



Seed nanopriming as a strategy to mitigate salinity stress: Physiological, biochemical, and molecular mechanisms

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ABSTRACT

Salinity is a significant abiotic factor limiting agricultural productivity worldwide, affecting nearly one-third of global agricultural land. The problem is becoming more severe through climate change, improper irrigation, and urbanization-induced soil alkalization. Salinity stress reduces seed germination through osmotic imbalance and ionic toxicity, which impair water uptake and metabolic activation. Seed priming technologies, including hydropriming, chemopriming, biopriming, and nanopriming, have emerged as strategies to mitigate salinity stress and improve crop establishment. Nanopriming involves soaking seeds in, or coating them with, a formulation containing nanoparticles (1–100 nm). This review discusses the mechanisms underlying nanopriming-mediated enhancement of seed performance under salinity stress. Physiologically, nanopriming improves osmotic homeostasis by regulating seed imbibition, increasing water potential, and enhancing ionic balance through reduced Na⁺ and Cl⁻ accumulation and improved K⁺ uptake. It modulates hormonal balance by decreasing abscisic acid (ABA) while increasing gibberellic acid (GA), promoting germination. Biochemically, nanopriming enhances metabolic activation through increased α-amylase activity and mitigates oxidative damage by reducing reactive oxygen species (ROS) accumulation and strengthening antioxidant defense systems, including enzymatic antioxidants (superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR)) and non-enzymatic components. At the molecular level, nanopriming activates stress-responsive signaling pathways involving ABA, GA, ethylene, Ca²⁺ signalling, ROS-mediated regulation, mitogen-activated protein kinase (MAPK)-cascades, and endoplasmic reticulum (ER)-stress responses. These pathways upregulate genes related to aquaporins, ion transporters, osmolyte biosynthesis, antioxidant enzymes, and growth regulation. Nanoprimed seeds exhibit increased germination percentages, faster germination rates, improved vigour indices, enhanced growth, and increased stress tolerance. Despite these benefits, research gaps remain. Field-scale evaluations are limited, and understanding of nanoparticle fate in soil ecosystems is insufficient. Inappropriate nanoparticle parameters may induce phytotoxicity, oxidative damage, and ecological risks. Some studies report excessive ROS production and nanoparticle accumulation in plants, raising food safety concerns. While nanopriming represents an innovative strategy for enhancing seed germination under salinity stress, further research is needed to optimize formulations, establish safety thresholds, and develop standardized protocols for sustainable agricultural application.

1. Introduction

Soil salinization has emerged as one of the most serious environmental and socioeconomic problems around the world, which is likely to be more problematic in the future under predicted climatic change [1].

Salt-affected lands account for an estimated one-third of agricultural land, and some of that is attributable to the widespread irrigation of brackish, saline, or reclaimed water for crop production [2]. These trends in climatic change and global warming have raised the frequency of extreme weather events such as drought, heat, which also limits

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availability of water resources for sustainability [3]. Furthermore, the large human land use, with urbanization, and oxidation of organic matter in waste water runoff, has also increased alkalization of soils and salinization of soils [4]. Salt-affected soils contain excess soluble salts, which impairs crop growth and productivity while risking salinization spread to unaffected regions [5]. Soil salinization mainly involves saline, alkaline and saline-alkaline soils with high salt content, raised pH and increased sodium content [6]. The high concentration of micro salt ions creates osmotic stress, which is one of the most common adverse effects, thereby restricting water availability to plants [7]. This restricted water uptake can markedly delay or suppress seed germination and seedling establishment, resulting in a crop establishment challenge that quite adversely impacts crop production. Germination of seeds is one of the important stages of the plant lifecycle during which plants go from an inactive or dormant seed to an actively growing seedling (Fig. 1). Seed germination takes three stages under normal conditions. During Phase I of germination, dry seeds imbibed water rapidly (Fig. 1 A, B). In phase II, metabolism resumes and water uptake is restricted (Fig. 1 A, B). The third phase is the post-germination period, in which a reversal of water occurs until complete germination. Phase I osmotic stress and phase II ionic stress are generally regarded to cause seed germination inhibition or delay of germination occurring in response to salinity stress (Fig. 1 A, B) [8,9]. Nevertheless, even if the seed has been germinated, embryo development organs, seedling growth and vigor are compromised in phase III by both ionic and osmotic stress (Fig. 1 A, B) [10,11]. All these change the physiological, biochemical, and molecular traits of seed germination.

Plants must enhance physiological and biochemical responses involved in osmotic adjustment, oxidative damage scavenging, and detoxification in order to adapt to high salt stress [12–14]. Generation of ROS, including H_2O_2 , $O_2^{\cdot-}$ and $\cdot OH$ occurs in salt-treated plant cells. This could lead to undesired harm to the organelles in cells, DNA, lipid and

enzymatic structure [15,16]. Seed germination involves complex pathways crucial for plant survival, particularly vulnerable to environmental stresses [17]. Successful germination under stress may facilitate subsequent developmental phases. Seedling growth rate and uniformity significantly affect plant growth and productivity, providing resilience against salinity challenges, ultimately ensuring robust root system establishment [18,19]. To manage seeds effectively from the very beginning of the germination process, it is essential to adopt new and innovative approaches.

For the management of seed germination under saline soil conditions, nanotechnology has become an emerging technology which helps in the promotion of seed germination with the application of nanoparticles (NPs) [20]. NPs, materials with high bioactivity and biosafety properties due to their size (particle size < 100 nm) and high surface-to-volume ratio, are natural or engineered materials [21]. NPs have found numerous applications in diverse areas like agriculture, pharmaceuticals, food technology, and environmental protection [21]. Owing to their distinct physical-chemical properties, NPs are gaining interest for applications in agriculture. Numerous engineered nanoparticles have been studied as nanofertilizers, nanopesticides and nanosensors evaluating the impact of these nanoproducts on growth, yield, and quality of important agricultural crops [22]. NPs have been assessed in relation to germination and the germination stage of seedling growth. Nonetheless, the effectiveness of NPs in addressing salinity stress is heavily influenced by the methods of application, highlighting the importance of choosing the right approach.

Seed priming is one such useful technique that increases the germination percentage, promotes uniform germination, improves seed quality, and stimulates seedling establishment and enzyme activity to transform the macromolecules into available forms for embryonic growth [23]. Seed priming also increases and synchronizes the germination of the damaged, diseased, or aged seeds under environmental

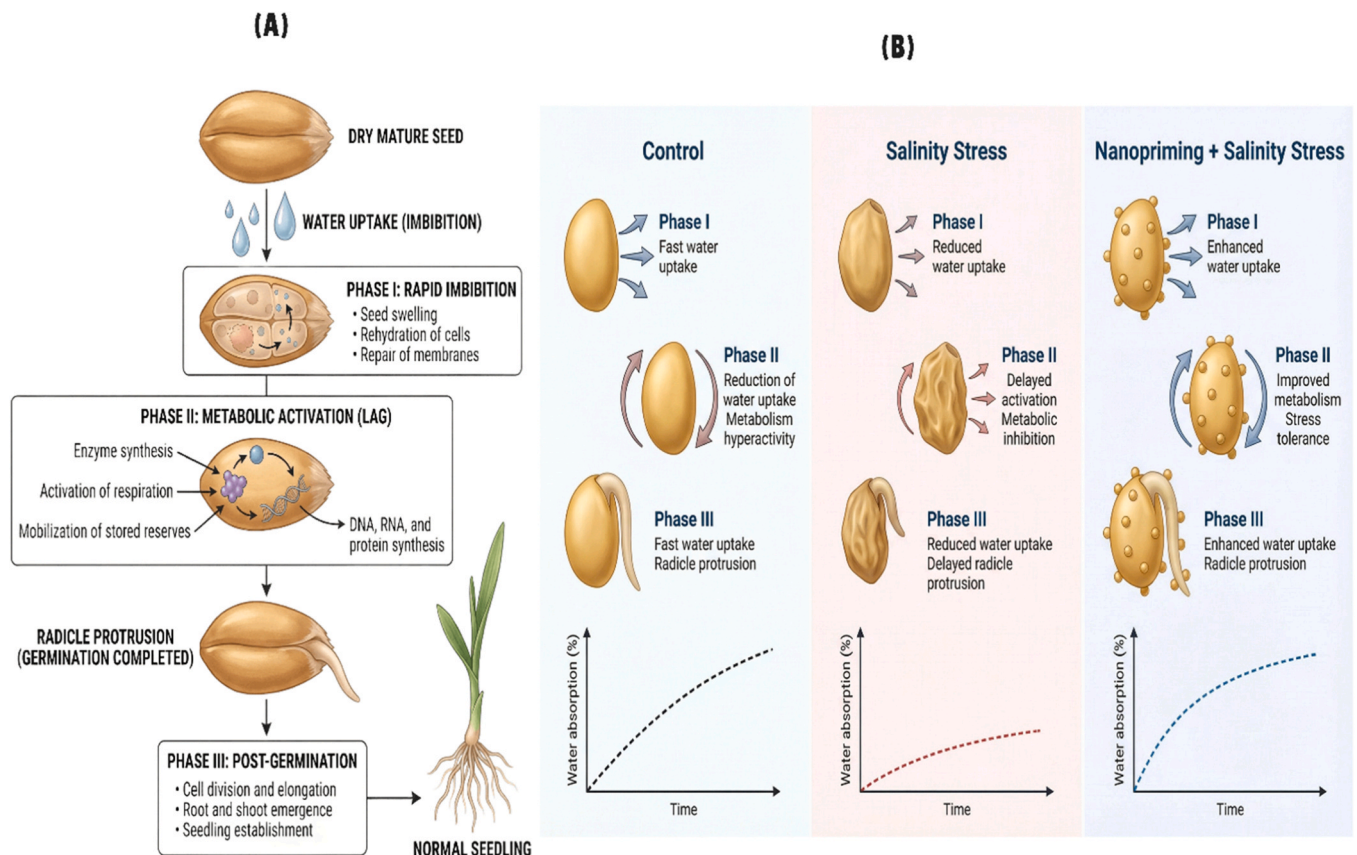


Fig. 1. Effect of salinity stress and nanoprimer on seed germination, plant growth and development.

stress conditions [24]. Nanopriming improves seed health, helps seeds grow into seedlings, and increases plant size. This is because of the small size and unique properties of NPs [25,26]. The effect of NPs on germination depends on the NP level, exposure duration, inherent plant characteristics, and interactions between the plant and the environment [27]. Additionally, nanopriming triggers specific metabolic processes that naturally occur during the early germination phase, resulting in increased germination rate, water-use efficiency, and nutrient uptake, thereby improving crop development, productivity, and quality [27,28].

In this review, we primarily aim to explore how salinity stress impacts key aspects of seed germination, including physiological, biochemical, and molecular parameters and how these parameters are influenced by nanopriming technology under saline conditions.

2. Effect of nanopriming on morpho-physiological traits of seed germination indices under salinity stress

2.1. Seedling growth and biomass

The reduction in seedling shoots and root lengths (SL and RL) under saline conditions is a common response in many plants, as roots are the first organs exposed to salinity [29]. Roots are the first organs in contact with the soil and are responsible for absorbing water from the soil and supplying it to the shoot [29]. Furthermore, salinity may negatively influence cell, tissue, and organ ultrastructure [30]. In addition, salinity has also been reported to arrest germination due to osmotic and specific ion toxic effects, the latter of which disrupt maintaining desirable levels of necessary nutrients for plant growth, restricting root emergence and seedling development [31,32]. SL and RL of the sorghum genotype decreased with an increase in salt concentration. The reductions in FW and DW observed are consistent with the earlier studies where the impact of salinity on sorghum plants was studied [33–35]. The impacts of salinity on root length were more severe than that of shoot length. This difference could be attributed to the fact that the effect of NaCl is more suppressive on root growth than shoot growth [36]. Previous study show that the decrease in FW and DW is attributed to the toxic effect of increased Na^+ concentrations on the photosynthesis rate of barley plant [37,38]. Increasing salt concentration from 0 to 120 mM reduced all growth parameters of roselle plants like plant height, leaf and root fresh and dry weights, respectively. The concentration of 90 mg/L of silver NPs within 60 mM and 120 mM salt contributed to an increase in the plant height. At this level (90 mg/L) of silver NPs, salinity-induced reductions in the leaf and root fresh and dry weights were reduced compared with the other concentration (60 mg/L). Meanwhile, the effective concentration of silver NPs varied primarily with plant characteristics under the effect of 120 mM salt [39]. Research reveals that pre-soaking of barley seeds in a solution containing 40 mg/L Ag-NPs at 25 °C for 2 h completely ameliorated the detrimental effects of salt stress and improved germination parameters to a considerable extent during salinity stress (150 and 200 mM) condition [40]. Such an effect may be attributed to the deep penetration of Ag-NPs into seed pore spaces, which may have enhanced water uptake efficiency and subsequently, led to a significant increase in germination speed of barley seeds [41]. This is well reflected by literature data, showing that under nanopriming, seeds take up water faster and are able to emerge through the covering tissue as a radicle sooner than in conventional seed priming methods. For instance, *Oryza sativa* L. seeds with Ag-NPs (10 ppm) priming increased the germination rate [42]. Likewise, with the use of cerium oxide nanoparticles coated with poly-(acrylic) acid (PNC, at a concentration 0.1 mM), nanopriming promoted water imbibition and germination of *Brassica napus* under salt stress conditions [43]. In a different study, nanopriming of *Triticum aestivum* L. along with ZnO-nanoparticles was found to enhance germination and shoot height, as well as plant physiology under salinity stress [44]. The salinity stress imposed at different levels showed significant reductions in SL, RL, seedling fresh weight (SFW), and seedling dry weight (SDW) of maize

hybrid; CS–20 at $P > 0.05$. Under normal and salinity stress conditions both nanopriming with TiO_2 (60 ppm) and hydropriming showed higher RL, SH, SFW and SDW. The significance marked difference in all above characteristics in control and TiO_2 treated plants. Under normal and salinity stress conditions, the effectiveness of nanopriming is greater than that of hydropriming on RL, SL, SFW and SDW [45]. This acceleration may be due to enhancement of metabolic activities at the pre-germination stages exercised during the priming process, which results in primed seeds having greater levels of seed germination and higher levels of growth of the seedling [46,47]. Other experiments also show that TiO_2 enhanced seed germination and seedling radicle and plumule growth in canola and wheat crops [48,49].

2.2. Water content

In dry areas, the main limiting factor is water deficit that is linked to high salinity in irrigation water, which exposes the plants to extreme water deficit during the dry season [50]. Such conditions led to the accumulation of salts in the soil, due to a high evaporation rate and the lack of ion leaching. Improved knowledge of the physiological responses of the crop plants to such stressful conditions may help in developing efficient crop improvement programs for salt stress. So far, several physiological mechanisms linked to tolerance to abiotic stresses have been described, e.g., sensitive stomata regulating water loss and salt uptake, upregulation of the antioxidants' system, and active accumulation of compatible solutes such as amino acids, polyamines, and carbohydrates. The latter is also linked to maintaining plant water status and to cell turgor, which is essential for continued growth and function under stress. High RWC of crop plants under salinity stress could also be correlated with salt tolerance [51]. The RWC describes the water level of a leaf based on the maximum amount that a leaf can absorb in full turgid condition. Thus, the RWC shows an appropriate stress measurement for analyzing the plant water status under the salinity stress condition. Leaf water potential has been widely used as an approximation of plant water status as far as water movement in the soil-plant-atmosphere condition but does not consider osmotic adjustment (OA) condition, which is frequently achieved in plant roots and leaves exposed to stress. OA is an important process for cellular water conservation, which could be presented in leaf RWC measurements during salinity stress. Therefore, the RWC can be considered as a better estimate of plant water status which occupies the leaf water potential, as well as OA [52]. Responses of plants to salt stress in the short term, as for instance at the early seedling stage, share many features with water stress responses [51]. This is because there are two phases of plants' responses to salt stress under saline conditions; the first one is a classical water stress response due to the high osmotic potential of the soil solution, which is caused by the accumulation of soluble salts, and second is the physiological injury resulting from the ionic stress that mainly manifests as ion toxicity and nutritional imbalances. Thus, application of NPs for salt tolerant function in plants can be selected based on RWC during the early phase of salt stress. Samples of leaves and shoots were collected to evaluate RWC. The youngest fully expanded leaf was used in RWC. Green leaf samples of one-centimeter size were collected from the region approximately one-third from the leaf tip. FW was recorded for samples, then the tissues were soaked in distilled water at 25 °C for 4 h to obtain the turgid weight (TW), and then were oven dried for 24 h at 80 °C to determine the dry weight (DW).

An experiment result showed that salinity stress decreased the RWC of leaves of maize. This explains that nano-priming with TiO_2 (60 ppm) led to an increase in the RWC status of the leaf in compared to control under salinity stress [45]. Similar another explains RWC was 80.05% higher with SiNPS-primed seeds under 30% saline condition compared to hydroprimed *Lathyrus odoratus* seeds [53]. Si NPs reduce plant transpiration because Si accumulates in external layers over the leaf and stem cell walls, resulting in the leaves and stems getting thicker with higher cuticles [54]. Silicon changes osmotic pressure, and this factor

promotes plant tolerance to salinity stress conditions [55,56]. The increased volumes of water in Si-plants cultivated under salinity results in plant growth promotion since Si mainly functions to dilute the salts within the plant [55]. Thus, it can be concluded that the advantageous role of NPs would result in enhancing the leaf water status and alleviating the osmotic stress effect of salinity stress in plants by improving the RWC.

2.3. Photosynthetic pigments contents

It is known that photosynthesis is the fundamental and most essential physiological process of green plants as the source of energy for their growth and development [57]. Salt stress has a severe adverse effect on photosynthesis in plants [58]. High Na^+ and Cl^- in the leaves are responsible for loss of water from the guard cells, thus altering the guard cell and stomatal structure, and activity density numbers, thereby restricting or reducing the entry of CO_2 , which in turn may lead to impaired or inhibited normal photosynthesis [59,60]. In addition, salt stress causes ion toxicity and oxidative stress, especially in chloroplasts, which are the principal sites of ROS production. Salt stress induces deficits along the electron transport chain (ETC) from the photosynthetic complex photosystem II (PSII) to PSI, leading to massive accumulation of ROS that can inflict oxidative damage on nucleic acids, proteins, lipids, membranes, and some photosynthetic enzymes, decreasing CO_2 oxidation and crop yield [61,62]. Salt stress also destroys chloroplast integrity, an organelle critical for the photosynthetic light reactions and carbon assimilation [63]. Salt-tolerant plants can maintain the normal morphology of photosynthesis structures under salt stress to support their function [63]. Salinity stress is known to reduce chlorophyll *a* and *b* and carotenoids levels, which are the essential molecules for proper functioning of the plant photosynthetic machinery [64]. Salinity stress-based oxidative stress state is responsible for

delayed pigment production or accelerated destruction due to lesser light absorption, rearrangements in pigment-protein complexes, and enhanced activity of chlorophyllase [65,66]. CeO_2 NPs act as a catalyst involved in the production of chloroplasts and protects the structure of chloroplasts over salinity injury [67]. Another experiment results showed that the application of CeO_2 NPs (0, 25, and 100 mg/L) enhanced the photosynthetic pigments in Moldavian Balm (*Dracocephalum moldavica* L.) plants under salinity stress (50–100 mM NaCl) [68]. Accumulation of Na^+ and Cl^- ions inhibits chlorophyll synthesis because this process impacts the production of some chlorophyll synthesizing enzymes containing Fe^{3+} in physic nut plant [69]. Under salt stress conditions (0–250 mM), rice seedlings from seeds primed with chitosan nanoparticles (CNPs) (50 $\mu\text{g/mL}$) had significantly increased chlorophyll and carotenoid content compared to those of control hydroprimed seeds, suggesting that the enhancement of chlorophyll and carotenoid can make a contribution to offsetting the lethal effects of ROS species to regulate a high germination rate and seedling vigour chlorophyll content [70]. Application of biogenic Ag-NP concentrations (0, 20, 40, 80, and 100 ppm) and different salinity levels (0, 50, 100, and 150 mM NaCl) can improve chlorophyll content that enhances the seed germination and growth of the spinach (*Spinacia oleracea* L.). Another experiment with 0.1% concentration of selenium nanoparticles (Se-NPs) showed that it enhanced the chlorophyll *a*, chlorophyll *b* and total chlorophyll over salt stress and control in wheat plants [71].

3. Effect of nanoprimering on biochemical traits of seed germination under salinity stress

Biochemical component changes of seeds for several crop species were documented based on soluble and reducing sugars, fatty acids, tocopherol, H_2O_2 and MDA (malondialdehyde) contents due to aging (Fig. 2) [72–74]. Various factors and their interactions have been

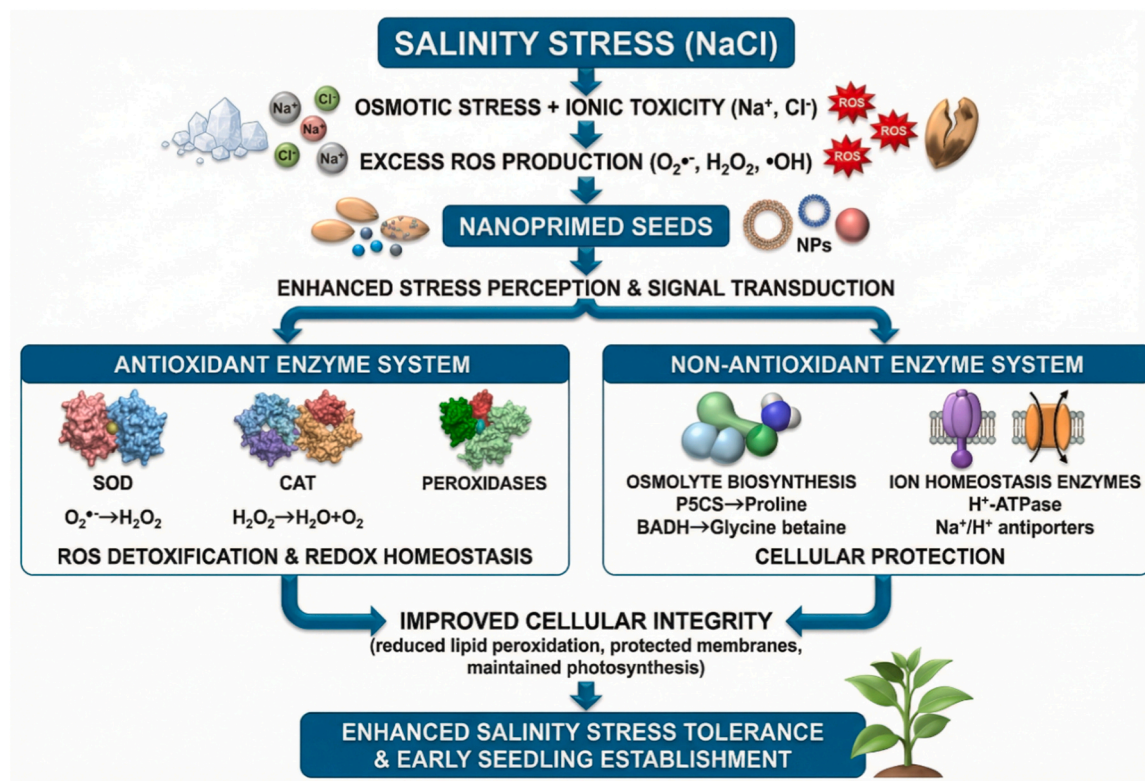


Fig. 2. Biochemically, nanoprimering increases metabolism through α -amylase enzyme activity, which ultimately leads to fast starch hydrolysis and availability of soluble sugars for embryo germination. Additionally, oxidative stress is alleviated by decreasing ROS accumulation and increasing antioxidant defense, which is confirmed by the increased activities of enzymatic antioxidants such as SOD, CAT, APX, GR along with an elevation in the levels of non-enzymatic antioxidants like GSH, compatible solutes, phenolics, α -tocopherol (vitamin E), carotenoids flavonoids, proline.

implicated in seed ageing-induced decline in viability [74]. The production of ROS results in lipid peroxidation through free radicals and the oxygen they produce, leading to changes in cell membranes through the oxidation of lipids, affecting the structure and function of membranes [75]. In addition to soluble sugars, seeds also contain phenols, glutathione and tocopherols to promote oil stability and to increase the time and levels at which seed longevity and germination are attainable. Through enzyme activation that aids in ROS scavenging and conversion of macromolecules for energy production, seed treatments have been implemented to counteract portions of aging damage [75–77]. Various studies indicate that using different NPs as priming agents can enhance seed germination by reducing ROS levels (Table 1).

3.1. α -amylase activity and soluble sugars

Starch is the main component of mature cereal grains. When the seeds are soaked in water, the enzymes present in dry seeds become activated. Starch-hydrolyzing enzymes are called amylases (α - and β -amylases). Alpha-amylases, beta-amylases, and limit dextrinases are the three classes of starch-degrading enzymes in germinated grains [78]. The main enzyme produced during germination is α -amylase, which functions to mobilize the starch reserves present in the endosperm. Alpha-amylases function by randomly hydrolyzing α -1,4-glucan linkages present in the starch polymers: amylose and amylopectin [78]. In the end, all the amylose turns into maltose after hydrolysis. The breakdown of amylopectin is more complicated and the breakout products are glucose, maltose, and alpha-limit dextrins [78]. Studies on amylase-rich foods based on wheat and barley have shown that α -amylase degrades starch granules and reduces their water-binding capacity, resulting in lower gruel viscosity [79,80]. Beta-amylase, an exoenzyme, attacks starch at the nonreducing ends of the dextrin products generated by alpha-amylase and limit dextrinase. It cleaves α -1–4 glucosidic bonds and every second bond to produce maltose but cannot cleave α -1–6 bonds resulting in beta-limit dextrins [78]. Salt stress suppresses seed germination by restricting seed water uptake, which inhibits the main enzyme for germination, α -amylase which is responsible for hydrolyzing the stored starch during seed germination [81]. During seed germination stage, α -amylase cleaves the endosperm starch to metabolizable sugars that supply the energy for the roots and shoots to grow. Thus, the inhibition of α -amylase activity and inability of seeds to absorb water under salinity stress may lead to the inhibition or failure of seed germination [82–85]. The pretreatment by NPs can reduce the negative effect of salinity on amylase enzymes [86].

α -Amylase activity assays showed that nanoprimering was the best treatment to improve starch metabolism of rice seeds and seedlings. As before, results were consistent with published data, which reported that priming was able to positively influence starch metabolism in germination [87,88]. α -Amylase is a hydrolytic enzyme responsible for the degradation of reserve carbohydrate to soluble sugars to maintain active respiratory metabolism for seed germination and subsequent seedling growth until photosynthesis is sufficient to support growth [89]. After the application of 5 and 10 ppm Ag-NPs the increase in germination rate and seedling vigor of nanoprimered rice seeds observed in this study could be partly explained by increased activity of α -amylase allowing a faster rate of starch hydrolysis in germinating nanoprimered seeds. This resulted in greater availability of soluble sugars necessary for generating the energy required for seedling growth, thereby leading to increased speed of germination [90]. Under 200 mM salinity stress, priming of rapeseed seeds with PNC showed increased α -amylase activity during the seed germination stage of the experiment (by 175%, 309%, and 295% after 1, 3, and 8 h of priming, respectively) compared with the control [91]. Another experiment with NanoZnO priming of two rice varieties (CY1000 and LLY506) under different salinity levels (0, 1.5, and 3%) showed upregulation of α -amylase activity [86]. NanoZnO nanoprimering directly stimulated seed water absorbance and increased the metabolic activity by activating germination enzymes such as α -amylase; it

upregulated starch hydrolysis and significantly increased seed germination.

3.2. NPs-mediated antioxidant and non-antioxidant enzymatic regulation of ROS homeostasis in seeds

3.2.1. NPs-mediated antioxidant enzyme-based ROS homeostasis

During seed aging, the structural alterations at the macromolecular level cause an imbalance between the activities of antioxidant enzymes and free radicals, leading the seed to oxidative stress [92,93]. Under aging conditions, antioxidant enzymes, including the superoxide dismutase (SOD), detoxify hydrogen peroxide and superoxide [72]. Like scavenging enzymes, peroxidases (POD) also deplete reactive oxygen species (ROS), but they also serve as sources of these molecules [94]. These enzymes are involved in the basic mechanism of degrading excessive ROS and minimizing their toxicity to seeds [95]. Lipid peroxidation triggered by ROS may hamper the activities of antioxidant enzymes. The activities of antioxidant enzymes may be regulated and have consequences for germination, seedling growth and development [96]. During germination, seed storage reserves are moved by mobilization to the embryo for development, an event common to all seeds. During germination, these reserves (e.g. carbohydrates, amino acids, fatty acids, and inorganic nutrients) are mobilized in varying amounts between different crop species. The rate of mobilization for this process, however, decreases with aging. Seed deterioration is quantified by measuring changes in biochemical and enzyme activities. It has also been shown that the decline in germination and seedling growth caused by seed aging is associated with reduced mobilization of seed reserves irrespective of seed reserve utilization efficiency [97]. These treatments are suggested to cope with deterioration of seed reserves and increase ROS scavenging enzyme activities in aged seeds with the chemicals and antioxidant compounds inducing translocation of organic substances to various parts of the embryo that would facilitate restoring seed vigor. Balancing the production of ROS with their scavenging is relevant for plant tolerance to stress. However, ROS production under environmental stress conditions exceeds the scavenging capacity of the cellular redox potential, and leads to oxidative stress [98–100]. A significant threat of ROS over-production is enzyme inhibition, lipid peroxidation, protein oxidation, damaging nucleic acids and initiation of programmed cell death (PCD pathway), consequently culminating in cell death [101–103]. Plant capacity to retain ROS homeostasis under different stresses has been correlated with plant stress tolerance [104]. In fact, the enhancement of salt tolerance in plants gained by nanoprimering is always facilitated by the greater ROS scavenging capacity. A study investigates the effect of poly (acrylic acid)-coated cerium oxide nanoparticles (PNC) on stress tolerance of plant seeds. This study observed a significant increase in root length, fresh weight, dry weight, altered root architecture, and *in vitro* root activity under salt stress conditions following seed priming with PNC. Accompanied by this decrease in ROS levels in roots, both root morphological and physiological alterations were mitigated [105]. Over all, the study indicated that ROS and conserved Ca^{2+} plant signaling pathways are involved in PNC-mediated improvement in salinity tolerance [105]. Three different concentrations of nanocellulose (NC) (0, 0.3%, and 0.6%) were used for the priming of wheat seeds to assess seed germination at different saline concentrations (0.7, 5, 10, 15, and 20 dSm^{-1}) show positive effects of NC seed priming treatments on growth, root morphology, water relation, SOD, and nutrient influx of wheat seedlings under salt stress respectively. Results showed that the germination percentage, root length, root surface area, and water content decreased under salt stress. In addition, root radius, Na uptake and SOD activity were increased. The maximum germination percentage, root length, root surface area and Na^{+} influx were obtained from seeds primed with NC at 0.3%. However, NC at 0.3% was also found to be the best treatment for these traits. Seed priming at 0.6% was the most effective treatment for reducing SOD enzyme activity. In conclusion, the results of this study confirmed that seed priming with NC can be a

Table 1

Effect of nanoprimering on managing salinity stress, considering salinity levels and different NPs.

Types of NPs	NPs concentration	Salinity concentration	Effects of NPs	References
Ag-NPs	1 L ⁻¹	25, 100 mM	Stimulate the germination and growth of wheat grains, improve growth index, pigment contents and chlorophyll stability index (CSI), auxins, cytokinins and ABA contents, enhance photosynthetic efficiency as well as phytohormones balance, and reduce the harmful consequences of salinity stress	[197]
ZnO NPs	50 L ⁻¹	200 mM	Increased trapped energy flow and electron transport flow, along with sucrose production, stimulated the antioxidant system.	[198]
TiO ₂ NPs	60 ppm	200 mM	TiO ₂ priming significantly improved maize seed germination percentage, germination energy, seedling vigor index, root and shoot lengths, and fresh and dry weights of seedlings under salinity stress. It also enhanced K ⁺ ion concentration, RWC, total phenolic, proline contents, and activities of SOD, CAT, and phenylalanine ammonia lyase (PAL). Furthermore, mean emergence time (MET), sodium ion (Na ⁺) concentration, membrane electrolyte leakage (MEL), and malondialdehyde (MDA) content were reduced compared to the control	[45]
ZnO-NPs	50, 100 and 500 mg L ⁻¹	150 mM NaCl	Enhanced wheat growth indicators help counteract the impact of salt by modifying growth patterns, photosynthetic pigments, photosynthetic performance, and the ultrastructure of leaves.	[199]
ZnO-NPs	50 L ⁻¹	0.52, 4.42, 6.84 and 9.3 dS m ⁻¹	The uptake of macronutrients (N, P, and K) by wheat straw and grains increased significantly with salinity levels up to 6.84 dS m ⁻¹ , especially in primed seeds	[200]
Cerium oxide nanoparticles (nanoceria)	0.1 mM	200 mM NaCl	PNC treatment of rapeseeds (<i>Brassica napus</i>) resulted in increased water absorption (52%, 14%, 12% at 1, 3, and 8 h of priming) and enhanced α-amylase activity (175%, 309%, 295% at the same intervals) compared to control seeds. Under salt stress, PNC-primed seeds exhibited decreased levels of MDA, H ₂ O ₂ , and *O ₂ in both shoots and roots. Additionally, they showed improved K ⁺ retention (29%) and reduced Na ⁺ accumulation (18.5%) and Na ⁺ /K ⁺ ratio (37%) compared to controls	[91]
PVP-coated Ag nanoparticles (PVP-AgNPs)	40 L ⁻¹	150 and 200 mM	Increased barley seed germination was linked to elevated antioxidants in NPs treatments, including SOD, CAT, GR, and GPX, which were reflected in both gene expression (<i>HvSOD</i> , <i>HvCAT</i> , <i>HvGR</i> , <i>HvGPX</i>) and protein levels, as well as glutathione content that scavenged ROS	[40]
ZnO NPs	50 and 100 L ⁻¹	50 and 100 mM NaCl	The study highlights the impact of salt-stressed soil on maize, noting an increase in cumulative germination percentage, germination energy, imbibition rate, grain weight, potassium (K ⁺) content, and α-amylase activity. Conversely, it significantly reduces germination time, days to 50% emergence, Na ⁺ uptake, and the Na ⁺ /K ⁺ ratio	[201]
Cerium oxide nanoparticle (CeO ₂ -NP)	50 mg/L	200 mM	CeO ₂ -NP priming enhanced α-amylase activity and osmoregulatory substances in alfalfa (<i>Medicago sativa</i>), reduced reactive oxygen species and malonaldehyde levels, and improved catalase enzyme activity	[202]
Nanocellulose (NC)	0, 0.3%, and 0.6%	0.7, 5, 10, 15, and 20 dSm ⁻¹	Enhancing germination rate, seedling development, root length, root surface area, and sodium influx.	[106]
NanoZnO	200 L ⁻¹	0, 1.5, and 3‰	ZnO nanoprimering enhances rice salt tolerance by increasing α-amylase, soluble sugar, and soluble protein levels, along with boosting antioxidant enzyme activities, thus promoting better seed germination and seedling growth	[86]
Poly acrylic acid coated selenium doped carbon dots (PAA@Se-CDs)	25, 50, and 75 L ⁻¹	200 L ⁻¹	Increased rapeseed germination (20%) and seedling fresh weight (161%) under saline conditions were observed with PAA@Se-CDs nanoprimering compared to the NNP control. This treatment significantly enhanced endo-β-mannanase activities (255% increase), total soluble sugars, and protein contents, supporting germination under salt stress. Additionally, respiration rate and ATP content rose by 76% and 607%, respectively. PAA@Se-CDs nanoprimering alleviated oxidative damage from ROS by boosting antioxidant enzyme activities (SOD, POD and CAT). It also improved salt tolerance by reducing sodium accumulation and enhancing potassium retention, increasing the K ⁺ /Na ⁺ ratio	[203]
Carbon dots (CDs)	0, 20, 50, 80, 100 and 120 mg/L	0.3 % NaCl	CDs priming improved germination in cotton seeds by reducing salt-induced oxidative damage through decreased O ₂ ⁻ and MDA levels. This process involved the upregulation of stress-response genes (<i>GhRboh</i> s, Ca ²⁺ influx channels, <i>SOS1/NHX7</i>) and enhanced Na ⁺ efflux via Ca ²⁺ -dependent Na ⁺ /H ⁺ antiporter, thereby boosting salinity tolerance	[204]
Nano-(Zinc EDTA)	12% and 170 ppm	0, 5, 8, and 11 dS m ⁻¹	Improved the germination, vigor index, and seedling biomass trait of rice	[205]
ZnO NPs	100 ppm	200 mM NaCl	Increased osmolyte accumulation and mineral absorption were observed, with tolerant barley genotypes showing strong induction of <i>NHX</i> and <i>SOS</i> genes, specifically <i>HvNHX3</i> and <i>HvSOS1</i> . Additionally, antioxidant genes such as <i>CAT1</i> , <i>APX</i> , and <i>GR</i> were upregulated	[206]
Graphene quantum dot (GQD)	0, 50, 100, 200, and 400 mg L ⁻¹	0 and 100 mM NaCl	Improved radicle and plumule emergence, along with a increased germination percentage and MGT, were observed in chickpea	[207]
Se-CS NPs	0, 10 and 20 L ⁻¹	0, 50 and 100 mM NaCl	Increased transcriptional levels of <i>WRKY1</i> , <i>SOS1</i> , <i>PM H⁺-ATPase</i> , <i>SKOR</i> , <i>Mc5PTase7</i> , <i>SOAR1</i> , <i>MAP30</i> , <i>α-MMC</i> , <i>polypeptide-P</i> and <i>PAL</i> increased growth parameters, photosynthesis parameters (SPAD _{IV} /F _m , Y (II)), antioxidant enzymatic activity (POD, SOD, CAT) and nutrient homeostasis (Na ⁺ /K ⁺ , Ca ²⁺ , and Cl ⁻) and induced the expression of genes in bitter melon plants	[153]

(continued on next page)

Table 1 (continued)

Types of NPs	NPs concentration	Salinity concentration	Effects of NPs	References
Zn/g-C ₃ N ₄	250 µg/L	0 mM, 25 mM, 50 mM, 75 mM, 125 mM, and 150 mM	Nano-priming triggered redox-regulatory pathways through Ca ²⁺ and ABA, leading to increased expression of genes like <i>OsCu/ZnSOD</i> , <i>OsPOX1</i> , and <i>OsAPX</i> , which enhanced antioxidant production. The distinct regulation of <i>OsSOS1</i> and <i>OsNHX1</i> improved Na ⁺ transport and vacuolar storage, helping to avoid ionic toxicity	[181]

beneficial method for enhancing germination, promoting seedling growth, and protecting wheat seedlings under salinity stress [106]. Nanopriming with ZnO NPs (10 mg/L) reduced the oxidative status of plants by upregulating the activity of antioxidant enzymes such as POD, CAT and SOD, which decreased membrane lipid peroxidation and significantly lowered ROS levels in nanoprimed wheat plants, thereby enhancing seed germination and photosynthetic performance [107].

3.2.2. NPs-mediated non-antioxidant enzyme-based ROS homeostasis

Some of the most harmful ROS, such as ¹O₂ and •OH, are not efficiently removed by enzymatic antioxidant systems [108]. Thus, to eliminate these ROS from plant cells, plants must rely solely on non-enzymatic mechanisms. In most cases, ROS leads to lipid peroxidation, which significantly increases MDA overproduction [109]. Non-enzymatic molecules such as GSH (glutathione), compatible solutes, phenolics, α-tocopherol, carotenoids, flavonoids, and proline act cooperatively to scavenge excessive ROS generated under stress conditions [110]. Different studies suggest that seed priming technology can upregulate the activity of the GSH system, thereby improving the tolerance of cucumber [111] and chickpea [112] seeds under salinity stress. Additionally, previous findings suggest that GSH is an essential antioxidant that plays a crucial role in seed quality and germination. Water uptake and oxidative metabolism in two recalcitrant-seeded species, *Avicennia marina* and *Trichilia dregeana*, were studied in relation to germination rate and storage duration [113]. *A. marina* had a shorter storage duration and faster germination rate than *T. dregeana*, which corresponded to increased water uptake and ROS levels in the former of both species combinations. Slow *T. dregeana* germination was characterized by decreased water uptake and ROS behavior. ROS generation is directly related to water imbibition and germination in a single positive correlation, while ROS scavengers inhibited seedling germination, supporting the notion that elevated ROS are crucial for the process of germination phylogenetically. Hence, ROS-driven germination during storage, including hard seeds such as *A. tenezica* and *A. marina*, is promoted by rapid water uptake and reduced ROS scavenging, which results in poor storage performance of these resistant seeds [113]. Breaking of apple seed dormancy is associated with increased GSH pool in embryonic axes [114]. Seed priming with GSH, either alone or in combination (0.5% Zn) was able to mitigate the effects of 120 mM NaCl salinity on salt-negative attributes of seedling establishment and seed germination traits [115]. GSH-mediated amelioration of seed germination parameters appears to be due to its increased uptake by seeds when used in combination with Zn than alone, and is involved in enhancing water absorption via a decrease in the osmotic potential of seeds, which is necessary for sustaining better activity of hydrolytic enzymes [116–118]. In another work investigating the influence of Ag-NPs on salinity-stressed barley seeds, the effect of seed priming with PVP-Ag-NPs on salinity stress was examined. Seedling germination was completely inhibited under 150 and 200 mM salt conditions compared with the control. A 2 h seed priming treatment with PVP-Ag-NPs (40 mg/L) alleviated the effects of salinity stress at different NaCl levels. The control showed lower levels of ROS than salinity-treated samples. Scavenging of ROS by GSH was induced by NPs treatments [40]. Proline is a well-known osmoprotective free amino acid in plants that accumulates in response to salt stress. It also acts as an osmolyte, playing an important role in maintaining the osmotic potential and protecting cellular

structures from damage under high salinity [119].

Proline is a ROS scavenger and plays a role in alleviating oxidative damage and maintaining cellular redox homeostasis [120]. Proline has also been suggested as a regulator of many physiological factors related to salt tolerance. It can change ion transport components, such as the activation and blocking of ion channels and transporters, thereby helping to maintain ion balance under salt stress. It is also known that proline may modulate the activity of enzymes involved in antioxidant defense, as well as stress signaling pathways and hormone biosynthesis and signaling [119,121]. Ag-NPs nanopriming preserved increased levels of soluble proteins, supporting better metabolic processes and increasing soluble protein content, thereby enhancing the salt tolerance of lettuce [122]. Similarly, positive effects on proline content in different crops under stress conditions via seed priming have been well documented in rapeseed [123] and *Leymus chinensis* [124] under salinity stress. An investigation reported that salt stress reduced proline levels in two rice varieties (Chaoyou 1000 (CY1000) and Longliangyou 506 (LLY506)) during growth chamber and field experiments [86]. Primed treatments also reduced proline content compared with non-primed treatments. However, the rate of proline reduction under saline conditions was much higher than that of NanoZnO nanoprimed seeds under salinity stress [86]. In contrast, NanoZnO nanopriming increased proline content in lupine species under salt stress [125]. Seed nanopriming of pearl millet with Ag NPs (20 mM concentration) was also reported to elevate proline content under salt stress (0, 120, and 150 mM NaCl) [126]. Correspondingly, TiO₂ NPs increased proline content in maize under salt stress conditions [127]. A possible explanation is that the nanopriming may activate distinct salt tolerance mechanisms in different crop species. In general, results from growth chamber and field experiments indicated that seed nanopriming with NanoZnO caused a remarkable increase in α-amylase activity [86]. The superior effect of NanoZnO nanopriming compared with hydropriming (H₂O) and chemical priming (ASA, SA, GABA) under salt stress, with respect to soluble sugar and soluble protein contents, might be attributed to the rapid mobilization of rice seedling growth due to enhanced endosperm breakdown and metabolism [86].

4. Effect of nanopriming on signalling and molecular features of seed germination under salinity stress

Currently, the mechanisms behind the improvement of seed germination by nanopriming technology for salinity stress management are: (1) increasing the relative expression of aquaporin and ion transporter genes to regulate osmotic and ionic stress homeostasis, (2) increasing the relative expression of hydrolytic enzyme genes, (3) increasing and decreasing the relative expression of GA biosynthesis genes and ABA biosynthesis genes, respectively, and (4) maintaining ROS homeostasis by altering the relative expression of antioxidant enzyme genes (Fig. 3). Nanopriming does not bring about phenological or genomic changes in the plant. However, stress-tolerant memory is maintained and is mediated transcriptionally, translationally and epigenetically. This adjustment is conserved at the molecular level, enabling plants to respond more quickly and efficiently when facing stress down the line (Table 1, Fig. 3).

Transcription factor gene families, such as bZIP, WRKY, APETALA2/Ethylene Response Factor (AP2/ERF), MYB, basic helix-loop-helix

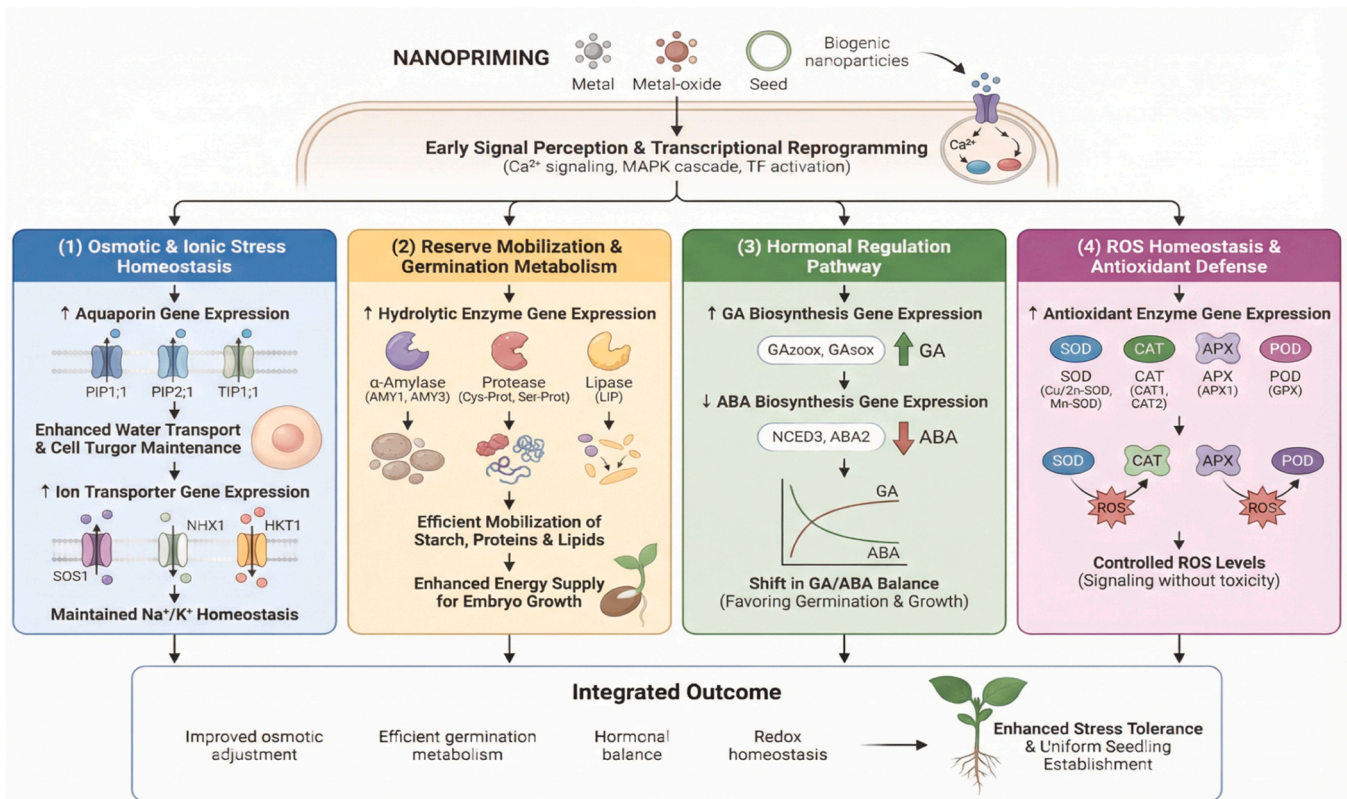


Fig. 3. The molecular effects of nanopriming are summarized in this schematic diagram. Nanopriming elicits early signalling and transcriptional reprogramming, thereby regulating multiple biological processes in a synchronized manner. On one hand, the up-regulation of expression of aquaporin (PIP1;1, PIP2;1, TIP1;1) and ion transporter genes (SOS1, NHX1, HKT1) is increased by nanopriming process which helps to maintain osmotic balance, cellular turgor and Na^+/K^+ homeostasis during stress. Secondly, the expression of hydrolytic enzyme genes such as α -amylase (AMY1 and AMY3), proteases and lipases is up-regulated leading to effective mobilization of seed-stored reserves in support of early embryo growth. Third, nanopriming regulates hormonal signaling by upregulating the biosynthesis genes of gibberellins (GA2ox, GA3ox) and downregulating those of abscisic acid (NCED3, ABA2), rebalancing the ratio of GA/ABA to stimulate germination and seedling growth. Antioxidant enzyme genes, including SOD, CAT, APX, and POD, are differentially expressed to maintain ROS homeostasis in plant cells and their moderate levels do not impair cellular activity, while ROS continue to function as signaling molecules. Their combined action ideally stabilizes cells, makes them more resistant to stress, and ensures the even growth of seedlings.

(bHLH), NAC and HD-ZIP, play an important role in determining the expression level of genes involved in salt tolerance by regulating the antioxidant and phytohormone system (Fig. 4) [128]. Water uptake by seeds is an essential process in dry seeds to trigger various metabolic activities of seed germination that promote the growth of seedlings [129]. Aquaporins (AQP) are channel proteins from the Major Intrinsic Protein (MIP) superfamily regulating plant water relations [130]. They transport water and small neutral molecules across membranes, conducting water at increased rates than selective ion channels [130]. Their expression and distribution in plant cells are regulated under abiotic stresses like salinity, drought, and temperature extremes [130–132]. AQPs enable efficient water flow and facilitate transport across water potential gradients. There are five main plant AQP subfamilies: plasma membrane intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), nodulin 26 like intrinsic proteins (NIPs), small basic intrinsic proteins (SIPs), and X intrinsic proteins (XIPs) [131,132]. AQPs are found in all living cells of plants, but mainly in the tonoplast and plasma membrane [130]. AQP gene expression is dynamically regulated through responses to external and internal signals by AP2/ERF, MYB, NAC and WRKY families, stress- and development-responsive transcription factors (TFs) are primarily involved in the transcriptional reprogramming process under salinity stress [133]. In Arabidopsis seedlings, the expression of aquaporin genes such as *PIP 1;2*, *PIP 2;1*, *PIP 2;2*, *SIP 1;1* and *TIP 1;1* demonstrated a ~ two-fold increase compared to their respective controls after exposure for one week to Ag-NPs at concentrations ranging between 0.2 or 0.5mg/L [134]. Another study reported the use of Ag-NPs

at 5 and 10 ppm with nanopriming of rice recorded that two aquaporin (*PIP1; 1* and *PIP2;11*) genes, which are associated with water uptake, had increased expression in germinated seeds after 24 h imbibition under salinity stress [129]. Similarly, the study investigated the influence of Se-NPs on the expression levels of aquaporin genes (*BnPIP1-1*, *BnPIP2-1*) and propounded it on a molecular basis to change seed metabolism during response to Se-NPs was up-regulated in nanoprimed seeds particularly 150 $\mu\text{mol/L}$ as compared with hydroprimed seeds imbibition stage (4 and 8 clear priming) [135]. Aquaporins (trans-membrane proteins) have been shown to play an important role in mediating water permeability across biological membranes [136], adjusting water homeostasis and ROS production, CO_2 diffusion and nutrient component contents (boron and silicon) of plants together with radical scavenging [137,138], thereby maintaining cellular water homeostasis in response to different abiotic stresses [136].

After osmotic homeostasis needs a balance of ionic uptake, so application of NPs via a priming method can improve the ionic homeostasis-related transporter genes, e.g., plasma membrane $\text{H}^+ - \text{ATPase}$ (ATPase), Ca^{2+} protein exchanger (CAX1), sodium/proton exchanger (NHX1), and salt overly sensitive (SOS1) gene expression [139]. Since Na^+ and Cl^- have toxic effects on cellular metabolism, high K^+/Na^+ and low cytosolic Na^+ content are preferred traits for efficient plants [140]. Moreover, Ca^{2+} is a major signalling element related to plant responses to salt stress [141]. Ca^{2+} promotes plant tolerance to salt stress by stabilizing cell wall structure [142], maintaining the structural and functional integrity of plant membranes during environmental

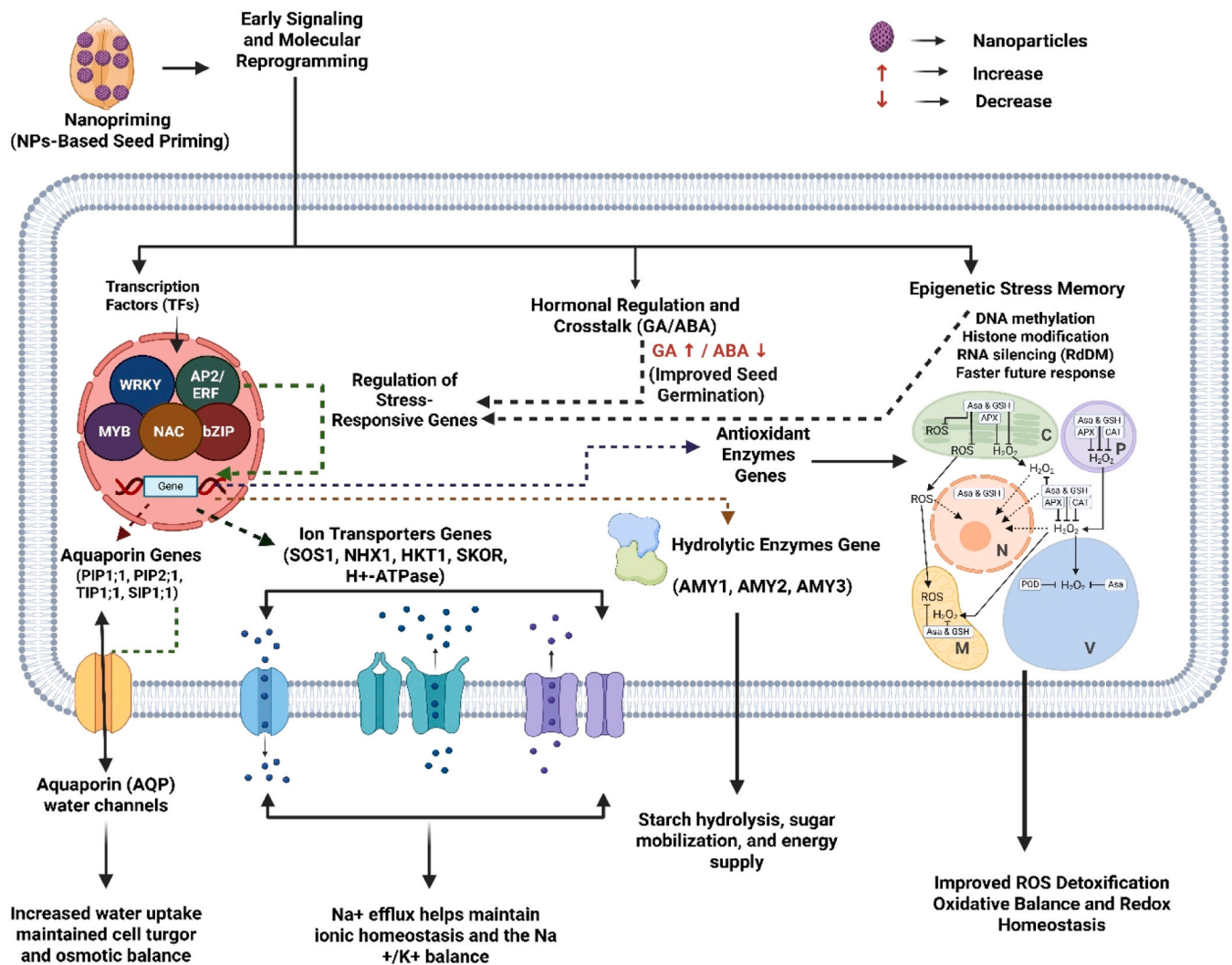


Fig. 4. Schematic representation of nanopriming-mediated molecular regulation during seed germination under salinity stress. Nanopriming activates early signaling and transcriptional reprogramming through stress-responsive transcription factors (WRKY, AP2/ERF, MYB, NAC, and bZIP), which regulate aquaporin and ion transporter genes to maintain osmotic and ionic homeostasis. Simultaneously, hydrolytic enzyme genes enhance reserve mobilization, while hormonal regulation increases GA and decreases ABA biosynthesis to promote germination. Nanopriming also regulates antioxidant genes to maintain ROS homeostasis, resulting in improved seed germination, seedling establishment, salinity tolerance, and stress memory.

stress [143], regulating ion selectivity and transport, also controlling ion-exchange behaviour in roots and plant organs [144]. Cytosolic Ca^{2+} accumulation in response to salinity serves as a secondary messenger within the stress signaling pathway [145]. In the salt overly sensitive (SOS) pathway, SOS3 (Salt Overly Sensitive3 [SOS3]-like calcium-binding proteins [SCaBPs; also named calcineurin B-like protein [CBL]]) [146] binds with Ca^{2+} and associates with the protein kinase SOS2 (serine/threonine protein kinase) [147]. SOS3-SOS2 complex activates SOS1 (a Na^+/H^+ -Antiporter), and the expression of SOS1 regulates cytosolic Na^+ concentration [148,149]. However, considering that reducing Na^+ influx into the root is the most promising method to avoid Na^+ accumulation in plants, there is also a plasma membrane located Na^+/H^+ antiporter (SOS1), which can efflux excess Na^+ from the cell. The cytosolic ion-homeostasis under saline conditions is also maintained by PM H^+ -ATPase which transports a H^+ gradient due to Na^+ efflux and H^+ influx to carry out Na^+/H^+ antiport across the plasma membrane [150]. K^+ plays many important roles in plant metabolism and SKOR is a K^+ channel that mediates K^+ efflux from root cells [151]. Thus, the normal K^+/Na^+ ratio in cells is maintain under salt stress that essential for plant growth and development. All these transporters are regulated by various types of TFs, which are crucial for the expression of genes

related to ionic homeostasis by nanopriming. A previous experiment suggested 20 L^{-1} Se-CS NPs bitter melon (*Momordica charantia* L. 'Palee F1') seed nanopriming which help to upregulation WRKY1 TFs that coordinates SOS1 (Na^+/H^+ antiporter), PM H^+ -ATPase (proton gradient), and SKOR (K^+ efflux) related genes for ionic balance under 100 mM salinity level [152,153]. In a study, NHX1, CAX1, SOS1 and H^+ -ATPase genes were down-regulated in non-stressful conditions but activated upon salt exposure and amendment treatment with stronger expression under combined application of SB + Se-NPs. It indicates that there is crosswise of SB and Se-NPs protection on membrane potential to maintain the H^+ -ATPase gene activity at an optimum level for K^+ uptake by which, the wheat plants might be protected from NaCl-induced damage [154]. The transcript of the high-affinity K^+ transporter (HKT1) gene showed an increasing pattern across the CSNPs and salinity treatments. A similar pattern to that of the (HKT1) gene was found for the Na^+/H^+ exchangers (NHX1) [155]. CSNPs treatment was associated with up-regulation of the plasma membrane proteolipid 3 (PMP3) gene, as compared to salinity controls in maize [155]. The molecular mechanism of salt-responsive genes (HKT1, SOS1 and NHX1) suggest that application of IONPs (iron oxide nanoparticles) increases transcript levels either by efflux of Na^+ ions from the cell or by internal

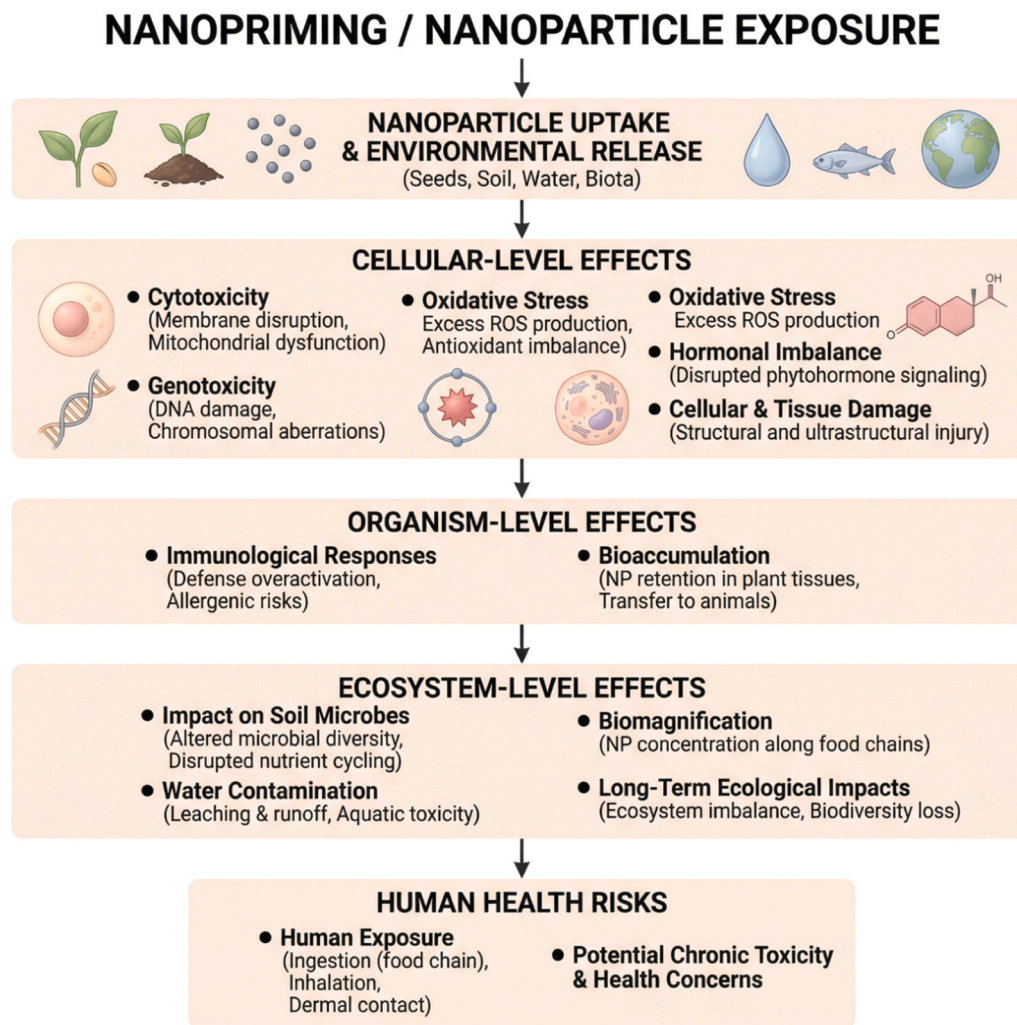


Fig. 5. Cytotoxic and genotoxic effects of NP-based seed priming and ecological and environmental risks of nanopriming technology.

sequestration into vacuole under stress, resulting improved morpho-physiological growth parameters including shoot length and chlorophyll levels in *Eucalyptus tereticornis* [156].

α -Amylase in the aleurone layer is crucially involved in cereal-seed germination by hydrolyzing endosperm starch to metabolizable sugars, which supply energy for new root and shoot growth [157]. In the seeds of plants, *AMY1* and *AMY2* genes encode α -amylases enzymes that degrade starch to provide a source of energy during germination; *AMY1* and *AMY2* demonstrate distinct expression patterns that are influenced by hormones (e.g. gibberellic acid) or sugar concentration levels: *AMY1* is known for its presence during germination while *AMY2* occurs through development. Both work to hydrolyze starch in endosperm in this growth period [158–162]. Salinity stress down-regulated the expression of *AMY1*, *AMY2* and *AMY3* genes in barley germinated seeds, which inhibited α -amylase activity [163]. Polyacrylic acid-coated nanoceria (PNC) nanopriming increased the expression of α -amylase genes (*AMY1* and *AMY2*), and more α -amylase activity promoted reserve metabolism, as well as provided more soluble sugar for germinating under salt stress [91]. ROS generated during the stimulation of plants can function as signal molecules for other messengers, including GA and ABA that may ultimately lead to the direct or indirect regulation of secondary metabolism processes [164]. Crucial to the stability of this 'stress memory' are the presence of signaling molecules and active or repressed transcription factors [165]. The differential expression of priming-induced genes is controlled via several ways, such as RNA-induced transcriptional gene silencing,

RNA-dependent DNA methylation (RdDM), positioning/spacing alteration of nucleosome or histone variants, DNA methylation and histone modifications [166]. In addition to inhibiting the water uptake of seed, salt also affects seed germination by decreasing the GA content and increasing the ABA content related to gene expression [167–169]. In rice, NaCl treatment was shown to decreased bioactive GA levels, leading to inhibition of seed germination by inhibiting α -amylase activity through down-regulation of the α -amylase gene expression such as *OsAmy1A* (*RAmy1A*), *OsAmy1C* (*RAmy1C*), *OsAmy3C* (*RAmy3C*), and *OsAmy3E* (*RAmy3E*) [170]. In addition, down-regulation of the α -*Amy1* and α -*Amy2* gene transcription in wheat grain was observed, together with reduced content of GA, which is caused by ectopic expression of *PcGA2ox1* (gibberellin 2-oxidase gene) [171]. Silicon-primed rice in the presence of nanosilver (Ag-NPs) resulted in an accumulation of ROS and promoted several hormones signaling pathways [172].

The expression of the *APETALA2* (*AP2*) domain-containing protein, the DOF zinc finger domain-containing protein and the *WRKY* TFs was also facilitated by this priming. The transcription factors, in turn, modulate the genes of defence response proteins, such as heat shock proteins (HSP), glutathione S-transferase (*GST*), F-box proteins (*FBP*), and late embryogenesis abundant (*LEA*) proteins, for enhancing the defence. They are also involved in the regulation of glutathione and -cytokinin-O-glucosyltransferase (CGTs) to facilitate seed germination. Rice seeds primed with Ag-NPs exhibited improved germination speed, seedling vigor, biomass, and root length under salt stress. Metabolomic analyses showed that Ag-NPs reprogrammed seed metabolism,

enhancing signaling (MAPK signaling) metabolites and activating stress defense pathways [172]. The phytohormone, ABA, governs diverse plant responses to stress and triggers the gene expression of genes such as encoding an ABA-responsive element-binding protein [173], which controls ABA-regulated gene expression required for better management of stress [174,175]. Similarly, the results also showed that the nanoprimer application of Se-NPs and ZnO-NPs NPs changed ABA levels after sowing and reducing ABA contents, reversing the germination of *Brassica napus* [176]. Also, this experiment also showed that Se NPs and ZnO NPs down-regulated abscisic acid-related genes (*BnCYP707A1*, *BnCYP707A3* and *BnCYP707A4*), ROS-related genes (*BnPER*), but up-regulation of gibberellin-related genes (*BnGA20ox*, *BnGA3ox*, *BNCPS*), germination-related gene (*BnCAM*) cell wall loosening-related genes (*BnEXP4*), germination rate-related genes (*BnRAB28*), and also positive regulations of genes expression improved the seed germination of *Brassica napus* under salinity stress [176]. Transcriptomic analysis revealed 4779 differentially expressed genes (DEGs) linked to ROS pathways and ion homeostasis under salinity stress. The findings suggest that PNC seed priming potentially enhances salinity tolerance through specific molecular mechanisms involving ROS and calcium signaling pathways in cotton (*Gossypium hirsutum* L.) seedlings [177].

Nanoprimer plant seeds and consequent seedlings express a well-regulated ROS homeostasis and antioxidant system to provide protection against oxidative damage to germinated seeds and seed longevity [178,179]. An earlier study indicated that nanoprimer bitter melon (*Momordica charantia* L. 'Palee F1') seeds with 20 L^{-1} Se-CS NPs aids in the upregulation of *WRKY1* transcription factors, which in turn enhances the activity of antioxidant enzymes such as SOD, CAT, and POD when exposed to salinity stress [153]. *OsDREB1A* is a transcription factor in rice that regulates tolerance to multiple abiotic stresses including high-salt [180]. Functioning by binding of dehydration-responsive element (DRE) and C-repeat (CRT), cis-acting elements present in promoters to enhance expression of stress-inducible genes [180]. Zn/g-C₃N₄ NPs based primed rice seedlings significantly activated the *OsDREB1A* stress-responsive transcription factor, which led to the further upregulation of stress-responsive genes. This, in turn, resulted in a proportional overexpression of antioxidant genes (*OsSOD*, *OsPOX*, *OsAPX*) and redox-recycling non-enzymatic antioxidants (*OsDHAR1* and *OsGST1*), aligning with the enhanced biochemical activity for detoxification of ROS under salinity stress [181].

The POD-related gene (*GhD09G1420*, *GhA03G2152*, *GhD08G2330*, *GhA03G1517*, *GhD09G1415*, *GhD11G2183* and *GhA10G2288*) expression was up-regulated in CeO₂ NPs-primed cotton with salt stress than control plants [177]. Salt stress hinders Mn uptake by plants, which can disturb the active Mn-SOD form and result in a negative effect on cell division and plant growth [182]. Nanoprimer of Mn-NPs increased SOD enzyme activity by upregulating the relative expression level of Mn-SOD gene and protected plant cells from ROS damage, which surpassed phytotoxic effects in pepper [183]. On the same line, MnO NPs nanoprimer enhanced antioxidant profiles and seedling the growth in watermelon seedlings [184]. AgNPs-treated seeds significantly enhanced the expression of *SOS2* and subsequently increased salt tolerance in tomato [185]. Research showed that ZnO NPs nanoprimer could trigger *miR156* and *miR159* generation in barley, which play crucial roles in the plant protective responses towards abiotic and biotic stress [186]. Similarly, in *Eruca sativa* seedlings, chlorophyll fluorescence was increased and *miR159c* expression was remarkably up-regulated by Fe₃O₄ NPs [186]. The *miR159* was upregulated by the treatment of TiO₂ NPs in tobacco, which is indispensable for plant development and stress issues, including abiotic response [187]. An et al. demonstrated that the down-regulation of *AKT1*, which was associated with a suppression of K⁺ loss, due to NPs nanoprimer, prevented further K⁺ decrease and enhanced cotton salt tolerance [177].

Phenylalanine ammonia-lyase (PAL) is the primary first enzyme in

phenylpropanol biosynthesis and catalyzes the conversion of L-phenylalanine to cinnamic acid [188,189]. PAL is the first step in the phenylpropanoid biosynthetic pathway, and it is essential to synthesize secondary metabolites such as phenols and flavonoids [190]. The ROS–polyphenols homeostasis assures the adaptation of plants against salt stress [191,192]. Phenolic compounds act as a ROS scavenger and substrate of peroxidase-like enzymes, which are part of the complex antioxidant system of the plants [193,194]. In this perspective, induction of phenolic synthesis is an important part of the response to salt stress. A previous study indicates that using 20 L^{-1} Se-CS NPs as a priming agent for bitter melon enhances PAL expression under saline conditions [153]. Nano-Se upregulated *dehydration response element B1A* (*DREB1A*) transcription factor and (*PAL*, *HCT1*, and *HQT1*) associated with secondary metabolism in chicory (*Cichorium intybus* L.) [195]. Nano-Se also upregulates the expression of the *WRKY1* transcription factor, phenylalanine ammonia-lyase (*PAL*), and 4-Coumarate: CoA-ligase (*4CL*) genes in bitter melon plants [196].

However, the results obtained from such studies are predominantly limited to morphological and physiological characteristics. Additional experimental studies are therefore required to investigate the molecular pathways associated with the positive effects of seed nanoprimer on crop salinity tolerance.

5. Concerns regarding nanoprimer-induced cytotoxicity and genotoxicity

The effects of nanoparticles on plant growth represent a double-edged sword. Due to their distinct size and composition, NPs may directly interact with diverse molecular and biochemical pathways in plants, causing phytotoxic effects such as cytotoxicity and genotoxicity, which can influence plant development (Fig. 4) [208]. Nanoprimer, which improves seed germination, stress tolerance, and crop productivity in various crops has emerged as a promising practice; however, growing evidence indicates the potential toxicological and ecological effects associated with NP exposure. One of the principal concerns is cytotoxicity, as NPs may induce deleterious effects on cellular architecture and function, ultimately affecting cell viability. These effects may arise from NP interactions with cellular membranes, organelles and metabolic pathways, resulting in the disruption of normal physiological functions [209]. Genotoxicity is also strongly associated with cytotoxic effects and includes DNA damage, chromosomal abnormalities, and mutations induced by NPs. Such genetic alterations may have long-term consequences by disrupting gene expression, and cell division, as well as causing heritable mutations that could ultimately affect plant health, food safety, and ecosystem stability [209,210]. NPs can also trigger immune responses in plants, partly through the activation of defense-related signaling pathways. Although these responses may initially enhance stress tolerance, excessive or chronically activated immune responses can lead to allergenicity, increased metabolic costs, and immune system dysregulation, all of which are known to hinder plant growth and productivity [210]. Another important concern is the induction of oxidative stress, namely the overproduction of ROS following NP exposure. Elevated ROS levels can exceed the capacity of endogenous antioxidant systems, thereby inducing lipid peroxidation, protein oxidation, and nucleic acid damage, ultimately resulting in cellular dysfunction and tissue injury [211,212]. Long-term oxidative stress may further aggravate cytotoxic and genotoxic effects. Nanoprimer has also been suggested to disrupt hormonal balance due to the ability of nanoparticles to interfere with phytohormone biosynthesis, transport or signaling pathways. Hormonal imbalances, particularly involving auxins, gibberellins, abscisic acid, and cytokinins, adversely affect plant growth, development, and physiological homeostasis, potentially counteracting the beneficial effects of nanoprimer under certain conditions [213].

At a structural scale, NPs may detrimentally affect cells and tissues through either direct physical interactions or indirect biochemical

processes. This damage may harm membrane structural integrity, organelle ultrastructure, and a normal cellular organization then this situation leads to decreased function of tissue and reduced performance of plantings [211,212]. In addition to single plants, bioaccumulation of NPs in plant tissues is a major risk for the ecosystem as well as humans' food chain safety. Retained NPs can accumulate in edible plant tissues, or animal organs over the long term, causing systemic toxicity and increasing the risks of cumulative exposure to consumers and bystanders [214]. This could be exacerbated through biomagnification, where the particle concentration continues to increase along consecutive trophic levels and also logarithmically cause harming effects in increased life forms and system health [214]. NPs residues from nanoprimered seeds can negatively influence soil microbial communities, resulting in changes of microbial diversity, enzymatic activity and nutrient cycling processes. This type of disruptions could lead to poor soil fertility, disruption in plant-microbe interactions and failure of the soil ecosystem [209,210]. Furthermore, water pollution is one of the major environmental threats because NPs have potential to leach down into groundwater or runoff from agroecosystems. This may have an effect on aquatic ecosystems by exerting severity upon microbial populations, invertebrates and aquatic increased organisms [209,210]. Together, these factors result in long-term effects on ecosystems such as synergistic and cumulative toxicity of metals, altered ecological equilibrium and changes in species interactions above ground and below water. These impacts highlight the requirement for full-fledged life-cycle assessments and ecological risk analyses prior to large-scale acceptance of nanoprimering systems [209, 212]. Last but not least, human exposure to nanoparticles in nanoprimered crops or environmental stalks carries health concerns due to ingestion, inhalation, and dermal loss. Despite the scantiness of available information, potential risk of chronic exposure, bioaccumulation, and systemic toxicity should be addressed in order to justify sustainable and responsible use of nanoprimering technology in agriculture [209,210].

6. Conclusion

All current results suggest that nanoprimering successfully influences seed germination and seedling vigor by synchronizing the physiological, biochemical and molecular responses. The nanoprimering ameliorates osmotic and ionic stresses, restores hormonal equilibrium (ABA down-regulation and GA increasing) and facilitates effective water intake during imbibition. Increased α -amylase activity, elevated antioxidant capabilities and modulated ROS homeostasis are additional evidence for metabolic activation and stress amelioration. Stress signaling pathways are activated to induce expression of multiple aquaporins, ion-transporters, antioxidants, and growth-related genes at the molecular level, and stress tolerance regarding germination rate and seedling establishment is enhanced. Overall, nanoprimering may serve as a potential sustainable and environmentally-friendly approach to improve seedling performance and crop resilience in harsh saline environments.

CRedit authorship contribution statement

Abhishek Singh, Roland Bol, Karen Ghazaryan: Conceptualization, Project administration, Direction and Supervision, Funding acquisition, Writing - Review & Editing, Resources. **Rupesh Kumar Singh, João Ricardo Sousa:** Writing - Original Draft, Methodology, Investigation, Data curation, Writing - Review & Editing. **Hasmik Movsesyan, Sakshi Singh:** Writing - Original Draft, Methodology, Investigation, Data curation, Writing - Review & Editing.

Declaration of Generative AI and AI-assisted technologies in the writing process

Not used any AI during preparation of manuscript.

Declaration of Competing Interest

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

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Data availability

Data will be made available on request.

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