

Role of Metal-Based Nanoparticles in *Capsicum* spp. Plants

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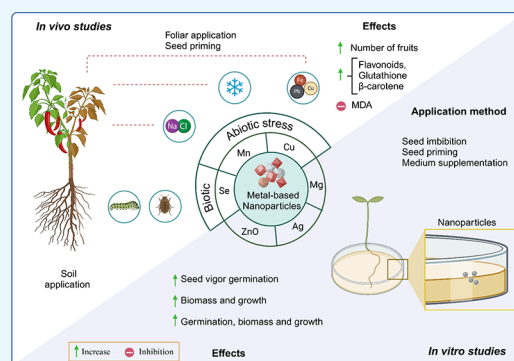
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ABSTRACT: Agriculture is a core activity in human civilization, constantly facing challenges with the main objective of increasing crop production; to solve this, different strategies and technologies have been used. Currently, metal-based nanoparticles (MNPs) have great potential to be used as agricultural inputs to mitigate the negative effects on crops caused by different stresses. However, studies about their impact on plants and agroecosystems require a comprehensive understanding of their effects. Chili pepper (*Capsicum* spp.) is a crop of global economic importance that could benefit from the use of MNPs in order to increase its production. The effects of MNPs depend on factors such as their composition, morphology, size, concentration, and application method. Both *in vitro* and greenhouse studies have demonstrated improvements in plant growth, response to abiotic stresses, and the induction of resistance to different pathogens. However, results vary considerably from one study to another, probably due to heterogeneity in synthesis, characterization, and application methods. This review examines recent findings about the effects of MNPs on chili pepper crops, focusing on growth, development, bioaccumulation, and response to biotic and abiotic stresses.



1. INTRODUCTION

Nowadays, metal-based nanoparticles (MNPs) are being used in various biological systems due to their physical, chemical, and biological properties.¹ Although MNPs can lead to developments that allow current technologies to evolve, they can also have negative side effects on the environment and living beings. However, there is still no concrete evidence about the possible consequences that may occur shortly due to the indiscriminate use of this type of particle. When current technologies become obsolete and the components are discarded, they will have a worrying impact on the environment.² Recently, concerns have been raised about the impact of everyday nanotechnologies, such as those found in pharmaceuticals, cosmetics, and fertilizers, which, at the end of their useful life, could release nanoparticles (NPs) that contaminate soils and aquifers.³ Plants are being exposed to MNPs, either in a targeted and planned way or indirectly, by encountering NPs debris or the uncontrolled disposition of products that nowadays carry a load of these nanomaterials. The potential effects on plant crops depend on the type of metal, composition, morphology, size, and concentration of the MNPs. Besides the nanoparticles itself, the method used for the delivery of the MNPs, the stage of plant development, and the time of exposure to the nanoparticles are in direct relation

to the effects observed in plants. Chili pepper (*Capsicum* spp.) is one of the most important economic crops in several countries where a culture related to the consumption of spicy foods exists. According to the data of the Food and Agricultural Organization of the United Nations, FAOSTAT (2022), countries such as China, Mexico, Turkey, and Indonesia produce around 18 million tons of chili peppers annually. Among the species in the genus, *Capsicum annuum* L. is the most important, including bell, poblano, cayenne, pimiento (including those used to make paprika), jalapeño, serrano, and a variety of other chili species.⁴

There is relatively little information to date on the effects (positive or negative) of nanoparticle supplementation on chili pepper crops; there have been some studies on phytopathogenic control and some about the mitigation of abiotic stress. Nevertheless, the lack of uniformity in the application of nanoparticles, the multiple morphologies of MNPs, and the

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Table 1. Effect of Metal-Based Nanoparticles on *Capsicum* spp. Plants^a

nanoparticle	assay	treatment	effect	ref
AgNPs (12.9 ± 9.1 nm)	<i>in vivo</i>	This study tested AgNPs and AgNO ₃ solutions in the range of 0.01 to 1 mg/L.	Both AgNPs and Ag ⁺ ions significantly increased the total content of Ag ⁺ in pepper tissues and decreased both plant height and biomass.	5
ZnONPs (12–24 nm)	<i>in vitro</i>	Germination of <i>C. annuum</i> L. was determined using filter paper imbibed with 0 to 500 ppm ZnONPs.	The seed vigor germination increased 123.50%, 129.40%, and 94.17% by treatment with ZnONPs suspensions at 100, 200, and 500 ppm, respectively.	14
ZnONPs (12–24 nm)	<i>in vivo</i>	Foliar applications of Zn at 1000 and 2000 mg/L concentrations of ZnSO ₄ and ZnONPs.	At a concentration of 1000 mg/L, ZnONPs positively affected plant height, stem diameter, and chlorophyll content and increased fruit yield and biomass accumulation.	6
Al ₂ O ₃ (40 nm) and ZnONPs (40–100 nm)	<i>in vitro</i>	Seeds were placed in damp filter paper moistened with 5 mL of sterile one-half-MS medium (pH 6.0) containing 0, 0.5, 2.5, and 5 mM Al ₂ O ₃ or ZnONPs.	None of the treatments showed statistical differences compared to the control group seeds.	8
MgONPs (20 nm, polyhedral shape)	<i>in vitro</i>	Seeds were grown in the Murashige and Skoog (MS) medium supplemented with 75, 225, and 675 mg/L NPs	The treatment increased biomass accumulation in shoots and roots.	13
AgNPs (48 nm, spherical shape)	<i>in vivo</i>	<i>C. annuum</i> plants were fertilized with wastewater and regular water and sprinkled with 80 mg/L AgNPs.	The treatment increased biomass accumulation in shoots and roots. The most significant improvements were recorded using normal water for fertigation.	29
CS-ZnO (10–50 nm) and ZnONPs (10–30 nm) (spherical shape)	<i>in vitro</i>	Seeds were cultured in a hormone-free MS medium supplemented with 1 mg/L ZnONPs or nanocomposite or without supplementation for control group.	Supplementation with the CS-ZnONPs drastically increased stem length and total leaf area compared to the control and bare ZnONPs groups.	15
	<i>in vitro</i>	In a micropropagation experiment, explants (shoot tips with two leaves) were cultured in an MS medium containing hormones ZnONPs (0 and 1 mg/L) or CS-ZnONPs.	The supplements significantly increased stem fresh mass, total leaf area, total leaf fresh mass, and root fresh mass, particularly the CD-ZnONPs.	
Ag (100 nm), Cu (150 nm), and Ag-CuNPs (100 nm) (spherical form)	<i>in vivo</i>	Seeds were primed with Ag, Cu, and Cu-AgNPs for 24 h (at 0, 1, 10, and 20 ppm). They were then sown and grown for 45 days.	The seedling showed maximum biomass and growth with primed nanoparticles at 20 ppm.	11
CS-Cu (150 nm) and CS-AgNPs (100 nm) (spherical form)	<i>in vitro</i>	Seeds were primed with varying concentrations of nanoparticles (0, 1, 10, and 20 ppm).	The seedling showed maximum biomass and growth with primed nanoparticles at 20 ppm.	30
Fe ₃ O ₄ and CS-Fe ₃ O ₄ NPs (3–22 nm)	<i>in vitro</i>	Two different culture methods using Petri dishes and paper towels were performed in concentrations of 0, 200, 400, 800, and 1600 mg/kg.	In both cases, 200 and 400 mg/kg concentrations significantly impacted seed germination and seedling growth.	12
TiO ₂ NPs (4–8 nm)	<i>in vivo</i>	Sweet pepper seedlings were exposed to TiO ₂ NPs via foliar (2.5% suspension) and root (0.5% suspension) methods.	Foliar application caused a higher accumulation of Ti in leaves than stems, while root exposure led to a higher increase of Ti content in stems than in leaves.	31
ZnO (35–40 nm, spherical), TiO ₂ (100 nm, cylindrical), and AgNPs (85 nm, needle morphology)	<i>in vivo</i>	Chili seeds were dry dressed in bulk and nanomaterials each at 750, 1000, and 1250 mg/kg.	Chili seeds invigorated with ZnO nanoparticles at 1000 mg/kg enhanced the germination and seedling vigor in aged seeds.	10
ZnO (nanorods) and TiO ₂ NPs (43 nm)	<i>in vivo</i>	Seeds were coated with the nanomaterials at 0, 50, 100, and 150 mg/L.	Maximum transplant lengths and fresh and dry weight were recorded at the level of 100 mg/L.	32
ZnONPs	<i>in vitro</i>	<i>C. chinense</i> seeds were exposed to 100, 200, 300, 400, and 500 mg/L.	Germination and fresh biomass highest levels were observed at 400 mg/L.	33
CuONPs	<i>in vivo</i>	Seedlings were transplanted to agricultural soil with 0, 125, 250, and 500 mg/kg CuONPs, bulk CuO, and ionic copper (CuCl ₂).	None of the treatments significantly affected stem elongation, plant dry biomass, or foliar area.	19
green synthesized AgNPs (25 and 45 nm, spherical polydisperse form)	<i>in vivo</i>	Seeds were immersed in AgNPs at 0, 10, 30, and 50 ppm for 24 hours at 25 °C.	Green synthesized AgNPs improved seed germination, plant growth, and photosynthesis and chlorophyll content.	34
Ag (10–20 nm), Cu (66–86 nm), and Cu-AgNPs (35–50 nm)	<i>in vitro</i>	Seeds were grown in MS medium supplemented with NPs at 1, 10, 25, and 50 ppm.	Priming with metal nanoparticles improved <i>in vitro</i> and <i>ex vitro</i> germination, photosynthesis and chlorophyll content, as well as antioxidant enzyme activity, favoring growth.	35
	<i>in vitro</i>	Seeds were primed in the same concentrations of NPs for 24 h. Then, MS medium was used to inoculate the seeds.		
	<i>ex vitro</i>	Seeds primed with 0, 10, 30, and 50 ppm NPs were cultivated in a greenhouse.		

^aNPs: nanoparticles; NCs: nanocomposites.

variety of concentrations used in those studies make this review seek to systematically organize the latest findings on the impact of MNPs on this crop.

2. APPLICATION EFFECT ON GROWTH AND DEVELOPMENT

Several experiments have been conducted in which chili pepper cultures are exposed to metal nanoparticles both *in vivo* and *in vitro*. These studies concluded that the contact method between nanoparticles and plants produces specific effects. In other words, the way in which the nanoparticles are prepared and applied to the crop (the treatment) directly influences their impact on the plants. Therefore, it is not sufficient to only discuss the types, concentrations, or shapes of the MNPs; it is also essential to specify how the nanoparticles were incorporated whether directly into the substrate,⁵ through foliar exposure,^{6,7} by fortifying the culture media,^{8,9} or by embedding them into the seeds.¹⁰ This detail is necessary to relate the potential effects on the crops.

2.1. In Vitro Treatment. *In vitro* studies are characterized by short-lapse evaluations, which may include adding the MNPs to the seed or during germination and seedling growth. They generally serve as background for subsequent field evaluation. They have the advantage of being quick and less expensive than *in vivo* studies. However, they do not reliably reproduce the crop growth conditions or long-term effects on plants. Numerous *in vitro* studies have suggested primarily positive effects of MNPs on the *Capsicum* crop at early growth stages.^{7,11–14} For example, adding zinc oxide nanoparticles (ZnONPs) to *Capsicum* seedlings increased root and seedling biomass, stem length, and total leaf area.¹⁴ On the other hand, it is not always easy to predict what concentration of MNPs would be beneficial for the plant; for instance, similar effects on biomass accumulation, increment of stem length, and leaf area were reported either at “low” nanoparticle concentrations (if ZnO,¹⁴ aluminum oxide (Al₂O₃),⁸ and magnesium oxide (MgO)¹³ nanoparticles were used) or at high nanoparticle concentrations (if chitosan/ZnO nanocomposite,¹⁵ iron oxide (Fe₃O₄), and chitosan-coated Fe₃O₄NPs¹² were applied). For specific details, see Table 1. Overall, the *in vitro* results suggest potential for the application of nanoparticles to improve the propagation and early growth of *Capsicum* spp. plants.

2.2. In Vivo Treatment. *In vivo* treatment is characterized by experiments carried out in more advanced plant stages to evaluate the use of nanoparticles as nanofertilizers, nanopesticides, nanosensors, or nanocarriers.¹⁶ Under *in vivo* conditions, nanoparticles also exhibit remarkable effects on the growth, pest resistance, and disease response of *Capsicum* spp. plants. Silver nanoparticles (AgNPs) increase biomass accumulation at 20 ppm, while copper nanoparticles enhance growth and biomass at a concentration of 20 ppm;¹¹ foliar application of titanium oxide nanoparticles (TiO₂NPs) at 150 µg/mL helped significantly decrease the concentration of tobacco mosaic virus in chili pepper leaves.¹⁷

2.3. Effect on Growth and Development. In chili crops, the germination percentage and germination time are critical parameters for the viability and yield of newly germinated plants. Typically, phytochemicals that promote germination are added to the seeds.¹⁸ However, some studies have demonstrated that nanoparticles can produce similar effects on germination as these phytochemicals. For example, Dileep Kumar et al. studied ZnO, TiO₂, and AgNPs at concentrations between 750 and 1250 mg/kg to improve the seed quality of

aged chili seeds. Using the dry-dressing method, they only observed favorable results with ZnONPs at 1000 mg/kg.¹⁰ On the other hand, foliar application of ZnONPs can generate higher yields in *C. annuum* L. crops, increasing the number of fruits per plant and the size and biomass of harvested chili peppers.⁷ Nevertheless, some studies have detected no appreciable effects when MNPs are applied. Rawat et al. explored the impact of different copper oxide nanoparticles (CuONPs) doses on the *in vivo* growth of bell pepper plants grown in enriched agricultural soils. The results indicated that, under their conditions, no significant effects on plant growth and development were observed, suggesting that the interaction between nanoparticles and the biological system may depend on multiple factors specific to the experimental environment.¹⁹ Otherwise, some researchers have reported negative effects of MNPs in the chili crop, such as reduction in plant size, root number, and biomass.⁵ An interesting example of how adverse effects are directly related to the concentration of MNPs applied can be observed in habanero pepper (*C. chinense*), as reported by García-López et al. When a foliar application of 2000 mg/L ZnONPs was used, plant size and chlorophyll content were diminished. However, when lower concentrations of MNPs were applied, the fruits harvested at the end of the growing cycle showed increased biomass compared to the control group.⁶ It is currently known that nanoparticles do not have a generalized effect on the chili pepper crop. Table 1 compiles the effects of different nanoparticles on the genus *Capsicum*, considering the application format, concentration, and nanoparticle type. A general trend toward increased germination rate, biomass accumulation, and plant size is observed in most of the cases studied.

3. UPTAKE, BIOACCUMULATION, AND TOXICITY

3.1. Uptake. NPs can enter the plant system through various routes, such as the root hairs, stomata, porosity in the leaf cuticle, or even cracks on the surface of the leaves.²⁰ Once inside the plant, NPs can move through the plant system by diffusion, bulk flow, and phloem loading. The transport of NPs is influenced by the size and shape of the NPs, their surface properties, the pH of the solution, and the presence of other ions or compounds in the solution.^{21,22}

When NPs are in contact or immersed within the soil, transport is mainly mediated on the root surface. The root epidermal cells are semipermeable, with pore sizes typically between 3 and 8 nm. Cell walls act as a selective barrier, allowing essential small molecules to enter while blocking larger particles. This characteristic plays a significant role in the plant's ability to absorb nutrients and water while protecting against potentially harmful large particles and pathogens. Besides, root hairs can release chemicals, such as mucus or organic acids, to help the adsorption of NPs. It is also possible that the negative charges of the root surface mediate the adsorption of positively charged NPs.²³ Same-way formation of lateral roots can create a new adsorption interface, thus allowing NPs to enter the root column. Finally, some NPs can enter and destroy the plasma membrane and induce the formation of new pores in the epidermal cell wall to facilitate the entry of NPs.^{21,24}

The composition and function of the plant leaf surface are similar to those of the plant root epidermis. When NPs are exposed in this area, uptake is accomplished by the cuticle or the stomata on the leaf surface.^{21,25} The cuticle of the leaf

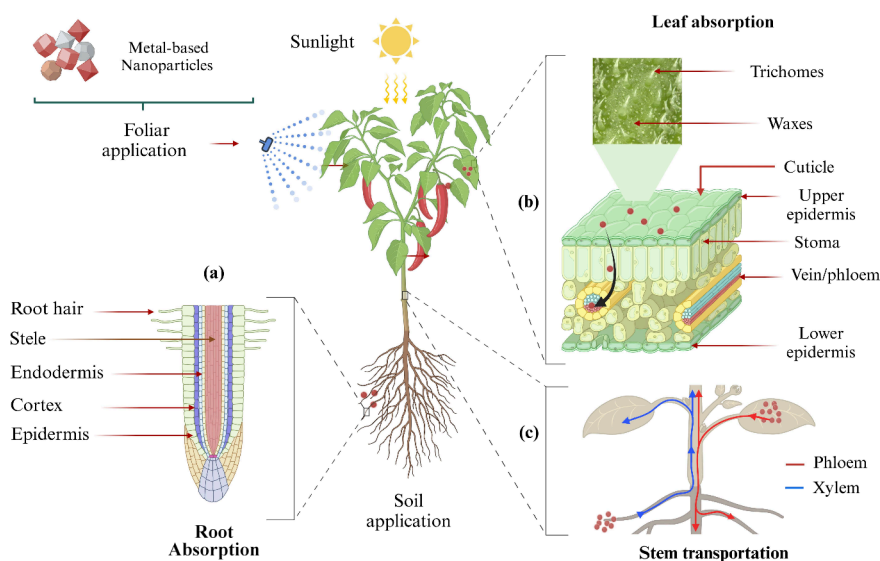


Figure 1. Uptake, bioaccumulation, and translocation of nanoparticles (NPs) in plant systems, highlighting key pathways through (a) root uptake, (b) leaf surface uptake, and (c) xylem and phloem transport in the stem. Created with [BioRender.com](https://www.bio-render.com/).

epidermis is composed mainly of wax, cutin, and pectin, and one of its functions is to form a protective barrier to prevent external agents from entering the cuticle. However, leaves have two types of channels on the surface of the waxy stratum corneum: hydrophilic and lipophilic, with diameters varying between 0.6 and 4.8 nm.^{21,26,27} This allows hydrophilic NPs smaller than 4.8 nm in diameter to pass through hydrophilic channels.²¹

Although NPs can enter through the cuticle, the main route of leaf uptake is through the stomata. Since the epidermis restricts passage due to its small pores, particles larger than 20 nm are limited to passing through the cell wall. However, the possibility of absorption increases in species with stomata on both leaf surfaces. Young leaves with a thinner wax layer can absorb nutrients and NPs more. NPs in aerosol form can penetrate stomata, although at a rate lower than that of suspensions. Small particles (10–50 nm) enter mainly through the symplast, while larger particles (50–200 nm) use the apoplast.^{16,21} Studies have detected intact NPs in tissues such as the mesophyll and vascular system and have shown their transport to new roots and leaves.^{21,28} Uptake of NPs may involve endocytosis, protein complexes, or redox reactions that alter their morphology.¹⁶

3.2. Bioaccumulation. Bioaccumulation refers to the gradual buildup of substances, such as nanoparticles (NPs), within an organism, often leading to concentrations that exceed those found in the surrounding environment. In plants, this process can raise significant concerns, as the accumulation of NPs may impact plant health and, consequently, the safety of the food supply for consumers. As NPs are absorbed by plants, a second step is necessary: their translocation through plant vascular systems, including the xylem and phloem, which could potentially lead to aerial parts, such as stems, leaves, flowers, and fruits. Xylem plays a pivotal role in NPs translocation, and plants exhibit a variety of xylem structures (see [Figure 1](#)).

Transport and accumulation of NPs are complex processes influenced by various physicochemical modifications among plant species such as cell wall pore size and hydraulic conductivity. Depending on the concentration and behavior,

some NPs could induce morphological and anatomical changes in plants.^{36–38} Some commonly studied metal oxide NPs, such as CuO and TiO₂NPs, are stable and remain inside the plant without undergoing any structural change.³⁹ Meanwhile, metal oxide NPs such as ZnO, NiO₂, CeO₂, La₂O₃, and Yb₂O₃ are unstable and competent to complex with organic compounds and reactive oxygen species (ROS).⁴⁰ The ability of NPs to enter plant systems and potentially induce oxidative stress by generating ROS makes understanding bioaccumulation critical for assessing environmental and health risks. When NPs encounter terrestrial plants, they predominantly adhere and aggregate near the roots or root surface;^{39,40} many biotic or abiotic factors modify their properties, such as their aggregation state and surface chemistry.^{41,42}

Despite the significant findings in the field, the influence of plant species and environmental factors on NPs uptake, translocation, and accumulation mechanisms remains a largely unexplored area. Understanding these influences is crucial, as the pathways through which plants absorb NPs are diverse, and their selection depends on many factors. While upward NPs translocation via the xylem and downward movement through the phloem have been extensively studied, there is a pressing need for more research on the mechanisms of NPs movement across cell membranes and other barriers, including channels and transporters. This significant gap in our current knowledge presents a compelling opportunity for future investigation.^{43,44}

For plants of the genus *Capsicum*, the transport pathways of nanoparticles have not been described yet, but in recent research, it has been found that by adding CuONPs to the growing soil, it is possible to detect the presence of copper in root, leaf, and fruit.¹⁹ By adding TiO₂NPs, titanium was detected in the stem and leaf.³¹ By impregnating seeds with Fe₃O₄NPs, iron was found in the root;¹² and by adding AgNPs to irrigation water, silver was identified in the root and leaves.⁵

3.3. Toxicity. Bioaccumulation of NPs in plants raises significant concerns about their adverse effects on plant health. Numerous studies have elucidated the interactions between NPs and plant species and their effects on plant tissues. These reports encompass nanostructure accumulation, speciation, and the overall impact on plants. In addition to documenting

the beneficial effects of NPs, some research also highlights their phytotoxic potential.⁴⁵ Phytotoxicity associated with NPs manifests in a range of symptoms, including diminished photosynthetic activity, generation of ROS, DNA damage, obstruction of apoplastic pathways, and, consequently, impaired nutrient uptake and hydraulic transfer.^{45–49} Furthermore, NPs–plant interactions can modify gene expression and induce genotoxic effects.^{43,44}

The impact of NPs on plants is related to their size, concentration, and application method.³⁹ So far, some reports indicate that metal-based nanoparticles applied to chili pepper plants have shown a toxic impact. For instance, in *C. annuum* plants treated with SeNPs, a restrictive development of organs in the apical meristem was observed, resulting in the arrest or reduction of plant development. Additionally, the authors reported changes in DNA methylation patterns, overexpression of transcription factors related to defense against abiotic stress sources, and alteration of different enzymes, like catalase and peroxidase (involved in antioxidant defense) and nitrate reductase (changing of nitrogen assimilation processes).⁵⁰ Similar results were observed when ZnONPs and Al₂O₃NPs were applied to chili peppers; both nanoparticles downregulate the dehydrin gene transcription in stems and roots, potentially weakening the plant's resilience to abiotic stress. Besides, when ZnONPs were administered at concentrations exceeding 0.5 mM, aquaporin genes in root tissues experience reduced expression.⁸ Meanwhile, FeNPs have been found to cause structural and physiological disturbances, such as deformed chloroplasts, damaged vascular bundles, and reduced chlorophyll content.⁵¹ On the other hand, applying CuONPs to *C. annuum* L. plants hinders nutrient assimilation. Interestingly, if bulk or ionic copper form is used instead of CuONPs, the uptake of essential elements is promoted.¹⁹ Altogether, these findings underscore the need to further explore the mechanisms underlying NPs toxicity in chili pepper plants.

4. EFFECT ON BIOTIC AND ABIOTIC STRESS

Plants constantly interact with different microorganisms, including pathogens such as oomycetes, fungi, bacteria, viruses, and nematodes.^{52,53}

Nevertheless, only a few taxa of microorganisms are capable of infecting and establishing themselves in plants. To fight against pathogens, plants have developed both passive and active defense mechanisms. Passive mechanisms include physical barriers such as the cuticle and trichomes, as well as the storage of compounds with antimicrobial activity called anticipins.⁵⁴ Active mechanisms include an immune system that regularly operates in two stages. In a plant–pathogen interaction, the plant, through pattern recognition receptors (PRRs), can recognize both pathogen-produced molecules known as pathogen-associated molecular patterns (PAMPs) and plant-derived molecules due to damage known as damage-associated molecular patterns (DAMPs), thereby activating pattern-triggered immunity (PTI). Certain pathogens can evade or suppress PTI by producing effector molecules. However, some plants can trigger a second mechanism known as effector-triggered immunity (ETI), where intracellular NLR immune receptors are able to recognize the effectors produced by pathogens.^{55–57}

These mechanisms activate immune responses, such as the production of ROS, the *de novo* biosynthesis of antimicrobial compounds called phytoalexin, the reinforcement and repair of the cell wall, callose deposition, the production of the

hypersensitive response (HR), and transcriptional reprogramming.^{52,54,58}

4.1. Defense against Biotic Stress. To obtain an optimal crop yield, plants must maintain a stable and balanced physiological state, where the immune system, a crucial component, plays an important role. Different methods are used to regulate, enhance, or help plant immunity, such as using resistant germplasm through conventional plant breeding, fertilization, fungicides, pesticides, elicitors, and beneficial microorganisms. However, it is essential to continue to search for new strategies to manage pathogens. Using nanomaterials in agriculture is a viable alternative to regulate plant defense mechanisms.^{59,60} Numerous studies have been carried out on the effect of MNPs on plants in recent years, although here, we focus on work related to the *Capsicum* genus.

So far, different types of metal-based nanoparticles have been studied; these were used as preventive or curative treatments against various pathogens such as oomycetes (*Phytophthora capsici*), fungi (*Fusarium oxysporum*, *Colletotrichum capsici*, *C. truncatum*, *C. gloeosporioides*, *Alternaria alternata*, *Sclerotium rolfsii*, *Oidiopsis sicula*), bacteria (*Xanthomonas campestris*, *X. vesicatoria*, *X. euvesicatoria*, *Pectobacterium carotovorum*, *Clavibacter michiganensis* subsp. *capsici*), viruses (Alfalfa Mosaic Virus, Tobacco Mosaic Virus, Pepper Huasteco Yellow Vein Virus, Pepper Mild Mottle Virus), nematodes (*Meloidogyne incognita*), and thrips (see Table 2).

It has been reported that nanomaterials can act directly on a pathogen with an antimicrobial effect or indirectly as an elicitor molecule that can activate different defense mechanisms or even cause a priming impact on plants. *In vitro* studies analyze nanoparticles' antimicrobial effect; although many studies have reported this effect, only a few have performed analyses at the cellular level. *F. oxysporum* treated with 100 µg/mL AgNPs inhibited 100% of its mycelial growth.⁶¹ Chitosan silver nanocomposites (CS-AgNPs) concentrations of 1, 0.5, and 0.25% inhibited spore germination and appressorium formation completely in *C. truncatum*.⁶² *X. euvesicatoria* treated with 50 µg/mL reduced graphene oxide with copper and silver composite (rGO-Cu-Ag) inhibited growth entirely.⁶³ In all cases, changes in the morphology of bacterial cells or fungi mycelium were observed. These changes were associated with a direct effect of the nanoparticles on the pathogen cell membranes.

Diverse works reported suggest that nanomaterials have great potential to be used as agricultural inputs that contribute to obtaining food worldwide (information summarized in Figure 2). However, to achieve this, it is necessary to continue studying the effects of these nanomaterials on the different interactions between plants and microorganisms, whether beneficial or pathogenic, mainly to try to elucidate the molecular mechanisms involved in the nanomaterial–plant–microorganism interactions (Figure 3).

4.2. Defense against Abiotic Stress. Plants need favorable abiotic environmental factors for optimal development; however, these environmental factors constantly change over time, leading to unfavorable conditions that cause abiotic stress. Abiotic stresses include drought, salinity, low and high temperatures, the presence and accumulation of heavy metals, and nutrient deficiencies, among others (Figure 3). These stress factors can negatively affect different developmental processes during the life cycle of plants, such as germination, vegetative development, reproductive development, and crop

Table 2. Effects of Metal-Based Nanomaterials on Infection by Pathogens in *Capsicum* spp. Plants

organism	nanoparticle	assay	treatment	effect	ref
<i>Fusarium oxysporum</i>	AgNPs (12.4 nm, spherical shape)	<i>in vitro</i>	Agar well diffusion assay. Minimum inhibitory concentration (MIC) 25 to 200 $\mu\text{g/mL}$.	At 100 $\mu\text{g/mL}$, it inhibited 100% of the growth. It severely damages the hyphae's cell wall and promotes the conidia's deformation.	61
		<i>in vivo</i>	Two weeks after pathogen inoculation, seedlings were foliar sprayed three times (every 10 days) at 25 and 50 $\mu\text{g/mL}$.	At 50 $\mu\text{g/mL}$, the disease severity was reduced by 72%.	
	ZnONPs (15–30 nm, spherical shape)	<i>in vitro</i>	Antifungal tests were performed using the agar dilution method and 0, 4, 6, 8, and 12 mg/L NPs, and the inhibition percent of growth was calculated.	Direct exposure to 12 mg/L ZnONPs exhibited a significant inhibitory effect on the growth of <i>F. oxysporum</i> , 80.73% compared with the control.	64
<i>Colletotrichum capsici</i>	SeNPs (60.48 to 123.16 nm, spherical shape)	<i>in vitro</i>	After inoculation, all treatments were applied by drenching the soil with 100 mL of water/pot.	Applying ZnONPs significantly reduced the disease severity of <i>F. oxysporum</i> and improved the quality and quantity of sweet pepper yield.	65
		<i>in vitro</i>	Detached leaves were moistened with 10–100 ppm SeNPs. After drying the leaves were inoculated.	The fungal growth expansion was inhibited to the maximum extent at a concentration of 50 ppm.	
	CS-AgNPs (4.43 $\pm$ 1.44 nm, spherical shape)	<i>in vitro</i>	Chili fruits were dipped for 10 min in coating formulation with CS-AgNPs composites or chitosan before or after pathogen inoculation.	Colony formation was completely inhibited in the PDA plates treated with nanoparticles from 1% to 0.031% concentrations.	62
<i>C. gloeosporioides</i>	AgNPs, CuNPs, AgCuNPs	<i>in vitro</i>	Each NP was added to PDA for growth inhibition assay.	CS-AgNPs at 1% resulted in maximum inhibition of 60.5% and 51.4% of anthracnose disease in curative and preventive coatings, respectively.	66
		<i>in vitro</i>	10 mL of 106 spores/mL spore suspension was dropped on potato dextrose (PA) liquid media supplemented with NPs for spore germination assay.	AgNPs, CuNPs, and the Ag-CuNPs mix at concentrations of 125, 75, and 50 ppm, respectively, inhibited the growth of fungal hyphae by 100%.	
	CuNP-E (42 nm, triangular shape) CuNP-M (33 nm, cluster shape)	<i>in vitro</i>	The different NPs were sprayed on chili fruits 30 min after pathogen inoculation and air-dried.	After 48 h of incubation, AgNPs, CuNPs, and the Ag-CuNPs mix at 75, 25, and 12.5 ppm, respectively, inhibited the spore germination rate by 100%.	67
<i>C. capsici</i>	AgNPs	<i>in vitro</i>	CuNP-E and CuNP-M were added to PDA for growth inhibition assay with 0 to 1000 ppm.	AgNPs, CuNPs, and the Ag-CuNPs mixed at concentrations of 125, 75, and 50 ppm inhibited disease incidence by 50%, 72.72%, and 86.70%, respectively.	68
		<i>in vitro</i>	250, 500, and 1000 ppm CuNP-E and CuNP-M were sprayed on detached chili fruits 48 h before or after pathogen inoculation.	The highest inhibition (99.78%) of mycelial growth was recorded in CuNP-M 1000 ppm, followed by 93.75% in CuNP-E 1000 ppm and CuNP-M 500 ppm.	
	ZnONPs (9 to 25 nm, wurtzite-like structure)	<i>in vitro</i>	The antifungal activity was assessed using the agar dilution technique at 0%, 25%, 50%, and 75% (w/v) concentrations. The percent growth inhibition was estimated.	CuNP-M 500 and 1000 ppm applied before inoculation and CuNP-M 1000 ppm applied after inoculation inhibited the disease completely.	69
<i>Sclerotium rolfsii</i>	AgNPs (300 nm, cylindrical and spherical shape)	<i>in vitro</i>	Conidial germination was determined after 8 h of ZnONPs treatment on cavity slides. Poisoned food methods were carried out, and mycelium growth inhibition was determined.	All the concentrations almost inhibited growth. The MGI had the maximum value (685.65%) at the 75% (w/v) dose.	70
		<i>in vitro</i>	100, 250, 500, 750, 1000, and 1250 ppm AgNPs were added to PDA for growth inhibition assay.	Best inhibition results were observed at 500 ppm, for conidial at 63.66%, for mycelial growth at 57.77%, and mycelial dry weight at 0.19 g.	
	MgONPs (53 nm, cubic shape), ZnONPs (79 nm)	<i>in vitro</i>	Naturally infected plants were sprayed with 0, 100, 150, and 200 mg/L MgO and ZnONPs twice at two-week intervals.	AgNPs inhibited mycelial growth, induced mycelial malformations, and inhibited sclerotial production at 100 and 250 ppm concentrations. At 750 ppm, mycelial growth was inhibited by 100%.	71
Alfalfa Mosaic Virus	CS-AgNCs (11.3 nm, spherical shape)	<i>in vitro</i>	Seedlings were foliar sprayed with CS-AgNCs 24 h before or after and during pathogen inoculation at 50, 100, 150, and 200 ppm.	MgO and ZnONPs reduced disease severity and disease progress.	72
		<i>in vitro</i>	ZnONPs were applied by foliar application in water suspension at 72 h before and after pathogen inoculation.	At 200 ppm, it inhibited 91% of viral proliferation when applied 24 h after inoculation.	73
	TiO ₂ NPs	<i>in vitro</i>	TiO ₂ NPs were foliar sprayed at 72, 144, and 216 h after pathogen inoculation at 50, 100, 150, and 200 g/mL .	At 100 and 150 mM, it significantly decreased disease severity. However, at 200 mM, it significantly reduced the viral titer.	74
Pepper Mosaic Virus	AgNPs (36 nm, spherical shape)	<i>in vitro</i>	AgNPs were exogenously applied at 0, 200, 300, and 400 $\mu\text{g/L}$ to natural and artificial infestation.	At 150 g/mL , the appearance of the symptoms caused by TMV was reduced.	75
		<i>in vitro</i>	MIC was determined by broth microdilution technique. MBC was evaluated by subculturing 5–10 μL of wells on the Mueller–Hinton agar plate.	Infected leaves treated with 400 $\mu\text{g/L}$ AgNPs were recorded as having an inferior buildup of total soluble proteins compared to 200 $\mu\text{g/L}$ AgNPs and the control.	76
	AgNPs (50 nm, spherical shape)	<i>in vitro</i>	Leaves were sprayed with different concentrations of AgNP two days after the bacterial infection.	MIC and MBC were recorded at 0.0625 and 0.125 mg/mL , respectively.	
<i>Pectobacterium carotovorum</i>		<i>in vitro</i>		AgNPs inhibited soft rot disease development and promoted the growth of pepper plants.	

Table 2. continued

organism	nanoparticle	assay	treatment	effect	ref
<i>Xanthomonas euvesicatoria</i>	rGO-Cu-Ag	in vitro	MIC for AgNPs was determined by broth microdilution technique. MICs were evaluated by subculturing on the agar plate.	MIC and MBC of rGO-Cu-Ag were recorded at 5 and 50 $\mu\text{g/mL}$, respectively. Reduction in DNA content was observed at concentrations of 25 $\mu\text{g/mL}$ rGO-Cu-Ag.	77
<i>X. campestris</i> pv. <i>vesicatoria</i>	CuNPs, ZnNPs, Cu-ZnNPs	in vivo	24 h before the bacterial infection, leaves were sprayed with sterilized filter paper, and circular discs were dipped into nanoparticle solutions.	rGO-Cu-Ag at 500 $\mu\text{g/mL}$ significantly reduced the bacterial spot severity on pepper plants without visible adverse effects.	78
		in vitro	Sterilized filter paper circular discs were dipped into 0%, 0.25%, 0.50%, and 0.75% nanoparticle solutions.	Cu-ZnNPs exhibited the most significant inhibition zone, measuring 13.73 mm, followed by ZnNPs with 7.93 mm and CuNPs with 7 mm.	
		in vivo	Three days after inoculation, the NPs solution was sprayed on the leaves.	The lowest disease incidence was observed with Cu-Zn (17.9%), followed by Zn (22.9%) and CuNPs (27.6%).	
trips	CS, CS-Ag, and CS-CuNPs (20–100 ppm)	in vivo	Foliar application of nanoparticles at 20, 40, 60, 80, and 100 ppm to the infected plants.	All NPs over 60 ppm concentration significantly inhibited sporulation by 70–85%.	30
seed-borne pathogens	AgNPs (55–350 nm, rod shape)	in vitro	Seed health testing for fungal infection was carried out using a blotter technique with AgNPs at 0, 750, 1000, and 1250 mg/kg.	AgNPs at 750 mg/kg and above significantly inhibited the growth of seed-borne pathogens.	79
<i>Meloidogyne incognita</i>	ZnONPs (15–30 nm)	in vitro	The bioassay was conducted in 10-well cell culture plates, with 35 J2s/mL each treatment.	The maximum mortality of <i>M. incognita</i> (J2s) was recorded by the treatment 12 mg/L ZnONPs, which showed 11.82%, 37.63%, 40.86%, and 89.65% after 6, 12, 24, and 72 h.	64
		in vivo	After inoculation, all treatments were applied by drenching the soil with 100 mL of water/pot.	The application of 12 mg/L significantly reduced the number of nematode galls, egg masses per root, eggs/egg mass, and females by 98%, 99%, 99.9%, and 95.5%, respectively.	

yield, through modifications in biochemical, morphological, and physiological processes and gene expression. The type and intensity of these modifications depend on the type of stress, duration, degree of stress, and the kind of crop.^{80–82} Morphological modifications include changes in total biomass, plant height, root length, number of leaves and branches, and flowering time, while physiological changes include a reduction in photosynthetic rate and modification of photosynthetic pigment content such as carotenoids and chlorophyll a and b. Within the biochemical changes, the generation and accumulation of reactive oxygen species (ROS) plays an important role, as it can serve as a signal for optimal plant response or can cause direct damage to different cellular components through the process known as oxidative burst.^{83,84}

4.2.1. Defense against Extreme Temperature Stress. Each plant species has an optimum temperature range for its development; in the case of *C. annuum*, temperatures below 15 °C and above 32 °C are considered stress conditions. These conditions affect plant growth, especially flower formation and fruit development, negatively impacting crop yield.⁸⁵

There are few studies dealing with cold stress relief using nanoparticles in *C. annuum*. Sayed et al. found that a combination of arbuscular mycorrhizal fungus (*Glomus mosseae*) inoculation and foliar application of a mixture of ZnO and SeNPs significantly improved the growth characteristics, productivity, and fruit quality of chili plants under cold stress conditions. Moreover, the total ascorbic acid and capsaicin content increased, as well as the activity of peroxidase (POD) and nitrogen glutamate dehydrogenase (GDH), while hydrogen peroxide (H_2O_2) and lipid peroxidation (MDA) content decreased.⁸⁶

Meanwhile, regarding research on hot stress relief using nanoparticles, we only found a study on *Solanum lycopersicum* (a closely related organism), in which exposing tomato plants to 0.01 CuNPs at 42 °C for 1 h accelerated the change of vegetative phase and the process of leaf senescence.⁸⁷

4.2.2. Defense against Saline Stress. Soil salinity is caused by the accumulation of soluble salts in the soil water; this parameter is measured by the electrical conductivity of a saturated soil paste extract (ECe), which is expressed in decisiemens per meter (dS/m) at 25 °C and gives an estimate of the concentration of soluble salts such as the cations sodium (Na^+), potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}) and the anions chloride (Cl^-), carbonate (CO_3^{2-}), sulfate (SO_4^{2-}), and nitrate (NO_3^-), considered the main soluble mineral salts in soil.^{83,88} Plant salinity stress depends on factors such as soil–water balance properties, climatic conditions, genotype, and developmental stage. Salinity values of ECe 2–4 dS/m can cause stress in plants considered very sensitive, while values of ECe 4–8 dS/m cause stress in most crops.⁸⁸ Salinity stress negatively affects seed germination, plant development, photosynthesis, senescence, lipid metabolism, and protein synthesis by causing osmotic stress, restricted water uptake, and unbalanced nutrient absorption.^{83,89}

The effect of nanoparticles on salt stress is the most studied phenomenon in chili. Seed priming with manganese(III) oxide nanoparticles (MnNPs) improved root elongation and alleviated salt stress during germination,⁹⁰ while the application of manganese-doped graphene quantum dots (GQD-Mn) offset the reduction of fruit number and total weight by 41 $\pm$ 0.55% and 58 $\pm$ 0.83%, respectively.⁹⁰ The application of nanoparticles of different compositions, such as Se, Cu, and ZnO, efficiently improved the pepper plants' physiological

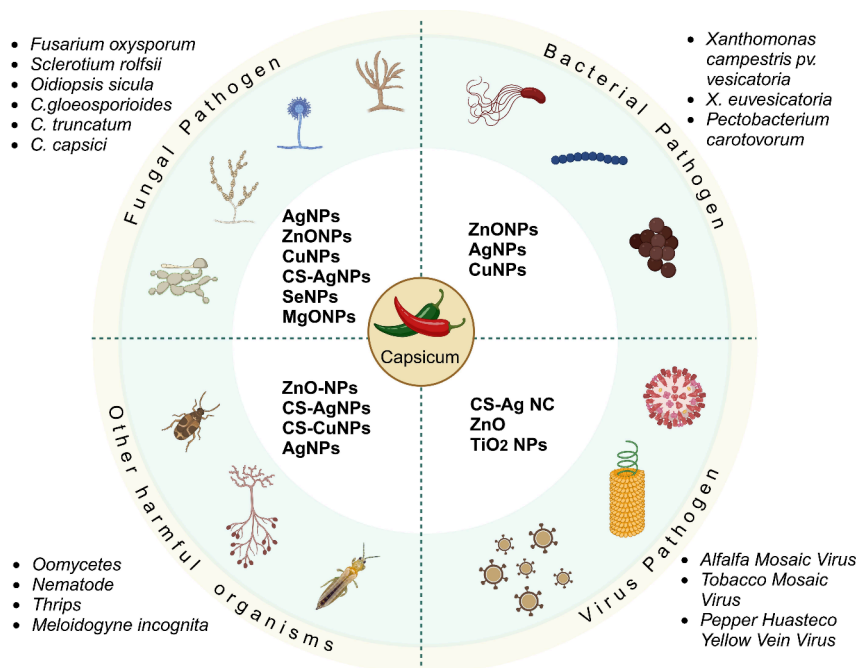


Figure 2. Different NPs for pathogens and microorganisms in *Capsicum* spp. plants. Created with BioRender.com.

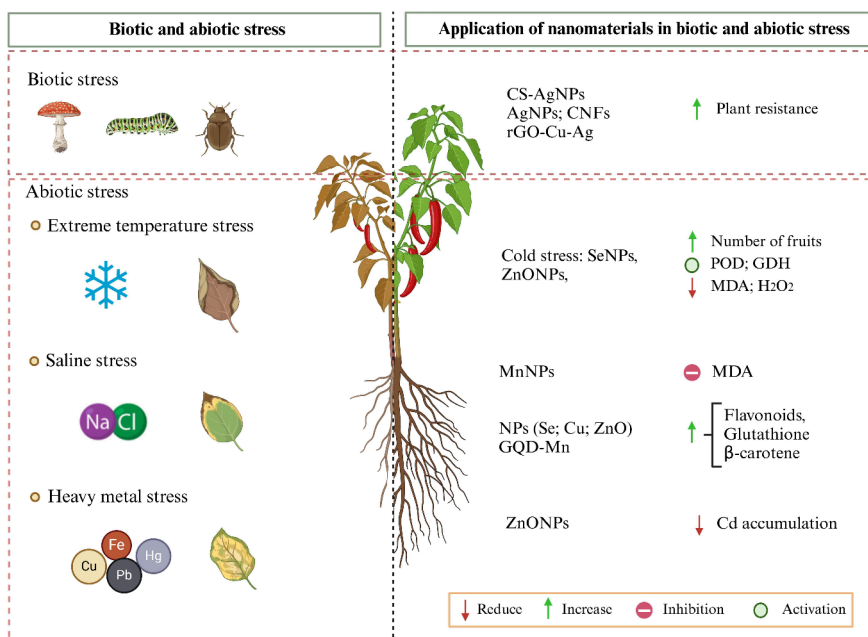


Figure 3. Types of nanomaterials used in the biotic and abiotic stress of *Capsicum* spp. plants. Created with BioRender.com.

responses under salinity through increased carotenoids, chlorophyll a and b content, or chlorophyll index (SPAD) values, fortifying the antioxidant defense system by the stimulation of enzymatic activities such as catalase, guaiacol peroxidase (GPX), ascorbate peroxidase (APX), superoxide dismutase (SOD), glutathione reductase (GR), dehydroascorbic acid (DHA), and oxidized glutathione (GSSG) activities.^{91,92} Se and Cu nanoparticles increased the content of bioactive compounds in fruits, such as phenols, flavonoids, glutathione, β-carotene, and yellow carotenoids.⁹² Also, the combined application of two nanofertilizers, one made from limestone, which is rich in calcium (Ca) and magnesium (Mg), and the other rich in micronutrients such as zinc (Zn), Mn, Fe,

Mg, Ca, nitrogen (N) source (amino-acids), and ascorbic acid, had a positive effect on the number of fruits, fresh and dry weights of fruit, yield per plant, and fruit dimensions.⁹³

4.2.3. Defense against Drought Stress. Drought is a multifactorial problem that affects different human activities and needs. Drought is classified into four categories: meteorological, hydrological, socioeconomic, and agricultural drought. The latter is an abiotic stress factor that affects agricultural production every year, and with the global increase in temperature, this condition will continue to worsen in the future.^{94,95} Drought stress affects biochemical and physiological processes in plants, such as chlorophyll content, gas exchange, respiration rate, and photosynthetic rate, which

decreases growth. In the case of chili, even short periods of drought stress can negatively affect yield quantity and quality.^{96,97}

Although we did not find information about the effect of MNPs against chili drought stress, some information corresponds to the Solanaceae family. In the case of eggplant, a study showed that foliar application of green synthesized AgNPs increased the growth of the plants, photosynthetic pigments, and antioxidant activity and decreased the proline content in plants under drought stress.⁹⁸ Foliar application of ZnONPs to water-stressed eggplants resulted in an increased relative water content and membrane stability index associated with improved stem and leaf anatomical structures and enhanced photosynthetic efficiency. Under drought stress, 50 and 100 ppm ZnONPs supplementation improved growth characteristics and increased fruit yield by 12.2% and 22.6%, respectively.⁹⁹

4.2.4. Defense against Heavy Metal Stress. Heavy metal pollution negatively affects different living species within ecosystems, including plants. For these organisms, heavy metals are classified into essential metals such as copper (Cu), zinc (Zn), manganese (Mn), iron (Fe), molybdenum (Mo), and nickel (Ni) that serve as micronutrients and nonessential metals such as aluminum (Al), cadmium (Cd), chromium (Cr), lead (Pb), and mercury (Hg) that have adverse effects on plant cells.¹⁰⁰ Cadmium is highly toxic due to its high solubility, plant uptake dynamics, and soil persistence.^{101,102} *C. annuum* has a moderate tolerance to cadmium; however, its accumulation in the plant affects its growth and physiological processes, such as photosynthesis.^{103,104}

Recently, two independent papers described the effect of ZnONPs on cadmium stress. Applying ZnONPs increased both the fresh shoot and root weights and the root dry biomass production. In the pot experiment, the foliar spray of ZnO nanoparticles reduced the negative effect on chlorophyll a, chlorophyll b, and total chlorophyllan. On the other hand, *in vitro* experiments showed that in the shoots, the treatment with ZnONPs significantly enhanced all antioxidant enzymatic activities of CAT, GPX, POD, APX, and GR. However, in the roots, the supplementation of ZnONPs reduced the activities of all antioxidant enzymes. The data generated in both papers suggest that ZnONPs ameliorate the effect of cadmium in chili.^{101,105} However, one of the main problems of cadmium contamination is that humans consume this metal by ingesting contaminated vegetables, such as chili. So far, it has not been analyzed in chili whether nanoparticles reduce cadmium accumulation in plants, which is an important aspect that should be considered in future work. However, it has been reported that the application of nanoparticles reduces cadmium accumulation in other species, such as rice, maize, and lettuce.^{106–108}

5. CONCLUSIONS AND PERSPECTIVES

This review highlights that most reports indicate positive effects of various metal nanoparticles in both *in vivo* and *in vitro* studies on chili plants. However, only a few studies have focused on changes at the global metabolite level in mature plants or on alterations in gene expression patterns. Additionally, the effects observed when nanoparticles are applied to chili peppers depend on factors such as the type, shape, and concentration of the nanoparticles, the method of application, and even the plant's genotype.

There is a need for more research to explore the effects of transgenerational exposure to nanoparticles and to conduct medium- and long-term evaluations. A significant gap in our understanding is the lack of information regarding where nanoparticles accumulate in plants and how they are transformed. It remains unclear whether the secondary metabolites produced by the plant promote the formation of macroscopic clusters or create a coating on the nanoparticles that passivates their surfaces, potentially leading to their accumulation or transformation within the plant.

Furthermore, the frequency and extent of accumulation, transformation, and speciation of different nanoparticle variables that depend on the type of study and the concentrations used are still unknown.

In conclusion, while metal nanoparticles present promising benefits for chili cultivation, it is crucial to standardize their synthesis, characterization, and application methods. Comprehensive studies are essential to fully understand their impact on plant health, environmental safety, and food security.

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ABBREVIATIONS

APX	ascorbate peroxidase
DAMPs	damage-associated molecular patterns
DHA	dehydroascorbic acid
ETI	effector-triggered immunity
GDH	glutamate dehydrogenase
GPX	guaiacol peroxidase
GR	glutathione reductase
GSSG	oxidized glutathione
HR	hypersensitive response
MDA	lipid peroxidation
MNPs	metal-based nanoparticles
NPs	nanoparticles
PAMPs	pathogen-associated molecular patterns
POD	peroxidase
PRRs	pattern recognition receptors
PTI	pattern-triggered immunity
ROS	reactive oxygen species
SOD	superoxide dismutase
SPAD	chlorophyll index

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