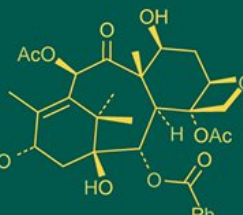
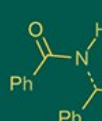


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Nano priming effects on seed vigour and disease resistance in cereal crops

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Abstract

In order to promote crop establishment, stress tolerance, and plant health, Nano priming a novel method to seed enhancement combines nanotechnology with seed priming techniques. This review focuses on how Nano priming improves cereal crops' physiological performance, disease resistance, and seed vigor. Zinc oxide (ZnO), iron oxide (Fe), silver (Ag), titanium dioxide (TiO₂), and carbon-based nanomaterials are examples of nanoparticles with special physicochemical characteristics that allow them to control metabolic and biochemical processes during seed germination. These characteristics include high surface area, increased reactivity, and improved penetration ability. It has been shown that Nano priming increases enzyme activity, especially α -amylase, which improves seed reserve mobilization and speeds germination. Additionally, it affects the balance of plant hormones by raising gibberellin (GA) activity and decreasing abscisic acid (ABA) levels, which encourages seedling development and emergence. Additionally, superoxide dismutase, catalase, and peroxidase enzyme activity are elevated in Nano primed seeds, indicating improved antioxidant defense mechanisms that support cellular redox homeostasis under stressful situations. Additionally, research has shown that Nano priming enhances micronutrient accumulation, photosynthetic efficiency, chlorophyll production, root growth, and nutrient absorption in crops including wheat, maize, and rice. By activating defense-related enzymes and signalling pathways, Nano priming not only promotes growth but also strengthens plant defences against bacterial, nematode, and fungal diseases. Despite these benefits, there are still challenges with long-term deposition in soil and plant tissues, environmental safety, and ideal nanoparticle concentrations that prevent widespread agricultural application. In order to guarantee the safe and efficient use of Nano priming in sustainable agricultural systems, future research should prioritize field-based validation, biosafety evaluation, and the creation of standardized application methods.

Keywords: Nano priming, Nanotechnology, Seed priming, Nanoparticles, Seed germination, Seed vigor, Stress tolerance, Cereal crops, Zinc oxide nanoparticles

Introduction

Researches have shown that biochemical, physiological, and morphological processes are involved in plant systems (Kottegoda et al., 2017) [22]. When a boom in agricultural output is achieved, nanotechnology has boosted a number of plant life nodes, including seed germination, plant fresh and dry weight gain, reduction of pest and insect incidence, and activation of antioxidant systems (Haghighi et al., 2012; Siddiqui and Al-Wahaibi, 2014; Wang et al., 2015, 2016a, b; Shalaby et al., 2016) [12, 21]. Nanotechnology has the potential to enhance green farming methods and boost food security by allowing for easier penetration into seeds. Nanotechnology has several benefits for plants, including increased reactivity, precise targeting, and the ability to encapsulate nutrients and plant protection products for long-term release and resistance (Ocsoy et al., 2013; Anusuya and Sathiyabama, 2015; Corsi et al., 2018) [27]. Eco-friendly use of nanotechnology in agriculture could contribute to sustainable development. To assure safe usage of nanotechnology, confocal microscopy and biochemical studies of plant-nanomaterial interactions are conducted *in vivo* using quantum dots (Wu et al., 2017) [10].

Seed Priming and its Effects in Agriculture

Seed is the main input used in agricultural production, hence, ensuring its quality is crucial to increasing crop productivity. According to Makhakham et al. (2017), the pathway from seed

To plant involves a complex collection of responses and physiology that determine agricultural field stand. The ancient Greek civilization used seed priming (SP), a physiological and biochemical seed invigoration technique (Evenari, 1980)^[11], to quickly transition to full germination. This process involves starch hydrolysis, osmotic adjustments, and enzymatic activation mediated by imbibition (Araújo et al., 2016; Hussain et al., 2015, 2016)^[5, 14], which activates and strengthens the plant's cellular defense system against various stresses (Jisha et al., 2013)^[16]. The most important requirement for sufficient crop growth that guarantees the effective use of input resources that define the final yield potential and the fundamentals of a sustainable agricultural economy is quick germination and a similar crop stand in the field (Bose et al., 2018)^[6]. According to Bose et al. (2018)^[6], Singhal et al., and Kumar

et al., SP is a well-known, inexpensive, readily adaptable, and highly effective method for improving germination and crop vigor that ensures better yield of significant agricultural products under both normal and stressful conditions. Partially hydrating and dehydrating seeds without allowing radicle initiation is known as SP, a pre-sowing technique. By soaking in water or other priming agents under carefully regulated conditions, this advancement of seeds (hydration) starts the premetabolic activity (Bose et al., 2018)^[6]. The length of the soaking period and the reaction's termination have a significant impact on this treatment. For SP treatment, which establishes the seed's storability and metabolic activities, this treatment adhered to a set duration for soaking and constantly quick-drying to their initial moisture level.

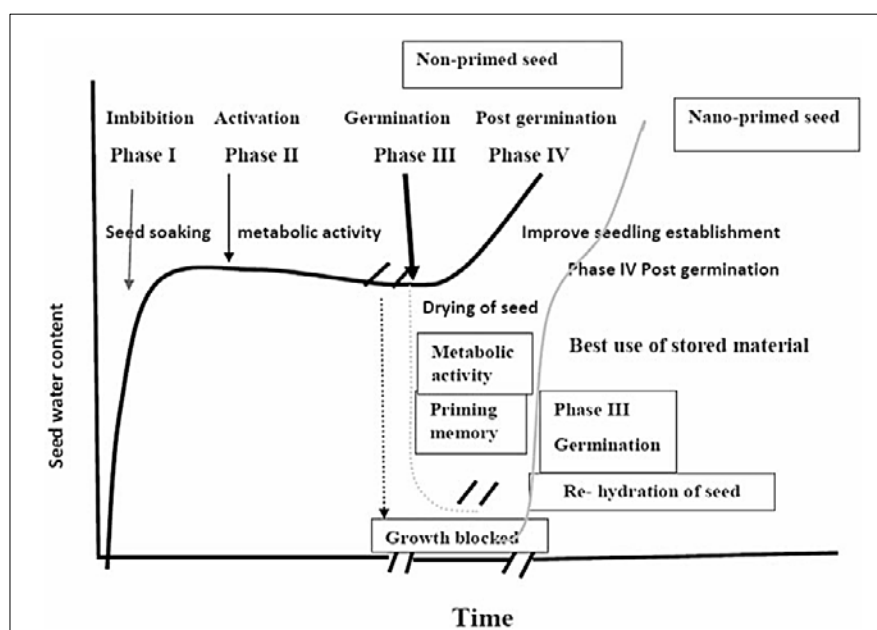


Fig 1: Illustrates the mechanism of SP in relation to the regulated seed germination process.

Figure 1.: A simplified depiction of the controlled germination and nanopriming-induced germination process (imbibition phase, phase I; activation phase, phase II; germination phase, phase III; postgermination phase, phase IV) (Bose et al., 2018)^[6].

Due to the hydration and rehydration process, the nanopriming phase II takes longer than the typical seed germination process. There are two hydration processes in primed seed and only one in control. While seedling growth is inhibited during the drying process, metabolic activity which is essential for metabolite synthesis, antioxidant activity, solubilization of stored material, priming and stress memory, and repair mechanisms remains active. It improves climate acclimation, stress tolerance, and quick and consistent seedling establishment. Priming agents are the substances that are most frequently employed in priming treatments. They might include water, inorganic chemical salts, hormones, sugars, vital nutrients, plant organic sources, water or nutrients, biofertilizer, and other helpful microorganisms (Jisha et al., 2013)^[16].

SP has been classified on the basis of priming agents like-hydropriming (priming with water), osmopriming (priming with osmotic salts like poly-ethylene glycol (PEG), KNO₃), matrix priming (priming with solid and semisolid matrices), nutripriming (priming with plant nutrients like

micronutrients and macronutrients), biopriming (priming with biological compounds), hormopriming (priming with plant growth regulators (PGRs)), and nanopriming (priming with carbon or metal-based nanomaterials).

Primed seeds exhibit increased crop establishment rates, enhanced seedling vigor, and greater rates of seedling emergence (Singhal and Bose, 2020). Additionally, SP helped developing seedlings overcome the detrimental effects of environmental challenges and increase their stress tolerance (Bose et al., 2018)^[6]. Additionally, because SP reduces the usage of chemicals on agricultural land, it addresses a variety of agricultural pollution issues, including heavy metal toxicity. These days, using NPs for SP has proven beneficial in the aforementioned areas (Zuverza-Mena et al., 2017)^[41]. By promoting cellular metabolic activities, water absorption, cell molecule and osmolyte repair, and other processes, priming seeds improves their physiological and growth performance as well as their potential for production (Canfield et al., 2010)^[7].

Nanopriming and Nanomaterials Used in Seed Priming

Numerous innovative applications in biotechnology and agriculture made possible by nanotechnology improve soil health, lower production inputs, and encourage sustainability in the agricultural system. Additionally, it is

assisting other agricultural-related businesses such food processing and packaging, the creation of a biosensor for pathogen detection, the manufacturing of nanofoods, and nanofertilizers (Dehkourdi and Mosavi, 2013). Leaching, hydrolysis, degradation, and decomposition processes prevent plants from consuming nutrients in bulk, so it's critical to minimize these losses by utilizing this cutting-edge technology. NPs have the ability to increase plant metabolism because of their unique characteristics, which include increased surface area, high reactivity, tenable pore size, and particle structure.

According to Wang et al. (2016a, b) [37, 38], nanoparticles are particulate nanomaterials with a nanoscale size of at least 1 to 100 nm. The two forms of NP that have been used as SP agents are metal-based (Zuverza-Mena et al., 2017) [41] and carbon-based (such as carbon nanotubes) (Mahakham et al., 2017) [24]. In significant crops like wheat and maize, carbon nanotube priming can boost germination, growth, water/nutrient uptake, and yield (Tiwari et al., 2014; Joshi et al., 2018) [35].

Compared to other materials, nanoparticles like zinc oxide nanoparticles (nZnO), iron nanoparticles (nFe), copper nanoparticles (nCu), silicon nanoparticles (nSi), and magnesium nanoparticles (nMg) can be quickly absorbed, transported, and accumulated in plant parts. These nanoparticles control the physiological and biochemical processes of plants, resulting in improved plant growth and development (Rastogi et al., 2017) [30]. However, the NP's effectiveness varies from plant to plant depending on its particle size, concentration, chemical structure, and surface coating (Rastogi et al., 2017) [30]. NPs are used as SP agents because they are affordable, nontoxic, biocompatible, and environmentally benign. Crop germination, seedling establishment, shoot/root elongation, fresh and dry weight, growth, chlorophyll content, photosynthetic activity, water uptake, biomass production, flowering, and antioxidant qualities can all be affected by various nanopriming agents, including silver nanopriming (AgNP) and nanotitanium dioxide (TiO₂) (Dehkourdi and Mosavi, 2013).

The feasibility of using nanoprimed seeds with micronutrient nanoparticles for sustainability has recently been investigated by scientists. Increased root characteristics like root length and root volume (Adhikari et al., 2013) [1], increased drought tolerance, increased micronutrient retention in the leaves (Anita and Rao, 2014) [4], increased

antioxidant activity followed by increased jasmonate, decreased time to flowering and increased seed weight.

According to Mahakham et al. (2017) [24], aged rice seeds primed with AgNPs greatly enhanced germination performance, seedling vigor, and α -amylase activity, which guarantees more soluble sugar to support the growth of newly emerged seedlings. By interacting with the sulfhydryl and COOH-groups of proteins, metal nanoparticles reduce the efficiency of enzymes (Shaw et al., 2014) [31]. In many crops, nanopriming also increases stress tolerance. Nano-ZnO priming with the concentration 60 mg L⁻¹ improved salinity tolerance by reducing the malondialdehyde (MDA) and Na⁺ concentrations in *Lupinus termis* but reduce sodium concentration and increased leaf water potential in wheat (Wang et al., 2016a, b) [37, 38]. According to Ali et al. (2019) [2], these nanoparticles can also reduce the buildup of other heavy metals in crops like rice. According to Mahakham et al. (2017) [24], nano priming promoted the induction of aquaporin genes and reactive oxygen species (ROS) generation in germinated seeds, both of which are crucial for improving seed germination. In spinach seeds, iron pyrite (FeS₂/Py) priming enhanced the quantity of leaves, leaf size, chlorophyll, and mineral content (Ca, Mn, and Zn) (Srivastava et al., 2014). Additionally, it increased grain output in rice, bio mass production in fenugreek and alfalfa, and the seed yield of oilseed crops like sesame and mustard. Additionally, defensive responses connected to jasmonates can be induced by nanoiron oxide. By increasing the activities of sodium dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), nano-ZnO priming affected an efficient ROS scavenging system that maintained cellular homeostasis and increased the activity of phosphoglucosyltransferase and cytoplasmic invertase enzymes involved in sucrose biosynthesis under salinity. A novel approach to iron biofortification in wheat was suggested by Nano SP with iron oxide (25–600 ppm), which increases iron absorption, deposition, and translocation in plants as well as iron buildup in grain (Sundaria et al., 2019) [32]. According to Munir et al. (2018) [25], ZnO nanopriming also raises Zn concentration in wheat. According to Rizwan et al. (2019) [14], iron oxide and zinc oxide both enhance plant development and lessen oxidative damage during cadmium stress.

Nanotechnology's shining future in precision agriculture has the potential to usher in a second sustainable green revolution.

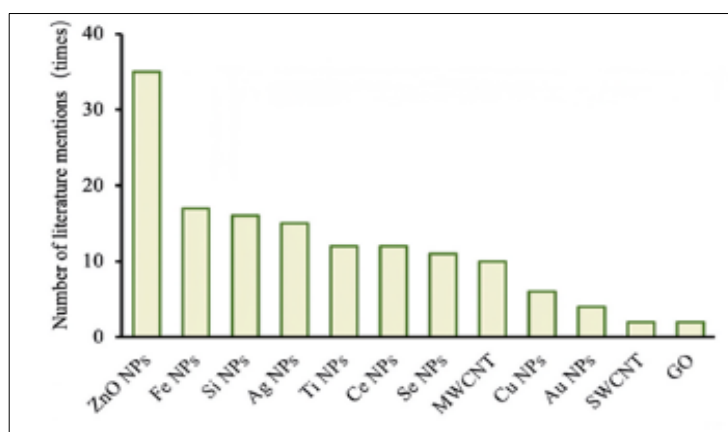


Fig 2: Statistics of seed priming with different nanoparticles

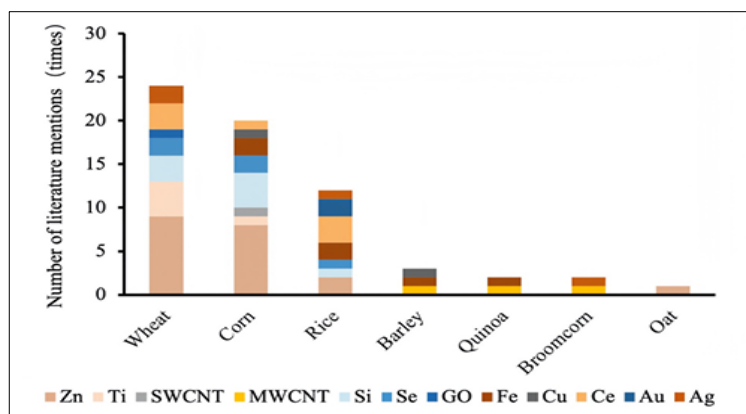


Fig 3: Statistics of nanopriming grain crop variety

Physiological Mechanisms of Nanopriming

A. Nanopriming boosts enzyme activity, controls hormone levels, loosens cell barriers, and provides vital nutrients

Nanopriming improves seed germination by activating enzymes, proteins, and lipids in seeds (Jisha et al., 2013) [16]. This involves increasing amylase activity to produce more soluble sugars, as documented in rice (Sharma et al., 2021), canola (Khan et al., 2024) [20], and chickpea seeds (Das and Dutta, 2022) [9]. Nanopriming regulates the balance of abscisic acid (ABA) and gibberellin (GA) by increasing the production of GA and cytokinin-related genes while decreasing ABA levels (Abdel-Aziz and Rizwan, 2019) [14]. A study found that priming rice seeds with selenium (Se) and salicylic acid (SA) at low temperatures increased GA3-amylase activity, content, and expression of OsGA3ox1 and OsGA20ox1. There is a decrease in both ABA content and expression of OsNCED1. Induction enhances GA-mediated α -amylase by raising GA3 levels while lowering ABA expression (Nie et al., 2022) [26]. The current work did not

explore whether nanopriming uses the same GA signaling mechanism. Nanoparticles need to get through the seed coat, which is made up of physicochemically stable sclerenchyma.

According to Schwab et al., this structure works as a barrier to protect seeds from external environmental threats. Zinc oxide nanoparticles (ZnO NPs) and titanium dioxide nanoparticles (nano-TiO₂) have been proven in experiments to penetrate seed coats and induce cell differentiation by triggering enzymes that break down seed dormancy. Seed priming increases hydroxyl radical ($\bullet$ OH) production, weakening seed cell walls and improving germination rates (Mahakham et al., 2017) [24].

Nanoparticles deliver critical nutrients to plant cells, including zinc, iron, potassium, and calcium. These nutrients boost plant chlorophyll content, speed up photosynthesis, and promote leaf growth, leading to higher yields. Figure 4. illustrates the intrinsic mechanism of nanopriming on plant cells.

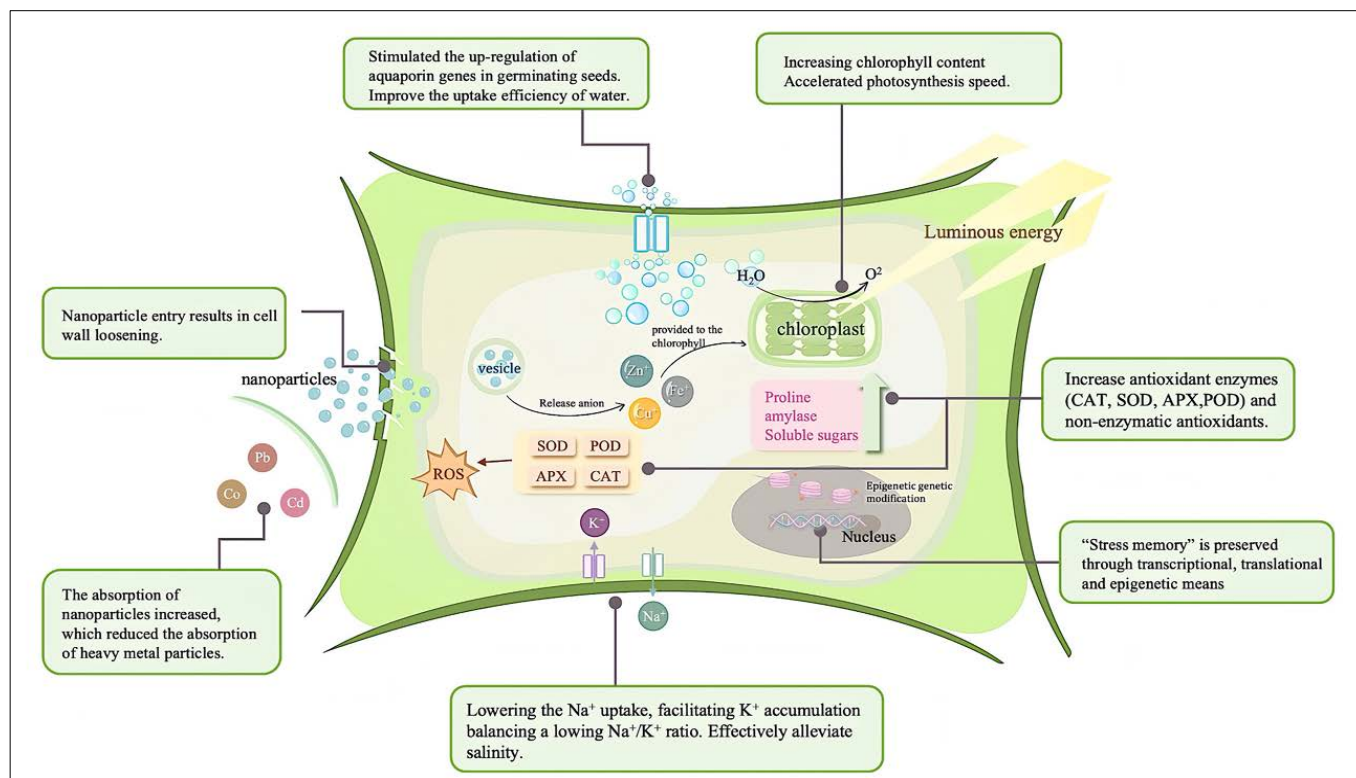


Fig 4: Diagrammatic illustration of intrinsic process of nanopriming for promoting plant growth.

B. Nanoprimering promotes the expression of genes involved in seed imbibition, plant defense, and antioxidation

Nanoprimering does not alter the plant's phenology or genomics. Johnson and Puthur (2021)^[17] found that stress-tolerant memory is sustained by transcription, translation, and epigenetic mechanisms. This molecular change allows plants to respond more quickly and efficiently to future stressors. Plants produce reactive oxygen species (ROS) that signal other messengers like ethylene (ET), salicylic acid (SA), nitric oxide (NO), jasmonic acid (JA), and oleoresinol stanols (BRs). These messengers can regulate secondary metabolism (Chung et al., 2018)^[8]. Signaling proteins and transcription factors have a crucial role in maintaining "stress memory". Priming-induced genes can be regulated at various levels, including RNA-induced transcription silencing, RNA-dependent DNA methylation (RdDM), changes in nucleosome or histone variant positioning, DNA methylation, and histone modifications.

Yan et al. (2022)^[42] discovered that priming rice with nanosilver (Ag NPs) raised reactive oxygen species (ROS) levels and activated hormone signaling pathways. This priming also increased the expression of APETALA2 (AP2) domain-containing protein, dof zinc finger domain-containing protein, and WRKY. Transcription factors increase protection by regulating the genes of defense-related proteins such as HSP, GST, FBP, and LEA. They also control glutathione and cytokinin-O-glucosyltransferase (CGTs) to enhance seed germination.

During the suckering stage of seed germination, the seed absorbs significant amounts of water, which can activate aquaporin genes (Salam et al., 2022a). El-Badri et al. (2022)

^[10] found that selenium nanoparticles (Se NPs) can boost the expression of aquaporin genes (BnPIP1-1 and BnPIP2-1), leading to increased water absorption. The researchers examined the impact of zinc oxide nanoparticles (ZnO NPs) on two rapeseed cultivars. El-Badri et al. (2021)^[43] discovered that ZnO NPs increased seed germination by upregulating BnCAM and affecting the seed imbibition gene BnPER.

Nanoprimering induces moderate ROS generation, which improves plant resilience to abiotic stress. This promotes the synthesis of secondary metabolites. Nile et al. suggest that serial analysis of gene expression (SAGE) can help understand the impact of nanoparticles on plants. Ulhassan et al. (2023)^[36] discovered that silicon nanoparticles (Si NPs) can increase chlorophyll synthesis genes (BnCAO, BnCHLG, BnPOR), inhibit the expression of senescence associated genes (BnSAG12), and increase the expression of defense genes (BnPAL, BnCAD, BnPPO, BnMT-1), reducing chlorophyll degradation and leaf senescence under chromium stress.

The literature reveals that nano-priming approaches have favourable effects by regulating ROS and enhancing the enzymatic antioxidant system. Non-enzymatic antioxidants work alongside enzymatic antioxidants to regulate ROS levels. This could explain why their levels spiked when antioxidant defenses were compromised after a hazardous event. The molecular mechanisms of enzymatic and non-enzymatic antioxidant systems regulating ROS levels in response to NPs remain unclear. Figure 5 illustrates how nano-priming modulates antioxidant defenses and regulates ROS levels.

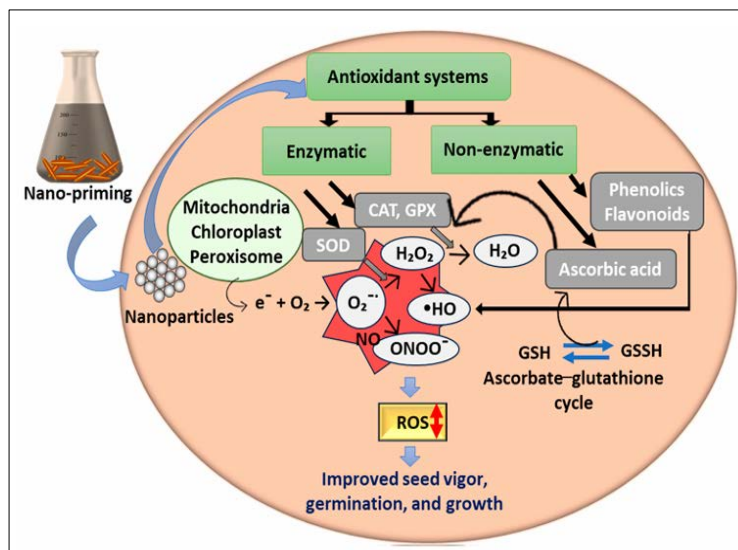


Fig 5: Schematic representation of nano-priming-induced modulation of antioxidant systems in seeds. Nanoparticles interact with cellular organelles (mitochondria, chloroplasts, and peroxisomes) to influence the production of reactive oxygen species (ROS), including $O_2^{\bullet-}$, H_2O_2 , $\bullet OH$, NO , and $ONOO^-$. ROS levels are regulated by enzymatic antioxidants (SOD, CAT, GPX) and non-enzymatic antioxidants (ascorbic acid, phenolics, and flavonoids), along with the ascorbate–glutathione cycle. This coordinated regulation maintains redox balance and enhances seed vigor, germination, and early seedling growth.

C. Nano-Priming as a Strategy for Enhancing Plant Disease Resistance

Annual crop losses caused by pathogen infections are significant, ranging from 20–40%, and involve a wide range of organisms such as fungi, bacteria, viruses, nematodes, and oomycetes. Conventional management strategies include chemical and biological approaches, as well as the

use of disease-resistant varieties. Recently, nanotechnology-based methods, particularly seed priming with nanomaterials, have emerged as promising alternatives for enhancing disease resistance in crops.

Seed priming with nanoparticles has been shown to improve plant defense against fungal, bacterial, and nematode pathogens. For example, in cumin, priming with chitosan

and silver nanoparticles enhanced antioxidant enzyme activities (SOD, CAT, peroxidase, and polyphenol oxidase), thereby reducing Fusarium wilt. Similarly, selenium nanoparticle-primed tomato seeds exhibited strong resistance to late blight through increased accumulation of lignin, callose, and hydrogen peroxide, along with elevated levels of defense-related enzymes such as SOD, LOX, β -1,3-glucanase, and PAL.

Pathogen infection in tomato plants by organisms like *Xanthomonas campestris*, *Pseudomonas syringae*, *Alternaria solani*, and *Fusarium oxysporum* negatively affected plant growth and biochemical parameters, including pigments and enzyme activities. However, seed priming with titanium dioxide nanoparticles improved growth, restored biochemical attributes, and reduced disease severity. Likewise, silicon dioxide nanoparticles were effective under greenhouse conditions in reducing diseases caused by pathogens such as *Pectobacterium*, *Meloidogyne*, and *Rhizoctonia*, while enhancing plant growth, photosynthesis, and defense enzyme activities, ultimately lowering disease incidence and nematode proliferation.

Field studies further demonstrated that advanced nanoparticle formulations, such as triazole-conjugated silver nanoparticles, reduced the incidence of bakanae disease in rice. However, the comparative effectiveness of seed priming versus foliar application of nanomaterials remains inconsistent across studies.

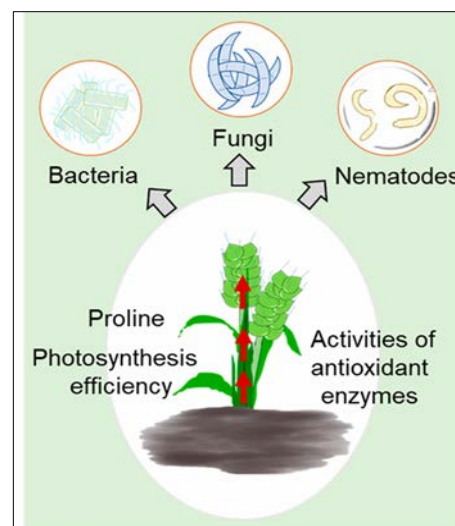


Fig 6: Nano-priming confers enhanced resistance to bacterial, fungal, and nematode pathogens through the upregulation of key physiological and biochemical processes, including improved photosynthetic efficiency, elevated proline accumulation, and increased activity of antioxidant defense enzymes. In the schematic, upward red arrows signify an increase in the respective parameters, whereas the bidirectional red arrows denote dynamic modulation of these levels.

Table 1: The effects of various nanomaterials employed as priming agents on various crop attributes and systems

Nanoprimer	Plant	Concentration	Trait influenced	Mechanism	References
AgNPs	Rice	5 and 10ppm	Improve germinating seedling performance, seedling vigor, and soluble sugar content	Enhance the α -amylase activity and up-regulation of aquaporin genes	Mahakham et al. (2017) [24]
Multiwalled C nanotubes	Wheat	0,70,80and 90 μ gof MWCNT/mL	Improved number of grains, Uptake of water, plant biomass, The densityof stomata, and size of xylem-phloem and epidermal cells	Increased cell elongation, development of excessive root hairs	Joshi et al. (2018)
ZnO	Maize	100mg/L	Increased germination rate, root shoot length and width, and dry matter production	ZnO nanoparticles alleviate Zn deficiency	Ittroutwar et al. (2020)

Conclusion

Nanoprimer technology applied to crop seeds offers a promising approach for sustainable agriculture, as it is considered safer, eco-friendly, and efficient. This pre-sowing treatment improves seed vigor, leading to enhanced plant growth, increased tolerance to both biotic and abiotic stresses, and ultimately improved yield and crop quality. Ongoing research efforts are directed toward developing nanoparticle synthesis methods that are environmentally benign, reliable, non-toxic, and economically viable.

Despite its potential, nanoprimer remains at an early stage of development. Most existing studies have been conducted under controlled experimental conditions, with primary emphasis on seed germination and early growth responses. In contrast, there is a lack of comprehensive research addressing its long-term effects on crop yield, quality, and nutritional composition. Critical concerns, such as heavy metal accumulation in plant tissues and possible soil contamination, have not been sufficiently explored. Additionally, optimal concentrations and toxicity thresholds of nanoparticles for different crop species remain unclear, necessitating careful consideration before large-scale application.

Future research should prioritize studies under controlled and simulated field conditions to better evaluate the

implications of nanoprimer on plant performance and human health. It is essential to establish standardized guidelines regarding nanoparticle dosage and treatment conditions to ensure safe application. Expanding nanoprimer studies to include aromatic, medicinal, and forage crops may also be beneficial, particularly in understanding nanoparticle transfer across trophic levels and generations.

At the mechanistic level, knowledge of nanoprimer remains limited. Further investigations are needed to elucidate the underlying molecular mechanisms, including the roles of regulatory genes, signaling networks, and epigenetic modifications. Moreover, understanding how primed seeds develop stress memory and whether such traits can be transmitted to subsequent generations represents an important area for future research.

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