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Interactive Influence of Silicon and Salicylic Acid on Physiological and Biochemical Responses of Cucumber Seedlings Under Salt Stress Condition

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ABSTRACT

This study evaluated the individual and combined effects of salinity stress (80 mM NaCl), salicylic acid (SA; 10 and 15 µM), and silicon (Si; 1.5 mM) on growth, physiological, ionic, and biochemical traits of cucumber (Cucumis sativus L.) seedlings using a factorial experimental design. Salinity stress alone significantly reduced leaf area (36%), shoot and root dry mass (32%), total chlorophyll (19%), and carotenoids (8%), while markedly increasing Na^+ accumulation and oxidative stress indicators. A significant salinity × SA × Si interaction was observed for all measured traits. Under saline conditions, the combined application of Si + SA at 10 µM (Si+SA10) produced the strongest positive responses, resulting in the highest values of growth parameters, photosynthetic pigments, K^+ content, and non-enzymatic antioxidants. Compared with the saline control, Si+SA10 increased leaf area (40%), shoot dry mass (57%), total chlorophyll (44%), carotenoids (61%), and shoot K^+ (62%), while reducing shoot Na^+ accumulation (36%), lipid peroxidation (61%), hydrogen peroxide (50%), and ion leakage (50%), indicating effective mitigation of salt-induced oxidative damage. Notably, under non-saline conditions, the SA × Si interaction also enhanced plant performance, although to a lesser extent. Si+SA10 increased leaf area (≈8%), shoot dry mass (≈13%), and chlorophyll content (≈10%) relative to the control, improved silicon accumulation, and moderately enhanced phenolic and anthocyanin contents, while oxidative stress markers remained at basal levels. Overall, these findings demonstrate that cucumber growth and salt tolerance are maximized through a synergistic interaction between salinity stress, low-dose salicylic acid, and silicon, primarily via improved growth, enhanced photosynthetic capacity, optimized ion homeostasis, and strengthened non-enzymatic antioxidant defense mechanisms.

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Abbreviations: APX- Ascorbate peroxidase; CAT – catalase; GPX – guaiacol peroxidase; H_2O_2 – hydrogen peroxide; MDA – malondialdehyde; NBT- nitro blue tetrazolium –; PVP – polyvinyl pyrrolidone; ROS – reactive oxygen species; RDM – root dry mass; SA – salicylic acid; Si – silicon; SOD – superoxide dismutase; SDM – shoot dry mass; TBA – thiobarbituric acid, TCA – trichloroacetic acid.

1. Introduction

Salinity is one of the most important non-living factors that can hinder plant growth and greatly decrease the yield of many crops. It negatively affects seed germination, seedling health, and final output (Kopecká *et al*., 2023, Malekzadeh et al., 2023). The harmful effects of salt stress come from several issues: osmotic stress from lower soil water levels, the toxic impact of excess sodium that competes with potassium (K^+) for important binding sites in cells, and the negative effect on nutrient uptake due to high concentrations of Na^+ and Cl^- (Balasubramaniam *et al*., 2023, Malekzadeh et al., 2024). In nearly all plant species, salinity and drought lead to the production of reactive oxygen species (ROS), including superoxide radicals (O_2^-). These can then create hydrogen peroxide (H_2O_2), hydroxyl radicals (OH•), and other highly reactive substances (Sachdev *et al*., 2021). Without effective detoxification methods, ROS buildup can cause serious damage to cells, including lipid membrane breakdown, protein degradation, DNA damage, and ultimately cell death (Engwa *et al*., 2018).

To protect against ROS toxicity, plants depend on a complex system of natural defenses made up of enzymes like superoxide dismutase (SOD; EC 1.15.1.1), catalase (CAT; EC 1.11.1.6), and ascorbate peroxidase (APX; EC 1.11.1.11). They also use non-enzymatic antioxidants such as ascorbate, glutathione, phenolics, anthocyanins, and flavonoids, which together help maintain a balance of ROS within cells (Berwal *et al*., 2021). Adding external compounds can enhance these protective components and improve plant resilience to salinity. A plant's ability to survive stress largely depends on how well it can sense stress signals, send them through its system, and set off a series of physiological and biochemical responses (Mudrilov *et al*., 2021). Various chemicals, especially silicon (Si) (Alsaeedi *et al*., 2019; Yin *et al*., 2019; Zhu *et al*., 2020; Shalaby *et al*., 2021; Mousavi *et al*., 2022; Anwar *et al*., 2025; Hussain *et al*., 2025) and salicylic acid (SA) (Kim *et al*., 2017; Gurmani *et al*., 2018; Miao *et al*., 2020; Ansari *et al*., 2025; Salama *et al*., 2025), have shown effectiveness in lessening the negative effects of saline environments.

Silicon, the second most common element in soil, is seen as a helpful nutrient for many plant species (Pavlovic *et al*., 2021; Souri *et al*., 2021). Using Si—whether through foliar sprays or nutrient solutions—has consistently been shown to promote plant growth and improve tolerance to both living and non-living stresses (Lozano-González *et al*., 2021; Hassan *et al*., 2024; Hussain *et al*., 2025). Its positive effects are especially noticeable in stressful growing conditions (Liu *et al*., 2019). Rather than being a passive element, Si acts as both a physical and physiological barrier in the plant. Si levels often rise when plants experience tough environmental challenges, like drought or root zone stress (Lux *et al*., 2020). Earlier research by Lux *et al*. (2002; 2020) found that drought-tolerant sorghum genotypes accumulate much more Si in the endodermis than sensitive ones. Beyond strengthening cell walls, Si plays a role in metabolic changes and physiological regulation, especially when plants face multiple stress factors (Souri *et al*., 2021; Mostofa *et al*., 2021). Boosting antioxidant defenses is one of the key ways Si reduces stress and improves overall plant performance (Mir *et al*., 2021; Bhardwaj *et al*., 2023; Kumar *et al*., 2025). Similarly, extensive research shows that salicylic acid helps increase plant tolerance to difficult conditions.

SA assists plant processes by improving photosynthetic efficiency (Kim *et al*., 2017; Miao *et al*., 2020), stabilizing membranes, and promoting the growth of salt-stressed cucumber plants (Gurmani *et al*., 2018; Youssef *et al*., 2018). It also lowers the levels of Na^+ and Cl^- in cucumber exposed to salinity (Liu *et al*., 2021; Oliveira *et al*., 2023). Miao *et al*. (2020) discovered that longer exposure of cucumber roots to low SA concentrations enhanced salt tolerance. Many of SA's salt-mitigating effects come from its ability to trigger antioxidant responses and decrease ROS production and lipid peroxidation (Song *et al*., 2023). However, SA works in a dose-dependent way: low amounts boost growth (Quamruzzaman *et al*., 2021), but high amounts can stress the plant (Ren *et al*., 2022). Notably, SA helps form proline-rich proteins, which may aid in the process of converting Si into silica structures (He *et al*., 2022).

Given the unique and complementary roles of Si and SA in reducing salinity stress, this study tested the idea that the combination of silicon (Si) and salicylic acid (SA) enhances salt tolerance in cucumber seedlings by improving antioxidant balance and maintaining ion homeostasis in saline conditions.

2. Materials and Methods

2.1. Plant material

Cucumber (cv. Sina) seeds (Cucumis sativus L) were purchased from Sepahan Rooyesh Co in Isfahan, Iran. The seeds were rinsed thoroughly with distilled water, soaked in water for 4 hours, and then germinated on moist filter paper in an incubator set at 28°C. After six days, the uniform seedlings were transplanted into hydroponic plastic pots containing 7000 ml of half-strength modified Hoagland nutrient solution (Hoagland, 1920), which was

aerated continuously using an air pump. Three plants were placed in each plastic pot, and three replications were used for each treatment. The nutrient solution included 5 mM KNO3, 5 mM Ca (NO3)2, 2 mM MgSO4, 1 mM KH2PO4, 9 µM MnCl2, 2 µM ZnSO4, 0.8 µM CuSO4, 0.8 µM Na2MoO4, 25 µM Fe-EDDHA, and 25 µM H3BO3. This solution was applied to the seedlings right after transplanting, and fresh solution was added every two days to avoid nutrient deficiency. The pH of the nutrient solution was adjusted daily to 6.0 using 0.01 mol/L KOH or HCl. The seedlings were allowed to grow for three weeks in a greenhouse with temperatures of 25/18 ℃ (day/night), a photoperiod of 16 hours of light and 8 hours of dark (200 mol m-2s-1 photon flux density), and a relative humidity of 50±5%.

Pretreatment started by adding silicon from Na2SiO3 (MC1056212500; Merck, Germany) at two levels (0 or 1.5 mM) and salicylic acid (Code: 100631, Merck Germany) at three levels (0, 10, or 15 µM) into the hydroponic system. After 72 hours of pretreatment, the pots were split into two groups and exposed to two salinity levels: 0 and 80 mM NaCl (MC1064041000, Merck Germany). Twelve different treatments with three replicates were used in the experiment: control, silicon 1.5 mM (Si), salicylic acid 10 µM (SA10), salicylic acid 10 µM + silicon 1.5 mM (SiSA10), salicylic acid 15 µM (SA15), and salicylic acid 15 µM + silicon 1.5 mM (SiSA15) under both salinity stress levels. All plants were harvested 7 days after the NaCl treatments and separated into leaves, stems, and roots. The growth parameters, including shoot and root dry weights and leaf area, were measured. The plant materials were washed with distilled water, quickly preserved in liquid nitrogen, and stored at −80℃ before measuring various biochemicals. The greenhouse and lab experiments took place at Shahid Bahonar University of Kerman in Kerman city, southeastern Iran. The experimental site's geographical coordinates are approximately 30.25° N latitude and 57.10° E longitude, with an elevation of about 1,755 m above sea level. This experiment was organized as a factorial study using a completely randomized design in 2024.

2.2. Measurement of the growth parameters

After harvesting in 30 days after transplanting, the plants were divided into shoots and roots. Total leaf area (LA) was measured using a leaf area meter (Portable Leaf Area Meter LI/3000A, LI-COR, Lincoln, Nebraska, USA). Roots and shoots were washed three times with distilled water, dried at 70 ℃ for 72 hours, and their dry weights were determined.

2.3. Chlorophyll contents

The amounts of photosynthetic pigments (chlorophyll a, b, total, and carotenoids) were determined using the method of Lichtenthaler (1987). Fresh leaves (250 mg) from every three plants in different replicates (in total nine plants) were homogenized in 80% acetone, centrifuged at 10,000×g for 5 minutes, and absorbance was recorded at wavelengths of 646.8 and 663.2 nm for chlorophyll and 470 nm for carotenoids using a UV–Vis spectrophotometer (Carl-Zeiß-Promenade, Jena, Germany).

2.4. Lipid peroxidation and aldehyde determination

Lipid peroxidation was measured by assessing malondialdehyde (MDA) content using the thiobarbituric acid (TBA) reaction, based on the method of Heath and Packer (1968) with minor changes. Fresh shoot tissues (1.0 g) from every three plants in different replicates (in total nine plants) were homogenized in 10 mL of 20% (w/v) trichloroacetic acid (TCA) containing 0.5% (w/v) TBA. The homogenate was incubated at 95 ℃ for 30 minutes in a water bath and then immediately cooled in an ice bath. Samples were then centrifuged (Thermo Scientific, Finland) at 10,000 × g for 15 minutes. The absorbance of the supernatant was measured at 532 nm and 600 nm using a UV–Vis spectrophotometer (Carl-Zeiß-Promenade, Jena, Germany). MDA concentration was calculated after adjusting for nonspecific turbidity (A600), using an extinction coefficient of 155 $mM^{-1} cm^{-1}$, and expressed as µmol g^{-1} fresh weight (FW).

2.4.1. Determination of other aldehydes

Other aldehydes produced during lipid peroxidation were measured from the same TBA reaction mixture by checking absorbance at 450 nm, following the method described by Hodges *et al*. (1999). Aldehyde content was calculated using the formula:

Other aldehydes = A450 − (A532 − A600)

Values were given in absorbance units per gram of FW and served as an index of non-MDA lipid peroxidation products.

2.5. Hydrogen peroxide (H_2O_2) content

Hydrogen peroxide concentration was determined according to Velikova *et al*. (2000). Shoot tissues (0.5 g) from every three plants in different replicates (in total nine plants) were homogenized in 5 mL of 0.1% (w/v) TCA and centrifuged at 12,000 × g for 15 minutes. An aliquot of the supernatant (0.5 mL) was mixed with 0.5 mL of 10 mM potassium phosphate buffer (pH 7.0) and 1.0 mL of 1 M potassium iodide (KI). Absorbance was measured

at 390 nm using a UV–Vis spectrophotometer (Carl-Zeiß-Promenade, Jena, Germany). H_2O_2 concentration was calculated using an extinction coefficient of 0.28 $\mu M^{-1} cm^{-1}$ and expressed as $\mu mol\ g^{-1}$ FW.

Electrolyte leakage (EL) was assessed following the method by Ben Hamed *et al.* (2007). Fresh shoot samples (200 mg) from every three plants in different replicates (in total nine plants) were incubated in 10 mL of deionized water at 32 °C for 2 hours, and the initial electrical conductivity (EC_1) was measured. Samples were then autoclaved at 121 °C for 20 minutes to release all electrolytes, cooled to room temperature, and the final conductivity (EC_2) was recorded. Electrolyte leakage was calculated as:

$$EL (\%) = EC1/EC2 \times 100$$

2.6. Enzyme extraction and antioxidant enzyme assays

Fresh leaf tissues (0.5 g) from every three plants in different replicates (in total nine plants) were homogenized in 5 mL of ice-cold 50 mM potassium phosphate buffer (pH 7.0) that contained 1% (w/v) polyvinylpyrrolidone (PVP), 1 mM EDTA, and 1 mM phenylmethylsulfonyl fluoride (PMSF). For APX assays, 10 mM ascorbic acid was added to the extraction buffer. The homogenates were centrifuged (Thermo Scientific, Finland) at 20,000 × g for 20 minutes at 4 °C, and the supernatant was used to determine enzyme activity. SOD activity was evaluated by measuring the inhibition of nitro blue tetrazolium (NBT) reduction at 560 nm (Giannopolitis & Ries, 1977). CAT activity was assessed by monitoring the breakdown of H_2O_2 at 240 nm using a UV–Vis spectrophotometer (Carl-Zeiß-Promenade, Jena, Germany) (Dhindsa *et al.*, 1981). APX activity was determined by tracking the decrease in absorbance at 290 nm due to ascorbate oxidation with a UV–Vis spectrophotometer (Carl-Zeiß-Promenade, Jena, Germany) (Nakano & Asada, 1981). Protein content was measured using the Bradford (1976) method.

2.7. Determination of total phenolic compounds

Total phenolic content was measured using the Folin–Ciocalteu method (Singleton & Rossi, 1965). Fresh tissues (100 mg) from every three plants in different replicates (in total nine plants) were extracted in 5 mL of 80% (v/v) methanol with 1% (v/v) HCl, centrifuged at 3,000 × g for 10 minutes, and the supernatant was collected. An aliquot (0.5 mL) was combined with Folin–Ciocalteu reagent and sodium carbonate solution, and absorbance was read at 765 nm using a UV–Vis spectrophotometer (Carl-Zeiß-Promenade, Jena, Germany). Gallic acid served as a standard, and results were expressed as mg gallic acid equivalents (GAE) per gram of FW.

2.8. Determination of total flavonoids

Total flavonoid content was assessed according to Zhishen *et al.* (1999). Extracts were treated sequentially with $NaNO_2$, $AlCl_3$, and NaOH, and absorbance was read at 510 nm using a UV–Vis spectrophotometer (Carl-Zeiß-Promenade, Jena, Germany). Rutin served as a standard, and results were expressed as mg rutin equivalents (RE) per 100 g FW.

2.9. Determination of total anthocyanins

Total anthocyanins were measured using the acidified methanol method (Wagner, 1979). Samples (100 mg) from every three plants in different replicates (in total nine plants) were extracted in methanol:HCl (99:1, v/v), and absorbance was recorded at 550 nm. Total anthocyanins were calculated using an extinction coefficient of 33,000 $M^{-1} cm^{-1}$ and expressed as $\mu mol\ g^{-1}$ FW.

2.10. Elemental analysis and silicon determination

Dried shoot and root samples (0.5 g) from every three plants in different replicates (in total nine plants) were digested in 10 mL of concentrated 65% (v/v) HNO_3 using a block digestion system until a clear solution formed. Elemental concentrations (Na^+, K^+, and Si) were determined with ICP-OES (Varian, Australia) following the protocol outlined by Khan *et al.* (2022). Although hydrofluoric acid (HF) digestion can offer better Silicon recovery, nitric acid digestion is often accepted for comparing Silicon levels in plant tissues and gives reliable relative differences among treatments. Thus, this method was deemed suitable for evaluating treatment-induced changes in Silicon accumulation.

Table 1. Individual and combined effects of silicon (1.5 mM), salicylic acid (10 and 15 µM) and NaCl (80 mM) on leaf area, shoot dry mass, root dry mass, total chlorophyll and carotenoids

Treatment	Leaf area (cm^2)		Shoot dry mass (g plant^{-1})		Root dry mass (g plant^{-1})		Total chlorophyll (mg g^{-1} FW)		Carotenoids (mg g^{-1} FW)	
	–NaCl	+NaCl	–NaCl	+NaCl	–NaCl	+NaCl	–NaCl	+NaCl	–NaCl	+NaCl
Control	444±1^{b}	284±3^{h}	2.22±0.06^{b}	1.51±0.06^{g}	0.44±0.03^{ab}	0.30±0.02^{c}	3.76±0.08^{de}	3.05±0.06^{f}	0.53±0.03^{cd}	0.49±0.03^{d}
Si	469±3^{a}	351±2^{f}	2.39±0.09^{a}	1.90±0.1^{c}	0.45±0.02^{ab}	0.37±0.02^{bc}	3.89±0.09^{cd}	3.63±0.05^{e}	0.60±0.04^{bcd}	0.61±0.02^{bc}
SA10	477±4.8^{a}	366±2^{e}	2.50±0.12^{a}	1.95±0.05^{cde}	0.48±0.04^{a}	0.38±0.01^{abc}	4.02±0.06^{bc}	4.01±0.09^{bc}	0.82±0.03^{ab}	0.84±0.03^{a}
Si+SA10	479±7.8^{a}	398±3^{d}	2.51±0.07^{a}	2.12±0.06^{bcd}	0.45±0.02^{ab}	0.36±0.01^{bc}	4.13±0.07^{b}	4.40±0.10^{a}	0.81±0.04^{ab}	0.79±0.02^{ab}
SA15	405±4^{d}	320±2^{g}	2.05±0.06^{cd}	1.61±0.07^{fg}	0.41±0.03^{ab}	0.35±0.02^{bc}	3.72±0.07^{de}	3.92±0.08^{bcd}	0.63±.02^{bcd}	0.82±0.04^{ab}
Si+SA15	431±5^{c}	364±1^{e}	2.16±0.10^{bc}	1.75±0.03^{f}	0.41±0.02^{ab}	0.35±0.01^{bc}	3.89±0.08^{cd}	3.66±0.11^{e}	0.71±0.06^{abc}	0.61±0.03^{bcd}

Values followed by the same letter within a column are not significantly different according to Duncan's multiple range test ($p \leq 0.05$). Comparisons were made among all treatment combinations within each salinity level separately.

Table 2. Individual and combined effects of silicon (1.5 mM), salicylic acid (10 and 15 µM) and NaCl (80 mM) on Shoot and root- Na^+, K^+ and Si

Treatment	Shoot Na^+ (% DW)		Shoot K^+ (% DW)		Shoot Si (mg g^{-1} DW)	
	–NaCl	+NaCl	–NaCl	+NaCl	–NaCl	+NaCl
Control	1.14±0.15^{e}	34.28±2.4^{a}	40.03±1.12^{b}	25.32±1.91^{e}	0.50±0.18^{e}	0.24±0.05^{e}
Si	1.10±0.2^{e}	23.60±1.7^{d}	42.00±1.45^{ab}	33.98±2.1^{cd}	11.21±0.11^{a}	5.57±0.42^{c}
SA10	1.31±0.1^{e}	26.61±1.5^{c}	40.02±1.71^{b}	32.28±1.07^{cd}	0.28±0.12^{e}	0.26±0.03^{e}
Si+SA10	1.03±0.19^{e}	22.10±0.96^{d}	44.28±1.9^{a}	41.04±1.6ab	8.02±.91^{b}	9.41±0.98^{b}
SA15	0.91±0.31^{e}	29.20±1.8^{bc}	35.02±2.98^{c}	30.37±0.98^{d}	0.51±0.04^{e}	0.19±0.02^{e}
Si+SA15	1.59±0.31^{e}	23.30±1.2^{d}	40.88±1.34^{ab}	39.92±1.56^{b}	3.81±0.7^{d}	6.09±0.53^{c}

	Root Na^+ (% DW)		Root K^+ (% DW)		Root Si (mg g^{-1} DW)	
	–NaCl	+NaCl	–NaCl	+NaCl	–NaCl	+NaCl
Control	1.10±0.2^{d}	26.29±2.31^{a}	20.31±2.31^{de}	11.31±0.89^{g}	0.25±0.16^{d}	0.27±0.1^{d}
Si	1.29±0.24^{d}	18.61±1.34^{c}	22.59±1.65^{bcd}	19.04±1.23^{def}	7.14±0.88^{a}	4.12±0.45^{bc}
SA10	0.87±0.32^{d}	16.32±1.67^{c}	24.30±2.12^{abc}	17.62±1.32^{ef}	0.31±0.11^{d}	0.15±0.08^{d}
Si+SA10	1.41±0.3^{d}	21.62±1.89^{b}	27.32±1.87^{a}	20.63±1.1^{de}	4.30±0.35^{b}	4.19±0.37^{bc}
SA15	0.89±0.25^{d}	18.08±1.65^{c}	21.71±1.12^{cd}	15.51±1.4^{f}	0.30±.09^{d}	0.15±0.07^{d}
Si+SA15	1.32±0.26^{d}	22.91±1.48^{b}	26.05±1.48^{ab}	19.32±1.7^{de}	3.29±0.27^{c}	3.61±0.29^{bc}

Values followed by the same letter within a column are not significantly different according to Duncan's multiple range test ($p \leq 0.05$). Comparisons were made among all treatment combinations within each salinity level separately.

2.11. Statistical analysis

The experiment was conducted as a 2 × 3 × 2 factorial arrangement (silicon × salicylic acid × salinity) in a completely randomized design with three replicates. Data were analyzed using three-way analysis of variance (ANOVA) with SPSS software (version 26.0; IBM Corp., USA). Prior to ANOVA, data were checked for normality using the Shapiro–Wilk test and for homogeneity of variances using Levene's test, and all data met the assumptions required for ANOVA. The ANOVA model included the main effects of silicon (Si), salicylic acid (SA), and salinity (NaCl), as well as all possible interaction effects (Si × SA, Si × NaCl, SA × NaCl, and Si × SA × NaCl). When significant interaction effects were observed ($p \leq 0.05$), mean comparisons were performed using Duncan's multiple range test (DMRT) implemented in MSTAT-C software (version 2.10). For clarity and consistency, mean separation was conducted within each salinity level when interactions involving salinity were significant.

3. Results

In the present study, the interaction of salinity stress, salicylic acid, and silicon on all growth and physiological traits of cucumber was significant. Under non-saline conditions, a significant interaction between silicon and salicylic acid was seen for most growth, photosynthetic, and biochemical parameters. When compared to the non-saline control, the combination of silicon and 10 µM salicylic acid increased leaf area by 8%, shoot dry mass by 13%, and total chlorophyll content by 17%. In contrast, the interaction with 15 µM salicylic acid showed only marginal or no significant changes compared to the control (Table 1). The silicon and 10 µM salicylic acid interaction also improved non-enzymatic antioxidant compounds under non-stress conditions. Total phenolic content rose by 15%, flavonoids by 9%, and anthocyanins by 17% relative to the control. Meanwhile, the interaction with 15 µM salicylic acid led to increases of less than 5% or no significant difference (Table 3). No significant interaction effect was found for antioxidant enzyme activities (SOD, APX, CAT) under non-saline conditions (Fig. 2).

These results show that even without salinity, salicylic acid had a positive impact on cucumber seedlings only when applied at a low concentration (10 µM) alongside silicon. Under salt stress (80 mM NaCl), the interaction between silicon and salicylic acid was significant for all major growth, ion balance, and oxidative stress parameters. Compared to the salt-stressed control, the combination of silicon and 10 µM salicylic acid increased leaf area by 40%, shoot dry mass by 57%, and root dry mass by 20%. The interaction with 15 µM salicylic acid improved these parameters by only 15-25% (Table 1). Photosynthetic pigment content changed notably with the interaction. Under salinity, the combination of silicon and 10 µM salicylic acid raised total chlorophyll by 44% and carotenoids by 61% compared to the control. In contrast, the combination with 15 µM salicylic acid improved these parameters by only 20-26% (Table 1). The silicon and 10 µM salicylic acid interaction reduced shoot sodium accumulation by 36% and increased shoot potassium concentration by 62% (Table 2). On the other hand, the combination with 15 µM salicylic acid reduced sodium by only 18% and increased potassium by 31%.

Table 3. Individual and combined effects of silicon (1.5 mM), salicylic acid (10 and 15 µM) and NaCl (80 mM) on Shoot total phenolic, total flavonoids and anthocyanin content

Treatment	Total phenolic (mg GAE g^{-1} FW)		Total flavonoids (mg rutin equivalents (RE) per 100 g^{-1} FW)		Anthocyanin (µmol g^{-1} FW)	
	–NaCl	+NaCl	–NaCl	+NaCl	–NaCl	+NaCl
Control	1.2±0.10^{de}	1.34±0.11^{cd}	32±1.3^{d}	39±2.7^{cd}	7.23±0.89^{c}	8.1±0.62^{c}
Si	1.31±0.09^{cd}	1.62±0.13^{bc}	37±1.4^{cd}	44±1.9^{b}	7.69±0.67^{c}	9.38±0.72^{bc}
SA10	1.45±0.11^{c}	1.66±0.12^{bc}	36±1.1^{d}	43±2.2^{bc}	8.12±0.84^{c}	9.78±0.57^{bc}
Si+SA10	1.38±0.10^{cd}	2.13±0.20^{a}	35±2.1^{d}	51±3.2^{a}	8.45±0.61^{bc}	12.12±0.94^{a}
SA15	1.42±0.11^{c}	1.41±0.18^{c}	36±1.2^{d}	40±1.7^{c}	7.45±0.62^{c}	10.1±0.85^{b}
Si+SA15	1.10±0.08^{e}	1.34±0.12^{cd}	34±1.3^{d}	41±2.1^{bc}	6.98±0.72^{c}	9.81±0.69^{bc}

Values followed by the same letter within a column are not significantly different according to Duncan's multiple range test ($p \leq 0.05$). Comparisons were made among all treatment combinations within each salinity level separately.

Markers of oxidative damage showed the strongest interactive response. Compared to the salt-stressed control, the interaction with silicon and 10 µM salicylic acid lowered malondialdehyde content by 61%, hydrogen peroxide by 50%, ion leakage by 50%, and aldehyde accumulation by 60% (Fig. 1). These reductions were significantly greater than those seen with the 15 µM salicylic acid interaction, which ranged from 25% to 35% (Fig. 2). The accumulation of non-enzymatic antioxidants, with phenolics, flavonoids, and anthocyanins increasing by 58%, 30%, and 49%, respectively, compared to the salt-stressed control (Table 3). Additionally, the shoot silicon concentration under the combination of silicon and 10 µM salicylic acid increased by about 39 times compared to the control (Table 2).

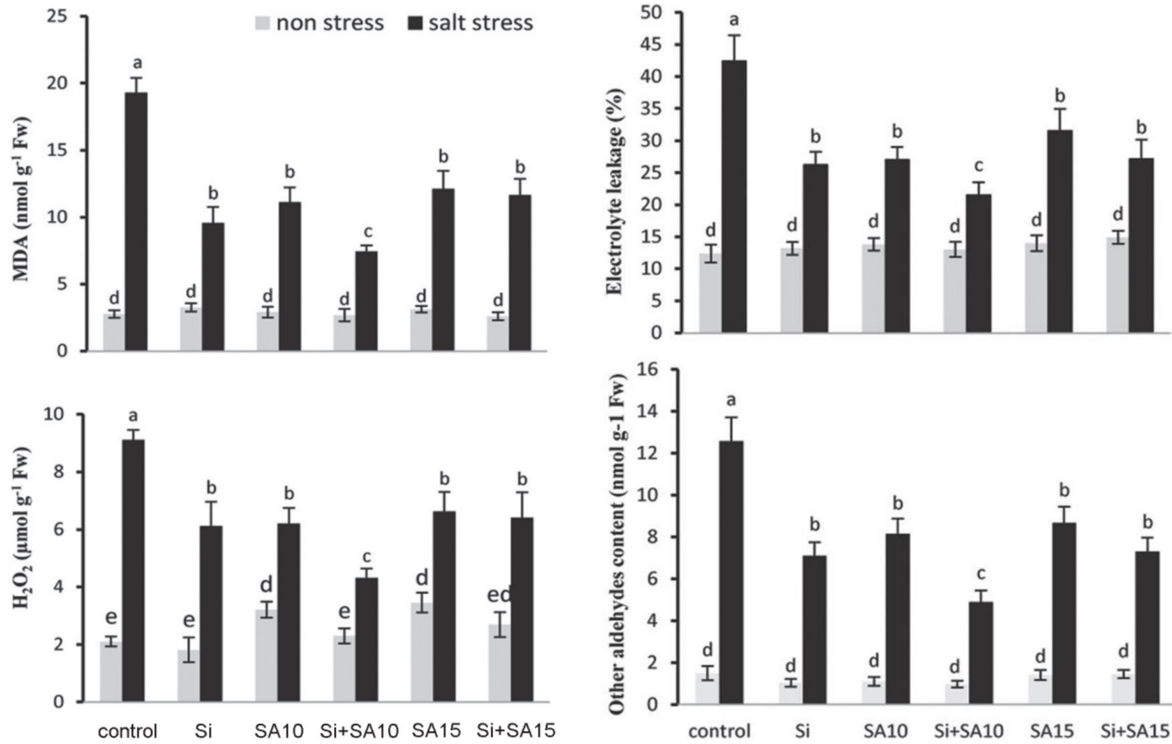

Figure 1. Individual and combined effects of silicon (1.5 mM), salicylic acid (10 and 15 µM) and NaCl (80 mM) on lipid peroxidation (MDA), hydrogen peroxide (H_2O_2), ion leakage and other aldehydes. Bars with the same letter are not significantly different according to Duncan's multiple range test ($p \leq 0.05$). Comparisons were made among all treatment combinations within each salinity level separately.

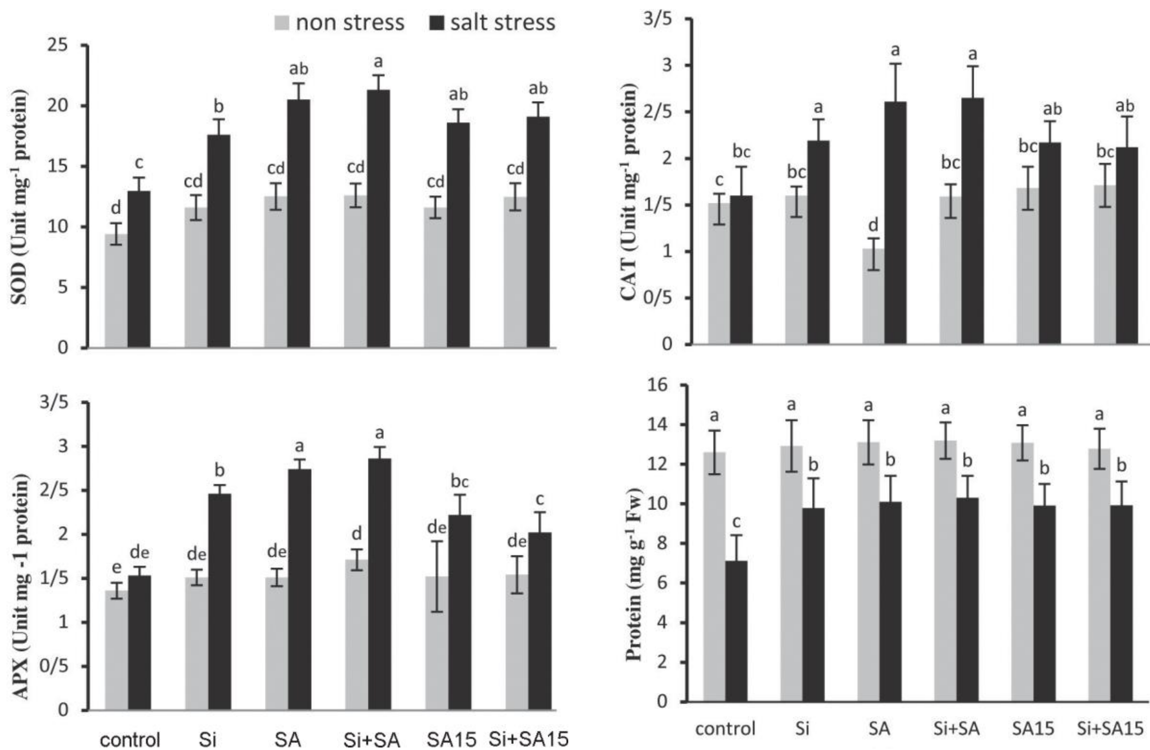

Figure 2. Individual and combined effects of silicon (1.5 mM), salicylic acid (10 and 15 µM) and NaCl (80 mM) on superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), and protein content. Bars with the same letter are not significantly different according to Duncan's multiple range test ($p \leq 0.05$). Comparisons were made among all treatment combinations within each salinity level separately.

4. Discussion

Salt stress is a major constraint on agricultural productivity worldwide because of its toxic effects on plant growth and metabolism (Kopecká *et al*., 2023, Sharafi, 2024; Khaleghi, 2024a and 2024b). Salinity imposes a complex stress environment characterized by ionic toxicity, nutrient imbalance, osmotic stress, and excessive production of reactive oxygen species (ROS), all of which severely impair photosynthetic efficiency and plant growth (Shahid *et al*., 2020, Malekzadeh et al., 2024). In the present study, salt stress markedly reduced growth and photosynthetic traits in cucumber seedlings, accompanied by increased Na^+ accumulation, elevated malondialdehyde (MDA), higher electrolyte leakage, and disruption of K^+ homeostasis. Under non-saline conditions, the application of silicon (Si), salicylic acid (SA), and especially their combination (Si + SA), promoted growth and physiological performance. Even in the absence of stress, Si supplementation improved cucumber growth, confirming previous findings that Si can enhance plant development under optimal conditions (Alsaeedi *et al*., 2019; Hu *et al*., 2022; Saeedi et al., 2024). Similar growth-promoting effects of Si have been reported in other crops and are often associated with improved hormonal balance and metabolic efficiency (Hamayun *et al*., 2010). Under salinity stress, Si markedly alleviated NaCl-induced oxidative damage. The protective role of Si may involve regulation at the gene expression level (Song *et al*., 2021, Rezaei and Erfani Moghadam, 2025) as well as the polymerization of silicic acid into silica, which reinforces cell walls and enhances tissue rigidity (Epstein, 2009). In this study, Si application significantly reduced Na^+ accumulation while increasing K^+ concentrations in both roots and shoots, thereby improving ionic balance. Similar Si-mediated regulation of Na^+ and K^+ has been reported in cucumber (Alsaeedi *et al*., 2018; Yan *et al*., 2025) and zucchini (Zhang *et al*., 2025). Maintaining higher cellular K^+ levels is crucial for membrane stability and enzymatic activity under salinity, and Si appears to play a key role in this process (Bu *et al*., 2024; Yan *et al*., 2025).

In addition, Si treatment reduced MDA, hydrogen peroxide (H_2O_2), and electrolyte leakage, indicating improved membrane integrity and lower lipid peroxidation. Previous studies have shown that Si protects chloroplast ultrastructure under salinity, preventing membrane collapse and grana disintegration (Cao *et al*., 2015). Si has also been reported to enhance membrane fluidity and reduce lipid peroxidation in cucumber, thereby preserving cellular function under stress (Bu *et al*., 2016; Gou *et al*., 2020). In the present study, improved performance of Si-treated plants was associated with enhanced antioxidant enzyme activities (SOD, APX, and CAT), consistent with earlier reports in cucumber (Khoshgoftarmanesh *et al*., 2014; Mousavi *et al*., 2022). Moreover, Si increased the accumulation of non-enzymatic antioxidants such as phenolics, flavonoids, and anthocyanins, which function as ROS scavengers and metal chelators (Hu *et al*., 2022). These findings collectively indicate that Si enhances salinity tolerance through both enzymatic and non-enzymatic antioxidant mechanisms.

Salicylic acid acts as a signaling molecule that can function either as a pro-oxidant or antioxidant, depending on its concentration and plant species (Wani *et al*., 2017). At appropriate concentrations, SA induces a controlled increase in H_2O_2, which serves as a signal to activate antioxidant defenses and improve stress tolerance (Szalai and Janda, 2007). In the present study, the 10 µM SA treatment effectively mitigated salinity stress, whereas the higher concentration (15 µM) was less effective, highlighting the dose-dependent nature of SA action. Similar optimal concentration effects of SA have been reported in cucumber and other crops (Kang *et al*., 2014; Khan *et al*., 2015). Notably, the combined application of Si and SA produced stronger protective effects than either treatment alone. However, the superior performance of Si + SA–treated plants was not associated with further stimulation of antioxidant enzyme activities or a pronounced additional reduction in Na^+ accumulation. Instead, the synergistic effect was mainly linked to enhanced accumulation of non-enzymatic antioxidants, including phenolics, flavonoids, anthocyanins, and carotenoids. These compounds play a critical role in protecting cellular structures by scavenging ROS, binding toxic ions, and reducing lipid peroxidation (Giordano *et al*., 2021). Another possible explanation for the enhanced effectiveness of the combined treatment is increased silica deposition. Salicylic acid is known to induce systemic acquired resistance and stimulate genes encoding proline-rich proteins that facilitate silica accumulation in plant tissues (Zhu and Gong, 2014). In this study, SA application significantly increased shoot Si concentration under salinity, which likely contributed to the improved stress tolerance observed in the combined treatment. Previous studies on spinach, maize, and potato have also reported interactive effects between Si and SA, although responses varied depending on species and stress type (Eraslan *et al*., 2008; Mohsenzadeh *et al*., 2011; Arvin *et al*., 2014). Overall, the present findings demonstrate that the combined application of Si and low-dose SA enhances salinity tolerance in cucumber primarily through improved ion balance, reinforced cellular structures, and elevated non-enzymatic antioxidant capacity.

Conclusion

Salt stress severely impaired growth, photosynthetic performance, ion balance, and membrane stability in cucumber seedlings, while intensifying oxidative damage. The present study demonstrates that these adverse effects are most effectively alleviated through the synergistic interaction between silicon (Si) and a low concentration of salicylic acid (10 µM). This combined treatment consistently outperformed individual applications and the higher SA concentration (15 µM), highlighting the importance of optimizing SA dosage. Under saline conditions, the Si + 10 µM SA combination significantly enhanced leaf area, biomass accumulation,

chlorophyll and carotenoid contents, and K^+ retention, while markedly reducing Na^+ accumulation. These improvements resulted in a more favorable K^+ /Na^+ ratio and improved physiological performance. Notably, the enhanced salt tolerance was not associated with further activation of antioxidant enzymes but was primarily linked to increased levels of non-enzymatic antioxidants, including phenolics, flavonoids, anthocyanins, and carotenoids, along with greater Si accumulation in shoot tissues. In conclusion, low-dose salicylic acid acts as an effective enhancer of silicon-mediated protection against salinity stress by improving ion homeostasis, strengthening membrane stability, and promoting metabolic antioxidant defenses. The combined application of Si and 10 µM SA represents a practical and biologically sound strategy for improving cucumber performance under saline growing conditions.

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