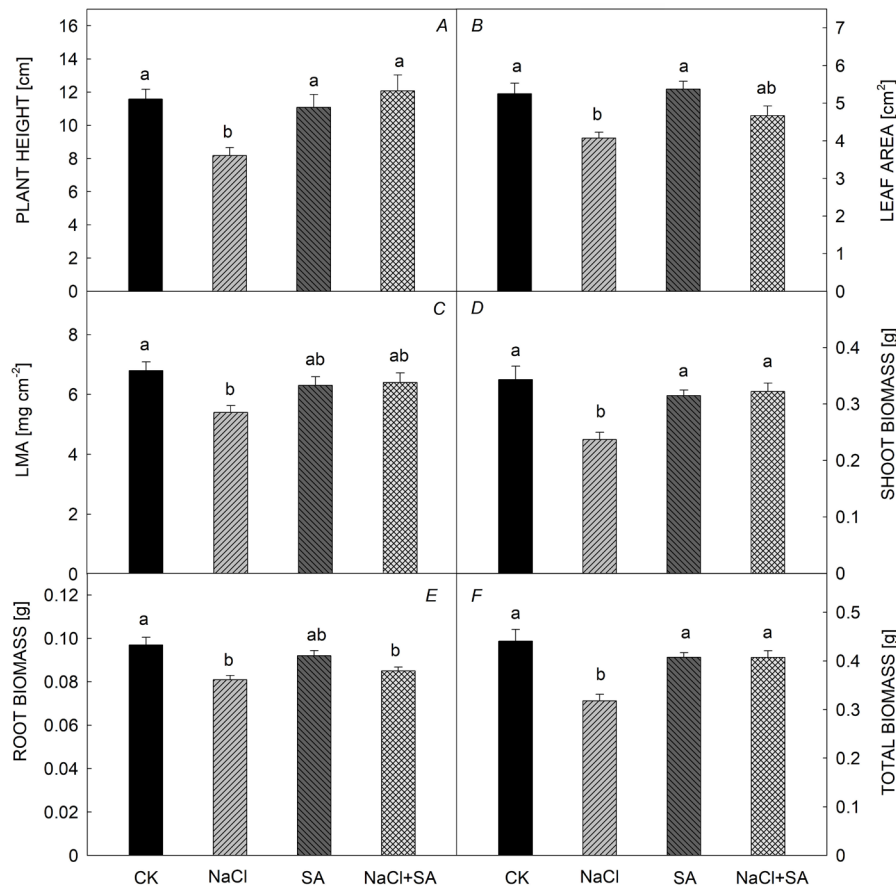


Fig. 1. Effects of exogenous salicylic acid (SA) on plant height (A), leaf area (B), leaf mass per area (LMA) (C), shoot biomass (D), root biomass (E), total biomass (F) of *Osmanthus fragrans* seedlings under salt stress. Data are means $\pm$ SE ($n = 6$), different lowercase letters indicate statistically significant differences at the $p < 0.05$ level. CK – control; NaCl – 100 mmol L⁻¹ NaCl; SA – 0.5 mmol L⁻¹ SA; NaCl+SA – 100 mmol L⁻¹ NaCl plus 0.5 mmol L⁻¹ SA.

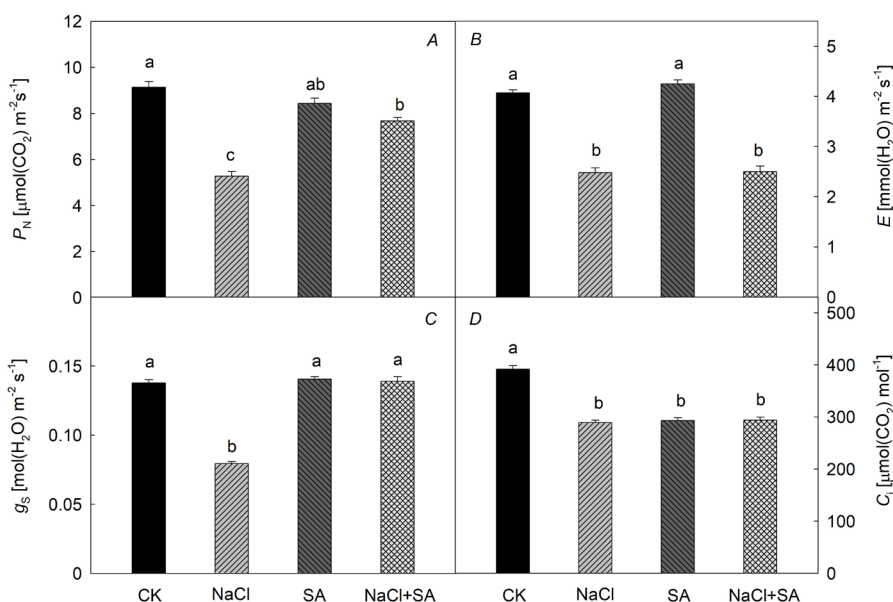


Fig. 2. Effects of exogenous salicylic acid (SA) on the gas-exchange parameters of *Osmanthus fragrans* seedlings under salt stress. Data are means $\pm$ SE ($n = 6$), different lowercase letters indicate statistically significant differences at the $p < 0.05$ level. (A) Net photosynthetic rate: P_N ; (B) transpiration rate: E ; (C) stomatal conductance: g_s ; (D) intercellular CO_2 concentration: C_i . CK – control; NaCl – 100 mmol L^{-1} NaCl; SA – 0.5 mmol L^{-1} SA; NaCl+SA – 100 mmol L^{-1} NaCl plus 0.5 mmol L^{-1} SA.

Table 1. Effects of different treatments on water-use efficiency (WUE) in leaves of *Osmanthus fragrans*. Data are means $\pm$ SE ($n = 6$), different lowercase letters indicate statistically significant differences at the $p < 0.05$ level. CK – control; NaCl – 100 mmol L^{-1} NaCl; SA – 0.5 mmol L^{-1} SA; NaCl+SA – 100 mmol L^{-1} NaCl plus 0.5 mmol L^{-1} SA.

Treatment	WUE [$\mu\text{mol}(\text{CO}_2) \text{mmol}(\text{H}_2\text{O})^{-1}$]
CK	2.24 $\pm$ 0.05 ^b
NaCl	2.14 $\pm$ 0.10 ^b
SA	1.99 $\pm$ 0.04 ^b
NaCl+SA	3.10 $\pm$ 0.12 ^a

treatments (Fig. 3E,F). Compared with CK, NaCl, SA, and NaCl+SA treatments significantly enhanced the plant Car/Chl ratio by 52.5, 18.5, and 28.8%, respectively.

Antioxidant enzymes: NaCl treatment significantly increased SOD, POD, CAT, and APX activities by 70.6, 31.0, 102.7, and 108.7% compared with CK, respectively (Fig. 4). SA treatment significantly affected SOD and CAT activities (Fig. 4A,C). Compared with NaCl treatment, NaCl+SA treatment significantly enhanced SOD and CAT activities by 23.7 and 12.7%, respectively, indicating that exogenous SA promoted *O. fragrans* antioxidant enzyme activities under salt stress (Fig. 4A,C).

Leaf MDA and H_2O_2 : SA treatment did not significantly affect MDA and H_2O_2 contents (Fig. 5A,B). In contrast, NaCl treatment significantly increased MDA and H_2O_2 contents by 101.4 and 97.2% compared with CK, respectively. The contents of MDA and H_2O_2 were obviously lowered by 31.5 and 45.2% under NaCl+SA treatment in comparison with NaCl treatment alone.

RWC and ψ_w : There was no significant difference in the RWC between the different treatments (Fig. 5C).

SA treatment did not significantly affect ψ_w (Fig. 5D). But ψ_w was reduced significantly by 156.3 and 219.4% in the NaCl and NaCl+SA treatments compared with that in CK, respectively.

Proline, glycine betaine, soluble sugar, and protein contents: SA treatment did not significantly affect proline contents (Fig. 6A). NaCl treatment significantly increased proline contents by 172.5% compared with CK. Proline contents were 14.4% higher under NaCl+SA treatment compared with NaCl treatment. Glycine betaine concentrations increased significantly by 82.3, 40.5, and 131.2% in the NaCl, SA, and combined NaCl+SA treatments, respectively, compared with CK (Fig. 6B). Relative to the NaCl treatment, NaCl+SA treatment markedly elevated glycine betaine contents by 26.9% (Fig. 6B). Soluble sugar contents significantly increased by 159.0, 128.2, and 185.2% in the NaCl, SA, and NaCl+SA treatments compared with CK, respectively (Fig. 6C). NaCl treatment significantly restrained soluble protein content (Fig. 6D). Compared with NaCl treatment, NaCl+SA treatment increased soluble protein content by 33.0%.

Discussion

Soil salinity represents a major and prevalent abiotic stress, which severely restricts plant growth and yield. NaCl stress was found to inhibit *O. fragrans* growth, plant height, shoot biomass, root biomass, and total biomass decreased significantly with the NaCl stress. Growth inhibition is a typical physiological response of plants under stress (Ogunsiji *et al.* 2023). Plants tend to shift energy allocation from biomass formation to stress defense (Munns and Tester 2008). It has been documented that SA serves as a growth regulator and enhances plant resistance to salinity (Ma *et al.* 2023, Ogunsiji *et al.* 2023, Sharma *et al.* 2023, Pai and Sharma 2024). Our results showed that the increase in biomass was due to the alleviating

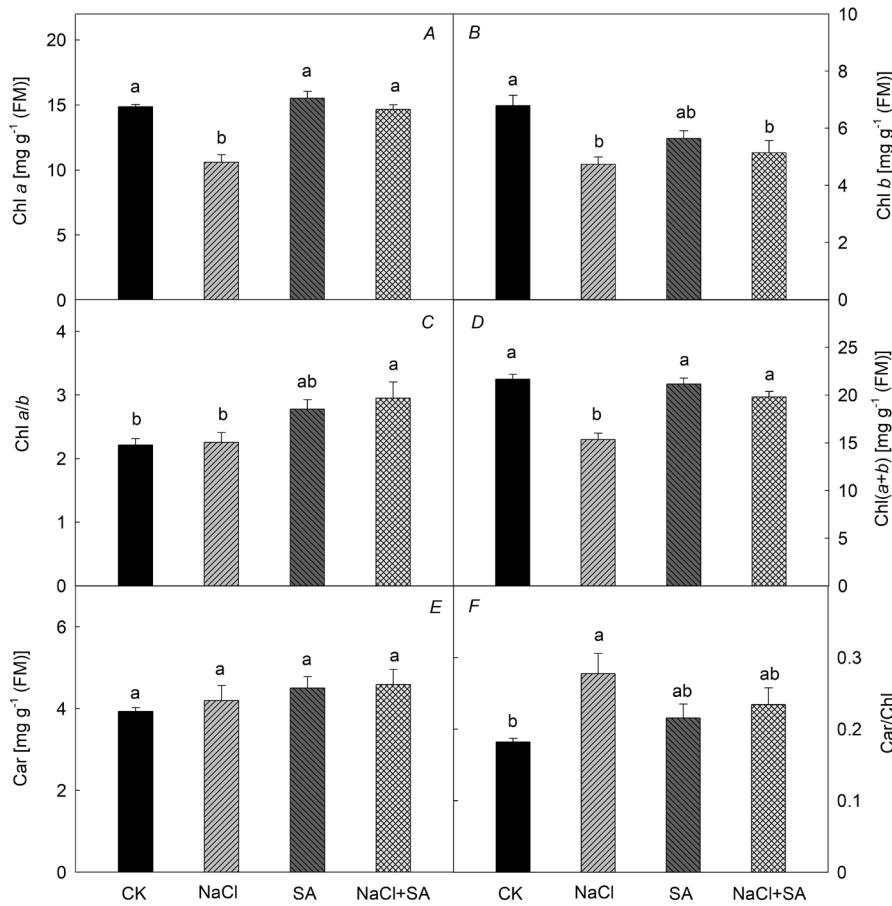


Fig. 3. Effects of exogenous salicylic acid (SA) on the contents of photosynthetic pigments in *Osmanthus fragrans* seedlings under salt stress. Data are means $\pm$ SE (*n* = 6), different lowercase letters indicate statistically significant differences at the *p* < 0.05 level. (A) Chlorophyll *a*: Chl *a*; (B) chlorophyll *b*: Chl *b*; (C) Chl *a/b*; (D) Chl (*a+b*); (E) carotenoids: Car; (F) Car/Chl. CK – control; NaCl – 100 mmol L⁻¹ NaCl; SA – 0.5 mmol L⁻¹ SA; NaCl+SA – 100 mmol L⁻¹ NaCl plus 0.5 mmol L⁻¹ SA.

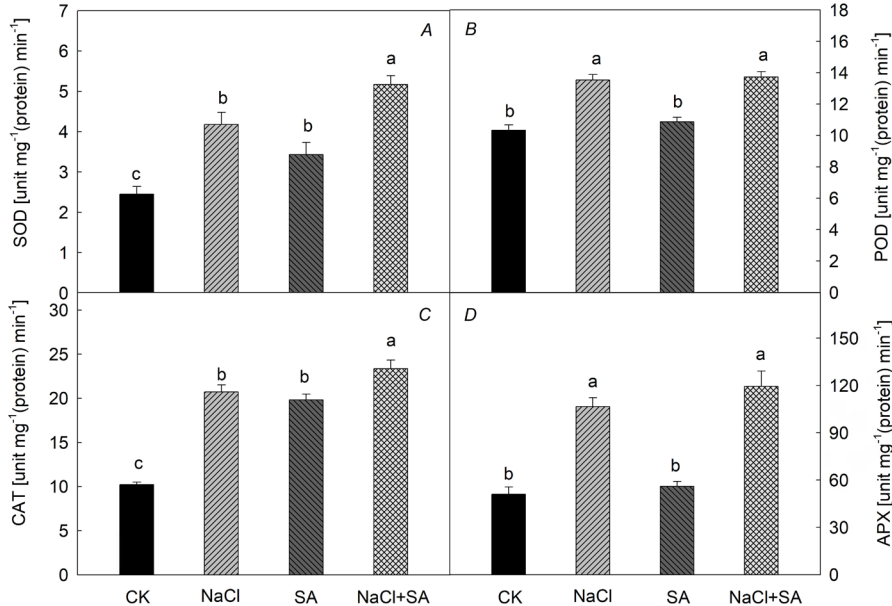


Fig. 4. Effects of exogenous salicylic acid (SA) on the contents of antioxidant enzymes in *Osmanthus fragrans* seedlings under salt stress. Data are means $\pm$ SE (*n* = 6), different lowercase letters indicate statistically significant differences at the *p* < 0.05 level. (A) Superoxide dismutase: SOD; (B) guaiacol peroxidase: POD; (C) catalase: CAT; (D) ascorbate peroxidase: APX. CK – control; NaCl – 100 mmol L⁻¹ NaCl; SA – 0.5 mmol L⁻¹ SA; NaCl+SA – 100 mmol L⁻¹ NaCl plus 0.5 mmol L⁻¹ SA.

effect of SA under salinity stress. Exogenous SA mitigated salt-triggered damage to *O. fragrans* seedlings. The positive effects of SA application on plant growth have been reported in *Brassica juncea* (Fariduddin *et al.* 2003), strawberry (Dakheel *et al.* 2025), wheat (Sharma 2017), and lemongrass (Idrees *et al.* 2010).

NaCl-induced biomass declined in *O. fragrans*, revealing growth restriction, which was also evidenced by leaf area and leaf mass per area (LMA). The LMA is an important indicator of plant survival strategies and a core trait in plant growth (Poorter *et al.* 2009, da Cruz *et al.* 2025). In this study, NaCl was shown to

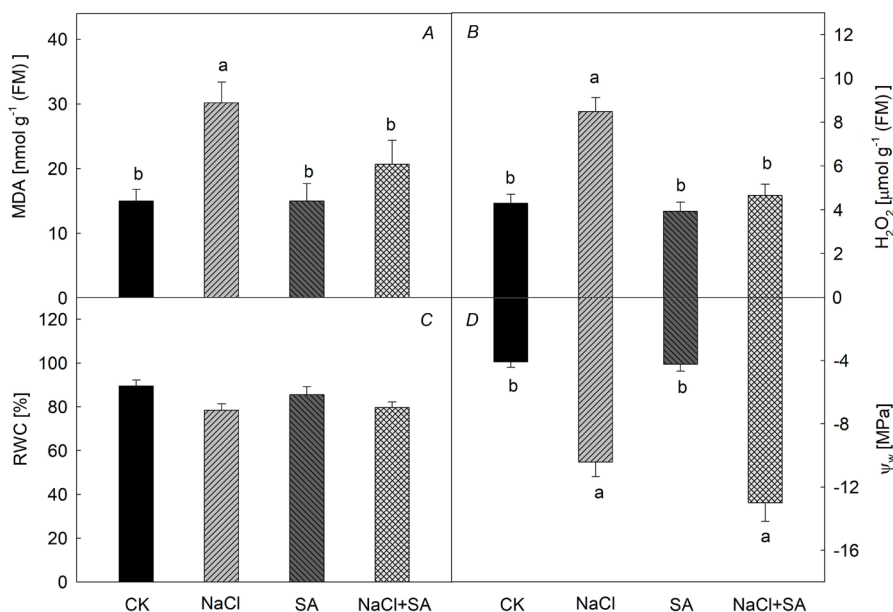


Fig. 5. Effects of exogenous salicylic acid (SA) on the leaf MDA, H₂O₂, RWC, and ψ_w of *Osmanthus fragrans* seedlings under salt stress. Data are means ± SE (*n* = 6), different lowercase letters indicate statistically significant differences at the *p* < 0.05 level. (A) Malondialdehyde content: MDA; (B) H₂O₂; (C) relative water content: RWC; (D) water potential: ψ_w. CK – control; NaCl – 100 mmol L⁻¹ NaCl; SA – 0.5 mmol L⁻¹ SA; NaCl+SA – 100 mmol L⁻¹ NaCl plus 0.5 mmol L⁻¹ SA.

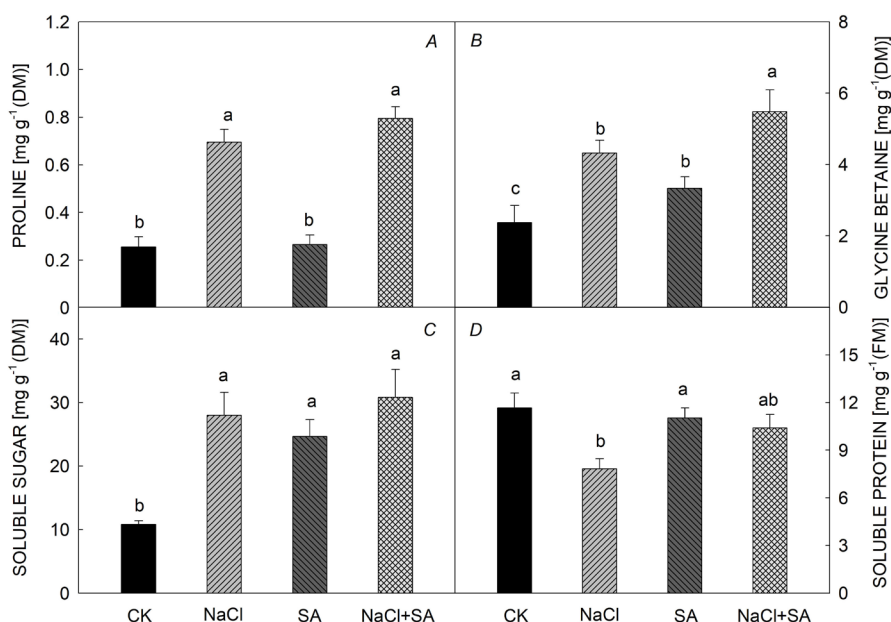


Fig. 6. Effects of exogenous salicylic acid (SA) on the contents of compatible solutes in *Osmanthus fragrans* seedlings under salt stress. Data are means ± SE (*n* = 6), different lowercase letters indicate statistically significant differences at the *p* < 0.05 level. (A) Proline; (B) glycine betaine; (C) soluble sugar; (D) soluble protein. CK – control; NaCl – 100 mmol L⁻¹ NaCl; SA – 0.5 mmol L⁻¹ SA; NaCl+SA – 100 mmol L⁻¹ NaCl plus 0.5 mmol L⁻¹ SA.

directly inhibit the LMA in *O. fragrans*, while NaCl+SA treatment promoted the LMA, leading to more adaptability to NaCl stress. The higher LMA enables plants to maintain high leaf water content under stress (Wang *et al.* 2011). In our previous study, higher LMA, contributing to higher tolerance in unfavorable conditions, was proved to be a main adaptive strategy to salt stress in two *O. fragrans* cultivars (Guo *et al.* 2023). Therefore, SA enhanced the LMA to alleviate the damage caused by salt stress in *O. fragrans*. An increase in LMA under combined NaCl and SA treatment is indicative of greater allocation to assimilatory tissues to improve photosynthetic performance (Fernández-García *et al.* 2014).

The decline in photosynthetic capacity under salt stress generally stems from the inhibition of photosynthetic rate. In our study, NaCl treatment significantly suppressed

photosynthetic rate (P_N) and stomatal conductance (g_s). The response of the g_s plays an important role in plant performance under salt stress (Fernández-García *et al.* 2014). The g_s is an indicator of water, energy, and CO₂ cycles between plants and the atmosphere (Saradadevi *et al.* 2017, Potkay *et al.* 2025). Lower g_s reduced the capacity of plants to take up CO₂ from the atmosphere and subsequently reduced photosynthetic carbon assimilation (Guo *et al.* 2015). Nevertheless, in our study, NaCl-induced negative effects on P_N and g_s were significantly attenuated in the NaCl+SA treatment. This result was in agreement with some earlier studies that found that exogenous application of SA increased the photosynthetic rate in different plants (Khodary 2004, Najafian *et al.* 2009, Kiremit *et al.* 2026). This showed that exogenous SA application may enhance photosynthesis,

which is a major controlling factor for plant growth. SA plays a fundamental role in promoting the synthesis of photosynthetic pigments (chlorophyll and carotenoids), which are essential for photosynthesis (Khodary 2004, Yang *et al.* 2023).

Under salt stress, destabilization of thylakoid membranes, elevated chlorophyllase activity, and aggravated oxidative stress jointly cause dramatic declines in chlorophyll and carotenoids (Moharekar *et al.* 2003, Hameed *et al.* 2021). In our experiment, NaCl treatment led to substantial pigment degradation. Our findings were consistent with earlier reports demonstrating that salinity greatly decreased Chl contents in cabbage and lettuce (Seymen *et al.* 2023, Kiremit *et al.* 2026). Such declines are probably caused by the combined actions of accumulated ROS, hormonal changes (especially higher contents of ABA and ethylene), and ionic imbalance, which disrupt pigment–protein complexes (Ma *et al.* 2017, 2024). However, NaCl+SA treatment significantly enhanced plant Chl *a* and Chl (*a*+*b*) contents compared with NaCl treatment. SA improves thylakoid membrane stability and restrains Chl decomposition *via* modulating the ascorbate–glutathione cycle and enhancing antioxidant enzyme activity (Kang *et al.* 2014, Peng *et al.* 2021). Exogenous SA can effectively alleviate pigment damage in *O. fragrans* and also in other plants under salinity (Borsani *et al.* 2001, Li *et al.* 2014b, Ma *et al.* 2017). The variation in the Chl *a/b* ratio is used as a pointer for relative photosystem stoichiometry (Pfannschmidt *et al.* 1999). Chl *a/b* ratio increased significantly in the NaCl+SA treatment, indicating that SA affected light-harvesting antenna size under salt stress. The higher Chl *a/b* ratio suggests that the light-harvesting antenna size is smaller (Moharekar *et al.* 2003). The Car/Chl ratio increased significantly under the NaCl. Salt-induced oxidative stress leads to an increased ROS production, which causes cell death (Munns and Tester 2008). Carotenoids, in higher plants, protect the photosynthetic apparatus from excessive photons and oxidative stress (Young 1991, Moharekar *et al.* 2003, Ashikhmin *et al.* 2023). Therefore, the significant increase in the Car/Chl ratio under the NaCl treatment might be of some protective value. In our experiment, SA and NaCl+SA treatment enhanced plant carotenoid content and the Car/Chl ratio. The exogenous SA can influence carotenoid accumulation and alleviate salt stress injury in *O. fragrans*.

Salt exposure stimulates excessive generation and accumulation of ROS in plant tissues. Plants eliminate excess ROS *via* enzymatic and nonenzymatic antioxidant systems to mitigate oxidative damage triggered by salt stress (Mittler 2002). The typical response of plants to various environmental stresses is to enhance the activity of antioxidant enzymes (Roussos *et al.* 2013). This study showed that NaCl treatment increased SOD, POD, CAT, and APX activities in *O. fragrans*, indicating that the antioxidant enzyme defense system of *O. fragrans* was activated by salt. Increasing the activities of POD, CAT, and APX under stress may be the result of increasing ROS generation, which activates the plant protective mechanism to reduce oxidative damage (Farhadi and

Ghassemi-Golezani 2020). The activities of SOD and CAT were further significantly increased when *O. fragrans* was treated with exogenous SA, indicating that plants with NaCl+SA treatment maintained higher antioxidant enzyme activities than plants with NaCl treatment, which was crucial for them to scavenge more reactive oxygen species and maintain low oxidative damage under salt. By boosting both gene expression and enzymatic activity of antioxidant proteins, SA treatment facilitates the elimination of excess ROS (Pai and Sharma 2024). In this study, combined SA and NaCl treatment effectively mitigated salt-caused oxidative stress damage. Reduction of H₂O₂ and MDA contents in SA-treated plants was the result of enhancing antioxidant enzyme activities and osmotic adjustment (Farhadi and Ghassemi-Golezani 2020).

The nonenzymatic mechanisms involve the synthesis of compatible solutes such as proline, glycine betaine, soluble sugar, and protein. The increase of proline, glycine betaine, and soluble sugar contents in *O. fragrans* indicated the capacity for dehydration tolerance, and the osmotic adjustment was enhanced with the NaCl treatment. Osmotic adjustment is known as one of the pivotal processes for plants to adapt to water deficit, decreasing cell water potential, and allowing the maintenance of the water absorption and cell turgor under salt and water stresses (Chaves *et al.* 2003). In this study, the contents of proline, glycine betaine, and soluble sugar were further increased when *O. fragrans* was treated with exogenous SA, indicating that SA had a critical role in the regulation of physiological and biochemical responses of plants to salt stress and improved plant adaptation to adverse situations (Ma *et al.* 2017, Farhadi and Ghassemi-Golezani 2020). Previous study suggested that exogenous SA improved proline content due to increasing P5CR activity, which converted pyrroline-5-carboxylate to proline (Misra and Saxena 2009, Iqbal *et al.* 2014). Proline, as one of the key osmolytes, is important in plant adaptation to adverse conditions through protecting the Rubisco and membrane structure by scavenging of singlet oxygen and osmotic adjustment (Matysik *et al.* 2002, Abdelrady *et al.* 2024). Another study had shown that SA treatment led to an increase in glycine betaine content through stimulation of the methionine pathway and inhibition of ET production in response to salt stress (Khan *et al.* 2014). Glycine betaine has an important role in the protection of membrane integrity and PSII complex under oxidative stress, the activation of antioxidant enzymes, and Rubisco (Ashraf and Foolad 2007). SA relieved salt damage in *O. fragrans* by activating the nonenzymatic mechanisms. Our experimental observations substantiated the former hypothesis regarding SA's salt-protective function on *O. fragrans*. Under salt stress, exogenously supplied SA ameliorated photosynthetic depression and activated antioxidant enzymatic systems. These integrated physiological regulations ultimately alleviated salt-caused damage of *O. fragrans* seedlings, solidly confirming our research conjecture.

The present experiment was conducted only with *O. fragrans* seedlings under controlled greenhouse pot conditions, and the conclusions obtained may not

fully represent the physiological performance of adult *O. fragrans* under complex field saline environments. In addition, this study focused primarily on physiological and antioxidant indexes at the phenotypic level, while the underlying molecular regulatory pathways responsible for SA-induced salt tolerance remain unexplored. Further multi-year field trials are required to supplement and validate our experimental results.

Conclusions: Salinity is one of the major abiotic stresses limiting plant growth and productivity worldwide. This study emphasizes the remarkable potential of exogenous SA in alleviating salt stress injury in *O. fragrans*. Our experimental study indicated that NaCl stress inhibited *O. fragrans* performance, plant height, shoot biomass, root biomass, total biomass, photosynthetic rate, and pigments, and leaf ψ_w decreased with the NaCl stress. On the other hand, antioxidant enzymes (SOD, POD, CAT, and APX), MDA, H_2O_2 , proline, glycine betaine, and soluble sugar contents of *O. fragrans* increased with the NaCl stress. Exogenous SA alleviated salt-induced injury in *O. fragrans* seedlings by regulating photosynthetic rate and pigments contents, enzymatic antioxidant system, membrane injury, water status, and compatible solutes. Therefore, application of exogenous SA could be a promising treatment for improving *O. fragrans* plant performance, especially under salt conditions. For subsequent research, multi-site field experiments covering seedling, juvenile, and mature stages of *O. fragrans* on diverse saline soils are recommended to clarify how SA alleviates salt injury in *Osmanthus*. From a practical perspective, exogenous SA can be developed as an economical plant growth regulator to facilitate the popularization and landscaping application of *O. fragrans* in salinized soil.

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