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REVIEW ARTICLE

Recent advances in nano-priming induced plant growth promotion and environmental stress tolerance

Nilanjana Ghosh[1] · Swarnali Dey[1] · Titir Guha[2] · Surupa Paul[1] · Rita Kundu[1]

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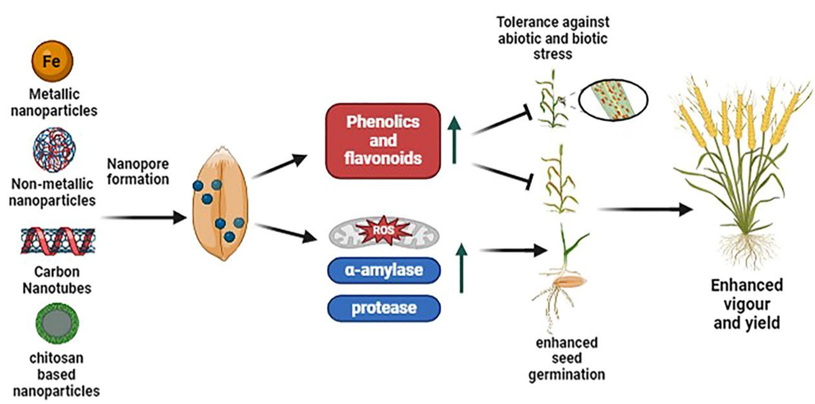
Abstract

The increasing demand for sustainable agriculture has propelled researchers to envision novel technological innovations. In this situation, the implementation of nanoparticles eventually gained huge importance and proved to be beneficial in the field of sustainable agriculture. To date, there have been numerous reports that have focused on utilizing the nanotechnological approach for positively influencing plant growth, development, and yield-associated parameters. Over the years there have been several successful applications of nanoparticles to mitigate the toxic effects imposed by abiotic and biotic stress factors on plants. Among the three major approaches of nanoparticle application to plants, seed priming has played an important role in plant growth promotion owing to its ability to activate signaling pathways concerned with phytohormone and ROS synthesis. So far, the reports available on the role of nano-priming in boosting plant growth and tolerance against environmental stress have been mostly associated with Zn, Fe, Cu, and other essential micronutrients. But in recent years application of metallic and non-metallic nanoparticles like silver, gold, platinum, titanium, and carbon nanotubes is also worth mentioning. The outcome of nano-priming is also subject to the appropriate concentration, charge, and size of NPs used. Besides, nano-priming can elicit a plethora of physiological, biochemical, and molecular responses in the germinating seeds that require proper understanding. Hence this review aims to document the progress made in the nano-priming research and pave the way for other advancements that can be made in the future.

Graphical abstract



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This article is dedicated to Prof. Arun Kumar Sharma to commemorate his Birth Centenary.

Nilanjana Ghosh and Swarnali Dey both have contributed equally.

Extended author information available on the last page of the article

Keywords Abiotic factors · Biotic agents · Heavy metals · Nanotechnology · Nutrients

Introduction

Agriculture is one of the indispensable domains of life. According to FAO (https://www.fao.org/fileadmin/templates/wsfs/docs/Issues_papers/HLEF2050_Global_Agriculture.pdf), about 60% of the world's population depends on agriculture for survival. The World Bank has identified agricultural development as a compelling tool to purge poverty & hunger, boost shared prosperity, and ensure global food security. With the existing population growth rate, the food supply should be increased by 50–70% to ensure food for all [58]. Agriculture is challenged by unfavorable climate, anthropogenic activities, shrinking arable lands, soaring temperatures, and frequent spells of drought and floods. Flanked by this situation, the obsession to create and adopt new technologies for agricultural intensification and extension should be intended. However, sustainability should be of prime consideration to protect against environmental fragmentation. Thus, sustainable agriculture holds the key to global food security [54].

Since its advent, nanotechnology has been an innovative and groundbreaking tool to tackle transpiring global issues and agriculture is no exception. With a characteristic dimension of 100 nm or less, nanomaterials serve as an excellent toolset to render efficient and targeted delivery of nutrients and ions to living cells, which makes them a propitious candidate for implementation in agricultural sector. Nanomaterials have been widely used in agriculture and allied fields for precision farming, as nano-sensors, nano-pesticides, nano-fertilizers, nano-herbicides, and agents for seed encapsulation and priming. Slow and controlled release, targeted delivery, and micro resources have bestowed nanomaterials as potential alternatives for chemical fertilizers which usually lead to leaching, bioaccumulation, residual effects, and long-term detrimental effects on soil health and the micro-environment [73].

Seed invigoration has been of profound importance in the past decade and seed priming has emerged as a salient and widely used technique for seed invigoration. Seed germination can be divided into 3 distinct phases: imbibition phase (rapid water uptake phase), activation or preparatory phase (low rate of water uptake, synthesis of new proteins and other essential organelles & molecules) & germination phase (protrusion of radical and plumule). Seed priming is a controlled hydration of seeds that allows germination to extend till the activation phase but restricts the initiation of the third phase [57]. Thus priming 'prepares' the seed for future sowing and stress atrocities. Hydropriming (with water), Osmo-priming (with osmolytes like PEG, sugar alcohols), Hormo-priming (with gibberellic acid, polyamines, salicylic acid), Chemical priming (with salts like sodium selenite, silicon), Vitamin priming (with thiamine, ascorbate), Nutri-priming (with various micro and macronutrients), Redox priming (with hydrogen peroxide), Bio priming are some of the well-documented priming techniques till date [48, 72].

With the advent of nanotechnology, nanomaterials have been extensively used as seed priming agents, and the technique, termed 'nano-priming' has been serving as a useful and innovative tool for sustainable agriculture by enhancing seedling establishment, seed quality, and crop yields as well as increasing tolerance to environmental stresses. Nano-priming has been implemented in a wide range of plants and various metallic and non-metallic elements have been used as priming agents to improve the growth of the plants or mitigate abiotic and biotic stresses since the past decade. Numerous research and review articles have been published in last 5 years on nano-priming that has improved our current understanding of this technique and also highlighted several unresolved research gaps (Fig. 1). The molecular basis of nanopriming involves inducing a cascade of mechanisms within seeds that lead to enhanced germination and growth. These mechanisms include forming nanopores for improved water uptake, modulating reactive oxygen species (ROS) and antioxidant systems, generating hydroxyl radicals for cell wall loosening, and accelerating starch metabolism by enhancing starch catalysing enzymes [4]. Additionally, nano-priming has been shown to stimulate the production of growth-promoting metabolites, trigger hormone secretion, and reduce ROS levels, ultimately enhancing disease resistance in plants [72]. Seed priming with AgNP enhances aquaporin genes (PIP) and cotton seeds primed with (PNCs) exposed to salt stress showed induction of genes involved in ROS signaling and ion homeostasis [72] Despite the fact, that extensive research needs to be performed to accentuate the positive and negative impacts of nano-priming on sustainable agriculture, few countries have commercialized this approach by developing nanomaterials to amplify crop productivity. For instance, Nanovec TS80 curated by Laboratórios Bio-Médicin, Brazil, is a nanocapsule composed of Mo, Mn, and Zn which has been considered to be efficient in promoting seed germination, root development, nutrient uptake, and biological nitrogen fixation in leguminous plants [71]. Therefore, this comprehensive review provides a holistic view of the role of commonly used nanoparticles in growth enhancement and stress amelioration. It also highlights the mode of action of the nano-priming mediated responses. Although there are previous reviews on nano-priming [20, 38, 55], this review stands out as it discusses the most recent advances and summarizes the findings and research gaps to serve as a cue for future research direction.

Growth enhancement through nano-priming

Nanoparticles (NPs) have indeed become an integral part of sustainable agriculture owing to their superior physical and chemical properties compared to its bulk counterparts. Over the years a wide range of nano-formulations have been curated where different carriers have been efficiently employed for gradual and specific release of macro as well as micronutrients. Depending upon their size, shape, surface charge, and degree of hydrophobicity nanoparticles can be taken up either by passive diffusion, active transport via transmembrane carrier proteins like aquaporins, or by endocytosis into the cell membrane. The entry of NPs can even be facilitated by creating small pores on the cell membrane or by forming a complex with organic compounds of root exudates [20, 55]. Post entry through the root cells, NPs are translocated to various plant tissues either via apoplastic (from root via xylem to shoot) or symplastic pathways (transport of water and substances between two cells via plasmodesmata). NPs can positively influence crucial physiological and metabolic activities in plants that make nano-priming a significant tool to facilitate breaking seed dormancy, enhancing seed germination, and seedling vigor (Table 1). NPs possibly function by creating nanopores that assist the uptake of water and nutrients into the seeds. Besides it triggers the formation of ROS (OH^-, O_2^- radicals) that makes the seed coat permeable and facilitates germination (Fig. 2) [55]. They even initiate a downstream signaling cascade which includes upregulation of α- amylase or other hydrolytic enzyme activity to break down the reserve food present in the endosperm essential for optimum germination. Besides, it might also help in the production of secondary metabolites like phenols to eventually promote seedling growth and development. Nano-priming upregulates the expression of aquaporin genes; establishes cell-to-cell communication and allows the diffusion of H_2O_2 through the cell membrane which contributes to better and synchronized seedling emergence [36, 48]. The diffusion of ROS across the seeds can be interlinked with the phytohormonal GA/ABA balance (enhanced GA accumulation and lower ABA formation) which is considered to be indispensable for degradation of starch and initiate germination of the embryo. Though phytohormones including ABA and auxin have no positive impact on the germination of nano-primed seeds but they have been found to aid the attachment of nanoparticles to the seed coat [46]. Nano-priming has been recognized for its ability to enhance root development which eventually facilitates efficient nutrient uptake and mobilization within the plants. Moreover, they assist the activity of enzymes associated with increased nutrient accessibility and boost crop productivity [8].

The merits of nano-priming have further intrigued researchers to investigate targeted and sustained delivery of essential nutrients through nano-priming for growth promotion in plants. These nano-micronutrients have been found to improve the germination percentage, seedling emergence rates, seedling vigor, photosynthetic activity, carbon and nitrogen assimilation, antioxidative machinery, and even support reproductive growth. Among the several nano-micronutrients, Zn and Fe have been used extensively in various forms (Zinc oxide, Zerovalent Iron, Fe_3O_4, FeS_2, etc.), concentrations, in different plant species (like rice, wheat, capsicum, maize, etc.).. Zn and Fe, both are responsible for maintenance of several important physiological functions in plants like photosynthesis, nitrogen assimilation, respiration and DNA metabolism [14], Priming of seeds by

Fig. 1 Bar graph representing the number of articles published related to nano-priming in the last 5 years (Data *source*: PubMed)

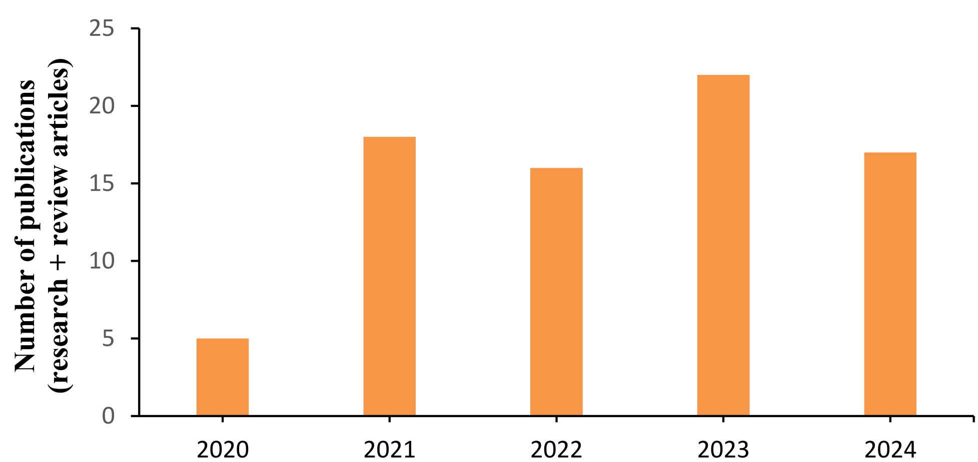

Table 1 Summary of reports highlighting the application of nano priming for promoting germination, seedling emergence, and overall plant health (arrowheads indicate ↑ increment and ↓ reduction in physiological and biochemical parameters)

Nanoparticles	Plants	Treatment conditions	Result achieved	Refs.
ZnO NP Diameter: ≤ 10 nm	*Oryza sativa*	Concentration: 10 µM (Applied singly and in combination with 50 µM of sodium selenite and sodium selenate) Soaked for 24 h	Germination ↑ Seedling vigor ↑ Total chlorophyll, phenol, and soluble protein contents of seedlings ↑ Nutrient uptake ↑ Yield parameters ↑ Grain Yield ↑	[5]
ZnO NP	*Triticum aestivum*	Concentration: 5, 10, 15, 20 mg/L Soaked for 18 h	Germination percentage (100%) Germination rate ↑ Growth ↑ α-amylase activity ↑ Chlorophyll content ↑ CAT ↑ and SOD ↓ activity Oxidative stress ↓	[64]
ZnO NP Diameter: 20 nm	*Zea mays*	Concentration: 20, 40, 80, 160 mg/L Soaked for 8 h	Germination rate ↑ Growth ↑ Biomass ↑	[20]
ZnO NP Diameter: 20, 40, 60 nm	*Phaseolus vulgaris*	Concentration: 1, 10, 100, 1000 & 5000 mg/L Soaked for 20 min	Biomass ↑ Zn content ↑	[73]
ZnO NP Diameter: 12–20 nm	*Capsicum annuum*	Concentration: 100, 200 & 500 ppm Soaked for 72 h	Seed germination ↑ Seed vigor ↑ Secondary metabolites ↑	[24]
FeO NP (Biosynthesized from *Cassis occidentalis* flower extract) Diameter: 28 nm	*Oryza sativa*	Concentration: 20 and 40 mg/L Soaked for 24 h	Germination rate ↑ Growth ↑ α-amylase activity ↑ Total soluble sugar ↑ SOD, CAT, APX ↑ Nutrients like Fe, Zn, K, Ca, and Mn content ↑	[39]
FeNPs (Biosynthesized from onion extract) Diameter: 19–30 nm	*Citrullus lanantus*	Concentration: 20, 40, 80, 160 mg/L Soaked for 14 h	Non-enzymatic lipophilic antioxidant activity ↑ Chlorophyll a and b content ↑ 12-oxophytodienoic acid content (OPDA) (3 days seedlings) ↑ OPDA and (Jasmonic acid) JA levels ↑	[44]

Table 1 (continued)

Nanoparticles	Plants	Treatment conditions	Result achieved	Refs.
Nanopyrite (nano FeS_2) Diameter: 5–10 nm	*Cicer arientinum*	Concentration: 100 µg/ml	Plant root and shoot length ↑ Root nodules ↑ Yield ↑ Macro and micronutrient content ↑	[41]
Nano-zero valent Fe (nZVI) Diameter: 33.8 ± 3.59 nm	*Oryza sativa*	Concentration: 10, 20, 40, 60, 80, 160 mg/L Soaked for 72 h	At 20 mg/L, Water imbibition % ↑ α-amylase, protease activity ↑ (maximum at 24 h and 48 h respectively) Plant growth, RWC% ↑ Photosynthetic pigment content ↑ MDA, Proline content in seedlings ↓ SOD, CAT, POD activity in seeds ↑ and seedlings ↓ Cell death ↓ Root dehydrogenase activity in seeds and seedlings↑	[31]
PEG-coated and uncoated Fe_3O_4 NPs Diameter:12 nm (PEG-coated Fe_3O_4 NPs) and 11 nm for uncoated Fe_3O_4 NPs	*Phaseolus vulgaris*	Concentration: 1, 10, 100, 1000 mg/L Soaked for 120 h	Germination % ↑ Radical length ↑ (in PEG-coated FeNPs) Fe uptake ↑	[15]
SeNP (Biosynthesized from raisins of *Vitis vinifera* L. extracts)	*Oryza sativa* L	Concentration: 20 µM, 25 µM Soaked for 24 h	Percentage of water imbibition↑ α amylase activity ↑ Total soluble sugar content↑ and starch content ↓ Embryo viability ↑ Seedling growth ↑ ROS ↑ SOD, CAT, APX ↑	[75]

Table 1 (continued)

Nanoparticles	Plants	Treatment conditions	Result achieved	Refs.
Mn_2O_3 NPs Diameter: 30 nm	*Artemisia annua*	Concentration: 25, 50, 100 mg/L Soaked for 3 and 6 h	Germination index and percentage ↑ RWC% ↑ Photosynthetic pigment content ↑ MDA, H_2O_2 content ↓, and proline content ↑ Protein content maximum at 120 days SOD, APX activity ↑ PPO activity ↓ (up to 60 days) ↑ (till 90 days) Phenol content initially ↓ later ↑ at 120 days Flavonoid content ↑	[69]
MnO NP (Biosynthesized from onion bulb extracts) Diameter: 22–39 nm	*Citrullus lanatus*	Concentration: 10, 20, 40, 80 mg/L Soaked for 14 h	Germination rate ↑ Total chlorophyll content ↑ DPPH, ABTS activity ↑ Phytohormones (ABA, GA, SA, ZA, OPDA) ↑ Metabolites content ↑	[45]
SiO_2 NPs $nSiO_2$(I) Diameter: 128 nm $nSiO_2$(II) Diameter: 248 nm	*Stevia rebaudiana* Bertoni	Concentration: 1, 5, 10, 25, 50, 100 ppm Soaked for 20 h	Germination %, vigor index ↑ Seedling dry weight ↑ α-amylase activity ↑ Starch and sucrose content ↑ H_2O_2 content at low conc. ↓ and at high conc. ↑ CAT, POX activity ↑	[36]
MgO NPs Size:2–5 nm	*Brassica juncea*	Concentration: 10, 50, 100, 150 μg/ml Soaked overnight	In one-month-old plants: Plant growth, leaf area, fresh biomass↑ Photosynthetic pigment content and carbohydrate content ↑ Total phenolics and flavonoid content ↑ Total grain yield, pod and seed size ↑ APX, CAT, SOD and Free radical scavenging activity (FRSA) ↑ From plants obtained by harvesting nano-primed seeds: Carbohydrate, and protein content ↑ Oxidative stress ↓, FRSA, phenolics ↑	[25]

Table 1 (continued)

Nanoparticles	Plants	Treatment conditions	Result achieved	Refs.
MgO NPs (Biosynthesized from *Syzygium aromaticum* extracts) Size: 2–5 nm	*Cicer arientinum*	Concentration: 10, 50, 100, 150 µg/ml Soaked overnight	Fresh biomass and RWC% ↑ Chlorophyll and carotenoid content↑ Total carbohydrate content ↑ Total phenol and flavonoid contents ↑ Free radical scavenging activity↑ SOD, CAT, APX ↑ Total soluble protein content ↑	[79]
CuNP, AgNP and Cu-AgNP Size: CuNP:66-86 nm AgNP:25–35 nm Cu–AgNP:35–50 nm	*Capsicum spp.*	Concentration: 1, 10, 20 ppm Soaked for 24 h	Germination rate ↑ Total chlorophyll and carotenoid content ↑ Antioxidant activity ↑ Total phenolic and flavonoid content ↑	[56]
Alfalfa extracts capped and light-induced AgNPs (Biosynthesized from alfalfa extracts) Particle Size: 50–55 nm Crystal size of pink AgNPs: 39.17 nm	*Medicago sativa*	Concentration: 12.5, 25, 50, 100, 200 mg/L Soaked for 3 h	Water uptake rate ↑, α-amylase activity ↑ and altered morphology of seed surface ↑ Germination rate, germination index, and seedling vigor index I and II ↑ Root, shoot length ↑ Root dehydrogenase activity ↑ Cell death ↓ at lower conc. of NPs and ↑ at high conc. of NPs Chlorophyll content ↑ MDA content ↓ till 12.5 mg/L NPs, proline content ↑ (25 mg/L) SOD, POD, CAT activity ↑ At low conc. of NPs: Ag^+ content in shoots > roots At high conc. of NPs: Ag^+ content in roots > shoots	[85]
AgNPs and TiO_2 NPs (Biosynthesized from *Trichoderma citrinoviridie*) AgNPs Diameter: 50–100 nm TiO_2 NPs Diameter: 10–400 nm	*Solanum lycopersicum*	Concentration: 25, 50, 100, 200, and 400 µg/mL Soaked for 24 h	Germination %, vigor index, Chlorophyll a content ↑ at low conc Carotenoid content ↑ Protein and proline content ↑ SOD, CAT, POD activity ↑	[84]

Table 1 (continued)

Nanoparticles	Plants	Treatment conditions	Result achieved	Refs.
Ag NP (Biosynthesized from onion peel extract) Diameter: 29 nm	*Citrullus lanatus*	Concentration: 31.3 ppm Soaked for 12 h, dried and germinated	Germination percentage ↑ Growth ↑ Phenol & ROS scavenging activity (-) Yield (31.6%) ↑ Macro- & micro-nutrient (-)	[4]
Ag and Au NP (Biosynthesized from onion peel extract) Diameter: Ag NP: 19–37 nm, Au NP: 30–113 nm	*Allium cepa*	Concentration: Ag NP: 31.3 ppm, Au NP: 5.4 nm Soaked for 12 h and germinated	Germination percentage ↑ Growth ↑ Yield (23.9%) ↑ Chlorophyll content ↑ Pungency ↓ Superiority: Au > Ag	[3]
AgNP Diameter: 40 ± 2 nm	*Vicia faba*	Concentration: 10, 50, 100 mg/L Soaked for 6 h, germinated directly	Antioxidant ↑ Mitotic index ↑ Genotoxic, mutagenic aberrations ↓ Seedling vigor ↑	[94]
AgNP Diameter: 40 ± 2 nm	*Vicia faba*	Concentration: 10, 50, 100 ppm Soaked for 6 h, germinated directly	Soluble sugar ↓ Photosynthetic pigment ↑ Starch accumulation ↑ Changes in chloroplast ultrastructure	[1]
AgNP (Biosynthesized from Kafffirlime leaf extract) Diameter: 6–36 nm	*Oryza sativa* L. cv. KDML 105	Concentration: 10, 20 ppm Soaked for 24 h, germination after surface drying	ROS ↑ Water uptake ↑ Aquaporin ↑ Antioxidants ↑ Amylase ↑ Germination ↑ Seedling vigor ↑	[53]
PVP-coated PtNP Diameter: 3.2 ± 0.8 nm	*Pisum sativum*	Concentration: 1 mM Pt NP Soaked for 1, 2 & 3 h	Fruit number ↑ Seed number ↑, weight ↓ Biomass ↑ Colonization of Arbuscular Mycorrhizal Fungi ↓ Seed germination ↓	[63]
MWCNTs Diameter: 6.6 nm	*Pennisetum glaucum*	Concentration: 30, 60, 90, 120, 150 ppm Soaked for 24 h	CAT, POD, SOD activity ↑ Enzyme activities at 120, 150 mg/L ↓ DPPH free radical scavenging ability ↑	[78]

Table 1 (continued)

Nanoparticles	Plants	Treatment conditions	Result achieved	Refs.
Carbon nanotubes and graphene Diameter of carbon nanotubes: 30–50 nm Diameter of graphene: 2 µm	*Solanum lycopersicum*	Concentration: 10, 100, 250, 5000, 1000 mg/L Soaked for 24 h	Chlorophyll content ↑ H_2O_2 content ↓ Vitamin C, GSH, phenol, flavonoid, β-carotene content ↑ (superior in graphene 1000 mg/L) DPPH activity ↓ SOD, CAT, GPX activity ↑ APX, PAL activity ↓	[51]
MWCNTs	*Momordica charantia*	Concentration: 50, 100, 200 mg/L. Cold plasma:0.84W/cm^2 Soaked for 48 h	Growth parameters ↑ Uptake of CNTs ↑ when co-applied with cold plasma Diameter of metaxylem ↑ Reproductive ability (flower number, floral diameter) ↑ Floral emergence time ↓	[74]
Chitosan NPs containing Cu^{2+} (NP Cu), Chitosan NPs Hydrodynamic size: 174.2 ± 1.5 nm	*Zea mays*	Concentration: 0.0625 mM/L Cu^{2+}	Shoot length, leaf area, shoot dry weight ↑ In accelerated-aged seeds Germination % ↑ MDA content↓ SOD, APX, POD activity↑ CAT activity ↓	[26]
Chitosan NPs Diameter: 80–200 nm	*Triticum aestivum*	Concentration:1, 5, 10, 50, 100 µg/ml Soaked for 8 h	Germination percentage ↑ Root, shoot length, and no. of adventitious root ↑ Chlorophyll content and soluble protein content ↑ IAA content in roots and shoot ↑ Transcript levels of YUCCA, ARF ↑ in roots and shoots Transcript of AUX1 in shoots ↑ and ↓ roots non-significantly	[48]

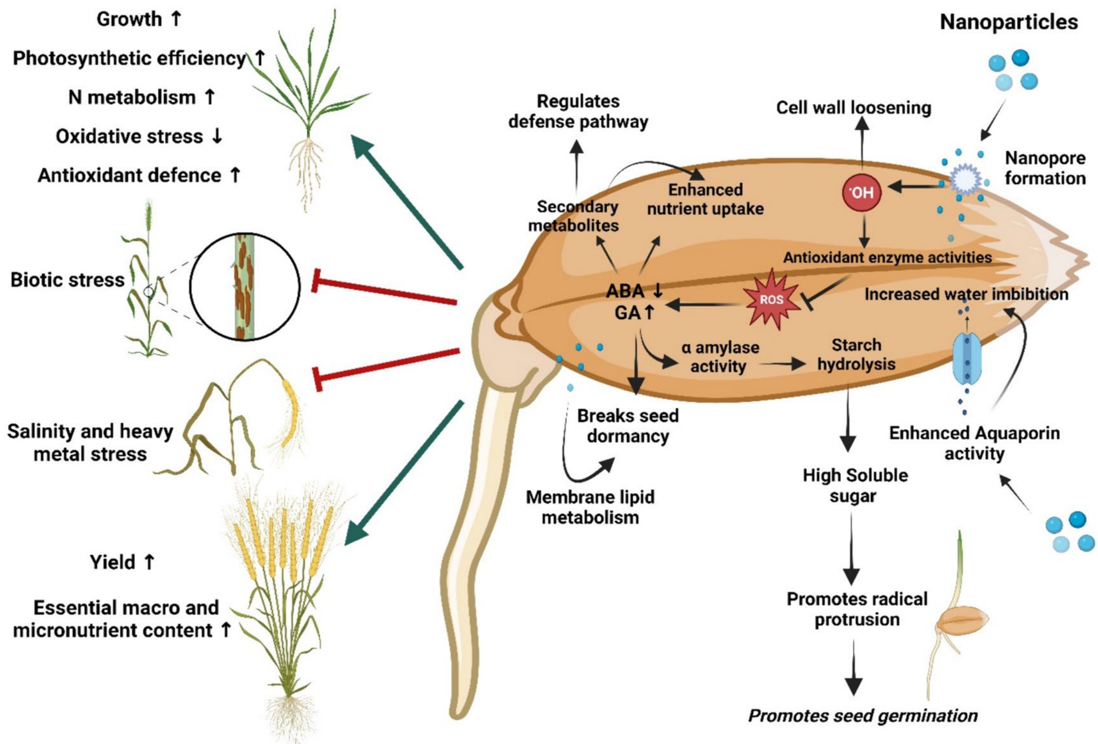

Fig. 2 Mode of action of nano-priming induced germination, growth, and stress resistance in plants. Nano-priming provides a 'headstart' to the seeds that promote germination and plant growth. It also 'prepares' the plant for future incidences of abiotic and biotic stress. NPs usually diffuse across the seed coat or create nanopores which facilitate their uptake into the seed. As soon as nanoparticles enter the seed, they can enhance the aquaporin gene expression which positively influences the uptake of water. NPs also initiate ROS formation at an optimum level which is regulated by elevated enzymatic antioxidative activities and they tend to act as a signaling molecule to activate GA and downregulate ABA synthesis. GA directly upregulates α-amylase activity and allows starch hydrolysis into soluble sugar which is indispensable for seed germination. This eventually leads to improvement in physiological parameters associated with growth. NP priming also activates the defense system against abiotic and biotic stress in plants by accumulation of secondary metabolites and strengthening the antioxidant system

these nutrients impart a plethora of advantages to the plants. Nano-Nutri-priming is therefore a beneficial and sustainable approach to boost plant growth compared to their bulk counterparts [31, 37, 40, 60, 62, 64]. Often the beneficial effects of nano-nutrients depend on the rate of biotransformation of NPs into organically bound nutrients within plant cells and can be governed by the shapes, dimensions, and surface charge of NPs [64]. In addition, nano-macronutrients have also been utilized as efficient seed-priming agents to enhance biochemical parameters for overall growth and productivity [70]. However, it is imperative to assess the optimum concentration of NP to be used as a priming agent because NPs in large concentrations can result in toxicity [31]. Besides, an excess of one nutrient is often known to interact and inhibit the uptake of other essential nutrients. These should be taken into consideration before implementing nano-priming to ensure optimum results.

NPs synthesis also plays a pivotal role in ensuring proper nutrient delivery with minimal environmental residue. The coating material, thus, plays a crucial role in determining the efficacy of NPs. PEG-coated NPs are superior to other NPs in promoting germination and supplementing nutrients due to the hydrophilic nature of PEG, which makes them incapable of interacting with cell membranes and plant proteins, thus eliminating the chances of toxicity. PEG coating also helps water uptake by seeds and prevents the amalgamation of NPs that can otherwise restrict their usual functions [64]. Nano-priming has also provided exemplary results in field experiments. Wheat seeds treated with Fe_2O_3 NPs not only promoted seedling growth, vigor, and photosynthetic efficiency but also accelerated nutrient absorption by plants which eventually led to the biofortification of grains with Fe [77]. Similar results have been documented with rice [30]. But still, most of the reports on Nano-Nutri-priming are limited to the laboratories and lack proper field trials to validate the findings. While seedling performance is improved with nano-priming, it is also pertinent to assess whether the effect is persistent till maturity.

Besides the nutrients known to have significant roles in plants, some elements that are not utilized by plants directly, have also been tested as priming agents viz. Ag, Au, Ti, and Pt. These metals are biologically nonessential for plants as they are not required for their growth or maintenance but owing to their antioxidative potential and free radical scavenging activity they have been implemented to combat several abiotic and biotic stress incidences. For example, AgNPs reportedly augment photosynthetic activities by altering chloroplast ultra-structures [1], AuNPs increase the germination rate, overall growth of plant morphologically, chlorophyll content and yield by 23.9% [3], and TiO_2 NPs increased seedling vigor, water content of leaves and antioxidant enzyme functioning in maize [39].

In recent decades carbon nanomaterials (CNMs), including single-walled carbon nanotubes (CNTs) (SWCNTs), multi-walled carbon nanotubes (MWCNTs), graphene (GR), and fullerenes have been reported to aid plant growth and can generate multiple responses which can also lead to increased stress tolerance [46]. MWCNTs alone or synergistically with cold plasma exposure can induce the xanthophyll cycle (β-carotene, α carotene, zeaxanthin, and lutein) to protect the photosynthetic machinery and improve the photosynthetic activity; enhance carotenoid content and upregulate the genes associated with terpenoid metabolism [74].

Chitosan nanoparticles have also become quite relevant in the agricultural sector due to their non-toxic, biocompatible properties, prolonged stability, and better delivery of micronutrients in plant tissues thus enhancing their efficacy in metabolic activities. Chitosan nanoparticles have shown promising effects on seed germination and at the same time enhanced plant photosynthetic efficiency and chlorophyll contents. NP priming with chitosan also increased auxin levels by upregulation of auxin synthetic genes [44]. Copper-loaded chitosan nanoparticles also found to have a profound role in promoting germination, seedling length, photosynthesis, and enhanced activity of enzymatic antioxidants in comparison to hydro-primed seeds [25].

Thus, the ability of nano-priming to serve as a propitious growth enhancer is quite evident from the previous discussions. However, most of such advancements are limited to preliminary laboratory findings and require proper validations through field trials for commercialization or agronomic use. Besides, another key determinant is the nutritional profiling of the product obtained through seed priming as well as analyzing its safety levels for consumption.

Abiotic stress management

Abiotic factors such as climate fluctuations, soil conditions, nutrient availability, and heavy metal contamination have inflicted dreadful impacts on the growth, development, and yield of plants. Hence to bridge the gap between population growth and food production, stress tolerance of crop plants must be improved. In this respect, nanotechnology can play a huge role in crop improvement through the alleviation of stresses. Seed priming can ameliorate adverse effects of abiotic (drought, salinity, flooding, heat, cold, heavy metal) stress in plants by triggering antioxidant metabolism, accumulation of non-enzymatic antioxidants, imparting stress memory and synthesis of stress proteins like late embryogenesis abundant (LEA), dehydrin and aquaporin (AQP) [36]. Among several abiotic stresses that can be mitigated through nano-priming, salinity, and heavy metal stress have been highlighted in detail.

Salinity stress

Globally around 20% of cultivated land and 33% of irrigated land have been ruthlessly affected by salinity stress which has raised a lot of concerns regarding global food security [12]. Salinity stress has been characterized by an exorbitant rise in Na^+, Cl^- ions in the soil which eventually alters soil porosity, and hydraulic conductivity and lowers the osmotic potential of soil. The toxic concentration of ions significantly alters the ionic balance, membrane stability and leads to rapid loss of water from cells [34] This leads to physiological conditions analogous to drought which is also delineated by restricted uptake of essential ions and minerals crucial for growth and development. In addition, salinity stress instigates ROS accumulation which triggers the destruction of proteins, nucleic acids, and lipids. The water deficit intervenes stomatal conductance thus hampering the photosynthetic activities and other associated parameters. Plants have an intrinsic defense mechanism that allows them to amplify the synthesis of osmotic solutes, endogenous hormones (ABA, BR, SA, GA), antioxidative capacity, compartmentalize ions, release secondary metabolites to lessen toxicity, and even interact with plant growth promoting rhizobacteria (PGPR) [22, 59, 82]. Depending upon the concentration of solute and the genetic potential of plants, the expression of stress resistance genes is upregulated to acclimatize themselves to the severity of stress [32].

Nanoparticles have been accredited for their profound role in salinity stress amelioration in plants. Metal oxide NPs, metal NPs, carbon nanomaterials, and nanocomposites have been utilized for the same owing to their ability to maintain ion homeostasis, induce an influx of K^+, regulate water absorption as well as upregulate the expression of genes like NHX1 (Na^+/H^+ antiporter) for sequestration of excess Na^+ in the vacuoles [21, 82]. Besides, they increase stomatal conductance, chlorophyll content, activity of enzymes (RuBisCo, carbonic anhydrase) and maintain the ultrastructure of chloroplasts, thus enhancing the photosynthetic efficiency. This subsequently prompted nano-priming with essential micronutrients to boost germination, enhance radical and plumule growth, lateral root formation, and enzymatic antioxidant activities (SOD, POD, CAT) to minimize the detrimental effects of ionic imbalance (Fig. 2) [36]. The mechanism of action of nanopriming in salinity stress extends to balancing reactive oxygen species production and enzymatic antioxidant activity, thereby enhancing the ability of plants to withstand water deficit conditions [60]. Nano-priming promotes α-amylase activity, GA synthesis, aquaporin gene expression, free amino acid, and plasma membrane lipid content as well as restricts the ABA levels to elevate the imbibition of water which eventually supports germination [18]. Therefore, Zn [17], Fe, Se [16], Si [56], and Mn [86] NPs have been utilized successfully to alleviate salt stress. Nanoparticles are often coated with plant extracts, phytohormones, and amino acids which impart stability and biocompatibility to NPs. The capping agents tend to alter the surface properties and pore space which makes them efficient for environmental stress remediation. For example, *Vigna radiata* L. seeds primed with glutamic acid-coated FeNPs regulated growth under salinity stress by facilitating antioxidant enzyme activities and osmolyte content. Glutamic acid has been speculated to have a crucial role in photosynthesis and nitrogen metabolism which was substantiated by improved chlorophyll content, morphological attributes, and yield [79].

Besides being potential growth regulators, Ag and Ti have been perceived for their response to osmotic stress. Nano-priming wheat and pearl millet with an optimum concentration of AgNPs increases tolerance to stress by increasing photosynthetic efficiency, reprogramming phytohormonal balance, decreasing Na^+/K^+ ratio, and enhancing secondary metabolite production [2, 41]. Ti_2O NPs have also been recognized for their enzymatic antioxidant activity to scavenge ROS, increase K^+ and phenolics content as well as reduce MDA and Na^+ levels thus maintaining membrane stability [68].

To date, chitosan NPs have been well acclaimed as a biostimulant and elicitor as they assist the defense mechanism as well as regulate associated signal transduction pathways under salinity stress. They modulate enzymatic antioxidants, secondary metabolite production, and enzymes corresponding to their synthesis. Nanopriming Cu-chitosan NPs has been effective in wheat seedlings by boosting chlorophyll content, sugar levels, α-amylase, and SOD activity [23]. Chitosan nanoparticles loaded with curcumin too have been ascertained to counteract the toxic effects of salinity stress in wheat owing to the growth-enhancing properties of chitosan and the antioxidative activity of curcumin [33].

The constructive purpose of carbon nanomaterials to combat salinity-induced water deficits has also been verified by their antioxidative potential and enhanced osmolyte levels. This eventually aided nutrient uptake, maintenance of osmotic potential, and membrane integrity. For instance, polyhydroxy fullerene nanoparticles (PHF) and carbon nanotubes, graphene can easily mitigate oxidative stress generated by toxic Na^+ concentrations in wheat and tomato respectively [26, 67].

Thus, nano-priming has emerged as a successful and sustainable alternative to bulk chemicals for imparting salinity stress tolerance to plants for efficient agriculture (Table 2). To date, micronutrients and metal NPs have been exploited for the same but the application of macronutrients still needs to be investigated. However, it is obligatory to assess the benefits of nano-priming in salinity stress alleviation through field experiments for implementation on a larger scale.

Heavy Metal Stress

Heavy metal contamination in soil has raised a lot of concerns in the agricultural sector due to its deep-rooted negative impact on the overall growth and development of plants. Non-essential heavy metals like Pb, Cr, Cd, and As are accumulated in the soil owing to several anthropogenic activities and natural disasters which inevitably hamper the productivity and quality of yield of commercially important crops. These metals get easily transported into the plant utilizing the transporters, channel proteins, and pathways responsible for the uptake of vital micronutrients like Fe, Zn, etc. owing to their analogous chemical structure. Their aggravated content not only affects the physiological and metabolic activities of a plant but can also cause potential harm to human beings. Therefore, amelioration of heavy metals in plants and reducing the health risk factors associated with the consumption of heavy metal-contaminated crops becomes the need of the hour. NPs are widely known to reduce heavy metal toxicity by reducing the bioavailable metals in soil, regulating the expression of genes associated with transport, and enhancing the antioxidative machinery as well as secondary metabolic pathways. Foliar spraying and root application of various metal oxide NPs were found to be effective in minimizing the adverse effects of heavy metals by upregulating the transport of essential nutrients and decreasing the translocation of heavy metals by adsorption. Apart from two common approaches, nano-priming has also grabbed a lot of attention for not only reducing heavy metal content in plants but also rescuing the yield-related parameters (represented in Table 3) [8, 23]. It has been established that seed priming with metal oxide NPs can promote the formation of a complex with the metal and the synthesis of metallothionine which eventually forms a complex with the heavy metals to restrict their uptake and translocation (Fig. 2) [45]. They even promote the antioxidative machinery to detoxify ROS produced excessively, maintain the ionic homeostasis of the cells as well as promote photosynthetic activity to induce tolerance against metal toxicity [36]. The reduced rate of germination in toxic metal-contaminated soil can even be

Table 2 Summary of reports highlighting the benefits of nano-priming in salinity stress alleviation (arrowheads indicate ↑ increment and ↓ reduction in physiological and biochemical parameters)

Nanoparticles	Plants	Treatment conditions	Results achieved	Refs.
ZnONPs Diameter: 20 nm	*Brassica napus*	Concentration: 25, 50, 100 mg/L with 150 mM NaCl Soaked for 8 h	Germination rate and final germination percentage↑, RWC% ↑, Photosynthetic pigment↑, Soluble sugar content↑, Oxidative stress↓, proline↑, K^+↑, Na^+ ↓, Ca^{2+}↑, Zn^{2+}↑, SOD↑, CAT↑, APX↑, Linolenic and Linoleic acid content in nano-primed seeds↑, Expression of *BnCAM* and *BnPER* genes↑	[18]
SeNPs and ZnONPs Diameter of SeNPs: 10 to 55 nm, Diameter of ZnONPs: ~20 nm	*Brassica napus*	Concentration of SeNPs: 150 µM/L with 150 mM/L NaCl Concentration of ZnONPs: 100 mg/L with 150 mM/L NaCl Soaked for 8 h	Germination rate and final germination percentage↑, Plant growth↑, In SeNPs: SOD↑, POD↑, APX↑, CAT↑, In ZnONPs: SOD↓, POD↓, APX↓, CAT↑, Protein metabolism↑, *BnGA20ox*↑, *BnGA3ox*↑, *BnCAM*↑, *BnRAB28*↑, *BnEXP4* genes↑, *BnPER*↓, *BnCYP707A1*↓, *BnCYP707A3*↓, *BnCYP707A4*↓, *BnCPS*↓ (during germination)	[17]
Bio SeNPs	*Brassica napus*	Concentration: 150 µM/L with 150 mM/L NaCl Soaked for 8 h	Water uptake↑, Imbibition potential↑, Seed germination↑, α-amylase activity↑, Free amino acids↑, Enzymatic and non-enzymatic antioxidants↑, ROS scavenging activity↑ Expression of aquaporin genes (*BnPIP1-1* and *BnPIP2-1*)↑, Na^+ levels↓ Photosynthesis↑, biomass↑	[16]
Glutamic-Acid-Functionalized Iron Nanoparticles (Glu-FeNPs) Diameter: 23–52 nm	*Vigna radiata*	Concentration: 150 mg/L with 40, 60, 80 mM NaCl Soaked for 5 h	Root and shoot length↑, Biomass↑, moisture content↑, leaf area↑, Chlorophylls↑, Carotenes↑, Proteins↑, Sugar↑, Proline↑, SOD↑, POD↑, Number of pods↑	[87]
MnNPs Diameter: 50 nm	*Capsicum annuum*	Concentration: 0.1, 0.5, 1 mg/L with 100 mM NaCl Soaked for 4-6 h	Root elongation↑, Na, K, and Ca in shoot↑, MnSOD expression ↑	[93]
AgNPs Diameter: 50–100 nm	*Pennisetum glaucum*	Concentration: 10, 20 and 30 mM with 0, 120, 150 mM NaCl Soaked for 20 h	Plant growth↑, RWC↑, Biomass↑, MDA↓, H_2O_2↓, Proline content↓, SOD↑, CAT↑, GPX↑, GR↑, POD↑, Phenol content↑, Flavonoid content↓, K^+↑, Na^+↓, Na^+/K^+ ratio↓	[46]
AgNPs (Biosynthesized from *Capparis spinosa* L.) Diameter: 15–30 nm	*Triticum aestivum*	Concentration: 1 mg/L with 25 mM and 100 mM NaCl Soaked for 24 h	Germination percentage↑, Root and shoot length↑, Biomass of root and shoot↑, Photosynthetic pigments↑, Chlorophyll Stability Index↑, Chlorophyll fluorescence↑, Auxin (1-Naphthalene acetic acid and Indole- 3-butyric acid)↑, Cytokinin (Benzylaminopurine)↑, ABA↓	[2]
TiO_2NPs Diameter: 10–25 nm	*Zea mays*	Concentration: 40, 60, 80 ppm with 200 mM NaCl Soaked for 24 h	Germination percentage↑, Germination energy↑, Mean emergence time↑, Seedling vigor index↑, Root and shoot length↑ Fresh and dry weights of seedling↑, RWC↑ Proline↑, Total phenolics↑, SOD↑, CAT↑, PAL↑, K^+↑, Na^+↓, Membrane electrolyte leakage↓, MDA↓	[77]

Table 2 (continued)

Nanoparticles	Plants	Treatment conditions	Results achieved	Refs.
Chitosan NPs encapsulated with curcumin Diameter: ~ 50 nm	*Triticum aestivum*	Concentration: 0.02 and 0.04% with 150 mM NaCl Soaked for 8 h	Final germination↑, Vigor↑, Germination index↑, Mean germination time↓, Photosynthetic pigments↑, Lycopene↑, Tannins↑, Flavonoids↑, Protein↑, CAT↑, POD↑, APX↑, SOD↑	[35]
Cu-Chitosan NPs Diameter: 19–21 nm	*Triticum aestivum*	Concentration: 0.12% and 0.16% with 150 mM NaCl Soaked for 8 h	Root and shoot length↑, Total protein and soluble sugar content↑, α-amylase activity↑, Protease activity↑, Chlorophyll a, b, total carotenoids, and β carotene content↑, MDA and total phenolic content↓, SOD↓, POD↓, CAT ↑	[23]
Plastic derived Carbon nanomaterials (CNMs)- Carbon Dots (CDs) and Carbon Nanotubes (CNTs) Diameter of CNMs: 10–40 nm, Diameter of CD: 10 nm	*Pisum sativum*	Concentration: 0.25 and 0.75 mg/ml with 200 mM NaCl Soaked for 8 h	Seed water uptake↑, Seed germination↑, Root-shoot elongation↑, Biomass↑, Photosynthetic process↑, Carbohydrate accumulation↑, Na^+↓, Na^+/K^+ ratio↓, Membrane integrity↓, Root vitality↑, Proline content↑, Antioxidants enzymes activity↑	[50]
Carbon nanoparticles (CNPs) Diameter: 20–130 nm	*Raphanus sativus*	Concentration: 80 mM with 25 mM NaCl Soaked for 12 h	Seed sprouting↑, Biomass↑, pigments content↑, Anthocyanin↑, Phenylalanine↑, Cinnamic acid↑, Coumaric acid↑, Naringenin↑, Chalcone synthase↑, Cinnamate-4-hydroxylase↑, 4-coumarate:CoA ligase↑, Proline↑, P5CS↑, PRODH↑, Sucrose↑, Sucrose P synthase↑ and Invertase↑, Polyamine metabolism↑, Polyphenol↑, Flavonoids↑, Enzymatic antioxidant activity↑, Phenylalanine ammonia lyase↓	[34]
Carbon nanomaterials (CNT) and graphene (GP) Diameter of CNTs: 30–50 nm, Diameter of GP: 8–12 nm	*Solanum lycopersicon*	Concentration: 50, 250, and 500 mg/L with 50 mM NaCl Soaked for 24 h	Photosynthetic pigments↑, Ascorbic acid↑, Glutathione↑, Protein↑, Phenols↑, Flavonoids↑, CAT↑, APX↑, GPX↑, PAL↑, Electrical conductivity↑, Oxidation–reduction potential↑, Total soluble sugars↑, Titratable acidity of fruits↑	[27]
Polyhydroxy fullerenes nanoparticles (PHF)	*Triticum aestivum*	Concentration: 10, 40, 80, and 120 nM with 150 mM NaCl Soaked for 10 h	Root-shoot length↑, Plant biomass↑, Chlorophyll content↑, Free amino acids↑, Soluble sugars↑, K^+↑, P↑, MDA↓, H_2O_2↓ Ascorbic acid↑, SOD↓, CAT↑, APX↑, POD↑	[76]

Table 3 Summary of successful case studies highlighting the benefits of nano-priming in the remediation of heavy metal stress in plants (arrowheads indicate ↑ increment and ↓ reduction in physiological and biochemical parameters)

Nanoparticles	Plant system	Treatment conditions	Results achieved	Ref
Aspartic Acid-Based Nano-Copper (Asp-CuNPs) Diameter: 46–120 nm	*Zea mays*	Concentration: 1.0, 5.0, and 10 µg/mL of Asp-CuNPs with 0, 500, and 1000 mg/L Lead stress	Germination percentage↑, Germination time↓, Plant growth↑, Leaf area↑, Chlorophyll content↑, SOD↑, POD↑, APOX↑, ROS↓, Pb content↓	[88]
TiO_2 NPs singly and in combination with *Bacillus mycoides* PM35	*Hordeum vulgare*	Concentration: 25, 50 µg/ml TiO_2 NPs and 10, 20 µl of *Bacillus mycoides* PM35 with 0, 50, 100 mg/Kg Cadmium stress Soaked for 24 h	Plant height, fresh and dry weight, leaf area↑, Chlorophyll, carotenoid content, net photosynthetic rate, transpiration rate, stomatal conductance, intercellular CO_2 conc. ↑, MDA content, electrolyte leakage ↓	[52]
ZnONPs Diameter: 20 nm	*Zea mays*	Concentration: 500 mg/L ZnONPs with 300 µM Cobalt stress Soaked for 24 h	Plant growth↑, Biomass↑, Photosynthetic rate↑, SPAD value↑, Chlorophylls content↑, transpiration rate↑, stomatal conductance↑, Intracellular CO_2 concentration↑, SOD↑, CAT↑, APX↑, ROS↓, MDA↓, Co↓, Zn↑, Improvement in stomatal aperture and ultrastructure of cell organelles	[68]
ZnO and Fe_3O_4 NPs Diameter: ZnONPs is ~ 193 nm and Fe_3O_4 NPs is ~ 210 nm	*Basella alba*	Concentration: 50, 100, 200, 300 and 500 mg/L ZnONPs and Fe_3O_4 NPs with 2, 4, 6, 8, 10, 15, 20 mM Lead stress Soaked for 16 h	Seed germination↑, Seedling vigor↑, Root and shoot length↑, Biomass↑, ROS↓, MDA↓, H_2O_2↓, Proline↑, SOD↑, CAT↑, POD↑, Pb accumulation↓	[33]
Titanium dioxide (TiO_2 NPs)	*Coriandrum sativum*	Concentration: 40, 80 and 160 mg/L TiO_2-NPs with Cadmium stress	Plant growth↑, Biomass↑, Chlorophyll content↑, Photosynthetic rate↑, Proline↑, Yield↑, Electrolyte leakage↓, MDA↓	[71]
Multiwall carbon nanotubes (MWCNTs) Inner diameter: 3 to 5 nm Outer diameter: 8–15nm	*Zea mays*	Concentration: 100, 200 mg/L MWCNTs with 100 and 200 mg/L cadmium stress Soaked for 24 h	Seed germination↑, Root- shoot growth↑, Fresh and dry biomass↑, SOD↑, CAT↑, POD↑, MDA↓	[8]
Polysuccinimide NPs (PSI-NPs) Size: 20.6 ± 0.6 nm	*Zea mays*	Concentration: 50, 100, 200, 400, 800 mg/L PSI-NPS with 5, 10, 20, 40, 80, 160 mg/L copper stress	Water uptake efficiency by seed↑, Seed germination percentage↑, Germination rate↑, Mean germination time↓, Root-shoot growth, Biomass↑, SOD↑, CAT↑, POD↑, Cu uptake↑	[91]
SiNPs	*Triticum aestivum*	Concentration: 300, 600, 900, 1200 mg/L SiNPs with 0.93 mg/kg soil available cadmium stress Soaked for 20 h	Shoot length↑, Biomass↑, Photosynthetic pigments↑, Transpiration rate↑, Stomata conductance↑, Electrolyte leakage↓, H_2O_2↓, MDA↓, CAT↑, SOD↑, POD↑, grain length↑, spike length↑, Spike dry weight↑ Si↑, Cd↓	[38]
ZnO and FeNPs Diameter of ZnONPs: 20–30 nm Diameter of FeNPs: 50–100 nm	*Triticum aestivum*	Concentration: 25, 50, 75, and 100 mg/L ZnONPs and 5, 10, 15, and 20 mg/L FeNPs with 0.93 mg/kg soil available cadmium stress Soaked for 24 h	Plant height↑, Root-shoot-spike-grain weight↑, Electrolyte leakage↓, Photosynthetic pigments↑, SOD↑, POD Cd↓, Zn↑, Fe↑	[67]

retrieved by these NPS as they accelerate α-amylase activity to break down starch, promote germination, and increase seedling vigor.

The antioxidative potential of Zn and Fe (as they serve as co-factors of several antioxidant enzymes) reportedly decreased the oxidative damage induced by Cd, improved the agronomic parameters, enhanced Zn, Fe content, and reduced Cd in vegetative parts as well as grains [30, 62]. It was also found to assist growth and maintain the metabolomic profile of fragrant rice varieties when subjected to Cd stress [45]. Besides, nano-priming reduces Cd accumulation and upregulates the pathways associated with purine, pyrimidine, amino acids, flavonoids, polyunsaturated fatty acids, and other metabolite biosynthesis. Atrocities involved with As stress can also be mitigated by nano-priming with Zn. Nano-priming increases germination percentage and seedling growth, reduces cell damage, and boosts antioxidant levels [6].

Silicon (Si), an essential component of plant cell walls often serves as the first line of defense against several abiotic and biotic stress factors. The role of Si in heavy metal toxicity amelioration has been confirmed by its ability to reduce the soil pH and reduce bioavailable heavy metal uptake into plants. Either independently or in congruence with other essential nutrients, metabolites, and hormones SiNPs can downregulate transporters responsible for their translocation from root to shoot and express genes responsible for heavy metal sequestration in cell vacuoles. These features led to further application of SiNPs in seed priming resulting reduction of Cd content in wheat grains and eventually improved morpho-physiological, photosynthetic, and yield-related parameters [35]. Application of nano-priming with MWCNT has also been established for the amelioration of Cd toxicity in plants [7]. Other NPs that have been used as priming agents against heavy metal stress include TiO_2NPs [47], polysuccinimide NPs [83], and aspartic acid-derived CuNPs [80].

Nano-priming in biotic stress amelioration

Biotic stress is an umbrella term that encompasses damage caused to crops by biotic agents such as fungi, viruses, bacteria, parasitic nematodes, insects, and weeds on other plants. Plants have developed sophisticated immune systems to fight against such biotic agents. Physical obstacles like waxes, dense cuticles, hairs, and special trichomes serve as the first line of defense to restrict pathogen entry [85]. However, pathogen invasion triggers varied immune responses in plants such as Hypersensitive Response (HR), Systemic Acquired Resistance (SAR), Induced Systemic Resistance (ISR) via activation of several mediators like Jasmonic Acid (JA), Salicylic Acid (SA), Ethylene (ET), Pathogenesis Related proteins (PR proteins) and secondary metabolites (tannins, alkaloids, phenols). Plants also restrict herbivory or growth of weeds in proximity by either secreting chemicals (allele-chemicals) or through specialized structures (thorns, raphides). Biotic stress leads to massive economic losses every year (20–40% yield loss worldwide). Among several approaches to control biotic agents, the most propitious ones to date have been chemical, biological, genetic, agricultural control, and integrated pest management. Chemical control (pesticide, fungicide, herbicide) is however the most preferred and convenient mode of control but is challenged by the increasing resistance of pathogens and residual effects on animals, humans, and the environment (soil and water contamination). Besides, climate change has confronted locally adapted crop genotypes with migrant pathogens, thereby introducing new biotic stress factors [53].

NPs can either function as nanocide, by killing or restricting the growth of phytopathogens or they might elicit a defense response in treated plants by upregulating responsive genes or triggering anti-oxidant enzyme activities. *In-vitro* assays demonstrate the efficacy of NPs in killing or inhibiting microbial growth whereas, in vivo*,* studies highlight the potential of NP-mediated seed priming in imparting enhanced disease resistance to the treated plants. Not necessarily, the NPs follow a particular mode of action, but rather different NPs, with characteristic functions might follow one or more of the above-mentioned routes alone or in combination. The mode of action of NPs as nanocides against seed-borne pathogens might be as follows:

- The NPs are known to interact directly with the walls of the microbes, resulting in ion uptake and cellular damage. Reports claim that most of the microbes have negative zeta potential compared to the employed NPs that possess a positive potential. These two opposing forces result in strong electrostatic attraction and powerful binding between the NP and the microbial cell. It has also been claimed that Gram-negative bacteria are more susceptible to NPs due to the presence of the external lipopolysaccharide layer imparting a negative charge to the cell [76]. However, other interactions such as receptor ligand, and hydrophobic interactions may serve as a potential cause.
- The second major cause of NP-mediated stress control could be due to ROS-induced cellular destruction. Uncontrolled ROS leads to cytotoxicity by inducing oxidative damage to the cellular proteins, membranes, and nucleic acid, thereby causing cell death [76].
- Inactivation of major metabolic enzymes and transporters may be another way of combating biotic agents. Gold NP has been found to disrupt the proton pump in fungi [81].
- Another plausible mode of action can be NP-induced changes in the cell wall of the microbes. Depolarization

of the cell increases cellular permeability leading to the unregulated flow of ions, culminating in cell disintegration and death [76].

Nano-priming has also been effective in eliciting enhanced defense response *in planta*. Reports reveal that priming with nanomaterials is of greater importance than soil or foliar application as NPs show greater penetration via seed coat leading to enhanced water and nutrient uptake, enzyme activation, and cellular damage repair [75]. Blending bioactive compounds into nanostructures to ensure slow release to target cells is one of the most promising nanotechnological tools. Commonly employed NPs in this regard are Chitosan NPs, CuO NPs, SiO_2 NPs, ZnO NPs, MgO NPs and TiO_2NPs. However, there are major crevices in understanding the mechanism of action of NPs in imparting resistance to several pathogens and thus disease tolerance [61].

Chitosan is known to impart tolerance against several pre- and post-harvest diseases to different crops by inducing phytoalexin synthesis, callose deposition, activities of reactive oxygen species, lignification, enhanced defense enzymes, and PR proteins. The conversion of chitosan to nano-chitosan alters certain characteristics of the molecule. Features like biocompatibility, reduced toxicity, biodegradability, and physiochemical properties like size, cationic nature, and surface area make it a potent elicitor of systemic resistance in plant responses by altering its biological activity. Cu-Chitosan nanoparticle primed seeds were effective in boosting plant growth along with building up a defense system against *Curvularia* leaf spot (CLS) disease of maize [9] by upregulating antioxidant levels including SOD, POD, PAL, and PPO. Priming of pearl millet seeds with chitosan nanoparticles has also been found beneficial in conferring resistance against downy mildew disease caused by the biotrophic oomycete *Sclerospora graminicola*. In comparison to bulk chitosan, trace amounts (250 mg/kg) of chitosan nanoparticles (CN) were able to generate a similar response in the plants against pathogens. Besides, CNs being tiny in size could easily enter the tissues, thus reducing the time of resistance induction in the treated plants [74]. Nitric oxide (NO) is responsible for generalized stress response in plants. NO, either by post-translational modification (S-nitrosylation, carbonylation, tyrosine nitration) of target proteins or together with secondary messengers in a signaling cascade (c-GMP) can alter specific defense gene expression [63]. It is also known to induce the synthesis of phytoalexins (an endogenous antimicrobial substance of plants), which lead to the accumulation of secondary metabolites and trigger the activities of antioxidant enzymes [19]. NO molecules are the key mediator of CNs-induced resistance response as evident from the increase in NO content in primed seeds and suppression of defense response on treatment with NO scavenger. CN-mediated defense response had been correlated with the enhanced activity of the defense genes and antioxidant enzymes such as Phenyl Ammonia Lyase (PAL), Polyphenol oxidase (POX), peroxidase, SOD, and catalase. Increased expression of PR proteins (PR-1 & PR-5) also provided an important cue towards augmented defense machinery post-treatment.

Zinc is associated with a plethora of biological processes in plants such as the maintenance of structural and functional integrity of biological membranes, protection of cellular proteins and lipids from oxidative damage, regulates expression of antioxidant enzymes like SOD, POD, GR and also known to induce lignification on pathogen invasion. CLS disease inflicts severe leaf necrosis and ROS accumulation in maize, thus hampering the photosynthetic efficiency, which leads to massive yield loss (60% yield loss yearly). The symptoms and outbreak of the disease are intensified in alkaline soil conditions where the bioavailability of Zn is limited. Zn-chitosan NPs had been found to inhibit spore germination and mycelial growth of *C. lunata* in-vitro. Pot experiments and field studies with maize seeds primed with Zn-chitosan NPs inoculated with CLS-causing pathogen, delivered improved resistance against CLS. Upregulation of SOD, POD, PAL & PPO expression with enhanced lignification might be the plausible mechanism that abated the microbial infection and its associated atrocities [10].

Silicon is a quasi-essential mineral nutrient for plant growth and development that helps in a better adaptation of plants under environmental stress conditions. Si-NPs besides enhancing the growth & development of plants, also serve as nanocides, herbicides, fertilizers & delivery agents for amino acids, and proteins [27]. Si NPs act as a physical barrier to prevent pathogen entry as they get deposited in a thick layer beneath the cuticle, subcuticular layer, cell wall, and intercellular spaces or develop a biofilm at the epidermal cell wall. This mechanism strengthens the cell wall and restricts pathogen invasion efficiently. Besides, a higher surface-to-volume ratio of Si-NPs increases the reactivity and bioavailability of Si and also spikes up its biological and molecular functions in the cell. Seed priming with SiO_2 NPs is more beneficial than foliar application in reducing nematode multiplication, galling, and disease indices in beetroot [42]. Besides, the superior functioning of the antioxidant and defense enzymes contributes to the management of three harmful pathogens causing a disease complex in beetroot viz. *Pectobacterium betavasculorum* (a pathogenic bacterium causing vascular necrosis, wilting and black streaks on the leaves and petioles, soft rots due to secretion of various extracellular digestive enzymes), *Meloidogyne incognita* (a root-knot nematode causing severe damage to epidermis, cortex, and stele in root cells, thereby hindering water and nutrient absorption) and *Rhizoctonia solani* (a pathogenic fungus responsible for crown and root rot diseases). SiO_2 NPs priming is also found effective against pathogens (*Alternaria dauci* and *Pectobacterium carotovorum)* causing diseases of carrots that cause massive yield losses [75]. However, how the resistance is imparted is yet to be revealed.

FeS-NPs serve as an antifungal agent against *Fusarium verticillioides*, causing sheath rot and seed discoloration of rice by inhibiting its growth at a much lower concentration (ED_{50} 18 ug/ml) than the standard fungicide Carbendazim (ED_{50} 230 ug/ml) in vitro [5]. Discolored rice seeds primed with such NPs, showed a significant reduction in seedling blight and seed rot symptoms with no morphologically visible signs of treatment-induced toxicity. SEM micrographs revealed that FeS-NPs led to mycelial disintegration, disruption of hyphal cell membrane, and inhibition of macroconidial growth of the fungus thereby restricting fungal proliferation and impeding fungal growth [5].

Cu has been used for ages as a bio-control agent owing to its insecticidal and fungicidal properties [13]. Cu NPs are the most affordable among various transition metals under examination like gold, silver & platinum. Cu-NPs are known to penetrate microbial cells and cause damage due to the inactivation of crucial enzymes by substituting essential ions and blocking functional groups of proteins, generating hydro-peroxide free radicals, modifying membrane integrity, and interacting with P and S-containing macromolecules like DNA, RNA, and lipids [13]. CuO NPs have been used as seed priming agents in forage sorghum (*Sorghum bicolour*), cowpea (*Vigna unguiculata*) [49] and wheat [87] and have been effective in improving seedling germination traits. *In-vitro* assays revealed that CuO could potentially inhibit the mycelial growth and spore germination of *Alternaria solani* (a fungal pathogen causing leaf blight in wheat) [87] and seed-borne fungal pathogens of sorghum and cowpea [49]. It is believed that CuO NP primed seeds will be more resistant to pathogen attack than unprimed seeds; however, the lack of *in-vivo* trials fails to validate the hypothesis in these studies.

Advantages and disadvantages of nano-priming

Advantages

Nano-priming indeed possesses the potential to steer a new era of crop productivity and sustainable agriculture. Studies reveal a plethora of advantages bestowed by nano-priming over conventional agricultural practices. Plants are known to provide a potential pathway for NP transportation that closely mimics that of endogenous nutrients. Besides the fact that the binding properties of seeds and nano-priming agents are higher than those of traditional priming agents like water, PEG, results in better seed water uptake in nano-primed seeds, resulting in rapid and synchronized germination ensuring a stable and successful crop stand. Nano-priming assures targeted and smart delivery of the nutrients or desired molecules to the seeds that control and minimize the harmful effect of such chemicals on the environment or the soil microflora. Nano-priming agents possess some unique physical, chemical, and mechanical properties that make them electrochemically more active than bulk materials of the same composition. Due to the presence of a higher proportion of atoms on the surface of nanomaterials, they tend to differ in surface composition and reactivity from their bulk counterparts. Another striking feature of NPs is their requirement in trace amounts and their ability to pass through biological membranes and interact with biomolecules owing to their minute sizes. Nano-priming has been found to influence biochemical pathways, reactive oxygen compound equilibrium, and plant growth hormones, thereby impacting the production of phytochemicals in plants [24]. Research has demonstrated that nano-priming can modulate physiological responses, including antioxidant systems and hormonal pathways, leading to enhanced stress resistance and disease resistance in plants [43]. Additionally, nano-priming has been associated with increased production of secondary phytochemicals, suggesting a potential for enhancing the natural production of these compounds in plants. For instance, priming *Momordica Charantia* L. seeds with ZnONPs has been speculated to upregulate the expression of genes associated with the shikimate phenylpropanoid pathway which elevates the phenolic and flavonoid content [51]. The positive effects of nano-priming on agriculture have been elucidated by field trials which have demonstrated the nano primed seeds as superior to hydro primed seeds owing to their feasibility in promoting yield as well as nutritional value of grains with negligible effect on soil microbiota [29].

Disadvantages

Nano-priming has been considered to be a prudent alternative to foliar or root application of nanoparticles owing to their minimized chances of environmental exposure. However, it is imperative to assess the optimal concentration and duration of treatment in seeds to ensure maximum growth, development of plants and eliminate chances of interference with beneficial soil microbial community. The adverse effects of nano-priming on soil microbiota have been explained by the significant alterations in nitrogen fixation, phosphate solubilization, downregulation in enzyme activities, and factors associated with soil fertility. The interaction and associated risks of nano priming with human and animal health have been a matter of prime importance and are debatable. It is essential to constantly monitor whether the nano-priming agents can impose any negative implications in future but the lack of any rules or standards has made this task perplexing. Nano-priming has been well acknowledged for its feasibility in augmenting the synthesis of secondary metabolites to defend the pathogens. Nevertheless, this approach may lead to the release of other phytochemicals which may protect the plant against pathogens but simultaneously can have adverse effects on human health [71]. Various priming approaches including UV-B [66], Plant growth promoting rhizobacteria (PGPR) [11], *Trichoderma* [78], INA [50], etc. have been substantiated to have a profound trans-generational impact on plants which include major transcriptional, post-translational and epigenetic changes. These trans-generational changes create a memory that enables the plants to enhance their growth and vigor as well as act as a defense system against abiotic and biotic stress factors. Priming rice seeds with AgNPs has also been revealed to create a defense memory against salinity stress and rice blast pathogen *Magnaporthe oryzae* [84]. AgNPs create this defense memory against the pathogen by triggering a significant alteration in the glutathione metabolism, MAPK and phytohormone signaling pathway associated with defense in addition to secondary metabolites like falvones, and flavonol. However, transcriptional changes in these signal transduction pathways persisted for only a few weeks. Lately, carbohydrate-coated CeO_2 NPs have been confirmed to have a trans-generational impact on *Chenopodium rubrum* L. and *Sinapis alba* L. seeds which were substantiated by elevated seed germination and enhanced morphological as well as physiological characteristics in subsequent generations [52].

Future perspectives and conclusion

The seed priming technique is innovative, cheap, and easy to apply in farmer's field conditions. Also, many successful case studies have been reported regarding seed priming for the amelioration of biotic and abiotic stress to date. However, we have yet to understand the molecular mechanism of seed priming. Future research must be oriented toward identifying the underlying mechanism of nano seed priming more vividly to popularize its application. Besides, the use of mono-metallic NPs has been taken over by the use of multi-metallic NPs [15] owing to their enhanced benefits. Such NPs can be applied as priming agents to develop multifaceted outcomes. Proper field trials, elucidation of a detailed mode of action for the NP-mediated response, and depiction of the environmental consequence of NPs application are the need of the moment. Thus, an orchestrated approach is required to render nano seed priming as an effective and promising strategy to replace the use of bulk synthetic pesticides to I protect the crop plants against biotic agents.

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Declarations

Conflict of interest All authors have read and approved the manuscript. The authors declare that there is no conflict of interest. RK is the member of the Editorial Board, but was not involved in decision process at any stage.

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Authors and Affiliations

Nilanjana Ghosh[1] · Swarnali Dey[1] · Titir Guha[2] · Surupa Paul[1] · Rita Kundu[1]

✉ Rita Kundu
rkbot@caluniv.ac.in

[1] Advanced Cell Biology Laboratory, Department of Botany, University of Calcutta, 35 Ballygunge Circular Road, Kolkata 700019, India

[2] Indian Institute of Science Education and Research, Karakambadi Road, Opposite Sri Rama Engineering College, Rami Reddy Nagar, Mangalam, Tirupati, Andhra Pradesh 517507, India