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Smart Nano-Fertilisers and Enzyme Activation: Revolutionising Crop Stress Management Under Climate Change Conditions

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Abstract **Original Research Article**

Drought, salinity, extreme heat and heavy metal toxicity which are caused by climate change, pose threats to food crops around the globe. They disturb the normal functioning of the plant, boost ROS production and destroy the structure of plant cells. The best defense against these results is the activity of enzymes in antioxidant systems such as SOD, CAT and APX in plants. Lately, the use of smart NFs has helped strengthen the defense systems of plants and assist in the delivery of nutrients. At the molecular level, NFs make sure that nutrients are released slowly and only when needed by the plant. This review covers blending nano-fertilizers through various methods, focusing on how they are compatible with living things, environmentally friendly and safe. Impacts of ZnO, Fe, SiO_2 and nano-NPK are reviewed for assisting root development, photosynthesis and improving harvests under stressful environment. To enhance the way plants reach fertilizers, science also uses encapsulation, pH-responsive coatings and foliar applications. When taken up into cells, NFs engage in activities with chloroplasts and mitochondria, activate certain ROS-removing genes and modify stress-responsive genes. Case studies find that they impact antioxidant action, balance the redox state in plant cells and boost crop yields for wheat, rice and maize. Furthermore, utilizing nano-sensors and precision agriculture means nutrient monitoring is possible at any time and farming can be adapted to different fields. In total, smart nano-fertilizers help agriculture become more sustainable and adapt to climate change by boosting enzymes, causing minimal damage to the environment and allowing farmers to produce more crops.

Keywords: Smart nano-fertilizers, abiotic stress, antioxidant enzymes, ROS, green synthesis, nutrient delivery, precision agriculture, redox homeostasis, crop resilience, climate-smart agriculture.

1. INTRODUCTION

Climate change is profoundly reshaping global agricultural systems, presenting urgent challenges to food security, crop productivity, and environmental sustainability. The rising concentration of greenhouse gases, particularly carbon dioxide (CO_2), has led to elevated global temperatures, irregular precipitation patterns, and an increased frequency of extreme weather events. These climate-induced changes impose multiple forms of abiotic stress, such as drought, salinity, extreme heat, and heavy metal toxicity, on crops, thereby threatening plant development, yield stability, and, ultimately, the livelihoods of farming communities (Shiade *et al.*, 2024; Verma *et al.*, 2022). Soil degradation and water scarcity, exacerbated by increased evapotranspiration, further compound these threats. At the physiological level, these stresses hinder vital functions such as photosynthesis, nutrient uptake, and cellular homeostasis, often resulting in oxidative damage, membrane destabilisation, and crop failure (Cao *et al.*, 2025).

One of the plant's key survival mechanisms under abiotic stress is the activation of its antioxidant defence system. Stress conditions lead to the excessive accumulation of reactive oxygen species (ROS) like hydrogen peroxide (H_2O_2) and superoxide radicals, which damage cellular macromolecules, including proteins, lipids, and nucleic acids. To combat this oxidative burden, plants utilise a complex enzymatic system that includes superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) to detoxify ROS and maintain redox equilibrium (Türkoğlu *et al*., 2024). Research has demonstrated that boosting the activity of these enzymes can significantly improve plant resilience under abiotic stress. For example, nano-fertiliser applications have been shown to enhance antioxidant enzyme activities in crops facing drought and salinity stress, thereby supporting plant growth and yield maintenance (Mustafa *et al*., 2022; Shoukat *et al*., 2025). In addition, nano-agrochemicals can modulate the expression of stress-responsive genes, indicating that biochemical regulation through nanotechnology holds great promise for engineering climate-resilient crops (Seeda *et al*., 2021).

In this context, smart nano-fertilisers emerge as an innovative and sustainable solution. These are specially engineered nanomaterials capable of delivering macro- and micronutrients, such as nitrogen, phosphorus, zinc, and silicon, in a controlled and targeted manner. Compared to conventional fertilisers, nano-formulations significantly enhance nutrient uptake efficiency, reduce nutrient leaching, and support consistent plant development under challenging environmental conditions (Patil *et al*., 2024; Saleh *et al*., 2021). For instance, nano-Zno and nano-silicon have been shown to improve root development, photosynthesis, grain yield, and osmotic regulation in crops exposed to drought and salinity, while simultaneously upregulating the antioxidant defence system (Alhasan *et al*., 2021; Shoukat *et al*., 2025). Furthermore, these advanced fertilisers contribute to ecological sustainability by minimising the overuse of chemical inputs and reducing the risk of environmental contamination. Controlled-release formulations and foliar applications are especially effective in limiting runoff and preserving soil and water quality (Miguel-Rojas & Pérez-de-Luque, 2023; Giri *et al*., 2023).

Beyond nutrient delivery, smart nano-fertilisers integrate well with precision agriculture technologies. Nanosensors embedded in agricultural systems can detect nutrient deficiencies, soil ph, or plant stress markers in real time, guiding the application of nano-fertilisers with high spatial accuracy. This integration enhances resource use efficiency and aligns agricultural practices with modern sustainability goals (Singh *et al*., 2023). Overall, the strategic deployment of smart nano-fertilisers represents a transformative approach to mitigating climate-induced crop stress, enhancing food security, and promoting sustainable agriculture in a warming world.

2. Plant Stress Physiology under Climate Change:

2.1 Major Abiotic Stressors: Drought, Salinity, Heat, Heavy Metals:

Abiotic stresses refer to non-living environmental factors that negatively impact plant health and productivity. Among the most impactful in the context of climate change are drought, salinity, heat, and heavy metal contamination (Jing *et al*., 2024). These stressors often occur simultaneously, placing a compounded burden on plant systems. Drought stress, aggravated by erratic rainfall and increasing temperatures, restricts water availability and nutrient transport, causing osmotic imbalance, reduced turgor, and impaired photosynthesis. This results in elevated ROS levels, triggering oxidative stress and cellular injury (Hussain *et al*., 2019; Lukić *et al*., 2020). Salinity stress, exacerbated by rising sea levels and poor irrigation practices, imposes both osmotic and ionic stress on plants. High concentrations of sodium (Na^+) and chloride (Cl^-) ions disrupt enzymatic functions, interfere with nutrient balance, and lead to ROS accumulation. Biotic interventions such as endophytic fungi (*Piriformospora indica*) have been shown to mitigate salinity effects by enhancing antioxidant responses and osmolyte synthesis (Nurrahma *et al*., 2024).

Heat stress impacts cellular membranes, accelerates respiration, and disrupts reproductive processes. It damages photosystems and denatures proteins, while also increasing ROS production through interrupted electron transport in chloroplasts and mitochondria (Rahman *et al*., 2024). Heavy metal stress, resulting from industrial pollution and agrochemical misuse, introduces toxic ions such as cadmium (Cd), arsenic (As), and lead (Pb) into the soil. These metals interfere with essential nutrient uptake, destabilise metabolic functions, and promote oxidative injury by inducing ROS generation and impairing the antioxidant defence mechanisms (Mareri *et al*., 2022).

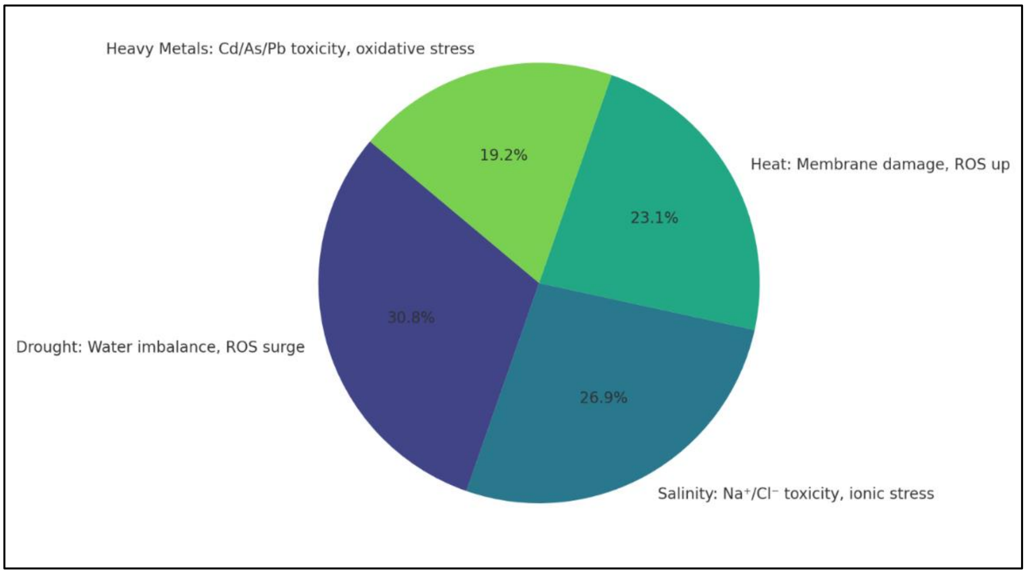


Figure: Relative Impact of Abiotic Stressors on Plant Physiology

2.2 Oxidative Stress and ROS Generation in Plants:

Abiotic stresses such as drought, salinity, heat, and heavy metal toxicity commonly trigger an overproduction of reactive oxygen species (ROS) in plant cells. These include superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radicals (•OH), and singlet oxygen ($^1O_2$). While ROS are essential signalling molecules at low concentrations, regulating various physiological processes such as stomatal movement, hormone signalling, and gene expression, their uncontrolled accumulation leads to oxidative stress and substantial cellular damage (Cassia *et al*., 2018; Kar, 2011). Thus, the balance between ROS generation and detoxification is crucial for plant survival under stress conditions.

The major sources of ROS in plant cells are chloroplasts (particularly photosystems I and II during photosynthesis), mitochondria (via the electron transport chain during respiration), and peroxisomes (during photorespiration). Under stress conditions, impaired electron transport leads to electron leakage, which reacts with molecular oxygen to form ROS (Gill & Tuteja, 2010). Additionally, enzymes like NADPH oxidases (respiratory burst oxidase homologs, RBOHS) located on the plasma membrane, along with apoplastic peroxidases, contribute significantly to ROS production during environmental stress episodes (Rahman *et al*., 2024). ROS are not merely toxic byproducts; they serve as critical messengers in complex signalling networks. Hydrogen peroxide (H_2O_2), due to its moderate reactivity and ability to diffuse through membranes, is especially important in signal transduction. It modulates stress-responsive gene expression, initiates systemic acquired resistance, and contributes to the closure of stomata to reduce water loss (Gechev & Petrov, 2020; Wang *et al*., 2023). This signalling role of ROS is tightly linked with hormonal pathways involving abscisic acid (ABA), ethylene, and salicylic acid, which regulate both ROS production and the activity of antioxidant systems (Sewelam *et al*., 2019; Liu & Yang, 2020).

However, when ROS levels surpass the threshold that cellular antioxidants can neutralise, oxidative stress ensues. This imbalance causes severe damage to essential biomolecules—lipid peroxidation compromises membrane integrity, carbonylation modifies protein structure and function, and ROS-induced strand breaks damage nuclear and organellar DNA (Dar *et al*., 2017; Kostecki *et al*., 2020). Persistent oxidative damage can initiate programmed cell death (PCD), a regulated mechanism that removes irreparably damaged cells but also reduces overall plant fitness under prolonged stress (Qamer *et al*., 2021). Modern advancements in molecular biology have further illuminated the role of ROS in plant responses. Tools like ROSMETER have helped decode ROS-specific transcriptomic responses based on their subcellular origin, allowing precise insights into how different organelles contribute to stress signalling (Rosenwasser *et al*., 2013). Furthermore, real-time ROS detection technologies—including electron paramagnetic resonance (EPR), ROS-specific fluorescent dyes, and biosensors—have enabled spatiotemporal mapping of ROS dynamics in subcellular compartments (Prasad *et al*., 2019).

2.3 Role of Endogenous Antioxidant Enzymes in Defence:

Plants are continuously challenged by a wide array of abiotic stressors such as drought, salinity, heavy metals, and temperature extremes, which disrupt normal physiological processes and stimulate the excessive generation of reactive oxygen species (ROS). In response, plants have developed a highly efficient and multi-tiered antioxidant defence system composed of both enzymatic and non-enzymatic components. Among the enzymatic defenses, superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione peroxidase (GPx), and glutathione reductase (GR) serve as the primary line of defense to scavenge ROS, sustain redox homeostasis, and ensure plant survival under stress conditions. SOD acts as the first enzymatic barrier against oxidative stress by catalysing the conversion of superoxide radicals (O_2^-) into hydrogen peroxide (H_2O_2) and molecular oxygen (O_2). This action reduces the potential toxicity of superoxide radicals and forms H_2O_2, which is subsequently detoxified by downstream enzymes. SOD exists in multiple isoforms—Mn-SOD, Fe-SOD, and Cu/Zn-SOD—distributed in various organelles such as mitochondria, chloroplasts, and the cytosol (Rajput *et al*., 2021). Experimental studies have shown that transgenic plants overexpressing SOD exhibit significantly enhanced tolerance to oxidative damage during drought and salinity stress (Sharma *et al*., 2017).CAT complements this system by decomposing H_2O_2 into water and oxygen without requiring a reducing substrate. Due to its high turnover rate, CAT efficiently detoxifies large quantities of H_2O_2, especially during intense oxidative bursts. However, its response is both organ- and species-specific; in some plant species, CAT activity is elevated under salt stress, while in others it is suppressed, reflecting tightly regulated expression patterns (Ahmad *et al*., 2017; Hanaka *et al*., 2018).

APX, another crucial enzyme, is part of the ascorbate–glutathione cycle and functions in various cellular compartments, including chloroplasts, mitochondria, and the cytosol. It reduces H_2O_2 to water using ascorbate as an electron donor and exhibits high sensitivity to oxidative cues. Isoform-specific regulation of APX has been linked to different types of environmental stress, and genome-wide analyses of desiccation-tolerant species have highlighted its essential role in drought resistance (Gupta *et al*., 2019; Rajput *et al*., 2021). GPx plays a vital role in detoxifying both H_2O_2 and lipid hydroperoxides by utilising glutathione (GSH) as a reducing agent. It is particularly important in protecting cellular membranes against lipid peroxidation. The upregulation of GPx under abiotic stress has been associated with improved membrane integrity and enhanced tolerance to environmental stressors. Moreover, its activity is functionally linked to GR, which regenerates reduced glutathione from its oxidised form (GSSG), maintaining the cellular redox environment (Sahoo & Tiwari, 2022).

GR serves as a critical component of the ascorbate–glutathione cycle by sustaining the GSH pool required for APX and GPx activity. Its expression and activity are upregulated under various stress conditions such as salinity and heavy metal toxicity, facilitating the restoration of antioxidant capacity and redox equilibrium after ROS detoxification (Ahmad *et al*., 2017). Collectively, these enzymes operate in a coordinated and dynamic manner to modulate stress responses across different cellular compartments. Importantly, antioxidant enzyme activities vary depending on tissue type and specific stress conditions. In maise, SOD and CAT levels were markedly elevated in salt-tolerant genotypes. In contrast, sensitive genotypes showed reduced enzyme activity and higher oxidative damage, emphasising the adaptive role of these enzymes (Neto *et al*., 2006). In mangrove species such as *Bruguiera parviflora*, NaCl stress induced the expression of specific SOD and GR isoforms, while CAT activity decreased, suggesting stress-type-specific enzymatic adjustments (Parida *et al*., 2004).

Beyond their detoxifying function, antioxidant enzymes interact with hormonal signalling pathways such as abscisic acid (ABA), ethylene, and salicylic acid. These hormones regulate the transcription of antioxidant genes and participate in priming the plant's defence mechanisms, allowing a more robust and rapid response upon subsequent stress exposure (Mahapatra, 2021). This hormonal crosstalk plays a central role in fine-tuning ROS levels and optimising the plant's physiological resilience. Advances in biotechnology have made it possible to enhance the antioxidant capacity of plants through genetic engineering. Overexpression of antioxidant enzymes—particularly SOD, APX, and GR—has proven successful in generating transgenic plants with improved stress tolerance, growth performance, and productivity under adverse environmental conditions (Sharma *et al*., 2017; Rajput *et al*., 2021). These genetic interventions represent a promising strategy for developing climate-resilient crops capable of withstanding increasingly unpredictable environmental challenges.

Nano-Fertilisers: Definition, Types, and Principles:

3.1 Definition and Characteristics of Nano-Fertilisers:

Nano-fertilisers represent a significant leap in the field of sustainable agriculture and plant nutrition. Developed through the application of nanotechnology, these fertilisers are designed to overcome the limitations of traditional formulations, such as nutrient leaching, volatilisation, and low bioavailability. Engineered with particle sizes typically ranging from 1 to 100 nanometers, nano-fertilisers exhibit enhanced solubility, reactivity, and targeted interaction with plant tissues, thereby improving nutrient delivery efficiency and minimising environmental impact (Chahande & Sharma, 2023). Defined as fertilisers that contain essential macro- or micronutrients synthesised or coated at the nanoscale, nano-fertilisers often incorporate carriers or encapsulation systems that facilitate controlled release. They are available in various physical forms, including nano-emulsions, nano-gels, and nano-encapsulated liquids or solids. Their compositions are tailored to supplement or correct specific nutrient deficiencies in crops. They can improve the uptake efficiency of both macronutrients (N, P, K) and micronutrients (Zn, Fe, B, etc.) (Jakhar *et al*., 2022). Typically, nano-fertilisers fall into three main categories: (1) nano-sized traditional fertilisers such as nano-urea and nano-Zno; (2) nutrient-loaded nanocarriers like chitosan or silica nanoparticles; and (3) nanocomposites that combine both nutrient and carrier functionalities (Kekeli *et al*., 2025).

The unique physicochemical characteristics of nano-fertilisers underlie their enhanced performance. Their high surface area-to-volume ratio provides a greater reactive surface for nutrient interactions, promoting higher solubility and absorption efficiency at the root-soil interface (Razauddin *et al*., 2023). Surface charge and chemical reactivity are crucial in enhancing adhesion to root cells and interaction with negatively charged soil particles and root exudates, thus improving nutrient bioavailability. Furthermore, advanced nano-formulations can be engineered with smart-release mechanisms that respond to environmental cues such as ph, temperature, or enzymatic activity. This allows synchronisation of nutrient release with plant developmental stages and environmental needs (Taware *et al*., 2024). One of the most valuable attributes of nano-fertilisers is their potential to improve nutrient use efficiency (NUE) significantly. Traditional fertilisers often suffer from inefficient uptake—nitrogen uptake, for instance, rarely exceeds 30–50%, and phosphorus use efficiency can be as low as 20%. In contrast, nano-fertilisers, through slow release and targeted delivery, have been shown to increase NUE to over 80% (Sadhukhan *et al*., 2022). These enhancements translate into improved root absorption, increased photosynthetic activity, elevated chlorophyll content, and greater enzyme expression. For example, foliar application of nano-urea has been shown to improve nitrogen uptake and chlorophyll content in rice. In contrast, nano-Zno application has promoted root elongation and shoot biomass in maize (Sharma *et al*., 2021).

Application methods for nano-fertilisers are versatile and can be adapted to specific crop requirements and soil conditions. Foliar application enables rapid absorption through leaf stomata, making it especially effective under stress conditions or in soils with low fertility (Ahmed, 2022). Soil application is suitable for slow-release formulations and root-targeted delivery. Seed priming, wherein seeds are coated with nano-fertilisers, enhances early seedling growth and improves tolerance to environmental stress. These diverse application methods also make nano-fertilisers highly compatible with precision agriculture technologies, enabling site-specific, data-driven nutrient management. In addition to improving crop productivity, nano-fertilisers contribute to ecological sustainability by reducing the environmental footprint of fertilisation. Their targeted delivery means that smaller quantities are needed, thus minimising runoff, nitrogen volatilisation, and nutrient leaching—key contributors to water eutrophication and greenhouse gas emissions (Yaseen *et al*., 2020). Moreover, biodegradable coatings such as those made from chitosan not only facilitate slow nutrient release but also promote soil microbial activity and rhizosphere health (Gupta & Prakash, 2020). Despite their numerous benefits, the use of nano-fertilisers does raise important concerns. At high concentrations, nanoparticles may become phytotoxic, damaging plant tissues due to their elevated reactivity. There is also ongoing debate about their impact on soil microflora, as nanoparticles may unintentionally disrupt beneficial microbial communities (Kekeli *et al*., 2025). Additionally, the potential accumulation of nanoparticles in edible plant parts raises questions about food safety and long-term human health risks. The lack of international standards and regulatory frameworks for defining particle size, permissible concentrations, and environmental behaviour of nano-fertilisers presents further challenges to their commercialisation and widespread adoption (Tang *et al*., 2023).

3.2 Types of Nano-Fertilisers (ZnO, Fe, SiO_2, NPK):

Nano-fertilisers are not a single category but rather a broad spectrum of nanoscale nutrient delivery systems, each designed to enhance nutrient use efficiency, crop performance, and environmental sustainability. These formulations vary by nutrient type—macronutrients (e.g., nitrogen, phosphorus, potassium) or micronutrients (e.g., zinc, iron, silicon)—as well as by structure, such as solid nanoparticles, nano-emulsions, or encapsulated carriers. Depending on their application, nano-fertilisers are used to promote plant growth, mitigate stress, or target specific deficiencies. Among the most widely studied nano-fertilisers are those based on zinc oxide (Zno), iron (Fe), silicon dioxide (SiO_2), and nano-formulated NPK blends. Each type exhibits unique physicochemical and biological properties that enhance plant uptake, stimulate growth, and improve soil health.

3.2.1. Zinc Oxide (Zno) Nano-Fertilisers

Zinc is an essential micronutrient for plant metabolic processes, including enzyme activation, protein synthesis, and hormone regulation. However, zinc deficiency is a major constraint in crop production, affecting nearly half of the world's cultivable soils. Zno-based nano-fertilisers offer a significant improvement over conventional zinc sources due to their smaller size and increased reactivity, which enhances zinc bioavailability. Numerous studies have reported the benefits of Zno nanoparticles on crop physiology. For example, biosynthesised Zno nanoparticles have significantly enhanced shoot and root length, leaf area, and protein content in maize (Sabir *et al*., 2020). In crops such as wheat and black carrot, foliar-applied Zno NPs have improved chlorophyll levels, biomass accumulation, and nutrient uptake compared to traditional zinc salts (Upadhyay *et al*., 2023).

Additionally, Zno NPs promote lateral root development and enhance root architecture under drought conditions, contributing to better water and nutrient absorption (Yang *et al*., 2018). These particles also regulate gene expression linked to stress tolerance in wheat. However, their effectiveness is concentration-dependent. While moderate doses are beneficial, excessive application may lead to phytotoxicity, oxidative stress, or disruptions in beneficial soil microbial communities (Liu *et al*., 2022; Li *et al*., 2025).

3.2.2. Iron (Fe) Nano-Fertilisers:

Iron is critical for chlorophyll synthesis, mitochondrial function, and overall plant energy metabolism. However, iron deficiency remains a prevalent problem in calcareous and alkaline soils, leading to chlorosis and reduced crop productivity. Conventional iron fertilisers often suffer from poor mobility and low plant uptake. In contrast, nano-iron fertilisers—including Feo, Fe_2O_3, and nano-chelated iron complexes—offer improved solubility and bioavailability. Studies have shown that nano-Fe significantly boosts iron uptake by roots, increases leaf chlorophyll content, and enhances biomass in both cereals and legumes (Khalid *et al*., 2021).

In comparative studies with other nanoparticles such as Zno and Mgo, Feo nanoparticles applied through seed priming and soil amendment markedly improved the morphological characteristics of *Caesalpinia bonducella*. Growth parameters increased by up to 93%, and chlorophyll content rose by 80% when nano-fertilisers were used instead of conventional $FeSO_4$ (Khalid *et al*., 2021), confirming their superior efficiency.

3.2.2. Silicon Dioxide (SiO_2) Nano-Fertilizers:

Although silicon is not classified as an essential nutrient, it plays an important role in improving plant structure, strengthening cell walls, and enhancing resistance to various abiotic stresses. Nano-silicon (SiO_2) fertilisers are increasingly recognised for their ability to mitigate stress, particularly under saline, drought, and heavy metal conditions. In a field study, maize plants treated with sol-gel synthesised SiO_2 nanoparticles showed a 110% increase in biomass and a 106% increase in yield compared to untreated controls. These results significantly outperformed those obtained using conventional silicon fertilisers (Shoukat *et al*., 2025).

Mechanistically, nano-SiO_2 reinforces the plant epidermis and vascular structures, reduces water loss, and improves ion regulation. By limiting sodium uptake and improving potassium balance, these particles enhance plant tolerance under salinity stress, making them especially useful in regions with poor water quality or degraded soils.

3.2.3. NPK Nano-Fertilisers:

The nano-formulation of macronutrients—nitrogen (N), phosphorus (P), and potassium (K)—is of major importance in precision farming. Nano-NPK fertilisers are typically encapsulated in carriers like chitosan, cellulose, or silica, which allow slow and controlled release of nutrients, thereby reducing the frequency and quantity of fertiliser applications. These nano-formulations have been shown to outperform bulk NPK fertilisers in wheat, maise, and rice. For example, nano-NPK fertilisers improved grain yield and nutrient uptake efficiency by 25–40% and reduced fertiliser requirements by up to 50% in field trials (Madzokere *et al*., 2021).

The slow-release and targeted nature of nano-NPK formulations also minimises nutrient leaching and runoff, which are major contributors to water pollution and eutrophication. By improving nutrient use efficiency and reducing environmental impact, nano-NPK plays a central role in climate-smart and resource-efficient agriculture (Ahmed, 2022). Furthermore, nano-NPK fertilisers can be tailored for site-specific applications using GPS and sensor-based precision systems, enabling real-time fertilisation adjustments based on plant needs and environmental conditions. Beyond the mainstream options, newer nano-materials are being explored for their potential in multi-nutrient delivery and biostimulant applications. These include titanium dioxide (TiO_2) nanoparticles, carbon nanotubes, and biochar-based nanocomposites. TiO_2 nanoparticles, in particular, have shown the ability to boost photosynthetic activity and improve oxidative stress tolerance, especially in chloroplast-rich crops like spinach and carrots (Upadhyay *et al*., 2023). These advanced materials are paving the way for multifunctional nano-fertilisers that not only supply nutrients but also improve plant health and productivity under challenging conditions.

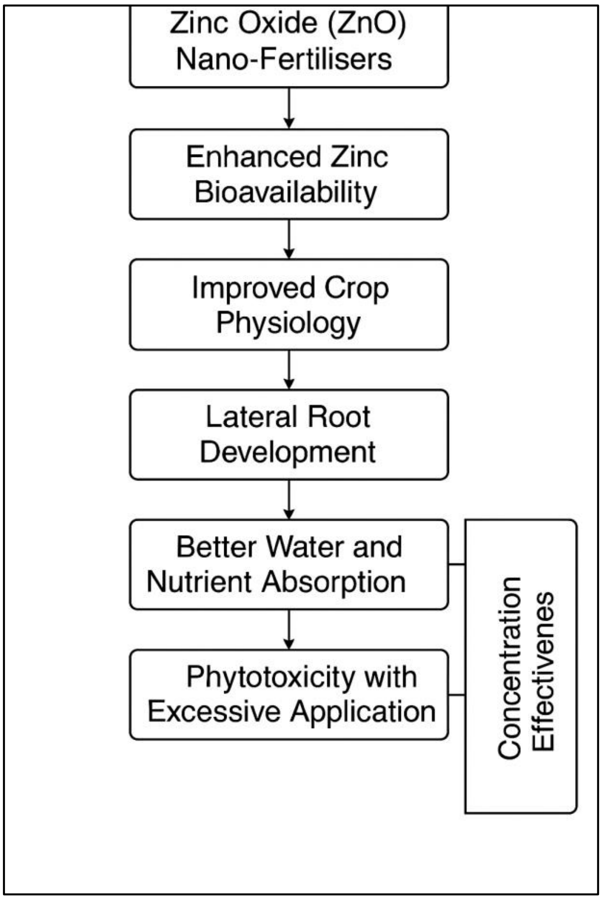


Figure: "Mechanism and Effects of Zinc Oxide (ZnO) Nano-Fertilizers on Crop Physiology"

3.3. Mechanisms of Controlled Nutrient Delivery:

Nano-fertilisers represent a transformative advancement in agricultural technology, offering an unprecedented level of precision in nutrient delivery to crops. Unlike conventional fertilisers, which often suffer from nutrient losses through leaching, volatilisation, or fixation, nano-fertilisers are engineered to release nutrients in a controlled, targeted, and environmentally responsive manner. Their nanoscale structures, characterised by high surface area and reactivity, enable efficient interaction with plant tissues and soil systems. This targeted delivery not only synchronises nutrient availability with plant growth stages but also reduces environmental waste, aligning with the goals of sustainable and precision agriculture. A foundational mechanism in nano-fertiliser technology is nano-encapsulation, where nutrients are enclosed within or bound to carriers such as chitosan, alginate, cellulose nanofibers, mesoporous silica, or hydroxyapatite. These nanocarriers protect the nutrients from degradation and release them in response to environmental stimuli such as ph, temperature, and microbial activity in the rhizosphere. This allows for sustained nutrient availability throughout various growth phases. For instance, chitosan-based nanoparticles have demonstrated efficient ph-responsive delivery of micronutrients like zinc and iron, enhancing plant bioavailability while minimising toxicity and nutrient loss (Riseh *et al*., 2024).

Another major innovation lies in the targeted delivery and functional coating of nano-fertilisers. These formulations can be designed for root-zone application or foliar sprays and are often modified with bioactive ligands or surfactants. Such coatings enable the particles to interact with root exudates, bind with soil components, or target specific receptors on plant membranes. Materials like graphene oxide and silica nanoparticles enhance nutrient delivery and contribute to soil structure and moisture retention (Bhattacharya *et al*., 2022). The ability to direct nutrient release toward the root-soil interface or into vascular tissues ensures maximum uptake with minimal loss. Controlled and slow-release mechanisms are another cornerstone of nano-fertiliser technology. These formulations are engineered to respond to chemical and physical cues such as soil moisture, temperature, or enzymatic activity. By gradually releasing nutrients over time, nano-fertilisers maintain consistent nutrient levels in the rhizosphere, reducing the need for frequent reapplication. For example, cellulose nanofibers embedded in biodegradable matrices have been used to release nitrate and potassium over 80 days, significantly reducing leaching (França *et al*., 2022). Similarly, hydrogel-based nano-formulations swell in response to soil moisture, enabling slow and efficient nutrient diffusion. A significant advancement is the integration of nano-fertilisers with real-time sensor systems that allow them to respond to specific environmental or physiological triggers. Some nano-carriers are designed to become permeable under specific ph ranges, redox potentials, or enzymatic signals from nutrient-deficient roots. This feedback-responsive system ensures that nutrient release is precisely matched to plant demand, enhancing nutrient use efficiency and reducing overapplication (Sivarethinamohan & Sujatha, 2021). These smart-release mechanisms are particularly suited for integration into precision agriculture platforms.

In addition to single-nutrient formulations, multi-nutrient nano-platforms are increasingly being developed. These systems co-encapsulate macronutrients like nitrogen and phosphorus alongside micronutrients such as zinc or iron, and sometimes even biostimulants or growth regulators. This co-delivery minimises nutrient antagonism and promotes synergistic uptake. Carbon nanotubes and hydroxyapatite have effectively delivered nitrogen and phosphorus, improving yield while maintaining soil ph and microbial balance (Goyal *et al*., 2022). Such systems enhance overall nutrient efficiency and crop performance. Nano-fertilisers can be enhanced with protective or functional modifications, such as UV-blocking coatings to prevent photodegradation, or magnetic particles for post-harvest recovery and reuse. Biodegradable materials like polyhydroxybutyrate (PHB) and starch have effectively encapsulated nutrients for slow release, while maintaining soil ecological integrity (França *et al*., 2022). These advancements add a sustainability dimension to nano-fertiliser design, aligning nutrient delivery with circular economy principles.

Foliar application of nano-fertilisers represents an effective method for quickly correcting nutrient deficiencies. Once applied to leaves, nanoparticles penetrate the cuticle and reach the vascular tissues, which are translocated via the phloem to other plant parts. This mechanism ensures rapid delivery of nutrients to areas of highest metabolic need, especially during critical stages of stress or reproductive development. Moreover, foliar-applied nano-nutrients reduce runoff and volatilisation losses compared to traditional sprays, enhancing their environmental safety (Singh & Singh, 2018). In summary, the delivery mechanisms of nano-fertilisers—ranging from nano-encapsulation and root-targeting to smart-release and multi-nutrient co-delivery—offer a highly efficient and sustainable approach to crop nutrition. These systems enhance nutrient use efficiency, minimise environmental losses, and enable site-specific and stage-specific fertilisation. Their integration into modern farming practices holds great promise for addressing food security challenges amid population growth, resource depletion, and climate variability (Aparanjitha *et al*., 2023; Chahande & Sharma, 2023).

4. Synthesis of Nano-Fertilisers:

4.1 Chemical and Physical Synthesis Approaches:

Chemical and physical synthesis methods are conventional strategies for engineering nanoparticles with controlled composition and structure. These techniques allow precise particle size, crystallinity, surface area, and morphology tuning—all critical factors for nutrient delivery efficiency in soil and plant systems.

The sol-gel process is widely used for synthesising metal oxide nanoparticles, particularly silica- and zinc-based nano-fertilisers. This method involves the hydrolysis and polycondensation of metal alkoxides or inorganic salts, forming a colloidal suspension (sol) that gradually transitions into a gel. Its advantages include low synthesis temperatures and excellent control over porosity and surface structure, making it suitable for nutrient encapsulation and controlled release applications (Tailor *et al*., 2022). Hydrothermal methods utilise aqueous precursor solutions subjected to high temperature and pressure inside sealed autoclaves. This technique is beneficial for synthesising highly crystalline and thermally stable nanoparticles such as iron oxide (Fe_2O_3) and titanium dioxide (TiO_2). Nano-Fe_2O_3 produced via hydrothermal synthesis has enhanced long-term iron availability in alkaline soils, supporting chlorophyll synthesis and plant growth (Ojha, 2022).

A top-down approach, ball-milling mechanically reduces bulk material into nanoscale particles through high-energy collisions in a rotating chamber. This technique is cost-effective, scalable, and suitable for producing oxide nanoparticles such as Zno and Cuo. However, due to particle agglomeration, stabilising agents or surfactants like polyvinyl alcohol (PVA) are often required, especially in wet milling conditions, to improve dispersibility and nutrient reactivity (Sebastian *et al*., 2023). This relatively simple and efficient bottom-up method involves the simultaneous precipitation of multiple metal salts by adjusting ph or adding precipitating agents. It is frequently used for synthesising multi-nutrient nano-composites. For instance, co-precipitation enables the formation of uniform NPK nano-formulations where ammonium, phosphate, and potassium ions are embedded in a consistent matrix, resulting in enhanced nutrient compatibility and synchronised release profiles (Channab *et al*., 2024).

These are advanced techniques used for producing highly uniform nanoparticles on a large scale. In flame spray pyrolysis, a precursor solution is atomised and combusted, generating ultra-fine particles with high crystallinity and surface area. This method is effective for synthesising nano-silica, nano-iron, and nano-manganese fertilisers. Although energy-intensive and costly, the particles produced by this method exhibit superior physical characteristics ideal for high-performance applications (Chahande & Sharma, 2023).

Despite their advantages, chemical and physical synthesis methods often involve using hazardous solvents, high energy input, and elevated processing temperatures. These factors can raise environmental and safety concerns, particularly due to the generation of toxic by-products. The need for post-synthesis surface functionalisation or coating to improve biocompatibility and dispersibility may further increase production costs. Therefore, while these methods provide high control over material properties, their implementation must consider sustainability and ecological risks.

4.2 Green Synthesis Using Plant Extracts and Bio-Agents:

Green synthesis represents a sustainable and biocompatible alternative to conventional chemical and physical nanoparticle fabrication methods. By utilising naturally occurring biological agents—such as plant extracts, fungi, bacteria, and algae—as reducing and stabilising agents, green synthesis offers an eco-friendly, low-cost, and scalable approach to producing nano-fertilisers. These biologically derived nanoparticles are environmentally safe and highly effective in improving nutrient delivery and reducing toxicity in soil ecosystems (Jiang *et al*., 2022).

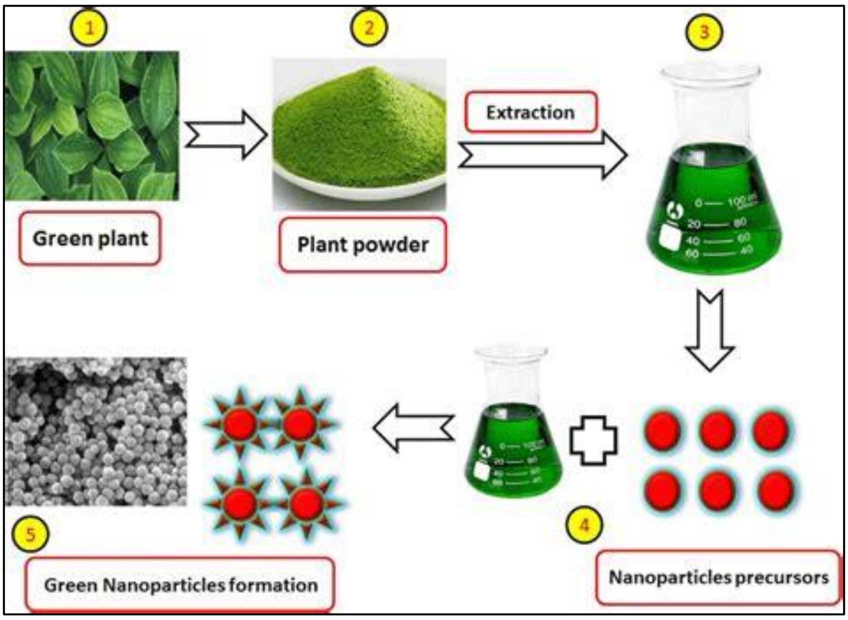
One of the core motivations for adopting green synthesis lies in mitigating the environmental risks posed by traditional reducing agents like sodium borohydride or hydrazine, which leave behind toxic residues. In contrast, green synthesis leverages phytochemicals, such as flavonoids, tannins, alkaloids, and terpenoids, found in plant extracts. These biomolecules act as reducing and capping agents, eliminating the need for synthetic chemicals while stabilising nanoparticles for agricultural use (Mawthoh *et al*., 2023).

Phytosynthesis, or plant-based nanoparticle synthesis, is the most widely studied and applied green method. It is favoured for its simplicity, accessibility of plant material, and broad applicability. Plant parts such as leaves, roots, seeds, fruit peels, and even agricultural waste have been successfully used to synthesise zinc oxide (ZnO), copper (Cu), iron (Fe), and silver (Ag) nanoparticles. For example, green tea (*Camellia sinensis*) extract has been effectively used to produce iron nanoparticles with controlled nutrient release properties and enhanced bioavailability for plant uptake (Biswas *et al*., 2023). In another study, waste materials such as banana rind and pomegranate peel were employed to synthesise potassium-enriched nitrogenous nano-fertilisers, resulting in improved plant growth and slow nutrient release even at lower application rates (Sebastian *et al*., 2023). Beyond plant-based synthesis, microbial biosynthesis using fungi, bacteria, and algae has emerged as another promising route. Fungi, particularly from the *Trichoderma* genus, are exceptionally efficient due to their extracellular enzymes and proteins facilitating metal ion reduction and nanoparticle stabilisation. These biogenic metal nanoparticles—such as iron and silver—have improved nutrient uptake and offer antimicrobial benefits, contributing to plant nutrition and protection (Sonawane *et al*., 2022). The fungal biosynthesis process typically involves intracellular or extracellular mechanisms wherein enzymes like nitrate reductase convert metal ions into stable nanoparticles. Fungi's filamentous structure also provides a high surface area and continuous metabolic activity, making them well-suited for large-scale nanoparticle production (Baazaoui & Sghaier-Hammami, 2021).

Bacterial-mediated synthesis, while less common in nano-fertiliser development, has also shown promise. *Pseudomonas*, *Bacillus*, and *Lactobacillus* can reduce metal salts into nanoparticles under controlled conditions. These biogenic nanoparticles serve as nutrient carriers and enhance soil microbial activity and plant health, functioning as dual-purpose agents—fertilisers and bio-inoculants (Jeevanandam *et al*., 2022). One of the most significant advantages of green-synthesised nano-fertilisers is their biocompatibility and low ecological toxicity. They are inherently safer for non-target organisms, soil microbiota, and aquatic environments, and they typically decompose into harmless byproducts over time. A comprehensive review by Pudhuvai *et al*. (2024) reported that green-synthesised nano-fertilisers reduced nutrient runoff, minimised soil acidification, and lower heavy metal accumulation compared to conventionally synthesised counterparts. Green synthesis also supports the principles of a circular bioeconomy by converting agricultural waste into value-added materials. For instance, banana peel ash and coconut coir extract have been successfully used to synthesise potassium and iron nanoparticles with sustained nutrient release characteristics (Sharma *et al*., 2023). This reduces dependency on synthetic inputs and lowers production costs and waste generation. Despite the benefits, several challenges remain. Green synthesis methods often suffer from nanoparticle size, shape, and yield variability due to differences in metabolite content across plant species and growth stages. Standardisation of synthesis protocols and optimisation of parameters like pH, temperature, extract concentration, and scalability for industrial production need further research. Hybrid approaches combining green and chemical methods are gaining traction to address these issues. These methods integrate natural reducing agents with controlled chemical conditions to enhance reproducibility and efficiency. For example, iron nanoparticles synthesised using both plant extract and ph-controlled co-precipitation techniques have demonstrated improved dispersion and bioavailability in soil systems (Babali *et al*., 2024).

Figure: Green Synthesis Using Plant Extracts and Bio-Agents.

Green synthesis begins with collecting plant parts rich in phytochemicals, like leaves or peels, followed by preparing an extract through boiling or soaking. This extract is mixed with a metal salt solution (e.g., Ag^{+} or Fe^{3+}), where plant compounds reduce the metal ions to form nanoparticles. These nanoparticles are stabilized by biomolecules, then purified and used as eco-friendly nano-fertilizers.



4.3 Surface Functionalization and Stabilisation Techniques:

Surface functionalisation and stabilisation are essential in the design and performance optimisation of nano-fertilisers. These strategies directly influence the colloidal stability, dispersibility, biocompatibility, and targeted nutrient delivery efficiency of nanoparticles (NPs) in agricultural systems. Functionalization refers to modifying nanoparticle surfaces with molecules, polymers, or ligands to improve their interaction with plant or soil components and regulate their release behavior. Stabilization, on the other hand, ensures that nanoparticles remain uniformly suspended in liquid or soil media without agglomerating, thereby retaining their efficacy over time. One of the most widely adopted approaches to functionalization involves coating nanoparticles with polymers such as chitosan, polyethylene glycol (PEG), dextran, and poly(maleic anhydride-alt-1-octadecene). These coatings provide steric stabilization, regulate surface charge, and offer reactive sites for further conjugation. Amphiphilic copolymers like PMAO-PEGMA have been employed to generate multifunctional coatings that improve stability across diverse environmental conditions while also enabling attachment of biomolecules or sensing elements for smart nutrient release (Culver *et al*., 2016).

Graphene oxide (GO) nanosheets have emerged as promising carriers in agricultural nano-delivery due to their high surface area, mechanical strength, and chemical versatility. Functionalisation of GO with hydrophilic polymers or bio-ligands enables controlled release of nutrients and improves water dispersibility, making them suitable for foliar and soil applications (Bhattacharya *et al*., 2022). Smart coatings that respond to environmental stimuli such as ph, temperature, or enzymatic activity are also gaining attention. For instance, bilayer coatings with oleate and amino-functionalized molecules have stabilised upconversion nanoparticles and enhanced their responsiveness to field conditions, allowing real-time nutrient release when needed (Schroter *et al*., 2023). Maintaining nanoparticle dispersion in high ionic strength environments like soil is challenging due to agglomeration caused by Van der Waals forces. Surface charge modification and steric hindrance are commonly applied stabilization techniques to address this. Functional groups such as carboxyl, sulfate, and phosphate can be introduced to nanoparticle surfaces to enhance electrostatic repulsion and improve dispersion. For example, lignin-based colloidal particles functionalised with sodium dodecyl sulfate (SDS) demonstrated excellent hydrophobicity and colloidal stability, significantly enhancing nutrient retention and slow release when applied as coatings for diammonium phosphate (DAP) fertilisers (El Bouchtaoui *et al*., 2025). Nanocellulose and Biodegradable Stabilisers Nanocellulose-based systems are gaining traction due to their biodegradability, mechanical strength, and surface modifiability. Chemically crosslinked nanocellulose hydrogels can serve as nutrient reservoirs, gradually releasing macronutrients like nitrogen and potassium under moisture-sensitive conditions, thus aiding in drought stress mitigation and enhancing nutrient use efficiency (Channab *et al*., 2024). These biopolymer-based systems also support microbial activity and contribute to soil health.

For hydrophobic nanoparticles such as ZnO and Fe_2O_3, surface functionalisation is necessary to transfer them into aqueous environments suitable for foliar or fertigation applications. Amphiphilic polymers with dual hydrophobic-hydrophilic domains are often employed, forming core-shell structures that stabilise the nanoparticles in water and prevent precipitation. PEG and zwitterionic coatings are frequently used, especially in saline or alkaline soils where ionic strength challenges colloidal stability (Cartwright *et al*., 2020). Surface coatings also function as barriers to oxidation and leaching, improving the longevity and performance of nano-fertilisers. For instance, chitosan-sepiolite nanocomposites have been used to coat urea granules, creating a semi-permeable matrix that slows nitrogen release. This modification extended nitrogen availability from 3 days (in conventional urea) to over 25 days, significantly improving nitrogen use efficiency in maize (Mohammadi *et al*., 2020). Advanced surface functionalisation can enable targeted nutrient delivery using ligands that interact specifically with root exudates or soil enzymes. This targeted approach ensures site-specific nutrient release, optimising absorption and minimising losses. Additionally, smart polymers that respond to soil pH or temperature can be engineered to release nutrients only under conditions favourable for root uptake. Despite the promising potential of functionalised and stabilised nano-fertilisers, several challenges remain. Scaling up lab-scale functionalization processes while maintaining uniform coating and cost-effectiveness is a major hurdle. Compatibility with existing fertilizer production systems, the cost of specialized polymers, and the need for long-term field validation of environmental safety are critical concerns. Moreover, understanding the interaction of these functional materials with diverse soil microbiomes and plant genotypes will be essential for optimizing their real-world performance.

5. Nano-Fertilizer Interaction with Plant Systems:

5.1 Absorption and Uptake Pathways in Plants:

The application of nano-fertilizers (NFs) marks a significant advancement in sustainable agriculture, offering enhanced nutrient delivery mechanisms through unique physicochemical properties such as nanoscale dimensions, increased surface area, tunable surface charge, and high reactivity. These attributes enable more efficient and targeted nutrient uptake than traditional fertilizers, thus minimizing waste and environmental impact. Among the primary uptake routes, root absorption remains the dominant pathway for most nano-fertilizer applications. NFs typically enter plant roots through apoplastic (extracellular) or symplastic (cytoplasmic) routes. In the apoplastic pathway, nanoparticles traverse intercellular spaces without breaching cell membranes, while in the symplastic pathway, they enter cells via endocytosis and are translocated through plasmodesmata connections. The dominance of either pathway is primarily influenced by the nanoparticle's size, charge, and surface coating. Particles smaller than 50 nm and those possessing neutral or slightly positive charges tend to penetrate cell walls more effectively, facilitating internalisation through ligand exchange or redox reactions at the root surface (Dey & Sadhukhan, 2024).

Once internalised, nanoparticles exhibit diverse behaviors depending on their chemical composition and the plant species involved. For instance, transmission electron microscopy (TEM) and X-ray fluorescence studies have revealed that iron phosphate nanoparticles ($FePO_4$ NPs) can localise at the root epidermis and endodermis, suggesting active transport mechanisms like endocytosis (Sega *et al*., 2020). Similarly, molybdenum nanoparticles (Mo NPs) have demonstrated superior uptake through root irrigation compared to foliar application, significantly enhancing plant growth by promoting root lignification and increasing the development of vascular tissues (Chen *et al*., 2023). A critical process facilitating nanoparticle entry is endocytosis, particularly the clathrin-mediated pathway, which enables nanoparticles to circumvent the plant cell wall barrier. Both xylem parenchyma and non-conductive cells contribute to the internalization and radial translocation of nanoparticles from the epidermis to the vascular bundles (Słupianek *et al*., 2019). Notably, surface modifications such as citrate-coating improve nanoparticle migration while minimizing root toxicity; for example, trisodium citrate-coated CuO nanoparticles showed higher vascular transport efficiency with minimal root inhibition compared to uncoated forms (Huang *et al*., 2022).

Environmental conditions and the plant's nutritional status also regulate nanoparticle uptake. Deficiencies in essential micronutrients like iron can upregulate endocytotic and transporter proteins, thereby enhancing iron nanoparticle absorption (Zheng *et al*., 2023). In addition to root-mediated pathways, foliar uptake offers an alternative route, particularly advantageous under abiotic stress conditions such as drought or salinity. Nanoparticles can be absorbed through stomata, cuticular waxes, trichomes, and hydathodes. Particles with diameters less than 20–40 nm have been observed entering leaves via stomatal pores, dispersing into mesophyll tissues and contributing to systemic nutrient delivery (Avellan *et al*., 2021). Hydrophobic nanoparticles exhibit improved penetration through the cuticle, especially when their surface energy matches that of the cuticular wax. This compatibility is further enhanced with stimuli-responsive nanoparticles that respond to redox potential, pH, or enzymatic triggers in the phyllosphere (Thirugnanasambandan *et al*., 2024).

Following absorption, long-distance translocation of nutrients occurs via xylem loading. Nanoparticles have been found to activate specific transporter proteins like magnesium-related MGR transporters, promoting upward translocation of nutrients from roots to shoots (Meng *et al*., 2022). Nano-interventions also enhance the expression of aquaporins and other membrane-associated proteins, improving water and nutrient flux through vascular tissues (Chen *et* *al*., 2023). Interestingly, elemental analysis of foliar-treated plants has identified nanoparticles in the phloem, suggesting not only unidirectional upward movement through xylem but also bidirectional distribution via phloem tissues, allowing for more dynamic nutrient redistribution throughout the plant system (Rani *et al*., 2022).

Uptake efficiency is highly dependent on both plant-specific and nanoparticle-specific factors. Different plant species exhibit distinct absorption behaviors due to variations in root architecture, membrane transporter proteins, and exudate profiles. Strategy I plants such as cucumber differ markedly in nanoparticle uptake mechanisms compared to Strategy II species like maize (Sega *et al*., 2020). Additionally, nanoparticle parameters such as size, surface coating, charge, and morphology significantly influence their bioavailability and toxicity. Coated nanoparticles have been shown to reduce phytotoxic effects while increasing absorption efficiency, a critical consideration in food safety, particularly in edible crops like *Ipomoea aquatica* (Huang *et al*., 2022).

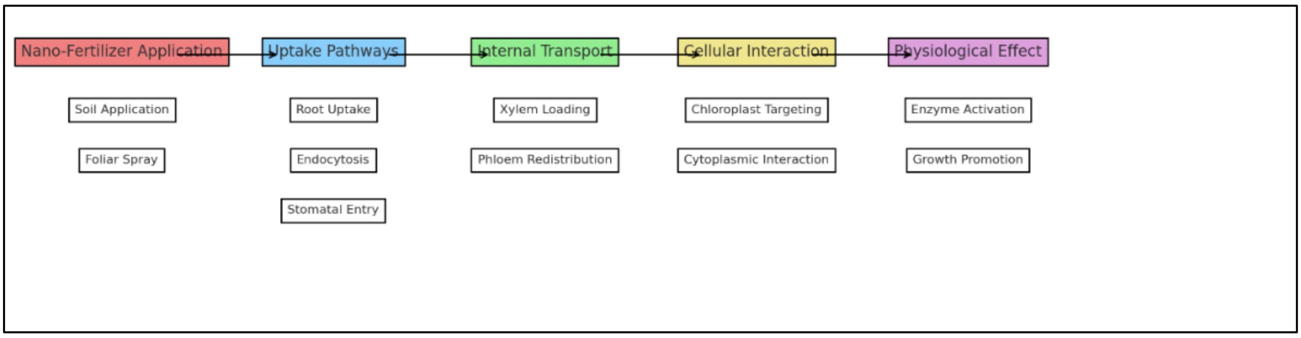


Figure: Interaction of Nano-Fertilisers with Plant Systems:

5.2 Translocation and Distribution within Plant Tissues:

Once nano-fertilizers (NFs) are absorbed through roots or leaves, their subsequent translocation within plant systems becomes a critical determinant of their efficacy. Unlike conventional nutrient ions, nanoparticles (NPs) face complex biological barriers and follow distinct transport routes, primarily involving xylem- and phloem-mediated movement. These processes are significantly influenced by nanoparticle characteristics such as size, surface charge, and coating, as well as by plant-specific traits including growth stage, transpiration rate, and anatomical structure.

The xylem serves as the primary conduit for unidirectional root-to-shoot transport of water and solutes, including nano-enabled fertilizers. Once inside the plant root, nanoparticles are loaded into the xylem either through apoplastic pathways or via symplastic movement across endodermal cells, depending on their size and surface interactions. Particles smaller than 40 nm, such as iron oxide or zinc oxide nanoparticles, have demonstrated successful root-to-shoot movement via the xylem, as confirmed by experiments in pumpkins where Fe_2O_3 nanoparticles in the 20–40 nm range showed superior accumulation in leaves compared to larger particles (Tombuloglu *et al*., 2022; Rani *et al*., 2022). Environmental variables such as soil pH and transpiration rates also influence this movement, as higher transpiration generates a stronger upward pull in the xylem, especially favoring hydrophilic and negatively charged nanoparticles that remain stably dispersed in the xylem sap (Khan *et al*., 2022).

In contrast, the phloem provides a bidirectional transport system, distributing nutrients and nanoparticles to sink tissues, including roots, reproductive structures, and young leaves. Recent research has confirmed the phloem's role in nanoparticle mobility through advanced visualization techniques and radiolabeling. For example, mesoporous silica-encapsulated ZnO nanoparticles (~70 nm) applied on leaves were tracked moving to distal tissues, including younger leaves and roots, with increased translocation observed when applied to the abaxial surface, which has higher stomatal density (Gao *et al*., 2023). Similarly, sucrose-functionalized quantum dots applied to wheat demonstrated that over 70% of phloem-targeted particles reached roots within 40 minutes, showcasing the effectiveness of ligand-functionalized NPs for systemic movement (Jeon *et al*., 2023). Co-applications with amino acids like lysine have further enhanced phloem mobility and nutrient redistribution, as demonstrated in manganese-based foliar treatments (Samane, 2019).

The physical and chemical properties of nanoparticles profoundly affect their mobility. Smaller nanoparticles (<20 nm) typically pass more easily through plant vasculature, whereas larger particles may require surface functionalization to aid in transport. Coating chemistry also determines distribution patterns; for instance, polyvinylpyrrolidone (PVP)-coated gold nanoparticles exhibited enhanced leaf cuticle adhesion but limited systemic translocation, accumulating primarily in mesophyll tissues. In contrast, citrate-coated nanoparticles demonstrated more efficient phloem mobility, revealing a trade-off between adhesion and long-distance movement (Avellan *et al*., 2019).

Moreover, deformable nanoparticles functionalized with arginine have shown the ability to bypass lysosomal degradation and avoid endocytic trapping, thereby improving systemic delivery across plant tissues (Ghosh *et al*., 2018).

The translocation of nanoparticles is not uniform across all plant developmental stages. Young, actively growing tissues serve as strong nutrient sinks, actively pulling nanoparticles through phloem pathways. Time-resolved studies indicate that nanoparticle accumulation in roots peaks within the first 24–48 hours post-application, followed by redistribution to shoots and reproductive organs (Avellan *et al*., 2021). Species-specific traits also play a role; dicot plants typically exhibit more efficient phloem transport due to their vascular architecture, which contrasts with the relatively limited mobility observed in monocots. For instance, studies on cucumber and maize revealed differential utilization of iron phosphate nanoparticles—cucumber favored phosphorus uptake while maize prioritized iron, demonstrating how species-specific metabolism influences NP distribution (Sega *et al*., 2020).

Despite these advances, several challenges limit precise control of nanoparticle distribution in planta. Aggregation within the xylem sap, retention within mesophyll tissue, and variable phloem loading efficiencies are notable constraints. Moreover, the molecular mechanisms governing phloem loading of nanoparticles remain poorly understood. However, innovative strategies such as phloem protein-fusion systems are emerging as promising solutions. For example, engineered phloem-mobile proteins like CsPP16 have been used to ferry bioactive compounds long distances, opening new avenues for the targeted delivery of nano-formulated fertilizers and therapeutics (Calderón-Pérez *et al*., 2022).

5.3 Interaction with Cellular Structures and Organelles:

Once nano-fertilizers (NFs) penetrate plant tissues, their interaction with internal cellular structures becomes essential for determining their bioavailability, physiological efficacy, and safety. These interactions, occurring at the nano–bio interface, involve dynamic engagement between nanoparticles and biological systems at the cellular and subcellular levels. Upon internalization via endocytosis or passive diffusion, nanoparticles encounter the cytoplasmic environment, where they may remain dispersed, form agglomerates, or be trafficked to specific organelles. The behavior of these nanoparticles is influenced by their physicochemical properties such as size, charge, and surface functionalization. For instance, arginine-functionalized nanoparticles can bypass typical endocytotic routes and directly translocate into the cytosol, avoiding vesicular entrapment and preserving bioactivity for effective nutrient delivery (Ghosh *et al*., 2018).

Within the cytoplasm, nanoparticles engage in multiple interactions that influence cellular homeostasis and stress signaling pathways. Metal-based nanoparticles such as ZnO, Fe_2O_3, and CuO may dissolve or participate in redox reactions, releasing ions that are subsequently incorporated into metabolic pathways. In contrast, carbon-based nanomaterials like graphene oxide and carbon nanotubes exhibit structural stability and often interact physically with intracellular proteins or membranes, influencing molecular organization without undergoing degradation (Bhaskar *et al*., 2023). These interactions may modulate cytoskeletal architecture, enzyme activities, and oxidative stress responses. Notably, nanoparticles have been found to enhance the activities of antioxidant enzymes like superoxide dismutase and peroxidase, contributing to increased tolerance against abiotic stresses (Mutalik *et al*., 2020). However, the potential cytotoxicity of poorly designed or high-dose nanoparticles cannot be overlooked, as excessive reactive oxygen species (ROS) production can disrupt cellular functions and lead to oxidative damage (Razauddin *et al*., 2023). Moreover, nanoparticles can affect calcium signaling and activate transcription factors that regulate stress adaptation and nutrient assimilation, including auxin and ethylene-responsive genes, thereby influencing root elongation and leaf expansion (El-Saadony *et al*., 2021).

Targeting chloroplasts represents a promising avenue for enhancing photosynthetic efficiency in nano-agriculture. As pivotal for photosynthesis and nitrogen metabolism, chloroplasts benefit significantly from the precise delivery of functional nanoparticles. These particles may reach chloroplasts via cytoplasmic streaming or specialized protein transport systems, exceptionally when engineered with surface coatings that facilitate organelle targeting. Studies have demonstrated that carbon-based and cerium oxide nanoparticles enhance photosynthetic activity by improving light absorption and mitigating photooxidative stress, partly due to their inherent antioxidant properties (Bhaskar *et al*., 2023). Iron- and magnesium-containing nanoparticles have been shown to integrate into chlorophyll biosynthesis pathways, resulting in elevated SPAD values and improved light use efficiency (Al-Tameemi *et al*., 2019).

Apart from chloroplasts, mitochondria interact with nanoparticles, particularly those supplying micronutrients like zinc, manganese, or iron. These interactions can enhance ATP synthesis, nitrogen metabolism, and overall energy availability in plant tissues. However, mitochondria are sensitive to nanoparticle-induced toxicity; overexposure to reactive particles may lead to membrane depolarization, inhibition of the electron transport chain, and reduced respiration efficiency (Mutalik *et al*., 2020). Thus, appropriate dosing and nanoparticle design are essential to maximize benefits while minimizing potential harm.

Although nuclear uptake by nanoparticles is limited, indirect effects on genetic activity have been documented. Nano-fertilizer exposure can result in altered gene expression profiles, including the upregulation of genes involved in stress tolerance, ion transport, and metabolic enzyme production. While the use of functionalized nanoparticles as gene delivery vectors remains largely theoretical in plant systems, early-stage studies suggest their potential for future biotechnological applications (El-Saadony *et al*., 2021).

The long-term fate of internalized nanoparticles is another critical aspect of their interaction with plant cells. Nanoparticles may undergo biotransformation, be compartmentalized in vacuoles to mitigate toxicity, or become integrated into cellular structures. Advanced techniques such as electron microscopy and spectroscopy have revealed that nanoparticles can persist in subcellular compartments for extended periods, gradually releasing nutrients or interacting with metabolic systems (Mahesha *et al*., 2023). This prolonged retention raises important considerations for controlled-release efficiency, bioaccumulation, and overall food safety in agricultural systems. Understanding these intracellular dynamics is essential for optimizing nano-fertilizer formulations and ensuring their safe and effective use in crop production.

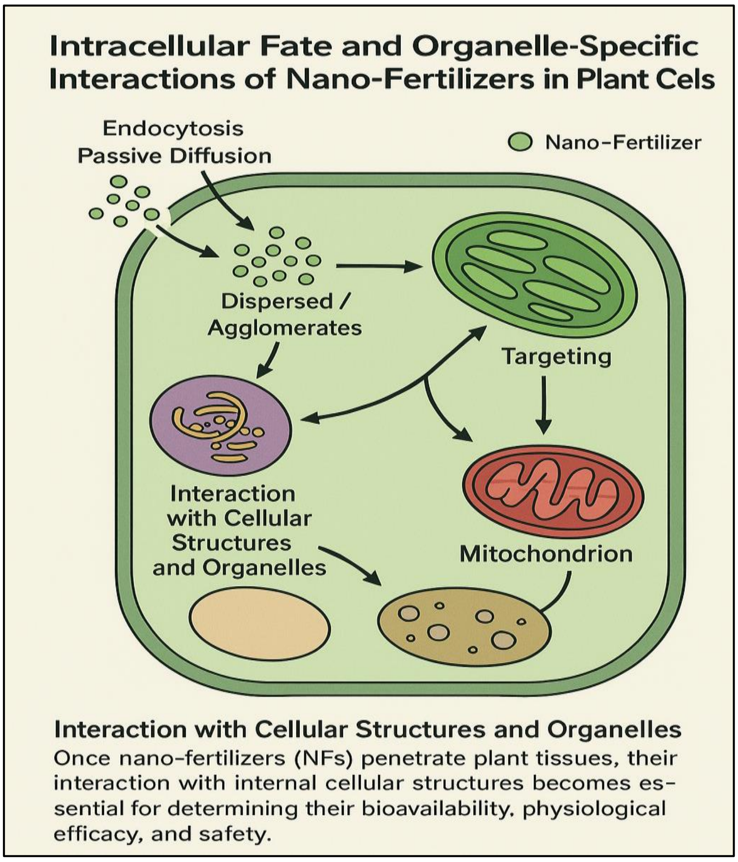


Figure: "Intracellular Fate and Organelle-Specific Interactions of Nano-Fertilizers in Plant Cells"

6. Modulation of Enzymatic Antioxidant Defense:

6.1 Activation of Antioxidant Enzymes by Nano-Fertilizers:

The modulation of antioxidant enzyme activity through nano-fertilizers has emerged as a critical strategy in modern agriculture, particularly for enhancing plant resilience under abiotic stress conditions such as drought, salinity, and heavy metal exposure. Nano-fertilizers, due to their high surface reactivity and bioavailability, can effectively stimulate key enzymatic defense mechanisms including superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and glutathione peroxidase (GPx). These enzymes play vital roles in mitigating reactive oxygen species (ROS), thereby reducing oxidative damage and improving plant health and productivity.

Zinc- and iron-based nano-formulations have been extensively studied for their antioxidative roles. In wheat subjected to salinity stress, the application of nano-Zn and nano-Fe oxides significantly upregulated the activities of CAT, POD, and polyphenol oxidase (PPO), while simultaneously increasing the levels of proline and soluble sugars, leading to a 17.4% improvement in yield (Babaei *et al*., 2017). Similarly, in triticale under high salinity, co-application of nano zinc oxide and biofertilizers enhanced enzymatic antioxidant activity and increased grain yield by as much as 39% (Arough *et al*., 2016). Supporting this, Nazir *et al*. (2024) demonstrated that green-synthesized ZnO nanoparticles from *Withania coagulans* extract substantially boosted wheat growth by enhancing SOD, CAT, and POD activity, confirming the particles' effective ROS scavenging potential.

The synergistic role of nano-magnesium and chitosan in modulating antioxidant defenses has also gained attention. In sesame plants under water-limited environments, foliar sprays of nano-Mg and chitosan led to significant elevations in CAT, POD, and ascorbate peroxidase (APX) activities. This combination improved seed yield and oil content, suggesting that nano-chelated magnesium can act as a potent enhancer of antioxidant enzyme expression under drought stress (Varamin *et al*., 2020). Likewise, ferric oxide nanoparticles (Fe_2O_3 NPs) have proven beneficial not only in improving tomato plant growth and chlorophyll content but also in activating SOD, CAT, POD, and PPO enzymes. These biochemical changes resulted in enhanced systemic resistance against *Fusarium* wilt, achieving over 80% disease protection (Elbasuney *et al*., 2022).

Under heavy metal stress, particularly cadmium (Cd) exposure, nano-silicon has demonstrated efficacy in protecting rice seedlings by regulating antioxidant enzymes. SOD, POD, and CAT activities were modulated in response to nano-Si foliar treatments, resulting in improved redox balance and lower malondialdehyde (MDA) levels, indicating reduced lipid peroxidation and oxidative damage (Wang *et al*., 2015). A similar pattern was observed in alfalfa under cadmium stress, where calcium oxide nanoparticles (CaO-NPs) enhanced plant biomass and increased SOD (29%), POD (41%), CAT (36%), and APX (49%) activities. These effects were accompanied by the upregulation of antioxidant-related genes such as Cu/Zn-SOD, MtCAT, and MtAPX, underlining the molecular impact of calcium-based nano-fertilizers (Hussan *et al*., 2024).

Titanium dioxide (TiO_2) nanoparticles have also shown lifecycle-wide benefits. In wheat under phosphorus-deficient conditions, TiO_2 application significantly enhanced root and shoot growth, and elevated SOD and POD activities. The most pronounced effects occurred at intermediate concentrations (50 mg/kg), emphasizing the importance of optimal dosing to avoid toxicity and to harness TiO_2's oxidative metabolism-regulating properties (Ullah *et al*., 2020). Similarly, in peanuts exposed to drought stress, foliar application of Zn nano-chelate fertilizers not only elevated SOD, CAT, and POD activities but also increased non-enzymatic antioxidant components like soluble sugars, proline, and anthocyanins, contributing to greater yield performance and overall plant resilience (Sharif *et al*., 2024).

Together, these findings underscore the decisive role that nano-fertilizers play in activating enzymatic defense pathways, highlighting their potential to promote sustainable agriculture through enhanced stress tolerance and productivity. The consistent upregulation of antioxidant systems across multiple crops and stress conditions illustrates the broad applicability of nano-enabled nutrient delivery strategies.

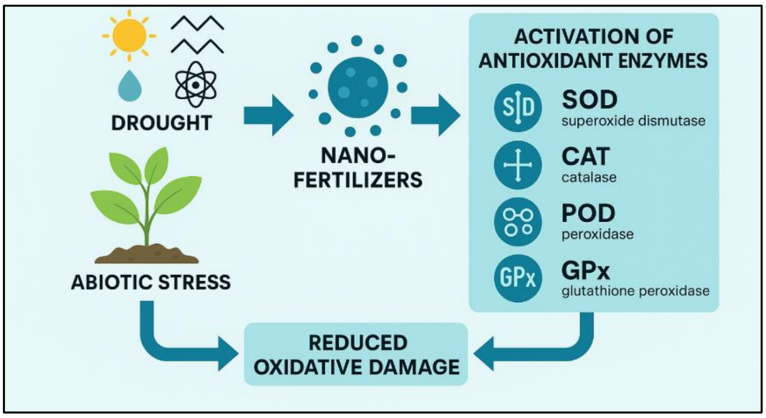


Figure: Activation of Antioxidant Enzymes in Plants by Nano-Fertilizers Under Abiotic Stress

6.2 Gene Expression Regulation under Nanoparticle Influence:

The impact of nanoparticles (NPs) on plants extends beyond traditional nutrient supplementation, influencing gene expression patterns related to enzymatic defense, stress signaling, and metabolic pathways. Recent studies have increasingly demonstrated that NPs can modulate the transcription of enzyme-encoding and stress-responsive genes, offering novel strategies for enhancing stress tolerance and crop productivity. This gene-level regulation, often confirmed through qPCR and transcriptomic analyses, reflects the intricate crosstalk between nanomaterials and plant molecular systems.

Titanium dioxide (TiO_2) nanoparticles are the most studied in this context. In *Vitex agnus-castus*, TiO_2 NPs applied at 800 µg/mL significantly upregulated antioxidant-related genes such as SOD, CAT, and the WRKY transcription factor, a key regulator of stress responses. The expression was dose-dependent, confirming the role of TiO_2 NPs as molecular elicitors that prime plants for oxidative stress defense (Farahi *et* *al*., 2021). Similarly, in *Dracocephalum kotschyi*, TiO_2 nanoparticle treatment led to the upregulation of RAS, TAT, and PAL—genes involved in the biosynthesis of rosmarinic acid. This genetic modulation was accompanied by enhanced activity of antioxidant enzymes like SOD, CAT, and APX, indicating that NPs can simultaneously influence primary defense systems and secondary metabolite production (Salar *et al*., 2021).

Cerium oxide (CeO_2) nanoparticles have also demonstrated the ability to reprogram gene expression in favor of stress mitigation. In wheat, green-synthesized CeO_2 NPs enhanced drought tolerance by upregulating drought-responsive genes such as DREB2, MYB33, and SnRK2.4. This molecular activation was supported by reduced biochemical indicators of oxidative stress, including hydrogen peroxide and malondialdehyde, establishing a clear link between transcriptional reprogramming and physiological resilience (Boora *et al*., 2024). Interestingly, other studies using hepatotoxicity models found that CeO_2 NPs downregulated antioxidant regulators like Nrf-2 and HO-1 while increasing cellular antioxidant reserves such as glutathione, GPx, CAT, and SOD, highlighting the nuanced and sometimes dose-specific effects of NPs on redox gene networks (Hashem *et al*., 2015).

Zinc sulfide nanoparticles (ZnS-T NPs) have also been shown to elicit significant transcriptional changes. In rice, ZnS-T NPs upregulated CuZn-SOD, CAT, and APX, alongside transcription factors like GRF and CKX that are involved in cell division and cytokinin signaling. These genetic changes were associated with improved germination rates and early seedling vigor, demonstrating that nanoparticle treatment can effectively activate growth and defense programs (Khepar *et al*., 2024). Similarly, bio-synthesized silver nanoparticles (AgNPs) promoted shoot and root elongation in rice and triggered an upregulation of CAT and APX while concurrently downregulating CuZn-SOD, suggesting a shift in the antioxidant pathway favoring the ascorbate cycle (Gupta *et al*., 2018).

Broader transcriptional effects have also been observed at the whole-plant level. Transcriptome-wide profiling of lettuce treated with a combination of TiO_2 and ZnO nanoparticles revealed over 3,600 differentially expressed genes (DEGs) in roots alone. Many of these genes were associated with antioxidant production, nitrogen metabolism, and photosynthetic pathways, indicating that NP treatment can modulate entire regulatory networks across multiple physiological processes (Wang *et al*., 2017). Furthermore, research on soybean seeds exposed to iron and cobalt nanoparticles uncovered not only changes in gene expression but also alterations in DNA methylation patterns. These epigenetic changes corresponded with the upregulation of genes involved in ethylene biosynthesis and mobilization of storage reserves, suggesting that NPs can influence early developmental stages via both genetic and epigenetic mechanisms (Linh *et al*., 2021).

6.3 Maintenance of Redox Homeostasis and Stress Alleviation:

Redox homeostasis plays a critical role in maintaining cellular integrity and physiological functionality in plants, especially under adverse environmental conditions. The accumulation of reactive oxygen species (ROS) during abiotic stress events—such as drought, salinity, or heavy metal exposure—can lead to severe oxidative damage, resulting in membrane lipid peroxidation, enzyme inhibition, and ultimately, growth suppression. In this context, nano-fertilizers have emerged as potent agents in regulating the cellular redox state. Due to their high reactivity and ability to activate antioxidant pathways, nanoparticles (NPs) effectively mitigate oxidative stress and promote resilience by balancing ROS production and scavenging.

Numerous studies have confirmed the ability of nanoparticles to stabilize redox conditions in crops under environmental stresses. Nanoparticles such as zinc oxide (ZnO), silicon dioxide (SiO_2), iron oxide (Fe_2O_3), selenium, and boron-based compounds have been shown to improve the antioxidant capacity of plants, reduce ROS accumulation, and limit oxidative injury. For example, in maize subjected to salinity stress, the application of B_2O_3 nanoparticles significantly enhanced the glutathione–ascorbate cycle and increased the synthesis of flavonoids and tocopherols, leading to a marked reduction in ROS biomarkers like hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) (El-Shafey *et al*., 2023). Similarly, in barley grown on contaminated soils, Fe_2O_3 nanoparticles mitigated oxidative damage by upregulating enzymatic antioxidants in both roots and shoots, restoring cellular redox equilibrium and promoting biomass accumulation (Rodríguez-Seijo *et al*., 2021).

Selenium nanoparticles (SeNPs) have also demonstrated robust redox-protective effects. In spinach under arsenic stress, SeNP application elevated the activities of catalase, glutathione peroxidase (GPx), and ascorbate peroxidase (APX), while improving photosynthesis and growth performance (Kumar *et al*., 2024). These nanoparticles detoxified arsenic-induced ROS and stimulated metabolic and photosynthetic recovery. In another instance, the use of SiO_2 nanoparticles counteracted the oxidative damage caused by graphene quantum dots in maize, resulting in enhanced photosynthetic efficiency and increased expression of antioxidant genes, demonstrating their efficacy even under combined or compound stress conditions (Yan *et al*., 2024).

Beyond direct ROS detoxification, nanoparticles influence redox homeostasis through crosstalk with plant hormonal signaling pathways. Reviews and experimental studies have documented NP-mediated modulation of abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA) signaling, which are key regulators of stress responses. Nanoparticles often trigger redox-sensitive transcription factors and signal cascades that activate antioxidant machinery (Banerjee & Roychoudhury, 2021). For instance, co-application of brassinosteroids and ZnO nanoparticles in tomatoes resulted in an improved glutathione redox state (higher GSH: GSSG ratio) and the upregulation of critical antioxidant genes, including *Cu/Zn-SOD*, *CAT1*, and *GSH1*, enhancing both enzymatic and non-enzymatic defenses (Li *et al*., 2016).

Synergistic strategies involving nanoparticles and biofertilizers further strengthen redox regulation. In safflower, integrating ZnO-NPs with biofertilizers significantly lowered MDA content, restored Na^+/K^+ ion balance under salt stress, and improved overall plant productivity (Yasmin *et al*., 2021). These effects exemplify how nanoparticles can work with biological agents to optimize redox homeostasis under challenging soil and climatic conditions. Importantly, nanoparticles scavenge ROS and serve as priming agents that mildly stimulate the plant's intrinsic defense systems. Cerium oxide, silver, and copper oxide nanoparticles, for example, have been shown to enhance the plant's antioxidant capacity through low-dose stimulation of redox signaling pathways. This priming effect increases the plant's preparedness for future stress without inducing toxicity, effectively enhancing stress memory and resilience (Zhao *et al*., 2022).

7. Smart Nano-Fertilizers and Crop Yield Improvement:

7.1 Growth and Physiological Parameters under Stress Conditions:

Smart nano-fertilizers have emerged as pivotal tools in modern crop management, particularly under abiotic stress conditions such as drought, salinity, nutrient depletion, and temperature extremes. These nanomaterials are specifically engineered to enhance nutrient use efficiency and physiological performance in plants. Key parameters such as leaf area, root-shoot ratio, and stomatal conductance—essential indicators of plant health and stress adaptation—are significantly improved through nano-fertilizer application, enabling crops to sustain growth and yield under challenging environments.

Numerous studies confirm that nano-fertilizers contribute to morphological enhancement and biomass accumulation in stressed crops. In sandy soils prone to nutrient leaching, foliar application of potassium-based nano-fertilizer led to notable increases in shoot fresh and dry weight, root length and circumference, and total chlorophyll content in peanut plants, indicating robust growth under suboptimal conditions (Anonymous, 2019). Similarly, in *Senna angustifolia* (cassia), a dual application of foliar and soil-based nano-fertilizers significantly improved plant height, leaf count, stem thickness, root biomass, and chlorophyll levels. Notably, a multi-nutrient nano-fertilizer containing Zn, Mn, Fe, Cu, and citric acid increased root dry weight by an impressive 261% compared to untreated controls (Kahlel *et al*., 2021).

Nano-fertilizers also exhibit remarkable influence on physiological traits such as leaf area and the root-to-shoot ratio. In *Myrtus communis* (myrtle), nano-NPK treatment led to a considerable increase in stem diameter and leaf area, accompanied by elevated chlorophyll and carbohydrate levels, signaling enhanced photosynthetic and metabolic activity (Fadalah *et al*., 2023). Under drought conditions in tomatoes, nano-vermicompost application not only improved shoot biomass and chlorophyll content but also stabilized cell membranes, reduced lipid peroxidation, and increased antioxidant enzyme activity. These physiological enhancements reflected a more balanced distribution of resources between root and shoot systems and improved water-use efficiency (Ahanger *et al*., 2021).

Stomatal conductance, a vital trait for water regulation under drought stress, is also modulated by smart nano-fertilizers. In rice plants exposed to alternating drought and flood conditions, nano-hydrogel nitrogen fertilizers improved enzymatic activity, root area development, and water retention capacity. This treatment maintained elevated catalase activity and enhanced cellular turgidity, indicating improved stomatal performance and reduced oxidative damage (Hamoud *et al*., 2024). Furthermore, gene-level analyses support these physiological findings. In *Arabidopsis thaliana*, foliar application of nano-urea increased plant biomass by 51% and chlorophyll content by 29.5%, while upregulating over 200 genes involved in growth, chlorophyll biosynthesis, and stress resilience—demonstrating a strong molecular basis for the observed physiological benefits (Dey *et al*., 2024).

The effectiveness of nano-fertilizers is closely linked to application method and frequency. In *Cucumis melo* (rock melon), foliar use of MARDI's nanoemulsion-based fertilizer enhanced plant height, stem diameter, leaf area, and chlorophyll content by more than 40% in optimal treatments. However, excessive application led to diminishing returns, emphasizing the importance of dosage optimization (Fadzil *et al*., 2024). Integration of nano-fertilizers with biological inoculants further amplifies growth outcomes. In cowpea, co-application of nano-DAP with zinc EDTA and biofertilizers increased pod weight, grain yield, and leaf count, outperforming conventional fertilization strategies and offering synergistic advantages under real-world field conditions (Balachandrakumar *et al*., 2024).

7.2 Yield Traits and Reproductive Development:

Smart nano-fertilizers have emerged as transformative agents in crop productivity by significantly enhancing yield traits and reproductive development, especially under variable field and stress-prone conditions. By enabling precise and efficient nutrient delivery at key developmental stages, nano-fertilizers improve flowering time, grain yield, and harvest index (HI), all while reducing fertilizer use and environmental burden. Their ability to optimize nutrient use efficiency (NUE) and physiological performance positions them as a cornerstone of sustainable and high-efficiency agriculture.

Several studies have reported notable grain yield increases resulting from applying nano-fertilizers. In cowpea, foliar spraying of nano-diammonium phosphate (nano-DAP) and zinc EDTA during crucial reproductive phases led to significant improvements in yield-related parameters, including pod length, pod number per plant, and seeds per pod. This intervention achieved a peak grain yield of 1,720 kg/ha with a remarkable benefit-cost ratio of 3.25, demonstrating strong economic and agronomic returns (Balachandrakumar *et al*., 2024). Likewise, three foliar applications of nano-NPK in transplanted puddled rice achieved grain and straw yields equivalent to those obtained with full conventional fertilizer doses. These results emphasized nano-fertilizers' potential to sustain high yield levels while reducing input quantities and environmental impact (Babu *et al*., 2025).

Beyond yield magnitude, nano-fertilizers influence reproductive timing and crop phenology. For instance, in wheat, late-stage foliar application of nano-urea in combination with nano-selenium extended the grain-filling period, increased chlorophyll content, and enhanced photosynthetic performance, thereby improving final grain yield (Singh *et al*., 2024). Similarly, a study on flax genotypes revealed that higher concentrations of NPK nano-fertilizer delayed flowering and improved both biological and seed yields, suggesting a direct role of nano-inputs in fine-tuning phenological events to boost productivity (Ali & Jassim, 2024).

Nano-fertilizers have also demonstrated consistent improvements in harvest index (HI), a critical trait reflecting the efficiency of converting biomass into harvestable yield. In tomato crops, foliar application of nano-iron (Fe) fertilizer enhanced fruit yield and HI while boosting phytochemical content, including carotenoids and flavonoids, indicating that nano-interventions improve both yield quantity and nutritional quality (Rahman *et al*., 2023). Similarly, using nano-titanium dioxide (TiO_2) and nano-silicon (SiO_2) significantly improved sunflower seed yield, oil content, chlorophyll levels, and HI. These treatments enhanced reproductive metrics such as seed count per head and accelerated physiological maturity, highlighting nano-fertilizers' capacity to support vegetative vigor and reproductive output (Sabaghnia *et al*., 2018).

The integration of nano-fertilizers with organic amendments further amplifies reproductive success. In sunflower, 20 tons per hectare of organic manure with zinc-based nano-fertilizers improved flowering duration, achene yield, and HI. TT biplot analysis confirmed this integrated approach as superior for maximizing yield-related traits under field conditions (Sabaghnia *et al*., 2018).

The versatility of nano-fertilizers across crops and environmental scenarios is particularly noteworthy. In saline-stressed maize, the application of nano-zinc and nano-silicon fertilizers increased cob length and grain yield by up to 110%, while simultaneously enhancing nutrient uptake and reducing sodium accumulation in plant tissues (Shoukat *et al*., 2025). Moreover, in rice, precision nitrogen management using nano-urea sprays yielded a 16.68% improvement in grain production compared to conventional fertilization methods, demonstrating how nano-enabled strategies can optimize productivity in diverse agroecological zones (Sagar *et al*., 2023).Together, these findings underscore the potential of smart nano-fertilizers to improve crop yield, reproductive timing, and resource-use efficiency, making them invaluable tools for climate-resilient and high-efficiency agriculture.

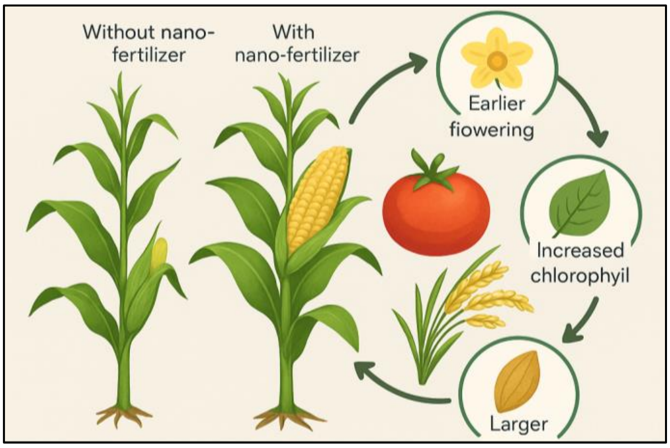


Figure: Impact of Smart Nano-Fertilizers on Yield Traits and Reproductive Development.

This figure compares crop performance with and without nano-fertilizers, showing improved flowering, larger grains, and increased chlorophyll. Smart nano-fertilizers enable efficient nutrient delivery during critical growth stages. They enhance productivity while reducing environmental burden in stress-prone conditions.

7.3 Enhanced Photosynthesis and Chlorophyll Retention:

Smart nano-fertilizers have demonstrated significant potential in enhancing photosynthesis and chlorophyll retention, crucial determinants of crop productivity and plant vitality, particularly under environmental stress conditions. Through their nanoscale size, increased surface area, and controlled-release capabilities, nano-fertilizers provide precise and sustained nutrient delivery. This targeted availability supports more efficient chlorophyll synthesis, stabilizes photosynthetic complexes, and enhances light-harvesting efficiency, ensuring the maintenance of photosynthetic capacity even in suboptimal conditions.

Numerous studies have highlighted nano-fertilizers' ability to boost chlorophyll content and promote photosynthetic activity. In lettuce, treatment with *Rosa roxburghii*-derived carbon dots (RR-CDs) led to a 31.8% increase in chlorophyll concentration and a 60.8% rise in net photosynthetic rate. Notably, electron transport in photosystem II improved by 38.7%, indicating enhanced light absorption and energy conversion efficiency, which contributed to overall biomass gains (Xu *et al*., 2024). A similar outcome was observed in pomegranate, where foliar application of nano-nitrogen significantly increased chlorophyll content and fruit yield using a fraction of the nitrogen typically required with conventional urea fertilizers. This demonstrated the superior efficiency of nano-N in supporting chloroplast function and reducing input requirements (Davarpanah *et al*., 2017).

Beyond chlorophyll synthesis, smart nano-fertilizers also improve the functional efficiency of the photosynthetic machinery. Under cold stress, maize plants treated with zinc and mineral-based nanoparticles exhibited rapid recovery in photosystem II efficiency. Chlorophyll fluorescence analysis revealed a 15–19% increase in net photosynthetic rate during the recovery phase, confirming the ability of nanoparticles to protect and stabilize the photosynthetic apparatus under environmental fluctuations (Ratajczak *et al*., 2023). In another study, CuZn bimetallic nanoparticles applied to tomato leaves enhanced PSII functionality without inducing phototoxicity. At low concentrations, these nanoparticles preserved the plastoquinone pool, minimized H_2O_2 accumulation, and maintained consistent electron transport during both low- and high-light conditions, thereby supporting optimal photosynthetic performance (Antonoglou *et al*., 2018).

The structural stability of photosynthetic complexes is further reinforced through nano-fertilizer application. In cotton, nano-phosphorus fertilizers combined with humic acid enhanced chlorophyll A and B concentrations, promoted root growth, and increased nutrient uptake. These physiological improvements suggest improved thylakoid membrane integrity and stabilization of photosystem structures under field conditions (Mohamed & El-Mgaed, 2020). Complementary findings in lettuce demonstrated that integrating 25–50% conventional fertilizers with nano-formulations significantly elevated chlorophyll a and b levels (by up to 51%) and improved PSII quantum efficiency. This partial replacement strategy also boosted antioxidant enzyme activity and nutrient assimilation, underscoring the dual benefits of enhanced photoprotection and productivity (Abdel-Hakim *et al*., 2023).

Mechanistically, nano-zinc fertilizers have been shown to support chlorophyll retention through improved micronutrient bioavailability and activation of key biosynthetic enzymes such as chlorophyll synthase and ALA synthetase. These effects are particularly valuable under nutrient-deficient and saline conditions, where enhanced enzyme activity aids in sustaining chlorophyll content and preserving photosynthetic output (Jakhar *et al*., 2022). Thus, smart nano-fertilizers not only boost photosynthetic capacity but also offer resilience against stress-induced chlorosis and yield decline, making them indispensable in climate-smart and precision agriculture practices.

8. Case Studies in Climate-Smart Crop Management:

8.1 Wheat: ZnO and SiO_2 Nanoparticles for Salinity and Drought:

Wheat, as one of the most widely cultivated cereal crops globally, faces significant yield reductions due to increasing occurrences of abiotic stresses, particularly drought and salinity. These stresses negatively impact physiological processes such as water uptake, chlorophyll biosynthesis, nutrient assimilation, and oxidative balance. However, the application of zinc oxide (ZnO) and silicon dioxide (SiO_2) nanoparticles (NPs) has shown notable potential in enhancing wheat resilience by modulating antioxidant activity, improving nutrient efficiency, and stabilizing physiological traits under stress.

Zinc oxide nanoparticles have emerged as particularly effective in enhancing drought tolerance in wheat. In a study involving two wheat cultivars—Anaj-2017 and FSD-2018—foliar application of ZnO NPs at concentrations ranging from 100 to 150 ppm significantly increased root and shoot biomass and improved chlorophyll a and b levels by over 70%. Peroxidase activity was also markedly elevated, especially in drought-sensitive cultivars, confirming the nanoparticles' role in oxidative stress mitigation (Haq *et al*., 2023). Similarly, wheat varieties Ujala-16 and

Zincol-16 showed enhanced drought tolerance when treated with ZnO NPs at 120 ppm. Treated plants displayed elevated chlorophyll content and improved uptake of essential nutrients such as calcium, magnesium, iron, and zinc. Among these, Zincol-16 performed particularly well under severe drought (50% field capacity), highlighting the genotype-dependent efficacy of nanoparticle treatments (Abbas *et al*., 2023).

Silicon dioxide nanoparticles also contribute to drought resilience by enhancing several physiological and biochemical parameters. In wheat genotypes Kalar1 and Kalar2, SiO_2 NPs improved specific leaf area, catalase activity, and soluble carbohydrate accumulation. When compared to copper nanoparticles, both ZnO and SiO_2 NPs offered superior osmoprotection and membrane stability, suggesting that their combined use may yield synergistic protective effects under water-deficit stress (Jasem & Khalil, 2022).

Beyond physiological improvements, ZnO nanoparticles influence gene expression patterns involved in drought tolerance. Notably, ZnO application was found to upregulate critical stress-responsive genes such as DREB2, CAT1, and P5CS—associated with proline synthesis, antioxidant response, and dehydration tolerance. These molecular adaptations translated into improved physiological performance under extreme drought at 35% field capacity (Sadati *et al*., 2022). Furthermore, nanopriming with ZnO has been reported to enhance seedling vigor through hydrogen peroxide (H_2O_2) signaling. This stimulation activated α-amylase and various antioxidant enzymes, contributing to better seedling establishment and protection of photosystem II from oxidative damage (Rai-Kalal *et al*., 2021).

The beneficial effects of ZnO NPs are amplified when co-applied with plant growth-promoting rhizobacteria (PGPR). In wheat, combined treatment with ZnO nanoparticles and *Azospirillum brasilense* led to significant increases in antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) by 38–44%. This dual treatment also improved membrane stability, chlorophyll content, and grain zinc accumulation, ultimately enhancing both stress tolerance and nutritional quality (Muhammad *et al*., 2022).

ZnO nanoparticle priming has also shown promise in combating salinity stress. In durum wheat, seed priming with ZnO NPs improved grain yield by up to 36% under saline conditions reaching 9.3 dS/m. The treatment facilitated better nitrogen and potassium uptake—two essential nutrients for osmotic and ionic balance under salinity stress (Al-Salama, 2022). Complementary results have been observed under combined drought and heat stress, where SiO_2 and ZnO nanoparticle treatments improved chlorophyll fluorescence and photosynthetic efficiency while reducing lipid peroxidation markers such as malondialdehyde (MDA) and hydrogen peroxide (H_2O_2). These improvements indicate superior oxidative stress management and enhanced physiological integrity under multiple stress conditions (Azmat *et al*., 2022).

Collectively, the application of ZnO and SiO_2 nanoparticles offers a multi-faceted approach to strengthening wheat's tolerance to drought and salinity. Through antioxidant activation, nutrient uptake enhancement, gene regulation, and stress signal modulation, these nanomaterials contribute significantly to sustainable wheat production under increasingly challenging agro-climatic conditions.

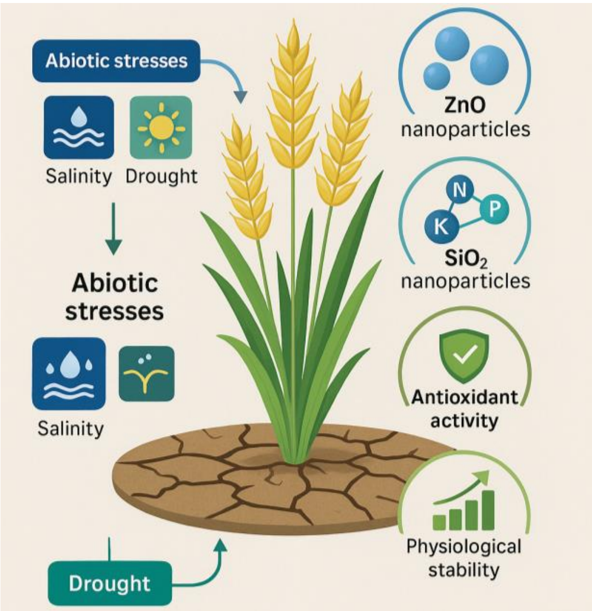


Figure: Enhancing Wheat Stress Tolerance with ZnO and SiO_2 Nanoparticles

This figure illustrates how zinc oxide (ZnO) and silicon dioxide (SiO_2) nanoparticles help wheat combat abiotic stresses such as salinity and drought. These nanoparticles enhance antioxidant activity, nutrient uptake, and physiological stability, resulting in improved resilience and growth. Their application supports climate-smart crop management under water- and salt-stressed conditions

8.2 Rice: Nano-Iron and Phosphate Fertilizers Under Flooding Stress:

Rice cultivation in lowland and flood-prone agroecosystems presents specific nutritional challenges due to the anaerobic conditions that arise under continuous flooding. These conditions alter redox potential, limit nutrient solubility—particularly phosphorus (P)—and exacerbate micronutrient imbalances such as iron (Fe) toxicity or deficiency. Smart nano-fertilizers, particularly nano-iron and nano-phosphates, offer targeted solutions by improving nutrient bioavailability, reducing oxidative stress, and enhancing yield quality under flooded conditions.

Nano-iron formulations have demonstrated substantial success in mitigating stress and improving productivity in waterlogged rice systems. A key study involving maghemite (γ-Fe_2O_3) nanoparticles applied to fluoride-contaminated rice fields found that FeNPs effectively reduced fluoride uptake, restored Hill reaction efficiency, and increased chlorophyll and carotenoid levels. These improvements were accompanied by enhanced activities of antioxidant enzymes including superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), as well as increased proline content and decreased ROS accumulation—resulting in significantly improved grain and panicle development compared to both stressed and control plants (Banerjee & Roychoudhury, 2021). Complementing this, nano-iron-loaded *Spirulina* biomass (a nano phyco-fertilizer, NPF) boosted shoot length by 37.6%, grain yield by 47%, and grain iron content by up to 44% over conventional NPK fertilizers, indicating dual benefits in iron delivery and stress mitigation (Mondal *et al*., 2024).

Further advancing this strategy, another algal-based nano-phyco-fertilizer improved grain yield by 2.5 times and significantly increased the nutritional value of polished rice. Iron content rose by 45% while essential amino acids increased by 20–40%, demonstrating the synergistic effect of combining nanoparticle-based micronutrients with organic carriers under flooded cultivation (Mondal *et al*., 2024).

Phosphorus solubility, a major limiting factor in anaerobic soils, can also be improved through nanotechnology. Under reducing conditions, conventional ferric-phosphate complexes often precipitate, becoming unavailable to plants. However, nano-phosphate formulations have been shown to bypass these constraints. In Egyptian rice fields, foliar application of nano-phosphatic fertilizers significantly improved both grain and straw yield across several rice varieties. Notably, the Giza 179 variety exhibited higher productivity compared to those treated with conventional superphosphate, confirming the higher uptake efficiency of nano-sized phosphorus sources (Sorour *et al*., 2020). In upland rice, combining nano-ZnO with phosphorus-solubilizing bacteria (PSB) resulted in improved root development, tiller count, and nutrient uptake, increasing phosphorus use efficiency (PUE) by 31.5%—a promising outcome for low-input or marginal soils (Jamadar *et al*., 2024).

The role of nano-fertilizers becomes even more critical in alternating drought-flood scenarios typical of monsoon-based agriculture. Application of smart nitrogen nano-hydrogel fertilizers maintained nitrogen availability during fluctuating moisture conditions, enhanced catalase activity, increased glutamine synthetase, and stabilized photosynthetic protein levels. As a result, treated rice plants achieved the highest levels of grain protein (12.4%), amylose content (17.6%), and milling recovery rate (87.3%), demonstrating that nano-formulations can support both physiological stability and grain quality under dual-stress regimes (Hamoud *et al*., 2024).

Additionally, nano-chelated iron fertilizers have shown remarkable agronomic and nutritional synergy. One study reported a 27% increase in grain yield and a 254% reduction in hollow grain formation. These fertilizers improved the nutrient content (N, P, K, Fe, Zn) of grains by up to 50% and enhanced rice protein and starch profiles, highlighting their value in biofortification and post-harvest quality enhancement (Fakharzadeh *et al*., 2020). Overall, the application of nano-iron and nano-phosphorus fertilizers presents a powerful strategy for sustaining rice productivity in flooded and alternating moisture environments. Through improved nutrient availability, photosynthetic efficiency, stress resilience, and grain quality, these innovations support climate-resilient and nutritionally enriched rice production systems.

8.3 Maize and Soybean: Heat and Drought Response to Nanoparticles:

Maize and soybean, two of the world's most important staple crops, are particularly susceptible to abiotic stresses such as drought and high temperatures. These stressors severely impact photosynthetic efficiency, enzyme function, and overall plant metabolism. Recent advances in nanotechnology have shown that nanoparticle (NP) applications—especially involving metal oxides, silicon, chitosan, and carbon-based materials—can substantially enhance thermal and drought tolerance in these crops by modulating antioxidant defense systems, stabilizing photosynthetic processes, and regulating stress-responsive gene expression.

In maize, copper nanoparticles (CuNPs) have been found highly effective in mitigating drought stress. CuNP-treated plants exhibited increased water retention, enhanced biomass, and improved grain yield. Biochemically, these plants showed elevated levels of chlorophyll, carotenoids, and anthocyanins, along with reduced reactive oxygen species (ROS) accumulation, due to increased activities of key antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX). The number of seeds per cob and total grain mass were significantly higher compared to untreated drought-stressed plants (Nguyen *et al*., 2021). Another promising intervention involved chitosan-fulvic acid nanoparticles (Ch-FANPs), which improved shoot and root biomass by 20%, reduced H_2O_2 content by 10%, and doubled APX activity. These treatments also triggered transcriptional changes, upregulating critical drought-related genes including *ZmDREB1A*, *ZmbZIP1*, and *ZmCIPK3* (Brown *et al*., 2024). Similarly, glycine betaine-loaded chitosan nanoparticles (LNPs) elevated antioxidant enzyme levels and proline accumulation while reducing malondialdehyde (MDA), a marker of oxidative damage. Gene expression analyses revealed upregulation of *ZmSOD*, *ZmCAT*, and *ZmAPX*, confirming their role in maintaining cellular homeostasis under 20% drought stress (Jabeen *et al*., 2024).

Metal oxide and silicon-based nanoparticles have also shown strong protective effects in maize under drought conditions. Silicon dioxide (SiO_2) nanoparticles enhanced relative water content, stimulated chlorophyll biosynthesis, and boosted activities of antioxidant enzymes such as SOD, CAT, and peroxidase (POD). These effects were associated with increased expression of photosynthetic genes, including *PsbD*, indicating enhanced photosystem stability (Sharf-Eldin *et al*., 2023). Manganese oxide (Mn_3O_4) nanoparticles improved root apex mitotic activity by 35.5%, reduced H_2O_2 content by 40.9%, and lowered MDA levels by 74.7%, highlighting their capacity to regulate oxidative stress and promote cell division under drought (Sun *et al*., 2023). Likewise, zinc oxide (ZnO) nanoparticles improved photosynthesis, water use efficiency, and carbohydrate metabolism by stimulating key metabolic enzymes such as UDP-glucose pyrophosphorylase and cytoplasmic invertase, leading to improved drought adaptation (Sun *et al*., 2020).

In soybean, nanoparticles have similarly shown multifaceted benefits in improving drought resilience. Treatments with iron, zinc, copper, and cobalt nanoparticles increased relative water content, biomass retention, and drought tolerance index. Iron nanoparticles, in particular, triggered a widespread upregulation of drought-responsive genes in both roots and shoots, including *GmERD1*, enhancing the plant's dehydration resistance mechanisms (Linh *et al*., 2020). Selenium nanoparticles (SeNPs), when applied during reproductive stages, improved photosynthetic pigment levels, antioxidant enzyme activities, and relative water content while reducing oxidative stress markers like ROS and MDA. These treatments preserved leaf ultrastructure and stomatal function, ultimately boosting drought resilience and yield potential (Zeeshan *et al*., 2024).

Further advancements include combining iron oxide nanoparticles with the beneficial endophytic fungus *Piriformospora indica*, which enhanced photosynthetic gas exchange, increased sucrose phosphate synthase activity, and improved phosphorus accumulation under water stress. This symbiotic nano-bio formulation stabilized cellular membranes and maintained leaf function during drought (Delavar *et al*., 2023).

9. Integration with Plant Biotechnology:

9.1 Genetically Enhanced Antioxidant Systems:

Enhancing plant antioxidant capacity through transgenic technology has emerged as a strategic and targeted approach to combat abiotic stressors such as drought, heat, salinity, and oxidative damage. By enabling the overexpression of specific antioxidant enzymes and stress-responsive genes, genetic engineering offers precise molecular interventions that enhance plant resilience, improve stress tolerance, and maintain physiological stability under adverse environmental conditions. Significant breakthroughs have been made in developing transgenic crops with superior antioxidant defense systems that outperform non-transgenic lines under stress.

A primary area of focus has been the genetic enhancement of classical antioxidant enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (APX), and catalase (CAT), which are central to reactive oxygen species (ROS) detoxification. For instance, in transgenic tall fescue, the simultaneous overexpression of *CuZnSOD* and *APX* under the control of an oxidative stress-inducible promoter conferred broad-spectrum resistance against salinity, heavy metals, and oxidative stress. These transgenic lines exhibited reduced lipid peroxidation, retained chlorophyll content, and maintained lower ROS levels compared to wild-type plants, confirming the success of targeted antioxidant pathway activation (Lee *et al*., 2007). Similarly, in potato, overexpression of the *GalUR* gene from strawberry enhanced ascorbate content and activated the ascorbate-glutathione cycle by upregulating APX, dehydroascorbate reductase (DHAR), and glutathione reductase (GR), leading to improved proline accumulation and reduced oxidative stress under salt and metal toxicity (Hemavathi *et al*., 2011).

The deployment of stress-responsive antioxidant genes has also been successfully demonstrated in food crops. In rice, transgenic lines overexpressing genes encoding SOD, APX, and glutaredoxin showed enhanced ROS scavenging efficiency and improved tolerance to drought and salinity. These physiological improvements were supported by the upregulation of protein kinases and transcription factors involved in oxidative stress signaling pathways (Morita, 2019). In another notable example, *CuZnSOD* from the halophytic mangrove *Avicennia marina* was introduced into *indica* rice, resulting in transgenic plants that demonstrated superior tolerance to both 150 mM NaCl salinity and drought stress. These plants retained chlorophyll levels and displayed less wilting than wild-type controls, even under prolonged salt exposure (Prashanth *et al*., 2008).

Beyond direct enzymatic enhancement, transgenic strategies have also leveraged transcriptional and hormonal regulatory mechanisms. In wheat, expression of the harpin-derived protein *Hpa110–42* induced thermotolerance through enhanced antioxidant enzyme activity. This response was attenuated by inhibitors of abscisic acid (ABA) biosynthesis and calcium signaling, indicating that the improved thermotolerance was mediated through hormone-regulated and calcium-dependent signaling cascades (Wang *et al*., 2017). This highlights the importance of integrating stress response elements at both the molecular and hormonal levels for maximal stress adaptation.

Innovative studies have also explored non-plant gene sources for antioxidant enhancement. In one such case, tobacco plants were genetically modified to express a versatile peroxidase (VP) gene from the white-rot fungus *Bjerkandera adusta*. These transgenic plants exhibited up to 10.8-fold higher manganese peroxidase (MnP) activity and showed exceptional tolerance to drought, salt, and oxidative stress, demonstrating the functional compatibility of fungal antioxidant systems within higher plants (Hernández-Bueno *et al*., 2021).

In addition to enzymatic strategies, metabolic engineering of compatible solute pathways has also proven effective. For instance, transgenic tobacco expressing the *PgP5CS* gene from pearl millet accumulated higher levels of proline—a key osmoprotectant—and maintained chlorophyll stability, lower MDA levels, and greater photosynthetic efficiency under drought and heat stress. These physiological benefits were correlated with improved water retention and upregulation of stress-regulated genes, highlighting the central role of proline metabolism in abiotic stress tolerance (Sellamuthu *et al*., 2024).

9.2 CRISPR/Cas-Based Engineering for Stress Traits:

The development of CRISPR/Cas-based genome editing has revolutionized plant biotechnology, offering a powerful and highly precise tool for improving abiotic stress resilience in crops. Unlike conventional breeding or transgenic approaches, CRISPR technology allows targeted editing of stress-responsive genes, cis-regulatory elements, and entire transcriptional networks. This enables rapid, efficient, and marker-free development of climate-resilient cultivars tailored for specific environmental challenges.

A major application of CRISPR/Cas9 involves editing both structural and regulatory genes associated with stress response. Structural genes encode proteins directly involved in physiological adaptation, while regulatory genes modulate broader signaling cascades. In rice, wheat, and maize, targeted editing of regulatory genes such as *DREB*, *AREB*, and *NAC* transcription factors has significantly enhanced drought, heat, and salinity tolerance (Zafar *et al*., 2020). In soybean, the knockout of *GmAITR* genes—members of an ABA-induced transcription repressor family—using CRISPR/Cas9 led to improved salinity tolerance without compromising yield. This genetic modification modulated ABA sensitivity and upregulated stress-associated genes, resulting in enhanced germination and seedling vigor under saline conditions (Wang *et al*., 2021).

CRISPR's utility also extends to promoter targeting and transcriptional regulation. Editing of cis-regulatory elements such as stress-responsive promoters has allowed fine-tuning of gene expression under specific environmental cues, without introducing foreign DNA. These modifications improve stress defense while minimizing energy costs and growth trade-offs (Zafar *et al*., 2020). Furthermore, advanced CRISPRi (interference) and CRISPRa (activation) platforms provide gene expression control without altering the DNA sequence, facilitating epigenetic modulation of stress networks and offering dynamic regulation of tolerance traits (Ahmad *et al*., 2021).

Next-generation editing tools like base editing and prime editing have further expanded CRISPR's capabilities. These systems enable single-nucleotide alterations within stress-associated genes with reduced off-target effects, offering precise allele modification for fine-tuning tolerance. In wheat and tomato, base editing has been used to enhance alleles linked to salt and drought response, improving crop survival and metabolic efficiency under severe stress (Kumar *et al*., 2023).

Multiplex CRISPR editing—where multiple genes are targeted in a single transformation event—has enabled the development of crops with combined resistance to multiple stressors. In tomato, simultaneous editing of *SlHyPRP1* and *SlDEA1* enhanced drought and disease tolerance by improving chlorophyll retention, reducing ROS accumulation, and stabilizing photosynthetic function. These results demonstrate the practical utility of gene stacking for addressing the increasingly complex nature of climate-induced stresses (Saikia *et al*., 2024).

Emerging strategies such as RNA editing and transgene-free CRISPR platforms are also gaining momentum. These methods allow transient or heritable genetic alterations without incorporating foreign DNA, addressing regulatory and consumer concerns. As these transgene-free technologies gain wider acceptance, they are poised to accelerate the release of improved crop varieties with reduced biosafety risks and greater public trust (Ahmad *et al*., 2021).

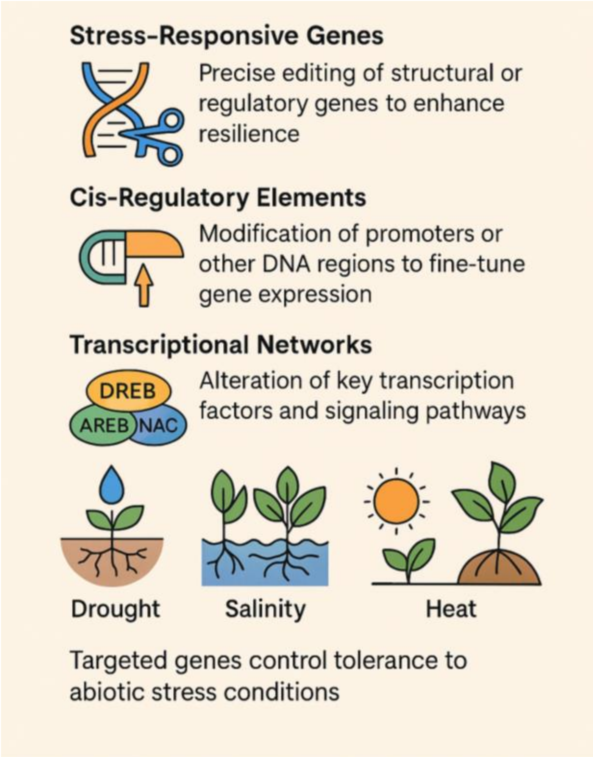


Figure: CRISPR/Cas-Based Engineering for Abiotic Stress Tolerance in Crops

This figure illustrates how CRISPR/Cas technology enhances crop resilience to drought, salinity, and heat by editing stress-responsive genes, cis-regulatory elements, and transcriptional networks. Targeted modifications improve stress tolerance without introducing foreign DNA, enabling precise, efficient, and sustainable crop improvement.

1.3 Combined Application of Nano-Fertilizers and Biostimulants:

The integrated use of nano-fertilizers and biostimulants represents a forward-looking strategy in sustainable agriculture, harnessing the precision of nanotechnology and the biological efficacy of microbial and organic inputs. This synergistic approach enhances nutrient use efficiency, modulates plant hormone signaling, and improves stress tolerance and crop productivity under variable environmental conditions. Recent research demonstrates that the co-application of nano-fertilizers with biostimulants—including algal extracts, microbial consortia, and hormone-based formulations—consistently outperforms the effects of either component when applied individually. In onion cultivation, for example, the foliar co-application of Nano-NPK (1.0 g/L) with algae extract (0.5 g/L) significantly enhanced plant height, fresh biomass, and bulb yield. This dual treatment improved bulb diameter by over 140% and total yield by 154% compared to untreated controls, outperforming conventional fertilization strategies. The algae-derived biostimulant facilitated superior nutrient uptake, while the nano-fertilizer ensured controlled nutrient release, maximizing nutrient bioavailability (Afify, 2023).

In maize, the combination of microbial biostimulants—including arbuscular mycorrhizal fungi (*Rhizophagus irregularis*), *Trichoderma koningii*, and plant growth-promoting rhizobacteria—with a protein hydrolysate (PH) induced profound changes in plant metabolism. Metabolomic analysis revealed significant alterations in phenylpropanoid and terpene pathways, increased shoot biomass by 16.6%, and root dry weight by 48% over untreated plants. The co-application also modulated phytohormonal balance and nitrogen utilization efficiency, contributing to improved growth and stress resilience (Rouphael *et al*., 2020).

Hormone-based biostimulants have also shown consistent long-term benefits when combined with nano-fertilizers. In tomato, a formulation containing gibberellins, auxins, and cytokinins led to a stable 15% increase in fruit yield across five consecutive growing seasons. When paired with nano-chelated micronutrients, the treatment amplified vegetative vigor, chlorophyll biosynthesis, and reproductive success, confirming the additive effects of hormonal stimulation and nanotechnology-enabled nutrient delivery (Smith & Argerich, 2019).

The synergy between microbial inoculants and nano-fertilizers is also evident under abiotic stress conditions. In greenhouse-grown pepper plants, co-application of *Rhizoglomus irregularis*, *Funneliformis mosseae*, and *Trichoderma koningii* with micronutrient nanoparticles led to a 23.7% increase in yield. The improved performance was attributed to hormonal rebalancing—elevated levels of gibberellins, auxins, and cytokinins—and enhanced production of carotenoids and phenolic compounds. Additionally, the presence of nanoparticles promoted microbial colonization and nutrient acquisition, further enhancing plant resilience (Bonini *et al*., 2020). Biopolymer–nanoparticle combinations have also shown promise. In green beans, foliar application of chitosan—a naturally derived biopolymer—with Fe and Zn nanoparticles increased nitrate reductase activity, nitrogen assimilation, and amino acid content. This synergistic treatment improved nutrient mobility and internal utilization, particularly under nutrient-limited or environmentally stressful conditions (Agüero-Esparza *et al*., 2022).

Interestingly, many nanoparticles themselves possess intrinsic biostimulant properties. Nanomaterials such as ZnO, SiO_2, and carbon-based nanoparticles can interact with plant membranes and ion channels, modulating ROS scavenging pathways, enhancing osmolyte accumulation, and activating stress-responsive gene networks. When applied in conjunction with microbial or organic biostimulants, these nanoparticles exhibit amplified physiological and molecular responses, positioning them as next-generation biostimulants in integrated nutrient and stress management systems (Bhatla *et al*., 2023). Overall, the co-application of nano-fertilizers and biostimulants offers a potent synergy for enhancing crop performance. By uniting the biochemical complexity of biological enhancers with the precision and efficiency of nanotechnology, this integrated approach addresses modern agricultural challenges with a systems-based, climate-smart solution.

10. Environmental and Safety Considerations:

10.1 Soil Health and Microbial Diversity Impacts:

The widespread application of nanoparticles (NPs), particularly metal-based nanofertilizers such as zinc oxide (ZnO), titanium dioxide (TiO_2), and silver nanoparticles (AgNPs), has introduced new dimensions to agricultural productivity. While these nanomaterials offer targeted nutrient delivery and improved crop performance, their effects on soil microbial health and ecological balance have raised significant environmental concerns. Soil microbial communities are integral to key processes such as nutrient cycling, organic matter decomposition, and overall soil fertility. Therefore, disruptions to microbial biomass, respiration, or functional diversity may threaten long-term soil health and sustainability.

Numerous studies have documented the negative impacts of metal-based nanoparticles on soil microbial biomass and enzymatic activity. For instance, prolonged exposure to AgNPs over a four-month period led to substantial declines in microbial biomass, alongside increased basal respiration and metabolic quotients (qCO_2), indicating reduced microbial efficiency in substrate utilization and heightened metabolic stress (Hänsch & Emmerling, 2010). Similar findings were reported for TiO_2 and ZnO nanoparticles, which significantly reduced microbial biomass and functional diversity in a California grassland soil. These nanoparticles also altered bacterial community structure and suppressed overall soil respiration, revealing their potential to interfere with carbon cycling and microbial equilibrium (Ge *et al*., 2011).

Nanoparticles also affect microbial community composition, particularly at higher application rates. In flooded paddy soils, elevated concentrations of CuO and TiO_2 nanoparticles reduced total microbial biomass, as measured by phospholipid fatty acid (PLFA) profiles, and decreased the activity of key enzymes such as urease, phosphatase, and dehydrogenase. Among the tested nanoparticles, CuO demonstrated stronger inhibitory effects on microbial diversity than TiO_2, likely due to its higher bioavailability and interaction with soil colloids (Xu *et al*., 2015). Similarly, ZnO nanoparticles suppressed microbial respiration and significantly decreased the abundance of actinobacteria and fungi. Dehydrogenase activity, a marker of microbial metabolic function, dropped by nearly 50%, accompanied by a sharp decline in microbial biomass carbon and total colony-forming units (Verma *et al*., 2021).

Exposure to cerium dioxide (CeO_2) nanoparticles in cambisol soils produced metabolic stress symptoms, including elevated basal respiration and reduced microbial carbon content. The resulting metabolic quotient (qCO_2) increase reflected inefficient microbial energy usage, a condition detrimental to microbial growth and long-term soil fertility (Antisari *et al*., 2011). Parallel observations were made with AgNPs, which triggered substantial reductions in bacterial and fungal colony-forming units, microbial respiration, and soil nitrogen content. These effects were particularly pronounced under conditions of higher NP concentration and extended exposure durations, suggesting the possibility of cumulative and chronic toxicity (Toularoud *et al*., 2025).

Interestingly, some studies have noted the potential for microbial adaptation in response to prolonged nanoparticle exposure. In soils treated with sub-lethal doses of ZnO nanoparticles, initial suppression of microbial activity was followed by the proliferation of metal-tolerant bacterial strains. While this shift implies some degree of microbial resilience, it also points to a community structure dominated by lower diversity and higher functional specialization, potentially impairing ecosystem multifunctionality and long-term nutrient cycling efficiency (Huang *et al*., 2021).

10.2 Bioaccumulation and Risk Assessment:

The environmental persistence of nanoparticles (NPs) and their capacity for bioaccumulation and trophic transfer pose serious concerns regarding long-term ecological safety and potential health impacts. Numerous studies have documented bioaccumulation of engineered nanoparticles in a wide range of aquatic and soil organisms, with the extent of accumulation largely influenced by factors such as particle size, surface coating, functionalization, and the specific exposure route. Notably, nanoparticles such as silver (AgNPs), titanium dioxide (TiO_2), and gold (AuNPs) have demonstrated significant bioaccumulation in aquatic organisms including algae, snails, and fish (Lekamge *et al*., 2020; Perrier *et al*., 2020; Skjolding *et al*., 2015). The physicochemical properties of nanoparticles, particularly hydrophobic surface modifications, are known to enhance uptake and retention within biota (Skjolding *et al*., 2015).

However, while bioaccumulation is frequently observed, biomagnification through trophic levels does not appear to be a consistent outcome. For example, AgNPs have been shown to accumulate in snails and planarians, yet the nanoparticles do not biomagnify across these trophic levels (Silva *et al*., 2021). Similar patterns have been reported in simplified aquatic food chains involving algae and *Daphnia magna*, where trophic transfer occurred but did not result in higher concentrations in predators compared to prey (Yoo-iam *et al*., 2014). This suggests that while trophic movement is possible, bioavailability and retention in higher organisms may be moderated by species-specific metabolism or excretion mechanisms. Moreover, engineered nanoparticles may act as carriers for co-contaminants such as polycyclic aromatic hydrocarbons (PAHs), enhancing their environmental mobility and bioavailability during trophic transfer. This co-exposure scenario can intensify toxicity in higher-level predators, thereby compounding ecological risk (Lu *et al*., 2020). Such interactions underscore the complexity of nanoparticle behavior in real-world ecosystems.

These insights make it clear that environmental risk assessments of nanoparticles must move beyond traditional models. Critical parameters such as aggregation state, dissolution kinetics, and surface chemistry must be incorporated to more accurately predict ecological impacts. Existing regulatory toxicity thresholds, often developed for bulk materials or conventional chemicals, are inadequate to capture the unique behaviors of engineered nanomaterials. Consequently, there is an urgent need to revise current regulatory frameworks to account for the specific environmental fate and bioactivity of nanoparticles (Baun, 2019).

10.3 Regulatory Frameworks and Safe Use Guidelines:

With the rapid expansion of nanotechnology in agriculture and industry, there is an increasing need for comprehensive regulatory frameworks that address the environmental and biosafety implications of nanoparticles (NPs). Due to their ultra-small size, unique surface reactivity, and novel physicochemical behaviors, nanoparticles present risks that often fall outside the boundaries of conventional regulatory systems. Their long-term effects remain uncertain, particularly regarding bioaccumulation, persistence, and ecosystem-level interactions, necessitating nano-specific governance mechanisms.

In response to these challenges, several strategic initiatives have emerged to fill regulatory gaps. One of the most prominent efforts is the Nano Risk Governance Framework (NRGF), developed under the Horizon 2020 projects NanoRigo, RiskGONE, and Gov4Nano. The NRGF proposes an integrated model that combines risk assessment with concern assessment, incorporating socio-technical perspectives and real-world stakeholder engagement. It offers operational tools for life cycle analysis, grouping methodologies, and risk-benefit evaluations applicable across industrial, regulatory, and public domains (van Broekhuizen *et al*., 2022). This multi-dimensional framework aims to support informed decision-making in nanomaterial production, use, and disposal.

There is also growing recognition of the inadequacy of existing legislation to effectively manage nanomaterial risks. Singh *et al*. (2024) have highlighted the need for specialized regulatory measures, particularly concerning nanoparticle contamination in drinking water, noting that traditional frameworks fail to capture the specific transport, transformation, and biological interactions of engineered nanomaterials. Similarly, Dhall *et al*. (2024) have advocated for stricter, more explicit guidelines governing the production, handling, occupational exposure, and end-of-life disposal of nanoparticles in both industrial and research contexts.

International regulatory approaches remain fragmented, with countries adopting varying levels of oversight. For example, Taiwan and several European Union member states have initiated labeling systems, workplace safety regulations, and national policy frameworks aimed at incorporating nanoparticle risk governance into existing environmental and public health protocols (Roig, 2018; Song & Pan, 2010). These country-specific models reflect an increasing policy-level awareness but also highlight inconsistencies in global regulatory harmonization.

Despite these developments, significant limitations persist. Many governments and regulatory bodies continue to follow a cautious "wait-and-see" approach due to scientific uncertainties, insufficient chronic toxicity data, and the ongoing lack of a universally accepted definition for nanomaterials (Helland, 2004; Reimhult, 2017). Furthermore, without robust data on nanoparticle fate and ecological effects, policymaking remains reactive rather than precautionary. To overcome these barriers, it is essential to foster greater public participation in nano-governance, integrate concern assessment into industry and governmental protocols, and advance inclusive, science-informed regulation. As suggested by Grieger *et al*. (2012), meaningful stakeholder involvement can enhance the legitimacy and effectiveness of nanoparticle risk governance, paving the way for more adaptive and responsible technological innovation.

11. Challenges, Limitations, and Knowledge Gaps:

11.1 Variability in Field Results Across Regions:

The inconsistent and sometimes contradictory outcomes observed from nanomaterial applications across agricultural regions remain one of the foremost challenges limiting the widespread adoption of nanotechnology in agriculture. Although nanotechnology offers immense potential to enhance crop productivity, nutrient use efficiency, and stress resistance, its translation from controlled laboratory environments to diverse open-field conditions often yields unpredictable results. This variability is primarily attributed to environmental, soil, climatic, biological, and management-related heterogeneity across geographies, all of which influence the behavior, stability, and efficacy of nanoparticles post-application.

Soil heterogeneity is a major factor affecting the variable performance of nanomaterials in the field. Critical soil parameters such as texture, pH, organic matter content, mineral composition, and microbial community dynamics govern nanoparticle interactions with the soil matrix and plant roots. For instance, sandy soils with low organic content may facilitate leaching, reducing nanoparticle-root contact, while clay-rich or organic matter-rich soils may strongly adsorb nanoparticles, limiting their mobility and bioavailability (Mukhopadhyay, 2014). Furthermore, soil pH can significantly alter nanoparticle surface charge and solubility. Acidic soils may enhance the dissolution of metal-based nanoparticles like ZnO and Fe_2O_3, improving nutrient uptake, whereas alkaline conditions can cause aggregation or precipitation, reducing effectiveness.

Climatic variables also play a crucial role in influencing nanoparticle behavior after application. Temperature affects nanoparticle reactivity, solubility, and plant-nanoparticle interactions, while rainfall and humidity impact their movement and persistence in soil. In humid or high-rainfall regions, increased leaching may reduce nanoparticle concentrations in the root zone. In contrast, arid regions may expose nanoparticles to UV degradation and oxidation at the soil surface, limiting their intended functionality (Zain *et al*., 2023). These climate-driven factors contribute significantly to region-specific performance variability and complicate the formulation of universal nanoparticle application protocols.

Crop type and agronomic practices introduce another layer of complexity. Different crops vary in root architecture, exudation patterns, transporter expression, and physiological sensitivity to nanomaterials. For example, a nanoparticle formulation that enhances nitrogen uptake in maize may not yield the same results in rice due to differing root and metabolic systems. Additionally, variations in planting density, irrigation schedules, fertilization regimes, and pest control measures influence the behavior and bioavailability of nanoparticles. In intercropping or mixed systems, interspecific interactions may further affect nanoparticle uptake and distribution, potentially leading to competition or phytotoxicity.

The formulation and source of the nanomaterials themselves are also critical determinants of field performance. Nanoparticles synthesized via different techniques—chemical, physical, or green synthesis—can differ significantly in size, morphology, surface functionalization, and stability, even when composed of the same core material. These physicochemical differences influence how nanoparticles interact with soil colloids, microbes, and plant surfaces. As a result, nanoparticle formulations that demonstrate high efficiency in one trial using industrial-grade materials may perform poorly in another using green-synthesized alternatives, even under comparable environmental conditions (Hofmann *et al*., 2020). Finally, the composition and activity of soil microbial communities further influence the outcome of nanoparticle use. Microorganisms are key mediators of nutrient cycling, organic matter decomposition, and plant health. Nanoparticles can disrupt or stimulate microbial processes depending on their type, concentration, and environmental context. Some may inhibit beneficial microbes, while others enhance functions like nitrogen fixation or phosphorus solubilization. These interactions are site-specific and vary with microbial diversity, soil type, and nanoparticle chemistry. Consequently, the same nanomaterial may improve crop yield in one region while reducing it in another due to differing microbial dynamics (Mukhopadhyay, 2014; Zain *et al*., 2023).

11.2 Limitations in Standardization and Dosage Optimization:

One of the most persistent challenges in the practical application of nanotechnology in agriculture is the lack of standardized guidelines and protocols for dosage optimization. Nanoparticles—while promising in enhancing nutrient uptake, pest resistance, and crop productivity—present a complex set of interactions with biological systems. Their efficacy and safety hinge not only on their physicochemical properties but also on their concentration and mode of delivery. Without clear standards, farmers and researchers face considerable uncertainty about how much, how often, and in what form nanoparticles should be applied to crops. The absence of universally accepted threshold concentrations is a primary concern. Nanoparticles, especially those composed of metals like zinc, copper, and iron, can exhibit both stimulatory and inhibitory effects depending on the dose. At low concentrations, these nanoparticles often serve as micronutrients or biostimulants, promoting plant growth and stress tolerance. However, at higher concentrations, they become phytotoxic—causing cellular damage, oxidative stress, and even plant death. For example, Shiran *et al*. (2024) demonstrated that green synthesized nitrogen-enriched zinc nanocomplexes (Zn-NC) enhanced wheat growth at concentrations up to 300 ppm, while traditional ZnO nanoparticles began exhibiting toxicity above 200 ppm. The shoot length and biomass increased significantly at optimal levels, but excessive doses led to reduced root growth and biochemical imbalance, illustrating the fine line between efficacy and toxicity.

These findings align with other studies that assess metal oxide nanoparticles such as ZnO, CuO, and Al_2O_3. Yang *et al*. (2015) evaluated their phytotoxic effects on maize and rice, reporting that root elongation was severely inhibited by CuO and ZnO nanoparticles at concentrations of 2000 mg/L, while other oxides like TiO_2 had minimal toxicity. Importantly, the toxic effects were not attributable solely to metal ion dissolution, suggesting that nanoparticle-specific properties such as size, surface charge, and reactivity play significant roles in their bioavailability and toxicity. This introduces complexity in defining a “safe” application rate, as nanoparticle formulation and plant species significantly influence outcomes.

Further complicating matters is the lack of uniformity in nanoparticle synthesis and characterization. Commercial and research-grade nanoparticles often vary in size distribution, surface area, and coating materials—even when labeled as the same compound. These variations can cause significant discrepancies in experimental outcomes and hinder reproducibility. Ruttkay-Nedecky *et al*. (2017) emphasized that plant uptake, bioaccumulation, and toxicity differ based on these variables. For instance, smaller nanoparticles have higher surface reactivity and are more likely to penetrate plant cells, increasing both their potential benefits and risks. Thus, even the same dose of a nanomaterial might produce different effects depending on its source and synthesis method. Another critical issue is the non-linear dose–response relationship exhibited by many nanoparticles. Unlike traditional agrochemicals, where responses often follow a predictable curve, nanoparticles frequently display hormetic effects—where low doses stimulate growth but higher doses inhibit it. This non-linearity makes it difficult to predict outcomes and necessitates rigorous testing across a range of concentrations for each specific nanoparticle-crop combination. Madanayake and Adassooriya (2021) argued that without such detailed profiling, any field application of nanoparticles carries inherent risks of underperformance or unintended toxicity.

Additionally, plant species-specific responses further challenge standardization. For example, a dose of nanoiron that enhances maize productivity might be phytotoxic to soybean, as Thomé *et al*. (2020) observed in their study. Corn plants tolerated moderate levels of nanoiron with minor toxicity, whereas the same concentration completely inhibited soybean seedling emergence. These interspecies differences stem from variations in root architecture, metabolic rates, and transporter expression profiles. Therefore, a one-size-fits-all dosage model is not feasible and must be replaced with crop-specific guidelines. The delivery method also plays a crucial role in determining the outcome. Nanoparticles can be applied via foliar spray, soil amendment, or seed priming. Each method influences nanoparticle behavior and plant interaction differently. Tabatabaee *et al*. (2021) found that foliar application of copper nanoparticles led to increased biomass at low doses but induced oxidative stress and lipid peroxidation at higher concentrations. These effects were linked to altered expression of stress-related genes and accumulation of reactive oxygen species, underscoring the importance of optimizing not only the dose but also the route of exposure.

Another overlooked aspect is the cumulative effect of repeated applications. Most studies focus on single-season or short-term experiments, but in real-world agriculture, nanoparticles might be applied across multiple crop cycles. This raises concerns about soil accumulation, changes in microbial community structure, and long-term phytotoxicity. Parthasarathi (2011) emphasized that in vitro testing should precede field application to mitigate cumulative risks and establish long-term safety profiles for each nanomaterial. Still, comprehensive multi-season field studies are rare, further complicating dosage recommendations.

Moreover, regulatory frameworks are not yet equipped to guide dosage optimization. Unlike traditional fertilizers and pesticides, which have established maximum residue limits and field-use protocols, nanoparticles lack such regulatory clarity in most countries. The absence of official guidelines leaves room for arbitrary application practices, increasing the risk of environmental contamination and crop toxicity. Rajpal *et al*. (2024) stressed the need for clear international standards that mandate rigorous toxicity testing, optimal dosing strategies, and safe disposal mechanisms. Standardization must also consider environmental variables, such as soil type, pH, and microbial activity. Jośko and Oleszczuk (2014) showed that the method of nanoparticle application (powder vs. suspension) significantly alters phytotoxicity outcomes. For example, nano-ZnO was more toxic in soil than in water, and this toxicity varied further depending on how the particles were introduced. These findings highlight that standardized dosing must account not just for nanoparticle properties but also for environmental context—a daunting but necessary task.

11.3 Insufficient Multi-Omics and Real-Time Monitoring Tools:

The successful integration of nanotechnology into agriculture hinges on understanding how nanoparticles interact with plants at the molecular level. However, a significant barrier to optimizing nanoparticle-based agricultural products is the limited use of multi-omics technologies—including transcriptomics, proteomics, and metabolomics—as well as real-time biosensors to monitor plant responses. These tools are essential for deciphering how plants metabolize, respond to, and potentially suffer from nanoparticle exposure. Yet, their incorporation into routine agricultural research and field use remains minimal.

Multi-omics approaches provide high-resolution insight into plant physiology and can identify early biomarkers of stress or benefit after nanoparticle treatment. For example, transcriptomics can reveal whether genes related to stress responses, nutrient uptake, or hormone signaling are activated or suppressed after exposure to specific nanoparticles. Similarly, metabolomics can detect changes in plant metabolites like flavonoids, amino acids, and antioxidants, which help interpret plant responses to nano-inputs. However, despite these advantages, most studies still rely on basic physiological or morphological endpoints, such as shoot length or biomass, instead of molecular markers (Majumdar & Keller, 2020).

Several factors contribute to this gap. First, omics platforms are resource-intensive, requiring advanced instrumentation, technical expertise, and substantial funding. Many agricultural labs, especially in developing regions, lack access to next-generation sequencing or mass spectrometry systems. Additionally, analyzing and interpreting omics data demands sophisticated bioinformatics tools and expertise that are often unavailable to field-level agronomists. As a result, only a limited number of studies use omics approaches to evaluate nanoparticle safety or efficacy comprehensively.

Moreover, omics studies are often not standardized. Differences in experimental design—such as nanoparticle type, concentration, exposure time, and plant species—make it difficult to compare results across studies. This inconsistency prevents the creation of comprehensive databases or models that could predict nanoparticle behavior in diverse agricultural environments. The development of centralized data repositories and agreed-upon protocols is needed to make omics approaches more impactful and reproducible in agricultural nanotechnology. Complementing omics approaches are biosensors, particularly those designed to provide real-time feedback on plant or soil health. Nanotechnology-enabled biosensors offer unprecedented sensitivity for detecting pH, nutrient levels, water status, or the presence of pathogens and stress biomarkers. These sensors use materials like carbon nanotubes, graphene, or metal oxides to create nanoscale detection platforms. For example, Kordrostami *et al*. (2021) describe biosensors capable of monitoring environmental stress indicators in crops, which could allow for on-the-spot adjustments in nano-agrochemical application.

However, while the concept of using biosensors in precision agriculture is appealing, practical challenges hinder widespread deployment. Biosensors must be robust, cost-effective, and easy to integrate into existing farming systems. Most prototypes remain confined to laboratory research due to issues like fragility, high production costs, and limited long-term stability under real-world conditions (Das *et al*., 2024). Additionally, rural agricultural regions may lack the digital infrastructure—such as wireless networks or cloud-based platforms—required to support continuous data collection and analysis from sensor arrays.

A further challenge is the disconnection between omics data and sensor output. Ideally, biosensors would detect specific stress signals—such as reactive oxygen species or hormone imbalances—and these findings could be cross-referenced with omics data to confirm and characterize plant responses. Yet, very few systems currently integrate these data streams. Establishing real-time feedback loops that combine sensor data with molecular diagnostics could revolutionize nanoparticle application by enabling precision dosing and early stress detection.

To overcome these limitations, researchers advocate for interdisciplinary collaboration between plant scientists, materials engineers, data scientists, and agronomists. Projects that combine omics technologies with biosensing and AI-driven decision-support tools could provide scalable solutions for nanoparticle management in the field. For instance, platforms that use omics-informed biomarkers to calibrate sensor thresholds could optimize nano-fertilizer application, reducing both costs and environmental risks (Majumdar & Keller, 2020; Kansotia *et al*., 2024).In summary, the current underutilization of multi-omics tools and real-time biosensors represents a critical gap in agricultural nanotechnology. Bridging this gap will require technological investment, standardized protocols, and integration of omics data with sensor outputs. Only through such holistic approaches can we ensure safe, precise, and efficient application of nanoparticles in agriculture.

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