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REVIEW ARTICLE

Recent advances in the alleviation of salt stress in plants

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Abstract

Salt stress is one of the crucial abiotic factors limiting plant growth and production. It is caused by high salt levels in the soil, which limit the availability of irrigated water and other minerals required for plant growth. It can cause poor crop yields and food insecurity, particularly in coastal and desert areas. Mitigating plant salt stress is critical for increasing agricultural yields and maintaining food security. There are numerous approaches to reducing the negative consequences of salt stress, including genetic modification, hormone therapy and improved soil management practices. Recent discoveries in the field include microbial consortia, nanotechnology, metabolomics, systems biology and CRISPR-Cas technologies for improving plant salt tolerance. Minimising salt stress in plants is crucial for enhancing agricultural output and food security and several quantitative methods can be utilised to accomplish this goal. This review will address recent findings on salt tolerance in plants, utilising microbial, morpho-physical, biochemical and genetic approaches and nanoparticle applications.

Keywords: biochemical; morpho-physical; nanotechnology; plant growth promoting bacteria; salt stress; transgenic

Introduction

Being a critical factor of the global economy, agriculture is essential for human existence and national development. Steady-state rise in the global population, drastic decline in the arable land and devastating effects of stressors, including pests, drought, salt and flooding, threaten food security (1–6). Among these, salt-affected soils have been the major issue in agricultural production since it is mostly prevalent in arid and semi-arid regions where irrigation remains the major source of raising crops (7). Nearly 26.10 million hectares (Mha) of land is affected by salt stress in India (8). Annually, one-fifth of the global area and 1.5 Mha of cultivable land become degraded owing to high salinity in the soil (9). Soil salinisation is induced by both natural and artificial processes such as water deficiency, low-quality irrigation, mineral weathering and excessive evaporation. High salinity in the soil leads to several detrimental impacts, including decreased water uptake, reduced photosynthesis, impaired nutrient absorption and perturbed microbial population (10–17). One of the significant ways that salt stress impacts plants is through its influence on water intake. Soil salinisation arrests the water inflow through the gradual loss of water from the cell interior to the outside because of the higher salt content in the soil than that of the roots, which creates the differences in the water potential (18). The chloroplast is the major organelle impaired under salt stress that directly impacts net photosynthetic rate, thereby arresting plant growth through the production of reactive oxygen species (ROS), which affects stomatal closure and photosynthesis (19). Higher salt content also interferes with the absorption of macro nutrients like nitrogen, phosphorus and potassium by obstructing the function of nutrient transporters, which also hinders plant development (20). Agronomic practices like effective irrigation management, mulching, foliar spray of calcium, magnesium and zinc and using soil amendments such as gypsum or sulfur can reduce soil salinity by eliminating excess sodium from the soil (21).

Extensive signalling pathways have been orchestrated inside the plant cells to cope with salt stress (22). These pathways mainly include signal perception, transduction and stress-responsive gene expression. At the cellular level, the components of salt stress, such as ionic and osmotic stresses, are perceived by the hypothetical sensors (23). The osmotic component of the salt stress arises due to excessive salt content in the soil, which reduces the water uptake and arrests cell expansion, whereas the ionic component of salt stress leads the cells to accumulate excessive sodium, which affects leaf photosynthesis and metabolic processes (24). Through signalling mechanisms, plants coordinate the salt-responsive physiological processes such as sodium exclusion, sodium compartmentalisation, turgor maintenance and osmotic adjustment through the production of key osmolytes like proline, trehalose and glycine betaine (25).

In this review, we aimed to cover the key events of salt-responsive mechanisms mediated by plants at the molecular, physiological and biochemical levels. We have summarised few pieces of evidence on the transgenic approaches and genome editing aspects for generating salt-tolerant plants. Further, we have addressed the recent application of plant growth-promoting bacteria (PGPB) and bio-stimulants such as nanoparticles for salt stress management.

Responses of salt stress on plants

Effect on the morphological and anatomical level (Root and leaf)

The salt stress reduced the number of lateral roots, which resulted in poor nutrient use efficiency (26). It severely inhibits root growth and function by causing osmotic stress, ion toxicity, nutrient imbalance and oxidative damage. Since roots control water and mineral uptake, salt-induced root damage ultimately reduces overall plant growth and productivity. Salt stress affects leaves by reducing growth, impairing photosynthesis, inducing ionic toxicity, oxidative damage and premature senescence (27). As leaves are a source of energy production, these effects ultimately result in reduced plant productivity and yield.

Effect on physiological parameters (Photosynthetic, plant water relation sand stomatal physiology)

It restricts CO_2 diffusion, damaging chlorophyll and the PSII system, disrupting electron transport and inhibiting carbon assimilation enzymes (28). The combined decline in photosynthetic parameters ultimately leads to reduced growth and development. It lowers the water potential, restricts water uptake, reduces hydraulic conductance and induces osmotic stress (29). It ultimately leads to water deficit, growth inhibition and reduced productivity. It affects stomatal physiology by inducing abscisic acid (ABA) mediated stomatal closure, disrupting guard cell ion homeostasis and reducing stomatal conductance and density (30). It also restricts CO_2 uptake and contributes to reduced photosynthesis, leading to reduced growth.

Effect on biochemical responses (Plant growth hormones and antioxidant enzymes)

The stress up-regulates stress-associated hormones -ABA, ethylene, Jasmonic acid (JA), Salycilic acid (SA) and down-regulates growth-promoting hormones (auxins, cytokinins, gibberellins) (31). Which prioritises survival and stress adaptation over growth, ultimately shaping plant tolerance or sensitivity to salinity.

Effect on oxidative stress

It enhances ROS production beyond the scavenging capacity of plant cells, leading to membrane damage, enzyme inactivation and genetic instability (32). The strength and efficiency of the antioxidant defence system play an important role. The stress triggers oxidative compounds, counteracted by the coordinated modulation of antioxidant enzymes. These include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), general peroxidases (PRX) (e.g. guaiacol peroxidase GPX), glutathione reductase (GR) and Peroxidase (POD), which reduce ROS accumulation and protect cellular structures (33).

Effect on gaseous molecules (Nitric oxide and hydrogen sulfide)

It acts as a central gaseous regulator in plants under salt stress. By interacting with ROS, hydrogen sulfide and carbon monoxide, nitric oxide reduces oxidative damage, maintains ion homeostasis and strengthens antioxidant defences (34). While hydrogen sulfate modulates a wide array of genes that orchestrate morphological, anatomical, physiological and biochemical changes to enhance tolerance, with gaseous signalling molecules playing a central role in this regulation (35). Morphologically and anatomically, stress-responsive genes regulate root architecture (e.g. deeper roots, altered lateral root formation) and leaf structure to improve water uptake and reduce ion toxicity.

Mechanisms of salt tolerance

Morpho-physiological responses to salt stress

Morphological and physiological responses to salt tolerance involve modifications in root and shoot growth and architecture such as profound root growth or the formation of specialist salt-excluding roots, as well as changes the ways, they transport and store water and nutrients (Table 1 and Fig. 1). Physiological factors such as the accumulation of solutes and the regulation of ion transporters also play a role in salt tolerance (42).

Table 1. Morpho-physical modifications in plants for survival under salt stress

Name of the plant	Type of experiment	Concentration of salt applied	Major outcome of the study	Reference
Tomato (Transgenic, SOD overexpressing)	Controlled pot experiment under NaCl stress	150 mM NaCl	Overexpression of SOD mitigated salt-induced structural damage in chloroplasts and improved cellular integrity	(36)
Paddy (Rice)	Pot experiment with rhizosphere bacteria	100 mM NaCl	Zinc-mobilising bacteria improved plant physiology and growth parameters under salt stress	(37)
Arabidopsis	Laboratory microscopy and molecular study	100–150 mM NaCl	Microtubule reorganisation plays a vital role in salt tolerance and adaptive growth	(38)
Barley (Aleurone cells)	High-salt germination experiment	200 mM NaCl	High salt altered actin cytoskeleton organisation and induced vacuolisation changes	(39)
Arabidopsis	Molecular and cytoskeleton analysis	150 mM NaCl	The microfilament cytoskeleton plays an essential role in osmotic and salt stress tolerance	(39)
Barley	Comparative proteomic study	100–200 mM NaCl	Differential root proteome changes associated with salt tolerance mechanisms	(40)
Pistachio (Rootstocks)	Field/pot morpho-physiological study	EC 8–16 dS m^{-1} (salinity levels)	Sodium compartmentalisation and morpho-physiological adjustments improved tolerance	(41)

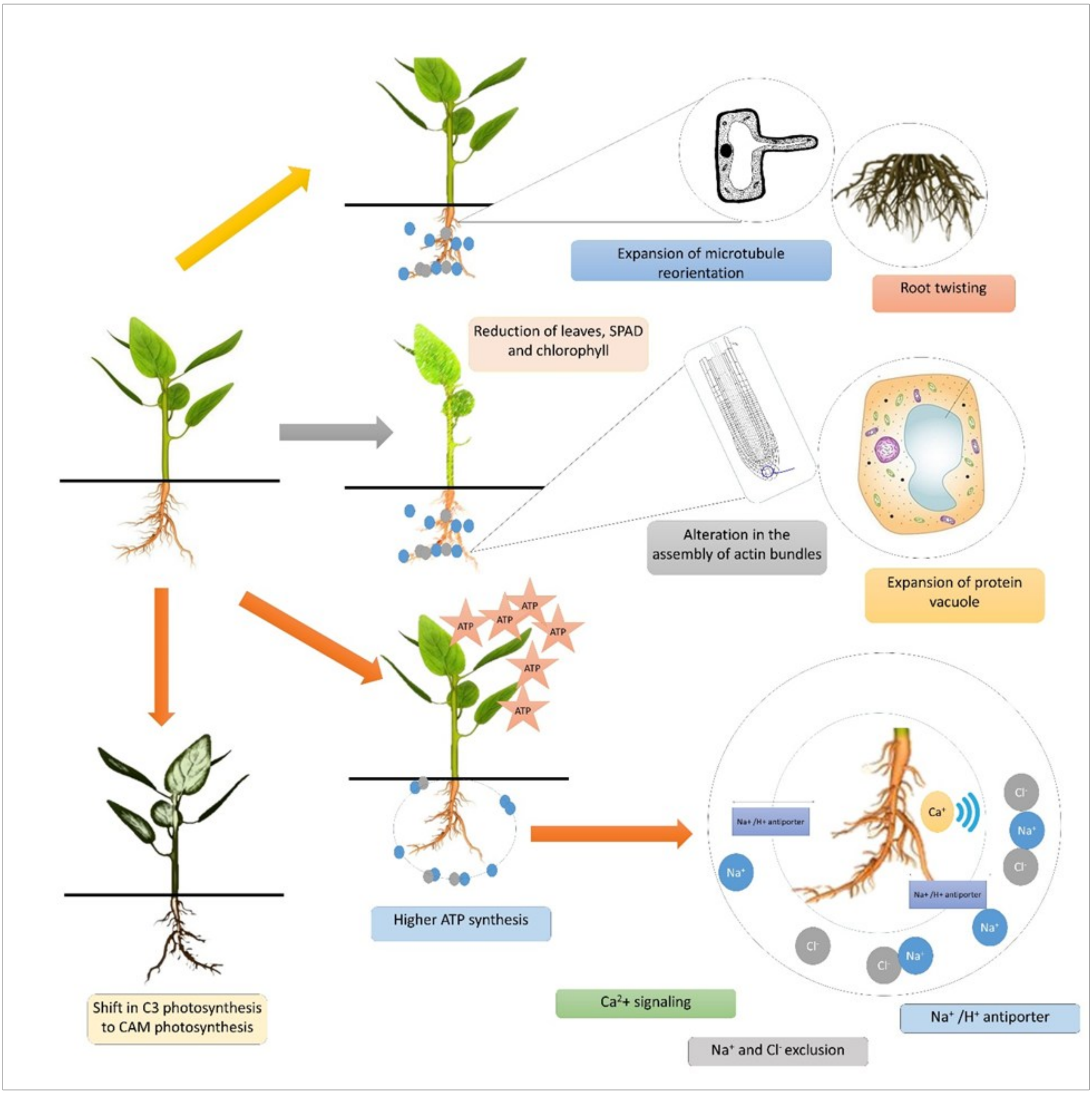

Fig. 1. Morpho-physiological modifications in plants under salt stress conditions.

Table 2. Use of plant growth-promoting bacteria in the alleviation of salt stress

Name of the plant	Name of the bacteria (PGPB)	Type of experiment	Major outcome of the study	Reference
Triticum aestivum (Wheat)	ACC deaminase–producing PGPR (e.g. *Pseudomonas*, *Bacillus*)	Review-based analysis of experimental studies	Reduced stress ethylene levels, improved root elongation, better Na^+/K^+ balance, enhanced biomass and yield under salt stress.	(44)
Pisum sativum (Pea)	ACC deaminase-containing endophytic bacteria	Pot experiment under salt stress	Reduced oxidative damage (MDA), enhanced antioxidant enzymes (SOD, CAT, POD) and improved shoot/root biomass under salinity.	(45)
Olea europaea (Olive)	Beneficial rhizobacteria (PGPB consortium)	*In vitro* plantlet experiment	Improved photosynthetic efficiency, enhanced ROS scavenging, better chlorophyll retention and growth under salt stress.	(46)
Solanum lycopersicum (Tomato)	ACC deaminase–producing PGPR (e.g. *Pseudomonas putida*)	Pot experiment	Improved plant height, root length, chlorophyll content; reduced ethylene accumulation; enhanced salt tolerance.	(47)
Panax ginseng	*Paenibacillus yonginensis* DCY84T	Controlled pot experiment	Activated antioxidant defence-related genes, enhanced enzymatic activity (SOD, CAT) and improved biomass under salinity.	(48)
Trigonella foenum-graecum (Fenugreek)	*Priestia endophytica* SK1	Pot experiment	Improved nitrogen assimilation increased secondary metabolites, enhanced growth and salt tolerance.	(49)

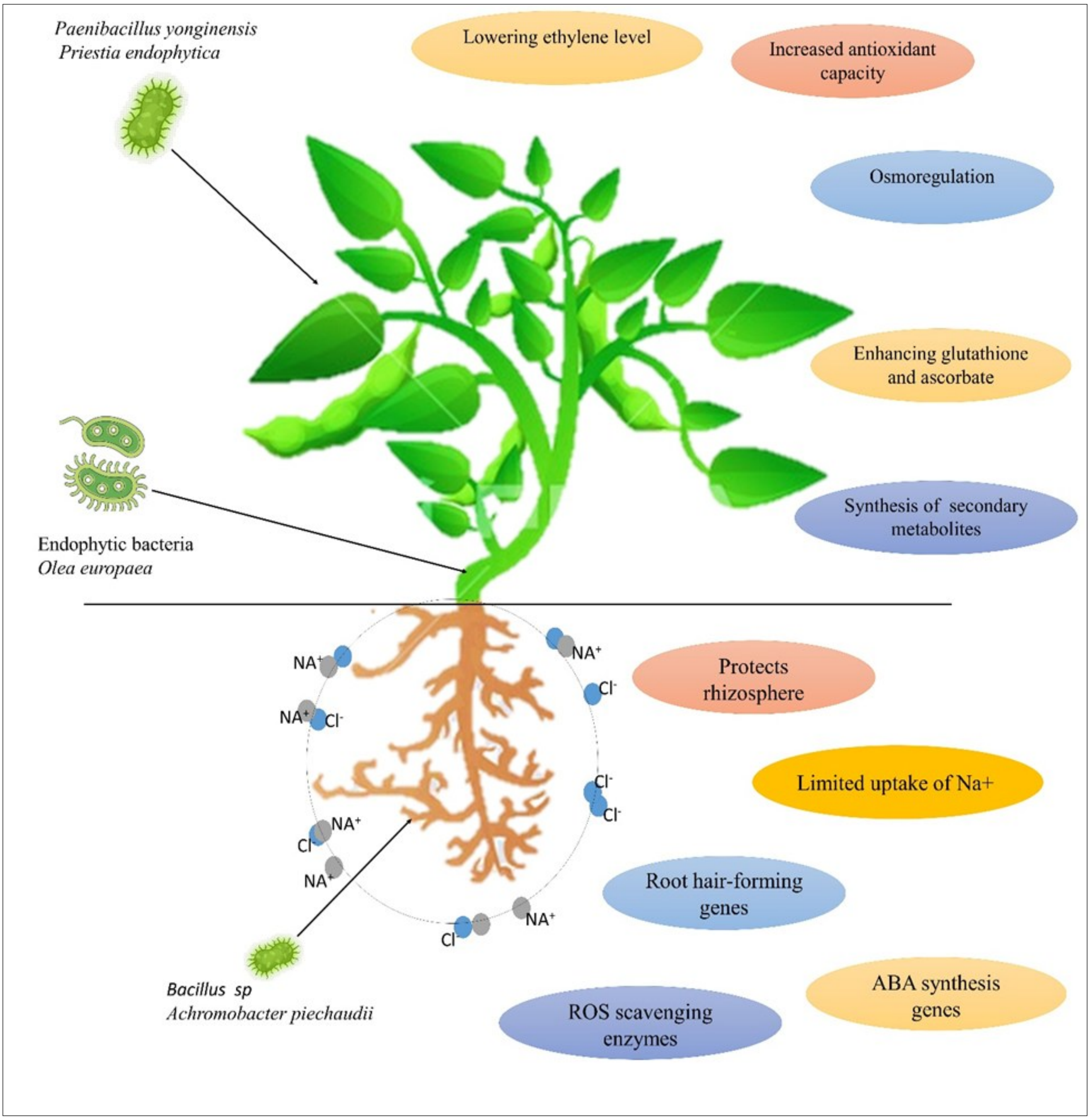

Fig. 2. Role of plant growth-promoting bacteria in salt stress tolerance.

Microbe-mediated salt tolerance

Using PGPB is one of multiple ways to enhance plant salt tolerance (Fig. 2). Plant growth promoting bacteria are naturally prevalent in the soil and provide an environmentally friendly approach to get rid of soil salinity and restore soil health as well (43). They can boost plant resistance against salt stress by several mechanisms, which are listed in Table 2. Applying PGPB in agriculture can provide a sustainable crop yield and food security in salt-affected areas.

In *Pisum sativum* L., endophytic bacteria are involved in the mitigation of salt stress by boosting the plant's ability to absorb and transport water, lowering water loss through stomata and enhancing the synthesis of hormones such as indole acetic acid (IAA) and gibberellins (GA). These hormones stimulate root development, which increases the absorption of nutrients and enhances the plant's ability to cope with environmental challenges (50). The bacteria were also discovered to strengthen the plant's antioxidant defence system, by triggering the synthesis of antioxidant enzymes viz. POD and superoxide dismutase SOD, which lower the levels of ROS under salt stress. Plant growth promoting rhizobacteria also help to minimise the accumulation of sodium ions by lowering the intake of sodium ions and boosting the capacity to reject sodium ions (51, 52).

In addition to PGPRs, *Azospirillum* and *Bacillus* have been demonstrated to control photosynthesis and reactive ROS levels in *Olea europaea* L. (olive tree) (53). These bacteria colonise the rhizosphere and influence photosynthesis by boosting the activity of photosynthetic enzymes. The regulation of photosynthesis and ROS together leads to enhancing stress tolerance. Rhizosphere bacteria from rice improved salt tolerance by the mechanism of solubilising the salt crystals mediated through proteases and increasing nutrient availability (54). Further, these bacteria increased the accumulation of solutes such as proline and glycine betaine in the leaves for osmotic stress tolerance. Similarly, *Paenibacillus yonginensis* (DCY84T) modulates the plant's antioxidant defence mechanism in *Panax ginseng* C.A.Mey. by altering numerous defence-related genes related to ion transport, root hair formation, solute accumulation, ROS scavenging, total sugars and ABA synthesis (55, 56).

Mung bean *(Vigna radiata* (L.) R.Wilczek) is well known crop that performs better under saline soils (57). The rhizosphere microbiome of *V. radiata* comprises a vast population of microorganisms such as bacteria, fungi and archaea, which increase resistance against salt stress. Fungi such as *Penicillium* and *Aspergillus* can also enhance the plant's resistance to salt stress by producing enzymes such as chitinases, glucanases and exopolysaccharides (EPS) that can help to boost water retention in the soil. *Priestia endophytica* SK1 is a bacterium that was discovered to increase the salt tolerance of fenugreek (*Trigonella foenum-graecum* L.) under salt stress by increasing the accumulation of compatible solutes, modulating the plant's antioxidant defence system and producing plant growth-promoting compounds (58).

Studies have demonstrated that plants with high levels of 1-Aminocyclopropane 1-carboxylic acid (ACC) deaminase are better able to handle salt stress, with increased growth and development than plants without ACC (59). Additionally, the enzyme has been demonstrated to boost the plant's capacity to absorb and transport water, further minimising the harmful consequences of salt stress. Similarly, *Achromobacter piechaudii* is a soil-borne bacterium that has been demonstrated to have a favourable influence on the growth and development of tomato plants through regulating the synthesis of IAA and GA. It was shown that *A. piechaudii* could promote the growth and development of tomato plants by promoting root growth and increasing the absorption of nutrients. These bacteria can also boost the plant's resistance to salt stress by enhancing water intake and lowering water loss through stomata (60).

Also, Biochar has proven to be beneficial against abiotic stress. It is a form of charcoal created by pyrolysis, a technique of heating organic materials under oxygen-poor conditions. It has been discovered to have a good influence on the growth and development of plants and can also aid in mitigating the detrimental effects of environmental pressures, such as salt stress. It mitigates the harmful impacts of salt stress by improving soil structure, boosting nutrient availability, lowering the buildup of sodium ions and promoting plant defence systems (61).

Wheat exhibits physiological and anatomical modifications-including osmotic adjustment, proline accumulation, enhanced root architecture, stomatal closure, leaf senescence and activation of the antioxidant defence system-to cope with salt stress. Similarly, pistachio nut plants subjected to elevated salt concentrations demonstrate sodium compartmentalisation in leaf cells, which minimises damage to the photosynthetic machinery (36). However, the reduction in the number of developing leaves, The soil plant analysis development (SPAD) index of leaves, chlorophyll content and stomatal conductance is still detected under salt stress conditions in salt-tolerant plants. A similar technique of excluding the salt level by root cells through the apoplastic barrier was also reported in olive plants. A study has also demonstrated that the alteration of root cells in connection to the function of exodermis and endodermis is elevated in response to salt stress in the olive tree, indicating that these barriers play an essential part in the olive tree's salt tolerance mechanism (62).

Apoplastic modifications in roots also lead to lower ion fluxes, including the inflow of sodium ions (Na^+) and chloride ions (Cl^-), which can contribute to plant salt tolerance. This system manages ion transport and homeostasis by preventing excess ion intake and allowing the plant to actively exclude ions when needed (63). The Apoplast operates as a barrier and synthesises apoplastic ascorbate oxidase (AAO) which plays a role in the antioxidant defence mechanism in response to salt stress (64). It catalyses the conversion of ascorbate to dehydroascorbate (DHA) and hydrogen peroxide (H_2O_2). The elevated H_2O_2 acts as a signalling molecule that stimulates additional antioxidant enzymes and prevents cell damage.

Studies in *Mesembryanthemum crystallinum* L., a C_3 plant, revealed a shift in the photosynthetic system to crassulacean acid metabolism (CAM) under salt stress within 2 weeks (65). The *Kalanchoe* (Crassulaceae family, CAM plants) plants adjusted the leaf succulence and stomatal closure during the day to reduce the water loss through transpiration and instead opened them at night to allow carbon dioxide. This permits the plant to conserve water and thrive in areas with limited water supplies, such as salt-affected soils. Further, it also revealed modulation of photosynthetic metabolic plasticity and chloroplast ultrastructure (66). The *Kalanchoe* plants maintained their chloroplast ultrastructure even under high salt conditions (2 % w/v) and the changes included increased stacking of thylakoid membranes through the upregulation of heat shock proteins (HSPs) (67, 68). Salt stress leads the plants to remodel their cytoskeleton to preserve standard cell shape and prevent excessive salt uptake (69). Under salt stress, 10–50 dS/m ECe in the microtubule cytoskeleton in the root cells (wheat or *Kalanchoe*) would be changed in a process termed root twisting, also known as gravitropic bending in which the root cells encounter a change in their form and orientation, through which plants can redirect their root growth to escape areas of high salt concentration and obtain water from deeper soil layers (70). According to root twisting in response to salt stress is mediated by changes in the activity of microtubule-associated proteins (MAPs) by the overexpression of FBA8, TUB3 and TUB4 genes, which can modify the stability and orientation of microtubules (71). In *Arabidopsis* plants, research has also demonstrated that the cytoskeleton, particularly actin microfilaments, plays a crucial role in the plant's response to salt stress. The actin cytoskeleton can also aid in pumping away excess salt from the cell. Additionally, microfilaments can assist in reinforcing the cell wall to avoid damage from the salt (72).

Salt tolerance through a transgenic approach

Genomics, transcriptomics, proteomics and metabolomics have been applied to explore different components involved in the response to high salt concentration to understand the underlying salt tolerance mechanisms (73–77). Transgenic tomato plants have been genetically engineered with ROS transporters, showing the phenotype of specialised salt-excluding roots or the growth of deeper roots to access water from deeper soil layers, an increased size or number of chloroplasts to support the increased biosynthesis of compatible solutes (78). The overexpression of the SOD genes in sweet potato plants has been found to increase tolerance to salt stress, drought and other environmental conditions (79).

Table 3. Genetical and transcriptional changes in plants for sustaining under salt stress

Name of the gene/ transcript	Name of the source plant	Mode of expression (Upregulation/ downregulation)	Important outcome of the study (specific to salt stress)	Reference
MdPR6	*Malus domestica*	Upregulation	Enhanced chloroplast structure stability, improving photosynthetic efficiency and salt tolerance	(82)
WRKY23	*Solanum lycopersicum*	Upregulation	Modulated ethylene and auxin signalling pathways, improving stress adaptation	(83)
BES1 (Transcription factor)	*Vitis vinifera*	Upregulation	Reduced malondialdehyde (MDA) levels and increased proline accumulation, lowering oxidative damage	(84)
CmCIPK18 (CIPK gene)	*Chrysanthemum*	Upregulation	Decreased ROS accumulation and enhanced antioxidant defence	(85)
PwNAC1	*Arabidopsis*	Upregulation	Regulated ABA-dependent stomatal conductance, improving water use efficiency under salinity	(86)
OsDSR2	*Oryza sativa*	Downregulation / Suppression	Modulated ABA and IAA signalling pathways, enhancing salt stress tolerance	(87)
R2R3-MYB transcription factor	*Setaria italica*	Upregulation	Regulated phenylpropanoid pathway, strengthening antioxidant and structural defence	(88)
BnGRP7 (Glycine-rich RNA-binding protein 7)	*Brassica napus*	Post-transcriptional modulation	Regulated mRNA stability and stress-responsive gene expression under salinity	(89)
Anthranilate Synthase α-Subunit (*ASA1*)	*Catharanthus roseus*	Overexpression	Enhanced jasmonic acid biosynthesis and altered metabolic pathways improve salt stress response	(90)
Phytoene Synthase (PSY) / β-Carotene Hydroxylase (BCH)	*Dunaliella salina*	Upregulation	Increased carotenoid biosynthesis leading to improved photoprotection and oxidative stress tolerance	(91)
HSP70 and LEA Proteins (Late Embryogenesis Abundant Proteins)	*Solanum tuberosum*	Upregulation	Enhanced cellular protection and multi-protein regulatory mechanisms under salt stress	(92)
SHE1 and *CESA6*	*Arabidopsis*	Upregulation	Enhanced cellulose synthesis, improving cell wall integrity under salinity	(93)
PtNAC10	*Populus trichocarpa*	Downregulation of lignin-related genes	Reduced lignin synthesis, modifying cell wall composition for improved stress adaptation	(94)

Genetic and transcriptional modification

Salt tolerance in plants can be increased by genetic manipulation, where specific genes involved in salt tolerance are introduced, overexpressed or silenced to enhance growth, survival and production under salt stress (80, 81) (Table 3).

There are numerous strategies used to achieve salt tolerance through genetic changes by introducing genes encoding for sodium-transporting ATPases or other transporters, over-expression of genes involved in osmoregulation and stress response, over-expression of transcription factors and antioxidant enzymes and by gene silencing through RNA interference (RNAi) for salt sensitivity, metabolic engineering to modify the plant's metabolic pathways and increase its ability to tolerate salt (95). In apples, the chloroplast-localised MdPRP6 protein (naturally encoded gene, not genetically modified) stabilises chloroplast structure under salt stress, preserving its integrity, supporting photosynthesis and aiding cellular stress responses (96). Specifically, it has been identified as important in controlling the plant's response to extreme salt stress via altering gene expression and ion transport. Similarly, in *Arabidopsis*, the WRKY23 gene has been demonstrated to affect genes related to ethylene and auxin signalling pathways. By discussing WRKY TFs like SlWRKY23 (tomato ortholog) in NGS-enabled breeding, where its overexpression modulates hormone crosstalk for osmotic/NaCl tolerance (e.g., via root architecture changes). Studies confirm effects in *Arabidopsis* transgenics ties to wheat/ linseed salt stress (97). The BES1 transcription factor reduces malondialdehyde (MDA) levels-a marker of oxidative stress and lipid peroxidation that damages plant cell membranes-under salt stress. In *Arabidopsis*, BES1 directly regulates salt-responsive genes for antioxidant defence (SOD, POD) and ion homeostasis, as shown in *bes1-D* gain-of-function mutants (150 mM NaCl) with lower MDA/electrolyte leakage vs. RNAi knockdowns. BES1 overexpression in birch (*BpBZR1-6*) and wheat homologs (*TaBZR2*) enhances salt tolerance by scavenging ROS and cutting MDA accumulation. Further salt-specific crop engineering using BES1 is warranted to develop salinity-resilient varieties like previous wheat/ linseed studies. It is also found similar downregulation of ROS occurs in *Chrysanthemums* by CmCIPK8 (98). The downregulation has resulted in enhancing the expression of genes related to ion transport. Similar downregulation of the phenylpropanoid pathway was found in foxtail millet by R2R3-MYB, consequently influencing the generation of these secondary metabolites (99). The phenylpropanoid pathway is responsible for forming secondary metabolites, including flavonoids, lignins and tannins, which play critical functions in plant growth, development and defence against biotic and abiotic stress (100).

The combination of PwNAC1 and the RNA-binding protein has been discovered to modulate gene expression implicated in the ABA signalling pathway, leading to variations in stomatal conductance. By modifying the stomatal conductance, PwNAC1 and the RNA-binding protein may aid in increasing water use efficiency and free radical scavenging during drought and salt stress (101). Further study is needed to thoroughly understand the processes by which PwNAC1 and the RNA-binding protein control ABA-dependent stomata conductance and to identify their potential for generating drought-tolerant crops (102, 103). Overexpression of the anthranilate synthase (AS) gene in *Catharanthus roseus* (L.) G.Don hairy roots increases anthranilate synthesis, boosting indole-3-acetic acid (auxin/IAA) and JA precursors in tryptophan metabolism. Under salinity (100–200 mM NaCl), endogenous IAA drops due to disrupted transport and *YUCCA/P450* downregulation, impairing root halotropism and osmotic adjustment. AS-OE elevates IAA levels, promoting lateral root growth to access deeper water, enhancing K+/Na+ ratios and activating JA-mediated ROS scavenging/ABA signalling for ionic homeostasis (104). Hairy roots have been genetically engineered to generate huge quantities of useful metabolites. The increase in anthranilate production by AS overexpression can also lead to up-regulation of the endogenous biosynthesis of JA, which is a signalling chemical implicated in plant stress responses. This up-regulation alters the metabolic networks in the hairy roots by modifying the expression of genes involved in secondary metabolism and the production of metabolites (105).

Interestingly, amplifying cellulose production has been proven to improve plant salt tolerance (106). It was observed that there was an overexpression of a gene *At1g45688* (*CC1*), which might have helped in cell wall development. Cellulose is a significant component of plant cell walls and is vital in maintaining cell shape and stiffness. Increased cellulose production can lead to thicker cell walls, which can give more protection to the plant against salt stress. In addition, cellulose production can also modify the regulation of other genes involved in plant stress responses and enhance water-use efficiency, which can further contribute to salt tolerance (107). At the same time, an increase in cellulose production has shown promise as a technique for strengthening salt tolerance (106). In contrast, the downregulation of lignin production has been demonstrated to promote salt tolerance.

Likewise, Lignin is a complex polymer that provides structural support and reinforces the cell walls of plants. However, excessive quantities of lignin can also impair water intake and limit the capacity of roots to absorb nutrients, making it more difficult for the plant to endure salt stress. Downregulation of lignin production can lead to lower lignin concentration and higher water-use efficiency, which can aid in enhancing plant salt tolerance (108). However, lignin is also crucial for plant defence against pathogens. Therefore, lowering lignin concentration also makes the plant more vulnerable to disease. And the overexpression of cellulose by gene OsNHX1 in *Arabidopsis* and downregulation of lignin by PtNAC101 transcription factor in *Populus trichocarpa* Torr. & A.Gray ex Hook. were reported (93, 109). In pomegranate, transcriptional regulation of *NHX1* leads to sequestering Na^+ in vacuoles and effluxing Na^+ from mature leaves (110).

Biochemical alterations

Salt stress can induce numerous metabolic modifications in plants, thereby impairing their development and survival. These abnormalities include ion imbalances, osmotic stress, oxidative damage and changes in gene expression (Table 4). These alterations can lead to cellular damage, diminished growth and lower agricultural yields (119–121).

Salt stress in plants generates a hormonal response that involves the regulation of multiple plant hormones (122). Abscisic acid levels increase in response to salt stress, whereas GA levels fall (123). This leads to diminished root development and increased oxidative stress (124). Similarly, a rise in ethylene has a role in regulating ion transport, perhaps contributing to salt stress tolerance. While GA levels drop during salt stress, limiting cell division and root development (124, 125). The response of plants to external hormone treatment under salt stress has been antagonistic with the application of GA and ABA, where GA stimulates growth and ABA reduces it and synergetic with the administration of SA and ABA, where they act together to enhance stress tolerance (126). Also, it was discovered that simultaneous application of GA and cytokinins (CK) under salt stress resulted in an overall impact equivalent to the sum of the effects of each hormone alone, where GA and CK have different and unique effects on plant growth and development. It was also observed that a rise in IAA and amino flunitrazepam levels in response to salt stress was associated with increased salt tolerance in plants (127). Both have been identified as crucial functions in altering the activity of signalling pathways involved in stress response and regulating the production of stress-responsive genes. Root system design is a key aspect in plant survival and development, especially under stressful circumstances like salt stress (128). It refers to the morphological and structural properties of a plant's root system, including root length, branching pattern, root diameter and root hairs. Several

Table 4. Biochemical alterations in plants under salt stress

Name of the plant	Type of experiment (pot / field / lab)	Concentration of salt applied	Major outcome of the study	Reference
Brassica juncea (Seedlings)	Pot experiment	100 mM NaCl	Nitric oxide accumulation, increased osmolytes, enhanced antioxidant defense and reduced ROS damage	(111)
Arabidopsis thaliana	Controlled lab experiment	150 mM NaCl	Flavonoid overaccumulation, reduced oxidative stress and enhanced tolerance	(112)
Pennisetum glaucum (Pearl millet)	Pot experiment with fungal inoculation	150 mM NaCl	Secondary metabolite modulation, improved osmotic balance and enhanced antioxidant activity	(113)
Mustard (Green & Purple)	Pot experiment (melatonin application)	100–150 mM NaCl	Enhanced anthocyanin accumulation, upregulation of antioxidant enzymes and improved ROS scavenging	(114)
Arabidopsis thaliana	Laboratory genetic & physiological study	100–150 mM NaCl	Upregulation of cellulose synthesis genes (CESA6, CSI1) improved cell wall integrity and enhanced salt tolerance	(115)
Wheat (Seedlings)	Pot experiment	100 mM NaCl	Hydrogen sulfide improved antioxidant defence, activation of the SOS pathway and reduced ion toxicity	(116)
Maize (Seedlings)	Laboratory germination study	150 mM NaCl	Auxin seed priming improved ROS detoxification, enhanced carbohydrate metabolism and improved germination under salinity	(117)
Rice (*Oryza sativa*)	Laboratory molecular study	100 mM NaCl	JA-Ile metabolism regulation, hormonal signalling adjustment and improved salt stress adaptation	(118)

plant hormones, including auxin, CK, ABA and GA, can also impact the modification of root system architecture through activating multiple key pathways (129). Studies have shown the relationship between hormones and root system architecture for tolerance to salt stress (130). The administration of exogenous auxin and/or cytokinin has been found to enhance root system architecture and salt tolerance in *Arabidopsis* (128).

(JA-Ile) is a JA facilitates the functions in plant growth, development and under stress conditions (129). It has been reported that, in rice, using exogenous JA-Ile can increase salt tolerance by activating defence mechanisms and boosting antioxidant activity (131). Additionally, compared to control plants, transgenic rice plants overexpressing the gene encoding the enzyme responsible for JA-Ile production demonstrated enhanced salt tolerance (132). Further, in soybeans, SA and JA were revealed to play a role in the plant's response to different environmental challenges, including salt stress (133). Salicylic acid is implicated in producing systemic acquired resistance (SAR), a plant defence mechanism against salt stress. Salicylic acid is shown to activate the production of defence-related genes, leading to an increase in antioxidant activity and better salt stress tolerance (134). Zwitterionic osmolytes are tiny, neutral molecules that function critically to maintain cellular osmotic equilibrium and resist salt stress in plants, including glycine betaine, proline and other amino acids with a zwitterionic structure. Under salt stress, they can operate as osmoprotectants, preventing osmotic stress and the buildup of harmful ions in the cytoplasm (135). It has been observed that glycine betaine can desorb salt ions from the root surface of barley by interacting with the surface, lowering the buildup of harmful ions and enhancing osmotic balance (136). They were also shown to be vital in regulating different stress-responsive genes (*SOS5*; *JAS*) and signalling pathways, enabling plant survival and adaptability to salt stress (132). Another osmolyte, proline, has been found to activate stress-responsive genes (*P5CS1 and P5CS2*) and enhance plant tolerance to salt stress by boosting cellular antioxidant defence systems and lowering oxidative damage (137, 138). Nitric oxide is another key osmolyte and signalling molecule that has been found to have a role in plant responses to various stress situations, particularly salt stress (138). Nitric oxide has been demonstrated to influence the activity of nitrate reductase (NR), a critical enzyme involved in nitrate absorption and plant development (138). During salt stress situations, NO can control NR activity by lowering its activity, resulting in reduced nitrate absorption and plant development. In tomato plants, NO donors like sodium nitroprusside (SNP) enhance NR activity under salt stress, which helps delay ammonium accumulation and supports nitrogen metabolism (139).

This NR activity is expected to help lessen the harmful effects of salt stress on plant development and survival. Also, NO has been demonstrated to activate antioxidant defence systems and minimise oxidative damage. The buildup of anthocyanin in plants has been found to guard against oxidative stress and lower the accumulation of ROS. The buildup of anthocyanin in response to stressful circumstances is a complicated and dynamic process that plays a critical function in protecting plants against oxidative stress and boosting their tolerance to diverse stress situations (140). Flavonoids and lignin precursors have been demonstrated to increase in response to salt stress and enhance tolerance to stress in *Zea mays L.* (141). Similarly, lignin precursors, such as p-coumaric acid and ferulic acid, have also increased in response to salt stress. The formation of lignin precursors has been demonstrated to reinforce the plant cell wall, giving greater protection against environmental stresses, including salt stress (111, 112, 142–144).

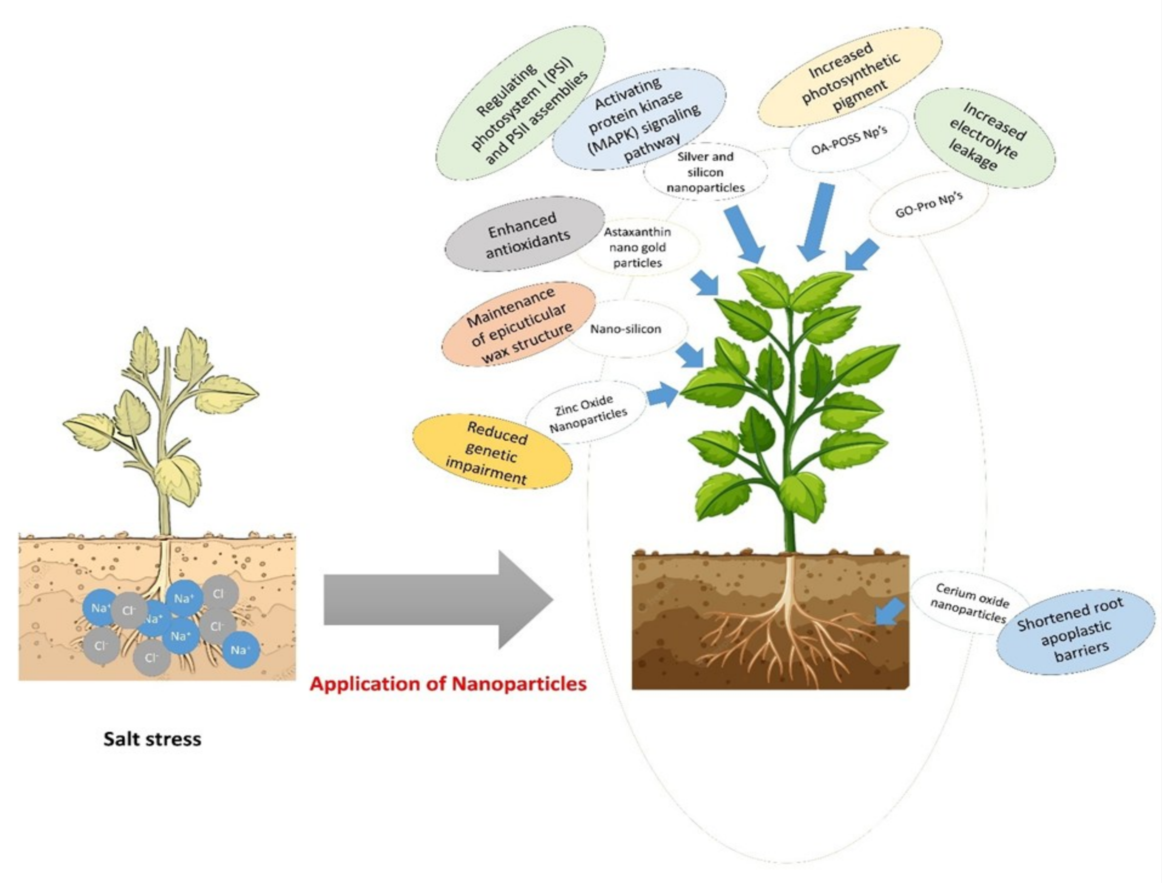

Fig. 3. The action of different nanoparticles in alleviating the salt stress.

Under stressful circumstances like salt stress, plants engage multiple signalling pathways to activate their defensive systems and minimise oxidative damage. The synchronisation of these signalling pathways is critical for the efficient activation of antioxidant defence mechanisms and the increased tolerance to stress (98, 145). Calcium ions (Ca^{2+}) act as pivotal secondary messengers in response to salt stress. Increased salinity instigates temporary surges in cytosolic Ca^{2+}, detected by calcium-binding proteins like calmodulins and calcium-dependent protein kinases (CDPKs) (146).

These proteins phosphorylate downstream targets to modulate ion transporters, such as Na^+/H^+ antiporters, thereby preserving ion homeostasis and mitigating Na^+ toxicity in cells. Similarly, SA is a versatile signalling molecule that mitigates salt stress by enhancing antioxidant defences, promoting osmolyte accumulation (e.g. proline, soluble sugars) and modulating nutrient uptake.

Application of nanoparticles

Nanoparticles have emerged as a possible approach for alleviating the harmful effects of salt stress in plants (Fig. 3). Nanoparticles are microscopic particles with a size range of 1 to 100 nanometers. They have unique features that make them valuable for diverse purposes, including plant growth and stress tolerance (Table 5). There are numerous ways, such as lowering oxidative stress, harmful chelating ions, boosting water and nutrient absorption and promoting photosynthesis. The use of nanoparticles in agriculture has the potential to provide a sustainable and environmentally friendly solution to increase crop yields and food security in salt-affected areas.

Silicon Nanoparticles (Si-NPs) have been found to boost the activity and stability of photosystems I (PS-I) and II (PS-II) in plants under stress conditions, including salt stress (152). As per the studies, Si-NPs can boost the movement and strength of PS-I and PS-II (153), raise the expression of genes involved in PS-I and PS-II repair and enhance the activities of antioxidant enzymes that protect the photosystems from oxidative damage (154–156). Seed priming of Pigeon pea with AgNPs has been proposed to boost seed resistance to salt stress (157). The processes by which AgNPs increase salt tolerance may include benefits in root development, photosynthesis and antioxidant defence systems (158, 159). A Study has demonstrated that nSi treatment can improve soybean resistance to salt stress by regulating ion balance, increasing K+ concentration, antioxidant activities, non-enzymatic chemicals and decreasing Na+ concentration (160). Increased potassium (K+) ions in plant tissues have been related to enhanced plant salt stress tolerance. This is because K+ helps control cellular water balance and maintain ion homeostasis in salty circumstances. Some Nanoparticles, such as potassium-based nanoparticles, have been found to raise K+ content in plant tissues and improve salt tolerance (161).

Zinc oxide nanoparticles have also proved to boost salt tolerance in plants. These particles alleviate salt stress by enhancing root development and controlling the movement of ions in the plant. They can also scavenge reactive oxygen species and strengthen the overall antioxidant defence system in the plant, hence minimising the harmful effects of salt stress (162, 163). They function as scavengers of ROS and boost plants' overall antioxidant defence system, lowering oxidative stress produced by salt stress. Also, it may control the ion balance in plants, allowing for better management of salt intake and decreasing its damaging effects (164). Further, they modulate gene expression of the biosynthesis pathway of carotenoids and chlorophylls, leading to changes in plant growth and development that improve tolerance to salt stress, can enhance root growth and development, which can improve the plant's ability to absorb water and nutrients, reducing the adverse effects of salt stress (165).

Conclusion

Recent advances in alleviating salt stress in plants highlight a clear shift from single-factor solutions toward integrated, multi-level strategies. Progress in plant physiology, molecular biology and biotechnology has deepened our understanding of how plants perceive and respond to salinity, particularly through ion

Table 5. Recent advances in the application of nanotechnology in the alleviation of salt stress in plants

Name of the nanoparticles	Plant studied	Type of experiment	Magnitude of salt stress applied	Outcome with respect to amelioration by nanoparticles	Reference
Silver nanoparticles (AgNPs)	Pearl millet (*Pennisetum glaucum*)	Controlled pot experiment + transcriptome analysis	NaCl-induced salinity stress	Improved biomass, enhanced antioxidant defence system, reduced ROS accumulation, regulated stress-responsive genes and improved ion homeostasis.	(147)
Proline-functionalized graphene oxide nanoparticles (GO-Pro NPs)	Grape (*Vitis vinifera*)	Pot experiment	NaCl-induced salinity	Increased proline accumulation, enhanced ROS scavenging, improved chlorophyll content and photosynthesis, reduced membrane damage	(148)
Octa-aminopropyl polyhedral oligomeric silsesquioxanes (OA-POSS) nanoparticles	Sweet basil (*Ocimum basilicum*)	Pot experiment	NaCl salinity stress	Improved growth parameters, enhanced antioxidant enzymes, better osmotic adjustment, reduced lipid peroxidation	(149)
Astaxanthin-synthesised gold nanoparticles (AuNPs)	Rice (*Oryza sativa*)	*In vitro* experiment	NaCl salinity stress	Enhanced tetrapyrrole biosynthesis, improved chlorophyll content, increased ROS scavenging and improved salt tolerance.	(150)
Cerium oxide nanoparticles	*Brassica* sp.	Pot experiment	NaCl salinity stress	Inhibited salt uptake by salt	(151)

homeostasis, osmotic adjustment, antioxidant defence and hormonal signalling. Genetic and genomic approaches-including marker-assisted breeding, QTL mapping and modern gene-editing tools-have enabled the development of salt-tolerant cultivars with improved yield stability under saline conditions. At the same time, beneficial plant–microbe interactions, such as the use of plant growth-promoting rhizobacteria and mycorrhizal fungi, have emerged as eco-friendly tools that enhance nutrient uptake and stress resilience. Agronomic innovations, including priming techniques, optimised nutrient management and the application of biostimulants and nanoparticles, further complement genetic strategies by improving plant performance in salt-affected soils. It is a severe barrier to plant growth, development and yield, particularly in coastal and dry environments. However, many techniques have been developed to reduce their impacts, including genetic modification, hormone therapy, soil management practices and salt-tolerant crops. Recent breakthroughs in the field, including the utilisation of microbial consortia, nanotechnology, metabolomics, systems biology and CRISPR-Cas technology, offer the potential to increase plant tolerance to salt stress significantly. Addressing salt stress is vital for guaranteeing food security and enhancing agricultural output in impacted areas.

Authors' contributions

AS drafted the primary manuscript. SSP and JREC participated in the literature review. PKS and PS prepared the final draft. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

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References

1. Bruce TJA. Tackling the threat to food security caused by crop pests in the new millennium. Food Secur. 2010;2(2):133–41. https://doi.org/10.1007/s12571-010-0061-8
2. Newton AC, Johnson SN, Gregory PJ. Implications of climate change for diseases, crop yields and food security. Euphytica. 2011;179:3–18 https://doi.org/10.1007/s10681-011-0359-4
3. Enenkel M, See L, Bonifacio R, Boken V, Chaney N, Vinck P, et al. Drought and food security-improving decision-support via new technologies and innovative collaboration. Glob Food Secur. 2015;4:51–5. https://doi.org/10.1016/j.gfs.2014.08.005
4. Kumar P, Sharma PK. Soil salinity and food security in India. Front Sustain Food Syst. 2020;4:533781. https://doi.org/10.3389/fsufs.2020.533781
5. Reed C, Anderson W, Kruczkiewicz A, Nakamura J, Gallo D, Seager R, et al. The impact of flooding on food security across Africa. Proc Natl Acad Sci USA. 2022;119 (43):e2119399119.
6. Prasad SS. Enzyme dynamics in aerobic plants under flood stress (review). Biologiya. 2025;60(5). https://doi.org/10.15389/agrobiology.2025.5.792eng
7. Prasad SS, Kurubar AR, Hugar A, Ramesh G, Umesh MR, Meena MK. Cost effectiveness of gladiolus production under drip fertigation and planting geometry. Indian J Hortic. 2022;79(3):353–62. https://doi.org/10.5958/0974-0112.2022.00048.2
8. Singh G, Bundela DS, Sethi M, Lal K, Kamra SK. Remote sensing and geographic information system for appraisal of salt-affected soils in India. J Environ Qual. 2010;39:5–15. https://doi.org/10.2134/jeq2009.0032
9. Hossain A, Pamanick B, Venugopalan VK, Ibrahimova U, Rahman MA, Siyal AL, et al. Emerging roles of plant growth regulators for plants adaptation to abiotic stress–induced oxidative stress. In: Aftab T, Naeem M, editors. Emerging plant growth regulators in agriculture. Cambridge (MA): Academic Press; 2022. p. 1–72. https://doi.org/10.1016/B978-0-323-91005-7.00010-2
10. Medina N, Rouhi Rad M, Nozari S, Suter JF, Bailey RT, Sahoo D. Water scarcity compounds the negative effects of salinity on irrigated agriculture. Water Resour Res. 2025;61. https://doi.org/10.1029/2024WR038504
11. Cetin M, Kirda C. Spatial and temporal changes of soil salinity in a cotton field irrigated with low-quality water. J Hydrol. 2003;273(1–4):238–49. https://doi.org/10.1016/S0022-1694 (02)00268-8
12. Rhoades JD, Krueger DB, Reed MJ. The effect of soil-mineral weathering on the sodium hazard of irrigation waters. Soil Sci Soc Am J. 1968;32:643–77. https://doi.org/10.2136/sssaj1968.03615995003200050020x
13. Nassar IN, Horton R. Salinity and compaction effects on soil water evaporation and water and solute distributions. Soil Sci Soc Am J. 1999;63:752–8. https://doi.org/10.2136/sssaj1999.634752x
14. Sun J, Yang G, Zhang W, Zhang Y. Effects of heterogeneous salinity on growth, water uptake and tissue ion concentrations of alfalfa. Plant Soil. 2016;408:211–26. https://doi.org/10.1007/s11104-016-2922-1
15. Pearcy RW, Ustin SL. Effects of salinity on growth and photosynthesis of three California tidal marsh species. Oecologia. 1984;62:68–73. https://doi.org/10.1007/BF00377375
16. Grattan SR, Grieve CM. Salinity-mineral nutrient relations in horticultural crops. Sci Hortic. 1998;78:127–57. https://doi.org/10.1016/S0304-4238 (98)00192-7
17. Mukhtar S, Mirza BS, Mehnaz S, Mirza MS, Mclean J, Malik KA. Impact of soil salinity on the microbial structure of halophyte rhizosphere microbiome. World J Microbiol Biotechnol. 2018;34 (9):136. https://doi.org/10.1007/s11274-018-2509-5
18. Sheldon AR, Dalal RC, Kirchhof G, Kopittke PM, Menzies NW. The effect of salinity on plant-available water. Plant Soil. 2017;418:477–91. https://doi.org/10.1007/s11104-017-3309-7
19. Tripathi S, Tiwari K, Mahra S, Victoria J, Rana S, Tripathi DK, et al. Nanoparticles and root traits: mineral nutrition, stress tolerance and interaction with rhizosphere microbiota. Planta. 2024;259:112. https://doi.org/10.1007/s00425-024-04409-y
20. Sha S, Wang G, Liu J, Wang M, Wang L, Liu Y, et al. Regulation of photosynthetic function and reactive oxygen species metabolism in sugar beet (*Beta vulgaris* L.) cultivars under waterlogging stress and associated tolerance mechanisms. Plant Physiol Biochem. 2024;211:108651. https://doi.org/10.1016/j.plaphy.2024.108651
21. Gangaiah B, Yadav AK. Modern crop management practices for pearl millet cultivation in Asia. In: Tonapi VA, Thirunavukkarasu N, Gupta S, Gangashetty PI, Yadav O, editors. Pearl Millet in the 21st Century. Singapore: Springer; 2024. p. 445–72. https://doi.org/10.1007/978-981-99-5890-0_18
22. Yang Y, Guo Y. Unraveling salt stress signaling in plants. J Integr Plant Biol. 2018;60:796–804. https://doi.org/10.1111/jipb.12689
23. Wang CF, Han GL, Yang ZR, Li YX, Wang BS. Plant salinity sensors: current understanding and future directions. Front Plant Sci. 2022;13:859224. https://doi.org/10.3389/fpls.2022.859224
24. Boussora F, Triki T, Bennani L, Bagues M, Ben Ali S, Ferchichi A, et al. Mineral accumulation, relative water content and gas exchange are the main physiological regulating mechanisms to cope with salt stress in barley. Sci Rep. 2024;14:14840. https://doi.org/10.1038/s41598-024-65967-5

25. Rasheed Y, Khalid F, Ashraf H, Asif K, Maqsood MF, Naz N, et al. Enhancing plant stress resilience with osmolytes and nanoparticles. J Soil Sci Plant Nutr. 2024;24:1871–1906. https://doi.org/10.1007/s42729-024-01821-x
26. Habibi N, Tayobong RRP, Parneel, Terada N, Sanada A, Koshio K. Novel insights into seed priming for tomato plants: restoring root vitality in the face of salt stress. Hortic Environ Biotechnol. 2025;66:361–80. https://doi.org/10.1007/s13580-024-00651-1
27. Munns R, Tester M. Mechanisms of salinity tolerance. Annu Rev Plant Biol. 2008;59:651–81. https://doi.org/10.1146/annurev.arplant.59.032607.092911
28. Zahra N, Al Hinai MS, Hafeez MB, Rehman A, Wahid A, Siddique KHM, et al. Regulation of photosynthesis under salt stress and associated tolerance mechanisms. Plant Physiol Biochem. 2022;178:55–69. https://doi.org/10.1016/j.plaphy.2022.03.003
29. Parida AK, Das AB. Salt tolerance and salinity effects on plants: a review. Ecotoxicol Environ Saf. 2005;60(3):324–49. https://doi.org/10.1016/j.ecoenv.2004.06.010
30. Seshagiri S, Varma A, Tallapragada P. *Piriformospora indica*-mediated amelioration of salt stress in *Solanum melongena* L. plants under greenhouse-a study on stomatal opening/closure. Geomicrobiol J. 2025;42:213–23. https://doi.org/10.1080/01490451.2025.2452568
31. Başak H, Aydin A, Yetişir H, Turan M. Salt stress effects on hybrid bottle gourd (*Lagenaria siceraria*) rootstock candidates plant growth, hormones and nutrient content. J Crop Health. 2025;77:1–15. https://doi.org/10.1007/s10343-024-01087-4
32. Chrouqi L, Sammama H, Azenzem R, Koussa T, Alfeddy MN. Impact of *Bacillus thuringiensis* (S48) in enhancing the oxidative stress defence systems of two wheat varieties against salt stress. Russ J Plant Physiol. 2025;72:1–12. https://doi.org/10.1134/S1021443725600059
33. Ajila-Celi GE, Lata-Tenesaca LF, Calzada KP, de Cassia Alves R, da Cruz MCP, Junior JSP, et al. Exogenous ascorbic acid mitigates salt-induced damage in soybean by modulating photosynthesis, antioxidant defense and ionic homeostasis. Acta Physiol Plant. 2025;47:1–14. https://doi.org/10.1007/s11738-025-03770-z
34. Kumari R, Rakhra G, Alsahli AA, Bhat JA, Ahmad P. Exploring the potential of signalling molecules hydrogen sulfide and nitric oxide in augmenting salt stress resilience in bitter gourd. BMC Plant Biol. 2025;25:42. https://doi.org/10.1186/s12870-025-06942-8
35. Kumari R, Khan MN, Parrey ZA, Kapoor P, Mir BA, Taziun T, et al. Synergistic effects of hydrogen sulfide and nitric oxide in enhancing salt stress tolerance in cucumber seedlings. Physiol Plant. 2025;177:e7010. https://doi.org/10.1111/ppl.70109
36. Goel D, Singh AK, Yadav V, Babbar SB, Bansal KC. Overexpression of osmotin gene confers tolerance to salt and drought stresses in transgenic tomato (*Solanum lycopersicum* L.). Protoplasma. 2010;245:133–41. https://doi.org/10.1007/s00709-010-0158-0
37. Sherpa MT, Sharma L, Bag N, Das S. Isolation, characterization and evaluation of native rhizobacterial consortia developed from the rhizosphere of rice grown in organic state Sikkim, India and their effect on plant growth. Front Microbiol. 2021;12:713660. https://doi.org/10.3389/fmicb.2021.713660
38. Quesada V, García-Martínez S, Piqueras P, Ponce MR, Micol JL. Genetic architecture of NaCl tolerance in *Arabidopsis*. Plant Physiol. 2002;130:951–63. https://doi.org/10.1104/pp.006536
39. Dermendjiev G, Schnurer M, Weiszmann J, Wilfinger S, Ott E, Gebert C, et al. Tissue-specific proteome and subcellular microscopic analyses reveal the effect of high salt concentration on actin cytoskeleton and vacuolization in aleurone cells during early germination of barley. Int J Mol Sci. 2021;22(17):9642. https://doi.org/10.3390/ijms22179642
40. Witzel K, Weidner A, Surabhi GK, Varshney RK, Kunze G, Buck-Sorlin GH, et al. Comparative analysis of the grain proteome fraction in barley genotypes with contrasting salinity tolerance during germination. Plant Cell Environ. 2010;33:211–22. https://doi.org/10.1111/j.1365-3040.2009.02071.x
41. Akbari M, Karbor S, Afshar A, Ferguson L, Farajpour M, Dillard T, et al. The role of rootstock selection in pistachio cultivation. Horticulturae. 2024;10(12):1278. https://doi.org/10.3390/horticulturae10121278
42. Li X, Xu Y, Zhang J, Xu K, Zheng X, Luo J, et al. Integrative physiology and transcriptome reveal salt-tolerance differences between two licorice species: ion transport, Casparian strip formation and flavonoids biosynthesis. BMC Plant Biol. 2024;24:391. https://doi.org/10.1186/s12870-024-04911-1
43. Xie X, Gan L, Wang C, He T. Salt-tolerant plant growth-promoting bacteria as a versatile tool for combating salt stress in crop plants. Arch Microbiol. 2024;206:312. https://doi.org/10.1007/s00203-024-04071-8
44. Nadeem SM, Zahir ZA, Naveed M, Asghar HN, Arshad M. Rhizobacteria capable of producing ACC-deaminase may mitigate salt stress in wheat. Soil Sci Soc Am J. 2010;74:533–42. https://doi.org/10.2136/sssaj2008.0240
45. Sofy MR, Aboseidah AA, Heneidak SA, Ahmed HR. ACC deaminase-containing endophytic bacteria ameliorate salt stress in *Pisum sativum* through reduced oxidative damage and induction of antioxidative defense systems. Environ Sci Pollut Res. 2021;28:40971–91. https://doi.org/10.1007/s11356-021-13585-3
46. Dias MC, Silva S, Galhano C, Lorenzo P. Olive tree belowground microbiota: plant growth-promoting bacteria and fungi. Plants. 2024;13(13):1848. https://doi.org/10.3390/plants13131848
47. Yan J, Smith MD, Glick BR, Liang Y. Effects of ACC deaminase containing rhizobacteria on plant growth and expression of Toc GTPases in tomato (*Solanum lycopersicum*) under salt stress. Botany. 2014;92:775–81. https://doi.org/10.1139/cjb-2014-0038
48. Sukweenadhi J, Balusamy SR, Kim YJ, Lee CH, Kim YJ, Koh SC, et al. A growth-promoting bacteria, *Paenibacillus yonginensis* DCY84T enhanced salt stress tolerance by activating defense-related systems in *Panax ginseng*. Front Plant Sci. 2018;9:813. https://doi.org/10.3389/fpls.2018.00813
49. Sharma K, Sharma S, Vaishnav A, Jain R, Singh D, Singh HB, et al. Salt-tolerant PGPR strain *Priestia endophytica* SK1 promotes fenugreek growth under salt stress by inducing nitrogen assimilation and secondary metabolites. J Appl Microbiol. 2022;133:2802–13. https://doi.org/10.1111/jam.15735
50. Acharya BR, Gill SP, Kaundal A, Sandhu D. Strategies for combating plant salinity stress: the potential of plant growth-promoting microorganisms. Front Plant Sci. 2024;15:1406913. https://doi.org/10.3389/fpls.2024.1406913
51. Siddika A, Rashid AA, Khan SN, Khatun A, Karim MM, Prasad PVV, et al. Harnessing plant growth-promoting rhizobacteria, *Bacillus subtilis* and *Bacillus aryabhattai* to combat salt stress in rice: a study on the regulation of antioxidant defense, ion homeostasis and photosynthetic parameters. Front Plant Sci. 2024;15:1419764. https://doi.org/10.3389/fpls.2024.1419764
52. Pan J, Peng F, Xue X, You Q, Zhang W, Wang T, et al. The growth promotion of two salt-tolerant plant groups with PGPR inoculation: a meta-analysis. Sustainability. 2019;11:20378. https://doi.org/10.3390/su11020378
53. Galicia-Campos E, García-Villaraco Velasco A, Montero-Palmero MB, Gutiérrez-Mañero FJ, Ramos-Solano B. Modulation of photosynthesis and ROS scavenging response by beneficial bacteria in *Olea europaea* plantlets under salt stress conditions. Plants. 2022;11(20):2748. https://doi.org/10.3390/plants11202748
54. Ji J, Zhang J, Wang X, Song W, Ma B, Wang R, et al. The alleviation of salt stress on rice through increasing photosynthetic capacity, maintaining redox homeostasis and regulating soil enzyme activities by *Enterobacter* sp. JIV1 assisted with putrescine. Microbiol Res. 2024;278:127590. https://doi.org/10.1016/j.micres.2023.127590

55. Gohari G, Jiang M, Manganaris GA, Zhou J, Fotopoulos V. Next generation chemical priming: with a little help from our nanocarrier friends. Trends Plant Sci. 2024;29(4):464–77. https://doi.org/10.1016/j.tplants.2023.11.024

56. Riaz N, Yousaf Z, Younas A, Hyder S, Aftab A, Maqbool Z, et al. Microbiomes: a road map of medicinal plant growth, disease control and abiotic stress management. In: Symbiotic association of microorganisms with medicinal and herbal plants. Boca Raton: CRC Press; 2024. p. 97–116. https://doi.org/10.1201/b23155-6

57. Anand G, Goel V, Dubey S, Sharma S. Tailoring the rhizospheric microbiome of *Vigna radiata* by adaptation to salt stress. Plant Growth Regul. 2021;93(1):79–88. https://doi.org/10.1007/s10725-020-00667-4

58. Patel M, Islam S, Husain FM, Yadav VK, Park HK, Yadav KK, et al. *Bacillus subtilis* ER-08, a multifunctional plant growth-promoting rhizobacterium, promotes the growth of fenugreek (*Trigonella foenum-graecum* L.) plants under salt and drought stress. Front Microbiol. 2023;14:1208743. https://doi.org/10.3389/fmicb.2023.1208743

59. Orozco-Mosqueda MC, Glick BR, Santoyo G. ACC deaminase in plant growth-promoting bacteria (PGPB): an efficient mechanism to counter salt stress in crops. Microbiol Res. 2020;235:126439. https://doi.org/10.1016/j.micres.2020.126439

60. Mayak S, Tirosh T, Glick BR. Plant growth-promoting bacteria confer resistance in tomato plants to salt stress. Plant Physiol Biochem. 2004;42:565–72. https://doi.org/10.1016/j.plaphy.2004.05.009

61. El-Ramady H, Prokisch J, Mansour H, Bayoumi YA, Shalaby TA, Veres S, et al. Review of crop response to soil salinity stress: possible approaches from leaching to nano-management. Soil Syst. 2024;8 (1):11. https://doi.org/10.3390/soilsystems8010011

62. El Yamani M, Cordovilla MP. Tolerance mechanisms of olive tree (*Olea europaea*) under saline conditions. Plants. 2024;13:2094. https://doi.org/10.3390/plants13152094

63. Wagan S, Ali M, Khoso MA, Alam I, Dinislam K, Hussain A, et al. Deciphering the role of WRKY transcription factors in plant resilience to alkaline salt stress. Plant Stress. 2024;13:100526. https://doi.org/10.1016/j.stress.2024.100526

64. Hadizadeh I, Peivastegan B, Nielsen KL, Auvinen P, Sipari N, Pirhonen M. Transcriptome analysis unravels the biocontrol mechanism of *Serratia plymuthica* A30 against potato soft rot caused by *Dickeya solani*. PLoS One. 2024;19(11):e0308744. https://doi.org/10.1371/journal.pone.0308744

65. Guan Q, Tan B, Kelley TM, Tian J, Chen S. Physiological changes in *Mesembryanthemum crystallinum* during the C3 to CAM transition induced by salt stress. Front Plant Sci. 2020;11:283. https://doi.org/10.3389/fpls.2020.00283

66. Ahmad B, Mukarram M, Choudhary S, Petrík P, Dar TA, Khan MMA. Adaptive responses of nitric oxide (NO) and its intricate dialogue with phytohormones during salinity stress. Plant Physiol Biochem. 2024;211:108504. https://doi.org/10.1016/j.plaphy.2024.108504

67. Atul S, Pradeep KS, Shiva SP, Satendra S, Pragati M, Rajeshwar JR, et al. Differential effects of high-temperature stress on the morpho-physiological traits of different wheat (*Triticum aestivum* L.) genotypes. Plant Sci Today. 2025;12(1):1–10. https://doi.org/10.14719/pst.6103

68. Adishesha K, Umesh BC, Jeevitha D, Sujatha HT, A, Prasad SS, et al. Temperature regime impacts on reproductive performance in various chickpea (*Cicer arietinum* L.) genotypes. Indian J Agric Res. 2025;59:1–7. https://doi.org/10.18805/IJARe.A-6367

69. Tariq F, Ma C, Zhao S. Integrative dynamics of cell wall architecture and plant growth under salt stress. Front Plant Sci. 2025;16:1644412. https://doi.org/10.3389/fpls.2025.1644412

70. Iqbal U, Daad A, Ali A, Gul MF, Aslam MU, Rehman FU, et al. Surviving the desert's grasp: decipherment of phreatophyte *Tamarix aphylla* (L.) Karst. adaptive strategies for arid resilience. Plant Sci. 2024;348:112201. https://doi.org/10.1016/j.plantsci.2024.112201

71. Yagi N, Fujita S, Nakamura M. Plant microtubule nucleating apparatus and its potential signaling pathway. Curr Opin Plant Biol. 2024;81:102624. https://doi.org/10.1016/j.pbi.2024.102624

72. Sun Y, Xiao Z, Chen B, Zhao Y, Dai J. Advances in material-assisted electromagnetic neural stimulation. Adv Mater. 2024;36 (40):2400346. https://doi.org/10.1002/adma.202400346

73. Bohnert HJ, Ayoubi P, Borchert C, Bressan RA, Burnap RL, Cushman JC, et al. A genomics approach towards salt stress tolerance. Plant Physiol Biochem. 2001;39:295–311. https://doi.org/10.1016/S0981-9428 (00)01237-7

74. Zhao C, Sandhu D, Ferreira JFS. Transcript analysis of two spinach cultivars reveals the complexity of salt tolerance mechanisms. ACS Agric Sci Technol. 2021;1:64–75. https://doi.org/10.1021/acsagscitech.0c00063

75. Chen F, Fang P, Peng Y, Zeng W, Zhao X, Ding Y, et al. Comparative proteomics of salt-tolerant and salt-sensitive maize inbred lines to reveal the molecular mechanism of salt tolerance. Int J Mol Sci. 2019;20 (19):4725. https://doi.org/10.3390/ijms20194725

76. Yang D, Zhang J, Li M, Shi L. Metabolomics analysis reveals the salt-tolerant mechanism in *Glycine soja*. J Plant Growth Regul. 2017;36:460–71. https://doi.org/10.1007/s00344-016-9654-6

77. Ingle KP, Singh A, Sahni T, Aakanksha K, Kumar S, Geethika P, et al. Genome editing in synthetic biology for sustainable production of biomolecules. In: Biomanufacturing for sustainable production of biomolecules. Singapore: Springer Nature; 2023. p. 315–29. https://doi.org/10.1007/978-981-19-7911-8_16

78. Bogoutdinova LR, Lazareva EM, Chaban IA, Kononenko NV, Dilovarova T, Khaliluev MR, et al. Salt stress-induced structural changes are mitigated in transgenic tomato plants over-expressing superoxide dismutase. Biology. 2020;9(9):297. https://doi.org/10.3390/biology9090297

79. Yan H, Li Q, Park SC, Wang X, Liu YJ, Zhang YG, et al. Overexpression of CuZnSOD and APX enhance salt stress tolerance in sweet potato. Plant Physiol Biochem. 2016;109:20–7. https://doi.org/10.1016/j.plaphy.2016.09.003

80. Prasad SS, Singh A, Patil K, Ramteke PW, Kumar N, Shukla PK, et al. Next-generation sequencing (NGS) application in plant breeding. In: Advances in plant genomics. Cham (CH): Springer; 2024. p. 149–71. https://doi.org/10.1007/978-3-031-68586-6_6

81. Prasad SS. Enhancing the throughput of design–build–test–learn cycle for the future perspective of synthetic biology in plants (review). Sel'skokhozyaistvennaya Biologiya. 2024;59(5):831–46.

82. Zhao B, Liu Q, Luo L, Zhou H, Zhang X, Ma F, et al. Suppression of MdPRP6 enhances adaptation of apple plants to long-term drought. Physiol Plant. 2025;177:e70099. https://doi.org/10.1111/ppl.70099

83. Singh D, Debnath P, Sane AP, Sane VA. Tomato (*Solanum lycopersicum*) WRKY23 enhances salt and osmotic stress tolerance by modulating the ethylene and auxin pathways in transgenic *Arabidopsis*. Plant Physiol Biochem. 2023;195:330–40. https://doi.org/10.1016/j.plaphy.2023.01.002

84. Cao X, Ma W, Zeng F, Cheng Y, Ma Z, Mao J, et al. Grape BES1 transcription factor gene VvBES1-3 confers salt tolerance in transgenic *Arabidopsis*. Gene. 2023;854:147059. https://doi.org/10.1016/j.gene.2022.147059

85. Ding X, Liu B, Liu H, Sun X, Sun X, Wang W, et al. A new CIPK gene CmCIPK8 enhances salt tolerance in transgenic chrysanthemum. Sci Hortic. 2023;308:111562. https://doi.org/10.1016/j.scienta.2022.111562

86. Yu M, Liu J, Du B, Zhang M, Wang A, Zhang L. NAC transcription factor PwNAC11 activates ERD1 by interaction with ABF3 and DREB2A to enhance drought tolerance in transgenic Arabidopsis. Int J Mol Sci. 2021;22(13):6952. https://doi.org/10.3390/

ijms22136952

87. Luo C, Akhtar M, Min W, Alam Y, Ma T, Shi Y, et al. The suppressed expression of a stress-responsive gene OsDSR2 enhances rice tolerance to drought and salt stress. J Plant Physiol. 2023;282:153927. https://doi.org/10.1016/j.jplph.2023.153927

88. Muthamilarasan M, Khandelwal R, Yadav CB, Bonthala VS, Khan Y, Prasad M. Identification and molecular characterization of MYB transcription factor superfamily in C4 model plant foxtail millet (*Setaria italica* L.). PLoS One. 2014;9(10):e109920. https://doi.org/10.1371/journal.pone.0109920

89. Lühmann KL, Seemann S, Martinek N, Ostendorp S, Kehr J. The glycine-rich domain of GRP7 plays a crucial role in binding long RNAs and facilitating phase separation. Sci Rep. 2024;14:66955. https://doi.org/10.1038/s41598-024-66955-5

90. Sun J, Manmathan H, Sun C, Peebles CAM. Examining the transcriptional response of overexpressing anthranilate synthase in hairy roots of *Catharanthus roseus* by RNA-seq. BMC Plant Biol. 2016;16:79. https://doi.org/10.1186/s12870-016-0794-4

91. Zhou X, Rao S, Wrightstone E, Sun T, Lui ACW, Welsch R, et al. Phytoene synthase: the key rate-limiting enzyme of carotenoid biosynthesis in plants. Front Plant Sci. 2022;13:884720. https://doi.org/10.3389/fpls.2022.884720

92. Chen Y, Li C, Zhang B, Yi J, Yang Y, Kong C, et al. The role of the late embryogenesis-abundant (LEA) protein family in development and abiotic stress response: comprehensive expression analysis of potato (*Solanum tuberosum*). Genes (Basel). 2019;10(2):148. https://doi.org/10.3390/genes10020148

93. Zhang SS, Sun L, Dong X, Lu SJ, Tian W, Liu JX. Cellulose synthesis genes CESA6 and CSI1 are important for salt stress tolerance in *Arabidopsis*. J Integr Plant Biol. 2016;58:623–6. https://doi.org/10.1111/jipb.12442

94. Qu D, Wu F, Yang J, Li M, Yang L, Xie R, et al. Transcription factor PtNAC101 negatively regulates lignin synthesis and salt tolerance in *Populus trichocarpa*. Environ Exp Bot. 2023;205:105149. https://doi.org/10.1016/j.envexpbot.2022.105149

95. Ren JP, Li L, Cai XL, Huang W, Chao DY, Zhu MZ, et al. A rice quantitative trait locus for salt tolerance encodes a sodium transporter. Nat Genet. 2005;37(10):1141–6. https://doi.org/10.1038/ng1643

96. Zhang X, Gong X, Yu H, Su X, Cheng S, Huang J, et al. The proline-rich protein MdPRP6 confers tolerance to salt stress in transgenic apple (*Malus domestica*). Sci Hortic. 2023;308:111581. https://doi.org/10.1016/j.scienta.2022.111581

97. Ren Y, Lv J, Wang H, Li L, Peng Y, Qu LJ. A comparative proteomics approach to detect unintended effects in transgenic *Arabidopsis.* J Genet Genomics. 2009;36:629–39. https://doi.org/10.1016/S1673-8527 (08)60155-1

98. Adarme-Vega TC, Thomas-Hall SR, Schenk PM. Towards sustainable sources for omega-3 fatty acids production. Curr Opin Biotechnol. 2014;26:14–8. https://doi.org/10.1016/j.copbio.2013.08.003

99. Yu Y, Guo DD, Min DH, Cao T, Ning L, Jiang QY, et al. Foxtail millet MYB-like transcription factor SiMYB16 confers salt tolerance in transgenic rice by regulating the phenylpropanoid pathway. Plant Physiol Biochem. 2023;195:310–21. https://doi.org/10.1016/j.plaphy.2022.11.032

100. Treutter D. Significance of flavonoids in plant resistance: a review. Environ Chem Lett. 2006;4:147–57. https://doi.org/10.1007/s10311-006-0068-8

101. Cui X, Cao Y, Zhang H, Zhang L. *Picea wilsonii* NAC transcription factor PwNAC1 interacts with RNA-binding protein PwRBP1 and synergistically enhances drought and salt tolerance in transgenic *Arabidopsis*. Environ Exp Bot. 2023;206:105174. https://doi.org/10.1016/j.envexpbot.2022.105174

102. Jiao K, Han J, Guo B, Wu Y, Zhang L, Li Y, et al. MbNAC22, a *Malus baccata* NAC transcription factor, increases drought and salt tolerance in Arabidopsis. Agronomy. 2023;13(5):1374. https://doi.org/10.3390/agronomy13051374

103. Huang Y, Du B, Yu M, Cao Y, Liang K, Zhang L. *Picea wilsonii* NAC31 and DREB2A cooperatively activate ERD1 to modulate drought resistance in transgenic *Arabidopsis*. Int J Mol Sci. 2024;25(4):2037. https://doi.org/10.3390/ijms25042037

104. Iqbal MZ, Liang Y, Anwar M, Fatima A, Hassan MJ, Ali A, et al. Overexpression of auxin/indole-3-acetic acid gene TrIAA27 enhances biomass, drought and salt tolerance in *Arabidopsis thaliana*. Plants. 2024;13(19):2684. https://doi.org/10.3390/plants13192684

105. Awere CO, Rakkammal K, Mwaura MM, Anadebe VC, Ramesh M. Hairy-root technology: a metabolic engineering tool for specialized metabolite pathway elucidation and production of secondary metabolites. Results Eng. 2024;24:102697. https://doi.org/10.1016/j.rineng.2024.102697

106. Endler A, Kesten C, Schneider R, Zhang Y, Ivakov A, Froehlich A, et al. A mechanism for sustained cellulose synthesis during salt stress. Cell. 2015;162:1353–64. https://doi.org/10.1016/j.cell.2015.08.028

107. Lou T, Lv S, Wang J, Wang D, Lin K, Zhang X, et al. Cell size and xylem differentiation regulating genes from *Salicornia europaea* contribute to plant salt tolerance. Plant Cell Environ. 2024;47(11):4184–204. https://doi.org/10.1111/pce.14905

108. Chun HJ, Baek D, Cho HM, Lee SH, Jin BJ, Yun DJ, et al. Lignin biosynthesis genes play critical roles in adaptation of *Arabidopsis* to high-salt stress. Plant Signal Behav. 2019;14(10):e1625697. https://doi.org/10.1080/15592324.2019.1625697

109. Kim B, Cho SH, Shim Y, Yoon H, Paek NC, Kang K. Rice OsMYB9 enhances salt stress tolerance by regulating the vacuolar Na+/H+ antiporter. Crop J. 2025;13:1718–3. https://doi.org/10.1016/j.cj.2025.08.002

110. Calzone A, Cotrozzi L, Pellegrini E, Lorenzini G, Nali C, Maathuis F. Transcriptional regulation of NHX1, SOS1 and HKT1 genes in two pomegranate cultivars under moderate salt stress. Sci Hortic. 2021;288:110309. https://doi.org/10.1016/j.scienta.2021.110309

111. Ahmad P, Hashem A, Abd-Allah EF, Alqarawi AA, John R, Egamberdieva D, et al. Role of *Trichoderma harzianum* in mitigating NaCl stress in Indian mustard (*Brassica juncea* L.) through antioxidative defense system. Front Plant Sci. 2015;6:868. https://doi.org/10.3389/fpls.2015.00868

112. Van Delden SH, Nazarideljou MJ, Marcelis LFM. Nutrient solutions for *Arabidopsis thaliana*: a study on nutrient solution composition in hydroponic systems. Plant Methods. 2020;16:66. https://doi.org/10.1186/s13007-020-00606-4

113. Ndiaye M, Mollier A, Diouf A, Diop TA. Mycorrhizal inoculation and fertilizer microdosing interactions in pearl millet (*Pennisetum glaucum*) under greenhouse conditions. Front Fungal Biol. 2024;5:1448156. https://doi.org/10.3389/ffunb.2024.1448156

114. Park HS, Kazerooni EA, Kang SM, Al-Sadi AM, Lee IJ. Melatonin enhances tolerance and recovery mechanisms in *Brassica juncea* under saline conditions. Front Plant Sci. 2021;12:593717. https://doi.org/10.3389/fpls.2021.593717

115. Yaschenko AE, Alonso JM, Stepanova AN. *Arabidopsis* as a model for translational research. Plant Cell. 2025;37(5):koae065. https://doi.org/10.1093/plcell/koae065

116. Genc Y, Taylor J, Lyons G, Li Y, Cheong J, Appelbee M, et al. Bread wheat with high salinity and sodicity tolerance. Front Plant Sci. 2019;10:1280. https://doi.org/10.3389/fpls.2019.01280

117. Tian Y, Guan B, Zhou D, Yu J, Li G, Lou Y. Responses of seed germination, seedling growth and seed yield traits to seed pretreatment in maize (*Zea mays* L.). Sci World J. 2014;2014:834630. https://doi.org/10.1155/2014/834630

118. Zuo G, Huo J, Yang X, Mei W, Zhang R, Khan A, et al. Photosynthetic

mechanisms underlying NaCl-induced salinity tolerance in rice (*Oryza sativa*). BMC Plant Biol. 2024;24:723. https://doi.org/10.1186/s12870-024-04723-3

119. Dabravolski SA, Isayenkov SV. The regulation of plant cell wall organisation under salt stress. Front Plant Sci. 2023;14:1118313. https://doi.org/10.3389/fpls.2023.1118313
120. Läuchli A, Grattan SR. Plant growth and development under salinity stress. In: Advances in molecular breeding toward drought and salt tolerant crops. Dordrecht: Springer; 2007. p. 1–32. https://doi.org/10.1007/978-1-4020-5578-2_1
121. Francois LE, Grieve CM, Maas EV, Lesch SM. Time of salt stress affects growth and yield components of irrigated wheat. Agron J. 1994;86:100–7. https://doi.org/10.2134/agronj1994.00021962008600010019x
122. Yang Z, Wang Y, Wei X, Zhao X, Wang B, Sui N. Transcription profiles of genes related to hormonal regulation under salt stress in sweet sorghum. Plant Mol Biol Rep. 2017;35:586–99. https://doi.org/10.1007/s11105-017-1047-x
123. Shu K, Qi Y, Chen F, Meng Y, Luo X, Shuai H, et al. Salt stress represses soybean seed germination by negatively regulating GA biosynthesis while positively mediating ABA biosynthesis. Front Plant Sci. 2017;8:1372. https://doi.org/10.3389/fpls.2017.01372
124. Choudhary P, Pramitha L, Rana S, Verma S, Aggarwal PR, Muthamilarasan M. Hormonal crosstalk in regulating salinity stress tolerance in graminaceous crops. Physiol Plant. 2021;173(4):1587–96. https://doi.org/10.1111/ppl.13558
125. Ellouzi H, Ben Slimene Debez I, Amraoui S, Rabhi M, Hanana M, Alyami NM, et al. Effect of seed priming with auxin on ROS detoxification and carbohydrate metabolism in salt-stressed maize. BMC Plant Biol. 2024;24:541. https://doi.org/10.1186/s12870-024-05413-w
126. Yuan K, Rashotte AM, Wysocka-Diller JW. ABA and GA signaling pathways interact and regulate seed germination and seedling development under salt stress. Acta Physiol Plant. 2011;33:261–71. https://doi.org/10.1007/s11738-010-0542-6
127. Medeiros BO, Silva LAS, Sarmento SN, Rosa DA, de Souza Barbosa LC, Machado M, et al. Antagonistic interactions between cytokinin and gibberellin during initial stem growth and leaf structure of royal poinciana (*Delonix regia*). Trees (Berl). 2024;38:1–14. https://doi.org/10.1007/s00468-024-02562-1
128. Koevoets IT, Venema JH, Elzenga JTM, Testerink C. Roots withstanding their environment: exploiting root system architecture responses to abiotic stress to improve crop tolerance. Front Plant Sci. 2016;7:1335. https://doi.org/10.3389/fpls.2016.01335
129. Ryu H, Cho YG. Plant hormones in salt stress tolerance. J Plant Biol. 2015;58:147–55. https://doi.org/10.1007/s12374-015-0103-z
130. Garrido-Vargas F, Godoy T, Tejos R, O'Brien JA. Overexpression of the auxin receptor AFB3 in *Arabidopsis* results in salt stress resistance and modulation of NAC4 and SZF1. Int J Mol Sci. 2020;21(24):9528. https://doi.org/10.3390/ijms21249528
131. Roychowdhury R, Hada A, Biswas S, Mishra S, Prusty MR, Das SP, et al. Jasmonic acid (JA) in plant immune response: unravelling complex molecular mechanisms and networking of defence signalling against pathogens. J Plant Growth Regul. 2024;43:1–22. https://doi.org/10.1007/s00344-024-11264-4
132. Hazman M, Sühnel M, Schäfer S, Zumsteg J, Lesot A, Beltran F, et al. Characterization of jasmonoyl-isoleucine (JA-Ile) hormonal catabolic pathways in rice upon wounding and salt stress. Rice. 2019;12:45. https://doi.org/10.1186/s12284-019-0303-0
133. Farhangi-Abriz S, Ghassemi-Golezani K. How can salicylic acid and jasmonic acid mitigate salt toxicity in soybean plants? Ecotoxicol Environ Saf. 2018;147:1010–6. https://doi.org/10.1016/j.ecoenv.2017.09.070
134. Sadhukhan A, Prasad SS, Mitra J, Siddiqui N, Sahoo L, Kobayashi Y, et al. How do plants remember drought? Planta. 2022;256:7. https://doi.org/10.1007/s00425-022-03924-0
135. Sarkar S, Guha A, Narayanan TN, Mondal J. Zwitterionic osmolytes revive surface charges under salt stress via dual mechanisms. J Phys Chem Lett. 2022;13(24):5660–8. https://doi.org/10.1021/acs.jpclett.2c00853
136. Thabet SG, Alomari DZ, Alqudah AM. Exploring natural diversity reveals alleles to enhance antioxidant system in barley under salt stress. Plant Physiol Biochem. 2021;166:789–98. https://doi.org/10.1016/j.plaphy.2021.06.030
137. El Moukhtari A, Cabassa-Hourton C, Farissi M, Savouré A. How does proline treatment promote salt stress tolerance during crop plant development? Front Plant Sci. 2020;11:1127. https://doi.org/10.3389/fpls.2020.01127
138. Ahmad P, Latef AAA, Hashem A, Abd Allah EF, Gucel S, Tran LSP. Nitric oxide mitigates salt stress by regulating levels of osmolytes and antioxidant enzymes in chickpea. Front Plant Sci. 2016;7:347. https://doi.org/10.3389/fpls.2016.00347
139. Manai J. Role of nitric oxide in saline stress: implications on nitrogen metabolism. Afr J Plant Sci. 2012;6 (14):376–82. https://doi.org/10.5897/AJPS12.079
140. Santisree P, Adimulam SS, Sharma K, Bhatnagar-Mathur P, Sharma KK. Insights into the nitric oxide mediated stress tolerance in plants. In: Khan MIR, Khan NA, editors. Plant signaling molecules: role and regulation under stressful environments. Cambridge (MA): Academic Press; 2019. p. 385–406. https://doi.org/10.1016/B978-0-12-816451-8.00024-1
141. Javaid MH, Chen N, Yasin MU, Fan X, Neelam A, Rehman M, et al. Green-synthesized lignin nanoparticles enhance *Zea mays* resilience to salt stress by improving antioxidant metabolism and mitigating ultrastructural damage. Chemosphere. 2024;359:142337. https://doi.org/10.1016/j.chemosphere.2024.142337
142. Nkomo M, Badiwe M, Niekerk LA, Gokul A, Keyster M, Klein A. p-Coumaric acid differentially alters the ion-omics profile of chia shoots under salt stress. Plants. 2024;13(11):1564. https://doi.org/10.3390/plants13111564
143. Linić I, Mlinarić S, Brkljačić L, Pavlović I, Smolko A, Salopek-Sondi B. Ferulic acid and salicylic acid foliar treatments reduce short-term salt stress in Chinese cabbage by increasing phenolic compounds accumulation and photosynthetic performance. Plants. 2021;10(11):2346. https://doi.org/10.3390/plants10112346
144. Yang J, Zhang Y, Jia J, Wang C, Fu Y. Flavonoid-lignin crosstalk: engineering metabolic flux for optimised plant growth and stress resilience. Plant Cell Environ. 2025;48:8141–60. https://doi.org/10.1111/pce.70106
145. Liu S, Liu J, Wang Y, Deng F, Deng Z. Oxidative stress: signaling pathways, biological functions and disease. MedComm. 2025;6:e702. https://doi.org/10.1002/mco2.70268
146. Gao W, Xu FC, Guo DD, Zhao JR, Liu J, Guo YW, et al. Calcium-dependent protein kinases in cotton: Insights into early plant responses to salt stress. BMC Plant Biol. 2018;18:12. https://doi.org/10.1186/s12870-018-1230-8
147. Khan I, Awan SA, Rizwan M, Akram MA, Zia-ur-Rehman M, Wang X, et al. Physiological and transcriptome analyses demonstrate the silver nanoparticles mediated alleviation of salt stress in pearl millet (*Pennisetum glaucum* L.). Environ Pollut. 2023;318:120863. https://doi.org/10.1016/j.envpol.2022.120863
148. Zahedi SM, Abolhassani M, Hadian-Deljou M, Feyzi H, Akbari A, Rasouli F, et al. Proline-functionalized graphene oxide nanoparticles (GO-Pro NPs): A new engineered nanoparticle to ameliorate salinity stress on grape (*Vitis vinifera* L. cv Sultana). Plant Stress. 2023;7:100128. https://doi.org/10.1016/j.stress.2022.100128
149. Gohari G, Panahirad S, Mohammadi A, Kulak M, Dadpour MR,

Lighvan ZM, et al. Characterization of octa-aminopropyl polyhedral oligomeric silsesquioxanes (OA-POSS) nanoparticles and their effect on sweet basil (*Ocimum basilicum* L.) response to salinity stress. Plant Physiol Biochem. 2023;196:89–102. https://doi.org/10.1016/j.plaphy.2023.01.019

150. Song Y, Zheng C, Basnet R, Li S, Chen J, Jiang M. Astaxanthin synthesized gold nanoparticles enhance salt stress tolerance in rice by enhancing tetrapyrrole biosynthesis and scavenging reactive oxygen species in vitro. Plant Stress. 2022;6:100122. https://doi.org/10.1016/j.stress.2022.100122

151. Rossi L, Zhang W, Lombardini L, Ma X. The impact of cerium oxide nanoparticles on the salt stress responses of *Brassica napus* L. Environ Pollut. 2016;219:28–36. https://doi.org/10.1016/j.envpol.2016.09.060

152. Mukarram M, Petrik P, Mushtaq Z, Khan MMA, Gulfishan M, Lux A. Silicon nanoparticles in higher plants: Uptake, action, stress tolerance and crosstalk with phytohormones, antioxidants and other signalling molecules. Environ Pollut. 2022;310:119855. https://doi.org/10.1016/j.envpol.2022.119855

153. Ahsan M, Radicetti E, Jamal A, Ali HM, Sajid M, Manan A, et al. Silicon nanoparticles and indole butyric acid positively regulate the growth performance of *Freesia refracta* by ameliorating oxidative stress under chromium toxicity. Front Plant Sci. 2024;15:1437276. https://doi.org/10.3389/fpls.2024.1437276

154. Rizwan A, Zia-ur-Rehman M, Rizwan M, Usman M, Anayatullah S, Areej, et al. Effects of silicon nanoparticles and conventional Si amendments on growth and nutrient accumulation by maize (*Zea mays* L.) grown in saline-sodic soil. Environ Res. 2023;227:115740. https://doi.org/10.1016/j.envres.2023.115740

155. Siddiqi KS, Husen A, Zahra N, Moheman A. Harnessing silicon nanoparticles and various forms of silicon for enhanced plant growth performance under salinity stress: Application and mechanism. Discov Nano. 2025;20:42. https://doi.org/10.1186/s11671-025-04270-2

156. Shahpari M, Mohammadi Torkashvand A, Ghanbari Jahromi M. Silicon nanoparticles-modulated salinity stress in sage (*Salvia officinalis* L.) plants through optimizing biochemical status and essential oil yield. J Plant Nutr. 2026;49:522–35. https://doi.org/10.1080/01904167.2025.2558891

157. Ibrahim EA. Seed priming to alleviate salinity stress in germinating seeds. J Plant Physiol. 2016;192:38–46. https://doi.org/10.1016/j.jplph.2015.12.011

158. Avestan S, Ghasemnezhad M, Esfahani M, Byrt CS. Application of nano-silicon dioxide improves salt stress tolerance in strawberry plants. Agronomy. 2019;9(5):246. https://doi.org/10.3390/agronomy9050246

159. Khan M, Jannat A, Munir F, Fatima N, Amir R. Biochemical and molecular mechanisms of abiotic stress tolerance. In: Hasanuzzaman M, editor. Plant ecophysiology and adaptation under climate change: Mechanisms and perspectives II. Singapore: Springer; 2020. p. 187–230. https://doi.org/10.1007/978-981-15-2172-0_9

160. Peña-Calzada K, Olivera-Viciedo D, Calero-Hurtado A, de Mello Prado R, Habermann E, Lata Tenesaca LF, et al. Silicon mitigates the negative impacts of salt stress in soybean plants. J Sci Food Agric. 2023;103:4360–70. https://doi.org/10.1002/jsfa.12503

161. Wang Q, Shan C, Zhang P, Zhao W, Zhu G, Sun Y, et al. The combination of nanotechnology and potassium: Applications in agriculture. Environ Sci Pollut Res Int. 2024;31:1–18. https://doi.org/10.1007/s11356-023-31207-y

162. Hosseinpour A, Haliloglu K, Cinisli KT, Ozkan G, Ozturk HI, Pour-Aboughadareh A, et al. Application of zinc oxide nanoparticles and plant growth promoting bacteria reduces genetic impairment under salt stress in tomato (*Solanum lycopersicum* L. 'Linda'). Agriculture. 2020;10(11):521. https://doi.org/10.3390/agriculture10110521

163. Jalil SU, Ansari MI. Nanoparticles and abiotic stress tolerance in plants: Synthesis, action and signaling mechanisms. In: Khan MIR, Khan NA, editors. Plant signaling molecules: Role and regulation under stressful environments. Cambridge (MA): Academic Press; 2019. p. 549–61. https://doi.org/10.1016/B978-0-12-816451-8.00034-4

164. Mishra M, Afzal S, Yadav R, Singh NK, Zarbakhsh S. Salinity stress amelioration through selenium and zinc oxide nanoparticles in rice. Sci Rep. 2025;15(1):27554. https://doi.org/10.1038/s41598-025-12106-3

165. Guo X, Shi Y, Zhu G, Zhou G. Melatonin mitigated salinity stress on alfalfa by improving antioxidant defense and osmoregulation. Agronomy. 2023;13(7):1727. https://doi.org/10.3390/agronomy13071727

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