Silicon (2023) 15:93–107
https://doi.org/10.1007/s12633-022-01988-x

ORIGINAL PAPER

Relationship between Silicon through Potassium Silicate and Salinity Tolerance in *Bellis perennis* L

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Received: 12 February 2022 / Accepted: 16 June 2022 / Published online: 5 July 2022

Abstract

Salt stress is considered as one of the critical factors threatening the growth and development of plants worldwide. The present study was aimed to evaluate the effect of potassium silicate (K_2SiO_3) on some physio-chemical characteristics of daisies under different levels of salinity stress. For this purpose, daisies (*Bellis perennis* 'Rob Roy') plants were treated with K_2SiO_3 (0, 2, and 4 Mm) and grown under salt stress (0, 30 and 60 mM NaCl). The results showed that salt stress stimulated mineral uptake, while application of 4 mM K_2SiO_3 reduced leaf Na^+ and Cl^- content (54 and 164%) at 60 mM salinity compared to unsprayed plants. Leaf osmotic potential was more negative in 60 mM salinity treatment than in the other treatments. Increasing salt stress level reduced the photosynthetic parameters (chlorophyll, *A*, *E*, *gs*, and WUE) in leaves, while K_2SiO_3 treatment improved the parameters. Application of 4 mM K_2SiO_3 increased plant's tolerance to stress by increasing carbohydrate, proline, phenolics and flavonoids. Application of K_2SiO_3 reduced malondialdehyde levels at 30 and 60 mM salt stress by 23.4 and 23%, respectively, by increasing membrane stability. However, application of K_2SiO_3 significantly increased the ability of plants to withstand salt stress by enhancing the accumulation of silicon (Si) and potassium (K) in plants compared to the unsprayed plants, which was due to the significant exclusion of Na+. The activity of peroxidase, ascorbate peroxidase, catalase, and superoxide dismutase exhibited positive increase as a result of K_2SiO_3 application under salt stress. In general, our results indicated that use of K_2SiO_3 can be considered as a common strategy to maintain the growth of plants under salt stress.

Keywords Antioxidant defense system · Daisy · Osmotic regulation · Photosynthesis · Silicon

1 Introduction

Daisy (*Bellis perennis* L.) is an autumn perennial that grows wild in meadows, wetlands, and forests in Europe and western Asia [1]. The plant is easy to propagate, does not require intensive care, and blooms profusely. As a medicinal plant, it contains blood purifying, mild laxative, anti-inflammatory, sedative, tonic, diaphoretic, expectorant and mild diuretic properties. It is also used to treat rheumatism. Blooming from March to October, it can also bloom throughout the year if the winter is mild [2].

Several interrelated factors including lack of fresh irrigation water, soil salinization, and increased evapotranspiration can affect the development of plant in arid and semiarid regions [3]. The production of plants is a global trade, so that the economic value of such plants has increased significantly in the last two decades and there has been intense competition for their continued cultivation in the world. Plant growth and productivity are significantly affected by environmental conditions associated with biotic and abiotic stresses [4]. Salinity is the second non-biological stress factor affecting the yield of horticultural crops in various ways. According to statistical data, about 20% of the world's cultivated land and 33% of the irrigated land are threatened by salinity stress [5]. However, an annual increase is being observed in the area of salinized land throughout the world, and these soils are being destroyed and rendered unusable. Salinization of soils occurs naturally or through agricultural intervention in the form of fertilization and irrigation with saline water [6, 7].

Salt stress (e.g., soil salinization and saline irrigation water) has affected the growth and development of plants in green spaces, leading to changes in soil physicochemical properties and plant morphological, physiological, and

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biochemical characteristics [8]. Salt stress promotes osmotic stress, low soil water potential and nutrient imbalance. Moreover, high sodium and chloride concentrations and oxidative stress reduce soil quality and impair plant growth. Therefore, to overcome the harmful effects of salt stress and maximize the production, use of alternative techniques is a practical method [9]. There is a great need for cost-effective and environmentally friendly approaches to agriculture on saline soils worldwide. The negative effects of salt stress can be minimized by using K_2SiO_3, which is one of the most promising options for improving soil health, and plant growth and development [10].

The second most abundant element in the lithosphere is silicon (Si). Due to its role in improving pest and disease control, increasing abiotic stress tolerance, and enhancing photosynthesis in plants, it is commonly classified as a beneficial element. Silicon can mitigate the negative effects of oxidative stress, particularly under abiotic stress conditions, by regulating reactive oxygen species (ROS) in the antioxidant system [11]. Another mechanism for increasing stress tolerance by Si element is improving physiological regulation, namely increasing stomatal efficiency and transpiration [12]. Silicon mediates salt-induced ion imbalance by regulating Na^+ uptake, transport, and distribution [13]. Potassium (K), one of the most important and consumed elements in plants, stimulates root length, vegetative growth, and osmoregulation. It also controls numerous metabolic activities such as photosynthesis, protein production, pore movement, water status, and carbohydrate synthesis [14]. Besides, potassium is actively involved in many functions such as enzyme activation and uptake of deleterious ions like Na^+. Therefore, it can be used to minimize the negative effects of salt stress in plants [15].

Potassium silicate is a plant biostimulant and a source of highly soluble potassium and silicon [16]. In agricultural products, it is generally used as a modifier and supplier of small amounts of potassium to improve quality and yield [17]. Potassium silicate improves vegetative growth, yield components, and concentrations of mineral nutrients, namely nitrogen, phosphorus, and potassium. It also affects physiological functions such as sugar and starch formation, protein synthesis, cell division, growth, and fruiting [18, 19]. According to some studies, K_2SiO_3 maintains plasma membrane function by increasing the activity of enzymatic antioxidants during salt stress [20]. It is widely reported to attenuate environmental stress, but its benefits are controversial due to differences in species, genotypes, and environmental conditions [21].

We hypothesized that non-essential element of silicon and essential element of potassium may mitigate the effect of salt stress on daisies (*B. perennis* 'Rob Roy'). If this hypothesis proves to be true, the use of K_2SiO_3 in saline areas can be expanded, and thus crop sustainability can be increased. The objective of the study was to investigate the effects of K_2SiO_3 on some physical-chemical characteristics of daisies under different levels of salinity stress.

2 Materials and Methods

2.1 Experimental Layout and Growth Conditions

B. perennis 'Rob Roy' seeds were grown on wet filter paper in an incubator at 22 °C for 3 days. Seeds after germination in the incubator were cultivated in a bed containing coco peat and perlite. Seedlings at 3–4 leaf stage were then transferred to pots containing a mixture of peat, coco peat, and perlite (1:1:1 v:v). The average temperature during the experimental period was 19.7 ± 2 °C (mean ± SD). The plants were provided with a full-strength Hoagland nutrient solution (EC 1.7 dS m^{-1}, pH 6.0–6.5) every two days [22]. Tables 1 and 2 show the chemical properties of media and nutrient solution.

2.2 Potassium Silicate and Salinity Treatments

Laboratory compounds such as K_2SiO_3 were purchased from Sigma-Aldrich, Steinheim, Germany. In April 2021, K_2SiO_3 treatment was applied every week until *B. perennis* 'Rob Roy' plant flowered (three times), and the salt stress was applied after the flowering stage for one month. Potassium silicate was prepared at two concentrations (2 and 4 mM) as

Table 1 Chemical properties of media

Media (%)	N	P	K	Mg	Ca	Na	Cl	Si	Mn	Fe	B	Zn
	2.85	0.44	1.98	0.57	1.56	**	**	0.02	**	**	**	**

**not reported

Table 2 Chemical properties of solution

Solution (ppm)	N	P	K	Mg	Ca	Na	Cl	Si	Mn	Fe	B	Zn
	218	30	240	44.7	180	0.02	0.14	**	0.1	2.7	0.3	0.03

**not reported

described above. Seedlings in the greenhouse were sprayed separately with each concentration using hand-held plastic spray pumps. The plants sprayed with distilled water served as control. For foliar fertilization, the whole shoots of the plants were fertilized using a pressurized sprayer to ensure that the foliar fertilization covered the leaf. After three weeks, the salinity treatment was applied by adding 30 and 60 mM NaCl to the solution while the control plants continued to grow in salt-free nutrient solution. The salinity treatment was applied gradually to avoid osmotic stress. All the treatments repeated three times. Finally, about eight months after the start of the experiment, 5 plants from each treatment were randomly selected for physiological and biochemical measurements.

2.3 Determination of Osmotic Potential and Minerals

The osmotic potential of three leaves was measured using a freezing-point depression osmometer (Digital Osmometer, Roebling, Berlin) at 25 ± 1 °C [23]. To measure Na^+ and K^+, the leaves were first powdered with 300 mg of dried leaf samples. Then, 2 ml of pure nitric acid was added to the pulverized samples in the test tube and the vials were kept under the same conditions for 24 hours. To evaporate the nitric acid, the samples were placed in a digestion oven at 100 °C and filtered with filter paper after two hours, and were finally diluted with 50 ml of distilled water. For the determination of Na^+ and K^+, 1 and 0.5 ml, respectively, of the clear extract of the samples were taken and were diluted with 10 ml of distilled water. Finally, the amounts of Na^+ and K^+ were determined by atomic absorption spectrophotometry using a flame photometer [24]. To measure Cl^-, the extract was diluted twice with twice distilled water and the amount of Cl^- in each extract was determined by titration. For this purpose, the dry weight of the plant was first mixed with silver nitrate, nitric acid, and potassium permanganate, then diluted and added to the ferric solution in acetone, and finally titrated with potassium thiocyanate solution [25].

2.4 Measurement of Photosynthesis Parameters

To determine chlorophyll content, 100 mg of fresh leaves were crushed in 10 ml of acetone and centrifuged at 4000 rpm for 10 min. A spectrophotometer was used to measure the absorbance at a wavelengths of 653 and 666 nm [26]. A portable plant photosynthesis system (KR8700 system; Korea Tech Inc., Seoul, Korea) was used to evaluate photosynthetic traits. Photosynthetic characteristics were evaluated by measuring traits such as photosynthesis rate (A), transpiration rate (E), and stomatal conductance (g_s). Furthermore, intrinsic water use efficiency (WUEi) was calculated.

2.5 Measurement of Proline and Carbohydrate Concentrations

The proline content was measured using the method proposed by Bates et al. [27] with some modifications. In brief, 1 ml of the alcoholic extract was mixed with 10 ml of distilled water, 5 ml of ninhydrin, and 5 ml of acetic acid. The sample obtained was placed in a water bath for 45 minutes. Ten ml of toluene was added to each sample. The absorbance of the samples was measured at 515 nm using a spectrophotometer. The calibration curve was calculated using the L-proline standard, and the amount of free proline in the samples was calculated in µmol per gram of leaf dry weight. Total carbohydrate were measured according to the method of Yemm and Willis [28]. The extract was obtained from 100 mg dry powder samples with 25 ml ethanol. Ten ml of a 0.15% anthrone solution (containing pure anthrone and 72% sulfuric acid) was added to one ml of the extract, and the samples were then heated to 95 °C. The absorbance of the samples was then measured using a spectrophotometer at 625 nm, and the total sugar concentration of the samples was calculated using the standard glucose curve based on mg per g of dry matter of samples.

2.6 Measurement of Phenol, Flavonoid and Anthocyanin

The phenol assay was performed according to the method of Dewanto et al. [29] with slight modification. An amount of 4.5 ml of distilled water and 0.1 ml of Fullen-Cicalto reagent were added to 0.1 of the methanolic extract of each sample. After 3 minutes, 0.3 ml of a 2% sodium bicarbonate solution was added and the samples were kept in the dark for 120 minutes. Different concentrations of gallic acid were used to prepare the standard curve, and the standard concentrations were prepared according to the extracts. The absorbance was measured using a spectrophotometer at 760 nm. The total phenolic content was calculated based on mg gallic acid per mg dry weight.

A plant extract of flavonoids was prepared from 50 mg of leaves and 5 ml of methanol. The extracts were shaken on a shaker for 24 hours and then centrifuged at 6000 rpm for 10 minutes. 300 μL of the above extract was mixed with 3.4 mL of 30% methanol, 150 μL of 0.5 M NaNO2, and 150 μL of 0.3 M $AlCl_3 \cdot 6H_2O$. After 5 minutes, 1 mL of NaOH (1 M) was added. Finally, light absorbance was measured at a wavelength of 510 nm [30]. To measure the amount of leaf anthocyanin, the method proposed by Wagner was used. To assay total anthocyanin, two buffer solutions (25 mM K-chloride pH 1.0 and 0.4 M Na-acetate pH 4.5) were used according to the method of Sukwattanasinit et al. [31].

2.7 Measurement of Electrolyte Leakage and Membranes Lipid Peroxidation

Five leaf pieces were placed in vials containing 50 ml of double-distilled water for 24 hours at laboratory temperature. Initial leakage was then measured using an EC meter (EC_1). The vials were placed in an autoclave for 20 minutes (with a pressure of 1.2 bar and a temperature of 120 °C) and the final leakage (EC_2) was measured after 24 hours. The percentage of electrolyte leakage was calculated using the following equation [32].

$$EL\% = EC1/CE2 \times 100$$

The membranes lipid peroxidation assay was conducted based on the method of Madhava Rao and Sresty [33]. The extract was prepared from 0.2 g of leaf tissue with 5 ml of 0.1% trichloroacetic acid (TCA). Then 4 ml of a 20% TCA solution containing 5 ml of thiobarbituric acid (TBA) was added to 1 ml of the centrifuged supernatant. The samples were placed in a hot water bath for 30 minutes and then quickly placed in ice for 10 minutes. The absorbance of this solution was measured by using spectrophotometer at the wavelengths of 532 and 600 nm.

2.8 Quantification of Antioxidant Enzyme Activities

To measure superoxide dismutase (SOD) activity, the method of Sairam et al. [34] was used with some modifications. The enzymatic reaction mixture consisted of 935 µl of 50 mM phosphate buffer containing 0.1 mM EDTAA, 13 mM methionine, 75 mM nitroblutetrazolium, 15 µL riboflavin 0.12 mM, and 50 µl of the enzymatic extract. After preparing the control and blank samples for measurement of enzymatic activity, the blank sample was stored in the dark for 15 minutes and the control and enzyme extracts were stored in a shaker at 25 °C for 15 minutes with two 20-watt fluorescent lamps and shaken at 100 rpm. The absorbance of the supernatant was measured at 560 nm. An amount of extract capable of 50% inhibition of nitroblue tetrazolium is equivalent to one enzyme unit. The activity of catalase (CAT) was measured as described by Abedi and Pakniyat [35]. The reaction solution consisted of a 50 mm phosphate buffer (pH 7.0), 10 mm H_2O_2, and 50 ml enzyme extract. With some modifications, the method of Srinivas et al. [36] was used to measure the peroxidase enzyme. After the formation of tetraguaiacol by adsorption at 471 nm and the extinction coefficient of 26.6 mm, the amount of tetraguaiacol was calculated. One ml of the reaction mixture contained 0.1 ml of enzyme extract, 50 ml of 20 mM guaiacol, and 2.8 ml of 10 mM phosphate buffer (pH 7.0). The reaction was carried out within one minute. One unit of peroxidase activity is defined as the activity of an enzyme oxidizing one µmol of guaiacol in one minute. The activity of ascorbate peroxidase (APX) was measured as described by Nakano and Asada [37].

2.9 ABA Content and Dry Weight

Endogenous abscisic acid [ABA] was extracted and purified using the method described by Yang et al. [38]. ABA level was determined using an HPLC system based on the previously reported methods with some modifications [39]. The dry weight of the plants was determined by placing the samples in an oven at 72 °C.

2.10 Data Analysis

All data were subjected to an analysis of variance (ANOVA) using SAS 9.0 software. The significance of differences between the treatments means was tested with the least significant difference (LSD) test at 1% and 5% probability levels. All graphs were generated using Microsoft Excel software v. 2010 (Microsoft Corporation, USA).

3 Results

3.1 Leaf Osmotic Potential and Mineral Concentrations

The osmotic potential and the contents of Na^+, Cl^- and K^+ elements were significantly ($P < 0.05$) affected by K_2SiO_3 and salt stress (Table 3). Leaf osmotic potential

Table 3 Analysis of variance on some traits of the daisy (*Bellis perennis* L.) as affected by potassium silicate and salinity

Source of variation	df	Osmotic potential	Na^+	Cl^-	K^+	Si	Carbohydrate	Proline
Salinity	2	0.176**	77685**	209157**	139459**	130*	302**	19.6**
Silicate potassium	2	0.11**	162401**	131297**	95**	1368239**	1590**	22.9**
Salinity* Silicate potassium	4	0.002*	4506**	27056**	16*	122**	82**	3.81**
Error	18	0.0004	48	38	5	24	2.18	0.112
Total	26							

*, ** – significant at the 5% and 1% probability levels respectively; ns – not significant

Table 4 Effect of potassium silicate and salinity on osmotic potential, Na^+, Cl^-, and K^+, and Si in daisy leaves

Treatments (mM NaCl)	Potassium silicate (mM)	Osmotic potential (MPa)	Na^+ (μ mol g^{-1} DW)	Cl^- (μ mol g^{-1} DW)	K^+ (μ mol g^{-1} DW)	Si (μ mol g^{-1} DW)
0	0	−1.19 ± 0.03ab	454 ± 1.85e	269 ± 0.577e	728 ± 2.23f	50 ± 1.53d
	2	−1.17 ± 0.02a	437 ± 8.08e	223 ± 5.19e	732 ± 7.81ef	629 ± 1.64c
	4	−1.15 ± 0.04a	281 ± 3.52 h	70 ± 2.84f	738 ± 2.90e	704 ± 1.45b
30	0	−1.3 ± 0.02c	580 ± 2.03c	371 ± 2.12c	940 ± 1.86d	51 ± 0.33d
	2	−1.24 ± 0.02bc	520 ± 4.48d	354 ± 4.16c	944 ± 2.60d	621 ± 0.58c
	4	−1.2 ± 0.04ab	315 ± 3.2 g	267 ± 2.64d	944 ± 1.15 cd	717 ± 1.86ab
60	0	−1.5 ± 0.1e	715 ± 4.25a	715 ± 0.33a	952 ± 3.05ab	51 ± 1.20d
	2	−1.4 ± 0.2d	625 ± 2.64b	426 ± 1.20b	950 ± 3.33bc	632 ± 0.78c
	4	−1.45 ± 0.03de	388 ± 1.53f	270 ± 3.33d	957 ± 2.90a	723 ± 1.20a

Means within each column followed by the same letter are not statistically different at ≤0.05 by Least Significant Difference test

(Table 4) was more negative in 60 mM salinity treatment than in the other treatments, and showed an increase in K_2SiO_3 treatment compared with the control. The highest amounts of Na^+ and Cl^- were obtained in unsprayed plants under 60 mM salinity stress. Increasing salt stress level to 60 mM enhanced the content of Na^+, Cl^-, and K^+ in the leaves by 57.4, 198.3, and 29.7%, respectively. However, the application of K_2SiO_3 reduced Na^+ in the plants subjected to salt stress, so that the amount of Na^+ in the plants sprayed with 4 mM was 38% under non-stress conditions and reduced by 46% under stress levels of 30 and 60 mM compared to sprayed plants. Potassium silicate at 4 mM had the greatest effect on the reduction of Cl^- level, but it showed no significant difference under non-stress and stress conditions (30 mM) at the level of 2 mM. Use of 4 mM K_2SiO_3 caused a 46% reduction in Cl^- accumulation in leaves under salt stress levels of 30 and 60 mM. Not only did the application of 2 and 4 mM not differ significantly regarding K^+ accumulation under stress-free conditions, but also the effect of this substance on K^+ accumulation, under salt stress conditions, did not make a significant difference compared to sprayed plants. Under stress-free conditions, the application of 4 mM K_2SiO_3 resulted in a 13.7% increase in K^+ compared to unsprayed plants (Table 4).

3.2 Parameters of Photosynthesis

Photosynthesis parameters (*A*, *E*, *gs*, WUEi and chlorophyll content) were also found to vary widely ($P < 0.05$) (Table 5). The highest value of *A* was 3.33 μmol m^{-2} s^{-1} obtained from 4 mM K_2SiO_3 under non-stress conditions, and it was 132% higher than that in non-sprayed plants. The lowest value of *E* was obtained from 2 and 4 mM (15.74 mmol m^{-2} s^{-1}) K_2SiO_3 treatments under 60 mM NaCl, in which the value was 78% lower than the control (0.56 mmol m^{-2} s^{-1}) which contained the highest *E* value. The highest *gs* content was obtained from 2 and 4 mM (0.057 mol m^{-2} s^{-1}) K_2SiO_3 treatments under non-stressed conditions, and this value was 40% higher than that of the control (0.04 mol m^{-2} s^{-1}); the lowest value was obtained from non-sprayed plants under 60 mM NaCl (0.03 mol m^{-2} s^{-1}). The highest WUEi was observed in 4 mM K_2SiO_3 which was 41% higher than the control (13.6 μmol CO_2 mm^{-1} H_2O) under 60 mM salinity level. In non-sprayed plants, 60 mM salinity caused a 28.4% decrease in total chlorophyll content compared to the control treatment. At 30 mM, application of 2 and 4 mM K_2SiO_3 brought about 8.9 and 5.76% increases in total chlorophyll, respectively, compared to the unsprayed treatment. However, at higher salt levels (60 mM), K_2SiO_3 treatment did not cause a significant effect on total chlorophyll (Table 6).

Table 5 Analysis of variance on photosynthesis parameters of the daisy (*Bellis perennis* L.) as affected by potassium silicate and salinity

Source of variation	df	Total chlorophyll	*A*	*gs*	*E*	*WUEi*
Salinity	2	10.4**	1.29**	0.001**	0.443**	1.07**
Silicate potassium	2	0.273**	4.04**	0.0002**	0.002**	4.18**
Salinity* Silicate potassium	4	0.981**	0.528**	0.0001*	0.001**	0.300*
Error	18	0.015	0.20	0.00003	0.00001	0.077
Total	26					

Means within each column followed by the same letter are not statistically different at ≤0.05 by Least Significant Difference test (A: Photosynthesis rate, gs: Stomatal conductance, E: Transpiration rate, WUE: intrinsic Water Use Efficiency)

3.3 Compatible Osmolytes

Potassium silicate and salt stress significantly ($P < 0.01$) affected the content of total carbohydrate and proline, so that an increase in salt stress level increased the content of both parameters (Table 3). The highest amounts of total carbohydrate were obtained in foliar spraying with 4 mM K_2SiO_3 under no stress conditions. Application of 2 and 4 mM K_2SiO_3 increased total carbohydrate content by 23.8 and 5.7%, respectively, compared to the control treatment. The lowest and highest amounts were obtained in the control (1.63 mg g^{-1}DW) and in the plants sprayed with 4 mM K_2SiO_3 at salinity level of 60 mM (9.3 mg g^{-1}DW) (Fig. 1a). Application of 4 mM K_2SiO_3 resulted in a 2.7-fold enhancement in proline content compared to stress-free conditions. Furthermore, 1.5 and 2.1-time increases were found in proline content compared to the unsprayed plants at 30 and 60 mM salinity levels, respectively (Fig. 1b).

3.4 Secondary Metabolites

Phenol, flavonoid, and anthocyanin contents were significantly ($P < 0.01$) affected by K_2SiO_3 and salt stress (Table 7). Application of 2 mM K_2SiO_3 decreased the amount of phenol under salt-free conditions, but 4 mM treatment increased the phenol. Under salinity conditions, K_2SiO_3 application increased phenolic content compared to unsprayed plants, so that at 30 mM salt stress, application of 2 and 4 mM K_2SiO_3 increased this index by 75 and 115%, respectively, while at high level of salt stress (60 mM), phenolic contents increased by 82 and 150%, respectively (Fig. 2a). Application of K_2SiO_3 under stress-free conditions did not affect the flavonoid content, but at 60 mM salinity, the application of 2 and 4 mM K_2SiO_3 increased the flavonoid content by 14.7 and 13.9%, respectively. The highest amount of flavonoids was obtained at 4 mM K_2SiO_3 under 60 mM salinity (Fig. 2b). Salt stress level of 60 mM decreased anthocyanin by 30.9% compared to stress-free plants. However, fertilization at 4 mM had the greatest effect on anthocyanin.

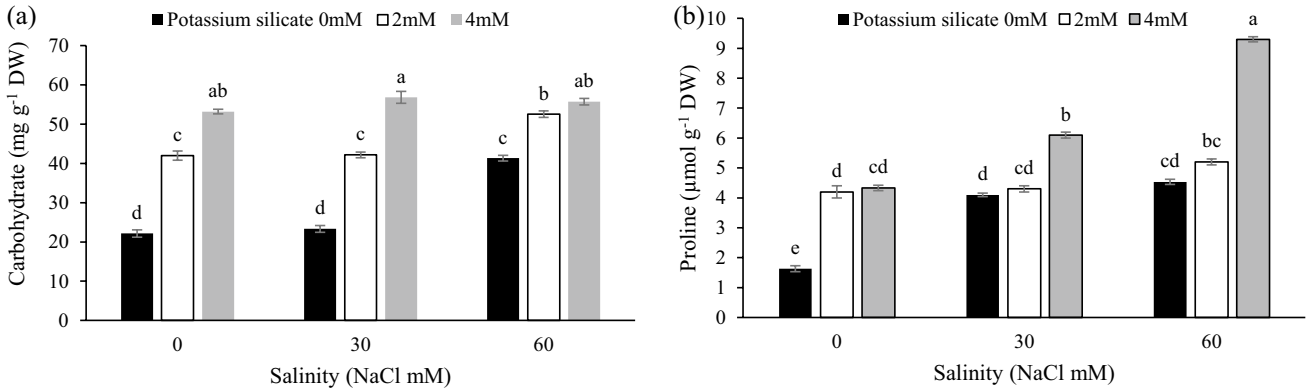

Fig. 1 Effect of salinity and potassium silicate on carbohydrate (**a**), and proline (**b**) in one-year-old daisy. Data (means ± SE, n = 3) followed by different small letters above the bars indicate a significant difference at P ≤ 0.05

Table 6 Effect of potassium silicate and salinity on total chrolophyll, *A*, *gs*, *E*, *iWUE* of daisy

Treatments (mM NaCl)	Potassium silicate (mM)	Total Chlorophyll (mg g^{-1} FW)	*A* (µmol m^{-2} s^{-1})	*gs* (mol m^{-2} s^{-1})	*E* (mmol m^{-2} s^{-1})	*WUEi* (µmol CO_2 mm^{-1} H_2O)
0	0	6.01 ± 0.11b	1.43 ± 0.09de	0.04 ± 0.003bcd	0.523 ± 0.003b	2.73 ± 0.15e
	2	6.60 ± 0.6a	3.03 ± 0.03ab	0.057 ± 0.002a	0.533 ± 0.007b	5.68 ± 0.07d
	4	6.40 ± 0.8a	3.33 ± 0.12a	0.057 ± 0.003a	0.563 ± 0.01a	5.91 ± 0.12d
30	0	5.55 ± 0.4c	1.3 ± 0.08e	0.046 ± 0.002abc	0.427 ± 0.003c	3.04 ± 0.02e
	2	6.04 ± 0.6b	2.66 ± 0.09bc	0.053 ± 0.007ab	0.431 ± 0.00c	6.21 ± 0.21d
	4	5.87 ± 0.8bc	2.26 ± 0.09c	0.043 ± 0.003abcd	0.430 ± 0.003c	5.23 ± 0.20d
60	0	4.32 ± 0.1d	1.51 ± 0.06de	0.03 ± 0.00d	0.110 ± 0.001d	13.6 ± 0.52c
	2	4.27 ± 0.1d	1.81 ± 0.06d	0.035 ± 0.002 cd	0.113 ± 0.003d	15.88 ± 0.26b
	4	4.21 ± 0.04d	2.33 ± 0.1c	0.039 ± 0.0007bcd	0.121 ± 0.001d	19.17 ± 0.96a

Means within each column followed by the same letter are not statistically different at ≤0.05 by Least Significant Difference test (*A*: Photosynthesis rate, *gs*: Stomatal conductance, *E*: Transpiration rate, *WUEi*: intrinsic Water Use Efficiency)

Table 7 Analysis of variance on photosynthesis parameters of the daisy (*Bellis perennis* L.) as affected by potassium silicate and salinity

	df	Phenol	Flavonoid	Anthocyanin	Electrolyte leakage	MDA	POD	APX	CAT	SOD	ABA	Dry weight
Salinity	2	0.624**	3.32**	905**	2755**	5868**	71712**	22150**	4.18**	90.1**	117**	3.92**
Silicate potassium	2	1.32**	0.848**	691**	136**	908**	583280**	5554**	0.627**	4.43*	38.04**	17.2**
Salinity* Silicate potassium	4	0.404**	0.371**	31.2**	10.22**	21.1**	54232**	4314**	0.228**	11.2**	8.09*	1.08**
Error	18	0.005	0.009	1.79	1.59	2.63	6441**	18.5	0.012	0.798	2.41	0.146
Total	26											

Means within each column followed by the same letter are not statistically different at ≤0.05 by Least Significant Difference test (MDA; malondialdehyde, POD; peroxidase, APX; ascorbate peroxidase, CAT; catalase, SOD; superoxide dismutase, ABA; abscisic acid)

Compared to unsprayed plants, application of K_2SiO_3 at 4 mM increased anthocyanin by 30, 44.7, and 45.6% under stress-free conditions, and at 30 and 60 mM saline stress levels, respectively (Fig. 2c).

3.5 Electrolyte Leakage and Membranes Lipid Peroxidation

The results showed that K_2SiO_3 and salt stress caused significant effects on electrolyte leakage, malondialdehyde (MDA), and antioxidant activity ($P < 0.01$) (Table 7). Application of K_2SiO_3 under stress-free conditions and 30 mM salinity level reduced electrolyte leakage, so that 4 mM K_2SiO_3 reduced electrolyte leakage by 23.6 and 14.9%, respectively, in control plants and plants under 30 mM stress compared to unsprayed plants. However, the application of K_2SiO_3 at 60 mM salinity did not cause a significant difference in electrolyte leakage (Fig. 3a). Increasing salt stress increased the amount of MDA so that the highest value of this index was observed at 60 mM salinity. In the control group and plants under salt stress, the amount of MDA tended to decrease as a result of K_2SiO_3 application, so that this index decreased by 60, 30 and 24%, respectively, in plants sprayed with 4 mM K_2SiO_3 in control, and 30 and 60 mM salinity levels (Fig. 3b).

3.6 Antioxidant Enzyme Activities

Regarding the effects of salt stress on antioxidant enzymes (Table 7), the activities of SOD, CAT, and APX exhibited significant 26.6, 23.7, and 91% increases under 60 mM salinity, respectively (Fig. 4). In general, K_2SiO_3 use increased the activities of these enzymes, but the increase was higher at 4 mM under 60 mM salinity level. Application of 4 mM K_2SiO_3 under stress-free conditions and 30 mM salt stress increased the activity of SOD enzyme by 11.9 and 9.3%, respectively, compared to unsprayed plants. No significant difference was found regarding the effect of K_2SiO_3 on the activity of SOD enzyme under high salinity (60 mM) compared to untreated plants (Fig. 4a). Spray of K_2SiO_3 at 2 and 4 mM significantly improved the activity of CAT in daisies grown at 60 mM by 63.6 and 63%, respectively, compared to non-sprayed plants (Fig. 4b). Although use of K_2SiO_3 under no stress conditions and salt stress (30 mM) increased the activity of POD enzyme, no significant difference was observed between sprayed and non-sprayed plants under severe salt stress level (60 mM). Application of 2 and 4 mM K_2SiO_3 under 30 mM salt stress increased peroxidase activity by 96 and 74%, respectively, compared to unsprayed plants (Fig. 4c). Spray of K_2SiO_3 at both levels significantly improved the activity of APX under salinity conditions. The activity of APX increased at 30 and 60 mM salinity levels compared

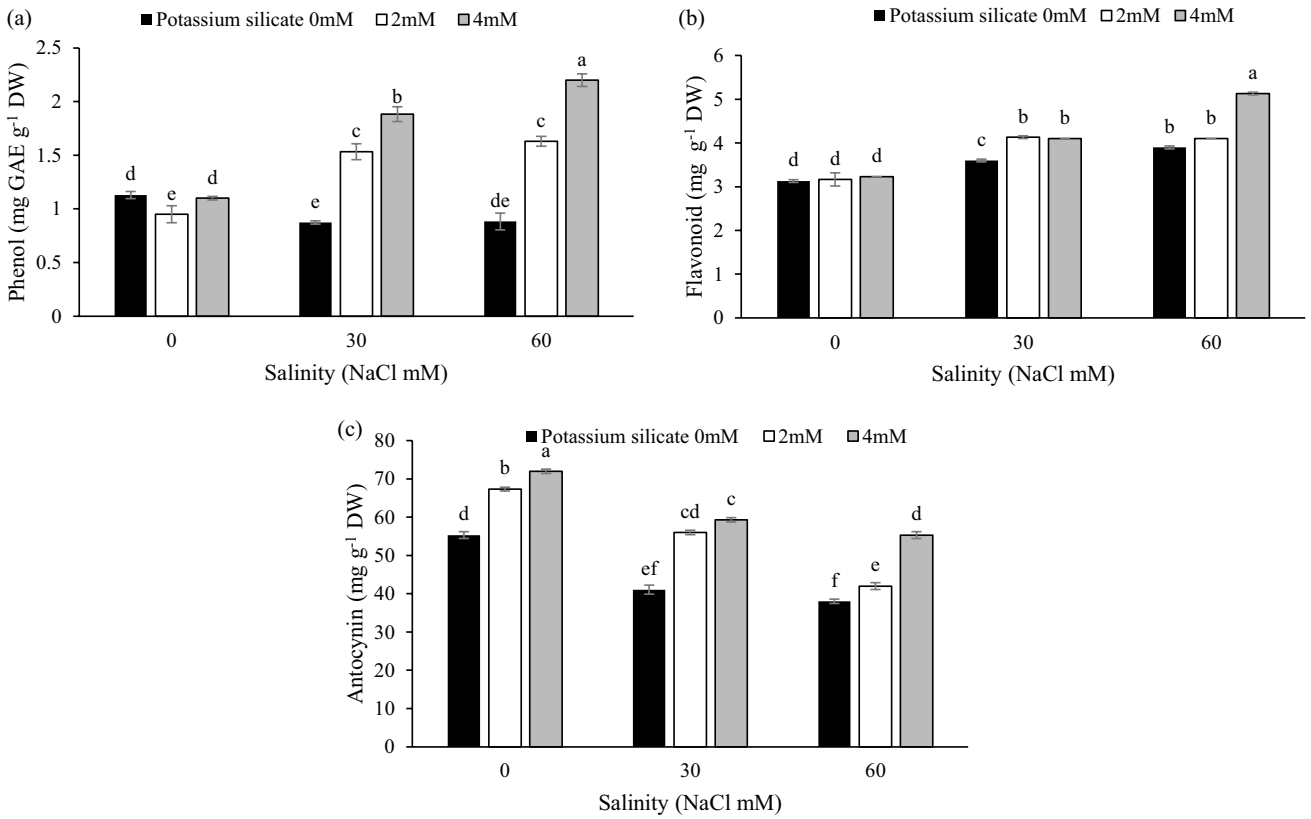

Fig. 2 Effect of salinity and potassium silicate on phenol (**a**), flavonoid (**b**), and anthocyanin (**c**) in one-year-old daisy. Data (means ± SE, n = 3) followed by different small letters above the bars indicate a significant difference at $P \leq 0.05$

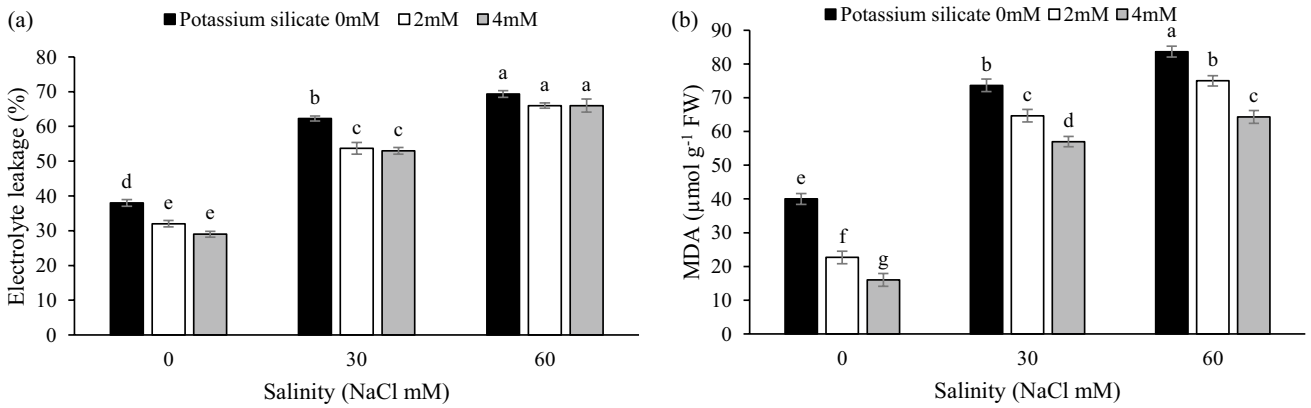

Fig. 3 Effect of salinity and potassium silicate on electrolyte leakage (**a**) and MDA (**b**) in one-year-old daisy. Data (means ± SE, n = 3) followed by different small letters above the bars indicate a significant difference at $P \leq 0.05$

to the control. As shown in Fig. 4d, the activity of APX increased by 81 and 113% in the plants sprayed with 2 and 4 mM K_2SiO_3, respectively, compared to the plants not sprayed at 30 mM salinity.

3.7 ABA and Dry Weight

ABA and dry weight were significantly ($P < 0.05$) affected by K_2SiO_3 and salt stress (Table 7). Potassium silicate

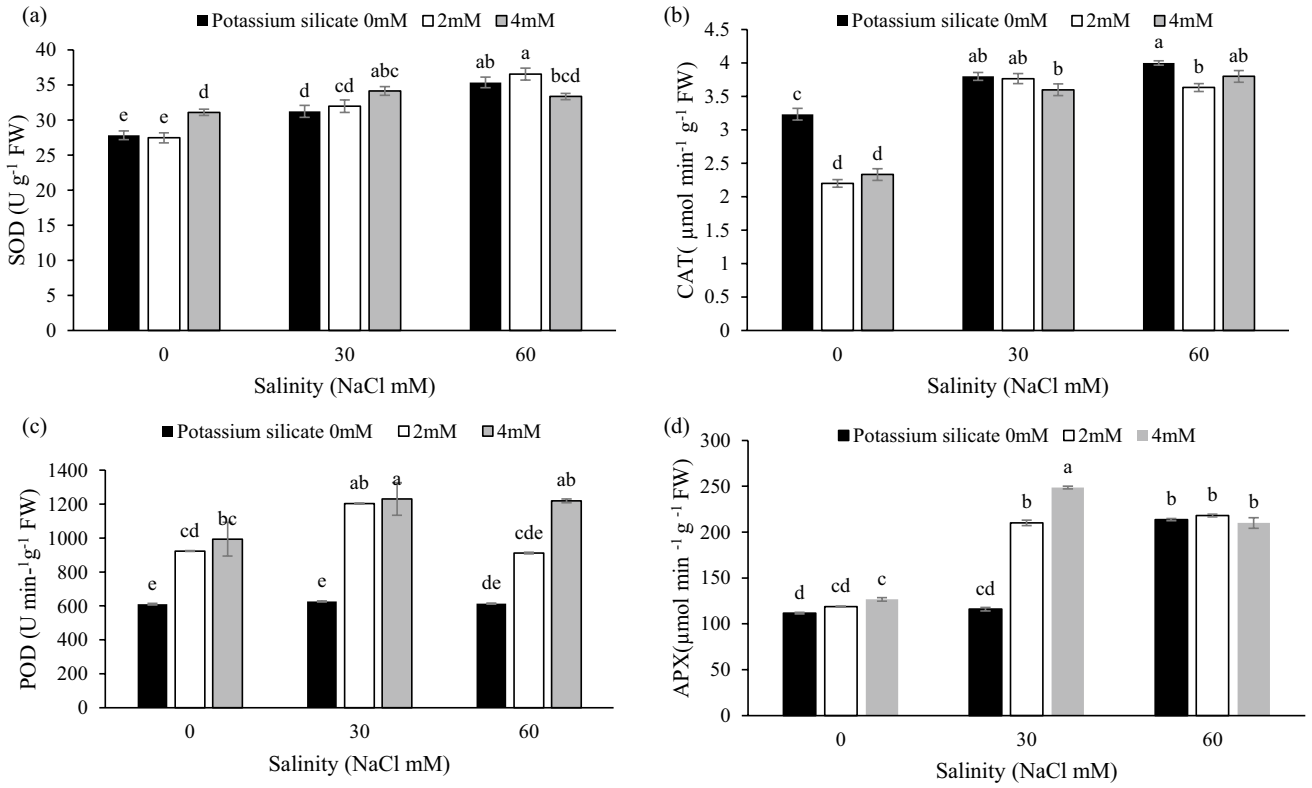

Fig. 4 Effect of salinity and potassium silicate on SOD (**a**), CAT (**b**), POD (**c**), and APX (**d**) in one-year-old daisy. Data (means ± SE, n = 3) followed by different small letters above the bars indicate a significant difference at $P \leq 0.05$

treatments decreased ABA values generally. Maximum ABA content (20.1 ng g^{-1} DW) was obtained from 2 mM K_2SiO_3 treatment, which was 39.5% higher than the control plants (14.33 20.1 ng g^{-1} DW) under 60 mM salinity (Fig. 5a). The increase in salt stress reduced plant weight, but no significant difference was observed between 30 mM and control. However, the application of K_2SiO_3 increased plant dry weight in control treatment by 24 and 39.5%, respectively. Salt stress at 30 and 60 mM levels increased dry weight by 21.9 and 47%, respectively, compared to unsprayed plants (Fig. 5b).

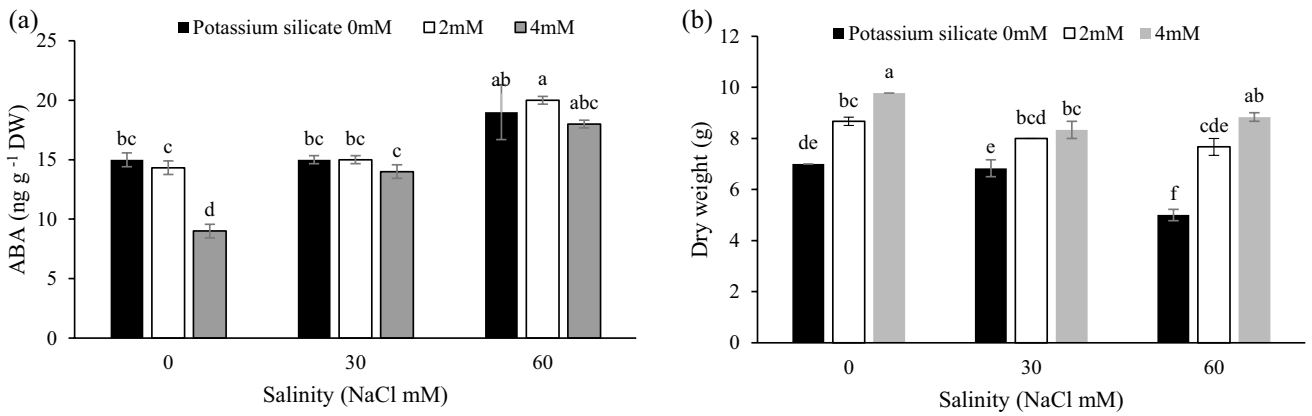

Fig. 5 Effect of salinity and potassium silicate on ABA (**a**) and dry weight (**b**) of one-year-old daisy. Data (means ± SE, n = 3) followed by different small letters above the bars indicate a significant difference at $P \leq 0.05$

4 Discussion

Salt stress triggers osmotic imbalances, lack of water use efficiency and nutrient deficiency, and finally leads to oxidative stress in plants [40]. In the current study, salt stress negatively affected different parameters in daisy plant. Increasing Na^+ and Cl^- concentrations under NaCl treatments led to a significant reduction in K^+ content of plants. However, the application of K_2SiO_3 reduced the accumulation of Na^+ and Cl^- in the leaves. The toxicity of Na^+ and Cl^- in metabolic processes results from their competition with K^+ for binding sites, which, in turn, disrupt the activities of enzymes and essential cellular functions. Consequently, the plants growing in saline soils may suffer from the dual injury of Na^+ toxicity and low K^+ concentrations [41, 42]. In the present study, plants sprayed with K_2SiO_3 had higher leaf K^+ and Si content compared to the control. This was the result of significant Na^+ exclusion and better maintenance of leaf K^+ concentration under NaCl stress, which may be associated with higher salt tolerance.

The accumulation of Si and K in the leaves of the daisy is in agreement with the results of Currie and Perry [43], who reported the accumulation of K and Si in the plant. However, high rate of Si accumulation in seedlings grown in K_2SiO_3 treatment can be partially explained by the increase in the endoderm, which can restrict the flow of elements to the shoot [44], so the application of silica by foliar spray using the K_2SiO_3 source helps to increase the accumulation of silica in the leaves. We also observed an increase in growth and relative water content along with the increase in K concentration (Table 4) in seedlings exposed to K_2SiO_3 in this study. In addition, K_2SiO_3 decreased the accumulation of Na^+ and Cl^- in leaves and increased the amount of K^+ and Si. Nevertheless, the improvement of K status was documented to be involved in the mitigating effects of K_2SiO_3 on salt stress in plants.

Several reports have shown that the application of Si significantly reduces Na^+ accumulation in the root, and prevents its transfer to sensitive plant tissues [45, 46]. By precipitating in epidermal cells and creating a barrier to ion movement or the forming a complex between freely available Na^+ and Si ions, Si prevents sodium transfer and increases potassium uptake [47]. Many nutrients show synergistic effects and facilitate the uptake of another element in the plant. The synergistic effect has been found between Si and K+, so that Si has been reported to improve K nutrient status under salt stress in many plant species [48, 49]. Therefore, the genes and proteins responsible for K^+ uptake and translocation from root to shoot appear to be the potential targets of K_2SiO_3 in improving the K^+ status of plants under salt stress. Yan et al. [50] showed that the addition of Si improved K^+ accumulation in the shoot, K^+ uptake index in the root, and K^+ translocation index from the root to the shoot in oochikara and T-65, but not in the lsi1 and lsi2 mutants, which is consistent with the different alleviating effects of Si on salt stress between WT and mutants of rice. The contrasting effects of Si on rice growth and K^+ status in WTs and their mutants suggest that the possible mechanism responsible for Si-induced alleviation of K deficiency in rice under salt stress may be promotion of K^+ uptake and root-shoot translocation. The Na^+/H^+ antiporter also plays an important role in maintaining low Na^+ concentrations by removing Na^+ from the cytosol or transferring it to the vacuole [51]. The activity of H^+- ATPase decreases under salt stress, but the application of Si increases its activity and improves the transfer of Na^+ from the cell. In addition, Si application increases the activity of H^+ -ATPase which, in turn, improves potassium uptake under salt stress [49].

Salt stress effect was clearly reflected in the elevated Na^+ and Cl^- levels in daisy leaves. Indeed, the osmotic potential in the leaves was significantly more negative in the salt treatment than in the control. All these results are consistent with the previous studies in *Crocus sativus* L. [49] and *Zea mays* L. [52], showing a clear relationship between potentials, solute accumulation, and salt stress [49]. This increase in solutes in leaf cells and the increased flow of water to them together lead to an increase in cell turgor, which is consistent with the maintenance of the growth of daisy plant under these conditions. In the leaves, an increase in osmotic potential (increased solute accumulation) was observed in the K_2SiO_3 treatment under salinity compared to the control, suggesting an increased water transport through the roots according to a previous study [53]. Moreover, salt stress significantly increased proline content throughout the experiment (Fig. 2b), which could be due to the increased rate of hydrolysis of proteins as the protein synthesis machinery is redirected into accumulating proline [54]. Many plants under stress conditions form and accumulate various osmoprotectants to maintain water in cells for normal physio-biochemical processes [55]. Under salt stress, the activities of pro-synthesising enzyme P5CS and pro-degrading enzyme ProDH were strongly induced and inhibited, respectively, which were accompanied by an increase in proline. Several studies suggest that the addition of Si can increase the salt tolerance of plants by regulating the content of osmolytes and adjusting the osmotic potential [56, 57]. Furthermore, the addition of K_2SiO_3 can actively participate in altering proline and carbohydrate metabolism in plant tissues by modulating the activities of metabolic enzymes [21, 58]. In daisies, K_2SiO_3 treatment, compared to the control, increased the accumulation of carbohydrate and proline (Fig. 2) and decreased the osmotic potential of leaves under salt treatments, thus contributing to the maintenance of the relative water content of leaves.

A significant decrease in leaf chlorophyll was observed along with the increase of leaf Cl^- and Na^+ concentrations. However, the plants subjected to high K_2SiO_3 showed a significant increase in leaf chlorophyll (Table 6). It seems that NaCl toxicity was the main reason for the degradation of chlorophyll in the plants, and the decrease in chlorophyll was caused by increased Cl^- and Na^+ concentrations. The addition of K_2SiO_3 significantly reduced the negative effects of NaCl on chlorophyll content; this can be interpreted as the effect of K_2SiO_3 on the biosynthesis of new chlorophylls and the protection of existing chlorophyll from oxidative stress caused by salinity [59]. The increasing effects of K_2SiO_3 on K and Si accumulation and Na and Cl reduction in leaves, found in the present study, are in agreement with the previous studies reporting the positive effect of Si on chlorophyll and photosynthesis due to high K^+ concentration and lower Na^+ concentration under salt stress [60]. The results of our study showed the inhibition of *A*, *gs*, and *E* under NaCl stress compared to the control; the results are in line with those of Seeman and Critchley [61] who associated the reduction in photosynthetic capacity at a given internal CO_2 concentration under salt stress to the reduction in leaf chlorophyll. The substomatal CO_2 content and stomatal conductance decreased in accordance with an increase in salinity. The reduction in photosynthesis under salt stress is due to the closure of stomata, resulting in a reduction in leaf transpiration rate and lower internal leaf CO_2 concentration. However, the plants facing NaCl treatment showed a reduction in *Ci* (leaf internal CO_2 concentration) in parallel with a reduction in *gs*, indicating specific deleterious effects of Cl^- on chloroplast function in addition to stomata limitations. Similarly, other studies have shown that both stomatal and non-stomatal factors affect photosynthesis at moderate and high salinity levels [62, 63]. When K_2SiO_3 was applied, *gs* and *E* increased under salinity, so the deleterious effect of salt on *A* decreased. In leaves, an increase in ABA and significantly lower *gs* were detected under salt treatment compared to the control, indicating a decrease in the photosynthesis rate. ABA accumulates in plant tissues to prevent water loss by closing stomata during salt stress. Interestingly, the current study found that use of K_2SiO_3 under NaCl stress reduced the amount of endogenous ABA and also reversed the stomatal closure induced by ABA. In addition, the induction of low ABA accumulation indicated that K_2SiO_3 significantly attenuated the hazardous effects of salinity, which is consistent with the previous studies [64]. In contrast, Kim et al. [65] showed that ABA content in rice increased significantly after 6 and 12 hours and then decreased 24 hours after Si application. Therefore, the effect of K_2SiO_3 on ABA concentration in salt-stressed plants depends on the plant species and K_2SiO_3 concentration.

In the present study, we analyzed the concentration of compounds such as phenolics, anthocyanins, and flavonoids. Salt stress and K_2SiO_3 increased secondary metabolites such as phenol and flavonoids. Phenyl compounds, including flavonoids and phenolic acids, formed through the phenylpropanoid pathway are well-known examples of phytochemicals that not only act as phytoalexins or phytoantipins against biological stress, but also play an important role as non-enzymatic antioxidant compounds in plant defense mechanisms against salt stress [66]. It also highlights the higher concentration of total phenolics in plants sprayed with K_2SiO_3. The Si supplied by K_2SiO_3could increase the synthesis and accumulation of phenols as suggested by the study of Yaghubi et al. [67]. Thus, the higher antioxidant capacity observed in the plants supplied with K_2SiO_3 could be related to the higher concentrations of these compounds compared to the control plants. Feeding plants with K_2SiO_3 has been shown to alter the expression pattern of many genes, particularly genes encoding enzymes involved in the phenylpropanoid pathway [68]. Increased phenylalanine ammonia lyase activity has also been reported as an alternative mechanism due to the effect of Si on the synthesis of phenolic compounds [69]. As shown in Fig. 3, salt stress decreased anthocyanin in daisy petals, but K_2SiO_3 had a positive effect on anthocyanin under stress and stress-free conditions. In our study, ABA concentration in the leaf increased under salt stress. There is a close relationship between ABA metabolism and phenylpropanoid, flavonoid, and ascorbic acid metabolic pathways under salt stress [70, 71], which may be one of the main reasons for improved tolerance of plants to salt stress.

The lowest membrane stability and the highest MDA content were obtained at 50 mM salt stress level with no K_2SiO_3, and the highest membrane stability and the lowest MDA content were obtained at 2 mM K_2SiO_3 under non-stress conditions. Salt stress decreased membrane stability and increased MDA content in daisies (Fig. 3). Under salt stress, cell membranes are damaged as a result of lipid peroxidation, and membrane selective permeability is disrupted, leading to higher permeability and electrolyte loss in cells. In the current study, K_2SiO_3 decreased MDA content and increased membrane stability of daisy cells in the treated plants. It was found that Si caused lower permeability of the plasma walls of leaves, which can be associated to lower lipid peroxidation under salt stress [72]. Application of K_2SiO_3 under salt stress conditions reduced electrolyte leakage by decreasing Na^+ and Cl^- absorption and accumulation in cell walls, thus increasing stability. Silicon has also been shown to inhibit lipid peroxidation of cell membranes by inducing amino acids, such as proline, to detoxify free radicals, which reduces MDA levels [73]. As the results reported by Soleimannejad [74] suggest, Na_2SiO_3 application improves plasma membrane activity by reducing electrolyte loss, possibly by increasing H^+ -ATPase activity, which may contribute to the excretion or removal of Na^+

from sensitive tissues. This curative effect on cellular damage may be due to an enhanced antioxidant response and activity of ROS inhibitory enzymes, resulting in protection of cells from free radicals [70].

Overproduction of ROS under salt stress poses a threat to cells through lipid peroxidation and enzyme inhibition. Several researchers have reported increased activity of antioxidant machinery in plants to counteract salinity-induced oxidative stress [75, 76]. In a similar context, K_2SiO_3 was reported to mitigate the adverse effects of salinity by enhancing the antioxidant defenses of crops. It is believed that the reduction of lipid peroxidation under stress is the result of antioxidant enzymes production in plants. Addition of exogenous K_2SiO_3 reduced MDA accumulation in salt-stressed plants. In our study, the activities of SOD, CAT, POD and APX increased under salt stress. The same increase was reported in antioxidant enzymes SOD, APX, DHAR and GR following Si application in salt-stressed cucumber (*Cucumis sativus* L.) leaves [77]. The results of this study indicated that salt-induced low ROS concentrations activated SOD, APX, and POD, with or without Si application. Therefore, K_2SiO_3 can suppress chlorophyll degradation in chloroplasts by activation of POD. Studies show that use of Si can reduce the negative effects of salinity by regulating antioxidant defense system, leading to a reduction in lipid peroxidation and ultimately maintenance of membrane integrity [78, 79]. In the present study, exogenous application of K_2SiO_3 showed significant positive effects on reducing MDA production and electrolyte loss, as well as on enhancing the antioxidant activities of SOD, APX, POD, and CAT under salt stress. Our results suggest that the addition of K_2SiO_3 could significantly enhance the ability of daisy seedlings to protect themselves against stress-induced oxidative damage.

Under severe salt stress conditions, leaf damage was observed in the form of marginal burns that gradually spread to larger areas, and the dry weight of plants decreased in response to salinity. In general, K_2SiO_3 application was found to be effective in increasing total dry weight under salt stress (Fig. 5). Necrosis was responsible for the decrease in dry weight under salt stress. Most likely, the accumulation of Cl and Na in toxic amounts, ion imbalance, and water stress are the main reasons for the occurrence of the leaf necrosis [67]. The reduced leaf necrosis in plants treated with K_2SiO_3 could be due to the inhibition of Na and Cl translocation to shoots and/or accumulation of Na in roots [80] and/or improved cell turgor due to maintenance of K^+ flux to leaf cells [81]. The present study showed that plant growth, chlorophyll content, and photosynthetic parameters of daisy plants were improved by the addition of K_2SiO_3 under salt stress conditions, demonstrating the positive and beneficial effects of Si and K on daisy growth. These beneficial effects could be direct (improved nutrition). Silicon promoted the growth of rice plants by increasing the extensibility of cell walls [82]. It appears that maintenance of photosynthetic activity increases dry weight under salt stress. Accumulation of toxic Cl^- and Na^+ concentrations, nutrient deficiency, ion imbalance, and water stress are most likely the main causes of dry weight loss [83]. The higher dry weight of K_2SiO_3-treated plants could be owing to the inhibition of Na^+ transport to shoots or the improvement of cellular turgor pressure due to the maintenance of K^+ flux [84]. Moreover, K_2SiO_3 enhances photosynthesis in plants under salt stress by modifying the gas exchange process, increasing chlorophyll content [70], removing ROS [59], and also regulating carbohydrate metabolism [85].

5 Conclusion

In conclusion, Si and K from K_2SiO_3 sources are beneficial for daisy growth under salt stress. The ameliorative effects of K_2SiO_3 on growth, and physiological and oxidative responses of salt-stressed daisy plants could be due to the improvement of photosynthetic parameters and the activation of antioxidant enzymes, as well as osmotic adjustment. These mitigating effects on most variables evaluated were more pronounced at 4 mM K_2SiO_3. Increased growth under salt stress by the application of K_2SiO_3 was associated with a decrease in Cl^- and Na^+ and an accumulation of K^+. The promotion of K in the leaf is not only the result of leaf application, but also of the effect of Si on K uptake from the nutrient solution. Therefore, our results suggest that K_2SiO_3 application to plants could be used as a promising strategy to maintain growth under salt stress.

Acknowledgments Authors thank Dr. Toktam Oraee and Ferdowsi Universty for encouragement and facilities.

Author Contributions A. Oraee: Performed the data acquisition, Writing - review & editing. A. Tehranifar: Project administration, Supervision and scientifically supported.

Data Availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication Not applicable.

Conflict of Interest The authors declare no conflict of interest.

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