

Morphological, Biochemical and Nutritional Responses of Potato (*Solanum tuberosum* L. cv. Agria) to SiO₂ Nanoparticles under Alkalinity Stress Conditions

Mahdi Bikdeloo

mahdi.bikdeloo@gmail.com

Arak University <https://orcid.org/0000-0002-3048-1066>

Fahimeh Feizi

Arak University

Hamid Reza Roosta

Arak University

Research Article

Keywords: SiO₂-NPs, Alkalinity stress, Potato, Hydroponics, Nutrient uptake

Posted Date: February 27th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-8941525/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Morphological, Biochemical and Nutritional Responses of Potato (*Solanum tuberosum* L. cv. Agria) to SiO₂ Nanoparticles under Alkalinity Stress Conditions

Mahdi Bikdeloo¹, Fahimeh Feizi¹, Hamid Reza Roosta¹

¹Department of Horticultural Sciences, Faculty of Agriculture and Natural Resources, Arak University, 38156-8-8349 Arak, Iran

***Corresponding author:** Mahdi Bikdeloo (mahdi.bigdelo@gmail.com)

Abstract

Considering the destructive effects of alkalinity stress on plants and the important role of silicon in stress alleviation, this study investigated the effects of foliar-applied silicon dioxide nanoparticles (SiO₂-NPs) at 0, 2, and 4 mM, under alkalinity stress induced by NaHCO₃ at 0, 5, 15, and 30 mM, on hydroponically grown potato (*Solanum tuberosum* L. cv. Agria). Under non-stress conditions, SiO₂-NPs, particularly at 4 mM (N4), significantly enhanced plant growth, increasing plant length (8.5%), dry weight (15.3%) and root biomass (up to 38.6%) compared to the control (N0). Alkalinity stress alone exhibited a dose-dependent detrimental effect, severely suppressing growth parameters by up to 65% at 30 mM NaHCO₃. Importantly, SiO₂ nanoparticles significantly interacted with stress and provided a strong protective effect. This protective role extended to mini-tuber yield, where N4 maintained higher productivity under moderate and severe stress. Biochemically, SiO₂-NPs enhanced the antioxidant defense system, elevating carotenoids, total phenolics and flavonoids. Nanoparticles also preserved chlorophyll content and significantly reduced the depletion of mineral ions under stress conditions. The 4 mM SiO₂-NP treatment reduced the severe loss of key nutrients and retained magnesium (21.0%), iron (31.6%), potassium (33.2%) and calcium (42.6%) compared to the untreated control under high alkalinity conditions. The results demonstrate that foliar application of SiO₂-NPs, especially at 4 mM, increases alkalinity tolerance in potato plants by

improving growth, antioxidant activity and nutrient uptake. Also, 5 mM NaHCO₃ acted as a beneficial root carbon source and showed a slight increase in some parameters compared to non-stress conditions. These results provide a suitable strategy for sustainable seed potato production in soilless systems with alkaline water.

Keywords: SiO₂-NPs; Alkalinity stress; Potato; Hydroponics; Nutrient uptake.

Introduction

Potato (*Solanum tuberosum* L.) holds a critical position in global food security, being the largest non-cereal food crop and the fourth most cultivated food crop worldwide after rice, wheat and maize (Li et al. 2025). Potato yield is influenced not only by prevailing climatic conditions during the growing season but also by the intrinsic health status of the plant. Notably, seed potato quality represents the most influential yield-determining factor under farmer control and remains a primary constraint to production in many potato-growing regions (Wasilewska-Nascimento et al. 2020). Potato tubers function as a unique seed material, capable of transmitting numerous pathogenic organisms. Soil-borne pathogens, including bacteria, fungi, and nematodes, can accumulate in the soil and infect the subterranean portions of the plant throughout the growing cycle. The foundation of productive potato agriculture is the consistent availability of high-quality, pathogen-free seed tubers (Thomas-Sharma et al. 2016). Modern seed potato production systems rely on biotechnological interventions, such as meristem culture, to eliminate pathogens, particularly viruses (Shrestha et al. 2026). The subsequent acclimatization of these plantlets under protected greenhouse conditions is a critical step to initiate the formation of pre-basic seed tubers (the first generation of mini-tubers in the seed certification pyramid). The acclimatization and initial growth phase are a period of high vulnerability. Conventional cultivation in natural soil presents significant agronomic risks, primarily contamination with soil-borne pathogens. Such contamination can compromise the

phytosanitary status of the pre-basic material, negate the benefits of previous stages of in vitro cultivation, and jeopardize the entire seed multiplication program (Hossain et al. 2017). To overcome the limitations of soil, the optimal medium for acclimatizing potato plantlets is soilless cultivation. Utilizing sterile substrates such as peat moss, vermiculite, perlite and coconut fiber ensures a controlled rhizosphere environment. This approach effectively eliminates the risk of introducing soil-borne pathogens, thereby preserving the axenic status of the plantlets and ensuring the production of genetically pure and phytosanitary pre-basic tubers (Cioloca et al. 2022; Rajendran et al. 2024). These systems facilitate precise control over nutrient delivery, water availability, and root zone oxygenation. This optimized growth environment often results in a multifold increase in the yield of seed tubers per plant compared to conventional methods. It also allows for more efficient use of water and fertilizer and supports sustainable agricultural practices (Kusnierek et al. 2023).

Nanoparticles (NPs) are used in agriculture to improve nutrient management and increase crop production (Seleiman et al. 2020). Due to their large surface area and high reactivity, nanoparticles provide nutrients to the plant in soluble and accessible forms, leading to better nutrient availability (Badawy et al. 2021). Nanoparticles have been shown to alter critical plant responses such as germination, seedling vigor, root development, and photosynthesis (Yang et al. 2025). Furthermore, several studies have shown that nanoparticles may enhance plant defense against oxidative stress, a property that complements their role in ameliorating the detrimental effects of major abiotic stresses such as salinity, alkalinity, and drought by improving overall plant tolerance (Salam et al. 2022). These benefits are relevant not only to soil but also to soilless systems; for example, nanoparticles have been used in hydroponic systems to accelerate the growth of plants such as spinach and melon (Wu et al. 2023; Amjad et al. 2025).

Silicon nanoparticles (Si-NPs) have demonstrated significant potential in sustainable agriculture for improving crop growth, yield, and resilience to environmental challenges such as drought, salinity, heavy metal toxicity, and pathogen attack. Their application can be effectively achieved through both root and foliar pathways (Miao et al. 2025). Foliar application of Si-NPs has been shown to reduce the adverse effects of salinity stress in potato crop and significantly enhances crop yield, a response correlated with improved photosynthetic performance, favorable biochemical indices, and increased water use efficiency (Kafi et al. 2021; Seleiman et al. 2023).

Saline-alkali waters constitute an important resource for agricultural production in water-scarce regions. Effectively integrating such waters into agricultural systems can play a vital role in reducing competition for scarce freshwater resources, preventing environmental degradation from the overexploitation of groundwater aquifers, and enhancing long-term food security (Sharma and Minhas 2005). Using saline-alkaline water in hydroponics cultivation requires precise management. When implemented correctly, this approach enables productive use of marginal water resources, aligning with the goals of sustainable agriculture in water-scarce regions (Roosta 2011). The integration of saline-alkaline water into hydroponic systems induces a complex suite of abiotic stresses on plants, primarily ionic toxicity (Na^+), high pH, osmotic stress, and oxidative damage (Fang et al. 2021). The application of silicon nanoparticles acts as a multifunctional "Phyto-protector" in hydroponic cultivation using saline-alkaline water. They do not remove the salts from the water but instead enhance the plant's inherent ability to tolerate the stress. By providing a nano-enabled shield against ionic imbalance, oxidative damage, and nutrient deficiency, nanoparticles can be a powerful tool to unlock the potential of marginal water resources for sustainable soilless agriculture (Laane 2018). Nanoparticles have great potential for use in agriculture, but raise concerns about unknown long-term and ecotoxicological effects, especially for crops consumed by humans or

animals. Seed potato production in a hydroponic cultivation system using saline-alkali water and nanoparticle foliar spraying offers a lower-risk scenario (Haghighi and Pessarakli 2013). Mini-tubers are produced in a fully controlled greenhouse, and the resulting tubers are not for direct consumption but for multi-generation field propagation. This enclosed system minimizes environmental and food-safety risks, making nanoparticles a potentially favorable tool to boost stress tolerance and tuber yield during early seed multiplication. While high bicarbonate concentrations (≥ 5 mM) inhibit growth in hydroponic systems, recent studies demonstrate that lower concentrations can enhance plant performance by enriching the root zone with CO₂. This root-derived CO₂ enrichment subsequently improves overall growth, intracellular water metabolism, nutrient transport efficiency, and photosynthetic capacity in various horticultural species (Chen et al. 2020; Li et al. 2023). Therefore, by evaluating a combined strategy using silicon nanoparticles (SiO₂-NPs) to reduce stress and low-concentration bicarbonate as a photosynthetic carbon source, we can identify a suitable strategy to enable sustainable cultivation of potato mini-tubers with alkaline water in a hydroponic system.

Materials and methods

Experimental site and treatments

The experiment was conducted in October 2024 in a research greenhouse and the advanced physiology laboratory of the Horticulture Department at Arak University, Arak (34° 5' N, 49° 41' E), Iran. This experiment employed a randomized complete block design (RCBD) with a factorial arrangement and three replications. The two experimental factors were: (1) alkaline stress, imposed by adding sodium bicarbonate (NaHCO₃) to the nutrient solution at concentrations of 0, 5, 15, or 30 mM; and (2) foliar application of silicon dioxide nanoparticles (SiO₂-NPs) at concentrations of 0, 2, or 4 mM. The foliar silicon was applied weekly in the morning until the leaves were fully wet. For foliar application, SiO₂-NP suspensions were

freshly prepared in deionized water. A few drops of Tween-20 were added to the spray solution as a surfactant to ensure complete and effective coverage.

Plant material and growth conditions

Tissue-cultured plantlets of potato (*Solanum tuberosum* L. cv. Agria) were obtained from Sepahan Royesh Isfahan Company, Iran. Following the removal of agar by gentle washing with distilled water, individual plantlets were transplanted into seedling trays. They were then acclimatized for one week in a greenhouse environment with high humidity. Thereafter, the plantlets were transplanted into 20-liter pots (40 cm height, 25 cm diameter) containing a 1:1 (v/v) mixture of perlite and cocopeat. After transplanting, the plantlets were irrigated with half strength Hoagland solution (Majidi et al. 2025) for one week and then subjected to alkaline stress for four weeks, which was applied by adding sodium bicarbonate (NaHCO_3) to the nutrient solution at four levels. Greenhouse conditions were maintained at 26/18 °C (day/night, ± 4 °C) with a relative humidity of 40 $\pm$ 10%.

Provision of SiO₂ nanoparticles

Silicon dioxide nanoparticles (SiO₂-NPs) with an average primary particle size of 8 nm and a specific surface area of 185 m² g⁻¹ were procured from US Research Nanomaterials, Inc. (Houston, TX 77084, USA). Attenuated total reflectance Fourier-transform infrared (ATR-FTIR) spectroscopy analyses were performed using a Bruker ALPHA FTIR Spectrometer in the 400–4000 cm⁻¹ range (Fig. 1). The characteristic peaks at 1104, 812, and 471 cm⁻¹ are attributed to the asymmetric stretching, symmetric stretching, and bending vibrations of Si-O-Si bonds, respectively, confirming the successful formation of the SiO₂ structure (Toledo-Manuel et al. 2025). The broad peak around 3400 cm⁻¹ indicates the presence of surface hydroxyl groups, which are common in silica nanoparticles (Shi et al. 2022).

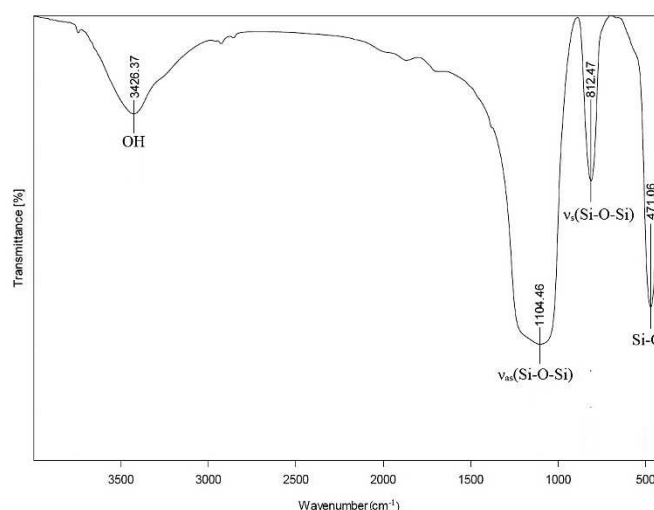


Fig. 1. FT-IR spectra of SiO₂ NPs.

Dynamic light scattering (DLS) and transmission electron microscopy (TEM) were employed to characterize the size distribution and morphology of the SiO₂ nanoparticles, respectively (Fig. 2).

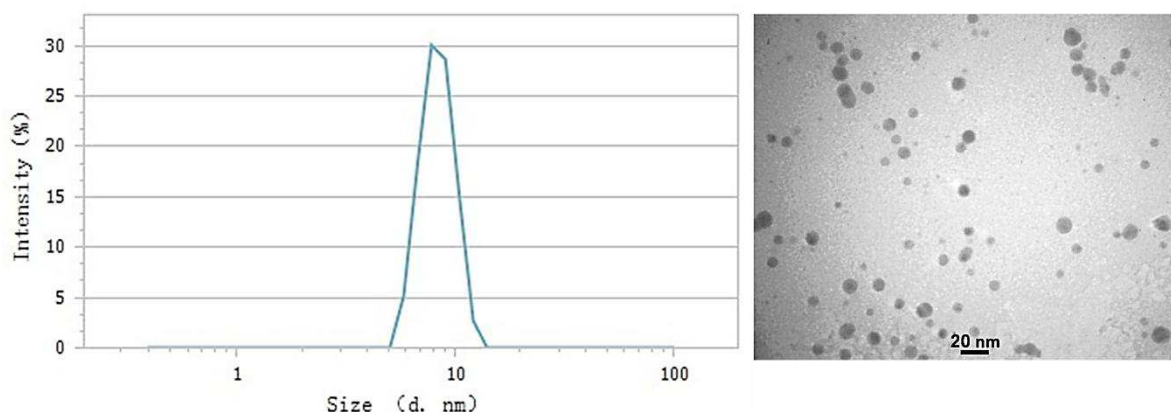


Fig. 2. DLS and TEM images of SiO₂ NPs.

Morphological assay

Morphological parameters were measured at the end of the experimental period. Plant length (PL) was measured in centimeters using a ruler. Plant fresh weight (PFW), plant dry weight (PDW), root fresh weight (RFW), root dry weight (RDW), and mini-tuber yield were determined using a digital scale with a precision of 0.01 g.

Chlorophyll and carotenoids

Chlorophyll a (Chla), chlorophyll b (Chlb) and carotenoid contents were extracted and quantified according to the method of Costache et al. (Costache et al. 2012). Briefly, 200 mg fresh leaf tissue was homogenized in 80% methanol at 4°C. The homogenate was centrifuged at $3,000 \times g$ for 15 min at 4°C, and the supernatant was stored in a refrigerator for 24 hours. The absorbance of the supernatant was then measured at 653, 666, and 470 nm using a UV/Vis spectrophotometer (Analytic Jena, model Specord 200 Plus, Germany). The concentrations of Chla, Chlb and carotenoids were calculated using the formula and expressed in mg per g fresh weight.

Total phenolic content

Total phenolic content (TPC) of potato leaf samples was determined using the Folin-Ciocalteu method with slight modifications (Rossi and Singleton 1965). Briefly, 200 µL of the leaf methanolic extract (2%, w/v) was mixed with 1000 µL of freshly prepared Folin-Ciocalteu reagent (10%) and 800 µL of sodium carbonate solution (7.5%). The mixture was incubated for 30 minutes in the dark, after which the absorbance was measured at 760 nm using a UV/Vis spectrophotometer (Analytic Jena, Specord 200 Plus, Germany). Gallic acid was used as the standard, and the results were expressed as micrograms of gallic acid equivalents per gram of fresh weight (µg GAE/g FW).

Total flavonoid content

The total flavonoid content (TFC) was determined using the aluminum chloride (AlCl₃) colorimetric method (Sumaiyah et al. 2018). A reaction mixture was prepared by combining 2 mL of the leaf methanolic extract (2%, w/v) with 2 mL of AlCl₃ solution (2%) and 0.1 mL of potassium acetate (1 M). After incubation at room temperature for 30 minutes, the absorbance was measured at 415 nm using a UV-Vis spectrophotometer (Analytic Jena, Specord 200 Plus,

Germany). Quercetin was used as the standard, and the TFC was expressed as micrograms of quercetin equivalents per gram of fresh weight ($\mu\text{g QE/g FW}$).

Antioxidant activity

The antioxidant activity of the leaf extracts was evaluated using the DPPH radical scavenging assay. Briefly, the leaf methanolic extract (2%, w/v) was mixed with a methanolic solution of DPPH (0.1 mM). The reaction mixture was vortexed and then incubated in the dark for 30 minutes. The absorbance was measured at 517 nm using a UV-Vis spectrophotometer (Analytic Jena, Specord 200 Plus, Germany). The scavenging activity was calculated based on the decrease in absorbance of the sample compared to a DPPH control solution and expressed as a percentage of DPPH radical scavenging activity using the following formula:

$$\% \text{ DPPH Radical Scavenging} = [(A_0 - A_s) / A_0] \times 100$$

where A_0 is the absorbance of the control (DPPH solution without extract) and A_s is the absorbance of the sample.

Leaf mineral content

The leaf concentrations of potassium (K), calcium (Ca), magnesium (Mg) and iron (Fe) were measured. Leaf samples (0.5 g of dried, ground material) were dry-ashed in a muffle furnace at 250°C for 30 minutes, followed by 550°C for 3 hours. The resulting ash was dissolved in 5 mL of 2N hydrochloric acid, and the volume was brought to 50 mL with distilled water (Pequerul et al. 1993). The prepared extracts were analyzed directly by ICP-OES (Analytik Jena, 9001, Germany).

Data analysis

All data were analyzed using SAS software (version 9.4, SAS Institute Inc., Cary, NC, USA). A two-way analysis of variance (ANOVA) was employed to evaluate the main effects of SiO_2 -

NP foliar application, alkalinity stress, and their interaction. Where significant effects were found, post-hoc comparisons were made using Tukey's test at ($p \leq 0.05$). Multivariate analyses, including principal component analysis (PCA) and heatmap visualization, were performed using Origin Pro software (v2024).

Results

Plant growth and mini-tuber yield

The data in Table 1 demonstrate that silicon dioxide nanoparticles (SiO_2 -NPs) significantly enhanced potato growth under non-stress conditions. Application of 4 mM SiO_2 -NPs (N4) increased plant length, plant dry weight, root dry weight, and root fresh weight by 8.5%, 15.3%, 27.6%, and 38.6%, respectively, compared to the control (N0). A lower dose of 2 mM SiO_2 -NPs (N2) also promoted growth, resulting in significant increases of 6.0% in plant length, 3.1% in plant dry weight, 15.6% in root dry weight, and 9.4% in root fresh weight.

In addition, these data demonstrate a dose-dependent detrimental effect of alkalinity stress on potato growth. Under severe stress (B30), all growth parameters were significantly suppressed, with reductions of 13.7% in plant length, 27.6% in plant dry weight, 50.9% in root fresh weight, and 65.1% in root dry weight compared to the unstressed control (B0). This negative impact was already evident at a moderate stress level (B15), which decreased plant length, plant dry weight, root fresh weight, and root dry weight by 4.2%, 18.4%, 45.8%, and 45.6%, respectively. In contrast, low stress (B5) did not significantly inhibit shoot growth, showing slight increases in plant length (2.6%), plant dry weight (4.7%), and root fresh weight (4.3%) compared to the unstressed control (B0). However, a minor decrease in root dry weight (1.4%) was observed, indicating that the root system was the first parameter affected by rising alkalinity.

Table 1. Plant length (PL), Plant dry weight (PDW), Root fresh weight (RFW) and Root dry weight (RDW) of potato as affected by silicon dioxide nanoparticles and alkalinity stress.

Treatment	PL (cm)	PDW (g)	RFW (g)	RDW (g)
N0	157.2±4.1b	58.8±3.6b	41.7±5.3b	3.52±0.56b
N2	166.6±4.9a	60.6±2.9b	45.6±4.7b	4.07±0.47a

N4	170.6±3.4a	67.8±2.6a	57.8±5.8a	4.49±0.46a
B0	171.3±4.2a	69.6±2.1a	62.9±3.8a	5.59±0.18a
B5	175.8±4.0a	72.9±1.9a	65.6±3.9a	5.51±0.28a
B15	164.1±3.1a	56.8±2.2b	34.1±3.1b	3.04±0.24b
B30	147.9±3.3b	50.4±2.3b	30.9±3.2b	1.95±0.21c

N0, N2 and N4 indicate silicon dioxide nanoparticles levels, B0, B5, B15 and B30 indicate alkalinity levels. Within columns and for each treatment, means with same letters are not different at significance level of 0.05.

The data in Table 2 demonstrate a significant interaction between alkalinity stress and SiO₂-NPs, with the beneficial effect of nano-silicon becoming most pronounced under stress conditions. Under unstressed control (B0) and low stress (B5) conditions, SiO₂-NPs (particularly N4) showed a positive but often non-significant trend towards increased plant growth parameters. Under severe alkalinity stress (B30), SiO₂-NPs exhibited a clear protective effect. The 4 mM SiO₂-NPs treatment significantly increased plant length (11.8%), plant dry weight (29.3%), root fresh weight (70.9%), and root dry weight (73.3%) compared to the stressed control (B30N0).

Table 2. Plant length (PL), Plant dry weight (PDW), Root fresh weight (RFW) and Root dry weight (RDW) of potato as affected by silicon dioxide nanoparticles and alkalinity stress.

Alkalinity	Nano Si	PL (cm)	PDW (g)	RFW (g)	RDW (g)
B0	N0	162.3±7.2abc	68.7±3.8ab	62.0±3.1abc	5.85±0.22ab
	N2	173.0±4.3ab	66.0±7.6abc	53.3±5.5bcd	5.01±0.19ab
	N4	178.7±7.3ab	74.0±5.8a	73.3±6.0ab	5.91±0.23ab
B5	N0	161.7±5.6abc	70.7±2.9a	54.7±4.4a-d	4.65±0.45bc
	N2	186.1±2.1a	71.3±4.4a	64.6±4.8ab	5.79±0.38ab
	N4	179.6±4.5ab	76.7±1.7a	77.3±4.1a	6.09±0.14a
B15	N0	164.0±7.2abc	52.6±1.2cd	26.7±3.5e	2.26±0.32efg
	N2	161.6±7.1abc	53.0±1.1cd	35.3±3.2de	3.61±0.23cd
	N4	166.7±0.9abc	64.7±2.6abc	40.3±6.2cde	3.26±0.20de
B30	N0	140.7±6.2c	43.3±2.6d	23.4±1.8e	1.31±0.11g
	N2	145.6±3.5c	52.0±3.1cd	29.3±5.4e	1.84±0.17fg
	N4	157.3±2.7bc	56.0±2.1bcd	40.0±4.6cde	2.27±0.07efg

N0, N2 and N4 indicate silicon dioxide nanoparticles levels, B0, B5, B15 and B30 indicate alkalinity levels. Within columns and for each treatment, means with same letters are not different at significance level of 0.05.

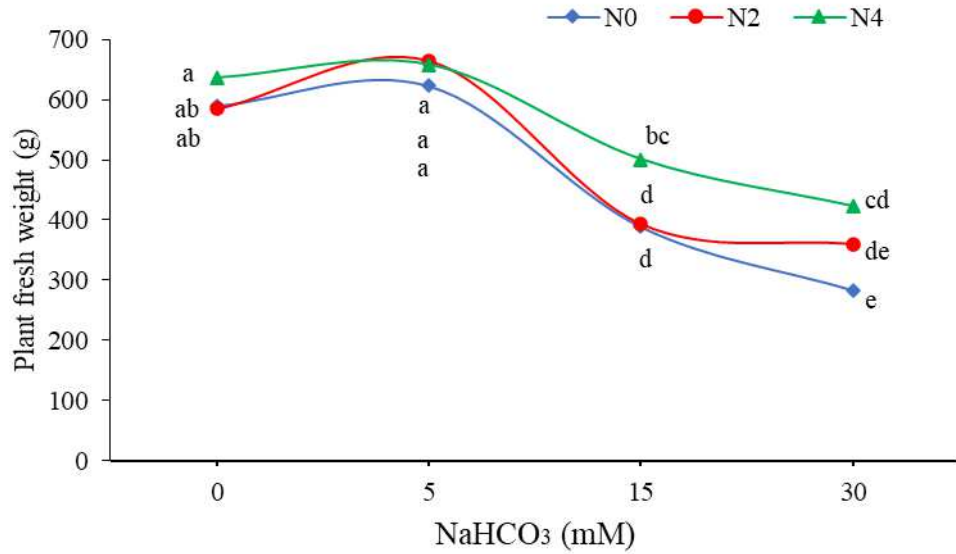


Fig. 3. The interaction between silicon dioxide nanoparticles (N0=0 mM, N2=2 mM and N4=4 mM SiO₂-NPs) and alkalinity stress on potato plant fresh weight. Different letters on top of columns refer to significantly different (Tukey's HSD, $p \leq 0.05$).

The effect of alkalinity stress and SiO₂-NPs on plant fresh weight was significant (Fig. 3). Increasing alkalinity stress from B0 to B30 led to a progressive decline in plant fresh weight. SiO₂-NP application had no significant effect under unstressed control (0 mM NaHCO₃) or low stress (5 mM NaHCO₃), although a significant effect was observed for the N4 treatment at moderate stress (15 mM NaHCO₃). Under severe alkalinity stress (30 mM NaHCO₃), plant fresh weight for the N4 treatment was significantly higher than N0 treatment. These results show that SiO₂-NPs confer a dose-dependent protective effect against severe alkaline stress.

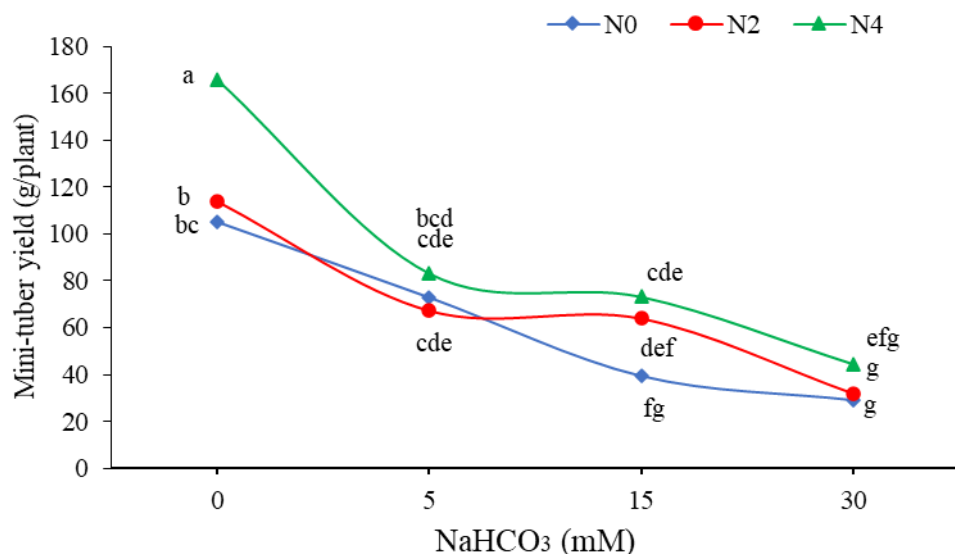


Fig. 4. The interaction between silicon dioxide nanoparticles (N0=0 mM, N2=2 mM and N4=4 mM SiO₂-NPs) and alkalinity stress on mini-tuber yield of potato. Different letters on top of columns refer to significantly different (Tukey's HSD, $p \leq 0.05$).

Figure 4 shows the interaction between SiO₂-NPs and alkalinity stress on potato mini-tuber yield. Mini-tuber yield declines as alkalinity increases from B0 to B30, indicating that higher alkalinity suppresses tuber production. Under unstressed condition (0 mM NaHCO₃) foliar application of N4 produced the highest mini-tuber yield, significantly higher than N0 and N2, which were not significantly different from each other; at low stress (5 mM NaHCO₃) yields remain relatively high and similar among N0, N2, and N4, suggesting limited or no clear benefit of SiO₂-NPs at this level; under moderate stress (15 mM NaHCO₃) clear differences emerge, with N4 producing higher mini-tuber yield than N0 and often N2, indicating a protective effect of the higher dose of SiO₂-NPs; under severe stress (30 mM NaHCO₃) there is a significant reduction in N0, whereas N2 and especially N4 maintain higher mini-tuber yield; however, their effects were statistically similar.

Biochemical traits

The data presented in Table 3 show that the application of SiO₂-NPs and exposure to alkaline stress significantly affected the biosynthesis of biochemical traits in potato leaves. The application of SiO₂-NPs consistently increased all measured parameters compared to the

control without nanoparticles (N0). Carotenoids, total phenolic content, total flavonoid content, and antioxidant activity were significantly increased by nanoparticle treatment. The findings indicate a positive, dose-dependent response up to N4 for most biochemical traits, especially for total phenolic content and total flavonoid content, where N4 achieved the highest values (74.8 mg GAE/g FW and 24.9 mg QE/g FW respectively). For carotenoids and antioxidant activity, N2 and N4 were statistically similar and superior to N0. This suggests that SiO₂-NPs likely reduced oxidative stress, thereby stimulating the plant's secondary metabolism and enhancing its antioxidant defense system. Alkaline stress had more complex and different effects on biochemical traits. Low stress (B5) produced a significant increase in carotenoids and total phenolic content compared to the unstressed control (B0), while total flavonoid content and antioxidant activity remained unchanged. Moderate stress (B15) represented a critical point and caused a significant increase in total phenolic content, total flavonoid content, and antioxidant activity reaching the highest values among all alkalinity treatments (76.6 mg GAE/g FW, 26.9 mg QE/g FW and 18.8% respectively). Severe stress (B30) resulted in reduced carotenoids and antioxidant activity compared to moderate stress (B15) and even unstressed control (B0), indicating a possible breakdown of defense mechanisms or severe physiological disturbance. Although total phenolic content and total flavonoid content reduced from their B15 peaks, they remained higher than in the control.

Table 3. Carotenoids (CARs), Total flavonoid content (TFC), Total phenolic content (TPC) and Antioxidant activity (AA) of potato as affected by silicon dioxide nanoparticles and alkalinity stress.

Treatment	CARs (mg/g FW)	TFC (mg QE/g FW)	TPC (mg GAE/g FW)	AA (%)
N0	2.94±0.26b	18.5±0.61c	60.6±1.8c	13.8±0.52b
N2	3.50±0.14a	20.9±1.97b	69.9±2.7b	18.1±0.51a
N4	3.57±0.18a	24.9±1.68a	74.8±3.7a	17.7±0.89a
B0	3.35±0.11b	18.1±1.06c	56.6±1.3c	15.3±0.69b
B5	4.14±0.13a	16.8±1.07c	64.8±2.3b	15.4±0.92b
B15	3.22±0.19b	26.9±1.99a	76.6±3.2a	18.8±0.94a
B30	2.62±0.21c	24.1±1.11b	75.9±3.4a	16.5±0.98b

N0, N2 and N4 indicate silicon dioxide nanoparticles levels, B0, B5, B15 and B30 indicate alkalinity levels. Within columns and for each treatment, means with same letters are not different at significance level of 0.05.

The interaction effects of SiO₂-NPs and alkalinity stress on biochemical traits of potato leaves are presented in Table 4. The data show a significant effect between these two factors, such that SiO₂-NPs consistently modulated the leaf response to alkalinity. Under severe stress (B30), the application of SiO₂-NPs effectively reduced the severe reduction in carotenoids and antioxidant activity observed in the untreated control (B30N0). Conversely, a synergistic increase was observed under moderate alkaline conditions (B15) combined with a high dose of nanoparticles (N4), resulting in maximum values for total phenolic content (86.2 mg GAE/g FW), total flavonoid content (32.3 mg QE/g FW), and antioxidant activity (21.2%).

Table 4. Carotenoids (CARs), Total flavonoid content (TFC), Total phenolic content (TPC) and Antioxidant activity (AA) of potato as affected by silicon dioxide nanoparticles and alkalinity stress.

Alkalinity	SiO ₂ NPs	CARs (mg/g FW)	TFC (mg QE/g FW)	TPC (mg GAE/g FW)	AA (%)
B0	N0	3.29±0.16bcd	15.9±0.19ef	53.3±1.8d	13.5±0.77cd
	N2	3.55±0.24abc	16.3±0.97ef	59.1±0.9cd	16.4±0.38a-d
	N4	3.23±0.21bcd	21.7±0.14cde	57.5±1.5cd	15.9±1.28bcd
B5	N0	4.05±0.26ab	18.1±0.91def	58.1±2.1cd	13.2±1.46d
	N2	4.04±0.28ab	13.9±1.27f	67.7±3.5bc	18.1±1.07a-d
	N4	4.33±0.14a	18.4±1.18def	68.6±2.2bc	14.9±0.94bcd
B15	N0	2.59±0.16de	19.1±0.62def	66.1±2.1bcd	15.4±0.98bcd
	N2	3.26±0.04bcd	29.3±0.92ab	77.4±3.3ab	19.9±0.19ab
	N4	3.82±0.19abc	32.3±1.17a	86.2±2.3a	21.2±0.73a
B30	N0	1.82±0.08e	20.9±0.53de	65.1±2.1bcd	13.2±0.57d
	N2	3.16±0.18bcd	24.1±1.82bcd	75.4±2.8ab	17.7±1.15a-d
	N4	2.89±0.17cd	27.2±0.96abc	87.1±2.5a	18.6±1.17abc

N0, N2 and N4 indicate silicon dioxide nanoparticles levels, B0, B5, B15 and B30 indicate alkalinity levels. Within columns and for each treatment, means with same letters are not different at significance level of 0.05.

The results in Figure 5 indicate a significant interaction between SiO₂-NPs and alkalinity stress on chlorophyll content (Chl.a+Chl.b) in potato leaves. Under non-stressed and low stress conditions (B0 and B5), the application of nanoparticles had no significant effect and all treatments (N0, N2, N4) maintained similarly high chlorophyll content. However, as alkalinity stress increased, the protective role of SiO₂-NPs became evident. At moderate and severe stress levels (B15 and B30), treatments containing SiO₂-NPs (N2 and N4) maintained significantly higher chlorophyll content compared to the control treatment without nanoparticles (N0). These findings indicate that SiO₂-NP application helps protect chlorophyll from degradation

under alkalinity stress, thereby potentially supporting photosynthetic performance and plant survival under adverse growth conditions.

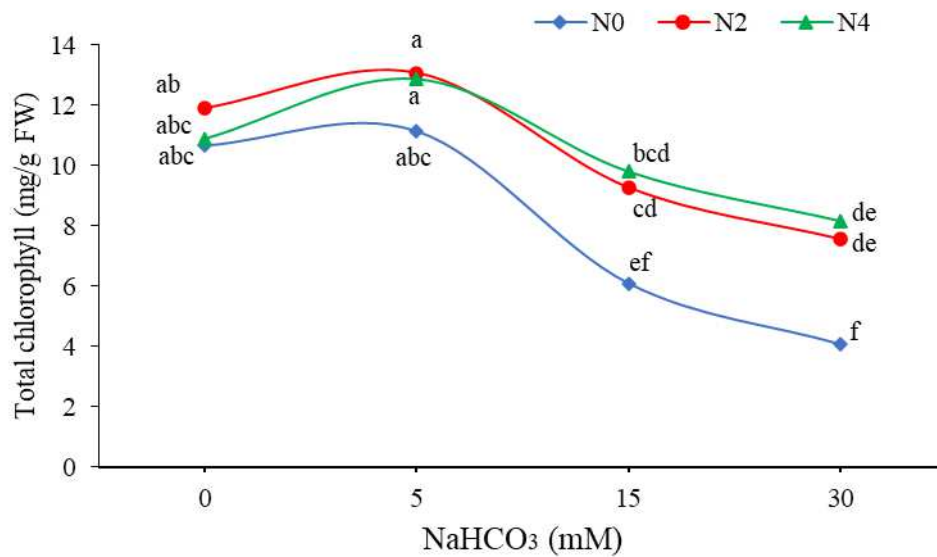


Fig. 5. The interaction between silicon dioxide nanoparticles (N0=0 mM, N2=2 mM and N4=4 mM SiO₂-NPs) and alkalinity stress on chlorophyll content in potato leaves. Different letters on top of columns refer to significantly different (Tukey's HSD, $p \leq 0.05$).

Heatmap with hierarchical clustering

Heatmap with hierarchical clustering analysis of all measured morphological, biochemical, and yield parameters revealed four distinct response groups among the twelve treatments (combinations of NaHCO₃ and SiO₂-NP levels), indicating a complex interaction between alkalinity stress severity and silicon dioxide nanoparticle amendment (Fig. 6). Group A included plants treated with high alkalinity stress (15 and 30 mM NaHCO₃) without SiO₂-NP supplementation (B15-N0, B30-N0), as well as with a low dose (2 mM NPs; B30-N2). This group was characterized by a significant decrease in growth parameters and chlorophyll content. The levels of antioxidant metabolites (TPC, TFC and AA) in these plants showed moderate levels, indicating that the endogenous antioxidant response was activated but not sufficient to prevent major physiological damage. Group B comprised plants treated with high alkalinity treatments amended with higher doses of SiO₂-NPs (B15-N2, B15-N4, B30-N4).

These plants showed low improvement in growth parameters and chlorophyll content, along with significant increases in antioxidant metabolites. This suggests that SiO₂-NPs at these concentrations, by strongly stimulating the plant's antioxidant defense system, likely reduce oxidative damage. Group C showed optimal performance under unstressed (0 mM NaHCO₃) and low-stress (5 mM NaHCO₃) treatments with or without low SiO₂-NPs (B0-N0, B0-N2, B5-N0). This group showed moderate values for vegetative parameters and photosynthetic pigments accumulation, with low levels of antioxidant metabolites. This confirms that under minimal alkalinity stress, photosynthetic and growth parameters operate at maximum efficiency without the need for increased antioxidant defense. Group D, which included low-stress treatments with SiO₂-NPs (notably at 4 mM), exhibited the highest growth, chlorophyll levels, and mini-tuber yield. These plants not only matched or exceeded the superior growth and photosynthetic performance of group C but also maintained balanced and relatively high levels of antioxidant compounds. This group represents a state where SiO₂-NPs act not only as a stress reducer but also as a biostimulant, enhancing overall plant performance and productivity under both unstressed and low stress conditions.

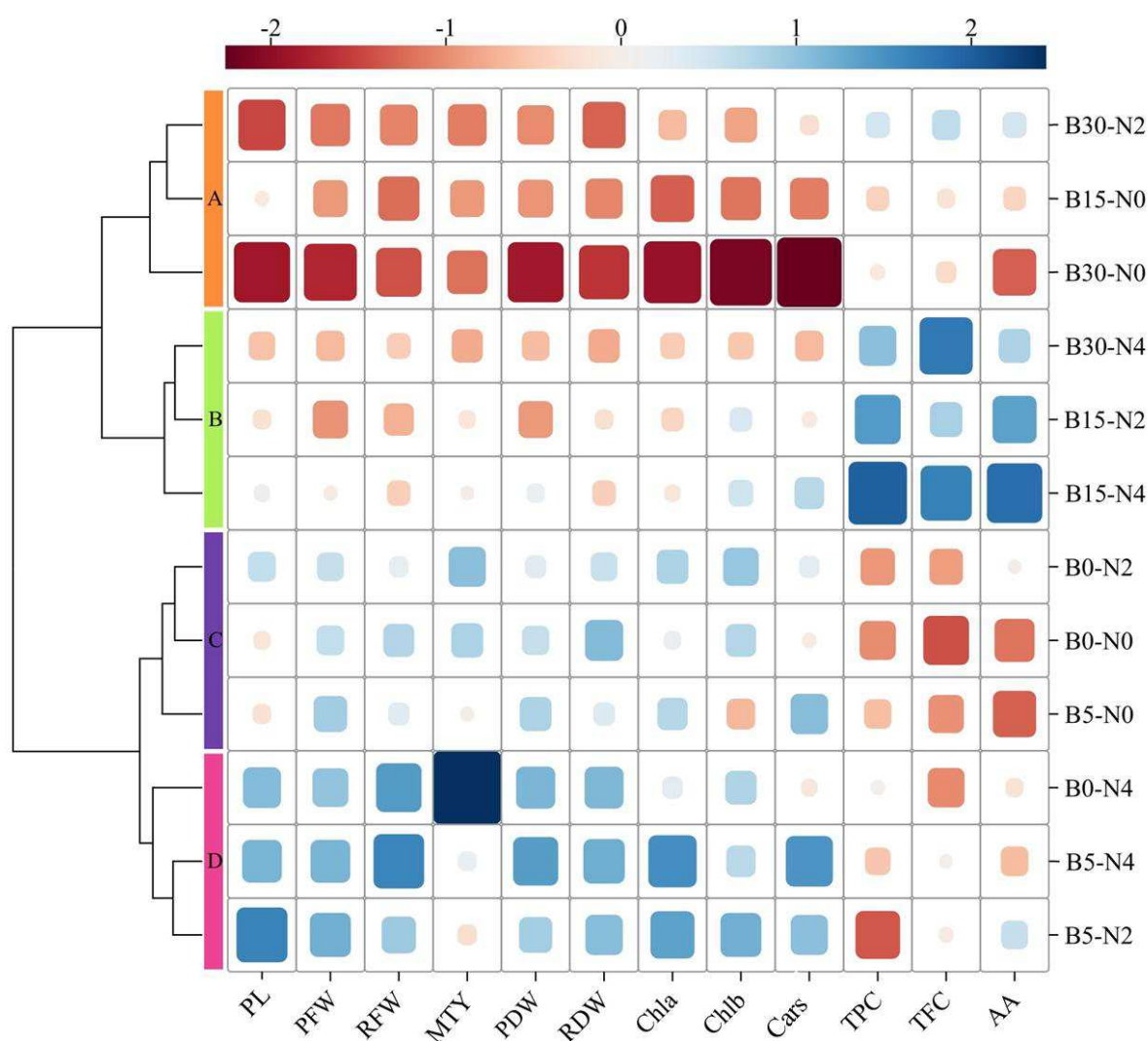


Fig. 6. Heatmap with hierarchical clustering showing the response of potato plants to combined alkalinity stress and silicon dioxide nanoparticle (SiO₂-NP) treatments across multiple morphological and biochemical parameters. The coding system in treatments (rows) is as follows: The first letter indicates the alkalinity stress (B0=0 mM, B5=5 mM, B15=15 mM and B30=30 mM NaHCO₃), the second letter represents silicon dioxide nanoparticles (N0=0 mM, N2=2 mM and N4=4 mM SiO₂-NPs). Also, Columns represent the measured traits: PL (plant length), PFW (plant fresh weight), RFW (root fresh weight), MTY (mini-tuber yield), PDW (plant dry weight), RDW (root dry weight), Chl.a (chlorophyll a), Chl.b (chlorophyll b), Cars (carotenoids), TPC (total phenolic content), TFC (total flavonoid content), and AA (antioxidant activity). Color scale indicates relative values across treatments, with blue representing higher values and red representing lower values after column-wise Z-score normalization.

Principal component analysis

Principal component analysis allowed us to demonstrate the effect of SiO₂ nanoparticles application and alkalinity stress in a more integrated way among the twelve measured parameters (Fig. 7). PC1 accounted for 65.44% and was associated positively with growth parameters and photosynthetic pigments and negatively with the antioxidant compounds. PC2

explained 21.08% of the total variance and showed a negative correlation with plant fresh weight, root fresh weight, root dry weight and mini-tuber yield and positively with the other parameters. In addition, distribution of treatments across the biplot's two-dimensional space revealed four distinct response regions. Treatments positioned in the first quadrant (positive PC1, positive PC2) correspond to low-stress conditions supplemented with SiO₂-NPs, particularly B5-N4 and B5-N2. This spatial separation confirms that under low alkalinity stress, SiO₂-NPs exert a synergistic biostimulant effect, elevating physiological performance beyond that of unstressed controls. The second quadrant (positive PC1, negative PC2) includes unstressed treatments, with or without application of SiO₂-NPs (B0-N0, B0-N2, B0-N4), reflecting optimal growth conditions. The inclusion of B5-N0 in this region further indicates that low stress alone does not significantly alter the measured parameters compared to the unstressed control. Treatments in the third quadrant (PC1 negative, PC2 positive) indicate high stress conditions with increased antioxidant metabolites due to SiO₂-NPs application (B15-N2, B15-N4, B30-N2, B30-N4). This result suggests that SiO₂-NPs application, especially at higher concentrations, reduces severe stress to some extent by increasing antioxidant capacity. Finally, the fourth quadrant (negative PC1, negative PC2) is occupied by high stress treatments without the application of SiO₂-NPs (B15-N0, B30-N0). This region is associated with the most pronounced stress impact, characterized by reduced growth and photosynthetic parameters, highlighting the severity of alkalinity stress in the absence of SiO₂-NPs application.

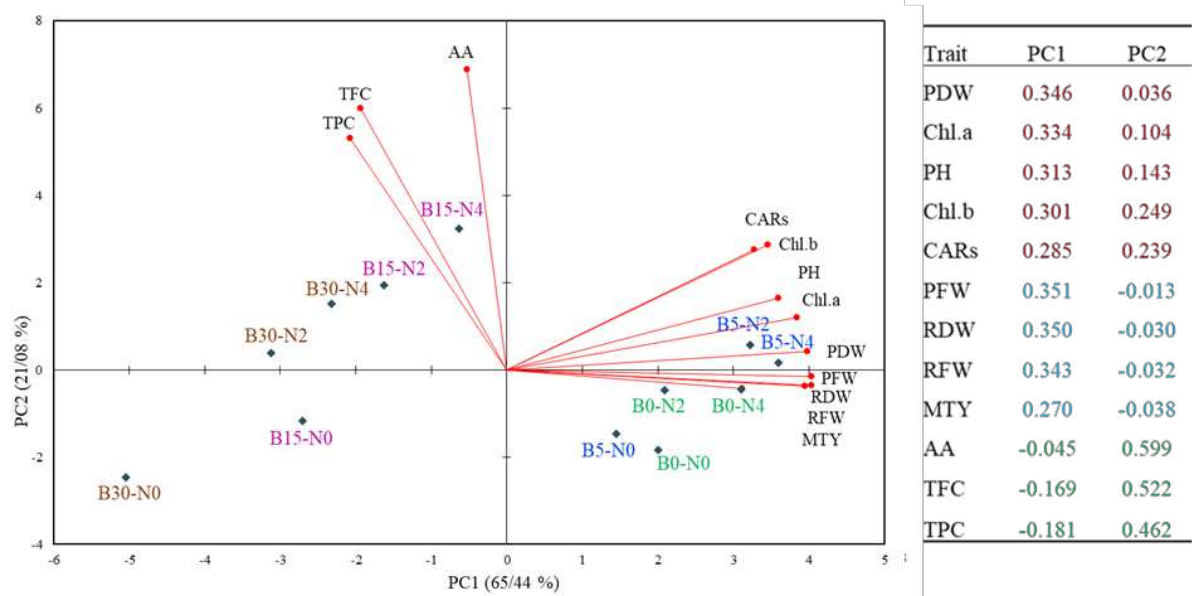


Fig. 7. Principal component analysis based on all morphological and biochemical parameters measured under alkalinity stress and SiO₂-NP concentrations (The abbreviations are explained in Fig. 4).

Mineral Element Contents

The application of silicon dioxide nanoparticles (SiO₂-NPs) significantly interacted with alkalinity stress and affected the content of mineral elements in potato leaves. Foliar spraying with 4 mM SiO₂-NPs (N4) effectively reduced the severe ion depletion under high alkaline conditions (30 mM NaHCO₃). Compared to the untreated control (N0), N4 maintained higher leaf Mg (21.0%), Fe (31.6%), K (33.2%), and Ca (42.6%). Notably, N4 uniquely maintained or increased Ca and Fe levels relative to N0 at all levels of alkalinity stress. The 2 mM SiO₂-NP treatment (N2) was particularly effective under moderate stress conditions (15 mM NaHCO₃), and its effectiveness decreased under severe stress (Fig. 8).

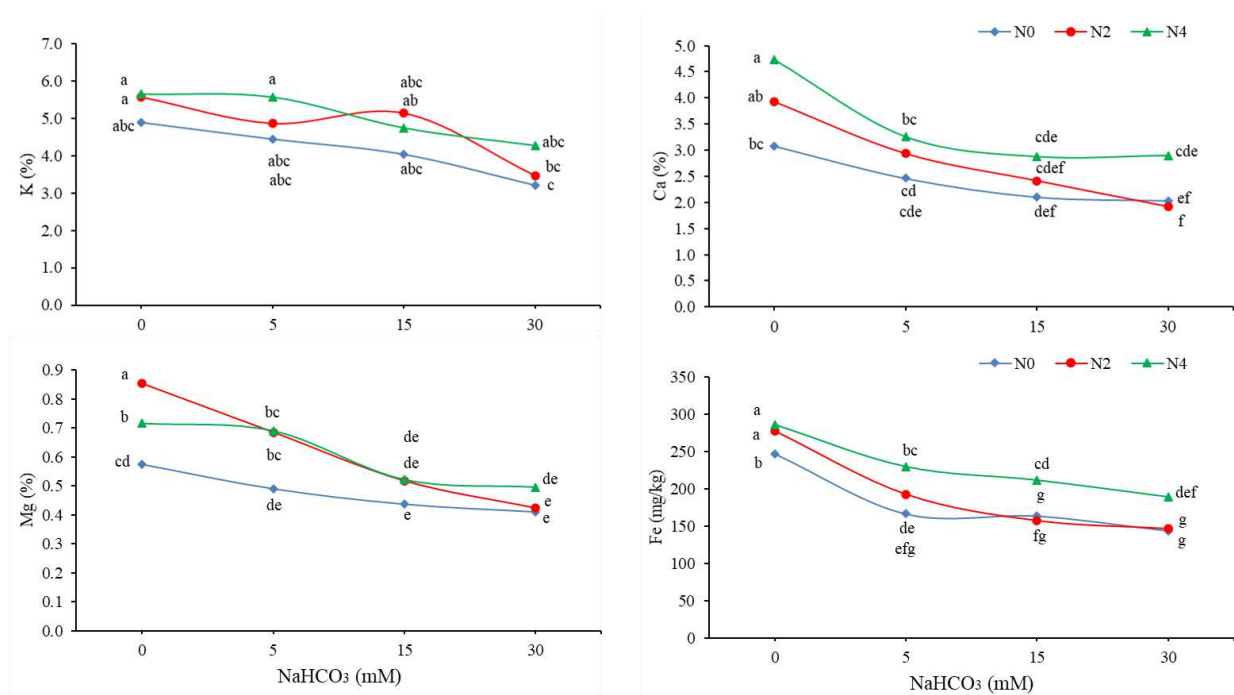


Fig. 8. The interaction between silicon dioxide nanoparticles (N0=0 mM, N2=2 mM and N4=4 mM SiO₂-NPs) and alkalinity stress on mineral element contents in potato leaves. Different letters on top of columns refer to significantly different (Tukey's HSD, $p \leq 0.05$).

Discussion

Effects of SiO₂-NPs and alkalinity stress on plant growth and mini-tuber yield

This study shows that foliar application of silicon dioxide nanoparticles (SiO₂-NPs) significantly enhances the growth parameters, biochemical resistance, and yield of potato (*Solanum tuberosum* L. cv. Agria) mini-tuber under alkalinity stress in a hydroponic system. Our findings confirm that SiO₂-NPs act as both a biostimulant under non-stress conditions (Yassen et al. 2017) and a protective agent under alkaline stress conditions (Deshmukh et al. 2017), offering a promising strategy for sustainable seed potato production using marginal quality water resources.

Under non-stress conditions, SiO₂-NPs, especially at a concentration of 4 mM, significantly improved plant length, dry weight, and root biomass. This is consistent with previous reports on the role of silicon in promoting root structure, nutrient uptake, and overall plant vigor (Miao et al. 2025). Also, studies indicate that silicon application increases cellular gibberellic acid levels. This phytohormone is vital for processes such as cell division and subsequent

430 elongation(Soundararajan et al. 2014). Interestingly, plants exposed to a low concentration of
431 bicarbonate (5 mM NaHCO_3), showed a slight increase in these same parameters compared to
432 the non-stressed control (As visualized in the heatmap analysis). This challenges the
433 conventional view of bicarbonate as merely an alkalinity stressor. Instead, it suggests that at
434 low, non-toxic concentrations, bicarbonate can serve as a beneficial carbon supplement for the
435 roots. This root-based inorganic carbon uptake represents a previously underutilized
436 photosynthetic pathway. This concept is supported by recent studies showing that, across
437 multiple species and soilless cultivation systems, enriching the root zone with inorganic carbon
438 can significantly enhance plant growth, photosynthesis, and nitrogen metabolism (Dąbrowska-
439 Bronk et al. 2016; Poschenrieder et al. 2018; Éva et al. 2019; Han et al. 2022). For example,
440 root-zone enrichment with low levels of bicarbonate increased shoot dry weight by 10–20% in
441 lettuce, pepper, and *Arabidopsis thaliana* (Leibar-Porcel et al. 2020; Gamarra Reinoso et al.
442 2024). In poplar (*Populus canescens*), root supply of low HCO_3^- concentrations, enhanced root
443 nitrate uptake and nitrogen transfer to shoots (Wanek and Popp 2000). How this additional
444 carbon promotes plant growth is still unclear. However, recent findings support the hypothesis
445 that inorganic carbon (HCO_3^-) absorbed by roots acts as a photosynthetic "carbon subsidy".
446 According to this hypothesis, inorganic carbon (HCO_3^-) is taken up by root anion channels and
447 transported via the xylem to the shoots, where leaf carbonic anhydrase enzymes convert it back
448 to CO_2 . This internally supplied CO_2 is then fixed by RuBisCo and directly supplements
449 photosynthesis (Gamarra Reinoso et al. 2024). However, potential mechanisms of action such
450 as increased rates of photosynthesis, altered amino acid concentrations and changes in
451 phytohormone concentrations should be investigated in future studies (Leibar-Porcel et al.
452 2020). In contrast, alkalinity stress induced by 15 and 30 mM NaHCO_3 concentrations
453 gradually inhibited plant growth, especially severe stress (30 mM) caused a significant decrease
454 in all measured morphological parameters. This reduction is attributed to ion toxicity, osmotic

stress, and impaired nutrient homeostasis, common responses to alkaline conditions (Fang et al. 2021; Malik et al. 2021). Importantly, SiO₂-NPs reduced these adverse effects, especially under severe stress, where the 4 mM treatment restored growth parameters and mini-tuber yield to levels comparable to those under moderate stress. This protective effect is likely due to silicon's role in stabilizing cell membranes, increasing antioxidant defense, and improving ion selectivity under stress conditions (Shahnaz et al. 2011; Saadatian et al. 2022). According to our results, silicon-based biostimulants also enhance tuber number and weight under drought conditions and increase yield by up to 23% under water deficit conditions (Wadas 2021). Similar positive effects have been reported under salt stress conditions, where nano-silicon formulations further improved potato tuber performance (Crusciol et al. 2009; Kafi et al. 2019). Overall, foliar silicon reduces abiotic stress and enhances potato productivity under various growing conditions.

Effects of SiO₂-NPs and alkalinity stress on antioxidant activity, total phenolics and flavonoids contents

The biochemical data show a clear interaction between alkalinity stress and SiO₂-NPs application. Under moderate alkalinity (15 mM), plants exhibited an upregulation of antioxidant metabolites, total phenolics, flavonoids, and antioxidant activity, indicating an activated stress response. SiO₂-NPs further enhanced this response, leading to the highest recorded values of these compounds. This synergistic effect suggests that SiO₂-NPs enhance the plant's capacity to counteract oxidative stress, possibly through improved silicon-mediated signaling and enzyme activation (Kafi et al. 2021). Flavonoids act as key antioxidants and help plants reduce abiotic stresses. Studies confirm that exogenous silicon supplementation enhances the flavonoid biosynthesis pathways in leaves and roots (Jiang et al. 2022). According to our results, foliar application of silicon in a greenhouse study increased proline levels and

antioxidant enzyme activities (CAT and SOD) in potato plants under water stress. This response effectively reduced the concentration of hydrogen peroxide (H_2O_2). Overall, silicon treatment enhanced physiological resilience of potatoes to drought stress (Pilon et al. 2014).

Effects of SiO_2 -NPs and alkalinity stress on chlorophyll contents and carotenoids

Chlorophyll contents and carotenoids remained stable under low stress regardless of SiO_2 -NPs treatment but declined sharply under higher alkalinity in untreated plants. SiO_2 -NPs application preserved chlorophyll levels, supporting photosynthetic continuity under stress. This aligns with earlier findings that silicon reduces chlorophyll degradation and sustains photosynthetic efficiency under abiotic stress (Nasseri et al. 2012; Seleiman et al. 2023). Increasing sodium bicarbonate elevates the pH of the root environment, reducing the uptake of essential ions such as Fe, Mn, Zn, and Mg for chlorophyll synthesis. Additionally, sodium and bicarbonate ions directly compete with calcium and magnesium, further inhibiting their absorption. This combined disruption of ion availability impairs the chlorophyll synthesis process (Guo et al. 2024). Carotenoids serve as essential photosynthetic pigments and a primary antioxidant defense against ROS, directly reducing them through the xanthophyll cycle. They also act as precursors for stress hormones like ABA, enhancing plant resistance under adverse conditions. Notably, silicon can affect carotenoid pathways, altering key pigments such as zeaxanthin and lutein to enhance protective functions (Song et al. 2025).

Effects of SiO_2 -NPs and alkalinity stress on mineral contents

The results of this study indicate that foliar application of silicon dioxide nanoparticles (SiO_2 -NPs) can effectively reduce alkalinity-induced mineral disorders in hydroponically grown potatoes. The protective mechanism likely involves increased membrane integrity by SiO_2 -NPs, improved ion selectivity (especially for K^+/Na^+ and Ca^{2+}/Na^+), and potential

enhancement of key ion transporters under alkalinity stress (Malik et al. 2021; Pavlovic et al. 2021). By preserving critical elements such as K (essential for osmotic regulation and enzyme activation) and Fe (needed for chlorophyll synthesis), the application of SiO₂-NPs helped maintain physiological function and stress resistance (Wang et al. 2013; Alam et al. 2025). Consistent with the present findings, silicon fertilization improves mineral uptake in various crops such as potato, wheat, maize, rice, sunflower and cucumber (Maria 2019; Shaheen et al. 2019; Wadas and Kondraciuk 2023).

Conclusion

In summary, foliar application of SiO₂-NPs improves alkalinity tolerance of potatoes in hydroponic systems by improving growth, maintaining photosynthetic activity, strengthening antioxidant defense systems, and enhancing mineral nutrient uptake. The 4 mM concentration was optimal, especially under moderate to severe stress. These results support the sustainable incorporation of SiO₂-NPs in soilless potato seed production, using saline-alkaline water to enhance seed security in arid regions, with minimal risks of nanoparticles in controlled environments.

Funding

No funding was received for conducting this study.

CRedit authorship contribution statement

Fahimeh Feyzi: Investigation, Data curation. **Mahdi Bikdeloo:** Writing – original draft, Methodology, Supervision, Formal analysis. **Hamid Reza Roosta:** Writing – review & editing, Supervision. All authors reviewed the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

References

- Alam T, Jalil S, Jilani G, et al (2025) Enhancing crop resilience to water stress through iron nanoparticles: A critical review of applications and implications. *Plant Stress* 16:. <https://doi.org/10.1016/j.stress.2025.100905>
- Amjad M, Riaz M, Hussain S (2025) Iron Oxide Nanoparticles in Hydroponic Agriculture: Classification, Green Synthesis, Properties, and Impact on Plant Growth. *Pak J Agri Sci* 62:551–570
- Badawy SA, Zayed BA, Bassiouni SMA, et al (2021) Influence of nano silicon and nano selenium on root characters, growth, ion selectivity, yield, and yield components of rice (*Oryza sativa* L.) under salinity conditions. *Plants* 10:. <https://doi.org/10.3390/plants10081657>
- Chen X, Yin Z, Yin Y, et al (2020) Effects of elevated root-zone CO₂ on root morphology and nitrogen metabolism revealed by physiological and transcriptome analysis in oriental melon seedling roots. *Int J Mol Sci* 21:. <https://doi.org/10.3390/ijms21030803>
- Cioloa M, Tican A, Badarau CL, Popa M (2022) PRODUCTION OF HIGH-QUALITY SEED POTATOES IN PROTECTED AREA FOR TRUE SEED PROGENIES, WHO SHOWED TOLERANCE TO *IN VITRO* INDUCED WATER STRESS. *Sci Pap a-Agronomy* 65:235–244
- Costache MA, Campeanu G, Neata G (2012) Studies concerning the extraction of chlorophyll and total carotenoids from vegetables. *Rom Biotechnol Lett* 17:7702–7708
- Crusciol CAC, Pulz AL, Lemos LB, et al (2009) Effects of silicon and drought stress on tuber yield and leaf biochemical characteristics in potato. *Crop Sci* 49:949–954. <https://doi.org/10.2135/cropsci2008.04.0233>
- Dąbrowska-Bronk J, Komar DN, Rusaczonek A, et al (2016) β -carbonic anhydrases and carbonic ions uptake positively influence Arabidopsis photosynthesis, oxidative stress tolerance and growth in light dependent manner. *J Plant Physiol* 203:44–54. <https://doi.org/10.1016/j.jplph.2016.05.013>
- Deshmukh RK, Ma JF, Bélanger RR (2017) Editorial: Role of silicon in plants. *Front Plant Sci* 8:. <https://doi.org/10.3389/fpls.2017.01858>
- Éva C, Oszvald M, Tamás L (2019) Current and possible approaches for improving

567 photosynthetic efficiency. Plant Sci 280:433–440.
568 <https://doi.org/10.1016/j.plantsci.2018.11.010>

569 Fang S, Hou X, Liang X (2021) Response Mechanisms of Plants Under Saline-Alkali Stress.
570 Front Plant Sci 12:.. <https://doi.org/10.3389/fpls.2021.667458>

571 Gamarra Reinoso L, Majláth I, Dernovics M, et al (2024) Root-based inorganic carbon uptake
572 increases the growth of *Arabidopsis thaliana* and changes transporter expression and
573 nitrogen and sulfur metabolism. Front Plant Sci 15:..
574 <https://doi.org/10.3389/fpls.2024.1448432>

575 Guo R, Zhou Z, Cai R, et al (2024) Metabolomic and physiological analysis of alfalfa
576 (*Medicago sativa* L.) in response to saline and alkaline stress. Plant Physiol Biochem 207:..
577 <https://doi.org/10.1016/j.plaphy.2024.108338>

578 Haghighi M, Pessarakli M (2013) Influence of silicon and nano-silicon on salinity tolerance of
579 cherry tomatoes (*Solanum lycopersicum* L.) at early growth stage. Sci Hortic
580 (Amsterdam) 161:111–117. <https://doi.org/10.1016/j.scienta.2013.06.034>

581 Han X, Jing Y, Xu C, et al (2022) Root-Zone CO₂ Concentration Affects Partitioning and
582 Assimilation of Carbon in Oriental Melon Seedlings. Int J Mol Sci 23:..
583 <https://doi.org/10.3390/ijms231810694>

584 Hossain MS, Hossain MM, Haque MM, et al (2017) Varietal Evaluation of Potato Microtuber
585 and Plantlet in Seed Tuber Production. Int J Agron 2017:..
586 <https://doi.org/10.1155/2017/7520297>

587 Jiang H, Song Z, Su QW, et al (2022) Transcriptomic and metabolomic reveals silicon
588 enhances adaptation of rice under dry cultivation by improving flavonoid biosynthesis,
589 osmoregulation, and photosynthesis. Front Plant Sci 13:..
590 <https://doi.org/10.3389/fpls.2022.967537>

591 Kafi M, Nabati J, Ahmadi-Lahijani MJ, Oskoueian A (2021) Silicon Compounds and
592 Potassium Sulfate Improve Salinity Tolerance of Potato Plants through Instigating the
593 Defense Mechanisms, Cell Membrane Stability, and Accumulation of Osmolytes.
594 Commun Soil Sci Plant Anal 52:843–858.
595 <https://doi.org/10.1080/00103624.2020.1869768>

596 Kafi M, Nabati J, Saadatian B, et al (2019) Potato response to silicone compounds (Micro and
597 nanoparticles) and potassium as affected by salinity stress. Ital J Agron 14:162–169.
598 <https://doi.org/10.4081/ija.2019.1182>

599 Kusnierek K, Heltoft P, Møllerhagen PJ, Woznicki T (2023) Hydroponic potato production in
600 wood fiber for food security. npj Sci Food 7:.. [https://doi.org/10.1038/s41538-023-00200-](https://doi.org/10.1038/s41538-023-00200-7)
601 7

602 Laane HM (2018) The effects of foliar sprays with different silicon compounds. Plants 7:..
603 <https://doi.org/10.3390/plants7020045>

604 Leibar-Porcel E, McAinsh MR, Dodd IC (2020) Root-zone CO₂ enrichment increases biomass
605 accumulation in lettuce and pepper grown hydroponically and aeroponically. Acta Hortic
606 1273:93–100. <https://doi.org/10.17660/ActaHortic.2020.1273.13>

607 Li H, Lv J, Su Y, Wu Y (2023) Appropriate Sodium Bicarbonate Concentration Enhances the
608 Intracellular Water Metabolism, Nutrient Transport and Photosynthesis Capacities of
609 *Coix lacryma-jobi* L. Agronomy 13:.. <https://doi.org/10.3390/agronomy13071790>

610 Li L, Zhu T, Wen L, et al (2025) Biofortification of potato nutrition. J Adv Res 75:23–34.
611 <https://doi.org/https://doi.org/10.1016/j.jare.2024.10.033>

612 Majidi A, Shahhoseini R, Salehi-Arjmand H, Roosta HR (2025) Effect of Hoagland’s nutrient
613 solution strengths and sodium silicate on growth, yield and biochemical parameters of
614 Carla (Momordica Charantia L.) under hydroponic conditions. Sci Rep 15:.
615 <https://doi.org/10.1038/s41598-025-92616-2>

616 Malik MA, Wani AH, Mir SH, et al (2021) Elucidating the role of silicon in drought stress
617 tolerance in plants. Plant Physiol Biochem 165:187–195.
618 <https://doi.org/10.1016/j.plaphy.2021.04.021>

619 Maria Ł (2019) Effects of bio-stimulants on the yield of cucumber fruits and on nutrient
620 content. African J Agric Res 14:2112–2118. <https://doi.org/10.5897/ajar2019.14502>

621 Miao G, Han J, Han T (2025) Silicon Nanoparticles and Apoplastic Protein Interaction: A
622 Hypothesized Mechanism for Modulating Plant Growth and Immunity. Plants 14:.
623 <https://doi.org/10.3390/plants14111630>

624 Nasser M, Arouiee H, Kafi M, Neamati H (2012) Effect of silicon on growth and physiological
625 parameters in fenugreek (Trigonella foenum-graceum L.) under salt stress. Int J Agric
626 Crop Sci 4:1554–1558

627 Pavlovic J, Kostic L, Bosnic P, et al (2021) Interactions of Silicon With Essential and
628 Beneficial Elements in Plants. Front Plant Sci 12:.
629 <https://doi.org/10.3389/fpls.2021.697592>

630 Pequerul A, Pérez C, Madero P, et al (1993) A rapid wet digestion method for plant analysis.
631 Optim Plant Nutr 3–6. https://doi.org/10.1007/978-94-017-2496-8_1

632 Pilon C, Soratto RP, Broetto F, Fernandes AM (2014) Foliar or soil applications of silicon
633 alleviate water-deficit stress of potato plants. Agron J 106:2325–2334.
634 <https://doi.org/10.2134/agronj14.0176>

635 Poschenrieder C, Fernández JA, Rubio L, et al (2018) Transport and use of bicarbonate in
636 plants: Current knowledge and challenges ahead. Int J Mol Sci 19:.
637 <https://doi.org/10.3390/ijms19051352>

638 Rajendran S, Domalachenpa T, Arora H, et al (2024) Hydroponics: Exploring innovative
639 sustainable technologies and applications across crop production, with Emphasis on
640 potato mini-tuber cultivation. Heliyon 10: <https://doi.org/10.1016/j.heliyon.2024.e26823>

641 Roosta HR (2011) Interaction between water alkalinity and nutrient solution ph on the
642 vegetative growth, chlorophyll fluorescence and leaf magnesium, iron, manganese, and
643 zinc concentrations in lettuce. J Plant Nutr 34:717–731.
644 <https://doi.org/10.1080/01904167.2011.540687>

645 Rossi JAJ, Singleton VL (1965) Colorimetry of total phenolics with phosphomolybdic
646 phosphotungstic acid reagents. Am J Enol Vitic 16:144–158

647 Saadatian B, Kafi M, Bannayan M, Hammami H (2022) Effects of Foliar Spraying Nano and
648 Ionized Silicon on Physiological Characteristics and Yield of Potato (Solanum tuberosum
649 L.) Mini-tuber. Silicon 14:8067–8079. <https://doi.org/10.1007/s12633-021-01565-8>

650 Salam A, Afridi MS, Javed MA, et al (2022) Nano-Priming against Abiotic Stress: A Way
651 Forward towards Sustainable Agriculture. Sustain 14:.

652 <https://doi.org/10.3390/su142214880>

653 Seleiman MF, Al-Selwey WA, Ibrahim AA, et al (2023) Foliar Applications of ZnO and SiO₂
 654 Nanoparticles Mitigate Water Deficit and Enhance Potato Yield and Quality Traits.
 655 Agronomy 13:. <https://doi.org/10.3390/agronomy13020466>

656 Seleiman MF, Alotaibi MA, Alhammad BA, et al (2020) Effects of ZnO nanoparticles and
 657 biochar of rice straw and cow manure on characteristics of contaminated soil and
 658 sunflower productivity, oil quality, and heavy metals uptake. Agronomy 10:790

659 Shaheen AM, Ragab ME, Rizk FA, et al (2019) Effect of some active stimulants on plant
 660 growth, tubers yield and nutritional values of potato plants grown in newly reclaimed soil.
 661 J Anim Plant Sci 29:215–225

662 Shahnaz G, Shekoofeh E, Kourosh D, Moohamadbagher B (2011) Interactive effects of silicon
 663 and aluminum on the malondialdehyde (MDA), proline, protein and phenolic compounds
 664 in borago officinalis L. J Med Plant Res 5:5818–5827

665 Sharma BR, Minhas PS (2005) Strategies for managing saline/alkali waters for sustainable
 666 agricultural production in South Asia. Agric Water Manag 78:136–151.
 667 <https://doi.org/10.1016/j.agwat.2005.04.019>

668 Shi B, Xie L, Ma B, et al (2022) Preparation and Properties of Highly Transparent SiO₂
 669 Aerogels for Thermal Insulation. Gels 8:. <https://doi.org/10.3390/gels8110744>

670 Shrestha S, Manandhar D, Dawadi N, et al (2026) Selection of Optimal 6-Benzylaminopurine
 671 (BAP) and 1-Naphthaleneacetic Acid (NAA) Combination for in vitro Propagation of
 672 ‘*Solanum tuberosum* L. cv. Cardinal’ Under Nepalese Laboratory Conditions. Asian J
 673 Agric Hortic Res 13:1–16. <https://doi.org/10.9734/ajahr/2026/v13i1430>

674 Song R, Chen X, He Y, et al (2025) The carotenoid biosynthesis pathway revealed to respond
 675 to Na₂SiO₃ stress on cotton growth. Curr Plant Biol 43:.
 676 <https://doi.org/10.1016/j.cpb.2025.100532>

677 Soundararajan P, Sivanesan I, Jana S, Jeong BR (2014) Influence of silicon supplementation
 678 on the growth and tolerance to high temperature in *Salvia splendens*. Hortic Environ
 679 Biotechnol 55:271–279. <https://doi.org/10.1007/s13580-014-0023-8>

680 Sumaiyah, Masfria, Dalimunthe A (2018) Determination of total phenolic content, total
 681 flavonoid content, and antimutagenic activity of ethanol extract nanoparticles of
 682 *rhaphidophora pinnata* (L.f) schott leaves. Rasayan J Chem 11:505–510.
 683 <https://doi.org/10.7324/RJC.2018.1122068>

684 Thomas-Sharma S, Abdurahman A, Ali S, et al (2016) Seed degeneration in potato: The need
 685 for an integrated seed health strategy to mitigate the problem in developing countries.
 686 Plant Pathol 65:3–16. <https://doi.org/10.1111/ppa.12439>

687 Toledo-Manuel I, Pérez-Alvarez M, Cadenas-Pliego G, et al (2025) Sonochemical
 688 Functionalization of SiO₂ Nanoparticles with Citric Acid and Monoethanolamine and Its
 689 Remarkable Effect on Antibacterial Activity. Materials (Basel) 18:.
 690 <https://doi.org/10.3390/ma18020439>

691 Wadas W (2021) Potato (*Solanum tuberosum* L.) growth in response to foliar silicon
 692 application. Agronomy 11:. <https://doi.org/10.3390/agronomy11122423>

693 Wadas W, Kondraciuk T (2023) Effect of Silicon on Micronutrient Content in New Potato

- Tubers. *Int J Mol Sci* 24:.. <https://doi.org/10.3390/ijms241310578>
- Wanek W, Popp M (2000) Effects of rhizospheric bicarbonate on net nitrate uptake and partitioning between the main nitrate utilising processes in *Populus canescens* and *Sambucus nigra*. *Plant Soil* 221:13–24. <https://doi.org/10.1023/A:1004745823911>
- Wang M, Zheng Q, Shen Q, Guo S (2013) The critical role of potassium in plant stress response. *Int J Mol Sci* 14:7370–7390. <https://doi.org/10.3390/ijms14047370>
- Wasilewska-Nascimento B, Boguszevska-Mańkowska D, Zarzyńska K (2020) Challenges in the production of high-quality seed potatoes (*Solanum tuberosum* L.) in the tropics and subtropics. *Agronomy* 10:.. <https://doi.org/10.3390/agronomy10020260>
- Wu T, Zou G, Lan X, et al (2023) The Efficiency of Nanoparticles on Improving Seed Germination and Mitigating Ammonium Stress of Water Spinach (*Ipomoea aquatica* Forssk.) and Hami Melon (*Cucumis melo* L.). *Sustain* 15:.. <https://doi.org/10.3390/su151310083>
- Yang Y, Ye C, Zhao M, et al (2025) Nanoparticles in sustainable agriculture: enhancing nutrient use efficiency and abiotic stress resilience under climate change. *Plant Stress* 17:.. <https://doi.org/10.1016/j.stress.2025.100982>
- Yassen A, Abdallah E, Gaballah M, Zaghloul S (2017) Role of Silicon Dioxide Nano Fertilizer in Mitigating Salt Stress on Growth, Yield and Chemical Composition of Cucumber (*Cucumis sativus* L.). *Int J Agric Res* 12:130–135. <https://doi.org/10.3923/ijar.2017.130.135>