



Review Article

Recent strategies for mitigating salinity stress in plants: A review of exogenous compound applications

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Abstract

Soil salinity is a major abiotic stress that severely limits plant growth, development, and agricultural productivity worldwide. This review summarizes recent progress in alleviating salinity stress through the external application of various compounds, including phytohormones, organic and inorganic small molecules, and nanoparticles. The application of exogenous compounds to various crop species and experimental systems often improves plant salt tolerance by activating convergent physiological and molecular mechanisms: (1) activation of enzyme and non-enzymatic antioxidant defense systems, reducing ROS and MDA levels; (2) maintaining ion homeostasis by limiting Na⁺ accumulation and enhancing K⁺ and Ca²⁺ uptake; (3) inducing osmolyte accumulation; and (4) modulating the stress-responsive gene expression and hormonal crosstalk. Effectiveness depends on compound concentration, application method (seed priming, foliar spray, root absorption), plant species, and salinity severity. Many previous studies are short-term and conducted under controlled environments with limited field validation. Synergistic combinations are often applied to enhance plant tolerance under salt stress. Future research priorities include the multi-omics integration, CRISPR-based gene editing, and long-term environmental safety assessments. Practical applications provide accessible, low-cost strategies to sustain crop productivity in salt-affected regions.

Keywords: Antioxidants, exogenous compounds, nanoparticles, phytohormone, salinity stress.

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1. Introduction

Salinity is a measure of salt content in the soil or water. Salts can be transported via water movement and are highly soluble in surface and groundwater. Salinity conditions become the most serious environmental problem in agriculture. It is estimated 20% of cultivated and 33% of irrigated agricultural lands were affected by high salinity problems (1). The percentage will increase annually due to various reasons. The most common cause of salinity is a poor irrigation system. The use of soluble salt water and a poor drainage system prevents the salt from exiting from a root zone. The evaporation of water leaves the salt on the soil surface, increasing the salt deposits. Other causes such as water runoff from weathering rock and land, tide, or flooding containing salts to the agriculture area could damage the soil. Most plants are sensitive to saline conditions that can reduce crop productivity, which are threats for agricultural sustainability.

Salinity could influence plant productivity. As plants absorb water from the soil via root systems, the osmotic stress disturbs the movement of water into the roots. The ionic stress caused by the addition of ionic substances Na^+ and Cl^- disturbs processes in the cell, such as photosynthesis and metabolism. Plants must cope with the stress by activating various biochemical and physiological changes. Changes in reproduction, morphology, anatomy, growth rate, and ion toxicity distribution (2). In addition, salinity causes chlorosis and necrosis in the plant leaf. The effect of salinity inhibits plant growth, reducing leaf canopy and inhibiting florescence; therefore, it decreases plant productivity and crop yields.

The problem has a big influence on the social economy; therefore, strategies to maintain agricultural productivity are necessary. One of the solutions is improving plant tolerance by exogenous compounds against salinity stress to support plant productivity by developing a salinity-tolerant variety of crops. The approach is relatively simple and suitable to use for plants. Previous studies reported various compounds are able to improve plant tolerance and maintain plant productivity under saline conditions. Therefore, this review compares

previous research related to "exogenous compounds" under saline stress. This review gives valuable insights on explaining the underlying mechanism of how the compound influences the plant tolerance and productivity.

2. Mechanism of salinity stress and plant tolerance responses

Salt stress could make various impacts on plant growth and metabolism by ionic toxicity, osmotic stress, and oxidative damage through stomata and non-stomata (3, 4) (Figure 1). In saline conditions, stomatal conductance may reduce due to a decrease of intracellular CO_2 . The long-term exposure induces thylakoid membrane and photosynthetic pigment dissolution (5-7).

Excessive ion of Na^+ could disturb ion homeostasis by competing with K^+ and Ca^{2+} in the plant cell, influencing transport mechanisms (5, 8). Overaccumulation of Na^+ in the cell competes for the same enzyme binding site of K^+ , therefore inhibiting the activity of K^+ -dependent cytosolic enzymes, leading to nutritional imbalance and cellular injury (4). The decreasing of the K^+/Na^+ ratio in the cell disrupts membrane integrity and protein stability (3).

The saline condition lowers water potential, distressing the plant by giving osmotic shock and reducing the water uptake from the root. A previous study reported that 15-day-old tobacco seedlings under salt conditions reduce 46.8% of total biomass (4). The inhibition has a big impact on shoot biomass (50%) compared to root biomass (34.6%). The oxidative stress state by saline condition induces the production of free oxygen radicals, which then plants counteract by accumulating antioxidants (9). The excessive amount of production could damage the lipid membrane, proteins, and DNA (5, 10, 11).

A previous study reported that salt stress strongly inhibits photosynthetic pigments, such as Chl a, Chl b, and carotenoid levels (4). Moreover, the stress also reduces the photochemical efficiency by inhibiting the photosystem II (PSII) reaction center, especially restricting the electron transfer between quinone acceptors. The molecular analysis reveals that salinity reduces the expression of essential genes for carbon assimilation, such as *rbcS1*,

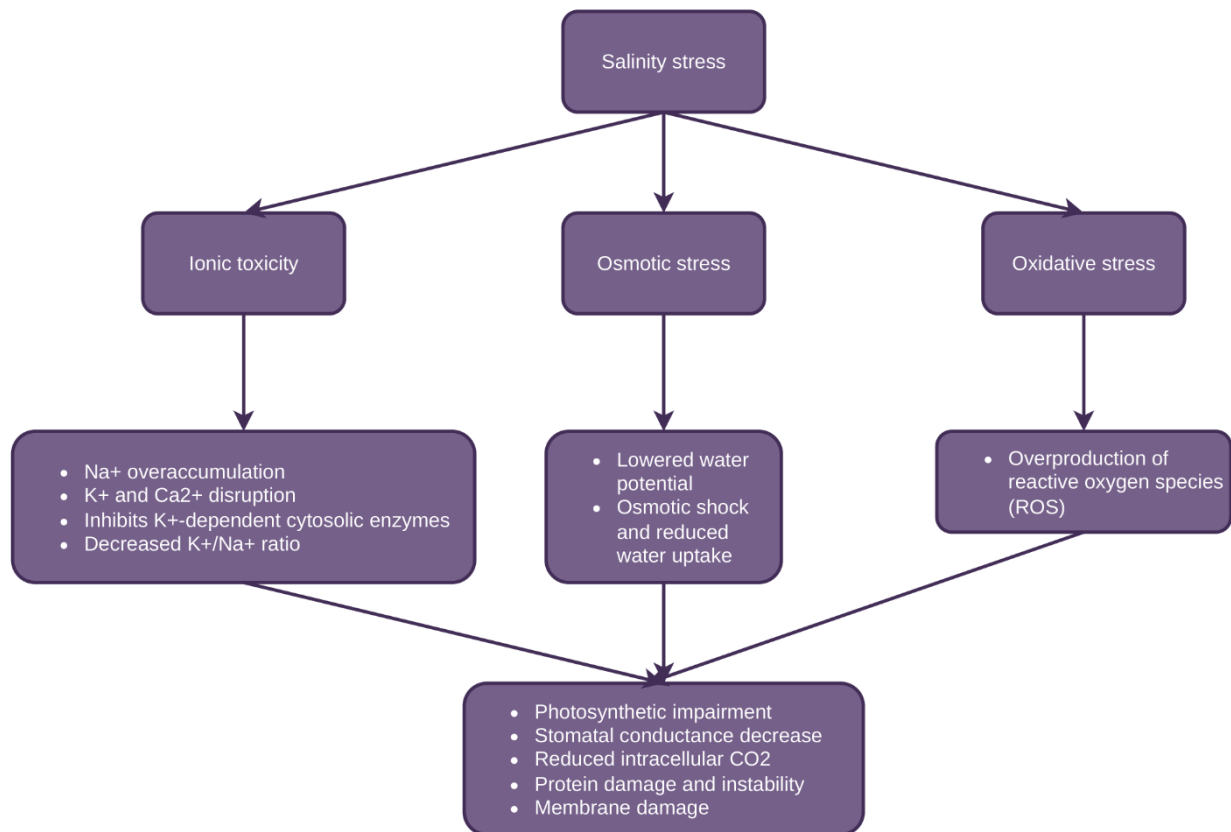


Figure 1. Impact of saline stress on plant.

pasbA, psaB, petA, and FNR, suppressing photosynthesis and respiration, leading to reduced plant energy metabolism (3).

3. Exogenous phytohormones for salinity mitigation

Phytohormones play a major role in plant signaling. The plants generate phytohormones to induce adaptation-gene response. They don't work separately, but they work interconnectedly with each other. Previous studies have reported various applications of phytohormones on salinity stress in plants (Table 1).

3.1 Gibberellins

Gibberellic acid is a class of tetracyclic diterpenoid phytohormones that acts as a plant growth regulator, stimulating cell elongation, seed germination, stem elongation, and flowering. Among the various gibberellins, gibberellic acid (GA₃) has been extensively studied. Gibberellic acid is able to promote the primary growth and germination under salt stress. A study from Attia and Alamer (12) applied seed priming of *Foeniculum vulgare*

using 3 μM of gibberellic acid (GA₃). The results reported that gibberellic acid enhanced germination rate by elongating the radicle and hypocotyl and preventing the polyamine accumulation. The GA₃ prevented the production of H₂O₂ from polyamine metabolism. The effect compensates for the negative impact of salinity stress on early plant growth. The foliar application of GA₃ demonstrated improved salt tolerance in wheat (*Triticum aestivum*) through enhanced growth, ionic partitioning, photosynthesis, yield, and hormonal homeostasis (13). The GA₃ mitigated the salt stress damages by stimulating cell division and enlargement, promoting growth, and improving stomatal movement (14).

3.2 Cytokinins

Application of a cytokinin-like compound, 6-benzyl adenine (BA), was also reported to improve plant growth and photosynthesis under salt conditions (15). The application of different concentrations (0.5, 1.0, and 1.5 mg/L) of BA regulated the homeostasis of the sodium-potassium ratio while also increasing the activity of

antioxidant enzymes for reducing the hydrogen peroxide levels. The increase in growth and grain yield from kinetin-primed seeds was also positively correlated with leaf auxin concentration and negatively with abscisic acid concentration under both saline and non-saline conditions (16). The most effective cytokinin application is to mitigate salt-induced leaf senescence. A study reported that the application mitigated the salt-induced leaf senescence by activating the antioxidant systems and improving the ionic balance in perennial ryegrass (17). The delaying of senescence can maintain the photosynthetic capacity for longer periods under stress conditions and sustained productivity. Cytokinins contribute to cell division and differentiation. In *Tropaeolum majus*, the cytokinin application attenuated salt stress by promoting the osmolytes like proline and inducing the energy absorption (18). At the molecular level, cytokinins modulate the stress-responsive gene expression and interact with other hormonal pathways. The role of cytokinin metabolism in stress tolerance.

3.3 Auxins

Auxins are a class of phytohormones that regulate cell elongation, division, and differentiation and play central roles in plant growth and development. Indole-3-acetic acid (IAA) is the primary naturally occurring auxin and has been widely investigated for its capacity to mitigate salinity stress when applied exogenously. Recent studies demonstrate that exogenous IAA application via foliar spray, seed priming, or culture medium supplementation improves multiple physiological and biochemical traits under saline conditions.

Foliar application of IAA has consistently enhanced growth and yield in salt-stressed crops. In faba bean (*Vicia faba*), foliar IAA (1.15 mM or 200 ppm) improved shoot and root growth, increased soluble sugars, proteins, and free amino acids, and enhanced nodulation under 60–150 mM NaCl (19, 20). Similarly, IAA foliar sprays (100–200 ppm) rescued plant height, chlorophyll content, and fruit yield in tomato under 30–60 mM NaCl (21). In olive plantlets, IAA pretreatment restricted root-to-shoot Na^+ transport,

improved leaf K^+/Na^+ ratio, and increased proline and biomass under 100–200 mM NaCl (22).

Seed priming with IAA improved germination dynamics, radicle and coleoptile growth, α -amylase activity, and sugar mobilization in maize under saline germination conditions (23). In vitro supplementation of IAA (7–14 μM) mitigated NaCl-induced growth reduction and increased soluble protein and antioxidant enzyme activities in potato (24).

Exogenous IAA consistently upregulated antioxidant enzyme activities superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), and ascorbate peroxidase (APX) across multiple species, reducing lipid peroxidation and malondialdehyde (MDA) accumulation (20, 24, 25). In rice, combined boron nanoparticles and IAA synergistically enhanced AsA–GSH cycle enzyme activities and upregulated auxin transporter and antioxidant genes under NaCl stress (26). IAA also improved photosynthetic efficiency and pigment content, particularly when combined with nitric oxide (NO) donors in *Brassica juncea* (25).

Ion homeostasis was improved by IAA through enhanced K^+ , Ca^{2+} , and Mg^{2+} uptake and reduced Na^+ accumulation in shoots (20, 22). Synergistic combinations of IAA with nitric oxide or boron nanoparticles often exceeded single-treatment effects, suggesting promising combinatory strategies for enhancing salinity tolerance (25, 26).

3.4 Jasmonate

Jasmonates are a family of lipid-derived phytohormones, principally jasmonic acid (JA) and its volatile methyl ester methyl jasmonate (MeJA), that regulate plant defense, stress signaling, and developmental processes. Their exogenous utilization is increasingly being investigated as a practical strategy to improve salinity tolerance in plants. Recent studies have shown that application of JA and MeJA by foliar spraying, seed preparation, or irrigation consistently improves growth, photosynthesis, antioxidant defense, and ionic homeostasis in many species grown under saline conditions. Exogenous seed priming of MeJA (10 to 15 μM)

in sorghum (*Sorghum bicolor*) prevented salt-induced growth inhibition, maintained chlorophyll content, reduced oxidative damage, and reduced the Na⁺/K⁺ ratio by more than 70% under 200 mM NaCl (27). In soybean (*Glycine max*), seed priming and foliar application of JA (60 μM) significantly increased the net photosynthetic rate up to 77%, improved stomatal conductance, and reduced leaf Na⁺ accumulation under 100 mM NaCl (28). Similarly, hemp foliar MeJA (0.001–0.01 mM) improved root biomass by 50%, chlorophyll content by 20%, and photosynthetic efficiency by 23% under moderate salinity (29).

At the antioxidant level, exogenous MeJA consistently increased the activities of superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX) and decreased the accumulation of malondialdehyde (MDA) and H₂O₂. In walnut (*Juglans regia*), MeJA increased SOD, POD, and CAT activities by 11.6%, 10.7%, and 22.3%, respectively, while decreasing MDA by 16.8% and further upregulated antioxidant enzyme genes by 1.2- to 2.0-fold (30). Molecular studies in *Crithmum maritimum* L. revealed that MeJA improves Ca and K uptake and translocation to the leaves of saline-treated plants and alleviates the negative effects of salt stress (31).

However, the effect of jasmonate depends on the dose and type. In *Arabidopsis thaliana*, exogenous JA impaired seedling salt tolerance through MYC2-mediated repression of CAT2 expression, resulting in increased HO and reduced tolerance, highlighting the importance of signaling context in determining outcomes (32). Overall, moderate application of JA/MeJA represents a promising strategy to improve salt tolerance, particularly in crops where jasmonate signaling supports antioxidant and ion homeostasis pathways.

3.5 Salicylic acid

Salicylic acid (SA) is a phenolic phytohormone that functions as an important signaling molecule in plant defense and adaptation to stress. Exogenous AS has been widely studied for its role in alleviating salt stress, with

applications ranging from foliar spraying to seed preparation to delivery to the root zone. Recent studies show that SA, typically applied at 0.25–2.0 mM, consistently improves plant growth, photosynthesis, antioxidant capacity, and ionic homeostasis under saline conditions for a wide range of species.

Foliar application of SA significantly improved growth and biomass in several low-salt crops. In strawberry (*Fragaria vesca*), 0.25 mM SA improved biomass, leaf water potential, relative water content, and photochemical efficiency (Fv/Fm) with 80 mM NaCl (33). In rapeseed (*Brassica napus*), foliar SA (10–20 mM) under 200 mM NaCl increased shoot fresh weight, root dry weight, and chlorophyll content, with cultivar-dependent responses (34). In pepper (*Capsicum annuum*), optimal foliar SA attenuated salinity-induced reductions in gas exchange, fruit size, and yield at irrigation salinity of 0.8–3.2 dS m⁻¹ (35). In perennial ryegrass (*Lolium perenne*), foliar SA (0.25–0.5 mM) restored grass quality, photosynthesis, and growth under a NaCl concentration of 250 mM (36).

Exogenous SA consistently increased enzymatic antioxidants (SOD, CAT, POD, APX, and glutathione reductase (GR)) while reducing MDA, H₂O₂, and electrolyte losses. In gladiolus (*Gladiolus grandiflorus*), SA (100–150 ppm) increased the accumulation of proline and glycine betaine with an EC salinity of 2–6 dS m⁻¹, supporting osmotic adjustment (37). SA with IAA also improved ion homeostasis by limiting Na⁺ transport from root to shoot and improving K⁺/Na⁺ ratios, as reported in olive seedlings with NaCl below 100 and 200 mM (22). However, the effect of jasmonate depends on the dose and type. In *Arabidopsis thaliana*, exogenous JA impaired seedling salt tolerance through MYC2-mediated repression of CAT2 expression, resulting in increased HO and reduced tolerance, highlighting the importance of signaling context in determining outcomes (32). Overall, moderate application of JA/MeJA represents a promising strategy to improve salt tolerance, particularly in crops where jasmonate signaling supports antioxidant and ion homeostasis pathways.

Table 1. Application of exogenous phytohormones on plants under salt stress condition.

Compounds	Concentration used	Type of Application	Plant used	Effects	Reference
Gibberellic acid (GA3)	3 μ M	Gibberellic acid (GA 3) was applied for seed priming	Fennel (<i>Foeniculum vulgare</i>)	-The germination rate was significantly higher, showing a decrease of 33% compared to the control. -It improved the elongation of radicle and hypocotyl organs. -GA3 seed priming was highly effective in reducing polyamine (PA) levels in salt-stressed seedlings compared to the control.	Attia et al., 2022 (12)
6-benzyl adenine (6-BA)	0.5, 1.0, and 1.5 mg/L	Solution was sprayed onto the upper and lower epidermis of the leaves	<i>Limonium bicolor</i>	-1.0 mg/L 6-BA significantly improved plant growth and photosynthesis. -It significantly increased the fresh and dry weight of shoots and roots, leaf area, and number of blades. -It significantly decreased the Na ⁺ content by 18.2% and increased the K ⁺ content by 55.6%. -It also significantly reduced the content of ROS such as H ₂ O ₂ and O ₂ ⁻ by 23.1% and 34.2% respectively, and increased the activities of antioxidant enzymes like SOD, CAT, APX, and POD.	Liu et al., 2023 (15)
Indole-3-acetic acid (IAA)	200 ppm	Foliar application of IAA was also implemented	Faba bean (<i>Vicia faba</i> L.)	-IAA application significantly enhanced root fresh weight (RFW), stem fresh weight (SFW), root dry weight (RDW), stem dry weight (SDW), fresh yield, dry yield, and number of nodules (NOD). -It increased the contents of total soluble sugars (TSS) in the roots, stem, and seeds in salt-stressed plants. -It also increased total soluble proteins (TSP), proline, total free amino acid, antioxidant enzyme activity, K ⁺ , Ca ²⁺ , and Mg ²⁺ content. -It reduced Na ⁺ content and malondialdehyde (MDA).	Latef et al., 2021 (20)

Table 1. Cont.

Compounds	Concentration used	Type of Application	Plant used	Effects	Reference
Methyl jasmonate (MeJ)	100 μ M	Foliar spraying	Tomato (<i>Solanum lycopersicum</i>) cultivar (Baraka F1)	-Application of MeJ increased enzymatic antioxidant activity, such as SOD, CAT, APX, and POD, moreover boost non-enzymatic antioxidants like phenolic, flavonoid, and anthocyanin contents under salinity stress. -MeJ application prevented the reduction of total chlorophyll content. It reduced H ₂ O ₂ , O ₂ ⁻ , MDA levels by 53.8%, 39.1%, 48.5%, respectively.	Hamidian et al., 2025 (60)
Jasmonic acid	200 μ M	Foliar spraying	<i>Tropaeolum majus</i> L.	Jasmonic acid application improved plant height and leaf area under moderate salt stress (50 mM NaCl) and severe stress (100 mM NaCl), with jasmonic acid also improving stem dry mass and total dry mass	Silva et al., 2022 (18)
Salicylic acid	2 mM	Foliar spraying	<i>Tropaeolum majus</i> L.	Salicylic acid did not improve plant height or leaf area under moderate salt stress.	Silva et al., 2022 (18)

4. Organic, inorganic compounds, and nanoparticles

Organic metabolites have been studied previously able to improve plant tolerance against salt stress. Previous studies used different approaches to apply organic, inorganic compounds and nanoparticles, such as seed priming, foliar spraying, and delivering to the root systems (Table 2). Previous study reported applying 10 mM of calcium chloride (CaCl_2) to the root zone of buckwheat seedlings able to reduce the NaCl toxicity and increase the plant growth (39). Furthermore, the CaCl_2 induced the antioxidant defense, soluble protein and proline contents under salt stress.

4.1 Salts that are inorganic

Inorganic salts, particularly those with vital mineral elements like calcium (Ca) and silicon (Si), are commonly utilized to counteract the adverse impacts of salinity on plants. Their primary mechanisms involve enhancing physical barriers, preserving ionic equilibrium, and triggering antioxidant defense systems.

Calcium chloride (CaCl_2) is vital in mitigating salt toxicity by decreasing sodium (Na^+) uptake and enhancing plant growth and antioxidant enzyme functions (40). For instance, the extreme use of 10 mM CaCl_2 on Tartar buckwheat seedlings facing NaCl stress enhanced growth and raised proline and soluble protein levels (39). The protective role of Ca^{2+} is largely due to its function as an important second messenger in signaling pathways that regulate stress response gene expression (41). It stabilizes cell walls and membranes, prevents Na^+ -induced destabilization, and helps restore K^+/Na^+ homeostasis, which is crucial for metabolic function.

Potassium silicate (K_2SiO_3) is another effective inorganic compound. As a foliar application, it reduces Na^+ uptake while improving potassium (K^+) concentration, compatible solutes, photosynthetic performance, and water use efficiency in plants such as olive trees (42). The positive impacts of Si are linked to its capacity to co-precipitate with Na^+ , thereby decreasing its transport to shoots, and to the enhancement of key antioxidant enzymes' activity such as superoxide dismutase (SOD) and catalase (CAT) (43). The combination of enhancing nutrient

balance and lowering oxidative stress renders K_2SiO_3 an effective resource for addressing salt stress.

4.2 Small organic compounds

This category encompasses a varied collection of organic substances, such as vitamins, polyamines, amino acids, and phytohormones. They primarily serve as osmolytes, antioxidants, and signaling molecules to safeguard plants against salt-induced harm.

Ascorbic acid (AA) and riboflavin are effective seed priming agents. In *Brassica rapa*, AA priming (100 mg L^{-1}) improved shoot dry weight by 130%, enhanced water and mineral (K^+ , Ca^{2+}) content, and boosted total antioxidant activity (44). Riboflavin (2 mM) also improved growth, potassium nutrition, and guaiacol peroxidase (GPX) activity while decreasing sodium and chloride accumulation and oxidative stress markers (44). These vitamins act by reinforcing both enzymatic and non-enzymatic antioxidant defense systems, reducing reactive oxygen species (ROS) and lipid peroxidation.

Putrescine (Put), a polyamine, is highly effective as a seed priming agent. In rapeseed, it improves salt tolerance during germination, improves seedling growth, and regulates ion homeostasis and ROS accumulation. Putrescine modulates the expression of key genes involved in ion exchange (e.g., *BnHKT1*, *BnSOS1*), thereby reducing the Na^+/K^+ ratio (45).

Melatonin, GABA, proline and glutathione are powerful stress-relieving molecules. Melatonin (0.2 mM) applied as a foliar spray on gerbera significantly increased shoot length and leaf mass while reducing H_2O_2 and MDA levels (46). GABA (2 mM) reduces Na^+ and Cl^- levels in roots, improves chlorophyll content, and increases SOD activity (47). Exogenous proline, when applied to Aloe vera, improves the K^+/Na^+ ratio, protects photosynthetic pigments and activates antioxidant enzymes (48). Glutathione, in turn, strengthens antioxidant defense systems and ATPase enzymes, thereby improving the growth and osmotic regulation of pepper plants (49).

4.3 Nanoparticles

Nanoparticles (NPs) are an innovative method to enhance plant salt tolerance, owing to their elevated specific surface area, reactivity, and capacity to effectively supply trace elements. Their processes involve optimizing ionic balance, boosting photosynthesis, and increasing regulation.

Selenium nanoparticles (Se-NPs) have shown significant efficiency in reducing salt stress in different crop species. Alharbi et al. (2025) researched the effects of foliar application of Se-NPs at concentrations between 0.25 and 1.5 mM on cowpea (*Vigna unguiculata* L.) cultivated in saline environments. The findings showed that Se-NPs notably enhanced the activities of antioxidant enzymes, boosted plant height and yield, mitigated salinity stress, and improved the water status and nutrient levels in leaves (50). The protective role of Se-NPs is linked to their capacity to modulate reactive oxygen species (ROS) scavenging mechanisms and preserve membrane integrity during salt stress. Additionally, Se-NPs have been shown to boost the function of key antioxidant enzymes, including catalase (CAT), ascorbate peroxidase (APX), and superoxide dismutase (SOD), while lowering oxidative stress markers such as malondialdehyde (MDA) and H₂O₂ in faba bean plants (51).

Silicon nanoparticles have attracted considerable attention due to their ability to function as physical barriers and physiological modulators under salt stress conditions. A crucial process involves reducing the flow of sodium (Na⁺) from roots to shoots, thereby protecting photosynthetic tissues from ionic damage. Earlier studies showed that applying silica nanoparticles (SiO₂-NPs) foliar at 200 mM to rice plants markedly decreased oxidative stress indicators (MDA by 78%, H₂O₂ by 67%), while enhancing the activities of antioxidant enzymes (SOD, POX, CAT) and boosting chlorophyll levels and photosynthesis rate (52). Application of SiO₂-NPs at 50 ppm through foliage 30–35 days after planting reduced salt stress toxicity by reducing H₂O₂ and MDA contents and increasing biomass, root growth, shoot growth, photosynthetic parameters, and antioxidant enzyme activities (53). The application of 400 mM Si-NPs improved root growth, increased the contents of chlorophyll, Na⁺

cotransporter (*CsSOS1*, *CsSOS2*, *CsSOS3* and *CsNHX1*) and aquaporin (*CsPIP1;1*, *CsPIP2;3* and *CsTIP4;1*); therefore, photosynthesis, water status, and regulation of ion content improve in NaCl-treated plants (54).

Furthermore, Si NPs play a crucial role in regulating water relations and osmotic balance. They regulate the expression of aquaporin genes (e.g., *CaPIP1-1* and *CaTIP1-1*) to maintain water balance and increase the accumulation of compatible solutes such as proline and soluble sugars (55). A synergistic effect was also observed when Si NPs were combined with other drugs. For example, the combined application of green synthesized SiNPs with melatonin significantly improved the salt tolerance of parsley (*Petroselinum crispum*) by improving germination energy (70%), shoot length (83%), and antioxidant enzyme activities (SOD and APX by 69.5% and 123.7%, respectively) while decreasing H₂O₂ and MDA levels (56). These results demonstrate that Si NPs are an environmentally friendly and effective strategy for improving plant resistance to salinity, especially in salt-polluted agricultural regions.

Foliar treatment with 100 mg/L ZnO NPs in rice improved growth, photosynthesis and nutrient uptake under salt stress conditions. Zinc is an essential cofactor for many enzymes and its nano form provides improved bioavailability, leading to a reduction in oxidative damage. Zinc oxide nanoparticles are well-known for their functions as vital micronutrient fertilizers and stress alleviators. They enhance salt tolerance by stimulating both enzymatic and non-enzymatic antioxidant defenses, thereby minimizing oxidative damage. Research on *Salvia leriifolia* revealed that foliar application of 4 mg/L ZnO NPs notably enhanced the levels of soluble sugars, total phenolics, and activities of antioxidant enzymes (catalase, phenylalanine ammonia lyase, and guaiacol peroxidase), whereas high salinity (200 mM NaCl) led to significant reductions in hydrogen peroxide and MDA levels (57). Likewise, ZnO NPs have demonstrated the ability to boost tolerance in black gram (*Vigna mungo* L.) by stabilizing photosynthetic pigments, improving potassium uptake, and managing ion transport to mitigate sodium toxicity (58).

Table 2. Application of organic, inorganic compounds and nanoparticles on plants under salinity stress

Compounds	Dose/Concentration	Type of Application	Plant used	Effects	Reference
Calcium chloride (CaCl₂)	10 mM	Administered to the roots of the seedlings	Tartary buckwheat seedlings cv. Xinong9920 and cv. Xinong 9909	-Exogenous CaCl ₂ reduced NaCl toxicity. It promoted the growth and antioxidant enzyme under the stress. -The CaCl ₂ increased the proline and soluble protein contents in the seedlings.	Zhang and Yang, 2022 (39)
K₂SiO₃ (Si 38%)	150 mg L ⁻¹	Foliar application of silicon (Si) as a pretreatment for 28 days with 10 mg L ⁻¹ Si(OH) ₄ , followed by root treatment with 100 mM NaCl for 51 days	'Frantoio' and 'Leccino' olive (<i>Olea europaea</i> L.)	Si reduces Na ⁺ uptake and enhances K ⁺ concentration. Si increases compatible solutes, enhance photosynthetic performance and water use efficiency.	Fidalgo-Illesca et al., 2025 (42)
Putrescine	0.1, 0.3, 0.5, 0.7, and 1 mM	Priming during seed germination stage.	Rapeseed (<i>Brassica napus</i> L.)	-Exogenous Put enhances salt tolerance during seed germinations, improves seedling growth and prevents photosynthetic pigment degradation, regulates ion exchange-related genes (BnCPK4, BnCPK10, BnATP1, BnGID1, BnSUS1, BnABF, BnPFK2, BnGLU19), and improving Na ⁺ /K ⁺ homeostasis. Put-priming reduces oxidative stress by modulating the ROS accumulation.	El-Badri et al., 2025 (45)
Ascorbic acid	100 mg L ⁻¹	seed priming	<i>Brassica rapa</i> L.	-Improved shoot dry weight to 130%, increased 1.35-fold water content, enhanced the potassium and calcium content, improved the ratio of Na ⁺ /K ⁺ and Na ⁺ /Ca ²⁺ ratios, increased a total antioxidant activity and chlorophyll content, while reduced the stress markers such as MDA and EL	Oueslati et al., 2025 (44)

Table 2. Cont.

Compounds	Dose/Concentration	Type of Application	Plant used	Effects	Reference
Riboflavin	2 mM	seed priming	<i>Brassica rapa</i> L.	Increase shoot dry weight 93%, potassium nutrition, total chlorophyll, increase guaiacol peroxidase (GPX) activity, while decrease sodium and chloride accumulation, and electrolyte leakage and MDA.	Oueslati et al., 2025 (44)
Melatonin	0.1 mM and 0.2 mM	Foliar spraying	Gerbera (<i>Gerbera jamosonii</i> L. cv. Yunnanhong)	-MT (0.2 mM) increased shoot length by 89%, leaf fresh mass by 68%, and leaf dry mass by 141% compared to untreated salt-stressed plants. Furthermore, MT application mitigated oxidative stress by reducing malondialdehyde and H ₂ O ₂ concentrations by up to 46% and 56% respectively, while enhancing antioxidant enzyme activities by up to 61%	Zulfiqar et al., 2023 (46)
GABA (γ -aminobutyric acid)	2 mM	administered as a solution to each pot	Chufa seedlings	-Exogenous GABA application significantly improved growth in chufa seedlings under saline stress, increasing shoot length by 11.2-16.6% and shoot fresh weight by 18.6-20% under 0-100 mM saline stress, respectively. It also reduced Na ⁺ and Cl ⁻ levels in roots by 18-32.5% and 13-15%, respectively, under 100-200 mM saline stress, while enhancing chlorophyll a and b by up to 11.5% and 15% respectively, and increasing antioxidant enzyme activities like SOD by 28-32.8%	Askari et al., 2023 (47)

Table 2. Cont.

Compounds	Dose/Concentration	Type of Application	Plant used	Effects	Reference
Proline	10 mM and 30 mM	Proline was applied on foliage twice every 7 days	<i>Aloe vera</i> (L.)	Proline reduced leaf Na content, improved the K/Na Ratio and relative water content (RWC), alleviated the inhibitory effect of salinity on chlorophyll a and carotenoids contents, improved the oxygen-evolving complex efficiency of PSII (Fv/Fo) and the quantum yield of electron transport. Proline reduced the accumulation of H ₂ O ₂ and MDA by activation of SOD, CAT, and APX.	Nakhaie et al., 2020 (48)
Glutathione	0.5 mM	Seedling spray	<i>Capsicum annuum</i> L.	Exogenous glutathione (GSH) application significantly alleviates salt stress in <i>Capsicum annuum</i> by enhancing antioxidant defense systems and ATPase enzymes, which leads to improved plant growth and expression of <i>CaXTH</i> genes. It also reduces oxidative damage (H ₂ O ₂ and MDA content) and improves osmotic regulation by increasing proline and soluble sugar levels.	Ramzan et al., 2023 (49)
Selenium nanoparticles (Se-NPs)	0.25, 0.5, 1.0, and 1.5 mM Se-NPs	Foliar application of selenium nanoparticles (Se-NPs) was utilized	<i>Cowpea (Vigna unguiculata</i> L.)	Se-NPs improved antioxidant enzyme activities significantly, enhanced the height and plant yield, alleviated salinity stress, improving water status and leaf nutrient uptake, and reduced sodium accumulation	Alharbi et al., 2025 (50)

Table 2. Cont.

Compounds	Dose/Concentration	Type of Application	Plant used	Effects	Reference
Silicon dioxide nanoparticles (SiO ₂ -NPs)	50 ppm	Foliar application at 30-35 days after sowing	<i>Solanum lycopersicum</i>	-SiO ₂ -NPs reduced the MDA and H ₂ O ₂ levels under salt stress -They enhanced biomass, root, shoot growth, photosynthetic parameters, antioxidant enzyme activities under salt stress.	Alam et al., 2025 (52)
Zinc oxide nanoparticles (ZnO-NPs)	100 mg/L	Foliar treatment for five consecutive days (26-30 DAS)	Rice (<i>Oryza sativa</i>)	ZnO-NPs enhanced growth, photosynthesis, and nutrient uptake under salt stress They lowered the oxidative stress and antioxidant enzyme activity.	Dogan et al., 2024 (61)

Recent research has also explored the combined application of ZnO-NPs with other nanomaterials for enhanced efficacy. Previous study reported that a combination of Se-NPs and ZnO-NPs in rice provided a more pronounced alleviation of salt stress than individual treatments, leading to significant improvements in plant height (46.32%), root length (70.53%), and grain yield (59). Furthermore, the functionalization of ZnO-NPs has been shown to boost their protective effects. For instance, melatonin-functionalized ZnO nanoparticles (MZ NPs) demonstrated a greater ability than bare ZnO-NPs to restore photosynthetic pigments, optimize antioxidant enzyme activities, and reduce excessive osmoprotectant accumulation, indicating a more balanced and effective stress response in black gram (58). These findings underscore the potential of ZnO-NPs as a versatile nano-fertilizer for improving crop resilience and nutritional quality in saline soils. Overall, the application of nanoparticles is a promising strategy for sustainable agriculture under saline conditions, but further research is needed to understand their long-term environmental impact and optimize delivery methods.

The exogenous compounds including phytohormones (gibberellins, cytokinins, auxins, jasmonates, salicylic acid), organic and inorganic small molecules (CaCl₂, K₂SiO₃, ascorbic acid, riboflavin, putrescine, melatonin, GABA, proline, glutathione), and nanoparticles (Se-NPs, Si-NPs, ZnO-NPs) constitutes a highly effective and versatile strategy for alleviating salinity stress in plants (Figure 2). Despite their chemical diversity, these compounds converge on a core set of physiological and molecular mechanisms that collectively restore cellular homeostasis under saline conditions.

Application of exogenous compounds including phytohormones (GA3, CK, IAA, JA/MeJA, and Sa), organic and inorganic small molecules (CaCl₂, K₂SiO₃, ascorbate, riboflavin, putrescine, melatonin, GABA, proline, and glutathione), and nanoparticles (Se-NPs, S-NPs, and ZnO-NPs) exhibits an effective and simple strategy to alleviate salinity stress in plants (Figure 2). The effective exogenous compounds enhance antioxidant defense systems. They consistently upregulate the activity of enzymatic antioxidants (superoxide dismutase, catalase, peroxidase, and glutathione reductase) and non-enzymatic

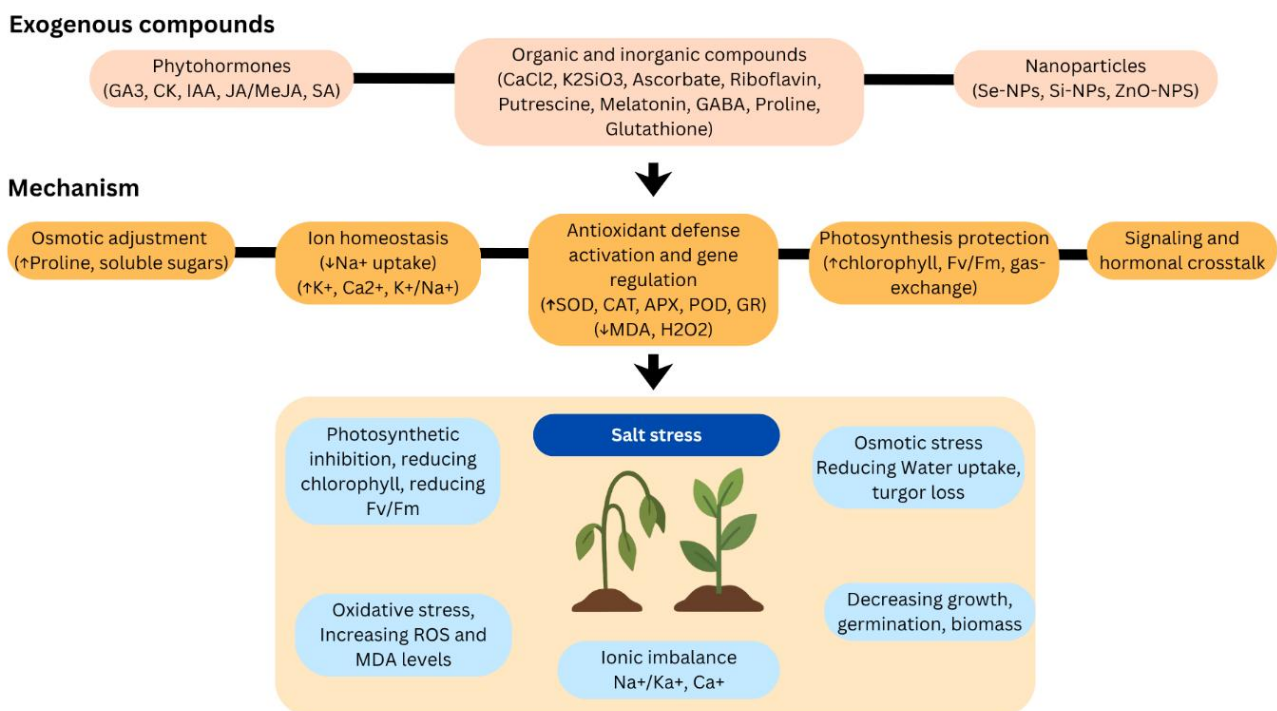


Figure 2. Exogenous compounds mechanism under salt stress conditions.

antioxidants (ascorbate, glutathione, and phenolics), leading to reduced accumulation of ROS and lipid peroxidation products (MDA). They adjust the osmotic balance by increasing the osmolytes (proline and soluble sugars). They promote osmotic adjustment via accumulation of compatible solutes including proline, soluble sugars, glycine betaine, and polyamines, thereby maintaining cell turgor and water balance. Moreover, increase the balance of ions by reducing the Na⁺ uptake and increasing the ratio of potassium and sodium ions and potassium and calcium ions. They increase the chlorophyll content, the photosynthetic efficiency, and gas exchange, thereby increasing the photosynthesis protection. Many compounds act as signaling molecules that modulate stress-responsive gene expression and hormonal crosstalk, particularly between SA, JA, IAA, ABA, and cytokinins. Importantly, the effectiveness of these compounds is highly dependent on dose, application method (seed priming, foliar spray, root drench), timing, plant species, and salinity severity. Synergistic combinations, such as IAA with nitric oxide or boron nanoparticles. Si-NPs with melatonin (36), or Se-NPs with ZnO-NPs (39) often outperform single treatments, indicating that integrated approaches hold greater promise for field applications.

5. Conclusion

Salinity stress showed significant physiological and biochemical influence, impacting plant growth and biomass. This review demonstrates that exogenous compounds have significant impacts on reducing saline toxicity by various mechanisms: (1) activation of enzyme and non-enzymatic antioxidant defense systems, reducing the ROS and MDA content; (2) maintaining ion homeostasis by limiting Na⁺ accumulation and enhancing K⁺ and Ca²⁺ uptake; (3) inducing the osmolytes; (4) modulating the stress-responsive gene expression and hormonal crosstalk. The effectiveness of the compounds depends on concentration, application method (seed priming, foliar spray, and root absorption), plant species, and salinity severity. Synergistic combination applications are frequently used to enhance the plant tolerance. In summary, exogenous compound application represents a

versatile and effective strategy to enhance plant salinity tolerance. Future study will refine these promising approaches for practical agricultural use.

Author Contributions

Muchamad Imam Asrori: Conceptualization, Analysis, Writing-Original, Visualization; Ender Hidayat: Review.

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No data was used for the research described in the article.

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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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