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Review

Synthesis of Zinc Oxide Nanoparticles and Their Applications in Enhancing Plant Stress Resistance: A Review

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Abstract: Biotic and abiotic stress factors are pivotal considerations in agriculture due to their potential to cause crop losses, food insecurity, and economic repercussions. Zinc oxide nanoparticles (ZnO nanoparticles) have gained substantial attention from researchers worldwide for their capacity to alleviate the detrimental impacts of both biotic and abiotic stress on plants, concurrently reducing dependence on environmentally harmful chemicals. This article provides an overview of methods for synthesizing ZnO nanoparticles, encompassing physical vapor deposition, ball milling, hydrothermal methods, solvothermal methods, precipitation methods, microwave methods, microbial synthesis, and plant-mediated synthesis. Additionally, it delves into the absorption, translocation, and biotransformation pathways of ZnO nanoparticles within plants. The emphasis lies in elucidating the potential of ZnO nanoparticles to safeguard plants against biotic and abiotic stress, enhance plant performance, and modulate various plant processes. The article also offers a preliminary exploration of the mechanisms underlying plant stress tolerance mediated by ZnO nanoparticles. In conclusion, ZnO nanoparticles present an environmentally friendly and cost-effective strategy for plant stress management, paving the way for the integration of nanotechnology in sustainable agriculture. This opens new possibilities for leveraging nanotechnology to bolster plant resilience against stress in the ever-changing climate conditions, ensuring global food security.

Keywords: zinc oxide; nanoparticles; agriculture; plants; biotic stress; abiotic stress

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1. Introduction

With the continuous changes in the global climate and the increasing impact of human activities, agriculture is facing unprecedented challenges [1–4]. Climate change and global warming have led to an increase in extreme weather events, posing threats to crop yields and soil fertility [5,6]. Simultaneously, biotic stresses such as viruses, bacteria, fungi, and parasites, as well as abiotic stresses including drought, salinity, high and low temperatures, and heavy metal toxicity, have severely compromised the health and productivity of crops [7–11]. In order to overcome these challenges, the agricultural sector has been actively exploring innovative methods to bolster crop resilience, increase yields, and decrease dependence on chemical pesticides and fertilizers [12–18].

In recent years, the emergence of nanotechnology has opened up new possibilities for addressing these challenges [19–22]. Specifically, zinc oxide nanoparticles (ZnO nanoparticles) have garnered considerable attention as a promising tool, demonstrating significant potential in effectively addressing both biotic and abiotic stresses [23]. The preparation methods for ZnO nanoparticles encompass various approaches, incorporating physical techniques such as vapor deposition and ball milling [24]. Chemical methods include solvothermal, hydrothermal, precipitation, and microwave procedures [25]. Additionally, there are biological synthesis methods that utilize organisms or their byproducts as mediums for nanoparticle synthesis [26,27]. These preparation techniques have their individual strengths and weaknesses but collectively furnish ample resources for employing ZnO nanoparticles in handling biotic and abiotic stresses.

Biotic and abiotic stresses stand as two primary limiting factors for crop growth and yield in agricultural production [28–32]. Biotic stresses encompass various invasions by viruses, bacteria, fungi, and pests, posing significant threats to crop growth [33–37]. Simultaneously, abiotic stresses primarily arise from environmental factors such as drought, high temperatures, low temperatures, salinity, and others, severely impacting plant growth and yield [38–42]. Recent research has underscored the significant potential of ZnO nanoparticles in mitigating biotic and abiotic stress in agriculture [43–46]. These nanoparticles have displayed the capacity to hinder the growth of different pathogenic microorganisms, such as bacteria, fungi, pests, and viruses [47–53]. Additionally, the immune system of plants can be enhanced by ZnO nanoparticles, which reduces the incidence of diseases effectively [54]. More importantly, in addressing abiotic stress, ZnO nanoparticles play a crucial role in managing plant water balance and preserving cell osmotic equilibrium, resulting in heightened plant resilience against stressors (such as heavy metals, cold, drought, and salinity) [55–59]. Beyond stress mitigation, ZnO nanoparticles have also exhibited the capacity to stimulate root growth, diversify the population of microorganisms in the rhizosphere, and contribute to the enhancement of soil structure and fertility [60–66]. These combined effects create a more favorable growth environment for crops, ultimately promoting healthier and more productive agricultural outcomes.

Through continued research and practical implementation, ZnO nanoparticles are poised to emerge as a vital component of agricultural sustainability. The nanoparticles hold the potential to boost crop productivity while reducing dependence on environmentally harmful chemicals. The purpose of this review is to consolidate the synthesis methods of ZnO nanoparticles, clarify their uptake and transport mechanisms in plants, and extensively delve into their diverse applications in bolstering plant resistance against both biotic and abiotic stresses. This review can serve as a valuable reference for the safe and effective utilization of ZnO nanoparticles in agricultural production, thus paving the way for the integration of nanotechnology in sustainable agriculture.

2. Preparation of ZnO Nanoparticles

The methods employed for synthesizing ZnO nanoparticles encompass physical, chemical, and biological approaches, as depicted in Figure 1. During the synthesis process, ZnO nanoparticles may undergo contamination, such as the introduction of iron ions, resulting in a notable change in the solubility of ZnO nanoparticles. Impurities in ZnO nanoparticles can arise from factors like the purity of reactants or the type of reaction vessel utilized in the synthesis process. Utilizing diverse synthesis methods and reactants enables the production of nano zinc oxide with varying impacts on plants, even while maintaining consistent particle sizes and shapes [67].

2.1. Physical Methods

2.1.1. Physical Vapor Deposition (PVD)

Physical vapor deposition (PVD) is a procedure used for the preparation of ZnO nanoparticles. Common PVD techniques involve the cathode arc physical vapor deposition electron beam, physical vapor deposition, ion beam sputtering, and pulse laser deposition [68–70]. The process begins with the sublimation of the source material, typically zinc metal, where it is transformed into a vapor state through high temperatures, often achieved within a furnace. Subsequently, this resulting vapor is directed towards a substrate and deposited onto it. The substrate is maintained at a lower temperature compared to the sublimation process, which facilitates the formation of ZnO nanoparticles on its surface. The size and shape of these nanoparticles can be controlled by adjusting the deposition conditions, such as substrate temperature, pressure, and evaporation rate. This technique is suitable for the mass production of ZnO nanoparticles.

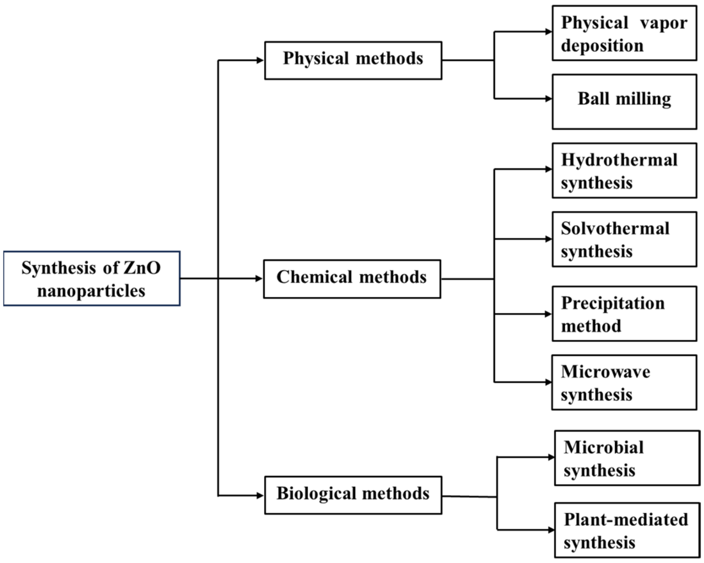

Figure 1. Various strategies for the fabrication of ZnO nanoparticles.

2.1.2. Ball Milling

Ball milling, a physical method for preparing ZnO nanoparticles, is a technique that refines particles and enables the acquisition of metastable materials [71]. In the specific case of ZnO nanoparticle synthesis using ball milling, ZnO powder is subjected to mechanical milling inside a ball mill. The milling process promotes the formation of ZnO nanoparticles with smaller sizes and improved crystallinity compared to the starting material. Moreover, ball milling can be combined with other methods, such as PVD, to strengthen the quality and uniformity of the ZnO nanoparticles. The mechanochemical procedure of ball milling is relatively simple and suitable for producing nanoparticles in large quantities [72].

2.2. Chemical Methods

2.2.1. Hydrothermal Synthesis

Hydrothermal synthesis is an efficient technique for the fabrication of ZnO nanoparticles, known for its relatively low process temperature requirement and the capability to regulate particle size and morphology [73]. In this technique, zinc precursor compounds are solubilized in a suitable solvent and exposed to elevated temperature and pressure in a closed reactor. Hydrothermal synthesis enables accurate manipulation of the size and morphology of the resultant ZnO nanoparticles by modifying reaction parameters like temperature, duration, and precursor concentrations [74,75]. It can also be combined with other methods, like ball milling to improve the quality and uniformity of the particles further [76]. The hydrothermal technique provides several advantages over other synthesis methods, including low cost, the utilization of simple equipment, uniform production, catalyst-free growth, ecofriendliness, and reduced hazards.

2.2.2. Solvothermal Synthesis

The solvothermal technique is derived from the hydrothermal method. In this approach, the reaction occurs within an enclosed system, such as an autoclave, where the initial mixture undergoes a reaction at a precise temperature and with the inherent pressure of the solution, employing organic substances or a nonaqueous solvent as the medium [77]. Typically, in solvothermal synthesis, zinc precursor compounds like zinc nitrate or zinc acetate are solubilized in an appropriate solvent and exposed to elevated temperature and pressure. The interaction of the zinc precursor with the solvent results in the generation of

ZnO nanoparticles [78]. Solvothermal synthesis regulates the size and morphology of the resultant nanoparticles [79,80].

2.2.3. Precipitation Method

The precipitation technique is a widely employed chemical synthesis method for the fabrication of ZnO nanoparticles [81,82]. It involves adding a precipitant to a soluble salt solution that contains one or more ions, inducing the generation of insoluble hydroxides, hydrated oxides, or salts that form a precipitate in the solution. The resulting precipitate is then washed, and the desired oxide nano powder is acquired via thermal decomposition or dehydration. By adjusting the reaction parameters and choice of precursors, it is possible to obtain nanoparticles with desired properties such as size, morphology, and composition [83–85]. The precipitation method is convenient and widely adopted by researchers for synthesizing ZnO nanoparticles.

2.2.4. Microwave Synthesis

Compared to conventional heating methods, microwave radiation synthesis is widely acknowledged for its numerous advantages, including rapid heating, brief reaction times, minimal side reactions, high efficiency, exceptional reaction selectivity, environmental friendliness, and suitability for morphology control [86]. In their study, Wojnarowicz et al. utilized zinc acetate as the raw material, ethylene glycol as the solvent, and employed microwave-assisted synthesis to fabricate ZnO nanoparticles. Operating at 190 °C and 600 W, varying reaction times obtained ZnO nanoparticles with particle sizes ranging from 20 to 120 nm, achieving a remarkable yield of 94–98%. Notably, the sole by-products generated throughout the entire reaction were water and esters [87].

2.3. Biological Methods

2.3.1. Microbial Synthesis

Extensive research has been conducted on the synthesis of ZnO nanoparticles through the biomineralization process, utilizing microorganisms such as bacteria or fungi. [88,89]. During biomineralization, the microorganisms uptake zinc ions from the growth medium and convert them into ZnO nanoparticles by secreting organic compounds. Enzymes synthesized or secreted by microorganisms play a crucial role in acting as nano-factories by reducing metal ions into metal nanoparticles. However, not all microbes possess the ability to synthesize nanoparticles due to variations in their metabolic processes and enzyme activities [90]. Therefore, careful selection of appropriate microbes is necessary for successful nanoparticle formation, irrespective of their enzyme activities and biochemical pathways. Typically, cultures are cultivated in a suitable culture medium, and metal precursors in the form of soluble salts are supplied. These precursors are then precipitated in suspensions comprising microorganism cells or biological compound extracts from the microbes. The synthesis process generally takes minutes to hours, contingent upon the culture conditions, and can be identified by visual changes such as the deposition of a white substance within the lower portion of the flasks or shifts in the color of the suspensions, indicating a positive transition. Numerous factors, including temperature, pH, metal precursor concentration, and reaction duration, influence the rate of production, yield, and morphologies of nanoparticles [91].

2.3.2. Plant-Mediated Synthesis

Plant-mediated synthesis is a biological method utilized for the fabrication of ZnO nanoparticles [92]. The existence of phytochemicals in plant extracts can act as potent reducing agents, enabling the transformation of metal precursors into metal nanoparticles [93]. Plant-secreted compounds, such as organic acids, can impact the dimensions and morphology of the nanoparticles [94]. Plant-mediated synthesis is not only a green and sustainable approach but also enables the functionalization of nanoparticles with biologically active compounds. Plant systems provide renewable and sustainable sources for nanoparticle synthesis and are recognized to contain various antioxidant secondary metabolites that have untapped potential for nanoparticle synthesis. Plant-based methodologies present multiple benefits compared to microbial systems, as the latter frequently involve expensive upkeep of cultures and subsequent processing, while plants offer a sustainable and renewable resource for nanoparticle synthesis [95,96].

3. Absorption and Transfer of ZnO Nanoparticles in the Plant

Nanoparticles, particularly those composed of ZnO, possess an array of diverse characteristics, including particle size, shape, and surface area, that render them highly significant in their interactions with plant tissues [97–99]. These interactions are influenced by the plant cell walls, which serve as natural barriers with pores spanning a size range of 3 to 8 nm and a thickness of 5 to 20 nm [100–102]. The size of nanoparticles is of paramount importance, as those smaller than the pore size can efficiently penetrate plant tissues. In the case of larger nanoparticles, there are two possible mechanisms through which they can enter plants. Firstly, the nanoparticles may induce the formation of new pores, which could be slightly larger than the usual ones [103–105]. Secondly, the loosening of cell walls induced by reactive oxygen species (ROS) may enable larger nanoparticles to pass through [106].

Root application and foliar application are the most commonly employed methods for delivering ZnO nanoparticles to plants [107–110]. For root application, Arruda et al. reviewed research indicating several possible mechanisms [111]. ZnO nanoparticles may decompose directly in the soil, releasing ions that can be taken up by plants. Larger ZnO nanoparticles may decompose in the soil, forming smaller nanoparticles that can be incorporated into plant tissues. Alternatively, these smaller ZnO nanoparticles may further decompose, releasing ions that can be incorporated into plant tissues [112]. Upon exposure to plant tissues, nanoparticles can penetrate the cell wall and cell membrane of the root epidermis and cortex, undergoing a series of complex events to enter the plant's vascular bundle (xylem) and move towards the stele (Figure 2B) [113–117]. A higher concentration of nanoparticle accumulation was observed in the epidermis, cortex, endodermis, cambium, and xylem compared to other plant tissues [118,119]. The uptake of these nanoparticles is believed to occur via an active transport mechanism involving various cellular processes, such as signaling, recycling, and regulation of the plasma membrane [120–122]. Meanwhile, ZnO nanoparticles can be taken up by root hair cells and transported through the endodermis and xylem vessel elements, eventually reaching the plant's underground parts [98]. For instance, ZnO nanoparticles (20 ± 5 nm) nm can initially adhere to the surface of the root cap and occupy the epidermal crypts on the root surface [119,123]. Subsequently, they penetrate the endodermis and vascular cylinder, gradually spreading into other tissues. In the elongation zone of rice roots, larger-sized ZnO nanoparticles (<50 nm) can be observed in the intercellular space between cell walls and cytoplasm of cortical cells, indicating that ZnO nanoparticles can traverse the epidermis and cortex via the apoplastic pathway [124].

In the case of foliar application, ZnO nanoparticles are sprayed onto the leaf surface and can be absorbed through the stomata and cuticle (Figure 2A). Subsequently, they are further transported within the plant through phloem sieve tubes, facilitating their whole-plant conduction [125]. Zhu et al. demonstrated that ZnO nanoparticles can penetrate the epidermis through stomata, accumulate in plastid exosomes, and then translocate to chloroplasts [65]. Before applying nanoparticles to leaves, it is essential to consider their size to prevent the blocking of stomata, which can impact transpiration [126]. Additionally, an excessively thick cuticle can act as a barrier to nanoparticle penetration [102]. To effectively absorb and utilize nanoparticles, it is necessary to overcome or adapt to these defense mechanisms in plants. Therefore, more comprehensive research is essential to elucidate the intricate mechanisms underlying the absorption and movement of ZnO nanoparticles within plant tissues [127].

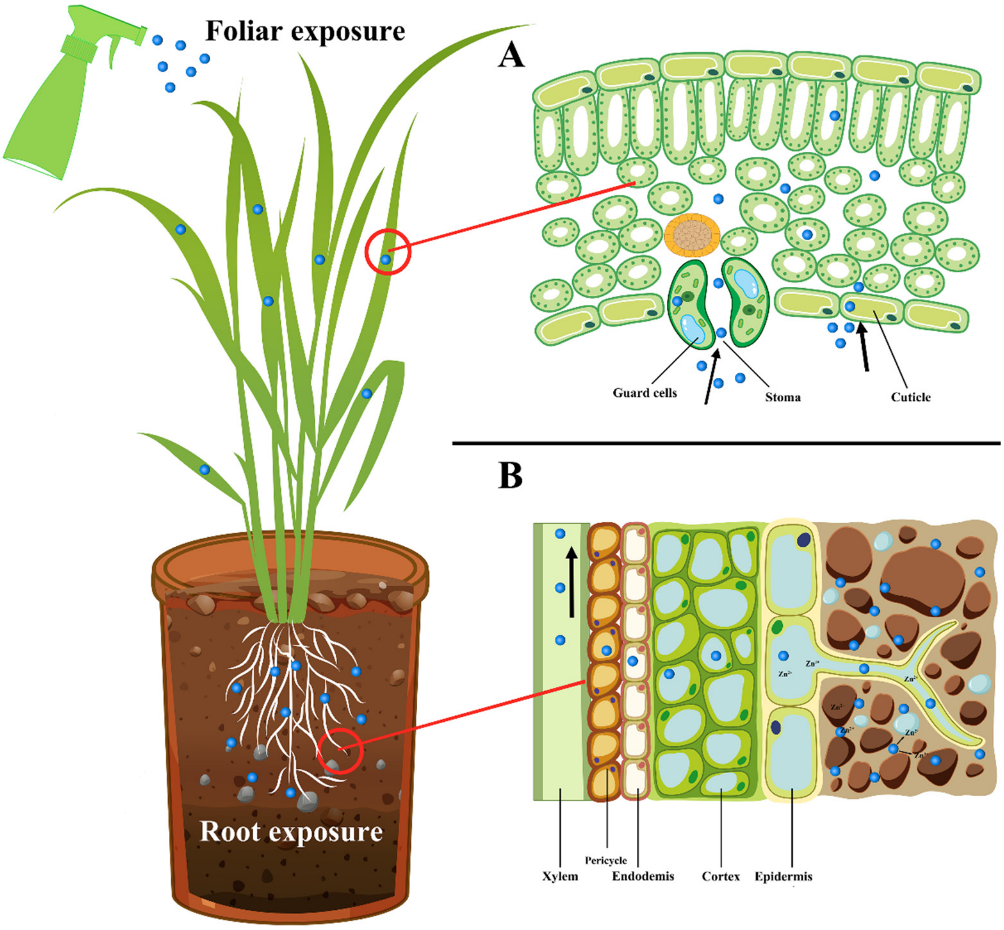

Figure 2. Mechanisms of ZnO nanoparticles uptake and transport in plant tissues. Transverse cross-section of the leaf showing entry of nanoparticles through stomata, cuticle penetration (**A**). Transverse cross-section of the root showing entry of nanoparticles through the root epidermis and cortex or biotransformation into zinc ions (**B**).

For ZnO nanoparticles, the particles undergo two primary transformations in the environment: dissolution and chemical modifications [128]. Dissolution involves the release of ions and chelation with organic matter, while chemical modifications encompass processes such as reduction, oxidation, and sulfidation [129,130]. Studies on cowpea have revealed that ZnO nanoparticles undergo rapid dissolution when introduced into the soil, with dissolved zinc primarily binding to compounds like citrate, histidine, and phytate [131]. Hernandez-Viezcas et al. have found zinc bound to oxygen in a form reminiscent of zinc-citrate, a common zinc complex found in soybean grains [132]. Regarding the secondary transformation process, zinc ions (Zn^{2+}) can attach to the sulfur present in phytochelatins, thus alleviating the effects of excessive zinc stress [133]. High concentrations of zinc were observed in the roots and shoots of rice seedlings upon exposure to ZnO nanoparticles, likely due to the ongoing biotransformation of ZnO nanoparticles into soluble salts, which are more easily assimilated by plants [124]. In summary, ZnO nanoparticles can be absorbed and stored in plants through various pathways, exerting influences on plant growth and development. Nevertheless, there are still unresolved questions concerning the specific mechanisms through which ZnO nanoparticles penetrate the cell wall and subsequently undergo transformation within plants. This underscores the necessity for further research to enhance our comprehension of these processes.

4. Impact of ZnO Nanoparticles against Biotic and Abiotic Stress

Plants are consistently exposed to challenging environmental conditions from the moment of emergence. Various unfavorable factors impede the normal growth, development, and reproduction of plants, encompassing both biotic stress (diseases, pests, and weeds) and abiotic stress (high temperature, drought, salinity, low temperature, heavy metals, etc.) [134]. These adverse elements can result in considerable losses in crop yield and quality. Nanotechnology emerges as a powerful tool to counteract the detrimental effects of both biotic and abiotic stress on plants. In particular, ZnO nanoparticles exhibit considerable promise owing to their low cost, simple preparation methods, and environmental friendliness [135]. They hold substantial potential for mitigating the impact of both biotic and abiotic stress, offering a diverse range of applications and the prospect of addressing significant challenges in plant cultivation (Figure 3).

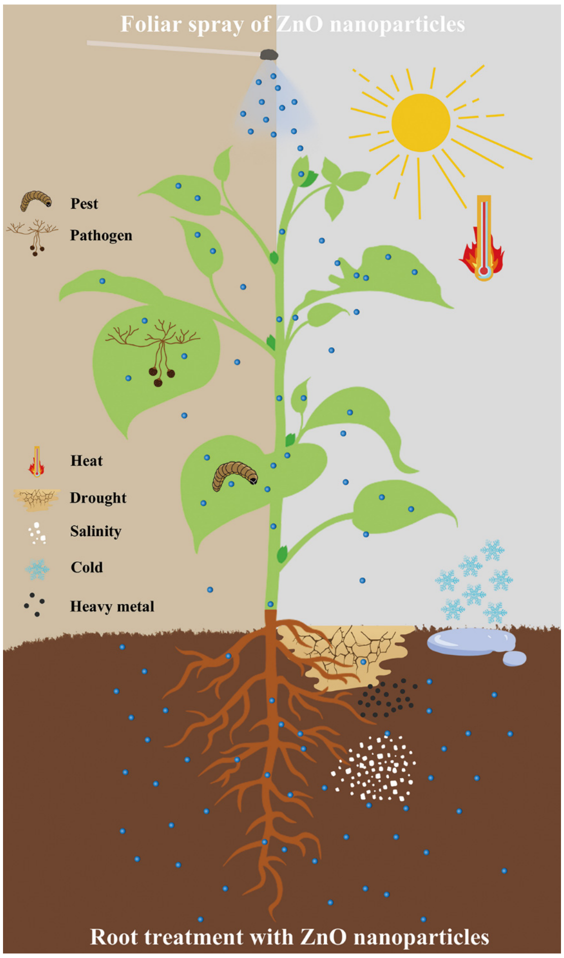

Figure 3. Effects of ZnO nanoparticles reducing abiotic and biotic stress in plants.

4.1. Impact of ZnO Nanoparticles against Biotic Stress

4.1.1. Pests

In recent years, nanotechnology has garnered considerable attention as biological pesticides for pest control to promote sustainable agriculture and delay the emergence of resistance. The fall armyworm (*Spodoptera frugiperda*) is an immensely devastating pest that inflicts substantial harm to crops globally, particularly maize and rice. Previous research has reported that the application of ZnO nanoparticles not only possesses the capacity to manage *Spodoptera frugiperda* but also can significantly reduce its abundance in ecosystems through various mechanisms, including physical distortion, diminished fertility, decreased egg deposition, and viability [136,137]. Senbill et al. demonstrated that ZnO nanoparticles can reduce the reproductive capacity and hatching rate of two-spotted spider mites, prolong their reproductive duration, and demonstrate significant insecticidal activity. More importantly, ZnO nanoparticles exhibit a high level of safety for nontarget mite species. In addition, ZnO nanoparticles can also be used for the control of stored grain pests. Malaikozhundan et al. reported that ZnO nanoparticles coated with *Bacillus thuringiensis* or *Ongamia pinnata* leaf extract exhibited significant insecticidal effects against the pulse beetle (*Callosobruchus maculatus*). Treatment with 25 μg/mL of ZnO nanoparticles not only caused a significant delay in the fecundity, hatchability, and larval and pupal development period of *Callosobruchus maculatus* but also led to complete mortality of *Callosobruchus maculatus*. Furthermore, ZnO nanoparticles can reduce the activities of midgut α-amylase, cysteine protease, α-glucosidase, and glutathione S-transferase (GST) in *Callosobruchus maculatus*, which are closely related to insect food digestion and pesticide detoxification [138,139]. In another study, ZnO nanoparticles have been proven to exhibit efficient insecticidal activity in the combined form with pesticides against insects [140]. Jameel et al. successfully synthesized nanocomposites of ZnO nanoparticles with thiacloprid. When fourth instar larvae of *Spodoptera litura* (Lepidoptera: Noctuidae) were exposed to castor leaves treated with these nanocomposites at various concentrations (ranging from 10 to 90 mg/L), their mortality rates showed a significant increase, with the highest increase reaching 27%. Moreover, pupae and adult insects exhibited physical deformities, delayed pupation, reduced reproductive capacity, and diminished fertility. Concurrently, the biochemical parameters in the larvae, such as superoxide dismutase (SOD), glutathione-S-transferase (GST), and thiobarbituric acid reactive substances (TBARS) were substantially impacted. Information in Table 1 describes the potential application of ZnO nanoparticles as insecticides. Consequently, ZnO nanoparticles have the potential to function as a viable substitute for pest control, presenting an effective alternative to conventional approaches.

Table 1. The insecticidal activity of ZnO nanoparticles against various pests.

Method of Synthesis	Particle Size (nm)	Target Pest	References
Commercial purchase	25–50 nm	*Spodoptera frugiperda*	[136]
Synthesized using *Paspalum scrobiculatum* grains extract	15–30 nm	*Tribolium castaneum*	[141]
Synthesized using *Aspergillus niger* biomass	76.2–183.8 nm	*Holotrichia* sp.	[142]
Synthesized using *Pongamia pinnata* leaf extract	21.3 nm	*Callosobruchus maculatus*	[139]
Synthesized using *Bacillus thuringiensis*	300 nm–1 μm	*Musca domestica*	[143]
Synthesized using *Azadirachta indica* leaf extract	10–70 nm	*Helicoverpa armigera*	[144]
Synthesized using *Zingiber officinale* rhizome extract	50–100 nm	*Spodoptera litura* and *Macrosiphum euphorbiae*	[145]
Synthesized using fungus *Fusarium solani* extract	8–33 nm	*Callosobruchus*	[146]
ZnO nanoparticles with a thiamethoxam nanocomposite	30 nm	*Spodoptera litura*	[140]
Synthesized using *Eucalyptus globulus* leaf extract	186.7 nm	*Rhyzopertha dominica*	[147]
Synthesized using *Spinacia oleracea* leaf extract	87.94 nm	*Corcyra cephalonica*	[148]
Synthesized using *Eriobotrya japonica* leaf extract	5–27 nm	*Sitophilus oryzae and Tribolium castaneum*	[149]
Synthesized using *Lemna minor* hydroalcoholic extract	10–20 nm	*Nezara viridula*	[150]
Synthesized using *Sargassum wightii* leaf extract	20–62 nm	*Helicoverpa armigera*	[151]

4.1.2. Plant Pathogens

The antimicrobial properties of ZnO nanoparticles have been extensively studied and well documented, and they play a vital role in the management of plant pathogenic microorganisms. Keerthana et al. reported that ZnO nanoparticles synthesized using aqueous peel extract of *Citrus medica* have excellent antimicrobial potential against plant pathogenic organisms (including *Streptomyces sannanesis*, *Bacillus subtilis*, *Pseudomonas aeruginosa*, *Salmonella enterica*, *Candida albicans*, and *Aspergillus niger*) [152]. Green tomato, as a substance rich in alkaloids and ascorbic acid, has been employed for the synthesis of ZnO nanoparticles and used for the control of bacterial leaf blight in rice. ZnO nanoparticles exhibited effective antibacterial activity against *Xanthomonas oryzae* pv. *oryzae* [153]. Soliman et al. utilized a one-pot wet synthesis technique to fabricate sub-5 nm ZnO-based nanoparticles, which showed excellent dispersibility and remarkable antibacterial activity against citrus huanglongbing (HLB) disease. The nanoparticles were capable of translocating within the phloem and xylem of citrus trees. Treatment with 400 mg/L of ZnO nanoparticles markedly decreased the severity of the disease in infected citrus plants, leading to an estimated 60% reduction in disease occurrence [154]. Qiu et al. utilized commercially acquired ZnO nanoparticles for the management of rice blast disease, observing their direct antifungal activity in inhibiting the formation of conidia and appressoria in the *Magnaporthe oryzae* [155]. Commercially purchased 30 nm zinc oxide has been proven to exhibit antifungal activity against *Sclerotinia homoeocarpa*. At a concentration of 200 μg/mL, there was a significant inhibition of mycelial growth, with an inhibition rate exceeding 60% [156]. ZnO nanoparticles, as a substitute for chemical fungicides, showed great potential in the field of preharvest preservation for strawberries. At a concentration of 5×10^{-3} M, these nanoparticles displayed a 16% inhibition rate on mycelial growth under dark conditions, while under light conditions, the inhibition rate increased to 80%. Upon application of ZnO nanoparticles in strawberry fields on sunny days, compared to the control, the incidence of gray mold disease decreased by 43%, crop yield increased by 28.5%, and the occurrence of decay during fruit storage was reduced by 8 days. The treatment was deemed safe for the plants themselves, demonstrating an efficacy equivalent to the conventional chemical fungicide fenhexamid [157]. The above studies reveal that phytogenic ZnO nanoparticles prove to be an efficient alternative to existing fungicides.

Several mechanisms have been postulated to elucidate their capacity to hinder the growth of fungi and bacteria and mitigate the intensity of infections and diseases. One proposed mechanism is the disruption of cell membranes and interference with metabolic processes in the pathogens. ZnO nanoparticles have the ability to penetrate bacterial cells and release Zn^{2+}. These ions can exert toxic effects by inhibiting active transport, bacterial metabolic processes, and enzyme functionality. The toxicity of Zn^{2+} on bacterial cellular biomolecules ultimately leads to cell death [158,159]. Another mechanism entails the production of reactive oxygen species (ROS) upon UV irradiation. ZnO nanoparticles possess the ability to generate ROS, such as superoxide anion (O^{2-}), hydroxyl ion (OH^-), and hydrogen peroxide (H_2O_2). These active species interact with cellular constituents like lipids, proteins, and DNA, resulting in cell impairment or mortality. The entry of ZnO nanoparticles into bacterial cells triggers oxidative stress and the generation of ROS, resulting in the disruption of the bacterial cell membrane and suppression of cellular proliferation [160–164]. Additionally, it has been revealed that ZnO nanoparticles can stimulate the immune system of plants and bolster their defense mechanisms against pathogens. These nanoparticles have the ability to trigger the expression of defense-related genes and promote the production of defense compounds, including phytoalexins and pathogenesis-related proteins. These substances play a crucial role in empowering plants to combat attacks from pathogens effectively [165,166]. In the case of perennial ryegrass (*Lolium perenne*), ZnO nanoparticles have been noted to be internalized in the endoderm and vascular tissues. This internalization allows for efficient delivery of the nanoparticles to the site of infection or colonization by microbial pathogens. Once internalized, ZnO nanoparticles come into direct contact with the pathogens, interacting with their cell membranes or cell walls and resulting in membrane impairment and disruption of cellular mechanisms. Moreover, the aggregation of ZnO nanoparticles and the induction of phytochemical production in the endoderm and vascular tissue create a hostile environment for pathogens, inhibiting their growth and colonization. The reinforcement of physical barriers, such as additional cell wall materials and strengthened cell walls, further hinders pathogen penetration and spread within the plant. The antimicrobial effects of ZnO nanoparticles can contribute to a reduction in the abundance of pathogenic microorganisms, ultimately leading to increased crop yield. Additionally, the nutritional value of ZnO nanoparticles, providing essential micronutrients, can contribute to supporting host defense mechanisms [167]. Another potential mechanism underlying the antimicrobial activity of ZnO nanoparticles involves their adherence to the bacterial cell membrane via electrostatic forces. Due to the positive zeta potential of ZnO nanoparticles, they can easily bind to the negatively charged bacterial cell surface. This attachment enables the infiltration of ZnO nanoparticles into the bacterial cells, leading to subsequent intracellular effects and potential disruption of cellular functions [168]. Furthermore, the accumulation of ZnO nanoparticles within bacterial cells can interfere with their metabolic functions, ultimately leading to cell death. The bactericidal mechanisms exhibited by ZnO nanoparticles offer distinct advantages over conventional therapeutic agents. Therefore, the ability of ZnO nanoparticles to disrupt bacterial metabolism and induce cell death provides alternative and potentially more effective modes of action for combating bacterial infections. Table 2 summarizes the antimicrobial activity of ZnO nanoparticles against various phytopathogenic microbes.

Table 2. The antimicrobial activity of ZnO nanoparticles against various phytopathogenic microbes.

Method of Synthesis	Particle Size (nm)	Target Pathogen	References
Synthesized using *Citrus medica* aqueous peel extract	29 nm	*Streptomyces sannanesis*, *Bacillus subtilis*, *Pseudomonas aeruginosa*, *Salmonella enterica*, *Candida albicans*, and *Aspergillus niger*	[152]
Commercial purchase	300–800 nm	*Botrytis cinerea*	[157]
Synthesized using *lycopersicon esculentum* aqueous extract	31.3–88.9 nm	*Xanthomonas oryzae* pv. *oryzae*	[153]
Synthesized using *Aegle marmelos* leaf extract	18 ± 2 nm	*Aspergillus flavus* and *Aspergillus niger*	[169]
Synthesized using one-pot wet-chemical method	2.5–5 nm	*Candidatus Liberibacter asiaticus*	[154]
Synthesized using *Thymbra spicata* plant extract	426–540 nm	*C. michiganensis* subsp. *Michiganensis*, *Pseudomonas cichorii*, *Pseudomonas syringae* pv. *Phaseolicola and Pectobacterium carotovorum* subsp. *Carotovorum*	[170]
Synthesized using *Garcinia mangostana* or *Eichhornia crassipes* extract	50–100 nm	*Xanthomonas oryzae* pv. *oryzae*, *Xanthomonas axonopodis* pv. *citri, and Ralstonia solanacearum*	[171]
Commercial purchase	30 nm	*Sclerotinia homeocarpa*	[156]
Commercial purchase	30 nm	*Magnaporthe oryzae*	[155]
Synthesized using *Azadirachta indica* leaf extract	101.6 nm	*Puccini triticina*	[172]

4.2. Impact of ZnO Nanoparticles against Abiotic Stress

4.2.1. Drought Stress

Drought, a prevalent abiotic stress, can considerably diminish crop yields by inducing prolonged water scarcity. Water, functioning as a medium for plant survival and nutrient transportation, is pivotal for the robust growth of crops. Drought stress influences diverse physiological and biochemical processes in plants, thus jeopardizing their typical survival capabilities. The quest for innovative approaches to tackle drought stress has become significantly crucial. Previous research has reported that ZnO nanoparticles can enhance drought-stress tolerance in plants, mitigating the negative impacts of drought on crop yield and biomass accumulation. Sun et al. investigated the effect of ZnO nanoparticles on drought tolerance in plants and revealed their ability to stimulate the synthesis of the endogenous hormone melatonin. Alterations in the activity of antioxidant enzymes were also noted, including malondialdehyde, catalase, and ascorbate peroxidase, thus activating the plant's internal antioxidant system [173,174]. Dimkpa et al. investigated the effects of ZnO nanoparticles on sorghum development, nutrient acquisition, and grain fortification. The results indicated that ZnO nanoparticles can enhance the absorption of essential crop nutrients (N, K, Zn), expedite plant growth and development, boost crop yield, and augment the Zn content in sorghum [175]. Studies have also revealed that ZnO nanoparticles can enhance the activities of antioxidant enzymes, related metabolites, total chlorophyll, total proteins, soluble sugars, lysine, and arginine at the physiological level in wheat. At the molecular level, they can upregulate the expression levels of drought-related genes Wdhn13, CAT1, P5CS, and DREB2, thereby mitigating the damage caused by drought to plants and improving wheat yield under drought conditions [176]. In addition, ZnO nanoparticles can regulate plant carbohydrate metabolism and enhance the activities of enzymes associated with carbohydrate synthesis and glycolytic metabolism (UDP-glucose pyrophosphorylase, phosphoglucoisomerase and cytoplasmic invertase), thus enhancing plant drought tolerance [177]. ZnO nanoparticles can also function as seed priming agents to enhance wheat's drought resistance. Rai-Kalal et al. reported that wheat seed pretreated with ZnO nanoparticles can prevent chlorophyll degradation under drought conditions, improve plant photosynthesis, and stimulate plant growth. Physiologically, wheat treated with nano zinc oxide significantly improved the efficiency of PSII primary photochemistry under drought stress, reducing the production of reactive oxygen species within the plant, thereby safeguarding the plant's photosynthetic apparatus from oxidative damage during drought stress [178].

4.2.2. Heat Stress

In recent years, the increasing levels of carbon dioxide emissions have intensified the greenhouse effect, resulting in severe high-temperature weather conditions. When temperatures exceed the optimal range for specific time periods or when plants are exposed to prolonged high-intensity light, they undergo heat stress, which adversely affects the normal growth and yield of crops. The application of ZnO nanoparticles has been observed to effectively enhance the heat stress tolerance in a few plant species (alfalfa, mungbean, chickpea, and wheat). A sufficient supply of zinc under heat stress can regulate the PSII efficiency of plants, improve water relations, increase free proline in leaves, enhance antioxidant enzyme activities (SOD, MDA, H_2O_2, and APX), and elevate the concentration of zinc ions in leaves. This can help mitigate the detrimental impacts of heat stress on plants, leading to improved plant growth and photosynthesis [179,180]. Furthermore, foliar application of ZnO nanoparticles not only increases chlorophyll content and gas exchange properties but also enhances the number of seeds per pod (SPP) and pods per plant (PPP), thus improving grain yield under heat stress [181]. Research has also indicated that heat stress primarily affects normal plant growth and physiological parameters by generating toxic reactive oxygen species. The application of zinc oxide is beneficial in enhancing plant yield and upregulating the plant's antioxidant defense system. The 20 nm ZnO nanoparticles can be absorbed and translocated in alfalfa, leading to osmolyte accumulation, further upregulating chlorophyll content and IRGA properties to maintain membrane stability. This not only aids in the reconstruction of cellular osmotic regulation but also improves plant biomass, heat injury index, and electrolyte leakage [182].

4.2.3. Salinity Stress

Salt stress, as one of the most prevalent abiotic stresses globally, is exacerbated by various factors such as climate change, irrigation water contamination, and improper fertilizer application, resulting in soil salinization and subsequent crop yield reduction. Soil salinization typically disrupts plant osmotic balance, induces ion toxicity, and diminishes water availability, leading to disturbances in plant physiological and biochemical processes and causing structural damage to plant morphology. ZnO nanoparticles can enhance plant salt tolerance by improving membrane integrity, scavenging reactive oxygen species generated by stress, regulating cell division, nutrient and water transport, and modulating levels of carbohydrates, amino acids, protein metabolism, photosynthetic pigments, and osmoregulators. Extensive research has reported the potential of ZnO nanoparticles in mitigating the adverse impacts of salinity stress on various crops, such as safflower, wheat, tomato, pea, rice, rapeseed, and so on [183–190]. Faizan et al. revealed that the application of ZnO nanoparticles on tomato plants facing salt stress resulted in significant improvements compared to untreated salt-stressed plants. These improvements were observed in various growth parameters of tomato, including shoot and root length, biomass, and leaf area, as well as enhancements in chlorophyll content and photosynthetic characteristics. Moreover, the levels of proline and protein content, along with the activities of antioxidant enzymes such as peroxidase (POD), superoxide dismutase (SOD), and catalase (CAT), were notably elevated [184]. Furthermore, the foliar administration of ZnO nanoparticles on salt-stressed rice led to a remarkable increase in the uptake of vital nutrients like phosphorus (P), potassium (K), and zinc (Zn) while concurrently reducing the absorption and adsorption of sodium ions. Additionally, the agronomic traits of rice, including plant height, panicle length, tiller number, grain weight, aboveground dry weight, and root dry weight, exhibited significant improvement. Physiological and biochemical parameters, such as chlorophyll content (91%), photosynthetic rate (113%), transpiration rate (106%), stomatal conductance (56%), and internal CO_2 (11%), were also substantially enhanced compared to the control group under salt stress [191]. Research has also explored the role of ZnO nanoparticles in regulating plant hormone signaling pathways. El-Badri et al. examined the influence of ZnO nanoparticles on the expression of genes associated with brassinosteroids and abscisic acid in canola. These findings demonstrated that ZnO nanoparticles promoted the expression of brassinosteroid-related genes (nGA20ox, BnGA3ox, and BnCPS) as well as abscisic acid-related genes (BnCYP707A1, BnCYP707A3, and BnCYP707A4), thereby enhancing the salt tolerance of the plants [192].

4.2.4. Cold Stress

Cold stress hinders the growth and reduces the yield of crops by affecting their physiological, biochemical, molecular, and metabolic processes [193–195]. Some studies have reported that ZnO nanoparticles can alleviate the harm caused by cold stress in various plants [58,196,197]. At the physiological level, foliar application of ZnO nanoparticles can alleviate the inhibitory effect of low-temperature stress on the growth of rice seedlings (including plant height, root length, and dry biomass). At the physiological level, ZnO nanoparticles can restore rice chlorophyll accumulation under cold stress, increase the activity of antioxidant enzymes (SOD, POD, CAT), and reduce intracellular H_2O_2, MDA, and proline content. At the molecular level, foliar application of ZnO nanoparticles can induce the expression of antioxidant systems (OsCu/ZnSOD1, OsCu/ZnSOD2, OsCu/ZnSOD3, OsPRX11, OsPRX65, OsPRX89, OsCATA, and OsCATB) and cold-responsive transcription factors (such as OsbZIP52, OsMYB4, OsMYB30, OsNAC5, OsWRKY76, and OsWRKY94) in young rice leaves under cold treatment. This leads to the restoration of the expression of all the mentioned genes to the control level after cold stress, effectively mitigating the harm of cold stress to plants [197]. Elsheery et al. reported the potential of ZnO nanoparticles in ameliorating the detrimental effects of cold stress in sugarcane. The study found that foliar application of ZnO nanoparticles enabled the plants to mitigate the adverse impacts of cold stress by increasing the content of photosynthetic pigments (chlorophyll and carotenoids), maintaining the maximum photochemical efficiency of PSII (F_v/Fm), maximum photo-oxidation of PSI (P_m), and photosynthetic gas exchange [196].

4.2.5. Heavy Metal Stress

The contamination of terrestrial soil by heavy metals (arsenic (As), Pb (plumbum), Cd (cadmium), mercury (Hg), and chromium (Cr)) has become a significant global environmental issue, adversely affecting ecological integrity, soil quality, and agricultural productivity [198–200]. The resulting food security concerns pose a substantial risk to ecosystems and human health. Consequently, the remediation or immobilization of toxic heavy metals in contaminated farmlands has become an urgent and critical issue [201,202]. Li et al. reported that the treatment of rice seeds with ZnO nanoparticles affects the physiological, biochemical, and molecular characteristics of plants under cadmium stress. At the physiological level, ZnO nanoparticles can increase plant fresh weight and root crown length. At the biochemical level, ZnO nanoparticles can enhance the activity of antioxidant enzymes (SOD, POD) in rice, as well as the content of metallothioneins (ROS scavengers) and chlorophyll (chlorophyll a, chlorophyll b, a + b, and carotenoids). At the metabolic level, ZnO nanoparticles primarily alleviate the harm of cadmium to rice by affecting the metabolism of amino acids (alanine, aspartate, and glutamate), taurine, subtaurine, and phenylpropanoid biosynthesis. Additionally, the application of zinc oxide can effectively increase the activity of α and β-amylase (in seeds) and total amylase (in seedlings), which may be beneficial for seed germination [203]. In mung bean plants, ZnO nanoparticles reduce the harm of cadmium to plants by regulating cellular homeostasis. ZnO nanoparticles enhance the activity of ROS scavenging enzymes (such as CAT, APX, GR, glutathione peroxidase (GPX), and guaiacol peroxidase (GPOX)) to reduce plant toxicity caused by cadmium stress. ZnO nanoparticles also regulate redox enzymes (such as NADPH-dependent thioredoxin reductase (NTR), ferredoxin (Fd), ferredoxin-NADP reductase (FNR), and thioredoxin (Trx)), effectively improving plant growth under cadmium stress [203]. ZnO nanoparticles exhibit a high affinity for heavy metals, enabling them to bind and immobilize these toxic substances in the soil. This capability effectively mitigates the adverse effects of heavy metal pollution on plant growth and overall soil quality. At the molecular level, the expression levels of OsNRAMP1, OsNRAMP4, and OsNRAMP5 genes involved in cadmium transport in rice under cadmium stress decreased significantly with treatment using zinc oxide nanomaterials, while the expression of the OsZIP1 gene related to zinc transport exhibited upregulation. This suggests that zinc oxide nanomaterials can alleviate cadmium toxicity in rice by enhancing the expression levels of resistance-related genes [204]. Similarly, effects have been observed in soils contaminated with As, Pb, Hg, and Cr, where the application of ZnO nanoparticles has been found to promote the development of antioxidant defense systems in plants to counter the oxidative damage caused by heavy metals. Simultaneously, it mitigates metal toxicity in various plants, leading to an improvement in plant growth parameters (Table 3).

Table 3. Examples of ZnO nanoparticle applications to confer heavy metal stress tolerance in different plant species.

Heavy Metal	Plant	Alteration in Plant Parameters	References
As	*Oryza sativa*	Enhanced plant growth parameters, gas exchange parameters, chlorophyll content (SPAD value), fluorescence efficiency (Fv/m), and antioxidant enzyme activities	[205]
As and Hg	*Pleioblastus pygmaeus*	Increased antioxidant activity, proline content, glycine betaine content, tyrosine ammonia-lyase activity, phenylalanine ammonia-lyase activity, chlorophyll indices, and plant biomass	[206]
As	*Brassica juncea*	Enhanced plant growth, photosynthesis-related parameters, protein content, carbonic anhydrase, nitrate reductase, and RuBisCO	[207]

Table 3. *Cont.*

Heavy Metal	Plant	Alteration in Plant Parameters	References
As	*Vigna mungo*	Enhanced seed germination rate, germination rate, seedling vigor, plant biomass, shoot length, root length, antioxidant enzymes activity (SOD, CAT, POX, APX), and osmoregulators	[208]
Pb	*Persicaria hydropiper*	Enhanced plant growth, chlorophyll content, carotenoid content, free proline, phenolics, flavonoids, and antioxidative enzymes (CAT, GR, GST, SOD)	[209]
Pb	*Triticum aestivum*	Increased plant height, fresh weight, dry weight, total chlorophyll content, proline content, SOD content, CAT content, H_2O_2 content, and lipid peroxidation content	[210]
Pb	*Solanum lycopersicum*	Increased germination rate, seedling vigor index, relative water content, chlorophyll content, protein, sugars, nitrate reductase, SOD, POD, and APX activity	[211]
Cd	*Perilla frutescens*	Increased SOD, POD, nutrient elements contents, organic acids (citric acid, malic acid and maleic acid), and amino acids (arginine, glutamate and phenylalanine), root and leaf dry weight	[212]
Cd	*Oryza sativa*	Increased plant height, biomass, photosynthetic attributes, oxidative stress (MDA, H_2O_2), antioxidant enzymes (SOD, POD, CAT, GSH. APX)	[204,213]
Cd and Pb	*Gossypium hirsutum* and *Leucaena leucocephala*	Enhanced plant growth and biomass, level photosynthetic pigments, MDA, protein content, and oxidative enzymes (POD, SOD, POX, and APX)	[214,215]
Cd	*Portulaca oleracea*	Improved the activity of antioxidant enzymes, the glyoxalase system, photosynthetic pigments, and the glyoxalase cycle	[216]
Cd	*Triticum aestivum*	Increased the growth of wheat, chlorophyll content, zinc content, POD, and SOD	[217]
Cd	*Oryza sativa*	Enhanced mean root fresh weight, root-shoot length, SOD, POD, metallothionein content, α-amylase, and total amylase activity	[203]
Cd	*Lycopersicon esculentum*	Enhanced plant height, fresh and dry weight of plant, leaf area, SPAD chlorophyll, photosynthetic attributes, protein content, and activities of nitrate reductase and carbonic anhydrase	[218]
Cr	*Oryza sativa*	Increased biomass accumulation, antioxidants (SOD, CAT, POD), nutrient acquisition (zinc, ferrum), and brassinosteroids	[219]
Cr	*Glycine max*	Enhanced biomass, antioxidant system, altered enzymatic (SOD, POD, CAT) and non-enzymatic antioxidant activities (GR, GSH, GSSH), and nutrient uptake	[220]
Cr	*Zea mays*	Increased fresh shoot weight, fresh root weight, shoot length, root length, chlorophyll content, total soluble sugars, proline content, POD, CAT, and APX enzyme activities	[221,222]

5. Conclusions

Nanotechnology offers a more cost-effective, efficient, and environmentally friendly approach to bolstering agricultural practices. This review outlines diverse methods for preparing ZnO nanoparticles and examines their absorption, translocation, and conduction mechanisms within plant systems. Furthermore, it explores the positive impact of ZnO nanoparticles in mitigating both biotic and abiotic stress on plants. At the physiological level, ZnO nanoparticles can enhance the agronomic traits of plants under stressful conditions, promoting increased plant growth and biomass. At the biochemical level, ZnO nanoparticles exhibit the ability to boost the activity of plant antioxidant enzymes, scavenge ROS generated under stress, regulate osmotic balance, and maintain cellular homeostasis, thereby alleviating the impact of both biotic and abiotic stress on plants. On the molecular level, ZnO nanoparticles can influence plant hormone signaling pathways, modulate stress-responsive genes, and enhance plant stress tolerance. Hence, the utilization of ZnO nanoparticles is anticipated to offer a novel, environmentally friendly, and cost-effective method to enhance agricultural productivity while mitigating the impact of various stressors on plants.

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