

Effects of Silicon Application at Nano and Micro Scales on the Growth and Nutrient Uptake of Potato Minitubers (Solanum tuberosum var. Agria) in Greenhouse Conditions

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Abstract Silicon has shown to have significant improving effects on nutrient uptake in plants. In this research, the effects of four different silicon compounds (nanosilica, sodium silicate, nanoclay, and Bentonite) in two concentrations (1000 and 2000 ppm) on the growth characteristics and nutrient uptake of potato (Solanum tuberosum var. Agria) plants have been investigated. Silicon treatments, except sodium silicate, improved leaf properties (up to 18% in leaf dry weight in Bentonite (1000 ppm)) and increased stem diameter (up to 17% in nanoclay and Bentonite (1000 ppm)). All root characteristics were enhanced when silicon was applied (up to 54% in root area per plant in sodium silicate (1000 ppm)). Although minituber production was not affected by silicon treatments, minituber quality characteristics were improved by silicon application in comparison with the control plants. Si, Mo, K, and P contents increased, while Al and Mn contents decreased in both tuber and plant in Si application treatments. Whereas Mg, Zn, and Fe contents were lower in Si-treated plants, Si content favorably increased in tubers. Si content in plants showed an increasing pattern of nanosilica < Bentonite < nanoclay < sodium silicate with regard to the Silicon source.

Keywords Bentonite . ICP-OES . Nanosilica . Nanoclay . **Nutrients**

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1 Introduction

Silicon is the second abundant element in the soil [[1](#page-8-0), [2\]](#page-8-0). It may comprise up to 70% of the soil mass in the form of silicate minerals and water-soluble orthosilicic acid $[Si(OH)₄]$ [[3\]](#page-8-0). In a recent definition of essential elements, silicon is listed as an essential element, since plants with silicon deficit show abnormalities in growth, development, and reproduction [[3\]](#page-8-0). Many experiments have shown that silicon can reduce the effect of both biotic and abiotic stresses in plants [[3](#page-8-0)–[5\]](#page-9-0). It has also been indicated that silicon has a beneficial role in plant nutrition by enhancing the absorption of nitrogen, phosphor, potassium, and zinc [\[5,](#page-9-0) [6\]](#page-9-0). Savvas and Ntatsi (2015) [\[1\]](#page-8-0) reported that the key mechanisms involved in Si-mediated alleviation of abiotic stresses in higher plants are as follows:

- & Silica deposition inside the plant tissues which provides mechanical strength and erectness to leaves and modulates nutrient and water mobility inside the plants
- Stimulation of antioxidant systems in plants
- Complexion or co-precipitation of toxic metals with Si both in plant tissues and in the soil
- Modulation of gene expression and signaling through phytohormones

The beneficial effects of silicon application on plant growth and physiology have tempted farmers and researchers to use it as a fertilizer [\[5](#page-9-0)]. Silicon fertilizers are applied as slag, compost, rice straw, calcium, and sodium silicates [[2\]](#page-8-0), in both foliar and soil applications [[1\]](#page-8-0). Si application may be beneficial in hydroponic production due to the absence of soil in the root environment [[1,](#page-8-0) [5](#page-9-0)]. These beneficial effects of Si supplementation on greenhouse and soil productivity depend on the form and rate of the applied Si [\[7](#page-9-0), [8](#page-9-0)].

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Compared to other crops, potato has a more shallow and less dense root distribution in the field [\[9](#page-9-0)]. Potato root length density is generally about one third of that produced by cereal crops, and is generally higher in the top soil [\[10](#page-9-0)], which makes it sensitive to drought stress [\[11\]](#page-9-0) and reduces element uptake. Therefore, expanded root and its distribution is a key trait to drought stress in potato. Due to the large need for virus-free potato seeds, mass production of potato minitubers in green house is a normal procedure [[5,](#page-9-0) [12](#page-9-0)–[16](#page-9-0)].

The main source of Si in the soil is silicate minerals [[17\]](#page-9-0), which are mostly non-absorbable for plants [[1](#page-8-0)]. In order to test the effect of nanosizing on Si release in a soluble media, nanoclay and nanosilica were used in this research. The bulk of research so far has focused on K_2SiO_3 (potassium silicate); therefore, it was not clear whether the beneficial effect was due to the silicon or potassium application [\[5](#page-9-0)]. In the current research project, sodium silicate was applied to avoid the interaction of potassium with Si in potato plants. The aim of this research was to check the effect of Si on the morphology of potato minitubers, as well as the mineral content in both plant and minitubers; it was also evaluated whether which Si could be considered as a source of silicon to be used in greenhouse production?

2 Materials and Methods

This experiment was conducted at the Research Greenhouse and Advanced Physiology Lab in the Agronomy Department, Ferdowsi University of Mashhad, Iran, in 2014.

2.1 Materials

2.1.1 Nanoclay

Nanoclay (hydrophilic Bentonite) was obtained from Sigma-Aldrich Company with product number of 682659. The general formula is $H_2A_2O_6Si$ and its molecular weight is 180.1 gmol⁻¹. The interlayer space in the nanoclay sample was 1.8 to 2 nm. Nanoclay was used at a concentration of 1000 ppm (1 gL^{-1}) and 2000 ppm (2 gL^{-1}) in distilled water. XRF analysis of element content was conducted by Philips Analytical X-Ray B.V. and shown in Table [1](#page-2-0).

2.1.2 Bentonite

The Bentonite was obtained from Chah-Amir mine (code: 29100167), in South Khorasan province, Iran. It was grounded and sifted with 70 μm Mesh. XRF analysis of element content was arranged using Philips Analytical X-Ray B.V. The SEM picture of Bentonite is presented in Fig. [1.](#page-2-0)

2.1.3 Nanosilica

Nanosilica was obtained from Nanosuv co. with the production code of SAV20201. This powder is water soluble and amorphous with 98% purity and its size is 20–30 nm in water (Fig. [2](#page-2-0)). Nanosilica was used at a concentration of 1000 and 2000 ppm in distilled water.

2.1.4 Sodium Silicate

Sodium silicate (Na₂O₃Si) with 96% purity was used at a concentration of 1000 and 2000 ppm in distilled water.

2.1.5 Minitubers

Potato minitubers (var. Agria) were all from the same harvest of same tissue cultured plants, with relatively the similar size. Minitubers were placed in a cold storage unit for 3 months in order to break probable dormancy.

2.1.6 Sowing Media and Growth Conditions

Washed sand with average size of 0.1 mm was used as sowing media to avoid the possible damage to roots at the time of washing media from the root surface. Sands were placed in plastic bags in pots made of polyvinyl chloride (PVC) tubes (100 cm height and 10 cm diameter). These pots were chosen in order to direct roots to grow vertically to facilitate further root measurements (Fig. [3](#page-3-0)). One minituber was planted in each bag, in three replicate (27 plant), and after emergence, it was nurtured with Hoagland solution on a weekly basis. Day and night temperatures were respectively 24 ± 2 and 18 ± 2 , and relative humidity was 40%.

2.2 Plant Sampling and Analysis

2.2.1 Plant Sampling

Ninety days after emergence, plants were harvested and the plastic bags were brought out of the pots. Leaf area, leaf dry weight, stem dry weight, stem height, average stem diameter (average of three measurements in each stem), number of minitubers, average diameter of minitubers, average minituber length, average minituber dry weight, and volume of all minitubers of a plant were measured.

2.2.2 Root Preparation and Analysis

Sands on the roots and minitubers were washed off gently and the roots were placed in distilled water in a refrigerator for further analysis. The roots were prepared for scanning based on the scanner manual and protocols [\[18\]](#page-9-0). They were scanned with root scanner (Delta-D scan, Somatco), and their

SiO ₂ %	$Al_2O_3\%$	Na ₂ O%	MgO%	$K_2O\%$	TiO ₂ %	$MnO\%$	$CaO\%$	$P_2O_5\%$	Fe ₂ O ₃ %	$SO_3\%$	$LOI\%$ ^a
53.46	18.16	0.95	2.18	l.32	0.69	0.11	1.85	0.15	6.16	0.58	14.15
43.62	10.15	1.76		0.43	0.45	0.11	11.27	0.09	3.04	0.43	25.10
Ba (ppm)			Cr (ppm)			Ni (ppm)			Cl (ppm)		
1270	Q		92	72		50			22	64	
187			40	N		95	10		4418	70	
			Co (ppm)			Cu (ppm)			Mo (ppm)		Zn (ppm)

Table 1 XRF analysis of element content of nanoclay and Bentonite

^a Loss on ignition

characteristics were measured by root analysis software (Delta-D scan software).

2.2.3 Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES)

In order to completely digest the organic matter of dried shoot and minitubers, a digestion method with an acid mixture (including HNO3, HClO4, and HF) was used. The digestion was carried out in a Teflon vessel on 1.0 g of sample by treatment with 5 ml of HNO3 and the solution was evaporated to dryness. Then, the solid samples were treated by strong oxidation with fuming $HCIO₄$. Subsequently, the silica salts were digested with HF, until white fumes were observed. The residue was diluted to 25 ml with ultrapure water in a plastic volumetric flask and filtered [\[19](#page-9-0)]. Nine samples of whole plant (leaf, root, shoot) and 9 samples of minituber were tested for 8 element content including Si, K, Zn, P, Al, Fe, Mn, and Mg with ICP-OES (Spectro Arcos). Wave lengths used for element determination are represented in Table [2.](#page-3-0)

2.3 Treatments

Wilson [\[20\]](#page-9-0) reported that ultrasonification contributes to achieve more homogenous clay suspensions. Therefore, nanomaterial suspensions were stirred by an ultrasonification probe (sonicator xl2020), at a frequency of 20 kHz for 5 min. Fifty milliliters of each suspension was applied to treatments every 30 days; the first application was 10 days after plant emergence (3 applications in total).

2.4 Statistical Analysis

Statistical analysis was conducted using SPSS software program, version 18 (2011), SAS software, version 9.1.3 (2005) and Minitab software, version 16.2.2 (2010). Oneway analysis of variance (ANOVA) was performed to discern significant difference at the 95% level of confidence among different treatments and the statistically different groups were determined by Duncan multiple range test. Cluster analysis was performed to find possible similarities and dissimilarities among the treatments based on more than one property. Cluster analysis has the potential to evaluate the groupings on the basis of more than two properties in a single run. The scaled indicator in each cluster analysis shows differences among the treatments; lower scale numbers show more similarities while higher ones indicate dissimilarities [[21](#page-9-0)].

Fig. 1 SEM picture of Bentonite Fig. 2 SEM picture of nanosilica

Fig. 3 PVC pots used for minituber growing

3 Results and Discussion

3.1 Leaf Growth

All treatments, except sodium silicate, improved both leaf dry matter and leaf area compared to the control group (Table [3\)](#page-4-0). This finding is in line with the findings reported by Pilon [[5\]](#page-9-0). The leaf samples were collected in the time of minituber harvest, and except sodium silicate and control, leaf senesces was slowed in other treatments (data not shown). The results obtained by Shaterian et al. [\[22](#page-9-0)] also indicated that potato exposed to $Na⁺$ stress accumulated $Na⁺$ mostly in the lower leaf, causing their early damage and deceasing.

Cluster analysis based on leaf area and dry matter demonstrated that control and sodium silicate (1000 ppm) were clustered significantly different (Fig. [5a](#page-6-0)), which implies that sodium silicate (1000 ppm) did not significantly affect the overall leaf properties and therefore, it was clustered close to the control specimens. Both treatments containing Bentonite (1000 and 2000 ppm) clustered differently from the other treatments. It can therefore be concluded that all the other treatments had significantly improved leaf properties so that they were clustered differently from the control group. Treatments with Bentonite (1000 and 2000 ppm) had the highest impact on leaf area and dry matter accumulation.

3.2 Stem Performance

Stem height in all silicon treatments increased up to 10 cm (Table [3](#page-4-0)). Average stem diameter did not show any particular pattern in the treatments and stem dry weight was also not significantly different among the treatments (Table [3](#page-4-0)). Even though the stem height varies significantly from the control plants and stem diameter showed no increase in the same pattern, but there was no lodging in taller plants (data not shown). Mechanical strength [\[23\]](#page-9-0) and lodging reduction in potato [[24](#page-9-0)] and other plants, especially rice, has been reported in silicon application [\[4](#page-8-0), [5](#page-9-0), [25\]](#page-9-0).

3.3 Root Characteristics

The black and white pictures of the root of a randomly chosen plant from each treatment are shown in Fig. [4.](#page-5-0) On average, control plants produced lower root diameter and accumulative root length and subsequently less root area and root volume (Table [4](#page-5-0)). This small root net is not problematic in wellwatered systems. However, in any sudden drought stress, plants with fewer roots net will be much more sensitive. In nanoclay treatments (especially 1000 ppm), root growth enhanced significantly (Table [4\)](#page-5-0).

Relatively low root diameter, high accumulative root length and high root volume leads to higher root surface area and increases root efficiency in both nutrient and water uptake. Sodium silicate and Bentonite significantly increased the average root diameter (Table [4\)](#page-5-0). Although average root volume was not significantly different in nanosilica treatments, both root surface area and average accumulative length of plants roots were higher in 1000 ppm treatment compared to 2000 ppm treatment (Table [4\)](#page-5-0). Root hairs are largely responsible for nutrient uptake in plants [[26](#page-9-0)] but in this research the treatments with higher average root diameter demonstrated more Si content in plants shoot (Table [4](#page-5-0) and Table [5\)](#page-6-0). The analyses on rice also yielded the same results [\[17,](#page-9-0) [27,](#page-9-0) [28\]](#page-9-0).

Recently, the gene $(LsiI)$ that is responsible for active Si uptake in rice has been identified [[28](#page-9-0)], which is mainly expressed in the roots supplying Si, main roots and lateral roots but not in root hairs. This is consistent with the results of other physiological studies which indicated that root hairs do not play a significant role in Si uptake, while lateral roots contribute significantly to Si uptake [[25,](#page-9-0) [27](#page-9-0)]. Transporter StLsi1 was also isolated from the potato genome and it was mainly expressed in potato roots and leaves [\[29\]](#page-9-0).

Table 2 Wave lengths (nm) employed for element determination

*Numbers with same letter are not significantly different based on Duncan multiple range test

Cluster analysis based on stem properties indicated the same insignificant effect of sodium silicate (1000 ppm). Therefore, the control and sodium silicate (1000 ppm) were clustered rather close to each other (Fig. [5](#page-6-0)b). Both treatments containing Bentonite (1000 and 2000 ppm) were also clustered closely and significantly different from the rest, showing the same effects of the treating materials on stem properties as on the leaf properties.

3.4 Minitubers

Average minitubers per plant were very few in all treatments, perhaps caused by the sowing media and the shape of pots. Although the plants were not in drought or nutrient stress conditions, soils with low density enhance vegetative growth and limit storage root development [[30](#page-9-0)]. Despite the low number of minitubers, all forms of silicon application increased minituber properties compared to control plants (Table 3). Crusciol [[24](#page-9-0)] maintains that Si application increases the number of tubers and dry weight as a consequence of greater production of photo-assimilates, or due to changes in photo-assimilates partitioning. Nevertheless, there are other reports showing no changes in potato organs [[29\]](#page-9-0) and minituber dry weight [\[5\]](#page-9-0) after Si fertilization. Except nanoclay (2000 pm) treatment, minitubers produced in all other treatments were significantly larger with higher dry weight (Table 3). Bentonite (1000 ppm) treatment produced the highest number of minitubers (Table 3). Nanosilica (1000 ppm) treatment has the largest average minituber size (Table 3), and larger minitubers are likely to sprout and emerge faster. They also have the potential to be sowed deeper for more protecting proposes [\[31\]](#page-9-0). The leaf properties of sodium silicate treatments were similar to control (Table 3), but the production

of minitubers in sodium silicate treatments was better than control. This may be due to the increase in photosynthesis rate in the plants treated with silicon [\[5](#page-9-0)].

However, cluster analysis based on the minituber properties demonstrated rather different results; the control treatment was clustered closely with nanoclay (2000 ppm) treatment; furthermore, Bentonite treatments were clustered not as close as in the previous cluster analysis (Fig. [5](#page-6-0)c). This clearly illustrated that the effects of the materials used in the present study on the morphology and tuber formation of potato were significantly different.

3.5 Mineral Content

3.5.1 Silicon Content

Silicon (Si) concentration in both shoots and tubers increased compared to control in all Si treatments (Table [5](#page-6-0) and Table [6](#page-7-0)), which is consistent with the findings of several other experimental studies on potato [\[5](#page-9-0), [24\]](#page-9-0), and other plants [\[4,](#page-8-0) [6](#page-9-0)]. Silicon accumulation in tuber peels can increase the tuber quality due to delay in tuber skin senescence and increase tuber storage time [[29](#page-9-0)]. It has been suggested that both transporter mediated transport and passive diffusion of Si are involved in the radial transport of Si. Carrier-mediated transport is an energy-dependent process [[25\]](#page-9-0), since metabolic inhibitors and low temperature inhibit Si transport [\[32\]](#page-9-0). It seems that xylem loading is the most important determinant of a high accumulation of Si in the plant [[33\]](#page-9-0). Lower accumulation of Si in nonaccumulator plants may be due to lower density of the transporter from the external solution to the cortical cells, a defective transporter or a lack of one from cortical cells to the xylem (SIT1 and SIT2 transporters) [\[33](#page-9-0), [34](#page-9-0)].

Fig. 4 Root scan of potato plants under different silicon applications (1—control, 2—nanoclay (1000 ppm), 3—nanoclay (2000 ppm), 4— Bentonite (1000 ppm), 5—Bentonite (2000 ppm), 6—nanosilica

3.5.2 Magnesium

Magnesium (Mg) content in potato plant decreased in all Si treatments compared to control (Table [5](#page-6-0)). Since previous studies have reported that in the presence of Si, there is lower Mg content in the aerial parts of plants like leaves [[7\]](#page-9-0), decreasing Mg content in the whole plant may result from its decrease in the shoot and not the roots. In this study, additional Si resulted in an increase in Mg content of tubers in comparison with

(1000 ppm), 7—nanosilica (2000 ppm), 8—sodium silicate (1000 ppm), 9—sodium silicate (2000 ppm))

control plants (Table [6\)](#page-7-0). This is mainly because as a phloemmobile element, magnesium is readily translocate to fruits, seeds, and tubers [\[35\]](#page-9-0). Magnesium is often stored in root cells and released to the xylem when shoots become Mg deficient [\[36](#page-9-0)]. The plants used in this experiment were nurtured with Hoagland nutrient solution which did not result in any Mg deficit. Since cytosolic Mg^{2+} approximates 0.4 mM, it was possible for Mg^{2+} to enter root cells through Mg^{2+} permeable cation channels [[36](#page-9-0), [37](#page-9-0)]. It seems that xylem loading is the

	Average root diameter (mm)	Accumulative root length per plant (km)	Root area per plant (m^2)	Root volume per plant (cm ³)
Control	0.108d	2.43a	3.13 _b	4.33 _b
Nanoclay (1000 ppm)	0.116d	2.79a	3.22 _b	6.33a
Nanoclay (2000 ppm)	0.134cd	2.53a	3.74ab	5.67ab
Bentonite (1000 ppm)	0.166ab	2.49a	3.90ab	5.83ab
Bentonite (2000 ppm)	0.167ab	2.62a	4.20ab	5.44ab
Nanosilica (1000 ppm)	0.137 bcd	2.86a	3.91ab	5.33ab
Nanosilica (2000 ppm)	0.124d	2.46a	3.49 _b	5.33ab
Sodium silicate (1000 ppm)	0.184a	2.76a	4.84a	5.17ab
Sodium silicate (2000 ppm)	0.165abc	2.65a	4.24ab	5.17ab

Table 4 Mean comparison of potato root characteristics of four different silicon compounds (nanosilica, sodium silicate, nanoclay, and Bentonite) in two concentrations (1000 and 2000 ppm) with control

*Numbers with same letter are not significantly different based on Duncan multiple range test

Table 5 Element content of potato plant in control and treatments with 1000 and 2000 ppm of nano and micro clay, nanosilica and sodium silicate $(\mu gg^{-1}$ dry weight)

	Si	K	Zn	P	Al	Fe	Mn	Mg
Control	25.67(0.8)	205.41(1.3)	40.96(0.3)	484.13 (0.9)	996.52 (1.07)	376.56 (4.5)	12.38(3.7)	1308.18 (6.6)
Nanoclay (1000 ppm)	37.36(1.6)	266.37 (2.04)	11.67(0.3)	554.56 (1.5)	149.91 (1.4)	476.71(2.2)	4.66(2.2)	490.39 (2.07)
Nanoclay (2000 ppm)	39.12(4.1)	396.04(0.6)	42.78(3.8)	1328.47 (2.2)	383.48 (2.9)	367.22 (0.009)	12.97(0.01)	843.18 (0.8)
Bentonite $(1000$ ppm $)$	32.3(2.1)	304.83(0.4)	24.94(1.7)	991.94 (0.7)	911.94(0.3)	147.12(0.9)	6.26(1.09)	979.78 (1.4)
Bentonite (2000 ppm)	34.66 (1.01)	293.19 (2.2)	13.84 (1.03)	745.79 (1.3)	289.3(1.4)	347.63(1.6)	4.21(2.3)	575.83(1.4)
Nanosilica (1000 ppm)	27.22(4.2)	223.68(1.8)	17.72(1.5)	551.74 (0.01)	309.74 (2.01)	208.16(1.5)	4.09(2.4)	599.79 (2.8)
Nanosilica (2000 ppm)	28.52(7.1)	285.74(0.7)	15.66(1.5)	448.23 (4.8)	311.48(2.5)	181.90(6.7)	4.00(10.1)	566.14 (7.9)
Sodium silicate $(1000$ ppm $)$	41.65(5.6)	396.38 (1.4)	18.59(4.4)	768.00(2.7)	490.26(3.1)	266.23 (2.01)	7.10(2.6)	879.70 (2.1)
Sodium silicate (2000 ppm)	50.33(3.6)	330.07(1.1)	10.71(1.02)	568.99 (0.06)	290.04 (1.9)	213.34 (1.07)	3.75(1.5)	607.70(1.6)

Average $(n = 2)$ with standard deviation (SD) in parenthesis

Fig. 5 Cluster analysis based on leaf properties (a), stem properties (b), and minituber properties (c) of the treatments

Table 6 Element content of tuber in control and treatments with 1000 and 2000 ppm of nanoclay, Bentonite, nanosilica, and sodium silicate (μ gg⁻¹ of dry weight)

	Si	K	Zn	P	Al	Fe	Mn	Mg
Control	37.40(0.5)	224.80(2.3)	45.69(2.6)	560.02 (0.6)	$965.06(1.3)$ 258.48 (0.3)		19.84(0.7)	2092.83 (0.18)
Nanoclay (1000 ppm)	42.10(0.1)	391.18 (0.9)	64.14(1.6)	848.88 (1.2)	$842.67(0.5)$ 940.89 (0.3)		27.21(0.8)	4771.35 (0.18)
Nanoclay (2000 ppm)	40.05(0.1)	342.46(0.5)	43.54(3.5)	775.54 (2.4)		$916.10(0.5)$ 603.64 (0.16)	16.19(0.02)	2274.92(0.7)
Bentonite (1000 ppm)	41.31(15.1)	316.57(0.8)	46.95(1.9)	816.91 (1.5)	$712.80(0.7)$ $765.76(1.2)$		23.26(1.2)	3288.18 (0.02)
Bentonite (2000 ppm)	45.80(1.6)	414.14(0.1)	53.16(1.2)	852.47 (0.7)	609.13(0.7)	586.24 (0.26)	18.43(0.03)	3974.78 (0.24)
Nanosilica (1000 ppm)	40.96(0.4)	281.28 (0.3)	46.68(1.05)	878.39 (0.8)	603.58(1.2)	689.81 (1.06)	27.95(1.3)	3900.33 (1.5)
Nanosilica (2000 ppm)	40.74(0.3)	211.70 (1.06)	43.50(0.4)	598.08 (0.9)	327.62(0.3)	426.26(1.25)	18.08(1.5)	2137.09 (1.08)
Sodium silicate (1000 ppm)	41.00(1.2)	305.21(0.1)	83.52(0.2)	689.78 (1.6)	936.42(0.3)	546.98 (1.3)	18.14(1.2)	3865.42 (0.82)
Sodium silicate (2000 ppm)	45.70(2.1)	232.49(0.3)	48.20(2.03)	643.55(1.9)	249.46 (0.8)	516.35(0.9)	7.77(1.3)	1392.01 (1.2)

Average $(n = 2)$ with standard deviation (SD) in parenthesis

most important determinant of a high accumulation of Si in the shoots [\[33\]](#page-9-0) and Si competition in cation transporters with Mg can effect Mg upload to xylem and shoots.

3.5.3 Iron

Iron (Fe) content of plants under Si application was reduced except nanoclay (1000 ppm) while Fe content in tubers was greater in Si application treatments compared to control (Table [5](#page-6-0)). Although it has been suggested that Si application in cotton, canola, and wheat could increase Fe uptake [\[6](#page-9-0)], it is mostly known as a preventer of Fe uptake [\[25,](#page-9-0) [38](#page-9-0)–[40](#page-10-0)]. Previous studies have shown that low or high concentration of Si has different effects on Fe uptake in plants [\[38](#page-9-0), [41](#page-10-0)]. However, the findings of the current study did not indicate any significant correlation between Si content and Fe content in potato plants. Fe uptake by plants depends largely on the pH of the root zone [[42](#page-10-0), [43](#page-10-0)], and it appears that Si increases the oxidizing capacity of roots, which converts ferrous into ferric iron, thereby preventing the high uptake of iron and limiting its toxicity [\[44\]](#page-10-0). Iron is not readily mobile among different plant organs [\[33\]](#page-9-0). Under planting conditions similar to this research, in which there is no toxic iron in the root zone, Si could cause physiological abnormality for the plant by preventing Fe uptake.

3.5.4 Zinc

Except for nanoclay (2000 ppm) treatment, Si application reduced zinc (Zn) uptake in potato plant tissues (Table [5\)](#page-6-0). This finding is similar to a number of studies on different plants [\[40,](#page-10-0) [45](#page-10-0)–[47\]](#page-10-0), and in contrast with the results obtained for wheat and canola [[6](#page-9-0)]. Zn content of minitubers was larger than control in all the treatments (Table 6). Si influenced the amount of zinc inside the plant, since zinc can co-precipitate with Si in the cell, leading to less soluble zinc [\[48\]](#page-10-0). Since the deposition

of silica in the endodermis and pericycle of roots seems to play an important role in the tolerance of maize to cadmium (Cd) and Zn stress [[47\]](#page-10-0), it can be concluded that the formation and storing of Zn-silicate [[48\]](#page-10-0), in cell walls and vacuoles [[25](#page-9-0)], is correlated with Si treatments.

3.5.5 Aluminum

Aluminum (Al) content in both plant and minitubers decreased by Si application to root zone (Tables [5](#page-6-0) and 6). This reduction may be due to the external plant mechanism. Si and Al interact in the soil, creating sub-colloidal and inert aluminosilicates, thereby reducing phytotoxic aluminum concentration [[49\]](#page-10-0). Another causing factor might be the stimulation of phenolic exudation by roots that would chelate and thus reduce Al ab-sorption [[50\]](#page-10-0). It is evident that under many conditions, the presence of Si in the culture solution does decrease Al uptake in Norway spruce (Piceaabies (L.) Karst.), which suggests that some solution effects are involved [\[51](#page-10-0)].

3.5.6 Manganese

The manganese (Mn) content of plants reduced in Si presence in all treatments (Table [5](#page-6-0)). The Mn content in tubers was not significant and in three treatments (Bentonite 1000 ppm, nanoclay 1000 ppm, nanosilica 100 pm), there was an increase in Mn content compared to control (Table 6). The decrease in plant manganese content in the presence of higher silicon content is due to the effects on uptake and transport mechanisms [\[38\]](#page-9-0). The possible toxicity of Mn causes the plants to regulate the manganese content (e.g., calcium) in the cytoplasm by sequestration and active transport into the vacuole [\[52](#page-10-0)].

The sum of Mn content of plant and tubers in all the treatments was close to Mn content of the control plants (Table [5\)](#page-6-0). Most probably, since a wide variety of metal transporter family members have the ability to transport Mn^{2+} in plant cells [\[52\]](#page-10-0),

the Si application did not significantly influence Mn uptake in plants. Si amelioration role in this study can be described as increases of Mn binding to cell walls, which limits cytoplasmic concentrations of Mn in plant cells [[25](#page-9-0), [48,](#page-10-0) [53](#page-10-0)].

3.5.7 Phosphorus

Phosphorus (P) content increased in plant and tubers (Table [5\)](#page-6-0), which is similar to the findings of several other research studies [[54](#page-10-0)–[57](#page-10-0)]. Several explanations have been presented for the impact of Si on P uptake; some believe that increases in P content and uptake resulting from Si application may lead to improved membrane functionality and increased H+ -ATPase activity [\[54](#page-10-0), [55](#page-10-0)], which in turn facilitates P uptake by the transporters. However, it seems that the facilitation of P uptake by Si depends on the availability of P in the root zone, and P utilization in the plant may be improved by Si when the available amount of P is low. There have been two viewpoints regarding the impact of Si on P uptake in situations where there is low availability of P. According to the first view, certain facts suggest that when P is low, P availability may be controlled by the levels of Mn and Fe in plants Hence, Si caused a decrease in Fe and Mn uptake and thus promoted P availability within the plant [\[56\]](#page-10-0). The other explanation maintains that enhanced P uptake in the presence of Si was due to increased transpiration rate when P levels are low [[57\]](#page-10-0).

According to the findings presented in Table [5](#page-6-0), the amount of Fe and Mn reduced in plants with Si treatments, which suggests that Si enhanced P uptake in plants by reducing Mn and Fe availability.

3.5.8 Potassium

Potassium (K) content in plants and tubers was higher in the presence of Si in all the treatments except for the tuber of nanosilica (2000 ppm) (Tables [5](#page-6-0) and [6](#page-7-0)). The results of this study are similar to previous experiments on potato [\[5](#page-9-0)], and other plants [\[6](#page-9-0), [58](#page-10-0)]. The possible mechanism of the stimulating effect of Si on K uptake is assumed to be the activation of H+ -ATPase in the membranes [\[59](#page-10-0)]. This effect improves electrochemical gradient and increases the transcellular uptake of K^+ through greater activity of K^+ channels and carriers across the plasma membrane [[54](#page-10-0)]. Activation of H⁺-ATPase in the membranes by Si is also an effective factor in increasing P and Mg in plants [\[6\]](#page-9-0). Moreover, the P content of both plants and tubers and the Mg content of tubers increased in Si treatments (Tables [5](#page-6-0) and [6\)](#page-7-0). Accordingly, in the current study, K uptake enhances due to H⁺-ATPase activation in Si presence.

3.6 Conclusion

The results of the current study indicated that Silicon application in potato changes the morphology and physiology of potato plants. The most important role of Si was improving of the root characteristics in treated plants which can make the plants more resistant to drought and element deficit stresses. Si content in plants showed an increasing pattern of nanosilica < Bentonite < nanoclay < sodium silicate with regard to the silicon source (Tables [5](#page-6-0) and [6\)](#page-7-0). The Si, Mg, K, and P content increased while Al and Mn content decreased in both tuber and shoot in Si application treatments. Although Mg, Zn, and Fe content were lower in Si treatments, Si increased the amount of Mg, Zn, and Fe content in tubers. Overall, the positive effects of applied substances on intensification of essential elements and alleviation of toxic elements accumulation in both potato shoot and tubers followed a pattern of nanoclay > sodium silicate > Bentonite > nanosilica. Enhanced effect of nanoclay on the element content of plants is the result of increased cation exchange capacity (CEC) in nano-sized minerals [[60](#page-10-0)]. Higher CEC in minerals is a favorable feature in up-taking essential elements but the mineral chemistry always includes other elements which are considered non-essential or toxic for plants (Table [1\)](#page-2-0). Therefore, in choosing the size of minerals (nano or micro) in agricultural activities, the effect and uptake of each element on plant growth has to be considered. Silicon uptake of potato plants was higher in the existence of sodium silicate compared to nanosilica due to the chemical form of silicon which can be absorbed more easily by roots [\[34\]](#page-9-0). Potato is a salt-susceptible crop and sodium has shown a negative effect on its growth rates, especially leaves (Table [3\)](#page-4-0). It can be concluded that higher silicon content in the plants treated with sodium silicate alleviates the negative effects of sodium accumulation in potato plant tissues [[55](#page-10-0)].

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References

- 1. Savvas, D., & Ntatsi, G. (2015). Biostimulant activity of silicon in horticulture. Scientia Horticulturae, 196, 66–81. [https://doi.org/10.](https://doi.org/10.1016/j.scienta.2015.09.010) [1016/j.scienta.2015.09.010](https://doi.org/10.1016/j.scienta.2015.09.010).
- 2. Hashemi, A., Abdolzadeh, A., & Sadeghipour, H. R. (2010). Beneficial effects of silicon nutrition in alleviating salinity stress in hydroponically grown canola, Brassica napus L., plants. Soil Science and Plant Nutrition, 56(2), 244–253. [https://doi.org/10.](https://doi.org/10.1111/j.1747-0765.2009.00443.x) [1111/j.1747-0765.2009.00443.x](https://doi.org/10.1111/j.1747-0765.2009.00443.x).
- 3. Van Bockhaven, J., De Vleesschauwer, D., & Höfte, M. (2013). Towards establishing broad-spectrum disease resistance in plants: silicon leads the way. Journal of Experimental Botany, 64(5), 1281–1293. <https://doi.org/10.1093/jxb/ers329>.
- 4. Zhao, D., Hao, Z., Tao, J., & Han, C. (2013). Silicon application enhances the mechanical strength of inflorescence stem in herbaceous peony (Paeonia lactiflora Pall.) Scientia Horticulturae, 151, 165–172. [https://doi.org/10.1016/j.scienta.2012.12.013.](https://doi.org/10.1016/j.scienta.2012.12.013)
- 5. Pilon, C., Soratto, R. P., & Moreno, L. A. (2013). Effects of soil and foliar application of soluble silicon on mineral nutrition, gas exchange, and growth of potato plants. Crop Science, 53(4), 1605– 1614. [https://doi.org/10.2135/cropsci2012.10.0580.](https://doi.org/10.2135/cropsci2012.10.0580)
- 6. Mehrabanjoubani, P., Abdolzadeh, A., Sadeghipour, H. R., & Aghdasi, M. (2015). Silicon affects transcellular and apoplastic uptake of some nutrients in plants. Pedosphere, 25(2), 192–201. [https://doi.org/10.1016/S1002-0160\(15\)60004-2.](https://doi.org/10.1016/S1002-0160(15)60004-2)
- 7. Kamenidou, S., Cavins, T. J., & Marek, S. (2009). Evaluation of silicon as a nutritional supplement for greenhouse zinnia production. Scientia Horticulturae, 119(3), 297–301. [https://doi.org/10.](https://doi.org/10.1016/j.scienta.2008.08.012) [1016/j.scienta.2008.08.012.](https://doi.org/10.1016/j.scienta.2008.08.012)
- 8. Nanayakkara, U. N., Uddin, W., & Datnoff, L. E. (2008). Application of silicon sources increases silicon accumulation in perennial ryegrass turf on two soil types. Plant and Soil, 303(1– 2), 83–94. <https://doi.org/10.1007/s11104-007-9488-x>.
- 9. Iwama, K. (2008). Physiology of the potato: New insights into root system and repercussions for crop management. Potato Research, 51(3–4), 333–353. <https://doi.org/10.1007/s11540-008-9120-3>.
- 10. Gregory, P. J., & Simmonds, L. P. (1992). Water relations and growth of potatoes. In P. M. Harris (Ed.), The potato crop: the scientific basis for improvement (pp. 214–246). Dordrecht: Springer Netherlands.
- 11. Palta, J. A., Chen, X., Milroy, S. P., Rebetzke, G. J., Dreccer, M. F., & Watt, M. (2011). Large root systems: are they useful in adapting wheat to dry environments? Functional Plant Biology, 38(5), 347– 354. <https://doi.org/10.1071/FP11031>.
- 12. Chang, D., Cho, I., Suh, J.-T., Kim, S., & Lee, Y. (2011). Growth and yield response of three aeroponically grown potato cultivars (Solanum tuberosum L.) to different electrical conductivities of nutrient solution. American Journal of Potato Research, 88(6), 450– 458. <https://doi.org/10.1007/s12230-011-9211-6>.
- 13. Chang, D., Park, C., Kim, S., Kim, S., & Lee, Y. (2008). Physiological growth responses by nutrient interruption in aeroponically grown potatoes. American Journal of Potato Research, 85(5), 315–323. [https://doi.org/10.1007/s12230-008-](https://doi.org/10.1007/s12230-008-9024-4) [9024-4.](https://doi.org/10.1007/s12230-008-9024-4)
- Corrêa, R. M., Pinto, J. E. B. P., Pinto, C. A. B. P., Faquin, V., Reis, É. S., Monteiro, A. B., & Dyer, W. E. (2008). A comparison of potato seed tuber yields in beds, pots and hydroponic systems. Scientia Horticulturae, 116(1), 17–20. [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.scienta.2007.10.031) [scienta.2007.10.031.](https://doi.org/10.1016/j.scienta.2007.10.031)
- 15. Gonçalves, J. F., Antes, F. G., Maldaner, J., Pereira, L. B., Tabaldi, L. A., Rauber, R., & Nicoloso, F. T. (2009). Cadmium and mineral nutrient accumulation in potato plantlets grown under cadmium stress in two different experimental culture conditions. Plant Physiology and Biochemistry, 47(9), 814–821. [https://doi.org/10.](https://doi.org/10.1016/j.plaphy.2009.04.002) [1016/j.plaphy.2009.04.002](https://doi.org/10.1016/j.plaphy.2009.04.002).
- 16. Park, S. W., Jeon, J. H., Kim, H. S., Hong, S. J., Aswath, C., & Joung, H. (2009). The effect of size and quality of potato microtubers on quality of seed potatoes in the cultivar 'superior'. Scientia Horticulturae, 120(1), 127–129. [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.scienta.2008.09.004) [scienta.2008.09.004.](https://doi.org/10.1016/j.scienta.2008.09.004)
- 17. Ma, J. F., & Yamaji, N. (2006). Silicon uptake and accumulation in higher plants. Trends in Plant Science, 11(8), 392-397. [https://doi.](https://doi.org/10.1016/j.tplants.2006.06.007) [org/10.1016/j.tplants.2006.06.007](https://doi.org/10.1016/j.tplants.2006.06.007).
- 18. Bouma, T., Nielsen, K., & Koutstaal, B. (2000). Sample preparation and scanning protocol for computerized analysis of root length and diameter. Plant and Soil, 218(1–2), 185–196. [https://doi.org/10.](https://doi.org/10.1023/A:1014905104017) [1023/A:1014905104017.](https://doi.org/10.1023/A:1014905104017)
- 19. Gomez, M. R., Cerutti, S., Sombra, L. L., Silva, M. F., & Martínez, L. D. (2007). Determination of heavy metals for the quality control in Argentinian herbal medicines by ETAAS and ICP-OES. Food and Chemical Toxicology, 45(6), 1060–1064. [https://doi.org/10.](https://doi.org/10.1016/j.fct.2006.12.013) [1016/j.fct.2006.12.013.](https://doi.org/10.1016/j.fct.2006.12.013)
- 20. Wilson, M. J. (2007). Handbook of clay science, F. Bergaya, B.K.G. Theng, G. Lagaly (Eds.). Elsevier, Amsterdam.
- 21. Ada, R. (2013). Cluster analysis and adaptation study for safflower genotypes. Bulgarian Journal of Agricultural Science, 19(1), 103– 109.
- 22. Shaterian, J., Waterer, D., Jong, H. D., & Tanino, K. K. (2005). Differential stress responses to NaCl salt application in early- and late-maturing diploid potato (Solanum sp.) clones. Environmental and Experimental Botany, 54(3), 202–212. [https://doi.org/10.1016/](https://doi.org/10.1016/j.envexpbot.2004.07.005) [j.envexpbot.2004.07.005.](https://doi.org/10.1016/j.envexpbot.2004.07.005)
- 23. Dakora, F. D., & Nelwamondo, A. (2003). Silicon nutrition promotes root growth and tissue mechanical strength in symbiotic cowpea. Functional Plant Biology, 30(9), 947–953.
- 24. Crusciol, C. A. C., Pulz, A. L., Lemos, L. B., Soratto, R. P., & Lima, G. P. P. (2009). Effects of silicon and drought stress on tuber yield and leaf biochemical characteristics in potato. Crop Science, 49(3). doi: [https://doi.org/10.2135/cropsci2008.04.0233.](https://doi.org/10.2135/cropsci2008.04.0233)
- 25. Guntzer, F., Keller, C., & Meunier, J.-D. (2012). Benefits of plant silicon for crops: a review. Agronomy for Sustainable Development, 32(1), 201–213. [https://doi.org/10.1007/s13593-011-0039-8.](https://doi.org/10.1007/s13593-011-0039-8)
- 26. Libault, M., Brechenmacher, L., Cheng, J., Xu, D., & Stacey, G. (2010). Root hair systems biology. Trends in Plant Science, 15(11), 641–650. [https://doi.org/10.1016/j.tplants.2010.08.010.](https://doi.org/10.1016/j.tplants.2010.08.010)
- 27. Feng, J., Ma, S. G., Tamai, K., & Ichii, M. (2001). Role of root hairs and lateral roots in silicon uptake by rice. Plant Physiology, 127(4), 1773–1780. <https://doi.org/10.1104/pp.010271>.
- 28. Ma, J. F., Tamai, K., Ichii, M., & Wu, G. F. (2002). A rice mutant defective in Si uptake1. Plant Physiology, 130(4), 2111–2117. [https://doi.org/10.1104/pp.010348.](https://doi.org/10.1104/pp.010348)
- 29. Vulavala, V. R., Elbaum, R., Yermiyahu, U., Fogelman, E., Kumar, A., & Ginzberg, I. (2015). Silicon fertilization of potato: expression of putative transporters and tuber skin quality. Planta, 1–13. doi: [https://doi.org/10.1007/s00425-015-2401-6.](https://doi.org/10.1007/s00425-015-2401-6)
- 30. Lebot, V. (2009). Tropical root and tuber crops: cassava, sweet potato, yams and aroids: CABI.
- 31. Lommen, W. J. M. (1994). Effect of weight of potato minitubers on sprout growth, emergence and plant characteristics at emergence. Potato Research, 37(3), 315–322. [https://doi.org/10.1007/](https://doi.org/10.1007/bf02360524) [bf02360524](https://doi.org/10.1007/bf02360524).
- 32. Mitani, N., & Ma, J. F. (2005). Uptake system of silicon in different plant species. Journal of Experimental Botany, 56(414), 1255– 1261. <https://doi.org/10.1093/jxb/eri121>.
- 33. Ma, J. F. (2005). Plant root responses to three abundant soil minerals: silicon, aluminum and iron. Critical Reviews in Plant Sciences, 24(4), 267–281. [https://doi.org/10.1080/](https://doi.org/10.1080/07352680500196017) [07352680500196017](https://doi.org/10.1080/07352680500196017).
- 34. Ma, J. F., & Yamaji, N. (2008). Functions and transport of silicon in plants. Cellular and Molecular Life Sciences, 65(19), 3049–3057. [https://doi.org/10.1007/s00018-008-7580-x.](https://doi.org/10.1007/s00018-008-7580-x)
- 35. White, P. J., & Broadley, M. R. (2009). Biofortification of crops with seven mineral elements often lacking in human diets—iron, zinc, copper, calcium, magnesium, selenium and iodine. New Phytologist, 182(1), 49–84. [https://doi.org/10.1111/j.1469-8137.](https://doi.org/10.1111/j.1469-8137.2008.02738.x) [2008.02738.x.](https://doi.org/10.1111/j.1469-8137.2008.02738.x)
- 36. Karley, A. J., & White, P. J. (2009). Moving cationic minerals to edible tissues: potassium, magnesium and calcium. Current Opinion in Plant Biology, 12(3), 291–298. [https://doi.org/10.](https://doi.org/10.1016/j.pbi.2009.04.013) [1016/j.pbi.2009.04.013.](https://doi.org/10.1016/j.pbi.2009.04.013)
- 37. Shaul, O. (2002). Magnesium transport and function in plants: the tip of the iceberg. Biometals, 15(3), 307–321. [https://doi.org/10.](https://doi.org/10.1023/A:1016091118585) [1023/A:1016091118585](https://doi.org/10.1023/A:1016091118585).
- 38. Brackhage, C., Schaller, J., Bäucker, E., & Dudel, E. G. (2013). Silicon availability affects the stoichiometry and content of calcium and micro nutrients in the leaves of common reed. SILICON, 5(3), 199–204. <https://doi.org/10.1007/s12633-013-9145-3>.
- 39. Ma, J., & Takahashi, E. (1993). Interaction between calcium and silicon in water-cultured rice plants. Plant and Soil, 148(1), 107– 113. [https://doi.org/10.1007/BF02185390.](https://doi.org/10.1007/BF02185390)
- 40. Meharg, C., & Meharg, A. A. (2015). Silicon, the silver bullet for mitigating biotic and abiotic stress, and improving grain quality, in rice? Environmental and Experimental Botany, 120, 8–17. [https://](https://doi.org/10.1016/j.envexpbot.2015.07.001) doi.org/10.1016/j.envexpbot.2015.07.001.
- 41. Mali, M., & Aery, N. C. (2009). Effect of silicon on growth, biochemical constituents, and mineral nutrition of cowpea. Communications in Soil Science and Plant Analysis, 40(7–8), 1041–1052. [https://doi.org/10.1080/00103620902753590.](https://doi.org/10.1080/00103620902753590)
- Kobayashi, T., & Nishizawa, N. K. (2012). Iron uptake, translocation, and regulation in higher plants. Annual Review of Plant Biology, 63(1), 131–152. [https://doi.org/10.1146/annurev-arplant-](https://doi.org/10.1146/annurev-arplant-042811-105522)[042811-105522](https://doi.org/10.1146/annurev-arplant-042811-105522).
- 43. Briat, J.-F., Curie, C., & Gaymard, F. (2007). Iron utilization and metabolism in plants. Current Opinion in Plant Biology, 10(3), 276–282. <https://doi.org/10.1016/j.pbi.2007.04.003>.
- 44. Ma, J. F., & Takahashi, E. (2002). Soil, fertilizer, and plant silicon research in Japan: Elsevier.
- 45. Anwaar, S., Ali, S., Ali, S., Ishaque, W., Farid, M., Farooq, M., & Sharif, M. (2015). Silicon (Si) alleviates cotton (Gossypium hirsutum L.) from zinc (Zn) toxicity stress by limiting Zn uptake and oxidative damage. Environmental Science and Pollution Research, 22(5), 3441–3450. [https://doi.org/10.1007/s11356-014-](https://doi.org/10.1007/s11356-014-3938-9) [3938-9](https://doi.org/10.1007/s11356-014-3938-9).
- 46. Kaya, C., Tuna, A. L., Sonmez, O., Ince, F., & Higgs, D. (2009). Mitigation effects of silicon on maize plants grown at high zinc. Journal of Plant Nutrition, 32(10), 1788–1798. [https://doi.org/10.](https://doi.org/10.1080/01904160903152624) [1080/01904160903152624](https://doi.org/10.1080/01904160903152624).
- 47. da Cunha, K., & do Nascimento, C. (2009). Silicon effects on metal tolerance and structural changes in maize (Zea mays l.) grown on a cadmium and zinc enriched soil. Water, Air, and Soil Pollution, 197(1–4), 323–330. <https://doi.org/10.1007/s11270-008-9814-9>.
- 48. Neumann, D., & zur Nieden, U. (2001). Silicon and heavy metal tolerance of higher plants. Phytochemistry, 56(7), 685–692. [https://](https://doi.org/10.1016/S0031-9422(00)00472-6) [doi.org/10.1016/S0031-9422\(00\)00472-6.](https://doi.org/10.1016/S0031-9422(00)00472-6)
- 49. Liang, Y., Sun, W., Zhu, Y.-G., & Christie, P. (2007). Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: a review. Environmental Pollution, 147(2), 422–428. [https://doi.org/](https://doi.org/10.1016/j.envpol.2006.06.008) [10.1016/j.envpol.2006.06.008.](https://doi.org/10.1016/j.envpol.2006.06.008)
- 50. Kidd, P. S., Llugany, M., Poschenrieder, C., Gunsé, B., & Barceló, J. (2001). The role of root exudates in aluminium resistance and

silicon-induced amelioration of aluminium toxicity in three varieties of maize (Zea mays L.) Journal of Experimental Botany, 52(359), 1339–1352. [https://doi.org/10.1093/jexbot/52.359.1339.](https://doi.org/10.1093/jexbot/52.359.1339)

- Prabagar, S., Hodson, M. J., & Evans, D. E. (2011). Silicon amelioration of aluminium toxicity and cell death in suspension cultures of Norway spruce (Picea abies (L.) Karst.) Environmental and Experimental Botany, 70(2–3), 266–276. [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.envexpbot.2010.10.001) [envexpbot.2010.10.001.](https://doi.org/10.1016/j.envexpbot.2010.10.001)
- 52. Pittman, J. K. (2005). Managing the manganese: molecular mechanisms of manganese transport and homeostasis. New Phytologist, 167(3), 733–742. <https://doi.org/10.1111/j.1469-8137.2005.01453.x>.
- 53. Doncheva, S., Poschenrieder, C., Stoyanova, Z., Georgieva, K., Velichkova, M., & Barceló, J. (2009). Silicon amelioration of manganese toxicity in Mn-sensitive and Mn-tolerant maize varieties. Environmental and Experimental Botany, 65(2–3), 189–197. [https://doi.org/10.1016/j.envexpbot.2008.11.006.](https://doi.org/10.1016/j.envexpbot.2008.11.006)
- 54. Liang, Y., Zhang, W., Chen, Q., Liu, Y., & Ding, R. (2006). Effect of exogenous silicon (Si) on H+−ATPase activity, phospholipids and fluidity of plasma membrane in leaves of salt-stressed barley (Hordeum vulgare L.) Environmental and Experimental Botany, 57(3), 212–219. <https://doi.org/10.1016/j.envexpbot.2005.05.012>.
- 55. Tuna, A. L., Kaya, C., Higgs, D., Murillo-Amador, B., Aydemir, S., & Girgin, A. R. (2008). Silicon improves salinity tolerance in wheat plants. Environmental and Experimental Botany, 62(1), 10–16. [https://doi.org/10.1016/j.envexpbot.2007.06.006.](https://doi.org/10.1016/j.envexpbot.2007.06.006)
- 56. Ma, J., & Takahashi, E. (1990). Effect of silicon on the growth and phosphorus uptake of rice. Plant and Soil, 126(1), 115-119. [https://](https://doi.org/10.1007/BF00041376) [doi.org/10.1007/BF00041376.](https://doi.org/10.1007/BF00041376)
- 57. Jianfeng, M. A., & Takahashi, E. (1991). Effect of silicate on phosphate availability for rice in a P-deficient soil. Plant and Soil, 133(2), 151–155. [https://doi.org/10.1007/BF00009187.](https://doi.org/10.1007/BF00009187)
- 58. Miao, B.-H., Han, X.-G., & Zhang, W.-H. (2010). The ameliorative effect of silicon on soybean seedlings grown in potassium-deficient medium. Annals of Botany. [https://doi.org/10.1093/aob/mcq063.](https://doi.org/10.1093/aob/mcq063)
- 59. Liang, Y. (1999). Effects of silicon on enzyme activity and sodium, potassium and calcium concentration in barley under salt stress. Plant and Soil, 209(2), 217–224. [https://doi.org/10.1023/A:](https://doi.org/10.1023/A:1004526604913) [1004526604913.](https://doi.org/10.1023/A:1004526604913)
- 60. Uddin, F. (2008). Clays, nanoclays, and montmorillonite minerals. Metallurgical and Materials Transactions A, 39(12), 2804–2814. [https://doi.org/10.1007/s11661-008-9603-5.](https://doi.org/10.1007/s11661-008-9603-5)