Journal of Plant Process and Function, Vol. 10, No. 46, Year 2022 Page: 41-49

Research Article

Silicon and selenium supplementations modulate antioxidant systems and mineral nutrition to mitigate salinity-alkalinity stresses in cucumber (*Cucumis sativus* L.) plants under hydroponic conditions

Seyed Ali Asghar Mousavi[1*], Hamid Reza Roosta[2], Majid Esmaeilizadeh[1] and Saeid Eshghi[3]

[1] Department of Horticultural Science, Faculty of Agriculture, Vali Asr University, Rafsanjan. Iran
[2] Department of Horticultural Science, Faculty of Agriculture and Natural Resources, Arak University, Arak
[3] Department of Horticultural Science, Faculty of Agriculture, Shiraz University, Shiraz. Iran
(Received: 10/07/2021-Accepted: 13/09/2021)

Abstract

This experiments was conducted to investigate the role of silicon (Si, 75, 100 mg. L^{-1} sodium silicate) and selenium (Se, 4, 6 mg. L^{-1} sodium selenate) in ameliorating the salinity (75 mM NaCl and 75 mM $NaHCO_3$) causing strong detrimental effects on mineral ions uptake and the oxidative damage in cucumber (*Cucumis sativus* L.) plants. Salinity and alkalinity stresses reduced macro and micro elements content which were significantly improved by Si and Se supplementation. Furthermore, peroxide hydrogen was more in salinity- alkalinity stressed plants without Si and Se as compared to those supplemented with Si and Se. Si protected cucumber plants from NaCl induced oxidative damage by improving the activity of antioxidant enzymes (glutathione reductase, guaiacol peroxidase, ascorbate peroxidase). More importantly Si and Se supplementation improved the accumulation of P, Mg, Ca, Fe, Zn, Mn and Cu. In conclusion, Si and Se mitigate the negative effects of NaCl and $NaHCO_3$ in cucumber plants by modifying nutrient uptake and up-regulating antioxidant system.

Keywords: Ascorbate peroxidase, NaCl stress, $NaHCO_3$ stress, Nutrient uptake, Selenate

Introduction

The normal growth patterns of plants are often encountered by a wide range of environmental stresses resulting in challenge to the sustainable agricultural system. Among the abiotic stresses, salinity and alkalinity have been considered as the major factors leading to damage plant metabolism and inferior yield (Akladious and Mohamed, 2018). Plants exposed to salt and alkalinity stresses caused strong detrimental effects on plant biomass (Basyuni *et al.,* 2019), physiology (Butcher *et al.,* 2016), mineral ions uptake (Naher and Alam, 2010; Ahmad *et al.,* 2016) and destroy PSII reactions (Yan *et al.,* 2018). Apart from the restrictions in the uptake of essential mineral nutrients and the disruptions in key physiological processes, the production of reactive oxygen species (ROS) is an important indicator for plants under salinity-alkalinity stress conditions (Noctor *et al.,* 2014; Alqarawi *et al.,* 2014). High levels of ROS sternly hinder cell membranes and influence photosynthetic pigments, membrane lipids, proteins and DNA (Hashem *et al.,* 2015; Li *et al.,* 2017; Cao *et al.,* 2018; Abdel Latef *et al.,* 2016). To prevent salt-induced damages, plants utilize a multifaceted and strong antioxidant defense system where non-enzymatic and enzymatic components perform their function in sensing and elimination/detoxification of excess ROS. The nonenzymatic component include Ascorbic acid (AsA), glutathione (GSH), phenolics, alkaloids, tocopherols, and free amino acids (Roychoudhury and Banerjee, 2015). Superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), glutathione peroxidase (GPX), and guaiacol peroxidase (GuPX) represent enzymatic participant of this machinery (Hasanuzzaman *et al*., 2014; Pedranzani *et al.,* 2016).

Various methods are being utilized to mitigate the toxicity of abiotic stresses and the utilization of various micronutrients either as fertilizer or foliar spray is one of these approaches to confront abiotic stresses (Abbas *et al*., 2015; Negm and Eltarabily, 2017; Tei *et al.,* 2017). Selenium (Se) and silicon (Si) are beneficial elements for higher plants (Swain and Rout, 2017). These elements have been recently used in ameliorating the toxic effects of salinity and alkalinity stresses (Habibi, 2017; Sattar *et al.,* 2017). Foliar selenium and silicon in combination or alone advanced transpiration rate, water relations, photosynthetic attributes, chlorophyll contents, and the growth of plants under stressed conditions (Sattar *et al.,* 2017). Dual

*Corresponding Author, Email: mousavihort@yahoo.com

[DOR: 20.1001.1.23222727.1400.10.46.7.7]

application of Se and Si alleviated the adverse effects of NaCl on the annual herb, *Anethum graveolens* (Shekari *et al.*, 2015). Addition of 1.5 mM Na_2SiO_4 and 5 µM of selenate enhanced the K^+: Na^+ ratio and the activities of antioxidant enzymes in the stressed plants (Banerjee and Roychoudhury, 2018).

Numerous researches indicated that the presence of Si in the growth medium can provide partial protection from the effects of salinity stress in barley (*Hordeum vulgare* L.) (He *et al.*, 2020), spinach (*Spinacia oleracea* L.), tomato (*Solanum lycopersicum* L.) (Gunes *et al.*, 2007), *Zea mays* (Moussa, 2006), wheat (*Triticum aestivum* L.) (Tuna *et al.*, 2008), grapevine rootstock (*Vitis vinifera* L.) (Liu *et al.*, 2015) and cucumber (*Cucumis sativus* L.) (Zhu *et al.*, 2004). Moreover, it has also been found that Si nutrition is necessary to balance plant nutrient deficiencies such as iron (Pavlovic *et al.*, 2013). However, Si application under high salinity stress induces resistance in plants against oxidative injury (Kusvuran *et al.*, 2016) by suppressing ROS generation, regulating antioxidant enzyme activities (particularly, catalase and ascorbate peroxidase activities) and by decreasing the contents of malondialdehyde and H_2O_2 (Kamran *et al.*, 2019).

Previous studies have reported the ameliorating effects of Se against some abiotic stresses such as drought (Schiavon *et al.*, 2017), salinity (Habibi, 2017; Sattar *et al*., 2017), high temperature (Balal *et al.*, 2016), as well as oxidative damage (Balakhnina and Nadezhkina, 2017). Hence, most of the positive effects of Se have been related to decrease in oxidative stress by enhancing the activity of antioxidants (Balakhnina and Nadezhkina, 2017). Mozafariyan *et al.* (2016) showed that the exogenous application of Se at very low concentrations (5 or 10 µM) could alleviate the deleterious effects of 25 mM and 50 mM NaCl stress on tomato plants.

Cucumber [*Cucumis sativus* (L.)] is a highly substantial commercial horticultural commodity, but its growth and productivity are highly susceptible to different abiotic factors like drought, salt stress and alkalinity stress during both vegetative and reproductive growth stages (Balal *et al.*, 2016). Recently, many studies have reported the role of Si and Se in the alleviation of salt-induced phytotoxicity in various plant species such as tomato (Haghighi and Pessarakli, 2013; Mozafariyan *et al.*, 2016), cucumber (Zhu *et al.*, 2020), and rice (Yan *et al.*, 2020). Meanwhile, their roles and responsible mechanisms in alleviating salt and alkalinity stresses in cucumber plants under hydroponic conditions are rarely reported in the literature. Therefore, the aim of this investigation was to assess the potential of Se and Si to ameliorate the adverse effect of salinity and alkalinity damages on mineral nutrients and enzymatic activities in cucumber plant.

Materials and methods

Plant material and experimental design: This experiment investigated the response of *cucumber* cv. Nagen plants to the effects of two beneficial elements (Se and Si) and salinity and alkalinity stress levels in the nutrient solutions. Cucumber seeds were grown in a transplant tray containing coco peat and peat moss (70+30% v). The plants were grown in a greenhouse of Zarghan city with maximum, minimum and average temperatures of 43, -4, 25 °C respectively, an average rainfall of 107.7 mm and 1528 m above mean sea level (AMSL) during the spring and summer, 2018. The hydroponic system includes separate tanks with a Hoagland's nutrient solutions (Hoagland and Arnon, 1950) in each tank. After 14 days of cultivation, five transplants of "Nagen" cucumber were sown in pots filled with coco peat and perlite (70% + 30% v). Afterwards, the plants were regularly fed with Hoagland's nutrient solution through the nozzles into the pots for two weeks. Subsequently, the treatments were applied in each tank in addition to Hoagland's nutrient solution. The experiment treatments consisted of control (without sodium chloride and sodium bicarbonate), 75 mM sodium chloride as salinity stress and 75 mM sodium bicarbonate as sodic-alkalinity stress, and simultaneous application of selenium at concentrations of 0, 4 and 6 mg. L^{-1} of sodium selenate and silicon at concentrations of 75 and 100 mg. L^{-1} of sodium silicate. All sub branches and fruits were thinned up to 30 to 50 cm (node 2) above the cultivation bed to improve vegetative growth and improving plant vigor. Plant responses were evaluated 60 days after the salinity and alkalinity stress treatments. Leaf samples were randomly taken from each plant and were immediately placed inside an aluminum foil and frozen in liquid nitrogen and then placed in a -80 °C refrigerator for further analysis.

Determination of H_2O_2 Content: Hydrogen peroxide content in leaves was determined according to Loreto and Velikova (2001) with some modifications. Leaf tissues (0.3 g) were homogenized in an ice bath with 3 mL of 0.1% (w/v) trichloroacetic acid (TCA). The homogenate was centrifuged at 10,000g for 10 min and 0.75 mL of the supernatant was added to 0.75 mL of 10 mm potassium phosphate buffer (pH 7.0) and 1.5 mL of 1 m KI. The absorbance of the supernatant was measured at 390 nm. The content of H_2O_2 was calculated by comparison with a standard calibration curve previously made by using different concentrations of H_2O_2.

Determination of ascorbate peroxidase activity: The reaction mixture for the peroxidase contained 50 mM potassium phosphate, pH 7.0, 0.5 mM ascorbate, 0.1 mM hydrogen peroxide and 50 µM ascorbate in a total volume of 1 ml and 0.1 mL plant extract. The reaction was started by adding the enzyme or hydrogen peroxide, and the absorbance was recorded 10 to 30 sec after this addition at 265 nm (Garcia-Limones *et al*., 2002).

Guaiacol peroxidase activity: Guaiacol peroxidase was assayed according to the method developed by Dazy *et al*. (2008). The reaction mixture consisted of

[DOR: 20.1001.1.23222727.1400.10.46.7.7]

100 µL plant extract, 100 µL guaiacol (22 mM), 100 µL H_2O_2 (100 mM) and completed to 1 mL final volume with 125 mM potassium phosphate buffer (pH 7.0). The increase in absorbance was measured spectro photometrically at 470 nm ($e = 26.6\ mM^{-1}\ cm^{-1}$).

Glutathione reductase activity: Glutathione reductase activity was assayed by monitoring glutathione- dependent oxidation of NADPH in 0.15 mM NADPH, 3 mM $MgCl_2$, 0.5 mM oxidized glutathione, and 50 mM Tris-HCl (pH 7.5). The absorbance was measured spectrophotometrically at 340 nm (Schaedle and Bassham, 1977); units were expressed as U/mg protein. min.

Mineral analysis: Concentrations of inorganic ions were determined in 1.0 g of oven dried leaf samples. The samples were ashed at 550 °C and digested in hydrochloric acid (Munns *et al.,* 2010). Phosphorus (P) was analyzed spectrophotometrically (Shimadzu UV 240, Japan) (Pratt and Chapman, 1982). The concentrations of calcium (Ca), iron (Fe), zinc (Zn), magnesium (Mg) and manganese (Mn) ions were determined by atomic absorption spectroscopy (GBC 1.33, Avanta, Australia).

Statistical analysis: The experiment was a completely randomized design factorial experiment in four replications. Data were subjected to analyses of variance (ANOVA) and the means were separated by Duncan's multiple range test multiple at $P \leq 0.05$. Data analysis were performed by SAS, v 9.2 software.

Results

According to the results of data analysis of variance, the effects of salinity and alkalinity stresses and selenium and silicon elements on all of the studied traits were statistically significant and also the effects of salinity and alkalinity stresses as well as selenium and silicon interactions were significant at $P < 0.01$ (Table 1).

Peroxide hydrogen: The results revealed that peroxide hydrogen concentration was increased in cucumber leaves under salinity and alkalinity stresses. The lowest content of peroxide hydrogen was recorded in the control treatment and peroxide hydrogen concentration was remarkably decreased by addition of selenium and silicon under salinity and alkalinity stresses (Fig. 1).

Ascorbate peroxidase activity: The effects of application of selenium and silicon treatments on ascorbate peroxidase activity of cucumber plants grown in salinity and alkalinity stress conditions are shown in Fig. 2. Ascorbate peroxidase activity in leaves of NaCl stressed plants significantly enhanced with the application of sodium silicate and sodium selenate. The highest enzyme activity was recorded in 100 mg. L^{-1} sodium silicate under 75 mM NaCl condition. Meanwhile application of sodium silicate and sodium selenate increased this enzyme activity of cucumber plants under 75 mM alkalinity stress. Whilst, under non-stress conditions, the ascorbate peroxidase activity was declined in leaves of the control plants compared with stressed plants.

Guaiacol peroxidase activity: Guaiacol peroxidase activity increased with either Si or Se in salinity and alkalinity stressed plants; the highest increase was observed in the 100 mg L^{-1} sodium silicate at the 75 mM NaCl. Both sodium silicate and sodium selenate improved the guaiacol peroxidase activity in the 75 mM $NaHCO_3$ treatment. Also, both levels of sodium silicate and sodium selenate improved the guaiacol peroxidase activity in the 75 mM NaCl treatment (Fig. 3).

Glutathione reductase: Sodium silicate and sodium selenate significantly increased glutathione reductase activity under control and both alkalinity and salinity stress conditions, whilst, the effects of beneficial elements under stressed conditions were more remarkable. 100 mg L^{-1} sodium silicate had the greatest effect on increasing glutathione reductase activity in the 75mM NaCl treatment and 75 mM $NaHCO_3$ as well (Fig. 4).

Mineral elements: Phosphorous concentration in cucumber plants changed with sodium silicate and sodium selenate application. Sodium silicate and sodium selenate increased phosphorous content in non-stressed and salinity and alkalinity stress conditions; However, the highest amount of P was in 100 mgL^{-1} sodium silicate treatment under non-stressed conditions (Table 2).

Sodium silicate and sodium selenate improved Mg content in both stressed plants and non- stress plants. The highest concentration of Mg was seen under non-stressed conditions, when 100 mg L^{-1} sodium silicate was applied. Sodium silicate and sodium selenate improved Mg content in the 75 mM $NaHCO_3$ and NaCl treatments, while no application of both sodium silicate and sodium selenate decreased it in 75 mM $NaHCO_3$ and NaCl treatment (Table 2).

Sodium silicate and sodium selenate significantly increased Ca content under both alkalinity and saline conditions. 75 mgL^{-1} sodium silicate had the greatest effect on increasing Ca content in the 75mM NaCl treatment in comparison with 75 mM $NaHCO_3$ (Table 2).

Table 3 presents the effects of salinity and alkalinity stress and different concentrations of beneficial elements on Mn, Fe, Zn, and Cu concentrations in leaf of cucumber plants. Stress conditions reduced the concentrations of Mn, Fe, Zn and Cu compared with non- stressed conditions.

As shown in Table 3, sodium silicate and sodium selenate improved Fe concentration in stressed plants, while the highest content was seen in no salinity or alkalinity stress conditions when 100 mgL^{-1} sodium silicate was applied.

Zn content improved with sodium silicate and sodium selenate applications in plants grown in alkalinity or salinity medium, with more significant efficiency in cucumber plants grown in salinity medium in comparison to that in alkalinity medium. The highest Zn concentration was recorded in non-stressed

[DOR: 20.1001.1.23222727.1400.10.46.7.7]

Table 1. Analysis variance of some properties of cucumber plants under salinity and alkalinity stresses

Source	D.F	Mean of Square										
		Peroxide hydrogen	Ascorbate peroxidase activity	Guaiacol peroxidase activity	Glutathione reductase	P	Mg	Ca	Cu	Mn	Zn	Fe
Salinity (A)	2	109.00**	1481**	1466.00**	241.00**	8.48**	0.009**	2.5*	30.25*	698.6*	3019.0**	7991.0**
Beneficial Elements (B)	4	41.00**	268**	607.00**	71.20**	0.93**	0.96**	65.39**	14.02**	244.8**	301.00**	938.00**
A*B	8	9.16**	126**	145.00**	21.50**	0.12**	41.01**	21.67**	27.96**	372.6**	28.01**	166.00**
Error	45	0.28	4.2	4.12	0.60	0.006	0.01	0.61	6.9	218.5	1.5	18.61
C.V		3.8	2.3	3.6	2.9	2.71	12.19	2.3	16.66	14.1	2.5	2.5

* P <0.05, *** P <0.001

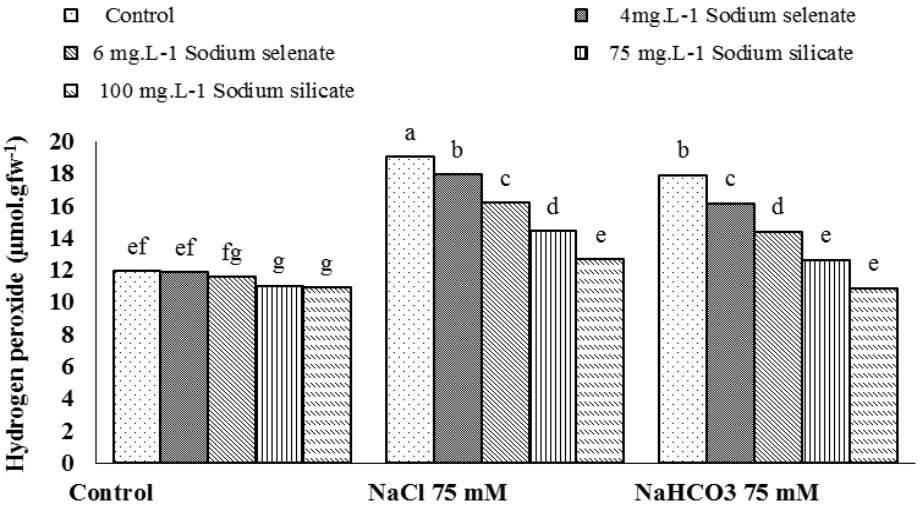

Fig. 1. Effects of application of sodium selenate and sodium silicate on peroxide hydrogen of cucumber plants grown in salinity and alkalinity stress conditions. Bars with different letters are significantly different according to the Duncan's multiple range test at P ≤ 0.05.

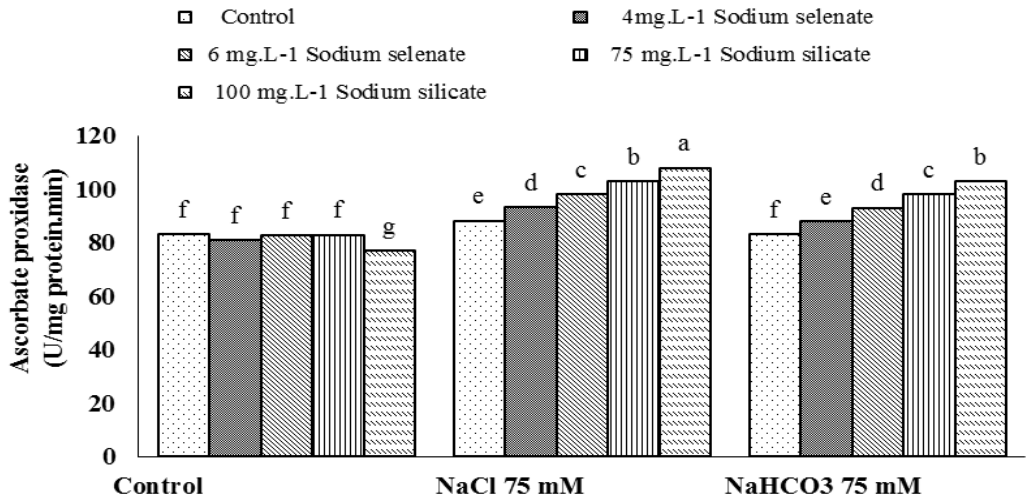

Fig. 2. Effects of application of sodium selenate and sodium silicate on ascorbate peroxidase activity of cucumber plants grown in salinity and alkalinity stress conditions. Bars with different letters are significantly different according to the Duncan multiple range test at P ≤ 0.05.

[DOR: 20.1001.1.23222727.1400.10.46.7.7]

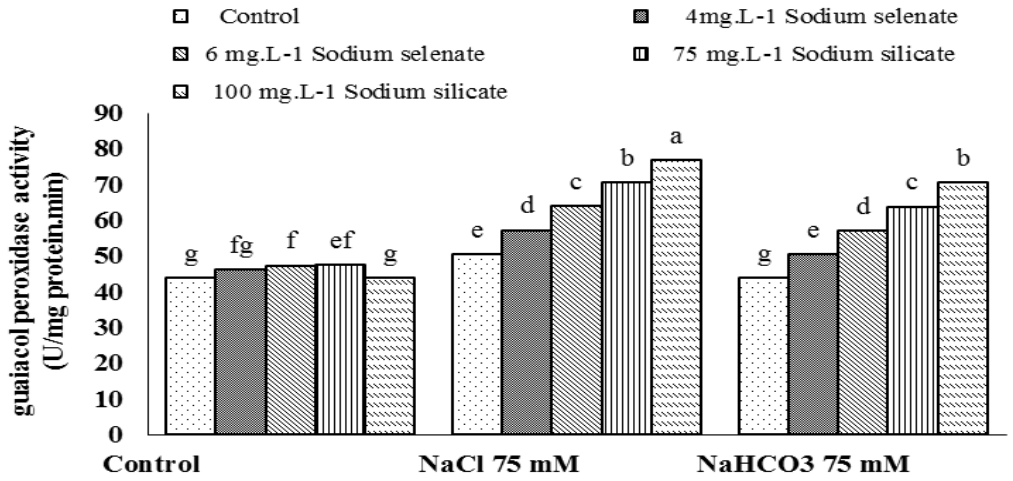

Fig. 3. Effects of foliar application of selenium and silicon on guaiacol peroxidase activity of cucumber plants grown in salinity or alkalinity stress conditions. Bars with different letters are significantly different according to according to the Duncan multiple range test at P ≤ 0.05.

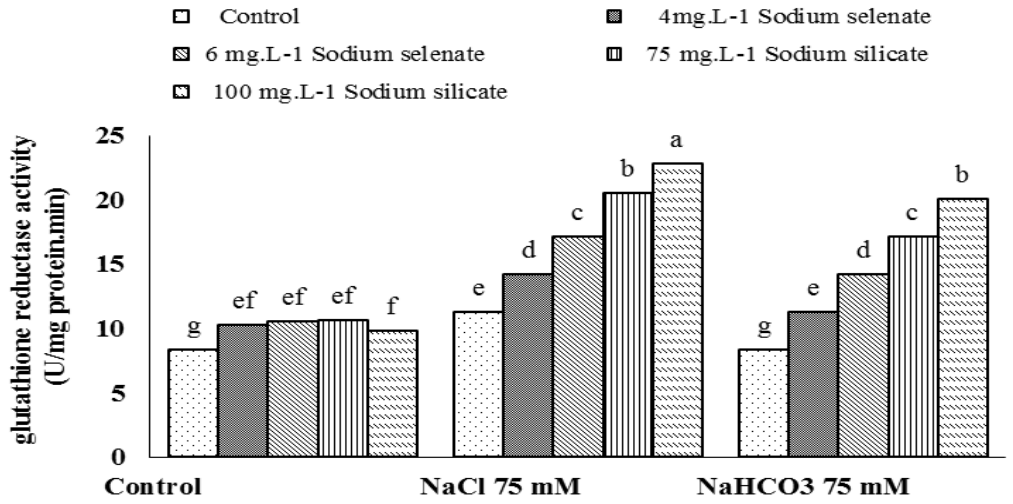

Fig. 4. Effects of application of sodium selenate and sodium silicate on glutathione reductase activity of cucumber plants grown in salinity and alkalinity stress conditions. Bars with different letters are significantly different according to the Duncan multiple range test at P ≤ 0.05

conditions when 100 mgL^{-1} sodium silicate was applied. The results revealed that salinity stress decreased Mn and Cu concentrations in cucumber plants and the lowest contents of Mn and Cu were recorded in the 75 mM $NaHCO_3$ treatment (Table 3). Under both stress conditions, sodium selenate and sodium silicate foliar applications remarkably increased Mn and Cu concentrations in cucumber leaves.

Discussion

Increased salinity in the growth medium has resulted in the decrease of plant growth features, physiological properties, and biochemical attributes, which eventually restricted the yield of crop plants (Kamran *et al.*, 2019). Another cause of the growth inhibition under abiotic stresses was changes in the plants' mineral composition. At the same time, silicon and selenate applications drastically mitigated the negative effect of salinity and alkalinity due to their beneficial roles in balancing morpho-physiological characteristics, mineral nutrition and antioxidant defense mechanism (Khorasaninejad *et al.*, 2020; Balakhnina and Nadezhkina, 2017).

Si-treated cucumber plants maintained high P and Fe levels even under salinity and alkalinity stress conditions which was in line with Farshidi *et al.* (2012) findings on canola plants. Hussein and Abou-Baker (2014) indicated that higher accumulation of P, K, Ca, and Mg in stressed *Moringa oleifera* compared to the non-treated stressed plants was induced by Si application. This experiment, an increment in Mn, Zn, and Fe contents in plant leaves under Se treatment could also be the reason for the improvement of photosynthetic apparatus and avoidance of chlorophyll degradation (Carvalho *et al.*, 2014).

[DOR: 20.1001.1.23222727.1400.10.46.7.7]

Table 2. Effect of combined different concentrations of sodium silicate, sodium selenate and salinity and alkalinity stress on macro elements content in cucumber leaf.

Salinity stress	Beneficial elements	mg/L	P	Mg	Ca
Control	Sodium selenate	0	2.91^{e†}	0.59^{j}	2.88^{h}
		4	3.05^{d}	0.90^{f}	3.14^{f}
		6	3.25^{c}	1.21^{d}	3.64^{c}
	Sodium silicate	75	3.53^{b}	1.41c	4.26^{b}
		100	3.99^{a}	1.74^{a}	4.47^{a}
75 mM Sodium chloride	Sodium selenate	0	1.72^{l}	0.48^{k}	2.66^{i}
		4	1.79l	0.73^{i}	2.96^{g}
		6	2.06^{k}	1.03^{e}	3.39^{e}
	Sodium silicate	75	2.26^{j}	1.23^{d}	3.74^{c}
		100	2.38^{i}	1.57^{b}	3.51^{d}
75 Mm Sodium bicarbonate	Sodium selenate	0	2.45^{i}	0.49^{k}	1.62^{l}
		4	2.56^{h}	0.80^{h}	2.11^{k}
		6	2.60^{g}	0.88^{g}	2.48^{j}
	Sodium silicate	75	2.76f^{g}	0.98^{d}	2.93^{g}
		100	2.80^{ef}	1.15^{b}	3.29^{e}

†Mean values followed by the same letters in each column are not significantly different at the 5% level (Duncan's multiple range test).

Table 3. Effect of combined different concentrations of sodium silicate, sodium selenate and salinity and alkalinity stress on micro elements in cucumber leaf.

Salinity stress	Beneficial elements	mg/L	Fe	Cu	Mn	Zn
Control	Sodium selenate	0	186.9^{d}	17.23^{g}	78.26^{g}	54.60^{de}
		4	189^{cd}	19.98^{f}	80.30^{f}	55.90^{d}
		6	192.6^{bc}	23.73^{d}	89.38^{e}	58.20^{c}
	Sodium silicate	75	198.0^{b}	29.73^{c}	108.94^{b}	61.30^{b}
		100	206.0^{a}	34.96^{a}	118.01^{a}	66.30^{a}
75 mM Sodium chloride	Sodium selenate	0	138.9^{j}	15.49^{h}	73.05^{h}	46.00^{h}
		4	154.5^{i}	17.04^{g}	79.32^{f}	47.06^{h}
		6	156.9^{h}	19.05^{f}	88.95^{e}	49.50^{g}
	Sodium silicate	75	162.9^{g}	24.82^{d}	93.82^{d}	51.36^{f}
		100	170.1^{e}	27.96^{c}	97.77^{c}	53.60^{e}
75 Mm Sodium bicarbonate	Sodium selenate	0	153.8^{i}	13.57^{i}	66.23^{i}	23.13^{l}
		4	166.0^{f}	18.88^{g}	77.85^{g}	33.50^{k}
		6	169.2^{e}	21.31^{e}	80.62^{f}	35.05^{k}
	Sodium silicate	75	172.0^{de}	27.88^{c}	90.48^{e}	38.86^{j}
		100	166.0^{f}	32.70^{b}	89.88^{e}	43.50^{i}

†Mean values followed by the same letters in each column are not significantly different at the 5% level (Duncan's multiple range test).

While salinity and alkalinity stresses induced oxidative stress and increased the levels of H_2O_2, addition of sodium selenate and sodium silicate decreased the harmful effects of stresses. Our findings were consistent with other researches that decreased generation of H_2O_2 under selenate supplementations has been confirmed (Hawrylak-Nowak, 2013). It has been well accepted that lower concentrations of selenate that cannot work as a pro-oxidant to induce oxidative stress help to protect plants from ROS-stimulated oxidative damage (Kamran *et al.*, 2019). In general., selenate could protect the metabolism and cellular functioning by up-regulating the ROS detoxifying pathways and the osmoregulatory mechanisms and silicate can develop antioxidant machinery by acting as a scavenger against H_2O_2 and O_2^- guaranteed ROS balance at the cellular level, which improved membrane stability and permeability (Kim *et al.*, 2017; Parveen *et al.*, 2020).

As salinity and alkalinity stresses induced oxidative stress, an increase in the activity of antioxidant enzymes including APX, GPX, and GuPX in the leaves of cucumber plants by application of the beneficial elements was observed. Research has shown that 75 mM salinity and alkalinity stresses induced oxidative stress due to the accumulation of ROS, which in turn induced free radicals that could not be controlled in damaging cell components and, eventually leading to cell death. Enhancement of H_2O_2 and other antioxidant enzymes have been reported for different plant species under salinity stress (Kamran *et al.*, 2019). Some elements such as Si and Se can act as the mediated improvement in the alleviation of ROS effect, improve the activities of oxidative enzymes resulting in increased antioxidative capacity in plants and survived them under abiotic stresses (Kamran *et al.*, 2019).

The neutralizing of H_2O_2 and lipid peroxide (MDA) into water and lipid alcohol is carried out by two substantial enzymes including glutathione peroxidase and glutathione reductase (Farooq *et al.*, 2015). Glutathione reductase is considered to be an important

[DOR: 20.1001.1.23222727.1400.10.46.7.7]

enzyme, which is strongly activated by Se in different plants under salinity stress (Kamran *et al.*, 2019). In the presence of Se, glutathione peroxidase suppresses H_2O_2 and then APX, CAT, and GR remove the leftover of H_2O_2. In line with our results, an increase in activity of glutathione reductase lowered the levels of H_2O_2 but improved the growth of rapeseed (*Brassica napus* L.), rice (*Oryza sativa* L.) and tomato (*Solanum lycopersicum* L.) plants by overcoming ROS-stimulated oxidative damage under salinity stress (Hasanuzzaman *et al.*, 2011; Kamran *et al.*, 2019).

Our results of increased activity of antioxidant enzymes by Silicon supplementation support the findings of Habibi and Hajiboland (2013) for *Pistacia vera*, Shekari *et al*. (2015) for *Anethum graveolens* and Abdel Latef and Tran (2016) for maize. Silicon stimulated the activity of GR and APX to prevent damage to photosynthetic apparatus by maintaining the optimal concentration of NADP for keeping the uniformity in electron flow resulted in hindering the generation of toxic superoxide radical (Abd_Allah *et al.*, 2015). Furthermore, it was stated that the access of proteases to internal membrane proteins as well as destruction and disturbance of cell membranes were inhibited by silicon (Ali *et al.*, 2021). Furthermore, our findings supported those obtained by Kamran *et al*. (2019), who concluded a significant reduction in H_2O_2 by Si application might be due to lower Na^+ uptake, improvement of plasma membrane stability and less exposure of maize roots to a saline environment.

Conclusion

Conclusively it can be said that supplementation of Si and Se protected cucumber plants from the ill effects of salinity and alkalinity stresses by causing significant improvement in nutrient accumulation. Stress triggered reduction in P, Mg, Ca, Mn, Fe, Zn and Cu were mitigated by Si and Se applications. Si mediated growth promotion under normal and salt stress conditions was supported by the modulation in the activity of antioxidant enzymes including glutathione reductase, guaiacol peroxidase and ascorbate peroxidase leading to reduced H_2O_2 content in them. It is noteworthy that elements other than those discussed here may also be beneficial for plants, but more validation is needed to support these results.

References

Abbas, T., Balal, R. M., Shahid, M. A., Pervez, M. A., Ayyub, C. M., Aqueel, M. A. and Javaid, M. M. (2015) Silicon-induced alleviation of NaCl toxicity in okra (*Abelmoschus esculentus*) is associated with enhanced photosynthesis, osmoprotectants and antioxidant metabolism. Acta Physiologiae Plantarum 37: 1-15.

Abd Allah, E. F., Hashem, A., Alqarawi, A. A., Bahkali, A. H. and Alwhibi, M. S. (2015) Enhancing growth performance and systemic acquired resistance of medicinal plant *Sesbania sesban* (L.) Merr using arbuscular mycorrhizal fungi under salt stress. Saudi Journal of Biological Sciences 22: 274-283.

Abdel Latef, A. A. H. and Chaoxing, H. (2014) Does inoculation with *Glomus mosseae* improve salt tolerance in pepper plants? Journal of Plant Growth Regulation 33: 644-653.

Abdel Latef, A. A. and Tran, L. S. P. (2016) Impacts of priming with silicon on the growth and tolerance of maize plants to alkaline stress. Frontiers in Plant Science 7: 243.

Ahmad, P., Latef, A. A. A., Hashem, A., Abd_Allah, E. F., Gucel, S. and Tran, L. S. P. (2016) Nitric oxide mitigates salt stress by regulating levels of osmolytes and antioxidant enzymes in chickpea. Frontiers in Plant Science7: 347.

Akladious, S. A. and Mohamed, H. I. (2018) Ameliorative effects of calcium nitrate and humic acid on the growth, yield component and biochemical attribute of pepper (*Capsicum annuum*) plants grown under salt stress. Scientia Horticulturae 236: 244-250.

Ali, M., Afzal, S., Parveen, A., Kamran, M., Javed, M. R., Abbasi, G. H. and Ali, S. (2021) Silicon mediated improvement in the growth and ion homeostasis by decreasing Na^+ uptake in maize (*Zea mays* L.) cultivars exposed to salinity stress. Plant Physiology and Biochemistry 158: 208-218.

Alqarawi, A. A., Abd Allah, E. F., Hashem, A., Al Huqail, A. A. and Al Sahli, A. A. (2014) Impact of abiotic salt stress on some metabolic activities of *Ephedra alata* Decne. Journal of Food, Agriculture and Environment 12:620-625.

Balakhnina, T. I. and Nadezhkina, E. S. (2017) Effect of selenium on growth and antioxidant capacity of *Triticum aestivum* L. during development of lead-induced oxidative stress. Russian Journal of Plant Physiology 64: 215-223.

Balal, R. M., Shahid, M. A. and Javaid, M. M. (2016) The role of selenium in amelioration of heat-induced oxidative damage in cucumber under high temperature stress. Acta Physiologiae Plantarum 38: 158-172.

Banerjee, A. and Roychoudhury, A. (2018) Plant Nutrients and Abiotic Stress Tolerance. Springer, Singapore.

Basyuni, M., Wasilah, M., Hasibuan, P. A. Z., Sulistiyono, N., Sumardi, Bimantara, Y., Hayati, R., Sagami, H. and Oku, H. (2019) Salinity and subsequent freshwater influences on the growth, biomass, and polyisoprenoids distribution of *Rhizophora apiculata* seedlings. Biodiversitas Journal of Biological Diversity 20: 288-295.

Butcher, K., Wick, A. F., DeSutter, T., Chatterjee, A. and Harmon, J. (2016) Soil salinity: A threat to global food security. Agronomy Journal 108: 2189-2200.

Cao, K., Yu, J., Xu, D., Ai, K., Bao, E. and Zou, Z. (2018) Exposure to lower red to far-red light ratios improve tomato tolerance to salt stress. BMC Plant Biology 18: 92.

[DOR: 20.1001.1.23222727.1400.10.46.7.7]

Carvalho, E. R., Oliveira, J. A., Von Pinho, E. V. D. R. and Costa Neto, J. (2014) Enzyme activity in soybean seeds produced under foliar application of manganese. Ciencia e Agrotecnologia 38: 317-327.

Dazy, M., Jung, V., Ferard, J. and Masfaraud, J. (2008) Ecological recovery of vegetation on a coke-factory soil: Role of plant antioxidant enzymes and possible implication in site restoration. Chemosphere 74: 57-63.

Farooq, M., Hussain, M., Wakeel, A. and Siddique, K. H. (2015) Salt stress in maize: Effects, resistance mechanisms, and management. Agronomy for Sustainable Development 35: 461-481.

Farshidi, M., Abdolzadeh, A. and Sadeghipour, H. R. (2012) Silicon nutrition alleviates physiological disorders imposed by salinity in hydroponically grown canola (*Brassica napus* L.) plants. Acta Physiologiae Plantarum 34: 1779-1788.

Garcia-Limones, C., Hervas, A., Navas-Cortes, J. A., Jimenez-Diaz, R. M. and Tena, M. (2002) Induction of an antioxidant enzyme system and other oxidative stress markers associated with compatible and incompatible interactions between chickpea (*Cicer arietinum* L.) and *Fusarium oxysporum*. sp. Ciceris. Physiological and Molecular Plant Pathology 61: 325-337.

Gunes, A., Inal, A., Bagci, E. G. and Pilbeam, D. J. (2007) Silicon-mediated changes of some physiological and enzymatic parameters symptomatic for oxidative stress in spinach and tomato grown in sodic-B toxic soil. Plant and Soil 164: 807-11.

Habibi, G. (2017) Selenium ameliorates salinity stress in *Petroselinum crispum* by modulation of photosynthesis and by reducing shoot Na accumulation. Russian Journal of Plant Physiology 64: 368-374.

Habibi, G. and Hajiboland, R. (2013) Alleviation of drought stress by silicon supplementation in pistachio (*Pistacia vera* L.) plants. Folia Horticulturae 25: 21-29.

Haghighi, M. and Pessarakli, M. (2013) Influence of silicon and nano-silicon on salinity tolerance of cherry tomatoes (*Solanum lycopersicum* L.) at early growth stage. Scientia Horticulturea 161: 111-117.

Hasanuzzaman M., Alam, M. M., Nahar, K., Jubayer-Al-Mahmud Ahamed, K. U. and Fujita, M. (2014) Exogenous salicylic acid alleviates salt stress-induced oxidative damage in *Brassica napus* by enhancing the antioxidant defense and glyoxalase systems. Australian Journal of Crop Science 8: 631-639.

Hasanuzzaman, M., Hossain, M. A. and Fujita, M. (2011) Selenium-induced up-regulation of the antioxidant defense and methylglyoxal detoxification system reduces salinity-induced damage in rapeseed seedlings. Biological Trace Element Research143: 1704-1721.

Hashem, A., Abd_Allah, E. F., Alqarawi, A. A., Aldubise, A. and Egamberdieva, D. (2015) Arbuscular mycorrhizal fungi enhance salinity tolerance of *Panicum turgidum* Forssk by altering photosynthetic and antioxidant pathways. Journal of Plant Interactions 10: 230-242.

Hawrylak-Nowak, B. (2013) Comparative effects of selenate and selenate on growth and selenium accumulation in lettuce plants under hydroponic conditions. Plant Growth Regulation70: 149-157.

He, Q., Li, P., Zhang, W. and Bi, Y. (2020) Cytoplasmic glucose-6-phosphate dehydrogenase plays an important role in the silicon-enhanced alkaline tolerance in highland barley. Functional Plant Biology 48: 119-130.

Hoagland, D. R. and Arnon, D. I. (1950) The water-culture method for growing plants without soil, second ed. Circular. California Agricultural Experiment Station.

Hussein, M. M. and Abou-Baker, N. H. (2014) Growth and mineral status of moringa plants as affected by silicate and salicylic acid under salt stress. International Journal of Plant and Soil Science 3: 163-177.

Kamran, M., Parveen, A., Ahmar, S., Malik, Z., Hussain, S., Chattha, M. S., Saleem, M. H., Adil, M., Heidari, P. and Chen, J. T. (2019) An overview of hazardous impacts of soil salinity in crops, tolerance mechanisms, and amelioration through selenium supplementation. International Journal of Molecular Sciences 21: 148.

Khorasaninejad, S., Zare, F. and Hemmati, K. (2020) Effects of silicon on some phytochemical traits of purple coneflower (*Echinacea purpurea* L.) under salinity. Scientia Horticulturae 264.

Kim, Y. H., Khan, A. L., Waqas, M. and Lee, I. J. (2017) Silicon regulates antioxidant activities of crop plants under abiotic-induced oxidative stress: A review. Frontiers in Plant Science 8: 510.

Kusvuran, S., Kiran, S. and Ellialtioglu, S. S. (2016) Antioxidant enzyme activities and abiotic stress tolerance relationship in vegetable crops. Abiotic and Biotic Stress in Plants - Recent Advances and Future Perspectives. Croatia: InTech 481-503

Li, H., Chang, J., Chen, H., Wang, Z., Gu, X. and Wei, C. (2017) Exogenous melatonin confers salt stress tolerance to watermelon by improving photosynthesis and redox homeostasis. Frontiers in Plant Science 8: 295.

Liu, P., Yin, L., Wang, S., Zhang, M., Deng, X., Zhang, S. and Tanaka, K. (2015) Enhanced root hydraulic conductance by aquaporin regulation accounts for silicon alleviated salt-induced osmotic stress in *Sorghum bicolor* L. Environmental and Experimental Botany 111: 42-51.

Loreto, F. and Velikova, V. (2001) Isoprene produced by leaves protects the photosynthetic apparatus against ozone damage, quenches ozone products, and reduces lipid peroxidation of cellular membranes. Journal of Plant Physiology 127: 1781-1787.

Moussa, H. R. (2006) Influence of exogenous application of silicon on physiological response of salt-stressed maize (*Zea mays* L.). International Journal of Agriculture and Biology 8: 293-297.

[DOR: 20.1001.1.23222727.1400.10.46.7.7]

Mozafariyan, M., Kamelmanesh, M. M. and Hawrylak-Nowak, B. (2016) Ameliorative effect of selenium on tomato plants grown under salinity stress. Archives of Agronomy and Soil Science 62: 1368-1380.

Munns, R., Richard A. J., Xavier, R. R. S., Robert, T. F. and Hamlyn, G. J. (2010) New phenotyping methods for screening wheat and barley for beneficial responses to water deficit. Journal of Experimental Botany 61: 3499-3507.

Naher, N. and Alam, A. (2010) Germination, growth and nodulation of mungbean (*Vigna radiata* L.) as affected by sodium chloride. International Journal of Agricultural Sustainability 5: 8-11.

Negm, A. M. and Eltarabily, M. G. A. (2017) Modeling of fertilizer transport through soil, case study. In: The Nile Delta, Hdb Env (ed. Negm, A. M.) Pp. 121-158. Chem Springer International Publishing, Cham.

Noctor, G., Mhamdi, A. and Foyer, C. H. (2014) The roles of reactive oxygen metabolism in drought: not so cut and dried. Plant Physiology 164: 1636-1648.

Parveen, A., Hamzah Saleem, M., Kamran, M., Zulqurnain Haider, M., Chen, J. T., Malik, Z., Shoaib Rana, M., Hassan, A., Hur, G., Tariq Javed, M. and Azeem, M. (2020) Effect of citric acid on growth, ecophysiology, chloroplast ultrastructure, and phytoremediation potential of jute (*Corchorus capsularis* L.) seedlings exposed to copper stress. Biomolecules 10: 592.

Pavlovic, J., Samardzic, J., Maksimovi´c, V., Timotijevic, G., Stevic, N., Laursen, K. H., Hansen, T. H., Husted, S., Schjoerring, J. K., Liang, Y. and Nikolic, M. (2013) Silicon alleviates iron deficiency in cucumber by promoting mobilization of iron in the root apoplast. New Phytologist 198: 1096-1107.

Pedranzani, H., Rodriguez-Rivera, M., Gutierrez, M., Porcel, R., Hause, B. and Ruiz-Lozano, J. M. (2016) Arbuscular mycorrhizal symbiosis regulates physiology and performance of *Digitaria eriantha* plants subjected to abiotic stresses by modulating antioxidant and jasmonate levels. Mycorrhiza 26: 141-152.

Roychoudhury, A., Banerjee, A. and Lahiri, V. (2015) Metabolic and molecular-genetic regulation of proline signaling and its cross-talk with major effectors mediates abiotic stress tolerance in plants. Turkish Journal of Botany 39: 887-910.

Sattar, A., Cheema, M. A., Abbas, T., Sher, A., Ijaz, M. and Hussain, M. (2017) Separate and combined effects of silicon and selenium on salt tolerance of wheat plants. Russian Journal of Plant Physiology 64: 341-348.

Schaedle, M. and Bassham, J. A. (1977) Chloroplast glutathione reductase. Plant Physiology 59: 1011-1012.

Schiavon, M., Lima, L. W., Jiang, Y. and Hawkesford, M. J. (2017) Effects of selenium on plant metabolism and implications for crops and consumers. In: Selenium in Plants, Plant Ecophysiology (ed. Pilon, S.) Pp. 257-275. Springer International Publishing, Cham.

Shekari, F., Abbasi, A. and Mustafavi, S. H. (2015) Effect of silicon and selenium on enzymatic changes and productivity of dill in saline condition. Journal of the Saudi Society of Agricultural Sciences 16: 367-374.

Swain, R. and Rout, G. R. (2017) Silicon in Agriculture. Sustainable Agriculture Reviews. Springer International Publishing, Cham.

Tei, F., Nicola, S. and Benincasa, P. (2017) Advances in Research on Fertilization Management of Vegetable Crops, Advances in Olericulture Series. Springer International Publishing, Cham.

Tuna, A. L., Kaya, C., Higgs, D., Murillo-Amador, B., Aydemir, S. and Girgin, A. R. (2008) Silicon improves salinity tolerance in wheat plants. Environmental and Experimental Botany 62: 10-16.

Yan, G., Fan, X., Peng, M., Yin, C., Xiao, Z. and Liang, Y. (2020) Silicon improves rice salinity resistance by alleviating ionic toxicity and osmotic constraint in an organ-specific pattern. Frontiers in Plant Science 11.

Yan, G., Nikolic, M., Ye, M., Xiao, Z. and Liang, Y. (2018) Silicon acquisition and accumulation in plant and its significance for agriculture. Journal of Integrative Agriculture17: 2138-2150.

Zhu, Y., Jiang, X., Zhang, J., He, Y., Zhu, X., Zhou, X., Gong, H., Yin, J. and Liu, Y. (2020) Silicon confers cucumber resistance to salinity stress through regulation of proline and cytokinins. Plant Physiology and Biochemistry 156: 209-220.

Zhu, Z., Wei, G., Li, J., Qian, Q. and Yu, J. (2004) Silicon alleviates salt stress and increases antioxidant enzymes activity in leaves of salt-stressed cucumber (*Cucumis sativus* L.). Plant Science 167: 527-533.

[DOR: 20.1001.1.23222727.1400.10.46.7.7]