Effects of Cerium Oxide Nanoparticle Seed Priming on Pepper Seed Germination and Seedling Growth Under Salt Stress: Postprint

Authors: Qin Zhongwei, Lin Xinqi, Wei Xiya, Liang Lamei, Li Yingzhi

Date: 2023-06-05T00:00:00+00:00

Abstract

Due to their strong free radical scavenging capacity and antioxidant enzyme-like properties, cerium oxide nanoparticles (CeO2NPS) have been proven to enhance plant salt tolerance, but their priming effects and mechanisms on pepper seeds remain unclear. To reveal the effects of CeO2 NPS seed priming treatment on germination and seedling growth of pepper under salt stress, the pepper cultivar (Capsicum annuum) 'Maoshu 360' was used as experimental material, and seven CeO2 NPS concentrations (0, 0.05, 0.1, 0.2, 0.3, 0.4, 0.5 mmol · L-1) were established, with the non-primed treatment group as control, to investigate the effects of different concentrations of CeO2NPS priming treatment on pepper seed germination, seedling biomass, and physiological and biochemical indices under salt stress. The results showed that: (1) Seeds treated with 0.5 mmol · L-1 CeO2NPS exhibited significantly increased soluble protein, proline content, catalase (CAT) activity, reduced ascorbic acid (AsA) content, and AsA/DHA ratio, while superoxide anion ($O2 \cdot -$) content was significantly decreased; under salt stress, this treatment resulted in the highest germination rate, germination potential, germination index, and vigor index. (2) Seedlings from seeds primed with 0.4 mmol · L-1 CeO2NPS showed the highest fresh weight, dry weight, and root length under salt stress, with significantly increased soluble protein, reduced ascorbic acid (AsA) content, and AsA/DHA ratio in the seedlings. In conclusion, CeO2NPS priming treatment can improve seed germination rate under salt stress by reducing seed water potential, promoting storage substance metabolism, and enhancing antioxidant capacity; simultaneously, it can promote seedling growth under salt stress during the seedling stage by enhancing protein synthesis and the ascorbate-glutathione cycle (AsA-GSH).

Full Text

Effect of Cerium Oxide Nanoparticle Seed Priming on Pepper Seed Germination and Seedling Growth Under Salt Stress

QIN Zhongwei, LIN Xinqi, WEI Qianya, LIANG Lamei, LI Yingzhi
Binhai Agricultural College, Guangdong Ocean University, Zhanjiang, Guangdong 524088, China*

Abstract

Cerium oxide nanoparticles (CeO_2NPs) have demonstrated the capacity to enhance plant salt tolerance through their potent free radical scavenging abilities and antioxidant enzyme-mimetic properties. However, the specific effects and underlying mechanisms of CeO_2NP seed priming in pepper remain unclear. To elucidate how CeO_2NP priming influences pepper germination and seedling development under saline conditions, we investigated the pepper variety *Capsicum annuum* 'Maoshu 360' using seven CeO_2NP concentrations (0, 0.05, 0.1, 0.2, 0.3, 0.4, and 0.5 mmol $\cdot$ L^{-1}), with an unprimed control group. Our study examined the impacts of different priming concentrations on seed germination, seedling biomass, and various physiological-biochemical parameters under salt stress. The results revealed: (1) Seeds primed with 0.5 mmol $\cdot$ L^{-1} CeO_2NPs exhibited significantly elevated levels of soluble protein, proline, catalase (CAT) activity, reduced ascorbic acid (AsA) content, and AsA/DHA ratio, while showing significantly reduced superoxide anion ($O_2 \cdot^-$) content. Under salt stress, this treatment achieved the highest germination rate, germination potential, germination index, and vigor index. (2) Seedlings derived from seeds primed with 0.4 mmol $\cdot$ L^{-1} CeO_2NPs demonstrated maximum fresh weight, dry weight, and root length under salt stress, with significantly increased soluble protein, AsA content, and AsA/DHA ratio. In conclusion, CeO_2NP seed priming enhances germination rates under salt stress by reducing seed water potential, promoting storage substance metabolism, and improving antioxidant capacity. Additionally, priming facilitates seedling growth during the nursery stage by enhancing protein synthesis and activating the ascorbate-glutathione (AsA-GSH) cycle.

Keywords: cerium oxide nanoparticles, pepper, seed priming, salt stress, seedling growth

Introduction

Soil salinization represents a major abiotic stress factor limiting crop productivity, adversely affecting both seed germination and seedling establishment [**?**, **?**]. Salt stress induces excessive accumulation of toxic ions (Na^+ and Cl^-) within plant cells, inhibits water absorption [**?**, **?**], and triggers overproduction of reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2) and superoxide anion ($O_2 \cdot^-$) [**?**, **?**]. This oxidative damage compromises membrane integrity

and elicits oxidative stress responses, impairing germination in pepper (*Capsicum annuum*), *Zygophyllum*, Chinese cabbage (*Brassica rapa*) [**?**, **?**, **?**, **?**] and hindering normal seedling growth in pepper, *Calotropis gigantea*, and wheat (*Triticum aestivum*) [**?**, **?**, **?**, **?**], ultimately reducing yield in crops such as rice (*Oryza sativa*) [**?**, **?**]. Therefore, investigating methods to improve germination rates and enhance salt tolerance is crucial for addressing soil salinization and ensuring food security and agricultural sustainability [**?**, **?**].

Seed priming is an emerging seed treatment technology that addresses salinity stress by inducing a specific physiological state before germination. Through a memory effect, primed plants can activate key signaling molecules and transcription factors to combat salt stress during growth [**?**, **?**, **?**]. Various nanomaterials, including zinc oxide nanoparticles (ZnONPs), selenium nanoparticles (SeNPs), and cerium oxide nanoparticles (CeO_2NPs), have been employed for seed priming [**?**, **?**, **?**, **?**]. Among these, CeO_2NPs are particularly promising due to their exceptional free radical scavenging capacity, which has been widely utilized in medical and cosmetic applications and more recently in nano-agriculture [**?**, **?**]. CeO_2NPs mitigate oxidative stress by mimicking antioxidant enzyme activities through Ce^{3+} and Ce^{4+} redox states, thereby reducing excessive ROS accumulation and enhancing plant stress tolerance. Khan et al. [**?**, **?**] demonstrated that CeO_2NP seed priming improved α-amylase activity and ROS scavenging in *Brassica rapa* seeds, increasing germination under salt stress. At the seedling stage, priming enhanced salt tolerance by elevating SOD and POD activities and soluble sugar content, ultimately promoting biomass accumulation. However, research on CeO_2NP seed priming effects on pepper growth and development under salt stress remains scarce.

Pepper (*Capsicum annuum*), a solanaceous crop valued for its appetite-stimulating, digestive, antimicrobial, and insecticidal properties, is widely cultivated and consumed [**?**, **?**]. China has become the world's largest producer of fresh peppers, with a cultivated area of 780,000 hectares and an annual output of 19 million tons [**?**, **?**]. Pepper fruits contain abundant bioactive compounds such as capsaicin, offering broad application prospects in food, pharmaceutical, and cosmetic industries [**?**, **?**].

To explore cultivation techniques and salt tolerance mechanisms in pepper, this study utilized the 'Maoshu 360' variety to investigate: (1) the effects of CeO_2NP seed priming on pepper germination and seedling growth under salt stress; (2) the optimal CeO_2NP concentration for enhancing pepper salt tolerance; and (3) the potential mechanisms underlying priming-induced salt tolerance.

Materials and Methods

Plant Materials

This experiment was conducted from March to August 2022 at Binhai Agricultural College, Guangdong Ocean University. The test material was pepper (*Capsicum annuum*) variety 'Maoshu 360'.

Seed Priming Treatment

Following the method of Newkirk et al. [**?**, **?**], cerium oxide nanoparticle (CeO_2NP) solution was synthesized and stored at 4°C. The solution was then diluted to concentrations of 0, 0.05, 0.1, 0.2, 0.3, 0.4, and 0.5 mmol $\cdot$ L^{-1} (designated S0, S0.05, S0.1, S0.2, S0.3, S0.4, and S0.5, respectively). The 0 mmol $\cdot$ L^{-1} solution (S0) served as an osmotic buffer control, consisting of 100 mmol $\cdot$ L^{-1} TES and 100 mmol $\cdot$ L^{-1} $MgCl_2$ adjusted to pH 7.5 with HCl. Approximately 2 g of uniform, plump pepper seeds were placed in beakers with 10 mL of each CeO_2NP solution, sealed, and incubated for 24 h to induce priming. Seeds were then rinsed with distilled water, blotted dry with filter paper, and re-dried to initial moisture content.

Seed Germination Assay

Both primed and unprimed control (CK) seeds were placed in standard germination boxes (10 cm × 10 cm × 5 cm) containing 5 mL of 100 mmol $\cdot$ L^{-1} NaCl solution to simulate salt stress. Germination was conducted in a light incubator at 25°C, with 60 seeds per treatment and three replicates.

Seedling Growth Assessment

Primed and unprimed seeds were sown in nursery trays containing a vermiculite-coconut coir mixture. Each tray received 50 germinated seeds (5 × 10 arrangement) and was irrigated with 100 mmol $\cdot$ L^{-1} NaCl solution to maintain salt stress conditions. Seedlings were grown at room temperature until the two-leaf-and-one-heart stage, when samples were collected for physiological measurements.

Germination Indices

Germination was defined as radicle emergence exceeding 2 mm. Daily germination counts were recorded until no further germination occurred. Germination potential (GP), germination rate (GR), germination index (GI), and vigor index (VI) were calculated according to Gammoudi et al. [**?**, **?**]:

- **Germination Potential (GP)** = (Number of germinated seeds within 3 days / Total seeds) × 100%
- **Germination Rate (GR)** = (Total germinated seeds at experiment end / Total seeds) × 100%
- **Germination Index (GI)** = Σ(Ni/ti)
- **Vigor Index (VI)** = GP × (Shoot height + Root length)

where Ni represents the number of germinated seeds on day i, and ti is the time from experiment start to day i.

Growth Parameters

At the two-leaf-and-one-heart stage, uniform seedlings were selected and whole plants were harvested. After washing and drying, shoot height and root length were measured with vernier calipers, fresh weight was determined with an electronic balance, and samples were oven-dried at 105°C for 30 min, then at 80°C to constant weight for dry weight measurement.

Physiological and Biochemical Analysis

Primed seeds and two-leaf-stage seedlings were sampled for physiological analysis. Malondialdehyde (MDA) content ($nmol \cdot g^{-1}$) was determined by the thiobarbituric acid method [**?**, **?**]. Superoxide anion ($O_2 \cdot^-$) content ($\mu mol \cdot g^{-1}$) was measured according to Schneider & Schlegel [**?**, **?**]. Soluble sugar content ($mg \cdot g^{-1}$) was assayed by anthrone colorimetry [**?**, **?**], and soluble protein content ($mg \cdot g^{-1}$) by Coomassie brilliant blue staining [**?**, **?**]. Reduced ascorbic acid (AsA) and dehydroascorbic acid (DHA) contents ($nmol \cdot g^{-1}$) were determined by the method of Wang et al. [**?**, **?**]. Ascorbate peroxidase (APX) activity [$U \cdot (g \cdot min)^{-1}$] was measured according to Nakano & Asada [**?**, **?**]. Superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) activities ($U \cdot g^{-1}$) were assayed using commercial kits (Solarbio). Proline content ($\mu g \cdot g^{-1}$) was also determined using a kit (Solarbio).

Statistical Analysis

Experimental data were processed using SPSS 26.0 statistical software, with figures prepared in Excel. Significance was assessed at $P < 0.05$.

Results

Effects of CeO_2NP Seed Priming on Pepper Seed Germination Under Salt Stress

The germination performance of primed versus unprimed pepper seeds under salt stress is presented in Table 1 . All CeO_2NP priming treatments enhanced pepper seed germination under saline conditions. The S0.5 treatment (0.5 $mmol \cdot L^{-1}$) achieved the highest germination rate, increasing by 34.59% compared to the unprimed control, with a germination potential 12 times greater than the control. CeO_2NP priming significantly improved the germination index (GI) across all concentrations. Both GI and vigor index (VI) were enhanced under salt stress, with the S0.5 treatment reaching peak values (increasing by 399.57 and 7.84, respectively, compared to the control).

Effects of CeO_2NP Priming on Pepper Seedling Growth Under Salt Stress

Seedling growth data for primed versus unprimed treatments under salt stress are shown in Table 2 . Appropriate CeO_2NP priming concentrations promoted

pepper seedling growth under saline conditions. The S0.4 treatment (0.4 mmol·L^{-1}) produced seedlings with maximum fresh weight, dry weight, and root length, significantly exceeding the unprimed control by 35.75%, 135.33%, and 35.48%, respectively. However, shoot height was significantly lower than the control, indicating that priming substantially promoted root system development.

Effects of CeO_2NP Seed Priming on Oxidative Stress Responses in Pepper Seeds

Analysis of superoxide anion and malondialdehyde (MDA) contents in primed versus unprimed seeds (Figure 1 [Figure 1: see original paper]) revealed that the S0.5 treatment significantly reduced superoxide anion content by 68.54% compared to the control, though MDA content increased by 21.74% (a non-significant difference). Antioxidant enzyme activity data (Table 3) showed that S0.5 treatment significantly increased CAT activity by 54.06% while decreasing POD and APX activities by 44.56% and 59.98%, respectively, compared to the control. Regarding antioxidant substances (Table 3), S0.5 treatment elevated AsA content by 8.89% and significantly increased the AsA/DHA ratio by 78.81% relative to the control.

Effects of CeO_2NP Seed Priming on Soluble Protein, Proline, and Soluble Sugar Contents in Pepper Seeds

As shown in Table 4 , the S0.5 treatment significantly increased soluble protein and proline contents by 119.62% and 114.50%, respectively, compared to the unprimed control, while soluble sugar content showed no significant difference.

Effects of CeO_2NP Priming on Soluble Protein, Proline, and Soluble Sugar Contents in Pepper Seedlings Under Salt Stress

Under salt stress, seedlings from primed seeds exhibited altered metabolite profiles (Table 5). The S0.4 treatment significantly increased soluble protein content by 20.51% compared to the control, while proline and soluble sugar contents decreased significantly by 75.02% and 41.16%, respectively.

Effects of CeO_2NP Priming on Oxidative Stress in Pepper Seedlings Under Salt Stress

Antioxidant enzyme activity data for salt-stressed seedlings (Table 6) indicated that the S0.4 treatment significantly reduced CAT, POD, APX, and SOD activities by 84.92%, 13.58%, 41.33%, and 61.79%, respectively, compared to the control. MDA content in S0.4-treated seedlings decreased by 20.38% relative to the control. AsA content and the AsA/DHA ratio in S0.4-treated seedlings (Figure 2 [Figure 2: see original paper]) were significantly elevated by 111.04% and 273.77%, respectively.

Discussion

Mechanisms of CeO_2NP Seed Priming Effects on Pepper Seed Germination Under Salt Stress

Salt stress disrupts cellular ionic and redox homeostasis through osmotic effects, leading to excessive ROS accumulation that causes lipid peroxidation, protein oxidation, and membrane damage, ultimately inhibiting seed germination [**?**, **?**]. Consequently, employing ROS-scavenging agents for seed priming represents a promising research direction. Studies have demonstrated that CeO_2NPs can facilitate seed germination under abiotic stress by scavenging ROS and enhancing the antioxidant enzyme system [**?**, **?**].

Our findings indicate that the S0.5 treatment was most effective for pepper seed priming, accelerating germination speed and improving overall germination under salt stress. Notably, the S0 control treatment (containing $MgCl_2$) also substantially improved germination compared to the unprimed control, likely because $MgCl_2$ has been used as an inorganic priming agent to promote sugar beet seed germination [**?**, **?**]. The slightly elevated MDA content in S0.5-treated seeds suggests that CeO_2NP priming may partially perturb oxidative stress balance, potentially due to nanoparticle toxicity. However, the significant reduction in superoxide anion content, coupled with increased proline, soluble protein, CAT activity, AsA content, and AsA/DHA ratio, demonstrates that CeO_2NP priming actively modulates seed physiological processes. Proline accumulation helps stabilize cytoplasmic osmotic balance, protects cells from oxidative damage, and supports stress-related protein synthesis [**?**, **?**, **?**]. This synergizes with enhanced CAT activity and the AsA-GSH cycle to scavenge excess ROS, maintain redox homeostasis, and reduce lipid peroxidation during germination, thereby preserving membrane integrity and facilitating successful seedling establishment. The significantly higher germination rates confirm that the beneficial effects of CeO_2NP priming outweigh potential toxicity, suggesting that pepper seeds possess protective mechanisms to adapt to CeO_2NP exposure. These results align with Khan et al. [**?**, **?**], who reported that 0.1 $mmol \cdot L^{-1}$ CeO_2NP priming improved *Brassica rapa* germination under salt stress, indicating that CeO_2NP seed priming generally benefits stress tolerance, though optimal concentrations vary among species.

Effects of CeO_2NP Priming on Pepper Seedling Growth and Physiology Under Salt Stress

Salt stress inhibits plant growth by disrupting antioxidant system establishment and suppressing protein synthesis [**?**, **?**, **?**]. CeO_2NPs have been shown to promote plant growth and development [**?**, **?**]. In our study, seedlings from S0.4-primed seeds exhibited maximum fresh weight, dry weight, and root length under salt stress, significantly surpassing the unprimed control. This demonstrates that optimal CeO_2NP priming concentrations enhance pepper seedling growth in saline conditions, consistent with Khan et al. [**?**, **?**] who reported sim-

ilar benefits in *Brassica rapa* seedlings primed with 0.1 mmol · L^{-1} CeO_2NPs. Furthermore, S0.4-treated seedlings outperformed the S0 control ($MgCl_2$) in these parameters, indicating that CeO_2NP priming is more effective than $MgCl_2$ alone.

MDA accumulation serves as an indicator of salt stress-induced oxidative damage [**?**, **?**]. The reduced MDA content in S0.4-treated seedlings suggests that CeO_2NP priming mitigates lipid peroxidation in pepper seedlings under salt stress. The concurrent decrease in CAT, SOD, POD, and APX activities may be attributed to the intrinsic antioxidant enzyme-mimetic activity of CeO_2NPs, which possess unique Ce^{3+}/Ce^{4+} redox cycling capabilities that directly scavenge ROS [**?**, **?**].

AsA functions as a non-enzymatic antioxidant that directly scavenges ROS and participates in the AsA-GSH cycle alongside reduced glutathione (GSH) [**?**, **?**]. The AsA/DHA ratio reflects AsA-GSH cycle efficiency and serves as a valuable indicator of antioxidant capacity and stress tolerance [**?**, **?**]. Our results show that S0.4 treatment significantly increased AsA content and the AsA/DHA ratio in salt-stressed seedlings, indicating that CeO_2NP priming enhances the AsA-GSH cycle to maintain oxidative stress balance. This finding parallels Gohari et al. [**?**, **?**], who reported that foliar CeO_2NP application on grapevine (*Vitis vinifera*) under 75 mmol · L^{-1} NaCl stress promoted the AsA-GSH cycle, reduced ROS content, and alleviated oxidative damage.

Conclusion

(1) All tested CeO_2NP concentrations improved pepper seed germination under salt stress, with 0.5 mmol · L^{-1} being optimal. (2) Appropriate CeO_2NP seed priming concentrations promoted root growth and biomass accumulation in salt-stressed seedlings, with 0.4 mmol · L^{-1} showing the best performance. (3) CeO_2NP seed priming enhanced germination by activating germination-related enzymes and increasing metabolic products, while improving seedling salt tolerance through a memory effect that elevated antioxidant content, promoted the AsA-GSH cycle, reduced lipid peroxidation, and mitigated oxidative stress. CeO_2NPs demonstrate potential as a nanoscale priming agent to enhance plant growth and development under saline conditions.

References

RAFFAELLA B, WALTER C, ANDREA G, et al., 2022. A stressful life: how plants cope with multiple biotic and abiotic adverse factors[J]. Plant Stress, 5: 10095.

SCHNEIDER K, SCHLEGEL HG, 1981. Production of superoxide radicals by soluble hydrogenase from *Alcaligenes eutrophus* H16[J]. Biochem J, 193(1): 99-107.

DEINLEIN U, STEPHAN AB, HORIE T, et al., 2014. Plant salt-tolerance mechanisms[J]. Trends Plant Sci, 19(6):

GAO JF, 2006. Plant Biology Experiment Guide[M]. Beijing: Higher Education Press: 208-230.

GAO ZQ, ZHANG JY, ZHANG J, et al., 2022. Nitric oxide alleviates salt-induced stress damage by regulating the ascorbate–glutathione cycle and Na^+/K^+ homeostasis in *Nitraria tangutorum* Bobr[J]. Plant Physiol Biochem: 173:

GAMMOUDI N, KARMOUS I, ZERRIA K, et al., 2020. Efficiency of pepper seed invigoration through hydrogen peroxide priming to improve in vitro salt and drought stress tolerance[J]. Hort, Environ Biotechnol, 61: 703-714.

GOHARI G, ZAREEI E, ROSTAMI H, et al., 2021. Protective effects of cerium oxide nanoparticles in grapevine (*Vitis vinifera* L.) cv. flame seedless under salt stress conditions[J]. Ecotoxicol Environ Safety, 220: 112402.

GOYAL V, JHANGHEL D, MEHROTRA S, 2021. Emerging warriors against salinity in plants: Nitric oxide and hydrogen sulphide[J]. Physiol Plant, 171(4): 896-908.

GUI X, ZHANG ZY, LIU ST, et al., 2015. Fate and phytotoxicity of CeO_2 nanoparticles on lettuce cultured in the potting soil environment[J]. PLoS One, 10(8): e0134261.

HASSANPOURAGHDAM MB, MEHRABANI LV, BONABIAN Z, et al., 2022. Foliar application of cerium oxide-Salicylic acid nanoparticles (CeO_2:SA Nanoparticles) influences the growth and physiological responses of *Portulaca oleracea* L. under salinity[J]. Int J Mol Sci, 23(9): 5093.

HUSSAIN S, NISAR F, BHATT A, et al., 2022. Redox priming alleviates dormancy and improves salinity tolerance of seeds and seedlings of medicinal halophyte *Zygophyllum simplex* L. [J]. J Appl Res Med Aromat Plant, 30: 100384

KE QB, YE J, WANG BM, et al., 2018. Melatonin mitigates salt stress in wheat seedlings by modulating polyamine metabolism[J]. Front Plant Sci, 9: 914.

KHAN MN, LI YH, KHAN Z, et al., 2021. Nanoceria seed priming enhanced salt tolerance in rapeseed through modulating ROS homeostasis and α-amylase activities[J]. J Nanobiotechnol, 19(1): 276.

LIU XH, WANG RH, WANG WC, et al., 2021. Effect of potassium sulfate and magnesium chloride combination on germination of sugar beet seeds[J]. Chinese Sugar Crops, 43(3): 61-65.

LIZZI D, MATTIELLO A, PIANI B, et al., 2020. Germination and early development of three spontaneous plant species exposed to nanoceria ($nCeO_2$) with different concentrations and particle sizes[J]. Nanomater Basel, 10(12): 2534.

NAKANO Y, ASADA K, 1981. Hydrogen peroxide is scavenged by ascorbate-specific peroxidase in spinach chloroplasts[J]. Plant Cell Physiol, 22(5): 867-880.

NEWKIRK GM, WU HH, SANTANA I, et al., 2018. Catalytic scavenging of plant reactive oxygen species in vivo by anionic cerium oxide nanoparticles[J]. J Visualized Exp: joVE, (138): 58373.

NOOR R, YASMIN H, ILYAS N, et al., 2022. Comparative analysis of iron oxide nanoparticles synthesized from ginger (*Zingiber officinale*) and cumin seeds (*Cuminum cyminum*) to induce resistance in wheat against drought stress[J]. Chemosphere, 292: 133201.

NOUMAN W, AZIZ U, 2022. Seed priming improves salinity tolerance in *Calotropis procera* (Aiton) by increasing photosynthetic pigments, antioxidant activities, and phenolic acids[J]. Biol, 77: 609-626.

PRAKASH V, PERALTA-VIDEA J, TRIPATHI DK, et al., 2021. Recent insights into the impact, fate and transport of cerium oxide nanoparticles in the plant-soil continuum[J]. Ecotoxicol Environ Safety, 221: 112403.

RAWASHDEH RY, HARB AM, AIHASAN AM, 2020. Biological interaction levels of Zinc oxide nanoparticles; lettuce seeds as case study[J]. Heliyon, 6(5): e03983.

RONG ZY, JIANG DJ, CAO JL, et al., 2022. Endophytic fungus *Serendipita indica* accelerates ascorbate-glutathione cycle of white clover in response to water stress[J]. Front Microb, 13: 967851.

ROSSI L, ZHANG WL, LOMBARDINI L, et al., 2016. The impact of cerium oxide nanoparticles on the salt stress responses of *Brassica napus* L[J]. Environ Pollut, 219: 28-36.

SARDAR R, AHMED S, SHAH AA, et al., 2022. Selenium nanoparticles reduced cadmium uptake, regulated nutritional homeostasis and antioxidative system in *Coriandrum sativum* grown in cadmium toxic conditions[J]. Chemosphere, 287(Pt 3): 132332.

SHA HJ, HU WC, JIA Y, et al., 2017. Effect of exogenous salicylic acid, proline, and γ-Aminobutyric acid on yield of rice under salt stress[J]. Acta Agronomica Sinica, 43(11): 1677-1688.

SHANG YF, HASAN MK, AHAMMED GJ, et al., 2019. Applications of nanotechnology in plant growth and crop protection: A Review[J]. Mol, 24(14): 2558.

VELIKOVA V, YORDANOV I, EDREVA A, 2000. Oxidative stress and some antioxidant systems in acid rain-treated bean plants: Protective role of exogenous polyamines[J]. Plant Sci, 151(1): 59-66.

WANG LH, MA YQ, ZHANG BX, 2019. Market demand and breeding trends of pepper varieties in China[J]. China Vegetables, (8): 1-4.

WANG SY, JIAO HJ, FAUST M, 1991. Changes in ascorbate, glutathione, and related enzyme activities during thidiazuron-induced bud break of apple[J]. Physiol Plant, 82(2): 231-236.

XIAO ZL, 2022. Effects of salt stress on growth, physiological characteristics, yield and quality of processing pepper[D]. Xinjiang Agricultural University: 7-34.

YAN SP, CHONG PF, ZHAO M, 2022. Effect of salt stress on the photosynthetic characteristics and endogenous hormones, and: A comprehensive evaluation of salt tolerance in *Reaumuria soongorica* seedlings[J]. Plant Signal Behav, 17(1): 2031782.

YANG H, DAI LJ, WEI YX, et al., 2020. Melatonin enhances salt stress tolerance in rubber tree (*Hevea brasiliensis*) seedlings[J]. Ind Crops Prod, 145(C): 111990.

YIN FM, ZHANG SY, CAO BL, et al., 2021. Low pH alleviated salinity stress of ginger seedlings by enhancing photosynthesis, fluorescence, and mineral element contents[J]. Peer J, 9: e10832.

ZHANG L, 2017. Effects of plant growth promoters on the growth and stress resistance of maize[D]. Wuhan: Huazhong Agricultural University: 3-27.

ZHANG TJ, CHEN YJ, LIU JZ, 2019. Characteristics of soil salinization in coastal wetlands based on canonical correspondence analysis[J]. Acta Ecologica Sinica, 39(9): 3322-3332.

ZHANG WH, XIE Y, WU Y, et al., 2022. Amelioration of salt-induced damage on alfalfa by exogenous application of silicon[J]. Grassland Sci, 68(1): 60-69.

ZHAO LJ, PENG B, HERNANDEZ-VIEZCAS JA, et al., 2012. Stress response and tolerance of *Zea mays* to CeO_2 nanoparticles: cross talk among H_2O_2, heat shock protein and lipid peroxidation[J]. ACS Nano, 6(11): 9615-9622.

ZHOU XD, JIA XR, ZHANG ZH, et al., 2022. AgNPs seed priming accelerated germination speed and altered nutritional profile of Chinese cabbage[J]. Sci Total Environ, 808: 151896.

ZOU XX, HU BW, XIONG C, et al., 2022. Review and prospects of pepper breeding for the past 60 years in China[J]. Acta Horticulturae Sinica, 49(10): 2099-2118.

Note: Figure translations are in progress. See original paper for figures.