



Morphological and Biochemical Properties, Leaf Nutrient Content, and Vase Life of Tuberose (*Polianthes tuberosa* L.) Affected by Root or Foliar Applications of Silicon (Si) and Silicon Nanoparticles (SiNPs)

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Abstract

Although the presence of silicon (Si) as a phyto-beneficial element is not essential in the nutrition of ornamental plants, its application may have many advantageous effects. Therefore, the present research was conducted to investigate the effects of Si and synthesized silicon nanoparticles (SiNPs) on the morphological and biochemical properties, leaf nutrient content, and vase life of tuberose (*Polianthes tuberosa* L.). Si and SiNPs were applied at 200 mg L⁻¹ and 400 mg L⁻¹ via root or foliar application under greenhouse conditions. The results showed that the application of two silicon sources by foliar or root, with increasing leaf phosphorus and Si contents, substantially enhanced total soluble carbohydrate and protein. Morphological parameters, including leaf fresh weight, root volume, root and bulblet dry weight, flowering stem length, flowering-stem dry weight, and floret number were improved. The flower vase life in treated plants was longer than non-treated ones and ranged from 32% for 200 mg L⁻¹ SiNPs by root application to 60% for 200 mg L⁻¹ Si and 400 mg L⁻¹ SiNPs by foliar. In most of the evaluated parameters, SiNPs had a relative superiority to Si, particularly when sprayed. A heat-map analysis of traits also revealed that the concentration of conventional Si has great prominence than its application method. In contrast, the method of applying SiNPs is more critical than its concentration. It is concluded that foliar application of SiNPs at 400 mg L⁻¹ can be recommend for improving the growth and flowering of tuberose plants, although the root application of Si at 200 mg L⁻¹ also had relatively acceptable results.

Keywords Bulbous plants · Nanoparticle · Silicon · Total soluble carbohydrate · Vase life

Abbreviations

ANOVA Analysis of variance
DW Dry weight

FW Fresh weight
POD Peroxidase
ROS Reactive oxygen species
Si Silicon
SiNPs Silicon nanoparticles
SOD Superoxide dismutase
TSC Total soluble carbohydrate
TSP Total soluble protein

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Introduction

Silicon (Si) as an element comprises 29% of the Earth's crust and, after oxygen, is the second-most abundant element therein. This element is taken up by plants in the form of orthosilicic acid (H₄SiO₄) and monosilicic acid [Si(OH)₄] (Ma and Yamaji, 2006), then translocated to the shoot by intermediation different Si transporter genes, i.e., *LSi1*, *LSi2* and *LSi6* (Rao and Susmitha 2017), thereafter, polymerized to form amorphous phytoliths similar to

silicon nanoparticles (SiNPs) (Sun et al. 2014; Nazaralian et al. 2017).

Apart from some species of the Equisitaceae family, Si is not a necessary element for plants. However, Si as an adaptable, green and eco-friendly alternative to different chemical fertilizers and its beneficial impacts on the plants, such as the production of more foliage, higher photosynthetic capacity, lower transpiration rate, and water loss and enhanced chlorophyll content (Etesami and Jeong, 2018; Rastogi et al. 2019). Furthermore, it has been well documented that Si could mitigate the adverse impacts of stresses, such as disease and pests (Etesami and Jeong 2018), drought (de Camargo et al. 2019), salinity (Yan et al. 2020), and metal toxicity (Tripathi et al. 2016) in plants.

Si nanoparticles (SiNPs) technology involves the engineering and employment of nano-sized silicon particles to produce of fungicides, bio-pesticides, and agro-fertilizer materials. SiNPs can be synthesized from several sources, including chemical compounds, such as tetraethyl orthosilicate [$[\text{Si}(\text{OC}_2\text{H}_5)_4]$], inorganic salts, such as sodium silicate [$[\text{Na}_2\text{SiO}_3]$], and organic materials, like rice (*Oryza sativa*) husk (Laane et al. 2018).

All sources of silicon are commonly applied in agriculture in three ways: drenching (root), foliar application, and incorporating to the growth medium. In the comparison of two methods of foliar or root application of Si or SiNPs, Artyszak (2018) reported that the advantages of the foliar application are that they are cheaper and more convenient to use than root application. It has also been indicated that the foliar application of Si is more efficient than soil application due to Si strong sorption to soil minerals and organics and relatively low solubility in soil (Syu et al. 2016).

The foliar application of monosilicic acid on some bedding flowers has been shown to enhance growth by increasing the number of lateral shoots, buds, and flowers (Wroblewska and Debicz 2011). Supplementing of Si improved the flower quality in gerbera (*Gerbera jamesonii*) (Kamenidou et al. 2010) and zinnia (*Zinnia elegans*) (Kamenidou et al. 2009).

Fitriani and Haryanti (2016) indicated when SiNPs, used as fertilizer, promoted plant height, leaf number, and root length of tomato (*Solanum lycopersicum*). The external application of SiNPs in plants can lead to enhanced growth and vegetative proliferation by the accumulating of proline, amino acids and nutrients (Luyckx et al. 2017). The application of SiNPs was observed to improve the growth rate, besides increasing the total soluble protein (TSP) content, and photosynthesis of lupin (*Lupinus angustifolius*) and wheat (*Triticum aestivum*) seedlings (Sun et al. 2016). The negative effect of SiNPs on plant height, shoot and root biomasses as well as its positive effect on shoot and root Si content, and peroxidase (POD) activity were reported by Le

et al. (2014) in transgenic and non-transgenic cotton (*Gossypium hirsutum*).

Roduner (2006), by comparing SiNPs with Si, reported that the SiNPs might exhibit different properties than Si, because of their small size, higher surface area-to-weight ratio, and different shapes. Previous comparative studies also have shown that due to greater availability of SiNPs than Si, SiNP is more effective in ameliorating of arsenate toxicity in maize (*Zea mays*) (Tripathi et al. 2016) and reducing of UV-B stress in wheat (Tripathi et al. 2017). Conversely, Haghghi and Pessarakli (2013) reported that the application of Si and SiNPs alleviated the adverse effect of salinity on cherry tomatoes, but they did not show any significant difference between these two forms of silicone. A comparison of two silicon sources (sodium silicate and SiNPs) on fenugreek (*Trigonella foenum-graecum*) has been shown that the putative silicon transporter (*PST*) gene was up-regulated at a greater level when sodium silicate was applied, but in some parameters, such as Si accumulation, POD activity, and SOD activity, no difference was found between the two silicon sources (Nazaralian et al. 2017).

The tuberose (*Polianthes tuberosa* L., Agavaceae), a summer-flowering bulbous plant is commercially used as a cut flower, garden plant, and in the perfume industry (Dole and Wilkins 2005). The flower quality in tuberose is evaluated by characteristics, such as flowering-stem length, diameter and weight, number of florets, and vase life. The short vase life is one of the limitations of this flower in production and marketing, so increasing the quality of this flower is vital for its prosperity in the floriculture industry. In addition to the importance of flower production in tuberose, the proper nutrition of the mother bulb as well as the production of bulblets should be considered in order to propagate for the next year. To the best of our knowledge, no comparing study has considered the effects of Si and SiNPs by foliar and root on growth and development of tuberose plants. Therefore, in the present study, our aims were (1) to evaluate whether two forms of silicon (Si and SiNPs) effect on the growth and development of the aerial (shoot and flower) and underground (bulb and root) parts of tuberose, and (2) to reveal the responses of biochemical properties, leaf nutrient content, and vase life of this plant to Si and SiNPs via two methods of application (root and foliar).

Materials and Methods

Preparation of Silicon (Si) and Silicon Nanoparticles (SiNPs)

Silicon dioxide (SiO_2) with a particle size of 10 to 45 μm was obtained from Merck Company. For the preparation of SiNPs, 3 mM nitric acid (HNO_3) solution was added as

a drip to 1 g of $\text{Si}(\text{OC}_2\text{H}_5)_4$ so that a pH value of 10 was achieved. This produced a pale yellow gel covered for two days, and was centrifuged at 4,000 g for 15 min, washed three times with distilled water, and finally dried at 60 °C in the oven (Heraeus Electric, Germany) for 24 h (Abdel-Haliem et al. 2017). The particle sizes of the resulting SiNPs (Fig. 1) were evaluated to be about 10 to 30 nm based on scanning electron microscopy (FE-SEM, MIRA3 TESCAN, Czech Republic) images.

Plant Materials and Growth Conditions

This study was carried out from May 2017 to September 2018 under greenhouse conditions at the University of Kurdistan, Iran (Sanandaj, 35°8'N, 46°51'E). The greenhouse was managed at $(25/17) \pm 3$ °C (day/night) temperature, $50 \pm 5\%$ relative humidity, $700\text{--}900 \mu\text{mol m}^{-2} \text{s}^{-1}$, and 14/8 h light/dark regime. Uniformly sized bulbs of tuberose

(*Polianthes tuberosa* cv. Dezful) with an average diameter of 2.5 to 3 cm were used for the experiments. On May 18, 2017, the bulbs were planted in 4.5 kg plastic pots in a mixture of soil, sand, and manure (v/v/v) (Table 1) and were irrigated every two to three days. The first fertilization involved the use of 200 mL of Kristalon fertilizer (38% K_2O , 12% N, 12% P_2O_5 , 0.07% Fe, 0.04% Mn, 0.028% B, 0.025% Zn, 0.01% Cu and 0.004% Mo) at a concentration of 0.25 g L^{-1} for each pot. After this date, 700 mL of the same fertilizer at 0.5 g L^{-1} was applied semimonthly to each pot.

Experimental Design and Treatments

This study was conducted in a completely randomized three-factor design. The factors included two types of silicon (Si and SiNPs), two methods of application (root and foliar), and two concentrations (200 and 400 mg L^{-1}), along with a control (distilled water). Each treatment was performed on

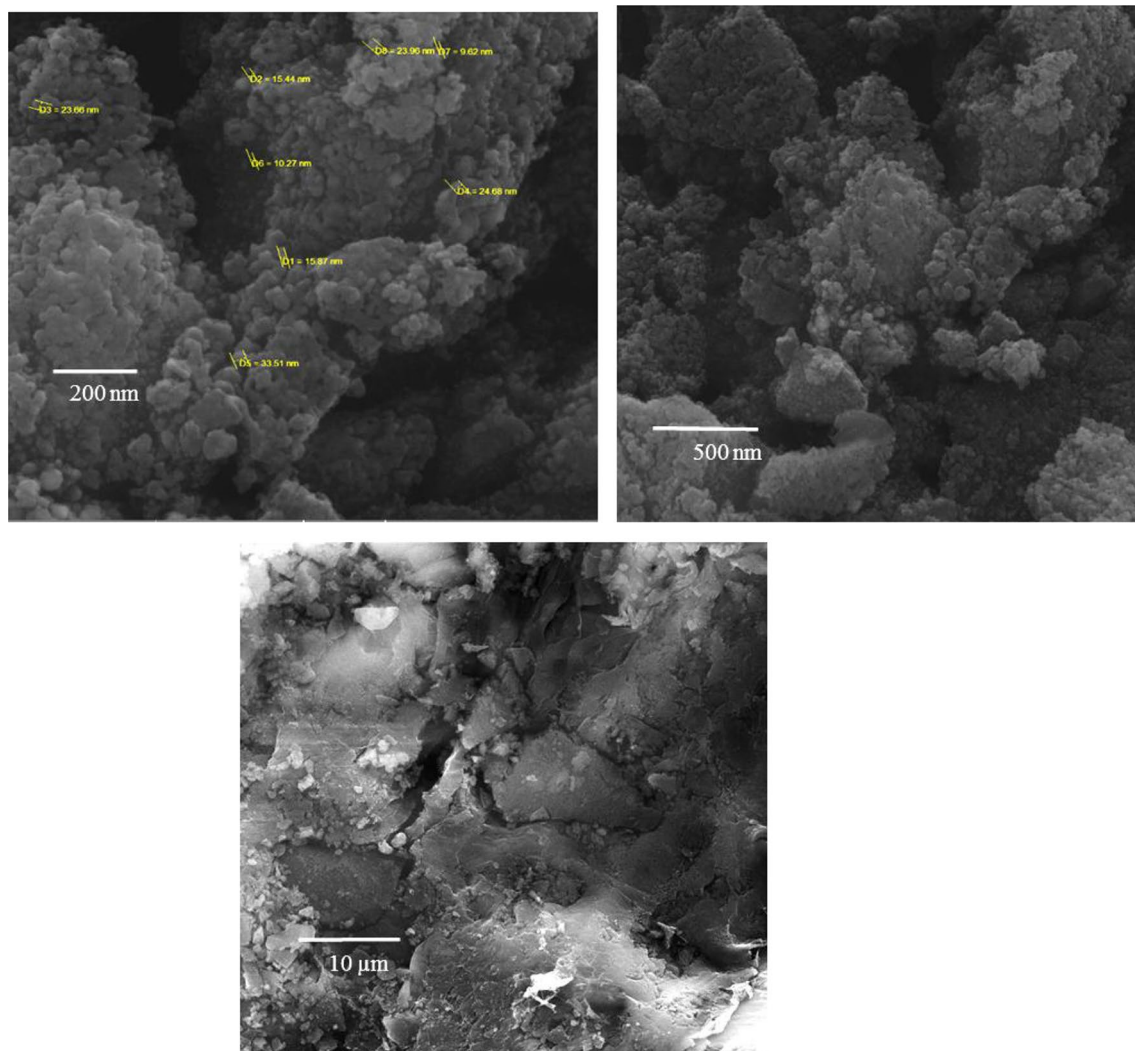


Fig. 1 The scanning electron microscopy (SEM) image of synthesized SiNPs

Table 1 Physical and chemical properties of the soil mixture used as pot media

| Ph | EC (dS m ⁻¹) | CEC (meq g ⁻¹ soil) | BD (g cm ⁻³) | PD (g cm ⁻³) | OM (%) | TP (%) |
|------|--------------------------|--------------------------------|--------------------------|--------------------------|--------|--------|
| 7.53 | 0.74 | 0.49 | 1.26 | 2.58 | 0.90 | 0.51 |

EC electrical conductivity, CEC cation exchange capacity, BD bulk density, PD particle density, OM organic matter, TPS total porosity

four replicates, and each replicate consisted of a pot with two bulbs. Si and SiNP solutions were prepared using a heater stirrer until the particles were completely dissolved in distilled water. Two drops of Tween 20 were added to 500 mL of each solution, and their pH was adjusted to 6 using phosphoric acid. Si and SiNP treatments started when the plants reached the 16-leaf stage (June 22, 2017). In the root application, 300 mL of both types of solution were poured over the entire pot surface. In the foliar method, the leaves were sprayed thoroughly up to runoff. This was repeated five times at intervals of 7 days (Mattson and Leatherwood 2010).

Physical and Chemical Properties of the Soil Mixtures

The soil mixtures' bulk and particle density, total porosity, pH, EC, and CEC (Harada and Inoko 1980) and the percentage of organic matter (Nelson and Sommers 1996) were evaluated. The pH and EC were measured using a pH meter (Metrohm Co., Herisau, Switzerland) and an EC meter (Inolab® Cond 7310, Germany), respectively. CEC was calculated according to the ammonium acetate method, in which the amount of Na in the soil is measured using a flame photometry (BWB Technologies Ltd., Newbury, UK).

Leaf Nutrient Content

After flowering (July 30, 2017), the amounts of N, P, K, and Si in dried leaves were measured. For total N, the Kjeldahl (2200 Kjeltex Auto Distillation, Denmark) method was used (Bremner 1965); the amount of P was measured using the colorimetric method and a spectrophotometer; K was also measured by flame photometry (Kalra 1998); and Si content was determined with the microwave-assisted digestion method (Frantz et al. 2008) using inductively coupled plasma optical emission spectrometry (ICP-OES).

Biochemical Properties

Chlorophyll Content

To measure the leaf chlorophyll content, 0.1 g of leaf tissue was ground and mixed with 0.1 g MgO and 10 mL of 80% acetone before being homogenized. The extract was centrifuged at 3,000 g for 10 min. Finally, the absorbance of the

supernatant extract was measured using a spectrophotometer at 663 and 646 nm, and the total chlorophyll content was calculated in mg g⁻¹ fresh weight (FW) according to the following formula (Lichtenthaler and Buschmanns (2001):

$$\text{Chl}_a (\text{mg g}^{-1} \text{FW}) = (12.25 \times A_{663}) - (2.79 \times A_{646}),$$

$$\text{Chl}_b (\text{mg g}^{-1} \text{FW}) = (21.21 \times A_{646}) - (5 \times A_{663}),$$

$$\text{Ch}_{\text{total}} (\text{mg g}^{-1} \text{FW}) = \text{Chl}_a + \text{Chl}_b.$$

Total Soluble Carbohydrate (TSC)

To determine leaf TSC, 0.5 g of leaf tissue was ground in a mortar and mixed with 5 mL of 95% ethanol. The grinding continued until the mixture became homogenous. The mixture was then centrifuged for 10 min at 3,500 g. Next, 1 mL of the supernatant was combined with 3 mL of inron and treated with 100 °C in a boiling-water bath (HYSC WD-11B, Korea) for 20 min. When the samples cooled, the light absorbance was read with a spectrophotometer at 625 nm. Different concentrations of glucose were used as standard solutions (Irigoyen et al. 1992).

Total Soluble Protein (TSP)

The leaf TSP was measured by grinding 0.5 g of leaf in a mortar to which 50 mg polyvinyl pyrrolidone was added. During stirring, 1.5 mL potassium phosphate buffer (pH 7) containing sodium metabisulfite was added and the grinding process continued to the point that the mixture became homogenized. The mixture was centrifuged at 10,000 g for 20 min at 4 °C. Next, 40 µL of the extract was mixed with 960 µL of Bradford solution, and the optical absorbance of the solution was read at 595 nm after 5 min (Bradford 1976).

Peroxidase (POD) Activity

To measure the POD activity, 400 µL of 50 mM potassium phosphate buffer (pH 7) was mixed with 40 µL of 1% guaiacol and 40 µL of 0.3% H₂O₂ in a cuvette on an ice bath. Then 65 µL of protein extract that contained plant enzymes was added to 960 µL of this reaction mixture. Changes in the absorbance were read at 470 nm for 120 s by

a spectrophotometer. Finally, the POD activity was recorded as unit mg^{-1} protein (Hemeda and Kelin 1990).

Superoxide Dismutase (SOD) Activity

The basis of Beyer and Fridovich's (1987) method of enzyme measurement is the inhibition of the SOD enzyme by the photoreduction of nitroblue tetrazolium (NBT). A reaction solution was prepared by mixing 25 mL of 50 mM phosphate buffer (pH 7.8), 3.5 mg L-methionine, 4 mg NBT, and 7.50 μL Triton X-100. Then 1 mL of the reaction solution was mixed with 400 μL riboflavin, and 100 μL of the extracted protein was mixed with the solution before being poured into a microtube. The absorbance was read at 560 nm using a spectrophotometer and the SOD activity was expressed in unit mg^{-1} protein.

Measurement of Morphological Parameters

After two or three lower florets had opened (Dole and Wilkins 2005), the flowering stem was harvested and the stem length and diameter and the vase life were measured. When all plants had flowered (October 2, 2017), the leaves were counted and their FW was measured. Then, mother bulbs were removed from each pot to calculate the bulblet number, root DW, and volume. To measure DW, the samples were dried at 72 °C with an oven (Heraeus Electronics, Hanau, Germany) for 48 h. To measure of root volume, the roots were immersed into the cylinder containing water and then the change in water volume was considered as the root volume (Javadi et al. 2017). All fresh and dry weight measurements of samples were performed using an electronic balance scale (FX400, Japan) with a precision of 0.001 g.

Table 2 The interaction effect of silicon types (Si and SiNPs), application methods (root and foliar), and two concentrations (200 and 400 mg L^{-1}) along with the control (deionized water) on leaf number, leaf FW, root DW, and volume of tuberose

| Silicon types | Con | Appli- cation method | Leaf number | Leaf FW (g) | Root DW (g) | Root volume (cm^3) |
|---------------------------------------|-----|----------------------------|----------------------------|-----------------------------|---------------------------|-------------------------------|
| Control | – | – | 28.60 ± 0.41 ^b | 66.52 ± 2.04 ^f | 0.34 ± 0.03 ^d | 3.85 ± 0.41 ^d |
| Si (mg L^{-1}) | 200 | Root | 27.50 ± 1.04 ^{cb} | 80.75 ± 1.22 ^{bc} | 0.48 ± 0.01 ^c | 5.50 ± 0.29 ^{bc} |
| | | Foliar | 34.25 ± 0.82 ^a | 84.50 ± 2.77 ^{abc} | 0.73 ± 0.05 ^{ab} | 8.00 ± 0.41 ^a |
| | 400 | Root | 27.00 ± 1.43 ^{cb} | 83.52 ± 0.24 ^{abc} | 0.66 ± 0.02 ^b | 8.00 ± 0.41 ^a |
| | | Foliar | 25.13 ± 1.13 ^c | 78.32 ± 1.62 ^{cd} | 0.70 ± 0.04 ^{ab} | 4.38 ± 0.38 ^{cd} |
| SiNPs (mg L^{-1}) | 200 | Root | 28.75 ± 0.82 ^b | 73.77 ± 4.08 ^{de} | 0.49 ± 0.04 ^c | 6.50 ± 0.61 ^b |
| | | Foliar | 33.13 ± 1.42 ^a | 86.09 ± 2.37 ^{ab} | 0.75 ± 0.02 ^a | 6.63 ± 0.31 ^b |
| | 400 | Root | 27.88 ± 0.97 ^{cb} | 70.84 ± 2.04 ^{ef} | 0.52 ± 0.01 ^c | 6.50 ± 0.61 ^b |
| | | Foliar | 33.38 ± 2.51 ^a | 88.32 ± 2.58 ^a | 0.76 ± 0.04 ^a | 8.75 ± 0.72 ^a |
| LSD ($P \leq 0.05$) | – | – | 3.28 | 6.50 | 0.08 | 1.33 |

Values represent the means ± standard error (n=5). In each column, values with the same letter (s) are not significantly different at LSD ($P \leq 0.05$)

Vase Life Evaluation

To measure vase life, the flowering stems were cut diagonally with a sharp knife under distilled water at 45 cm length, and each branch was placed in 200 mL of a vase solution of distilled water containing 4% sucrose. The environmental conditions were 23 ± 2 °C, $60 \pm 10\%$ relative humidity, and $17 \mu\text{mol m}^{-2} \text{s}^{-1}$ light with a photoperiod of 12 h. The vase life period was considered to extend from the first day of harvesting flower until the flowering stems showed signs of wilting and bending while the petals turned pale (Dole and Wilkins 2005).

The centrifugation of all samples was performed in a MIKRO 200 centrifuge (Hettich, Tuttlingen, Germany) and all spectrophotometric measurements were performed in a UV-2100 spectrophotometer (Unico, New Jersey, NJ, USA).

Data Analysis

The SAS software was used for statistical analysis, and the mean values were compared using the LSD test ($P \leq 0.05$). Pearson's correlation coefficient for evaluating the correlation between the study variables was executed using Minitab 17 software. In addition, a heat map of traits that had been prepared through the heat-map package in the R environment was used to better evaluate the measured traits under the interaction effect of all three factors.

Results

ANOVA Analysis

According to the analysis of variance (Supplemental Tables 1 and 2), the interaction effects of all three factors (silicon type, method of application, and concentration)

were significant on all measured traits except vase life, total chlorophyll content, and leaf Si content.

Heat-map Analysis

The heat-map analysis of traits (Fig. 2) revealed that Si concentration was more important than method of application. In contrast, the method of application was more effective than concentration when SiNPs were applied. According to this analysis, the measured traits were classified into six categories in response to the interaction effect of three main factors: (1) two types of silicon at 200 mg L⁻¹ by root application; (2) Si at 200 mg L⁻¹ by foliar application; (3) treatments in which distilled water was used instead of Si and SiNPs; (4) SiNPs at 200 and 400 mg L⁻¹ by foliar application; (5) SiNPs at 400 mg L⁻¹ by root application; and (6) Si at 400 mg L⁻¹ by root and foliar applications.

Effects of Silicon (Si) and Silicon Nanoparticles (SiNPs) by Foliar and Root Applications on Leaf Nutrient Content of Tuberose

The highest total N content was obtained with foliar application of SiNPs at 400 mg L⁻¹, although not significantly different from either root application of SiNPs at 200 mg L⁻¹ or foliar application of Si at 200 mg L⁻¹. Moreover, there was no significant difference among control and Si concentrations for both methods (Fig. 3a).

Supplying both silicon sources by different methods significantly increased leaf P content, compared to the control. Increasing the Si from 200 to 400 mg L⁻¹ significantly increased leaf P content with root application, but no significant difference was observed with foliar application. Conversely, the increase in SiNPs from 200 to 400 mg L⁻¹ with root application showed no significant increase in leaf P content, but leaf P content was significantly increased with foliar application. In general, the highest leaf P content was achieved with foliar application of SiNPs at 400 mg L⁻¹ (Fig. 3b).

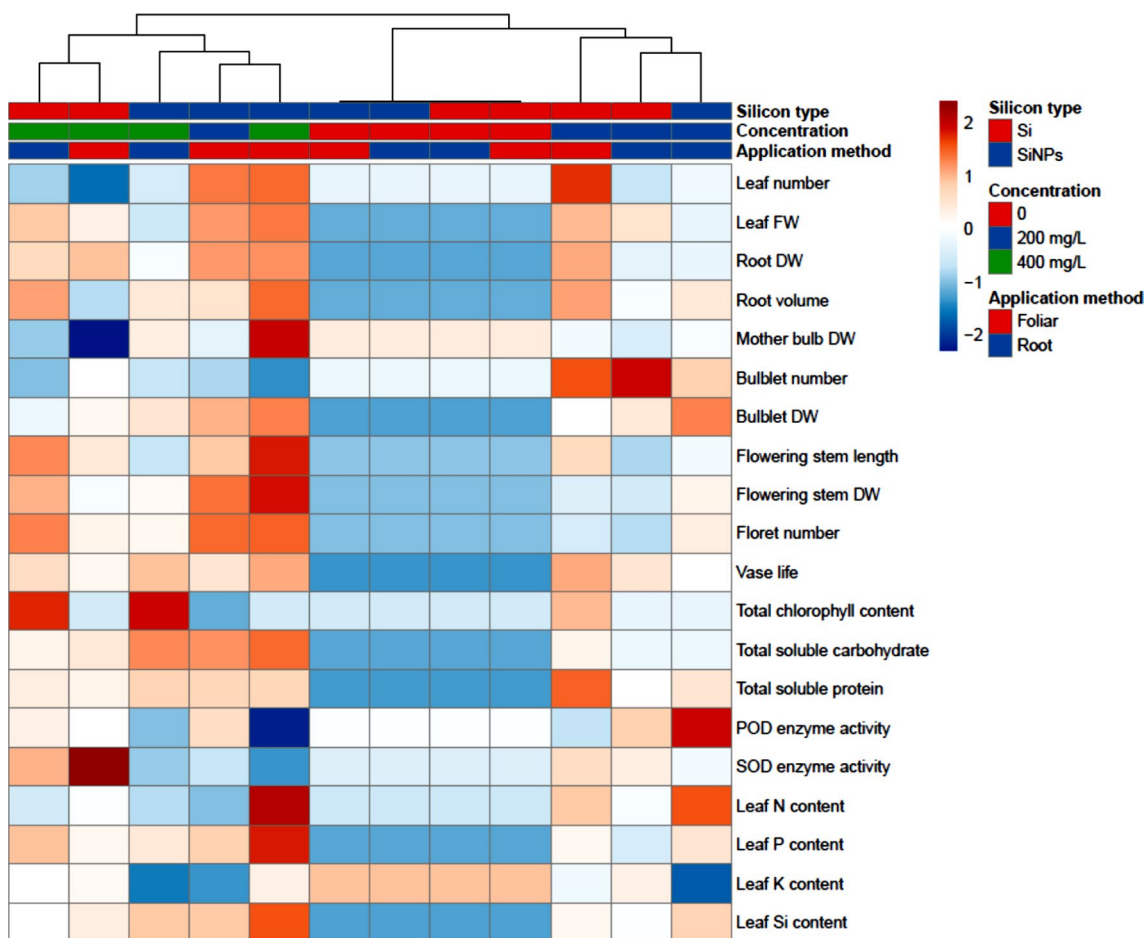


Fig. 2 The heat map of all measured traits in tuberose that affected by interaction effect between silicon types (Si and SiNPs), application methods (drenching and foliar), and concentrations (200 and 400 mg L⁻¹) along with the control (deionized water)

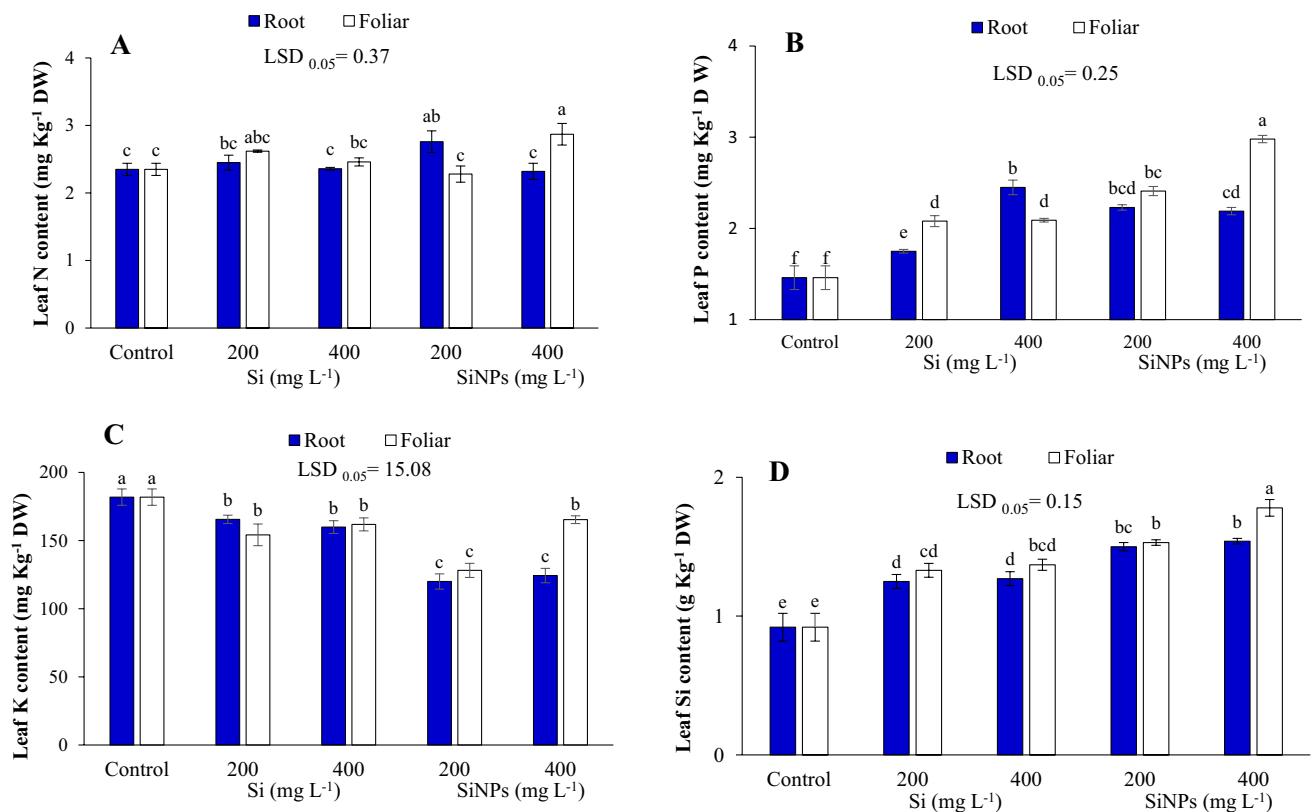


Fig. 3 The interaction effect of silicon types (Si and SiNPs), application methods (root and foliar), and concentrations (200 and 400 mg L⁻¹) along with the control (deionized water) on leaf N content (a), leaf P content (b), leaf K content (c), and leaf Si content (d) of tuberose.

Columns followed by the same letter (s) are not significantly different according to LSD ($P \leq 0.05$). Vertical bars represent the standard error of means ($n = 4$)

Both silicon sources had a negative effect on leaf K content. When both types of silicon sources and both supplementation methods were compared, a root drench of both concentrations of SiNPs and a foliar application of SiNPs at 200 mg L⁻¹ reduced the leaf K content compared to other treatments (Fig. 3c).

Both forms of silicon significantly increased leaf Si content compared to the control using foliar supplementation. As both silicon sources were increased from 200 to 400 mg L⁻¹, leaf Si content increased exponentially. In general, foliar application of both silicon sources increased leaf Si content more than root application; however, this difference was significant only for SiNPs at 400 mg L⁻¹ (Fig. 3d).

Effects of Silicon (Si) and Silicon Nanoparticles (SiNPs) by Foliar and Root Applications on Leaf Biochemical Properties of Tuberose

Total Chlorophyll Content

Both types of silicon can affect the leaf total chlorophyll content positively, negatively, or insignificantly.

Root application of both types of silicon improved total chlorophyll content. The highest value for this trait was obtained with root application of SiNPs at 400 mg L⁻¹ and Si, although these differed insignificantly with Si at 200 mg L⁻¹ using foliar application (Fig. 4).

Total Soluble Carbohydrate (TSC) and Total Soluble Protein (TSP)

Both types of silicon resulted in a significant increase in the leaf TSC and TSP content compared to control (Fig. 5a and b). For both supplementation methods, increasing the concentration from 200 to 400 mg L⁻¹ improved TSC. For both silicon sources, the SiNPs, in particular, foliar application, resulted in higher TSC than root application; the highest amount of leaf TSC was achieved with the foliar application of SiNPs at 400 mg L⁻¹ (Fig. 5a). However, Si increased TSP content more efficiently than SiNPs. Foliar application of Si at 200 mg L⁻¹ increased TSP content more than any other treatment (Fig. 5b).

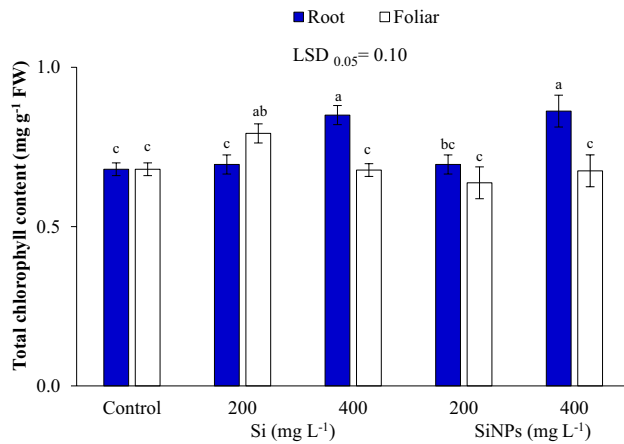


Fig. 4 The interaction effect of silicon types (Si and SiNPs), application methods (root and foliar), and concentrations (200 and 400 mg L⁻¹) along with the control (deionized water) on leaf total chlorophyll content of tuberose. Columns followed by the same letter are not significantly different according to LSD ($P \leq 0.05$). Vertical bars represent the standard error of means ($n = 4$)

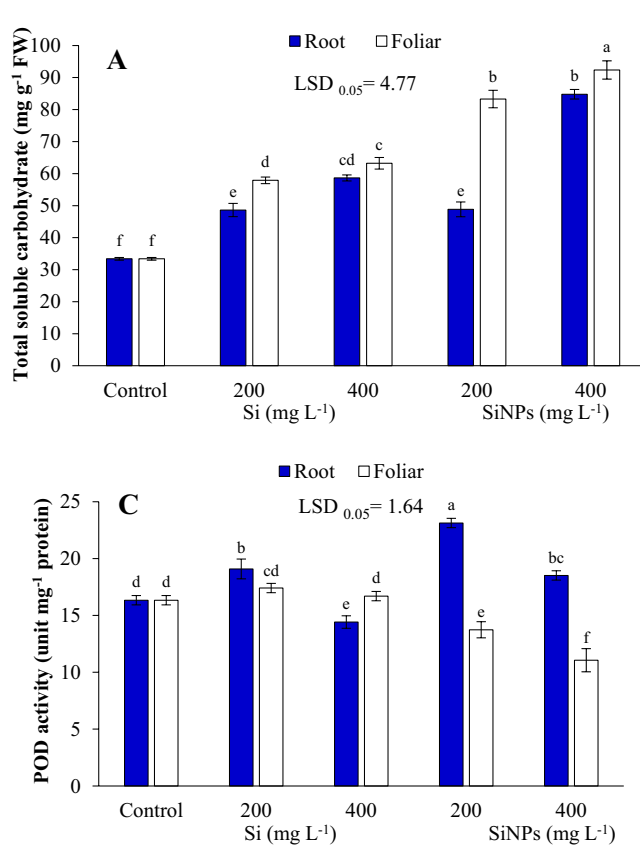
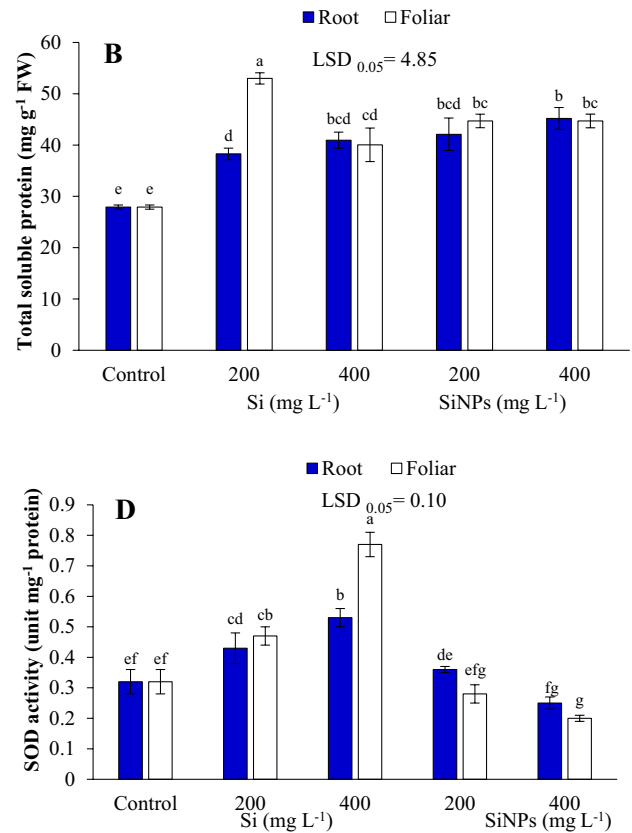


Fig. 5 The interaction effect of silicon types (Si and SiNPs), application methods (root and foliar), and concentrations (200 and 400 mg L⁻¹) along with the control (deionized water) on leaf total soluble carbohydrate (a), total soluble protein (b), POD (c), and SOD (d)

POD and SOD Activities

Increasing the concentration of both types of silicon led to a significant reduction in POD activity. The highest amount of POD activity was gained with root application of SiNPs at 200 mg L⁻¹, the lowest with foliar application of SiNPs at 400 mg L⁻¹ (Fig. 5c). The application of SiNPs significantly reduced SOD activity in comparison with Si. An increase from 200 to 400 mg L⁻¹ in both methods increased SOD activity for Si but decreased it for SiNPs. Absolutely, the highest and significant SOD activity was achieved by foliar of Si at 400 mg L⁻¹ (Fig. 5d). In general, SiNPs at high concentration in both application methods reduced the activity of both enzymes, especially SOD.



enzymes activity of tuberose. Columns followed by the same letter (s) are not significantly different according to LSD ($P \leq 0.05$). Vertical bars represent the standard error of means ($n = 4$)

Effects of Silicon (Si) and Silicon Nanoparticles (SiNPs) by Foliar and Root applications on Morphological Properties of Tuberose

Number and FW of Leaves

Foliar application of Si at lower concentration was more effective than root application in increasing leaf number and FW, but foliar application of SiNPs was more efficient than root drench at both concentrations. The highest leaf number and leaf FW were obtained with foliar application of Si at 200 mg L⁻¹ and SiNPs at 200 and 400 mg L⁻¹ (Table 2).

Root DW and Volume

The highest root DW was yielded from foliar application of both types of silicon and both concentrations, compared to control, but root DW was significantly reduced with root application. The highest root volume was recorded with foliar application of SiNPs at 400 mg L⁻¹; there was no significant difference between foliar application of Si at 200 mg L⁻¹ and root application of Si at 400 mg L⁻¹ (Table 2).

Bulblet Numbers and DW of Mother Bulb and Bulblets

Silicon sources variously had positive, negative, and insignificant effects on bulblet numbers and DW of the mother bulb and the bulblets. The highest number of bulblets per mother bulb was achieved by root and foliar application of Si at 200 mg L⁻¹. Apart from the foliar application of SiNPs at 400 mg L⁻¹, which resulted in the highest DW of the mother bulb, this trait was negatively affected by the treatments. The highest bulblet DW was obtained with root and foliar application of SiNPs at 200 and 400 mg L⁻¹, respectively (Table 3).

Table 3 The interaction effect of silicon types (Si and SiNPs), application methods (root and foliar), and two concentrations (200 and 400 mg L⁻¹) along with the control (deionized water) on mother bulb dry weight, bulblet number, and dry weight of tuberose

| Silicon types | Con | Application method | Mother bulb DW (g) | Bulblet number | Bulblet DW (g) |
|-----------------------------|-----|--------------------|---------------------------|---------------------------|---------------------------|
| Control | – | – | 3.85 ± 0.31 ^b | 5.50 ± 0.29 ^{cd} | 1.01 ± 0.02 ^g |
| Si (mg L ⁻¹) | 200 | Root | 3.18 ± 0.45 ^b | 9.00 ± 0.20 ^a | 3.22 ± 0.05 ^{cd} |
| | | Foliar | 3.42 ± 0.20 ^b | 8.38 ± 0.24 ^a | 2.47 ± 0.17 ^{ef} |
| | 400 | Root | 2.81 ± 0.41 ^{bc} | 4.50 ± 0.29 ^e | 2.11 ± 0.27 ^f |
| | | Foliar | 1.97 ± 0.14 ^c | 5.88 ± 0.31 ^c | 2.81 ± 0.11 ^{de} |
| SiNPs (mg L ⁻¹) | 200 | Root | 3.45 ± 0.34 ^b | 7.00 ± 0.20 ^b | 5.02 ± 0.27 ^a |
| | | Foliar | 3.26 ± 0.63 ^b | 4.75 ± 0.43 ^{de} | 4.39 ± 0.17 ^b |
| | 400 | Root | 3.83 ± 0.39 ^b | 4.88 ± 0.38 ^{de} | 3.25 ± 0.13 ^c |
| | | Foliar | 5.45 ± 0.34 ^a | 4.13 ± 0.24 ^e | 5.10 ± 0.18 ^a |
| LSD (P ≤ 0.05) | – | – | 1.05 | 0.85 | 0.43 |

Values represent the means ± standard error (n = 5). In each column, values with the same letter (s) are not significantly different at LSD (P ≤ 0.05)

Length and DW of Flowering Stems

The length of the flowering stem was increased in parallel with the increase in root application of Si from 200 to 400 mg L⁻¹, whereas a decrease in length was observed with foliar application. However, stem length was decreased with an increase in the root application of SiNPs from 200 to 400 mg L⁻¹, but increased with foliar application. The highest length and DW of flowering stems were obtained with foliar application of SiNPs at 400 mg L⁻¹, but not significantly different from other treatments. The lowest length and DW of flowering stems were observed in the control plants (Table 4).

Floret Numbers and Vase life

Floret numbers and vase life were positively affected by both types of silicon and both application methods. Foliar application of Si at 400 mg L⁻¹ and SiNPs at both concentrations led to the highest number of florets in inflorescence (Table 4). Foliar application of Si at 200 mg L⁻¹ and application of SiNPs at 400 mg L⁻¹ by both methods had stronger effects on prolonging vase life. The lowest number of florets and the shortest vase life were observed in control plants (Table 4).

Discussion

Leaf Macronutrient Contents of Tuberose Affected by Foliar and Root Applications of Silicon (Si) and Silicon Nanoparticles (SiNPs)

Our findings revealed an increase in leaf N, P, and Si contents by application of two sources of silicon especially the foliar application of SiNPs at 400 mg L⁻¹ (Fig. 3a–d). Si

Table 4 The interaction effect of silicon types (Si and SiNPs), application methods (root and foliar), and two concentrations (200 and 400 mg L⁻¹) along with the control (deionized water) on flowering-stem length and dry weight, floret number, and vase life of tuberose

| Silicon types | Con | Application method | Flowering stem length (cm) | Flowering stem DW (g) | Florets number | Vase life (day) |
|-----------------------------|-----|--------------------|-----------------------------|----------------------------|----------------------------|----------------------------|
| Control | – | – | 64.50 ± 1.22 ^e | 3.08 ± 0.09 ^d | 16.38 ± 0.63 ^c | 8.33 ± 0.44 ^f |
| Si (mg L ⁻¹) | 200 | Root | 65.18 ± 1.93 ^e | 3.24 ± 0.10 ^{cd} | 17.13 ± 0.77 ^c | 12.00 ± 0.29 ^{cd} |
| | | Foliar | 72.04 ± 1.29 ^{bc} | 3.30 ± 0.11 ^{cd} | 18.00 ± 1.22 ^{bc} | 13.33 ± 0.17 ^a |
| | 400 | Root | 75.05 ± 2.55 ^{ab} | 3.86 ± 0.07 ^{ab} | 24.63 ± 1.11 ^a | 12.33 ± 0.17 ^{bc} |
| | | Foliar | 71.01 ± 1.92 ^{bcd} | 3.43 ± 0.22 ^{bcd} | 20.63 ± 0.85 ^b | 11.33 ± 0.17 ^{de} |
| SiNPs (mg L ⁻¹) | 200 | Root | 68.33 ± 2.76 ^{cde} | 3.54 ± 0.31 ^{bc} | 21.00 ± 0.20 ^b | 11.00 ± 0.29 ^e |
| | | Foliar | 72.95 ± 1.85 ^{abc} | 4.01 ± 0.14 ^a | 25.25 ± 1.84 ^a | 12.00 ± 0.29 ^{cd} |
| | 400 | Root | 65.79 ± 2.65 ^{de} | 3.51 ± 0.20 ^{bcd} | 20.50 ± 0.96 ^b | 13.00 ± 0.29 ^{ab} |
| | | Foliar | 77.95 ± 1.56 ^a | 4.23 ± 0.12 ^a | 25.50 ± 2.18 ^a | 13.33 ± 0.17 ^a |
| LSD (P ≤ 0.05) | – | – | 5.37 | 0.44 | 3.18 | 0.93 |

Values represent the means ± standard error (n=5). In each column, values with the same letter (s) are not significantly different at LSD (P ≤ 0.05)

may modify the uptake and acquisition of nutrients in various plant species by stimulating the binding of nutrients in plant tissues, and by affecting their translocation into shoots (Greger et al. 2018). Si is also known to increase soil nutrient availability particularly P in plants and to maintain a balance between macro (N and P) and microelements such as zinc (Zn) and manganese (Mn) (White et al. 2017). Consistent with our results, an increase in the content of N in gerbera (*Gerbera jamesonii*) (Savvas et al. 2007), P in rice (Neeru et al. 2016) and grapes (*Vitis labrusca*) (Bhavaya et al. 2011), as well as Si in hybrid orchid (*Phalaenopsis* spp.) (Vendrame et al. 2010) and chrysanthemum (*Chrysanthemum* cv. Brighton) (Song and Jeong 2014) has been reported with the application of different sources of silicon. In the current study, the leaf P content was positively correlated with TSP value at P ≤ 0.01 (Supplemental Table 3). It is also capable of increasing the plant's total N content by increasing the amount of protein and amino acids and improving P uptake. It seems that the preference of SiNPs compared to Si on the content of these elements is due to (1) relative superiority effects of SiNPs than Si on root growth and (2) that SiNPs may be more effective in expressing a number of genes involved in the transport of these elements. In this regard, Kostic et al. (2017) suggested that the increase in P content of shoots and leaves of wheat is a result of the Si enhancing the expression of the root Pi transporter genes (*TaPHT1.1* and *TaPHT1.2*), and the root exudation of citrate and malate.

Rastogi et al. (2019) reported that one of the important factors affecting the performance of SiNPs is the method of application. In SiNPs and in the three elements mentioned above (N, P, and Si), foliar application was superior to root, but in Si, no specific trend was observed, although foliar application had better results at a 200 mg L⁻¹. It may be concluded that the foliar application of Si at high concentration

causes more Si deposition compared to SiNPs and exhibits antitranspirant effects (Kamenidou et al. 2010).

Similar to our results, Greger et al. (2018) reported that the application of Si decreased accumulation of K in the shoots of species with low Si accumulation capacity, such as lettuce, carrot, and pea. Conversely, they concluded that Si-accumulating plants, such as wheat, did not show a reduction in K. From our results, the decrease in K content caused by using both types of silicon may be that the plants were not subjected to any stress.

Responses of Leaf Biochemical Properties of Tuberose to Silicon (Si) and Silicon Nanoparticles (SiNPs) by Foliar and Root application

In the current study, all of the biochemical properties in tuberose were impacted by the use of two sources of silicon. Based on previous studies, silicon has positive effects on leaf chlorophyll content and prevents chlorophyll degradation as well as carbohydrate level (Savvas and Ntatsi 2015). In line with our results, silicon has been shown to increase the total chlorophyll content in the leaves of Changbai larch (*Larix olgensis*) (Bao-Shan et al. 2004), chrysanthemum (*Dendranthema grandiflorum*) (Sivanesan et al. 2013), and maize (Tripathi et al. 2016). Aminolevulinic acid (δ -aminolevulinic) is a precursor of chlorophyll production, and silicon sources may increase chlorophyll content in plant tissues by increasing the production of this precursor (Savvas et al. 2009). Si application has been shown to increase TSC content in impatiens (*Impatiens walleriana* “Accent White”) and petunia (*Petunia* × *hybrida* “Celebrity White”) (Whitted-Haag et al. 2014). Manivannan and Ahn (2017) reported that Si could up-regulate the expression of *osNAC* proteins that are responsible for stress tolerance, proline synthesis, and carbohydrate biosynthesis. Si nutrition

also plays an essential role in modulating the flux of 2-Oxoglutarate for amino-acid metabolism (Sweetlove and Fernie 2005). Accordingly, an increase in protein storage may be expected with the use of Si (Detmann et al. 2012). In our study, leaf Si content was positively correlated with TSC and TSP values at $P \leq 0.01$ (Supplemental Table 3). Nazaralian et al. (2017) also reported that silicate and SiNPs treatments increased protein synthesis in fenugreek seedlings and they concluded that silicon with expressing of phosphoenolpyruvate carboxykinase (*PEPCK*) gene in the roots and leaves affected nitrogenous compounds, like proteins (Beihaghi et al. 2009). Our results correspond to these reports.

There has been a great deal of research on the positive and negative effects of silicon on the activity of antioxidant enzymes Bokor et al. (2014), reported that Si application could reduce the reactive oxygen species (ROS) in plants by increasing SOD and decreasing POD. Increasing the activity of POD and SOD, by applying some concentrations of both silicon sources in the current study, confirmed the previous researches reporting an increase in activity of POD in asparagus (*Asparagus officinalis*) (Lu et al. 2008) and SOD in creeping bentgrass (*Agrostis stolonifera*) (Schmidt et al. 1999). Nevertheless, the observed decrease in SOD and POD activities that were obtained by the application of specific concentrations of two sources of silicon could be justified by the suggestion that some concentrations of two sources of silicon improve plant function under stress conditions, and thus, there is no need for the plant to produce SOD and POD to scavenge. In addition, in most applied treatments, the root application method increased POD activity more than foliar (Fig. 5c). Therefore, it can be assumed that this method has caused mild stress to some extent, and therefore, the activity of this enzyme has increased.

It is thought that the superiority of SiNPs compared to Si in the changes most of the biochemical traits is due to the smaller particle size of SiNPs because there is a high relationship between the extent of particle uptake and particle size (Abdel-Halim et al. 2017). Likewise, the smaller particle size of SiNPs is important in particle adhesion and interaction with cells (Smith et al. 2008).

Improved Morphological Parameters of Tuberose by Foliar and Root Application of Silicon (Si) and Silicon Nanoparticles (SiNPs)

It has been reported that Si with improving photosynthetic efficiency and producing more assimilates ultimately increase the number of leaves (Zhu and Gong 2014; Savvas and Ntatsi 2015) and leaf FW (Zhu and Gong 2014). A positive linear regression was observed between leaf Si content with TSC and leaf P content, with r-squared values of 0.82 and 0.81, respectively (Figs 6a and b). Similarly, Yassen et al. (2017) stated that foliar application of SiNPs at 60 mg L^{-1} on cucumber (*Cucumis sativus*) plants increased leaf number, leaf FW and DW. Meanwhile, de Oliveira et al. (2019) concluded that the increase in sorghum (*Sorghum bicolor*) growth with the use of Si is due to the reduction of water loss and respiration as well as its positive effect on gas exchange. Therefore, based on the higher content of Si that was obtained in the leaves with the use of SiNPs, it can be concluded that more Si adsorption causes the maintaining leaves upright and stretching leaf surfaces to capture maximum sunlight, thus optimizing photosynthesis (Siddiqui et al. 2020).

Application of Si can increase root DW and root volume by enhancing the level at which plants absorb elements

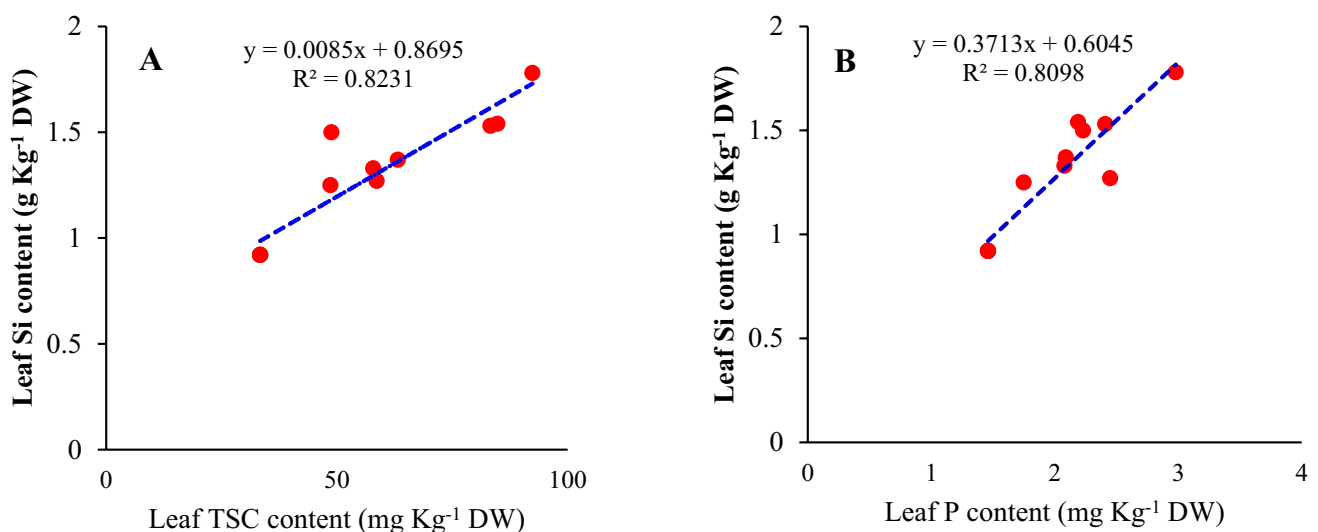


Fig. 6 The positive linear regression between leaf Si content with leaf total soluble carbohydrate (a) and leaf P content (b)

from the growing medium and by increasing the surface of root hairs (Ma et al. 2001). In this study, the increase in root DW and root volume maybe correlated with increased leaf FW, considering the positive correlation between these traits at $P \leq 0.01$ (Supplemental Table 3). In agreement with these results, Hu et al. (2019) found that the application of potassium silicate (K_2SiO_3) on stem cuttings of poinsettia (*Euphorbia pulcherrima*) improved the root FW and DW. However, the positive correlation observed between leaf P content and root DW and volume (Supplemental Table 3) suggests that two sources of silicon may also improve root growth by increasing P uptake (Fig. 3b).

In addition to various vegetative and physiological factors, bulblet production in bulbous plants is affected by the reproductive growth rate. In other words, the higher growth rate of the flowering stem can reduce bulblet production, and vice versa. In this study, the root application of Si at 200 mg L^{-1} resulted in shorter flowering stems, less DW, and fewer floret numbers, but better bulblet production. However, foliar application of SiNPs at 400 mg L^{-1} decreased bulblet production due to a better reproductive status and more efficient consumption of plant-derived assimilates. Even though there were fewer bulblet numbers in this treatment, the bulblet DW was greater due to the larger size of their tissues.

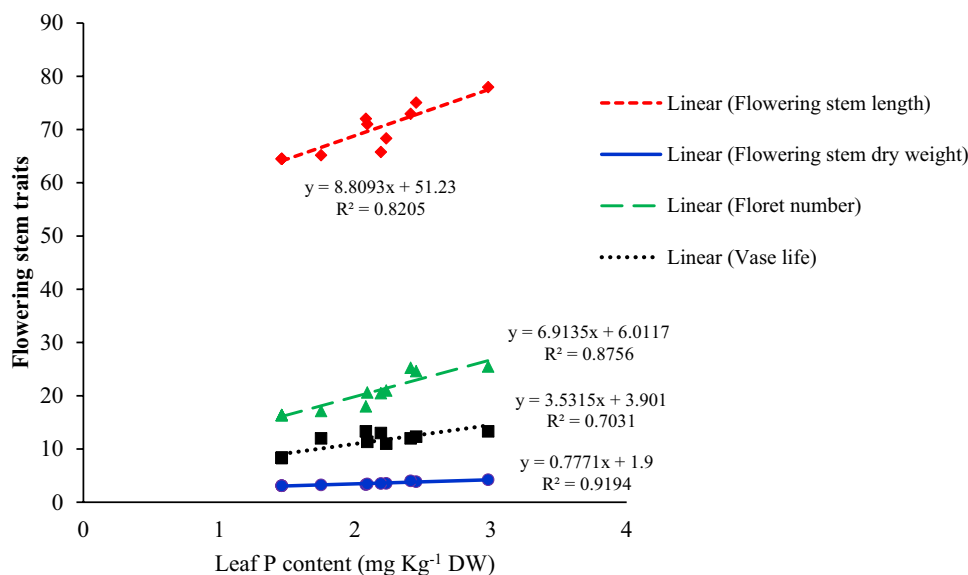
The increase in flowering-stem length was probably due to the role of Si in improving the water status of plants, thereby enhancing cell growth (Kamenidou et al. 2010). In accordance with the present study, Si application has been shown to increase stem length in New Guinea impatiens (*I. hawkeri*), portulaca (*Portulaca grandiflora*), and Lobelia (*Lobelia erinus*) (Mattson and Leatherwood 2010). Similarly, applying potassium metasilicate in the soil mixture of chrysanthemum (*D. grandiflora*) has been shown to increase their flower DW (Carvalho-Zanao et al. 2012).

The number of florets and vase life are two important traits that determine the quality of flower stems in tuberose. The amount of P in bulbous plants clearly affects their flowering-stem quality and values. In the present study, a positive linear regression was observed between flowering-stem features—i.e., flowering stem length ($R^2 = 0.82$), DW ($R^2 = 0.92$), floret numbers ($R^2 = 0.88$), and vase life ($R^2 = 0.70$)—with leaf P content (Fig. 7). These traits also were positively correlated with leaf Si content (Supplemental Table 3). It has previously been reported that using P fertilizers on olive (*Olea europaea*) trees can increase the number of flowers per inflorescence (Erel et al. 2016), confirming the data presented in our research.

Vase life is one of the most important features affecting the quality of cut flowers. In the present study, vase life was significantly extended from 8.3 days in non-treated (control) plants to 11.33 days (32%)–13.33 days (60%) in supplemented plants by either of the two types of silicon (Table 4).

Several factors may have been involved in extending the flower vase life of tuberose in our study by two sources of silicon: (1) given the positive and significant correlation between vase life and leaf FW, root DW, and root volume, silicon can positively affect the vegetative growth of plants by improving photosynthetic capacity, thereby increasing the vase life; (2) the decrease in POD and SOD enzyme activities as a result of these treatments is correlated with a longer vase life, suggesting that the flowering stems of these plants went through weaker levels of mechanical stress when being detached from the mother plant; (3) an enhanced uptake of P, N, and Si affected the processes of flower senescence; (4) high levels of TSC and TSP could improve the vase life, because in the current study the vase life was positively correlated with TSC and TSP values at $P \leq 0.01$ (Supplemental Table 3); (5) as in previous

Fig. 7 The positive linear regression between leaf P content with flowering-stem traits, including flowering-stem length and DW, floret number, and vase life in this experiment



studies, the increase in *iso*-pentenyladenine and *iso*-pentenyladenine riboside (Hosseini et al. 2019) as well as the decrease in the abscisic acid (Le et al. 2014) and indole-3-acetic acid (Guo et al. 2019) has been achieved with the use of Si or SiNPs, so it can be assumed that these changes have improved the flower vase life of tuberose. However, according to the little information available, the mechanism of the effect of silicon on the vase life of flowers is not yet fully understood and further studies are needed.

Similar to nutritional and biochemical properties, the SiNPs treatments more favored in the changes of most morphological traits than Si, and foliar application method was preferable to root. Therefore, it can be used as an alternative to various silicon sources in improving the growth status of ornamental plants for sustainable agricultural purposes.

Conclusion

In conclusion, both silicon sources, especially SiNPs, increased the levels of P and Si uptake, as well as TSC and TSP contents. SiNPs also improved leaf FW, root DW, and root volume. They reduced POD and SOD enzyme activity, thereby improving flowering-stem characteristics, such as flowering-stem length and DW, floret number, and vase life. The concentration of Si can be more important than its method of application. Surprisingly, however, the inverse seems to be true for SiNPs: the method of application is more important than the concentration. Si proved to be more beneficial at a low concentration by foliar application and at a high concentration by root application. In general, SiNP was more efficient than Si and is more suitable for foliar nutrition of plants because it is safe for the natural environment and can be used in organic farming. Finally, based on the results, we can recommend the foliar application of SiNPs at 400 mg L⁻¹ on growth and development of tuberose plants, although the results were almost satisfactory for the root application of Si at 200 mg L⁻¹. Nevertheless, in order to further investigate the role of silicon in improving physiological and biochemical properties of tuberose, more detailed research studies are needed on the role of silicon in altering the metabolism of phytohormones under stress and non-stress conditions.

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Author Contributions FN designed the experiment, analyzed the data, wrote, and edited the manuscript; NK performed the experiment; SS prepared the silicon nanoparticles (SiNPs). All the authors read and approved the final manuscript.

Compliance with Ethical Standards

Conflict of interest No potential conflict of interest was reported by the authors.

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