Agrotechniques in Industrial Crops

Journal Homepage: https://atic.razi.ac.ir

Combined Effects of Seaweed Extract and Selenium Nanoparticles on Mitigation of Cadmium and Chromium Stress in Fennel (*Foeniculum vulgare* Mill.)

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ARTICLE INFO

Original paper

Article history:
Received: 01 Oct 2025
Revised: 06 Feb 2026
Accepted: 07 Jun 2026

Keywords:
Fennel
Heavy metals
Seaweed extract
Seed yield
Selenium nanoparticles

ABSTRACT

Heavy metal contamination by cadmium (Cd) and chromium (Cr) threatens fennel productivity and seed safety through oxidative damage and metal accumulation. This study tested whether combined foliar application of seaweed extract (SWE) and selenium nanoparticles (SeNPs) provides enhanced protection against Cd- and Cr-stress in fennel. For this purpose, a greenhouse factorial experiment was conducted using a randomized complete block design (RCBD) with three replicates. Treatments included three soil metal levels (control, 20 mg Cd kg^{-1}, and 100 mg Cr kg^{-1}) and four foliar treatments (control, SWE at 1 mL L^{-1}, SeNPs at 20 mg L^{-1}, and SWE + SeNPs). Electrolyte leakage (EL), proline, malondialdehyde (MDA), catalase (CAT), superoxide dismutase (SOD), seed Cd/Cr concentrations, seed yield, and biological yield were measured. Results showed that Cd and Cr stress increased membrane and oxidative injury compared with the non-contaminated control, as reflected by higher EL, MDA, CAT, and SOD, and they reduced seed and biological yields. Foliar SeNPs and SWE improved stress tolerance by lowering oxidative damage indices and improving productivity, with SWE+SeNPs treatment showing greater improvements than individual applications. SWE+SeNPs decreased MDA by 27.8% (Cd) and 22.7% (Cr), reduced CAT by 32.8% (Cd) and 28.3% (Cr), and reduced SOD by 25.9% (Cd) and 30.3% (Cr) relative to stressed controls, indicating alleviation of oxidative pressure. The combined treatment also produced the greatest improvement in seed safety by lowering seed Cd by 63.5% and seed Cr by 41.1% relative to the foliar control. These biochemical improvements translated into higher productivity, with SWE+SeNPs increasing seed yield by 21.6% relative to the foliar control and improving biological yield under both Cd and Cr stress. In conclusion, SWE+SeNPs foliar strategy most effectively mitigated Cd/Cr toxicity by reducing oxidative damage, lowering metal transfer to seeds, and improving yield, supporting its potential use for safer fennel production in contaminated soils.

DOI: 10.22126/ATIC.2026.12771.1235

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1. Introduction

Medicinal and aromatic plants are increasingly cultivated under suboptimal soil conditions, where contamination by heavy metals threatens both productivity and quality (Mukherjee *et al.*, 2023). Fennel (*Foeniculum vulgare* Mill.) is a high-value medicinal crop used for essential oil and bioactive compounds, and its economic return depends strongly on stable growth and yield (Hajalizadeh *et al.*, 2019). Yet fennel is often grown in regions affected by industrial inputs, wastewater irrigation, and fertilizer-derived contaminants, making it a relevant model for testing practical mitigation strategies that can protect yield and physiological integrity under soil pollution (Safaei *et al.*, 2024; Rafieian *et al.*, 2024). Among toxic metals, cadmium (Cd) and chromium (Cr) are particularly damaging because they disturb nutrient balance, inhibit photosynthesis, and trigger excessive reactive oxygen species (ROS) formation (Mohamed *et al.*, 2025). ROS accumulation causes membrane

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disruption and metabolic dysfunction, commonly reflected by increased electrolyte leakage (EL) and elevated malondialdehyde (MDA) as an index of lipid peroxidation. Plants partially counteract this through osmotic adjustment and redox buffering, including accumulation of proline and activation of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT) (Zhang *et al.*, 2024). Although such responses are well documented in many crops, evidence remains limited and fragmented for fennel, especially regarding how biostimulants and nanonutrients can jointly stabilize these core stress indicators while sustaining yield.

Two promising, environmentally friendly approaches are selenium nanoparticles (SeNPs) and seaweed extracts (SWEs), but most studies examine them separately. SeNPs can act as a highly available Se source that strengthens enzymatic antioxidant defenses and improves redox homeostasis, potentially lowering ROS-driven damage (thereby reducing EL and MDA) while supporting growth (Abadi *et al.*, 2025). SWEs, rich in bioactive polysaccharides, minerals, and hormone-like compounds, can enhance nutrient uptake, stimulate metabolism, and prime stress signaling, often leading to improved osmoprotection (e.g., proline regulation) and stronger antioxidant capacity. A complementary interaction between SWE and SeNPs may occur, in which SWE improves overall physiological performance and stress signaling, while SeNPs support redox homeostasis and antioxidant efficiency. Such complementarity could result in greater mitigation of oxidative and membrane damage compared with individual applications, without necessarily implying strict statistical synergy across all traits (Ashour *et al*., 2024; Mishra *et al*., 2025).

Recently, SeNPs and SWE have been increasingly applied to modulate heavy metal toxicity in plants, with Se-based treatments improving stress tolerance in *Sargassum fusiforme* (Zhang *et al.*, 2020), faba bean (El Khattabi *et al*., 2023), and pepper (Pal *et al*., 2024), and SeNPs alleviating heavy metal–induced damage in wheat (Nasirzadeh *et al.*, 2022), rice (Basit *et al.*, 2023), and sage (Alawamleh *et al*., 2023) mainly by enhancing antioxidant capacity and limiting oxidative injury; however, their combined use remains largely unexplored, particularly for mitigating Cd and Cr toxicity in medicinal plants such as fennel. The novelty of the present work is to test whether SWE and SeNPs can act synergistically against two major contaminants with distinct toxic modes—Cd, a highly mobile and bioaccumulative metal that disrupts nutrient balance and membrane integrity, and Cr, a metal strongly linked to oxidative stress and metabolic dysfunction—thereby providing practical insight into fennel vulnerability and defense. Accordingly, we propose that SWE "primes" whole-plant performance while SeNPs strengthen enzymatic detoxification at the cellular level, together reducing oxidative membrane damage more effectively than either treatment alone.

Therefore, this study investigates the synergistic effects of SWE and SeNPs in mitigating Cd and Cr stress in fennel. Specifically, we quantify how single and combined treatments influence yield, EL, MDA, proline accumulation, and key antioxidant enzymes under heavy metal exposure. We hypothesize that co-application will (i) improve yield relative to untreated stressed plants, (ii) reduce membrane injury (lower EL and MDA), and (iii) enhance antioxidant defense and osmotic adjustment (higher enzyme activities and optimized proline), indicating a mechanistically coherent and agronomically relevant protective synergy.

2. Materials and methods

2.1. Growth conditions and treatment application

This investigation was conducted in 2023 as a factorial experiment arranged in a randomized complete block design (RCBD) with three replications under greenhouse conditions. The experiment evaluated the combined effects of heavy metal stress and foliar treatments on fennel growth. Three levels of heavy metal stress were applied: control (no heavy metal addition), cadmium stress (20 mg Cd kg^{-1} soil), and chromium stress (100 mg Cr kg^{-1} soil). The second factor consisted of three foliar treatments: SeNPs (20 mg L^{-1}), SWE (1 mL L^{-1}), and a non-sprayed control.

Fennel seeds were obtained from Pakan Bazr Company (Isfahan, Iran), surface-sterilized, and sown at a density of seven plants per pot in 3 L plastic pots. Plants were grown in a greenhouse under a 16/8 h light/dark photoperiod, with temperatures of 25 ± 2 °C (day) and 18 ± 2 °C (night), and relative humidity of 60–70%. The experiment was arranged as a factorial in a randomized complete block design (RCBD) with three replications; blocks were oriented according to the greenhouse environmental gradient created by the air conditioner located on one side, to minimize positional effects and reduce experimental error.

The growth medium was a sandy loam soil (pH 7.13; EC 1.18 dS m^{-1}) containing 0.19% total nitrogen, 11.9 mg kg^{-1} available phosphorus, 245 mg kg^{-1} potassium, 0.08 mg kg^{-1} cadmium, and 0.13 mg kg^{-1} chromium. Prior to sowing, the soil was oven-sterilized at 120°C and then artificially contaminated with cadmium chloride ($CdCl_2$, 99.9% purity) and potassium dichromate ($K_2Cr_2O_7$, 99.5% purity) (Merck, Germany) to achieve the desired metal concentrations.

The SWE (Ascophyllum nodosum) was obtained from Armadin Co. (Tehran, Iran). SeNPs were purchased from Nikzma Farind Parsian Co. (Tehran, Iran) and were produced via a chemical synthesis method as specified by the manufacturer. The nanoparticles had an average particle size of 15–40 nm, a specific surface area of 30–50 m^2 g^{-1}, a bulk density of 3.89 g cm^{-3}, and a purity of 99.9%, with no additional surface coating reported by the supplier.

Foliar applications were performed three times at 15-day intervals using a hand-held atomizer. The first foliar spray was applied 30 days after sowing, and heavy metal stress was imposed immediately after this first application by introducing Cd or Cr into the soil. Each pot received approximately 25 mL of spray solution, applied until full leaf wetting without runoff. Spraying was carried out in the early morning (08:00–10:00 h) under calm greenhouse conditions to ensure uniform deposition and minimize evaporation. Control plants were sprayed with distilled water only. Plants were harvested at 110 days after sowing, when fennel reached physiological seed maturity, characterized by fully developed umbels and hardened, brown-colored seeds. At harvest, seed yield and biological yield were recorded, and plant samples were collected for further analysis. Each treatment included three biological replicates (three pots). For dry weight determination, harvested plant material was shade-dried at room temperature until constant weight. Dry weight was recorded for the aerial parts (shoots).

2.2. Physiological and biochemical traits measured

2.2.1. Proline content determination

Proline was extracted from leaf tissues following the method of Bates et al. (1973). Fresh leaf samples were homogenized in 3% sulfosalicylic acid. Two milliliters of the resulting extract were mixed with 2 mL of ninhydrin reagent and 2 mL of glacial acetic acid in separate test tubes. The tubes were incubated in a water bath at 100°C for 1 h. After incubation, the reaction mixture was cooled, and 2 mL of toluene was added. Samples were placed on ice until two distinct phases formed. The chromophore-containing upper phase was carefully separated, and its absorbance was recorded at 520 nm using a UV–Vis spectrophotometer (UV-160A, Shimadzu, Japan) equipped with quartz cuvettes.

2.2.2. Electrolyte leakage measurement

EL, used as a marker of cell membrane injury, was determined following the method of Ben Hamed et al. (2007). Fresh aerial tissue (0.2 g) was carefully washed with deionized water to eliminate surface ions and transferred into tightly sealed test tubes containing 10 mL of deionized water. The samples were incubated in a water bath at 32°C for 2 hours, after which the initial electrical conductivity (EC_1) of the solution was recorded using a conductivity meter (Winlab Data Windaus). The tubes were then autoclaved at 121°C for 20 minutes to ensure complete cell lysis, cooled to 25°C, and the final electrical conductivity (EC_2) was measured. The percentage of EL was calculated using Equation 1.

$$EL = EC_1/EC_2 \times 100 \quad (1)$$

2.2.3. Malondialdehyde (MDA) content

Lipid peroxidation was estimated by measuring malondialdehyde (MDA) levels according to Heath and Packer (1968). Fresh leaf tissue (0.5 g) was homogenized in trichloroacetic acid (TCA) solution, and the homogenate was centrifuged at 14,000 rpm for 15 min. Subsequently, 1.5 mL of the supernatant was mixed with 20% TCA containing thiobarbituric acid (TBA) and incubated in a boiling water bath. After cooling, the mixture was centrifuged again, and absorbance of the supernatant was measured at 532 and 600 nm using a UV–Vis spectrophotometer. MDA concentration was calculated and expressed as µmol g^{-1} fresh weight.

2.2.4. Enzyme extraction and antioxidant enzyme assays

Fresh leaf tissue (0.5 g) was homogenized in 5 mL of ice-cold extraction buffer containing 50 mM potassium phosphate buffer (pH 7.0), 1 mM EDTA, and 1% (w/v) polyvinylpyrrolidone (PVP) using a pre-chilled mortar and pestle. The homogenate was centrifuged at 12,000 × g for 15 min at 4°C, and the resulting supernatant was collected and used as the crude enzyme extract for all antioxidant enzyme assays.

Catalase (CAT) activity was assayed following Eising and Gerhardt (1987) with minor modifications. The reaction mixture had a final volume of 2.31 mL, consisting of 2.0 mL of 50 mM potassium phosphate buffer (pH 7.0), 200 µL of 3% (v/v) H_2O_2, 100 µL of the same buffer, and 10 µL of enzyme extract. The decomposition of H_2O_2 was monitored by recording the decrease in absorbance at 240 nm for 1 min. One unit of CAT activity was defined as the amount of enzyme required to decompose 1 µmol of H_2O_2 per minute, and activity was expressed as U mg^{-1} protein.

SOD activity was determined following Dhindsa et al. (1981). The reaction system contained 100 mM phosphate buffer (pH 7.8), 12 mM methionine, 75 µM nitroblue tetrazolium (NBT), 100 µM EDTA, and 0.025% Triton X-100. Each reaction received 290 µL of this mixture, 2 µM riboflavin, and 10 µL of enzyme extract. After illumination, absorbance was measured at 560 nm, and one unit of SOD activity was defined as the amount of enzyme causing 50% inhibition of NBT photoreduction. The soluble protein content of the enzyme extracts was determined using the Bradford (1976) method with bovine serum albumin (BSA) as the standard. Enzyme activities were expressed on a protein basis (U mg^{-1} protein).

2.3. Determination of chromium and cadmium in seeds

To quantify heavy metal accumulation in fennel seeds, 0.2 g of dried tissue was digested with 4 mL of 65% HNO_3 for 24 hours at 25°C. The samples were then heated at 90°C for 5 hours to remove residual NO_2. After cooling, the digests were filtered and diluted to a final volume of 10 mL. Cadmium (Cd) and chromium (Cr) concentrations were subsequently measured using inductively coupled plasma mass spectrometry (ICP–MS, Agilent 4500 series, Santa Clara, CA, USA) following the method described by Wang et al. (2021).

2.4. Biological yield and seed yield

At maturity, plants were harvested, and the mean total dry biomass per pot was recorded as biological yield. Seeds were carefully separated and weighed to determine seed yield per pot.

2.5. Statistical analysis

All experimental data were analyzed using SAS software version 9.1. Data were subjected to two-way analysis of variance (ANOVA) to assess the main effects of heavy metal stress and foliar treatments, as well as their interaction. Mean comparisons were performed using Duncan's multiple range test at a significance level of $P \leq 0.05$. Interaction effects were interpreted to distinguish additive responses from treatment combinations showing comparatively stronger trends.

3. Results and discussion

The analysis of variance (Table 1) revealed that the interaction between foliar application and heavy metal treatment was highly significant ($p \leq 0.01$) for the activities of the CAT and SOD, and significant ($p \leq 0.05$) for MDA levels. Furthermore, the main effects of foliar treatments (SeNPs and SWE) and heavy metals (cadmium and chromium) were highly significant ($p \leq 0.01$) for both proline content and EL (Table 1).

Table 1. Analysis of variance (ANOVA) for electrolyte leakage, malondialdehyde concentration, and antioxidant enzyme activities of fennel plants under heavy metal stress as influenced by foliar application of selenium nanoparticles and seaweed extract

SOV	df	EL	Proline	MDA	CAT	SOD
Block	2	8.44^{ns}	641.77^{**}	0.46^{ns}	0.006^{ns}	2.25^{**}
Heavy metals (H)	2	308.77^{**}	6517.19^{**}	36.13^{**}	0.183^{**}	11.57^{**}
Foliar spraying (S)	3	47.43^{**}	1105.21^{**}	13.23^{**}	0.015^{**}	1.95^{**}
H × S	6	4.40^{ns}	54.71^{ns}	1.93^{*}	0.010^{**}	1.19^{**}
Error	22	9.32	60.35	0.53	0.002	0.31
CV (%)	-	0.8	2.4	6.7	11.1	11.2

Notes: * and ** indicate significance at the 5% and 1% probability levels, respectively.

3.1. Electrolyte leakage

According to the results presented in Table 1, the interaction between heavy metals and foliar application had no significant effect on electrolyte EL. Mean comparison results indicated that heavy metal stress increased EL compared to the control, with cadmium and chromium causing 29.81% and 23.13% increases, respectively. Foliar application of SeNPs, SWE, and their combined application reduced EL relative to the control, with the lowest EL (15.57%) observed under the combined application of SeNPs and SWE (Fig. 1).

The presence of heavy metals significantly reduces cellular membrane stability (Aroei *et al*., 2019). EL is an essential indicator of membrane integrity, reflecting photosynthetic carbon assimilation under oxidative stress conditions (Kumari *et al*., 2017). Previous studies reported that increasing cadmium concentration markedly decreased membrane stability by up to 75%. Such findings suggest that cadmium induces lipid peroxidation of membrane fatty acids, promotes MDA production, increases electrolyte leakage (EL), and consequently reduces membrane stability. Oxidative stress caused by cadmium and lead has also been shown to elevate EL in sage leaves, whereas SeNPs mitigated this effect (Aroei *et al*., 2019). Similarly, chromium stress increased the percentage of leaf EL in lettuce plants (Majnooni Harris *et al*., 2023), consistent with the present results. Furthermore, the application of SWE has been reported to decrease leEL by enhancing membrane integrity. which aligns with our findings. This improvement is likely due to the ability of seaweed-based biostimulants to reduce ROS levels, thereby stabilizing cellular membranes (Arab *et al*., 2023).

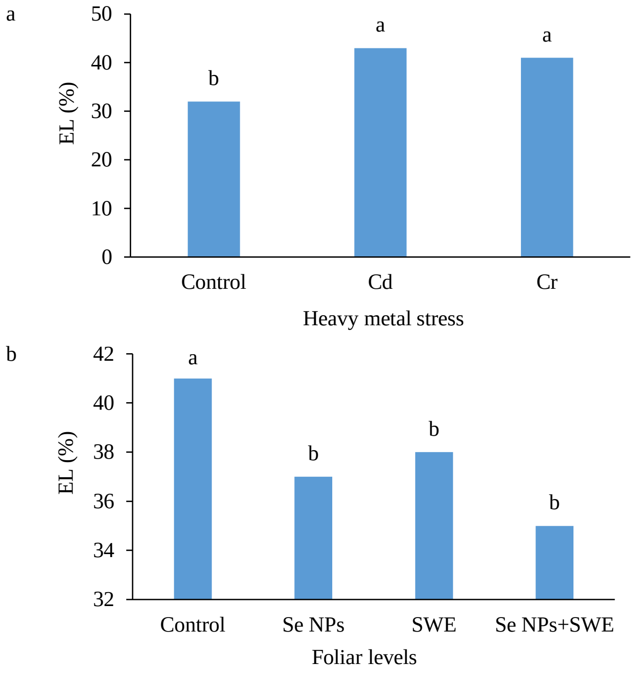

Figure 1. Electrolyte leakage (EL) of fennel as affected by heavy metal stress and foliar application. Means sharing the same letter within each column are not significantly different according to Duncan's multiple range test (p≤0.05)

3.2. Proline content

According to the analysis of variance results (Table 1), only the main effects of heavy metals and foliar application were highly significant (p≤0.01) for proline content. Mean comparisons revealed that proline content increased under Cd and Cr stress by 25.19% and 26.37%, respectively, compared to the control. Proline accumulation is one of the most common adaptive responses of plants to heavy metal stress (Tian *et al*., 2016). Plants modulate proline concentration to regulate cellular osmotic balance and protect themselves against various stresses. As a unique amino acid, proline accumulation has been reported in numerous plant species under stress conditions (El Rasafi *et al*., 2022). Previous studies have reported that cadmium exposure in Periwinkle plants enhances proline content and the activity of catalase (CAT) and superoxide dismutase (SOD) (Ahsan *et al*., 2025). Under high heavy metal stress, proline accumulation is induced, which in turn contributes to plant stress tolerance. This tolerance is attributed to proline functioning as an osmolyte, reactive oxygen species (ROS) scavenger, and molecular chaperone to preserve protein structure demonstrated that increasing cadmium concentrations decreased the activity of CAT, ascorbate peroxidase, guaiacol peroxidase, and polyphenol oxidase in coriander. The increased activity of antioxidant enzymes under cadmium stress is explained by reduced photosynthetic rate and consequent elevated ROS production, which stimulates the activity of detoxifying enzymes (Mansour and Salama, 2020; Głowacka *et al*., 2019). The reduction in CAT and SOD activities following SeNPs and SWE application under Cd and Cr stress should not be interpreted as suppression of antioxidant defense. Rather, it reflects an alleviation of oxidative pressure, as lower ROS production reduces the requirement for maintaining elevated enzyme activities. This interpretation is supported by the concurrent decline in MDA and electrolyte leakage, indicating improved membrane integrity and redox balance. The greater moderation of enzyme activities under the combined treatment suggests complementary action in restoring oxidative homeostasis (Sharma *et al*., 2024). Moreover, foliar application of SeNPs, SWE, and their combination increased proline content compared to the control, with the lowest (11.02%) and highest (15.27%) proline levels observed under SeNPs application and the combined application of SeNPs and SWE, respectively (Fig. 2). Researchers have reported that foliar-applied Se increases proline content in rosemary

(Shamsai *et al.*, 2021). Selenium nanoparticles influence osmotic regulators (free proline and soluble sugars), nutrient content, Se accumulation, and cellular integrity (water content and membrane stability), significantly enhancing growth-related indices in coriander plants (Sardar *et al.*, 2022). Additionally, aqueous extracts of the seaweeds *Fucus spiralis* and *Cystoseira ericoides* increased proline levels and improved plant responses to heavy metal stress, highlighting the potential of these SWE in phytoremediation processes (El Khattabi *et al.*, 2023). These findings align with the present study, where foliar application of SeNPs enhanced proline accumulation.

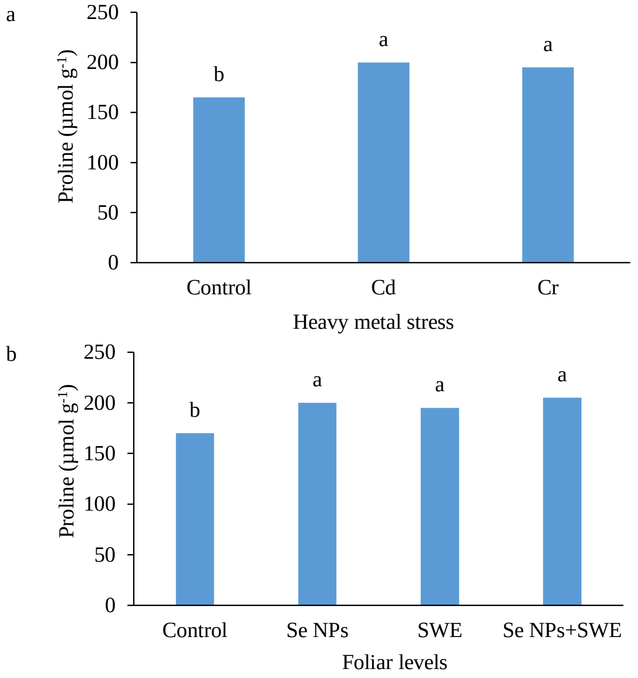

Figure 2. Proline content of fennel under heavy metal stress as affected by foliar application. Means sharing the same letters within each column are not significantly different according to Duncan's multiple range test ($p \leq 0.05$).

3.3. Malondialdehyde

Heavy metal stress markedly increased MDA content in fennel leaves. Under Cd contamination, MDA increased by 54.9%, rising from 9.53 µg g^{-1} FW in the non-heavy-metal control to 14.76 µg g^{-1} FW in Cd-stressed plants. Under Cr contamination, MDA increased by 40.6% compared with the non-stressed control (13.40 vs. 9.53 µg g^{-1} FW). Foliar application of SeNPs and SWE decreased MDA under heavy metal stress. Under Cd stress, SeNPs, SWE, and their combination decreased MDA by 13.8%, 24.4%, and 27.8%, respectively, compared with the Cd-stressed control. Under Cr stress, MDA decreased by 17.5% with SeNPs, 23.4% with SWE, and 22.7% with the combined treatment. Under non-heavy-metal conditions, foliar treatments caused only a slight decrease in MDA (7.0–9.1%) relative to the untreated control (Table 2).

These findings show that Cd and Cr triggered oxidative stress severe enough to damage membrane lipids in fennel leaves, as reflected by the elevated MDA levels, with Cd imposing a stronger peroxidative burden than Cr (Wang *et al.*, 2021; Hu *et al.*, 2023). The consistent decline in MDA after SeNPs and SWE spraying indicates that both inputs enhanced the plant's capacity to restrict ROS-driven lipid peroxidation and preserve membrane integrity under metal toxicity. The stronger protective trend observed with SWE and SeNPs—and the comparable or slightly enhanced response when they were combined—suggests that SWE likely contributed broad stress buffering through improved metabolic stability and stress signaling (Tian *et al.*, 2016), while SeNPs supported redox homeostasis by strengthening antioxidant defense (Wang *et al.*, 2021). The minimal change in MDA under non-stressed conditions further implies that these treatments act mainly as stress-mitigators rather than simply depressing baseline oxidative metabolism, supporting their use as targeted protectants when fennel is exposed to heavy metal contamination (Wang *et al.*, 2021; Fatima *et al.*, 2025).

Table 2. Mean comparison of the interaction effect of heavy metal stress × foliar application on malondialdehyde content and catalase (CAT) and superoxide dismutase (SOD) activities in fennel plants

Heavy metal	SeNPs & SE	MDA (µg g^{-1} FW)	CAT (U mg^{-1} protein min)	SOD (U mg^{-1} protein min)
Non-heavy metals	Control	9.53^{e}	0.22^{e}	3.56^{f}
	SeNPs	8.86^{e}	0.26^{e}	4.13^{ef}
	SWE	8.70^{e}	0.29^{e}	4.03^{ef}
	SeNPs + SWE	8.66^{e}	0.27^{e}	4.10^{ef}
Cd contamination	Control	14.76^{a}	0.61^{a}	7.10^{a}
	SeNPs	12.73^{b}	0.48^{bc}	5.46^{bcd}
	SWE	11.16^{c}	0.47^{bc}	5.73^{bc}
	SeNPs + SWE	10.66^{cd}	0.41^{cd}	5.26^{cd}
Cr contamination	Control	13.40^{b}	0.53^{b}	6.36^{ab}
	SeNPs	11.06^{c}	0.47^{bc}	4.83^{cde}
	SWE	10.26^{cd}	0.42^{cd}	5.26^{cd}
	SeNPs + SWE	10.36^{cd}	0.38^{d}	4.43^{def}

Note: Values within the same column sharing the same letter do not differ significantly ($P<0.05$). Abbreviations: Cd: Cadmium stress; Cr: Chromium stress; SeNPs: Foliar application of selenium nanoparticles; SWE: Seaweed extract.

3.4. Catalase activity and superoxide dismutase activity

Heavy metal contamination significantly increased CAT activity relative to non-stressed plants. Under Cd stress, CAT activity increased by 177.3%, from 0.22 to 0.61 U mg^{-1} protein min. Under Cr stress, CAT increased by 140.9%, reaching 0.53 U mg^{-1} protein min. Application of SeNPs and SWE decreased CAT activity under stress compared with stressed controls. Under Cd contamination, CAT decreased by 21.3% with SeNPs, 23.0% with SWE, and 32.8% with the combined treatment. Under Cr contamination, CAT decreased by 11.3%, 20.8%, and 28.3% with SeNPs, SWE, and their combination, respectively. In contrast, under non-heavy-metal conditions, CAT activity increased slightly by 18.2–31.8% following foliar application (Table 2).

Exposure to heavy metals strongly increased SOD activity in fennel leaves. Under Cd contamination, SOD increased by 99.4%, from 3.56 to 7.10 U mg^{-1} protein min. Under Cr contamination, SOD increased by 78.7%, reaching 6.36 U mg^{-1} protein min compared with the non-stressed control. Foliar application of SeNPs and SWE decreased SOD activity under heavy metal stress. Under Cd stress, SOD decreased by 23.1% with SeNPs, 19.3% with SWE, and 25.9% with the combined treatment relative to the Cd-stressed control. Under Cr stress, SOD decreased by 24.1%, 17.3%, and 30.3% with SeNPs, SWE, and their combination, respectively. Under non-heavy-metal conditions, SOD activity increased modestly by 13.2–16.0% following foliar treatments (Table 2).

The marked activation of CAT and SOD under Cd and Cr exposure reflects a classic oxidative-stress response in which fennel boosts enzymatic ROS scavenging to counter metal-induced superoxide and hydrogen peroxide accumulation, with the stronger induction under Cd suggesting a higher redox disturbance than Cr (Jawad Hassan *et al*., 2020). The reduction of both enzymes after SeNPs and SWE application under stress is best interpreted not as inhibition, but as stress alleviation—i.e., these treatments likely lowered ROS generation and membrane oxidative pressure, thereby decreasing the plant's need to maintain elevated antioxidant enzyme activities (Irani *et al*., 2023). The comparatively greater moderation observed with the combined treatment supports the idea of complementary modes of action: SWE may improve overall physiological stability and stress signaling, while SeNPs enhance redox buffering efficiency, together restoring a more balanced intracellular ROS state. In contrast, the modest enzyme stimulation in non-stressed plants indicates a priming effect, where foliar inputs elevate baseline antioxidant readiness without causing damage, potentially enabling a faster and more effective response when heavy metal stress occurs (Wang *et al*., 2021).

3.5. Analysis of variance for grain cadmium, grain chromium, and plant yield

According to the results of the analysis of variance (Table 3), the interaction effect between foliar application × heavy metals was significant only for biological yield at the 1% probability level. The main effects of foliar application (SeNPs and SWE) and heavy metals (cadmium and chromium) were highly significant (p≤0.01) for grain cadmium and chromium concentrations as well as grain yield (Table 3).

Table 3. Analysis of variance (ANOVA) for grain cadmium, grain chromium, and yield of fennel plants under heavy metal stress as influenced by foliar application of selenium nanoparticles and seaweed extract

SOV	df	MS			
		Seed Cd	Seed Cr	Seed yield	Biological yield
Block	2	0.003^{ns}	0.008^{**}	42.36^{**}	269.08^{**}
Heavy metal (H)	2	0.292^{**}	0.798^{**}	332.11^{**}	3173.25^{**}
Spraying (S)	3	0.023^{**}	0.016^{**}	22.00^{**}	241.43^{**}
H × S	6	0.022^{ns}	0.015^{ns}	111.0^{ns}	12.65^{**}
Error	22	0.0004	0.001	0.45	1.81
CV (%)	-	20.4	21.8	3.5	2.0

ns, * and ** indicate non-significant, significant at p≤0.05, and significant at p≤0.01, respectively.

3.6. Accumulation of heavy metals in plant tissues

Heavy metals affected seed Cd accumulation. Compared with the heavy-metal control (0.158 mg g^{-1}), Cd toxicity increased seed Cd to 0.2858 mg g^{-1}, an increase of 80.9%, whereas Cr toxicity slightly decreased seed Cd to 0.150 mg g^{-1}, a decrease of 5.1%. Foliar treatments reduced seed Cd compared with the foliar control (0.181 mg g^{-1}): SeNPs decreased seed Cd to 0.088 mg g^{-1} (51.4% decrease), SWE decreased it to 0.085 mg g^{-1} (53.0% decrease), and SWE + SeNPs decreased it to 0.066 mg g^{-1} (63.5% decrease).

Heavy metals strongly influenced seed Cr concentration. Relative to the heavy-metal control (0.025 mg g^{-1}), Cd toxicity decreased seed Cr to 0.016 mg g^{-1} (36.0% decrease), while Cr toxicity increased seed Cr to 0.467 mg g^{-1} (1768% increase). Foliar treatments decreased seed Cr compared with the foliar control (0.231 mg g^{-1}): SeNPs decreased seed Cr to 0.146 mg g^{-1} (36.8% decrease), SWE decreased it to 0.164 mg g^{-1} (29.0% decrease), and SWE + SeNPs decreased it to 0.136 mg g^{-1} (41.1% decrease) (Table 4).

Table 4. Mean comparison of the effects of heavy metal stress and foliar application on seed cadmium, seed chromium concentrations, and seed yield of fennel plants

Factor	Treatment	Seed Cd (mg g^{-1})	Seed Cr (mg g^{-1})	Seed yield (g pot^{-1})
Heavy metals	Control	0.0158^{b}	0.025^{b}	25.16^{a}
	Cd toxicity	0.2858^{a}	0.016^{b}	15.66^{c}
	Cr toxicity	0.0150^{b}	0.467^{a}	16.50^{b}
SWE & SeNPs	Control	0.181^{a}	0.231^{a}	17.00^{d}
	SeNPs	0.088^{b}	0.146^{b}	19.77^{b}
	SWE	0.085^{bc}	0.164^{b}	19.00^{c}
	SWE + SeNPs	0.066^{c}	0.136^{b}	20.66^{a}

Note: Means with the same letter are not significantly different ($P<0.05$). Abbreviations: Cd: Cadmium, Cr: Chromium stress, SeNPs: Foliar application of selenium nanoparticles, SWE: Seaweed extract.

The seed ion data indicate that Cd and Cr exposure not only increased the accumulation of their respective metals in seeds, but also altered cross-metal uptake patterns, implying competition and/or transporter-level interference during root uptake and long-distance translocation. The strong enrichment of seed Cd under Cd stress and of seed Cr under Cr stress suggests that fennel can transfer a substantial fraction of absorbed metals into reproductive tissues, which is agronomically important because it directly affects seed safety and marketability (Bakhtiari *et al*., 2023). The reductions observed with foliar SeNPs and SWE—most clearly when applied together—support the idea that these treatments limited metal entry into seeds by improving membrane integrity and root selectivity, modulating metal transporter activity, and/or enhancing detoxification and sequestration (e.g., binding in root cell walls and vacuoles) that restricts xylem loading and seed deposition (Tian *et al*., 2016). The fact that foliar treatments lowered both seed Cd and seed Cr suggests a broad protective mechanism rather than a metal-specific effect, consistent with strengthened antioxidant status and reduced stress-driven permeability that otherwise facilitates metal movement (Lam *et al*., 2025). Overall, the combined treatment appears most promising for minimizing edible/propagule contamination, highlighting its potential value for producing safer fennel seeds under contaminated soils.

3.7. Seed yield and biological yield

Heavy metal stress reduced seed yield. Compared with the heavy-metal control (25.166 g pot^{-1}), Cd toxicity decreased seed yield to 15.66 g pot^{-1} (37.7% decrease), and Cr toxicity decreased it to 16.5 g pot^{-1} (34.5% decrease). In contrast, foliar treatments increased seed yield relative to the foliar control (17 g pot^{-1}): SeNPs increased seed yield to 19.77 g pot^{-1} (16.3% increase), SWE increased it to 19 g pot^{-1} (11.8% increase), and SWE + SeNPs increased it to 20.66 g pot^{-1} (21.6% increase) (Table 4).

Cadmium and chromium toxicities adversely affected biological systems. In the absence of SWE and SeNPs, biological yield decreased by 40% and 33%, respectively, compared to the control. Foliar application of SWE and SeNPs significantly improved the biological yield of fennel plants. SWE, SeNPs, and their combined application (SWE + SeNPs) increased biological yield by 25%, 21%, and 30% under chromium stress, and by 20%, 18%, and 17% under cadmium stress, respectively, compared to the untreated plants (Table 5).

The yield responses confirm that Cd and Cr toxicity imposed a substantial constraint on fennel productivity, likely through combined disruption of photosynthetic efficiency, nutrient balance, and reproductive development, which together reduce assimilate supply to seeds and limit overall biomass formation (Mousavi *et al*., 2024). The recovery of both seed yield and biological yield following foliar SeNPs and SWE indicates that these treatments improved whole-plant performance under metal stress, consistent with a mitigation of oxidative damage and better maintenance of metabolic function during critical growth stages. The stronger improvement observed with the combined treatment—especially under Cr—supports a complementary action in which SWE enhances physiological vigor and resource acquisition (Ahmed *et al*., 2024) while SeNPs strengthen redox buffering and stress tolerance, resulting in more effective preservation of growth and reproductive allocation than either input alone (Babashpour-Asl *et al*., 2022). The comparatively stronger yield recovery observed under the combined treatment indicates a beneficial interaction between SWE and SeNPs. However, given that interaction effects were not significant for all yield-related traits, these responses are best described as additive with complementary physiological benefits rather than strictly synergistic across all parameters (Nasirzadeh *et al*., 2022; Wang *et al*., 2021).

Table 5. Mean comparison of the interaction effect of heavy metal stress and foliar application on the biological yield of fennel plants.

Heavy metal	SeNPs & SE	Mean biological yield (g pot^{-1})
Non-heavy metals	Control	77.67^{c}
	SeNPs	84.00^{b}
	SWE	83.66^{b}
	SeNPs + SWE	92.00^{a}
Cd contamination	Control	46.33^{h}
	SeNPs	56.34^{f}
	SWE	58.33^{ef}
	SeNPs + SWE	60.31^{de}
Cr contamination	Control	52.00^{g}
	SeNPs	58.66^{ef}
	SWE	56.23^{f}
	SeNPs + SWE	61.30^{d}

Note: Values with the same letter are not significantly different (P<0.05). Abbreviations: Cd: Cadmium, Cr: Chromium stress, SeNPs: Foliar application of selenium nanoparticles, SWE: Seaweed extract.

4. Conclusion

In summary, cadmium and chromium stress impaired fennel growth, yield, and seed safety by intensifying oxidative damage, membrane instability, and metal accumulation in seeds. Foliar application of selenium nanoparticles and seaweed extract mitigated these adverse effects by improving redox balance, stabilizing cellular membranes, and limiting metal transfer to reproductive tissues. Although not all traits exhibited statistically significant interaction effects, the combined application generally produced greater improvements than individual treatments, reflecting complementary physiological actions. These findings support the use of SWE and SeNPs as an effective and environmentally friendly strategy for improving fennel productivity and seed safety under heavy metal–contaminated conditions.

Conflict of interests

All authors declare no conflict of interest.

Ethics approval and consent to participate

No humans or animals were used in the present research. The authors have adhered to ethical standards, including avoiding plagiarism, data fabrication, and double publication.

Consent for publications

All authors read and approved the final manuscript for publication.

Availability of data and material

All the data are embedded in the manuscript.

Authors' contributions

All authors had an equal role in study design, work, statistical analysis and manuscript writing.

Informed consent

The authors declare not to use any patients in this research.

Funding/Support

This study was supported by University of Mohaghegh Ardabili, Ardabil, Iran.

Acknowledgement

The authors gratefully acknowledge all individuals and organizations that provided the necessary facilities for conducting this research.

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HOW TO CITE THIS ARTICLE

Raeisi Sadati S.Y., Jahanbakhsh-Godekahriz S., Tobeh A., Farzaneh S., Shafiei Y., Fazeli-Nasab B. 2026. Combined Effects of Seaweed Extract and Selenium Nanoparticles on Mitigation of Cadmium and Chromium Stress in Fennel (*Foeniculum vulgare* Mill.). *Agrotechniques in Industrial Crops* 6(2): 208-218. 10.22126/ATIC.2026.12771.1235