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NANOPRIMING WITH ZINC AND SELENIUM NANOPARTICLES: A PROMISING APPROACH FOR ENHANCED SEED GERMINATION AND STRESS RESILIENCE

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ABSTRACT
Nanotechnology is increasingly being explored as a modern approach to make agriculture more sustainable, especially through the use of zinc (Zn) and selenium (Se) nanoparticles in seed science. This review focuses on how these nanoparticles improve seed germination, early seedling growth, and the ability of plants to withstand environmental stresses. Zinc nanoparticles, particularly ZnO, support important plant processes such as enzyme activity, nutrient absorption, and hormone balance, which are essential for healthy early growth, while selenium nanoparticles, although not considered essential for plants, play a valuable role in strengthening antioxidant systems, controlling harmful reactive oxygen species, and helping plants tolerate stresses like drought, salinity, and heavy metal exposure. When applied through seed priming (nanopriming), these nanoparticles activate key internal processes such as enzyme function, hormonal regulation, and energy mobilisation, resulting in faster and more uniform germination. However, their effects are highly dependent on concentration, as optimal levels promote growth while excessive amounts may cause toxicity. The combined use of zinc and selenium nanoparticles often produces better results due to their complementary roles, improving photosynthesis, biomass accumulation, and overall plant resilience, although further research is still needed to optimise their use and ensure environmental safety for long-term agricultural applications.

KEYWORDS
Seed germination; Seedling growth; Stress tolerance; Antioxidant defence; Sustainable agriculture; Plant development.

1. INTRODUCTION

The global population is projected to reach about 9.7 billion by 2050, creating immense pressure on agriculture to provide food and nutrition for all(Kah, Kookana *et al*. 2018). Yet, climate change and environmental stresses such as rising temperatures, drought, soil salinity, and heavy metal pollution are increasingly threatening crop productivity (Calicioglu *et al*., 2019). While conventional fertilisers and pesticides have historically enhanced crop yields, their low use efficiency has contributed to serious environmental concerns, including eutrophication and the development of pest resistance (Tilman *et al*., 2002; Savci, 2012). Nanotechnology offers a promising solution for sustainable agriculture, with nano-enabled inputs improving nutrient use and crop protection (Adisa *et al*., 2019; Jakhar *et al*., 2022). Among these, selenium and zinc nanoparticles stand out in seed science for their roles in enhancing germination, seedling vigour, and early plant growth. Selenium nanoparticle seed priming strengthens antioxidant defences, balances reactive oxygen species, and increases tolerance to stresses like drought, salinity, and metal toxicity (Hawrylak-Nowak *et al*., 2018; Djanaguiraman *et al*., 2018; El-Ramady *et al*., 2021). Zinc nanoparticles, particularly ZnO, act as cofactors for enzymes involved in protein synthesis, carbohydrate metabolism, and hormone regulation, improving germination, nutrient uptake, and seedling development (Rizwan *et al*., 2017; Rameshraddy *et al*., 2020; Singh *et al*., 2021). However, knowledge on their mechanisms, optimal application methods, dose responses, and environmental impacts remains limited and fragmented. This review evaluates the synthesis, application, physiological mechanisms, and stress-mitigating effects of selenium and zinc nanoparticles in seed science and agricultural technology. It also highlights research gaps and future directions to guide their safe integration into sustainable crop production.

2 Physiological Roles of Zinc in Plants

Zinc is an essential micronutrient that plays a fundamental role in plant metabolism, growth, and development. It is a structural or catalytic cofactor for about 300 enzymes that are involved in important physiological and biochemical processes, including the regulation of nucleic acids, protein synthesis, membrane integrity, and glucose metabolism. (Rai-Kalal & Jajoo, 2021). Zinc is also critically involved in the biosynthesis of auxins, particularly indole-3-acetic acid (IAA), which regulates cell division, elongation, and overall plant morphogenesis (Marschner, 2012). Additionally, adequate zinc nutrition enhances photosynthetic efficiency, stabilises cellular membranes, and improves plant tolerance to both biotic and abiotic stresses such as drought, salinity, and oxidative damage (Broadley *et al.*, 2012). Seed priming with Zn boosts seed vigour, germination, early seedling development, biomass accumulation, photosynthetic performance, and levels of sugars, total nitrogen, proteins, and other micronutrients across various crops(Faizan *et al*., 2018)

The application of zinc in nanoparticle form, particularly zinc oxide nanoparticles (ZnO NPs), has emerged as a promising strategy to improve zinc bioavailability and utilisation in plants. Due to their nanoscale size and high surface-area-to-volume ratio, ZnO NPs interact more effectively with seed surfaces, root tissues, and cellular components, leading to enhanced uptake, translocation, and physiological efficiency compared to conventional zinc fertilisers (Sharma *et al*., 2021; Dimkpa *et al*., 2019; Raliya *et al*., 2017). This improved efficiency enables effective zinc delivery at lower application rates, thereby reducing potential toxicity risks while maintaining or enhancing plant growth and productivity, making ZnO NPs a sustainable alternative for modern agriculture (Kah *et al*., 2018; Subbaiah *et al*., 2016)

3. Physiological roles of selenium in plants.

While selenium is not officially considered an essential nutrient for plants, research has shown that it can offer notable benefits for plant growth and resilience when present in the right amounts(Hu, Su *et al*. 2022) . Selenium (Se), a component of selenoproteins, supports starch and ATP production (Turakainen *et al.,* 2006), maintains water balance, and protects chlorophyll under drought conditions (Kaklewski *et al*., 2008; Kuznetsov & Kuznetsov, 2003)

Transforming selenium from its ionic states—such as selenite and selenate—into nanoparticles has been found to lower its toxicity, all while preserving or even amplifying its beneficial effects (García-Locascio, Valenzuela *et al*. 2024). Compared to traditional ionic forms, selenium nanoparticles are less reactive, which means they can be used more safely at higher concentrations without causing harm to plants. This combination of greater safety and increased bioavailability makes selenium nanoparticles especially appealing for uses like seed priming and foliar sprays in agriculture.

4. Seed Priming with Zinc and Selenium Nanoparticles

4.1 Mechanisms of Nanopriming

Seed priming is an effective pre-sowing technique that enhances germination, seedling vigour, and stress tolerance by initiating early metabolic processes without radicle emergence. It involves partial hydration followed by redrying, which activates physiological and molecular mechanisms such as antioxidant defence systems and DNA repair, ultimately improving seed performance under diverse environmental conditions (Paparella *et al*., 2015). Studies have shown that seed priming significantly improves germination rate, uniformity, and crop establishment, making it a widely adopted strategy in modern agriculture (Farooq *et al*., 2019; Tian *et al*., 2023). Furthermore, primed seeds exhibit enhanced stress resilience and synchronised germination due to the accumulation of essential proteins and transcripts required for rapid growth (Afzal, 2023). The technique is also cost-effective and versatile, ranging from simple hydropriming methods to advanced biostimulant-based approaches, thereby benefiting both smallholder and commercial farming systems (Dawadi & Karki, 2023). Recently, researchers have begun adding nanoparticles to the priming solution—a method known as nanopriming. This allows the nanoparticles to penetrate the seed coat and interact directly with the embryo inside.

Through these interactions, nanopriming can set off a variety of beneficial changes within the seed, not only at the physiological level but also in terms of biochemistry and gene expression. Seeds treated this way often show better quality and performance. The improvements are believed to come from several factors: the seeds absorb water more efficiently, important metabolic pathways are activated, enzymes work more effectively, hormonal signals are better regulated, and the seed's antioxidant systems are prepared to handle stress.(Paparella, Araújo *et al*. 2015, Mahakham, Sarmah *et al*. 2017, Zulfiqar 2021)

Applying zinc oxide nanoparticles (ZnO NPs) during seed priming has been shown to improve both seed germination and early seedling growth through several interrelated mechanisms. These nanoparticles enhance the activity of key enzymes such as α-amylase, proteases, and dehydrogenases, which aid in breaking down and mobilising stored carbohydrates and proteins to nourish the growing embryo(Abdel Latef, Abu Alhmad *et al*. 2017, Salama, Osman *et al.* 2019). Additionally, optimal doses of ZnO NPs can promote the regulated production of reactive oxygen species (ROS), which function as signalling molecules involved in gene activation for germination and in overcoming seed dormancy (Ghafariyan, Malakouti *et al.* 2013). The gradual release of zinc ions from these nanoparticles also supports auxin synthesis, stabilises cellular membranes, and facilitates protein metabolism—factors that collectively drive cell division, elongation, and robust early seedling development (Alabdallah & Alzahrani, 2020)

Selenium nanoparticles (SeNPs) help seeds cope with oxidative stress by working through multiple, interconnected pathways. One of their main roles is to boost the plant's antioxidant defence system—they do this by increasing the activity of crucial enzymes like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione peroxidase (GPX). Together, these enzymes form a protective shield, helping germinating seeds handle the oxidative challenges they face during the early stages of growth. (Hawrylak-Nowak, Hasanuzzaman *et al*. 2018). This antioxidant support is especially important right after seeds begin to absorb water and during the initial stages of germination, periods when the restart of metabolism can cause a surge in reactive oxygen species. In addition to bolstering antioxidant defences, selenium nanoparticles also play a role in managing plant hormones. They help adjust the levels of abscisic acid (ABA) and gibberellic acid (GA), tipping the balance in favour of breaking dormancy and kickstarting germination. (Ishtiaq *et al*., 2023). By helping to maintain redox balance in the cell, selenium nanoparticles play a key role in switching on genes involved in germination and boosting seed vigour, whether conditions are ideal or stressful. Studies have shown that SeNPs can support these genetic and physiological processes across a range of environments (Hasanuzzaman, Bhuyan *et al*. 2020)
Overall, nanopriming with zinc and selenium nanoparticles represents a modern seed enhancement approach that integrates micronutrient delivery, redox regulation, hormonal modulation, and metabolic activation. The combined action of these nanomaterials results in faster and more uniform germination, improved seedling establishment, and enhanced tolerance to environmental stresses, highlighting nanopriming as a promising and sustainable strategy for improving crop productivity (Zulfiqar *et al*., 2021; García-López *et al*., 2024).

4.2 Effects on Germination Parameters

Substantial experimental evidence shows that nanopriming with zinc- and selenium-based nanoparticles has a pronounced positive effect on seed germination behaviour and early seedling development. In comparison with conventional priming techniques, nanoparticle-assisted priming consistently promotes faster radicle emergence, improved germination synchrony, and higher seedling vigour. These improvements are primarily associated with enhanced seed hydration, rapid initiation of metabolic processes, and more efficient utilisation of stored food reserves during the early phases of germination(Kah 2015, Rastogi, Zivcak *et al.* 2017, Tamindžić, Azizbekian *et al*. 2023). The shortening of mean germination time observed after nanopriming reflects more uniform germination, which is essential for achieving consistent crop establishment and competitive growth in field environments.
In horticultural crops, seed treatment with selenium nanoparticles has been widely reported to enhance key germination traits, including germination percentage and vigour indices. These positive responses are largely attributed to improved antioxidant defence, better maintenance of cellular redox balance, and reduced oxidative damage during seed imbibition and the onset of germination (Hawrylak-Nowak *et al*., 2015; Ahmad *et al*., 2021; El-Ramady *et al*., 2022). Improvements recorded under laboratory and nursery conditions often translate into superior early establishment in the field, underscoring the agronomic relevance of selenium-based nanopriming in vegetable production systems.
Cereal crops similarly exhibit strong responses to zinc-based nanopriming. Several studies have demonstrated that ZnO nanoparticle seed treatments significantly increase germination percentage, seedling length, and overall vigour, leading to more robust early growth compared with untreated seeds(Dimkpa, Singh *et al.* 2018, Faizan, Bhat *et al*. 2021). Enhanced chlorophyll accumulation and improved photosynthetic efficiency in young seedlings indicate that the benefits of nanopriming extend beyond germination and contribute to improved physiological performance during subsequent growth stages (Tripathi *et al*., 2017; Singh *et al.,* 2023). Comparable responses have been observed in oilseed crops, where the combined application of zinc and selenium nanoparticles under abiotic stress conditions resulted in higher final germination rates, faster germination, and increased antioxidant enzyme activities compared with hydroprimed and non-primed seeds (Rady *et al*., 2020; Abdel-Latef *et al*., 2022).
Overall , these findings clearly indicate that nanopriming with zinc and selenium nanoparticles consistently enhances germination efficiency, speed, and uniformity across a wide range of crop species. Improvements in early germination and seedling growth parameters are critical for successful crop establishment and stress tolerance, highlighting nanoparticle-based seed priming as a promising and sustainable approach for improving agricultural productivity under both optimal and stress-affected conditions (Khan *et al*., 2019; Nile *et al*., 2022).

4.3 Concentration-Dependent Effects

When applied at moderate concentrations, typically between 25 and 400 ppm, zinc oxide nanoparticles (ZnO NPs) generally promote seed germination and early seedling development, though the ideal dose varies depending on crop species and treatment method. ZnO NP seed treatment in soybeans improves root and shoot growth and supports physiological functioning in legume crops; however, excessive concentrations disrupt antioxidant balance, increase the accumulation of reactive oxygen species, and have a detrimental effect on plant growth (Ghafariyan *et al*., 2013; Latef *et al*., 2017 The effectiveness of nanoparticle priming is highly concentration-dependent, with both stimulatory and inhibitory effects possible depending on the dose applied. This biphasic response, often described as hormesis, is characteristic of many nanomaterial-plant interactions. At low to moderate concentrations, nanoparticles typically promote germination and growth, while excessive concentrations can induce phytotoxicity (Rico, Majumdar *et al.* 2011)
Seed priming using selenium nanoparticles (SeNPs) produces a distinctly dose-dependent effect, where positive physiological responses are observed only within an optimal concentration window. Across different crop species, low to moderate SeNP concentrations (approximately 1–50 mg L^{-1}) have been shown to enhance seed

germination, seedling vigour, and early growth performance. In cereal crops such as rice and maize, appropriately dosed SeNP priming improved seedling establishment by strengthening antioxidant defence systems and maintaining cellular redox balance, while excessive concentrations resulted in delayed germination and growth inhibition (Dong, Huang *et al*. 2025)). These studies collectively demonstrate that the success of SeNP seed priming is highly contingent upon precise dose optimisation, which varies according to plant species, developmental stage, and nanoparticle physicochemical properties.

Concentrations between 100 and 300 ppm enhanced germination, seedling vigour, and zinc bioavailability by improving metabolic activity during early growth stages(Sedghi, Hadi *et al*. 2013). For rice, concentrations around 100 ppm proved effective for promoting germination and starch metabolism (Sharma *et al*., 2021). However, concentrations exceeding 500 ppm often resulted in reduced germination or seedling abnormalities, highlighting the importance of dose optimisation.

5. Molecular and Biochemical Mechanisms

5.1 Hormone Regulation During Germination

The transition from seed dormancy to germination is controlled by a complex hormonal balance, mainly involving the antagonistic interaction between abscisic acid (ABA) and gibberellic acid (GA). ABA is responsible for maintaining dormancy, while GA promotes germination by stimulating embryo growth and enzymatic activity required for reserve mobilisation (Nonogaki *et al*., 2010; Shu *et al*., 2016). Recent studies have highlighted that nanoparticle-based seed priming (nanopriming) can influence these hormonal pathways, thereby enhancing germination and seedling establishment under both normal and stress conditions (Rico *et al*., 2011; Latef *et al*., 2017).

In rapeseed (*Brassica napus*), nanopriming with selenium nanoparticles (SeNPs) and zinc oxide nanoparticles (ZnO NPs) has been shown to significantly regulate the expression of ABA-related genes such as *BnCYP707A1*, *BnCYP707A3*, and *BnCYP707A4*, leading to reduced ABA accumulation and the release of seeds from dormancy (El-Badri *et al*., 2021). This reduction in ABA content plays a key role in initiating germination processes. Additionally, nanoparticles have been reported to enhance reactive oxygen species (ROS) signalling and antioxidant defence mechanisms, which further support hormonal regulation during seed germination (Bailly, 2004; Latef *et al*., 2017).

Conversely, nanopriming also promotes the upregulation of gibberellin biosynthesis genes such as *BnGA20ox*, *BnGA3ox*, and *BnCPS*, especially under stress conditions like salinity (El-Badri *et al*., 2021). These genes encode enzymes essential for GA production, and their increased expression leads to higher GA levels that stimulate embryo elongation and accelerate germination. The coordinated regulation of ABA degradation and GA biosynthesis demonstrates that nanoparticles act as key modulators of hormonal signalling pathways (Nonogaki *et al*., 2010; Shu *et al*., 2016).

Overall, nanoparticle-mediated seed priming enhances germination by fine-tuning hormonal balance, improving oxidative stress tolerance, and activating metabolic processes required for early seedling growth, making it a promising strategy for sustainable agriculture (Rico *et al*., 2011; Latef *et al*., 2017).

5.2 Antioxidant Defence System Activation

During germination, seeds undergo rapid metabolic activation, which leads to increased oxygen consumption and the generation of reactive oxygen species (ROS), resulting in oxidative stress. Nanoparticle-based seed priming has been shown to enhance antioxidant defence systems, thereby protecting cellular structures during germination and early seedling establishment (Bailly, 2004; Paparella *et al*., 2015).

Experimental evidence indicates that selenium nanoparticle (SeNP) priming significantly enhances antioxidant enzyme activities in germinating seeds. In rice, SeNP treatment increased the activities of superoxide dismutase (SOD) and catalase (CAT), particularly during later stages of germination, while ascorbate peroxidase (APX) activity remained relatively stable, suggesting selective regulation of antioxidant pathways (Hu *et al*., 2022). This targeted modulation helps maintain redox homeostasis without triggering excessive stress responses.

Similarly, in wheat exposed to drought stress, selenium nanoparticles have been reported to significantly enhance the activities of key enzymes involved in the ascorbate–glutathione cycle, including monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), glutathione peroxidase (GPX), and catalase (Ikram *et al*., 2020). These enzymes play a crucial role in detoxifying hydrogen peroxide and maintaining intracellular redox balance, thereby protecting cells from oxidative damage and improving stress tolerance (Gill & Tuteja, 2010; Noctor & Foyer, 1998).

In addition to selenium, zinc oxide nanoparticles (ZnO NPs) have also been reported to enhance antioxidant defence mechanisms by improving enzymatic activity and reducing oxidative damage in plants under stress conditions (Faizan *et al*., 2018). Zinc supplied through ZnO nanoparticles supports the activity of antioxidant enzymes and contributes to membrane stability, thereby minimising lipid peroxidation and cellular injury. Nanoparticle-mediated seed priming strengthens antioxidant defence systems by regulating key enzymatic pathways, maintaining redox homeostasis, and reducing oxidative damage, ultimately leading to improved germination performance and enhanced tolerance to environmental stresses (Paparella *et al*., 2015; Gill & Tuteja, 2010).

5.3 Enzyme Activation and Reserve Mobilisation

Successful germination depends on the efficient mobilisation of stored reserves such as starch, proteins, and lipids, which provide energy and essential metabolites for the developing embryo. This process is closely associated with the activation of hydrolytic enzymes, including α-amylase, proteases, and lipases, which are responsible for the breakdown of stored reserves during germination (Finch-Savage & Leubner-Metzger, 2006; Rajjou *et al*., 2012). Nanoparticle-based seed priming has been reported to influence germination processes and seedling establishment by enhancing physiological and biochemical activities within the seed. These improvements are often associated with increased metabolic efficiency and may contribute to enhanced activity of enzymes involved in reserve mobilisation (Weitbrecht *et al*., 2011). Higher α-amylase activity facilitates the hydrolysis of starch into sugars, supplying energy necessary for the developing embryo. (Rajjou *et al*., 2012). Protease enzymes play a key role in converting storage proteins into amino acids for protein synthesis, aiding cell division and seedling growth. Meanwhile, lipids are mobilised by lipases and undergo β-oxidation to provide energy via the glyoxylate cycle during early seedling establishment.(Graham, 2008; Eastmond & Graham, 2001).

6. Impact on Seedling Growth and Development

6.1 Root and Shoot Development

The benefits of nanoparticle-based seed priming extend beyond germination and significantly influence early seedling growth and development. In particular, enhanced root system development is essential for successful plant establishment, as it improves water and nutrient uptake, strengthens anchorage, and contributes to overall plant vigour (Ma *et al*., 2010; Nair & Chung, 2014). Studies have reported that nanoparticle-treated seeds exhibit improved root and shoot elongation due to enhanced metabolic activity and more efficient physiological functioning during early growth stages (Tripathi *et al*., 2017).

In direct-seeded rice, nanoparticle priming with selenium and zinc has been shown to significantly improve seedling growth parameters, including root and shoot length, within the initial weeks after sowing (Adhikary *et al*., 2022). The observed increase in seedling vigour was associated with enhanced metabolic processes, improved mobilisation of nutrients, and strengthened antioxidant defence systems during early development. These findings highlight the ability of nanoparticle priming to accelerate early growth and improve crop establishment under field conditions.

Selenium nanoparticles, in particular, have been reported to enhance root development and improve plant water status under both normal and stress environments (Feng *et al*., 2013). This effect is likely linked to the modulation of phytohormones such as auxins and the protection of actively dividing root meristem cells from oxidative damage. Additionally, nanoparticle treatments have been shown to improve root architecture by stimulating lateral root formation and increasing root surface area, thereby enhancing the plant's capacity for water and nutrient uptake (Nair & Chung, 2014).

6.2 Biomass Accumulation and Vigour

Biomass accumulation during the initial stages of plant growth is a key factor determining successful seedling establishment and overall crop yield. Seedling vigour, characterised by quick germination, uniform emergence, and strong early development, can be effectively enhanced through nanoparticle-based seed priming techniques (Paparella et al., 2015; Farooq et al., 2019). Zinc (Zn) and selenium (Se) nanoparticles have been extensively studied for their ability to improve these traits by regulating metabolic processes, strengthening antioxidant systems, and optimising nutrient availability during germination and early seedling growth (Rizwan et al., 2019; Hasanuzzaman et al., 2020).

Priming seeds with zinc oxide (ZnO) nanoparticles has been found to promote biomass accumulation by enhancing the activity of enzymes responsible for mobilising stored reserves. In wheat, treatment with ZnO nanoparticles resulted in noticeable increases in seedling dry weight, as well as improved root and shoot development, leading to higher overall vigour. These improvements are mainly linked to the stimulation of hydrolytic enzymes such as α-amylase, which play a key role in breaking down starch into usable energy. As a result, seedlings are able to grow more quickly and establish more effectively during the early stages (Raliya *et al.,* 2015).

Selenium nanoparticles also play an important role in enhancing biomass by supporting photosynthesis and reducing oxidative stress in plants. In rice, seeds treated with Se nanoparticles showed higher chlorophyll levels, improved photosynthetic activity, and increased overall biomass. These positive effects are mainly due to the protection of chloroplast structure and a reduction in oxidative damage, which together help improve carbon assimilation and maintain steady plant growth (Hartikainen *et al*., 2000; Feng *et al*., 2013).

Apart from improving physiological processes, nanoparticle priming also brings about noticeable changes in plant morphology that support biomass accumulation. Plants treated with zinc nanoparticles often show better root growth and increased branching, which helps them absorb water and nutrients more efficiently. For instance, in maize, Zn-based nanopriming improved root system development and nutrient uptake, ultimately resulting in higher biomass production and stronger early establishment of seedlings (Subbaiah *et al*., 2016).

6.3 Photosynthetic Efficiency

Nanoparticle-based interventions are increasingly recognised for their ability to enhance photosynthetic efficiency in developing seedlings, thereby promoting improved plant growth and productivity. Zinc (Zn) plays a fundamental role in chlorophyll biosynthesis, maintenance of chloroplast integrity, and activation of key enzymes involved in photosynthesis. In contrast, selenium (Se) contributes primarily through its role in reinforcing antioxidant defence systems, thereby protecting the photosynthetic machinery from oxidative damage. The nano-formulation of these micronutrients enhances their solubility, uptake, and translocation within plant tissues, resulting in improved physiological performance compared to conventional forms (Dimkpa & Bindraban, 2016; Hussain *et al*., 2019).

Experimental studies have demonstrated that zinc-based nanoparticles significantly improve photosynthetic parameters such as net photosynthetic rate, stomatal conductance, and chlorophyll fluorescence. These improvements are closely associated with enhanced chlorophyll accumulation and increased efficiency of photosystem II (PSII), which collectively contribute to improved energy conversion and biomass production in seedlings (Liu *et al*., 2021; Gao *et al*., 2018). Furthermore, zinc has been shown to alleviate stress-induced degradation of photosynthetic pigments, restoring chlorophyll a, chlorophyll b, and total chlorophyll content under adverse environmental conditions, thereby maintaining photosynthetic stability (Tavallali *et al*., 2010; Zhang *et al*., 2014).

Selenium nanoparticles further enhance photosynthetic performance by protecting chloroplast membranes and associated enzymes from reactive oxygen species (ROS)-induced damage, particularly under abiotic stresses such as drought, salinity, and high temperature. By improving antioxidant capacity and maintaining cellular redox homeostasis, selenium enables plants to sustain efficient photosynthetic activity even under stress conditions (Feng *et al*., 2013; Hasanuzzaman *et al*., 2011). The combined application of zinc and selenium nanoparticles often results in synergistic effects, where zinc supports structural and enzymatic processes while selenium enhances stress tolerance through antioxidative protection. This complementary interaction ultimately leads to superior photosynthetic efficiency and improved overall plant performance compared to individual treatments (Dimkpa & Bindraban, 2016; Gao *et al.,* 2018).

7. Stress Tolerance Enhancement

7.1 Drought Stress Mitigation

Drought stress is one of the most severe abiotic constraints limiting global crop productivity, significantly impairing plant physiological processes, growth, and yield stability. In this context, nanoparticle-based seed priming has emerged as an advanced strategy to enhance drought tolerance and sustain crop performance under water stress conditions. Selenium nanoparticles (SeNPs), owing to their enhanced bioavailability and surface reactivity, have been reported to improve plant stress tolerance by modulating antioxidant defence systems and maintaining cellular redox homeostasis under drought conditions (Zhang *et al*., 2019; Li *et al*., 2020).

In cereal crops such as wheat, selenium nanoparticle treatments have been shown to enhance drought tolerance by promoting root system development and improving water uptake efficiency. These adaptations enable plants to maintain higher relative water content (RWC) and reduce drought-induced wilting. Moreover, SeNP-treated plants exhibit significantly lower levels of oxidative stress markers, including malondialdehyde (MDA) and hydrogen peroxide (H_2O_2), indicating efficient scavenging of reactive oxygen species (ROS) and improved cellular protection under drought stress (Zhang *et al*., 2019; Wang *et al*., 2020).

Similarly, in tomato and other horticultural crops, selenium nanoparticle application enhances drought tolerance by strengthening antioxidant enzyme activities, stabilizing membrane integrity, and improving osmotic adjustment through increased accumulation of compatible solutes such as proline. These physiological responses support sustained cellular hydration and metabolic activity under water stress conditions, thereby enabling plants to maintain growth and productivity even under prolonged drought exposure (Li *et al*., 2020; Xu *et al.*, 2021).

The drought tolerance conferred by selenium nanoparticles is associated with multiple coordinated physiological and biochemical adjustments, including enhanced root architecture that facilitates efficient water acquisition and improved stomatal regulation contributing to better water use efficiency. In addition, SeNP-mediated enhancement of antioxidant defence systems plays a crucial role in minimising oxidative damage caused by drought-induced reactive oxygen species. These responses are further supported by improved osmotic adjustment through the accumulation of compatible solutes, which helps maintain cellular turgor and metabolic activity under water-deficit conditions. Together, these interconnected mechanisms enable plants to sustain functional stability and growth under drought stress (Hussain *et al*., 2021; Elkelish *et al*., 2020).

7.2 Salt Stress Tolerance

The accumulation of soluble salts creates osmotic pressure and ionic toxicity that severely hinder seed development. Nanoparticle seed priming has emerged as an efficient strategy to overcome these constraints by initiating physiological readiness. Priming with zinc oxide or selenium nanoparticles triggers controlled hydration and metabolic activation without immediate radicle emergence. This process facilitates the creation of seed coat nanopores, improving the influx of water and signalling molecules while stimulating hydrolytic enzymes like alpha-amylase to fuel rapid growth under saline conditions (Rane *et al*., 2022).

At the molecular level, the application of zinc and selenium nanoparticles helps maintain cellular homeostasis by regulating the transport of ions and the stabilisation of protein structures. Salinity stress typically leads to the displacement of essential potassium ions by sodium, disrupting enzymatic functions; however, nanoparticle-treated plants show an enhanced ability to exclude sodium at the root interface or sequester it within vacuoles. This is often achieved through the modulation of the salt overly sensitive signalling pathway and the upregulation of high-affinity potassium transporters (Hassan *et al*., 2022). Furthermore, selenium nanoparticles have been noted for their role in enhancing the thickness of the cell wall and increasing the deposition of lignin and hemicellulose, which provides a physical barrier against salt infiltration and prevents the collapse of vascular tissues under osmotic dehydration (Aparna *et al*., 2023).

The defensive capabilities provided by nanoparticle priming are largely centered on the mitigation of oxidative damage. Salinity triggers the production of reactive oxygen species that lead to lipid peroxidation and the degradation of chlorophyll pigments. Zinc oxide nanoparticles contribute to the structural integrity of superoxide dismutase, while selenium acts as a cofactor for glutathione peroxidase, creating a robust enzymatic shield that neutralises free radicals before they can damage the cellular machinery (Siddiqui & Al-Whaibi, 2023). Recent studies have demonstrated that this primed state allows for higher photosynthetic efficiency and the maintenance of leaf turgor even when soil salinity levels are high (Noman et al., 2020). By fostering a balance between hormonal signalling and antioxidant defence, these nanomaterials ensure that crop productivity is stabilised in marginalised agricultural landscapes (Gupta & Maurya, 2024).

7.3 Heavy Metal Stress Alleviation

Heavy metal contamination of agricultural soils poses serious threats to food security and human health. Selenium nanoparticles (SeNPs) have emerged as an effective strategy to alleviate heavy metal toxicity in plants through multiple physiological and biochemical pathways.

Studies have shown that selenium can significantly reduce the uptake of toxic metals by plant roots and limit their translocation to shoots, thereby protecting edible plant parts from contamination (Feng, Wei, & Tu, 2013; Elkelish *et al*., 2019). In nanoparticle form, selenium exhibits enhanced bioavailability and reactivity, allowing more efficient interaction with plant systems. SeNPs improve membrane stability, regulate mineral nutrient balance, activate antioxidant defence systems, and maintain photosynthetic efficiency under stress conditions. These combined effects enhance plant growth and tolerance in environments contaminated with metals such as cadmium, lead, arsenic, and chromium (Hasanuzzaman *et al.,* 2020).

The mechanisms of heavy metal stress alleviation include immobilisation and sequestration of metal ions, reducing their bioavailability in plant tissues; activation of antioxidant enzymes to counteract reactive oxygen species; improved uptake and utilisation of essential nutrients to maintain cellular homeostasis; and regulation of metal detoxification pathways (Filek *et al.,* 2012; Elkelish *et al.,* 2019). Additionally, selenium can compete with toxic elements for uptake sites or transporters, thereby reducing their accumulation and toxicity within plant tissues (Feng *et al*., 2013).

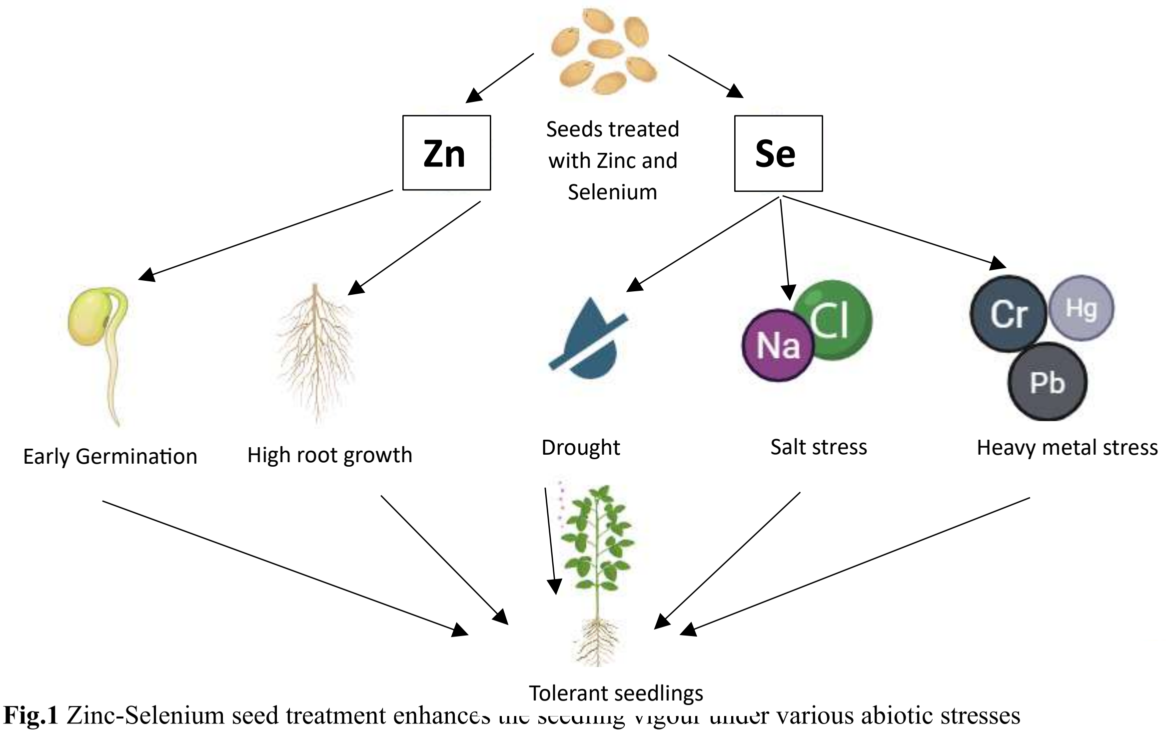

Fig.1 Zinc-Selenium seed treatment enhances the seedling vigour under various abiotic stresses
Zn:Zinc, Se: selenium ; NaCl: salinity ; Pb: Lead, Cr: Chromium , Hg: Mercury(Heavy metals)

8. Synergistic Effects of Combined Zinc and Selenium Nanoparticles

8.1 Complementary Mechanisms

The combined application of zinc and selenium nanoparticles has gained increasing attention due to their synergistic effects, which often surpass the outcomes of individual applications. This synergy is primarily attributed to the complementary physiological and biochemical roles of zinc and selenium in plants, particularly under environmental stress conditions. Zinc is an essential micronutrient involved in enzyme activation, protein synthesis, membrane stability, and regulation of growth hormones such as auxins, whereas selenium plays a critical role in enhancing antioxidant defence systems, maintaining cellular redox homeostasis, and protecting plants against oxidative damage (White & Broadley, 2009; Gupta & Gupta, 2017).

Recent studies have demonstrated that the combined application of zinc and selenium, particularly in nanoparticle or priming-based approaches, significantly improves seed germination, seedling vigour, and biomass accumulation compared to individual treatments (Rizwan *et al*., 2019; Hussain *et al*., 2020). These improvements are associated with enhanced metabolic activity, efficient nutrient mobilisation, and better early-stage plant establishment. Furthermore, co-application of Zn and Se has been shown to improve root development and nutrient uptake efficiency, enabling plants to better tolerate abiotic stresses such as heavy metal toxicity and salinity (Rizwan *et al*., 2019; Elkelish *et al*., 2019).

The synergistic interaction between zinc and selenium is mediated through multiple interconnected mechanisms. Zinc supports structural and catalytic functions by activating a wide range of enzymes and promoting auxin biosynthesis, thereby enhancing cell division and elongation (Cakmak, 2008). In contrast, selenium enhances antioxidant capacity by stimulating enzymes such as superoxide dismutase, catalase, and glutathione-related systems, which mitigate oxidative stress and protect cellular structures (Gupta & Gupta, 2017; Elkelish *et al.,* 2019). Additionally, both elements contribute to improved photosynthetic performance through distinct pathways, with zinc playing a key role in chlorophyll synthesis and enzyme regulation, while selenium protects chloroplast structures and maintains photosystem efficiency under stress conditions (Djanaguiraman *et al*., 2010; Hussain *et al.,* 2020).

8.2 Optimal Ratios and Concentrations

Determining optimal ratios and concentrations for combined nanoparticle treatments is essential for maximising plant growth benefits while minimising potential toxicity or antagonistic interactions. The effectiveness of zinc and selenium nanoparticle combinations is highly dependent on plant species, environmental conditions, and application methods such as seed priming or foliar application. Both micronutrients exhibit concentration-dependent behaviour, where insufficient levels may limit physiological processes while excessive concentrations can induce oxidative stress and disrupt cellular homeostasis, emphasising the need for precise optimisation (Wang *et al.,* 2016; Prasad *et al*., 2012).

Experimental studies have demonstrated that the combined application of zinc and selenium nanoparticles at moderate concentrations significantly enhances seed germination, seedling vigour, and biomass accumulation compared to individual treatments. In cereal crops, co-application of ZnO and Se nanoparticles improves enzymatic activity, accelerates metabolic processes during germination, and enhances nutrient mobilisation, resulting in improved early seedling establishment and uniform growth (Zhao *et al.*, 2017; Chen *et al.,* 2020). These responses are strongly dose-dependent, with moderate concentrations producing optimal outcomes, whereas higher concentrations may inhibit growth due to nanoparticle-induced toxicity. Furthermore, the optimal ratio of Zn and Se may vary across developmental stages, reflecting changing nutrient requirements during plant growth (Chen *et al*., 2020; Prasad *et al*., 2012).

Under abiotic stress conditions such as salinity, combined nanopriming with zinc and selenium has been shown to improve plant tolerance more effectively than individual applications. Studies in oilseed and horticultural crops indicate that balanced concentrations of Zn and Se nanoparticles enhance antioxidant enzyme activities, regulate ion homeostasis, and improve osmotic balance, thereby reducing stress-induced damage and maintaining cellular stability (Kumar *et al.,* 2018; Wang *et al*., 2016). In contrast, excessive application of single elements may lead to oxidative imbalance, metabolic disruption, and reduced plant growth. These findings highlight that moderate and well-balanced combinations of zinc and selenium nanoparticles are more effective than high-dose single-element applications due to improved coordination of physiological and biochemical processes (Zhao *et al*., 2017; Kumar *et al*., 2018).

Table 1: Effect of Zinc and Selenium nanoparticles in different crops under various abiotic stress conditions

Crop	Treatment	Dose	Application Method	Stress Condition	Key Observations	Reference
Wheat (*Triticum aestivum*)	ZnO nanoparticles	10–50 mg/L	Seed priming	Drought	Seeds showed better germination and improved photosynthetic activity under stress	(Rai-Kalal & Jajoo, 2021)
Wheat (*Triticum aestivum*)	ZnO nanoparticles	~100 mg/L	Soil application	Salinity	Helped plants manage salt stress by reducing sodium toxicity and improving defence systems	(Rizwan *et al*., 2017)
Rice (*Oryza sativa*)	ZnO nanoparticles	20–60 mg/L	Seed priming	Salinity	Improved seed vigour and supported enzyme activity during early growth	(Dimkpa *et al*., 2019)
Maize (*Zea mays*)	ZnO nanoparticles	25–100 mg/L	Seed priming	Drought	Supported better seedling growth and	(Prasad *et al*., 2012)

					improved tolerance to water stress	
Common bean (*Phaseolus vulgaris*)	ZnO nanoparticles	25–50 mg/L	Seed priming	Salinity	Helped maintain ion balance and improved overall seedling growth	(Rady *et al.*, 2020)
Groundnut(*Arachis hypogaea*)	ZnO nanoparticles	~1000 mg/L	Soil application	No stress	Increased yield and enhanced nutrient uptake under normal conditions	(RameshReddy *et al.*, 2020)
Tomato (*Solanum lycopersicum*)	ZnO nanoparticles	10–30 mg/L	Foliar spray	Salinity	Improved plant growth and boosted antioxidant activity	(Singh *et al.*, 2021)
Chickpea (*Cicer arietinum*)	ZnO nanoparticles	20–40 mg/L	Seed priming	Drought	Encouraged root development and improved metabolic activity	(Jakhar *et al.*, 2022)
Mustard (*Brassica juncea*)	ZnO nanoparticles	25–75 mg/L	Foliar spray	Salinity	Enhanced photosynthesis and reduced cellular damage	(Sharma *et al.*, 2021)
Barley (*Hordeum vulgare*)	ZnO nanoparticles	20–50 mg/L	Seed priming	Salinity	Improved early seedling growth and vigour	(El-Ramady *et al.*, 2021)
Lentil (*Lens culinaris*)	ZnO nanoparticles	10–30 mg/L	Seed priming	Drought	Promoted better root growth and early establishment	(Adisa *et al.*, 2019)
Sorghum (*Sorghum bicolor*)	Selenium nanoparticles	~500 mg/L	Foliar spray	Drought	Reduced oxidative damage and improved photosynthesis	(Djanaguiraman *et al.*, 2018)
Sunflower (*Helianthus annuus*)	ZnO nanoparticles	50 mg/L	Seed priming	Seed priming	Improved biomass and water-use efficiency	(Dimkpa *et al.*, 2019)
Canola (*Brassica napus*)	Selenium	10–40 µM	Seed priming	Drought	Reduced oxidative damage and improved yield	(Ahmad *et al.*, 2021)
Camelina (*Camelina sativa*)	Selenium	10–40 µM	Seed priming	Drought	Strengthened antioxidant system and supported growth	(Ahmad *et al.*, 2021)

9. Safety and Environmental Considerations

While nanoparticles offer significant advantages in agricultural applications, their safe and sustainable use requires careful evaluation of potential environmental and human health impacts. Biosynthesised nanoparticles, particularly those produced using plant-based extracts, are generally considered more biocompatible and environmentally friendly than chemically synthesised counterparts due to their surface-bound organic compounds, which can reduce toxicity and improve stability in biological systems (Iravani, 2011; Ahmed *et al*., 2016).

The environmental fate of nanoparticles in soil–plant systems remains a critical area of investigation. Once introduced into soil, zinc and selenium nanoparticles may undergo transformation processes such as dissolution, aggregation, or interaction with soil organic matter, influencing their mobility and bioavailability. Several studies have reported that these nanoparticles can release ionic forms that are absorbed by plants through conventional nutrient uptake pathways, while a fraction may persist in particulate form and accumulate in plant tissues (Servin & White, 2016; Lv *et al*., 2019). Such behaviour highlights the complexity of nanoparticle dynamics in agroecosystems and the need for controlled application strategies.

Experimental evidence has also demonstrated that nanoparticles are capable of penetrating seed structures and interacting with internal tissues. For instance, studies on crop seeds have shown that nanoparticles can traverse seed coats and localise within endosperm or embryonic tissues, thereby influencing germination and early seedling development (Ma *et al*., 2010; Rastogi *et al*., 2017). While this confirms their effectiveness in enhancing physiological processes, it also raises important concerns regarding nanoparticle translocation, persistence, and potential accumulation in edible plant parts. Consequently, comprehensive research on nanoparticle bioaccumulation, biotransformation, and long-term toxicity within food chains is essential to ensure the safe implementation of nanotechnology in agriculture (Kah *et al*., 2018; Servin & White, 2016).

10.CONCLUSION

Zinc and selenium nanoparticles show strong potential in enhancing seed performance, plant growth, and stress tolerance due to their high bioavailability and complementary physiological roles. Their combined application offers synergistic benefits, improving productivity and resilience in crops. However, their effective use requires careful optimisation of dosage and application methods to avoid toxicity. Further research on environmental safety and long-term impacts is essential to ensure their sustainable use in agriculture.

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REFERENCES

1. Abdel Latef, A. A. H., et al. (2017). "The possible roles of priming with ZnO nanoparticles in mitigation of salinity stress in lupine (Lupinus termis) plants." Journal of Plant Growth Regulation **36**(1): 60-70.
2. Adhikary, S., Kundu, S., & Bhattacharyya, P. (2022). Nanoparticle priming enhances seedling growth and stress tolerance in direct-seeded rice. *Environmental Nanotechnology, Monitoring & Management, 18*, 100702.
3. Adisa, I. O., Reddy Pullagurala, V. L., Rawat, S., Hernandez-Viezcas, J. A., Dimkpa, C. O., Elmer, W. H., White, J. C., & Gardea-Torresdey, J. L. (2019)
4. Role of engineered nanomaterials in agriculture: A review of recent advances and future perspectives. *Environmental Science: Nano, 6*(7), 2002–2034.https://doi.org/10.1039/C9EN00233K
5. Afzal, I. (2023). Seed priming: A review of recent advances in molecular mechanisms and agricultural applications. *Agronomy, 13*(5), 1–20.
6. Ahmed, S., Ahmad, M., Swami, B. L., & Ikram, S. (2016). A review on plants extract mediated synthesis of silver nanoparticles for antimicrobial applications. *Journal of Advanced Research, 7*(1), 17–28.
7. Ahmad, Z., Waraich, E. A., Akhtar, S., Anjum, S. A., Ahmad, T., & Rizwan, M. (2021). Selenium alleviates the adverse effect of drought in oilseed crops camelina (*Camelina sativa* L.) and canola (*Brassica napus* L.). *Molecules, 26*(6), 1699. https://doi.org/10.3390/molecules26061699
8. Ahmad, B., Shabbir, A., Jaleel, H., Khan, M. M. A., & Sadiq, Y. (2021).
9. Efficacy of zinc oxide nanoparticles in improving plant growth and alleviating abiotic stress: A review. *Environmental Science and Pollution Research, 28*(37), 50808–50827. https://doi.org/10.1007/s11356-021-14939-5
10. Alabdallah, N. M., & Alzahrani, H. S. (2020).
11. The potential mitigation effect of zinc oxide nanoparticles on salinity stress in plants: A review. *Environmental Science and Pollution Research, 27*(10), 10056–10072. https://doi.org/10.1007/s11356-020-07612-2
12. Aparna, K., Rajesh, T., & Kumar, S. (2023). Molecular perspectives of nanoparticle-mediated salt stress tolerance in agricultural crops. Journal of Nanobiotechnology, 21(1), 45-62. https://doi.org/10.1186/s12951-023-01811-0
13. Bailly, C. (2004). Active oxygen species and antioxidants in seed biology. *Seed Science Research, 14*(2), 93–107.
14. Broadley, M. R., Brown, P. H., Cakmak, I., Rengel, Z., & Zhao, F. J. (2012).

15. Function of nutrients: Micronutrients. In P. Marschner (Ed.), *Marschner's mineral nutrition of higher plants* (3rd ed., pp. 191–248). Academic Press.
16. Cakmak, I. (2008). Enrichment of cereal grains with zinc: Agronomic or genetic biofortification? *Plant and Soil, 302*(1–2), 1–17. https://doi.org/10.1007/s11104-007-9466-3
17. Calicioglu, O., Flammini, A., Bracco, S., Bellù, L., & Sims, R. (2019). *The future challenges of food and agriculture: An integrated analysis of trends and solutions*. **Sustainability, 11**(1), 222. https://doi.org/10.3390/su11010222
18. Chen, J., Dou, R., Yang, Z., You, T., & Gao, X. (2020). Interactive effects of zinc and selenium nanoparticles on plant growth and antioxidant responses. *Ecotoxicology and Environmental Safety, 204*, 111043.
19. Dawadi, B., & Karki, T. B. (2023). Seed priming: Current status and future prospects in crop production. *Journal of Agriculture and Food Research, 12*, 100–110.
20. Dimkpa, C. O., & Bindraban, P. S. (2016). Fortification of micronutrients for efficient agronomic production: A review. *Agronomy for Sustainable Development, 36*(1), 7.
21. Dimkpa, C. O., et al. (2018). "Exposure to weathered and fresh nanoparticle and ionic Zn in soil promotes grain yield and modulates nutrient acquisition in wheat (Triticum aestivum L.)." Journal of Agricultural and Food Chemistry **66**(37): 9645-9656.
22. Dimkpa, C. O., Singh, U., Bindraban, P. S., Elmer, W. H., Gardea-Torresdey, J. L., & White, J. C. (2019). Zinc oxide nanoparticles alleviate drought-induced stress in wheat by enhancing growth and nutrient acquisition. *Journal of Agricultural and Food Chemistry, 67*(19), 5665–5675. https://doi.org/10.1021/acs.jafc.9b01310
23. Djanaguiraman, M., et al. (2010). "Selenium protects sorghum leaves from oxidative damage under high temperature stress by enhancing antioxidant defense system." Plant Physiology and Biochemistry **48**(12): 999-1007.
24. Djanaguiraman, M., Nair, R., Giraldo, J. P., & Prasad, P. V. V. (2018).
25. Cerium oxide nanoparticles decrease drought-induced oxidative damage in sorghum leading to improved photosynthesis and growth. *Journal of Experimental Botany, 69*(21), 5145–5158. https://doi.org/10.1093/jxb/ery269
26. Dong, Q., et al. (2025). "Nano-priming with selenium nanoparticles reprograms seed germination, antioxidant defense, and phenylpropanoid metabolism to enhance Fusarium graminearum resistance in maize seedlings." Journal of Advanced Research.
27. Eastmond, P. J., & Graham, I. A. (2001). Re-examining the role of the glyoxylate cycle in oilseeds. *Trends in Plant Science, 6*(2), 72–78.
28. Elkelish, A., Qari, S. H., Mazrou, Y. S. A., Abdelaal, K. A. A., Hafez, Y. M., & El-Esawi, M. A. (2019).Selenium protects wheat seedlings against salt stress-mediated oxidative damage by upregulating antioxidant defense system and osmolyte accumulation. *Plants, 8*(9), 300. https://doi.org/10.3390/plants8090300
29. Elkelish, A., Qari, S. H., Mazrou, Y. S. A., Abdelaal, K. A. A., Hafez, Y. M., & El-Esawi, M. A. (2020). Selenium-induced antioxidant defense and osmotic adjustment in plants under abiotic stress conditions. *Plants, 9*(5), 1–16.
30. El-Badri, A. M., Batool, M., Wang, C., Hashem, A., Taha, R. S., & Kuai, J. (2021). Selenium and zinc oxide nanoparticles modulate hormonal balance and gene expression involved in seed germination of *Brassica napus*. *Environmental Pollution, 268*, 115–698.
31. El-Ramady, H., et al. (2016). "Selenium and nano-selenium in plant nutrition." Environmental Chemistry Letters **14**(1): 123-147.
32. El-Ramady, H., Abdalla, N., Alshaal, T., El-Henawy, A., Faizy, S. E.-D. A., Belal, E.-B. A., Shams, M. S., & Shalaby, T. (2021).
33. Nanotechnology in agriculture: Impacts, applications, and future prospects. *Environment, Biodiversity and Soil Security, 5*, 191–215. https://doi.org/10.21608/jenvbs.2021.70056.1140
34. Faizan, M., Faraz, A., Yusuf, M., Khan, S. T., & Hayat, S. (2018). Zinc oxide nanoparticle-mediated changes in photosynthetic efficiency and antioxidant system of tomato plants. *Photosynthetica, 56*(3), 678–686.
35. Faizan, M., et al. (2021). "Zinc oxide nanoparticles alleviates the adverse effects of cadmium stress on Oryza sativa via modulation of the photosynthesis and antioxidant defense system." Ecotoxicology and Environmental Safety **220**: 112401.
36. Farooq, M., Usman, M., Nadeem, F., Rehman, H., Wahid, A., Basra, S. M. A., & Siddique, K. H. M. (2019). Seed priming in field crops: Potential benefits, adoption and challenges. *Crop and Pasture Science, 70*(9), 731–771.
37. Feng, R., Wei, C., & Tu, S. (2013). The roles of selenium in protecting plants against abiotic stresses. *Environmental and Experimental Botany, 87*, 58–68.
38. Filek, M., Keskinen, R., Hartikainen, H., Szarejko, I., Janiak, A., Miszalski, Z., & Golda, A. (2012). The protective role of selenium in rape seedlings subjected to cadmium stress. *Journal of Plant Physiology, 169*(10), 1053–1060. https://doi.org/10.1016/j.jplph.2012.03.016
39. Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *New Phytologist, 171*(3), 501–523.

40. Gao, F., Liu, C., Qu, C., Zheng, L., Yang, F., Su, M., & Hong, F. (2018). Was improvement of photosynthesis in spinach plants treated with nano-TiO_2 associated with enhanced Rubisco activity? *Biological Trace Element Research, 119*(3), 183–192.
41. García-Locascio, E., et al. (2024). "Impact of seed priming with Selenium nanoparticles on germination and seedlings growth of tomato." Scientific Reports **14**(1): 6726.
42. Ghafariyan, M. H., et al. (2013). "Effects of magnetite nanoparticles on soybean chlorophyll." Environmental science & technology **47**(18): 10645-10652.
43. Gill, S. S., & Tuteja, N. (2010). Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiology and Biochemistry, 48*(12), 909–930.
44. Graham, I. A. (2008). Seed storage oil mobilisation. *Annual Review of Plant Biology, 59*, 115–142.
45. Gupta, M., & Gupta, S. (2017).An overview of selenium uptake, metabolism, and toxicity in plants. *Frontiers in Plant Science, 7*, 2074. https://doi.org/10.3389/fpls.2016.02074
46. Gupta, R., & Maurya, A. N. (2024). Mechanistic insights into metal-based nanoparticle seed priming for sustainable agriculture in saline terrains. Environmental Science: Nano, 11(2),
312-330. https://doi.org/10.1039/D3EN00712H
47. Hartikainen, H., Xue, T., & Piironen, V. (2000). Selenium as an antioxidant and pro-oxidant in ryegrass. *Plant and Soil, 225*, 193–200. https://doi.org/10.1023/A:1026512921026
48. Hasanuzzaman, M., Hossain, M. A., & Fujita, M. (2011). Selenium-induced up-regulation of the antioxidant defense and methylglyoxal detoxification system reduces salinity-induced damage in plants. *Biological Trace Element Research, 143*(3), 1704–1721.
49. Hasanuzzaman, M., et al. (2020). "Selenium in plants: Boon or bane?" Environmental and Experimental Botany **178**: 104170.
50. Hasanuzzaman, M., Bhuyan, M. H. M. B., Anee, T. I., Parvin, K., Nahar, K., Mahmud, J. A., & Fujita, M. (2020).
Regulation of ascorbate–glutathione pathway in mitigating oxidative damage in plants under abiotic stress. *Antioxidants,* *9*(5), 384.
https://doi.org/10.3390/antiox9050384
51. Hassan, M. U., Chattha, M. U., Khan, I., Chattha, M. B., Aamer, M., Nawaz, M., Ali, A., & Khan, S. T. (2022). Zinc oxide nanoparticles-mediated alleviation of salt stress in cereals: A review of physiological and molecular mechanisms. Plant Growth Regulation, 98(3), 411-429. https://doi.org/10.1007/s10725-022-00877-w

52. Hawrylak-Nowak, B., et al. (2018). "Mechanisms of selenium-induced enhancement of abiotic stress tolerance in plants." Plant nutrients and abiotic stress tolerance: 269-295.

53. Hu, W., et al. (2022). "Foliar application of silicon and selenium improves the growth, yield and quality characteristics of cucumber in field conditions." Scientia horticulturae **294**: 110776.
54. Hussain, A., Ali, S., Rizwan, M., Rehman, M. Z., Javed, M. R., Imran, M., & Chatha, S. A. S. (2019). Role of zinc in plant nutrition, growth, and stress tolerance. *Journal of Plant Growth Regulation, 38*(4), 1462–1476.
55. Hussain, S., Khan, F., Cao, W., Wu, L., & Geng, M. (2020).
Seed priming with zinc and selenium improves germination and growth under stress conditions. *Environmental Science and Pollution Research, 27*, 34337–34348.
56. Hussain, S., Khan, F., Cao, W., Wu, L., & Geng, M. (2021). Seed priming with selenium nanoparticles enhances drought tolerance through regulation of antioxidant metabolism and water relations in plants. *Plant Physiology and Biochemistry, 166*, 521–530.
57. Ikram, M., et al. (2021). "Biomedical potential of plant-based selenium nanoparticles: a comprehensive review on therapeutic and mechanistic aspects." International Journal of Nanomedicine: 249-268.
58. Ikram, M., et al. (2022). "Phytogenic selenium nanoparticles elicited the physiological, biochemical, and antioxidant defense system amelioration of Huanglongbing-infected 'Kinnow'mandarin Plants." Nanomaterials **12**(3): 356.
59. Iravani, S. (2011). Green synthesis of metal nanoparticles using plants. *Green Chemistry, 13*(10), 2638–2650.
60. Ishtiaq, M., et al. (2023). "Seed priming with the selenium nanoparticles maintains the redox status in the water stressed tomato plants by modulating the antioxidant defense enzymes." Plants **12**(7): 1556.
61. Jakhar, S., Jangra, S., Sangwan, P., & Duhan, J. S. (2022)
62. Nanotechnology in agriculture: Prospects and challenges. *Chemosphere, 286*, 131766.
https://doi.org/10.1016/j.chemosphere.2021.131766
63. Kah, M. (2015). "Nanopesticides and nanofertilizers: emerging contaminants or opportunities for risk mitigation?" Frontiers in chemistry **3**: 64.
64. Kah, M., et al. (2018). "A critical evaluation of nanopesticides and nanofertilizers against their conventional analogues." Nature nanotechnology **13**(8): 677-684.
65. Khan, I., Saeed, K., & Khan, I. (2019). Nanoparticles: Properties, applications and toxicities. *Arabian Journal of Chemistry, 12*(7), 908–931. https://doi.org/10.1016/j.arabjc.2017.05.011
66. Kaklewski, K., Nowak, J., & Ligocki, M. (2008). Effects of selenium content in green parts of plants on the amount of ATP and ascorbate–glutathione cycle enzyme activity at various growth stages of wheat and oilseed rape. *Journal of Plant Physiology, 165*(10), 1011–1022.

67. Kumar, A., Prasad, M. N. V., Sytar, O., & Brestic, M. (2018). Zinc and selenium nanoparticles: Potential role in improving plant stress tolerance. *Plant Physiology Reports, 23*(3), 321–330.
68. Kuznetsov, V., & Kuznetsov, V. (2003). Selenium regulates the water status of plants exposed to drought. *Doklady Biological Sciences, 390*, 266–268.
69. Latef, A. A. H. A., Srivastava, A. K., Saber, H., Alwaleed, E. A., & Tran, L. S. P. (2017). Sensing of environmental stress and reactive oxygen species signaling in plants: Role of nanoparticles. *Plant Physiology and Biochemistry, 121*, 75–85.
70. Li, J., Hu, J., Ma, C., Wang, Y., Wu, C., Huang, J., & Xing, B. (2020). Uptake, translocation, and physiological effects of selenium nanoparticles in plants under stress conditions. *Environmental Science: Nano, 7*(2), 456–465.
71. Liu, R., Zhang, H., & Lal, R. (2021). Effects of nanoparticles on plant growth and photosynthesis: A review. *Environmental Chemistry Letters, 19*(2), 1469–1488.
72. Lv, J., Zhang, S., Luo, L., Zhang, J., Yang, K., & Christie, P. (2019). Accumulation, speciation and uptake pathway of ZnO nanoparticles in plants. *Environmental Science: Nano, 6*(2), 486–495.
73. Ma, X., Geiser-Lee, J., Deng, Y., & Kolmakov, A. (2010). Interactions between engineered nanoparticles and plants: Phytotoxicity, uptake, and accumulation. *Science of the Total Environment, 408*(16), 3053–3061.
74. Mahakham, W., et al. (2017). "Nanopriming technology for enhancing germination and starch metabolism of aged rice seeds using phytosynthesized silver nanoparticles." Scientific Reports **7**(1): 8263.
75. Marschner, P. (Ed.). (2012). *Marschner's mineral nutrition of higher plants* (3rd ed.). Academic Press.
76. Mirza Hasanuzzaman, M. H., et al. (2010). "Selenium in higher plants: physiological role, antioxidant metabolism and abiotic stress tolerance."
77. Nair, R., & Chung, I. M. (2014). Regulation of plant growth and metabolism by zinc oxide nanoparticles. *Plant Cell, Tissue and Organ Culture, 118*(2), 209–222.
78. Nile, S. H., Thiruvengadam, M., Wang, Y., Samynathan, R., Shariati, M. A., Rebezov, M., Nile, A. S., Sun, M., & Kai, G. (2022).
79. Nano-priming as emerging seed priming technology for sustainable agriculture—Recent developments and future perspectives. *Journal of Nanobiotechnology, 20*, 254. https://doi.org/10.1186/s12951-022-01462-5
80. Noctor, G., & Foyer, C. H. (1998). Ascorbate and glutathione: Keeping active oxygen under control. *Annual Review of Plant Physiology and Plant Molecular Biology, 49*, 249–279.
81. Noman, M., Ahmed, T., Ijaz, U., Shahid, M., Li, D., & Song, F. (2020). Nanomaterial-based seed priming: A novel strategy to improve plant growth and response to abiotic stresses. ACS Sustainable Chemistry & Engineering, 8(23), 8443-8458. https://doi.org/10.1021/acssuschemeng.0c02821
82. Nonogaki, H., Bassel, G. W., & Bewley, J. D. (2010). Germination—Still a mystery. *Plant Science, 179*(6), 574–581.
83. Paparella, S., et al. (2015). "Seed priming: state of the art and new perspectives." Plant cell reports **34**(8): 1281-1293.
84. Prasad, T. N. V. K. V., Sudhakar, P., Sreenivasulu, Y., Latha, P., & Munaswamy, V. (2012). Effect of nanoscale zinc oxide particles on the germination, growth and yield of crops. *Journal of Plant Nutrition, 35*(6), 905–927.
85. Rady, M. M., Varma, C. B., & Howladar, S. M. (2020). ommon bean (*Phaseolus vulgaris* L.) seedlings overcome salt stress as a result of presowing seed treatment with zinc oxide nanoparticles. *Journal of Plant Growth Regulation, 39*(2), 740–753.
https://doi.org/10.1007/s00344-019-09941-0
86. Rajjou, L., Duval, M., Gallardo, K., Catusse, J., Bally, J., Job, C., & Job, D. (2012). Seed germination and vigour. *Annual Review of Plant Biology, 63*, 507–533.
87. Raliya, R., Nair, R., Chavalmane, S., Wang, W. N., & Biswas, P. (2015). Mechanistic evaluation of translocation and physiological impact of titanium dioxide and zinc oxide nanoparticles on the tomato plant. *Metallomics, 7*(12), 1584–1594. https://doi.org/10.1039/C5MT00168D
88. Raliya, R., Saharan, V., Dimkpa, C., & Biswas, P. (2017). Nanofertilizer for precision and sustainable agriculture: Current state and future perspectives. *Journal of Agricultural and Food Chemistry, 65*(36), 7210–7219. https://doi.org/10.1021/acs.jafc.7b02178
89. Rai-Kalal, P., & Jajoo, A. (2021). Priming with zinc oxide nanoparticles improve germination and photosynthetic performance in wheat. *Plant Physiology and Biochemistry, 160*, 341–351.
https://doi.org/10.1016/j.plaphy.2021.01.019
90. RameshReddy, S., Prasad, T. N. V. K. V., & Sudhakar, P. (2020). Effect of zinc oxide nanoparticles on growth, yield, and nutrient uptake in peanut (*Arachis hypogaea* L.). *Plant Physiology Reports, 25*(2), 260–267. https://doi.org/10.1007/s40502-020-00506-0
91. Rane, J., Bakshi, M., Loka, d. A., Reddy, V. R., & Singh, N. P. (2022). Nanopriming of seeds: A potential tool for enhancing germination and seedling vigor under abiotic stress. Frontiers in Plant Science, 13, 854512. https://doi.org/10.3389/fpls.2022.854512
92. Rastogi, A., et al. (2017). "Impact of metal and metal oxide nanoparticles on plant: a critical review." Frontiers in Chemistry **5**: 78.
93. Rico, C. M., et al. (2011). "Interaction of nanoparticles with edible plants and their possible implications in the food chain." Journal of Agricultural and Food Chemistry **59**(8): 3485-3498.

94. Rizwan, M., Ali, S., Ali, B., Adrees, M., Arshad, M., Hussain, A., Zia-ur-Rehman, M., Waris, A. A., & Martinez-Ballesta, M. del C. (2017).Zinc and iron oxide nanoparticles improved the plant growth and reduced the oxidative stress and cadmium concentration in wheat. *Environmental Science and Pollution Research, 24*(7), 6545–6554.
https://doi.org/10.1007/s11356-016-8327-4
95. Rizwan, M., Ali, S., Qayyum, M. F., Ok, Y. S., Adrees, M., Ibrahim, M., & Abbas, F. (2019). Effect of metal and metal oxide nanoparticles on plant growth and physiology. *Environmental Science and Pollution Research, 26*, 17631–17644. https://doi.org/10.1007/s11356-019-05059-2
96. Salama, D. M., et al. (2019). "Effect of zinc oxide nanoparticles on the growth, genomic DNA, production and the quality of common dry bean (Phaseolus vulgaris)." Biocatalysis and Agricultural Biotechnology **18**: 101083.
97. Sarker, P., Mahamud, M. A., Paul, N. C., Harine, I. J., Sumi, M. J., Chakrobortty, J., Rahman, M. A., Brestic, M., Rahimi, M., & Imran, S. (2025). Zinc application through seed priming and foliar spray enhanced germination, seedling growth, photosynthetic pigments, and reduced lead toxicity in tomato (*Solanum lycopersicum* L.). *BMC Plant Biology*, *25*, 1678. https://doi.org/10.1186/s12870-025-07733-x
98. Sedghi, M., et al. (2013). "Effect of nano zinc oxide on the germination parameters of soybean seeds under drought stress." Ann West Univ Timisoara Ser Biol **16**(2): 73.
99. Servin, A. D., & White, J. C. (2016). Nanotechnology in agriculture: Next steps for understanding engineered nanoparticle exposure and risk. *NanoImpact, 1*, 9–12.
100. Sharma, P., Jha, A. B., Dubey, R. S., & Pessarakli, M. (2021). Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. *Journal of Botany, 2021*, 1–26. https://doi.org/10.1155/2021/5381738
101. Shu, K., Liu, X. D., Xie, Q., & He, Z. H. (2016). Two faces of one seed: Hormonal regulation of dormancy and germination. *Molecular Plant, 9*(1), 34–45.
102. Singh, A., Singh, N. B., Hussain, I., Singh, H., & Yadav, V. (2021). Synthesis and characterisation of zinc oxide nanoparticles and their impact on plant growth and physiology. *Journal of Plant Nutrition, 44*(10), 1496–1511. https://doi.org/10.1080/01904167.2021.1871747
103. Subbaiah, L. V., Prasad, T. N. V. K. V., Krishna, T. G., Sudhakar, P., Reddy, B. R., & Pradeep, T. (2016). Novel effects of nanoparticulate delivery of zinc on growth, productivity, and zinc biofortification in maize (*Zea mays* L.). *Journal of Agricultural and Food Chemistry, 64*(19), 3778–3788.
https://doi.org/10.1021/acs.jafc.6b00838
104. Siddiqui, S. A., & Al-Whaibi, M. H. (2023). Role of nano-selenium in the regulation of plant metabolism and environmental stress tolerance. Journal of King Saud University - Science, 35(1), 102434. https://doi.org/10.1016/j.jksus.2022.102434
105. Tamindžić, G., et al. (2023). "Comprehensive metal-based nanopriming for improving seed germination and initial growth of field pea (Pisum sativum L.)." Agronomy **13**(12): 2932.
106. Tavallali, V., Rahemi, M., & Eshghi, S. (2010). Zinc alleviates salt stress and increases antioxidant enzyme activity in pistachio (*Pistacia vera* L.). *Scientia Horticulturae, 125*(3), 381–385.
107. Tian, Y., Guan, B., Zhou, D., Yu, J., Li, G., & Lou, Y. (2023). Bibliometric analysis of seed priming research: Trends and future perspectives. *Plants, 12*(3), 1–15.
108. Tripathi, D. K., Singh, S., Singh, V. P., Prasad, S. M., Chauhan, D. K., Dubey, N. K., & Singh, S. (2017). Silicon nanoparticles more effectively alleviate arsenate toxicity than silicon in maize. *Scientific Reports, 7*, 1–13.
109. Turakainen, M., Hartikainen, H., Ekholm, P., & Seppänen, M. M. (2006). Distribution of selenium in different biochemical fractions and raw darkening degree of potato (*Solanum tuberosum* L.) tubers supplemented with selenate. *Journal of Agricultural and Food Chemistry, 54*(23), 8617–8622.
110. Vanlalveni, C., et al. (2021). "Green synthesis of silver nanoparticles using plant extracts and their antimicrobial activities: A review of recent literature." RSC advances **11**(5): 2804-2837.
111. Wang, P., Lombi, E., Zhao, F. J., & Kopittke, P. M. (2016). Nanotechnology: A new opportunity in plant sciences. *Trends in Plant Science, 21*(8), 699–712.
112. Wang, X., Yang, X., Chen, S., Li, Q., Wang, W., Hou, C., Gao, X., & Wang, L. (2020). Zinc oxide nanoparticles affect biomass accumulation and photosynthesis in Arabidopsis. *Frontiers in Plant Science, 11*, 1–10.
113. Weitbrecht, K., Müller, K., & Leubner-Metzger, G. (2011). First off the mark: Early seed germination. *Journal of Experimental Botany, 62*(10), 3289–3309.
114. White, P. J., & Broadley, M. R. (2009). Biofortification of crops with essential mineral elements. *Trends in Plant Science, 14*(6), 286–295.https://doi.org/10.1016/j.tplants.2009.03.005
115. Xu, C., Tan, J., Wang, L., Liu, Z., & Wang, Y. (2021). Selenium nanoparticles regulate antioxidant systems and improve drought tolerance in plants. *Plant Physiology and Biochemistry, 164*, 27–35.
116. Zhang, Y., Chen, H., He, C., & Wang, Q. (2014). Exogenous zinc alleviates oxidative stress and improves photosynthesis in plants under environmental stress. *Plant Physiology and Biochemistry, 80*, 1–10.
117. Zhang, H., Zhao, Z., & Zhang, X. (2019). Effects of selenium nanoparticles on plant growth and oxidative stress under drought conditions. *Journal of Plant Growth Regulation, 38*(2), 589–599.
118. Zhao, L., Sun, Y., Hernandez-Viezcas, J. A., Hong, J., Majumdar, S., Niu, G., Duarte-Gardea, M., Peralta-Videa, J. R., & Gardea-Torresdey, J. L. (2017).

119. Monitoring the environmental effects of engineered nanoparticles in plants. *Trends in Biotechnology, 35*(6), 574–588.
120. Zulfiqar, F. (2021). "Effect of seed priming on horticultural crops." Scientia horticulturae **286**: 110197.