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The application of selenium enhances salt stress tolerance of sesame plants through regulation of key metabolic responses

Hamideh Heydari¹, Fatemeh Zarinkamar^{1*}, Maryam Rezayian² and Bahram M. Soltani³

Abstract

Salinity stress severely limits sesame productivity. Although selenium (Se) can alleviate the effects of salinity in many crops, its role in sesame remains unclear. This study is the first to systematically evaluate the physiological, biochemical, and molecular responses of sesame to Se under salt stress, highlighting its potential to enhance tolerance and crop performance. Sesame plants (*Sesamum indicum* L.) were exposed to varying NaCl concentrations (0, 75, and 150 mM) with or without Se supplementation (50 mg L⁻¹). Selenium application significantly mitigated the adverse effects of salt stress by increasing whole-plant length, dry and fresh biomass, and enhancing photosynthetic pigments (chlorophyll *a*, chlorophyll *b*, and carotenoids), thereby promoting growth and biomass accumulation. Salt stress induced oxidative damage, evidenced by elevated hydrogen peroxide content; however, Se treatment reduced oxidative stress by increasing enzymatic antioxidant activities (SOD by 36% and CAT by 46%) and non-enzymatic antioxidants (flavonoids by 27%). Under saline conditions, Se also stimulated the biosynthesis of auxin, abscisic acid, and gibberellin. Exogenous Se application significantly decreased levels of palmitoleic, linoleic, oleic, linolenic, arachidic, behenic, and lignoceric acids under salt stress. Moreover, Se upregulated the salt stress-responsive gene Na⁺/H⁺ exchanger 1 (*NHX1*), improving ionic homeostasis. Multivariate analyses, including principal component analysis (PCA) and Pearson correlation, confirmed distinct treatment separations and revealed strong positive and negative correlations among physiological and stress-related traits. These findings underscore the comprehensive protective role of Se in enhancing salt stress tolerance in sesame by modulating growth, photosynthesis, antioxidant defense, hormone regulation, fatty acid composition, and ionic balance.

Keywords Antioxidant mechanism, Growth, Phytohormone, Salt stress, Selenium, *Sesamum indicum* L.

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Introduction

Sesamum indicum L., commonly known as sesame, is an ancient oilseed crop prized as a source of high-quality edible oil. It is predominantly cultivated in tropical and subtropical regions, particularly throughout Asia [1, 2]. This annual herbaceous plant belongs to the *Pedaliaceae* family [3, 4]. Its seeds serve as a valuable source of essential nutrients, including proteins, carbohydrates, dietary fiber, minerals, and oils. In addition, they are rich in lipid-soluble antioxidants—such as sesamin, sesamol, and sesamolol—that contribute significantly to human health and nutrition [5, 6]. Scientific evidence confirms that sesame oil can reduce cholesterol levels and blood pressure [7, 8]. Various parts of the plant are also utilized in traditional medicine. Sesame growth decreases under salt stress [9]. In our country, sesame is a culturally and economically important crop, widely cultivated for both edible oil and local food products, making it a key component of agricultural sustainability and rural livelihoods. Approximately 6.8 million hectares of agricultural land in Iran are affected by salinity, which reduces crop growth and productivity, highlighting the need to identify effective strategies to enhance plant tolerance to salinity [10, 11]. Different strategies comprising phytohormonal applications, organic amendments, biostimulants [12], nanoparticles, and nutritional balance can be effective for sustainable productivity of various crops, focusing on sufficient growth and higher yield [12, 13].

Salinity stress represents a major abiotic constraint that disrupts key plant processes and inhibits growth [14]. Its detrimental effects are primarily manifested as secondary osmotic and ionic stress. To withstand saline conditions and maintain development and productivity, plants deploy an array of physiological, biochemical, morphological, and molecular adaptive strategies [15–17]. These compensatory mechanisms involve the modulation of signaling pathways, maintenance of ionic homeostasis, osmotic adjustment, and activation of antioxidant systems. The adverse impacts on growth and development arise from two interconnected factors: ionic stress caused by the accumulation of toxic ions (Na^+ and Cl^-) and the concomitant depletion of essential ions (K^+ and Ca^{2+}), as well as osmotic stress, which impedes root water absorption.

A further consequence is the overproduction of reactive oxygen species (ROS), which, at high concentrations, can cause oxidative damage to proteins, lipids, and DNA, as indicated by elevated malondialdehyde (MDA) levels. Conversely, at low concentrations, ROS function as signaling molecules that initiate defense pathways. To counteract the deleterious effects of ROS, plants activate a sophisticated antioxidant defense system. This includes enzymatic antioxidants—such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase

(APX)—and non-enzymatic molecules like ascorbate and glutathione. These components are crucial for detoxifying ROS and preserving cellular integrity and metabolic function. Furthermore, plants accumulate compatible solutes for osmotic adjustment and rigorously regulate mineral ions to mitigate osmotic stress, thereby sustaining water and ion homeostasis at the cellular level [18–21].

The strategic application of micro- and macro-elements represents a key approach for mitigating abiotic stress in plants. Among these, selenium (Se) is recognized as a beneficial element that supports plant growth and influences various physiological and biochemical processes [22–25]. Even at low concentrations, Se significantly enhances the accumulation of osmolytes and fortifies antioxidant systems in plants facing abiotic stress conditions [26]. For instance, Handa et al. [27] demonstrated that Se application boosted the production of secondary metabolites in *Brassica juncea* L., while other research has confirmed its role in elevating the activity of key antioxidant enzymes [28]. Several studies have highlighted the beneficial effects of Se in mitigating salt stress in plants. Se has been shown to enhance growth, yield-related traits, and protein content in crops such as *Zea mays* under saline conditions. It improves salt tolerance by regulating photosynthetic capacity, maintaining ion homeostasis (especially Na^+ and K^+ balance), and boosting antioxidant enzyme activities that reduce oxidative damage. Additionally, Se contributes to better mineral nutrition by influencing nutrient uptake and transporter function, protecting photosynthetic pigments, and lowering ROS accumulation. These multifaceted roles of Se help plants maintain physiological stability and improve stress resilience under salinity [23, 29].

Given these documented positive effects across various plant species, we hypothesized that Se supplementation could ameliorate the detrimental impacts of salinity in sesame, which is vital for sustaining crop yield and quality in our country. Consequently, the principal objective of this study was to determine the efficacy of Se treatment in enhancing salinity stress tolerance in sesame plants by elucidating the underlying mechanisms, including the effects of Se on secondary metabolites, fatty acids, and phytohormone profiles under both saline-stressed and non-stressed conditions.

Materials and methods

Plant material and experimental design

Seeds of sesame (*Sesamum indicum* L. cv. Ultan) were obtained from the Seed and Plant Improvement Research Institute, Karaj, Iran. Seeds were sown in pots containing a 1:1 (v/v) mixture of peat and perlite, and seedlings were thinned to five uniform plants per pot. The plants were cultivated under controlled conditions (25 °C day / 18 °C

night) and irrigated with half-strength Hoagland's solution for 4 weeks. Salinity stress was applied using NaCl at concentrations of 0, 75, and 150 mM [30, 31]. The potential role of selenium (Se) was assessed by adding sodium selenate (Na_2SeO_4) at 50 mg L^{-1} to the growth medium every other day for 3 weeks. Additionally, the effects of sodium selenate at 0, 25, and 50 mg L^{-1} were evaluated under salinity stress in 50% Hoagland's solution. Only the 50 mg L^{-1} concentration enhanced growth and reduced MDA levels and was thus selected for further investigation. Treatments were conducted in three biological replicates. After 21 days, shoots and roots were harvested for growth, biochemical, and molecular analyses, with tissues dried or flash-frozen as appropriate (Fig. 1).

Assessment of plant growth parameters and leaf pigment contents

The Fresh Weight (FW) of shoots and roots was recorded immediately after harvest, and Dry Weight (DW) was obtained after oven-drying at 48°C for 72 h. Leaf Relative Water Content (RWC) was determined following the method of Weatherley [32] using the formula:

$$\text{RWC (\%)} = [(\text{FW} - \text{DW}) / (\text{SW} - \text{DW})] \times 100.$$

Chlorophyll and carotenoid contents were extracted with 80% (v/v) acetone, and absorbance was measured at 663.2, 646.8, and 470 nm using a Unico 2100 UV spectrophotometer (Dayton, NJ, USA). Concentrations were calculated according to the established protocol [33].

Assessment of proline and soluble sugar content

Leaf proline content was determined following the method of Bates et al. [34]. Fresh leaf tissue (0.1 g) was homogenized in 3% sulfosalicylic acid and centrifuged at $13,000 \times g$ for 20 min. The supernatant was reacted with ninhydrin and glacial acetic acid, the chromophore

was extracted, and absorbance was measured at 520 nm. Proline concentration was calculated using a standard curve prepared with 50, 100, 200, 400, and $800 \mu\text{g mL}^{-1}$ of L-proline.

Total soluble sugar content was determined using the phenol–sulfuric acid method of Dubois et al. [35]. Leaf tissue (0.05 g) was extracted with 1.5 mL distilled water, reacted with phenol and concentrated sulfuric acid, and absorbance was measured spectrophotometrically. Soluble sugar concentration was calculated from a standard curve prepared with 20, 40, 60, 80, and $100 \mu\text{g mL}^{-1}$ of glucose.

Measurement of H_2O_2 and MDA

Hydrogen peroxide (H_2O_2 Content)

The H_2O_2 concentration was determined following Velikova et al. [36]. About 0.1 g of leaf tissue was homogenized in 1 mL of 0.1% (w/v) TCA. After centrifugation, the supernatant was mixed with potassium phosphate buffer (pH 7.0) and 1 M potassium iodide (KI) solution, and the absorbance was measured at 390 nm. H_2O_2 concentration was calculated using a standard curve prepared with 50, 100, 200, 400, and $800 \mu\text{M H}_2\text{O}_2$. Lipid peroxidation was estimated by measuring MDA concentration following the method of Heath and Packer [37]. About 0.2 g of leaf tissue was homogenized in 2 mL of 0.1% (w/v) TCA, and after centrifugation, the supernatant was reacted with 0.5% (w/v) thiobarbituric acid (TBA) in 20% TCA. The mixture was heated at 95°C for 30 min, cooled, and centrifuged. The absorbance of the supernatant was measured at 532 and 600 nm, and MDA concentration was calculated from the difference in absorbance ($A_{532} - A_{600}$) using an extinction coefficient of $155 \text{ mM}^{-1} \text{ cm}^{-1}$.

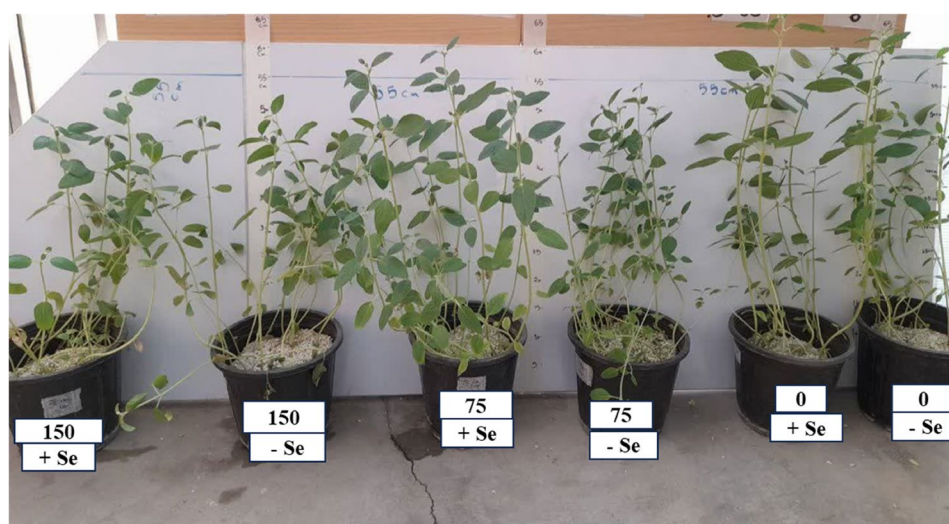


Fig. 1 Effect of 50 mg L^{-1} selenium on the morphology of sesame under salt stress (75 and 150 mM NaCl)

Antioxidant enzyme assay

For the analysis of total protein content and antioxidant enzyme activities, 0.1 g of leaf tissue was homogenized in ice-cold 50 mM potassium phosphate buffer (pH 7.8) containing 10 mM ethylenediaminetetraacetic acid (EDTA). The total soluble protein content of the extracts was quantified according to the method of Bradford [38] using bovine serum albumin (BSA) as a standard.

SOD activity

The activity of superoxide dismutase (SOD, EC 1.15.1.1) was measured according to [39] by assessing its ability to inhibit the photochemical reduction of nitroblue tetrazolium (NBT). The reaction mixture (3 mL) contained 50 mM potassium phosphate buffer (pH 7.8), 0.1 mM EDTA, 75 μ M NBT, 13 mM methionine, 2 μ M riboflavin, and 100 μ L of enzyme extract. The reaction was started by illumination for 16 min under 300 μ mol m⁻² s⁻¹ light. Absorbance was read at 560 nm. One unit of SOD activity was defined as the amount of enzyme causing 50% inhibition of NBT reduction, and results were expressed as U g⁻¹ protein.

CAT Activity: Catalase (CAT) Activity

Catalase (EC 1.11.1.6) activity was measured following Aebi [40] by monitoring H₂O₂ decomposition at 240 nm. The reaction contained 50 mM potassium phosphate buffer (pH 7.0), 3% H₂O₂, and 40 μ L of enzyme extract. Absorbance change was recorded for 1 min. One unit of CAT activity was defined as the amount of enzyme decomposing 1 μ mol H₂O₂ per minute, expressed as U mg⁻¹ protein.

Ascorbate peroxidase (APX) activity

APX (EC 1.11.1.11) activity was measured following Jebara et al. [41]. The reaction mixture contained 50 mM potassium phosphate buffer (pH 7.0), 0.5 mM ascorbic acid, 0.1 mM H₂O₂, and 40 μ L of enzyme extract. The decrease in absorbance at 290 nm over 1 min was used to track ascorbate oxidation. Activity was calculated using ϵ = 2.8 mM⁻¹ cm⁻¹ and expressed as U mg⁻¹ protein.

Glutathione S-Transferase (GST) activity

The activity of glutathione S-transferase (GST, EC 2.5.1.18) was determined following Habig et al. [42], based on the conjugation of glutathione (GSH) with 1-chloro-2,4-dinitrobenzene (CDNB). The reaction mixture contained 2 mM potassium phosphate buffer (pH 6.25), 1 mM CDNB, 1 mM GSH, and enzyme extract. The increase in absorbance due to GS-DNB conjugate formation was recorded at 340 nm for 3 min. Activity was calculated using an extinction coefficient of 9.6 mM⁻¹ cm⁻¹ and expressed as U g⁻¹ protein, where one unit equals the formation of 1 μ mol product per minute.

Determination of non-enzymatic antioxidant components

Quantification of total phenolics, flavonoids, and flavonols

Non-enzymatic antioxidant components were extracted from leaf samples for the quantification of total phenolic, flavonoid, and flavonol contents by following established protocols [43]. Briefly, 0.3 g of fresh leaf tissue was homogenized in 4 mL of 80% (v/v) aqueous methanol.

Total phenolic content The total phenolic content was determined using the Folin-Ciocalteu method [44]. An aliquot of 0.1 mL of the methanolic extract was mixed with 2.5 mL of 10% (v/v) Folin-Ciocalteu reagent and neutralized with 2 mL of 7% (w/v) sodium carbonate solution. The mixture was incubated in the dark for 60 min at room temperature, after which the absorbance was measured at 765 nm. The results were expressed as milligrams of gallic acid equivalent per gram of fresh weight (mg GAE g⁻¹ FW).

Total flavonoid content The total flavonoid content was determined following Chang et al. [45] with slight modifications. Briefly, 0.5 mL of extract was mixed with 1.5 mL methanol, 0.1 mL of 10% AlCl₃, 0.1 mL of 1 M potassium acetate, and 2.8 mL distilled water. After incubation at room temperature for 30 min, absorbance was recorded at 415 nm. Flavonoid concentration was calculated using a quercetin standard curve and expressed as mg quercetin equivalent per g fresh weight (mg QE g⁻¹ FW).

Anthocyanin content The anthocyanin content was extracted by homogenizing leaf tissue in methanol acidified with 0.3% (v/v) hydrochloric acid and incubating at 25 °C for 24 h in the dark [46]. The absorbance of the supernatant was measured at 550 nm. The anthocyanin concentration was calculated using the molar extinction coefficient of 33,000 M⁻¹ cm⁻¹ (or 33 cm² mol⁻¹) and expressed as micromoles per gram of fresh weight (μ mol g⁻¹ FW).

Measurement of phenolic acids and flavonoid compounds by HPLC

Extraction and analysis of phenolic acids Phenolic acids were extracted and analyzed according to the method of [47] with minor modifications. In brief, 0.5 g of fresh leaf tissue was homogenized in 1 mL methanol and centrifuged. The residue was re-extracted with 4 mL acetonitrile, defatted using 2 mL n-hexane, evaporated under nitrogen, and re-dissolved in 500 μ L methanol for HPLC analysis. Separation was performed on a Waters e2695 HPLC system with a Knauer C18 column (250 $\times$ 4.6 mm, 5 μ m) using a gradient of 2% acetic acid (A) and methanol (B) from 5% to 100% B over 50 min, at 1.0 mL min⁻¹ and 25 °C. Detection was carried out at 278 and 300 nm, and

compounds were quantified against external standards, expressed as mg g^{-1} FW.

Extraction and analysis of flavonoids Flavonoids were extracted following Keinänen et al. [48]. Fresh leaf tissue (0.5 g) was homogenized in 40% (v/v) aqueous methanol with 0.5% acetic acid and extracted for 3 h with shaking. The supernatant was filtered for HPLC analysis. Separation was performed as described by Gudej & Tomczyk [49] using the same HPLC system. The mobile phase consisted of deionized water with 0.01% phosphoric acid (A) and acetonitrile (B) with a gradient from 18% to 67% B, returning to 18% B. The flow rate was 0.8 mL min^{-1} at 25°C . Flavonoids were identified by retention times and UV spectra (280 and 350 nm) compared to standards and quantified using external standard curves, expressed as mg g^{-1} FW.

Measurement of PAL activity

PAL activity The activity of phenylalanine ammonia-lyase (PAL, EC 4.3.1.24) was measured following Berner et al. [50]. The reaction mixture contained 50 μL enzyme extract and 1 mL of 0.1 M boric acid buffer (pH 8.8) with 150 mM L-phenylalanine. After incubation at 40°C for 30 min, the reaction was stopped with 0.1 mL of 6 M HCl, and the formation of trans-cinnamic acid was monitored at 290 nm. Activity was calculated using a molar extinction coefficient of $10,000 \text{ M}^{-1} \text{ cm}^{-1}$. One unit of PAL activity corresponds to 1 μmol trans-cinnamic acid produced per min, expressed as $\text{U min}^{-1} \text{ mg}^{-1}$ protein.

Measurement of phytohormones

Endogenous phytohormones Phytohormones were extracted from 0.2 g fresh leaf tissue in 3 mL absolute methanol and incubated overnight at 4°C . After centrifugation, the supernatant was evaporated under nitrogen and re-dissolved in 20 μL methanol for HPLC analysis [51]. Quantification was performed using a Knauer HPLC system with a reverse-phase C18 column following Delavar et al. [52]. The mobile phase was a water-acetonitrile gradient with 0.1% acetic acid at 0.6 mL min^{-1} , and detection was at 220 nm. Compounds were identified by retention

times of standards and quantified using external calibration curves, expressed as ng g^{-1} FW.

Determination of fatty acid composition

Fatty acid composition

Fatty acids were analyzed by gas chromatography after transesterification to fatty acid methyl esters (FAMES). About 0.1 g of fresh leaf tissue was heated at 100°C for 1 h in 1 mL methanol/acetyl chloride (20:1, v/v), then FAMES were extracted with 1 mL n-hexane [53]. Separation and quantification were performed using a Shimadzu GC-17 A equipped with a flame ionization detector (FID) and a capillary column (e.g., DB-Wax). Injector and detector temperatures were set at 250°C , with the oven program as follows: 140°C for 5 min, ramped at 4°C min^{-1} to 240°C , then held for 10 min. Helium was used as the carrier gas. FAMES were identified by comparison to standards and expressed as a percentage of total fatty acids.

RNA extraction, cDNA synthesis, and qRT-PCR analysis

Gene expression analysis

The relative expression of Na^+/H^+ exchanger 1 (*NHX1*) and phenylalanine ammonia-lyase (PAL) was analyzed by qRT-PCR, using actin (ACT) as an internal reference. Since selenium combined with 75 mM NaCl had the greatest effect on growth parameters, this optimal level was selected for molecular analyses. Total RNA was extracted from 100 mg of frozen leaf powder using 1 mL TRIzol[™] (Zaver Zist Azma, Iran). RNA quality and concentration were checked with a Nanodrop (A260/A280: 1.8–2.0), and integrity was confirmed on 1% agarose gel. One microgram of RNA was reverse-transcribed to cDNA using oligo(dT) primers. qRT-PCR was performed with a SYBR Green master mix and gene-specific primers (Table 1) designed via Oligo Analyzer and IDT. Amplification efficiency was validated, and relative expression was calculated using the $2^{-\Delta\Delta\text{Ct}}$ method.

cDNA synthesis and qRT-PCR analysis

Complementary DNA (cDNA) was synthesized from 1 μg total RNA using a reverse transcription mix containing 1 μL random hexamers, 1 μL oligo(dT)₁₈ primers, 1.5 μL dNTP mix (10 mM each), and 0.5 μL reverse transcriptase. The reaction was incubated at 42°C for 70 min and then inactivated at 70°C for 12 min.

Table 1 Primer sequences used for this study

Treatments	0	75	150	0+Se	75+Se	150+Se
Chl a ($\text{mg g}^{-1}\text{FW}$)	0.0147 ± 0.0007^b	0.0139 ± 0.0004^b	0.0117 ± 0.0008^c	0.0178 ± 0.0002^a	0.0174 ± 0.0002^a	0.0114 ± 0.0001^c
Chl b ($\text{mg g}^{-1}\text{FW}$)	0.0115 ± 0.0004^b	0.0091 ± 0.0005^c	0.0070 ± 0.0005^d	0.0135 ± 0.0001^a	0.0118 ± 0.0003^b	0.0068 ± 0.0001^a
Chl T ($\text{mg g}^{-1}\text{FW}$)	0.0097 ± 0.0004^b	0.0076 ± 0.0004^c	0.0058 ± 0.0004^d	0.0113 ± 0.0000^a	0.0099 ± 0.0003^b	0.0057 ± 0.0001^d
Carotenoid ($\text{mg g}^{-1}\text{FW}$)	0.0062 ± 0.0003^{bc}	0.0062 ± 0.0001^{bc}	0.0062 ± 0.0001^{bc}	0.0083 ± 0.0002^{ab}	0.0102 ± 0.0009^a	0.0061 ± 0.0002^{bc}

Table 2 The influence of 50 mg L⁻¹ selenium on growth parameters in sesame under salt stress (75 and 150 mM NaCl)

Treatments	0	75	150	0+Se	75+Se	150+Se
Rosmarinic acid(μg g ⁻¹ FW)	46.44±6.321 ^b	65.69±3.11 ^a	49.61±3.89 ^b	52.49±4.9 ^b	65.75±3.23 ^a	42.99±3.95 ^{ab}
Benzoic acid(μg g ⁻¹ FW)	305.1±49.82 ^d	622.9±6.70 ^a	486.02±4024 ^{bc}	415.83±8.6 ^d	600.1±70.70 ^c	516.61±31.74 ^{a-c}
Salicylic acid(μg g ⁻¹ FW)	100.14±8.30 ^c	123.9±0.81 ^b	156.08±13.20 ^c	157.6±2.03 ^a	118.02±13.20 ^c	148.72±1.27 ^a
Cinnamic acid(μg g ⁻¹ FW)	9343±1577 ^b	15677±759 ^a	15108±1769 ^a	17607± 2072 ^a	14307±1286 ^a	15088±1515 ^a
Coumaric acid(μg g ⁻¹ FW)	37±8.19 ^c	246±13 ^a	234±16.07 ^{ab}	74±8.58 ^c	203±1.8 ^b	195±25.73 ^b

Data are expressed as means ± SE of three replicates. The same letter indicates no statistically significant difference at $P \leq 0.05$, while the same letter indicates no significant difference

Table 3 The influence of 50 mg L⁻¹ selenium on photosynthetic pigment contents in sesame under salt stress (75 and 150 mM NaCl)

Treatments	0	75	150	0+Se	75+Se	150+Se
Chl <i>a</i> (mg g ⁻¹ FW)	0.0147±0.0007 ^b	0.0139±0.0004 ^b	0.0117±0.0008 ^c	0.0178±0.0002 ^a	0.0174±0.0002 ^a	0.0114±0.0001 ^c
Chl <i>b</i> (mg g ⁻¹ FW)	0.0115±0.0004 ^b	0.0091±0.0005 ^c	0.0070±0.0005 ^d	0.0135±0.0001 ^a	0.0118±0.0003 ^b	0.0068±0.0001 ^a
Chl T (mg g ⁻¹ FW)	0.0097±0.0004 ^b	0.0076±0.0004 ^c	0.0058±0.0004 ^d	0.0113±0.0000 ^a	0.0099±0.0003 ^b	0.0057±0.0001 ^d
Carotenoid (mg g ⁻¹ FW)	0.0062±0.0003 ^{bc}	0.0062±0.0001 ^{bc}	0.0062±0.0001 ^{bc}	0.0083±0.0002 ^{ab}	0.0102±0.0009 ^a	0.0061±0.0002 ^{bc}

Data are expressed as means ± SE of three replicates. The same letter indicates no statistically significant difference at $P \leq 0.05$, while the same letter indicates no significant difference

qRT-PCR was performed on a StepOne™ Real-Time PCR System (Applied Biosystems) with SYBR Green Master Mix (Amplicon, Iran). Each 10 μL reaction contained 1 μL diluted cDNA, 1 μL primer mix (10 pmol/μL each), and 8 μL SYBR Green Master Mix. Thermal cycling conditions were: 95 °C for 15 min, followed by 40 cycles of 95 °C for 15 s, 57 °C for 25 s, and 72 °C for 30 s. Reactions were run in duplicate, with melting curve analysis and gel electrophoresis used to confirm specificity.

Relative expression of *NHX1* and *PAL* was normalized to actin (*ACT*) and calculated using the 2^{-(ΔΔCt)} method [54], comparing treated versus control ΔCt values.

Extraction and determination of ion concentrations

Mineral element analysis

Concentrations of Na⁺, Se, Ca²⁺, K⁺, and P were determined following Demirel et al. [55]. Approximately 50 mg of dried leaf powder was digested with 6 mL concentrated HNO₃ at 200 °C for 30 min. After cooling, 2 mL of 30% H₂O₂ was added, and digestion continued for 40 min. The digestate was diluted to 10 mL with ultrapure water. Elemental content was quantified using ICP-MS (HP 4500, Asx-520 Autosampler, England) with multi-element standards for calibration, and results were expressed as mg g⁻¹ DW.

Statistical analysis

All experiments were conducted with three independent biological replicates. Data were analyzed using one-way analysis of variance (ANOVA) in SPSS software (version 21). Differences among means were determined by Duncan's multiple range test at a 95% confidence level ($p < 0.05$). Results are presented as mean ± standard error (SE).

Principal component analysis (PCA) was performed to explore the relationships among the measured physiological and biochemical parameters under different treatments. PCA was conducted using both the SRplot online platform (<https://www.bioinformatics.com.cn>) and R software (version 3.5.0; <http://www.r-project.org>), and the results were visualized in a biplot to illustrate correlations between treatments and variables.

Results

Growth features and photosynthetic pigments

Salt stress reduced dry weight (DW), fresh weight (FW), and plant length by approximately 54%, 50%, and 28%, respectively, compared to the control. The simultaneous application of Se with 75 mM NaCl increased FW, DW, and plant length in sesame by approximately 41%, 59%, and 12%, respectively, compared to the 75 mM NaCl treatment without selenium (Table 2). Salinity and Se treatments had no significant effect on relative water content (RWC) (Table 2). Under salinity conditions, the chlorophyll *a* (Chl *a*) content in sesame plants significantly decreased compared to the control. Salt stress at 75 and 150 mM NaCl reduced chlorophyll *b* (Chl *b*) and total chlorophyll (Chl T) contents in the plants. The exogenous application of Se to plants treated with 75 mM NaCl resulted in a considerable increase in Chl *a*, Chl *b*, and Chl T by 25.17%, 29%, and 30%, respectively. Carotenoid content showed no significant change under salt stress; however, an increase in carotenoid content was observed in the combined treatment of 75 mM NaCl + Se (Table 3).

Oxidative injury and antioxidant defense

H₂O₂ content in plants increased by approximately 84% and 107% under 75 mM and 150 mM salinity treatments, respectively, compared to the control. Additionally,

under low salinity treatment, selenium application significantly reduced H_2O_2 content, whereas this reduction was not statistically significant under high salinity conditions (Fig. 2a). MDA content increased significantly in plants under both salinity concentrations compared to the control. However, selenium application combined with the 75 mM salinity treatment reduced MDA content by approximately 40% compared to the 75 mM salinity treatment without selenium (Fig. 2b).

SOD enzyme activity in plants increased by approximately 107% and 235% under 75 mM and 150 mM salinity treatments, respectively, compared to control plants. Moreover, selenium application enhanced SOD activity at both salinity levels, with a statistically significant increase observed under low salinity (Fig. 3a). Salinity stress increased CAT enzyme activity in plants by approximately 20% and 40% under 75 mM and 150 mM NaCl treatments, respectively, compared to non-saline plants. Furthermore, CAT activity showed a statistically significant increase following selenium application only under 75 mM salinity (Fig. 3b). APX activity in plants increased by approximately 200% under 150 mM salinity compared to control plants. However, at this salinity level, selenium treatment resulted in a reduction in APX activity (Fig. 3c). Salinity stress caused a non-significant change in GST activity. Moreover, the increase in GST activity observed under selenium treatment was not statistically significant (Fig. 3d). Protein content in plants decreased under 150 mM NaCl salinity compared to the control. Selenium application increased protein content in plants under 75 mM salt stress compared to salinity treatment alone (Fig. 4a).

These results indicate that antioxidant enzyme activities were elevated under salinity stress, reflecting the activation of plant defense mechanisms against oxidative damage. Selenium treatment, particularly under low salinity conditions, further enhanced SOD and CAT activities, demonstrating its protective role. Additionally, the increase in protein content following selenium application under moderate salinity suggests improved stress tolerance.

Salinity stress significantly increased the total phenol, flavonoid, and anthocyanin contents in plants. Selenium application in plants grown under salinity enhanced anthocyanin and flavonoid contents, while its effect on total phenol content was not statistically significant (Fig. 4b, c, and d). Salt stress caused an increase in salicylic acid content in sesame plants, whereas selenium application prevented this change. Salinity stress altered rosmarinic acid content in plants in a NaCl concentration-dependent manner. Treatment with 75 mM NaCl increased rosmarinic acid content in plants. Selenium application did not cause a significant change in rosmarinic acid content under salt stress conditions. Benzoic acid content was elevated in plants exposed to salt stress, and Se treatment did not significantly affect benzoic acid levels under salinity. Salinity stress increased coumaric acid content in plants. Both selenium and salt stress caused non-significant changes in cinnamic acid content in plants (Table 4). According to our results, diosmin content in plants under saline conditions decreased. Selenium application induced diosmin content in plants subjected to salt stress. Under salt stress, the alteration of resveratrol content was not significant in plants. Selenium application elevated resveratrol content in

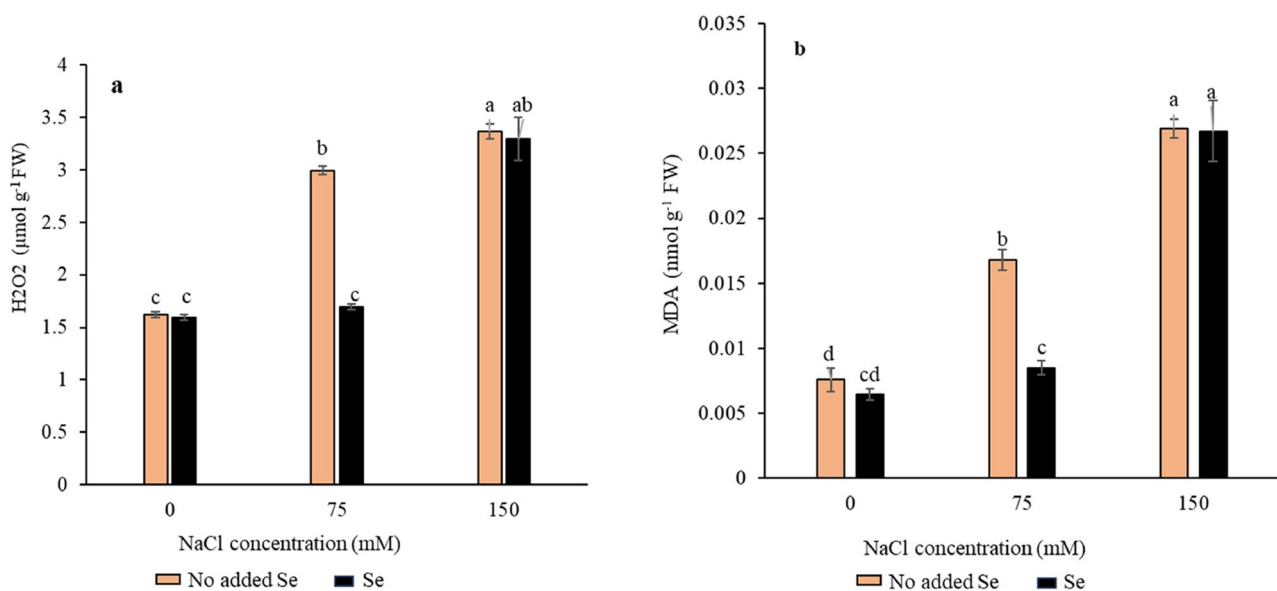


Fig. 2 The influence of 50 mg L⁻¹ selenium on hydrogen peroxide (a) and malondialdehyde (b) contents in sesame under salt stress (75 and 150 mM NaCl). Data are presented as means ± SE of three replicates. Different letters indicate significant differences at $P \leq 0.05$

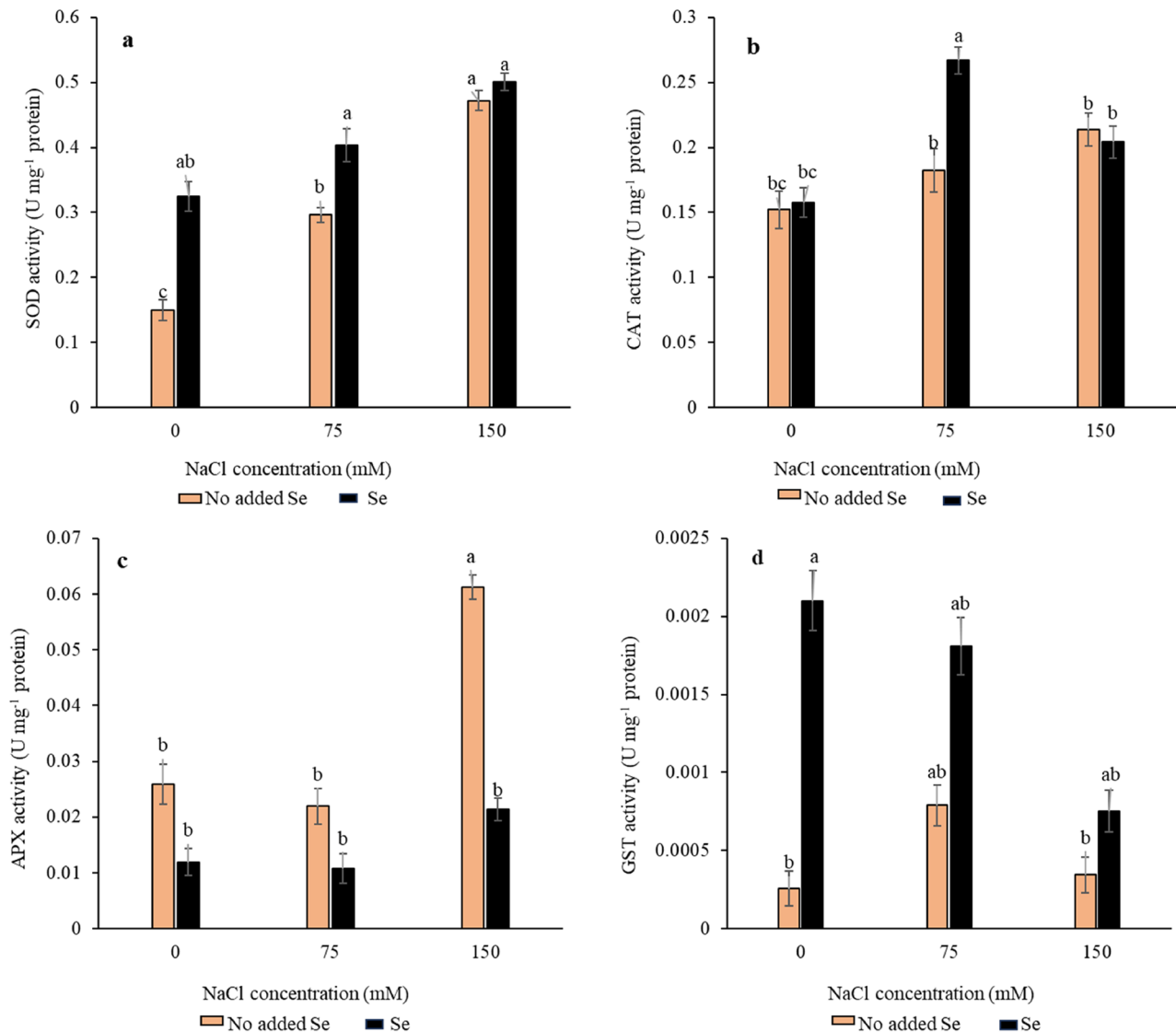


Fig. 3 The effect of 50 mg L⁻¹ selenium on activities of superoxide dismutase (SOD) (a), catalase (CAT) (b), ascorbate peroxidase (APX) (c), and glutathione S-transferase (GST) (d) in sesame under salt stress (75 and 150 mM NaCl). Data are presented as means $\pm$ SE of three replicates. Different letters indicate significant differences at $P \leq 0.05$

plants treated with 75 mM NaCl. Salinity stress significantly increased myricetin content in plants compared to untreated controls. Exogenous application of selenium reduced myricetin content in plants under saline conditions. Catechin content increased in plants during salt stress. Furthermore, plants treated with 150 mM NaCl and selenium exhibited lower catechin content than those treated with 150 mM NaCl alone (Table 5).

Compatible osmolytes

Proline content in the plants increased by approximately 121% and 183% under 75 mM and 150 mM salt stress treatments, respectively, compared to the control. Additionally, the simultaneous application of Se under 75 mM NaCl salinity resulted in an approximately 37% increase

in proline content compared to the 75 mM NaCl treatment without Se (Fig. 5a).

Soluble sugar content increased under salinity conditions. Se treatment resulted in a 25% increase in soluble sugars at 75 mM NaCl, while no significant change was observed in Se-treated control plants compared to the untreated control (Fig. 5b).

Ion concentrations

Salt stress caused a decrease in K⁺ content and an increase in Ca²⁺ content, while exogenous selenium application significantly increased potassium levels in plants under salt stress; however, the increase in calcium was not statistically significant. Salt stress also led to a significant increase in Na⁺ and phosphorus (P) contents

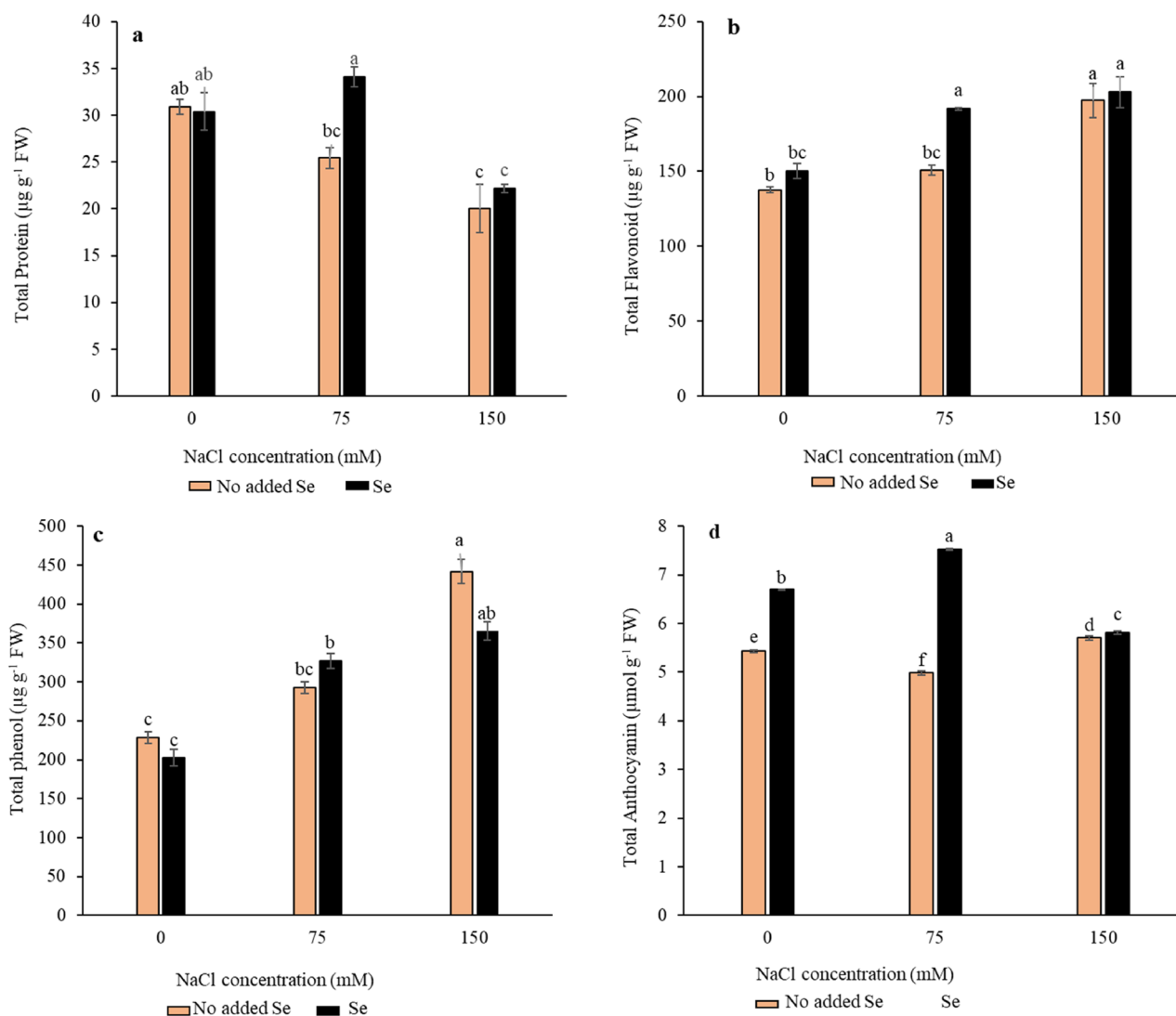


Fig. 4 The effect of 50 mg L⁻¹ selenium on total protein (a), phenol (b), flavonoid (c), and anthocyanin (d) contents in sesame under salt stress (75 and 150 mM NaCl). Data are presented as means $\pm$ SE of three replicates. Different letters indicate significant differences at $P \leq 0.05$

Table 4 The influence of 50 mg L⁻¹ selenium on phenolic acid compounds in sesame under salt stress (75 and 150 mM NaCl)

Treatments	0	75	150	0 + Se	75 + Se	150 + Se
Rosmarinic acid ($\mu\text{g g}^{-1}$ FW)	46.44 $\pm$ 6.32 ^b	65.69 $\pm$ 3.11 ^a	49.61 $\pm$ 3.89 ^b	52.49 $\pm$ 0.49 ^b	65.75 $\pm$ 3.23 ^a	42.99 $\pm$ 3.95 ^{ab}
Benzoic acid ($\mu\text{g g}^{-1}$ FW)	305.1 $\pm$ 49.82 ^d	622.9 $\pm$ 6.70 ^a	486.02 $\pm$ 4024 ^{bc}	415.83 $\pm$ 8.6 ^d	600.1 $\pm$ 70.70 ^c	516.61 $\pm$ 31.74 ^{a-c}
Salicylic acid ($\mu\text{g g}^{-1}$ FW)	100.14 $\pm$ 8.30 ^c	123.9 $\pm$ 0.81 ^b	156.08 $\pm$ 13.20 ^c	157.6 $\pm$ 2.03 ^a	118.02 $\pm$ 13.20 ^c	148.72 $\pm$ 1.27 ^a
Cinnamic acid ($\mu\text{g g}^{-1}$ FW)	9343 $\pm$ 1577 ^b	15677 $\pm$ 759 ^a	15108 $\pm$ 1769 ^a	17607 $\pm$ 2072 ^a	14307 $\pm$ 1286 ^a	15088 $\pm$ 1515 ^a
Coumaric acid ($\mu\text{g g}^{-1}$ FW)	37 $\pm$ 8.19 ^c	246 $\pm$ 13 ^a	234 $\pm$ 16.07 ^{ab}	74 $\pm$ 8.58 ^c	203 $\pm$ 1.8 ^b	195 $\pm$ 25.73 ^b

Data are expressed as means $\pm$ SE of three replicates. The same letter indicates no statistically significant difference at $P \leq 0.05$, while the same letter indicates no significant difference

Table 5 The influence of 50 mg L⁻¹ selenium on flavonoid compounds in sesame under salt stress (75 and 150 mM NaCl)

Treatments	0	75	150	0 + Se	75 + Se	150 + Se
Diosmin (μg g ⁻¹ FW)	28515 ± 1380.92 ^{ab}	26125 ± 1264 ^b	26604 ± 1141 ^b	15583 ± 963 ^c	30711 ± 86 ^a	1548 ± 24.67 ^d
Resveratrol (μg g ⁻¹ FW)	2217 ± 93.42 ^b	2079 ± 32.908 ^b	1923 ± 94.43 ^b	659 ± 170.31 ^c	3873 ± 270.77 ^a	196 ± 16.1658 ^d
Myricetin (μg g ⁻¹ FW)	3843 ± 441 ^b	6346 ± 74 ^a	7591 ± 921 ^a	4070 ± 100.17 ^b	2070 ± 154 ^c	5791 ± 20.20 ^c
Catechin (μg g ⁻¹ FW)	377773 ± 7407 ^c	482915 ± 10484 ^b	620519 ± 33329 ^a	310188 ± 3973 ^c	485991 ± 1398 ^b	39916 ± 48.20 ^d

Data are expressed as means ± SE of three replicates. The same letter indicates no statistically significant difference at $P \leq 0.05$, while the same letter indicates no significant difference

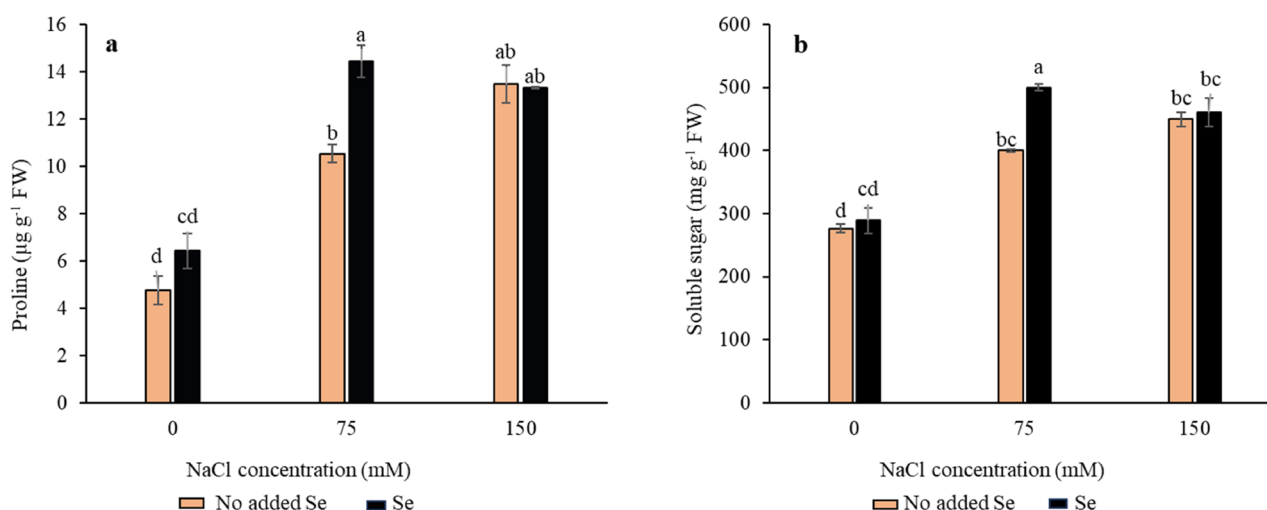


Fig. 5 The effect of 50 mg L⁻¹ selenium on proline content (a) and soluble sugar (b) in sesame under salt stress (75 and 150 mM NaCl). Data are presented as means ± SE of three replicates. Different letters indicate significant differences at $P \leq 0.05$

compared to the control. However, selenium treatment combined with salt stress reduced sodium levels in plants. Additionally, salt stress significantly decreased the K⁺/Na⁺ ratio. Selenium application effectively increased Se content in the plants (Fig. 6).

Transcript level of *NHX1*

In our study, salt stress caused a non-significant change in *NHX1* transcript levels in plants. Selenium application increased *NHX1* transcript levels by 53% in plants grown under saline conditions (Fig. 7).

Enzyme activity and gene expression of PAL

PAL enzyme activity showed a significant increase under salinity stress conditions. Specifically, at high salinity levels (150 mM), PAL activity increased by 41% compared to the control treatment. Additionally, selenium application under salinity stress did not cause a significant change in PAL enzyme activity. Salinity stress induced an approximately 57% increase in PAL gene expression compared to the control, while selenium application under salt stress led to an approximately 45% increase in the expression of this gene (Fig. 8).

Phytohormones content

Salinity and Se treatments had no significant effect on brassinosteroid (BR) content in plants. Salt stress increased BR content in plants, whereas Se application under salinity conditions decreased BR content (Fig. 9a). Salt stress caused a significant change in abscisic acid (ABA) content in the plants compared to the control. However, under 75 mM salinity, Se treatment increased ABA content in the plants (Fig. 9b). Salt stress reduced auxin (IAA) content in the plants, while Se application significantly increased IAA content in plants treated with 75 and 150 mM NaCl (Fig. 9c). Salt treatment with 75 mM NaCl increased gibberellin (GA) content in the plants, but this increase was not statistically significant. In addition, Se application at the same salinity level further increased GA content in the plants; however, this increase was not statistically significant (Fig. 9d).

Fatty acid profile

Salt stress significantly decreased the contents of palmitic acid (C16), palmitoleic acid (C16:1), and stearic acid (C18) in the plants. However, it increased the levels of oleic acid (C18:1), linoleic acid (C18:2), linolenic acid

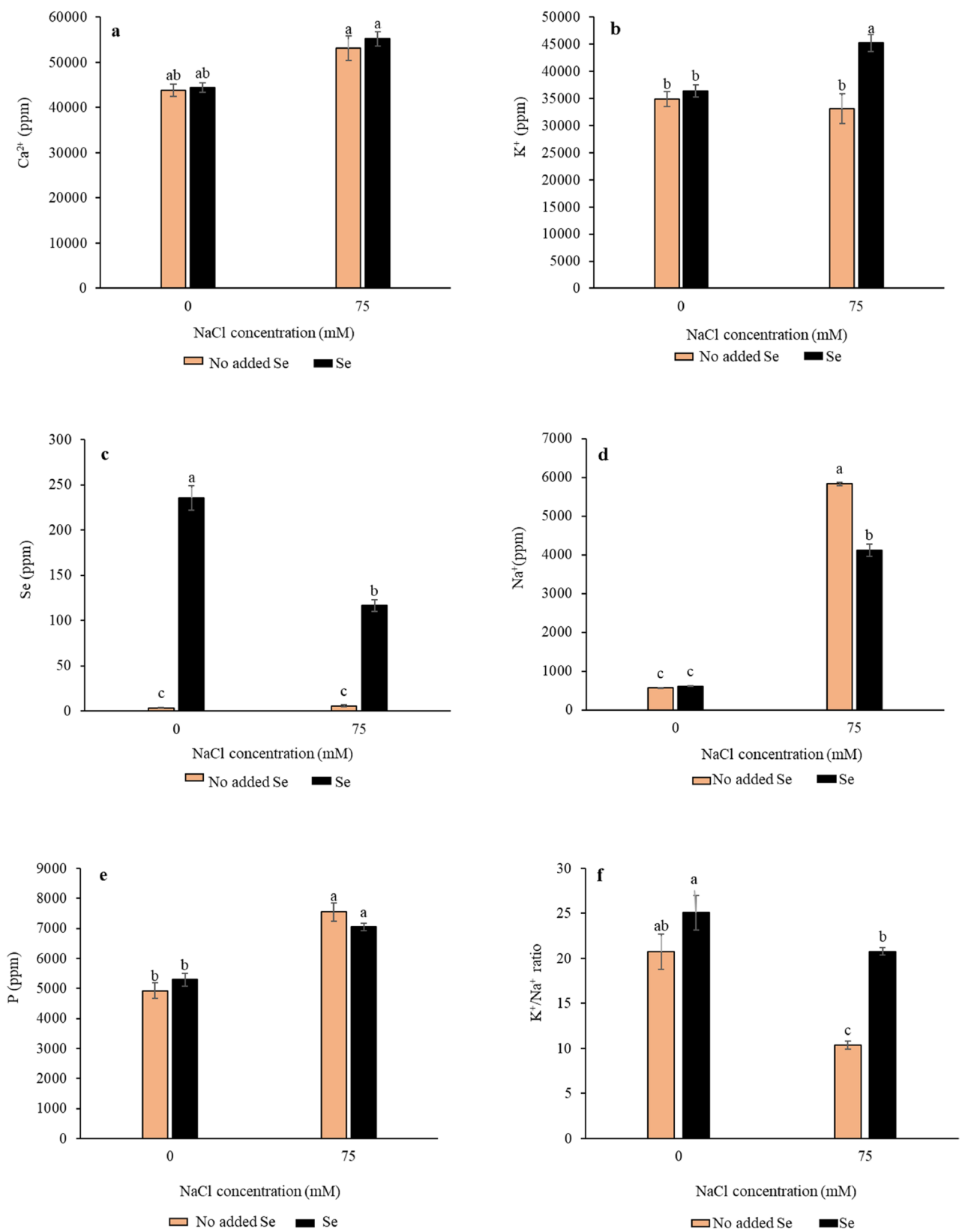


Fig. 6 The effect of 50 mg L⁻¹ selenium on ion contents in sesame under salt stress (75 and 150 mM NaCl). Data are presented as means ± SE of three replicates. Different letters indicate significant differences at *P* ≤ 0.05

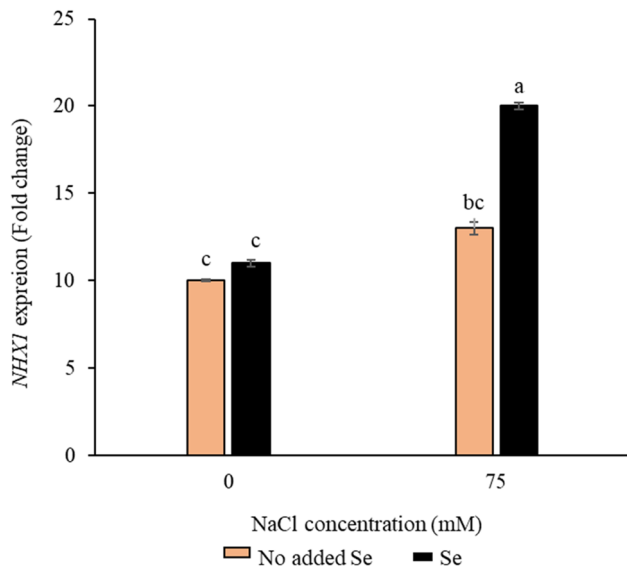


Fig. 7 The effect of 50 mg L⁻¹ selenium on transcript level of sodium/hydrogen exchanger 1 (NHX1) in sesame under salt stress (75 and 150 mM NaCl). Data are presented as means $\pm$ SE of three replicates. Different letters indicate significant differences at $P \leq 0.05$

(C18:3), and behenic acid (C22) compared to the control. Exogenous application of Se under salinity conditions led to a significant reduction in palmitoleic, oleic, linoleic, linolenic, arachidic acid (C20), behenic, and lignoceric acid (C24) contents in the plants (Table 6).

Principal component analysis (PCA) and correlation studies

The Pearson correlation matrix revealed strong positive correlations (blue) among growth-related traits, including dry weight (DW), indicating that improvements in one growth parameter were accompanied by increases in

others. Photosynthetic pigments (Chl *a*, Chl *b*, and Car) and phenolic compounds also showed positive correlations with growth attributes, while exhibiting negative associations (red) with oxidative stress indicators (H₂O₂ and MDA). Antioxidant enzymes (SOD, APX, and CAT) were positively correlated with proline and phenolic contents but negatively correlated with H₂O₂ and MDA, suggesting their protective role against oxidative damage. In contrast, ABA exhibited a negative relationship with growth traits, whereas secondary metabolites such as rosmarinic acid and p-coumaric acid were positively associated with antioxidant activity, reflecting their contribution to stress mitigation (Fig. 10).

To explore the overall relationships among salinity and selenium treatments and the physiological traits of sesame plants, a principal component analysis (PCA) was performed (Fig. 11). The first two principal components (PC1 = 52.4% and PC2 = 19.8%) together explained 72.2% of the total variance, indicating that these components were sufficient to distinguish between the treatments. The PCA biplot revealed a clear separation among treatments. The control and Salt0Se treatments were located close to each other in the upper left quadrant and showed positive correlations with growth-related traits, including shoot and root length, fresh and dry weight, leaf area, relative water content (RWC), and photosynthetic pigments (chlorophyll *a*, chlorophyll *b*, and carotenoids), reflecting a favorable physiological status and the positive influence of selenium under non-stress conditions. The Salt75 treatment was positioned in the lower right quadrant and was negatively correlated with growth and pigment traits, indicating the adverse effects of moderate salinity on plant performance. In contrast, the Salt75Se

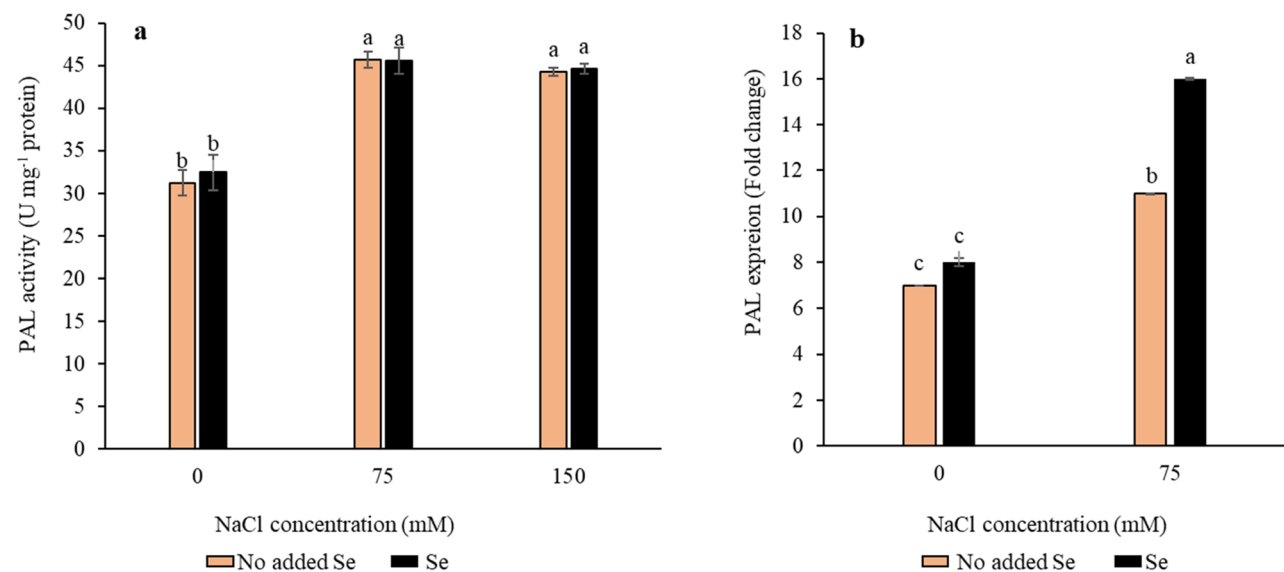


Fig. 8 The effect of 50 mg L⁻¹ selenium on phenylalanine ammonia lyase (PAL) activity (a) and gene expression (b) in sesame under salt stress (75 and 150 mM NaCl). Data are presented as means $\pm$ SE of three replicates. Different letters indicate significant differences at $P \leq 0.05$

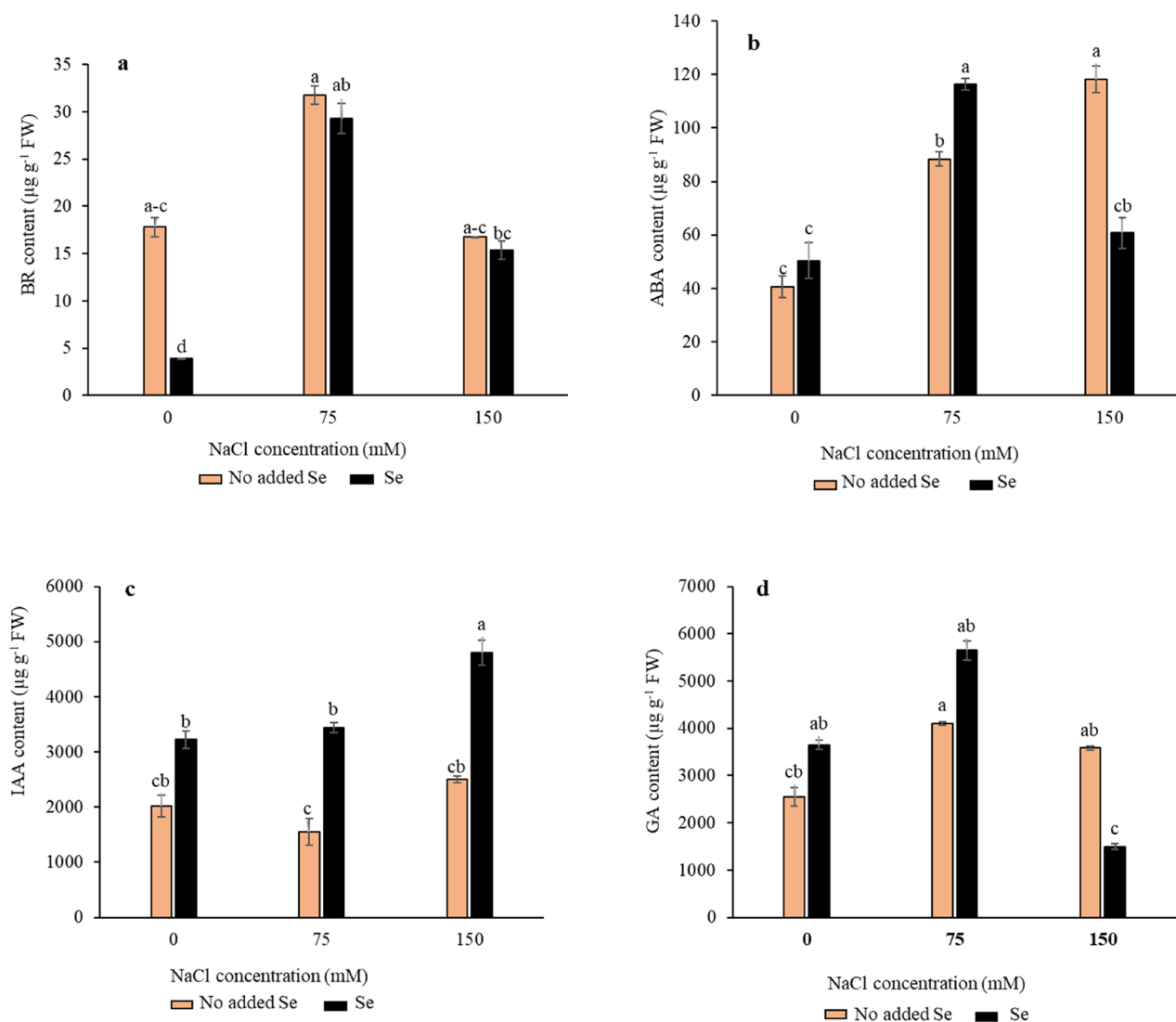
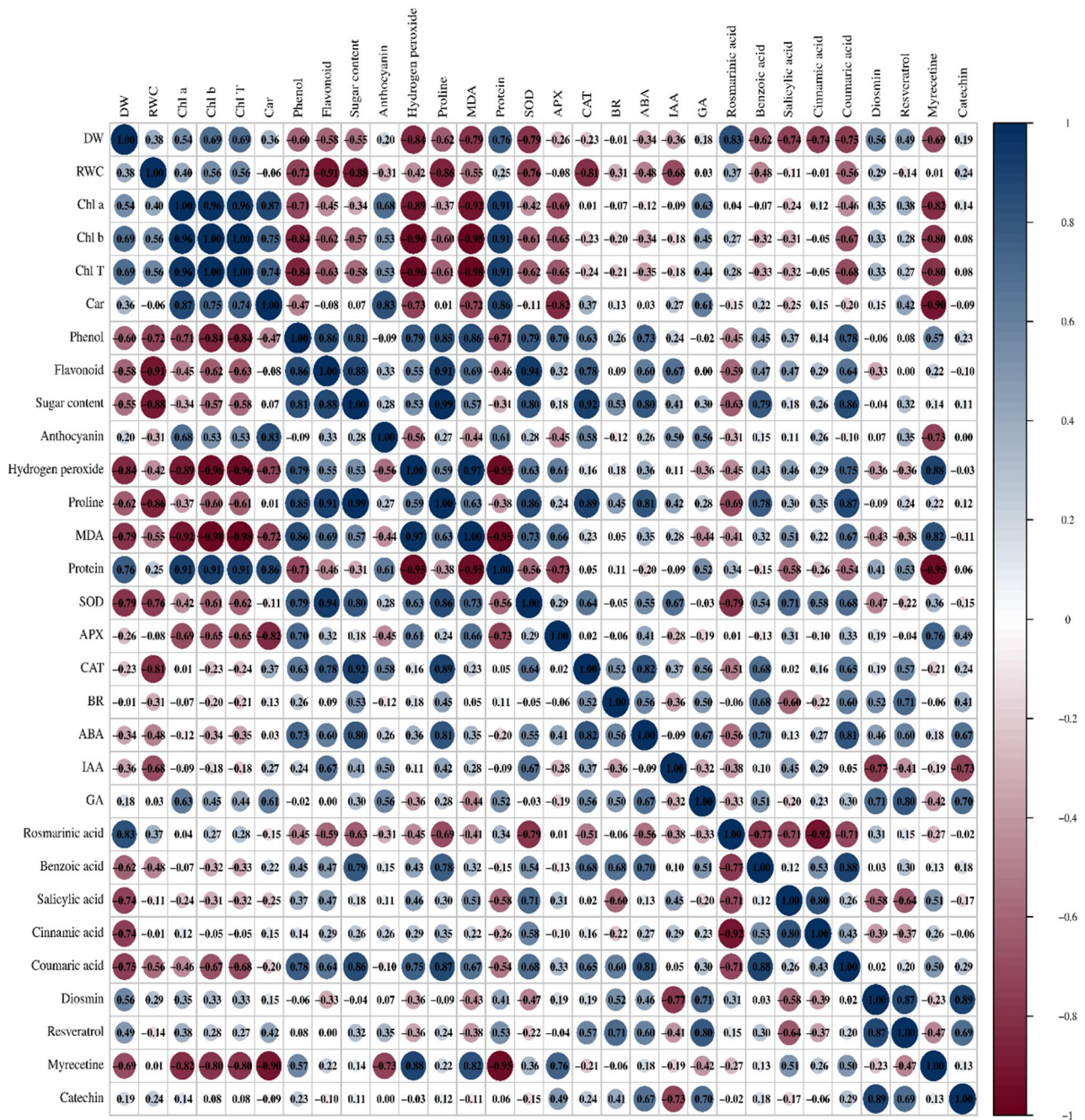


Fig. 9 The effect of 50 mg L⁻¹ selenium on brassinosteroid (BR) (a), abscisic acid (ABA) (b), indole-3-acetic acid (IAA) (c), and gibberellic acid (GA) (d) contents in sesame under salt stress (75 and 150 mM NaCl). Data are presented as means $\pm$ SE of three replicates. Different letters indicate significant differences at $P \leq 0.05$

Table 6 The influence of 50 mg L⁻¹ selenium on fatty acid profiles (%) in sesame under salt stress (75 and 150 mM NaCl)

Treatments	0	75	0+Se	75+Se
Palmitic acid(C ₁₆)	28.6 $\pm$ 1 ^a	23.73 $\pm$ 2.1 ^b	14.52 $\pm$ 1.2 ^c	21.07 $\pm$ 1.22 ^b
Palmitoleic acid(C _{16:1})	0.76 $\pm$ 0.08 ^a	0.54 $\pm$ 0.01 ^b	0.42 $\pm$ 0.03 ^c	0.45 $\pm$ 0.04 ^c
Stearic acid(C ₁₈)	16.34 $\pm$ 2 ^a	11.34 $\pm$ 2.13 ^b	6.92 $\pm$ 1.23 ^c	10.14 $\pm$ 2.11 ^b
Oleic acid(C _{18:1})	3.31 $\pm$ 0.13 ^b	5.91 $\pm$ 0.13 ^a	3.82 $\pm$ 0.12 ^b	3.98 $\pm$ 0.15 ^b
Linoleic acid(C _{18:2})	4.48 $\pm$ 1.1 ^b	5.67 $\pm$ 0.22 ^a	4.36 $\pm$ 0.11 ^b	4.33 $\pm$ 0.14 ^b
Linolenic acid(C _{18:3})	22.44 $\pm$ 1.90 ^c	28.07 $\pm$ 2.11 ^a	22.11 $\pm$ 3.20 ^c	25.06 $\pm$ 1.22 ^b
Arachidic acid (C ₂₀)	12.19 $\pm$ 1.22 ^b	11.13 $\pm$ 0.89 ^b	24.40 $\pm$ 2.11 ^a	9.14 $\pm$ 1.34 ^c
Behenic acid(C ₂₂)	2.90 $\pm$ 0.87 ^b	4.30 $\pm$ 1.09 ^a	4.79 $\pm$ 0.32 ^a	2.20 $\pm$ 0.11 ^b
Lignoceric acid(C ₂₄)	8.99 $\pm$ 1.23 ^b	9.31 $\pm$ 1.21 ^b	18.65 $\pm$ 2.56 ^a	7.30 $\pm$ 1.11 ^c

Data are expressed as means $\pm$ SE of three replicates. The same letter indicates no statistically significant difference at $P \leq 0.05$, while the same letter indicates no significant difference



treatment was located near the center of the plot, suggesting a partial alleviation of salinity-induced damage by selenium. The Salt150Se treatment appeared in the upper right quadrant and showed positive associations with stress-related traits such as increased proline and soluble sugar contents, indicating the activation of osmotic adjustment mechanisms under severe salinity in

the presence of selenium. Furthermore, elevated levels of MDA and H₂O₂ in the Salt150 and Salt150Se treatments indicated the induction of oxidative stress under high salinity conditions.

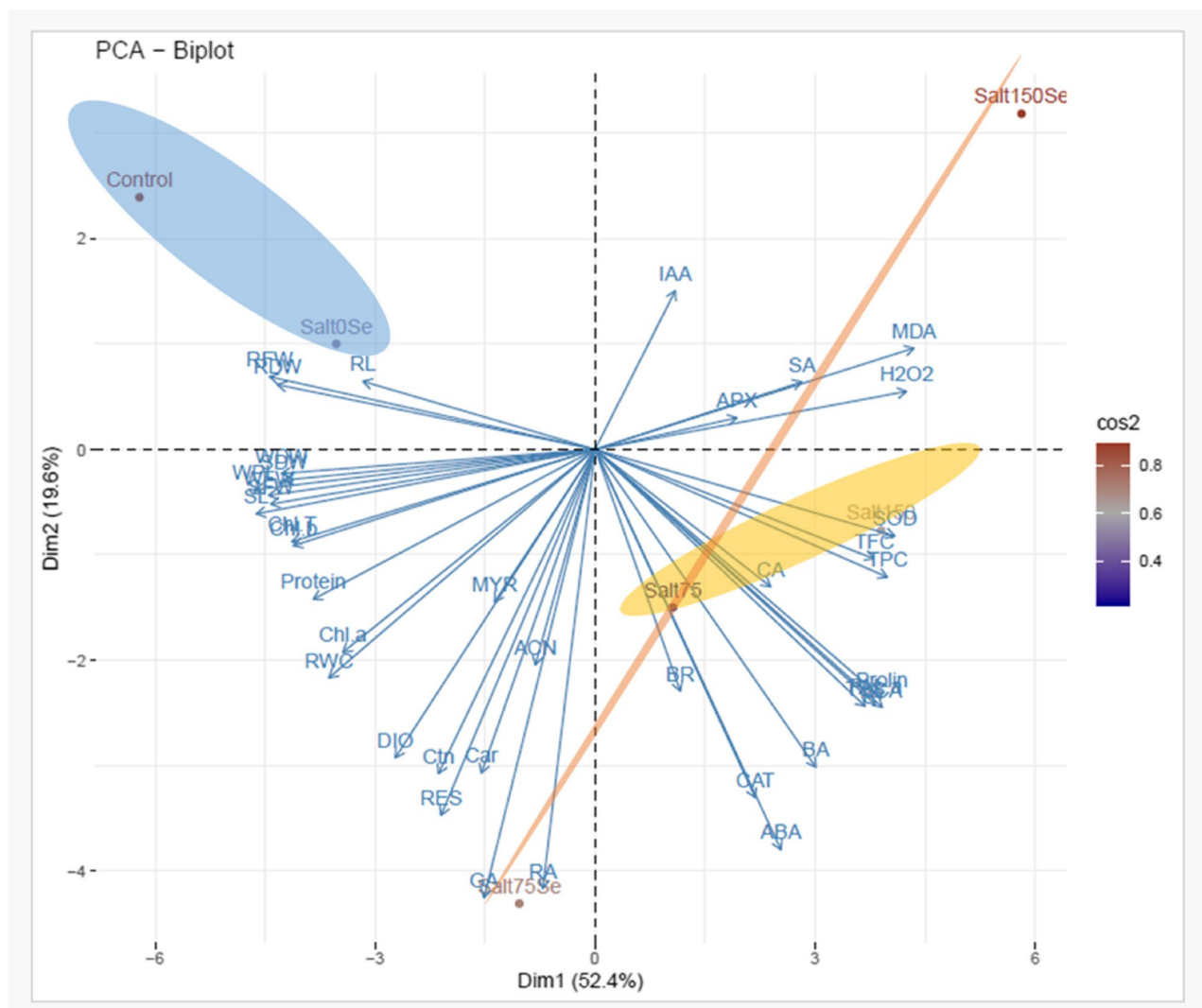


Fig. 11 Principal component analysis (PCA) biplot representing growth, physiological, and biochemical traits in sesame plants under salt stress (75 and 150 mM NaCl) and treatment with 50 mg L⁻¹ selenium. Abbreviations: Root length (RL); Shoot length (SL); Whole plant length (WPL); Relative water content (RWC); Shoot fresh weight (SFW); Root fresh weight (RFW); Whole plant fresh weight (WFW); Shoot dry weight (SDW); Root dry weight (RDW); Whole plant dry weight (WDW); Chlorophyll a (Chl a); Chlorophyll b (Chl b); Total chlorophyll (Chl T); Carotenoid (Car); Hydrogen peroxide (H₂O₂); Proline content (Proline); Malondialdehyde (MDA); Superoxide dismutase (SOD); Ascorbate peroxidase (APX); Catalase (CAT); Phenylalanine ammonia-lyase enzyme activity (PAL-a); Brassinosteroid (BR); Absciscic acid (ABA); Indole-3-acetic acid (IAA); Gibberellic acid (GA); Rosmarinic acid (RA); Cinnamic acid (CA); Salicylic acid (SA); p-Coumaric acid (p-CA); Benzoic acid (BA); Resveratrol (RES); Diosmin (DIO); Myricetin (MYR); Catechin (Ctn)

Discussion

Salt stress represents a major environmental constraint that impairs plant growth by inducing osmotic and ionic imbalances, resulting in physiological water deficits [15, 17]. These disruptions adversely affect numerous biochemical and physiological processes essential for normal development and growth [56]. In the present study, observed reductions in Fresh Weight (FW), Dry Weight (DW), and plant length under saline conditions demonstrated that salinity significantly inhibited growth in sesame plants. This growth inhibition is likely attributable to salinity-induced osmotic stress, which hampers water uptake and transport, triggering hormetic responses

including reduced CO₂ assimilation, decreased photosynthetic efficiency, and stomatal closure. Consequently, carbon allocation and carbohydrate homeostasis between source and sink tissues are altered to facilitate osmotic adjustment under stress conditions [57, 58]. The decline in biomass and growth parameters observed in our experiment likely resulted from Na⁺ toxicity, overproduction of reactive oxygen species (ROS) such as H₂O₂, and subsequent oxidative damage. Under saline conditions, cellular metabolism was disrupted, and excessive ROS generation induced oxidative stress. Our results demonstrated that selenium supplementation enhanced growth parameters in sesame plants by mitigating the adverse

effects of salinity, particularly at 75 mM NaCl. Previous studies have reported that the beneficial effects and mechanisms of Se-mediated salinity tolerance are concentration-dependent [29]. Our findings confirmed that Se application alleviates salt stress by reducing oxidative damage through enhanced ROS-scavenging activity. Moreover, Se promoted growth in sesame plants, which was associated with increased levels of photosynthetic pigments, elevated concentrations of phytohormones—including abscisic acid (ABA), indole-3-acetic acid (IAA), and gibberellic acid (GA)—upregulation of *NHX1* gene transcript levels, and a reduction in unsaturated fatty acid content [59]. These results are consistent with reports in maize, where Se mitigated salt stress by activating antioxidant defense mechanisms to reduce ROS damage, improving photosynthetic efficiency by minimizing chlorophyll degradation, preserving chloroplast ultrastructure, and regulating ionic homeostasis [60]. Numerous studies have established chlorophyll content as a reliable indicator of cellular metabolic status and a valuable biochemical marker for salinity tolerance. The suppression of plant growth under saline conditions is often correlated with a decline in chlorophyll levels and a consequent reduction in photosynthetic capacity, resulting from alterations in various physiological and biochemical pathways [61–63]. Our results corroborate these findings, demonstrating a significant decrease in chlorophyll content under salinity stress (Table 3). This reduction may be attributed to the disorganization of chlorophyll–protein complexes and degradation of pigment–protein assemblies. Furthermore, the accumulation of reactive oxygen species (ROS), such as H_2O_2 and O_2^- , under salt stress could disrupt chloroplast membrane integrity, leading to chlorophyll degradation [64]. In the present study, selenium application ameliorated the salt-induced reduction in chlorophyll content. An optimal exogenous concentration of Se appeared to mitigate damage to chloroplast ultrastructure and facilitated the preservation and biosynthesis of chlorophyll in plants subjected to salinity [65, 66]. This protective effect may be attributed to the positive influence of Se on chloroplast enzymes involved in pigment biosynthesis, as previously observed in cowpea, where Se supplementation enhanced the levels of both chlorophyll *a* and chlorophyll *b* [67]. By promoting chlorophyll synthesis and stabilizing the photosynthetic apparatus, Se contributed to an increased photosynthetic rate, thereby supporting improved plant growth under stress conditions. Our findings are consistent with earlier reports [68, 69], confirming a significant increase in photosynthetic pigments in Se-treated plants under salinity. This effect is likely driven by the role of Se in supporting vital processes such as the electron transport chain and cellular respiration [70]. Additionally, this study revealed that salt stress

induced the upregulation of phenylalanine ammonia-lyase (PAL) gene expression (Fig. 8). Notably, the combined treatment of selenium and salt stress resulted in a further significant increase in PAL transcript levels compared to salt stress alone. These findings are consistent with previous studies highlighting the critical role of PAL—a key enzyme in the phenylpropanoid pathway—in enhancing salt stress tolerance through the synthesis of protective phenolic compounds [71, 72]. Although Se application did not cause a statistically significant change in PAL enzyme activity (Fig. 8), our gene expression data indicated that it upregulated PAL gene transcription (Fig. 8). This suggests that Se may enhance the potential for phenolic compound synthesis through transcriptional regulation, aligning with earlier reports that Se can promote the expression of key stress-responsive genes, including those involved in secondary metabolism [73, 74]. In the present study, salt stress significantly induced the accumulation of total phenolics, flavonoids, and anthocyanins in sesame plants. Selenium application under saline conditions further amplified this response, resulting in a particularly notable increase in flavonoid and anthocyanin contents. This observation aligns with prior research indicating that Se can stimulate the biosynthesis and accumulation of anthocyanins [75, 76]. Furthermore, salinity stress caused a marked increase in salicylic acid (SA) concentration (Table 4); however, this effect was mitigated by Se supplementation. This result corroborates previous studies demonstrating that Se can modulate phytohormone pathways by reducing excessive SA accumulation under stress conditions [77, 78]. Analysis of specific phenolic acids revealed that the contents of rosmarinic, benzoic, coumaric, and cinnamic acids were significantly altered by salinity stress but were not substantially influenced by Se treatment. In contrast, Se specifically stimulated the accumulation of certain flavonoid metabolites, most notably diosmin (Tables 4 and 5). Overall, these results demonstrate that Se exerts a positive effect on the biosynthesis of specific classes of secondary metabolites—particularly flavonoids and anthocyanins—under salinity stress, while its influence on other compounds, such as resveratrol, myricetin, and catechin, was less pronounced or more variable. The impact of salt stress on metabolic profiles varies considerably across plant species, highlighting the complexity of adaptive responses to salinity and the potential role of Se in modulating these processes. As salinity induces osmotic stress, the accumulation of compatible osmolytes becomes a critical mechanism for re-establishing cellular osmotic equilibrium and maintaining turgor pressure [79, 80]. Among these osmolytes, proline and soluble sugars play pivotal roles in osmotic adjustment and in mitigating the adverse effects of stress on cellular functions [81, 82]. Concentrations of these osmolytes are

strongly correlated with stress tolerance (Fig. 5), making them reliable biochemical markers of the plant's resilience potential. Beyond their osmotic functions, these compounds contribute to stress mitigation by stabilizing protein structures, scavenging ROS, and protecting the photosynthetic apparatus [83–85]. Furthermore, soluble sugars can act as chelating agents, sequestering Na^+ ions within starch granules, thereby reducing ionic toxicity in plant cells under saline conditions [86]. In this study, selenium application under moderate salt stress (75 mM NaCl) stimulated a more pronounced accumulation of proline and soluble sugars compared to severe stress (150 mM NaCl). This suggests that sesame plants actively accumulate these compatible solutes to counteract salinity-induced osmotic stress and that Se treatment enhances this protective response. The observed increase in osmotically active metabolites indicates improved physiological adjustment to salinity facilitated by Se. These findings support the concept that Se contributes to maintaining turgor and preserving cell membrane integrity under salt stress, partly through the elevated synthesis of osmoprotectants such as proline [87]. It is postulated that selenium enhances proline biosynthesis by increasing nitrogen availability and the activity of key enzymes, such as nitrate reductase, both of which are essential for proline synthesis [88]. Furthermore, selenium appears to modulate the proline metabolic pathway by regulating the activities of γ -glutamyl kinase (γ -GK) and proline oxidase (PROX), thereby reducing proline degradation while simultaneously enhancing its production [87]. The observed accumulation of osmolytes at 75 mM NaCl with selenium application corresponded with mitigated salt injury and improved plant development, suggesting that selenium-facilitated osmotic adjustment contributed to enhanced growth under moderate salinity. In saline environments, excessive sodium ion uptake disrupts cellular homeostasis and leads to the accumulation of reactive oxygen species (ROS), resulting in oxidative stress. The present study demonstrated that salt stress induced oxidative damage in sesame plants, as evidenced by elevated H_2O_2 and MDA concentrations. Selenium application alleviated salinity-induced oxidative stress by enhancing both enzymatic and non-enzymatic antioxidant defense systems. Plants treated with selenium showed increased activity of ROS-scavenging enzymes [Fig. 3] and elevated levels of non-enzymatic antioxidants [Figs. 4 and 5], collectively reducing oxidative damage. Antioxidant protection mechanisms, comprising both enzymatic and non-enzymatic components, served to neutralize ROS and enhance plant resilience to abiotic stresses [89]. Our findings indicate that selenium application strengthened this oxidative defense network in sesame plants under salt stress. Selenium appeared to play a safeguarding role by suppressing ROS accumulation [88],

boosting the activity of antioxidant enzymes, and enhancing non-enzymatic scavenging of superoxide radicals [90]. This coordinated response limited excessive ROS buildup and mitigated oxidative damage to cellular membranes. Therefore, the reduction in hydrogen peroxide concentration following selenium treatment can be attributed to its positive regulation of antioxidant capacity in sesame plants. This study investigated the combined effects of salinity stress and Se application on the oxidative defense system in *Sesamum indicum* plants, integrating our findings with established literature [91, 92]. Under saline conditions, *Sesamum indicum* exhibited increased activity of key antioxidant enzymes, superoxide dismutase (SOD) and catalase (CAT). This reinforced previous research identifying a strong correlation between enhanced SOD and CAT activities and salinity tolerance across diverse plant species. For instance, salt-tolerant rice cultivars have been shown to maintain higher constitutive activities of these enzymes compared to salt-sensitive varieties [93, 94]. Our results further demonstrated that selenium supplementation strengthened the antioxidant defense system in *Sesamum indicum* under salt stress, particularly through the enhanced activities of SOD and CAT, thereby mitigating the detrimental effects of salinity on plant growth. This selenium-mediated boost in antioxidant enzyme activity, accompanied by a reduction in oxidative stress markers, has been consistently documented in other species including foxtail millet [95], soybean [96], *Brassica rapa* [97], and peanut [98]. Moreover, studies indicated that Se treatment specifically enhanced the functional capacity of SOD and CAT enzymes, leading to more efficient neutralization of superoxide radicals and an overall enhancement of the plant's antioxidant potential and adaptive response to salinity stress [99]. An interesting observation in our study was the decline in ascorbate peroxidase (APX) activity following Se application. Similar findings have been reported in ryegrass [100], where this phenomenon might be attributed to substrate competition between CAT and APX, as both enzymes utilize H_2O_2 as their substrate. The selenium-induced stimulation of catalase activity likely reduced cellular H_2O_2 concentrations, consequently diminishing substrate availability and activation of the APX pathway [101]. The influence of selenium on antioxidant enzyme activities is notably complex and context-dependent, as observed across various plant species. For example, in *Arabidopsis thaliana*, the effect of selenium varies significantly depending on environmental conditions [102]. Similarly, our findings in sesame demonstrated that selenium's modulation of antioxidant enzymes depended on the NaCl concentration, revealing a multifaceted interaction between selenium application and salinity levels in regulating these enzymatic responses. In this study, exogenous selenium application

differentially affected antioxidant enzyme activities in sesame plants, with specific response patterns contingent upon the severity of salt stress. Under saline conditions, selenium supplementation generally enhanced the overall antioxidant defense system, thereby mitigating the adverse effects of salinity on plant growth. This protective role is consistent with observations in wheat, where selenium upregulated SOD and CAT activities, enhancing superoxide radical scavenging capacity and improving overall antioxidant efficiency and salt stress resilience [99]. The selenium-mediated enhancement of antioxidant enzyme performance and the concomitant reduction of oxidative damage under salinity stress have been consistently documented across multiple plant species, including proso millet [95], soybean [96], *Brassica rapa* L [97], and peanuts [98]. Beyond direct enzymatic activation, selenium also appears to function at the transcriptional level by modulating the expression of genes encoding antioxidant enzymes. Studies in mustard have shown that selenium influences the expression of genes encoding CAT and SOD [103], while research in *Brassica napus* demonstrates that alterations in the expression of antioxidant enzyme genes enhance enzymatic activity, thereby improving salt resistance through reduced ROS accumulation [104]. Consequently, selenium serves as a comprehensive regulator of both enzymatic and non-enzymatic antioxidant systems, while simultaneously contributing to plasma membrane stability. This dual function represents a crucial mechanism for salt stress resilience, given that membrane lipid peroxidation constitutes a fundamental cellular injury under salinity stress [105, 106]. Selenium application results in a reduction of unsaturated fatty acids in sesame plants subjected to salt stress. This alteration in membrane lipid composition is thought to decrease membrane fluidity. It is hypothesized that this reduction in membrane elasticity may contribute to diminished uptake of cytotoxic ions, specifically Cl^- and Na^+ , potentially through the modulation of relevant membrane transporters. Furthermore, maintaining membrane stability is crucial for preventing the efflux of beneficial compatible solutes and restricting the influx of harmful ions, thereby helping to preserve essential osmotic homeostasis across the plasma membrane [107, 108]. Membrane stability is a critical component of plant salinity tolerance, as salt stress invariably induces oxidative damage to cellular membranes [109, 110]. In this study, selenium treatment was found to reduce the proportion of unsaturated fatty acids in the plasma membrane of salt-stressed sesame plants. This shift in lipid composition was associated with increased membrane rigidity. It is proposed that this enhanced membrane stability helps regulate the activity of ion channels and transporters, thereby limiting the passive influx of toxic ions such as Na^+ and Cl^- . Concurrently, a less fluid

membrane reduces the efflux of osmoprotectants, safeguarding the intracellular accumulation of compounds vital for osmotic adjustment. This dual mechanism—restricting ion entry and retaining solutes—is essential for maintaining cellular osmotic balance under saline conditions and enhances the plant's overall resilience. Additionally, a lower degree of fatty acid unsaturation is linked to reduced susceptibility to lipid peroxidation, further contributing to membrane integrity under oxidative stress conditions [111]. By modulating the fatty acid profile towards greater saturation, selenium may enhance membrane stability and fortify the barrier against ion leakage [112]. Our data also indicated that selenium application significantly altered the endogenous levels of key phytohormones, including indole-3-acetic acid (IAA), abscisic acid (ABA), and gibberellic acid (GA). This suggests that selenium influences the biochemical and physiological metabolism of sesame plants not only through direct antioxidant action and membrane stabilization but also via hormonal regulation, collectively enhancing the plant's capacity to tolerate salt stress. The regulatory influence of selenium on phytohormone biosynthesis and signaling represents a significant mechanism for enhancing stress tolerance. Our findings, which demonstrated selenium-induced modulation of IAA, ABA, and GA levels, are consistent with previous research. For instance, Luo et al. [113] reported that selenium application elevated IAA concentrations in *Nicotiana tabacum* under stress conditions, a response attributed to the upregulation of genes involved in IAA biosynthesis and efflux transport. By fine-tuning hormonal homeostasis, selenium optimizes key physiological processes—including stomatal regulation, water-use efficiency, and nutrient acquisition—thereby improving overall plant resilience. This aligns with agronomic studies across various species indicating that selenium ameliorates salinity stress through the reinforcement of phytohormone-mediated defenses and the regulation of ionic homeostasis [114–117]. The results of the present study demonstrated that selenium application under salinity stress significantly increased the K^+/Na^+ ratio in sesame plants. This finding is consistent with previous research in other species; for instance, Subramanyam et al. [64] observed enhanced K^+/Na^+ homeostasis in rice, while Elkesh et al. [87] reported similar improvements in ionic equilibrium in selenium-treated wheat under salt stress. These collective findings suggest that selenium plays a conserved role in promoting ionic balance across diverse plant species. However, the precise molecular mechanisms through which selenium regulates ion transporter activity and maintains ionic homeostasis under saline conditions remain incompletely characterized and warrant further investigation. To elucidate the mechanism by which selenium modulates ion homeostasis

under salinity stress, we analyzed the expression of the *NHX1* gene in sesame plants. The *NHX1* antiporter plays a pivotal role in plant ionic regulation by facilitating the sequestration of Na^+ ions from the cytosol into the vacuole, thereby reducing cytotoxic Na^+ accumulation and maintaining cytoplasmic K^+/Na^+ balance. The upregulation of *NHX1* expression under salt stress is a well-documented tolerance mechanism in various plant species [118]. Our results demonstrated that selenium application further upregulated *NHX1* transcription, suggesting that enhanced vacuolar Na^+ compartmentalization is a key mechanism through which selenium mitigates ionic stress. This increased *NHX1* expression likely facilitates more efficient Na^+ sequestration, thereby alleviating the disruption of water transport and osmotic balance caused by high Na^+ concentrations. This finding aligns with research in rice, where selenium treatment significantly enhanced *OsNHX1* expression under salinity stress, contributing to increased Na^+ storage in root vacuoles and reduced translocation to shoots [118, 119]. While these results clearly indicate that selenium promotes *NHX1*-mediated ion homeostasis, the precise signaling pathways through which selenium regulates this gene's expression under stress conditions require further investigation.

Overall, multivariate analyses further confirmed the physiological basis of the observed trends. Principal component analysis (PCA; Fig. 11) provided a comprehensive understanding of the relationships among salinity levels, selenium application, and physiological traits in sesame. The clear separation of treatments indicated distinct plant responses to different salinity–selenium combinations. The close clustering of the control and Salt0Se treatments reflected the positive effect of selenium in promoting growth and pigment accumulation even under non-stress conditions, likely due to its role in maintaining photosynthetic efficiency and water balance. In contrast, the Salt75 and Salt75Se treatments were positioned in opposite directions on the biplot, confirming that selenium application under moderate salinity partially alleviated the negative impacts of salt stress by enhancing antioxidant defense and osmotic regulation. Furthermore, the Salt150Se treatment was associated with stress-related traits such as proline and soluble sugars, suggesting activation of osmotic adjustment mechanisms under severe salinity. The Pearson correlation matrix (Fig. 10) supported these findings, showing strong positive correlations between growth-related and pigment traits (blue) and negative associations with oxidative stress indicators (red), consistent with the protective role of selenium in mitigating salt-induced oxidative damage.

Conclusion

The data demonstrated that selenium application can mitigate the detrimental effects of salinity on sesame plants. This protective effect may be attributed to selenium's role in enhancing photosynthetic pigments, promoting the accumulation of osmolytes, increasing the activity of both enzymatic and non-enzymatic antioxidants, and reducing unsaturated fatty acid content under salt stress conditions. Selenium treatment may regulate Na^+ compartmentalization and alleviate Na^+ toxicity by upregulating *NHX1* expression. Furthermore, selenium application plays a key role in nutrient uptake and maintaining ionic balance. Based on our findings, selenium modulates the tolerance mechanisms of sesame plants by altering the levels of phytohormones such as abscisic acid (ABA), gibberellic acid (GA), and indole-3-acetic acid (IAA), thereby contributing to the enhancement of these mechanisms. Considering the beneficial effects of selenium, further research is warranted to elucidate the selenium-triggered signaling pathways in plants.

Supplementary Information

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Supplementary Material 1.

Supplementary Material 2.

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Authors' contributions

H.H. performed the majority of the experiments, collected and critically analyzed the data, and drafted the manuscript. F.Z. equally contributed to the experimental design. M.R. and B.S. contributed to manuscript drafting and critically revised the final version. All authors read and approved the final manuscript.

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Data will be made available on request.

Declarations

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