

Physiological Responses and Nutritional Implications of *Physalis alkekengi* L. Under Varied Salinity Stress and Si and Se Nanoparticle Treatments

Mohammad Javad Abdi¹, Marzieh Ghanbari Jahromi^{1*}, Seyed Najmmaddin Mortazavi², Sepideh Kalateh Jari¹, Mohammad Javad Nazarideljou³

¹Department of Horticultural Science and Agronomy, Science and Research Branch, Islamic Azad University, Tehran, Iran

²College of Agriculture, Department of Horticulture, University of Zanjan, Zanjan, Iran

³Department of Horticultural Science, Mahabad Branch, Islamic Azad University, Mahabad, Iran

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*Corresponding author's email: ghanbari@srbiau.ac.ir

This study systematically investigates the physiological responses of *Physalis alkekengi* to diverse conditions of salinity stress (0, 50, 100, and 200 mM NaCl), coupled with the application of selenium (Se) nanoparticles at concentrations of 25 and 50 mg l⁻¹, as well as silicon (Si) nanoparticles at concentrations of 100 and 200 mg l⁻¹. The experiment involved a thorough examination of many characteristics connected to biomass, such as antioxidant enzyme activity, fatty acid composition, and elemental content. This analysis was conducted at varying levels of salinity and with the addition of nanoparticles. The findings revealed that exposure to salt stress has a detrimental effect on both plant development and fruit output, leading to changes in vegetative and morphological characteristics. The utilization of Se and Si nanoparticles had a significant alleviating impact on stress caused by salinity. The correlation matrix analysis revealed complex correlations among the examined parameters, emphasizing the interrelated responses of *P. alkekengi* to environmental stressors and nanoparticle interventions. Principal Component Analysis (PCA) revealed the hidden patterns and connections between variables, highlighting the significant influence of biomass-related features, antioxidant enzymes, and fatty acid content on the observed variability. The results of this study enhance our knowledge of the physiological processes that regulate *P. alkekengi*'s reaction to high salt levels. Additionally, it offers valuable information on the possible beneficial impacts of Se and Si nanoparticles in reducing the negative consequences of salinity stress. The study's comprehensive breadth increases its relevance to future research focused on optimizing growth circumstances and strengthening the resistance of *P. alkekengi* in demanding situations.

Abstract

Keywords: Antioxidant defense system, Fatty acid composition, Nanoparticle, Salinity stress.

INTRODUCTION

Physalis alkekengi L., a member of the solanaceae family, is notable in both ornamental and therapeutic applications. The plant's fruit, referred to as the bladder cherry, Chinese lantern, Japanese lantern, strawberry groundcherry, or winter cherry is known in different regions has a diverse range of uses including food, medicine, and industry (He *et al.*, 2023). This plant species is well-known in different regions, such as China, Japan, Korea, and portions of Europe. Fossils of its seeds have been found dating back to the miocene and pliocene geological periods (23 million to 5.3 million years ago) in Europe (Liang *et al.*, 2024). In addition to its visual attractiveness, *Physalis alkekengi* L. has been of great significance in traditional medicine worldwide (Bahmani *et al.*, 2016).

Physalis alkekengi L. is abundant in biologically active substances such as steroids, flavonoids, phenylpropanoids, alkaloids, nucleosides, terpenoids, megastigmane, aliphatic derivatives, organic acids, coumarins, and sucrose esters (Liang *et al.*, 2024). Throughout history, it has been widely used for its various therapeutic benefits. The applications of this substance include reducing fever, producing anti-inflammatory reactions, providing analgesic effects, possessing antibacterial capabilities, and exhibiting antiviral activity (Popova *et al.*, 2022). The field of Chinese medicine has effectively utilized the medicinal properties of the plant by harnessing the therapeutic potential of its fruit juice. *Physalis alkekengi* L. remedies have been used to treat a variety of ailments including abscesses, coughs, fevers, sore throats, acidic excretions, gout, arthritis, hemorrhoids, hepatitis, bronchitis, and to strengthen the liver. The plant's historical acknowledgment as a medicinal substance with the ability to induce fetal abortion and prevent pregnancy enhances its traditional importance (Bahmani *et al.*, 2016, He *et al.*, 2023). Moreover, the plant's chemical substances, such as physoaline and solenoid alkaloids, have shown effectiveness in inhibiting mycobacterium TB, highlighting its promise in fighting tuberculosis (Liang *et al.*, 2024).

Although, there is a significant amount of information available on the therapeutic benefits of *Physalis alkekengi* L., there is a lack of research on how it responds to environmental stresses, specifically salt (Bahmani *et al.*, 2016; Bosch *et al.*, 2016; Helvacı *et al.*, 2010; Li *et al.*, 2018). This study seeks to fill this void by investigating the influence of Si and Se nanoparticles on the physiological reactions of *Physalis alkekengi* L. in the presence of high salt levels. Despite its abundance in the Earth's crust, Si has not traditionally been considered necessary for plant growth. Recent findings demonstrate its importance in strengthening cell walls, increasing plant resistance to diseases, and raising overall plant quality (Abdoli *et al.*, 2020; Monroy-Velandia and Coy-Barrera, 2021). The presence of Si in plants has a dual purpose: It enhances the strength of cell walls and also functions as a mobile element inside the plant. This makes Si an important supplement for many plant species, especially when they are experiencing stressful conditions. The crucial importance of its potential lies in its ability to stimulate growth, increase photosynthesis, reduce evaporation and transpiration, strengthen leaves, and improve overall plant quality. This is particularly significant when considering environmental challenges like salinity (Al-aghabary *et al.*, 2005; Banerjee *et al.*, 2021).

Si has a complex impact on the ability of plants to withstand stress. Under unfavorable circumstances, it provides defense against harm caused by the sun, minimizes the loss of water through a dual cellulose layer in the leaf's outer covering, and improves the process of photosynthesis. In addition, Si enhances the ability to withstand biological and physical pressures, such as high salinity, heavy metals, and drought. The application of this technology

improves the efficiency of water consumption, stimulates the production of dry matter, and increases the water potential in leaves during periods of drought stress (Guerriero *et al.*, 2016; Karimi *et al.*, 2020; Khan *et al.*, 2021). The deposition of Si on the cell walls of xylem provides protection against water scarcity, particularly in dry environments. This process plays a crucial role in the metabolic, physiological, and structural functions of plants (Moradi *et al.*, 2022; Mushtaq *et al.*, 2020).

Se, at low concentrations, enhances plant growth and alleviates the adverse impacts of environmental stressors such as low temperature, water scarcity, high salinity, and toxicity caused by heavy metals. Se acts as a vital antioxidant, boosting the body's ability to withstand oxidative stress and maintaining the integrity and functionality of cells. Se's application mitigates heavy metal toxicity, enhances chloroplast enzymes, and promotes plant growth in stressful conditions. The recent application of nano-Se as a fertilizer in agriculture, due to its exceptional purity and absorption efficiency, demonstrates its potential to serve as a more efficient stress-reducing agent. The increased effectiveness of nano-Se is due to its greater specific surface area compared to conventional particles, which presents a promising opportunity for implementing environmentally sustainable stress management approaches (Badawy *et al.*, 2021; Golubkina *et al.*, 2022; Hajiboland and Keivanfar, 2012).

Se, although not directly engaged in the fundamental metabolic processes of plants, has shown a significant function in improving both the growth of plant structures and the production of offspring, particularly when plants are subjected to challenging environmental or biological circumstances (Bisht *et al.*, 2022; Ghasemian *et al.*, 2021). Se's positive effects are diverse and involve enhanced activity of antioxidant enzymes and increasing levels of antioxidant molecules. Research has indicated that Se is effective in improving growth under drought stress conditions and delaying aging caused by flowering in annual plants (Hawrylak-Nowak, 2022; Jiang *et al.*, 2017; Karimi *et al.*, 2020). However, further in-depth studies are necessary to fully understand the overall mechanisms by which Se helps to reduce environmental stress (Bisht *et al.*, 2022).

Nanotechnology is revolutionizing plant science in the modern era. Nanoparticles, with a size smaller than 50 nm, possess distinct characteristics that allow them to enter plant cell walls and impact physiological responses. The utilization of metal nanoparticles, specifically, has demonstrated potential in enhancing both the quantitative and qualitative attributes of plants, while also providing a method to counteract biological stressors (Sanzari *et al.*, 2019). This paper addresses the lack of research on the effects of Si and Se nanoparticles on *Physalis alkekengi* L. in saline environments.

The main goal of this work is to examine the previously unexamined impacts of nano-sized Si and Se particles on the physiological responses of *Physalis alkekengi* L. plants under saline circumstances, considering the gaps in knowledge mentioned earlier. Our objective is to clarify the mechanisms by which these nanoparticles can improve a plant's ability to withstand salt stress. This research will not only deepen our understanding of how plants respond to stress, but also potentially provide new approaches to alleviating environmental stress in agriculture. By examining the complex interaction of Si, Se, and *Physalis alkekengi* L. in the presence of saline circumstances.

MATERIALS AND METHODS

Plant materials

The seeds of *Physalis alkekengi* L. were obtained from Pakan Bazr Company, located

in Isfahan, Iran. The study employed Se nanoparticles (NPs) in the form of Se dioxide acquired from Sigma-Aldrich, USA. Described as having a spherical shape, with a CAS number of 7446-08-4, a size that falls between 10-40 nm, a purity level of 99.9%, a specific surface area of 30-50 m²g⁻¹, and a true density of 3.89 g cm⁻³. The Si dioxide used in this study was obtained from Sigma-Aldrich, USA. It consisted of Si nanoparticles (Si NPs) with a CAS number of 7631-86-9. The quality of the Si nanoparticles was 99.5%, and their particle size ranged from 10 to 20 nm. The active surface area of the nanoparticles was measured to be 450 g m⁻².

Conditions for growth and experimental design

The experimental design was organized in a factorial configuration, utilizing a randomized complete design (CRD) with three replicates in the year 2022. The seeds were planted in 4-L pots filled with a substrate consisting of a 2:1 ratio of cocoa to perlite. The greenhouse maintained a photoperiod of 16 hours of light and 8 hours of darkness, together with a relative humidity ranging from 65% to 80%. The experimental setting was the greenhouse of the University of Zanjan, Zanjan, Iran, located at an elevation of 1661 (36° 40' 25" N, 48° 29' 04" E). During the growth period, plants were nourished with a Hoagland solution and irrigated with distilled water until they reached the 4-leaf stage. Following that, the plants were subjected to saline conditions and exposed to varying concentrations of NaCl (50, 100, and 200 mM) every three days for a total of 50 days. In addition, the plants were treated with Si nanoparticles (Si NPs) at concentrations of 100 and 200 mg l⁻¹ and Se nanoparticles (Se NPs) at concentrations of 25 and 50 mg l⁻¹. These treatments were applied three times, with a 15-day gap between each application, starting from the stage when the plants had four leaves. The sampling was performed when the fruits reached maturity, and their physiological and biochemical features were assessed.

Shoot dry weight

After subjecting the plant aerial parts to dehydration in an oven set at 72 °C for a period of 24 hours, their weight in the dry state was measured using a digital scale with a precision of 0.01 g.

Fruit weight and yield

The individual weight of each fruit was measured using a digital scale, and the total fruit yield was calculated by adding all the weights of all the fruits on each plant.

Calyx size

The fruit calyx's dimensions, including its length and width, were precisely measured using a caliper.

Catalase enzyme activity measurement

The enzyme extraction process involved pulverizing plant leaf samples in an mortar using liquid nitrogen, resulting in a powdered form. Afterward, 0.5 ml of sodium phosphate buffer with a pH of 6 was introduced, and then the mixture was spun at a speed of 13,000 revolutions per minute. The supernatant obtained was used to measure the total protein content and catalase enzyme activity. The spectrophotometric determination of catalase activity was conducted at a wavelength of 240 nm for a duration of 30 seconds. This was achieved by utilizing a 20 mM sodium phosphate buffer with a pH of 7, along with 20 µL of 30% hydrogen peroxide (H₂O₂) as

the electron acceptors. The quantification of catalase activity was determined by measuring the enzyme units (mg^{-1} of protein), following the established procedure described by (Anderson, 2002).

Superoxide dismutase (SOD) enzyme activity measurement

The activity of the SOD enzyme was assessed in leaf samples by measuring its ability to inhibit the photochemical reduction process of nitrobuterazolium (NBT). The reaction mixture comprised 50 mM phosphate buffer (pH 7), 13 mM methionine, 0.1 mM sodium ethylenediaminetetraacetate (Na-EDTA), 75 μM nitrobuterazolium (NBT), 75 μM riboflavin, and 100 μL of the extract. Spectrophotometric measurements were conducted at a wavelength of 560 nm at two-minute intervals to determine absorbance. The SOD activity was quantified in enzyme units mg^{-1} of protein using the methodology developed by (Giannopolitis and Ries, 1977).

Anthocyanin measurement

The anthocyanin content was quantified using (Wagner, 1979) methodology. 1 g sample of fruit was combined with 10 mL of acidic methanol. The resulting mixture was then stored in darkness at a temperature of 4 °C for a duration of 24 hours. The absorbance of the supernatant was measured at a wavelength of 520 nm using a spectrophotometer after centrifugation. The anthocyanin content was determined by applying the formula $A = \epsilon bc$, where ϵ represents the extinction coefficient (3300 mM cm^{-1}), A is the absorption value, b is the width of the cuvette (1 cm), and c is the quantity of anthocyanin in milligrams of cyanidin-3-glucoside per 100 g.

Analysis of sodium and potassium content in leaves

The leaf samples were pulverized using a mortar after being completely dried in the air. Subjecting the sample to a temperature of 500 °C for a duration of 6 hours and subsequently dissolving it in a solution of 2 M nitric acid facilitated the measurement of sodium and potassium levels. The solution volume was ultimately modified to 25 ml by adding double-distilled water. Subsequently, measurements were carried out using a film-photometry apparatus (model PFP7, JENWAY, England) in accordance with the approach described by (Chapman and Pratt, 1962).

Leaf chlorine measurement

In order to determine the amount of chlorine present, a sample of 100 mg of powdered plant tissue was treated with 10 ml of 0.5 M nitric acid to extract the chlorine content. Following an hour of drying the extract at a temperature of 80 °C, a volume of one mL of the extract was utilized to measure the chlorine content utilizing a colorimetric method at a wavelength of 480 nm using the Epoch 2 instrument, in accordance with the procedure outlined by (Munns and Tester, 2008).

Quantification of phosphorus content in leaves

The phosphorus content was measured using a Unico spectrophotometer. The plant samples were incinerated in a furnace at a temperature of 550 °C. Subsequently, Barton's reagent and 70% perchloric acid were added. The spectrophotometric measurement of absorbance was conducted at a wavelength of 450 nm, following the methodology described by (Ryan *et al.*, 2009).

Fatty acid analysis

The determination of the fatty acid composition in the fruit involved the extraction of oil via the Soxhlet method, followed by gas chromatography (GC) for profiling. The GC analysis was conducted using a Thermo-UFM (Ultra Fast Model) gas chromatograph equipped with a Ph-5 capillary column measuring 10 meters in length, 0.1 mm inner diameter, and 0.4 μm thickness. The column featured a dimethyl stationary phase siloxane on its inner surface, with a 5% phenyl coating. The thermal program of the column ranged from 60 to 280 $^{\circ}\text{C}$, with a temperature increase rate of 80 $^{\circ}\text{C min}^{-1}$. Detection was carried out using a Flame Ionization Detector (FID), and helium served as the carrier gas with an inlet pressure to the column set at 0.5 kg cm^{-2} . The detector chamber maintained a temperature of 290 $^{\circ}\text{C}$, while the injection chamber was set at 280 $^{\circ}\text{C}$ (Sowmiya *et al.*, 2021).

Statistical analysis

The data obtained from measuring various variables in this study were initially recorded in Excel and then analyzed using SAS statistical software version 9.4. In order to evaluate the importance of average data, comparisons were carried out using Duncan's test at either the 1% or 5% level of significance. The graphs and figs were produced using Excel software. PCA and hierarchical clustering were performed using XLSTAT software version 2022-4 the clustering procedure utilized Ward's algorithm and Euclidean distance as the fundamental principles for grouping.

RESULT

Shoot dry weight

Salinity stress significantly reduced shoot dry weight ($P<0.01$), with the highest impact observed at 200 mM salinity, causing a 29% decrease compared to the control. Se and Si nanoparticles had a significant positive effect on shoot dry weight ($P<0.01$), increasing it by 8% and 10%, respectively, in 25 and 200 mg l^{-1} treatments compared to the control. The interaction between salinity stress and nanoparticles also significantly influenced shoot dry weight ($P<0.01$), indicating a mitigating effect of Se and Si on salinity-induced reduction. In the 200 mM salinity treatment, Se at 25 and 100 mg l^{-1} increased shoot dry weight by 34% and 22%, respectively, showcasing the potential of these nanoparticles in enhancing plant resilience to salinity stress (Fig. 1-a).

Fruit morphology

Calyx length: Salinity stress significantly impacted calyx length ($P<0.01$), causing a notable decrease at higher salinity levels, with the lowest value of 38.4 mm observed at 200 mM. Se and Si nanoparticles treatments significantly increased calyx length compared to the control, reaching the maximum at 50 and 200 mg l^{-1} Se treatments (Fig. 1-d).

Calyx width: Salinity stress ($P<0.01$) led to a substantial decrease in calyx width, with the lowest value of 31.6 mm at 200 mM. Se and Si nanoparticles treatments significantly increased calyx width compared to the control, with the highest values observed at 25 and 200 mg l^{-1} Se treatments (Fig. 1-e).

Fruit fresh weight: Salinity stress significantly reduced fruit fresh weight ($P<0.01$), showing a decreasing trend with increasing salinity levels. Se and Si nanoparticles treatments significantly increased fruit fresh weight compared to the control, with the highest fresh weight observed at 200 mg l^{-1} Se treatment (Fig. 1-b,c).

Fruit yield: Salinity stress significantly reduced fruit yield ($P < 0.01$), exhibiting a marked decline with increasing salinity levels, reaching the lowest at 200 mM. Se and Si nanoparticle treatments significantly increased fruit yield compared to the control, with the highest yield observed at 50 and 200 mg l⁻¹ Se treatments (Fig. 1-f,g).

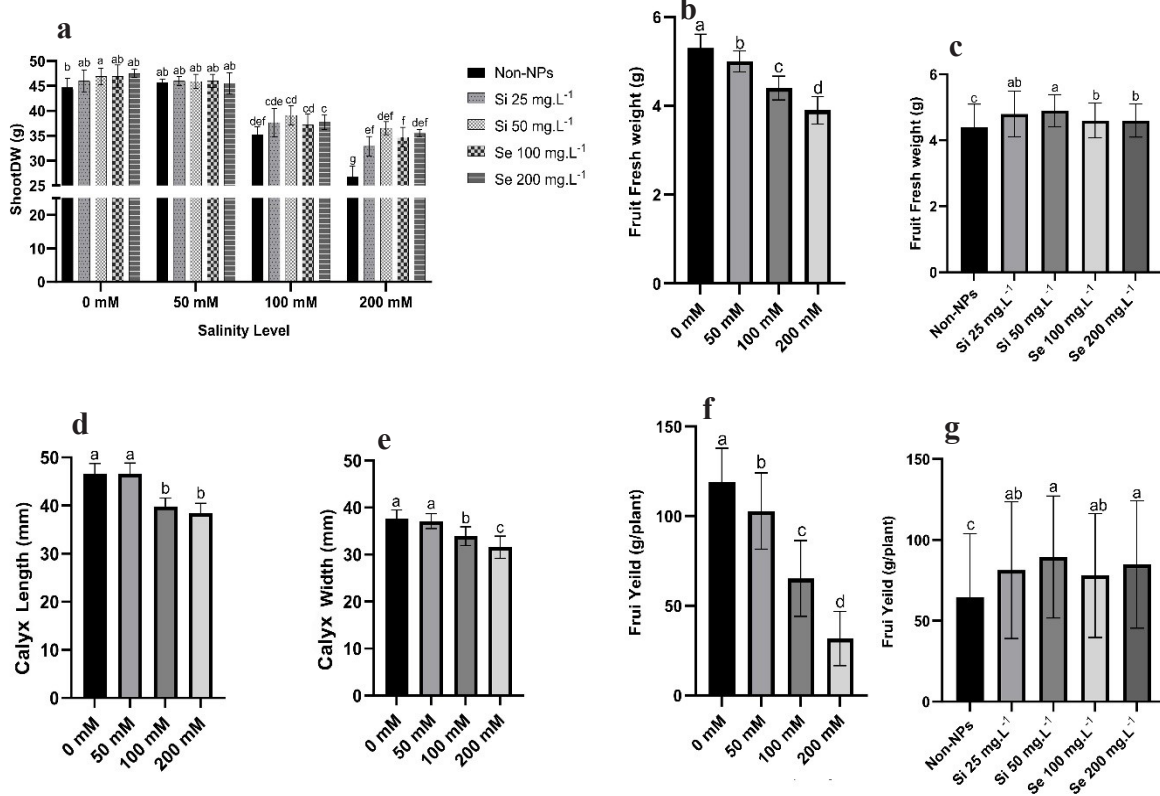


Fig. 1. Presents a comprehensive overview of key physiological parameters in *Physalis alkekengi* L. under varying salinity concentrations and nanoparticle treatments. The subplots include (a) Shoot dry weight, illustrating the impact of different treatments on plant biomass; (b) Fruit fresh weight under distinct salt concentrations, elucidating the correlation between salinity stress and fruit weight; (c) Fruit fresh weight under diverse nanoparticle concentrations, highlighting the effect of nanoparticles on fruit development; (d) Calyx length in response to varying salt concentrations, indicating the influence of salinity on fruit calyx morphology; (e) Calyx length under different nanoparticle treatments, emphasizing the role of nanoparticles in modulating calyx length; (f) Fruit yield in distinct salt concentrations, providing insights into the relationship between salinity stress and overall fruit productivity; and (g) Fruit yield under different nanoparticle concentrations, revealing the impact of nanoparticles on enhancing or mitigating fruit yield.

Biochemical traits

Catalase enzyme activity

The impact of salinity stress on catalase enzyme activity was statistically significant at the 1% level ($P < 0.01$). Salinity-induced stress led to a marked increase in catalase enzyme activity, with the highest observed activity at 200 mM salinity (0.532 enzyme units). Notably, treatments involving Se and Si nanoparticles resulted in a considerable reduction in catalase enzyme activity compared to the control treatment, where the highest activity was recorded in the control treatment (0.481). Specifically, Se treatments at 25 and 100 mg l⁻¹ exhibited an 11% and 12% decrease, respectively, relative to the control condition (Fig. 2-b,c).

Superoxide dismutase (SOD) enzyme activity

Salinity stress significantly heightened SOD enzyme activity ($P < 0.01$), peaking at 200 mM salinity (5.82 enzyme units). In contrast, treatments involving Se and Si nanoparticles demonstrated a significant reduction in SOD enzyme activity compared to the control expect in Se 100 mg l⁻¹, with the highest activity observed in the control treatment (4.64 enzyme units). Se treatments at 50 and 200 mg l⁻¹ resulted in a notable 7% and 10% reduction, respectively, in SOD enzyme activity relative to the control (Fig. 2-d,e).

Anthocyanin content

Salinity stress up to 50 mM elicited a significant increase in anthocyanin content, followed by a subsequent decline at higher stress levels ($P < 0.01$). Se and Si nanoparticle treatments induced a notable augmentation in anthocyanin content compared to the control condition, where the lowest amount was recorded (2.29 mg). Specifically, Se treatments at 25 and 200 mg l⁻¹ demonstrated a substantial 21% and 27% increase, respectively, in anthocyanin content relative to the control (Fig. 3-a).

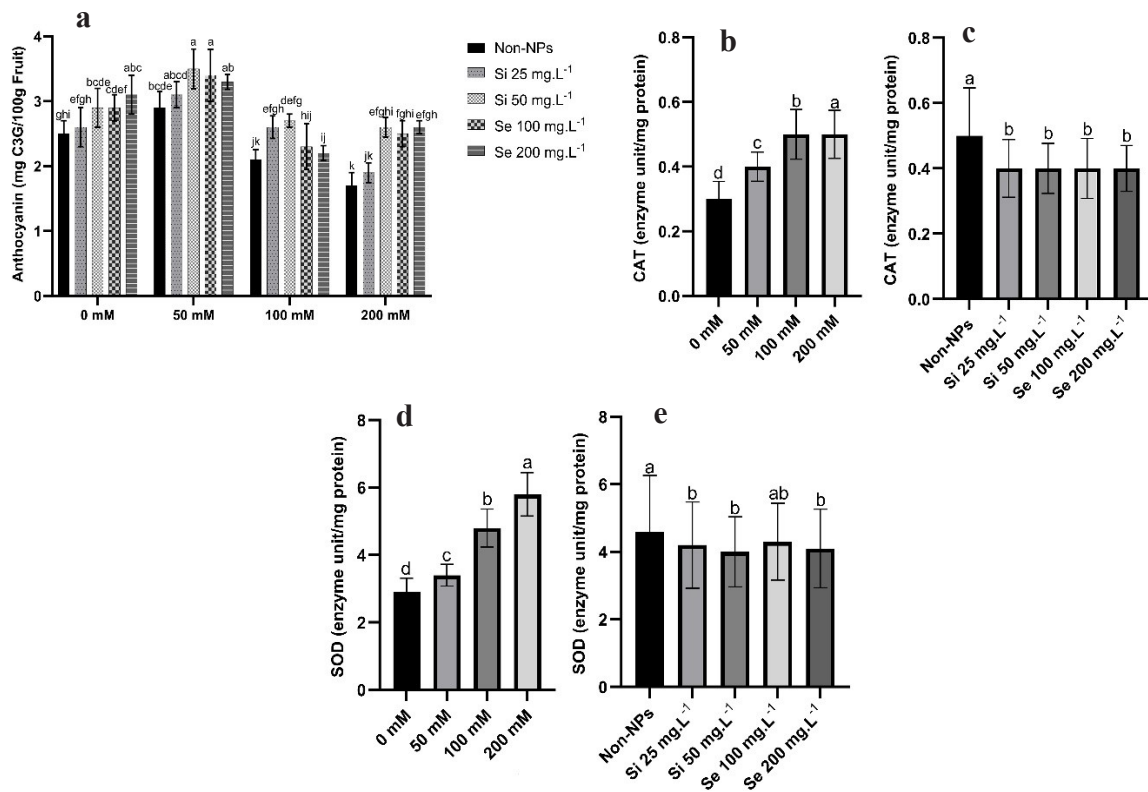


Fig. 2. Provides a detailed depiction of crucial biochemical parameters in *Physalis alkekengi* L. subjected to varying salinity concentrations and nanoparticle treatments. The subplots encompass (a) Anthocyanin levels, illustrating the influence of different treatments on the plant's anthocyanin content; (b) Catalase (CAT) activity under distinct salt concentrations, elucidating the correlation between salinity stress and CAT enzyme response; (c) CAT activity under diverse nanoparticle concentrations, highlighting the effect of nanoparticles on modulating CAT enzyme activity; (d) Superoxide dismutase (SOD) activity in response to varying salt concentrations, indicating the impact of salinity on the plant's antioxidant defense mechanism; and (e) SOD activity under different nanoparticle treatments, emphasizing the role of nanoparticles in regulating SOD enzyme activity.

Leaf elemental composition

Sodium (Na)

The impact of salinity stress on leaf sodium content was statistically significant at the 1% level ($P < 0.01$). Increasing salinity stress levels led to a substantial rise in leaf sodium content, reaching its peak at 200 mM salinity (7.54 mg g^{-1}), while the control treatment exhibited the lowest sodium content (1.86 mg g^{-1}). Se and Si nanoparticle treatments induced a significant reduction in leaf sodium content compared to the control. Specifically, Se treatments at 50 and 200 mg l^{-1} resulted in a noteworthy 27% and 32% decrease, respectively, in leaf sodium content relative to the control. The interaction effect of salinity stress and Se and Si nanoparticles on leaf sodium was also significant ($P < 0.01$), showcasing a notable reduction in leaf sodium levels in the presence of Se and Si (Fig. 3-a).

Chlorine (Cl)

Salinity stress significantly increased leaf chlorine content ($P < 0.01$), with the highest observed value at 200 mM salinity (50.33 mg g^{-1}). Conversely, Se and Si nanoparticle treatments caused a substantial reduction in leaf chlorine content compared to the control, demonstrating a pronounced decrease in chlorine levels. Se treatments at 25 and 200 mg l^{-1} resulted in a considerable 21% and 27% reduction, respectively, in leaf chlorine content relative to the control. The interaction effect of salinity stress and Se and Si nanoparticles on leaf chlorine was also significant ($P < 0.01$), revealing a mitigating influence on chlorine levels by Se and Si treatments (Fig. 3-b).

Potassium (K)

Salinity stress significantly decreased leaf potassium content ($P < 0.01$), reaching its lowest at 200 mM salt stress treatment (26.13 mg g^{-1}), while the control treatment exhibited the highest potassium content (35.73 mg g^{-1}). In contrast, Se and Si nanoparticle treatments induced a significant increase in leaf potassium content compared to the control. Se treatments at 200 mg l^{-1} demonstrated a notable 15% increase in leaf potassium content relative to the control (Fig. 3-c,d).

Phosphorus (P)

Salinity stress led to a significant decrease in leaf phosphorus content ($P < 0.01$), with the lowest observed value at 200 mM salinity (2.86 mg g^{-1}) and the highest in the control treatment (6.26 mg g^{-1}). Se and Si nanoparticle treatments induced a significant increase in leaf phosphorus content compared to the control. Se treatments at 25 and 100 mg l^{-1} resulted in a considerable 12% and 14% increase, respectively, in leaf phosphorus content relative to the control. Notably, no significant difference in leaf phosphorus was observed between different levels of Se and Si nanoparticles (Fig. 3-e,f).

Total essential fatty acid (TEFA)

The analysis of total essential fatty acids (TEFA) across different treatments revealed notable variations in fatty acid composition. Under salinity stress at varying levels (50, 100, and 200 mM), the TEFA content exhibited a discernible trend. Specifically, in the absence of nanoparticles (Without NP), TEFA values remained relatively stable, indicating a limited impact of salinity on the overall essential fatty acid profile. However, the introduction of Si nanoparticles (Si 25 and Si 50 mg l^{-1}) resulted in marginal decreases in TEFA, suggesting a potential modulating effect of Si on essential fatty acid composition. Se treatments (Se 100 and Se 200 mg l^{-1}) showed a tendency to maintain TEFA levels comparable to the control, hinting at a protective role against salinity-induced alterations in essential fatty acids. Further investigations may elucidate the specific mechanisms by which Si and Se nanoparticles influence TEFA synthesis and accumulation under salinity stress (Fig. 4-a,b).

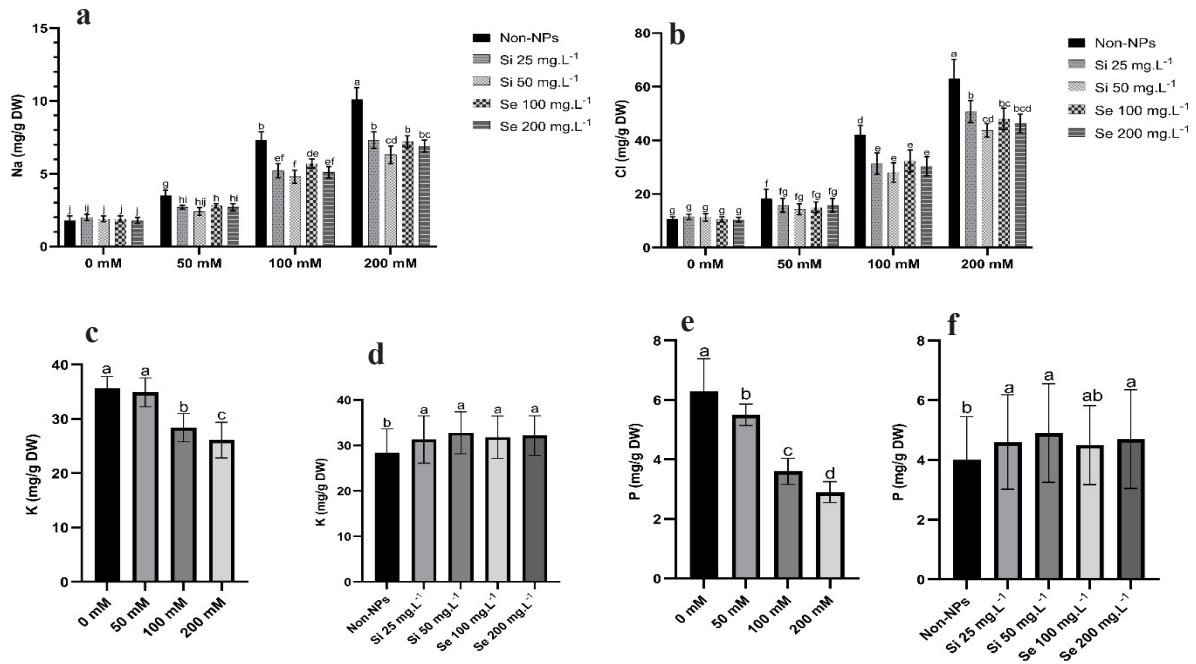


Fig. 3. Provides a comprehensive insight into the ionic profile of *Physalis alkekengi* L. under varying salinity conditions and nanoparticle treatments. The subplots encompass (a) Sodium (Na) levels, illustrating the plant's response to different salt concentrations; (b) Chloride (Cl) levels, depicting the variation in Cl content under different salt treatments; (c) Potassium (K) concentrations in response to diverse salinity levels, delineating the plant's K dynamics under salt stress; (d) K levels under various nanoparticle treatments, demonstrating the influence of nanoparticles on K uptake; (e) Phosphorus (P) content under different salinity conditions, providing insights into the impact of salt stress on P accumulation; and (f) P concentrations in response to distinct nanoparticle treatments, highlighting the role of nanoparticles in modulating P levels.

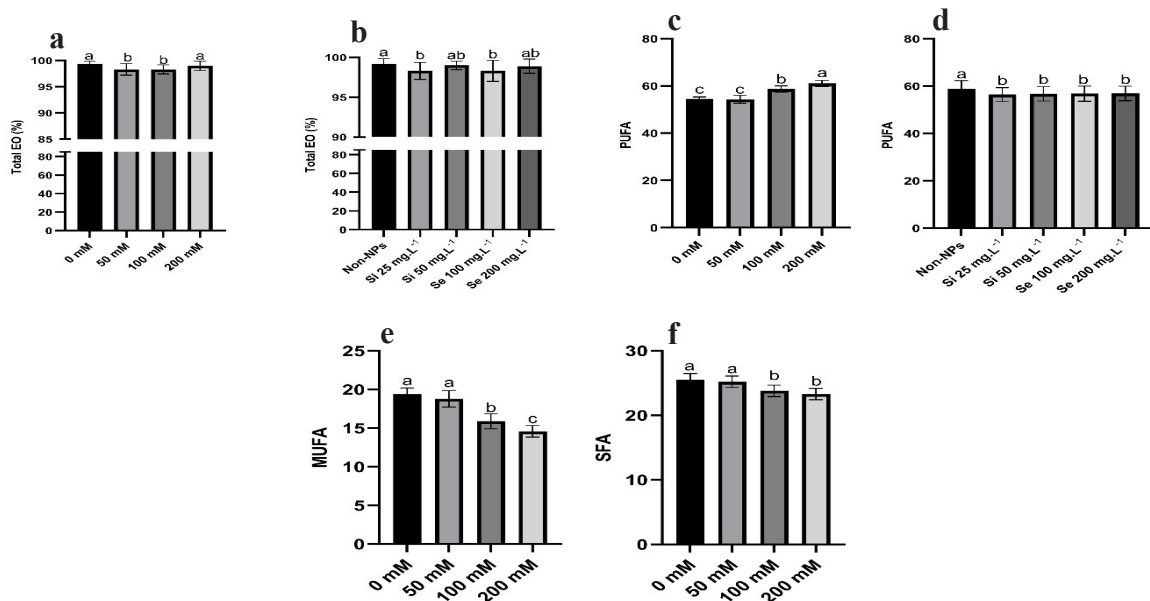


Fig. 4. Provides a detailed overview of the fatty acid composition in *Physalis alkekengi* L. under distinct salinity conditions and nanoparticle treatments. The subplots present (a) Total fatty acid levels, elucidating variations in the overall fatty acid content under different salt concentrations; (b) Total fatty acid concentrations in response to various nanoparticle treatments, illustrating the impact of nanoparticles on the total fatty acid profile; (c) Polyunsaturated fatty acids (PUFA) levels under different salt conditions, showcasing the plant's response to salt-induced stress; (d) PUFA concentrations under diverse nanoparticle treatments, indicating the role of nanoparticles in influencing PUFA content; (e) Monounsaturated fatty acids (MUFA) variations in different salinity concentrations, shedding light on the plant's MUFA dynamics under salt stress; and (f) Saturated fatty acids (SFA) alterations under different salt conditions, providing insights into how salt stress affects SFA composition.

Saturated fatty acids (SFAs)

The analysis of saturated fatty acids (SFAs) demonstrated nuanced responses to salinity stress and nanoparticle treatments. Across different salinity levels, SFAs exhibited fluctuations with variations in the type and concentration of nanoparticles. In the absence of nanoparticles (Without NP), SFAs experienced modest changes under increasing salinity. However, Si nanoparticle treatments (Si 25 and Si 50 mg l⁻¹) displayed a trend of maintaining SFAs at levels comparable to or slightly below the control, suggesting a potential mitigating effect on salinity-induced SFA alterations. Se treatments (Se100 and Se 200 mg l⁻¹) demonstrated a similar trend, highlighting the capacity of Se to regulate SFA content under salt stress conditions. Further investigations into the molecular pathways involved in SFA metabolism and regulation could enhance our understanding of the observed trends (Fig. 4-f).

Monounsaturated fatty acids (MUFAs)

The examination of monounsaturated fatty acids (MUFAs) revealed distinct patterns influenced by salinity stress and nanoparticle treatments. Salinity stress at varying levels prompted changes in MUFA content, with a general trend of decrease observed. In the absence of nanoparticles (without NP), the decline in MUFAs under salinity stress was notable. However, Si nanoparticle treatments (Si 25 and Si 50 mg l⁻¹) demonstrated a potential mitigating effect, with MUFA levels exhibiting moderation compared to the control. Se treatments (Se 100 and Se 200 mg l⁻¹) also showed a trend of preserving MUFA levels, suggesting a protective role against salinity-induced reductions in monounsaturated fatty acids. Exploring the underlying molecular mechanisms governing MUFA metabolism and regulation in response to nanoparticle treatments could provide valuable insights (Fig. 4-e).

Polyunsaturated fatty acids (PUFA)

Polyunsaturated fatty acids (PUFAs) exhibited dynamic responses to salinity stress and nanoparticle treatments. Salinity stress at varying levels led to fluctuations in PUFA content, indicating the sensitivity of these fatty acids to environmental stressors. In the absence of nanoparticles (without NP), PUFA levels displayed a general decreasing trend under salinity stress. However, Si nanoparticle treatments (Si 25 and Si 50 mg l⁻¹) showcased a potential mitigating effect, with PUFA content showing moderation compared to the control. Se treatments (Se 100 and Se 200 mg l⁻¹) also demonstrated a trend of maintaining PUFA levels, suggesting a protective role against salinity-induced alterations in polyunsaturated fatty acids. Exploring the molecular mechanisms involved in the synthesis and regulation of PUFAs under nanoparticle treatments could contribute to a comprehensive understanding of their role in plant responses to salinity stress (Fig. 4-c,d).

Correlation matrix

The Pearson correlation matrix analysis revealed intricate interrelationships among diverse physiological parameters in the experimental context. Strong positive correlations were observed between biomass-related traits (DW shoot, calyx dimensions, FW fruit, and fruit Y), indicating coordinated responses. Concurrently, a negative correlation between these traits and antioxidant enzymes (CAT and SOD) suggests a potential trade-off between growth and antioxidant activity. Sodium (Na) and chloride (Cl) exhibited a consistent co-occurrence, negatively correlating with antioxidant enzymes, implicating their role in ionic stress response. Potassium (K) and phosphorus (P) displayed positive correlations with biomass, emphasizing their significance in plant growth. Fatty acid composition (Total essential fatty acid, SFA, MUFA,

PUFA) exhibited weak correlations with other parameters, suggesting relative independence. Treatment effects, particularly Se, and Si nanoparticles, hinted at nuanced shifts in correlations, underlining their potential in modulating plant responses (Fig. 5-a).

Principal component analysis (PCA)

Principal component analysis (PCA) was conducted to elucidate intricate patterns within the extensive dataset derived from the experimental conditions. The eigenvalue analysis revealed that the first five principal components (F1-F5) collectively accounted for a substantial 97.44% of the total variability, highlighting their significance in capturing the underlying structure of the data. The eigenvectors associated with each parameter provided insights into their contributions to the respective principal components. Biomass-related traits, antioxidant enzymes, and fatty acid composition exhibited noteworthy contributions to specific principal components, emphasizing their distinctive roles in the observed variance. The cumulative percentage of variability further underscored the efficacy of the selected principal components in collectively representing the majority of the dataset. The loadings and squared cosines of the variables provided a nuanced understanding of the strength and reliability of the associations, guiding the nuanced interpretation of the PCA results (Fig. 5-b).

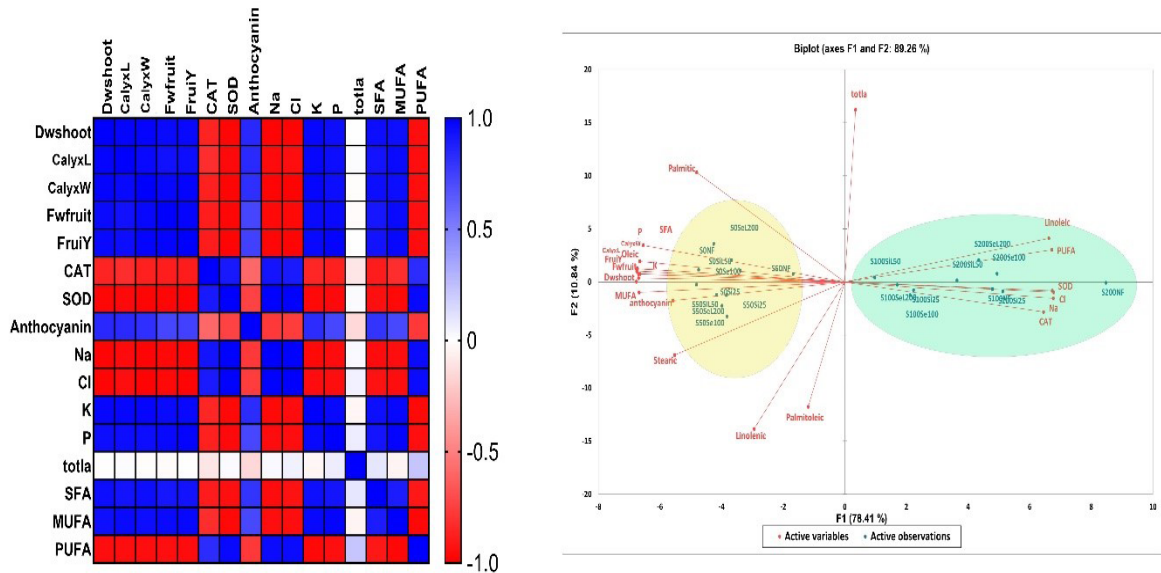


Fig. 5. Encapsulates two crucial analytical components: (a) a Correlation matrix and (b) PCA, both contributing to a comprehensive understanding of the intricate relationships and multivariate patterns within the dataset. Subplot (a) displays the correlation matrix, employing Pearson correlation coefficients to elucidate the interdependencies among diverse parameters, such as shoot dry weight, fruit yield, enzymatic activities (CAT, SOD), anthocyanin content, and elemental concentrations (Na, Cl, K, P). The correlation matrix aids in identifying potential associations or trends between these variables. Subplot (b) features principal component analysis. The eigenvalues, eigenvectors, and variable contributions are presented, offering insights into the major determinants shaping the observed patterns.

DISCUSSION

This experiment rigorously investigated the effects of salinity stress on the physiological and biochemical aspects of plant growth in *P. alkekengi* L. The findings demonstrate substantial changes in shoot dry weight, fruit morphology, and multiple biochemical characteristics, indicating the adverse impact of elevated salinity levels on plant well-being. Furthermore, the utilization of Se and Si nanoparticles exhibited encouraging remedial effects, alleviating the

detrimental outcomes of salinity stress (Afshari *et al.*, 2021; Ali *et al.*, 2021; Ghasemian *et al.*, 2021).

The augmentation of soil salinity levels instigates a cascade of physiological responses in plants, primarily through the elevation of external osmotic pressure. This results in a diminished capacity for water absorption, thereby compromising plant turgor and reducing femininity (Shomali *et al.*, 2021). Concurrently, salt stress disrupts water secretion processes, leading to the accumulation of salts within plant tissues, ultimately resulting in a decline in overall plant vigor. The accompanying perturbations in enzymatic activities and metabolic processes further contribute to the detrimental effects of salinity stress (Gaafar *et al.*, 2020; Hawrylak-Nowak, 2022; Monroy-Velandia and Coy-Barrera, 2021). However, the introduction of Se and Si nanoparticles serves as a strategic intervention, manifesting positive effects on plant aerial parts under salt stress conditions.

The incorporation of nanoparticles demonstrates notable enhancements in plant growth dynamics, water absorption, and nutrient assimilation, culminating in an overall increase in plant weight. Se nanoparticles, acknowledged for their essential role in plant physiology, exhibit a capacity to elevate enzyme activity and metabolic processes, thereby mitigating the adverse impacts of salinity stress on plants (Alsaedi *et al.*, 2019; Alsamadany *et al.*, 2022; Gaafar *et al.*, 2020). The current findings are consistent with previous studies highlighting the beneficial effects of Si and Se nanoparticles, underscoring their role in augmenting plant biomass under salinity stress conditions.

Salt stress-induced alterations in fruit quality, encompassing changes in color, texture, and phenolic content, pose considerable challenges to the commercial value of crops (Monroy-Velandia and Coy-Barrera, 2021; Mushtaq *et al.*, 2020). However, the application of Se and Si nanoparticles emerges as an effective strategy to counteract these adverse effects, contributing to increased plant weight and size (Afshari *et al.*, 2021; Alsamadany *et al.*, 2022; Kiumarzi *et al.*, 2022). Moreover, the discernible reductions in fruit yield attributed to diminished water and nutrient absorption, increased vulnerability to diseases, and compromised resistance under salt stress conditions can be effectively mitigated through nanoparticle interventions (Ghasemi-Soloklui *et al.*, 2023).

The multifaceted contributions of Se nanoparticles, characterized by their involvement in plant growth, development, and antioxidant activity, offer significant improvements in fruit yield (Abdoli *et al.*, 2020; Garza-García *et al.*, 2021; Ghasemian *et al.*, 2021; González-García *et al.*, 2021). The present study aligns with prior research reports, indicating increased fruit yield in strawberries with the application of Se nanoparticles. Notably, the concentration of nanoparticles proves to be a critical factor, with the 200 mg l⁻¹ level demonstrating superior efficacy in influencing plant performance. This underscores the importance of nanoparticle dosage in tailoring interventions for optimal plant responses under salinity stress conditions.

The discernible impact of salt, even in low concentrations within the roots and leaves, manifests in the heightened activity of the catalase enzyme. This catalytic response exhibits organ-specific variations, influenced by the diverse sodium concentrations present in different plant organs. A pivotal biochemical consequence of salinity stress in plants is the accumulation of reactive oxygen species (ROS), leading to perturbations in cellular redox balance and the onset of oxidative stress, as elucidated by previous research (Mushtaq *et al.*, 2020). In response to stressful environmental conditions, plants mobilize antioxidant compounds, with varying quantities among different plant species, to counteract the deleterious effects of activated oxygen

species. The delicate equilibrium between ROS generation and neutralization by antioxidants becomes disrupted under stress, resulting in oxidative damage at the cellular level (Alam *et al.*, 2022; Moradi *et al.*, 2022). Reactive oxygen species, including hydrogen peroxide, are formed during metabolic processes and environmental stress, underscoring the continuous exposure of photosynthetic aerobic organisms to these species. The catalase enzyme plays a pivotal role in eliminating hydrogen peroxide from plant cells, leading to a concurrent decrease in its activity. Consequently, the heightened activity of antioxidant enzymes, such as catalase, constitutes an essential adaptive mechanism employed by plants to combat salinity-induced stress (Ali *et al.*, 2021; Kiumarzi *et al.*, 2022). Also, the stability of SOD and CAT levels in nanoparticle treatments, despite harsh salt stress conditions, underscores the efficacy of nanoparticle interventions in mitigating cellular oxidative stress. By reducing ROS concentrations within the cells, nanoparticle treatments effectively dampen the need for significant alterations in SOD and CAT activity. This resilience highlights the potential of nanoparticle-based approaches in buffering against environmental stressors, thereby preserving cellular homeostasis even under challenging conditions (Zia-ur-Rehman *et al.*, 2023).

The adaptive response to salinity stress encompasses an augmentation in chlorophyll content and the enhanced activity of antioxidant enzymes like catalase, peroxidase, and polyphenol oxidase. The elevation in these antioxidant defenses serves as a strategic mechanism for plants to contend with the surge in reactive oxygen species triggered by salt stress (Zahedi *et al.*, 2019). Notably, the application of nanoparticles has garnered attention for its reported efficacy in increasing the content of antioxidant enzymes, as evidenced by various studies (Ghasemi-Soloklui *et al.*, 2023; Ghasemian *et al.*, 2021; Golubkina *et al.*, 2022; Hawrylak-Nowak, 2022; Moradi *et al.*, 2022). Researchers postulate that certain nanoparticles possess distinctive antioxidant enzyme-like properties, thereby aiding plants in mitigating oxidative conditions induced by environmental stressors (Zia-ur-Rehman *et al.*, 2023).

Salt stress induces the production of superoxide radical anions ($O_2^{\cdot-}$) within plant cells, primarily attributed to stomatal closure and diminished carbon dioxide fixation, leading to reduced growth. Concurrently, heightened respiration in these conditions contributes to the generation of detrimental ions within the cell's mitochondria. The pivotal response involves the elevation in superoxide dismutase enzyme activity, crucial for the detoxification of superoxide ions and consequent reduction in plant damage. Under stress conditions, superoxide dismutase efficiently reacts with superoxide anion radicals, producing water and oxygen as byproducts (Alam *et al.*, 2022; Moradi *et al.*, 2022). Si and Se nanoparticles exhibit the potential to mitigate oxidative damage by modulating antioxidant defense systems, encompassing both enzymatic and non-enzymatic components (Patel *et al.*, 2023; Sanjay and Shukla, 2021). Notably, the application of nanoparticles and Se under stress conditions led to a decrease in enzyme activity, indicative of their stress-moderating and ROS-reducing capabilities. This aligns with findings reporting reduced antioxidant enzyme activity with nanoparticle application under stress conditions in beans (Zadegan *et al.*, 2023). Although, antioxidant activity can enhance plant tolerance to harsh conditions, the presented data from this study suggest that nanoparticle treatments may not consistently influence this parameter across all treatments. The lack of significant differences in plant antioxidant concentrations between nanoparticle treatments compared to the control group underscores the variability in the effectiveness of nanoparticle strategies in modulating plant stress responses (Morales-Espinoza *et al.*, 2019).

The impact of salinity stress on fruit anthocyanins, crucial phenolic compounds contributing to red, blue, and purple hues in fruits and vegetables, is multifaceted. Salinity-

induced alterations in enzyme activity and plant metabolism can diminish anthocyanin production and concentration, especially under extreme stress levels like 200 mM. Elevated salinity conditions may heighten the oxidation potential of the environment, potentially oxidizing anthocyanins and reducing their content and activity in the fruit (Denaxa *et al.*, 2022). The observed nuanced response in the current study, where mild salinity levels increased anthocyanin content while severe levels decreased it, echoes findings reported by Denaxa *et al.* (2022) and Yaghubi *et al.* (2019) in strawberries. Encouragingly, the application of nanoparticles and Se emerges as a positive influence on fruit anthocyanins. Nanoparticles exhibit the capacity to augment anthocyanin production and concentration, while Se nanoparticles not only boost anthocyanin levels but also enhance their antioxidant activity (Banerjee *et al.*, 2021). Consistent with previous research, an augmentation in anthocyanin content with Se application has been reported (Fatemi *et al.*, 2021; Sheikhalipour *et al.*, 2021).

Plants respond to high levels of sodium ions in their surroundings by activating mechanisms that regulate the balance of sodium ion concentrations inside and outside of cells. Unlike potassium ions, which are maintained at high concentrations within cells, plants actively reduce sodium ion levels inside cells in order to achieve equilibrium (Muhammad *et al.*, 2022). The increase in salt concentration in the growth medium hinders the plant's ability to maintain a balance of sodium ions, leading to a higher accumulation of sodium ions in the leaves. The current findings are consistent with previous research conducted by (Alam *et al.*, 2022; Moradi *et al.*, 2022), which have demonstrated a decrease in sodium ion levels in leaves by using nanoparticles and Se.

Under conditions of elevated sodium chloride concentration in the root environment, there is an increase in the accumulation of chloride ions in plant organs. Nanoparticles and Se act as chlorine ion adsorbents, specifically attracting and absorbing these ions, including those that enter the plant through the soil. Nanoparticles and Se function as inhibitory agents on chlorine ion permeation channels in plant cells. This leads to a decrease in the penetration of chloride ions and subsequently reduces their accumulation in leaves (Kiumarzi *et al.*, 2022). In addition, these substances strengthen the plant's defense mechanism by promoting the production of antioxidants and improving its ability to withstand salinity stress. As a result, the accumulation of chlorine ions in the leaves is reduced (Hawrylak-Nowak, 2022; Kiumarzi *et al.*, 2022; Muhammad *et al.*, 2022).

Salinity stress, marked by an elevation in soil salt concentration, hampers the uptake of potassium by plant roots. The disparity in osmotic conditions between the soil and roots, coupled with the hindrance of potassium transportation within the plant, leads to a reduction in the transfer of potassium from the roots to the leaves. In addition, exposure to high levels of salt can cause cellular harm, leading to a decrease in the ability of damaged cells to transport potassium (Habibi and Aleyasin, 2020; Hawrylak-Nowak, 2022; Muhammad *et al.*, 2022). As a result, there is a decrease in the potassium levels in the leaves (Sardar *et al.*, 2023). Se nanoparticles enhance the antioxidant defense system, reducing oxidative damage, protecting cells and cell membranes from salt-induced stress, and promoting potassium uptake and transport in plants. Increased potassium uptake and transport contribute to heightened potassium concentrations in leaves during periods of salt stress. Nanoparticles have been shown to enhance plant tolerance to saline conditions by improving the activity of potassium transfer pumps in roots, leading to increased potassium absorption and transfer in plants (Wu *et al.*, 2018).

The presence of high levels of salt in the soil has a detrimental effect on the ability of plant roots to absorb phosphorus. This is caused by the disruption of the root's water balance

and an increase in the deposition of phosphate in the soil. Salinity stress causes changes in the tissue structure and function of roots, leading to a decrease in the movement of phosphorus within the plant (Okon, 2019; Yadav *et al.*, 2011). This limits the transport of phosphorus from the roots to the leaves and reduces the phosphorus content in the leaves. Moreover, alterations in enzyme activity caused by salinity, specifically phosphatase, result in reduced absorption and utilization of phosphorus by plants (Bouras *et al.*, 2022; Sardar *et al.*, 2023). Prior studies, exemplified by Golubkina *et al.* (2022), have demonstrated the effectiveness of nanoparticles and Se in enhancing the phosphorus content in leaves. This indicates their potential use in reducing the negative impact of salinity stress on the absorption and utilization of phosphorus by plants.

Beyond its gustatory appeal, the *P. alkekengi* fruit stands out for its nutritional richness, contributing to potential human health benefits. The discerned decline in fatty acids can be ascribed to the impeding influence on both unsaturated and saturated fatty acid synthesis, culminating in diminished oil content and consequential shifts in the fatty acid composition. The plant's adaptive responses to environmental and growth nuances extend beyond impacting performance metrics, influencing the intricate synthesis of secondary metabolites and bioactive compounds (Terletskaia *et al.*, 2021). In concordance with previous study on wheat (Weinstock *et al.*, 2006), our investigation illuminates a discernible inverse correlation between linoleic acid and oleic acid. Furthermore, our study reveals an augmentation in polyunsaturated fatty acids and a concurrent reduction in non-monounsaturated fatty acids under stress conditions, mirroring the trends documented by He and Ding (2020) and Zadegan *et al.* (2023). These consistent patterns underscore the universality of the observed alterations in fatty acid composition in response to environmental stressors and treatment modalities.

The correlation matrix analysis offers a thorough comprehension of the complex physiological relationships within the experimental framework, revealing insights into the dynamic reactions of *P. alkekengi* to different situations and treatments. The significant positive relationships reported across biomass-related parameters, such as shoot biomass, calyx dimensions, fruit fresh weight, and fruit yield, highlight a synchronized response to environmental stressors. The inverse relationship between these growth-related characteristics and antioxidant enzymes (CAT and SOD) implies a possible trade-off, indicating the allocation of resources between growth and stress response mechanisms. The elements sodium (Na) and chloride (Cl) consistently showed a negative connection with antioxidant enzymes, suggesting their participation in the plant's response to ionic stress. The discovered positive associations between potassium (K) and phosphorus (P) with biomass-related variables highlight the crucial roles of these nutrients in promoting plant growth. The fatty acid composition, including the total essential fatty acid, saturated fatty acid (SFA), monounsaturated fatty acid (MUFA), and polyunsaturated fatty acid (PUFA), showed relatively modest associations with other measures. This suggests that they exhibit a certain level of independence in their reactions. The introduction of Se and Si nanoparticles in treatment had subtle impacts on correlations, emphasizing their potential in influencing the complex physiological dynamics of *P. alkekengi*.

The PCA conducted on the broad range of parameters in this experiment reveals the complex interrelationships and underlying patterns among the variables. The primary eigenvalues corresponding to the initial five main components (F1-F5), which together account for 97.44% of the overall variability, highlight the crucial significance of these components in capturing the fundamental characteristics of the dataset. The specific principal components were primarily influenced by biomass-related features, antioxidant enzymes, and fatty acid

content, emphasizing their unique contributions to the observed variability. The loadings and squared cosines of the variables highlighted the robustness and validity of these correlations. The distinct responses to the treatment were evident by closely analyzing the eigenvectors. Parameters such as DW shoot, calyx L, and calyx W showed significant correlations with individual main components. The significant impact of fatty acids, such as palmitic, palmitoleic, stearic, oleic, linoleic, and linolenic, was demonstrated in determining the observed differences in various treatments. The cumulative proportion of variability demonstrates that the chosen principal components jointly captured most of the dataset's complexity. The effectiveness of PCA in identifying treatment-specific patterns improves our comprehension of *P. alkekengi*'s response to different conditions, offering a comprehensive perspective on the relationship between biomass-related characteristics, antioxidant enzymes, and fatty acid composition.

CONCLUSION

In conclusion, this study highlights the significant impact of salinity stress on *Physalis alkekengi* L., resulting in decreased growth and fruit yield alongside heightened activities of antioxidant enzymes as a response to oxidative stress induced by salt exposure. Application of Se and Si nanoparticles via foliar spraying demonstrated promising efficacy in mitigating salinity stress, particularly within the concentration range of 25 to 100 mg l⁻¹ respectively, indicating a potential avenue for enhancing plant tolerance to adverse conditions. The superior performance of Se and Si nanoparticles compared to the control underscores the potential of nanotechnology in optimizing plant responses to environmental stressors, with their surfaces exhibiting notable superiority in promoting overall plant health and performance. The ability of nanoparticles to modulate salinity stress and enhance antioxidant enzyme activities and boosting plant tolerance to abiotic stress such as alkaline or salt stress presents novel opportunities for sustainable agricultural practices aimed at improving crop yields and quality. Moving forward, further research should explore the molecular mechanisms underlying the positive effects of Se and Si nanoparticles on plant responses to salinity stress, paving the way for tailored interventions and nano-based solutions to bolster crop resilience in the face of environmental challenges. This study thus contributes valuable insights into the potential applications of nanotechnology in agriculture, offering a pathway towards sustainable and resilient crop production amidst changing environmental conditions.

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