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Unraveling the Mechanistic Basis of Nanoparticle Mediated Antioxidant Defense under Salinity Stress

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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Review Article

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Abstract

Soil salinity represents one of the most pervasive abiotic stresses, constraining global agricultural productivity, affecting over 1.4 billion hectares of arable land worldwide. The emergence of nanoparticle (NP)-based agronomic interventions has opened a compelling new frontier in stress physiology research, offering targeted, low-dose strategies to bolster plant defense machinery. This review critically examines the mechanistic basis by which various nanoparticles- including zinc oxide (ZnO), silicon dioxide (SiO_2), titanium dioxide (TiO_2), cerium oxide (CeO_2) and carbon-based nanomaterials-modulate reactive oxygen species (ROS) homeostasis, enzymatic antioxidant networks, osmoprotectant accumulation and ion transport dynamics in crop plants exposed to salinity stress. Despite the rapid growth of this field, a critical research gap considering the mechanistic hierarchy governing NP-mediated antioxidant enhancement remains poorly defined and it is unclear which molecular targets are primary drivers versus secondary consequences of improved salinity tolerance. This raises a pivotal question, if nanoparticles genuinely reprogram plant redox homeostasis at the transcriptional and enzymatic level or they primarily relieve osmotic and ionic constraints

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that otherwise suppress constitutive antioxidant capacity. Addressing this distinction is essential for rational nano-agronomic design. Hence, this review is the first to integrate nanoparticle-mediated regulation of ROS homeostasis, enzymatic antioxidant networks, proline metabolism, and ion transport into a unified mechanistic framework for salinity tolerance, while critically addressing dose-dependent phytotoxicity, NADPH availability and redox-sensitive transcription factor signaling.

Keywords: Stress; nanoparticle; antioxidant defence.; ROS; redox homeostasis

1. Introduction

Salinity stress imposes a dual burden on crop plants: an osmotic phase that limits water uptake almost immediately upon exposure to saline conditions, followed by an ionic phase characterized by the toxic accumulation of Na^+ and Cl^- in shoot tissues (Balasubramaniam *et al*., 2023). Together, these perturbations trigger a cascade of secondary oxidative stress events that damage lipids, proteins and nucleic acids, ultimately compromising yield and survival (Atta et al., 2023). Classical breeding and transgenic approaches have achieved meaningful gains in salt tolerance, yet the complexity of the trait- governed by hundreds of quantitative loci- has tempered expectations.

Nanoparticles, owing to their exceptionally high surface-area-to-volume ratios, tunable surface chemistries and capacity to interact directly with cellular membranes and enzymatic machinery, have attracted considerable attention as "nano-elicitors" capable of priming plant defense systems (Kumari *et al*., 2024). The literature has grown rapidly over the past decade, encompassing field crops such as wheat, rice, maize and soybean, as well as horticultural species including tomato, cucumber and pepper. However, mechanistic clarity- particularly at the level of antioxidant enzyme regulation, compatible solute metabolism and transporter gene expression- has remained fragmented. This review synthesizes current evidence across these interconnected domains. To integrate these mechanisms, we propose a conceptual framework that conceptualizes nanoparticle-mediated salinity tolerance as a coordinated, multi-layered regulatory network rather than a single biochemical adjustment (Fig. 1).

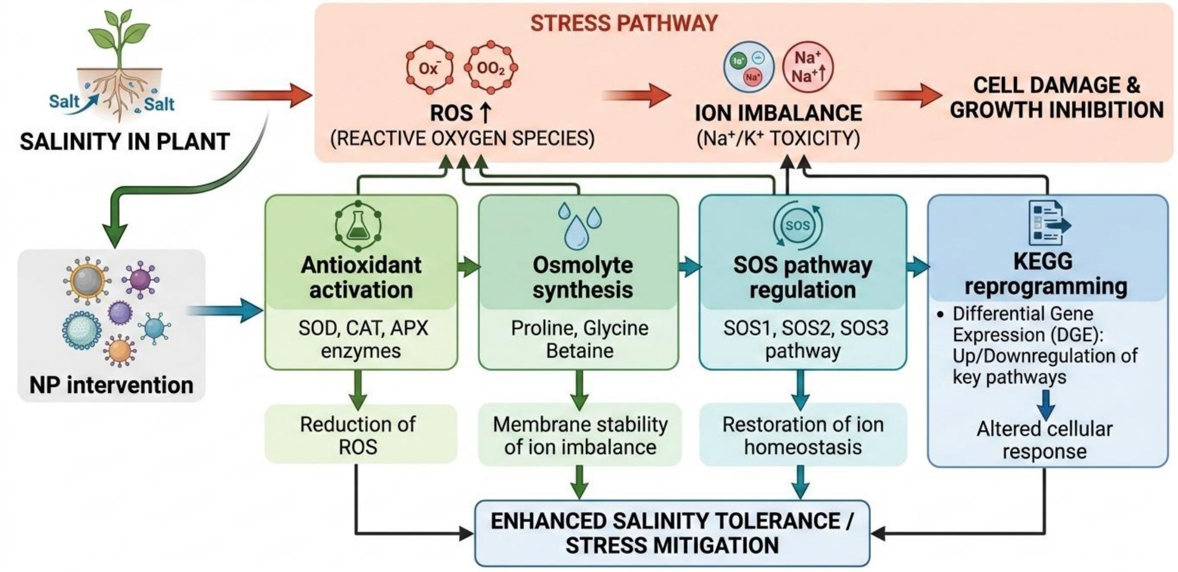

Fig. 1. Mechanism of Nanoparticle intervention for salinity stress mitigation in plants

2. Salinity-Induced ROS Accumulation: The Oxidative Penalty

2.1 Sources and Chemistry of ROS under Salinity

Reactive oxygen species are inevitable by-products of aerobic metabolism, but salinity dramatically amplifies their production beyond the capacity of baseline scavenging systems. The chloroplast is the primary site of ROS generation under salt stress, where disruption of the photosynthetic electron transport chain leads to over-reduction of ferredoxin and subsequent single-electron transfer to molecular oxygen, generating superoxide radicals (O_2•-). Simultaneously, the peroxisomes generate hydrogen peroxide (H_2O_2) during photorespiration, a pathway that is upregulated when stomatal closure under osmotic stress changes the CO_2/O_2 ratio unfavorably. Mitochondrial NADH oxidase complexes contribute additional $O_2^{\bullet -}$, while NADPH oxidases (respiratory burst oxidase homologs, RBOHs) at the plasma membrane serve as a signal-amplifying source of apoplastic ROS (Okoye *et al*., 2023).

The Haber-Weiss and Fenton reactions convert $O_2^{\bullet -}$ and H_2O_2 into the highly reactive hydroxyl radical (•OH), which initiates lipid peroxidation chain reactions measured biochemically as malondialdehyde (MDA) accumulation (Al-Hamood *et al*., 2023). Elevated MDA, together with increases in electrolyte leakage and protein carbonylation, constitutes the canonical oxidative damage signature of salt-stressed plants. The magnitude of this oxidative burden correlates with external NaCl concentration, exposure duration and the inherent antioxidant capacity of the genotype.

A dimension insufficiently discussed in most NP-salinity studies concerns the direct effect of NPs on NADPH availability. NADPH is a critical reductant for both the ascorbate-glutathione cycle (via glutathione reductase) and the NADPH oxidase (RBOH) system that generates signaling ROS. Salinity stress diverts NADPH from biosynthetic and photosynthetic reactions toward stress-response pathways, creating a reductant deficit that can impair enzymatic antioxidant capacity. Certain NPs, particularly those that enhance photosynthetic efficiency such as TiO_2 and SiO_2 NPs may indirectly restore NADPH pools by maintaining operational Calvin cycle activity and improving the rate of $NADP^+$ reduction (Imtiaz *et al*., 2025). This reductant-replenishment effect has not been systematically investigated but could account for a significant portion of the observed improvements in GR and APX activity under NP treatment.

The effects of NPs on redox-sensitive transcription factors (TFs) that serve as molecular sensors linking ROS levels to gene expression reprogramming are equally unexplored. Key TFs among these are NPR1 (nonexpresser of PR genes 1), TGA TFs, WRKY TFs (particularly WRKY18, WRKY40 and WRKY60) and the OXS (oxidative stress) zinc-finger proteins (Kumar *et al*., 2022). Under salinity, shifts in the cellular redox state, specifically changes in the GSH/GSSG ratio and H_2O_2 concentrations, modulate the oligomeric state and nuclear translocation of these factors, thereby altering the transcriptional landscape of stress-responsive genes including those encoding antioxidant enzymes. As NPs improve GSH/GSSG ratios and attenuate excess H_2O_2, they would be expected to influence this redox-TF signaling axis (Li *et al*., 2025). Direct evidence linking NP treatment to the activation state of specific redox-sensitive TFs remains sparse and represents an important mechanistic frontier for future investigation.

2.2 ROS as Signals and Stressors: A Dual Role

It is important to recognize that ROS are not exclusively damaging agents - they function as second messengers in stress signaling pathways. Low, spatiotemporally controlled bursts of H_2O_2 activate mitogen-activated protein kinase (MAPK) cascades, induce stomatal closure via guard cell signaling and prime systemic acquired stress tolerance. The challenge for plants - and for NP-based interventions - lies in maintaining ROS within this signaling window without allowing concentrations to escalate into the cytotoxic range. Nanoparticles that scavenge excess ROS while permitting residual signaling concentrations to persist may therefore offer superior outcomes compared to broad-spectrum chemical antioxidants that suppress ROS indiscriminately (Dai & Haque, 2025).

3. Enzymatic Antioxidant Defense: GR, APX and CAT as Central Players

3.1 The Ascorbate-Glutathione Cycle and APX

Ascorbate peroxidase (APX) catalyzes the conversion of H_2O_2 to water using ascorbate as the electron donor, producing monodehydroascorbate. It is the most abundant and kinetically competent H_2O_2-scavenging enzyme in chloroplasts and cytosol, making it the first line of enzymatic defense against photosynthetically derived H_2O_2. Multiple APX isoforms exist - cytosolic (cAPX), chloroplastic stromal (sAPX) and thylakoid-bound (tAPX) - each protecting specific subcellular compartments. Salt-stressed plants that maintain high APX activity show markedly reduced oxidative damage and numerous studies have demonstrated that NP treatment upregulates APX transcript abundance and specific enzyme activity (Li *et al*., 2025).

Zinc oxide NPs applied at concentrations of 25-100 mg/L have been shown to increase APX activity in wheat by 40-80% relative to salt-only controls, correlating with reduced H_2O_2 content and lower MDA (Singh *et al*., 2022). Silicon NPs similarly enhance APX in rice under 150 mM NaCl, likely through silicon-mediated strengthening of cell walls that reduces apoplastic ROS invasion and through transcriptional upregulation of APX gene families.

3.2 Glutathione Reductase and the Redox Buffering Function

Glutathione reductase (GR) sustains the ascorbate-glutathione cycle by reducing oxidized glutathione (GSSG) back to its reduced form (GSH) using NADPH as a cofactor. The GSH/GSSG ratio is a master redox buffer that influences the activity of numerous redox-sensitive proteins and transcription factors. Under salinity, GR activity often initially rises as an adaptive response, but prolonged or severe stress can decrease this capacity, shifting the glutathione pool toward the oxidized state with downstream consequences for ascorbate regeneration and thioredoxin-peroxiredoxin systems (Garcia *et al*., 2020).

Nanoparticle interventions have consistently been shown to maintain or enhance GR activity under saline conditions. Cerium oxide NPs (nanoceria), celebrated for their intrinsic superoxide dismutase and catalase-mimetic activities arising from Ce^{3+}/Ce^{4+} redox cycling on their surface, indirectly preserve GR function by reducing the total oxidative load that depletes GSH. Carbon-based nanomaterials, including fullerol and multi-walled carbon nanotubes, have also been reported to upregulate GR in soybean and maize under salt stress, with proposed mechanisms involving enhanced water uptake that relieves the osmotic stress component and reduces NADPH diversion to stress responses at the expense of GR activity. Importantly, higher GR activity under NP treatment is frequently accompanied by elevated total glutathione content and improved GSH/GSSG ratios, indicative of genuine redox improvement rather than mere compensatory upregulation (Horváth *et al*., 2023).

3.3 Catalase: The Peroxisomal Guardian

Catalase (CAT) dismutates H_2O_2 to water and oxygen without requiring a reductant, operating primarily in peroxisomes where photorespiratory H_2O_2 production is highest. Three CAT isoforms (CAT1, CAT2, CAT3) exist in most crop species, with differential expression patterns across tissues and stress conditions. CAT is particularly sensitive to inactivation by its own substrate at high H_2O_2 concentrations and by light-induced photo-oxidation, meaning that its activity can paradoxically decline at precisely the moment when its demand is greatest during intense salt stress (Dong *et al*., 2021).

Several NPs appear to partially compensate for this vulnerability. TiO_2 NPs, which have well-documented photocatalytic properties, have been reported to interact with peroxisomal membranes in ways that reduce localized H_2O_2 accumulation, thereby protecting CAT from substrate-mediated inactivation. ZnO NPs enhance CAT activity in salt-stressed maize, potentially through zinc's role as a cofactor in metalloenzyme stabilization and through transcriptional activation of CAT genes downstream of zinc-responsive elements. Selenium NPs represent a particularly interesting case: seleno-proteins possess intrinsic peroxidase activity analogous to glutathione peroxidase in animals and exogenous selenium supply enhances CAT expression in wheat and canola under salt stress, suggesting cross-talk between selenium metabolism and catalase gene regulation pathways (Deng *et al*., 2025). The concurrent enhancement of APX, GR and CAT by well-optimized NP treatments creates a synergistic antioxidant network where the limitations of individual enzymes are compensated by the collective activity of the system.

4. Proline Accumulation: Osmotic Adjustment and Beyond

4.1 Proline Biosynthesis and Its Multi-Functional Role

Proline is the quintessential compatible solute in salt-stressed plants, accumulating to millimolar concentrations in the cytosol through the Δ1-pyrroline-5-carboxylate synthetase (P5CS) pathway using glutamate as the primary precursor (Ayman et al., 2024). Its roles extend far beyond osmotic adjustment: proline stabilizes proteins and membranes through preferential exclusion mechanisms, quenches singlet oxygen and hydroxyl radicals directly, serves as a nitrogen and carbon reservoir for post-stress recovery and signals through proline dehydrogenase (ProDH)-mediated oxidation to influence MAPK cascades and cell death decisions. The ratio of P5CS to ProDH activity is therefore a key determinant of proline set-point under stress and both enzymes are subject to transcriptional and post-translational regulation by salt-responsive pathways including ABA signaling, calcium-dependent protein kinases (CDPKs) and the SOS pathway (Liu *et al*., 2020).

The majority of studies interpret elevated proline as evidence of adaptive osmotic adjustment and invoke it as a marker of improved stress tolerance. However, this interpretation conflates correlation with causation. The key unresolved question is whether NP-driven proline accumulation is a primary driver of tolerance, i.e., directly enabling cell turgor maintenance, ROS quenching and membrane protection, or whether it is a symptomatic consequence of the stress state itself, reflecting metabolic reprogramming that occurs in response to, rather than in anticipation of, osmotic imbalance. Evidence from transgenic plants overexpressing P5CS suggests that proline accumulation can confer genuine tolerance gains; however, the magnitude of these gains varies considerably with species, stress severity and developmental stage, indicating that proline is neither universally nor unconditionally protective (Ghosh *et al*., 2021).

Moreover, not all proline elevations are protective. Some literature reports that extreme proline hyper-accumulation, particularly in genotypes with compromised ProDH activity or in plants subjected to severe, sustained NaCl stress can itself become a physiological burden (Renzetti *et al*., 2024). Under these conditions, proline accumulation may reflect an inability of the plant to catabolize proline during recovery, impairing carbon and nitrogen remobilization. Furthermore, very high proline concentrations can disrupt cellular pH homeostasis and interfere with protein folding. Some authors therefore argue that hyper-accumulation of proline is better interpreted as a marker of severe physiological stress and metabolic dysfunction rather than a hallmark of adaptive tolerance (Renzetti *et al*., 2024; Spormann *et al*., 2023). Future NP studies should therefore report not only absolute proline concentrations but also the P5CS/ProDH activity ratio, total proline relative to stress severity and whether proline levels normalize appropriately upon stress removal, only through such multi-parameter analysis can the adaptive versus symptomatic nature of NP-induced proline accumulation be reliably distinguished.

4.2 Nanoparticle Enhancement of Proline Accumulation

The majority of NP studies report significantly elevated leaf proline content under combined NP plus salt stress treatment compared to salt stress alone. Silicon NPs are among the most consistently effective in this regard, with studies in tomato, barley and pepper showing 30-120% increases in proline under saline conditions following SiO_2 NP application (Sepasi *et al*., 2024). The proposed mechanism involves silicon-mediated enhancement of P5CS gene expression, potentially through silicon's modulation of ABA biosynthesis and signaling -ABA being a potent inducer of P5CS transcription through ABA-responsive elements (ABREs) in the promoter. Zinc NPs similarly increase proline, likely through zinc's role as a structural component of zinc-finger transcription factors that regulate P5CS expression (Mushtaq et al., 2023).

Titanium dioxide NPs have shown particularly interesting effects in wheat and rice, where TiO_2 treatment under salt stress not only increases total proline but also shifts the proline metabolic flux away from catabolism by suppressing ProDH activity, thereby extending proline accumulation through the stress period. This dual mechanism of enhanced synthesis combined with reduced degradation, results in greater and more sustained osmotic protection than would be achieved by either mechanism alone. The consequent maintenance of cell turgor and membrane integrity facilitates continued nutrient and water uptake, creating a positive feedback loop that further supports antioxidant enzyme activity by ensuring adequate NADPH availability from an operational Calvin cycle.

5. Ion Transport Modulation: Restoring Na^+/K^+ Homeostasis

5.1 The Ionic Toxicity Problem

The SOS (Salt Overly Sensitive) pathway governs the primary ionic homeostasis response to salinity, with SOS3 (CBL4) sensing cytosolic Ca^{2+} signals generated by salt stress, activating the SOS2 (CIPK24) kinase, which in turn phosphorylates and activates the SOS1 plasma membrane Na^+/H^+ antiporter to extrude Na^+ from root cells. Vacuolar sequestration of Na^+ by the tonoplast NHX antiporters provides an additional detoxification route, while HKT (high-affinity potassium transporter) family members - particularly HKT1;1 and HKT1;5 retrieve Na^+ from the xylem stream before it reaches shoot tissues, representing a critical long-distance protection mechanism for photosynthetically active leaves (Zhang *et al*., 2017).

K^+ homeostasis is equally critical: Na^+ competitively inhibits K^+ uptake through HAK/KUP transporters and AKT channels at the root plasma membrane, reducing cytosolic K^+/Na^+ ratios that are essential for enzyme function and membrane potential maintenance. Plants maintain this ratio through the integrated activity of SOS1, NHX and K^+ channels, all of which must remain functional under the energetically demanding conditions imposed by salinity (Tiwari *et al*., 2020; Fahmideh and Fooladvand, 2018).

5.2 Nanoparticle Effects on Ion Transport Systems

Emerging evidence indicates that NPs can modulate ion transporter gene expression and activity in ways that meaningfully improve Na^+/K^+ homeostasis. Silicon NPs, perhaps the most comprehensively studied in this regard, deposit in the apoplast and endodermal layer of roots, physically reinforcing the Casparian strip and reducing apoplastic bypass flow of Na^+ into the stele - a passive, non-selective pathway that circumvents active exclusion mechanisms and is particularly significant under high salinity. This structural effect complements transcriptional upregulation of HKT1 and SOS1 observed in silicon-treated rice and wheat under salt stress. ZnO NPs have been shown to increase K^+ content and decrease Na^+ in shoots of salt-stressed tomato and bean, correlated with transcriptional upregulation of NHX1 and SOS1 genes, suggesting that zinc may activate or stabilize components of the SOS signaling cascade (Zeid *et al*., 2023).

Iron oxide NPs are noteworthy for their effects in rice, where Fe_3O_4 NP treatment under saline conditions enhanced vacuolar Na^+ compartmentalization by upregulating OsNHX1 and OsNHX2, while simultaneously improving chloroplast ultrastructure integrity. The mechanistic link may involve iron's essential role in the electron transport chain, wherein adequate iron supply ensures sufficient ATP and reducing power for the H^+-ATPases that generate the proton motive force driving NHX antiporter activity. Calcium-based NPs represent another promising avenue: nano-calcium carbonate applications increased leaf Ca^{2+} content in salt-stressed soybean, which could amplify the initial Ca^{2+} signal activating SOS3 and thereby sensitize the entire SOS pathway to respond more rapidly and robustly to ionic challenge (Hameed *et al*., 2025).

6. Dose-Dependent Effects and Phytotoxicity Considerations

A recurring theme in the NP-plant stress literature is that the relationship between NP concentration and physiological benefit follows a hormetic dose-response pattern: low to moderate concentrations elicit protective responses, while high concentrations can themselves become phytotoxic, paradoxically exacerbating ROS production, damaging membranes and inhibiting growth. The optimal dose window varies considerably across NP type, crop species, growth stage and salinity severity, complicating straightforward recommendations. ZnO NPs, for instance, improve antioxidant enzyme activity and proline at 25-75 mg/L in most crops but become inhibitory above 200 mg/L due to Zn^{2+} ion release and direct ROS generation via nano-surface photocatalysis (Faizan *et al*., 2018). This concentration dependency underscores the necessity of rigorous dose-optimization studies and highlights the importance of surface coating and functionalization strategies that can modulate NP reactivity, uptake and intracellular behavior.

NP types reveal that optimal phytotoxicity thresholds differ substantially. ZnO NPs become inhibitory above approximately 200 mg/L in most crops (García-Gómez *et al*., 2018; Yang *et al*., 2015), whereas CeO_2 NPs exhibit toxicity thresholds an order of magnitude higher (1,000-2,000 mg/L) owing to their lower ion-release rates and intrinsic ROS-scavenging capacity (Mathur *et al*., 2023; Yang *et al*., 2015). TiO_2 NPs occupy an intermediate range, with phytotoxic effects are observed above 500 mg/L under high-light conditions, due to photocatalytic ROS generation (Zamora-Ledezma *et al*., 2025; Mathur *et al*., 2023). Carbon-based NPs (fullerols, carbon nanotubes) generally exhibit the widest safety windows, with most studies reporting benefit at concentrations of 5-50 mg/L and phytotoxicity only above 200 mg/L, although surface functionalization profoundly alters this profile (Mathur *et al*., 2023). Silicon NPs are arguably the safest, with reported phytotoxic thresholds exceeding 2,000 mg/L SiO_2 in most agricultural species (Lee *et al*., 2010). These comparative data underscore the importance of NP-type-specific dose optimization and highlight that blanket recommendations are scientifically unjustifiable.

The question of NP bioaccumulation represents a fundamental safety concern that is largely absent from the crop physiology literature. Metallic NPs applied to soils can persist for years; ZnO and TiO_2 NPs in particular show slow dissolution kinetics and accumulate in the rhizosphere (Sarabia-Castillo *et al.*, 2023). Plants can internalize NPs via root endocytosis and apoplastic transport, with subsequent translocation to shoots documented for ZnO, CeO_2 and carbon-based NPs in wheat, soybean and lettuce. The extent of shoot accumulation varies by species, NP size, surface coating and soil pH, but even low-level shoot loading raises concerns about grain contamination in food crops. Studies on ZnO NPs in wheat have detected zinc enrichment in grain tissues above control levels, referring to careful evaluation before agronomic deployment (Sun *et al.*, 2023). Therefore, translocation factor (TF-shoot concentration/root concentration) must become a standard reporting metric in NP-plant studies.

For crops treated with ZnO or TiO_2 NPs, the risk profile depends critically on whether NPs remain in particulate form within plant tissues or dissolve to release free metal ions during digestion, with the ionic forms generally more bioavailable and potentially more toxic (Leopold *et al.*, 2022). Regulatory frameworks have not yet established acceptable residue limits for NPs in food crops and this gap represents a significant barrier to commercial NP-based agronomic applications.

Soil microbiome disruption constitutes perhaps the most ecologically consequential risk associated with NP agricultural applications. The rhizosphere microbiome encompassing nitrogen-fixing bacteria, mycorrhizal fungi, nitrifying archaea and a broad community of decomposers underpins soil fertility and plant health in ways that cannot be replicated by agrochemical inputs alone (Das and Haque, 2025). ZnO NPs at concentrations as low as 100 mg/kg soil have been shown to reduce microbial biomass carbon, alter bacterial community composition by selectively suppressing Acidobacteria and Proteobacteria, and inhibit nitrification activity. TiO_2 NPs similarly disrupt fungal communities, including arbuscular mycorrhizal fungi that critically enhance plant nutrient acquisition and stress tolerance (Serov *et al.*, 2024). These microbiome-level effects may partially offset the direct plant stress-mitigating benefits of NP applications, producing a net outcome that is less favorable than controlled hydroponic studies suggest. Any comprehensive assessment of NP agronomic safety must therefore include soil microbial community profiling across application seasons, with particular attention to functional endpoints such as nitrogen cycling, phosphorus solubilization and organic matter decomposition rates.

7. Current Limitations and Future Directions

Despite significant progress, several critical gaps remain. First, most studies are conducted under hydroponic or controlled growth chamber conditions using single NP types and single salt concentrations, which poorly replicate the heterogeneous, fluctuating salinity of field soils. Mechanistic insights derived from these models may not translate directly to agronomic practice. Second, the fate, transformation and long-term soil accumulation of NPs, particularly metallic NPs such as ZnO and TiO_2, raise legitimate ecotoxicological concerns that have not been adequately addressed in most crop physiology studies.

Future research should prioritize field-level validation under realistic agronomic conditions, development of biodegradable and environmentally benign NP platforms (including chitosan, lignin and protein-based nanocarriers), multi-omics integration combining transcriptomics, proteomics, metabolomics and ionomics within cohesive KEGG-anchored analytical frameworks and mechanistic dissection of NP-membrane interactions using cryo-electron microscopy and surface-sensitive spectroscopic techniques. Understanding how different NP types interact with specific ion transporter proteins at the structural level could ultimately enable the rational design of nano-elicitors that precisely target the SOS pathway, NHX vacuolar sequestration and HKT xylem unloading to deliver maximum ionic homeostasis benefit at minimal concentration.

8. Conclusion

The collective evidence reviewed here supports a model in which nanoparticles of various compositions modulate salinity stress tolerance in crop plants through a coordinated multi-target mechanism: dampening excess ROS through both direct scavenging and enzymatic upregulation (APX, GR, CAT), enhancing osmotic adjustment through proline accumulation via P5CS induction and ProDH suppression and restoring ionic homeostasis through structural reinforcement of ion exclusion barriers and transcriptional upregulation of SOS1, NHX and HKT transporters. As research translatestoward field-level validation and ecologically safe NP designs, nanoparticle-based agronomic interventions hold genuine promise as a complementary strategy for sustaining crop productivity in the face of expanding soil salinity.

Disclaimer (Artificial Intelligence)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

Competing Interests

Authors have declared that no competing interests exist.

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