

Article

The Effect of Selenium Application on the Balance of Nutrients and Antioxidant Properties of ‘Malas Saveh’ Pomegranate Fruit

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Abstract

Selenium (Se) is a beneficial element that enhances plant antioxidant capacity, improves fruit quality, and contributes to the biofortification of horticultural crops. However, information regarding its effects on mineral nutrient balance and antioxidant metabolism in pomegranate remains limited. This study investigated the effects of foliar selenium (Se) application on fruit yield, mineral nutrient balance, antioxidant metabolism, and fruit quality of pomegranate (*Punica granatum* L.) cv. ‘Malas Saveh’ during the 2022 and 2023 growing seasons under orchard conditions in Iran. Trees were treated with sodium selenate at different concentrations using a randomized complete block design. In 2022, Se was applied at 0, 2, 4, and 6 mg L^{−1}, while in 2023, based on the results of the first-year screening phase, the concentration range was expanded to 0, 6, 8, and 10 mg L^{−1} to further investigate plant responses to higher Se levels. Foliar Se application significantly increased fruit yield, fruit number, and Se accumulation in both leaves and fruits, confirming the effectiveness of Se biofortification. Selenium treatments also improved the nutritional composition of pomegranate fruits by increasing the concentrations of nitrogen (N), phosphorus (P), potassium (K), iron (Fe), and zinc (Zn), whereas manganese (Mn) concentrations declined, suggesting an antagonistic interaction between Se and Mn uptake. Significant improvements were observed in fruit quality traits, including soluble solids content, titratable acidity, vitamin C, total phenolics, anthocyanins, and antioxidant activity. The 6 mg L^{−1} treatment in 2022 and the 8–10 mg L^{−1} treatments in 2023 resulted in the most pronounced physiological and biochemical responses, with 10 mg L^{−1} showing no further significant improvement for several key traits. Selenium application also enhanced the antioxidant defense system through increased activities of catalase (CAT), superoxide dismutase (SOD), peroxidase (POD), phenylalanine ammonia-lyase (PAL), and ascorbate peroxidase (APX), while reducing hydrogen peroxide (H₂O₂), malondialdehyde (MDA), and membrane ion leakage. Principal component analysis further confirmed the strong positive association between higher Se concentrations and improved mineral and biochemical characteristics. Overall, foliar Se application effectively enhanced pomegranate productivity, nutritional quality, antioxidant capacity, and physiological performance, highlighting its potential as a sustainable agronomic practice for the production of high-quality Se-enriched fruits.



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1. Introduction

Pomegranate (*Punica granatum* L.) is among the oldest cultivated fruit crops and is widely valued for its exceptional nutritional, sensory, and medicinal properties. Native to the Mediterranean and Middle Eastern regions, it has gained considerable commercial importance in recent decades owing to the increasing consumer demand for functional foods rich in bioactive compounds [1,2]. Pomegranate fruits contain high concentrations of phenolic compounds, flavonoids, anthocyanins, tannins, and vitamins, which contribute substantially to their antioxidant capacity and associated health-promoting properties, including anti-inflammatory, antimicrobial, and cardioprotective effects [2,3]. Fruit quality is determined by several physicochemical and biochemical attributes, including soluble solids content, titratable acidity, anthocyanin concentration, antioxidant capacity, and mineral composition, all of which are strongly influenced by preharvest environmental conditions and nutritional management practices [3,4].

In recent years, increasing attention has been directed toward sustainable agronomic practices that enhance fruit quality while simultaneously improving nutritional value and plant tolerance to environmental stresses. Among the beneficial micronutrients, selenium (Se) has received particular attention because of its dual role in plant physiology and human nutrition [5,6]. Selenium is an essential trace element for humans and animals, where it plays a fundamental role in antioxidant defense, immune function, and protection against oxidative stress-related disorders [6,7]. Although Se is not considered an essential element for higher plants, numerous studies have demonstrated that low concentrations can exert beneficial effects on plant growth, metabolism, and tolerance to abiotic stresses [8,9]. At appropriate concentrations, Se has been shown to enhance photosynthetic efficiency, maintain membrane integrity, improve nutrient acquisition, and stimulate antioxidant metabolism in a wide range of horticultural crops [10–12].

Selenium can be supplied to plants either through soil fertilization or foliar application. Among these approaches, foliar spraying is generally considered the more efficient strategy because it promotes rapid Se absorption and translocation while minimizing fixation and losses in the soil [13]. Once absorbed, Se enters sulfur metabolic pathways and contributes to the synthesis of antioxidant compounds and other stress-related metabolites [14]. Numerous studies have demonstrated that agronomic Se biofortification improves crop yield, nutritional quality, antioxidant capacity, and postharvest performance in a wide range of horticultural commodities, including strawberry, tomato, grape, apple, and ju-jube [15–19]. Agronomic biofortification, defined as the enrichment of edible plant tissues with essential micronutrients through fertilizer application, has emerged as an effective and sustainable strategy for alleviating micronutrient deficiencies in human populations worldwide [6,11–13]. Furthermore, Se supplementation has been associated with increased accumulation of phenolic compounds, anthocyanins, vitamin C, and soluble solids, together with enhanced activities of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX) [18–21].

Beyond its role in antioxidant metabolism, Se may substantially influence the uptake, translocation, and distribution of mineral nutrients within plant tissues. Previous studies have reported synergistic interactions between Se and several essential nutrients, including nitrogen (N), phosphorus (P), potassium (K), iron (Fe), and zinc (Zn), whereas antagonistic relationships have been observed with manganese (Mn) and sulfur (S) [22,23]. These interactions may modify the nutritional status of plants and consequently influence fruit quality, physiological performance, tolerance to environmental stresses, and postharvest behavior. Nevertheless, despite the increasing interest in Se biofortification, information regarding the effects of foliar Se application on mineral nutrient balance and antioxidant

metabolism in pomegranate remains scarce, particularly under field conditions and over consecutive growing seasons.

Although previous studies have demonstrated that foliar Se application can improve pomegranate yield and fruit quality [9], the physiological and biochemical mechanisms underlying these responses remain only partially understood. In particular, little information is available regarding the combined effects of Se on mineral nutrient balance, antioxidant metabolism, oxidative stress, and biofortification efficiency under orchard conditions. Furthermore, no previous study has comprehensively evaluated these responses over two consecutive growing seasons using different Se concentration ranges.

Therefore, we hypothesized that foliar Se application would enhance pomegranate productivity by improving mineral nutrient acquisition, strengthening antioxidant defense mechanisms, and promoting fruit nutritional quality. To test this hypothesis, the present study investigated the effects of different foliar Se concentrations on (i) fruit yield and selenium accumulation, (ii) macro- and micronutrient balance in leaves and fruits, (iii) antioxidant enzyme activities and oxidative stress indicators, and (iv) the physicochemical and biochemical quality characteristics of ‘Malas Saveh’ pomegranate grown under orchard conditions. The findings provide new insights into the role of Se as a sustainable agronomic biofortification strategy for improving both fruit quality and nutritional value.

2. Materials and Methods

2.1. Plant Material, Experimental Site, and Selenium Treatments

The experiment was conducted during the 2022 and 2023 growing seasons in a commercial pomegranate orchard located in Saveh, Markazi Province, Iran (35°01′ N, 50°21′ E; approximately 979 m above sea level). The region is characterized by a hot semi-arid climate (Köppen classification BSh), with an average annual precipitation of approximately 94 mm and summer temperatures reaching up to 38 °C. The orchard soil had a sandy loam texture.

Eleven-year-old pomegranate trees (*Punica granatum* L. cv. ‘Malas Saveh’), planted in 2011 at a spacing of 3 × 4 m, were used in this study. Trees were trained to an open-center system and managed according to standard commercial orchard practices, including drip irrigation, pruning, fertilization, and integrated pest management, following the recommendations of [2] and CABI (2020). Only healthy trees with uniform vigor, comparable fruit load, and no visible symptoms of pests or diseases were selected for the experiment.

The experiment was arranged in a randomized complete block design (RCBD) with three replications. Selenium (Se) was applied as sodium selenate (Na₂SeO₄; Sigma-Aldrich, St. Louis, MO, USA). In 2022, the treatments consisted of 0, 2, 4, and 6 mg L^{−1} Se, whereas in 2023 the concentration range was expanded to 0, 6, 8, and 10 mg L^{−1} based on the results obtained during the first growing season. The 6 mg L^{−1} treatment was retained as the reference concentration because it produced the most favorable responses during the initial screening experiment.

Each treatment consisted of two trees per replicate, resulting in a total of 24 experimental trees each year. Foliar sprays were applied three times at monthly intervals, beginning at fruit set (6 June), using approximately 5 L of spray solution per tree and a handheld high-pressure sprayer to ensure uniform canopy coverage. Control trees were sprayed with distilled water following the same application schedule. No surfactants or additional adjuvants were added to the spray solutions.

Fully expanded leaves were collected from the middle portion of current-season shoots exactly 48 h after each foliar application for mineral nutrient analysis. Fruits were harvested at commercial maturity on 5 November 2022 and 12 November 2023. For each growing season, 400 fruits (100 fruits per treatment) were randomly collected across the three repli-

cations and transported to the Physiology Laboratory, Faculty of Agriculture, University of Tehran. Fruits were selected for uniformity in size and color and for the absence of visible defects before analysis. All physicochemical and biochemical determinations were performed immediately after harvest.

2.2. Fruit Yield and Physical Characteristics

At harvest, the total number of fruits per tree was recorded, and fruit yield was expressed as kilograms per tree (kg tree^{-1}). Representative fruit samples from each treatment were subsequently used for physicochemical, biochemical, and mineral nutrient analyses.

2.3. Determination of Macro- and Micronutrient Concentrations

Leaf and fruit samples collected from both Se-treated and control trees were analyzed for macro- and micronutrient concentrations according to the procedures described by Chapman and Pratt [23]. Samples were oven-dried at 60 °C until constant weight, finely ground, and subsequently digested prior to elemental analysis.

Phosphorus (P) and potassium (K) concentrations were determined using a flame photometer (PFP7, Jenway, UK), whereas magnesium (Mg), iron (Fe), zinc (Zn), and manganese (Mn) concentrations were quantified by flame atomic absorption spectrophotometry (FAAS; Unicam AA-929, Cambridge, The Netherlands).

Selenium concentrations in leaf and fruit tissues were determined following microwave-assisted nitric acid digestion using inductively coupled plasma–optical emission spectrometry (ICP-OES; Varian VGA 77, Palo Alto, CA, USA), according to the method described by Mimmo et al. [24].

2.4. Fruit Chemical and Biochemical Characteristics

Fruit soluble solids content (SSC) was measured immediately after harvest (day 0) at 25 °C using a portable refractometer (Model RF-40, Waltham, MA, USA) and expressed as °Brix [25].

Titrate acidity (TA) was determined at harvest by diluting 10 mL of freshly extracted juice with 90 mL of distilled water and titrating the mixture with 0.1 N NaOH to an endpoint of pH 8.2. Citric acid was considered the predominant organic acid for TA calculations [26].

Fresh arils intended for the determination of total phenolic content and antioxidant activity were immediately frozen in liquid nitrogen and stored at −80 °C until analysis to prevent enzymatic degradation.

For extraction, 5 g of frozen arils was homogenized in 15 mL of 80% methanol using an analytical homogenizer and centrifuged at 10,000 rpm for 15 min at 4 °C. The resulting supernatant was collected and used for subsequent analyses.

Total phenolic content was determined using the Folin–Ciocalteu method, whereas antioxidant activity was evaluated using the DPPH radical scavenging assay according to Zhang et al. [27].

Ascorbic acid content was determined at harvest according to the 2,6-dichlorophenolindophenol (DCPIP) titration method [28]. Briefly, 5 g of frozen arils was extracted with 15 mL of 3% metaphosphoric acid and centrifuged at 10,000 rpm for 10 min at 4 °C. The extract was titrated with DCPIP solution until a stable pale-pink endpoint was obtained.

Total anthocyanin content was determined at harvest using the pH differential method described by Bucchini et al. [29]. Absorbance was measured at 510 and 700 nm after mixing diluted juice separately with potassium chloride buffer (0.025 M, pH 1.0) and sodium acetate buffer (0.4 M, pH 4.5). Anthocyanin concentration was calculated according to the standard equation described by Bucchini et al. [29]. Absorbance readings were recorded at 510 and 700 nm using distilled water as a blank after mixing 1 mL of diluted juice separately

with potassium chloride buffer (0.025 M, pH 1.0) and sodium acetate buffer (0.4 M, pH 4.5). Total anthocyanin concentration was calculated using the following equation:

$$\text{Anthocyanin content} = \frac{A \times MW \times DF \times 1000}{\epsilon \times l}$$

where $A = (A_{510} - A_{700})_{\text{pH}1.0} - (A_{510} - A_{700})_{\text{pH}4.5}$, MW = molecular weight of cyanidin-3-glucoside (449.2 g mol^{-1}), DF = dilution factor, ϵ = molar extinction coefficient ($26,900 \text{ L mol}^{-1} \text{ cm}^{-1}$), and l = path length (1 cm).

A_{510} pH 1.0 and A_{700} pH 1.0 are the absorbances at 510 nm and 700 nm in pH 1.0 buffer.

2.5. Determination of Antioxidant Enzyme Activities and Oxidative Stress Markers

All enzyme extractions and oxidative stress determinations were performed immediately after harvest using either fresh arils or samples previously frozen in liquid nitrogen.

Superoxide dismutase (SOD; EC 1.15.1.1) activity was determined by measuring the inhibition of nitroblue tetrazolium (NBT) photoreduction at 560 nm according to Tiwari et al. [30].

Catalase (CAT; EC 1.11.1.6) activity was determined by monitoring hydrogen peroxide decomposition at 240 nm [31].

Peroxidase (POD; EC 1.11.1.7) activity was quantified based on guaiacol oxidation at 470 nm, whereas polyphenol oxidase (PPO; EC 1.14.18.1) activity was determined using pyrocatechol as substrate and measuring absorbance at 420 nm [32].

Phenylalanine ammonia-lyase (PAL; EC 4.3.1.24) activity was assayed by monitoring the formation of cinnamic acid from L-phenylalanine at 290 nm [31].

Ascorbate peroxidase (APX; EC 1.11.1.11) activity was determined according to Corpas et al. [33] by monitoring the oxidation of ascorbic acid at 290 nm.

Hydrogen peroxide (H_2O_2) concentration was determined spectrophotometrically using titanium chloride reagent according to Zhu et al. [34]. Malondialdehyde (MDA) concentration and electrolyte leakage were also determined as indicators of oxidative damage and membrane integrity.

2.6. Statistical Analysis

Prior to statistical analysis, the assumptions of normality and homogeneity of variances were evaluated using the Shapiro–Wilk and Levene’s tests, respectively. As all datasets satisfied these assumptions ($p > 0.05$), no data transformation was required. If these assumptions had not been satisfied, appropriate data transformations or non-parametric statistical methods would have been considered.

Data were analyzed separately for each growing season using analysis of variance (ANOVA) according to a randomized complete block design (RCBD) with SAS software (version 9.4; SAS Institute Inc., Cary, NC, USA). Treatment means were compared using Tukey’s honestly significant difference (HSD) test at the 5% significance level ($p \leq 0.05$). The growing seasons were analyzed independently because different selenium concentration ranges were evaluated in 2022 and 2023.

Principal component analysis (PCA) was performed using R software (version 4.3.2; R Core Team, Vienna, Austria) to investigate the relationships between selenium treatments and mineral nutrient concentrations in leaves and fruits. PCA biplots were generated to visualize the associations among treatments and mineral variables based on the first two principal components.

3. Results

3.1. Fruit Yield and Selenium Accumulation

Foliar selenium (Se) application significantly enhanced fruit yield and selenium accumulation in both leaves and fruits during the two consecutive growing seasons (Tables 1 and 2). In 2022, fruit yield increased progressively from 27.12 kg tree⁻¹ in the control treatment to 34.15 kg tree⁻¹ following application of 6 mg L⁻¹ Se, representing an increase of approximately 26%. Likewise, the number of fruits per tree increased from 107 in the control to 119 under the highest Se concentration evaluated during the first season.

Table 1. Influence of the foliar spraying of Se, on Total fruit weight, Total number of fruits, and Leaf Se content, Fruit Se content of fruits pomegranate (*Punica granatum* L. CV. Malase Saveh) in the seasons of 2022.

Treatments	Total Fruit Weight (kg tree ⁻¹)	Total Number of Fruits (tree ⁻¹)	Leaf Se Content (µg Se kg ⁻¹ DW)	Fruit Se Content (µg Se kg ⁻¹ DW)
Control	27.118 ± 1.720 d	107.00 ± 1.15 c	17 ± 0.33 d	0.02 ± 0.03 d
2 mg/L Se	29.165 ± 1.730 c	112.00 ± 1.28 b	120 ± 1.73 c	58.00 ± 0.88 c
4 mg/L Se	32.883 ± 1.730 b	118.67 ± 1.17 ab	210 ± 2.33 b	115.00 ± 0.57 b
6 mg/L Se	34.145 ± 1.730 a	119.00 ± 1.18 a	250 ± 1.15 a	125.00 ± 1.45 a

Values are expressed as mean ± SE of three replicates ($n = 3$). Means followed by different lowercase letters within the same column differ significantly according to Tukey's HSD test ($p \leq 0.05$).

Table 2. Influence of the foliar spraying of Se, on Total fruit weight, Total number of fruits, and Leaf Se content, Fruit Se content of fruits pomegranate (*Punica granatum* L. CV. Malase Saveh) throughout 2023.

Treatments	Total Fruit Weight (kg tree ⁻¹)	Total Number of Fruits (tree ⁻¹)	Leaf Se Content (µg Se kg ⁻¹ DW)	Fruit Se Content (µg Se kg ⁻¹ DW)
Control	26.187 ± 1.310 d	101.667 ± 1.180 c	15 ± 0.23 d	0.1 ± 0.01 d
6 mg/L Se	33.520 ± 1.260 c	120.000 ± 2.770 b	232 ± 1.25 c	101.00 ± 0.93 c
8 mg/L Se	35.297 ± 1.560 b	130.000 ± 2.400 a	275 ± 1.82 b	142.00 ± 1.06 b
10 mg/L Se	37.670 ± 1.520 a	132.333 ± 2.420 a	320 ± 2.53 a	185.00 ± 1.49 a

Values are expressed as mean ± SE of three replicates ($n = 3$). Means followed by different lowercase letters within the same column differ significantly according to Tukey's HSD test ($p \leq 0.05$).

Foliar Se application also resulted in a marked increase in tissue Se concentrations. Leaf Se concentration increased from 17 to 250 µg kg⁻¹ DW, whereas fruit Se concentration increased from 0.02 to 125 µg kg⁻¹ DW, confirming the effectiveness of foliar Se biofortification.

During the 2023 growing season, increasing Se concentrations further enhanced both fruit productivity and tissue Se accumulation. Fruit yield increased from 26.19 kg tree⁻¹ in the control treatment to 37.67 kg tree⁻¹ following application of 10 mg L⁻¹ Se, whereas fruit number increased from 101.7 to 132.3 fruits tree⁻¹. Maximum Se concentrations of 320 µg kg⁻¹ DW in leaves and 185 µg kg⁻¹ DW in fruits were recorded in the 10 mg L⁻¹ treatment. However, fruit number did not differ significantly between the 8 and 10 mg L⁻¹ treatments, suggesting that the response approached a plateau within the tested concentration range.

3.2. Fruit Physicochemical and Biochemical Characteristics

Foliar Se application significantly improved several physicochemical and biochemical characteristics of pomegranate fruits during both growing seasons (Figures 1 and 2). Compared with the control treatment, Se application increased titratable acidity (TA), sol-

uble solids content (SSC), vitamin C concentration, total phenolic content, anthocyanin concentration, and antioxidant activity.

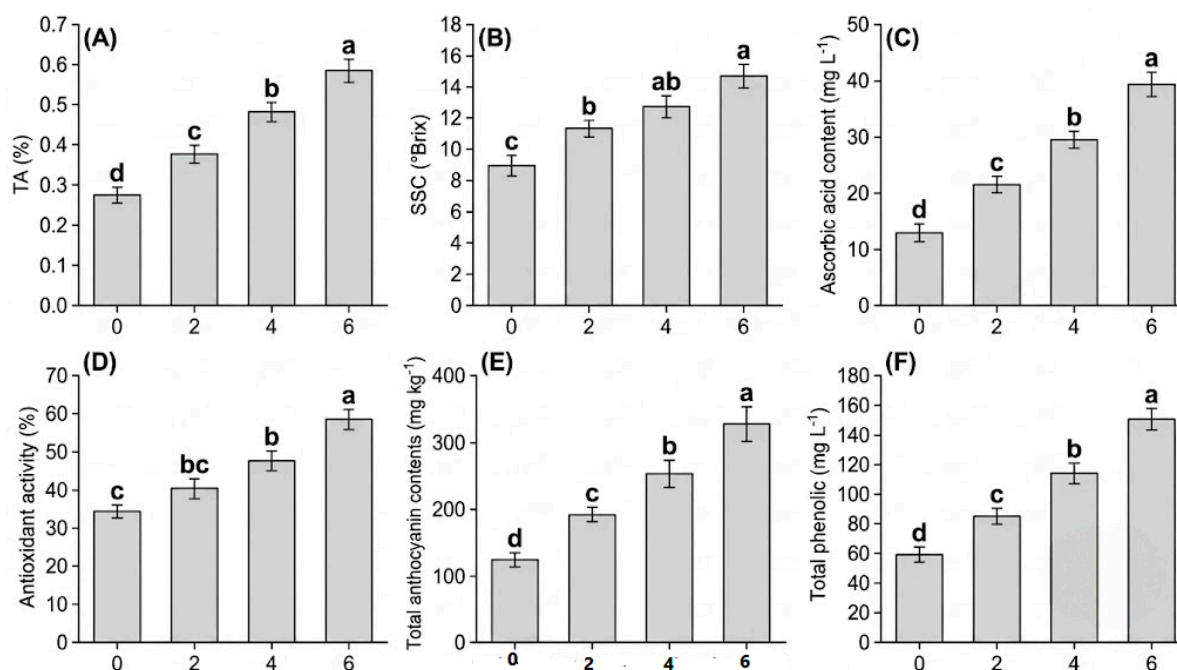


Figure 1. Impact of applying foliar selenium (Se) at varying concentrations on the pomegranate's (*Punica granatum* L.) titratable acidity (TA) (A), soluble solid content (SSC) (B), ascorbic acid content (C), antioxidant activity (D), anthocyanin contents (E), and total phenolic (F). The mean values of three replicates $\pm$ standard error are represented in the data for Malase Saveh during the 2022 seasons. Means followed by different lowercase letters differ significantly according to.

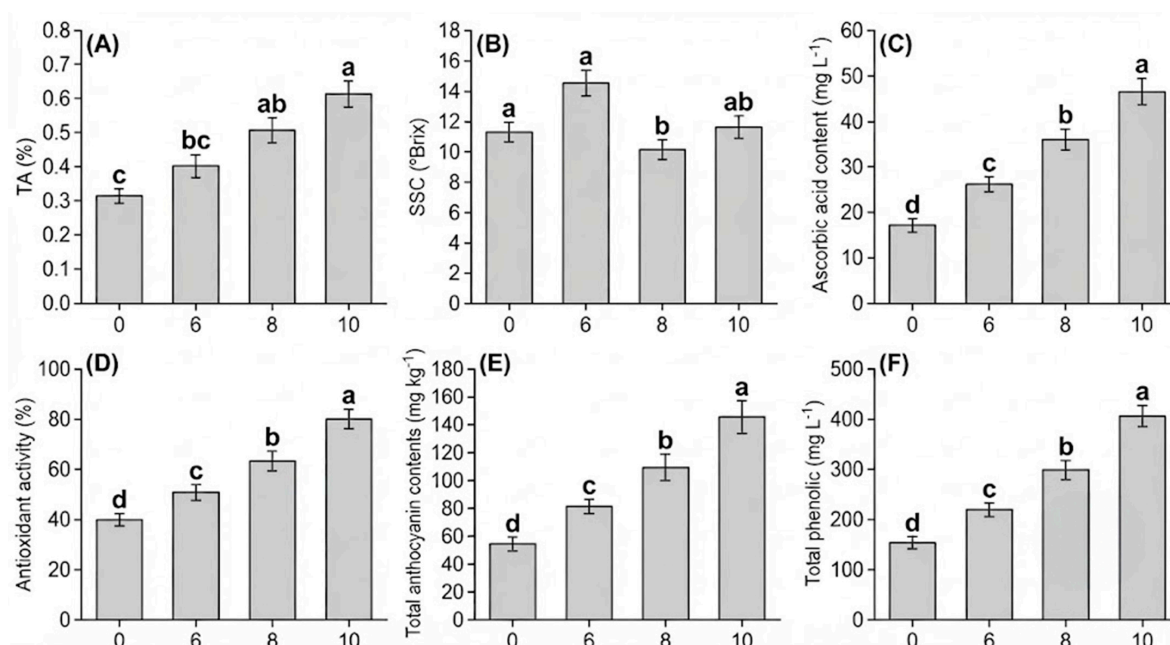


Figure 2. Titratable acidity (TA) (A), soluble solid content (SSC) (B), ascorbic acid content (C), antioxidant activity (D), anthocyanin contents (E), and total phenolic (F) of pomegranates (*Punica granatum* L.) are all affected by foliar selenium (Se) application at varying concentrations. cv "Malase Saveh") in the seasons of 2023. The data are the averages of three replicates plus standard error. Means followed by different lowercase letters differ significantly according to Tukey's HSD test ($p \leq 0.05$).

In 2022, the 6 mg L⁻¹ Se treatment produced the highest values for SSC, vitamin C, antioxidant activity, anthocyanin concentration, and total phenolic content (Figure 1).

During the 2023 growing season, increasing Se concentrations further improved most fruit quality parameters. The 10 mg L⁻¹ Se treatment resulted in the highest values for TA, antioxidant activity, anthocyanin concentration, and total phenolic content. In contrast, SSC showed a different response pattern. The highest SSC was recorded in fruits treated with 6 mg L⁻¹ Se, although this value did not differ significantly from those of the control and 10 mg L⁻¹ Se treatments. The 8 mg L⁻¹ Se treatment produced significantly lower SSC than the other treatments (Figure 2B).

Overall, foliar Se application consistently enhanced the nutritional quality and antioxidant potential of pomegranate fruits, although the response varied among individual quality attributes.

3.3. Oxidative Stress Indicators

Foliar Se application markedly reduced oxidative stress in pomegranate fruits during both growing seasons (Figures 3 and 4). Hydrogen peroxide (H₂O₂) concentrations decreased progressively with increasing Se concentrations, with the lowest values recorded in fruits treated with 6 mg L⁻¹ Se in 2022 and 10 mg L⁻¹ Se in 2023 (Figure 3). In contrast, control fruits consistently exhibited the highest H₂O₂ concentrations.

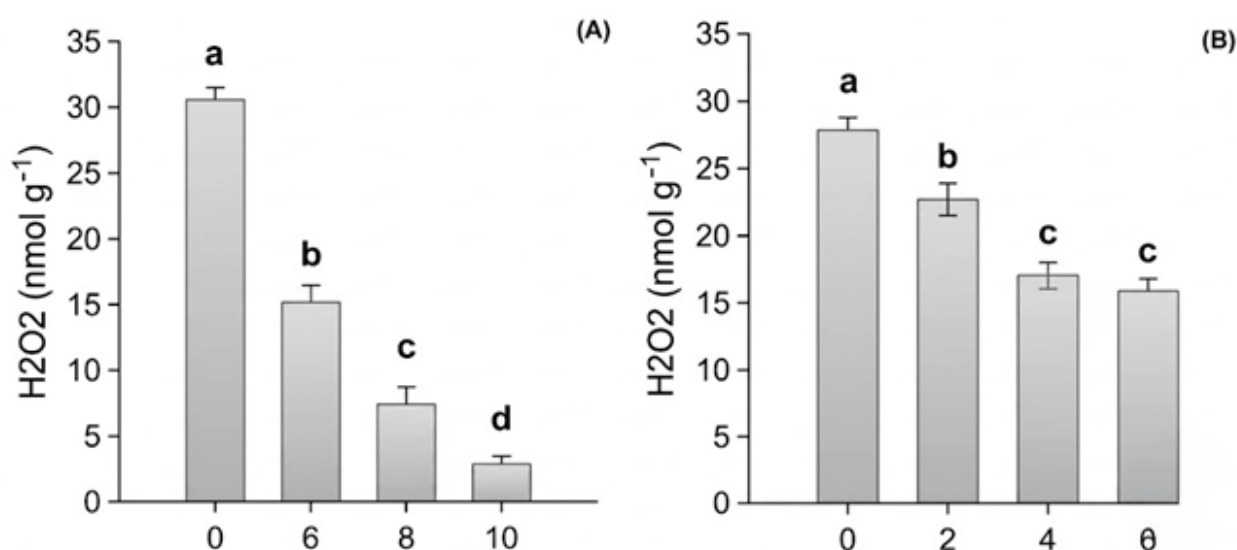


Figure 3. Impact of foliar application of selenium (Se) at varying concentrations on pomegranate (*Punica granatum* L.) H₂O₂ (A,B). cv “Malase Saveh”) in the seasons of 2022–2023. The data are the averages of three replicates $\pm$ standard error. Means followed by different lowercase letters differ significantly according to Tukey’s HSD test ($p \leq 0.05$).

A similar trend was observed for malondialdehyde (MDA) concentration and electrolyte leakage (Figure 4). Both parameters declined significantly following Se application, with the greatest reductions observed at the highest Se concentrations evaluated in each growing season. These results indicate that foliar Se application effectively alleviated oxidative damage and improved membrane stability in pomegranate fruits.

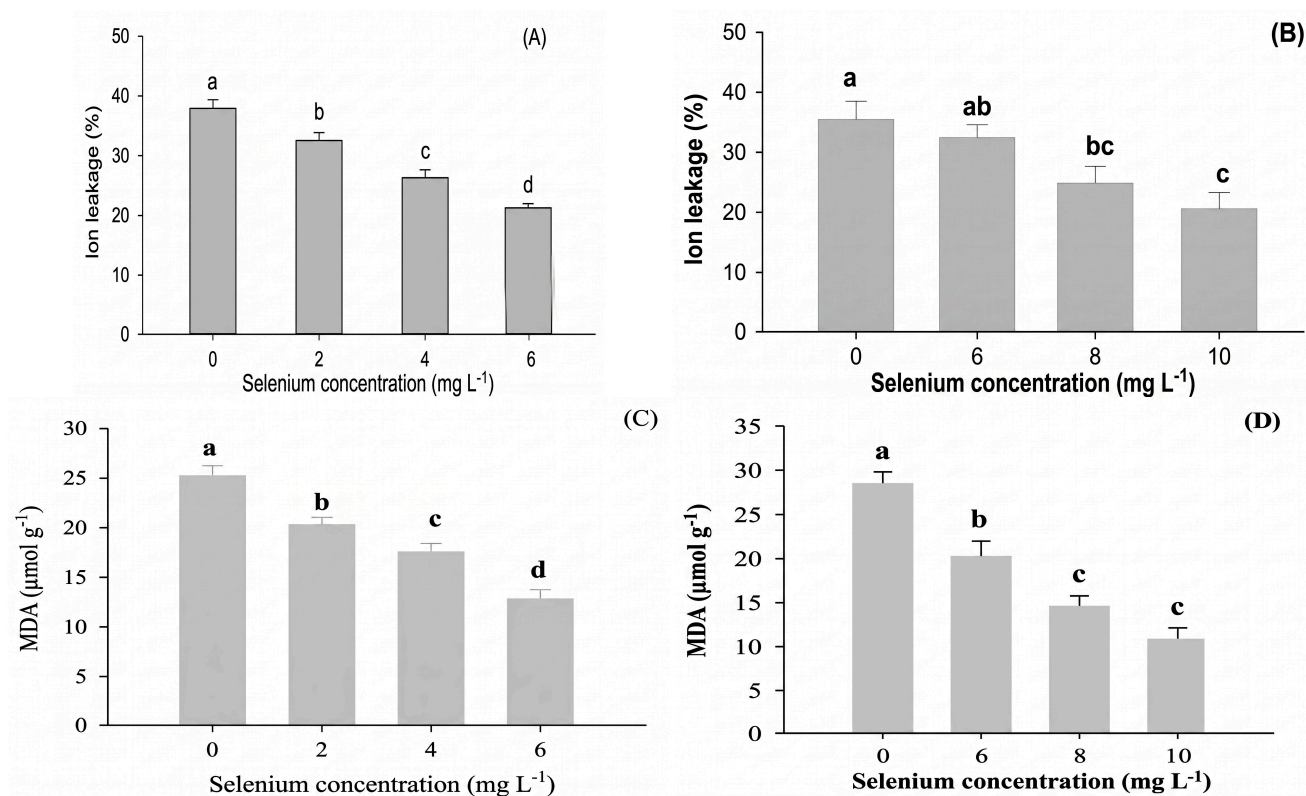


Figure 4. Malondialdehyde (MDA) content (C,D) and ion leakage percentage (A,B) of pomegranates (*Punica granatum* L.) following foliar selenium application (Se) application at varying concentrations. Data are the mean values of three replicates $\pm$ standard error for Malase Saveh during the 2022–2023 seasons. Means followed by different lowercase letters differ significantly according to Tukey's HSD test ($p \leq 0.05$).

3.4. Macro- and Micronutrient Concentrations

Principal component analysis (PCA) demonstrated that foliar Se application substantially modified the mineral nutrient composition of pomegranate leaves and fruits during both growing seasons (Figure 5). The first principal component explained 95.1% and 97.3% of the total variation in 2022 and 2023, respectively, indicating that Se treatments accounted for most of the variability in mineral nutrient composition.

The PCA biplots revealed strong positive associations between Se treatments and the accumulation of nitrogen (N), phosphorus (P), potassium (K), iron (Fe), zinc (Zn), and selenium (Se) in both leaves and fruits. In contrast, manganese (Mn) was consistently positioned opposite the Se treatment vectors, indicating a negative association between Se application and Mn accumulation.

The 10 mg L⁻¹ Se treatment was closely associated with the highest concentrations of Se, K, P, and Zn, whereas Mn concentrations were lowest under this treatment (Figure 5). These results demonstrate a clear shift in nutrient composition following foliar Se application.

3.5. Antioxidant Enzyme Activities

Foliar Se application significantly enhanced the activities of antioxidant enzymes in pomegranate fruits during both growing seasons (Figures 6 and 7). In 2022, the activities of superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), phenylalanine ammonia-lyase (PAL), and ascorbate peroxidase (APX) increased progressively with increasing Se concentration, whereas polyphenol oxidase (PPO) activity decreased. The 6 mg L⁻¹ Se

treatment consistently produced the highest activities of the antioxidant enzymes evaluated during the first growing season.

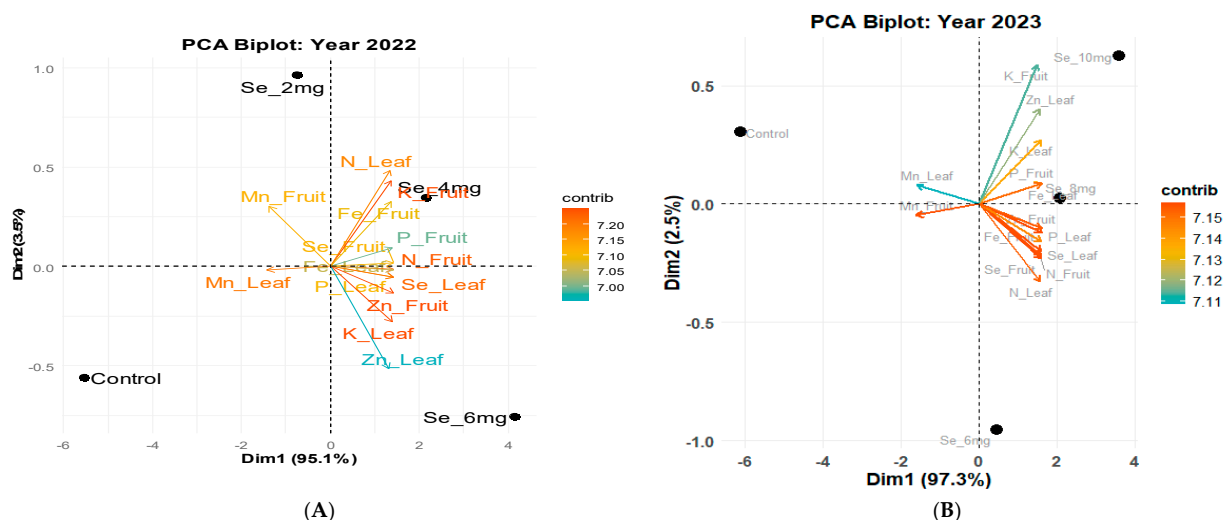


Figure 5. Principal component analysis (PCA) biplots showing the relationships between foliar selenium (Se) treatments and mineral nutrient concentrations in pomegranate leaves and fruits during (A) the 2022 season (treatments: 0, 2, 4, and 6 mg L⁻¹ Se) and (B) the 2023 season (treatments: 0, 6, 8, and 10 mg L⁻¹ Se). The first two dimensions (Dim1 and Dim2) account for 95.1% and 97.3% of the total variance for each year, respectively. Vectors represent the mineral elements (N, P, K, Fe, Zn, Mn, and Se), where the direction and length of the arrows indicate the strength of correlation with specific Se treatments. Color intensity of the vectors represents the contribution (contrib) of each variable to the principal components. Note the consistent synergistic clustering of N, P, K, Fe, Zn, and Se with higher Se dosages, contrasted by the antagonistic positioning of Mn vectors in the opposite quadrants.

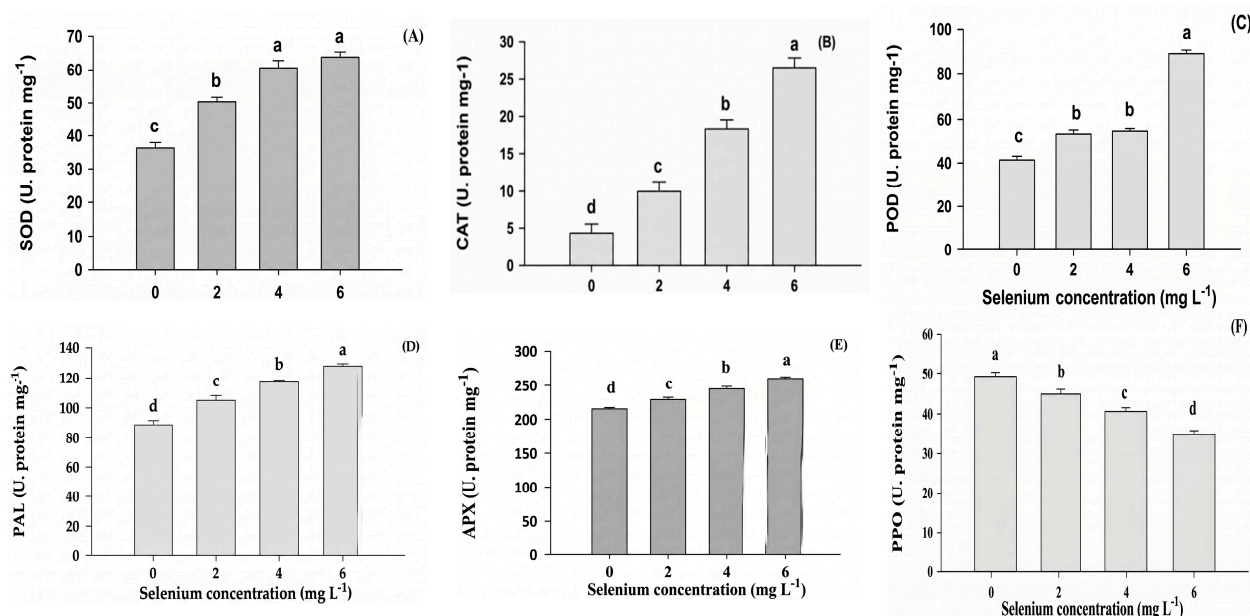


Figure 6. Impact of applying foliar selenium (Se) at varying concentrations on the activities of “pomegranate (*Punica granatum* L.)” enzymes, including superoxide dismutase (SOD) (A), catalase (CAT) (B), peroxidase activity (POD) (C), PAL activity (D), ascorbate peroxidase (E), and PPO activity (F). CV. Malase Saveh) in the seasons of 2022. The data are the averages of three replicates plus standard error. Means followed by different lowercase letters differ significantly according to Tukey's HSD test ($p \leq 0.05$).

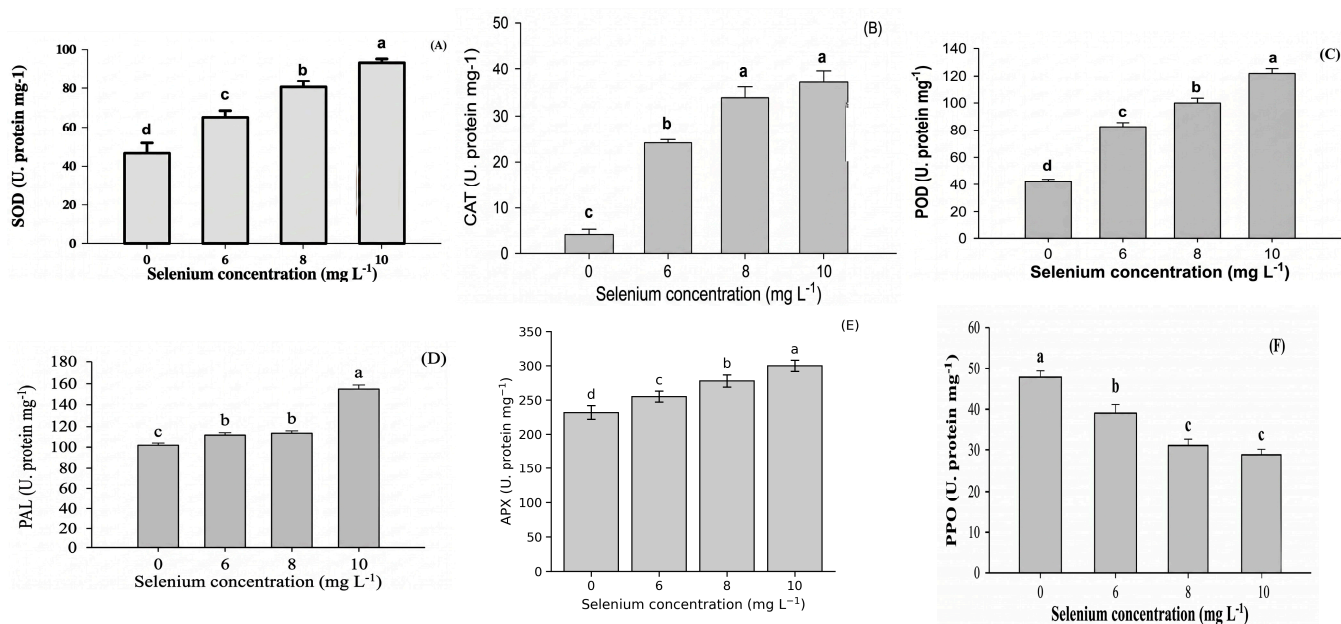


Figure 7. Impact of applying foliar selenium (Se) at varying concentrations on the activities of “pomegranate (*Punica granatum* L.)” enzymes, including superoxide dismutase (SOD) (A), catalase (CAT) (B), peroxidase activity (POD) (C), PAL activity (D), ascorbate peroxidase (E), and polyphenol oxidase activity (PPO) (F). CV. Malase Saveh) in the seasons of 2023. The data are the averages of three replicates plus standard errors. Means followed by different lowercase letters differ significantly according to Tukey’s HSD test ($p \leq 0.05$).

A similar response was observed in 2023, with the 10 mg L⁻¹ Se treatment producing the highest CAT, POD, SOD, PAL, and APX activities (Figure 7). Compared with the control treatment, CAT activity increased approximately ninefold, whereas POD and SOD activities increased by approximately two- to threefold. Conversely, PPO activity declined significantly following Se application.

The lowest PPO activity was recorded in the 6 mg L⁻¹ Se treatment in 2022 and in the 8 and 10 mg L⁻¹ Se treatments in 2023, with no significant differences between the latter two treatments. Likewise, no significant differences were observed between the 8 and 10 mg L⁻¹ Se treatments for several antioxidant enzymes, indicating that enzyme activities approached a plateau at higher Se concentrations.

4. Discussion

The present study demonstrates that foliar selenium (Se) application effectively improved pomegranate productivity, fruit nutritional quality, antioxidant metabolism, and mineral nutrient balance over two consecutive growing seasons. Selenium application increased fruit yield, promoted Se accumulation in both leaves and fruits, enhanced antioxidant capacity, and improved the concentrations of several essential mineral nutrients, while simultaneously reducing oxidative stress. Collectively, these findings highlight the multifunctional role of Se in plant physiology and support its use as an effective strategy for agronomic biofortification in pomegranate production.

The positive effects of foliar Se application on fruit yield indicates that selenium promoted reproductive development and fruit growth under orchard conditions. Yield improvement was most evident at 6 mg L⁻¹ during the first growing season and 10 mg L⁻¹ during the second, suggesting that pomegranate trees responded positively to increasing Se availability within the tested concentration range. Comparable responses have been reported in jujube, strawberry, tomato, and grape, where Se enhanced photosynthetic performance, carbon assimilation, and tolerance to environmental stresses [35–41].

Several physiological mechanisms may explain these responses. Selenium has been reported to protect chloroplast ultrastructure, improve photosynthetic efficiency, reduce oxidative damage, and enhance carbohydrate production, thereby increasing the availability of assimilates for fruit development [42–46]. The progressive increase in Se concentration observed in both leaves and fruits further confirms the high efficiency of foliar application as a biofortification strategy in pomegranate.

Foliar Se application markedly improved fruit quality by increasing soluble solids content, titratable acidity, vitamin C, total phenolic compounds, anthocyanins, and antioxidant activity. These improvements are particularly relevant because they directly influence fruit nutritional value, sensory characteristics, and consumer acceptance.

The increase in soluble solids content is likely associated with enhanced photosynthetic efficiency and carbohydrate accumulation resulting from improved physiological performance. Similar improvements have been reported in mango, tomato, apple, and strawberry following foliar Se application [20,42,47,48]. Likewise, the higher titratable acidity observed in Se-treated fruits may reflect delayed degradation of organic acids during fruit maturation, contributing to a more balanced flavor profile and potentially improved postharvest quality.

The substantial increases in total phenolic compounds, anthocyanins, vitamin C, and antioxidant activity indicate that Se stimulated secondary metabolism in pomegranate fruits. Selenium has been shown to activate the phenylpropanoid pathway, thereby promoting the biosynthesis of phenolic compounds and flavonoids in several horticultural crops [18,47,49].

The enhanced activity of phenylalanine ammonia-lyase (PAL) observed in the present study likely contributed to the greater accumulation of phenolic compounds and anthocyanins. Because anthocyanins are major contributors to both fruit coloration and antioxidant capacity in pomegranate, their increased accumulation represents an important improvement in overall fruit quality. Furthermore, the increase in vitamin C concentration supports previous reports indicating that Se contributes to maintaining cellular redox homeostasis and strengthening antioxidant metabolism [17,50].

Foliar Se application also markedly influenced mineral nutrient composition. Principal component analysis revealed strong positive associations between Se application and the accumulation of N, P, K, Fe, and Zn, whereas Mn exhibited an opposite distribution pattern. These findings agree with previous reports describing positive interactions between Se and several macro- and micronutrients [15,22,51–53].

The increased accumulation of nitrogen may be associated with enhanced nitrate assimilation and protein synthesis, whereas the higher Fe and Zn concentrations may reflect improved nutrient transport and greater protection of membrane transport systems under reduced oxidative stress. Although the mechanisms underlying these interactions remain incompletely understood, the present findings clearly demonstrate that Se application substantially modified the nutritional profile of pomegranate tissues.

A major finding of the present study was the pronounced enhancement of the antioxidant defense system following foliar Se application. Activities of CAT, SOD, POD, PAL, and APX increased markedly, whereas H₂O₂ concentration, MDA accumulation, electrolyte leakage, and PPO activity declined significantly. These coordinated responses indicate that Se effectively strengthened the enzymatic antioxidant machinery, thereby reducing oxidative damage and preserving cellular membrane integrity.

The observed increase in antioxidant enzyme activities is consistent with previous studies reporting that Se enhances reactive oxygen species (ROS) scavenging and maintains cellular redox homeostasis under both normal and stress conditions [31,44,48,53–56]. Catalase and APX are directly involved in H₂O₂ detoxification, whereas SOD constitutes the first line of enzymatic defense against superoxide radicals. Consequently, the simultaneous

activation of these enzymes provides an efficient antioxidant network capable of limiting oxidative injury and maintaining cellular function.

The reductions in MDA concentration and electrolyte leakage further support this interpretation, as both parameters are widely recognized indicators of lipid peroxidation and membrane damage. Collectively, these findings suggest that Se not only improves antioxidant metabolism but also enhances membrane stability, thereby contributing to improved physiological performance and fruit quality.

Beyond its physiological effects, foliar Se application has important practical implications for commercial pomegranate production. The simultaneous improvement in fruit yield, nutritional quality, antioxidant capacity, and Se biofortification indicates that Se fertilization may represent a valuable agronomic tool for producing fruits with enhanced market value and nutritional benefits.

From a human nutrition perspective, Se-enriched pomegranate fruits may contribute to increasing dietary selenium intake in regions where Se deficiency remains prevalent. At the same time, improved antioxidant capacity and membrane stability may enhance postharvest performance, thereby reducing quality losses during storage and marketing. Consequently, Se biofortification has the potential to generate both economic and nutritional benefits throughout the production chain.

Despite the promising results obtained in the present study, several limitations should be acknowledged. First, the experiment included only six trees per treatment (two trees per replicate, three replicates), which inevitably limits the statistical power of the study. Therefore, although significant treatment effects were detected, the present findings should be interpreted with caution and considered preliminary until validated in larger-scale experiments. Furthermore, the experiment was conducted using a single pomegranate cultivar under the environmental conditions of one production region in Iran. Consequently, the observed responses may vary among cultivars and under different climatic or soil conditions. In addition, the study evaluated Se application over two consecutive growing seasons but did not assess long-term effects on soil Se dynamics, repeated annual applications, or potential environmental impacts. Future multi-location trials including a larger number of experimental units are therefore required to confirm the robustness and wider applicability of the present findings.

5. Conclusions

The present study demonstrated that foliar selenium (Se) application effectively enhanced the productivity, nutritional quality, antioxidant metabolism, and mineral nutrient balance of 'Malas Saveh' pomegranate under orchard conditions. Selenium application significantly increased fruit yield, fruit number, and Se accumulation in both leaves and fruits, confirming the effectiveness of foliar Se biofortification.

In addition to improving productivity, Se application enhanced several important fruit quality attributes, including soluble solids content, titratable acidity, vitamin C, total phenolic compounds, anthocyanins, and antioxidant activity. Selenium also promoted the accumulation of essential mineral nutrients, particularly nitrogen, phosphorus, potassium, iron, and zinc, while reducing manganese concentrations, indicating that Se substantially influences mineral nutrient homeostasis in pomegranate.

Foliar Se application markedly strengthened the antioxidant defense system by increasing the activities of catalase (CAT), superoxide dismutase (SOD), peroxidase (POD), phenylalanine ammonia-lyase (PAL), and ascorbate peroxidase (APX), while simultaneously reducing hydrogen peroxide (H₂O₂), malondialdehyde (MDA), and electrolyte leakage. These responses indicate that Se effectively alleviated oxidative stress and improved

membrane stability, thereby contributing to enhanced physiological performance and fruit quality.

Among the evaluated treatments, 6 mg L⁻¹ Se was the most effective concentration during the first growing season, whereas 8–10 mg L⁻¹ Se produced the greatest overall responses during the second season. However, the absence of significant differences between the 8 and 10 mg L⁻¹ treatments for several measured variables suggests that the physiological response approached a plateau at higher Se concentrations.

A major strength of the present study is the comprehensive evaluation of Se effects on fruit productivity, mineral nutrient composition, antioxidant metabolism, oxidative stress indicators, and biofortification efficiency over two consecutive growing seasons under orchard conditions. These findings provide new evidence that foliar Se application simultaneously regulates mineral nutrient homeostasis and antioxidant metabolism, highlighting its multifunctional role in improving pomegranate performance.

Overall, foliar Se application represents a promising and sustainable agronomic strategy for producing high-quality, Se-enriched pomegranate fruits with improved nutritional and functional value. Future research should focus on validating these findings across different cultivars, environmental conditions, and production systems, while also evaluating the long-term effects of repeated Se applications on soil–plant interactions, fruit storage performance, and consumer health benefits.

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Abbreviations

The following abbreviations are used in this manuscript:

Abbreviation	Definition
APX	Ascorbate peroxidase
CAT	Catalase
DCPIP	2,6-Dichlorophenol indophenol
DPPH	2,2-Diphenyl-1-picrylhydrazyl

DW	Dry weight
FAAS	Flame atomic absorption spectrophotometry
Fe	Iron
H ₂ O ₂	Hydrogen peroxide
ICP-OES	Inductively coupled plasma–optical emission spectrometry
K	Potassium
MDA	Malondialdehyde
Mg	Magnesium
Mn	Manganese
N	Nitrogen
PAL	Phenylalanine ammonia-lyase
P	Phosphorus
PCA	Principal component analysis
POD	Peroxidase
PPO	Polyphenol oxidase
ROS	Reactive oxygen species
SOD	Superoxide dismutase
SSC	Soluble solids content
TA	Titrateable acidity
Zn	Zinc
Se	Selenium

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