# Recent advances in nano-enabled plant salt tolerance: Methods of application, risk assessment, opportunities and future perspectives

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**Abstract** Salinity is a big issue threatening global food security. Among the different strategies, nanotechnology has shown tremendous potential for crop production under abiotic stresses, such as salinity. In this review, we discussed the environmental challenges associated with the different methods of nanomaterials application, including seed nanopriming, foliar, and soil/root application. Based on the previous research, nanopriming uses less nanomaterials and has minimum concerns about environmental safety and the food chain. We discussed in detail the preventive measures based on the application methods for the safe and sustainable use of nanomaterials in agriculture. Furthermore, we summarized the role of antioxidant enzyme-triggering nanomaterials and direct reactive oxygen species (ROS) scavenging nanomaterials (nanozymes) in plant salt tolerance. Nanomaterials improve sodium ($Na^+$) and potassium ($K^+$) homeostasis through various anatomical, physiological, and molecular mechanisms while improving plant salt tolerance. The role of nanomaterials in modulating plant photosynthesis and hormonal balance is largely overlooked. We also identified research gaps, providing guidelines for future research work. This review aimed to provide guidelines for the researchers to understand better the proper designing of NPs and different plant-related factors while using NPs for plant stress tolerance. It will help to improve the delivery efficiency of NPs into plants. Furthermore, after gaining sufficient scientific knowledge and better understanding, NPs can be integral to sustainable agriculture, saving costs and reducing biosafety concerns and environmental pollution.

**Keywords:** nano-enabled plant salt tolerance, nanoparticles, biosafety concerns, delivery efficiency, sustainable agriculture[1]

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# 1. Introduction

Soil salinization is one of the major abiotic stresses affecting plant growth and development (Munns 2002; Munns and Tester 2008). It has been reported that around 50% of arable land will be lost by the middle of the 21st century due to the ongoing rise in salinity in arable land caused by poor agricultural practices and climate change (Parihar *et al*. 2015; Shrivastava and Kumar 2015; Seleiman *et al*. 2022; Liu *et al*. 2023). Salinity is considered a severe threat to agriculture as it has already adversely affected around 1,125 million hectares of agricultural land (Parihar *et al*. 2015; Shrivastava and Kumar 2015; Hossain and Shah 2019). The excessive salts in the soil lead to ionic and osmotic stresses affecting plant morphology, metabolic and physiological activities, and biomass, ultimately resulting in plant damage and yield reduction (Munns and Tester 2008; Seleiman *et al*. 2022). The osmotic stress inhibits seed and root water uptake from the soil. Salinity increases the sodium and chlorine uptake, increasing the $Na^+/K^+$ ratio (Munns and Tester 2008). Furthermore, ionic stress also affects plant nutrient uptake, such as calcium ($Ca^{2+}$), resulting in plant nutrient deficiency (Zhang *et al*. 2018). ROS (reactive oxygen species), including $H_2O_2$ (hydrogen peroxide), $^{\bullet}O_2^-$ (superoxide anion), $^{\bullet}OH$ (hydroxyl radicals), and $^1O_2$ (singlet oxygen) are the precursors of normal cellular metabolism (Ibrahim 2016). Plants have developed antioxidants for scavenging ROS under normal growing conditions (Läuchli and Grattan 2007; Gul *et al*. 2013; Ibrahim 2016). However, stress factors such as salinity disrupt this balance, and the ROS are over-generated, causing oxidative damage (Munns and Tester 2008; Parihar *et al*. 2015). The over-accumulation of ROS damages pigments, enzymes, membrane lipids, and DNA (Ashraf and McNeilly 2004; Parihar *et al*. 2015).

Recently, nanomaterials (NPs) applications in agriculture have gained much interest while enhancing plant stress tolerance. NPs are much smaller in size (100 nm or less) than their bulks (Hu *et al*. 2020; Wu and Li 2022). The electrical properties, high biochemical reactivity, smaller size, and high surface-to-volume ratio greatly distinguish NPs from bulks (Das *et al*. 2019; Dhenadhayalan *et al*. 2020; Pereira *et al*. 2021; Ndaba *et al*. 2022). These unique properties of NPs offer a novel concept in agriculture. Different strategies have been implemented to promote agricultural production and plant salt tolerance in salt-affected lands. For example, irrigation management strategies, growing salt tolerant crops, soil reclamation strategies, application of plant hormones and growth regulators, use of beneficial soil microorganisms, and breeding and genetics strategies. Although these strategies have shown potential to promote agricultural production, they require more time and cost more money, limiting their implementation to a wide range. In the near past, nanotechnology has gained more interest in plant stress tolerance from the perspectives of improving seed germination, photosynthesis,

plant growth and development, and an inevitable increase in crop production (Khan *et al*. 2023). However, applying nanotechnology strategies requires an accurate preventive assessment of NPs-plant interactions, understanding the mechanisms of their uptake, translocation, and accumulation and assessing any potential adverse effects on plant growth and development. For instance, plant uptake of NPs is challenging to predict because it depends on a variety of factors, including the NPs size, zeta potential, and surface functionalization, as well as the mode of application, interactions with the environment (water availability, microbiota soil texture), the restriction imposed by cell wall, the physiology, and the complexity of seed coat (nanopriming), leaf (foliar application), and root (root application) anatomy of the individual plant species (González-Melendi *et al*. 2008; Falsini *et al*. 2019; Khan *et al*. 2023). Because of the widespread use in industry and the simplicity of detection and tracking using microscopy techniques, most previous studies in plants have focused on the uptake of smaller-sized metal and metal oxide NPs. However, in contrast to the enormous amount of data on metazoans, only a few integrated comparative analyses have been designed to determine the role of NPs physicochemical characteristics (size, zeta potential, coatings, etc.) in plant-nanoparticle interaction (Song *et al*. 2013; Vidyalakshmi *et al*. 2017). This review briefly summarized the nanomaterials application methods, the barriers, environmental pollution, and the mechanism behind nanomaterials-enabled plant salt tolerance.

## 2. Methods of nanomaterials application: Factors affecting the uptake and translocation of NPs

### 2.1. Seed treatment

Nanopriming refers to imbibing seeds with nanoformulations/nanosuspensions to improve seed quality, germination, seedling establishment, and crop yields under different environmental stresses (Das *et al*. 2019; Khan *et al*. 2022, 2023; Sarraf *et al*. 2022). Nanopriming has been reported in many crops, such as rapeseed, wheat, maize, and pea (Nakasato *et al*. 2017; Munir *et al*. 2018). Previous studies have reported both the positive and negative effects of nanopriming, which were not only dependent on the concentration charge, and size, the zeta potential of the NPs used, but also the effect of nanopriming varied with different plant species (Khan *et al*. 2023). For example, selenium (Se NPs, 120-260 nm, (−32.4±2) mV, and 150 μmol $L^{-1}$) and zinc oxide nanoparticles (ZnO NPs, 25 nm, zeta potential not reported, and 100 mg $L^{-1}$) were used for seed nanopriming (8h imbibition with NPs) in rapeseed under 150 mM NaCl stress (El-Badri *et al*. 2021). The ZnO NPs and Se NPs significantly increased the germination ability of the rapeseed by 167 and 174%, respectively, in salt stress. Similarly, seed nanopriming (8 h imbibition) with nanoceria ($CeO_2$ NPs, (8.5±0.2) nm, (−43.3±6.3) mV, and 0.1 mmol $L^{-1}$) also increased the germination rate of the rapeseed to 84% under 200 mmol $L^{-1}$

NaCl stress (An *et al*. 2020). In cotton, seed soaking (24h) with nanoceria ($CeO_2$ NPs, (1.8±0.3) nm, (−51.7±11.5) mV, 500 mg $L^{-1}$) increased fresh weight (42%) and dry weight (38%) under 200 mmol $L^{-1}$ NaCl stress (An *et al*. 2020). Nanopriming with carbon-based nanoparticles such as multi-walled CNTs (MWCNT-COOH, OD 13-18 nm; length 1-12 μm) and graphene nanoplatelets (<3 layers; lateral dimensions 1-2 μm) were reported to have had a dose-dependent effect on the germination of switchgrass under saline growing conditions (Pandey *et al*. 2018). When the switchgrass seeds were placed in a medium supplemented with 100 mmol $L^{-1}$ NaCl for 21d, there was a 40% increase in seed germination at 200 μg $mL^{-1}$ of CNTs and 500 μg $mL^{-1}$ of graphene. The findings of these studies suggest that nanopriming-mediated increase in seed germination is highly dependent on the type, size, charge, and dose of the NPs. Moreover, the nanopriming-seed interaction of different plant species also matters while considering the effect of nanopriming as a tool to improve the seed germination of crop species in salt stress. For example, nanopriming with nanoceria in cotton ((1.8±0.3) nm, −51.7±11.5) and rapeseed ((8.5±0.2) nm, (−43.3±6.3) mV) needed different doses of the same NPs ($CeO_2$ NPs) to improve the salt tolerance of cotton (500 mg $L^{-1}$) and rapeseed (0.1 mmol $L^{-1}$).

Besides the characterization (size and charge) of the NPs, the seed coat anatomy of crop species may also influence the uptake of NPs. NPs penetrate the seed through the vacant places in the parenchyma cell layers (Das *et al*. 2019). Generally, different crop species have different seed coat anatomy. The seed coat thickness, different layers of parenchyma cells, and the empty spaces among the parenchyma cell layers are not uniform. The variations in the seed coat anatomy of rice and maize are clearly shown in Fig. 1. The number of parenchyma cell layers in maize is 5-7, while in rice is 3-4. The differences in the number of parenchyma cell layers in maize and rice seed coats also affect the total thickness of the seed coat. Generally, rice and maize seeds are imbibed for 24h during the priming treatments (Rajjou *et al*. 2012; Ibrahim 2016). In this case, during nanopriming, the NPs might be easily absorbed by the rice seed as compared to the maize seeds. In the case of maize nanopriming, NPs having smaller sizes, a higher magnitude of charge (+ or -), and a higher concentration (dosage) may favor the translocation of NPs across the seed coat. Therefore, designing NPs with different characterizations based on understanding the seed coat anatomy of the different crop species may only favor the positive role of nanopriming in improving seed germination under adverse environmental stresses.

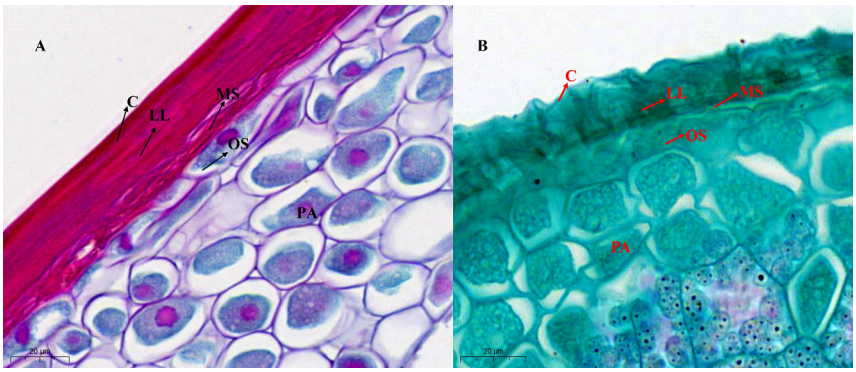


**Fig. 1** Seed coat anatomy differences. A, seed coat anatomy of maize and B) rice. Due to more parenchyma cell layers, total seed coat thickness is larger in maize seed compared to rice seed, which might interact with the efficiency of NPs uptake. C (cuticle), LL (light-line), MS (macrosclereid layer), OS (osteosclereid), and PA (parenchyma cell layers) are the different seed coat cell layers. Scale bar=20 µm.

## 2.2. Foliar application of NPs

NPs enter the plants through the stomata or leaf epidermis and then translocate via symplastic or apoplastic pathways (Fig. 2) (Hu *et al*. 2020). In different plant species, the foliar application of nanomaterials has been reported to mediate salt tolerance. For example, under 100 mmol $L^{-1}$ NaCl stress, the foliar application of $CeO_2$ NPs (10 nm, (14.5±1.1) mV, and 10 mg $L^{-1}$) improved the maize salt tolerance, reflected by a 69.5% increase in salt tolerance index (STI). However, the lower doses of $CeO_2$ NPs (1 and 5 mg $L^{-1}$) foliar application had no significant contribution to the maize salt tolerance (Liu *et al*. 2022). Chitosan-selenium nanoparticles (Cs-Se NPs, 50 nm, zeta potential not reported, and 20 mg $L^{-1}$) foliar application increased the shoot fresh weight (24%), root fresh weight (10%), and relative water content (28%) of bitter melon under 100 mmol $L^{-1}$ NaCl stress (Sheikhalipour *et al*. 2021a). Nonetheless, Cs-Se NPs at the concentration of 10 mg $L^{-1}$ also contributed to the salt tolerance of the bitter melon. However, the improvement in the salt tolerance of bitter melon was more evident at the concentration of 20 mg $L^{-1}$. Among the different concentrations (0.01, 0.02, and 0.03%) of titanium oxide nanoparticles ($TiO_2$ NPs, 25 nm, and zeta potential not reported), 0.01% concentration of $TiO_2$ NPs was the most effective in improving the salt tolerance of broad bean under 180 mM salt stress (Latef *et al*. 2018). Compared to the bare ZnO NPs, coating with a silicon shell (ZnO-Si NPs) enhanced the efficiency of PSII and PSI in pea plants in salt stress (Elshoky *et al*. 2021). The transmission electron microscopy (TEM) size of the ZnO and ZnO-Si NPs were (40±8) nm and (42±7) nm, with a zeta potential of (−9.21±3.38) and (+19.3±4.16) mV, respectively. Moreover, the foliar application of the sole ZnO NPs exhibited phytotoxicity at the concentration of 400 mg $L^{-1}$, while 400 mg $L^{-1}$ ZnO-Si NPs decreased the negative effects of salt stress. It is obvious from the findings of

this study that the Si coating changed the zeta potential of the ZnO NPs (from (−9.21±3.38) to (+19.3±4.16) mV). The positive charge may have influenced the interaction of ZnO NPs with the cells. Similarly, the foliar application of $TiO_2$ NPs (100 mg $L^{-1}$) and Cs-SeNPs (20 mg $L^{-1}$) improved the growth performance of *Stevia* under 200 mmol $L^{-1}$ NaCl stress (Sheikhalipour *et al*. 2021b). The findings of this study suggest that the efficiency of the foliar application of NPs varies depending on the type of NP and the coating agents of the NPs. Overall, the findings of the studies mentioned above show that the properties of the nanomaterials affect the efficiency of the foliar application of NPs.

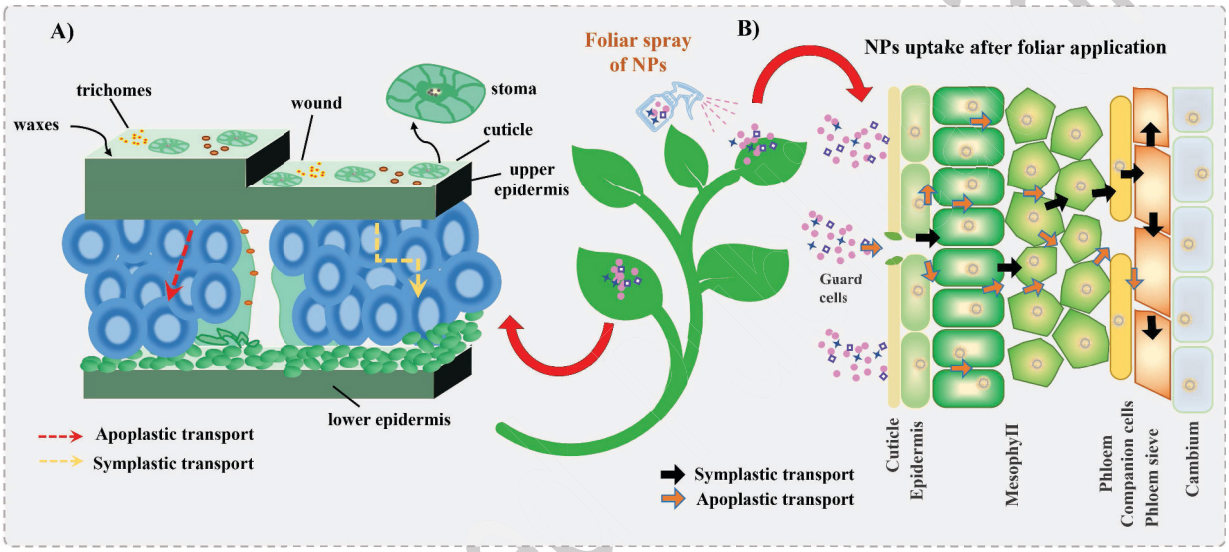


**Fig. 2** Factors affecting foliar uptake of NPs. A, the plant factors associated with NPs uptake include leaf anatomy, size of the stomatal aperture, the pore size of the cell wall, wax thickness, trichrome, and wound, while the physical factors affecting NPs leaf uptake include NPs size, shape, zeta potential, dosages, solubility, hydrophilicity, etc. B, the foliar uptake, internalization of NPs, and journey of NPs to reach phloem. The phloem further translocates the NPs into different parts (shoot and root) of the plant.

Hu *et al*. (2020) simultaneously studied foliar delivery efficiency by modifying NPs with different sizes and zeta potential in two contrasting leaf anatomies crops, such as cotton (dicotyledon) and maize (monocotyledon). They reported some exciting results that among the different sizes and zeta potentials, NPs with hydrodynamic sizes<20 and 11 nm for cotton and maize, respectively, with positive charge>15 mV, enhanced the efficiency of foliar application. Furthermore, NPs with the mentioned properties showed 100% delivery efficiencies into guard cells, 90.3% into extracellular space, and 55.8% into chloroplasts. Besides the characterization of NPs, the leaf anatomy also influences the uptake and translocation of NPs. Most commonly cultivated plant species are classified into C3 and C4 groups based on leaf anatomy and photosynthesis differences. The detailed differences in the leaf anatomy of C3 and C4 are briefly reported elsewhere (Cui 2021). In C3 plants,

there are more than two mesophyll cells between neighboring vascular bundles; in C4 plants, there are two mesophyll cells. The bundle sheath in C3 leaves is smaller, containing fewer chloroplasts. In contrast, the bundle sheath in C4 is bigger in size and has more chloroplasts (Cui 2021). Similarly, the foliar application of ZnO NPs mediated a dose-dependent salt tolerance in *Lycopersicon esculentum* (100 mg $L^{-1}$) (Faizan *et al*. 2021) and *Abelmoschus esculentus* L. *Moenc* (10 mg/L). According to the results of these investigations, various crop species require different dosages of the same nanomaterials in order to withstand salt stress better.

Higher plant leaves have a waxy cuticle layer that acts as a water barrier and is the first barrier against NP penetration (Pollard *et al*. 2008). The two common channels solutes use to cross the cuticle layer are the hydrophilic way for polar solutes and the lipophilic way for nonpolar solutes (Eichert *et al*. 2008). NPs<4.8 nm can enter directly via the cuticular way into the leaf (Lv *et al*. 2019). It has been shown that NPs larger than 5 nm were taken up by the cuticle, although the exact mechanism by which this happened is still unknown. Studies have also reported that the main barrier preventing NP entry into plant cells is the pore size of the cell wall (Etesami *et al*. 2021). Furthermore, stomatal apertures control the absorption of hydrophilic chemicals (Eichert *et al*. 2008). Stomatal apertures are estimated to be 3-10 μm wide and 25 μm long. Some researchers have documented that the radius of the stomatal pore is 20 nm (Eichert *et al*. 2008). Nonetheless, some plant species have trichrome and wounds on the leaf surface, which also influences the uptake of NPs (Hong *et al*. 2021). In addition, research showed that organic and inorganic substances generated by phyllosphere microorganisms could acidify, decrease, and chelate NPs and impact NP entrance into the leaves (Xiong *et al*. 2016). In conclusion, the differences in the properties of NPs (size, zeta potential, and dosage), plant species, stomatal sizes, and leaf structure affect the efficiency of the foliar application of NPs. Therefore, further efforts are highly recommended to explore the complexity of NPs foliar application while considering the properties of the NPs and leaf anatomy of the particular plant species to ensure safe and wide-range application in agriculture.

## 2.3. Root/soil application

Numerous strategies can be used to manage soil salinity at the nanoscale. These strategies mainly focus on improving soil structure and quality, increasing plant development, and increasing plant tolerance to salt stress. Using conventional techniques (such as nano-gypsum, nano-hydroxyapatite, nano-sulfur, etc.), nano-nutrients (such as calcium, selenium, silicon, ZnO, etc.), nano-amendments (such as nano-biochar, nano-compost, nano-chitosan, etc.), nano-halophytes, and salt-tolerant genotypes are a few examples of these approaches (Sári *et al*. 2023). Saline soils can be improved through the addition of nano-biochar, which is one of the sustainable options for environmental restoration. Through a variety of mechanisms, nano-biochar also improves plant salt tolerance.

These mechanisms include the preservation of ROS homeostasis, enhancement of $K^+$ retention and shoot $Na^+$ exclusion, stimulation of nitric oxide production, the elevation of α-amylase activity, reduction of lipoxygenase activity, etc. The role of nano-biochar and nanocomposites is briefly reported in our previous published work (Sultan *et al*. 2024). However, in the current review, we have focused on the constraints related to the soil application of NPs and the mechanisms of improving plant salt tolerance.

Root exposure to NPs has gained more research attention in some plant species than foliar application (Lv *et al*. 2019). NPs are absorbed on the root surface. Because of the root hairs, the root surface appears rough, and the root surface secretes organic acids and mucilage, causing a negative charge. Due to this phenomenon, roots make it more likely that negatively charged NPs will attach and absorb more onto the root (Zhou *et al*. 2011). For the uptake and translocation, NPs must pass through several physiological barriers to reach the xylem. The root barriers include the epidermis, endodermis, root cuticle, casparian strips, and cortex (Fig. 3). Although the root and leaf cuticle operates similarly, whether the NPs could absorb through this layer is still unclear. It has been found that the cuticles of developing root tips and root hairs have undeveloped cuticles, which may help NPs enter the epidermis directly (Schwab *et al*. 2016). Subsequently, the apoplastic and symplastic pathways transport NPs from the epidermis to the other various plant tissues.

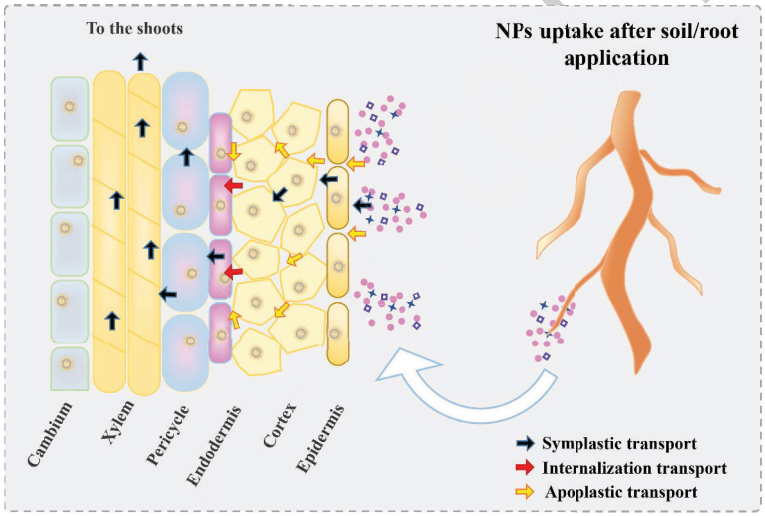


**Fig. 3** The root uptake, internalization, and the journey of NPs to reach the xylem. The xylem further translocates the NPs into different parts (shoot and leaf) of the plant.

Under hydroponic growth conditions, the root application of $CeO_2$ NPs ((5.4±2.9) nm, (−24.0±1.4) mV, and 0.1 mmol $L^{-1}$) contributed to the cucumber salt tolerance through better $Na^+/K^+$ ratio (Peng *et al*. 2022). Rossi *et al*. (2016) reported that the soil application of $CeO_2$ NPs (55.6 nm, -51.8 mV, 1,000 mg $kg^{-1}$ soil) increased rapeseed fresh and dry weight of rapeseed in salt stress. Moreover, the plant

Ce content increased with the Ce concentration in the soil mixture. The Ce concentration was 150% higher in salt-stressed plants compared to unstressed plants. Similarly, Rossi *et al*. (2017) used $CeO_2$ NPs with the same physicochemical properties but with different dosages (500 mg/kg dry sand) for rapeseed salt tolerance. They have reported that $CeO_2$ NPs modified the apoplastic root barriers, helping more transportation of $Na^+$ to shoot with less accumulation in the root. After three weeks of the trial, 35% higher Ce content was found in the leaves of plants treated with $CeO_2$ NPs+NaCl than those treated with $CeO_2$ NPs treatment alone. On the other hand, the Ce content in the roots was 40% lower in plants treated with $CeO_2$ NPs+NaCl. It is obvious from the findings of these studies that the root/soil application of NPs in plants is still controversial due to contradictory research findings. In root/soil application of the NPs, the plant growth conditions greatly influence the dosage and uptake of NPs. Such as, under hydroponic culture, $CeO_2$NPs at the dosage of 0.1 mM improved the cucumber salt tolerance (Peng *et al*. 2022). While under soil and sand growth conditions, the optimum dosages of $CeO_2$ NPs to improve rapeseed salt tolerance were 1,000 mg $kg^{-1}$ soil and 500 mg $kg^{-1}$ dry sand (Rossi *et al*. 2016; Peng *et al*. 2022). Besides the growing medium, different plant species have different root architectures, such as cucumber and rapeseed, which may also need different dosages of NPs.

The size of the NPs is another important factor that affects the root NPs uptake efficiency. The root uptake of Au NPs with size 3.5 nm was reported, whereas when the Au NPs size was 18 nm, no root uptake was observed owing to the agglomeration of NPs on the surface of the root (Sabo-Attwood *et al*. 2012). Similarly, in *Arabidopsis thaliana*, no root uptake was reported for Au NPs with sizes 7-108 nm (Taylor *et al*. 2014). Besides the uptake, the size of the NPs also determines the translocation of NPs into different plant parts. For example, $TiO_2$ NPs with a size of 36 nm were uptaken by roots and distributed aboveground parts of wheat (Larue *et al*. 2012). Furthermore, when the size of the $TiO_2$ NPs was 36-140 nm, the NPs were only accumulated in the roots with no translocation to the other parts of the wheat. However, the wheat roots even did not uptake $TiO_2$ NPs with a size of 140 nm.

The translocation and uptake of NPs are also affected by the surface charges on the roots. Mucilaginous layer covers the root cap, which secretes root exudate with negative charges. In *Arabidopsis*, NPs with positive charges were uptaken and translocated to the interior tissues of roots (Avellan *et al*. 2017). However, NPs with negative charges were transferred to the apoplast of the roots rather than absorbed by the mucilaginous layer of the roots (Avellan *et al*. 2017). In wheat and rice, similar findings were reported with different NPs (Koelmel *et al*. 2013; Spielman-Sun *et al*. 2017). Under different NPs applications, different plant species secrete different root exudates. As a result, the process of NP uptake by various plant species at various growth stages is quite complex. Several studies have examined the fate and distribution of NPs in the soil-plant system concerning many physiological parameters, including plant type, plant diseases, and the nature of the root architecture.

Due to differences in their physiological profiles, metabolic processes, and nature, several plant species displayed variation in their uptake of NPs. For instance, dicots uptaken and translocated $CeO_2$ NPs more efficiently than monocots (Layet *et al*. 2017). Judy *et al*. (2012) stated that Au NPs in size ranging from 10-50 nm were uptaken by tobacco roots, whereas the AuNPs with the same size characterization were not uptaken by wheat roots. Mycorrhizal fungus also enhances the root uptake of NPs. Mycorrhizal fungi form advantageous relationships with the roots of higher plants, increasing their potency by up to 10 times. As a result, plant roots absorb more water and nutrients, which may impact the uptake and bioavailability of NPs (Schwab *et al*. 2016). Tomato plants with mycorrhizal fungus accumulated less Ag in their root tissues when exposed to 2 nm Ag NPs (Noori *et al*. 2017). Root diseases also influence NPs uptake (Servin *et al*. 2015). In summary, compared to nanopriming and foliar application of NPs, root uptake of NPs is quite complex.

# 3. The reported mechanisms behind nano-enabled plant salt tolerance

## 3.1. Faster seed water uptake is important for nanopriming-induced salt tolerance

Osmotic stress, which lowers the seed capacity to absorb water, and ionic stress, caused by the excessive $Na^+$ and $Cl^-$ ions, are the two prominent effects of salt stress. Water must travel from outside the seed wall (higher water potential) to within the seed wall *via* diffusion and capillary action for the seed to germinate (lower water potential) successfully (Ibrahim 2016). Osmotic stress, due to salinity, reduces the water potential of the germination medium in comparison to the seed interior and slows the seed ability to absorb water (Parihar *et al*. 2015). The ionic stress caused by the high salt contents interferes with hormonal imbalance, metabolism, enzyme activity, and the use of stored energy and may also impact germination (Dehnavi *et al*. 2020). Under salinity, the seed water uptake is the primary reason behind seed germination failure in many crops. Furthermore, osmotic and ionic stress either delay or inhibit seed germination.

Recently published research suggested that absorption of NPs by the seed (nanopriming) promotes earlier radicle protrusion and faster water uptake (Khan *et al*. 2023). Ag NPs seed treatment increased the seed germination of rice (Mahakham *et al*. 2017). Seed treatment with Ag NPs regulated the *PIP1;1* and *PIP2;1* (aquaporin genes), resulting in speedy seed water absorption. Subsequently, the rapid water uptake accelerated the α-amylase enzyme activity to produce more soluble sugar for the emerging seedling growth. The results of our study showed that seed nanopriming with cerium oxide nanoparticles coated with poly (acrylic) acid (PNC) increased the germination rate and improved the rapeseed seedling growth in salt stress (Khan *et al*. 2021). The accumulation and distribution of PNC showed rapid seed water uptake during the imbibition period accompanied by higher α-amylase enzyme activity. PNC nanopriming upregulated the α-amylase

genes (*AMY1* and *AMY2*). The increase in α-amylase enzyme activity promoted reserve metabolism and provided more soluble sugar for the germinating seed in salt stress (Khan *et al*. 2021). As the PNC were accumulated in the cotyledon and radicle, the PNC significantly reduced the generation of ROS. These studies show that rapid seed water absorption, faster endosperm metabolism, and ROS homeostasis could be an integral component of the nanopriming-regulated mechanism to improve seed germination. Similarly, ZnO NPs also enhanced seed water uptake, increasing metabolic activities (Rai-Kalal and Jajoo 2021a). Improvement in wheat seed germination was ascribed to the ZnO NPs-regulated faster starch hydrolysis through increasing the α-amylase enzyme activity (Rai-Kalal and Jajoo 2021a).

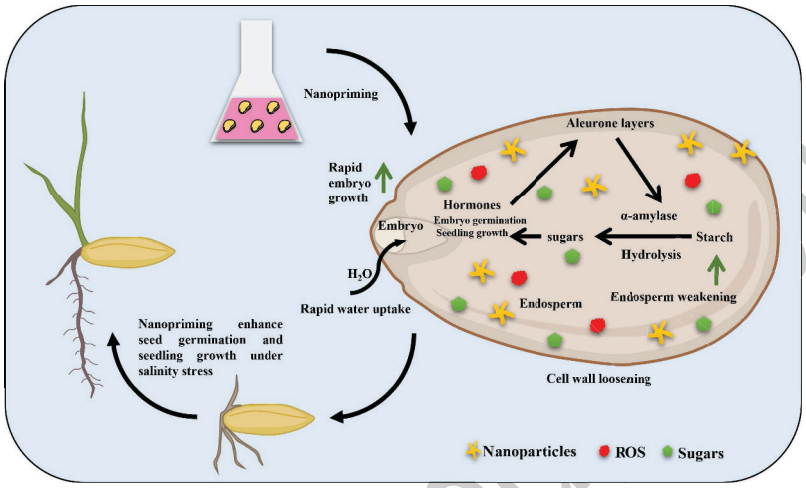


**Fig. 4** Nanopriming increases hormones production, hastens endosperm metabolism, and reduces ROS damage while enhances seed germination under salt stress.

Besides inhibiting seed water uptake, salinity affects seed germination by decreasing GAs levels and increasing ABA levels (Lee and Luan 2012; Lorrai *et al*. 2018; Shu *et al*. 2018). PNC nanopriming amplified $GA_3$ and SA levels to increase rapeseed germination in salt stress. In watermelon (diploid and triploid watermelon), manganese oxide nanopriming (MnO NPs) modulated GA and ABA, JA (Jasmonic acid), SA, OPDA (12-oxo phytodienoic acid), and ZA (zeatin) to improve the seedling growth (Kasote *et al*. 2021). MnO NPs nanopriming increased the JA level in diploid watermelon with decreased OPDA level. On the other hand, in triploid watermelon, MnO NPs nanopriming increased ABA and GA levels while decreasing SA and ZA levels (Kasote *et al*. 2021). Similarly, Ag NPs nanopriming enhanced wheat tolerance to salinity through increasing BAP (6-benzylaminopurine), IBA (indole-3-butyric acid), NAA (1-naphthalene acetic acid), whereas decreased ABA level (Ismail and Abou-Zeid 2018). Nanopriming with ZnO NPs and Se NPs enhanced the rapeseed salt tolerance at the germination stage (El-Badri *et al*. 2021). The increase in rapeseed germination under salt tolerance was associated with the upregulation of GA-allied genes (*BnGA20ox*, *BnGA3ox*, *and BnCPS*)

and the downregulation of ABA-related genes (*BnCYP707A1*, *BnCYP707A3*, and *BnCYP707A4*). As briefly mentioned above, salinity restricts seed water uptake, slower the endosperm metabolism, and imbalance the hormonal homeostasis (increased ABA levels and decreased GA levels). On the other hand, nanopriming expedites the seed water uptake, and endosperm metabolism increases GA levels and decreases ABA levels to improve seed germination in salt stress. Therefore, seed nanopriming could be adopted as a practical strategy while improving the seed germination and seedling growth of different crop species in salt-affected agricultural lands. The mechanisms behind nanopriming modulated plant salt tolerance at the germination stage are shown in Fig. 4.

## 3.2. ROS scavenging is one of the major mechanisms behind nanozymes-alleviated plant salt tolerance

Highly reactive oxygen derivatives termed reactive oxygen species (ROS) include oxygen radicals and non-radicals (Miller *et al*. 2010). Hydroxyl radicals ($^{\bullet}OH$), superoxide radicals ($^{\bullet}O_2^-$), and singlet oxygen ($^1O_2$) are examples of oxygen radicals, which are separate entities with unpaired electrons. Ozone ($O_3$) and $H_2O_2$ are examples of non-radicals ROS (Miller *et al*. 2010). Most plant cell compartments produce ROS, and regulating ROS generation is a defining feature of developing plant cells and organs. ROS takes part in signaling processes that govern ion channel function and gene expression (Liu *et al*. 2021a). ROS levels typically rise in plants under biotic and abiotic stress conditions, such as salinity. Excessive ROS interacts with macromolecules, including lipids, proteins, and nucleic acids, causing oxidative damage (Das and Roychoudhury 2014; Mittler 2017). Different tissues and cell compartments are anticipated to respond to salt stress with different ROS balances (Choudhury *et al*. 2017). Plants possess antioxidant defense systems to tolerate different stresses (Munns and Tester 2008). Superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), glutathione peroxidase (GPX), and ascorbate peroxidase (APX) are the key components of enzymatic antioxidants (Munns 2002). Glutathione, ascorbic acid, carotenoid, mannitol, and vitamin E are categorized as non-enzymatic antioxidants (Khan I *et al*. 2020). Therefore, controlling the over-accumulation of ROS through enhanced antioxidant defense is essential for achieving plant salt tolerance.

The role NPs in ROS scavenging is reported in many crop species (Wu *et al*. 2017; An *et al*. 2020; Hu *et al*. 2020; Khan *et al*. 2022; Peng *et al*. 2022). NPs can directly scavenge ROS (nanozymes) or indirectly by triggering plant antioxidant enzyme activities (Mittler 2017; Yao *et al*. 2018; Liu *et al*. 2021a). Among the nanozymes, $CeO_2$ NPs are the most widely used NPs for plant salt tolerance. $CeO_2$ NPs have many surface oxygen vacancies that can convert ROS ($H_2O_2$, $^{\bullet}O_2^-$, and $^{\bullet}OH$) to non-radical counterparts and thus are considered potent catalytic ROS scavengers. Newkirk *et al*. (2018)

determined the *in vivo* and *in vitro* ROS scavenging abilities of PNC. In the *in vivo* experiments, the live imaging (confocal microscopy) exhibited that PNC reduced the intensities of DCF (a dye used for imaging the intensity of general ROS) and DHE (a dye used for imaging the intensity of superoxide anion) in *Arabidopsis* leaf chloroplast. In the *in vitro* experiment, they checked the catalase (CAT) mimetic activity of PNC scavenging of $H_2O_2$. They found a decrease in resorufin, which indicates $H_2O_2$ level in the reaction mixture containing PNC. These *in vivo* and *in vitro* experiments confirmed the CAT mimetic activity of PNC. An *et al*. (2020) studied the mechanism of PNC seed treatment in cotton under salinity. PNC priming significantly scavenged the over-produced ROS in cotton seedlings in salt stress. When comparing seedlings in salt stress with water controls, 7 POD-related genes (*Gh_A03G2152*, *Gh_A03G1517*, *Gh_D08G2330*, *Gh_A09G1415*, *Gh_D09G1420*, *Gh_A10G2288*, and *Gh_D11G2183*) were significantly upregulated by PNC priming. PNC priming also upregulated two glutathione S-transferases GST tau (*GSTU8 Gh_A09G1508GSTU7* and *Gh_A02G0259*) genes. The results of a previous study showed that PNC nanopriming increased SOD and POD activities in rapeseed seedlings in salt stress (Pandey *et al*. 2018). However, PNC nanopriming reduced the activities of CAT, providing a clue that PNC might have CAT mimetic activity to enhance salt tolerance of rapeseed. Furthermore, the findings of our other study revealed that PNC nanopriming increased the SA levels in rapeseed seedlings in salt stress (Khan *et al*. 2022). SA has been widely reported to maintain ROS homeostasis and plant stress tolerance. Thus, the findings of our study concluded that the increase in endogenous SA levels might be another mechanism behind PNC-enabled plant salt tolerance. The foliar application of PNC significantly reduced MDA, $H_2O_2$, and $^{\bullet}O_2^-$ contents in cotton seedlings under saline growing conditions (Liu *et al*. 2021b). The PNC-mediated cotton salt tolerance was related to the increased activities of antioxidant enzymes. They further confirmed the PNC ROS scavenging through confocal microscopy and reported a significant decrease in the intensities of DCF and DHE. Wu *et al*. ( 2017) experimented with scavenging the over-production of $^{\bullet}OH$ (lacking enzymatic scavenging pathways) with PNC in *Arabidopsis* in salt stress. The mesophyll cells infiltrated with PNC demonstrated catalytic scavenging of $^{\bullet}OH$ and enhanced *Arabidopsis* salt tolerance.

Moreover, manganese oxide nanoparticles ($Mn_3O_4$ NPs) are also effective in scavenging ROS, with SOD-like and CAT-like mimicking enzymatic activities to scavenge $^{\bullet}OH$ (Yao *et al*. 2018). Lu *et al*. (2020) tested the ROS ($H_2O_2$, $^{\bullet}OH$, and $^{\bullet}O_2^-$) scavenging abilities of $Mn_3O_4$ NPs in cucumber in salt stress. They reported that $Mn_3O_4$ NPs at the concentration of 100 mg $L^{-1}$ had 46% scavenging ability of $^{\bullet}O_2^-$, indicating excellent SOD mimicking activity. Nonetheless, $Mn_3O_4$ NPs (100 mg $L^{-1}$) also had excellent CAT-mimicking activity, confirmed by a 40% $H_2O_2$ scavenging rate. Also, the scavenging rate of $^{\bullet}OH$ by $Mn_3O_4$ NPs (100 mg $L^{-1}$) was 30%. The finding of this study suggests that $Mn_3O_4$ NPs are excellent ROS scavengers with SOD-like or CAT-like mimicking activities. Similarly, Mn NPs seed nanopriming (1 mg $L^{-1}$) in *Capsicum annuum* increased the relative expression of *MnSOD* by 31.4-fold

in salt stress (Ye *et al*. 2020). A recent study reported that $Mn_3O_4$ NPs decreased ROS intensities (indicated by the significant decrease in DCF and DHE intensities) and improved rapeseed salt tolerance. $Mn_3O_4$ NPs triggered the antioxidant enzyme activities (CAT, SOD, and POD) to scavenge ROS ($H_2O_2$ and $^{\bullet}O_2^-$) and alleviate membrane damage. Other than nanozymes (direct scavenging of ROS), some NPs also play a role in ROS homeostasis by triggering the plant defense system. For example, seed nanopriming with Ag NPs improved pearl millet salt tolerance (Manickavasagam *et al*. 2019). The salt tolerance of pearl millet due to Ag NPs nanopriming was associated with increased antioxidant enzymes, including SOD, CAT, and GPX. The root application of $TiO_2$ NPs alleviated salinity stress in *Dracocephalum moldavica* by enhancing the antioxidant enzyme activities (Gohari *et al*. 2020). Priming seed with put-CQD NPs (putrescine-functionalized carbon quantum dot nanoparticles) improved the salt tolerance of grapevine by increasing the activities of SOD, CAT, GPX, and APX (Gohari *et al*. 2021). The foliar spray of Cs-Se NPs (chitosan-selenium nanoparticles) alleviated the salt tolerance of bitter melon by enhancing the antioxidant enzymes system (Sheikhalipour *et al*. 2021a). These summarized studies suggest that NPs with direct scavenging abilities (nanozymes) or indirect scavenging abilities (enhancing plant antioxidant defense system) are of broad interest in improving plant salt tolerance.

### 3.3. NPs modulates hormonal homeostasis to improve plant salt tolerance

It is well-recognized that phytohormones are important for plant ability to adapt to various environments through various mechanisms. Studies generally show that these phytohormones help to improve plant resistance to salt stress (Verma *et al*. 2016). Some recently published work reported that NPs could modulate phytohormones levels at seed germination and early seedling growth stage under salinity. Se NPs and ZnO NPs nanopriming modulated GA/ABA levels to improve rapeseed seed germination in salt stress (El-Badri *et al*. 2021). Their results showed that Se NPs and ZnO NPs nanopriming downregulated ABA-associated genes (*BnCYP707A1*, *3*, and *4*) while upregulated GA-associated genes (*BnCPS*, *BnGA20ox*, and *BnGA3ox*). Rapeseed seed nanopriming with $CeO_2$ NPs modulated the hormone levels, including $GA_3$, ABA, SA, JA, and IAA, in the germinating seedlings in salt stress (Khan *et al*. 2022). Among these hormones, the SA in the rapeseed seedlings was largely affected by $CeO_2$ NPs nanopriming. Furthermore, $CeO_2$ NPs nanopriming upregulated SA-biosynthesis-related genes [*SAR DEFICIENT1* (*SARD1*) and *phenylalanine ammonia-lyase* (*PAL*)] in rapeseed. This significant increase in the SA level reduced the ROS levels in rapeseed and was concluded as one of the mechanisms behind $CeO_2$ NPs-mediated plant salt tolerance.

Similarly, Ag NPs nanopriming reduced the ABA level while increasing BAP (6-benzyl amino purine), IBA (indole-3-butyric acid), NAA (1-naphthalene acetic acid) levels, improving the wheat salt

tolerance (Ismail and Abou-Zeid 2018). Ag NPs also increased the ABA and ethylene contents to improve rice salt tolerance (Manickavasagam *et al*. 2019). Se NPs foliar application increased ABA and indole-3-acetic acid levels, involving different physiological and molecular responses of strawberry salinity tolerance (Manickavasagam *et al*. 2019). Overall, the role of NPs in modulating phytohormones in improving plant salinity tolerance has rarely been described. Most studies related to the NPs-mediating plant salt tolerance through modulating endogenous plant hormones are limited to the regulation ABA/GA ratio during the seed germination stage. Therefore, scientists are encouraged to explore the role of NPs and the regulation of endogenous hormones while improving plant salinity tolerance. Furthermore, the role of NPs application from the perspectives of the regulation of salt-responsive hormones (ABA, SA, ethylene, and JA) and salt tolerance-promoting hormones (GA, BRs, CKs, and SLs) will provide more exciting insights into nano-enabled salinity tolerance of plant. Table 1 represents the application methods, characterization, dosage, and mechanisms behind NPs-improved plant salinity tolerance.

## 3.4. NPs modulates ion homeostasis to improve plant salt tolerance

A crucial strategy for plant salt tolerance is maintaining a high ratio of $K^+/Na^+$ (Munns and Tester 2008). On the one hand, excessive $Na^+$ is accumulated in plant tissues under salinity, causing $Na^+$ toxicity in plants. On the other hand, due to the competitive nature of $Na^+$ with $K^+$ ions, plants cannot uptake an adequate amount of $K^+$ for normal physiological and growth development (Munns and Tester 2008). $Na^+$ toxicity is the leading cause of cell damage in most salt-sensitive plants (Kader *et al*. 2006). Cytosolic concentrations of 1-10 mmol $L^{-1}$ $Na^+$ and 100-200 mmol $L^{-1}$ $K^+$; this $Na^+/K^+$ ratio is ideal for various metabolic cell processes (Munns and Tester 2008). Thus, maintaining a lower $Na^+$ or $Na^+/K^+$ ratio is vital for plant salt tolerance. Plants have developed a few strategies to reduce $Na^+$ toxicity in leaves. $Na^+$ is retained in the lower portion of leaves, transporting it into the vacuole, cycling $Na^+$ between shoots and roots, and inhibiting the transit of $Na^+$ to the xylem (Shi *et al*. 2002). To reduce $Na^+$ toxicity in stems, intracellular $Na^+$ is transported from the cell by the *SOS1* transporter (salt overly sensitive 1) or into the root xylem by the high-affinity potassium transporter (*HKT1;4*, *HKT1;5*) (Shi *et al*. 2002; Tian *et al*. 2010). The sodium-hydrogen exchanger in the tonoplast can also sequester the $Na^+$ in the vacuole (*NHX1*) (Apse *et al*. 1999).

**Table 1** The effects of NPs on plant salt tolerance mechanisms (↓ indicates decrease, ↑ indicates increase)

| Nanomaterials | Plant specie | Method of application | Characterization | Dosage | Observed mechanisms | Reference |
|---|---|---|---|---|---|---|
| Ag NPs | Rice | Nanopriming | 6-36 nm, zeta potential not reported | 10 ppm | Aquaporin genes (*PIP1; 1* & *PIP2; 1*)↑, α-amylase activity↑, ↑ROS-scavenging abilities | Rai-Kalal and Jajoo a(2021) |
| $CeO_2$ NPs | Rapeseed | Nanopriming | 8.5, -43.3 mV | 0.1 mmol $L^{-1}$ | Seed water uptake↑, α-amylase activity (*AMY1* & *AMY2* genes)↑, soluble sugar content↑, ROS scavenging abilities↑ | Pandey *et al*. (2018) |
| Se NPs & ZnO NPs | Rapeseed | Nanopriming | Se NPs, 120-260 nm, -32.4 mV, ZnO NPs, 25 nm, zeta potential not reported | SeNPs 150 µmol $L^{-1}$, ZnONPs 100 mg $L^{-1}$ | GA-related genes (*BnGA20ox*, *BnGA3ox*, & *BnCPS*)↑, ABA-related genes (*BnCYP707A1*, *BnCYP707A3*, & *BnCYP707A4*)↓ | An *et al*. (2020) |
| $CeO_2$ NPs | Rapeseed | Nanopriming | 9.2 nm, -38.7 mV | 0.1 mmol $L^{-1}$ | SA-biosynthesis-related genes (*SARD1* & *PAL*)↑, SA level↑ | Munir *et al*. (2018) |
| $CeO_2$ NPs | Cotton | Seed soaking | 2.1 nm, -51.7 mV | 500 mg $L^{-1}$ | POD-related genes (*Gh_A03G2152*, *Gh_A03G1517*, *Gh_D08G2330*, *Gh_A09G1415*, *Gh_D09G1420*, *Gh_A10G2288*, & *Gh_D11G2183*)↑, glutathione S-transferases GST tau (*GSTU8 Gh_A09G1508GSTU7* & *Gh_A02G0259*) genes↑ | Rajjou *et al*. (2012) |
| ZnO-Si NPs | Peas | Foliar application | 42 nm, +19.3 mV | 400 mg $L^{-1}$ | Quantum yield of photosystem II (PSII) & the photochemistry of photosystem I (PSI)↑ | Abdoli *et al*. (2020) |

| | | | | | | |
|---|---|---|---|---|---|---|
| $Mn_3O_4$ NPS & $CeO_2$ NPs | Rapeseed | Foliar application | $CeO_2$ NPs, 9.2 nm, -36.2 mV & $Mn_3O_4$ NPs, 10.2 nm, -35.2 mV | $CeO_2$NPs, 0.05 mmol $L^{-1}$ & $Mn_3O_4$NPs, 300 mg $L^{-1}$ | ROS scavenging abilities↑, leaf $K^+$ retention↑, $K^+/Na^+$ ratio↑, chlorophyll content & photosynthesis rate↑ | Wang *et al*. (2008) |
| Cs-Se NPs | Bitter melon | Foliar application | 50 nm, zeta potential not reported | 20 mg $L^{-1}$ | ROS levels↓, antioxidant enzyme activities↑, d chlorophyll content↑, $Na^+/K^+$ ratio↓ | Elshoky *et al*. (2021) |
| $CeO_2$ NPs | Maize | Foliar application | 10 nm, 14.5 mV | 10 mg $L^{-1}$ | Antioxidant system↑, ROS levels↑, photosynthetic rate↑, maintained $Na^+/K^+$ ratio↑ | Ye *et al*. (2020) |
| $TiO_2$ NPs | Stevia | Foliar application | 25 nm, zeta potential not reported | 0.01% | Antioxidant system ↑, chlorophyll↑, proline↑, soluble sugar↑, $Na^+/K^+$ ratio↓ | Sheikhalipour *et al*. (2021b) |
| MWCNTs | Rapeseed | Root application | Outer diameter, 6-12 nm, inter diameter, 2.5-5 nm, & length, 1-9 µm, zeta potential not reported | 20 mg $L^{-1}$ | Nitrate reductase-dependent nitric oxide biosynthesis↓, modulated expression of salt overly sensitive 1 (*SOS1*), $Na^+/H^+$ exchanger 1 (*NHX1*) & $K^+$ transporter 1 (*KT1*), $Na^+/K^+$ ratio↓ | Qi *et al*. (2013) |
| $CeO_2$ NPs | Rapeseed | Soil application | 55.6 nm, -51.8 mV | 1,000 mg $kg^{-1}$ | Modified the apoplastic root barriers, helping more transportation of $Na^+$ to shoot with less accumulation in the root, maintained $Na^+/K^+$ ratio↑, proline↑, efficiency of the photosynthetic apparatus↑ | Sabo-Attwood *et al*. (2012) |
| $CeO_2$ NPs | Cucumber | Root application | 5.4 nm, −24.0 mV | 0.1 mmol $L^{-1}$ | Modulated *AKT1* to $K^+$ maintenance↑, maintain $Na^+/K^+$ ratio↑ | Rossi *et al*. (2017) |
| $TiO_2$ NPs | Moldavian balm | Root application | 20-30 nm, zeta potential not reported | 100 mg $L^{-1}$ | Antioxidant enzymes activities↑, ROS levels↓, chl a, b & carotenoids | Kader *et al*. (2006) |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | | | | contents↑ | |
| $CeO_2$ NPs | Rapeseed | Dry sand application | 55.6 nm, -51.8 mV | 500 mg $kg^{-1}$ | Chlorophyll fluorescence↑ & photosynthetic efficiency↑ | Rossi *et al*. (2016) |

PNC treatment significantly increased cytosolic $K^+$ in cotton leaves and reduced cytosolic $Na^+$ fluorescence intensity (Liu *et al*. 2021b). These results were supported by the analysis of the leaf ions, which showed that cotton plants treated with PNC maintained a higher $K^+/Na^+$ by retaining lower $Na^+$ but higher $K^+$ contents in salt stress. While PNC-treated plants did not significantly exhibit higher mesophyll cell vacuolar $Na^+$, suggesting that the key mechanism underlying PNC-enhanced cotton salt tolerance is improved leaf $Na^+$ exclusion and leaf $K^+$ retention rather than vacuolar $Na^+$ sequestration. According to Liu *et al*. (2021b), the modulation of *HKT1* but not *SOS1* relative gene expression during salinity stress is more important to the PNC-mediated leaf $Na^+$ exclusion. The authors suggest $CeO_2$ NPs are better equipped to scavenge $^{\bullet}OH$ radical than other materials. The plasma membrane $K^+$-selective (*GORK*) channels that carry $K^+$ to the cell become more active as a consequence of this process (Wu *et al*. 2018). Multi-walled carbon nanotubes (MWCNTs) have been shown to alter the expression of salt overly sensitive 1 (*SOS1*) genes in rapeseed plants under salinity stress (Zhao *et al*. 2019). In addition to intensifying nitrate reductase-dependent nitric oxide biosynthesis, the application of MWCNTs in salt-stressed rapeseed seedlings also resulted in the restoration of redox and ion imbalance, as indicated by the reduction in the $Na^+/K^+$ ratio. The $Na^+/H^+$ exchanger 1 (*NHX1*) and $K^+$ transporter 1 (*KT1*) transcripts were altered as a result of MWCNTs exposure, which was linked to the beneficial impacts of the MWCNTs plant salt tolerance (Zhao *et al*. 2019). Under salinity stress, PNC priming decreased the expression of the $K^+$ channel *AKT1* (*Gh_A13G1762*) gene (An *et al*. 2020). Moreover, PNC priming in salt stress reduced the expression of the cation exchanger (*CAX1*) gene GhCAX1 (*Gh_D01G0422*). The vacuole contains the *CAX1* transporter, a crucial transporter that controls the amplitude and duration of cytosolic $Ca^{2+}$ levels. Salt sensitivity results from *CAX1* having a high level of expression. As a result, their findings suggest that PNC seed priming improves salt tolerance in cotton seedlings by decreasing *CAX1* levels, which increase cytosolic $Ca^{2+}$ levels. Maintaining high $K^+$ content in salt stress is also crucial in nano-enabled plant salinity tolerance. For example, seed nanopriming with $CeO_2$ NPs maintained high $K^+$ content in the rapeseed seedlings and maintained a higher $K^+/Na^+$ ratio for better salt tolerance (Khan *et al*. 2021). $CeO_2$ NPs modulated ROS-activated NSCC channels (non-selective cation channels) to enhance salt tolerance in *Arabidopsis* by decreasing $K^+$ loss (Wu *et al*. 2018). By increasing the leaf $K^+$ content, nano$SiO_2$ improved soybean seedling growth in salt stress (Farhangi-Abriz and Torabian 2018). Cu NPs foliar application in tomato plants reduced salt stress by enhancing growth and the $Na^+/K^+$ ratio (Quiterio-Gutiérrez *et al*. 2019). $Fe_2O_3$ NPs reduced the salinity damage in *Trachyspermum ammi* by increasing the $K^+/Na^+$ ratio (Abdoli *et al*. 2020). Mn NPs decreased the redistribution of $Na^+$, $Ca^{2+}$, and $K^+$ contents between the root and aerial parts while increasing root growth (Ye *et al*. 2020). Li *et al*. (2022) reported that higher $K^+$ retention was a shared mechanism between $CeO_2$ NPs and $Mn_3O_4$ NPs to enhance rapeseed salt tolerance. Overall, the

regulation of ion homeostasis ($Na^+$ and $K^+$) in nano-enabled plant salinity tolerance has been extensively reported. It is evident from the studies mentioned above that NPs have the potential to 1) exclude $Na^+$, 2) transport more $Na^+$ to shoot, 3) increase/sustain higher $K^+$ content, and 4) maintain a high $K^+/Na^+$ ratio to promote plant salt tolerance.

### 3.5. Nano-enabled plant photosynthesis under salt stress is an extensive research gap: Calling for more in-depth research work

One of the physiological processes in plants most vulnerable to environmental challenges is photosynthesis, which serves as the core component of metabolic functions. Consequently, maintaining an optimal photosynthetic rate is essential for plants to survive hostile situations. Plants treated with NPs exhibit enhanced rates of photosynthesis, stomatal conductance, transpiration, water use efficiency, Chl, and proline content, and carbonic anhydrase activity against various abiotic challenges (Qi *et al*. 2013; Tighe-Neira *et al*. 2018; Faizan *et al*. 2021). RuBisCO enzyme is one of the most significant factors in fixing carbon dioxide ($CO_2$) during the Calvin cycle. Wang *et al*. (2008) studied the effect of $TiO_2$ NPs on spinach growth. According to their findings, the results of bulk $TiO_2$ were not as significant as those of nano-anatase ($TiO_2$ NPs) in terms of promoting the expression of the RuBisCO small subunit (*rbcS*) and large subunit (*rbcL*) messenger RNA (*mRNA*) in the $TiO_2$ NPs-treated spinach. As a result, compared to the control, the protein expression of RuBisCO from the spinach treated with $TiO_2$ NPs increased by 40%. The $TiO_2$ NPs increased the activity of RuBisCO up to 2.33 times higher than bulk $TiO_2$. Enhancing RuBisCO mRNA amounts, protein levels, and activity was another molecular mechanism of carbon reaction enhanced by $TiO_2$ NPs. This improved RuBisCO carboxylation and the rate of photosynthetic carbon reaction (Wang *et al*. 2008). Similarly, the root application of $TiO_2$ NPs increased the contents of photosynthetic pigments in *Moldavian balm* in salinity stress (Gohari *et al*. 2020). Also, Fv/Fm and other chlorophyll fluorescence parameters were increased by applying $TiO_2$ NPs. It was found that transferring light energy absorbed by the chloroplast membrane from PSI to PSII, promoting light energy conversion to electron energy and electron transport, and the accelerating water photolysis and oxygen evolution was likely responsible for the increase in the examined chlorophyll fluorescence parameters after $TiO_2$ NPs root application in salt stress. The tomato tolerance was improved by applying $TiO_2$ NPs, which alleviated the chlorophyll content in salt stress (Khan 2016). $TiO_2$ NPs and Cs-Se NPs-treated *Stevia* plants exhibited a significant increase in chl a and b, total chlorophyll, carotenoid contents, and $P_n$ and $F_v/F_m$ (Sheikhalipour *et al*. 2021a).

Applying MWCNTs increased photosynthesis rate and water uptake to promote broccoli salt tolerance (Etesami *et al*. 2021). Sarkar *et al*. (2022) used carbon nano dots (CNDs) for the salt tolerance of *Vigna radiate*. They reported that the application of CNDs significantly increased Chl *a*, *b*, and carotenoid contents. In a study, *Arabidopsis* plants under salinity stress had considerably higher chlorophyll contents than control plants after receiving foliar applications of $CeO_2$ NPs (Wu *et al*. 2018). Also, this study found

that plants treated with foliar spray of $CeO_2$ NPs had better photosynthesis and carbon assimilation rates, compared with the control treatment. Rossi *et al*. (2007) found that $CeO_2$ NPs increased *Brassica* biomass and photosynthetic efficiency in salt stress. Rapeseed leaves treated with $CeO_2$ NPs and $Mn_3O_4$ NPs increased chlorophyll content (Chl *a* and *b*), $F_v/F_m$, carbon assimilation rate and increased leaf area in salt stress (Li *et al*. 2022). Similarly, in cotton, PNC treatment increased the CCI (chlorophyll content index), Chl *a* and *b* in salt stress (Liu *et al*. 2021b).

In tomato plants grown under salinity, foliar application of ZnO NPs significantly increased chlorophyll content (Faizan *et al*. 2021). Moreover, SPAD values and leaf area increased dramatically in the plants treated with ZnO NPs. ZnO NPs treatment significantly increased the levels of photosynthetic metrics such as $P_n$, $g_s$, $C_i$, and E. Thus, the NaCl-induced detrimental impacts on the various photosynthetic indices of tomato plants were reduced considerably by ZnONPs treatment. Through enhancing the electron transport flux, ZnO NPs priming improved the photosynthetic apparatus tolerance to subsequent salt stress (Wang *et al*. 2020). The phosphoglucomutase and cytoplasmic invertase activities were elevated by the ZnO NPs priming, which promoted sucrose production in stressed leaves. Also, the ZnO NPs treated plants had higher dry biomass than the control treatment. Thus, enhancing electron transport and sucrose biosynthesis efficiency in salt-stressed leaves improved the salt tolerance of wheat. Likewise, ZnO NPs increased RWC (relative water content), stomatal density, Hill reaction, and improved rapeseed salt tolerance (Hezaveh *et al*. 2019).

Fe NPs compensated for the damaging effects of salinity on morphological traits, leading to an increase in soluble carbohydrate content, RWC, and chlorophyll a, b, and total chlorophyll content (Mozafari *et al*. 2018). The Chl *b* and total chlorophyll contents positively correlated with RWC, which was crucial for the grape salt tolerance. $Fe_3O_4$ NPs increased plant height, number of branches, leaves/plant leaf area, stem diameter, and total biomass of *Moringa oleifera* under salinity stress (Tawfik *et al*. 2021). The improvement in the salt tolerance of *Moringa oleifera* was ascribed to enhancement in photosynthetic pigments. Similarly, the foliar application of $Fe_3O_4$ NPs increased Chl *a*, *b*, enhancing maize salt tolerance (Fathi *et al*. 2017). Compared to the control group, the $Fe_3O_4$ NPs spraying substantially increased the chlorophyll content up to 39% of the wheat plants growing in salt stress (Manzoor *et al*. 2021).

Ag NPs regulated the salt tolerance of wheat by enhancing stomatal traits and chlorophyll content (Wahid *et al*. 2020). The pearl miller plants established from seed nanopriming with Ag NPs were greenish, healthier, and grew well compared to the control (Khan I *et al*. 2020). The Ag NPs nanopriming improved the photosynthetic parameters, including Chl, carotenoids, stomatal conductance, transpiration rate, and hence photosynthetic rate in salt stress. When *Chenopodium quinoa* was grown under *in vitro* salt-stress conditions, the application of Ag NPs alleviated the salt damaging effects through increasing Chl *a*, *b*, and total Chl contents (Shibli *et al*. 2022). Similarly, the application of Ag NPs to salinized *Maerua* enhanced plant photosynthetic pigment (Shaikhaldein *et al*. 2022).

In general, enhancing photosynthetic pigments to increase the photosynthesis rate is one of the favorable effects of NPs. However, the research on NPs-enabled plant photosynthesis in salt stress is still

limited. Moreover, most experiments were conducted in laboratory growing conditions, reporting the beneficial impacts of NPs on the Chl *a*, *b*, and carotenoids contents. More research work is encouraged under open field conditions to unravel the role of NPs in improving plant photosynthesis correlated with the increase in crop yields in salt-affected agricultural lands. This will further explore the cost-benefit ratio of the adoption of nanotechnology and the net income return for the farmer's community. Nonetheless, an in-depth research is required to investigate the additional mechanisms of different NPs-mediated regulation of photosynthesis interrelated aspects in salt stress.

## 4. Risks and constraints associated with nanomaterials application in agriculture

With the rapid and massive progress of nanotechnology and nanomaterials, NPs may be exposed to plants for an extended period, damaging plant growth. In agriculture, nanotechnology aims to use NPs to improve plant growth and development under various abiotic and biotic challenges. Depending on the type, characterization, and dosage, NPs can be uptaken and accumulated in plants, leading to phytotoxicity. The NPs-induced phytotoxicity mechanisms are 1) the over-production of ROS and oxidative damage when the NPs interact with plants (Marslin *et al*. 2017), 2) transcriptional changes (Xun *et al*. 2017), and 3) genotoxicity (NPs interaction with DNA and organelles) (Xun *et al*. 2017). It is emphasized that using NPs is a sort of double-edged sword. If applied improperly, it may damage plant growth and development. For example, $TiO_2$ NPs with particle size 20 nm and application dosage of 2000 mg $L^{-1}$ had no significant effect on the germination and radicle growth, whereas it inhibited the plumule growth of *Brassica* (Mahmoodzadeh *et al*. 2015). In *Allium cepa*, the $TiO_2$ NPs with particle size 21 nm and application dosage of 30 mg/L increased the germination rate and root and shoot lengths (Lawre and Raskar 2014). Whereas, in *Sinapis alba*, $TiO_2$ NPs with particle size 25 nm and application dosage of 80 mg/L decreased the germination rate and inhibited the seedling growth (Hatami *et al*. 2014). ZnO NPs increased the germination rate of *Allium cepa* when the particle size was 20 nm, and the dosage was 40 mg $L^{-1}$ (Laware and Raskar 2014). However, when the particle size of ZnO NPs was <50 nm and the application dosage was 1,000 mg $L^{-1}$, it decreased the germination and inhibited the seedling growth of *Pennisetum glaucum* (Jain *et al*. 2017). These results clearly show that the adverse or positive effects of NPs are closely dependent on the size and dosage of NPs used for improving seed germination. Other than NPs related factors, different plant species may need a different amount of NPs to trigger germination. Such as, in *Vigna radiata* (Israel García-López *et al*. 2018) and *Cucumis sativus* (Deshpande *et al*. 2017), ZnO NPs needed 100 mg $L^{-1}$ and 1600 mg $L^{-1}$ to improve germination and seedling growth. Furthermore, these germination experiments are mostly conducted in petridishes, hydroponics, and well-controlled laboratory conditions. There is a lack of sufficient information regarding nanopriming-induced improvement in seed germination in real field conditions. The efficiency of nanopriming may vary under field conditions, as the

nanoprimed seed may face several factors (NPs interaction with soil, soil nutrition status, biota, and the intensity of salinity and drought, low temperature, high temperature etc.).

Besides nanopriming, foliar and root/soil application are the two other methods for delivering NPs into plants. Several factors, including the properties of NPs, leaf-related factors, and weather-related factors, influence the efficiency of foliar delivery of NPs. NPs sizes significantly influence their uptake via stomata transferring into plant cells (Deshpande *et al*. 2017). According to studies, small-sized NPs can be more effectively absorbed through leaf pores, increasing the amount of NPs taken into the plants (Larue *et al*. 2014). Comparing the effectiveness of the foliar application of the bulk ZnO ((40±8) nm and (−9.21±3.38) mV) with ZnO-Si NPs ((42±7) nm and (+19.3±4.16) mV), the bulk ZnO exhibited phytotoxicity (400 mg $L^{-1}$). In contrast, ZnO-Si NPs (400 mg $L^{-1}$) promoted the salt tolerance of peanuts (Elshoky *et al*. 2021). The foliar application of Cs-Se NPs (20 mg $L^{-1}$) and $TiO_2$NPs (100 mg $L^{-1}$) improved the *Stevia* salt tolerance (Sheikhalipour *et al*. 2021b). Hu *et al*. (2020) stated that the charge and size of NPs determine the foliar delivery efficiency of NPs. They observed that NPs with hydrodynamic sizes <11 and 20 nm for maize and cotton, respectively, with positive charge >15 mV, enhanced the efficiency of foliar application. These contrasting findings show that the foliar delivery of NPs depends on the characterization of NPs and plant species. The plant factors which interfere with the NPs uptake include leaf anatomy, stomatal size, waxes, wound, trichrome. Moreover, the weather conditions, such as rain, relative humidity, temperature, light, etc., will also affect the efficiency of the foliar delivery of NPs (Hong *et al*. 2021).

The root application of NPs is a complex method of NPs application. The possible reason could be the difficulty of NPs delivery to a large field. Even though some researchers have observed the root delivery of NPs in hydroponic cultures, it is still different from the real field conditions. In actual field conditions, the NPs interact with soil, which might change the behavior of the NPs. Under hydroponic culture, $CeO_2$ NPs needed 0.1 mmol $L^{-1}$ dosage to improve cucumber salt tolerance (Peng *et al*. 2022). However, to improve rapeseed salt tolerance, the optimum dosages under the soil (Rossi *et al*. 2016) and dry sand (Rossi *et al*. 2017) growing conditions were 1,000 and 500 mg $kg^{-1}$, respectively. These results clearly indicate that, compared to hydroponic experiments, in real soil/field conditions, the dosage of NPs needed for plant growth and development is quite huge. Moreover, the root uptake efficiency of NPs depends on the plant age, root architecture, rhizosphere conditions, root exudates, root surface, physicochemical properties of the soil, and plant species. Overall, compared to the root application method of NPs, seed nanopriming and foliar application of NPs are reliable regarding nanotechnology adaptability in agriculture.

Due to insufficient research work and understanding of the physical and chemical properties of NPs in complex matrix, there are certain constraints while completely adopting nanotechnology in agriculture. The first red flag about nanotechnology is whether the nanomaterials released into the soil and inside the crops are safe for humans and other animals. According to reports, NPs are used in more than 1,600 commercial food products (Koo *et al*. 2015). Applying NPs to terrestrial crops (foliar application) will increase the accumulation of NPs in plant tissues. In this way, these NPs will enter the food chain. However, limited research is available regarding the accumulation of NPs in edible plant parts and its

effects on human health. In this regard, will the NPs derived from biopolymers such as proteins and carbohydrates could be a way to reduce the toxicity of NPs on human health and the environment? In the agroecosystem, the soil is the major sink and the fate of NPs. The surface runoff, irrigation, and other water channels carry these NPs accumulated in the soil into large aquatic environments (ponds, rivers, lakes, and oceans). Thus, it is another route for NPs to reach the food chain. Moreover, the accumulation of NPs (root/soil application) in the soil also affects the soil microbial community. Another constraint to the wide range adaptability of nanotechnology in agriculture is the higher cost of the production of NPs. Many researchers have reported good results about the NPs role in improving plant stress tolerance. However, most of these studies were conducted *in vitro* due to the cost (both in time and money) of synthesizing large amounts of the NPs for greenhouse or field experiments.

In summary, we believe that to avoid nanotoxicity and the adverse effect of NPs on humans, animals, and soil biota, more research is still needed to design NPs with characterization based on the understanding of seed coat anatomy (nanopriming) and leaf anatomy (foliar application). This will improve plant growth and development under different abiotic and biotic stresses and reduce the cost of NPs (low dosage) and environmental hazards (less use of NPs). Furthermore, the soil/root application of NPs requires high doses of NPs, which will affect the soil biota, water quality, and marine life. Thus, root/soil application of NPs should possibly be avoided.

## 5. Conclusion and future perspectives

Salinity results in seed germination reduction, photosynthesis inhibition, hormonal and ion imbalance, ROS generation, and membrane damage. Therefore, salinity is a big threat to agricultural production. Among the different strategies, nanotechnology provides significant advantages in achieving plant salt tolerance. NPs and plant interaction occur through seed nanopriming, foliar application, and soil/root application. Among the NPs application methods in agriculture, nanopriming (use low dosages of NPs, easily practicable, and less biosafety concerns) and foliar application (compared to soil application, use low dosages, less biosafety concerns, and easily accessible) can be used to deliver NPs into plants. While the soil application of NPs should possibly be avoided as the soil/root application requires an excessively large amount of NPs, which not only increases the cost but also leads to the accumulation of NPs (soil is the biggest sink and fate of NPs); thus NPs have more chance to reach to the food chain. The effectiveness of NPs is largely dependent on the size, charge, and dosage. Nonetheless, different crop species may respond to NPs differently. Different factors such as seed coat anatomy, leaf anatomy, stomatal size, waxes, trichomes, wound, cell membrane pore size, root architecture, root surface, exudates, etc., affect the NPs uptake and translocation in different parts of the plant. According to the summarized studies, the NPs-induced plant salt tolerance mechanisms are 1) regulation of aquaporin genes and starch hydrolytic enzymes genes for faster seed water uptake and starch metabolism, 2) regulation of ABA/GA ratio to promote seed germination, 3) direct scavenging of ROS or regulation of antioxidant enzymes genes for the

detoxification of ROS, 4) reducing the membrane damage, 5) extrusion of $Na^+$, 6) increase the $K^+$ uptake or sustain higher $K^+$, 7) increase $K^+/Na^+$ ratio, and 8) increase the chlorophyll content, RuBisCo activity, stomatal conductance, transpiration rate, and photosynthesis rate. However, NPs application in plants also leads to phytotoxicity. The nano phytotoxicity may be ascribed insufficient scientific research and less focus on the physicochemical properties of NPs and the complexity of the response of different crop species. Further research work (combined analysis of transcriptome and metabolome) is highly encouraged to understand better the NPs-related and plant-related factors for the efficiency of NPs and plant interaction. Also, the concept of safe-by-design (Sbd) needs to be implemented for nano-enabled agriculture in order to identify potential risks during the early stages of the technology development. Moreover, the nano-based experiments in plants are mostly performed in controlled laboratory conditions. Trials under open-field are required to unravel the potential of NPs in increasing crop yields. More attention is needed to the application of NPs in agriculture, avoiding harm to the agroecosystem and human health.

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**Competing interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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