Zinc Oxide Nanoparticles in Enhancing Plant Stress Resistance

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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.

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

1. Introduction

With the continuous changes in the global climate and the increasing impact of human activities, agriculture is facing unprecedented challenges $^{[1][2][3][4]}$. 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 $^{[2][8][9][10][11]}$. 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 $^{[12][13][14][15][16][17][18]}$.

In recent years, the emergence of nanotechnology has opened up new possibilities for addressing these challenges [19][20] [21][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].

Biotic and abiotic stresses stand as two primary limiting factors for crop growth and yield in agricultural production ^{[26][27]} ^{[28][29][30]}. Biotic stresses encompass various invasions by viruses, bacteria, fungi, and pests, posing significant threats to crop growth ^{[31][32][33][34][35]}. Simultaneously, abiotic stresses primarily arise from environmental factors such as drought, high temperatures, low temperatures, salinity, and others, severely impacting plant growth and yield ^{[36][37][38][39][40]}. Recent research has underscored the significant potential of ZnO nanoparticles in mitigating biotic and abiotic stress in agriculture ^{[41][42][43][44]}. These nanoparticles have displayed the capacity to hinder the growth of different pathogenic microorganisms, such as bacteria, fungi, pests, and viruses ^{[45][46][47][48][49][50][51]}.

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 ^[52].

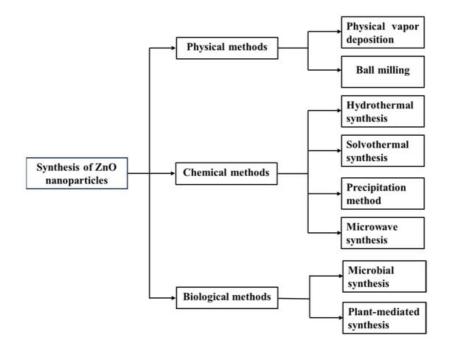


Figure 1. Various strategies for the fabrication of ZnO nanoparticles.

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 ^{[53][54][55]}. 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 ^{[56][57][58]}. 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 ^{[59][60][61]}. Secondly, the loosening of cell walls induced by reactive oxygen species (ROS) may enable larger nanoparticles to pass through ^[62].

Root application and foliar application are the most commonly employed methods for delivering ZnO nanoparticles to plants ^{[63][64][65][66]}. For root application, Arruda et al. reviewed research indicating several possible mechanisms ^[67]. 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 ^[68]. 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 2**) ^{[69][70][71][72][73]}.

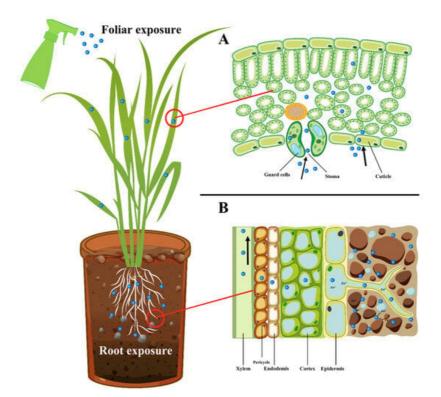


Figure 2. Mechanisms of ZnO nanoparticles uptake and transport in plant tissues. Transverse cross-section of the leaf showing entry of nanoparticles through stomata, cuticle penetration (**A**). Transverse cross-section of the root showing entry of nanoparticles through the root epidermis and cortex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

In the case of foliar application, ZnO nanoparticles are sprayed onto the leaf surface and can be absorbed through the stomata and cuticle (**Figure 2**A). Subsequently, they are further transported within the plant through phloem sieve tubes, facilitating their whole-plant conduction $\frac{74}{2}$.

For ZnO nanoparticles, the particles undergo two primary transformations in the environment: dissolution and chemical modifications ^[75]. Dissolution involves the release of ions and chelation with organic matter, while chemical modifications encompass processes such as reduction, oxidation, and sulfidation ^{[76][77]}.

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.) ^[78]. 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 ^[79]. 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**).

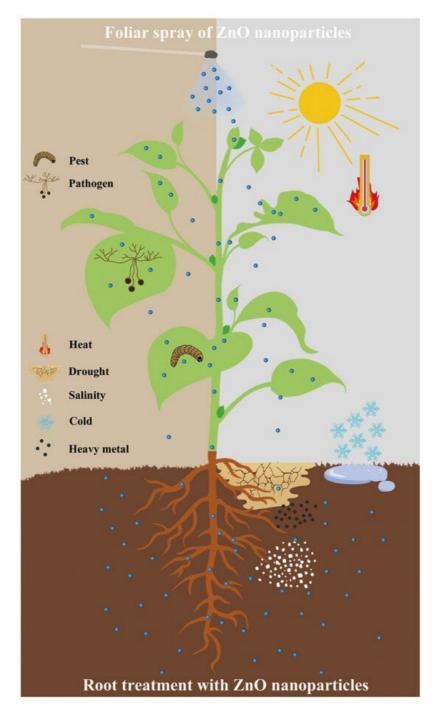


Figure 3. Effects of ZnO nanoparticles reducing abiotic and biotic stress in plants.

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 ^{[80][81]}.

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*) ^[82]. 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* ^[83]. 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 ^[84].

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 ^{[85][86]}. 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 ^{[87][88][89][90][91]}.

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 ^{[92][93]}.

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 improve plant growth and photosynthesis ^{[94][95]}.

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 [96][97][98][99][100][101][102][103].

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 [104][105][106]. Some studies have reported that ZnO nanoparticles can alleviate the harm caused by cold stress in various plants [107][108][109]. 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 H₂O₂, 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 ^[109].

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 [110][111][112]. 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 [113][114]. 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 [115]. 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 $\frac{115}{1}$. 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 guality. 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 resistancerelated genes [116].

5. Conclusions

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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