

The Role of Nanoparticles in Mitigating Abiotic Stress: Advances and Applications in Plant Science

Amit kumar Tiwari ^{1*}, Niketa Rajput¹, Shahnaz Bano², Shweta Jaiswal³

*1*Assistant Professor, Botany Department, Bundelkhand University, Jhansi, UP*

¹(M.Sc.), Institute of Basic Science, Vigyan Bhawan, Department of Botany, Bundelkhand university, Jhansi

²Research Scholar Institute of Basic science, Vigyan Bhawan, Department of Botany, Bundelkhand university, Jhansi

³Research Scholar (SRF), Shweta Jaiswal Institute of Basic Science, Vigyan Bhawan, Department of Botany, Bundelkhand university, Jhansi

Abstract- Abiotic stress is a major barrier to global agricultural output and food security. To address these challenges and achieve sustainability, innovative strategies like nanotechnology are essential. Nanotechnology leverages nanoscale items such as nanopesticides, nanofungicides, nanofertilizers, and nanoherbicides to enhance crop yield. The reduced size, easy solubility, and efficient uptake of nanoparticles make them valuable tools in modern agriculture. Studies have shown that nanoparticles can significantly improve both the qualitative and quantitative aspects of crop yield under various biotic and abiotic stress conditions. This review explores the significant physiological, biochemical, and molecular changes that nanoparticles induce in plants, helping them tolerate stress conditions. It also examines the different types of abiotic stresses that plants face and the role of nanoparticles in mitigating these stresses, highlighting the potential of nanotechnology in enhancing agricultural productivity and sustainability.

Keywords Abiotic stress, Nanoparticles, Nanopesticides, Nanofungicides, Nanofertilizers, and Nanoherbicides.

INTRODUCTION

Plant stress occurs when plants are unable to grow optimally due to adverse conditions, resulting in reduced crop yields, potential irreversible damage, or even death if the stress exceeds tolerance levels. Stress factors are categorized into abiotic and biotic. Abiotic factors include environmental elements like light, water, and temperature that affect plant growth. Biotic factors involve interactions with other species. Under suboptimal conditions, plants face increased demands,

leading to lasting damage, stunted growth, or yield shortfalls. Understanding and managing these stressors is crucial for maintaining healthy plant growth and agricultural productivity. In contrast, other species that coexist with plants and engage in interactions with them are known as biotic factors, and these include pathogens and pests. Complex molecular mechanisms, such as alterations in gene expression and regulatory networks, are typically involved in the response to stress [1]. Plant proteins, membranes, and other structural elements may be harmed by the increased ROS produced in response to abiotic stress, which may ultimately cause deficits in vital physiological functions [2].

Regardless of the stress, damage to photosynthetic systems and membrane peroxidation have been observed in a variety of plants. Therefore, the primary goal of plant defence mechanisms is to scavenge ROS by turning on antioxidant molecules [3]. Increased phenol and flavonoid production has been seen in numerous plants under a variety of abiotic stressors. The majority of the time, significant levels of phytochelatin formation were seen under diverse heavy metal stressors [4]. Additionally, it was discovered that proline content increased to function as an osmolyte and combat a variety of abiotic stressors. The activation of antioxidant enzymes to scavenge the ROS molecules is another significant biological alteration. Antioxidant enzymes such as SOD, APX, GPX, and catalase aid plants in withstanding oxidative stress.

Long-term stressors may negatively impair a plant's ability to grow and develop, which has an immediate effect on agricultural productivity. Since plants are thought to be the primary producers in the living kingdom, circumstances that negatively impact plants give rise to worries about the security of food [5]. Abiotic stresses are responsible for up to 50% of yield losses in important crops, which is a considerable contribution to yield losses [6]. In order to lessen abiotic stress, scientists are focusing their study on methods like genetic engineering and plant breeding. Nanotechnology has recently been applied to the resistance to abiotic stress [7]. As a way to protect plant growth from abiotic stresses such drought, salt, heavy metals, extremely high temperatures, and flooding, interest in nanomaterials is rapidly expanding globally [8]. In order to solve current and future production constraints in sustainable agriculture, nanoparticles (NPs) are considered to be helpful and promising methods for adjusting crop yield by improving a plant's capacity to withstand abiotic stress [9].

ABIOTIC STRESS IN PLANTS

The phrase "abiotic stress" refers to the detrimental effects that inanimate objects have on living organisms within a specific setting. Some of the possible stresses that are significant worldwide issues are drought, salt, heavy metals, extremely high or low temperatures, and other environmental extremes. Abiotic stress is increasingly likely to affect plants due to the changing global environment. Heat waves, droughts, and other abiotic stress conditions including flooding, salinity, and freezing are becoming more often of global warming [10]. Apart from natural factors, human disturbances of the biosphere, which show up as various worldwide occurrences like a swifter pace of industrialization, intensive farming, and massive mining, along with an expanding populace and swift

urbanisation, have resulted in global warming disasters. This has also indirectly contributed to abiotic stress and the serious pollution of the planet's vital components.

ROLE OF NANO PARTICLES IN ABIOTIC STRESS MANAGEMENT

Since they are sessile organisms, plants must withstand abiotic stresses including salt, drought, and extremely high or low temperatures [11]. Instead of being straightforward, linear pathways, stress responses are intricate, integrated circuits that involve several pathways, mainly cellular compartments, tissues, and interactions with other cofactors and/or signalling molecules to coordinate a particular response to a given stimulus [12]. The stress on a tissue or organ will dictate the plant's response. Furthermore, the length and severity of the stress can have a big impact on how complex the reaction is [13]. In order to counteract stress reactions and enhance tolerance, plants respond to abiotic challenges by activating early stress-signaling systems [14,15]. Second messengers, including calcium, phospholipids, reactive oxygen species (ROS), nitric oxide (NO), and several protein kinases, relay and intensify the signal when a plant cell senses stress [16]. By inhibiting energy-intensive activities and promoting plant stress tolerance, SnRk1 kinases alter the expression of about 1000 stress-responsive genes, aiding in the restoration of homeostasis. Because of this, they are able to withstand a variety of abiotic stresses, including salinity, flooding, drought, and nutrient shortage. Additionally, plant hormones like ABA and ethylene serve as the main messengers for defence mechanisms in plants, such as the shutting of stomata in response to drought stress. To combat the severe impacts of abiotic stress, these stress-signaling pathways activate transcription factors, which in turn activate a variety of stress-response genes.

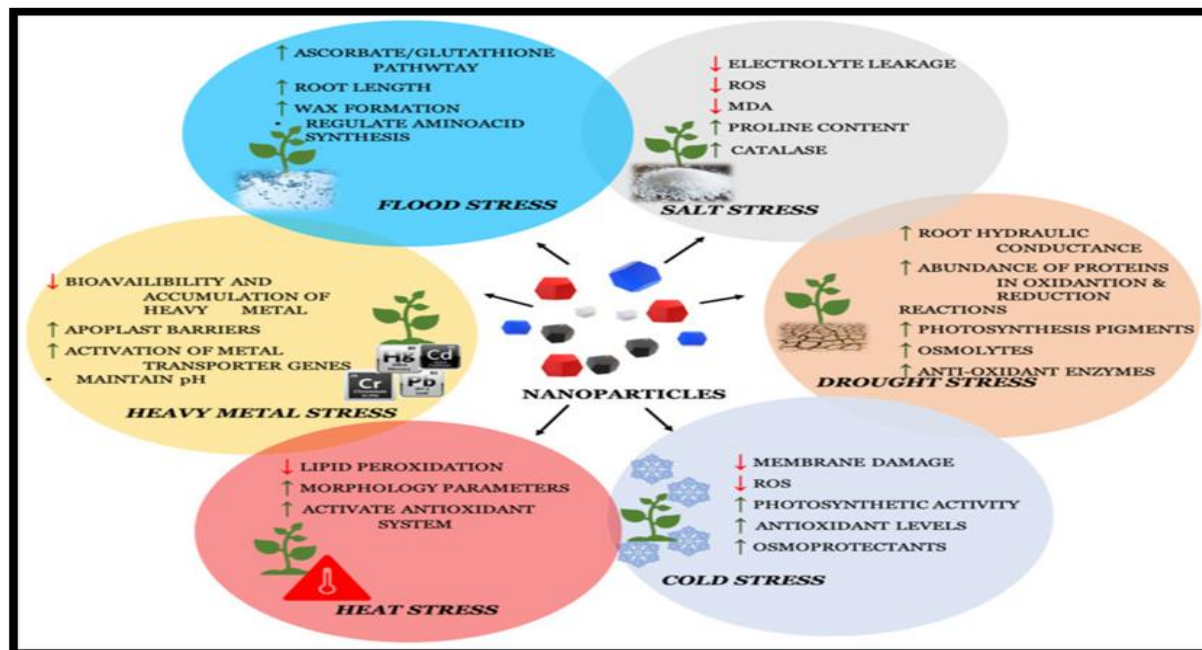


Figure 1 . Nanoparticles involved in combating abiotic stress. (Al-Khayri et al. ,2023)

Nanoparticles in Salt-Stress Tolerance

Due to water constraint brought on by global warming, agricultural regions worldwide are forced to be irrigated with saline water, which increases the salt content of the soil. One of the biggest obstacles to modern agriculture is salinity, or the accumulation of excessive salt in the soil, which eventually inhibits and damages plant growth and development and results in plant mortality [17, 18]. More than 200 mM of NaCl causes the majority of plants to perish. Every stage of a plant's life cycle—including seed germination, seedling development, vegetative growth, and blooming—is significantly impacted by salinity [19]. Salinity affects a wide range of horticultural crops, including fruits, vegetables, and spices. Salt stress imbalances ionic strength, which affects several biochemical, physiological, and metabolic processes in addition to producing osmotic stress, water stress, oxidative stress, nutritional stress, and decreased cell division [20,21].

The application of nanoparticles, such as Zn NPs, Ag NPs, SiO₂ NPs, Cu NPs, Fe NPs, Mn NPs, C NPs, Ti NPs, Ce NPs, and K NPs, was successful in reducing the harmful effects of salt stress in a variety of plants, claim Zulfiqar and Ashraf. The El-Sharkawy group [22] discovered that applying K NPs topically to salt-sensitive *Medicago sativa* enhanced the plant's ability

to withstand salt by decreasing electrolyte leakage and raising proline and antioxidant enzyme levels, including catalase. Similar to this, reduced oxidative stress was demonstrated by lower MDA and ROS levels as well as increased antioxidant activity in pearl millet plants treated with AgNPs; this reduction in Na⁺ absorption in the leaves may have been the cause. It was shown that cerium-oxide nanoparticles helped *Brassica napus* increase photosynthetic activity by changing the root cells and enhancing the intake of minerals [23]. A growing body of research indicates that treating plants with nanoparticles might significantly lessen the negative effects of salt stress and, as a result, regulate how plants adapt.

Nanoparticles in Drought-Stress Tolerance

Drought is regarded as the most detrimental environmental stress, reducing crop yield more than any other. According to the Intergovernmental Panel on Climate Change (IPCC), the average temperature will rise by 1.8 to 4.0 °C by 2100, and drought will affect vast areas of the world [24]. Drought affects agriculture when plants have insufficient moisture to develop normally and complete their life cycles. The severity of drought is further increased by a continuous decline in precipitation and increase in evapotranspiration demand [25]. For instance, drought

stress prevents plant development, because water is required for cell turgor, which is the pressure that a contained liquid exerts on cell walls, causing cells to expand [26]. The principal effects of drought on crop plants include slower rates of cell division and growth, smaller leaves, longer stems and roots, disordered stomatal oscillations, altered water and nutrient relationships with lower crop output and inefficient water usage .

As per previous studies, NPs cause a variety of morphological, physiological and biochemical changes in plants as they increase their resistance to drought stress by increasing plant root hydraulic conductance and water uptake and demonstrate a differential abundance of proteins involved in oxidation-reduction, ROS detoxification, stress signaling and hormone pathways [27]. The foliar application of metal-oxide nanoparticles, such as titanium dioxide (TiO₂), zinc oxide (ZnO) and iron oxide (Fe₃O₄), were found to be effective in enhancing the plant's physiological and metabolic activities under drought stress [28]. When Si NPs were applied to drought-stressed pomegranate plants, additional improvements were made to their photosynthetic pigments, nutrient status, physical and chemical parameters (especially those related to fruit cracking), phenolic content and concentrations of osmolytes, antioxidant enzymes and abscisic acid [29]. El-Zohri et al. [30] suggested that green ZnO-NPs administered topically at lower concentrations could successfully boost tomato tolerance to drought stress. In addition to nanofertilizers, green synthesized Fe₃O₄ NPs were also found to be effective in reducing the impact of drought stress on fenugreek plants [31]. However, a study by Potter et al. [32] indicates that the potential benefits of using NPs in enhancing plant drought resistance only actualize under specific environmental circumstances.

3. Nanoparticles in Cold-Stress Tolerance :-

The adverse effects of cold or low temperatures on plant growth and development are also a result of global climate change. Chilling and freezing are two common low-temperature stresses that plants encounter. Plants may withstand temperatures as low as 0 °C or as high as 15 °C, depending on the species. Other elements that influence chilling temperatures include the air temperature and wind speed during exposure. The plant will struggle in freezing

temperatures (below 0 °C), in contrast to how it reacts to chilling conditions. Low and nonfreezing temperatures can harm or even kill crop species, which can affect their survival, production, and ecological dispersal. Plant growth is slowed by cold stress because lower temperatures cause a reduction in the activity of enzymes and other proteins. Low temperatures affect many processes in these plants, such as those related to defence, respiration, secondary metabolism, and the synthesis of proteins and nucleic acids [33]. TiO₂ and chitosan nanoparticles have been widely used in numerous investigations due to their effectiveness in withstanding cold stress. Using transcriptional regulation, it was discovered that the administration of Ti NPs improved electrolyte leakage, photosynthetic activity, and membrane damage in chickpea plants under cold stress [34,35,36]. It is implied that TiO₂ NP treatment may help plants become more resilient to cold stress by regulating the pressure caused by temperature drops and changing their metabolism to promote plant growth [37]. When TiO₂ NPs are used in licorice plants, the negative effects of cold stress are lessened and the concentration of glycyrrhizin is increased. In banana plants under cold stress, the use of chitosan nanoparticles was found to be beneficial in lowering ROS with the build-up of osmoprotectants. Furthermore, through the antioxidative system and transcription factors involved in the chilling response, the foliar application of ZnO NPs may lessen chilling stress in rice plants. In a similar vein, using SiNPs can enhance sugarcane plants' capacity for photosynthetic processes during chilling stress [38].

Nanoparticles in Heavy-Metal-Stress Tolerance

One of the harmful elements that lowers agricultural output in the present era is heavy-metal (HM) stress. Globally, human activities including urbanisation and industry have led to HM pollution. The increased use of contemporary farming instruments, like chemical fertilisers and pesticides, has also increased crop plant susceptibility to HM stress. Plants suffer harmful effects from heavy metals such as Ag, Pb, Cd, Ni, Co, and Cr [39]. Since plants are at the base of trophic systems, there is a strong likelihood that these heavy metals (HMs) will be bioaccumulated along the food chain. This can eventually cause chronic health problems in humans and other animals, including damage to the kidneys and liver. Furthermore, HMs

directly affect plants by causing defects in their morphology and physiology as well as compromised metabolic pathways [40]. These have an impact on the amount and quality of plant-based goods, particularly on medicinal and agricultural plants. Numerous investigations have been carried out on the application of nanoparticles to reduce HM stress. By absorbing and changing the heavy metals (HMs) present in the soil, nanoparticles placed to the soil can lessen the HMs' mobility and bioaccumulation. Fe₃O₄ NP treatment has decreased the availability of Cd metal in soil. By releasing phosphate ions, the hydroxyapatite nanoparticles can both regulate the pH of the soil and lessen the harmful effects of metals in it. Additionally, NPs cause the apoplast barriers to develop, which lower the root's concentration of heavy metals. Additionally, plants can regulate the genes encoding metal transporters to intercept heavy metals. By forming complexes with the HMs, these NPs can prevent the HMs from translocating. NPs like SiNPs have encouraged the synthesis of organic acids, which lessen the harm caused by HM stress. Additionally, NPs stimulate the antioxidant system, which lessens the stress brought on by ROS.

Response of Plants to Nanoparticles under Abiotic Stress

Carbon nanotubes (CNTS), metal-based nanoparticles (Ag NPs and Au NPs), fullerenes, tiny crystalline powders (Fe, Co, and Cu), and metal-oxide nanoparticles (iron oxide, TiO₂ NPs, ZnO NPs, SiO₂ NPs, CuO NPs, and CaCO₃ NPs) are some of the most well studied functional nanoparticles [41]. Because NPs have a high surface energy and surface/volume ratio, their reactivity is enhanced and their biochemical activity is increased, which has a variety of effects on plants. NPs have a fast rate of plant interaction and molecular mechanism stimulation. Furthermore, the NMs perform a dual role, first defending against ROS and then inducing oxidative stress, which triggers the activation of plants' antioxidant defence mechanisms. By lessening the harmful effects of abiotic stress and by affecting many morphological, anatomical, physiological, biochemical, and molecular properties of plants, NPs help plants respond to harsh conditions more efficiently and yield more.

Morphological Changes under the Influence of Nanoparticles

Abiotic stressors that impact plant morphology, including salt, drought, high and low temperatures, and heavy metals, have a major impact on fresh and dry weight, leaf area, shoot and root length, total plant growth, and crop output [42]. The priming of seeds with low concentrations of NPs boosted root length, shoot length, and seed germination rate, according to [43]. Applying Se NPs helped to restore the sorghum's decreased pollen germination, seed set, and yield caused by temperature stress. Under high temperatures, plant-derived silver nanoparticles (NPs) increase the dry weight and leaf area of aerial structures. Under salinity stress, TiNPs have been shown to boost plant height in *Dracocephalum moldavica*. Under drought stress, FeNPs have been demonstrated to boost plant growth and biomass output overall in *Brassica napus* [44].

Anatomical Changes under the Influence of Nanoparticles

In response to abiotic stress, plants go through a variety of morphological changes. The kind of abiotic stress determines the anatomical reactions. Large substomatal chambers and an increase in the thickness of the upper-epidermal waxy cuticle, cuticular margins, and lignification of xylem tracheids are among the structural changes that occur in response to drought. Reduced cell size, stomata closing, and transcription rate are all inhibited by heat stress, although larger xylem vessels in roots and shoots and increased stomatal and trichomatous densities are seen. Under heat stress, *Vitis vinifera* L. CV. Jingx has damaged mesophyll cells and enhanced plasma membrane permeability [45]. In *Zygophyllum qatarense* Hadidi subjected to high temperatures, bimodal stomatal behaviour has been shown to minimise transpirational water loss. Applying nanoparticles supports the plant's anatomical adaptations, which enable the plant to tolerate stressful environments. In maize plants under heat stress, the stomatal opening has been successfully regulated by the TiO₂ nanoparticles, lessening its effects. The application of SiO₂ nanoparticles improved the strawberry plants' epicuticular wax layer (EWL), reducing the detrimental effects of salinity. Al₂O₃ nanoparticles decreased cell mortality in the soybean plant's hypocotyl area in the study. Under salt stress, ZnO NPs were demonstrated to be effective in

minimising damage to the vascular tissues and epidermis of *Sorghum bicolor*. There has been another study published on the impact of CeO₂ NPs in *Brassica napus* L. under salt stress. The former was found to have the ability to shorten root apoplastic barriers[46]. Nanoparticles are readily absorbed by plants in a variety of forms, including fertilizers, herbicides, and insecticides, because of their smaller size and strong reactivity. [47]

Physiological Changes under the Influence of Nanoparticles

Under stressful conditions, plants display a range of physiological reactions, including adjustments to their photosynthetic apparatus, transpiration, absorption of minerals and water, lipid peroxidation, and seed germination. Plants under cold stress display suppression of seed germination along with reduced levels of seed set, chlorophyll content, and pollen fertility, all of which have an impact on photosynthesis. Plant cells also experience plasmolysis, protoplasmic streaming, and electrolyte loss. Plants that are under heat stress may absorb nutrients at a slower rate. Because plants cannot absorb water while they are under a Cd stress, the buildup of Cd in the soil also affects the uptake of macro- and micronutrients. Because drought stress affects the thylakoid membranes, it is known to limit photosynthesis. Plant germination is inhibited by high soil salinity. In addition, heavy metals inhibit photosynthesis and seed germination, among other physiological processes in plants. When plants are stressed by dryness, Si nanoparticles speed up photosynthesis and stomatal conductance, which helps the plants endure the stress. Applying a fixed dose of nano-TiO₂ to tomato leaves under heat stress enhanced stomatal conductance, net photosynthetic rate, and leaf transpiration. Nano-TiO₂ boosted uncontrolled growth and reduced photosystem II (PS II) energy loss.

Major Biochemical Changes to Tolerate Abiotic Stress

Plants are subject to overlapping effects from abiotic stressors like salinity, drought, and high metal levels. These effects include increased reactive oxygen species levels, antioxidant system activation, and accumulation of inert solutes, or osmolytes, which include sugars, polyamines, secondary metabolites, and amino acids. Abiotic stress causes the proteins and

enzymes to get denaturated, which activates the enzymes, decreases protein synthesis, increases membrane lipid fluidity, and destroys membrane integrity. The response of the total carbohydrate concentration to various biotic stressors varies. It is known that the total carbohydrate content increases in reaction to lower temperature stress and decreases in response to salinity stress. Abiotically stressed plants release enzymes and secondary metabolites including lignins, anthocyanins, flavonoids, and phenolic acids, among other compounds, to mitigate the effects of the stress and control oxidative damage, so minimising cellular damage. Reports state that NPs alter plants' morphology, physiology, and biochemistry in a number of ways to strengthen their resistance to drought stress. The application of Ag NPs increased the stress tolerance of soybean seedlings by decreasing the misfolding of proteins caused by flooding stress. Under drought conditions, Zn NPs applied topically increased proline, glycine betaine, free amino acid levels, and sugar levels. It is discovered that proline concentration is high under a variety of abiotic stressors. It has been suggested that proline, when present in large concentrations as an osmoticum, protects cellular structures and enzymes. Such osmolyte buildup serves as a signal for the antioxidant response and aids in preserving the redox potential of cells in stressful situations.

The Drawbacks of Using Nanoparticles in Plants

Although nanoparticles are used in agriculture to combat environmental stress, there are worries over their accumulation and possible introduction into the food chain. The overuse of some manmade nanoscale elements in agriculture may be hazardous to human health and the environment, even though it is known that nanoscale materials like protein, fat globules, carbohydrates, and DNA found in food are not harmful. Plants absorb and bioaccumulate engineered nanoparticles (ENPs) when they come into contact with them in the soil. Consequently, plants are the basic building blocks of all ecosystems and are essential to the movement of ENPs that attach to the surface of plant roots and may pose a chemical or physical risk to the plants. Large pores on cell walls may grow as a result of the ENPs once they are attached to plant roots, making it easier for large ENPs to internalise through them. Additionally, it has been noted that in leguminous plants, the nitrogen-fixing

mechanism carried out by soybean crops is impeded by nano-cerium oxide particles that infiltrate the roots and root nodules. The long-term impacts of these nanoparticles on the food supply and the chemical harm to the plants are other issues that are brought up. Additionally, the nanoparticles have the potential to enter the food chain, disrupt it, and endanger both people and animals.

CONCLUSIONS

Nanoparticles present promising solutions for mitigating abiotic stress in plants, enhancing resilience and productivity. Advances in nanotechnology offer innovative approaches to improve plant health under adverse conditions. Continued research and application of nanoparticles can significantly contribute to sustainable agriculture, ensuring food security in the face of growing environmental challenges.

ACKNOWLEDGEMENT

The Vice-Chancellor, the Dean, and the Head of the Botany Department Institute of Basic Science Bundelkhand University are acknowledged by the authors for providing the facilities required to conduct the experiment and produce the publication.

REFERANCE

[1] Physiological and Molecular Plant Pathology, 2023

[2] Arbona V., Manzi M., Zandalinas S.I., Vives-Peris V., Pérez-Clemente R.M., Gómez-Cadenas A. Physiological, metabolic, and molecular responses of plants to abiotic stress. In: Al-Khayri J.M., Ansari M.I., Singh A.K., editors. *Stress Signaling in Plants: Genomics and Proteomics Perspective*. Volume 2. Springer; Cham, Switzerland: 2017. pp. 1–35. [CrossRef] [Google Scholar]

[3] Sachdev S., Ahmad S. *NanoBiotechnology*. Springer; Berlin/Heidelberg, Germany: 2021. Role of Nanomaterials in Regulating Oxidative Stress in Plants; pp. 305–326. [CrossRef] [Google Scholar]

[4] Bidi H., Fallah H., Niknejad Y., Tari D.B. Iron oxide nanoparticles alleviate arsenic phytotoxicity in rice by improving iron uptake,

oxidative stress tolerance and diminishing arsenic accumulation. *Plant Physiol. Biochem.* 2021;163:348–357. doi: 10.1016/j.plaphy.2021.04.020. [PubMed] [CrossRef] [Google Scholar]

[5] Ahmad J., Qamar S., Kausar N., Qureshi M.I. *Nanotechnology in the Life Sciences*. Springer; Berlin/Heidelberg, Germany: 2020. Nanoparticles: The Magic Bullets in Mitigating Drought Stress in Plants; pp. 145–161. [CrossRef] [Google Scholar]

[6] González-García Y., González-Moscoso M., Hernández-Hernández H., Méndez-López A., Juárez-Maldonado A. *Nanotechnology in Plant Growth Promotion and Protection*. John Wiley & Sons Ltd.; Hoboken, NJ, USA: 2021. Induction of stress tolerance in crops by applying nanomaterials; pp. 129–169. [Google Scholar]

[7] Rajput V., Minkina T., Kumari A., Harish, Singh V., Verma K., Mandzhieva S., Sushkova S., Srivastava S., Keswani C. *Coping with the Challenges of Abiotic Stress in Plants: New Dimensions in the Field Application of Nanoparticles*. *Plants*. 2021;10:1221. doi: 10.3390/plants10061221. [PMC free article] [PubMed] [CrossRef] [Google Scholar]

[8] Sarraf M., Vishwakarma K., Kumar V., Arif N., Das S., Johnson R., Janeeshma E., Puthur J.T., Aliniaiefard S., Chauhan D.K., et al. *Metal/Metalloid-Based Nanomaterials for Plant Abiotic Stress Tolerance: An Overview of the Mechanisms*. *Plants*. 2022;11:316. doi: 10.3390/plants11030316. [PMC free article] [PubMed] [CrossRef] [Google Scholar]

[9] Kandhol N., Jain M., Tripathi D.K. Nanoparticles as potential hallmarks of drought stress tolerance in plants. *Physiol. Plant*. 2022;174:e13665. doi: 10.1111/ppl.13665. [PubMed] [CrossRef] [Google Scholar]

[10] Zandalinas S.I., Fritschi F.B., Mittler R. Global Warming, Climate Change, and Environmental Pollution: Recipe for a Multifactorial Stress Combination Disaster. *Trends Plant Sci.* 2021;26:588–599. doi: 10.1016/j.tplants.2021.02.011. [PubMed] [CrossRef] [Google Scholar]

[11] Zhang H., Zhu J., Gong Z., Zhu J.-K. Abiotic stress responses in plants. *Nat. Rev. Genet.*

- 2022;23:104–119. doi: 10.1038/s41576-021-00413-0. [PubMed] [CrossRef] [Google Scholar]
- [12] Marothia D., Kaur N., Pati P.K. Abiotic Stress in Plants. IntechOpen; London, UK: 2021. Abiotic Stress Responses in Plants: Current Knowledge and Future Prospects; pp. 1–18. [CrossRef] [Google Scholar]
- [13] Cramer G.R., Urano K., Delrot S., Pezzotti M., Shinozaki K. Effects of abiotic stress on plants: A systems biology perspective. *BMC Plant Biol.* 2011;11:163. doi: 10.1186/1471-2229-11-163. [PMC free article] [PubMed] [CrossRef] [Google Scholar]
- [14] Molassiotis A., Fotopoulos V. Oxidative and nitrosative signaling in plants: Two branches in the same tree? *Plant Signal. Behav.* 2011;6:210–214. doi: 10.4161/psb.6.2.14878. [PMC free article] [PubMed] [CrossRef] [Google Scholar]
- [15] Mohanta T.K., Bashir T., Hashem A., Abd_Allah E.F., Khan A.L., Al-Harrasi A.S. Early Events in Plant Abiotic Stress Signaling: Interplay Between Calcium, Reactive Oxygen Species and Phytohormones. *J. Plant Growth Regul.* 2018;37:1033–1049. doi: 10.1007/s00344-018-9833-8. [CrossRef] [Google Scholar]
- [16] Zhang H., Zhao Y., Zhu J.-K. Thriving under Stress: How Plants Balance Growth and the Stress Response. *Dev. Cell.* 2020;55:529–543. doi: 10.1016/j.devcel.2020.10.012. [PubMed]
- [17] Isayenkov S.V., Maathuis F.J.M. Plant Salinity Stress: Many Unanswered Questions Remain. *Front. Plant Sci.* 2019;10:80. doi: 10.3389/fpls.2019.00080. [PMC free article] [PubMed] [CrossRef] [Google Scholar]
- [18] 18.. Mahmood R., Ijaz M., Qamar S., Bukhari S.A., Malik K. Abiotic stress signaling in rice crop. In: Mirza H., Masayuku F., Kamrun N., Jiban B., editors. *Advances in Rice Research for Abiotic Stress Tolerance*. Woodhead Publishing; Sawston, UK: 2019. pp. 551–569. [Google Scholar]
- [19] Mohamed H.I., Sajyan T.K., Shaalan R., Bejjani R., Sassine Y.N., Basit A. Plant-mediated copper nanoparticles for agri-ecosystem applications. In: Kamel A.A., Rajiv P., Rajeshkumar S., editors. *Agri-Waste and Microbes for Production of Sustainable Nanomaterials*. Elsevier; Amsterdam, The Netherlands: 2022. pp. 79–120. [Google Scholar]
- [20] Dong F., Yang F., Liu Y., Jia W., He X., Chai J., Zhao H., Lv M., Zhao L., Zhou S. Calcium Transport Elements in Plants. Academic Press; Cambridge, MA, USA: 2021. Calmodulin-binding transcription activator (CAMTA)/factors in plants; pp. 249–266. [Google Scholar]
- [21] Sinha R.K., Verma S.S. Stress Tolerance in Horticultural Crops. Woodhead Publishing; Sawston, UK: 2021. Proteomics approach in horticultural crops for abiotic-stress tolerance; pp. 371–385. [CrossRef] [Google Scholar]
- [22] Khan I., Raza M.A., Awan S.A., Shah G.A., Rizwan M., Ali B., Tariq R., Hassan M.J., Alyemeni M.N., Brestic M., et al. Amelioration of salt induced toxicity in pearl millet by seed priming with silver nanoparticles (AgNPs): The oxidative damage, antioxidant enzymes and ions uptake are major determinants of salt tolerant capacity. *Plant Physiol. Biochem.* 2020;156:221–232. doi: 10.1016/j.plaphy.2020.09.018. [PubMed] [CrossRef] [Google Scholar]
- [23] Rossi L., Zhang W., Ma X. Cerium oxide nanoparticles alter the salt stress tolerance of *Brassica napus* L. by modifying the formation of root apoplastic barriers. *Environ. Pollut.* 2017;229:132–138. doi: 10.1016/j.envpol.2017.05.083. [PubMed] [CrossRef] [Google Scholar]
- [24] Ozturk M., Unal B.T., García-Caparrós P., Khursheed A., Gul A., Hasanuzzaman M. Osmoregulation and its actions during the drought stress in plants. *Physiol. Plant.* 2020;172:1321–1335. doi: 10.1111/ppl.13297. [PubMed] [CrossRef] [Google Scholar]
- [25] Farooq M., Hussain M., Wahid A., Siddique K.H.M. *Plant Responses to Drought Stress*. Springer; Berlin/Heidelberg, Germany: 2012. Drought stress in plants: An overview; pp. 1–33. [Google Scholar]
- [26] Zhang H., Zhao Y., Zhu J.-K. Thriving under Stress: How Plants Balance Growth and the Stress Response. *Dev. Cell.* 2020;55:529–543. doi: 10.1016/j.devcel.2020.10.012. [PubMed] [CrossRef] [Google Scholar]
- [27] Kandhol N., Jain M., Tripathi D.K. Nanoparticles as potential hallmarks of drought stress tolerance in plants. *Physiol. Plant.* 2022;174:e13665. doi: 10.1111/ppl.13665. [PubMed] [CrossRef] [Google Scholar]

- [28] Alabdallah N.M., Hasan M., Hammami I., Alghamdi A.I., Alshehri D., Alatawi H.A. Green Synthesized Metal Oxide Nanoparticles Mediate Growth Regulation and Physiology of Crop Plants under Drought Stress. *Plants*. 2021;10:1730. doi: 10.3390/plants10081730. [PMC free article] [PubMed] [CrossRef] [Google Scholar]
- [29] Zahedi S.M., Hosseini M.S., Meybodi N.D.H., Peijnenburg W. Mitigation of the effect of drought on growth and yield of pomegranates by foliar spraying of different sizes of selenium nanoparticles. *J. Sci. Food Agric*. 2021;101:5202–5213. doi: 10.1002/jsfa.11167. [PubMed] [CrossRef] [Google Scholar]
- [30] El-Zohri M., Al-Wadaani N.A., Bafeel S.O. Foliar Sprayed Green Zinc Oxide Nanoparticles Mitigate Drought-Induced Oxidative Stress in Tomato. *Plants*. 2021;10:2400. doi: 10.3390/plants10112400. [PMC free article] [PubMed] [CrossRef] [Google Scholar]
- [31] Bishta S., Sharma V., Kumari N. Biosynthesized magnetite nanoparticles from *Polyalthia longifolia* leaves improve photosynthetic performance and yield of *Trigonella foenum-graecum* under drought stress. *Plant Stress*. 2022;5:100090. doi: 10.1016/j.stress.2022.100090. [CrossRef] [Google Scholar]
- [32] Potter M., Deakin J., Cartwright A., Hortin J., Sparks D., Anderson A.J., McLean J.E., Jacobson A., Britt D.W. Absence of Nanoparticle-Induced Drought Tolerance in Nutrient Sufficient Wheat Seedlings. *Environ. Sci. Technol*. 2021;55:13541–13550. doi: 10.1021/acs.est.1c00453. [PubMed] [CrossRef] [Google Scholar]
- [33] Aslam M., Fakher B., Ashraf M.A., Cheng Y., Wang B., Qin Y. Plant Low-Temperature Stress: Signaling and Response. *Agronomy*. 2022;12:702. doi: 10.3390/agronomy12030702. [CrossRef] [Google Scholar]
- [34] Mohammadi R., Maali-Amiri R., Abbasi A. Effect of TiO₂ Nanoparticles on Chickpea Response to Cold Stress. *Biol. Trace Elem. Res*. 2013;152:403–410. doi: 10.1007/s12011-013-9631-x. [PubMed] [CrossRef] [Google Scholar]
- [35] Mohammadi R., Maali-Amiri R., Mantri N. Effect of TiO₂ nanoparticles on oxidative damage and antioxidant defense systems in chickpea seedlings during cold stress. *Russ. J. Plant Physiol*. 2014;61:768–775. doi: 10.1134/S1021443714050124. [CrossRef] [Google Scholar]
- [36] Amini S., Maali-Amiri R., Mohammadi R., Shahandashti S.-S.K. cDNA-AFLP Analysis of Transcripts Induced in Chickpea Plants by TiO₂ Nanoparticles during Cold Stress. *Plant Physiol. Biochem*. 2017;111:39–49. doi: 10.1016/j.plaphy.2016.11.011. [PubMed] [CrossRef] [Google Scholar]
- [37] Hasanpour H., Maali-Amir R., Zeinali H. Effect of TiO₂ nanoparticles on metabolic limitations to photosynthesis under cold in chickpea. *Russ. J. Plant Physiol*. 2015;62:779–787. doi: 10.1134/S1021443715060096. [CrossRef] [Google Scholar]
- [38] Elsheery N.I., Sunoj V., Wen Y., Zhu J., Muralidharan G., Cao K. Foliar application of nanoparticles mitigates the chilling effect on photosynthesis and photoprotection in sugarcane. *Plant Physiol. Biochem*. 2020;149:50–60. doi: 10.1016/j.plaphy.2020.01.035. [PubMed] [CrossRef] [Google Scholar]
- [39] Yadav S.K. Heavy metals toxicity in plants: An overview on the role of glutathione and phytochelatins in heavy metal stress tolerance of plants. *S. Afr. J. Bot*. 2010;76:167–179. doi: 10.1016/j.sajb.2009.10.007. [CrossRef] [Google Scholar]
- [40] Tiwari S., Lata C. Heavy Metal Stress, Signaling, and Tolerance Due to Plant-Associated Microbes: An Overview. *Front. Plant Sci*. 2018;9:452. doi: 10.3389/fpls.2018.00452. [PMC free article] [PubMed] [CrossRef] [Google Scholar]
- [41] Singh A., Tiwari S., Pandey J., Lata C., Singh I.K. Role of nanoparticles in crop improvement and abiotic stress management. *J. Biotechnol*. 2021;337:57–70. doi: 10.1016/j.jbiotec.2021.06.022. [PubMed] [CrossRef] [Google Scholar]
- [42] Iqbal M., Raja N.I., Mashwani Z.-U., Hussain M., Ejaz M., Yasmeen F. Effect of silver nanoparticles on growth of wheat Under Heat Stress. *Iran. J. Sci. Technol. Trans. A Sci*. 2019;43:387–395. doi: 10.1007/s40995-017-0417-4. [CrossRef] [Google Scholar]
- [43] Hassanisaadi M., Barani M., Rahdar A., Heidary M., Thysiadou A., Kyzas G.Z. Role of

agrochemical-based nanomaterials in plants: Biotic and abiotic stress with germination improvement of seeds. *Plant Growth Regul.* 2022;97:375–418. doi: 10.1007/s10725-021-00782-w. [CrossRef] [Google Scholar]

[44] Palmqvist N.M., Seisenbaeva G.A., Svedlindh P., Kessler V.G. Maghemite Nanoparticles acts as nanozymes, improving growth and abiotic stress tolerance in *Brassica napus*. *Nanoscale Res. Lett.* 2017;12:631. doi: 10.1186/s11671-017-2404-2. [PMC free article] [PubMed] [CrossRef] [Google Scholar]

[45] Zhang J.-H., Huang W.-D., Yue-Ping L.I.U., Qiu-Hong P.A.N. Effects of temperature acclimation pretreatment on the ultrastructure of mesophyll cells in young grape plants (*Vitis Vinifera* L. Cv. Jingxiu) under cross-temperature stresses. *J. Integ. Plant Biol.* 2005;47:959–970. doi: 10.1111/j.1744-7909.2005.00109.x. [CrossRef] [Google Scholar]

[46] Qi M., Liu Y., Li T. Nano-TiO₂ improve the photosynthesis of tomato leaves under mild heat stress. *Biol. Trace Elem. Res.* 2013;156:323–328. doi: 10.1007/s12011-013-9833-2. [PubMed] [CrossRef] [Google Scholar].

[47] Al-Khayri JM, Rashmi R, Surya Ulhas R, Sudheer WN, Banadka A, Nagella P, Aldaej MI, Rezk AA, Shehata WF, Almaghasla MI. The Role of Nanoparticles in Response of Plants to Abiotic Stress at Physiological, Biochemical, and Molecular Levels. *Plants (Basel)*. 2023 Jan 7;12(2):292. doi: 10.3390/plants12020292. PMID: 36679005; PMCID: PMC9865530.