Golsa Alinejad[1], Jafar Amiri[1*], MirHassan Rasouli-Sadaghiani[2]

Potassium silicate counteracts salt-induced damage associated with changes in some growth characteristics, physiological, biochemical responses, and nutrient contents in two grapevines (*Vitis vinifera* L.) cultivars

Affiliations
[1]Department of Horticultural Science, Faculty of Agriculture, Urmia University, Urmia, Iran.
[2] Department of Soil Science, Faculty of Agriculture, Urmia University, Urmia, Iran.

Correspondence
Golsa Alinejad: golsa.alinejhad1@yahoo.com
Jafar Amiri*: j.amiri@urmia.ac.ir
MirHassan Rasouli-Sadaghiani: m.rsadaghiani@urmia.ac.ir

Summary

This study investigates the effects of potassium silicate on the growth characteristics, physiological parameters, biochemical parameters, and nutrient content of two grapevine cultivars, 'Bidaneh Ghermez' and 'Sahibi Gird', under NaCl stress conditions. The plants were exposed to NaCl solutions with concentrations of 0, 40, and 80 mM in a hydroponic system. Additionally, the plants were treated with potassium silicate sprays at concentrations of 0, 50, 100, and 200 mg L^{-1}. As NaCl levels increased, both 'Bidaneh Ghermez' and 'Sahibi Gird' cultivars exhibited reduced fresh and dry root weights. However, with potassium silicate application at 200 mg L^{-1}, the rate of root dry weight loss was reduced to 28% and 66.4% for 40 mM and 80 mM NaCl treatments, respectively. The maximum total protein content (1.65 mg L^{-1} fresh weight) was detected at the 80 mM NaCl level and potassium silicate application at 50 mg L^{-1}. The maximum ascorbate peroxidase activity was observed at a potassium silicate concentration of 50 mg L^{-1}. Based on the results, increasing NaCl levels significantly boosted plant Na^+ percentage. In treatments with 40 and 80 mM NaCl (without potassium silicate), nitrate levels decreased by 32.34% and 46.71%, respectively, compared to the control. The amount of leaf iron in the 40 mM salinity treatment increased and by 10.47% with potassium silicate at a concentration of 200 mg L^{-1}. The findings confirmed the role of potassium silicate in modulating the negative effects of NaCl, although more investigations in different grapevine cultivars under NaCl stress are required in this field.

Keywords

Growth parameters, Osmolyte, Potassium, Sodium, *Vitis vinifera* L.

Introduction

Salt stress is one of the main stressors that can lead to crop yield reductions (Zhu *et al.*, 2019b). Grapevine (*Vitis vinifera* L.) is a valuable crop with global significance, ranking among the world's most important fruit crops. However, it faces significant viticultural challenges, particularly soil salinization, which affects nearly 6% of the Earth's land area (Cuena-Lombraña *et al.*, 2022). Grapevines are typically grown in semi-arid regions, where drought and salinity are the most frequent issues (Cramer *et al.*, 2007). Field studies suggest that grapevines should be classified as moderately salt-sensitive (Stevens *et al.* 1999). While salt tolerance primarily derives from plant genetics, it is also influenced by various factors, including the plant's growth stage and the presence of other stressors (Grigore and Vicente, 2023). Negrao *et al.* (2017) discovered that NaCl ions are collected in young leaves and older leaves of salt-sensitive and salt-tolerant cultivars, correspondingly. The build-up of NaCl ions in the roots causes nutritional distinctions in the root tissue due to a reduced K^+-to-Na^+ ratio, resulting in increased salt levels. Quickly detecting excessive Na^+ signal is a precondition for beginning to restore cellular ionic balance under salt stress conditions (Yang and Guo, 2018). The undesirable impacts of excess salinity on plants are possibly attributed to osmotic stress, cytotoxicity provoked by excess Na^+ and Cl^-, nutritional imbalances, and decreased turgor (Kaur *et al.*, 2022; Farouk and AL-Huqail, 2022).

Salt stress also causes ionic imbalances, the osmotic effect, water use deficiency, and nutrient deficiency (e.g., N, Ca, K, P, Fe, and Zn), which ultimately leads to oxidative stress in plants (Rehman *et al.*, 2019). Silicon, which is the second most abundant element in soil, is well-known to increase plant tolerance to multiple abiotic stresses such as salinity (Thorne *et al.*, 2020). Furthermore, Silicon can be described as a "multi-talented" element and can improve soil conditions and nutrient content

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(e.g., N, P, and K) in plants, making it a valuable fertilizer for promoting ecologically sound agricultural practices (Zargar *et al.*, 2019). In several studies, foliar sprays of silicate (e.g., K_2SiO_3 or Na_2SiO_3), silica nanoparticles, and stabilized silicic acid have been shown to effectively increase plant growth (Laane, 2017). Foliar application of silicon (Si), including silicates, stabilized silicic acid, and silica nanoparticles, has been investigated in numerous studies. Similar to root application, foliar sprays with Si compounds effectively enhance growth and yield while mitigating biotic and abiotic stresses (Laane, 2018). However, the beneficial effects of foliar silicon on salt stress have only been experimentally tested in a few plant species. In cucumber, foliar spray of SiO2 nanofertilizers increased nitrogen (N) and phosphorus (P) content and uptake, and reduced sodium (Na^+) content and uptake under salt stress (Yassen *et al.*, 2017). Interestingly, Si's ability to alleviate various stresses has been confirmed even in species with low Si accumulation potential, such as tomatoes (Hoffmann *et al.*, 2020). Silicon also enhances plant tolerance to a wide range of biotic and abiotic stresses, including drought, salinity, heat, cold, metal toxicity, and nutrient stress (Bhat *et al.*, 2019; Hasanuzzaman *et al.*, 2018). Recently, the advancements and mechanisms of Si in alleviating various biotic and abiotic stresses in plants have been systematically reviewed by several researchers (Coskun *et al.*, 2019; Debona *et al.*, 2017; Luyckx *et al.*, 2017). In general, Si may improve salinity tolerance by regulating Na^+ and K^+ transport and accumulation, which are the primary salt tolerance mechanisms in plants (Zhu and Gong, 2014). Si has been shown to increase the concentration of macronutrients, such as Ca, P, and Mg, and micronutrients, such as B, Fe, Zn, and Mn, in a variety of plant species (Zhu and Gong, 2014). Si is known to reduce Na^+ uptake by stimulating the activity of the root plasma membrane H^+-ATPase (Xu *et al.*, 2015) and to minimize Na^+ translocation by enhancing its binding to cell walls, thus reducing Na^+ in the leaf apoplast. Coskun *et al.* (2016) reported that silicon-mediated stimulation of proton pumps located on the plasma membrane and tonoplast increases Na^+ efflux and K^+ influx to plant cells. In previous studies indicated that Si treatment enhanced the uptake of nutrients such as K (Chen *et al.*, 2016), Mg (Xu *et al.*, 2015), Ca (Mateos-Naranjo *et al.*, 2015), Fe (Pavlovic *et al.*, 2013), Zn (Pascual *et al.*, 2016), Mn (Wang and Han, 2007), and Cu (Gunes *et al.*, 2008) in plants under drought and salt stress. Exogenous silicon application has been shown to mitigate oxidative stress in many plant species, including tomatoes (Shi *et al.*, 2014), cucumber (Pavlovic *et al.*, 2013), strawberry (Muneer *et al.*, 2017), and rapeseed (Hasanuzzaman *et al.*, 2018). There are limited research studies on the effects of Si on woody plant responses to salinity stress. Therefore, the purpose of the current study was to elucidate the effects of exogenous silicon on growth, compatible solutes, enzymatic antioxidants, and mineral nutrient content under salinity stress in two grapevine cultivars (*Vitis vinifera* L.).

Material and Methods

Plant materials and growth conditions

Well-rooted cuttings of two grapevine cultivars, *Vitis vinifera* L. 'Bidaneh Ghermez' and 'Sahibi Gird', were transplanted into pots filled with a mixture of perlite and cocopeat (1:1 v/v) in an open hydroponic system. The pots were maintained in a greenhouse with a photoperiod of 16 hours of light and 8 hours of darkness, a relative humidity of 50 to 60%, and average minimum and maximum temperatures of 19 ± 3°C and 27 ± 3°C, respectively. The plants were fertigated with a modified ½ strength Hoagland nutrient solution consisting of 2.5 mM Ca (NO_3), 1 mM $MgSO_4$, 2.5 mM KNO_3, 0.5 mM KH_2PO_4, 0.3 µM $CuSO_4$, 6 µM $MnSO_4$, 0.7 µM $ZnSO_4$, 23 µM H_3BO_3, 32 µM Fe-EDTA, and 0.1 µM H_2MoO_4 (Hoagland and Arnon, 1950). The pH of the nutrient solution was maintained at 6.1. At the onset of the experiment, the plants were supplied with 150 mL of nutrient solution three times a week. The nutrient solution was renewed weekly.

Application of salt stress

Salinity stress was imposed on two-year-old grapevine plants fertilized with ½ strength Hoagland nutrient solutions. The final concentrations of NaCl salinity were 40 mM and 80 mM. Control plants received only nutrient solutions. The electrical conductivity (EC) of the salt-treated solutions at 25°C was 3.5 dsm^{-1} and 7.8 dsm^{-1}, respectively. To minimize salinity shock, NaCl was gradually added to the nutrient solutions at 40 mM per day to achieve the desired salinity level. The experiment lasted six weeks.

Potassium silicate treatments

Potassium silicate was applied to the foliage at rates of 0, 50, 100, and 200 mg L^{-1}. A control group of plants was grown without NaCl and sprayed with deionized water. Tween-20 (0.1%) was added to all solutions as a surfactant. The plants were sprayed with potassium silicate solutions at two-week intervals throughout the experimental period.

The fresh and dry weight of leaf, and root measurement

After harvesting, the leaves, stems, and roots of the plants from each pot were separated. They were then washed, and their fresh weights were recorded immediately after drying using a digital scale (PJ300, METTLER) with 0.001 g precision. To determine the dry weight of leaf and root, the samples were first oven-dried at 70°C for 72 hours and then reweighed using a digital scale.

Compatible solute content

Determination of proline content and soluble sugars

Proline content was determined following the method described by Irigoyen *et al.* (1992). Fresh leaf material (0.5 g) was homogenized in 5 mL of 75% ethanol, and the homogenate was centrifuged at 3,500 rpm. The alcoholic extract was stored in the refrigerator (4°C) until proline and soluble sugar measurements were conducted (Irigoyen *et al.*, 1992). One milliliter of the supernatant was combined with 5 mL of acid ninhydrin and 5 mL of glacial acetic acid in a test tube. The mixture was placed in a water bath for 45 min at

100°C. The reaction mixture was extracted with 10 mL of benzene, and the homogenate was centrifuged. The supernatant was cooled to room temperature, and the absorbance was measured at 515 nm using a UV/visible spectrophotometer. Appropriate proline standards were included to calculate the proline content of the samples (Paquin and Lechasseur, 1979). For soluble sugar quantification, 0.1 mL of the alcoholic extract stored in the refrigerator was added to a test tube using a micropipette and 3 mL of Anthon reagent (150 mg Anthon + 100 mL of 72% w/w sulfuric acid). The test tubes were placed in boiling water for 10 min. After cooling the samples, their absorption rate was determined at a wavelength of 625 nm using a spectrophotometer (Irigoyen *et al.*, 1992).

Determination of protein content

Mature leaves were utilized for protein content determination. Leaf segments were ground in cold phosphate buffer (pH 6.5) and filtered. The filtrate was centrifuged at 4,000 g for 20 minutes at 4°C. The supernatant was decanted, and then the Bradford Protein Kit was added. The mixture was vigorously shaken with a vortex. The sample absorbance was determined at 595 nm. The protein levels were estimated according to the Bradford (1976) method using bovine serum albumin as a standard and expressed in milligrams of protein per gram of fresh weight (FW).

Antioxidant Enzyme Activity

Leaves were sampled for the determination of antioxidant enzyme activities: catalase (CAT), Guaiacol Peroxidase (GPX), and Ascorbate peroxidase (APX). Plant extracts were prepared to assess enzymatic activity (Kang and Saltveit, 2002). Fresh leaf samples (0.5 g) were homogenized at 0-4°C in 3 mL of 50 mM Tris buffer (pH 7.8), containing 1 mM EDTA-Na_2 and 7.5% polyvinylpyrrolidone. Leaf samples were centrifuged at 12,000 rpm for 20 minutes, and the antioxidant enzyme activities were assayed in the supernatant using a spectrophotometer.

Catalase assay

Catalase (CAT) activity was determined according to the method described by Aebi (1984). The CAT reaction mixture included 2.5 mL of 50 mM phosphate buffer (pH = 7) and 0.2 mL of hydrogen peroxide (H_2O_2) at a concentration of 0.1%. This mixture was rapidly mixed with 0.3 mL of enzyme extract. Changes in absorbance at 240 nm were measured after 1 min using a spectrophotometer. The catalase activity was calculated using the following formula:

$$\text{CAT activity}\left(\frac{\text{U}}{\text{g}}.\ \text{F.W.}\ \text{min.}\right)=\frac{\Delta\ \text{OD/ min}\times\ \text{Vol of assay}\ (0.0003)}{\text{Extinction coefficient}\ (43.6)}$$

Guaiacol peroxidase assay

Guaiacol peroxidase (GPX) activity was determined using the method described by Updhyaya *et al.* (1985). The GPX reaction mixture included 2.5 mL of 50 mM phosphate buffer (pH = 7), 1 mL of guaiacol (1%), and 1 mL of hydrogen peroxide (H_2O_2). This mixture was rapidly mixed with 0.1 mL of enzyme extract. The light absorbance of the reaction solution was measured after 1 min at 420 nm. The guaiacol peroxidase activity was calculated using the following formula:

$$\text{GPX activity}\left(\frac{\text{U}}{\text{g}}.\ \text{F.W.}\ \text{min.}\right)=\frac{\Delta\ \text{OD/ min}\times\ \text{Vol of assay}\ (0.0001)}{\text{Extinction coefficient}\ (26.6)}$$

Ascorbate peroxidase assay

Ascorbate peroxidase (APX) activity was determined following the method described by Nakano and Asada (1981). The AXP reaction mixture consisted of 2.5 mL of 50 mM phosphate buffer (pH = 7), 0.1 mL of EDTA, 1 mM sodium ascorbate, and 0.2 mL of hydrogen peroxide (H_2O_2). This mixture was rapidly mixed with 0.1 mL of enzyme extract. The absorbance of the reaction solution was measured after 1 min at 290 nm. The APX activity was calculated using the following formula:

$$\text{APX activity}\left(\frac{\text{U}}{\text{g}}.\ \text{F.W.}\ \text{min.}\right)=\frac{\Delta\ \text{OD/ min}\times\ \text{Vol of assay}\ (0.0001)}{\text{Extinction coefficient}\ (2.8)}$$

Mineral nutrient analysis

Upon completion of the experiment, mature leaves from the mid-stem were harvested and oven-dried at 70°C for 48 hours. The dried tissues were subjected to analysis to determine their concentrations of NO_3-N, phosphorus, potassium, sodium, zinc, iron, and manganese. Sodium and potassium levels in the leaves were assessed via flame photometry (Fater 405 model, Iran) (Mizukoshi *et al.*, 1994). Nitrogen as nitrate (NO_3-N) was determined colorimetrically through the nitration of salicylic acid (Cataldo *et al.*, 1975). Phosphorus content was estimated using the colorimetric molybdenum vanadate method, employing a spectrophotometer (UV-2100) at 470 nm (Ohyama, 1991). Another set of samples was prepared to determine the concentrations of manganese, iron, and zinc. Dried samples (0.4 g) were individually ground and ashed in a porcelain crucible at 550°C for 5 hours. The white ash was subjected to digestion using 10 mL of 2 M hydrochloric acid (HCl). The digested solution was then filtered into a 50 mL volumetric flask and brought to a final volume of 50 mL with distilled water. The concentrations of manganese, iron, and zinc were determined using an atomic absorption spectrophotometer (Shimadzu AA-6300, Japan) (Ghazan Shahi, 1997).

Statistical analysis

The experiments were conducted as factorial trials utilizing a completely randomized design. Data analysis was performed using analysis of variance (ANOVA) in SAS v. 9.1 Statistical Software. Significant differences among the means were established at $p < 0.05$.

Results

Growth response to salt treatments

Fresh and dry weight of leaf

Increasing NaCl levels in the nutrient solution resulted in a decline in both fresh and dry leaf weights. The highest fresh weight (4.98 g) and dry leaf weight (2.4 g) were observed in the treatment with 200 mg L^{-1} potassium silicate and zero salinity (Fig. 1). As NaCl levels increased, both 'Bidaneh Ghermez' and 'Sahibi Gird' cultivars exhibited reduced fresh and dry root weights. In response to 40 mM salinity treatment, the rate of root fresh weight loss was reduced by 18.2%, 9%, and 7.2% for treatments with 50, 100, and 200 mg L^{-1} potassium silicate, respectively, compared to the control. Without potassium silicate application, the rate of root dry weight loss was 47.44% and 58.32% for 40 mM and 80 mM NaCl treatments, respectively. However, with potassium silicate application at 200 mg L^{-1}, the rate of root dry weight loss was reduced to 28% and 66.4% for 40 mM and 80 mM NaCl treatments, respectively. The application of potassium silicate at 80 mM NaCl level did not effectively mitigate the adverse effects of salinity on root dry weight (Fig. 1).

Compatible solutions

Proline

Increasing NaCl levels resulted in elevated proline levels in both cultivars. The peak proline concentration was observed in the treatment with 80 mM salinity (317.13 mg g^{-1} of fresh weight) and potassium silicate at 50 mg L^{-1} (Fig. 2).

Soluble sugars

Increased NaCl levels led to a substantial increase in soluble sugars content in both 'Bidaneh Ghermez' and 'Sahibi Gird' cultivars, with a 4.4-fold and 54.5-fold increase, respectively, compared to the control (Fig. 2).

Total protein

Total protein content in both cultivars exhibited an increasing trend with elevated NaCl levels. This upward trajectory was observed at the 80 mM salinity level for 'Bidaneh Ghermez' (1.49 mg L^{-1} fresh weight) and 'Sahibi Gird' (1.63 mg L^{-1} fresh weight). The maximum total protein content (1.65 mg L^{-1} fresh weight) was detected at the 80 mM NaCl level and potassium silicate application at 50 mg L^{-1} (Fig. 2).

Activities of antioxidant enzymes

Activity of Ascorbate peroxidase enzyme (APX)

With increasing NaCl concentrations in the external environment, the activity of ascorbate peroxidase (APX) in both 'Bidaneh Ghermez' and 'Sahibi Gird' increased by 3.53-fold and 4.7-fold, respectively, compared to the control (Fig. 3). The maximum APX activity (7.54 µmol min^{-1} fresh weight) was observed at a potassium silicate concentration of 50 mg L^{-1} (Fig. 3).

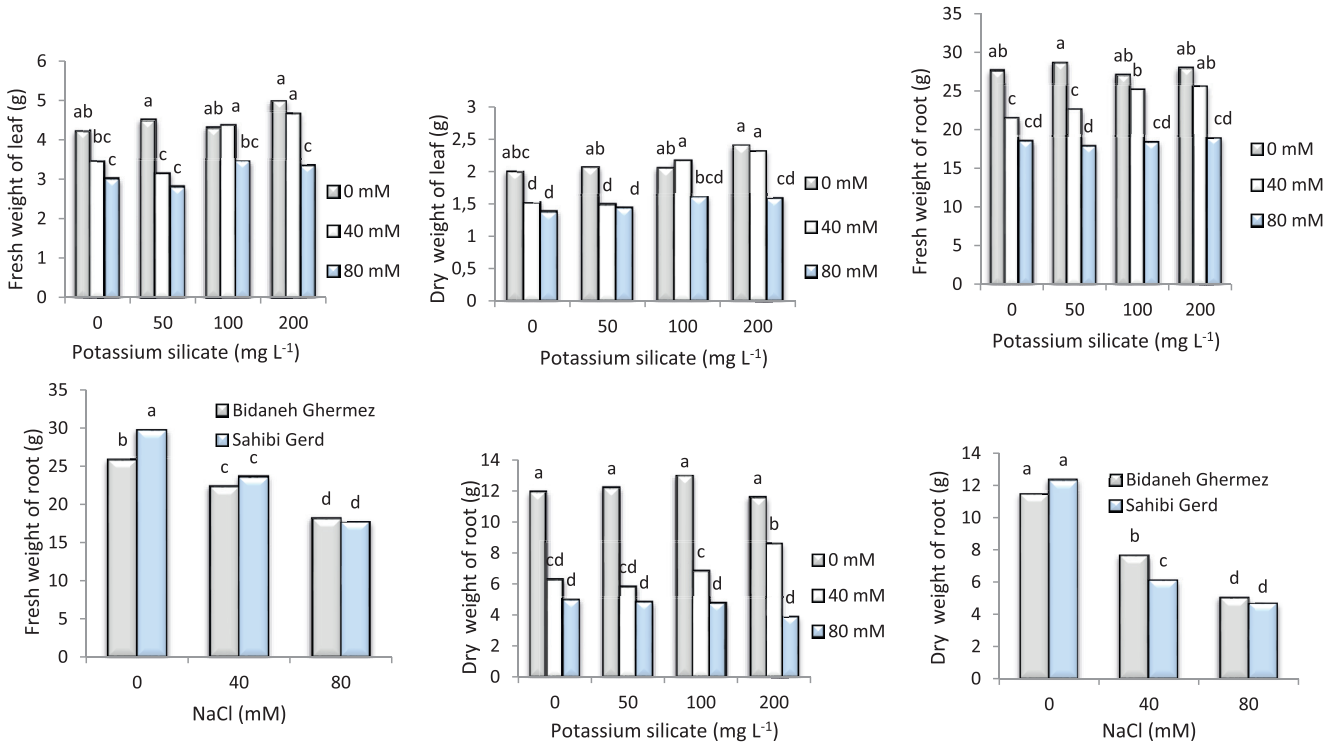

Fig. 1: Interaction effects of potassium silicate and NaCl on leaf and root fresh and dry weight in two grapevine cultivars ('Bidaneh Ghermez' and 'Sahibi Gird'). Different letters indicate a significant difference ($p<0.05$) between different treatments.

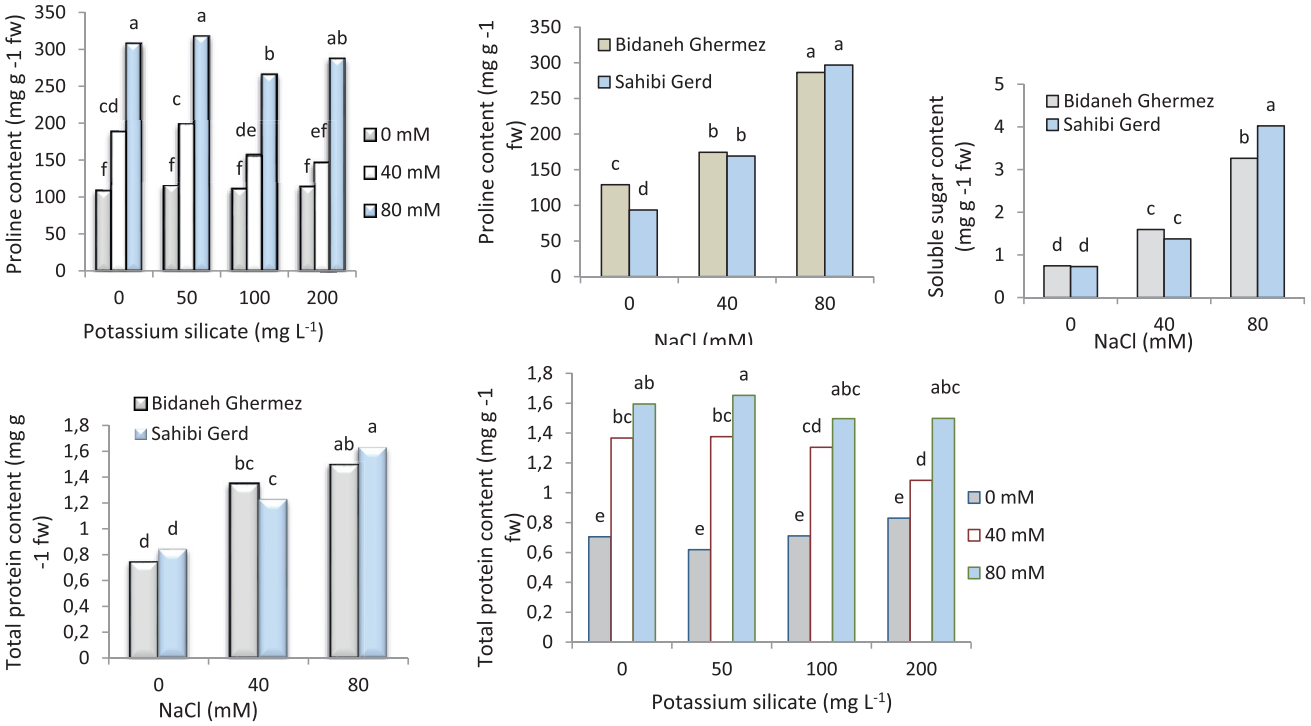

Fig. 2: Interaction effects of potassium silicate and NaCl on proline levels, soluble sugars content, and total protein content in two grapevine cultivars ('Bidaneh Ghermez' and 'Sahibi Gird'). Different letters indicate a significant difference ($p<0.05$) between different treatments.

Activity of Guaiacol peroxidase enzyme (GPX)

At an external NaCl of 80 mM, the application of potassium silicate at concentrations of 50, 100, and 200 mg L^{-1} resulted in a 2.76, 2.87, and 2.9-fold increase in GPX activity, respectively, compared to the control plants (Fig. 3).

Activity of Catalase enzyme (CAT)

In 50, 100, and 200 mg L^{-1} potassium silicate treatments, catalase enzyme activity in the 80 mM NaCl treatment was 4.19, 3.82, and 4.28-fold higher than the control treatment, respectively (Fig. 3).

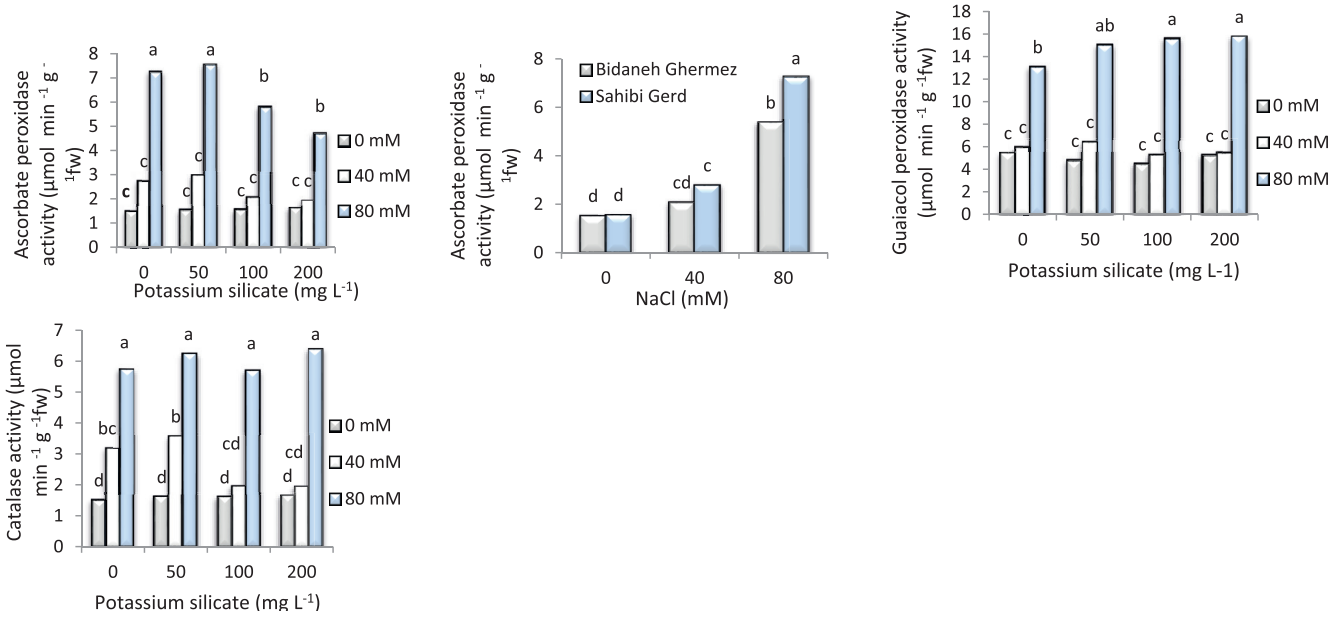

Fig. 3: Interaction effects of potassium silicate and NaCl on activity of ascorbate peroxidase, guaiacol peroxidase, and catalase enzymes in two grapevine cultivars ('Bidaneh Ghermez' and 'Sahibi Gird'). Different letters indicate a significant difference ($p<0.05$) between different treatments.

Effects of salinity on mineral contents

Nitrate

As NaCl levels in the nutrient solution increased, the amount of nitrate in the leaves decreased. In treatments with 40 and 80 mM NaCl (without potassium silicate), nitrate levels decreased by 32.34% and 46.71%, respectively, compared to the control group (Fig. 4). When potassium silicate was applied at concentrations of 100 and 200 mg L^{-1} in the 40 mM NaCl treatment, the rate of nitrate loss was 22.16% and 17.37%, respectively, compared to the control group.

Phosphorus

As NaCl levels increased, the amount of leaf phosphorus decreased. At 40 mM NaCl, phosphorus content was 7.43% lower than the control, and at 80 mM NaCl, it was 12.84% lower (Fig. 4). Phosphorus content in 'Bidaneh Ghermez' was 0.65% and in 'Sahibi Gird', 0.73%.

Potassium

The presence of sodium chloride (NaCl) in the root medium caused a decrease in potassium (K^+) content in the leaves of both cultivars. However, the application of potassium silicate at a concentration of 200 mg L^{-1} mitigated this reduction in potassium levels. At 40 mM NaCl, potassium levels were reduced by 9.02% with potassium silicate application, compared to the control without potassium silicate. At 80 mM salinity, the reduction in potassium levels with potassium silicate application was 22.54% compared to the control (Fig. 4).

Sodium

In both cultivars, the sodium (Na^+) content in leaves increased along with the increase in NaCl concentration in the nutrient solution. The highest Na^+ concentration was observed in the 80 mM NaCl treatment, regardless of whether potassium silicate was applied or not at a concentration of 50 mg L^{-1}. Potassium silicate treatment significantly reduced Na^+ concentration in leaves of both cultivars under NaCl stress conditions (Fig. 4).

Iron

The lowest iron content in both cultivars was observed in the 80 mM NaCl treatment. In this treatment, leaf iron concentration in 'Bidaneh Ghermez' and 'Sahibi Gird' cultivars decreased 1.60 and 1.48 times, respectively, compared to the control. The amount of leaf iron in the 40 mM NaCl treatment increased by 7.64% with potassium silicate at a concentration of 100 mg L^{-1} and by 10.47% with potassium silicate at a concentration of 200 mg L^{-1} (Fig. 4).

Zinc

In the 40 mM NaCl treatment, zinc content with the application of potassium silicate at concentrations of 100 and 200 mg L^{-1} showed an increase of 14.35% and 22.4%, respectively (Fig. 4).

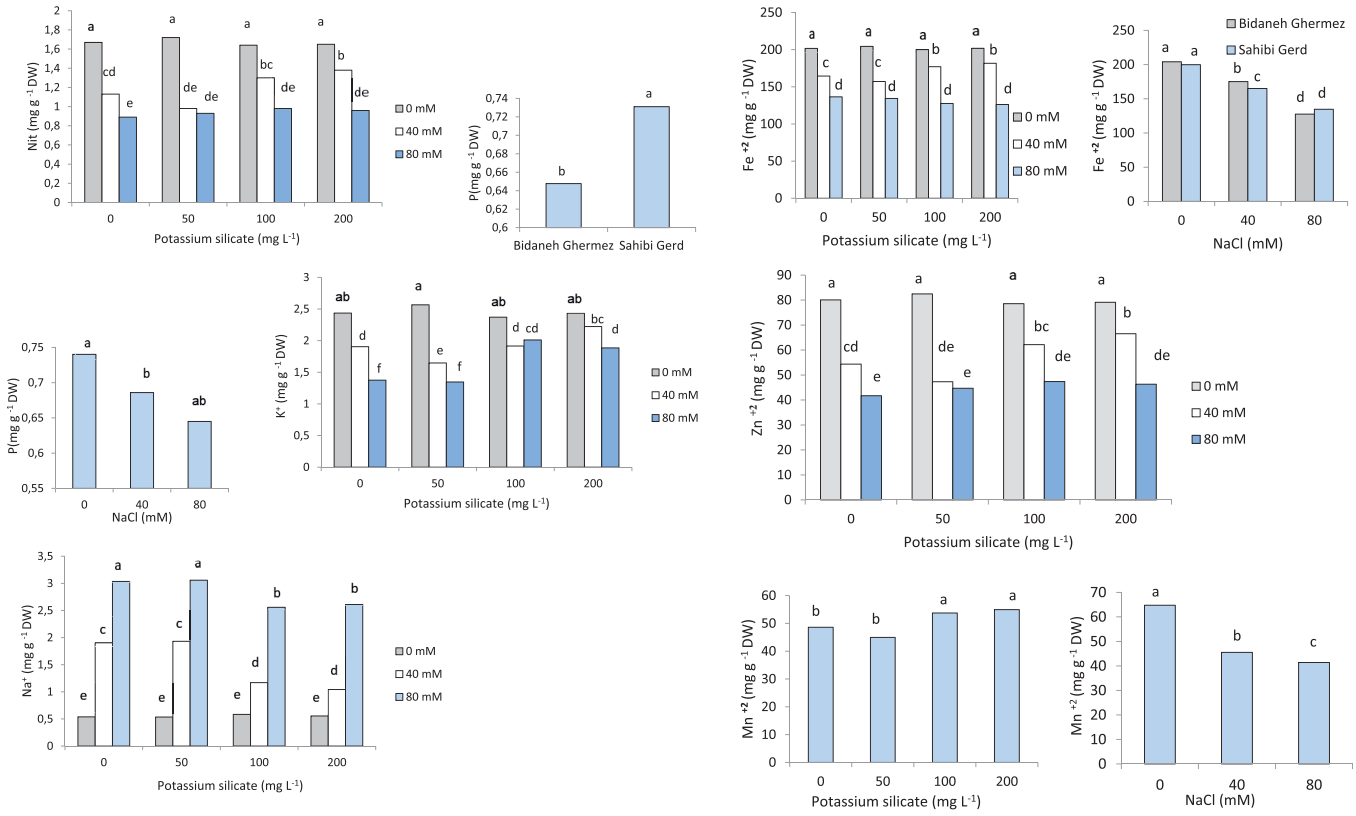

Fig. 4: Interaction of potassium silicate and NaCl on nitrate, phosphorus, potassium, sodium, iron, zinc, and manganese content in two grapevine cultivars ('Bidaneh Ghermez' and 'Sahibi Gird'). Different letters indicate a significant difference ($p<0.05$) between different treatments.

Manganese

With increasing NaCl concentration in the nutrient solution, manganese (Mn) concentration decreased by 29.7% in the 40 mM salinity treatment and by 36.1% in the 80 mM NaCl treatment. With increasing the concentration of potassium silicate, the amount of Mn increased, so that in the treatments with 100 and 200 mg L^{-1} of potassium silicate, this increase was 10.6% and 13.2%, respectively, compared to the control (Fig. 4).

Discussion

Salinity stress induces a diverse array of responses in plants, leading to morphological, physiological, biochemical, and molecular alterations. It can also impair physiological and biochemical processes such as photosynthesis, protein synthesis, transpiration, and lipid metabolism (Muchate *et al.*, 2016). Salinity has been shown to reduce dry root weight in both cultivars. This study revealed a negative correlation between salinity stress and vegetative growth parameters, including fresh and dry weight of leaves, shoots, and roots. The most detrimental effect of salinity on vegetative traits was observed at the highest NaCl level (80 mM), though this effect was evident in both cultivars. However, the responses of the two cultivars differed. In plants subjected to salinity stress, NaCl ions accumulate in the roots of both salt-tolerant and salt-sensitive crops. High salinity levels can significantly hinder plant growth and development (Lei *et al.*, 2015). High salt levels can lead to both water deficit and ion toxicity, adversely affecting various aspects of plant function, metabolism, and structure. In this study, the observed growth decline under salinity stress was attributed to nutritional imbalances and excessive sodium (Na^+) uptake. These findings align with previous studies on the detrimental effects of salinity on plant growth. Roots are the primary organs directly exposed to salinity stress, experiencing a more severe growth reduction than other plant tissues such as shoots. These findings are consistent with previous reports (Aazami *et al.*, 2023; El-Banna *et al.*, 2022; Liu *et al.*, 2020).

In recent years, research has focused on understanding the role of silicon (Si) in mitigating abiotic and biotic stresses, particularly drought and salinity, the two most prevalent stress factors. Si has been demonstrated to regulate root growth in salt-stressed plants (Zhu *et al.*, 2015). Applying silicon (Si) as a foliar spray mitigated the growth inhibition caused by added sodium chloride (NaCl). In cucumber, Si was found to increase the root-to-shoot ratio of salt-stressed plants and improve root hydraulic conductance, potentially contributing to enhanced plant water balance (Wang *et al.*, 2015). In rice and sorghum, Si may improve root growth by increasing casparian band formation, stimulating suberin and lignin biosynthesis, or promoting cell wall extensibility in the growth region (Fleck *et al.*, 2015). With increasing salinity levels, the levels of proline, an osmoprotectant, increased in both grapevine cultivars. The highest proline levels were observed at the highest salinity level (80 mM) and with the addition of 50 mg L^{-1} potassium silicate (317.13 mg g^{-1} fresh weight). This study demonstrated that both moderate (40 mM) and high (80 mM) salinity induced a significant increase in free proline content in the leaves of both grapevine cultivars. Proline synthesis is considered an adaptive mechanism to counteract salt stress. Osmolytes like proline help stabilize functional proteins, enzymes, protein complexes, and cell membranes under salt stress conditions (Rajasheker *et al.*, 2019). In this study, the enhancement in proline levels likely resulted from a combination of its osmotic and antioxidant properties. Similar observations have been reported in other crops, including *Brassica juncea* (Khan *et al.* 2012), *Linum usitatissimum* (Nasir Khan *et al.* 2009), *Morus alba* (Ahmad *et al.* 2013), and *Cicer arietinum* (Ahmad *et al.*, 2016).

Our results demonstrate that supplemental silicon (Si) enhanced proline accumulation in grapevine leaves exposed to salt stress. Si plays a crucial role in modulating the expression of silicon transporters (Lsi_1 and Lsi_2) and stress-related proteins, leading to increased silica accumulation and elevated levels of compatible solutes in plants fertilized with Si (Thorne *et al.*, 2020). Additionally, the elevated proline levels in the tissues may have further contributed to this effect by protecting cellular structures. Therefore, it is reasonable to conclude that Si improved the antioxidant capacity of grapevine plants under salt stress. In this experiment, we observed an increase in soluble sugars under stress, which aligns with the findings of other researchers studying various plant species. Numerous studies have reported that Si application can enhance plant tolerance to salinity stress by altering the levels of solutes such as carbohydrates (Ming *et al.*, 2012), proline (Yin *et al.*, 2013), glycine betaine (Torabi *et al.*, 2015), polyols, and antioxidant compounds like total phenolics (Hashemi *et al.*, 2010). These alterations help mitigate the osmotic shock induced by NaCl stress due to ion toxicity (Na^+ and Cl^-). In cucumber, treatment with Na + Na_2SiO_3_$9H_2O$ was found to increase the accumulation of soluble sugars (primarily sucrose and glucose) and reduce the osmotic potential of xylem sap in the root system compared with Na^+ treatment. This effect contributed to enhanced root water uptake (Zhu *et al.*, 2016).

As salinity levels increased, soluble protein content rose in both grapevine cultivars. Ali *et al.* (2013) observed that soluble protein content was alleviated by salinity and significantly increased in the presence of Si in sunflower. Al-Aghabary *et al.* (2004) proposed that Si acts as a promoter of protein synthesis, as the presence of this nutrient in salt-stressed plants enhances the synthesis of mRNA related to the synthesis of nitrogenous compounds. These findings suggest that grapevine plants similarly responded to Si, as evidenced by the increased soluble protein content in leaves of plants provided with Si. Salinity tolerance is contingent on an effective antioxidant system. In this study, as salinity increased, the activity of antioxidant enzymes followed an upward trend. To minimize ROS-induced damage to biomolecules, plants should efficiently utilize their antioxidant defense system, which consists of both enzymatic and non-enzymatic antioxidants (Hasanuzzaman *et al.*, 2019).

The present study demonstrates that supplemental silicon enhanced the activity of antioxidant enzymes in both grapevine cultivars. Hasanuzzaman *et al.* (2018) reported that exogenous Si application (1 mM) increased the activity of APX, MDHAR, GR, GST, DHAR, CAT, and GPX and boosted AsA and GSH levels in *Brassica napus*. These findings corroborate our

results, suggesting that Si can significantly augment the antioxidant capacity of grapevine plants under salt stress. Similar observations have been reported in other plant species, such as grapevine (Soylemezoglu *et al.*, 2009), tomato (Li *et al.*, 2015), and okra (Abbas *et al.*, 2015). These studies collectively indicate that Si has the potential to induce a robust antioxidant defense system that effectively counteracts reactive oxygen species (ROS) buildup and protects grapevine plants from salt stress-induced damage. Salt stress can exacerbate nutritional deficiencies in plants (Gupta and Huang, 2014). High levels of salts can lead to nutrient imbalances, as excessive sodium (Na^+) uptake can interfere with the uptake of essential nutrients.

This is because the hydrated ionic radii of K^+ and Na^+ are similar, making it challenging for the cell membrane transport system to distinguish between these two ions. This misidentification can cause Na^+ ions to be transported into cells via K^+ transporters, leading to Na^+ toxicity under high salinity conditions (Blumwald, 2000). Na^+ toxicity, particularly at salinity levels exceeding 40 mM, has been observed in both grapevine cultivars. Plants have developed various mechanisms to cope with salt stress, including ion-uptake regulation, vacuolar compartmentation, and ion exclusion. These strategies help maintain cellular ion balance and protect plants from the harmful effects of salinity (Blumwald, 2000). However, excessive accumulation of Na^+ and Cl^- ions during saline conditions can still hinder the uptake of essential nutrients (Ahanger and Agarwal, 2017).

When Na^+ concentration is elevated, K^+ uptake is often inhibited, leading to increased Na^+ accumulation in plant tissues. K^+ ions enter the cell through a series of ion channels located on the cell membrane, and these channels can easily be used for the penetration of Na^+ ions into the cell under salt stress conditions (Mita *et al.*, 2021). Supplemental Si can effectively block the uptake of Na^+ ions and act as a physical barrier to their root-to-shoot translocation through the apoplastic bypass route (Yeo *et al.*, 1999). This mechanism effectively prevents Na^+ accumulation in the shoots. Yan *et al.* (2021) investigated the role of Si in regulating Na^+ transport and its movement from roots to shoots in rice. They found that Si supplementation increased lignification and suberization of the casparian band, the barrier between the root cortex and stele. These structural modifications, driven by changes in gene expression related to phenol biosynthesis (Hinrichs *et al.*, 2017), further protect plants from uncontrolled Na^+ influx. This research suggests that Si can mitigate the negative effects of salinity by preventing Na^+ uptake by the roots and its subsequent movement to the shoots. Silicon protective effects are likely due to its ability to form a physical barrier, enhance lignification and suberization, and modulate gene expression to regulate Na^+ transport. Silicate, particularly potassium silicate, acts as a protective barrier against salt stress by preventing Na^+ translocation from roots to aerial parts of the plant. It achieves this by either depositing Na^+ in epidermal cells, forming a physical barrier to ion movement, or forming complexes with freely available Na^+ and Si ions. A recent study by Bosnic *et al.* (2018) demonstrated that Si supplementation to moderately NaCl-stressed maize plants effectively reduced Na^+ concentration in the root symplast by up-regulating the expression of *SOS1* (responsible for Na^+ efflux) and down-regulating the expression of *HKT1* (responsible for Na^+ influx). This mechanism helps prevent Na^+ accumulation in the plant, protecting it from the detrimental effects of salt stress.

In grapevines, the application of potassium silicate resulted in a significant increase in Na^+ exclusion, as evidenced by reduced Na^+ levels in leaves even at elevated salinity levels. This protective effect is likely due to Si's ability to form a physical barrier, enhance lignification and suberization of the casparian band, and modulate gene expression to regulate Na^+ transport. A sharp decline in potassium ion (K^+) content was observed in the leaves of both grape cultivars as salt concentration increased. It is now understood that K^+ ions can enter cells through channels that are often more permeable to sodium ions (Na^+) under saline conditions (Parida and Das, 2005). Due to the physicochemical similarity between Na^+ and K^+ (e.g., ionic radius and ion hydration energy), Na + competes with K^+ for different binding sites in crucial metabolic processes within the cytoplasm (Shabala and Cuin, 2008). This suggests competition between Na + and K^+ in grapevines. The depletion in K^+ uptake caused by Na^+ is likely to stem from the competitive influx of both ions into the cells. There are limited studies on the impact of silicon (Si) on enhancing K^+ ion uptake under salinity stress. However, silicon has been shown to improve K^+ nutrition under salt stress in various plant species (Rizwan *et al.*, 2015; Coskun *et al.*, 2016; Zhu *et al.*, 2019a).

A study by Liang (1999) demonstrated that supplemental Si can improve K^+ uptake in salt-stressed barley by ameliorating K^+ selectivity. In line with these findings, potassium silicate alleviated the detrimental effects of Na^+ in grapevine leaves by boosting K^+ content. The present study revealed a significant decline in NO_3-N content in salt-stressed grapevines. This reduction indicates that salinity disrupts ionic homeostasis in grapevines and negatively impacts N nutrition. The application of potassium silicate alleviated these disturbances by enhancing NO_3-N uptake, assimilation, and remobilization (Gou *et al.*, 2020). Haddad *et al.* (2018) reported that Si supplementation increased N uptake in *Brassica napus* plants, accompanied by an upsurge in the expression of a nitrate transporter gene in roots. Our findings corroborate these observations, as potassium silicate treatment resulted in elevated NO_3-N content in grapevine leaves. Along with NO_3-N, salinity also reduced leaf phosphorus content in both cultivars. At the highest salinity level of 80 mM, phosphorus content decreased by 12.84% relative to the control. Phosphorus deficiency is known to hinder plant growth and biomass production (Sulieman and Tran, 2015). However, potassium silicate treatments effectively counteracted this deficiency by increasing phosphorus concentration in grapevine leaves. Two primary mechanisms have been proposed to explain Si's ability to alleviate phosphorus deficiency: 1. Enhanced root uptake: Si can increase the expression of phosphorus transporters in root cells, leading to improved phosphorus uptake from the soil. 2. Enhanced utilization of phosphorus within plant tissues: Si may improve the efficiency of phosphorus utilization by enhancing phosphorus partitioning and metabolism.

Studies have demonstrated increased phosphorus uptake following Si fertilization in various crops (Neu *et al.*, 2017; Zhang

et al., 2019). These findings suggest that potassium silicate can be a valuable tool for mitigating the negative effects of salinity stress on grapevines by improving nitrogen and phosphorus nutrition. Silicon can enhance phosphorus availability in soil by modifying soil pH, reducing phosphorus absorption by soil minerals due to competition between phosphorus and silicon (depending on silicon speciation in soil solution) (Schaller *et al.*, 2021). With increasing salinity in the nutrient solution, iron (Fe) content in the leaves decreased. The lowest Fe amount was observed in both cultivars at 80 mM NaCl. In this treatment, leaf Fe concentration in 'Bidaneh Ghermez' and 'Sahibi Gird' cultivars decreased by 1.60 and 1.48 times, respectively, compared to the control. In cucumber, exogenous silicon application alleviates iron deficiency by coordinating the expression of genes involved in iron acquisition (Pavlovic *et al.*, 2013). The effect of silicon on iron nutrition has been demonstrated in various plant species grown under optimal, low, or high iron conditions (Becker *et al.*, 2020; Hernández-Apaolaza *et al.*, 2020).

Additionally, Stevic *et al.* (2016) showed that the addition of Si $(OH)_4$ to iron-deprived cucumber plants could enhance iron bioavailability by forming an iron-silicon complex and maintaining the redox potential in both root apoplastic and xylem fluids, thus facilitating iron translocation from roots to shoots via the xylem. Furthermore, Nikolić *et al.* (2019) recently reported that silicon alleviates iron deficiency in barley (a Strategy 2 species) by amplifying the expression of genes involved in iron uptake and transport in roots. In both cultivars, the amount of zinc (Zn^{2+}) and manganese (Mn^{2+}) decreased with increasing salinity levels in the nutrient solution. Potassium silicate application, particularly at concentrations of 100 and 200 mg L^{-1}, significantly boosted Zn^{2+} content in grapevine leaves. Pascual *et al.* (2016) proposed that Si treatment enhances Zn^{2+} accumulation in the root apoplast and its movement to shoots when soybean plants are subjected to Zn^{2+} deficiency, thereby alleviating stress symptoms. For instance, Si application has been shown to mitigate certain symptoms of Zn-deficiency in cucumber plants, most likely due to its indirect effect of enhancing the antioxidant defense capacity in plant tissues, rather than its direct effect on Zn mobility, uptake, and tissue distribution (Bityutskii *et al.*, 2014). Potassium silicate treatments effectively increased Mn^{2+} concentration in leaves of both grapevine cultivars. These findings are consistent with those of Greger *et al.* (2018), who demonstrated that Si application to soil increases Mn^{2+} availability and improves Mn^{2+} uptake and translocation to shoots in various plant species grown under conditions of adequate Mn^{2+} supply.

Conclusion

Salinity stress encompasses intricate and multifaceted mechanisms that are linked to distinct metabolic pathways in various plant organs. Plants respond to high-salinity stress by employing a variety of mechanisms, including the modulation of Na^+ uptake and translocation, activation of their antioxidant defense system, accumulation of compatible solutes, and osmotic regulation. These responses play a crucial role in plant adaptation to salt stress. Competition between Na^+ ions and K^+ ions, a consequence of salinity stress, impedes plant growth by disrupting nutrient accessibility. However, application of silicon (Si) mitigates these stress-induced detrimental effects by regulating various physiological and biochemical processes, such as Na^+ balance, enhancing the activity of antioxidant enzymes (CAT, APX, and GPX), and accumulation of compatible solutes, in both grapevine cultivars. In conclusion, the results of this study suggest that application of potassium silicate can be used as an effective strategy to reduce the negative effects of salinity stress on grapevines.

Conflicts of interest

The authors declare that they do not have any conflicts of interest.

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