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FULL LENGTH ARTICLE

Effect of silicon and selenium on enzymatic changes and productivity of dill in saline condition

Fariborz Shekari, Amin Abbasi *, Seyed Hamid Mustafavi

Department of Agronomy and Plant Breeding, Faculty of Agriculture, University of Maragheh, Maragheh, Iran

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KEYWORDS

Dill (*Anethum graveolens*);
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Abstract *Anethum graveolens* is an annual herb in the celery family Apiaceae. The experiment was carried out in a factorial design with two factors include salinity, which was applied to the root medium as NaCl (0 and 10 ds/m) and nutrition as sodium silicate (0 and 1.5 mM), and selenate (0, 5 μM). Supplementary Si or Se ameliorated the negative effects of salinity on plant dry matter and chlorophyll content. Application of Si or Se decreased Na^+ concentration and increased K^+ concentration in roots and shoots of dill plants. Salinity imposed oxidative stress and leaded to increase malondialdehyde (MDA) concentration. Under saline condition, addition of Si/Se significantly increased the activities of superoxide dismutase (SOD) and catalase (CAT) in salt-stressed plant when compared with plant subjected to salinity alone. Our results revealed that improvement in growth of salt stressed plants under the influence of Si and Se may be due to the improved ion balance, antioxidant enzymes activities and osmotic adjustment. These trace elements had negative effect on growth under non-saline conditions. Therefore, application of these trace elements (especially Silicon) under saline condition could be a better strategy for maintaining the crop productivity in these regions.

1. Introduction

Soil salinity is one of the most serious environmental problems limiting crop production mainly in arid and semiarid areas. About one-third of the world's irrigated lands are affected by salt (Flowers and Colmer, 2008). Salinity can be hazardous to plant growth and productivity especially in arid and semiarid areas, where irrigation of crops with saline water could accumulate salts in soil. The response of plants to salinity is multifaceted and involves changes in plant's morphology, physiology and metabolism (Hilal et al., 1998), resulted in diminishing growth and yield (Ashraf and Harris, 2004). Ahmad et al. (2012) reported that >65% yield losses in wheat occur due to salinity. Accumulation of salts in soil solution exerts an osmotic pressure and reduces the soil water potential making water unavailable to plants as reported by Munns et al. (2006). Ionic imbalance and specific ion toxicity due to excessive buildup of Na^+ and Cl^- is other factor that affects the uptake of other mineral nutrients (Grattan and Grieve, 1999; Chinnusamy et al., 2005), resulted in growth reduction.

* Corresponding author.
E-mail address: a.abbasi25@yahoo.com (A. Abbasi).
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Salt stress not only imposes the osmotic stress and ion toxicity, but is also marked as an oxidative stress (Gueta-Dahan et al., 1997) which can elevate membrane permeability (Tabaei-Aghdaei et al., 2000) and show reduction in chlorophyll contents (Hashemi et al., 2010).

Recently, various chemical, physical and biological strategies are adapted for stable productivity of crops in saline soils. Of all these strategies, exogenous application of nutrients has gained a considerable ground as an effective approach to ameliorate the adverse effects of salt stress (Grattan and Grieve, 1999). Silicon (Si) is the second most abundant mineral element in the soil after oxygen (Epstein, 1999; Liang et al., 2007), and also is a major structural component of the cell walls in some monocotyledonous species (Inanaga and Okasaka, 1996). Although Si is a major constituent of plants, to date its essentiality has not been completely established, but various studies have demonstrated that Si application significantly increased plant growth under stress condition including biotic and abiotic stresses as salt stress (Rodrigues et al., 2003; Ma, 2004). The exogenous application of Si has been shown to ameliorate the adverse effects of salinity in several plants, including *Oryza sativa* (Lekklar and Chaidee, 2011), *Triticum aestivum* (Tuna et al., 2008; Tahir et al., 2012), *Zea mays* (Moussa, 2006), *Brassica napus* (Hashemi et al., 2010) and *Lycopersicon esculentum* (Romero-Aranda et al., 2006). Hashemi et al. (2010) found that exogenous Si ameliorated the deleterious effects of salinity on the growth through lowering tissue Na^+ content, maintaining the membrane integrity and increased ROS scavenging capacity.

Selenium (Se) is considered to be an essential trace element for human, animals, and some species of microorganisms. Although, Se is not confirmed to be required by higher plants, several studies demonstrate that at low concentrations it plays an important role in antioxidative reactions and hormone balance in plant cells such as enhancing the activity of glutathione peroxidase (GPX) (Djanaguiraman et al., 2005; Cartes et al., 2010; Filek et al., 2008). Some studies show plants supplemented with Se have shown enhanced resistance to certain abiotic stresses including salinity (Djanaguiraman et al., 2005; Filek et al., 2008; Cartes et al., 2010; Chu et al., 2010; Djanaguiraman et al., 2010; Hasanuzzaman et al., 2011). For instance, Hawrylak-Nowak (2009) reported that low level of exogenous Se (5 and 10 μM) generally stimulates growth as well as photosynthetic pigments accumulation in NaCl-treated cucumber seedlings. Literatures have emerged that the protective role of Se ions in salt-stressed plants is not well-known and can be related to inhibited lipid peroxidation process, enhanced accumulation of free proline, and/or decrease in content of chloride ions in shoot issues (Hawrylak-Nowak, 2009; Hasanuzzaman and Fujita, 2011; Hasanuzzaman et al., 2011).

Dill (*Anethum graveolens* L.) is an annual aromatic and medicinal plant belonging to the Apiaceae (Umbilliferae) family. It contains a wide ranges of essential oils, Carvone, limonene, fatty oil, moisture (8.39%), proteins (15.68%), carbohydrates (36%), fiber (14.80%), ash (9.8%) and mineral elements such as calcium, potassium, magnesium, phosphorous, sodium, vitamin A and niacin (Kaur and Arora, 2010). The leaves of dill are used for prevention and treatment of diseases and disorders of the gastrointestinal tract, kidney and urinary tract, for spasms and sleep disorders. An aqueous dill extract, also is used for lowering blood pressure, dilates blood vessels, stimulates respiration and slows heart rate in animals (Khare, 2007).

Our previous research showed that dill is relatively sensitive to saline water at levels around the 10 ds/m; therefore, in the present research we investigated the ameliorative effect of silicon and/or selenium nutrition on growth and essential oils content of dill plants exposed to salinity.

2. Material and methods

The experiments were conducted during 2014 in a greenhouse at the University of Maragheh. Seeds of Dill (*A. graveolens*). The seeds were incubated in a moistened paper towel and germinated in the dark at 25 ± 5 °C for 48 h. Seedlings were initially hydro-cultured in the aerated water and were grown inside the growth chamber under light condition in ratio of 16:8 light and darkness, 25 °C, 65% relative humidity and light intensity of 6000 Lux. The experiment was carried out in a factorial completely randomized design. Factor one was salinity, which was applied to the root medium as NaCl (0 and 10 ds/m), and factor two was silicon nutrition, which was supplied as sodium silicate (0 and 1.5 mM), and selenium nutrition (0, 5 μM) which was applied as (Na_2SeO_4). Treatments were started 2 weeks after transplanting the seedlings to hydroponic culture. The pH of the nutrient solution was measured by a pH meter and adjusted to 5.5 through adding 1 N sulfuric acid (H_2SO_4). Plants were harvested 25 days after starting the treatments and used to assess growth parameters and for chemical analyses. Samples from the above ground organs and roots were weighed, oven-dried for 3 days at 70 °C, re-weighed and ground to determine the mineral contents. Fresh samples or deep-frozen samples were used for the biochemical assays.

2.1. Analysis of growth and essential oil content

The shoots and roots of seedlings from each jar were harvested separately and washed with distillated water, and then samples were weighted for their fresh weight determination. The samples were dried in an oven at 105 °C for 24 h and then the DW of both shoots and roots was measured for the different treatments. Aboveground organ samples were mixed with 300 ml of distilled water and the essential oil content was determined by hydro-distillation for 3 h, using a modified Clevenger apparatus.

2.2. Chlorophyll concentration

Chlorophyll a and b was determined according to Dere et al. (1998). One-hundred mg of fresh leaf material was taken from the aboveground organs and extracted with 99% methanol and read absorption recorded using spectrophotometer (Jenway Model 6305) at 653 and 666 nm wavelengths, for chlorophyll a and b, respectively. Chlorophyll concentrations were calculated by using the below equations (Dere et al., 1998):

Ch a = 15.65 A666 – 7.340 A653.
Ch b = 27.05 A653 – 11.21 A666.

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2.3. Proline content

Proline content of leaf tissues was estimated spectrophotometrically following the Ninhydrin method described by Bates et al. (1973) with minor modification. Fresh leaf samples (500 mg) were homogenized in 10 cm^3 of aqueous solution of 3% (w/v) sulphosalicylic acid. Thereafter, the solution was filtered and 2 cm^3 of the extract was reacted with 2 cm^3 of acidic ninhydrin and 2 cm^3 of glacial acetic acid for 1 h at 100 °C. Finally, the reaction was terminated in an ice bath. Thereafter, the reaction mixture was extracted with 4 cm^3 of toluene and mixed vigorously by vortexing for 20 s. After this, the chromophore containing toluene phase was sucked using a pipette and it was kept at room temperature to stabilize. Proline content was measured by a spectrophotometer at 520 nm using toluene as a blank and calculated as mg g^{-1} FW against standard proline.

2.4. Estimation of lipid peroxidation

Lipid peroxidation was measured in terms of malondialdehyde (MDA) content of shoots as described by Heath and Packer (1968) through a colorimetric method. Shoot samples were homogenized in 2 ml of 0.1% trichloroacetic acid (TCA) and centrifuged. Then, 0.5 ml of supernatant was mixed with 2 ml of 20% TCA containing 0.5% thiobarbituric acid. The mixture was incubated at 95 °C for 30 min. The samples were centrifuged at 10,000*g* for 10 min. The absorbance of the supernatant was read at 532 and 600 nm. The amount of MDA was calculated from the extinction coefficient of 155 mM^{-1} cm^{-1}.

2.5. Extraction and assay of antioxidative enzymes

The shoot tissues (0.5 g fresh weight) were homogenized in 2 mL of 100 mM potassium phosphate buffer, pH 7 containing 1 mM of EDTA and 1% (w/v) polyvinylpyrrolidone (PVP). The extract was then centrifuged at 4 °C for 15 min at 12.000*g* in a cooled centrifuge. This supernatant was used to measure the activities of superoxide dismutase (SOD), guaiacol peroxidase (POD), ascorbate peroxidase (APX) and catalase (CAT). Activity of SOD was assayed by using the photochemical nitro blue tetrazolium (NBT) method. The assay was performed in terms of SOD's ability to inhibit reduction of NBT to form formazan by superoxide radical as described by Beauchamp and Fridovich (1971). Activity of POD was determined at 25 °C with guaiacol (Bergmeyer, 1974). Activity of APX was measured by following the rate of hydrogen peroxide-dependent oxidation of ascorbic acid (Nakano and Asada, 1981). Finally, the activity of CAT was assayed following H_2O_2 decomposition.

2.6. Determination of inorganic ions

Potassium and sodium concentrations were determined in the roots and shoots after digesting 100 mg powder of the oven-dried tissues in a mixture of concentrated nitric acid and perchloric acid (3:1; v/v) at 175 °C. The potassium and sodium contents of the digested extracts were quantified using a flame photometer (model Jenway PFP7, UK).

2.7. Statistical analysis

Analysis of variance appropriate to the experimental design was conducted, using SPSS and MSTAT-C software. Means of each trait were compared according to Duncan multiple range test at $P \leqslant 0.05$. Excel software was used to draw figures.

3. Results

3.1. Growth and essential oil content

Fresh and dry weights of the plants were significantly decreased by salinity stress, and salinity appears to affect root more than shoots and causes lower root:shoot ratios (Table 1). Seedling dry weight decreased 70% as a result of salinity (Table 1). Inhibition in plant growth improved by addition of Si or Se to the medium; however, it was still lower than the control plants. Silicon or selenium nutrition, recovered salt-stressed plants growth by 2.7 and 1.9 folds, respectively. Under non-saline conditions, both trace elements had negative effect on dry matter accumulation. Essential oil percentage was slightly, but not significantly improved under salinity compared with control. Among the treatments, salt-treated plants fed with Se had high essential oil content (57%); however, differences were not statistically significant (Table 1).

3.2. Potassium and sodium uptake

Shoot and root Na content increased significantly under salinity (Table 2). For instance, shoot and root Na content at control were 10.7 mg g^{-1} dw and 5.2 mg g^{-1} dw and at saline condition were 22.1 mg g^{-1} dw and 39.9 mg g^{-1} dw, respectively. Si or Se application in saline media significantly reduced Na uptake and translocation by roots; however, Si was more effective than Se (Table 2). According to Table 2, under salinity, shoot and root K content showed the opposite trend of Na content and were decreased by 2.7 and 3.2 folds, respectively. Addition of Si or Se significantly mitigated the toxic effect of Na^+ and improved K^+ uptake, so, the concentration of K^+ increased under salinity in both shoots and roots by trace element nutrition. Salt stress caused a significant reduction in shoot and root K^+/Na^+ ratios. Shoot and root K^+/Na^+ ratios were partially increased by application of Si and Se in higher levels of salinity, and this ratio was markedly higher in the control condition where the Si and Se application reduced this ratio in the non-saline medium (Table 2). Under non-saline conditions, incorporation of Si or Se in nutrient media decreased K^+/Na^+ ratios; however, this was significant only by Se application.

3.3. Biochemical factors

Chlorophyll contents have been suggested as one of the parameters of salt tolerance in crop plants (Srivastava et al., 1988). The chlorophyll a and b content of salt-treated plants was 30% and 17% lower, respectively, when compared with the control. Under salinity, Si or Se nutrition could recover the leaf chlorophyll content of the plants so that the contents of chlorophyll a and chlorophyll b in the Si-fed plants were 28% and 14% more, respectively, compared with plants grown

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Table 1 Effect of salinity (control versus 10 ds/m NaCl) on fresh and dry weight and essential oil content of Dill plants fed with or without silicon and selenium.

Treatment	Fresh weight (g)			Dry weight (g)			Root:shoot ratio	Essential oil (%)
	Shoot	Root	Seedling	Shoot	Root	Seedling		
Control	62.9a	16.8a	79.7a	5.5a	2.11a	7.76a	0.37a	0.46
Si	48.7b	13.6ab	62.4a	4.9b	1.8b	6.7b	0.36a	0.49
NaCl	22.5d	5.40d	28.04d	2.0d	0.29d	2.3e	0.14c	0.54
Si + NaCl	48.6b	10.7bc	59.4b	4.6b	1.75b	6.3b	0.38a	0.51
Se	43.1b	9.40c	52.5b	4.4b	1.12c	5.5c	0.25b	0.48
Se + NaCl	30.2d	9.10c	39.4c	3.2c	1.17d	4.4d	0.36a	0.57

Different letters in each column indicate significant difference at $P \leqslant 0.05$.

Table 2 Na^+ and K^+ concentrations in the shoots and roots of control and salt-stressed (10 ds/m NaCl) dill plants fed with or without silicon and selenium.

Treatment	Na^+ (mg g^{-1} dw)		K^+ (mg g^{-1} dw)		K^+/Na^+ ratios	
	Shoot	Root	Shoot	Root	Shoot	Root
Control	10.7c	5.2c	5.5a	28.1a	3.5a	5.4a
Si	12.6c	7.3c	4.9b	24.6a	2.9ab	3.5b
NaCl	39.9a	22.1a	2.0d	8.6c	0.14c	0.4c
Si + NaCl	25.9b	12.0b	4.6b	18.3b	0.8c	1.5c
Se	13.7c	5.9c	4.4b	29.7a	2.1b	5.2a
Se + NaCl	26.5b	19.6a	3.2c	15.4b	0.5c	0.7c

Different letters in each column indicate significant difference at $P \leqslant 0.05$.

without Si and for Se nutrition, these values were 15% and 11%, respectively (Table 3).

The data for malondialdehyde (MDA) concentration are presented in Table 3. Lipid peroxidation increased markedly under salinity. In the 10 ds/m NaCl treatment, it increased approximately 3 folds compared with the control plants. However, inclusion of Si or Se significantly reduced MDA concentration of salt-stressed plants compared to the salt treatments alone (Table 3).

In the saline condition, proline content was 2 folds than control. Addition of Se in saline media increased leaf proline content (approximately 10%), but Si decreased its value (11%), however both of them had not significant difference with alone NaCl treatment (Table 3). The soluble sugar content in leaves partially increased in plants grown under salinity. Supplementation of salt-treated plants with Si slightly increased soluble sugar content, whereas Se supplementation decreased this value compared with control (18.1 mg g^{-1} dw) (Table 3).

Data for CAT activity of different treatments are illustrated in Fig. 1a. CAT activity of salt-stressed plants significantly increased compared to the control. The addition of Si or Se alone and in saline condition increased CAT activity, however it was noticeable in salinity. In the salt treatment, Ascorbate peroxidase activity increased significantly. Trace element nutrition could not cause any significant changes in APX activity, when added to non-saline and saline medium (Fig. 1b). Salinity significantly increased SOD activity, and it was approximately 2 fold greater when compared with the control. In saline condition, SOD activity of plant fed with Si or Se nutrition was enhanced higher than pure NaCl (Fig. 1c). Salinity significantly decreased ($p \leqslant 0.05$) peroxidase activity. The application of Si or Se did not influence all analyzed antioxidant enzymes activity under well-watered conditions. Under saline conditions, Si and Se application caused a significant increase in the activity of all analyzed antioxidant enzymes with the exception of APX. In addition, under non-saline conditions, application of mentioned trace elements slightly influenced enzymes activity (Fig. 1a–d).

4. Discussion

Salinity significantly suppressed shoot and root growth of plants, however root tissues received more stress than shoots (Table 1). It might be due to the direct contact of root tips with stress. Plant growth requires both proliferation and elongation of cells; so, growth reduction due to salinity stress may be

Table 3 Chlorophyll a, b, MDA, proline and soluble sugar concentrations in the shoots of control and salt-stressed (10 ds/m NaCl) dill plants fed with or without silicon and selenium.

Treatment	Chlorophyll (mg g^{-1} FW)		MDA (nmol g^{-1} FW)	Proline (mg g^{-1} FW)	Soluble sugar (mg g^{-1} dw)
	a	b			
Control	2.12ab	0.91a	18.8e	10.7c	70.1ab
Si	2.25a	0.88a	25d	12.3c	65.3b
NaCl	1.51e	0.76b	65a	24.1ab	81.2a
Si + NaCl	1.94c	0.87a	38.6b	21.9b	86.7a
Se	2.02bc	0.86ab	24d	12.5c	72.0ab
Se + NaCl	1.74d	0.85ab	33.3c	26.6a	63.1b

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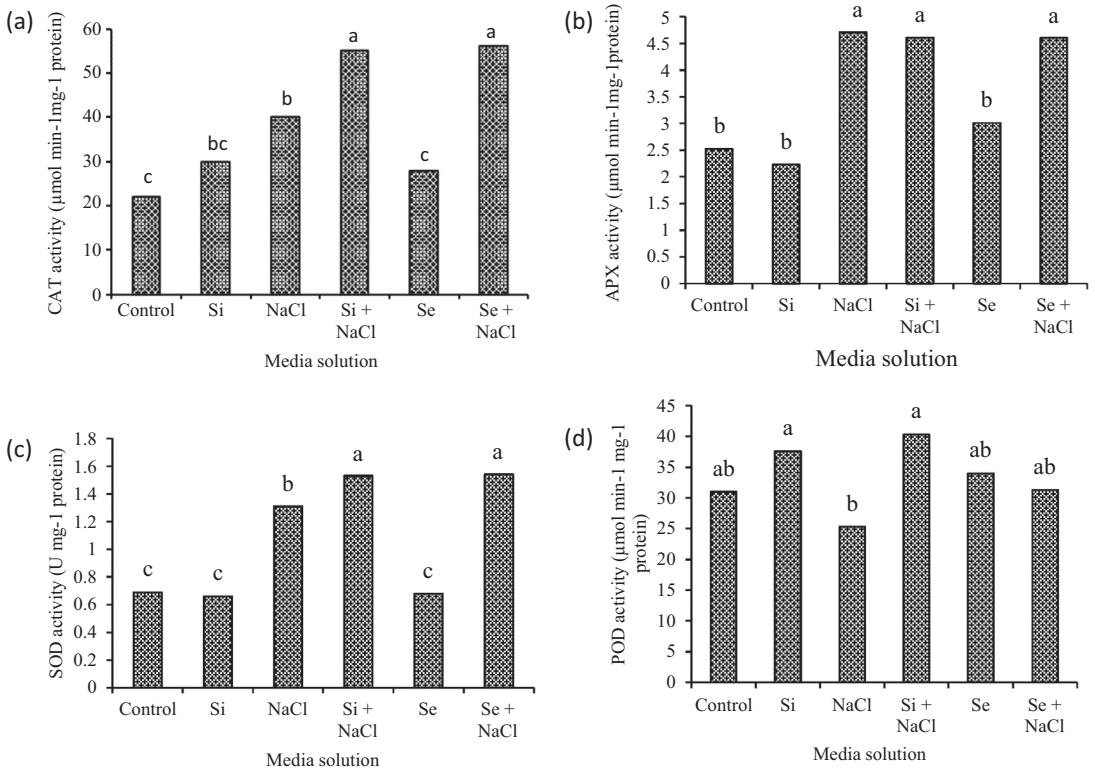

Figure 1 Effect of silicon or selenium on the activities of CAT (a), APX (b), SOD (c) and POD (d) of dill aboveground organs under salinity.

attributed to osmotic stress, ion imbalance and ion toxicity (Marschner, 1995; Tahir et al., 2006; Yazici et al., 2007), that resulted in loosing the turgor and DNA synthesis for cell growth. Hasanuzzaman et al. (2013) reported that the first phase of growth reduction is a quicker process which is due to osmotic effect, which is followed with much slower process induced by salt accumulation in leaves, leading to salt toxicity in the plants. Similar results were also reported by Kafi and Rahimi (2011) on purslane, Ashraf et al. (2010) on Sugarcane, Tahir et al. (2010) on wheat and Dolatabadian et al. (2011) on *G. max*.

Our results showed that addition of Si or Se to salt stressed plant greatly improved plant growth; however, between the two trace elements, Si was superior treatment from this view point. There are ample evidences that Si and Se play a favorable role in plant growth under biotic and abiotic stresses. For instance, Tahir et al. (2010) found that Silicon application significantly increased salt-treated plant biomass. Supplementation of salt-treated plants with Si ameliorated K^+/Na^+ ratio (kafi and rahimi, 2011; Tahir et al., 2010) and improved ROS scavenging capacity (Hashemi et al., 2010; Hasanuzzaman et al., 2013). Se treatments at 5 and 10 mM significantly improved the growth rate of cucumber plant when subjected to salt stress (Hawrylak-Nowak, 2009). One of the major effects of Se on abiotic stress tolerance is associated with its antioxidative capacity (Djanaguiraman et al., 2005; Hasanuzzaman et al., 2011; Hasanuzzaman and Fujita, 2011). Djanaguiraman et al. (2005) reported that Se enhanced the salt tolerance of *G. max* seedlings by protecting the cell membrane against lipid peroxidation.

For illustrating the mode of action of Si and Se in alleviating adverse effect of salinity on plant growth, in the present experiment, we investigate the key traits that were mainly affected by salinity.

Crop growth could be related to rate of photosynthesis which is directly proportional to chlorophyll contents in leaves. According to results, salinity reduced Chl a and Chl b contents; however, nutrition of these plants with Si or Se alleviates the adverse effect of salt stress on chlorophyll pigments (Table 3). The decrease in leaf chlorophyll content under salinity may be due to an increase of chlorophyll degradation or to a decrease of chlorophyll biosynthesis (Santos, 2004) as a result of oxidative stress (Bhattacharjee, 2005; Blokhina et al., 2003). The decrease in Chl content under salt stress is a commonly reported phenomenon and it was used as a sensitive indicator of the cellular metabolic state (Chutipaijit et al., 2011). Amirjani (2011) found that Chl a and b contents of leaves were reduced by salinity stress. Silicon or selenium nutrition can recover the chlorophyll content of dill plants under salinity, which suggests that they play a role in the suppression of oxidative stress. Added Si has also been shown to improve the chlorophyll content of canola, purslane and barley under salt stress (Hashemi et al., 2010; Kafi and Rahimi, 2010; Liang et al., 1996). Hawrylak-Nowak (2009) showed that Se treatments at 5 and 10 mM significantly increased the photosynthetic pigments in *Cucumis sativus* leaves when subjected to salt stress. As there was a positive relationship between chlorophyll contents and grain yield, so increase in chlorophyll contents led to increased photosynthesis and consequently grain yield.

Potassium is an important nutrient required for normal water uptake and transpiration flow (Marschner, 1995), cell expansion and osmoregulation, stomatal opening and carbon

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dioxide (CO_2) supply for photosynthesis (Munns and Tester, 2008). A suitable K^+/Na^+ ratio in plant tissues is important for the adjustment of cell osmoregulation, stomatal function, activation of many enzymes, protein synthesis, and photosynthesis (Hasanuzzaman et al., 2013). Sodium and potassium concentrations are good indicators of salinity tolerance (Saqib et al., 2004). In the present experiment, salinity stress significantly decreased K^+ concentration in shoots and roots of dill, whereas Na^+ content increased in mentioned organs (Table 2). Saqib et al. (2004) reported that in saline condition, high concentration of Na^+ in root environment can depresses K^+ uptake at root level due to the antagonism of Na^+ and K^+ at uptake sites in the roots. Added Si or Se significantly reduced Na^+ concentration in shoots as well as roots of dill plants, however reduction by Si was greater than Se (Table 2). This effect may result from formation of some complex between Si and Na^+ at root level resulted in hampering its upward movement through a reduction in apoplastic transport across the root and its translocation to the shoots (Gong et al., 2006). In addition, presence of these elements in saline medium alleviates the adverse effect of Na^+ on K^+ uptake (Table 2). Liang et al. (2003) also reported a significant increase in K^+ uptake and decrease in Na^+ uptake under salt stress when Si was included because of increased activity of plasma membrane H-ATPase. Saqib et al. (2008) in their study on wheat suggested that increased resistance to salinity by Si was due to reduced Na uptake and shoot/root Na partitioning. Silicon may also improve plant Na detoxification by increasing cell-wall Na binding (Kafi and Rahimi, 2011). Kong et al. (2005) revealed that application of Se to salt-stressed sorrel plants induced the accumulation of K^+ in leaves and a reduction in roots. However, a recent study by Hawrylak-Nowak (2009) showed that Se supplementation did not alleviate this adverse effect. Thus, it seems that growth-promoting effect of Se under salinity conditions can be related to improvement of K^+/Na^+ ratio. Amelioration of K^+/Na^+ ratio in salt-stressed plant by Se and Si was also previously reported by Ashraf et al. (2010), Hashemi et al. (2010), and Tuna et al. (2008).

One of the biochemical strategies to improve salt tolerance in plants is synthesis of compatible solutes. Proline and sucrose are the most commonly solutes that mainly accumulate at saline condition (Munns and Tester, 2008). In our experiment, under salinity stress both proline and soluble sugars concentration increased; however, for soluble sugars difference was not significant (Table 3). Incorporation of salt-stressed plant with Si increased both of the proline and soluble sugars concentration, whereas, Se application improved proline content only. However, proline concentration was affected greater by Se than Si. The results of this study are in line with previous findings which showed that added Si increased proline and soluble sugars concentration under salt stress (Liang et al., 2003). Hawrylak-Nowak (2009) reported that Se treatment at concentration of 5 and 10 μM increased proline content by 23% and 39%, respectively, when compared to NaCl-stressed plants grown without Se, whereas in the presence of 20 μM Se proline level was unchanged.

Salt stress can stimulate the production reactive oxygen species (ROS) such as superoxide, hydrogen peroxide, hydroxyl radical and singlet oxygen (Lee et al., 2001). One effect of free oxygen radicals accumulation in plant cells under stress is lipid peroxidation via oxidation of unsaturated fatty acids leading to membrane deterioration (Marschner, 1995). MDA is one of the final products of the peroxidation of unsaturated fatty acids in phospholipids and is responsible for cell membrane damage (Sharma et al., 2011). The MDA levels of salt-stressed plants were consistently higher, compared to the control; however, incorporation of Si or Se into salt-treatment decreased MDA content compared with the treatment with salt alone (Table 3). SOD, CAT, APX and POD are the major antioxidant enzymes associated with scavenging the reactive oxygen species (ROS) (Marschner, 1995). According to results, shoot CAT, APX and SOD activities were enhanced by adding the NaCl to nutrient medium, and POD activity decreased in this situation (Fig. 1a–d). This may be a general adaptive defense response of plants to salinity at early stages. Although antioxidant enzymes were stimulated in plants exposed to salt, MDA content was high. So, it seems that ROS production was higher than its scavenging by antioxidants. Exogenous Si and Se significantly increased the activities of SOD and CAT in salt-stressed plant compared with salinity treatment (Fig. 1a–d). The induction of these enzymes coincided with a decrease in concentration of MDA as well, suggesting that oxidative damage induced by salt be alleviated by the addition of Si or Se. The results of this study are in line with previous findings which showed that added Si decreased the permeability of the plasma membrane of leaf cells, enhanced leaf SOD activity and decreased MDA concentration under salt stress (Liang et al., 1996). It was reported that Si enhanced the stability of lipids in cell membranes of rice plants exposed to drought and heat stresses, suggesting that Si prevented the structural and functional deterioration of cell membranes when rice plants were exposed to environmental stress (Agarie et al., 1998). The evidence therefore suggests that Si decreases the permeability of plasma membranes and membrane lipid peroxidation and maintains the membrane integrity and functions of salt stressed barley, thus mitigating against salt toxicity and improving the growth of plants. The efficiency of antioxidant enzymes in the preservation of membranes against ROS injury was visibly reflected in the stable amount of MDA in salt-stressed plants and is likely another reason for the protective effect of Si and Se on the photochemistry of leaves observed in this study. The activation of antioxidant enzymes including SOD, CAT, APX and POD by Si or Se supplementation has been reported in some plant species (Gong et al., 2008; Habibi and Hajiboland, 2013).

5. Conclusion

In summary, our results revealed that improvement in growth of salt stressed plants under the influence of Si and Se may be due to the improved ion balance, antioxidant enzymes activities and osmotic adjustment. These trace elements had negative effect on growth under non-saline conditions. Therefore, application of these trace elements (especially Silicon) under saline condition could be a better strategy for maintaining the crop productivity in these regions.

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