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MJA designed the experiment; HZ performed the experiments and wrote the paper; AAJ: performed laboratory analysis; VA and AMT: analyzed data and helped writing and editing the manuscript

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ORIGINAL RESEARCH PAPER

The effect of methyl jasmonate and sodium silicate on the mineral composition of *Solanum lycopersicum* L. grown under salinity stress

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Abstract

Soil and water salinities have become a major problem for agricultural activities as they can negatively affect crop yield in different ways. The present study aimed to investigate the effect of methyl jasmonate (MeJA) and sodium silicate (Si) on the content of selected mineral elements in the leaves of tomato plants (*Solanum lycopersicum* L.) under salinity stress. A fully randomized block experimental design was used with three factors, including three levels of salinity (0, 4, and 6 dS m^{-1}), Si (0, 4, and 8 mM), and MeJA (0, 5, and 7.5 μM). Main plots were allocated to the three levels of salinity and the subplots were devoted to MeJA and Si levels. An increase in MeJA concentration was related to an 8.5% increase in leaf P content. When MeJA was applied at high salinity levels, the Na, Ca, and Mn concentrations decreased, but Fe increased. The application of 8 mM Si reduced the concentration of Cl by 50% at a salinity level of 4 dS m^{-1} in plants not treated with MeJA. The triple interaction of the factors was significant for K, Mg, and Cl ($p < 0.01$). Furthermore, the treatments used did induce significant differences in leaf Zn and N concentrations. The results indicate that MeJA and Si can partially mitigate the adverse impacts of salinity stress and contribute to an increased uptake of nutrients under saline conditions.

Keywords

salt stress mitigation; nutrients; leaves; jasmonates; silicon

Introduction

Soil and water salinity are the main obstacle and limiting factors for agriculture development in many countries around the world. Approximately 33 M ha of all agricultural lands (55%) in Iran are influenced by soil and water salinity [1]. Salinity is a major environmental stress that adversely affects plant metabolism and growth [2,3]. Yield reductions caused by salinity occur on an estimated 50% of crop lands worldwide [4]. Salinity affects plant physiological functions through changes in the water balance and ionic status in cells [5]. Under saline conditions, Na and Cl concentrations are usually higher than other mineral elements resulting in reduced uptake of essential nutrients including Ca, Mg, Mn, and K [6]. High concentrations of Na and Cl are usually the most injurious and predominant elements. High levels of Na cause direct damage to plant cell membranes, disrupt cell metabolism, and impair plant growth, fertility, and free radical generation [7]. Plants that are exposed to salinity stress should be able to optimally maintain K and Na at high and low levels, respectively [8]. The application of

Tab. 1 The results of water and soil analyses.

Water	
EC (µS cm^{-1})	280.00
TDS (mg L^{-1})	171.38
pH	7.35
CO_3^{2-} (mEq L^{-1})	0.00
HCO_3^- (mEq L^{-1})	0.85
Cl^- (mEq L^{-1})	0.80
SO_4^{2-} (mEq L^{-1})	0.82
Total anions (mEq L^{-1})	2.47
Ca^{2+} (mEq L^{-1})	1.25
Mg^{2+} (mEq L^{-1})	0.55
Na^+ (mEq L^{-1})	0.86
K^+ (mEq L^{-1})	0.01
Total cations (mEq L^{-1})	2.67
SSP	32.21
SAR	0.91
TH (mg L^{-1})	90.00
TA (mg L^{-1})	42.50
Soil	
EC (µS cm^{-1})	798
pH	7.25
TNV (%)	68.0
OC (%)	0.31
OM (%)	0.53
TN (%)	0.03
P (µg g^{-1})	3.28
K (µg g^{-1})	0.79
Clay (%)	13.5
Silt (%)	9.20
Sand (%)	77.3
Texture	Sand
Cu (µg g^{-1})	0.20
Mn (µg g^{-1})	5.30
Fe (µg g^{-1})	3.60
Zn (µg g^{-1})	0.80

According to water analysis, the EC of the applied water was 280 µS cm^{-1}. Using sodium chloride salt and calcium in 2:1 ratio, water EC was adjusted to 4 and 6 dS m^{-1}. The substrate was composed of coco–peat and perlite and the plants were first planted in seedling trays and when they reached the height of 10 cm, they were transplanted in the pots. They were irrigated with water having EC of 280 µS cm^{-1} to stimulate germination. For the water with an EC of 0, distilled water was 280 µS cm^{-1}. EC – electrical conductivity; TDS – total dissolved solids; SSP – sodium soluble percent; SAR – sodium adsorption ratio; TL – total hardness; TA – total alkalinity; TNV – total neutralizing value; OC – organic carbon; OM – organic matter content; TN – total nitrogen.

silicon can contribute to reduced Na and Cl accumulation in plants, increased K content and boost antioxidant activity in salinity-stressed plants [1,9–11]. Silicon supply is associated with a decreased mobilization of Na, Cl, and B from the roots to the stems of tomato plants in sodic soils [12]. Shahrzad et al. [13] reported that salinity causes Na^+ accumulation in the apoplast of leaves, but silicon application effectively reduces this accumulation. The application of silicon has been shown to decrease and increase Na and K contents, respectively in the stems of tomato plants [14]. Although it had no effect on the Na and Cl concentrations in the leaves of tomato, it did improve the water status [9].

Plants employ various methods and physiological mechanisms to adapt to salinity stress and to mitigate its adverse impacts [15,16]. Jasmonate is one of the most important plant growth regulators with different roles in plant growth and the alleviation of stress impacts on plants. Furthermore, jasmonate plays a crucial role in defense mechanisms against environmental stresses such as heavy metal and ion toxicities, drought, salinity, and low temperature [16–19]. Salinity stress can significantly disrupt the physiological and biochemical activity of the tomato plant. It has been demonstrated that methyl jasmonate (MeJA) alleviates the harmful effects of salinity in tomato by inducing biochemical and physiological resistance mechanisms [20]. Tomato production in different parts of Iran is limited by a variety of stresses such as salt, drought, cold, and heat. To the best of our knowledge, no study to date has investigated the effects of the simultaneous use of MeJA and sodium silicate (Si) on plants under salinity stress. The present study therefore aimed to investigate the combined effects of MeJA and Si on mineral content of tomato leaves under salinity stress.

Material and methods

The study was carried out at a commercial greenhouse in Jahrom, Fars Province, Iran, during 2017–2018. The greenhouse conditions were as follows: area of 300 m^2, thermostatic heating system, fan and pad cooling system with day and night temperatures of 26 ±3°C and 17 ±2°C, respectively, a relative humidity of 67 ±3%, and a plastic cover. The results of soil and water analyses are presented in Tab. 1. The experiment was organized with a fully randomized block design, and a split-plot factorial arrangement having three replications. The factors studied included three levels of salinity (0, 4, and 6 dS m^{-1}), MeJA [$C_5H_6(CH_2CH = CHC_2H_5)CH_2CONCH_3$] at 0, 5, and 7.5 µM and Si (supplied as Na_2SiO_3) at 0, 4, and 8 mM. The salinity factor was allotted to the main plots and the two other factors were allotted to the subplots.

Seeds of tomato *Solanum lycopersicum* L. 'Dafnis', a hybrid F_1 produced in India with 99% purity and 94% germination, were sown on a seed planting tray. After germination, seedlings were transferred to pots at the five–six leaf stage. The pots were filled with 8 kg of sand and arranged with an in-row and inter-row spacing of 35 cm and 75 cm, respectively. Two weeks after transplanting, salinity treatments were applied manually, until the end of the life cycle of the plants. The saline solution was composed of sodium and calcium chloride salts in a 2:1 ratio. Both Si and MeJA were applied three times at 1, 7, and 15 weeks after transplanting. All plants were fertigated according to Tab. 2. In addition, chelated iron fertilizer (350 g) and 0.04 kg of a mix of trace elements (containing 1.45% B, 3.2% Cu, 7.5% Fe, 8.15% Mn, 4.6% Mo, and 4.5% Zn) were dissolved in 500 L of water

Tab. 2 Fertigation programs used in Iran and China.

		Type and composition of fertilizer (mg dm^{-3}) and manufacturing country					
Planting type	Fertigation time (weeks after sowing)	Calcium nitrate $Ca(NO_3)_2$ Iran	Potassium nitrate KNO_3 Iran	Ammonium nitrate $(NH_4)\ (NO_3)$ China	Mono ammonium phosphate (MAP) $NH_4H_2PO_4$ China	Petassium sulfate K_2SO_4 China	Magnesium sulfate $MgSO_4$ China
Fall planting	1–4	15	16.0	1.5	5.5	-	12.5
	5–8	15	16.0	-	5.5	-	12.5
	9–10	15	16.0	-	5.5	-	12.5
	11–12	10	11.0	-	5.5	17.0	12.5
	13–14	10	6.0	-	5.5	27.0	12.5
	15–18	10	3.5	-	5.5	16.5	12.5
Total consumed fertilizer		75	66.5	1.5	33.0	60.5	75.0

and used for plant fertigation. During the experiment, leaves were sampled once at the late-flowering stage to measure the characteristics to be analyzed.

Leaf samples were dried in an oven at 75°C in order to determine mineral element concentrations. One g of each sample was placed in a furnace at 550°C for 6 h and then the ash was dissolved in 100 mL of 10% HCl. P concentrations were measured by a colorimetric method measuring absorbance at 459 nm [21]. The concentrations K and Na were measured by flame emission photometry (Jenway PFP7, UK). The final concentrations of these elements were calculated by the use of a standard curve [22]. The concentrations of Ca, Fe, Mg, Mn, Zn, and Cu in the digests were determined by atomic absorption spectrophotometry (Sensa AA, GBC, Australia) [23]. To determine Cl concentrations, a silver nitrate and potassium chloride method was used [22]. Total N content was assayed by the Kjeldahl method [24].

The normality of the data sets was evaluated by the Kolmogorov–Smirnov test using SPSS 25.0 software (SPSS Inc., Chicago, IL, USA). Analysis of variance was performed on the data using Statistical Analysis Software (version 9.1 for Windows; SAS Institute, Cary, NC, USA) and the treatment means were compared by the LSD test ($p < 0.05$). A heat map of the correlations was conducted using MetaboAnalyst [25].

Results

The ANOVA demonstrated that there were significant differences between the three levels of MeJA in P content ($p < 0.05$) and in Ca and Na concentrations with Si supply ($p < 0.01$; Tab. 3). In addition, the results revealed that the double interactions between MeJA with salinity were significant for Ca, Na, Fe, Cu, and Mn concentrations ($p < 0.01$). Moreover, the ANOVA showed that the triple interaction between the three factors was significant for K, Mg, and Cl concentrations ($p < 0.01$). According to Keppel and Wickens [26], when the triple or double interactions of factors are significant, then less attention can be paid to the main effects and the focus should be on the main interaction effects.

P, Ca, and Na

As the MeJA level increased, the P concentration also increased significantly (Fig. 1). The highest P value (0.26%) was observed in the plants treated with 7.5 µM MeJA. However, it was not significant in the 5 µM MeJA treatment. Calcium concentrations showed significant differences between the 0 mM Si and the two other Si treatments (Fig. 2).

Tab. 3 ANOVA of mineral element concentrations in tomato leaves from plants treated with Si and MeJA under salinity stress.

Source of variation	Degree of freedom	Mean squares										
		P	Ca	Na	Fe	Cu	Mn	K	Mg	Cl	Zn	N
Replication (R)	2	0.0035^{ns}	0.126^{ns}	0.0005^{ns}	67.4^{ns}	3.81^{ns}	108.0^{ns}	0.08^{ns}	0.022*	0.002^{ns}	70.2^{ns}	0.025^{ns}
Salinity (A)	2	0.0054^{ns}	0.202^{ns}	0.0520**	2,575.4^{ns}	79.78^{ns}	2,041.0^{ns}	0.05^{ns}	0.001^{ns}	1.497**	995.2^{ns}	0.259^{ns}
Error *a*	4	0.0019	0.035	0.0007	1,181.4	20.94	464.5	0.06	0.002	0.005	291.1	0.105
Na_2SiO_3 (B)	2	0.0012^{ns}	0.164**	0.0048**	93.7^{ns}	3.24^{ns}	48.5^{ns}	0.30**	0.064**	0.278**	40.1^{ns}	0.165^{ns}
MeJA (C)	2	0.0036*	0.091^{ns}	0.1736**	1,156.7*	35.71**	107.6^{ns}	0.16*	0.023**	0.072**	38.4^{ns}	0.014^{ns}
A × B	4	0.0014^{ns}	0.010^{ns}	0.0007^{ns}	92.9^{ns}	2.17^{ns}	12.2^{ns}	0.21**	0.007^{ns}	0.297**	80.8^{ns}	0.149^{ns}
A × C	4	0.0009^{ns}	0.124**	0.0455**	1,529.3**	28.16**	914.1**	0.05^{ns}	0.034**	0.152**	81.3^{ns}	0.168^{ns}
B × C	4	0.0009^{ns}	0.008^{ns}	0.0007^{ns}	37.2^{ns}	0.46^{ns}	68.0^{ns}	0.03^{ns}	0.027**	0.206**	7.0^{ns}	0.066^{ns}
A × B × C	8	0.0004^{ns}	0.024^{ns}	0.0010^{ns}	241.2^{ns}	0.55^{ns}	15.2^{ns}	0.18**	0.020**	0.183**	24.0^{ns}	0.073^{ns}
Error *b*	48	0.0009	0.028	0.0006	265.4	5.76	78.7	0.04	0.003	0.005	58.0	0.072
CV (%)		12.4	9.6	12.9	9.5	18.6	8.5	7.7	11.5	13.3	17.5	8.9

* and ** indicate significance at 5% and 1% levels, respectively; ns – nonsignificant.

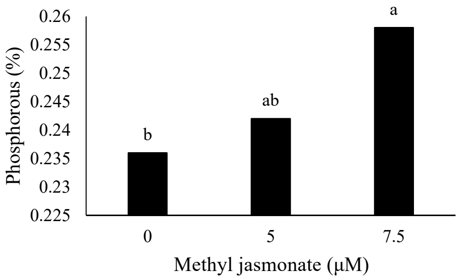

Fig. 1 Effect of methyl jasmonate on phosphorus percentage in tomato leaves.

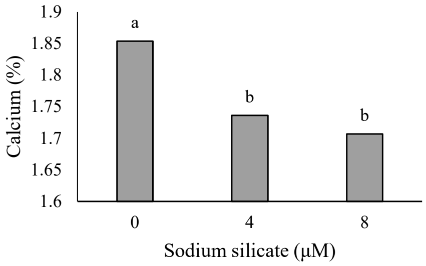

Fig. 2 Effect of sodium metasilicate on calcium percentage in tomato leaves.

Ca concentrations significantly decreased with increasing the Si concentrations. The lowest Ca concentrations of 1.71% and 1.74% were with the 8 and 4 mM Si, respectively. The interaction of salinity and MeJA for this element indicated that at salinity levels of 0 and 4 dS m^{-1}, an increase in MeJA first boosted Ca concentration but then it declined (Tab. 4). At a salinity level of 6 dS m^{-1}, an increase in MeJA resulted in a significant decline of Ca concentrations so that the lowest value (1.54%) was in plants treated with 6 dS m^{-1} salinity and 7.5 µM MeJA. The highest value (1.94%) was found with the interaction of 0 dS m^{-1} salinity and 5 µM MeJA. The results showed that as Si level increased, the Na concentration also increased (Fig. 3). The highest Na concentration (0.2%) was observed in plants treated with 8 mM Si. However, there was no significant difference between the 0 and 4 mM Si treatments. Moreover, the interaction of salinity and MeJA for Na concentrations showed that at salinity levels of 4 and 6 dS m^{-1}, greater MeJA treatment was associated with lower Na concentrations. The highest Na value (0.39%) was observed from the interaction of 6 dS m^{-1} salinity and the 0 µM MeJA treatment, followed by the interaction of 4 dS m^{-1} salinity and 0 µM MeJA. The other treatments had the lowest Na concentrations. Si application clearly reduced Na concentrations in the plants.

Fe, Cu, and Mn

The interaction of salinity and MeJA revealed that at 6 dS m^{-1} salinity, higher MeJA concentrations were related to significantly higher Fe concentrations, so that

Tab. 4 Effects of the interaction between salinity with MeJA on some mineral element concentrations in tomato leaves. All concentrations are expressed on a dry weight basis.

Salinity (dS m^{-1})	MeJA (µM)	Ca (%)	Na (%)	Fe (µg g^{-1})	Cu (µg g^{-1})	Mn (µg g^{-1})
0	0	1.718 ^{bc}	0.142 ^{c}	171 ^{abc}	11.29 ^{cd}	94.4 ^{bc}
	5	1.943 ^{a}	0.124 ^{c}	161 ^{c}	13.05 ^{bc}	97.2 ^{c}
	7.5	1.779 ^{bc}	0.141 ^{c}	174 ^{abc}	15.45 ^{a}	111.4 ^{a}
4	0	1.789 ^{abc}	0.296 ^{b}	183 ^{a}	10.68 ^{d}	115.9 ^{a}
	5	1.877 ^{ab}	0.144 ^{c}	186 ^{a}	10.48 ^{d}	114.6 ^{a}
	7.5	1.788 ^{abc}	0.139 ^{c}	180 ^{ab}	12.0 ^{cd}	113.2 ^{a}
6	0	1.827 ^{ab}	0.391 ^{a}	143 ^{d}	16.49 ^{a}	110.3 ^{a}
	5	1.630 ^{c}	0.140 ^{c}	167 ^{bc}	12.02 ^{cd}	97.3 ^{b}
	7.5	1.541 ^{d}	0.126 ^{c}	183 ^{a}	14.91 ^{ab}	87.6 ^{c}

Means with at least one similar letter were not significantly different according to the LSD test.

the highest and lowest elemental concentrations of 183 and 143 µg g^{-1} were obtained with 7.5 and 0 µM MeJA, respectively. Other MeJA concentrations did not show any significant effects at other salinity levels. Furthermore, salinity increases up to 4 dS m^{-1} were followed by increased Fe uptake, which may be associated with the function of this element in osmotic adjustment in response to salinity. The interaction of salinity and MeJA shows that at 0 dS m^{-1} salinity, an increase in MeJA concentration resulted in a significant increase in Cu concentrations so that the highest value (15.45 µg g^{-1}) was related to the application of 7.5 µM MeJA. At 6 dS m^{-1} salinity, the highest Cu concentration was 16.49 µg g^{-1} exhibited by plants not treated with MeJA, and at 4 dS m^{-1} salinity, it was the lowest value in all MeJA treatments. According to the interaction of salinity and MeJA, at a salinity level of 6 dS m^{-1}, the increase in MeJA concentration was related to a decline in Mn concentrations, but concentrations of this element significantly increased with MeJA increases at a salinity level of 0 dS m^{-1}. However, different MeJA treatments did not show any significant differences in Mn concentrations at a salinity level of 4 dS m^{-1}. The highest and lowest Mn concentrations were obtained with 0 µM MeJA (115.9 µg g^{-1}) at 4 dS m^{-1} salinity and with 7.5 µM MeJA (87.6 µg g^{-1}) at a salinity level of 6 dS m^{-1}, respectively.

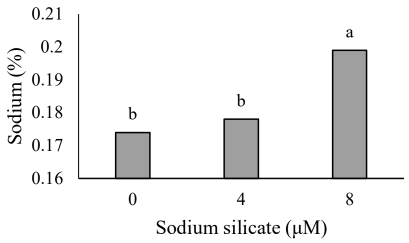

Fig. 3 Effect of sodium metasilicate on sodium percentage in tomato leaves.

K, Mg, and Cl

The triple interaction effects of K, Mg, and Cl are illustrated in Tab. 5. The interaction of salinity, Si, and MeJA was significant for K concentrations. The highest K value was 2.96% observed in plants treated with 6 dS m^{-1} salinity, 4 mM Si, and 7.5 µM MeJA. The lowest was 2.21% in plants treated with 0 dS m^{-1} salinity, 0 mM Si, and 5 µM MeJA. According to the interaction of these three factors, the highest Mg concentrations of 0.73% and 0.67% were obtained from plants subjected to the interaction of 4 dS m^{-1} salinity, 8 mM Si, and 0 µM MeJA and the interaction of 4 dS m^{-1} salinity, 4 mM Si, and 5 µM MeJA, respectively. The lowest Mg concentration was 0.35% noted in plants treated with 4 dS m^{-1} salinity, 8 mM Si, and 7.5 µM MeJA. The interaction of salinity, Si and MeJA indicated the highest Cl concentration (1.33 µg g^{-1}) was in plants simultaneously treated with 6 dS m^{-1} salinity, 8 mM Si, and 5 µM MeJA. The lowest values of Cl concentrations were found for two interactions including 4 dS m^{-1} salinity, 8 mM Si, and 0 µM MeJA and the interaction of 0 dS m^{-1} salinity and 4 mM Si (0.1 µg g^{-1}).

Tab. 5 Effects of the interaction among salinity, Si, and MeJA factors on K, Mg, and Cl concentrations in tomato leaves. All concentrations are expressed on a dry weight basis.

Salinity (dS m^{-1})	Si (mM)	MeJA (µM)	K (%)	Mg (%)	Cl (µg g^{-1})
0	0	0	2.347 $^{\text{fg}}$	0.403 $^{\text{fgh}}$	0.20 $^{\text{hi}}$
		5	2.210 $^{\text{g}}$	0.407 $^{\text{fgh}}$	0.13 $^{\text{i}}$
		7.5	2.370 $^{\text{fg}}$	0.420 $^{\text{e–h}}$	0.50 $^{\text{ef}}$
	4	0	2.733 $^{\text{a–e}}$	0.500 $^{\text{b–e}}$	0.20 $^{\text{hi}}$
		5	2.810 $^{\text{abc}}$	0.517 $^{\text{bc}}$	0.30 $^{\text{gh}}$
		7.5	2.790 $^{\text{a–d}}$	0.467 $^{\text{b–f}}$	0.10 $^{\text{i}}$
	8	0	2.473 $^{\text{d–g}}$	0.510 $^{\text{bcd}}$	0.17 $^{\text{i}}$
		5	2.617 $^{\text{b–f}}$	0.523 $^{\text{b}}$	0.55 $^{\text{e}}$
		7.5	2.773 $^{\text{a–d}}$	0.497 $^{\text{b–e}}$	0.70 $^{\text{d}}$
4	0	0	2.377 $^{\text{fg}}$	0.403 $^{\text{fgh}}$	0.40 $^{\text{fg}}$
		5	2.420 $^{\text{efg}}$	0.357 $^{\text{gh}}$	0.83 $^{\text{c}}$
		7.5	2.800 $^{\text{a–d}}$	0.380 $^{\text{gh}}$	0.40 $^{\text{fg}}$
	4	0	2.490 $^{\text{c–g}}$	0.527 $^{\text{b}}$	0.85 $^{\text{c}}$
		5	2.540 $^{\text{bc–g}}$	0.667 $^{\text{a}}$	0.50 $^{\text{ef}}$
		7.5	2.300 $^{\text{fg}}$	0.347 $^{\text{h}}$	0.40 $^{\text{fg}}$
	8	0	2.847 $^{\text{ab}}$	0.730 $^{\text{a}}$	0.10 $^{\text{i}}$
		5	2.373 $^{\text{fg}}$	0.373 $^{\text{gh}}$	0.70 $^{\text{d}}$
		7.5	2.800 $^{\text{a–d}}$	0.348 $^{\text{h}}$	0.40 $^{\text{fg}}$
8	0	0	2.337 $^{\text{fg}}$	0.427 $^{\text{d–h}}$	0.85 $^{\text{c}}$
		5	2.843 $^{\text{ab}}$	0.420 $^{\text{e–h}}$	0.40 $^{\text{fg}}$
		7.5	2.550 $^{\text{b–f}}$	0.473 $^{\text{b–f}}$	0.85 $^{\text{c}}$
	4	0	2.430 $^{\text{efg}}$	0.433 $^{\text{c–g}}$	0.50 $^{\text{ef}}$
		5	2.350 $^{\text{fg}}$	0.480 $^{\text{b–f}}$	0.40 $^{\text{fg}}$
		7.5	2.960 $^{\text{a}}$	0.473 $^{\text{b–f}}$	0.83 $^{\text{c}}$
	8	0	2.747 $^{\text{a–e}}$	0.480 $^{\text{b–f}}$	1.03 $^{\text{b}}$
		5	2.773 $^{\text{a–d}}$	0.523 $^{\text{b}}$	1.33 $^{\text{a}}$
		7.5	2.723 $^{\text{a–e}}$	0.500 $^{\text{b–e}}$	0.87 $^{\text{c}}$

Means with at least one similar letter were not significantly different according to the LSD test.

N and Zn

According to the results of analysis of variance, none of the effects including simple, double, and triple interactions of the three factors were significant for N and Zn concentrations.

Association and correlation analyses

The association analysis showed that EC was significantly correlated with P ($r = -0.314$, $p = 0.004$), Ca ($r = -0.253$, $p = 0.022$), Na ($r = 0.389$, $p = 0.0001$), Zn ($r = 0.326$, $p = 0.003$), and Cl ($r = 0.563$, $p = 0.0001$) concentrations (Tab. 6). The strongest associations were observed between EC and Cl, Na and Zn. Si has a significant association with Mg, K, Cl, and Ca concentrations; nonetheless, the association with Ca was inverse. MeJA showed the strongest association with Na concentrations ($r = -0.668$, $p = 0.0001$), and furthermore MeJA had a significant correlation with Fe and P concentrations. Correlation analysis was used to investigate the relationships between the elements analyzed (Fig. 4). The highest correlation coefficient between these elements was for Zn and Cu ($p < 0.01$). Zn was also significantly but negatively correlated with Mn and Fe ($p < 0.01$),

Tab. 6 Association analysis of treatment factor with elemental concentrations in tomato leaves.

Treatment	P	Ca	Na	Fe	Cu	Mn	K	Mg	Cl	Zn	N
EC (dS m^{-1})	−0.3**	−0.25*	0.29**	−0.02 ^{ns}	0.08 ^{ns}	0.02 ^{ns}	0.08 ^{ns}	−0.02 ^{ns}	0.56**	0.33**	−0.1 ^{ns}
Si (mM)	0.10 ^{ns}	−0.3**	0.110 ^{ns}	−0.02 ^{ns}	0.04 ^{ns}	0.05 ^{ns}	0.31**	0.36**	0.24*	0.01 ^{ns}	0.21 ^{ns}
MeJA (μM)	0.25*	−0.1 ^{ns}	−0.67**	0.25*	0.13 ^{ns}	−0.10 ^{ns}	0.19 ^{ns}	−0.22 ^{ns}	0.10 ^{ns}	−0.004 ^{ns}	0.06 ^{ns}

* and ** indicates significance at 5% and 1% levels, respectively; ns – nonsignificant.

Ca and Cl ($p < 0.05$). Fe was significantly correlated with Na and Cu ($p < 0.01$). Mn was significantly correlated with Na and Ca ($p < 0.01$), N and Fe ($p < 0.05$). P had a significant negative correlation with Na concentration.

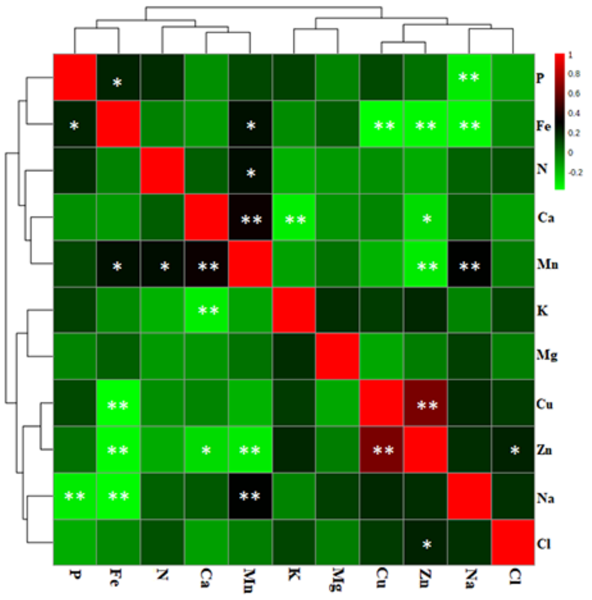

Fig. 4 Heat map of the correlations among the elemental concentrations in tomato leaves. * and ** indicate significance at the 5% and 1% levels, respectively.

Discussion

Our findings have shown that Si treatment improved salt tolerance in the tomato plants tested. This finding confirms that of Haghighi and Pessarakli [1] which revealed that silicon in the form of nano-silicon or silicon can affect salt tolerance and this effect has no relationship to the form of the silicon or silica supplied. The mechanism of the alleviation effect of silicon possibly contributes to its root deposition and a decrease in apoplastic bypass flow and metal-binding behavior, which could lead to a decrease in uptake and translocation of salts and metallic elements from the roots to shoots [27]. Satti et al. [28] suggested that the addition of K and Ca can improve the growth and yield of tomato plants growing in a saline medium. This observation may indicate the protective role of cellular contents and/or soil-borne K and Ca against the adverse effects of Na^+ ions in tomato plants. In the present study, we observed that treatment of tomato plants under saline conditions with MeJA and Si could increase the K content of leaves. However, the Ca content increased with MeJA treatment at lower concentrations and then declined. Si treatment has been shown to improve both the K and Ca concentrations in roots and shoots of wheat plants grown under high NaCl conditions [10], similar to our study. Si treatment improved the K status of plants, but the difference in the effects on Ca concentrations may be related to the different plant species employed and the different organs investigated. Our results showed that the application of Si improved K uptake. As K uptake by plants increases, more K is allocated to the fruits. Potassium is an essential cytoplasmic element and is usually regarded as a key element in saline conditions because of its function in osmotic adjustment and competition with Na. Thus, it is believed that a low Na:K ratio in leaves is closely related to salinity resistance. The increase in K content reflects higher selection potential for K mobilization to shoots, which is suggested as a mechanism for salinity tolerance [11,29,30]. It was found that Na content increased but Ca content decreased as the salinity level and Si application was increased. Therefore, the hydraulic resistance between stems and fruits increased with an increase in the level of salinity. As a result, the mobilization of water and Ca is not considered essential, and Na accumulation in salinity-exposed plants results in a decline in Ca and K contents. Although Na^+ can contribute to increasing turgor, it cannot replace essential ions, such as K^+ and Ca^{2+} in their specific functions, which include enzyme activation and protein synthesis. Therefore, the toxic effects of Na^+ cannot be caused only by the direct effects of Na^+; rather, they may be related to the decrease in such essential nutrients as K and Ca in plants [8,31]. The application of salinity up to 4 dS m^{-1} resulted in higher Mn uptake, which may be associated with its function in osmotic adjustment in response to salinity [32]. Micronutrient foliar sprays which include Fe, Mn, and Zn can increase salinity tolerance in wheat (*Triticum aestivum* L.)

[33] which suggests the important role of these micronutrients in salt-stressed plants. These elements have been shown to improve the root growth and prevent nutritional disorders and consequently bring about an increase in the uptake of nutrients [33]. In our study, applying the combination of MeJA and Si resulted in increased Fe and Mn contents in leaves under saline conditions which may enhance the plant tolerance to salinity. An optimal supply of silica helps the growth and development of root volume and weight, thereby increasing the total area for nutrient uptake. This is a likely reason for the higher Mg uptake in plants treated with Si. Similarly, it has been reported that silica application increased the Mg content of cucumber [34]. Increased absorption of Na, P, and Mg implies an important mechanism of salt tolerance in mycorrhizal *Sesbania* plants [35] which was probably due to the role of appropriate concentrations of them in continuing their physiological function under saline conditions. In the present study, we observed increased Mg and P contents in the treatments with MeJA and Si in salinity treatments. These treatments may be supplied to enhance the critical concentrations of Mg and P to bring about salt tolerance responses. Our results show that tomato lacks a mechanism to control Cl accumulation in leaves and salinity damage can be mainly attributed to Cl. One possible reason for salinity sensitivity is a lack of mechanisms to maintain the ion balance inside the plant. Thus, when plants are exposed to salinity stress, they lose their internal ion balance and a great deal of Cl is accumulated in their tissues [36].

Conclusions

This research demonstrated that leaf Na content in tomato plants increased with an increase in water salinity and under Si application, but that the Ca content decreased. An increase in exogenous MeJA could reduce Na, Ca, and Mn concentrations in leaves and increase their Fe content at higher salinity levels. When the irrigation water used was not saline, an increase in MeJA level to as high as 5 μM significantly increased Mn and Ca concentrations, but a further increase in MeJA application had no further effect. The lowest Cl concentration was obtained when the irrigation water was not saline. An application of 8 mM Si significantly reduced Cl at a salinity level of 4 dS m^{-1} without MeJA application. The results of this experiment lead to the conclusion that MeJA and Si can partially mitigate the adverse impacts of salinity stress on tomato plants and contribute to an increased uptake of some nutrients under saline conditions. Therefore, it can be recommended to apply them to saline soil or water. This research is one of the first reports of the simultaneous application of MeJA and Si. Further research, however, is needed to confirm our recommendation for the use of these combined treatments of MeJA and Si for other salt-stressed plants.

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Wpływ jasmonianu metylu i krzemianu sodu na skład mineralny *Solanum lycopersicum* L. rosnącego w warunkach stresu zasolenia

Streszczenie

Zasolenie gleb i wód stało się poważnym problemem dla działalności rolniczej. Wpływa negatywnie na plonowanie upraw. Celem niniejszej pracy było określenie wpływu jasmonianu metylu (MeJA) oraz krzemianu sodu (Si) na zawartość wybranych pierwiastków mineralnych w pomidorze (*Solanum lycopersicum* L.) w warunkach stresu zasolenia. W tym celu zastosowano całkowicie zrandomizowany układ blokowy z trzema czynnikami, w tym trzema poziomami zasolenia (0, 4 i 6 dS m^{-1}), Si (0, 4 i 8 mM) oraz MeJA (0, 5 i 7,5 μM). Poletka główne przydzielono do trzech poziomów zasolenia, a podpoletka zróżnicowano pod względem poziomu MeJA i Si. Wzrost stężenia MeJA był związany z 8,5% wzrostem zawartości P w liściach. Gdy MeJA był stosowany przy wysokich poziomach zasolenia, stężenia Na, Ca i Mn obniżyły się, ale zawartość Fe uległa podwyższeniu. Przy poziomie zasolenia wynoszącym 4 dS m^{-1} zastosowanie 8 mM Si zmniejszyło zawartość Cl o 50% w roślinach nietraktowanych MeJA. Interakcja trzech zastosowanych czynników była istotna w odniesieniu do zawartości K, Mg i Cl ($p < 0,01$). Zastosowane czynniki nie wywołały istotnych różnic w zawartości Zn i N. Uzyskane wyniki wskazują, że MeJA oraz Si mogą częściowo łagodzić niekorzystny wpływ stresu zasolenia i przyczyniać się do zwiększonego pobierania składników mineralnych w warunkach zasolenia.