Silicon Compounds and Potassium Sulfate Improve Salinity Tolerance of Potato Plants through Instigating the Defense Mechanisms, Cell Membrane Stability, and Accumulation of Osmolytes

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Silicon Compounds and Potassium Sulfate Improve Salinity Tolerance of Potato Plants through Instigating the Defense Mechanisms, Cell Membrane Stability, and Accumulation of Osmolytes

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ABSTRACT

Potato (*Solanum tuberosum* L.) as a strategic crop is moderately susceptible to salinity. Therefore, it is essential to recognize the defense mechanisms upon which potato plants respond to salinity stress and adopt strategies to enhance their salinity tolerance. An open field experiment was conducted at different saline irrigation water (0.5, 5, 8, and 12 $dS.m^{-1}$) to investigate the physicochemical traits and tuber yield of potato plants under antistress compounds application, including K_2SO_4, $NaSiO_3$ nanoparticles ($NaSiO_3$-NPs), and SiO_2. The results showed that gas exchange variables were suppressed by salinity stress, while they were alleviated by foliar application of K_2SO_4. The lowest leaf malondialdehyde content was observed at 5, and 12 $dS.m^{-1}$ in SiO_2 and $NaSiO_3$-NPs-treated plants showed 56% and 43% decreases, respectively, over control. The application of silicon under saline conditions increased leaf soluble carbohydrates and proline content compared with the control. While salinity increased the Na^+/K^+ ratio, the application of silicon reduced Na^+/K^+ more than twice compared with the control. The antioxidant enzyme activities were induced the most by $NaSiO_3$-NPs. It seems that the use of antistress compounds, especially nanoparticles, would be a practical approach to alleviate the detrimental effects of salinity stress on potato plants.

Introduction

Increasing population growth would double the need for food production by 2050 (Fróna, Szenderák, and Harangi-Rákos 2019). This will increase the pressure on the environment and groundwater resources and force the use of marginal lands for agricultural purposes, thereby negatively affect the quantity and quality of irrigation water, agricultural products, and food security, particularly in developing countries. On average, abiotic stresses reduce crop yield by 71% worldwide, of which salinity alone reduced yields by an average of 20% (Kafi et al. 2009). Irrigated lands are highly prone to salinization, while they provide more than a third of the world's food crops (Kafi et al. 2009).

Potato (*Solanum tuberosum* L.) is the fourth most important crop and is of particular importance in human and animal nutrition. In semi-arid regions, where potatoes are widely cultivated, salinity is a serious problem and drastically reduces plant productivity (Faostat 2014). Iran has the largest percentage of saline land after China, India, and Pakistan, and more than 75% of food production

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in this country is dependent on irrigated lands (Kafi et al. 2009). The salinization of irrigation water in the potato fields of Iran has damaged this crop in recent years, and farmers have been forced to use unusual and saline water. Therefore, it is necessary to adopt agronomic approaches and methods of alleviating salt stress and harmful minerals of irrigation water to make potato production more sustainable.

Salinity usually imposes osmotic stress to the plants leading to over-generation of reactive oxygen species (ROSs), such as hydroxyl radical, superoxide anion, singlet oxygen, and hydrogen peroxide, each of which can adversely affect the plant cell metabolism and damage the cell membranes, DNA, and enzymes (Gill and Tuteja 2010; Zushi, Matsuzoe, and Kitano 2009). Plants have a wide range of antioxidant defense systems to scavenge those ROSs. Ion balance in plants is disrupted by high levels of salt in the growing medium, and under non-stressed conditions, a high K^+/Na^+ ratio is maintained in the protoplasm; however, a competition would occur between Na^+ and K^+ due to their similarity, and it is difficult for the plant cell to discriminate between those ions. Therefore, the K^+/Na^+ ratio is altered through the higher influx of Na^+ by the K^+ pathway (Blumwald 2000).

One strategy to increase crop tolerance to salt stress is antistress compounds (Hussein, El-Faham, and Alva 2012). For example, potassium (Hussein, El-Faham, and Alva 2012) and silicon (Haghighi and Pessarakli 2013) are among the compounds with antistress effects under salinity stress conditions. Potassium has a synergistic effect on the uptake of other macro-nutrients such as nitrogen, phosphorus, and calcium, and positive effects on the osmotic adjustment process of plant root and shoot cells under adverse conditions. Potassium helps to absorb more water and nutrients required by the plant (Shabala and Cuin 2008) and regulates the stomatal aperture under salinity stress conditions (Kant et al. 2002).

The advantageous effects of silicon on plants have been reported, especially under salinity stress conditions (Kafi et al. 2019). Silicon increases chlorophyll concentration per unit leaf area and increases the plant's ability to light interception and photosynthesis (Haghighi and Pessarakli 2013). Silicon also imposes deposition on leaf cuticular layers to prevent extra water loss, enhances leaf physical resistance under stress conditions, and contributes to plant water balance (Silva et al. 2012). The application of silicon stimulated the antioxidant activity and decreased H_2O_2 levels in tomato (*Solanum lycopersicum*), maize (*Zea mays*), and cucumber (*Cucumis sativus*) under salt stress (Al-aghabary, Zhu, and Shi 2005; Moussa 2006; Zhu et al. 2004). The product of lipid peroxidation, *i.e.*, malondialdehyde, has been reported to be decreased by the application of silicon in maize (*Zea mays*), grapevine (*Vitis vinifera* L.), and barley (*Hordeum vulgare*) under salinity stress (Liang et al. 2003; Moussa 2006; Soylemezoglu et al. 2009). The decrease in lipid peroxidation mediated by silicon is attributed to its adjustment of the plant antioxidant activities, in which the effect is species and time-dependent (Liang et al. 2003).

Extensive researches have been performed to improve the agronomic and physiological performance of potato crop yield (Ahmadi-Lahijani et al. 2018a, 2018b; Kafi et al. 2019; Struik and Wiersema 1999). Many studies reported the capability of silicon to enhance salinity tolerance in some main crops, including rice (*Oryza sativa*), sugarcane (*Saccharum officinarum*), wheat (*Triticum aestivum*), soybean (*Glycine max*), barley (*Hordeum vulgare*), and tomato (*Solanum lycopersicum*) (Ahmad, Zaheer, and Ismail 1992; Liang Yongchao 1999a; Liang et al. 2003; Al-aghabary, Zhu, and Shi 2005; Liang, Si, and Römheld 2005; Gong, Randall, and Flowers 2006; Romero-Aranda, Jurado, and Cuartero 2006; Tuna et al. 2008; Ashraf et al. 2010; Lee et al. 2010). Nevertheless, to our knowledge, despite its agronomic and economic importance, less information has been released on the effects of antistress compounds such as potassium and silicon nanoparticles to improve potato tolerance to salinity. Due to the importance of the potato crop in feeding the growing population and meeting future food security, any possible strategy should be adopted to improve the salinity tolerance of this crop. Therefore, it was hypothesized that applying the antistress compounds (K_2SO_4, $NaSiO_3$-NPs, and SiO_2) modify the growth and tuber yield by ameliorating the adverse effects of salinity on the potato crop. The study was also aimed to recognize the mechanisms underlying the antistress compound-mediated amelioration of salinity stress through foliar application of the aforementioned

compounds. Furthermore, the efficiency of silicon nanoparticles compared with the conventional compounds on physiological and biochemical response and tuber yield of potato plants was also investigated.

Materials and methods

Experimental site and treatments

This study was conducted at the research farm of the Ferdowsi University of Mashhad, Iran, in 2016. Experimental treatments were salinity levels of 0.5 (control), 5, 8 and 12 dS.m^{-1} as the main plots, and foliar application of potassium sulfate (K_2SO_4) (1000 mg.l^{-1}), sodium silicate nanoparticles ($NaSiO_3$-NPs) (400 mg.l^{-1}), and silicon (SiO_2) (1000 mg.l^{-1}) as the sub-plots. The particle size of $NaSiO_3$-NPs was 68 nm (Figure 1). Spraying with distilled water was considered as the untreated (control) plants. The chemicals were foliar applied separately at each salinity level (4 × 4). Uniform potato mini tubers (*cv.* Agria, with the same physiological age, 1–1.5 cm in diameter, and 3–5 green buds) were sown with 20 cm intervals on four rows (5 m long and 75 cm apart) in plots of 15 m^2 area on May 20th. The soil texture was silty loam, and based on the physicochemical analysis of the soil (K = 397 mg.Kg^{-1}, P = 29.8 mg.Kg^{-1}, N = 0.07%, Na = 8 mg.Kg^{-1}, and pH = 7.8), phosphorus and potassium were enough to earn 40 ton.ha^{-1} potato tubers, therefore, only nitrogen was applied (200 Kg.ha^{-1}) at three-time intervals: planting, two, and four weeks after planting.

Irrigation with fresh water was made from the planting to three to four leaves stage (up to one month after cultivation). The irrigation water analysis is presented in Table 1. Then, salinity was applied through the dissolution of sodium chloride salt based on the ionization coefficient in the water supply. Foliar application of the antistress compounds was performed in two stages; 10 days (40 days after planting) and 20 days (50 days after planting) after salinity stress onset using a handheld sprayer after sunset. One week after the second foliar application of the antistress compounds, leaf samples
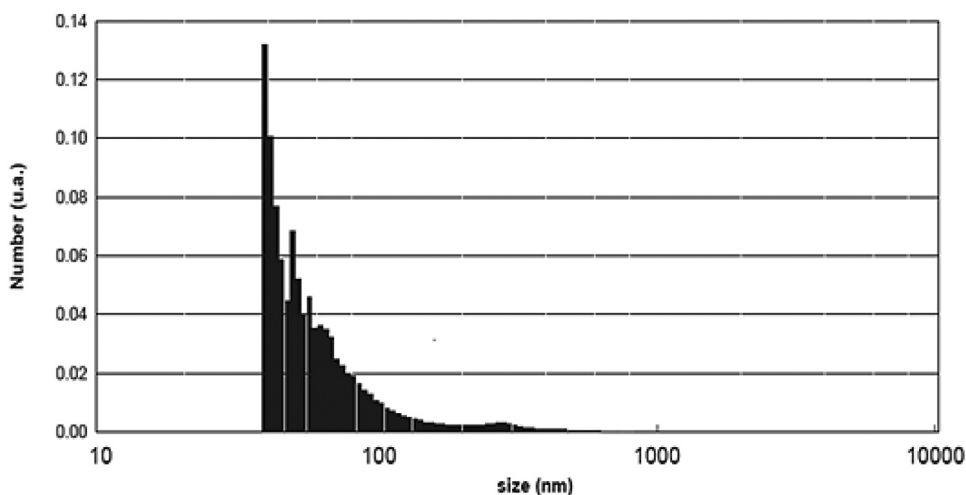

Figure 1. Sodium silicate nanoparticles diameter determined by particle size analyzer system.

Table 1. Physicochemical properties of irrigation water.

SO$_4^-$ (mg. L^{-1})	Cl$^-$ (mg. L^{-1})	HCO$_3^-$ (mg. L^{-1})	K$^+$ (mg. L^{-1})	Na$^+$ (mg. L^{-1})	Mg^{2+} (mg. L^{-1})	Ca^{2+} (mg. L^{-1})	SAR (%)	TDS (mg. L^{-1})	EC (dS. m^{-1})	pH
3.08	2.6	3.7	0.08	4.4	3	1.9	2.8	597	0.5	7.94

were taken from the fully developed young leaves (third), and the physiological and biochemical traits were measured.

Physiological traits

Leaf gas exchange variables

Gas exchange variables including net photosynthetic rate (Np), mesophyll conductance (g_m), intercellular CO_2 concentration (C_i), stomatal conductance (g_s), and intercellular to ambient CO_2 concentration (C_i:C_a) measured using a portable LCA4 photosynthesis system (ADC Bio Scientific Ltd, UK) at approximately 1000 μmol m^{-2}s^{-1} PAR, a relative humidity of 40 ± 5%, at the ambient CO_2 concentration, and leaf temperature of 25°C. The measurements were made between 10:00–12:00 am three times for each treatment. At the same time, leaf pigment content (SPAD) was measured on the same leaves using a handheld chlorophyll meter (SPAD 502, Spectrum Technologies, Inc.).

Leaf electrolyte leakage (EL)

The leaf samples were incubated in vials containing 100 ml distilled water for 24 h, and then, primary EL (EC1) was recorded using an EC meter (Jenway). Then, the vials were placed in an autoclave at 121°C and 1.2 atm for 20 min, and after cooling down, the secondary EL (EC2) was recorded. Leaf EL was calculated as Eq. (1):

$$EL = \left[\frac{EC1 - EC0}{EC2 - EC0}\right] \times 100 \tag{1}$$

Here, EC0 is the electrical conductivity of distilled water (Sairam 1994).

Leaf relative water content (RWC)

Leaf RWC was measured according to the method of Smart and Bingham (1974). The leaf samples were collected from the central rows of each plot, and RWC was calculated as Eq. (2):

$$RWC = \left[\frac{FW - DW}{TW - DW}\right] \times 100 \tag{2}$$

Here, DW, FW, and TW are the leaf dry weight, fresh weight, and turgid weight, respectively.

Leaf osmotic water potential (ψ_O)

The leaf ψ_O was determined according to the freezing point depression method using an osmometer (Wogel, model OM802.D). The leaf osmolytes content was calculated based on the van't Hoff equation, and the leaf ψ_O was measured by the Eq. (3):

$$mMol/g = [-Op/RT) \times (WC/(1 - WC)] \tag{3}$$

Here, the osmolytes content is based on mM g^{-1} dry weight, R is the gas constant (0.083), T is the temperature (°K), Op is the leaf osmotic potential (bar), and WC is the leaf water content.

Biochemical traits

Leaf malondialdehyde content (MDA)

Leaf MDA was measured by homogenizing leaf fresh weight in 5 ml of trichloroacetic acid (100 g^{-1}) containing 250 g l^{-1} thiobarbituric acid. The mixture was centrifuged at 20,000 g for 25 min at 4°C and then was heated to 95°C for 30 min. It was then cooled in an ice-bath and centrifuged at 10,000 g for 10 min at 4°C. The supernatant absorbance was read at 532 nm spectromatically (Jenway UV-Visible, Model 6305) and was corrected at *A600*. The extinction coefficient of 155 mM^{-1}cm^{-1} was applied to measure the MDA content and indicated as nM of MDA g^{-1} fresh weight (Heath and Packer 1968).

Leaf soluble carbohydrates content (SC)

The leaf SC was measured according to the method of Dubois et al. (1956). 100 mg fresh leaf was homogenized in ethanol 70% and was kept at 4°C for 24 h. The solids were removed by centrifuging at 3000 g for 5 min. The supernatant was mixed with phenol and sulfuric acid, and finally, after 30 min hot water bath (100°C), the absorbance was read at $A480$.

Leaf proline content

100 mg leaf fresh weight was homogenized in 1 ml sulfosalicylic acid (3%). After removing the insoluble solids by centrifuging in 3000 g for 5 min, 200 µl glacial acetic acid and 200 µl ninhydrin reagent (2, 2-dihydroxyindane-1, 3-dione) was added to the mixture. It was then heated to 100°C for 30 min in a hot water bath. After cooling down, 600 µl toluene was added to the mixture. The absorbance of the supernatant was read at $A520$ nm, and the proline content was calculated using the proline standard curve (Bates, Waldren, and Teare 1973),

Ion assay

Leaf sodium (Na^+) and potassium (K^+) was assayed by the method of Tandon and Tandon (1993). 100 mg leaf dry weight was ground and digested in a dense nitric acid for 60 min at 80°C. Na^+ and K^+ content were determined by a flame photometer (Jenway, UK) and the standard Na^+ and K^+ solutions. The ratio of sodium to potassium (Na^+/K^+) was also measured.

Antioxidant activity

100 mg leaf fresh weight was ground in liquid nitrogen, and 1 ml potassium phosphate (0.1 M, pH = 7.8) containing 1 mM EDTA were added. The insoluble solids were removed by centrifuging the mixture in 12,000 g at 4°C (Sigma, model K18-3). The supernatant was taken and kept at −80°C to assay the enzymatic antioxidant activities (Yamaguchi, Mori, and Nishimura 1995).

Ascorbate peroxidase (APX) activity (EC 1.11.1.11) was measured according to the method of Yamaguchi, Mori, and Nishimura (1995). The reaction mixture contained potassium phosphate buffer (50 mM, pH = 7), hydrogen peroxidase (1 mM), and ascorbate (0.5 mM). The APX activity was assayed according to a reduction in absorbance in $A290$ nm ascorbate oxidation (distinction coefficient 2.8 mM cm^{-1}). To measure the peroxidase (POX) activity (EC 1.11.1.7), 1 ml of the reaction mixture containing potassium phosphate buffer (20 mM, pH = 6), 5 mM guaiacol (2-methoxy phenol), and 1 mM hydrogen peroxidase was used. According to the method modified by Herzog (1973), the formation of tetraguaiacol at $A470$ nm and a distinction coefficient of 26.6 mM were used to calculate the tetraguaiacol amount. The reaction was monitored for 1 min. The POX activity was defined as the oxidation of 1 µM guaiacol in 1 min by the enzyme activity.

Leaf phenol content

100 mg leaf fresh weight was homogenized in ethanol (70%) and incubated at 4°C for 24 h. After centrifuging in 3000 g for 5 min, 20 µl of supernatant was mixed with 1 ml double distilled water (dd H_2O) and 20 µl the Folin–Ciocalteu reagent, and 5 min later, 120 µl carbonate sodium (20% w/v) was added to and kept in room temperature for 30 min. The total phenol content was determined based on absorbance in $A765$ nm and Gallic acid standard and reported as mg.g^{-1} dry weight (Singleton and Rossi 1965).

Harvesting and tuber yield

At physiological ripening (late September, 120 days after planting), two square meters of each experimental plot were harvested to determine the tuber yield considering the marginal effect.

Statistical analysis

The experiment was conducted in a split-plot arrangement based on a randomized complete block design with three replications. Analysis of variance and means comparison was performed by SAS *v.* 9.1 statistical software. Graphs were plotted using Sigma Plot 14.0. Means were compared with LSD at 5% probability level.

Results

Leaf gas exchange variables

Leaf N_p, g_s, and g_m were affected by salinity, antistress compounds, and their interactions (Table S1). Foliar application of K_2SO_4 significantly increased N_p by 90% compared with the control; however, it was decreased by increasing salinity level (Figure 2A). Application of antistress compounds alleviated the salinity effect on N_p at 8 dS.m^{-1}; N_p was higher by 59, 29, and 29% compared with the control when SiO_2, K_2SO_4, and $NaSiO_3$-NPs were applied, respectively. Generally, salinity stress suppressed g_s; however, foliar applying antistress compounds increased g_s compared with the control (Figure 2B). The highest g_s was recorded in K_2SO_4-treated plants at the control that was 18% higher than the untreated plants.

K_2SO_4 application significantly increased g_m by 90% compared with the untreated plants at 5 dS. m^{-1} salinity level; however, g_m was suppressed by increasing the salinity intensity (Figure 2C). At 12 dS.m^{-1}, the antistress compounds-treated plants were not different from the control; however, SiO_2-treated plants showed 51% greater g_m compared with the untreated plants at 8 dS.m^{-1} (Figure 2C). The effect of salinity was also significant on C_i and C_i:C_a (Table S1). Intercellular CO_2 concentration and C_i
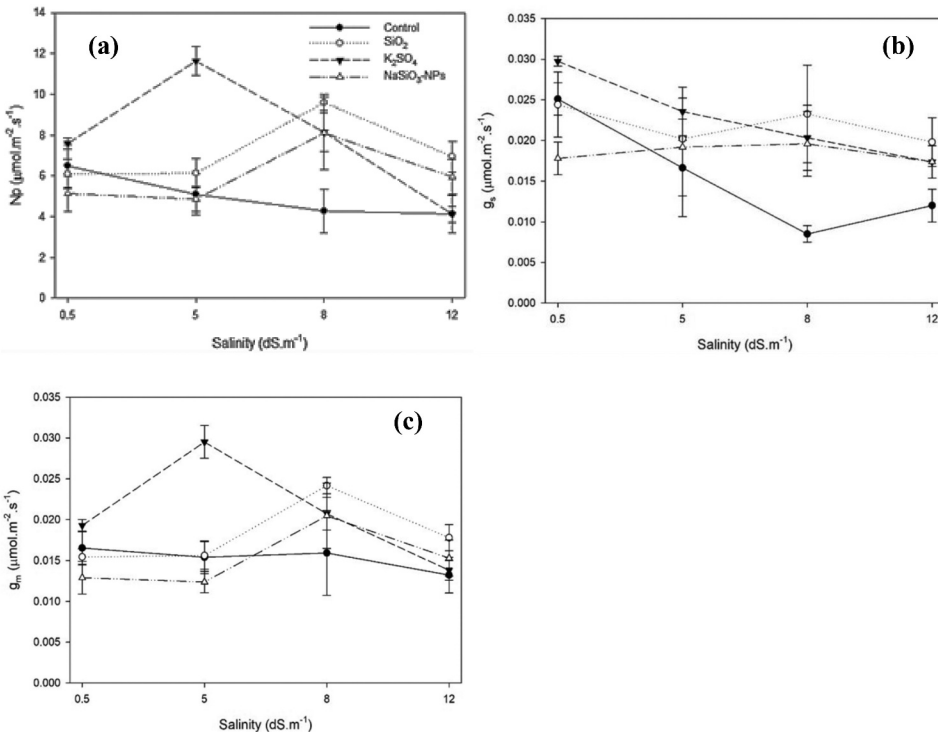
Figure 2. Net photosynthetic rate (A), stomatal conductance (B), and mesophyll conductance (C) of potato plants grown at salinity stress and foliar application of anti-stress compounds. NPs: nano-particles. The vertical bars represent the parameter's mean ± S. E. n = 3.
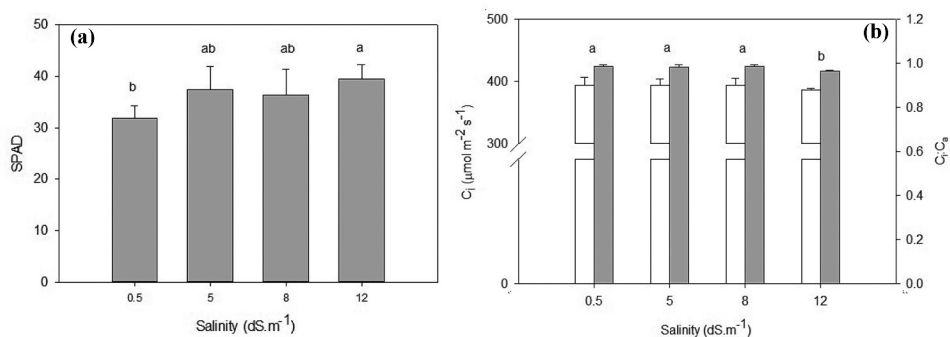
Figure 3. Leaf chlorophyll content (SPAD) (A), and intercellular CO2 concentration and intercellular to ambient CO2 concentration (B) of potato plants grown at salinity stress and foliar application of anti-stress compounds. White and gray columns represent Ci and Ci: Ca, respectively. Columns with the same letters are not significantly different, LSD 5%.

:C_a tended to decrease by increasing the salinity level (Figure 3B). SPAD values significantly increased by salinity stress (Table S1). The greatest SPAD values were recorded at 12 dS.m^{-1}, which was 24% higher than the control plants (Figure 3A).

Leaf RWC and ψ_O

Antistress compounds and salinity stress interacted to affect the ψ_O of leaves (Table S2). Leaf ψ_O was decreased by increasing salinity stress in untreated plants. In contrast, leaf ψ_O was stimulated in the antistress-treated plants (Figure 4A). The greatest leaf ψ_O was recorded in NaSiO$_3$-NPs-treated, followed by K$_2$SO$_4$-treated plants at 8 and 12 dS.m^{-1} salinity levels. NaSiO$_3$-NPs and K$_2$SO$_4$ increased leaf ψ_O 46 and 12%, compared with the untreated plants at 12 dS.m^1, respectively (Figure 4B). The leaf RWC was affected by salinity stress (Table S2); the lowest RWC was observed at 12 dS.m^{-1}, which was significantly lower than that under the control conditions (Figure 4B).

Leaf MDA and EL

Salinity stress increased the leaf EL; salinity stress levels of 5, 8, and 12 dS.m^{-1} increased this parameter by 30, 58, and 57%, respectively (Table S2 and Figure 4B). The interaction effect of salinity and foliar application of antistress compounds was significant on leaf MDA (Table S3). Under the control conditions, the lowest MDA was recorded in K$_2$SO$_4$-treated plants. However, at 5 and 12 dS.m^{-1},
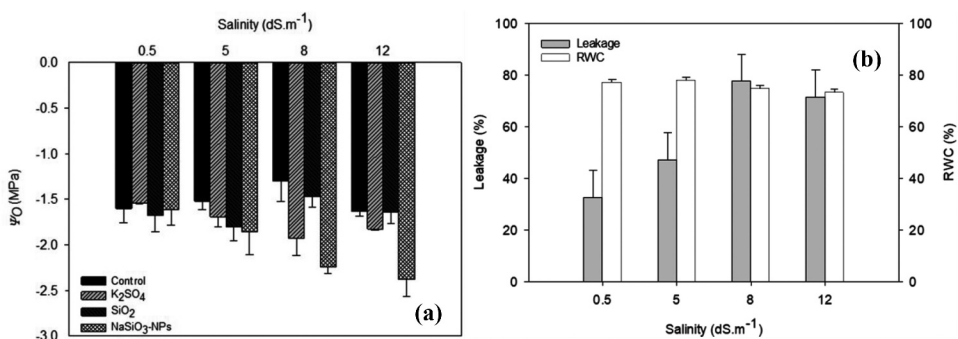
Figure 4. Leaf osmotic potential (ψ_O) (A), and electrolyte leakage (EL) and relative water content (RWC) (B) of potato plants grown at salinity stress and foliar application of anti-stress compounds. NPs: nano-particles. The vertical bars represent the parameter's mean ± S.E. n = 3.

Table 2. Effect of salinity and foliar application of anti-stress compounds on biochemical traits of potato plants.

Salinity level (dS. m^{-1})	Anti-stress compounds	MDA[†] (nm.g^{-1} Fw)	Soluble carbohydrates (mg. g^{-1} Fw)	Proline (mg.g^{-1} Fw)	Phenol (mg.g^{-1} Fw)
0.5	Control	27.8 ± 12.4	7.27 ± 0.37	2.04 ± 0.19	1.23 ± 0.17
	Nano-NaSiO$_3$	17.6 ± 2.80	5.14 ± 0.80	3.12 ± 0.23	1.76 ± 0.19
	K$_2$SO$_4$	11.8 ± 0.27	7.88 ± 0.69	1.20 ± 0.11	1.52 ± 0.05
	SiO$_2$	13.3 ± 1.55	8.01 ± 1.18	2.06 ± 0.61	1.80 ± 0.17
5	Control	14.4 ± 0.63	8.65 ± 1.07	2.29 ± 0.33	1.03 ± 0.31
	Nano-NaSiO$_3$	12.6 ± 0.42	5.07 ± 0.45	5.75 ± 0.66	1.47 ± 0.25
	K$_2$SO$_4$	12.4 ± 0.35	6.23 ± 1.10	2.83 ± 0.39	1.73 ± 0.42
	SiO$_2$	6.3 ± 0.80	5.64 ± 1.03	2.60 ± 0.02	1.62 ± 0.25
8	Control	28.4 ± 2.20	2.80 ± 0.07	3.32 ± 0.24	1.27 ± 0.07
	Nano-NaSiO$_3$	14.6 ± 1.35	6.22 ± 0.07	2.57 ± 0.42	1.55 ± 0.07
	K$_2$SO$_4$	15.3 ± 2.40	4.26 ± 0.43	2.89 ± 0.62	1.35 ± 0.56
	SiO$_2$	14.7 ± 0.63	4.66 ± 0.20	2.97 ± 0.17	1.57 ± 0.95
12	Control	15.7 ± 1.23	5.08 ± 1.03	2.56 ± 0.36	1.62 ± 0.22
	Nano-NaSiO$_3$	5.4 ± 0.30	4.11 ± 0.93	3.66 ± 0.25	1.56 ± 0.10
	K$_2$SO$_4$	9.0 ± 1.81	2.62 ± 0.28	4.10 ± 0.25	1.60 ± 0.11
	SiO$_2$	9.1 ± 0.28	6.30 ± 1.33	3.75 ± 0.57	1.86 ± 0.28

[†]Malondialdehyde, LSD 5%, means are indicated ±SE. n = 3.

the lowest MDA was observed in SiO$_2$ and NaSiO$_3$-NPs treatments by 56 and 43% decrease compared to the control, respectively (Table 2).

Leaf soluble carbohydrates content (SC)

Salinity and foliar application of antistress compounds interacted to affect leaf SC content of potato plants (Table S3). Overall, the greatest leaf SC content was observed at the salinity level of 12 dS.m^{-1}. Leaf SC content decreased by 61% at 8 dS.m^{-1}, but spraying NaSiO$_3$-NPs increased leaf SC content by 20% compared with the control (Table 2).

Leaf proline content

Salinity and foliar application of antistress compounds interacted to affect the leaf proline content (Table S3). In general, leaf proline content increased with increasing salinity stress. Antistress compounds application had various effects on the leaf proline content at the control conditions; the silicon compounds relatively increased, and potassium compound decreased leaf proline content over the untreated plants (Table 2). NaSiO$_3$-NPs application increased leaf proline content by 34% compared with the untreated plants under the control conditions (Table 2). At 12 dS.m^{-1}, the greatest increase in leaf proline content was observed when K$_2$SO$_4$ was applied (60% compared with the untreated plants).

Leaf phenol content

The leaf phenol content was influenced by foliar application of antistress compounds (Table S3). Although insignificantly, the leaf phenol content showed an ascending trend by increasing the salinity level. Generally, SiO$_2$-treated plants showed more significant leaf phenol content compared with the untreated plants. For instance, the leaf phenol content of SiO$_2$-treated plants was 45 and 57% greater than the untreated plants at the control (0.5 dS.m^{-1}) and 5 dS.m^{-1}, respectively (Table 2).

Ion assay

Leaf Na content and Na$^+$/K$^+$ ratio were affected by the salinity, foliar application of antistress compounds, and their interaction (Table S2). Interaction of salinity and the foliar application of
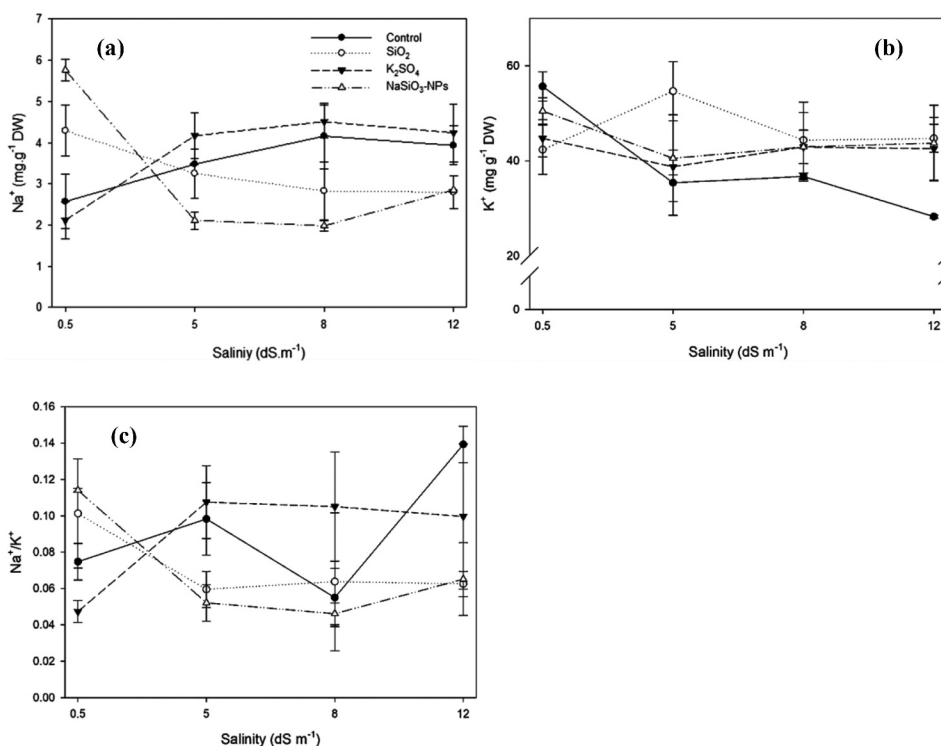
Figure 5. Leaf sodium content (Na^+) (A), and potassium content (K^+) (B), and sodium to potassium ratio (Na^+/K^+) of potato plants grown at salinity stress and foliar application of anti-stress compounds. NPs: nano-particles. The vertical bars represent the parameter's mean ± S.E. n = 3.

antistress compounds was also significant on leaf K^+ content (Table S3). The highest leaf Na^+ content was obtained by the application of K_2SO_4 at 8 dS.m^{-1} (Figure 5A). Under the control conditions, K_2SO_4 reduced leaf Na^+ content by 49%. In contrast, at 5 and 8 dS.m^{-1}, the application of $NaSiO_3$-NPs reduced leaf Na^+ content by 64 and 160% compared to the control (Figure 5A). Leaf K^+ content showed a descending trend by increasing the salinity levels (for instance, a 20% decrease at 12 dS.m^{-1} under the control conditions) (Figure 5B). Salinity decreased leaf K^+ content by 97% at 12 dS.m^{-1} compared with the control, but the application of SiO_2 increased leaf K^+ content by 37% compared to the untreated plants (Figure 5B). Salinity stress significantly increased the Na^+/K^+ ratio. Na^+/K^+ ratio of untreated plants increased by 50% at 12 dS.m^{-1} compared with the control (Figure 5C). The application of SiO_2 reduced the Na^+/K^+ ratio by more than twice at 12 dS.m^{-1} compared with the control.

Antioxidant activity

Leaf antioxidants were significantly influenced by the salinity, foliar application of antistress compounds, and their interaction (Table S2). SiO_2 increased APX 38% compared with the untreated plants at the control treatment (Figure 6A). At 12 dS.m^{-1}, the greatest APX activity was recorded in $NaSiO_3$-NPs- followed by K_2SO_4-treated plants by 120 and 41% over the untreated plants, respectively (Figure 6A). Salinity stress at 5 dS.m^{-1} significantly decreased leaf POX activity of untreated plants, while the application of $NaSiO_3$-NPs increased the POX activity by 90% compared with the control (0.5 dS.m^{-1}) (Figure 6B). Nevertheless, the higher salinity levels decreased POX activity.
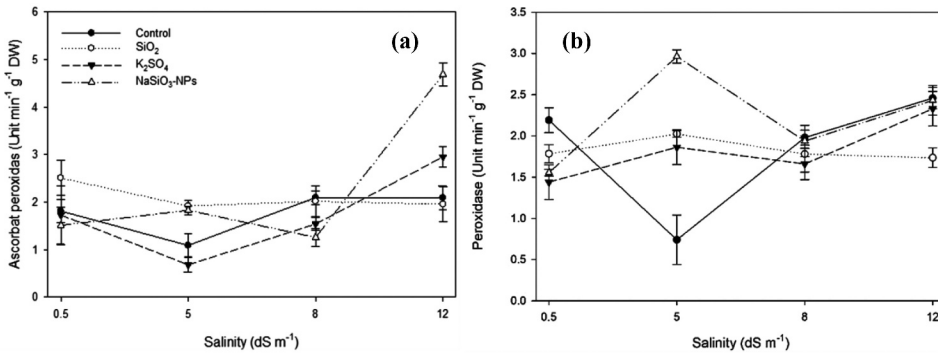
Figure 6. Leaf Ascorbate peroxidase (APX) (A), and peroxidase (POD) (B) activity of potato plants grown at salinity stress and foliar application of anti-stress compounds. NPs: nano-particles. The vertical bars represent the parameter's mean ± S.E. n = 3.
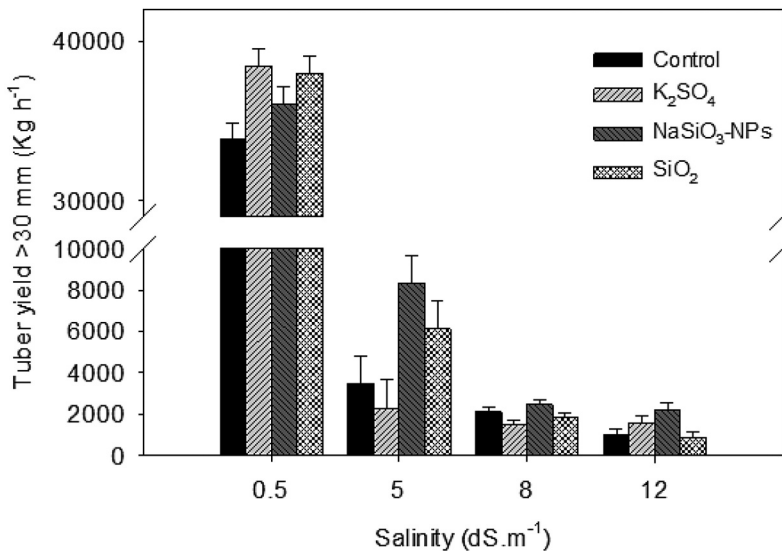

Figure 7. Tuber yield (>30 mm) of potato plants grown at salinity stress and foliar application of antistress compounds. NPs: nano-particles. The vertical bars represent the mean ±S.E.

Tuber yield

With increasing salinity stress, the yield of tubers larger than 30 mm drastically decreased. Tuber yield of 36 t.ha^{-1} under non-stress condition was diminished to 1.4 ton. ha^{-1} at 12 dS.m^{-1} (Figure 7); however, the application of antistress compounds improved the tuber yield. Under control conditions, the application of K_2SO_4 and SiO_2 increased the tuber yield by 13 and 12%, respectively. In contrast, the tuber yield was increased by 127% at 12 dS.m^{-1} by applying $NaSiO_3$-NPs compared with the control plants (Figure 7).

Discussion

Salinity stress reduces plant growth by inhibiting cell division and expansion and disrupting physiological and biochemical processes (Hajiboland, Norouzi, and Poschenrieder 2014). Under saline conditions, the plant water status is disrupted. It has been reported the application of silicon improved the plant water status under saline conditions through a decrease in cell sap concentration, indicating

a positive role of silicon in preserving water in the plant (Liang YC 1999). In tomato (*Solanum lycopersicum*) and wheat (*Triticum aestivum*), the silicon-treated plants showed an increase in relative water content compared with the control plants (Romero-Aranda, Jurado, and Cuartero 2006).

The mitigating effects of silicon under salinity conditions are not always imposed by preventing sodium and chlorine entry (Romero-Aranda, Jurado, and Cuartero 2006). For instance, it has been observed that silicon did not reduce sodium and chlorine amounts in tomato leaves but increased leaf water storage. This water content further dilutes salts and reduces salt toxicity, and improves plant growth (Romero-Aranda, Jurado, and Cuartero 2006). The present study showed that increasing salinity up to 5 dS.m^{-1} relatively improved the leaf RWC compared with the control plants. However, leaf RWC decreased with increasing the salinity intensity. Silicon has been found to improve wheat leaves RWC under salinity stress but did not affect the control plants (Zhu and Gong 2014). The results showed there was no significant effect on the RWC of potato leaves in the present study. However, the application of NaSiO$_3$-NPs increased the osmotic potential of the leaf. This indicates that silicon might improve the plant growth and tuber yield in potato plants by preventing the entry and accumulation of Na$^+$ ions. The role of salt dilution and water uptake was slight in this plant.

High levels of sodium damage the plant cell metabolism that slows down the growth, and hasten the production of the ROSs. Under salt stress conditions, a plant has to spend more energy to maintain a higher concentration of cytosolic potassium and a lower sodium concentration, which can reduce plant growth and productivity (Zhu and Gong 2014). Silicon can reduce sodium accumulation in the roots or shoots. It has been observed that the application of silicon reduced sodium and chloride and increased potassium ions in barley (*Hordeum vulgare*) and oat (*Avena sativa*) under saline conditions, resulting in a more equitable distribution of sodium and potassium in the root sections (Wang and Han 2007).

In the present study, salinity stress increased sodium and reduced potassium concentration in potato leaves. Shahzad et al. (2013) also observed that the sodium concentration of bean leaf (*Vicia faba*) significantly increased under salinity stress but improved with the application of silicon. The present study also showed that NaSiO$_3$-NPs application reduced the concentration of potato leaf sodium. Furthermore, antistress compounds, especially silicon, increased leaf potassium content compared with the control plants under salinity stress. The Na$^+$/H$^+$ antiporters play an essential role in maintaining low sodium concentrations by removing sodium from the cytosol or placing it in the vacuole supplied by ATP from H$^+$-ATPase membrane proteins. The ATPase pump activity was increased by applying silicon, which facilitates the expulsion of sodium from the cell (Zhu and Gong 2014).

Foliar application of K$_2$SO$_4$ significantly increased N$_p$, g$_s$, and g$_m$ compared with the untreated plants at salinity stress; however, they were suppressed by increasing the salinity level. NaCl can alter the cell's fine structure, *e.g.*, the chloroplasts, thylakoids membranes, and grana (Parida and Das 2005). Silicon may alleviate salt stress damages by protecting the photosynthetic apparatus partly due to increased K$^+$ uptake, improving antioxidant activities, and inhibition of excess Na$^+$ uptake under saline conditions (Liang Yongchao 1999a). The addition of silicon restored the chlorophyll content of salt-stressed wheat plants to or even higher than the control level (Tuna et al. 2008). The positive effects of silicon on alleviating the salinity stress effects on the photosynthetic apparatus, activity, and pigments have also been found in tomato and *Spartina densiflora* (Al-aghabary, Zhu, and Shi 2005; Mateos-Naranjo, Andrades-Moreno, and Davy 2013). Studies show that excessive ROS accumulation promotes chlorophyll degradation and reduces photosynthetic function (Woo et al. 2004). Silicon by reducing the regeneration of ROS through activating antioxidant enzymes may prevent the degradation of chlorophyll.

Accumulation of salt under salinity stress restricts the CO$_2$ supply, and consequently, inhibits the N$_p$ (Mahmoud et al. 2019a). Inhibition of photosynthesis can occur by either stomatal or non-stomatal factors, depending on the severity of the stressed conditions and the plant genotype (Lawlor and Cornic 2002). Furthermore, the electron transport chain, enzymatic activities, and photophosphorylation can also be adversely affected by salinity (Fadzilla, Finch, and Burdon 1997; Liang YC 1999;

Steduto et al. 2000). However, silicon has been observed to improve chlorophyll formation, net assimilation rate, intercellular CO_2 concentration, and stomatal conductance under salinity conditions (Mahmoud et al. 2019b, 2019a; Shah, Houborg, and McCabe 2017; Song et al. 2014; Yeo et al. 1999). In the present study, g_s was affected more than g_m exposed to salinity stress. Furthermore, the reduction in C_i and C_i:C_a ratio at the higher salt levels also showed that the carboxylation process was inhibited by the lower availability of CO_2, which indicates the stomatal factors more inhibited the N_p.

Increasing the nanoparticles' effectiveness compared to the conventional forms has been attributed to their unique properties, reactivity, and transportability in the plant tissues (Haghighi and Pessarakli 2013; Kafi et al. 2019). One reason for a decrease in the leaf ion leakage and MDA content treated with nanoparticles at 12 dS.m^{-1} and its relative difference with silicon and potassium sulfate treatments was nanoparticles' higher biological activity and high permeability in the plant tissues. Researches have linked the loss of cell membrane stability to increase membrane lipid peroxidation under stress conditions (Shabala and Cuin 2008). It has been reported that silicon reduces lipid peroxidation and helps to maintain membrane stability, and decreases membrane permeability under salinity stress (Liang et al. 1996; Zhu et al. 2004).

In the present study, the proline content of potato leaves was increased with increasing salt stress levels. Proline also plays a role in reducing the toxic effects of high concentrations of Na$^+$ on metabolites and the cell membranes and in scavenging ROSs to alleviate the detrimental effects of oxygen radicles under salinity stress (Mahmoud et al. 2019a; Munns and Tester 2008). The effects of silicon on different plant species and environmental conditions can be varied under salinity conditions. Application of silicon reduced leaf proline content of different plants; including soybean (*Glycine max*), wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), and sorghum (*Sorghum bicolor*) under salinity conditions, but a short-term application of silicon under salinity stress also increased compatible solutes, indicating their role in regulating cell osmotic potential (Gunes et al. 2007; Lee et al. 2010; Soylemezoglu et al. 2009; Tuna et al. 2008; Yin et al. 2013). The results showed that the application of NaSiO$_3$-NPs increased the leaf proline content of salinity-stressed plants compared with the control, possibly indicating the plant's effort to conserve leaf water and protect the cell against water desiccation, which the higher ψ_O under such salinity level may confirm this role. However, more investigation is required to elucidate the relationship between compatible solute metabolism and silicon (Zhu and Gong 2014).

NaSiO$_3$-NPs application increased POX and APX activity compared with the untreated plants. Salinity stress leads to membrane lipid peroxidation and oxidative damage by increased ROS production (Fadzilla, Finch, and Burdon 1997; Hernandez et al. 1993; Wang et al. 2013). Silicon induced the SOD activity and decreased MDA content in salt-stressed barley (*Hordeum vulgare*) plants (Liang YC 1999b). Silicon applications differently influenced antioxidants activity. For example, working on cucumber (*Cucumis sativus*) under salinity stress, the application of silicon enhanced the activity of glutathione reductase and ascorbate peroxidases, but the activity of catalase remained unaltered (Zhu et al. 2004). Soylemezoglu et al. (2009) have also reported that APX, CAT, and SOD activity were increased, decreased, and remained unchanged, respectively, in salt-stressed grapevine by application of silicon. We also observed that the application of silicon differently affected APX and SOD activity at different salinity levels so that the greatest activity of APX and SOD was recorded in NaSiO$_3$-NPs-treated plants at 12 and 5 dS.m^{-1}, respectively. Silicon can increase the activity of plasma membrane H$^+$-ATPase that might be related to a reduction in oxidative damage to proteins under salinity stress conditions (Gong, Randall, and Flowers 2006). However, the silicon-mediated enhancement in antioxidant activity may also be related to the involvement of silicon in the metabolic and physiological activities of plants, as it has been observed in some plants (Al-aghabary, Zhu, and Shi 2005; Gunes et al. 2007; Hashemi, Abdolzadeh, and Sadeghipour 2010; Liang et al. 2003; Zhu et al. 2004).

Due to the high salinity levels that were applied in this experiment, the loss of tuber yield was not unexpected. Accordingly, the results of other studies on potatoes in a stressful environment have shown the detrimental effects of stress on tuber yield (Hussein, El-Faham, and Alva 2012; Kafi et al. 2019). The yield reduction can be associated with both the reduction of the tuber weight and

number per plant (Jha, Choudhary, and Sharda 2017). The lower tuber yield under salinity stress is due to Na^+ and Cl^- accumulation in the plant cells (Nagaz et al. 2008). It seems that the application of $NaSiO_3$-NPs during the growing season has been coupled with the period of determination of the number and size of physiological sinks in the soil, which ultimately improved tuber yield per unit ground area. Supplying more photoassimilates possibly obviated the reduced production of carbohydrates to fill the tubers under salinity stress. Kafi et al. (2019) reported that photosynthesis and quantum yield were increased using nano-silicate and potassium sulfate compounds under salinity stress compared with the control plants. A long-term study on the field-grown potato plants also showed that the tuber yield was increased by 12% by applying K_2O_3Si (Liang et al. 2015).

Conclusion

The results showed that salinity negatively affected cell membrane and ion leakage of potato plant cells. However, the results indicated the beneficial effects of antistress compounds on alleviating the adverse effects of salinity on the potato plant physiology, growth, and tuber yield. Foliar application of nano-sodium silicate, potassium sulfate, and silicon compounds reduced the effects of salinity on traits such as leaf net photosynthetic rate, electrolyte leakage, MDA content, and Na^+/K^+ ratios. However, the effects varied between the treatments. These compounds significantly increase the retention of water in leaves and stimulated the antioxidant enzyme activity of salt-stressed plants. The tuber yield was improved, especially by applying $NaSiO_3$-NPs at 12 $dS.m^{-1}$ compared with the control plants. However, they could not manage the adverse effects of salinity to obtain a desirable tuber yield level. The improvement of the potato plant performance using the antistress compounds can briefly be due to: (a) the improved photosynthetic rate, (b) the higher K^+/Na^+ ratio, (c) the higher antioxidant enzymes activity, and (d) the increased soluble carbohydrates and compatible solute content, resulting in better salinity tolerance of the plants. According to the results, it can be concluded that silicon application will be an effective strategy to reduce the effects of salinity on the potato growth under stress conditions, and the use of nanoparticles will increase the efficiency of which. Therefore, such an effective strategy has been elucidated as a possible approach to face the increasing salinity issue but not more than 5 $dS.m^{-1}$. Nevertheless, further studies are recommended to carry out in different soil types, compound doses, and possible ecological impact.

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