






Review

Nanoparticles in Plant Abiotic Stress Resilience

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Abstract

Climate change, along with the increasing incidence of drought, salinity, nutrient depletion, and extreme temperatures, is severely constraining global agricultural productivity. In recent years, nanoparticles (NPs) have emerged as effective modulators of plant physiology; however, a comprehensive understanding of their comparative performance across different stress conditions remains limited. This review synthesizes recent advances on silicon dioxide (SiO₂), zinc oxide (ZnO), copper oxide (CuO), iron oxide (FeO), silver (Ag), and titanium dioxide/titania (TiO₂) NPs, emphasizing their mechanistic roles and quantifying their effectiveness in enhancing plant resilience. Evidence indicates that SiO₂ NPs primarily enhance antioxidant defense, regulate ion homeostasis, improve water-use efficiency, and promote root development under drought and salinity stress. For example, SiO₂ NPs at 250 mg L⁻¹ increased chlorophyll content and boosted antioxidant enzyme activity. ZnO NPs contribute to stress tolerance by strengthening antioxidant systems, maintaining membrane stability, improving osmotic adjustment, and enhancing nutrient uptake under drought, salinity, and nutrient-deficient conditions. Their effects on antioxidant defenses are consistently strong: plants treated with 100 mg L⁻¹ ZnO NPs exhibited marked increases in pigment concentrations (+58–73% for chlorophyll a, +142–149% for chlorophyll b, and +176–193% for carotenoids). Cu NPs also demonstrated protective effects: doses of 20 mg L⁻¹ can reduce cadmium (Cd) accumulation in leaves (-12.6%) and roots (-38.6%). Iron(II) oxide NPs (FeO NPs), applied at 20–100 mg L⁻¹, promote better growth and photosynthesis in barley by regulating gene expression. Additionally, TiO₂ NPs at 200 ppm have been shown to enhance salt tolerance in eggplant by improving antioxidant defense, protecting photosynthetic function, and reducing oxidative damage. By integrating these quantitative results with mechanistic insights, this review clarifies how NPs modulate plant performance under stress. It also identifies key knowledge gaps related to dose optimization, long-term environmental fate, and safety assessment. Overall, the findings highlight both the potential and the challenges of incorporating nanotechnology into future strategies aimed at strengthening crop resilience under accelerating climate stress.

Keywords: nanoparticles (NPs); plants; environmental exposure

1. Introduction

The application of nanotechnology in agriculture is a rapidly evolving field of research and innovation. It holds great promise for advancing sustainable agricultural practices and strengthening global food security [1,2,3]. In this context, nanotechnology applies nanoscale materials and techniques to multiple aspects of farming, including boosting crop productivity, improving soil health, and supporting sustainable agricultural systems. This innovative approach encompasses a wide range of uses, such as nanosensors for real-time plant health monitoring and nanofertilizers designed for precise and efficient nutrient delivery [3,4]. Nanoencapsulation enables the controlled release of essential nutrients, improving their absorption by plants and ultimately enhancing crop nutritional quality [5]. Crop protection represents another key area where nanotechnology can make a substantial impact [6,7]. In fact, crop protection is closely linked to the growing global population, which is expected to require a 70% increase in food pro-

duction [3]. The use of nanomaterials, including nanoparticles (NPs) and nanocomposites with sizes typically ranging from 1 to 100 nanometers, offers significant improvements in safeguarding plants against various threats [3,8,9]. In the context of nanotechnology, it is known that low concentrations of NPs induce hormesis in plants, which can stimulate their growth and increase resistance to various environmental stresses. Biochemical and physiological mechanisms regulate the plant hormesis, such as low concentrations trigger an increase in the activity of key antioxidant enzymes (e.g., superoxide dismutase (SOD) and peroxidase (POD) prime the plant's immune system improving its fitness), and high concentrations become toxic leading to inhibition of these enzymes and cellular damage [10]. Although scientific evidence dates back to the mid-2000s [11,12], the exact mechanisms are still under investigation. One of the hypothesized processes involves the modulation of nutritional status: NPs can alter the absorption and distribution of micro- and macronutrients in plant tissues [13]. It is important to note that this stimulation does not appear to re-



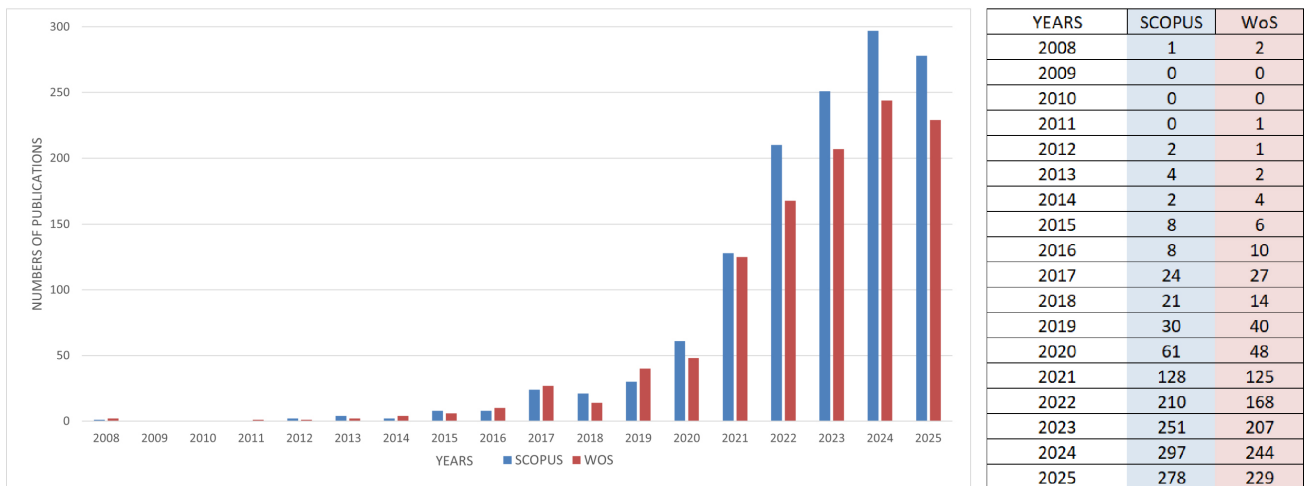


Fig. 1. Number of publications, indexed in the Web of Science (WoS) and Scopus databases, related to the terms ‘Nanoparticles’ and ‘Plants’, and ‘Abiotic Stress’ from 2008 to 2025. This figure was created using Microsoft Excel (Office 365).

sult primarily from the simple release of metal ions from the particles, but from the specific interaction of the nanoparticle itself. Despite the growth of physiological knowledge, current research still has limitations. For instance, the lack of “omics” analyses to understand plant response along a concentration-time continuum, and physicochemical variables to determine how the dose-response curve is influenced by the intrinsic properties of nanomaterials (e.g., particle size and shape, aggregates state and structure, surface functionalization and crystallinity, and metal concentration and type of stabilizer used) are necessary to be solved. The relevance of the topic is clearly illustrated in Fig. 1, which shows an increase in the number of articles published over the study period.

This review offers an updated and comparative perspective on the application of NPs in plant science, emphasizing their role in improving resilience to abiotic stress. It integrates a broader and more current set of references than previous works. Although nanotechnology in plant science has been extensively investigated, this article advances the discussion by providing a comprehensive and integrative overview of recent progress, with particular attention to plant-targeted delivery systems and their contribution to sustainable agricultural practices. In doing so, it explores emerging nanocarrier technologies including their distinctive properties and mechanisms that enable precise delivery within plants.

2. Major Abiotic Stress Conditions

Abiotic stresses are one of the main causes of reduced agricultural productivity globally, affecting crop growth and development. Factors such as drought, temperature stress, salinity, pollution, and nutrient deficiencies are particularly critical in the context of climate change [14,15]. The use of NPs is emerging as an innovative and promising strategy to reduce the negative effects of these stresses

on plants. Moreover, the physical characteristics of the soil, the microbial flora of the terrain, and consequently entire natural ecosystems are irreparably damaged by the excessive and unbalanced use of chemical fertilizers [16]. Thanks to their properties, NPs can modulate physiological and biochemical responses, improve resource use efficiency, and strengthen plant defense systems, providing an integrated approach to support growth and productivity under adverse environmental conditions [17]. However, there are still many aspects of how plants respond abiotic stress and how they influence plant growth under NPs treatments which are poorly understood [18].

2.1 Drought Stress

Drought stress is recognized as one of the most critical abiotic factors limiting agricultural productivity worldwide. Current crop growth models predict that the impacts of drought will become increasingly severe in the future, posing a major challenge to global food security [19]. Drought stress begins from a combination of low soil moisture, high rates of transpiration, and evaporation, all of which negatively affect plant growth and development. These conditions reduce water availability, reduce photosynthesis, and promote the excessive accumulation of reactive oxygen species (ROS), which can damage cellular structures and compromise plant health [20]. Under drought conditions, studies have shown that plants treated with iron NPs (Fe NPs) exhibit improved tolerance, maintaining sufficient production of photoassimilates and increasing overall biomass compared to controls, without showing any signs of potential toxicity [21] (Table 1, Ref. [21,22,23,24,25,26,27,28,29,30,31,32,33,34,35,36,37,38,39,40]). Similarly, research on zinc oxide NPs (ZnONPs) has confirmed their effectiveness in mitigating drought stress, particularly in tomato plants, where concentrations of 25 and 50 mg/L improved both biomass production

Table 1. Summary of major abiotic stresses and the most promising nanoparticle classes reported in Section 2.

Abiotic stress	Most effective NP classes	Main effects on plant physiology	Examples of plant specie	References
Drought stress	Fe NPs, ZnO NPs, Cu NPs	Increased biomass and growth; enhanced antioxidant enzyme activity; maintenance of photosynthesis and water status; improved drought tolerance at optimal doses	• Wheat, tomato, sorghum	[21,22,23,24]
Temperature stress (heat and cold)	Se NPs, TiO ₂ NPs, ZnO NPs, Ag NPs	Increased chlorophyll and carotenoids; improved gas exchange and photosynthetic efficiency; enhanced antioxidant defense; mitigation of heat, UV and cold stress	• Wheat, <i>Arabidopsis thaliana</i> , alfalfa, cereals	[25,26,27,28]
Salinity stress	ZnO NPs, Se NPs, Cu NPs, chitosan NPs	Improved growth and biomass; enhanced photosynthesis; reduced Na ⁺ accumulation; improved ion homeostasis and osmotic balance	• Rice, faba bean, sorghum	[29,30,31,32]
Pollution/heavy-metal stress	Fe NPs, ZnO NPs, bio-Se NPs, Cu NPs (with beneficial microbes)	Reduced uptake and accumulation of toxic metals (Cd, As); improved photosynthesis and nutrient uptake; strengthened antioxidant responses	• Rice, chili pepper, barley	[33,34,35,36]
Nutrient deficiency	ZnO NPs, Fe NPs, SiO ₂ NPs, nano-encapsulated fertilizers	Enhanced nutrient availability and uptake (Zn, Fe, N, P, K); improved growth and yield; increased nutrient use efficiency	• Rice, beet, wheat	[37,38,39,40]

NP, Nanoparticle; Fe NPs, iron NPs; ZnO NPs, zinc oxide NPs; Cu NPs, copper NPs; Se NPs, selenium NPs; TiO₂ NPs, titanium dioxide NPs; Ag NPs, silver NPs; Na⁺, sodium ion; bio-Se NPs, biologically synthesized selenium NPs; Cd, cadmium; As, arsenic; SiO₂ NPs, silicon dioxide NPs; N, nitrogen; P, phosphorus; K, potassium.

and the activity of antioxidant defense systems. However, higher concentrations, such as 100 mg/L, were found to be phytotoxic and negatively affected plant growth [22]. Three wheat cultivars (Faisalabad-08, Johar-16, and AaS-2011) were investigated to evaluate the effects of iron oxide (FeO) and zinc oxide (ZnO) NPs at concentrations of 20, 40, and 60 ppm under drought stress. The results reinforced the negative impact of drought stress, showing significant reductions in key growth parameters, including shoot length, biomass, and chlorophyll content across all cultivars [23]. In addition, copper NPs (CuNPs) have been observed to improve major physiological and growth traits in several wheat varieties (cultivars) at concentrations of 10, 20, and 30 ppm. The most pronounced effects were recorded at 30 ppm, with the varieties *Dharab* and *Watan 94* exhibiting the highest productivity and resilience to drought stress [24].

2.2 Temperature Stress

Climate change is also recognized as a major factor exerting pressure on crops, as both unusually high and low temperatures can have detrimental effects on plant growth, development, and overall productivity [18]. In this context, several studies have highlighted the potential of NPs to help plants tolerate temperature-related stress and maintain physiological performance under challenging conditions. For example, selenium NPs (Se NPs) applied at 100

µg/mL were shown to increase chlorophyll and carotenoid content in wheat plants by 12–32% compared to untreated controls (Table 1). In addition to pigment accumulation, other important physiological parameters like including gas exchange, transpiration, stomatal conductance, and photosynthetic efficiency, were also improved [25]. Furthermore, a study by Wang et al. [26] demonstrated that titanium dioxide NPs (TiO₂ NPs, 10 mg/L) provided protective effects against both UV and heat stress in *Arabidopsis thaliana*. The application of these NPs enhanced the activity of key antioxidant enzymes and promoted the accumulation of flavonoids, contributing to improved stress tolerance [26]. ZnO NPs were also found to be effective in *alfalfa seedlings*, alleviating heat-induced morpho-physiological and ultrastructural damages. Foliar application of ZnO NPs during the flowering stage improved chlorophyll activity, gas-exchange parameters, and overall plant resilience [27]. On the other end of the temperature spectrum, silver NPs (AgNPs) have been shown to mitigate the negative effects of low temperatures on cereal crops, enhancing their ability to withstand cold stress. In a study by Minić et al. [28], two winter cereal varieties—*Simonida (Triticum aestivum L.)* and *Nonius (Hordeum vulgare L.)*—were treated with AgNPs–H₂O at concentrations of 5 and 10 mg/mL. The treatment positively influenced antioxidant activity and increased proline levels compared to untreated plants, indicating improved stress adaptation and resilience [28].

2.3 Salinity Stress

Soil salinity begins both from natural processes, such as the gradual accumulation of salts in the soil and groundwater, and from human activities that alter the soil's hydrological balance, for example through unsustainable irrigation practices that promote salt concentration [41,42]. Salinity alone reduces vegetative growth, seed size, and germination. However, responses to salt stress vary among germplasm across different trait indices [43]. It also causes ionic imbalances, osmotic stress, lower photosynthesis and chlorophyll levels, and a reduction in respiration and enzyme activity [42]. A study conducted by Mishra et al. [29] proves the effectiveness of Se NPs and ZnO NPs on salinity stress in rice plants (Table 1). These NPs enhance physiological functions, photosynthesis activity and nutrient accumulation, promoting overall plant growth. Results illustrate that combined application of NPs was more effective than singular treatments [29]. Further studies on the use of ZnO NPs confirmed their role in improving plant tolerance to salt stress. In faba bean, foliar treatments with ZnONPs at 50 and 100 mg/L, applied alone or together with salt stress (150 mM sodium chloride [NaCl]), showed a clear increase in shoot length and fresh/dry weight. The highest levels of chlorophyll a, b, and carotenoids were recorded with the 50 mg/L dose [30]. Similarly, in sorghum (*Sorghum bicolor*) seeds pretreated with ZnONPs (5 and 10 mg/L) and then exposed to high salinity (400 mM NaCl), priming increased salt tolerance by reducing the negative effects caused by excessive sodium ion (Na^+) accumulation in cells, which leads to osmotic stress and reduced uptake of essential elements like K^+ . Under these conditions, ZnONPs helped reduce water loss and improved nutrient and water transport, supporting better plant growth [31]. Supporting the potential of nanotechnologies in managing salinity stress, seed priming with chitosan NPs (CS NPs) or chitosan (CS) biopolymers showed positive effects in rice, improving seedling growth under both normal and salt stress conditions, and helping maintain high levels of chlorophyll and carotenoids, with the best results observed for CS NPs at higher NaCl concentrations [32].

2.4 Pollution Stress

Environmental pollution caused by human activities is one of the main sources of abiotic stress for both agricultural and natural ecosystems. Pollutants coming from industrialization and urbanization accumulate in water, soil, and air, enter the food chain, and warn both the environment and human health. Despite the growing combined impact of pollution and climate change, their interactions are still not well understood [44]. Among the most dangerous contaminants are heavy metals, which are widely released from industrial areas in developing countries. For example, in rice (*Oryza sativa L.*), a crop grown submerged for long periods in contaminated water will show a significant reduction in plant growth [33]. Industrial pollution also changes the diversity

and structure of riparian vegetation, causing physiological stress and lowering ecosystem resilience. The degradation of riparian zones has deep consequences for water quality, biodiversity, and ecosystem services, and can even threaten the survival of some plant species [45]. A major contribution to the decline of agricultural environments also comes from textile industry effluents, which release untreated organic and inorganic pollutants, reducing soil fertility and negatively affecting agricultural productivity and public health [46]. Several studies have shown that using NPs together with beneficial microorganisms can reduce the toxic effects of heavy metals in crops. In a pot experiment on *Oryza sativa L.*, exposure to different cadmium levels (0, 50, and 100 mg kg⁻¹) caused strong negative effects on plant growth, photosynthesis, and oxidative balance. However, applying iron oxide NPs (50 and 100 mg L⁻¹) together with the bacterium *Bacillus megaterium* (5 and 10 ppm) significantly improved growth, gas exchange, and nutrient uptake, while also reducing cadmium accumulation in plant tissues [34]. A similar effect was observed in chili pepper (*Capsicum annuum var. conoides*) treated with biologically synthesized selenium NPs (Bio-Se NPs): at concentrations between 2 and 20 mg/L, these NPs increased seed germination (reaching 100% at 5 mg/L), whereas higher doses inhibited growth. When applied as a foliar spray, 5 mg/L Bio-Se NPs improved plant growth, photosynthetic efficiency, and antioxidant responses under cadmium stress [35] (Table 1). The combined treatment of beneficial bacteria (*Bacillus cereus* and *Lysinibacillus macroides*) with zinc oxide NPs (5–25 mg/L) also played an important role in reducing heavy-metal stress in rice plants grown in contaminated water. Seeds that were primed and grown in the presence of ZnO NPs (5 mg/L) showed lower uptake of heavy metals in roots, stems, and leaves, which improved overall plant growth. The joint action of bacteria and NPs also increased the plants' tolerance index [33]. Even excessive exposure of plants to arsenic stress (100 μM) reduces growth and photosynthesis, causing alterations in other physiological traits, including increased oxidative stress and nutrient disequilibrium. However, the addition of iron oxide NPs (20 and 100 mg L⁻¹) drastically reduced arsenic uptake and accumulation in the plants, improving growth, photosynthesis, and antioxidant capacity, while decreasing oxidative stress [36].

2.5 Nutrient Deficient Stress

Nutrients are essential for plants because they play key roles in biological processes, development, and growth. The main macronutrients include nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg). Insufficient supply of these elements causes nutrient deficiencies in plants, which appear as different types of symptoms. Nutritional disorders can also show atypical symptoms due to interactions between biotic and abiotic factors [47]. Deficiencies of specific nutrients show characteristic signs: Mg deficiency causes premature leaf drop, K defi-

ciency leads to interveinal chlorosis, Ca deficiency results in chlorosis with necrotic leaf tips, N deficiency causes yellowing of leaf tissues, and P deficiency produces dark green leaves with bronze or purple shades on the lower surface [48]. Among innovative strategies to improve plant nutrition, NPs have shown multiple roles. They can be used as nanofertilizers, releasing nutrients in a targeted way, or they can enhance the uptake of nutrients already present in the soil, increasing absorption efficiency and plant growth [37]. For example, ZnO NPs can increase zinc uptake in crops, promoting growth and productivity even at lower doses than conventional fertilizers. Similarly, nano-encapsulated nitrogen fertilizers reduce nitrogen losses and improve its use efficiency, lowering environmental impacts from leaching and greenhouse gas emissions [38] (Table 1). Guha et al. [39] showed that iron NPs (Fe NPs) derived from *Punica granatum* improve Fe availability and uptake in rice (*Oryza sativa*), increasing growth, yield, and nutrient concentration in tissues. Additionally, a dose of 2.0 mmol L⁻¹ of nanosilica, applied via foliar application to beet plants (*Beta vulgaris*), significantly improved N and P uptake, enhanced physiological performance, and increased growth compared to plants not treated with silicon NPs [40].

3. Effects on Key Plant Parameters

3.1 Growth and Morphological Traits

The use of NPs influences various key growth parameters and morphological traits of plants, often in a dose- and plant species-dependent manner [49,50,51,52]. The improvement in growth by NPs can be linked to several mechanisms, including boosted nutrient and water uptake [53,54,55], enhanced enzymatic activity [53,55], maintenance of water balance, protection of cell membranes [53], and modulation of growth hormones (such as auxins and cytokinins, which stimulate cell division and elongation) [50,55,56,57,58]. NPs, when used at suitable concentrations, generally enhance overall growth and morphology, promoting plant growth, enhancing seed germination, and strengthening stress resistance [53,56,59]. The use of NPs frequently resulted in a significant increase in stem (or plant height) and root length, as well as fresh weight and dry weight of both parts, an increase in leaf number and leaf area [50,53,54,55,56,60]. NPs can enhance root structure, essential for water and nutrient uptake [51,54]. Treatment with low-concentration silicon NPs (nSiL+cadmium [Cd]) enhances the quantity of root tips, root surface area, and root nodes in lettuce under Cd stress, alleviating the negative effects of Cd [51]. However, root growth is often inhibited by high doses of NPs, as the roots are directly exposed and more sensitive [57]. Numerous NPs, including AuNPs, ZnO NPs, and TiO₂ NPs, can enhance the germination rate and vigor of seedlings [50,61,62]. Indeed, NPs can create new pores in the seed coat, facilitating water absorption, which is essential for the resumption of cellular metabolic processes and growth [62,63]. CeO₂ NPs increased ear

length and grain and straw yield in wheat [59]. However, higher concentrations may result in adverse or phytotoxic effects [50,54,57,62]. Moreover, S-Au NPs concentrations greater than 200 μM decreased germination efficiency and morphological characteristics in spinach, likely because of aggregation and inhibition of cell division and elongation [50]. Similarly, Al₂O₃ NPs enhanced germination at lower concentrations but diminished it at higher concentrations [52]. High doses often lead to root growth inhibition since the roots are directly exposed and more sensitive [57]. Concerning the mitigation of heavy metal effects, NPs, such as SiO₂ NPs, ZnO NPs, TiO₂ NPs, and CeO₂ NPs, can counteract pollutant inhibition by increasing root and shoot lengths and biomass [49,51,56,60,64]. Thus, NPs offer a way to improve the morphological and growth characteristics of plants, especially under stress conditions, by acting as biostimulants and cellular protectors, but their effectiveness is finely tuned to the applied NP type, size and concentration [49,65].

3.2 Photosynthesis Performance

The impacts of NPs on plant photosynthetic efficiency is intricate and influenced by multiple factors, such as concentration, chemical composition, surface area, size and plant species [23,66]. In general, NPs can improve photosynthetic efficiency through several mechanisms, especially under stressful conditions, but can also lead to negative and toxic effects at high doses [23,54,67,68]. The use of NPs frequently results in a significant increase in chlorophyll (a and b) and carotenoid levels [66,69,70,71,72,73]. For example, magnetic iron oxide NPs (MIO NPs) enhanced total chlorophyll and carotenoid content in radish and mung bean plants exposed to UV-B stress [74]. Cerium oxide NPs (CeO₂ NPs) are well recognized for their ability to alter and improve photosynthetic pigment systems, greatly boosting the chlorophyll level in mustard leaves [75]. The efficiency of PSII, namely the maximum quantum yield (Fv/Fm) and the performance index, in NP-treated plants indicates that more reaction centers are maintained in an “open state” to perform light-dependent reactions [76]. Treatments with MgZnAl₂O₄ NPs showed a progressive increase in chlorophyll fluorescence characteristics [70], peaking at around 200 mg L⁻¹. Many NPs increase gas exchange parameters, contributing to more efficient carbon assimilation [35,75,77,78]. For instance, CeO₂²⁻ NPs significantly increased the net photosynthetic rate, stomatal conductance, transpiration rate, and internal CO₂ concentration in mustard [75,79]. Nickel-iron oxide (NiFe₂O₄) NPs at low and moderate doses increased the net photosynthetic rate by 132% and 107%, respectively, compared to the control in peanut [80]. Regarding biochemical and structural mechanisms, NPs often reduce oxidative stress [68,71,74] and protect chloroplast integrity, which is essential for photosynthetic function [54]. For instance, CeO₂ NPs increase the activity of key enzymes such

as Rubisco and carbonic anhydrase [75]. However, concentrations above the optimal threshold can induce phytotoxicity and genotoxicity [70]. For example, high concentrations of $\text{MgZnAl}_2\text{O}_4$ NPs (400 mg L^{-1}) reduced photosynthetic pigments due to NP-induced stress or potential dissociation into toxic Al^{2+} ions that accumulate and damage the cell [70]. Moreover, MIO NPs mitigate effects of exposure to UV-B, which reduces photosynthetic efficiency by damaging carotenoids, chlorophyll, PSII proteins and reducing enzymatic activity [74]. Cobalt tungstate NPs (CoWO_4 NPs) impaired the photosynthetic activity of the microalga *Raphidocelis subcapitata*, reducing the maximum electron transport rate (rETRmax) by approximately 53% at the highest concentrations and compromising the light capture efficiency [81]. Therefore, the specific properties of NPs play a crucial role in determining their effect on photosynthesis. For CeO_2 NPs in mustard, the smallest crystalline size (4.5 nm) at 100 ppm was found to be the most effective in improving photosynthetic parameters [75]. In summary, NPs offer the potential to improve crop resilience and photosynthetic performance under stressful conditions by serving as efficient nutrient sources and activating antioxidant defenses [68,74]. However, efficacy is critically dependent on dosage optimization and the specific properties of the nanoparticle [80,82].

3.3 Water-Use Efficiency

Water-use efficiency (WUE) is an essential factor for assessing plant productivity in drought scenarios [83]. A high WUE indicates the ability to generate greater biomass with reduced water consumption [84]. The ability of NPs to alleviate the negative impacts of water stress includes enhancing WUE via physiological regulation [85,86]. The impacts of NPs on WUE varies by source and is beneficial, especially in conditions of water stress. Nanoparticle applications during water stress has demonstrated remarkable potential, significantly enhancing crop WUE [87]. The type and concentration of NPs were found to be the most significant factors influencing WUE [87]. The optimal NP concentration for improving WUE was less than 50 mg L^{-1} , with a recorded increase of 112.6% [87]. The highest impact (148.3% increase) on WUE was noted when NPs were utilized through seed priming [87]. The combined application of NPs with arbuscular mycorrhizal fungi (AMF) through nanopriming has been demonstrated to increase water use efficiency in wheat [88,89]. NPs assist in regulating the water status of plants, mitigating water loss and improving drought tolerance [87]. Increased WUE is often related to the ability of NPs to regulate stomatal movement to reduce leaf transpiration rates [83,86]. NPs promote osmotic regulation through the accumulation of osmolytes, proline and soluble sugars [87], to maintain cell turgor and continuous CO_2 assimilation at low water potential, by improving WUE. Several NPs have been shown to improve WUE in various crops. Carbon NPs (CNPs)

led to an increase in WUE in rice, with a significant increase of 75% compared to untreated plants [90]. Carbon-based NPs improve photosynthetic efficiency by managing stomatal conductance and WUE [87]. However, not all NPs or concentrations aid in WUE. For example, titanium dioxide NPs (TiO_2 NPs/TNPs) dramatically reduced WUE in okra seedlings under water stress, showing reductions of 24.06% and 32.09% at concentrations of 30 and 70 mg kg^{-1} , respectively, in comparison to the untreated control [91]. In the Desi genotype of chickpea, the application of iron(III) oxide NPs (Fe_2O_3 NPs) lead to a decrease in WUE, with the untreated control showed greater effectiveness [92]. Whereas, in the Kabuli genotype of chickpea, the application of ZnO NPs induced high water use efficiency and photosynthetic rates [93]. Concentrations of CaCO_3 NPs higher than 150 mg L^{-1} diminish WUE in tomato cultivars [94]. Thus, NPs act as catalysts or nutrient promoters that improve drought tolerance mechanisms, increasing the efficiency with which the plant absorbs and uses water for biomass production [85,87]. This is accomplished primarily by adjusting the photosynthesis rate and decreasing transpiration via the modulation of stomatal conductance [87,95].

3.4 Biomass Accumulation

Biomass accumulation serve as an essential measure of plant growth and productivity, influenced by NPs' concentration, type, plant species and environmental stress factors [67,96,97,98,99]. NPs, especially when used at low or moderate concentrations or under stress conditions, frequently lead to significant increases in biomass [97,98,100,101,102]. For instance, the use of Se NPs has been shown to improve biomass and morpho-physiological attributes in rice under Cd stress conditions, in cotton seedlings subjected to arsenic (As) stress, and in *Helichrysum italicum* [55]. However, small amounts of Se NPs induced increase in plant growth by promoting water, macro- and micronutrient uptake, cell size and cell division [55]. The simultaneous application of Fe and Zn NPs resulted in a substantial enhancement in growth and biomass accumulation in wheat subjected to drought stress conditions [23,103]. In the cyanobacterium *Nostoc linckia*, low concentrations of ZnONPs (0.1 and 1 mg L^{-1}) stimulated biomass accumulation by 9.51% and 15.11%, respectively [104], while, TiO_2 NPs consistently promoted biomass growth at all tested concentrations (0.1 to 30 mg L^{-1}), with a maximum increase of 41.04% at 30 mg L^{-1} [104]. Low concentrations of nano-carbon (NC-5 and NC-10) enhanced the total biomass of poplar by 115.42% and 108.32%, respectively [105]. Also carbon dot NPs (CD NPs) and star-shaped polycation NPs (SPc NPs) promoted biomass production in sweet potato subjected to salt stress [106] and in maize and *Arabidopsis*, partly by modulating the aquaporin pathway to improve water transport efficiency [99], respectively. However, a dose-dependent effect is often observed,

where low doses have beneficial effects and high doses cause toxicity [67,96,97,101,102,104,107,108]. For example, moderate doses of potassium NPs improved dry matter accumulation in corn, but higher concentrations reduced it [107]. Decreased biomass was noted due to: high doses (500 mg/kg) of polyethylene NPs (PE-NPs) and polypropylene NPs (PP-NPs) in corn and soybean [67], high doses of PP-NPs in soybean [67], foliar application of polystyrene nanoplastics (PS, PSC, PSN) in *Chrysanthemum coronarium* plants [109], exposure to 200 mg kg⁻¹ of copper oxide NPs (CuO NPs) in soil showed the lowest values for the morphological parameters [67,96]. Furthermore, positively charged PSNs induced stronger phytotoxicity [109]. High concentration of Se NPs (75 mg L⁻¹) decreased the dry weight of the whole mung bean plant by 15.9% compared to the control in greenhouse conditions [110]. The simultaneous exposure to Cd and polystyrene NPs (PSNPs) in the submerged macrophyte *Vallisneria natans* did not change total chlorophyll levels, but significantly intensified oxidative stress, suggesting a potential synergistic toxicity that may negatively affect biomass [111]. Thus, biomass accumulation is a net outcome of the interplay between the positive effects (nutritional, hormonal stimulation, or stress protection) and the phytotoxic impacts (physical blockade, oxidative stress) of NPs [67,96,101]. In details, the biomass accumulation under stress factors (salinity, drought, heavy metals) frequently results from NPs stimulating antioxidant systems, safeguarding cell membranes and the photosynthetic apparatus, and enhancing ionic balance or water uptake (e.g., by modulating aquaporins), allowing the plant to overcome stress-induced growth inhibition [23,96,99,106,112,113]. Whereas, the growth inhibition at elevated concentrations is associated with restricted root functions, the induction of oxidative stress (increased levels of MDA and hydrogen peroxide [H₂O₂]), the suppression of enzymatic activity (such as catalase) and the reduction of photosynthetic efficiency, which compromise growth and accumulation of organic matter [67,96,109].

4. Mechanism and Applications of NPs Under Stress Conditions

Their unique physicochemical properties, including high surface area, reactivity, and the ability to interact with plant systems at the cellular level, make them effective agents in mitigating stress-induced challenges [114]. Recent studies have highlighted the multifaceted roles of NPs in plant stress management. For instance, NPs can enhance nutrient uptake, regulate phytohormone signalling pathways, and modulate gene expression related to stress responses. These interactions contribute to improved photosynthetic efficiency, antioxidant defense mechanisms, and overall plant growth under adverse conditions [115].

This section delves into the mechanisms through which NPs influence plant stress responses. It also explores their practical applications in agriculture, highlighting their

potential to improve crop yield and quality under challenging environmental conditions. Understanding these mechanisms and applications is essential for harnessing the full potential of NPs in sustainable agriculture.

NPs employed in plant science and agricultural applications can be produced through different synthesis approaches, commonly classified into physical, chemical, and biological (green) methods. The synthesis route plays a crucial role in determining nanoparticle properties such as size, shape, surface chemistry, stability, and reactivity, which in turn influence their biological behaviour, effectiveness, and potential phytotoxicity in plant systems [3,17,18].

Physical synthesis methods include techniques such as high-energy ball milling, laser ablation, and evaporation–condensation processes. These approaches generally avoid the use of chemical reagents and allow the production of relatively pure NPs; however, they often require high energy input and provide limited control over particle size distribution and surface functionalization [3,8].

Chemical synthesis methods are among the most widely used for producing metal and metal oxide NPs, including sol–gel processes, precipitation, hydrothermal synthesis, chemical reduction, and microemulsion techniques. These methods allow better control over nanoparticle morphology, composition, and crystallinity, making them suitable for tailoring NPs for specific applications in plant stress mitigation. Nevertheless, the use of chemical solvents and reducing agents may raise concerns regarding environmental impact and potential toxicity, especially in agricultural contexts [17,18].

In recent years, biological or green synthesis approaches have gained increasing attention as sustainable alternatives. These methods exploit plant extracts, algae, bacteria, or fungi as reducing and stabilizing agents for nanoparticle production. Green-synthesized NPs are often characterized by improved biocompatibility and reduced toxicity, which makes them particularly attractive for applications in plant science and stress physiology. Moreover, the presence of bioactive compounds on the nanoparticle surface may enhance their interaction with plant tissues and modulate stress-response pathways [22,116].

Overall, an understanding of nanoparticle production and synthesis methods is essential for interpreting their effects on plant physiology and for designing safe and effective nanomaterials for improving tolerance to abiotic stresses. The synthesis strategy must therefore be considered a key factor when evaluating nanoparticle performance, environmental fate, and applicability in sustainable agricultural systems [18,114,115].

Particular attention will be focused on the most widely studied NPs in plant stress research: SiO₂ NPs (silica NPs), Fe NPs (iron oxide NPs), Cu NPs (copper NPs), ZnO NPs (zinc oxide NPs), Ag NPs (silver NPs), and TiO₂ NPs (titanium dioxide NPs) [3,17,18].

SiO₂ NPs are primarily involved in improving antioxidant defense, regulating ion homeostasis, enhancing water-use efficiency, and promoting root development under drought and salinity stress [69,117,118,119,120,121]. Fe NPs mainly act as nano-fertilizers, improving iron availability, photosynthetic performance, and antioxidant capacity, while also reducing the uptake of toxic elements such as arsenic and cadmium [100,122,123,124,125]. ZnO NPs contribute to stress tolerance by strengthening antioxidant systems, maintaining membrane stability, enhancing osmotic adjustment, and improving nutrient uptake under drought, salinity, and nutrient-deficient conditions [22,30,31,126,127].

Copper-based NPs (Cu and CuO NPs) play a dual role, acting at low concentrations as micronutrient sources and stress-priming agents that enhance antioxidant activity and photosynthesis, while potentially inducing phytotoxic effects at higher doses [116,128,129,130,131]. Silver NPs (Ag NPs) mainly modulate reactive oxygen species (ROS) metabolism, improve seed germination, and enhance early plant development under drought and salinity stress [132,133]. TiO₂ NPs are known to enhance photosynthetic efficiency, stimulate antioxidant enzyme activity, and improve ion balance and nutrient use efficiency under salinity, drought, and nutrient stress conditions [134,135,136].

Overall, these NPs differ in composition, mode of action, and application strategies, but they share the ability to modulate key physiological, biochemical, and molecular processes involved in plant stress responses [18,114,115]. The following sections provide a detailed discussion of the mechanisms, features, and applications of each nanoparticle type under specific abiotic stress conditions.

4.1 SiO₂ NPs—Silica NPs

SiO₂ NPs have garnered significant attention in plant science due to their potential to mitigate the adverse effects of abiotic stresses such as drought, salinity, and oxidative damage. These nanomaterials, characterized by their high surface area and reactivity, interact with plant systems to enhance stress tolerance through various mechanisms, as summarized below:

- Antioxidant defense enhancement: SiO₂ NPs can bolster the plant's antioxidant system, leading to reduced oxidative stress. For instance, under copper (Cu) stress, SiO₂ NPs have been shown to enhance antioxidant enzyme activities and regulate proline metabolism, thereby mitigating oxidative damage and improving plant resilience [69].

- Regulation of ion homeostasis: in saline conditions, SiO₂ NPs help maintain ion balance by modulating the expression of genes involved in ion transport, such as HKT (High-affinity K⁺ Transporters), SOS (Salt Overly Sensitive signalling pathway), and NHX (Na⁺/H⁺ Exchangers). This regulation aids in reducing sodium accumulation and maintaining potassium levels, crucial for plant growth under salt stress [117].

- Promotion of osmolyte accumulation: SiO₂ NPs stimulate the synthesis of osmolytes like soluble sugars and proline, which play vital roles in osmoregulation and cellular protection under drought conditions. This accumulation helps in maintaining cellular turgor and stabilizing proteins and membranes [118].

- Enhancement of root architecture: application of SiO₂ NPs has been observed to improve root growth parameters, including root length and surface area. These improvements facilitate better water and nutrient uptake, contributing to enhanced plant growth under stress conditions [119].

The application of SiO₂ NPs in agriculture has shown promising results in improving crop yield and quality under stress conditions, as summarised in Table 2 (Ref. [120,137,138,139,140]). For example, foliar application of SiO₂ NPs has led to increased yield and improved stress tolerance in various crops, including lettuce and maize, under temperature extremes, salinity, and drought stress [120,121]. Additionally, SiO₂ NPs have been utilized to enhance the medicinal properties of plants like *Sophora tonkinensis* under drought stress, increasing the content of bioactive compounds such as matrine and genistein [118]. Recent research has demonstrated that SiO₂ NPs can effectively enhance plant tolerance to a variety of abiotic stresses, including drought, salinity, and combined stress conditions.

In maize (*Zea mays*) seedlings, foliar application of SiO₂ NPs at 0.25 g/L under drought conditions improved multiple growth indices, including chlorophyll content, relative water content (RWC), and biomass accumulation, while also enhancing the activity of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and guaiacol peroxidase (G-POX). These improvements were accompanied by reductions in oxidative damage markers, including hydrogen peroxide (H₂O₂) and malondialdehyde (MDA), indicating a strong protective effect against drought-induced oxidative stress [120].

Similarly, in ginger (*Zingiber officinale*), SiO₂ NPs applied at 100 mg/L enhanced photosynthetic efficiency, increased chlorophyll content, and improved water status, while significantly reducing oxidative stress markers such as H₂O₂, superoxide (O₂⁻), MDA, and methylglyoxal (MG) [137]. This was accompanied by activation of antioxidant enzymes (SOD, POD, CAT), enhancement of the ascorbate–glutathione (AsA–GSH) cycle, including increased activities of ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), and glutathione reductase (GR), and upregulation of glyoxalase system enzymes (Gly I, Gly II). Gene expression analysis confirmed the upregulation of ZoDHAR2 (dehydroascorbate reductase 2), ZoAPX1 (ascorbate peroxidase 1), ZoGR2 (glutathione reductase 2), and ZoGLY I (glyoxalase I), along with the downregulation of genes involved in methylglyoxal (MG) synthesis—

Table 2. Summary of recent studies on the application of silica NPs (SiO₂ NPs) in various plant species under abiotic stresses, including drought, salinity, and combined stress.

Plant species	Stress type	Nanoparticle concentration/application method	Main outcomes	References
Maize (<i>Zea mays</i>) seedlings	Drought	250 [mg/L] (foliar application)	<ul style="list-style-type: none"> Improved growth indices under drought: (i) increased chlorophyll content, (ii) higher RWC, (iii) enhanced antioxidant enzyme activities (SOD, CAT, GPOX), (iv) reduced levels of H₂O₂ and MDA. 	[120]
Ginger (<i>Zingiber officinale</i>)	Drought	100 [mg/L] (foliar application)	<ul style="list-style-type: none"> Alleviated drought stress by enhancing photosynthesis, lowering ROS (H₂O₂, O₂⁻), increasing activities of antioxidant enzymes (SOD, POD, CAT), elevating AsA–GSH cycle & glyoxalase system, reducing MDA and methylglyoxal. 	[137]
Cotton seedlings (<i>Gossypium hirsutum</i>)	Salt + Low Temperature (dual stress)	50, 100, 200 [mg/L] (foliar application)	<ul style="list-style-type: none"> Decreased growth/biomass. Improved effects on growth and photosynthesis under combined stress. 	[138]
Lettuce (<i>Lactuca sativa</i>)	Salinity	100, 200, 400 [mg/L] (foliar application)	<ul style="list-style-type: none"> Improved head diameter, plant height, dry matter. Reduced MDA (-21%). Increased Mg, Fe, Zn uptake. Reduced Na accumulation. 	[139]
Arabidopsis (<i>Arabidopsis thaliana</i>)	PEG-simulated drought <i>in vitro</i>	0–5000 [mg/L] (<i>in vitro</i> exposure)	<ul style="list-style-type: none"> At optimal dose (~1500 mg/L), increased root length, lateral roots, leaf area, shoot biomass. At highest dose (5000 mg/L) reduced germination. 	[140]

SiO₂ NPs, silicon dioxide NPs; RWC, relative water content; SOD, superoxide dismutase; CAT, catalase; GPOX, guaiacol peroxidase; POD, peroxidase; ROS, reactive oxygen species; H₂O₂, hydrogen peroxide; O₂⁻, superoxide anion; MDA, malondialdehyde; AsA, ascorbate; GSH, glutathione; PEG, polyethylene glycol; Mg, magnesium; Na, sodium.

namely ZoAMO1 (amadoriase 1), ZoAMO2 (amadoriase 2), and ZoMGS1 (methylglyoxal synthase 1)—collectively indicating a profound molecular regulation of stress tolerance mechanisms. This study highlights how silica NPs can act not only as physical or biochemical protectants but also as regulators of gene expression and detoxification pathways under water deficit.

Under combined salinity and low-temperature stress, cotton seedlings (*Gossypium hirsutum*) showed diminished growth and biomass; however, SiO₂ NPs treatment mitigated these negative effects, preserving photosynthetic performance and improving overall plant vigour [138]. In lettuce (*Lactuca sativa*) exposed to salinity, SiO₂ NPs at concentrations of 100–400 mg/L improved plant height, head diameter, and dry matter accumulation. These treatments also reduced oxidative damage (MDA decreased by 21%) and enhanced mineral uptake (Mg, Fe, Zn), while lowering sodium accumulation, indicating that SiO₂ NPs can modulate ionic homeostasis under salt stress [139].

In *Arabidopsis thaliana*, *in vitro* exposure to mesoporous SiO₂ NPs under polyethylene glycol (PEG)-simulated drought demonstrated a strong dose-dependent effect. At optimal concentrations (~1500 mg/L), SiO₂ NPs promoted root elongation, lateral root formation, leaf area expansion, and shoot biomass, whereas higher doses (5000

mg/L) negatively affected germination and growth [140]. This highlights the importance of careful optimization of nanoparticle concentration for achieving beneficial effects without inducing toxicity.

These studies demonstrate that SiO₂ NPs enhance plant tolerance to abiotic stress through multiple, complementary mechanisms. They improve water status by increasing RWC and root hydraulic conductivity, maintain photosynthetic efficiency, alleviate oxidative damage by boosting antioxidant enzyme activities, and regulate mineral nutrition and ionic balance. The beneficial effects of SiO₂ NPs are strongly influenced by dosage, plant species, and application method, highlighting the importance of precise optimization in agricultural practice. Despite their potential, the agricultural use of SiO₂ NPs still presents challenges concerning optimal concentrations, possible toxicity, and environmental safety. Further research is needed to refine application strategies, evaluate long-term impacts on soil health and microbial communities, and ensure their safe integration into sustainable crop management. With continued investigation and technological advancement, SiO₂ NPs could serve as versatile and effective tools for improving plant resilience and productivity under adverse environmental conditions.

4.2 Fe NPs—Iron Based NPs

Fe NPs represent a promising tool for enhancing plant tolerance to abiotic stress conditions, acting through multiple mechanisms that involve both nutrition and antioxidant defense. Iron is an essential micronutrient for numerous cellular processes, including chlorophyll synthesis, mitochondrial respiration, and the activity of antioxidant enzymes. Its availability can be limited in alkaline, saline, or chemically immobilized soils [122,141]. Fe NPs, due to their high surface area and reactivity (or when coated with organic molecules to improve solubility and bioavailability), can increase iron uptake in plants and improve physiological performance under stress, as demonstrated in tomato plants treated with magnetite iron oxide NPs (Fe₃O₄ NPs) coated with humic acid or citrate [123].

Fe NPs also positively modulate plant antioxidant systems: for example, flax plants primed with Fe NPs showed reduced H₂O₂ and MDA levels, along with increased activity of enzymes such as SOD, POD, and CAT under drought conditions [124]. Furthermore, these NPs can regulate the uptake of toxic ions (e.g., arsenic, cadmium) and modulate the expression of genes involved in iron transport and heavy metal stress responses, as observed in rice, where Fe NPs decreased arsenic accumulation while improving photosynthesis and iron content [125].

From an application perspective, studies have shown that Fe NPs can mitigate salinity stress (*Triticum aestivum*), alkalinity stress (*Capsicum annuum*), and drought stress (*Sorghum bicolor*) [100,122]. However, the effects of Fe NPs strongly depend on particle concentration, size, coating, and application method: excessive doses can induce phytotoxicity or additional oxidative stress [142]. A summary of studies investigating the application of Fe NPs is presented in Table 3 (Ref. [100,122,125,143,144,145,146,147,148,149]).

In soybean (*Glycine max*), foliar application of Fe₃O₄ NPs at 200 ppm under drought conditions significantly increased seed yield and improved seed oil and protein content, demonstrating the NPs' capacity to enhance productivity under water limitation [143]. Similarly, in *Sorghum bicolor*, seed priming with green-synthesized α -Fe₂O₃ NPs at 10 mg/L improved plant height, biomass, chlorophyll content, and nutrient uptake while reducing reactive oxygen species and oxidative damage, indicating that Fe NPs can effectively prime plants for improved stress tolerance [122].

In maize, Fe₂O₃ NPs showed the promotion of growth and modulated metabolic enzyme activity, highlighting their influence on plant metabolism under drought [144]. In grapevine (*Vitis vinifera*), exposure to Fe NPs under PEG-induced drought conditions enhanced chlorophyll content and fluorescence, reduced hydrogen peroxide and malondialdehyde levels, and boosted both enzymatic and non-enzymatic antioxidant defenses [145]. These findings underscore the dual role of Fe NPs in providing essential

micronutrients while simultaneously activating antioxidant mechanisms. In rice (*Oryza sativa*) and barley (*Hordeum vulgare*), Fe NPs not only improved iron nutrition but also reduced arsenic accumulation, enhanced photosynthetic pigment levels, and modulated the expression of genes involved in iron and heavy metal transport, illustrating their capacity to mitigate heavy metal stress alongside drought [125,146].

Wheat (*Triticum aestivum*) has also been extensively studied, with phytosynthesized iron(II) oxide NPs (FeO NPs) applied via seed priming or foliar sprays improving growth and yield attributes under drought [147]. In conditions of combined salinity and cadmium stress, bioengineered FeO NPs enhanced plant growth, reduced cadmium uptake, and improved nutrient status, while lowering sodium and chloride accumulation [148]. Bell pepper (*Capsicum annuum*) treated with foliar Fe₃O₄ NPs under alkaline stress exhibited significant increases in shoot length and root dry weight, accompanied by improvements in relative water content, membrane stability, carbohydrate metabolism, and antioxidant enzyme activity [100]. Similarly, cowpea (*Vigna unguiculata*) exposed to salinity stress showed reduced pigment degradation, elevated osmoprotectant levels, and enhanced seed dry matter and protein content following treatment with green-synthesized Fe and Zn NPs [149].

Altogether, the available evidence indicates that iron NPs contribute to plant tolerance under abiotic stress through a combination of nutritional, physiological, and biochemical mechanisms. Their role in enhancing iron availability, modulating ion homeostasis, and stimulating antioxidant defenses helps sustain photosynthetic activity, membrane integrity, and overall plant performance. However, the magnitude and direction of these effects vary considerably with nanoparticle characteristics, including size, composition, surface coating, and mode of application, highlighting the need for careful experimental calibration. While Fe NPs hold clear potential as sustainable nanofertilizers and stress-mitigation agents, a more comprehensive understanding of their long-term interactions with soil systems and crop metabolism remains essential before their broad adoption in agricultural practice.

4.3 Cu NPs—Copper Based NPs

Copper NPs (Cu NPs) and copper oxide NPs (CuO NPs) are emerging as dual-faced agents in plant stress science: on one hand, when applied at appropriate doses they can act as micronutrient-suppliers or stress-priming tools; on the other hand, at higher concentrations they may trigger phytotoxicity via oxidative stress. In terms of beneficial mechanisms, foliar application of CuO NPs in maize (*Zea mays*) grown in saline soil improved growth performance, photosynthetic attributes and nutrient (N, P, K, Ca, Mg) content in roots and shoots, thereby demonstrating how Cu NPs may help mitigate salt stress by supporting nutri-

Table 3. Summary of recent studies on the application of iron based NPs in various plant species under different abiotic stresses.

Plant species	Stress type	Nanoparticle concentration/application method	Main outcomes	References
Soybean (<i>Glycine max</i>)	Drought (40 % field capacity)	Fe ₃ O ₄ NPs 0/100/200 ppm (foliar spray)	• Increased seed yield by ~40% under drought, with higher seed oil and protein contents, at 200 ppm NPs.	[143]
<i>Sorghum bicolor</i>	Drought (water-deprivation)	Green-synthesized α-Fe ₂ O ₃ NPs 5/10/15 [mg/L] (seed priming)	• Best improvement: height, biomass, chlorophyll, nutrient uptake, reduced ROS and oxidative damage for 10 mg/L NPs.	[122]
Maize (<i>Zea mays</i>)	Drought stress	Fe ₂ O ₃ NPs (sprout exposure; concentration not reported)	• Improved growth under drought; altered NADP-ISDH enzyme activity (metabolic enzyme) in roots/leaves.	[144]
Grapevine (<i>Vitis vinifera</i> L.)	PEG-simulated drought	Fe NPs up to 10 μM (nutrient solution)	• Increased chlorophyll and fluorescence under drought. • Reduced H ₂ O ₂ and MDA; enhanced enzymatic antioxidants and non-enzymatic (AsA/GSH) systems.	[145]
Rice (<i>Oryza sativa</i>)	As heavy-metal stress	Fe NPs 20 and 100 [mg/L] (nutrient solution)	• Reduced As uptake/accumulation, improved Fe uptake, photosynthetic pigments, antioxidant enzyme activities, and growth.	[125]
Indian Mustard Plant (<i>Brassica juncea</i> L.)	As toxicity	Fe ₃ O ₄ NPs 500 [mg/L] (nutrient solution)	• FeO NPs action as nano-fertilizer. • Alleviated As toxicity. • Better growth and photosynthesis via gene regulation (Fe transporters up, As transporters down).	[146]
Wheat (<i>Triticum aestivum</i>)	Drought (rain-fed field)	Phytosynthesized FeO NPs 12.5–100 ppm (seed nanoprimering/foliar)	• Improved morphological and yield attributes under drought for higher doses. • FeO NPs contribution to drought resilience.	[147]
Wheat (<i>Triticum aestivum</i>)	Salinity + Cd stress	Bioengineered FeO NPs ~19–40 nm, 100 mg kg ⁻¹ (soil application in saline soil)	• Growth increase of 36.7% vs. control. • Reduced Cd uptake by ~72.5%. • Improved nutrient status (N, P, K). • Reduced Na ⁺ /Cl ⁻ content.	[148]
Bell pepper (<i>Capsicum annuum</i>)	Alkaline stress (high pH/CO ₃ ²⁻ /HCO ₃ ⁻)	Fe ₃ O ₄ NPs 100 [mg/L] (foliar application)	• Increased shoot length (24%) and root dry weight (127%), under alkaline stress, improving RWC, membrane stability, carbohydrate metabolism, and antioxidant enzyme activity.	[100]
Cowpea (<i>Vigna unguiculata</i>)	Salinity stress (saline irrigation water)	Green-synthesized Zn + Fe NPs (foliar spray; concentration not reported)	• Mitigated salt stress: slowed pigment degradation, increased osmoprotectants, improved seed dry matter and protein under salinity.	[149]

Fe₃O₄ NPs, magnetite iron oxide NPs; Fe₂O₃ NPs, iron(III) oxide NPs; FeO NPs, iron(II) oxide NPs; Zn + Fe NPs, zinc and iron NPs; PEG, polyethylene glycol; ROS, reactive oxygen species; H₂O₂, hydrogen peroxide; MDA, malondialdehyde; AsA, ascorbate; GSH, glutathione; NADP-ISDH, NADP-dependent isocitrate dehydrogenase; RWC, relative water content; As, arsenic; Cd, cadmium; N, nitrogen; P, phosphorus; K, potassium; Na⁺, sodium ion; Cl⁻, chloride ion; CO₃²⁻, carbonate ion; HCO₃⁻, bicarbonate ion.

ent assimilation and photosynthetic capacity [128]. Mechanistically, Cu NPs/CuO NPs can influence plant antioxidant systems: for example, in Brassica under cadmium stress, treatment with Cu NPs increased SOD, POD and CAT activities, while both Cu NPs and CuO NPs inhibited APX activity. Importantly, when combined with Cd, Cu NPs reduced cadmium accumulation in leaves and roots, whereas CuO NPs increased Cd uptake, indicating complex ion-interaction effects and highlighting dose/particle form importance [129]. On the other hand, higher concentrations of Cu NPs (10–30 nm size) applied to cucumber (*Cucumis sativus*) caused genotoxicity, increased H₂O₂

and MDA levels, root plasma membrane damage and decreased chlorophyll content and biomass, underscoring the fine threshold between benefit and toxicity [130]. Table 4 (Ref. [116,128,129,131,134,150,151,152]) summarizes the recent studies illustrating the applications and effects of Cu/CuO NPs.

In maize (*Zea mays*) and fenugreek (*Trigonella foenum-graecum*), foliar application of Cu NPs significantly alleviated the effects of salinity stress, leading to improved growth and enhanced physiological performance, including parameters related to photosynthesis and water status (Shafiq et al., 2024 [128]). Similarly, in a broader

Table 4. Summary of recent studies on the application of copper NPs (CuNPs and CuO NPs) in various plant species under different abiotic stresses, including drought, salinity, and heavy metal toxicity.

Plant species	Stress type	Nanoparticle concentration/application method	Main outcomes	References
Maize (<i>Zea mays</i>) and Fenugreek (<i>Trigonella foenum-graecum</i>)	Salinity	Cu NPs (foliar application; concentration not specified)	<ul style="list-style-type: none"> Significantly mitigated salt stress effects, improving growth and physiological parameters. 	[128]
Various species	Drought, salinity	CuO NPs (green synthesis; concentration not specified)	<ul style="list-style-type: none"> Improved germination, growth, photosynthesis, and nutrient uptake under stress. 	[116]
Brassica	Cd stress	Cu NPs and CuO NPs, 20 mg/L (growth medium exposure)	<ul style="list-style-type: none"> Reduced Cd accumulation (−12.6% leaves, −38.6% roots) for Cu NPs. Increased Cd accumulation (+73.1% in leaves, +22.5% in roots) for CuO NPs. Highlighted form- and dose-dependent effects for CuO NPs. 	[129]
Barley (<i>Hordeum vulgare</i>)	High Cu/CuO NP exposure	5–1000 [mg/L] (growth medium exposure)	<ul style="list-style-type: none"> Induced oxidative stress, hormonal imbalance, cellular damage. Demonstrated toxicity at excessive doses. 	[131]
Rice (<i>Oryza sativa</i>)	CuO NP toxicity	CuO NPs (concentration not specified) + H ₂ S treatment	<ul style="list-style-type: none"> Mitigation of CuO toxicity by hydrogen sulfide (H₂S), regulating oxidative metabolism and gene expression. 	[150]
Various species	Heavy metal and other abiotic stresses	Cu NPs (dose-dependent; application method not specified)	<ul style="list-style-type: none"> Improved stress tolerance by activating antioxidant enzymes and enhancing nutrient uptake. 	[134]
Various species	Various abiotic stresses	Cu NPs (dose-dependent; application method not specified)	<ul style="list-style-type: none"> Influenced seed germination, root growth, and photosynthesis. Strong dependence of effects on size, dose, and exposure duration. 	[151]
Various species	Drought, salinity, heavy metals	Cu NPs (dose-dependent; application method not specified)	<ul style="list-style-type: none"> Enhanced plant resilience via upregulation of antioxidant enzymes. Improved nutrient assimilation. 	[152]

Cu NPs, copper NPs; CuO NPs, copper oxide NPs; Cd, cadmium; Cu, copper; H₂S, hydrogen sulfide.

set of plant species, green-synthesized CuO NPs were reported to enhance germination, growth, photosynthetic efficiency, and nutrient uptake under both drought and salinity stress, demonstrating the versatility of CuO NPs as nano-agrochemicals in stress management [116].

The effects of CuNPs and CuO NPs are highly dependent on particle form and concentration. In Brassica plants exposed to cadmium stress, Cu NPs reduced Cd accumulation by 12.6% in leaves and 38.6% in roots, whereas CuO NPs increased Cd accumulation, highlighting the differential responses depending on nanoparticle type [129].

While moderate Cu/CuO NP treatments can enhance stress tolerance, excessive exposure can be detrimental. For instance, in barley (*Hordeum vulgare*), high concentrations of CuO NPs induced oxidative stress, hormonal imbalances, and cellular damage, underscoring the importance of careful dose optimization to avoid phytotoxicity [131].

Nanoparticle-mediated mitigation of stress can also involve biochemical regulation. In rice (*Oryza sativa*), the toxicity induced by CuO NPs was alleviated through hydrogen sulfide (H₂S) treatment, which modulated oxidative metabolism and gene expression, demonstrating that

Cu/CuO NP interactions with plant signalling pathways can influence stress responses [150]. Reviews and broader analyses have confirmed that Cu NPs, alone or in combination with other NPs, enhance plant resilience to heavy metal and other abiotic stresses by activating antioxidant enzymes and improving nutrient uptake [134]. Additional studies across various species reported that CuO NPs at variable doses influenced seed germination, root growth, and photosynthetic activity, with the magnitude of these effects strongly depending on nanoparticle size, concentration, and exposure duration [151]. Finally, Cu NP applications under combined drought, salinity, and heavy metal stresses were found to enhance overall plant resilience via upregulation of antioxidant enzymes and improved nutrient assimilation [152].

These findings demonstrate that Cu NPs and CuO NPs hold significant potential for enhancing plant tolerance to abiotic stresses. They promote growth, modulate biochemical and physiological processes, and reduce toxic ion accumulation. Nevertheless, the fine balance between their beneficial and toxic effects highlights the importance of optimizing nanoparticle type, concentration, and application method to ensure safe and effective agricultural use.

4.4 ZnO NPs—Zinc Oxide NPs

ZnO NPs represent one of the most promising nanotechnological approaches for enhancing plant resilience to abiotic stresses, due to their ability to act simultaneously as a highly bioavailable source of zinc and as modulators of antioxidant and metabolic systems [153]. It has been demonstrated that the application of ZnO NPs can mitigate the negative effects of conditions such as drought, salinity, and nutrient deficiency by strengthening antioxidant defenses, improving membrane stability, and maintaining photosynthetic efficiency [154].

ZnO NPs are emerging as valuable tools for enhancing plant resilience to abiotic stresses, owing to their ability to release Zn^{2+} ions in a controlled manner and to modulate key physiological processes involved in stress responses [153]. The application of ZnO NPs provides zinc in a highly bioavailable form, supporting essential metabolic functions such as the activation of key enzymes and the stabilization of cellular membranes, which are often compromised under adverse environmental conditions. At the same time, ZnO NPs directly influence the antioxidant system by increasing the activity of SOD, CAT, APX, and glutathione reductase (GR), while reducing oxidative stress indicators such as lipid peroxidation, measured as MDA. This reinforcement of the antioxidant defense system enhances the plant's ability to neutralize ROS, which tend to accumulate under drought, salinity, or nutrient-deficient conditions.

The method of ZnO NPs application is a crucial factor for treatment efficacy. Foliar application allows rapid absorption and immediate physiological responses, whereas seed nanopriming can improve germination and

early seedling vigour, preparing plants to better tolerate future stresses. It is essential to consider the strongly dose-dependent nature of ZnO NPs, as excessive concentrations can induce phytotoxicity. Additionally, factors such as environmental fate, interactions with soil microorganisms, and potential accumulation in plant tissues require further investigation. Overall, ZnO NPs show significant potential to enhance tolerance to abiotic stresses by improving antioxidant metabolism, osmotic regulation, and photosynthetic efficiency, but their application requires an integrated approach that considers agronomic effectiveness, ecotoxicological safety, and formulation standardization.

In this context, the studies conducted by El-Zohri et al. (2021) [22], Abdelkhalik et al. (2025) [126], and Raza et al. (2025) [127], reported in Table 5 (Ref. [22,126,127]), provide essential evidence, as they show across different crops and stress conditions how ZnO NPs can translate their physiological potential into measurable benefits. These studies report improvements in growth, photosynthesis, water status, and antioxidant activity, confirming the theoretical premises and offering a clearer understanding of the functional role of ZnO NPs under drought and salinity stress.

El-Zohri et al. (2021) [22] examined how zinc oxide NPs synthesized through a green method, obtained using *Coleus forskohlii* leaf extracts, can help tomato plants tolerate drought. The plants were subjected to four levels of water availability (from 100% to 25% field capacity) and, at the same time, treated with three different concentrations of ZnO NPs (25, 50 and 100 mg/L). Drought caused a marked reduction in plant growth and an increase in oxidative stress indicators such as MDA and H_2O_2 . The lower concentrations of ZnO-NPs (25 and 50 mg/L) proved effective in counteracting these effects, significantly improving both root and shoot biomass, even under the most severe stress conditions. The application of NPs also reduced the accumulation of MDA and H_2O_2 , suggesting decreased lipid peroxidation and greater stability of cellular membranes. Their beneficial effect was associated with an enhancement of the plant's antioxidant system: both non-enzymatic antioxidants (such as ascorbate and phenolic compounds) and key antioxidant enzymes, like SOD, CAT, and APX, increased. Under the most intense drought conditions, the activities of these enzymes rose to more than four times those of the untreated controls, demonstrating a strong capacity to neutralize ROS. This case study indicates that green-synthesized ZnO-NPs, when applied at low concentrations, represent a useful tool for enhancing tomato tolerance to drought by strengthening antioxidant defenses and protecting cellular structures [22].

In the case study by Abdelkhalik et al. (2025) [126], the use of ZnO NPs proved decisive in improving the response of *Cucurbita pepo* L. subjected simultaneously to drought (60% ETc) and salinity (EC 6.45 dS m^{-1}). The ZnO NPs were applied at 50 and 100 mg L^{-1} as foliar sprays prior to the moringa leaf extract (MLE 3%), allow-

Table 5. Effects of zinc oxide NPs (ZnO NPs) on plants under different abiotic stress conditions.

Plant species	Stress type	Nanoparticle concentration/application method	Main outcomes	References
<i>Solanum lycopersicum</i> (tomato)	Drought	25–100 [mg/L] (foliar application)	<ul style="list-style-type: none"> • Increased chlorophyll content • Enhanced photosynthesis • Higher antioxidant enzyme activity (SOD, CAT, APX) • Reduced oxidative stress (MDA) 	[22]
<i>Cucurbita pepo</i> (zucchini)	Water deficit	Combination of ZnO NPs 50–100 [mg/L] (foliar spray; combined with moringa leaf extract)	<ul style="list-style-type: none"> • Synergistic effects: increased photosynthesis, higher osmolyte accumulation (proline and soluble sugars), enhanced antioxidant activity, reduced ROS, improved yield 	[126]
<i>Triticum aestivum</i> (wheat)	Drought	Seed priming with ZnO NPs (~70 nm), various concentrations (0, 50, 100 and 150 ppm), applied at different phenological stages	<ul style="list-style-type: none"> • Improved yield • Increased nutrient uptake efficiency • Higher antioxidant activity • Reduced oxidative damage • Caution for phytotoxicity at high doses 	[127]

ZnO NPs, zinc oxide NPs; SOD, superoxide dismutase; CAT, catalase; APX, ascorbate peroxidase; ROS, reactive oxygen species; MDA, malondialdehyde.

ing rapid penetration of the micronutrient into leaf tissues and an effective activation of defense mechanisms [126]. Under combined drought and salt stress, the NPs markedly reduced oxidative damage: H₂O₂ decreased by 28–30% at 100 mg L⁻¹, while the membrane stability index (MSI) increased by 45–50%, showing clear protection of plasma membranes. At the same time, treated leaves maintained a RWC 30–34% higher than stressed untreated plants, indicating that ZnO NPs favoured the maintenance of tissue hydration. The most evident effect was observed in the photosynthetic system. Plants treated with 100 mg L⁻¹ ZnO NPs showed very high increases in pigment levels: +58–73% for chlorophyll a, +142–149% for chlorophyll b, and +176–193% for carotenoids. This strong protection of photosynthetic pigments led to significant improvements in fluorescence parameters: PSII efficiency (F_v/F_m) increased by 12–17%, while the Performance Index rose by 45–56%, indicating a more stable and functional photosynthesis even under severe stress. ZnO-NPs also promoted the accumulation of osmoprotectants, with increases in soluble sugars of 33–54% and in free amino acids of 13–20%, contributing to osmotic regulation and protection of cellular structures. Biochemically, the NPs enhanced the activity of antioxidant enzymes: CAT, SOD, APX, and GR increased by 28–38%, 29–37%, 29–41%, and 17–33%, respectively, at 100 mg L⁻¹, demonstrating that zinc directly stimulated the plant's enzymatic defense system. The integration of ZnO NPs with MLE further amplified the effects already induced by the NPs, but the decisive factor in counteracting stress was the zinc in nanoform. In this case study, most of the physiological improvements from membrane protection to pigment recovery, from increased photosynthetic efficiency to improved water retention, were directly dependent on the action of ZnO NPs. Overall, the treatment resulted in a remarkable increase in productivity, with both yield and water

use efficiency (WUE) increasing by 76–84%, compared to stressed untreated plants. This case provides clear evidence that the use of ZnO NPs, particularly at the dose of 100 mg L⁻¹, played a central role in enabling *Cucurbita pepo* to maintain key physiological functions and sustain productivity despite the combined challenges of drought and salinity [126].

Moreover, the application of ZnO NPs played a decisive role in improving the response of wheat (*Triticum aestivum* L.) subjected to drought, as evidenced by Raza et al. (2025) [127]. In their work, the NPs, with an average size of about 70 nm, were applied to the soil at concentrations of 50, 100 and 150 ppm, and the most effective dose was 150 ppm. Their nanoform allowed for a faster availability and a more efficient absorption of zinc, an essential element for numerous enzymes, thereby promoting the activation of physiological mechanisms that help counteract water deficit. Wheat plants treated with ZnO NPs showed a marked reduction in oxidative damage, as evidenced by the strengthening of the enzymatic antioxidant system: the activities of SOD, CAT, APX and GR increased between 29 and 41%, values clearly superior to those of stressed control plants. This enhancement supported the protection of cellular membranes, with a significant improvement in membrane stability and a notable increase in RWC, reaching rises of 30–34% at the 150 ppm dose, indicating a greater ability of plant tissues to retain water even under limited irrigation or rainfall conditions. The effect of the NPs was also evident in the root system and overall plant growth: root biomass and shoot biomass increased, with a particularly marked rise in shoot biomass during grain-filling stage (D2), reaching +81.2% compared to stressed untreated plants. The stronger root system facilitated water and nutrient uptake, supporting better overall plant physiology. One of the most relevant aspects concerns the protec-

tion of photosynthesis. ZnO NPs effectively supported photosynthetic pigments and processes, with chlorophyll content increasing by up to 139.4% during the tillering stage (D1). Gas-exchange parameters also positively responded, with very high increases in transpiration (+121.2%) and net photosynthesis (+67.3%) at the 150 ppm dose. These results indicate that the NPs helped maintain stomatal and chloroplast functionality even under drought stress, limiting pigment degradation and preserving photosynthetic efficiency. The positive impact on the photosynthetic apparatus and water relations translated into clear improvements in yield-related traits. The number of grains per spike increased by 11.2%, the thousand-grain weight by 5.1%, and the per-plant grain yield rose by 19.8% at the 150 ppm dose. Beyond yield, there was also an improvement in grain quality: protein content increased by 8.1%, and zinc concentration in the grains increased by 62.1% under D1 conditions, demonstrating a significant nutritional enhancement. These results show that zinc oxide NPs, especially at the dose of 150 ppm, supported wheat in a decisive manner during drought stress, due to their ability to improve photosynthetic efficiency, membrane stability, water status, root growth and antioxidant defense, enabling the crop to maintain growth, metabolic activity and productivity even under the most critical conditions [127].

4.5 Ag NPs—Silver NPs

Ag NPs are among the most extensively studied nanomaterials for enhancing plant tolerance to abiotic stresses. Ag NPs are particles of silver ranging from 1 to 100 nm in size, characterized by a high surface area-to-volume ratio, catalytic properties, and antimicrobial activity. These unique properties allow Ag NPs to interact with plant cells differently from bulk or ionic silver, modulating physiological, biochemical, and hormonal processes in plants under stress [18].

Several studies have documented the efficacy of Ag NPs across different plant species and stress conditions (Table 6, Ref. [132,133]). In tomato (*Lycopersicon esculentum*), exposure to Ag NPs and silver nitrate (AgNO_3) modulated both physiological and molecular responses associated with oxidative stress. Ag NPs increased antioxidant enzyme activity (SOD and CAT), decreased oxidative damage (H_2O_2 and MDA), and upregulated genes involved in oxidative stress defense, including peroxidases. Notably, AgNO_3 exhibited higher toxicity than Ag NPs, highlighting the relative safety and efficiency of nanoparticles in stimulating plant defense mechanisms [132].

Alabdallah et al. (2021) [133] examined the role of AgNPs in enhancing drought tolerance in eggplant (*Solanum melongena L.*). Drought stress was imposed using different field capacities (FC) 80% (control), 50% FC, 35% FC and 20% FC, while Ag NPs synthesized through green methods were applied foliarly at concentrations of 0, 0.1, 0.2 and 0.5 μmol . The NPs had spherical to hexago-

nal shapes and sizes ranging from 14 to 35 nm. Drought stress markedly reduced plant height, shoot fresh and dry mass, leaf area and photosynthetic pigments confirming severe physiological impairment. However, Ag NP application significantly counteracted these reductions, with 0.1 μmol being the most effective concentration in enhancing growth traits and pigment levels under drought [133]. In addition to morphological effects, Ag NPs influenced key biochemical responses. Drought stress increased proline by 28–49% and reduced protein content by 26–85% compared with the well-watered control. Foliar Ag NPs markedly reduced proline accumulation and restored protein content across all drought levels, indicating better osmotic regulation and metabolic stability. Oxidative damage markers, namely H_2O_2 and MDA, increased sharply under drought (up to 85% and 82% higher than the control), but Ag NPs significantly lowered both molecules, demonstrating strong protection against lipid peroxidation and ROS accumulation. Drought also induced increases in antioxidant enzymes, with SOD rising by 35–62% and CAT by 46–54%. Ag NP treatments further boosted SOD and CAT activities beyond drought-induced levels, suggesting reinforced antioxidant defense. The study shows that green-synthesized Ag NPs, especially at 0.1–0.2 μmol , effectively mitigate drought stress in eggplant by improving growth, maintaining photosynthetic pigments, reducing oxidative damage and enhancing antioxidant activity. The NPs improved water balance, protected cellular membranes and strengthened ROS-scavenging systems, resulting in significantly greater drought tolerance in *S. melongena* seedlings [133].

4.6 TiO_2 NPs—Titanium Dioxide NPs

TiO_2 NPs are emerging as a promising nanotechnological tool for enhancing plant tolerance to abiotic stresses due to their ability to modulate key physiological and biochemical processes. For example, TiO_2 NPs have been reported to enhance the activity of antioxidant enzymes such as SOD, CAT, APX, and GPX, thereby reducing lipid peroxidation (measured by MDA) and protecting cellular membranes from oxidative damage under stress conditions [155].

Numerous experimental studies demonstrate the ability of TiO_2 NPs to exert beneficial effects in different plant species and under various abiotic stress conditions, as reported in Table 7 (Ref. [135,136,156]).

Khalid et al. (2024) [156] examined the effect of TiO_2 NPs on *Solanum melongena L.* exposed to moderate (75 mM) and severe (150 mM) salt stress. The NPs, foliarly applied at 0, 200 and 400 ppm, had a clear protective effect, with 200 ppm being the most effective concentration (Khalid et al., 2024 [156]). Salt stress reduced growth, leaf greenness and photosynthetic efficiency, but plants treated with 200 ppm TiO_2 NPs maintained higher shoot and root growth and better chlorophyll fluorescence performance. The NPs strengthened antioxidant activity especially SOD, CAT, POD and APX and lowered oxidative stress mark-

Table 6. Summary of recent studies on the application of silver NPs (Ag NPs) in various plant species under different abiotic stresses.

Plant species	Stress type	Nanoparticle type and concentration	Main outcomes	References
<i>Lycopersicon esculentum</i> (tomato)	Oxidative Stress	Ag NPs vs. AgNO ₃ (concentrations not specified here, but applied in comparative form, application method not specified)	<ul style="list-style-type: none"> • Increased SOD and CAT • Decreased H₂O₂ and MDA • Upregulation of genes involved in oxidative stress defense, including peroxidase • Higher toxicity for AgNO₃: associated with impaired antioxidant responses 	[132]
<i>Solanum melongena</i> L. (eggplant)	Drought stress (80%, 50%, 35%, 20% FC)	0, 0.1, 0.2, 0.5 μmol (foliar application)	<ul style="list-style-type: none"> • Increased growth and pigments at 0.1–0.2 μmol • Decreased H₂O₂ and MDA at 0.1–0.2 μmol • Increased SOD and CAT at 0.1–0.2 μmol 	[133]

Ag NPs, silver NPs; AgNO₃, silver nitrate; FC, field capacity; SOD, superoxide dismutase; CAT, catalase; H₂O₂, hydrogen peroxide; MDA, malondialdehyde.

Table 7. Summary of recent studies on the application of titania NPs (TiO₂ NPs) in various plant species under different abiotic stresses, including salinity and phosphorus deficiency.

Plant species	Stress type	Nanoparticle concentration/application method	Main outcomes	References
<i>Solanum melongena</i> L. (eggplant)	Salt stress (75–150 mM NaCl)	0, 200, 400 ppm (foliar application)	<ul style="list-style-type: none"> • Improved shoot and root growth, chlorophyll fluorescence, antioxidant enzyme activity (SOD, CAT, POD, APX) at 200 ppm • Reduced H₂O₂, MDA, membrane damage at 200 ppm • Lowered Na⁺ accumulation at 200 ppm • Less effectiveness or stress at 400 ppm 	[156]
<i>Malus domestica</i> (MM106 rootstock)	Phosphorus deficiency (±P)	0, 10, 50, 100 [mg/L] (foliar application)	<ul style="list-style-type: none"> • Increased shoot growth, leaf area, root biomass, nutrient uptake at 10 mg L⁻¹ • Improved chlorophyll and growth-related hormones at 10 mg L⁻¹ • Less effectiveness for higher doses 	[135]
<i>Vicia faba</i> L. (faba bean)	Salt stress (75 mM, 150 mM NaCl)	40 mM, 80 mM (foliar application)	<ul style="list-style-type: none"> • Improved biomass, chlorophyll, photosynthesis (Pn, gs, Tr) at 40 mM • Reduced ROS, MDA, electrolyte leakage at 40 mM • Enhanced antioxidants (GSH, ASA, CAT, GR, SOD) at 40 mM • Reduced Na⁺ accumulation at 40 mM • Restored N, P, K at 40 mM 	[136]

NaCl, sodium chloride; SOD, superoxide dismutase; CAT, catalase; POD, peroxidase; APX, ascorbate peroxidase; H₂O₂, hydrogen peroxide; MDA, malondialdehyde; Na⁺, sodium ion; ROS, reactive oxygen species; P, phosphorus; Pn, net photosynthetic rate; gs, stomatal conductance; Tr, transpiration rate; GSH, glutathione; AsA, ascorbate; GR, glutathione reductase; N, nitrogen; K, potassium.

ers such as H₂O₂ and MDA, indicating reduced membrane damage. They also helped limit Na⁺ accumulation, improving ion balance under salinity. The 400 ppm dose did not provide similar benefits and sometimes showed stress-like effects, confirming the strong dose dependence of TiO₂ NP action. This study demonstrates that TiO₂ NPs at 200 ppm enhanced salt-stress tolerance in eggplant by improving antioxidant defense, protecting photosynthetic function and reducing oxidative injury [156].

Soliman et al. (2025) [135] investigated the effect of TiO₂ NPs on MM106 apple rootstock plants grown under conditions of sufficient or deficient phosphorus. The NPs, foliarly applied at concentrations of 0, 10, 50, and 100 mg L⁻¹, were assessed for their potential to alleviate the typical effects of phosphorus deficiency [135]. The treatment showed a clearly positive effect, particularly at the lowest concentration (10 mg L⁻¹). At this dosage, plants grown under phosphorus deficiency displayed more vigorous growth, with better-developed leaves and a more

robust root system trait usually compromised under low-phosphorus conditions. The impact on root development was especially notable: the 10 mg L⁻¹ application promoted greater root growth and improved nutrient uptake capacity. From a physiological standpoint, the same treatment helped maintain more balanced levels of chlorophyll and growth-related hormones, both of which are normally reduced under phosphorus deficiency. Higher concentrations, 50 and 100 mg L⁻¹, showed less pronounced or even diminished benefits, indicating that the optimal dose is the lowest one [135].

Elnaggar et al. (2025) [136], investigated the effect of TiO₂ NPs on faba bean plants (*Vicia faba L.*) subjected to salt stress, induced by irrigation with 75 mM and 150 mM NaCl, levels that markedly reduce growth, photosynthesis and nutritional status. The plants were treated with foliar applications of TiO₂ NPs at concentrations of 40 mM and 80 mM to evaluate the NPs' ability to mitigate salt-induced damage. Salt stress caused a strong accumulation of Na⁺ in leaf tissues, a decrease in N (nitrogen), P (phosphorus) and K (potassium), a reduction in chlorophyll content, and an increase in H₂O₂, MDA and membrane damage, together with a decline in photosynthetic parameters (net photosynthetic rate [Pn], stomatal conductance [gs], transpiration rate [Tr]). The treatment with 40 mM TiO₂ NPs proved to be the most effective: it improved plant height and biomass, increased photosynthetic pigments, restored photosynthetic performance and significantly reduced ROS, MDA and electrolyte leakage, indicating more intact membranes. At the same time, it enhanced antioxidants, strengthening the plant's defense against oxidative stress. TiO₂ NPs also reduced sodium accumulation and restored higher concentrations of essential nutrients. The study shows that TiO₂ NPs especially at 40 mM significantly enhance faba bean tolerance to salt stress by improving growth, photosynthesis, antioxidant capacity and ionic balance, making them an effective treatment to limit sodium-induced damage. These results highlight the multifunctional role of TiO₂ NPs in supporting plant physiology under abiotic stress by enhancing antioxidant defense, root growth, and photosynthesis, suggesting a significant potential for their application in agronomic strategies aimed at mitigating the effects of environmental stresses [136].

5. Advantages and Limitations

5.1 Benefits of NPs

The use of NPs offers advantages on improving agricultural efficiency, nutrient management, mitigating abiotic stress and reducing environmental impact [60,85,112,157,158]. NPs are considered a promising and transformative strategy for sustainable and precision agriculture [66,70,112]. The use of nano-fertilizers reduces application rates and fertilizer requirements compared to conventional fertilizers, with relevant benefit on soil contamination, environmental risks associated with chemical

fertilizers, and pollution caused by leaching, evaporation, and volatilization [66,157]. Some approaches employing NPs, such as the preparation of photothermal materials with Ag NPs, can contribute to the management of renewable resources and waste biomass [159]. NPs significantly improve the efficiency of nutrient uptake in plants due to their nanometric size (generally less than 100 nm), allowing effective penetration into cells and better transport across membranes [49,66,157]. Nano-fertilizers offer a controlled, gradual release of nutrients, by promoting sustainable nutrient management and ensures long-term access to essential elements [66]. Moreover, the small size of NPs gives them a high surface-to-volume ratio and greater reactivity, which increases nutrient absorption and retention compared to traditional fertilizers [66,157]. NPs enhance plant adaptation to various abiotic stresses, such as drought, salinity, extreme temperatures and UV-B radiation [61,70,112,160,161]. NPs, such as CeO₂-NPs, FeO-NPs, and ZnO-NPs, help maintain redox homeostasis and strengthen antioxidant defense systems [75,158,162]. The application of NPs is correlated with the reduction of the levels of reactive oxygen species (ROS), hydrogen peroxide (H₂O₂) and malondialdehyde (MDA) [60,74,112,162]. NPs can mitigate the toxicity induced by heavy metals and metalloids, such as cadmium (Cd) and arsenic (As), by reducing their accumulation and translocation in plants [49,51]. Some NPs, such as silver NPs (AgNPs) and copper oxide NPs (CuO NPs), have antimicrobial properties and can be used as fungicides or pesticides to reduce plant diseases [49,76]. The Fig. 2 summarizes the main mechanism of stress resilience induced by NPs to the plants.

5.2 Limitations of NPs

The issue of availability and production costs of NPs in agriculture is complex, as, although they are often characterized by a high initial cost, their unique properties can make them economically advantageous in the long term. Nano-fertilizers have a high cost [66], which, combined with limited accessibility, raises social equity concerns, and they can disadvantage smallholder farmers, exacerbating economic inequalities in the agricultural sector [66]. Although the initial cost of synthesizing nano-fertilizers is higher than conventional synthetic fertilizers due to the technology required [85], optimal and responsible use of NPs can potentially reduce production costs [66]. This is due to several factors that increase its efficiency and economic convenience. NPs can be applied at significantly lower concentrations (sometimes even a tenth or a fifteenth) than conventional fertilizers [157]. For example, the use of nano-fertilizers allows for significantly reduced application rates and fertilizer requirements compared to traditional fertilizers [66]. Nutrient absorption efficiency is higher due to the nanometer size of the particles, which reduces the inputs needed to achieve the desired results [66]. The controlled and gradual release system offered by nano-fertilizers re-

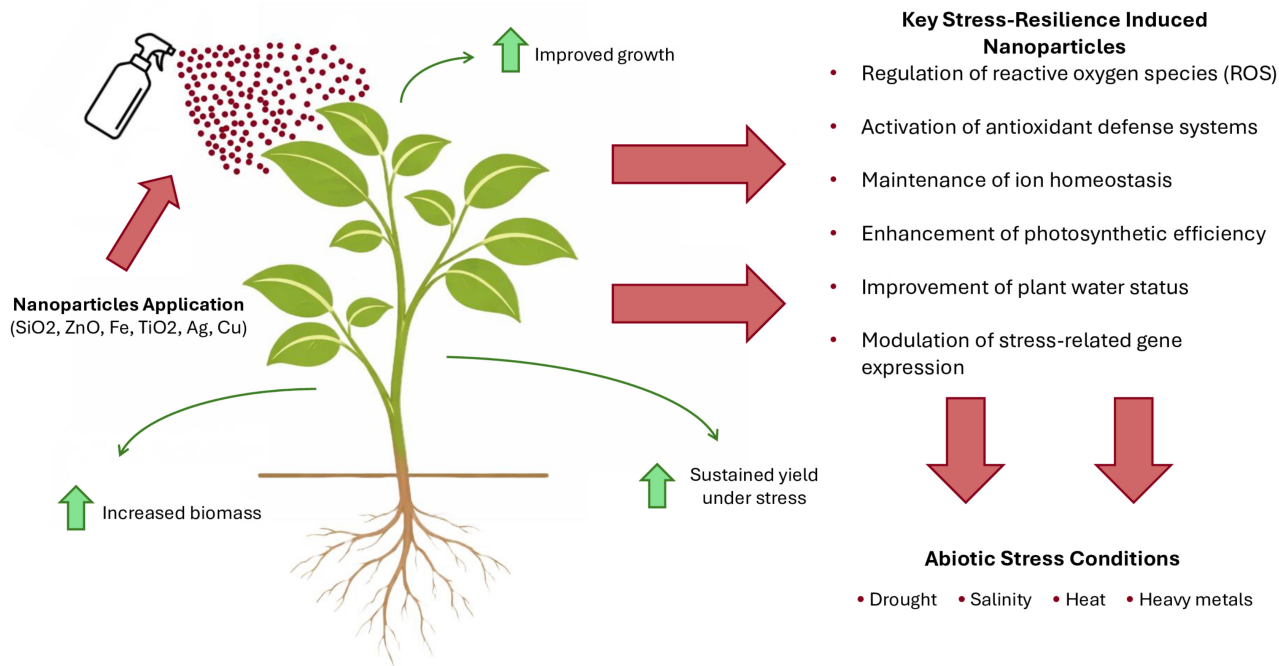


Fig. 2. Main mechanism of stress resilience induced by NPs. This figure was created using Microsoft PowerPoint (Office 365).

duces nutrient waste and ensures long-term access to essential elements [66]. Optimal application of NPs helps to increase crop yields [6,7,66], which, combined with the reduction of inputs, makes them cheaper than conventional synthetic fertilizers [85]. Furthermore, some sustainably produced NPs may represent a low-cost alternative. For example, biosynthesized silver NPs (bio-AgNPs) obtained by green methods are practical and economical, representing an important factor for cost reduction in biomass production in plant tissue cultures, especially compared to synthetic growth regulators [97]. Materials derived from renewable resources and biomass waste, such as carbon from corn straw (used for photothermal evaporators), are considered low-cost and readily available materials [159]. Therefore, the efficiency obtained by using nano-NPK at moderate concentrations (e.g., 1 and 1.5 mL/L) was shown to be equivalent or superior to that of high doses of conventional fertilizers (such as 2 g/L), suggesting that the use of nano-fertilizers may be a promising strategy for sustainable agriculture that optimizes growth while potentially reducing costs [66]. However, it remains very challenging to scale up green synthesis methods to industrial production for two main reasons. First, green-synthesized NPs often exhibit high variability in size, shape, and physico-chemical properties, due to the numerous factors influencing the process, such as pH, temperature, and the growth conditions of the bacterial and plant organisms used [163]. Second, green synthesis is likely more expensive than conventional industrial production methods; indeed, biological approaches involve the high cost of biological agents

employed in the process, as well as the longer synthesis times required [163]. Nevertheless, the need for further research is emphasized to investigate the long-term cost-effectiveness of nano-NPK applications for sustainable cultivation practices. The use of nanomaterials in the agri-food sector is strongly regulated both in the European Union and in the United States. In the EU, the competent authority is the EFSA (European Food Safety Authority), which has developed a risk assessment process composed of multiple phases. The main phase is the physico-chemical characterization of the materials, followed by several exposure assessment steps. After these phases, if the materials are fully dissolved in the matrix, *in vivo* and *in vitro* testing is carried out to evaluate potential toxicological hazards. If the previous assessments are not conclusive, an additional evaluation phase is required before proceeding to the testing phase [3]. In the United States, the regulation of nanomaterials involves more than one agency. The most important are the NNI (National Nanotechnology Initiative), the EPA (Environmental Protection Agency), and the FDA (Food and Drug Administration). Together, these authorities regulate exposure limits and provide both general and specific guidelines, for example through the submission of the TSCA (Toxic Substances Control Act). In addition, two other agencies address the impact of nanomaterials on consumers' and workers' health: the CPSC (Consumer Product Safety Commission) and the OSHA (Occupational Safety and Health Administration) [3]. NPs offer several promising advantages and limitations in agricultural applications: NPs can significantly enhance plant tolerance

to abiotic stresses such as drought, salinity, and heavy metal exposure by activating antioxidant defense systems and improving osmotic regulation, as also described in the previous sections [25]. Their ability to enhance nutrient uptake and bioavailability makes them effective as nano-fertilizers, supplying essential micronutrients like iron, zinc, and manganese with high efficiency. In addition, NPs can stimulate plant growth and photosynthesis, particularly at low concentrations, improving seed germination, root development, and chlorophyll synthesis. Through redox regulation and antioxidant enzyme activation, NPs help reduce oxidative damage and maintain cellular homeostasis [164]. Furthermore, certain NPs, especially Fe and Si-based types, can reduce heavy metal toxicity by limiting the accumulation of toxic ions such as cadmium and arsenic [165]. These combined effects often translate into higher yields and better crop quality, while promoting sustainable agricultural practices through reduced fertilizer use and improved resource efficiency. However, these benefits are counterbalanced by several limitations and risks. NPs exhibit dose-dependent toxicity, where excessive concentrations can cause oxidative stress, membrane damage, and inhibition of plant growth [166]. Their effects also depend strongly on particle size and morphology—smaller NPs (<50 nm) may more easily penetrate plant tissues, increasing reactivity and potential genotoxicity [167]. In environmental contexts, nanoparticle accumulation in soil can disturb microbial communities and alter nutrient cycling, posing long-term ecological concerns [168]. Additionally, non-biocompatible coatings may enhance nanoparticle persistence and toxicity, reducing biodegradability. The lack of standardized safety regulations and long-term ecotoxicological data further complicates their safe use. Moreover, the production of high-quality or green-synthesized NPs remains costly and difficult to scale up for large agricultural applications [56].

5.3 Potential Risks of NPs

Although NPs have shown considerable promise in improving plant tolerance to abiotic stresses, their toxicological effects remain one of the major limitations to their widespread and safe agricultural use. The toxicity of NPs is not only determined by their chemical composition but also by a combination of physicochemical properties, such as particle size, concentration, surface coating, solubility, and reactivity [152,169]. These factors influence nanoparticle mobility, uptake, translocation, and accumulation within plant tissues, ultimately shaping their biological effects. Among these parameters, particle size plays a critical role. Smaller NPs (typically <50 nm) exhibit higher surface-to-volume ratios, leading to greater reactivity and easier penetration through plant cell walls and membranes [170]. While this enhances nutrient delivery at low doses, it can also increase oxidative stress and DNA damage at higher concentrations. For example, CuO NPs smaller than

30 nm have been shown to induce severe oxidative damage, elevated H₂O₂ and MDA levels, and reduced chlorophyll content in *Cucumis sativus* [130]. Conversely, larger or aggregated NPs tend to have lower bioavailability but may accumulate in the rhizosphere, potentially disturbing soil-microbe interactions over time [171]. Concentration is another crucial determinant of nanoparticle toxicity. While low to moderate concentrations can promote growth, improve photosynthetic efficiency, and activate antioxidant enzymes, excessive doses often reverse these effects. The threshold between beneficial and toxic levels varies depending on the nanoparticle type and plant species. For instance, foliar application of Fe₃O₄ NPs at 100–200 ppm enhanced drought tolerance in soybean, whereas concentrations above 400 ppm led to oxidative imbalance and growth inhibition [143]. Similarly, ZnO NPs were beneficial to *Arabidopsis thaliana* up to 50 mg/L, but concentrations beyond 200 mg/L caused root growth inhibition and genotoxic effects [172]. These findings emphasize the dose-dependent duality of nanoparticle action, where the boundary between stimulation and toxicity is often narrow. The surface coating of NPs also critically influences their environmental behaviour and biological activity. Coatings made of biocompatible or organic molecules, such as humic acids, chitosan, or citrate, can enhance nanoparticle dispersion, reduce aggregation, and mitigate toxic ion release [123]. Coated Fe₃O₄ NPs, for example, displayed improved iron bioavailability in tomato plants with minimal oxidative stress compared to uncoated particles [123]. Conversely, uncoated metallic NPs or those with reactive oxide surfaces can catalyse Fenton-type reactions, producing excessive ROS and causing oxidative injury [170]. Moreover, coatings influence nanoparticle persistence in soil: while organic coatings tend to degrade and integrate into natural carbon cycles, inorganic or synthetic coatings may persist longer, raising environmental concerns [173]. The underlying mechanisms of nanoparticle-induced toxicity are primarily linked to oxidative stress and the subsequent activation of plant defense responses. Excess ROS production can damage lipids, proteins, and nucleic acids, alter gene expression, and impair photosynthesis [131]. High concentrations of CuO or Ag NPs have been shown to trigger oxidative bursts, hormonal imbalance, and cell ultrastructure disruption in *Hordeum vulgare* and *Oryza sativa*, respectively [174]. In parallel, NPs may interfere with ion transporters, disturb nutrient homeostasis, and compete with essential metals such as Zn, Fe, and Mn, further exacerbating physiological stress. Beyond plant-level impacts, environmental toxicity represents a growing concern. NPs released into the soil can interact with organic matter, roots, and microorganisms, potentially altering microbial diversity and enzymatic activities involved in nutrient cycling [171]. Persistent or bioaccumulative NPs might enter the food chain, leading to potential ecotoxicological risks. However, these outcomes depend strongly on particle persistence, aggrega-

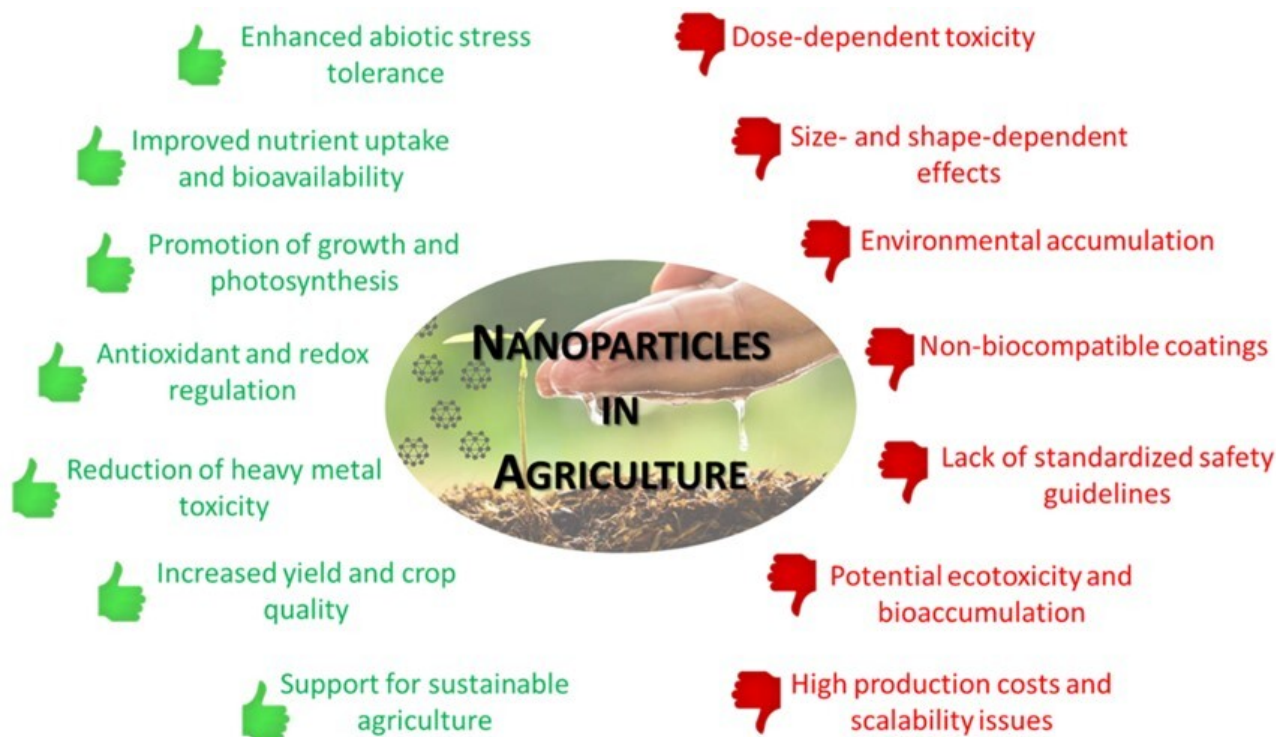


Fig. 3. Advantages and limitations of NPs in agriculture. This figure was created using Microsoft PowerPoint (Office 365).

tion dynamics, and transformation processes such as oxidation or dissolution [170]. To ensure the safe integration of nanotechnology into agriculture, future research must focus on establishing standardized dose-response relationships, defining safe particle size thresholds, and developing eco-friendly coatings that enhance functionality while minimizing toxicity. Moreover, comprehensive life-cycle and risk assessments are needed to understand long-term interactions with soil systems and plant-microbe ecosystems. The adoption of green synthesis techniques and biodegradable nanoparticle formulations represents a promising direction for reducing environmental persistence and ensuring sustainable use. In summary, nanoparticle toxicity is a dose-, size-, and coating-dependent phenomenon that requires precise control and careful optimization. While NPs can serve as powerful tools for enhancing crop resilience, their benefits can rapidly turn into detrimental effects if physicochemical parameters are not appropriately tuned. Balancing efficacy and safety will therefore be essential to fully exploit nanotechnology's agricultural potential without compromising environmental integrity. NPs used in agriculture represent a promising innovation: thanks to their unique properties, they can improve nutrient uptake in plants, enhance antioxidant defenses, and increase resilience to environmental stresses. However, alongside these agronomic advantages, concerns also arise regarding potential risks to human health, which require careful and balanced evaluation. Experimental evidence shows that, when properly calibrated in terms of dose, nanoparticle type, and appli-

cation method, NPs can modulate plant metabolism, nutrient dynamics, and defense systems, contributing to greater tolerance to abiotic stresses. Nevertheless, the risk benefit profile must be assessed on a case-by-case basis, integrating physiological, biochemical, and ecotoxicological data to define safe, effective, and sustainable application strategies. Several studies indicate that metal-based NPs such as TiO_2 and ZnO can accumulate in plant tissues, especially after foliar or soil application. For example, Šebesta et al. [175] demonstrated that foliar application of ZnO NPs significantly increases zinc content in edible plant parts such as leaves and seeds. This phenomenon raises the possibility of dietary exposure, as consumers may ingest vegetables containing engineered nanomaterials. Human health risks may be both direct, through ingestion of plant products containing NPs, and indirect, through environmental alterations. Soil application of nano-agrochemicals such as ZnO and Fe_2O_3 can modify microbial communities, reducing bacterial and fungal activity while promoting nanoparticle accumulation in crops [176]. Although some studies report estimated dietary exposure levels below risk thresholds (e.g., in red beet), questions remain regarding chronic exposure, bioaccumulation, and long-term effects. Therefore, although NPs offer important agronomic benefits such as increased micronutrient content, improved fertilizer efficiency, and enhanced stress tolerance the potential risks to human health cannot be overlooked. Fig. 3 provides a schematic overview of the advantages and limitations of NPs in Agriculture.

Table 8. Comparative overview about the NPs commonly used for plant abiotic stress resilience.

NPs type	Abiotic stress	Indicative effective dose range*	Key mechanisms	Reported efficacy	References
SiO ₂ NPs	Drought, salinity, temperature stress	~50–400 mg L ⁻¹ (species- and method-dependent)	• Enhancement of antioxidant defense; regulation of ion homeostasis (Na ⁺ /K ⁺ balance); osmolyte accumulation; improved root architecture and water status	High	[69,117,119,120,121,137,138,139,140]
Fe NPs/FeO NPs	Drought, salinity, heavy-metal stress	~10–200 ppm or mg L ⁻¹	• Improved Fe availability; activation of antioxidant enzymes (SOD, CAT, POD); reduced ROS and lipid peroxidation; decreased uptake of As and Cd	Moderate–high	[21,122,125,143,144,145,146,147,148]
Cu NPs/CuO NPs	Drought, salinity, heavy-metal stress	Low doses effective (≈10–30 ppm); higher doses phytotoxic	• Modulation of antioxidant enzymes; improved photosynthesis and nutrient assimilation; strong dose- and form-dependent effects	Moderate (highly dose-dependent)	[24,116,128,129,130,131,134,150,151,152]
ZnO NPs	Drought, salinity, nutrient deficiency	~25–150 mg L ⁻¹ or ppm	• Enhancement of antioxidant activity; membrane stabilization; improved photosynthesis, osmotic regulation and Zn uptake	High	[22,30,31,126,127]
Ag NPs	Temperature stress, drought	≤0.2 μmol	• Regulation of ROS metabolism; stimulation of antioxidant enzymes	Moderate	[28,132,133]
TiO ₂ NPs	Temperature stress, salinity, nutrient deficiency	~10–200 mg L ⁻¹ or ppm	• Protection of photosynthetic apparatus; enhancement of antioxidant enzymes; reduction of oxidative damage and Na ⁺ accumulation	Moderate–high	[26,135,136,156]
Chitosan NPs	Salinity stress	Low–moderate, species-dependent	• Seed priming effects; maintenance of chlorophyll and carotenoids; improved early growth and salt tolerance	Moderate	[32]

*Dose ranges are indicative and derived from the studies summarized in the text; efficacy and optimal concentration depend on plant species, nanoparticle properties, and application method.

6. Concluding Remarks and Future Perspectives

Nanotechnology is emerging as a transformative frontier in plant science, offering powerful tools to enhance crop resilience and productivity under increasingly challenging environmental conditions. In particular, nanotechnology offers a wide range of NPs with distinct physicochemical properties and biological functions that can be exploited to enhance plant tolerance to abiotic stresses. This review examines the use of NPs in agriculture, with a main focus on the mechanisms of abiotic stress mitigation and their effects on several plant parameters, such as growth and photosynthetic efficiency. Table 8 (Ref. [21,22,24,26,28,30,31,32,69,116,117,119,120,121,122,125,126,127,128,129,130,131,132,133,134,135,136,137,138,139,140,143,144,145,146,147,148,150,151,152,156]) provides a comparative analysis about all the most used NPs for plant abiotic stress resilience. The evidence discussed in this review demonstrates that NPs can effectively mitigate abiotic stresses by modulating physiological, biochemical, and molecular pathways in plants. According to the reviewed studies, the most effective NPs are silica-based

and metal-based NPs, particularly those containing copper, iron, titanium, zinc, and silver. SiO₂, CuO, ZnO, and TiO₂ NPs have shown promising capacity to reduce oxidative damage, improve water-use efficiency, regulate stress-related metabolites, and support adaptive morphological changes. These results collectively highlight the potential of NPs to contribute to a new sustainable agriculture, reduce losses in crop performance, and strengthen global food security. In addition to the applications discussed in this review, NPs offer many other potential uses in the agri-food sector, for example, for the development of new nanofertilizers and nanopesticides [3,177]. Despite these encouraging findings, potential negative effects must also be considered, and several challenges must be addressed to fully unlock the potential of nanotechnology in agriculture. Knowledge gaps remain regarding nanoparticle fate, environmental persistence, long-term effects on ecosystems, and potential risks to human health. We suggest more targeted investigations into the transport and fate of NPs within plant tissues, with particular emphasis on nanoparticle residues in seeds and fruits, especially for metal-based NPs. Such studies should also be extended

to aquifers, soils, and the human body. Most studies conducted to date have focused on nanoparticle behaviour under laboratory conditions; however, open-field environments are considerably more complex. Therefore, further research is required to evaluate the effects of variables such as temperature, soil texture, humidity, and other environmental factors. Moreover, the mechanisms that govern nanoparticle–plant interactions at the cellular and subcellular levels require further elucidation to optimize nanoparticle design for specific stress scenarios. Further in-depth studies are essential to test specific dosages and optimize the timing of NP application, and different NP application methods (such as nano-priming, foliar application, or soil application) should be evaluated to reduce toxicity and improve efficacy. It will be necessary to focus on the green synthesis of multifunctional NPs and on the optimization of composite formulations, such as the combination of Fe NPs with biochar or stabilization with biopolymers, such as chitosan (CS-IONPs). Regarding green synthesis methods, future research should focus on developing strategies to better engineer these processes, making them more affordable, scalable, and reproducible at an industrial level. Moreover, synergistic or additive effects between different NPs (e.g., CuO and SiO₂ NPs), or between NPs and other biostimulatory or microbial agents (such as rhizobacteria), need to be explored to maximize plant resilience. The coming years will be crucial for both nanotechnology research and its practical implementation in agricultural systems. Looking ahead, future research should prioritize the development of environmentally responsible NPs, explore synergistic effects with other sustainable agricultural practices, and integrate advanced monitoring tools—such as imaging, spectroscopy, and plant phenotyping—to better understand nanoparticle dynamics in planta. Interdisciplinary collaboration among plant physiologists, materials scientists, and environmental researchers will be essential to translate laboratory findings into scalable solutions. By addressing these scientific and regulatory challenges, nanotechnology holds the promise of becoming a backbone of next-generation agriculture, enabling crops to thrive in an era of accelerating climate change and increasing global demand.

Author Contributions

Conceptualization, MP, CC and IC; methodology, MP, FB, GM, CC, EL, MM and IC; formal analysis, MP, FB, GM, CC, EL, MM and IC; investigation, MP, FB, GM, CC, EL, MM and IC; data curation, MP, FB, GM, CC, EL, MM and IC; writing—original draft preparation, MP, FB, GM, CC, EL, MM and IC; writing—review and editing, MP, CC, EL, MM and IC; visualization, MP, FB, GM, CC, EL, MM and IC; supervision, MP, CC and IC. All authors contributed to editorial changes in the manuscript. All authors read and approved the final manuscript. All authors

have participated sufficiently in the work and agreed to be accountable for all aspects of the work.

Ethics Approval and Consent to Participate

Not applicable.

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Conflicts of Interest

The authors declare no conflicts of interest.

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