

REVIEW

Open Access



Nanomaterial strategies for enhancing plant resilience in the face of temperature stress

Amanpreet K. Sidhu^{1*}, Madhvi Sharma^{1*} , Sanskruthi Bhickchand Agrawal², Pranita Bhavsar³ and Mahesh Kumar Samota⁴

Abstract

Plant growth and productivity are greatly impacted by temperature stress, both high and low. These stresses impair biochemical, physiological, and molecular processes in the plant, eventually affecting plant growth, development, and productivity. Consequently, novel approaches are needed to overcome these problems and achieve sustainability. Nanotechnology is one such novel approach to improving crop production, by using nanoscale products. Nanoparticle size, nature, application mode, environmental conditions, rhizospheric and phyllospheric environments, and the species of plant make a significant impact on their action. With their easy soluble nature, smaller size, and excellent ability to penetrate plants, and their ability to cross cellular barriers, nanoparticles have become an increasingly popular agricultural tool. It has recently been observed that silver, silicon, titanium, and selenium nanoparticles can alter the physiological and biochemical response of plants in order to counteract high or low temperature stress. In this review, a description is provided of how nanoparticles are absorbed in different plant parts and how they are translocate along with the factors that influence their uptake and translocation. Also how plant response to nanoparticles in temperature stress and the various types of physiological, morphological, anatomical, biochemical and molecular modifications caused by nanoparticles. The review is going to provide researchers in agricultural sciences a glimpse into how to discover new nanoparticles to deal with heat stress.

Keywords Heat stress, Nanoparticles, Translocation, Silver, Titanium, Plants, Physiological, Molecular processes

Introduction

Temperature stress affects plant growth, development, and ultimately crop productivity, making it a major challenge to global agriculture. In plants, temperature is one

of the major abiotic stresses that limit growth and production (Hedhly et al. 2009). When plants are exposed extreme temperatures, they suffer from severe adverse effects, and sometimes even die. It is for this reason that plants have evolved sophisticated mechanisms to deal with temperature extremes. For instance there are several physiological processes affected adversely by heat stress, including respiration, transpiration, membrane thermo stability, and osmotic regulation (Liu et al. 2020, Akter et al. 2017). The presence of heat stress generally reduces photosynthetic efficiency, shortening the life cycle and decreasing productivity of plants (Hasanuzzaman et al. 2013; Hu et al. 2020a, b; Kumar et al. 2020). Yet, while much focus has been on addressing heat stress, the impact of low-temperature episodes, exacerbated by climate change, cannot be overlooked. Extremely

*Correspondence:

Amanpreet K. Sidhu
aman.preet1807@gmail.com

Madhvi Sharma
madhvisharma413@gmail.com

¹ Department of Biotechnology, Khalsa College, Amritsar, Punjab 143009, India

² Department of Biotechnology, K.T.H.M. College, Nashik, Maharashtra 422009, India

³ National Centre for Cell Science, SPPU Campus, Ganeshkhind Road, Pune 411007, India

⁴ ICAR-Central Institute of Post-Harvest Engineering and Technology, Regional Station, Abohar 152116, India



© The Author(s) 2024. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>. The Creative Commons Public Domain Dedication waiver (<http://creativecommons.org/publicdomain/zero/1.0/>) applies to the data made available in this article, unless otherwise stated in a credit line to the data.

low temperatures also have a significant effect on plant growth through physiological, anatomical, and morphological changes that alter nutrient uptake, root architecture, cell division, photosynthesis, water transport, and phytohormonal signaling (Ahmed et al. 2024). It is therefore a goal of Germplasm scientists and agronomists to develop extreme temperature tolerant varieties or cultivars in order to adapt to these effects and reduce their impact. A combination of conventional breeding techniques and physiological and biotechnological tools might be used to select and develop heat-tolerant genotypes that are more productive (Saeed et al. 2023). In recent years, advances in agricultural nanotechnology have raised expectations for sustainable productivity without altering the genetic make-up of plants. The study of nanotechnology is the field of material science that is the most dynamic, and nanoparticle (NP) production is rising quickly globally. Because of certain characteristics like size (1–100 nm), shape, and structure, nanoparticles exhibit entirely new or improved properties (Nejatzadeh 2021; Taran et al. 2017). The two types of nanoparticles that can be synthesized are inorganic and organic. Metallic nanoparticles like Au, Ag, Cu, Al, magnetic nanoparticles like Co, Fe, Ni, and semi-conductor nanoparticles like ZnO, ZnS, and CdS are examples of inorganic nanoparticles, whereas carbon nanoparticles like chitosan, cellulose acetate, quantum dots and carbon nanotubes are examples of organic nanoparticles (Taran et al. 2017; Chouhan 2018; Wang et al. 2021; Lima et al. 2022). These NPs can be used to produce sustainable crop yields because nanoparticles have unique properties (Nejatzadeh 2021, Parisi et al. 2015) such as more surface area, which increases the availability and promotes greater uptake of fertilizers by plants. This decreases fertilizer losses from leaching, emissions, and long-term incorporation by soil microorganisms (Liu et al. 2006, DeRosa et al. 2010). A novel method of increasing crop heat tolerance could be using biologically active nanoparticles (NPs). Recent research has demonstrated that NPs from silver, silicon, titanium, and selenium can significantly alter the physiological and biochemical responses of plants under heat stress. Many researchers have periodically conducted a number of studies to determine whether nanomaterial's can be used to reduce temperature stress. Application of selenium nanoparticles in low concentrations has been found to mitigate the effects of heat stress by enhancing plant development, chlorophyll content, and hydration (Haghighi et al. 2014). Additionally, plants can benefit from the antioxidative properties of selenium nanoparticles at low concentrations, whereas oxidative stress was brought on by selenium nanoparticles at high concentrations (Hartikainen et al. 2000; Hasanuzzaman et al. 2014). During times of heat stress,

plants produce a number of molecular chaperones and heat shock proteins (Schulze et al. 2005). Heat shock proteins help other proteins maintain their fidelity in stressful situations and are involved in the resistance to heat stress (Wahid et al. 2007). Multiwall carbon nanotubes have been shown to increase the gene expression of heat shock proteins, such as HSP90 (Khodakovskaya et al. 2011). Furthermore, maize plants that were exposed to CeO₂ nanoparticles showed excessive H₂O₂ production and up regulation of HSP70 (Zhao et al. 2012a, b). Additionally, the use of TiO₂ nanoparticles via stomata opening regulation lessened the impact of heat stress (Qi et al. 2013). Therefore, this study aims to investigate, how nanoparticles are being absorbed by plants and its translocation mechanisms, how plants respond to nanoparticles in temperature Stress, the various modifications like physiological, morphological, anatomical, biochemical and molecular caused by nanoparticles. The phytotoxic effect of nanoparticles on plants and how plants grow under both natural and environmental stress conditions has also been discussed.

Plant nanoparticle absorption and translocation

Nanomaterials have garnered escalated interest in recent times owing to their distinctive physical and chemical characteristics, enabling their utilization as multifaceted materials. The application of nanomaterials in the agricultural sector for enhancing crop yield and environmental preservation has surfaced as an urgent requirement. Using nanoparticles to enhance crop growth involves a number of techniques, including root application, foliar application, and seed priming. Finding out the best way to apply nanoparticles and whether they can reach different plant tissues from the root to the shoot are highly interesting questions. Several factors contribute to the effects of nanoparticles, such as their size, composition, method of application, surrounding conditions, as well as the rhizospheric and phyllospheric settings, and the specific plant species. To successfully traverse cell barriers and membranes, nanoparticles must possess specific chemical, physical, and dosage characteristics, among other essential attributes. Surface chemical reactions such as ion exchange, surface precipitation, and physical adsorption are among the commonly observed processes for the uptake of nanoparticles (Singh et al. 2021). For instance, at the plant cell wall, the initial interaction between nanoparticles and plants takes place. The plant's cell wall is equipped with numerous pores, ranging in diameter from 5 to 20 nm, which govern particle mobility and contribute to the plant's filtration capabilities. Nanoparticles falling within this diameter range can readily penetrate plant cells. Conversely, nanoparticles of larger diameters engage with proteins and polysaccharides in

cell walls, leading to the formation of novel pores and pathways for entry (Ali et al. 2021, Alnaddaf et al. 2023, Farooq et al. 2024). It has been reported that osmotic pressure, capillary forces, and direct passage through the root epidermis are some of the reasons why small nanoparticles (size 3–5 nm) enter plant roots. Large nanoparticles cannot pass through the semipermeable epidermal cells found in the walls of root cells because of their small pores. Certain nanoparticles were discovered to induce the formation of new pores in epidermal cells, allowing the particles to enter the cells. (Nag et al. 2024, Arumugam et al. 2023, Rehman et al. 2024). The process of absorption of metal nanoparticles by plants involves ion exchange, chelation, chemical precipitation, and endocytosis (Maine et al. 2001; Tani and Barington 2005, Aslani et al. 2014, Hong et al. 2021, Zhang et al. 2024). Additionally, ion transporters, such as carrier proteins, aquaporins, and ion channels (Somasundaran et al. 2010; Yadav et al. 2014, Ahmad et al. 2022, Omar et al. 2023), have been observed as alternatives for metal nanoparticles uptake by plants. We can enhance our comprehension of the penetration of nanoparticles into cells by gaining insights into the lipid exchange process occurring between the nanoparticles and the cell envelope, as elucidated through the utilization of a mathematical framework known as Lipid Exchange Envelope Penetration (LEEP) (Wong et al. 2016; Lew et al. 2018; Wang et al. 2019a, b; Arya et al. 2021).. Plants uptake nanoparticles by traversing through the epidermis, cytoplasm, and nucleus within their cellular structure. The alteration of nutrient absorption may occur if nanoparticles initially not absorbed on the root surface of soil aggregates. Nanoparticles have the capability to infiltrate through the coat by means of parenchymatic intercellular spaces, subsequently diffusing within the cotyledon, and ultimately penetrating the seed coat directly. (Nair et al. 2010a, b, Wang et al. 2012, Banerjee et al. 2019, Singla et al. 2019, Ramírez Anguiano et al. 2023). The targeted tissue is reached by the nanoparticles via both apoplastic and symplastic pathways. According to several studies (Schwab et al. 2016a, b, Pérez-de-Luque et al. 2017, Hubbard et al. 2020, Wu et al. 2022) the corresponding membrane carrier protein typically makes it easier for the nanoparticles to pass through xylem channels. Additionally, nanoparticles need to get ahead of the stomata and cuticle in order to access the leaf's internal system. The cuticular pathway is followed by particles smaller than 5 nm, while the latter pathway is followed by particles larger than 5 nm. The internal transportation system of a leaf is similar to that of roots. According to Ruttkay-Nedecy et al. (2017), Millán-Chiu et al. (2020), nanoparticles enter leaves through cuticle, stomata, hydathodes, and wounded tissues. They are then transported by phloem

tubes via apoplastic and symplastic pathways to the desired location or organs, such as shoots, roots, and fruit. The penetration of nanoparticles is followed by the processes like endocytosis, pore formation and some of the carriers proteins also participate during the process (Zhang et al. 2024). Before nanoparticles are being taken by the plants, it interacts with soil and soil microorganisms. The complete illustration of the translocation process has been presented in the Fig. 1.

Mechanism of absorption of nanoparticles in plant roots

The mechanisms of nutrient and ion uptake into the root cytosol are simple diffusion, facilitated diffusion, and active transport, which all work by generating an osmotic potential across the membrane. Currently, the two most well-known mechanisms for root uptake are apoplast and symplast transport. In symplast transport, plasmodesmata are utilised to transfer ions or water between the cytosol of plant cells. In apoplast transport, the region of continuous cell walls found inside cells is used (Doran et al. 2013, Aslani et al. 2014, López-Valdez et al. 2018, Bhatla et al. 2023). It is still unknown how different NPs cross the plant membrane—through endocytosis or through aquaporins and plasmodesmata channels, and when they move using symplastic pathways. Even though different NPs can travel long distances through the xylem (from roots to leaves) and the phloem (from leaves to roots), it is still unknown how the NPs cross the plant membrane—through endocytosis, through aquaporins and plasmodesmata channels, and when they move using symplastic pathways (Tripathi et al. 2017a, b). The highest leaf-root transport is observed for the most soluble NPs (Schwab et al. 2016a, b), suggesting that transport and solubility are related. Avellan et al. (2019) demonstrated that Au-NP transport from wheat leaves to roots is feasible and that Au-NPs smaller than 50 nm were exuded into the soil, regardless of their coating and sizes. In another study AgNPs of 40 nm were discovered accumulated in and around Arabidopsis root tip regions such as border cells, columella cells, root cap, axial/lateral root cap, and epidermis. The follow-up studies proposed that AgNPs were initially attached to the Arabidopsis primary roots surface during the initial phases of NPs exposure and later entered the root tips (Geisler-Lee et al. 2014, 2012; Schwab et al. 2016a, b; Zhai et al. 2014). Comparably, before entering the epidermis and after penetrating the root cortex of maize plants, a high concentration of ZnONPs aggregates was seen. In the root endodermis and later closer to the Casparian strip, a trace amount of ZnONPs aggregate was also detected (Schwab et al. 2016a, b; L. Zhao et al. 2012a, b) (Fig. 2).

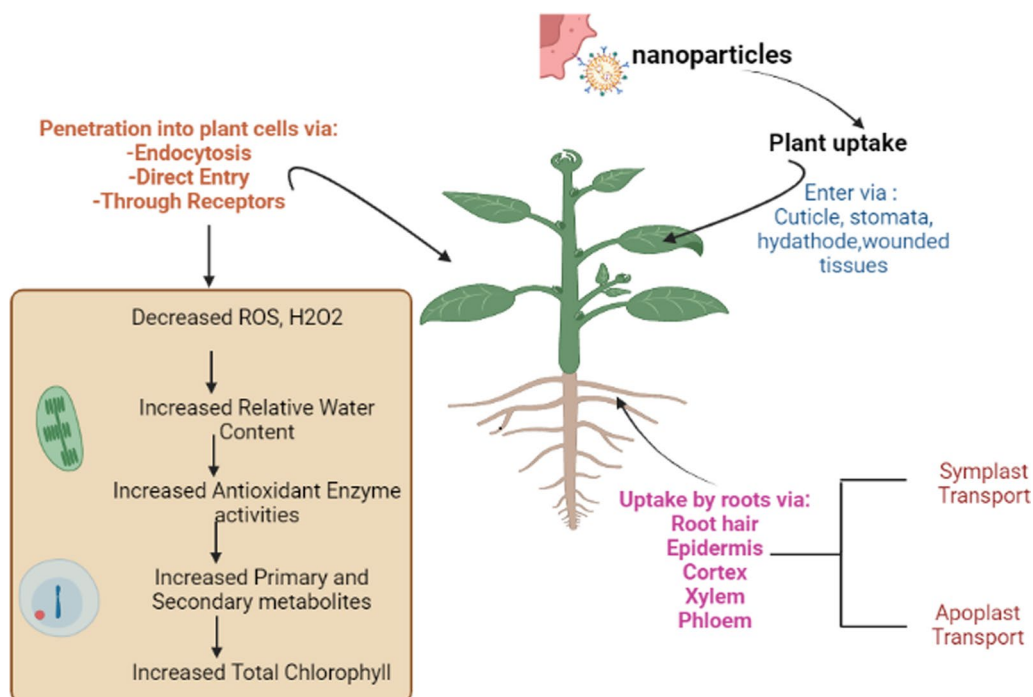


Fig. 1 The small NPs enter plant roots through root epidermal cells, capillary forces, or osmotic pressure. The semipermeable root cell wall's epidermal cells contain small pores that limit the movement of large NPs. Some NPs caused the epidermal cell wall to develop new pores, which aided in its entrance. NPs are apoplastically transported through extracellular spaces after passing through cell walls, eventually arriving at the central vascular cylinder and enabling the xylem to ascend unidirectionally. However, in order for NPs to enter the central vascular cylinder, they must symplastically cross the Casparian strip barrier. This is accomplished by endocytosis, pore formation, and transport, which bind to the carrier proteins of the endodermal cell membrane

Mechanism of foliar uptake of nanoparticles by plants

When used in agriculture, nanoparticles are usually sprayed onto the leaf surface where they deposit. From there, the plants absorb the particles through their stomata or cuticle (Yashveer et al. 2022). Plants need time to absorb and disperse NPs, which are primarily absorbed through foliar and root uptake by the xylem and phloem systems after being first taken up by the leaves or roots of the plant. The two most prevalent foliar uptake pathways are stomatal and cuticular. The cuticular pathway is composed of two parallel pathways: the lipophilic and hydrophilic uptake pathways. While the lipophilic pathway involves the diffusion of lipid-loving apolar and non-charged molecules in cutin and waxes, the hydrophilic pathway involves the dissolution of water-loving polar or ionic molecules through aqueous pores with a diameter of 0.6–4.8 nm. However, the stomatal pathway is a solid-state pathway that permits the hydrophilic and suspended molecules to be absorbed through diffusion (Uzu et al. 2010; Khan, et al. 2022a, b). Hu et al. 2020a, b, recently demonstrated, using confocal fluorescence microscopy with high spatial and temporal resolution, that carbon dots smaller than 2 nm could penetrate cotton leaves

through the cuticular pathway. However, plants can only absorb a certain amount of nanoparticles through the epidermis because of the tiny pore channels in the cuticle. The absorption behaviour of nanoparticles in plant leaves can be influenced by their characteristics, including size, chemical makeup, surface charge, and surface modification. For example, Zhu et al. 2020, applied 30 nm ZnO nanoparticles labelled with fluorescein isothiocyanate (FITC) to wheat leaves. Using confocal microscopy, they discovered that zinc oxide nanoparticles mostly entered wheat leaves through the stomata pathway and accumulated in the chloroplasts. Additionally, they looked into how stomatal opening and closing affected ZnO NP absorption. Avelian et al. 2019, applied coating-modified gold nanoparticles with varying diameters (3, 10, 50 nm) to wheat leaves. They discovered that wheat (*Triticum aestivum* cv. cumberland) leaves could absorb the coated gold nanoparticles of all sizes. Similar to this, AgNPs accumulation was seen in the cotyledons of Arabidopsis seedlings (Geisler-Lee et al. 2014; Larue et al. 2014; Avellan et al. 2021; Rani, et al. 2023; Guo et al. 2023). In another study, Rapeseed, maize, and lettuce were found to accumulate AuNPs, TiO₂NPs, CeO₂NPs, and PbNPs

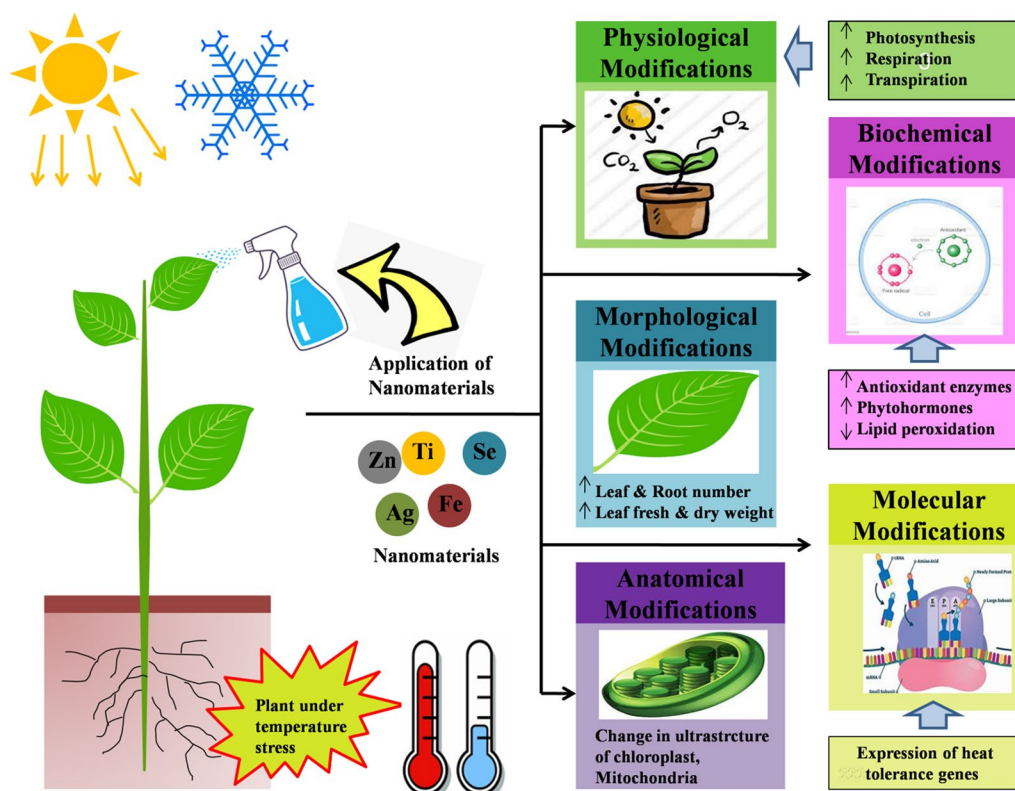


Fig. 2 Plants under temperature stress respond differently to nanoparticles applied to them; these responses assist the plant in overcoming the damage caused by high and low temperatures, as well as in acclimating to the temperature stress condition. Plants exhibit a variety of modifications, including: 1. Physiological modifications, which include an increase in the rate of photosynthesis, respiration, and transpiration; 2. Morphological changes that include an increase in the number of roots or leaves as well as an increase in their dry weight. 3. Anatomical changes such as changes in the ultrastructure of mitochondria and chloroplasts 4. Molecular modifications, such as heat tolerance gene expression; and 5. Biochemical modifications, such as antioxidant responses and phytohormone synthesis

aggregates in a manner similar to that described for foliar exposure (Larue et al. 2012; Yasmin et al. 2021).

Plant response to nanoparticles under temperature stress

The interaction between plants and nanoparticles in the context of temperature stress is a complex and emerging field of research. Nanoparticles, due to their unique physicochemical properties, can influence plant responses under temperature stress conditions. Temperature stress, whether in the form of heat or cold, can have profound effects on plant growth, development, and overall performance. Studies suggest that nanoparticles, when introduced to plants under temperature stress, may elicit both positive and negative responses. On the positive side, certain nanoparticles have been found to enhance the plant’s ability to cope with temperature extremes by acting as stress mitigators. These nanoparticles may facilitate improved water and nutrient uptake, enhance photosynthetic efficiency,

and bolster antioxidant defenses, thereby aiding the plant in adapting to temperature-induced challenges. Conversely, some nanoparticles may exacerbate the negative impacts of temperature stress on plants. They might interfere with cellular processes, disrupt membrane integrity, or induce oxidative stress, leading to impaired growth and reduced resilience to temperature extremes.

Understanding the intricate interplay between nanoparticles and plant responses under temperature stress is crucial for developing sustainable agricultural practices and optimizing nanoparticle applications in various environmental conditions. Further research is needed to elucidate the underlying mechanisms and identify nanoparticle characteristics that can be tailored for positive interactions with plants facing temperature stress, contributing to the development of resilient and adaptive crop varieties. Few modifications that are influenced by nanoparticles are explained below:

Physiological modifications under the influence of nanoparticles

Heat stress has a negative impact on a wide range of physiological processes, including photosynthesis, respiration, transpiration, osmotic regulation and reproductive capacity. One of the most heat sensitive physiological processes in plants is photosynthesis. It has been reported that the thylakoid membrane is damaged during heat stress, and important photosynthetic enzymes like 1, 5-bisphosphate carboxylase and Rubisco are inhibited. Given that the PSII complex is the most heat-intolerant, photosystem II (PSII) activity is significantly decreased or even completely stopped under HS (Song et al. 2014; Zhao et al. 2021a, b). Various nanoparticles have been reported to affect plant physiology under temperature stress.

Qi et al (2013) had presented a detailed account on use of Nano-TiO₂ in improving photosynthesis in tomato leaves under heat stress. The application of nano-TiO₂ increased the net photosynthetic rate, conductance to H₂O, and transpiration rate of tomato leaves. Additionally, it significantly reduced the relative electron transport in leaves and the minimum chlorophyll fluorescence. Under moderate heat stress, Nano-TiO₂ increased the energy dissipation of the regulated photosystem II (PS II) and decreased the energy dissipation of the non-regulated PS II.

One of the most widely explored nanomaterials is Nano-Selenium; the effect of it has been studied both under heat and cold stress. El-Saadony et al. (2021) have reported that under high temperature, the wheat treated with Bio-SeNPs (100 g/mL) had a 12–32% increase in total carotenoids and chlorophyll compared to control. Additionally, the gas exchange parameters transpiration (Tr), the stomata's conductance (gs) and net photosynthesis (Pn) have improved remarkably. According to a recently published research study, green synthesis of SeNPs was achieved using a *Lactobacillus casei* bacterial strain with dimensions ranging from 50 to 100 nm. They found that biogenic SeNPs improve the growth, physiological, and biochemical profiles of two sensitive chrysanthemum cultivars (sensual and Francofone) when subjected to heat stress (up to 41.6 °C). Additionally, the nano-Se-treated cut chrysanthemum flowers exposed to heat stress demonstrated the positive effects of nan-Se on flower quality and economic value (Seliem et al. 2020). Another study found that SeNPs reduce the negative effects of heat stress in grain sorghum. They discovered that foliar applications of 10 mg/L SeNPs to sorghum during the booting stage under heat stress improved the anti-oxidative defense system by improving the antioxidant enzyme action potential. Besides, SeNPs reduce high-temperature stress by increasing pollen

germination, seed set percentage, seed yield, photosynthetic rate, and decreasing oxidative stress (Djanaguira-man et al. 2018a, b).

In one comparative study, NPs such as silicon dioxide (nSiO₂; 5–15 nm), zinc oxide (nZnO;<100 nm), selenium (nSe; 100 mesh), graphene (graphene nanoribbons [GNRs] alkyl functionalized; 2–15 μm × 40–250 nm) were applied as foliar sprays on sugarcane leaves to understand the amelioration effect of NPs against negative impact of chilling stress on photosynthesis and photo protection. By maintaining the maximum photochemical efficiency of PSII (Fv/Fm), maximum photo-oxidizable PSI (Pm), and photosynthetic gas exchange, NPs treatments lessened the negative effects of chilling. Additionally, seedlings treated with NPs contained more light-harvesting pigments (chlorophylls and carotenoids). The nonphotochemical quenching (NPQ) of PSII was improved in seedlings treated with NPs due to higher carotenoid accumulation in the leaves. The nSiO₂ had the greatest amelioration effects of the NPs (Elsheery et al. 2020).

In mung bean, Kareem et al. (2022a) discovered that temperature increases above 28–30 °C, especially during the flowering stage, can disturb the plant's potential performance. The heat-stressed crops received a foliar spray of ZnO nanoparticles at various concentrations (0, 15, 30, 45, and 60 mg L⁻¹). The use of nano-ZnO NPs at high temperatures increased chlorophyll activity, gas exchange parameters, and enzymatic balance, resulting in an increase in pod number, size, and total grain yield, according to the researchers. Treatments with exogenous AgNPs have also demonstrated to increase plants' tolerance to cold temperatures. For instance, green beans exhibited quick and uniform germination in laboratory and field settings when exposed to low concentrations of AgNPs (0.25, 1.25 mg dm⁻³) under high temperature stress, which was evidently beneficial as evidenced by an increase in plant height, fresh and dry weight, and photosynthesis (Prazak et al. 2020).

Morphological modifications under the influence of nanoparticles

The morphological signs of heat stress include scorching and sunburns of leaves, twigs, branches, and stems, shoot and root growth inhibition, leaf senescence and abscission, fruit discoloration and damage (Rodríguez et al. 2005). NPs are effectively used as a nutrient source due to increased biomass production brought on by the amplification of metabolic, photocatalytic, and light energy conversion processes. TheTiO₂NP treatment, mung bean seedlings showed a noticeable increase in their shoot, root, and root nodule lengths as well as their total soluble protein and chlorophyll contents in the leaves. (Raliya et al. 2015). Under heat stress, the application of

biologically synthesized Ag-NPs at concentrations ranging from 25 to 75 mg/L resulted in a significant increase in plant fresh and dry weight, root and shoot length, leaf area, leaf number, leaf fresh weight, and leaf dry weight. At 100 mg/L, however, all of these characteristics showed a significant decrease (Iqbal et al. 2019).

Anatomical modifications under the influence of nanoparticles

Abiotic stress causes various anatomical changes in plants. The type of abiotic stress affects the anatomical reactions. Under heat stress, cells shrink, stomata close, and transcription rates slow down, but stomatal and trichomatous densities rise and larger xylem vessels are seen in the roots and shoots (Bañon et al. 2004). Nanoparticle application aids in the plant's anatomical adaptations, which helps the plant survive in stressful situations. In order to prevent heat-induced damage and maintain better plant growth, ZnO NPs were applied to alfalfa seedlings before they were put under heat stress. Application of 90 mg/L of ZnO nanoparticles before the onset of heat stress was more successful at reversing the ultra structural changes to chloroplast, mitochondria, and cell wall caused by the high temperature (Kareem et al. 2022b). Anatomical observations in heat stressed *Postia* plants show that the Multiwalled carbon nano tubes (MWCNTs) 200 mg/L treatment significantly slowed stomatal closure, and the stomata remained partially open, whereas the stomata remained close in control plants. Furthermore, the treatment significantly reduced mesophyll cell and chloroplast damage (Zhao et al. 2021a, b).

Responses at the molecular levels

Crop productivity is directly impacted by the regulation of plant stress response, which is mediated by gene expression and consequently affects the production of enzymes and proteins. Numerous proteins, transcription factors, and genes control how well an organism can withstand temperature stress. The stimulation of expression, whether it is up regulation or down regulation, has a direct impact on plant survival (Khalid et al. 2022). According to reports, treating plants with NPs when they are under temperature stress reduces the stress by triggering one or more molecular reactions.

The effects of silicon dioxide nanoparticles (SiNPs) and potassium silicate (K_2SiO_3) at concentrations of 1.66 mM and 1.5 mM respectively on wheat (*Triticum aestivum* L.) seedlings under heat stress (45 °C, 4 h) were evaluated in the study by Younis et al. (2020). The results of the reverse transcription polymerase chain reaction (RT-PCR) revealed that Si treatment, but not SiNP treatment, stimulated the overexpression of the genes for the aquaporins TaPIP1 (*Triticum aestivum* plasma membrane

intrinsic protein) and TaNIP₂ (*Triticum aestivum* nodulin 26-like intrinsic protein) in *Triticum aestivum* in parallel (Younis et al. 2020). In one study, *Arabidopsis thaliana* seedlings were cultured in medium containing zinc oxide nanoparticles (ZnO-NPs) and then subjected to heat stress at 37 °C in order to study the molecular impact of ZnO nanoparticles during heat stress. The study involved TGS (transcriptional gene silencing) in aerial leafy tissues. In *Arabidopsis thaliana* seedlings grown under ZnO NPs and subjected to heat stress (37 °C), the alleviation of TGS-GUS (-glucuronidase) genes was significantly improved (Wu and Wang 2020).

Differential expression of the genes involved in cellular defense, chromatin modification, cell signaling, and transcriptional regulation was observed when *Cicer arietinum* L. (Chickpea) was treated with TiO₂NPs under cold stress (Amini et al. 2017). The most significant of these was the up-regulation of the genes encoding for the large and small subunits of RUBISCO, Chlorophyll a/b binding proteins, and Phosphoenolpyruvate Carboxylase (PEPC), which in turn caused an increase in photosynthesis, altered energy metabolism, and a decrease in H₂O₂ concentration (Hasanpour et al. 2015). Another study showed how ZnO nanoparticles affected rice's susceptibility to cold stress. ZnO NPs applied topically induced the expression of genes related to the CAT, SOD, and POD antioxidative system and transcription factors involved in the cooling response, basic leucine zipper, N-terminal. Additionally, a reduction in H₂O₂, MDA, and proline levels as well as an increase in the activity of the main antioxidant enzymes was observed (Song et al. 2021).

Biochemical modifications under the influence of nanoparticles

Nanoparticles (NPs) positively influence various morphological, physiological, and biochemical processes that adversely affect crop productivity and plant development under different abiotic stresses. Cold or freeze stress causes ice crystal damage, creates disorder in plant metabolism, and increases the production of reactive oxygen species (ROS), thereby resulting in oxidative stress in plants. On the other hand, heat stress reduces photosynthetic and transpiration efficiencies, negatively regulates root development, reduces water utilisation efficiency, and decreases crop productivity. In order to avoid excess heat or cold stress, plants have to evolve different strategies and complex regulatory mechanisms to survive harsh conditions. Besides improving plant growth, NPs also safeguard plants from various types of stress. The NPs can alter the protein structures by developing bonds between heavy metal and sulfahydryl groups, thus, altering the enzymatic activity and metabolic processes like DNA damage and lipid peroxidation (Djanaguiraman

et al. 2018a, b; Al-Khayri et al. 2023; Hasanuzzaman et al. 2013; El-Saadony et al. 2022). Recent research has revealed that the NP seems to have a direct impact on the biochemical modifications of plants by modulating the antioxidant response and regulating phytohormone signalling under abiotic stress conditions.

Modulation of antioxidant response

Most of the enzymes are sensitive to various degrees of temperature, thus affecting different metabolic pathways. Therefore, there might be an accumulation of unwanted and harmful ROS like superoxide anion, hydrogen peroxide, hydroxyl radical, singlet oxygen, and lipid peroxidation free radicals. ROS formation severely damages lipid membranes and other molecules like nucleic acids and proteins, causing the death of cells in plants. In response to heat stress, β -oxidation of fatty acids, galatolipids, and phospholipids releases aldehyde especially malondialdehyde (MDA) and causes degradation of plant cell membranes (Hasaan et al. 2018). As a result, NPs stimulates different ROS scavenging systems, including superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX), glutathione peroxidase (GPx), glutathione reductase, and guaiacol peroxidase, as well as non-enzymatic pathways (flavonoids, compounds, proline, and phenolic) (Djanaguiraman et al. 2018a, b). Several studies have reported that plants produce more antioxidant molecules when exposed to NPs (El-Saadony et al. 2022). NPs are absorbed by plants and form a metal component or cofactor of enzymes, making it an essential micronutrient for plants. NPs stimulate nanoenzymes, which restrict the production of ROS under stress conditions. NPs at an appropriate concentration alter the antioxidant enzyme activity to improve its performance against heat stress. NPs provide sustenance to plants and mitigate stress-induced damage by activating some enzymatic antioxidant mechanisms, such as the detoxification pathway.

Zinc (Zn) is a co-factor in SOD and performs the scavenging of superoxide radicals, thereby playing an essential role in stabilising cell membranes against oxidative stress. Hassan et al. reported Zn as a co-factor for CAT, a hydrogen peroxide scavenging enzyme protecting membrane lipids and proteins from peroxidation. Thus, Zn affects the enzyme stability of the ROS scavenging system, thereby protecting the cell membrane from permeability alterations (Hassan et al. 2018).

UV-B exerts several impacts on the biochemical and molecular processes of plants, resulting in a high accumulation of ROS. Nitric oxide (NO) gets triggered in response to ROS-mediated oxidative damage but is not sufficient to induce antioxidants like SOD and APX. However, the addition of NPs like Si greatly triggers NO,

so ultimately there is an enhanced level of antioxidants counterbalancing the level of ROS. Thus, UV-B-mediated stress can be mitigated by pre-addition of Si NPs, leading to up-regulation of antioxidants due to enhancement of NO levels in wheat plants. Also, Si NPs lowered MDA and electrolyte leakage, suggesting their role in membrane lipid peroxidation (Tripathi et al. 2017a, b). Ascorbate, a non-enzymatic antioxidant, actively participates in managing ROS levels in plants, especially by maintaining hydrogen peroxide inside the cell. NPs addition significantly overproduces ascorbate and proline, reducing the lethal impact of ROS under different stress conditions. Thakur et al. reported that pretreatment with ZnO and TiO₂ NPs led to increased antioxidant potential and higher production of non-enzymatic antioxidants like flavonols and phenols in wheat plants. Therefore, improved heat stress resistance can be achieved by pre-treatment of ZnO NP at a lower concentration (1.5 ppm) and TiO₂NPs at a 10 ppm concentration increases SOD and GPX activity thereby lowering MDA and H₂O₂ levels (Thakur et al. 2021).

In addition to oxidative damage, ROS can also serve in MAPK signal transduction for a range of stresses. ROS activated by Cu induces SIMK and SAMK pathway activation (Yuan et al. 2013). Se-NPs stimulated the antioxidant defense system in sorghum under high temperature stress, decreasing the enzyme activity of SOD, CAT, POX, and GPX. Also, Se-NPs improved pollen germination and maintained the lipid bilayer and fluidity by facilitating higher levels of unsaturated phospholipids (Djanaguiraman et al. 2018a, b). Different doses of Ag-NPs and Cu-NPs (500, 750, and 1000 ppm) induces activation of stress enzymes CAT, POD and phenylpropanoid pathway increasing total phenolic content in peanut leaves to reduces ROS (Santos-Espinoza et al. 2020).

Regulation of biosynthesis of phytohormones

Phytohormones, being the versatile regulators of plant growth and development, present an unexplored field in NPs-induced abiotic stress. The levels of phytohormones reflect the abiotic stress level in plants. The plant's hormonal balance and metabolic pathways get altered in response to abiotic stress. NPs may regulate phytohormone biosynthesis positively or negatively, depending on their levels (Fig. 3). Plant antioxidant systems are composed of salicylic acid, jasmonic acid, methyl jasmonate, ABA, and other plant hormones (Santos-Espinoza et al. 2020; Yuan et al. 2013). Although there are few reports on the alteration of phytohormones by nanoparticles under temperature stress, there are high chances the future research holds potential to reveal many beneficial relationships in this direction. In general, nanoparticles

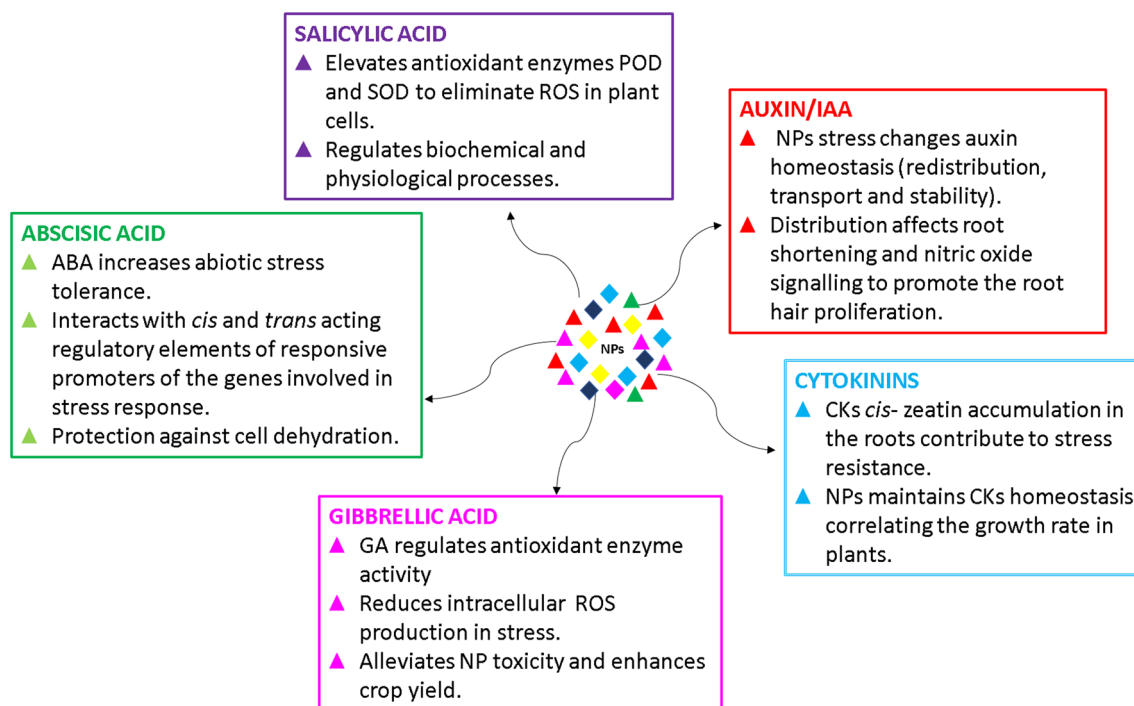


Fig. 3 Effect of NPs on regulation of biosynthesis of phytohormones. Plants sense nanoparticles (NPs) under severe stressed conditions and leads to elevation of stress hormone abscisic acid (ABA) and salicylic acid (SA); NPs gets accumulated in the apices and thus down-regulates growth due to decreased levels of auxin and cytokinins (CKs); Gibberellic acid (GA) reduces NPs accumulation by improving antioxidant response

are reported to cause changes in level of phytohormones expressed in plants.

For instance, plants sense nanoparticles (NPs) under severe stressed conditions and leads to elevation of stress hormone abscisic acid (ABA) and salicylic acid (SA); NPs gets accumulated in the apices and thus down-regulates growth due to decreased levels of auxin and cytokinins (CKs); Gibberellic acid (GA) reduces NPs accumulation by improving antioxidant response (Fig. 4).

NPs influence a wide range of auxin-regulated phenotypes, such as increased root hairs, inhibition of root elongation, and increased formation of lateral roots. It directly affects plant responses to stress through changes in auxin homeostasis, transport, and stability. Tryptophan, being the precursor for the Indole-3-acetic acid (IAA) synthesis pathway, regulates IAA levels required in many root functions. IAA is produced by the shoots and delivered to the root tips, where the redistribution occurs in an inverted fountain effect that allows the growth regulator to enter and exit the cells. IAA redistribution results in the accumulation of IAA in root tip cells and correlates with primary root elongation upon exposure of *Arabidopsis* roots to Cu ions (Yuan et al. 2013). Cu-NPs dissolution modifies IAA distribution in the rhizosphere, causing root shortening and nitric oxide signalling to promote the proliferation of root hairs (Adams et al.

2017). The auxin content was maintained in leaves during increased stress, and IAA levels were relatively high in the roots (Vankova et al. 2017; Santos-Espinoza et al. 2020).

Cytokinin, an essential phytohormone for plant growth and development, has also been conceded to play a significant role during plant acclimation to stress conditions. Stress tolerance in plants may be positively or negatively affected by cytokinins. It has been reported that cytokinins are most abundantly found in tissues exposed to various stresses (drought, heat). The cytokinin levels in plants are maintained by conversion between free bases, nucleosides, and nucleotides and by their inactivation, degradation, translocation, and de-novo synthesis. There was a significant increase in total cytokinins in the leaves of pepper plants treated with Ag-NPs, which affected their development by decreasing both plant height and biomass. It was suggested that the inhibition of plant growth may not have been caused directly by the phytotoxicity of Ag-NPs but rather by the interactions between plant transport pathways and Ag-NPs (Vinkovi et al. 2017). The cytokinin content in the roots and apices of *Arabidopsis* was increasing at higher ZnO-NPs levels due to the accumulation of *cis*-zeatin (Vankova et al. 2017).

Gibberellic acid (GA), an important signaling phytohormone, enhances plant development and physiological

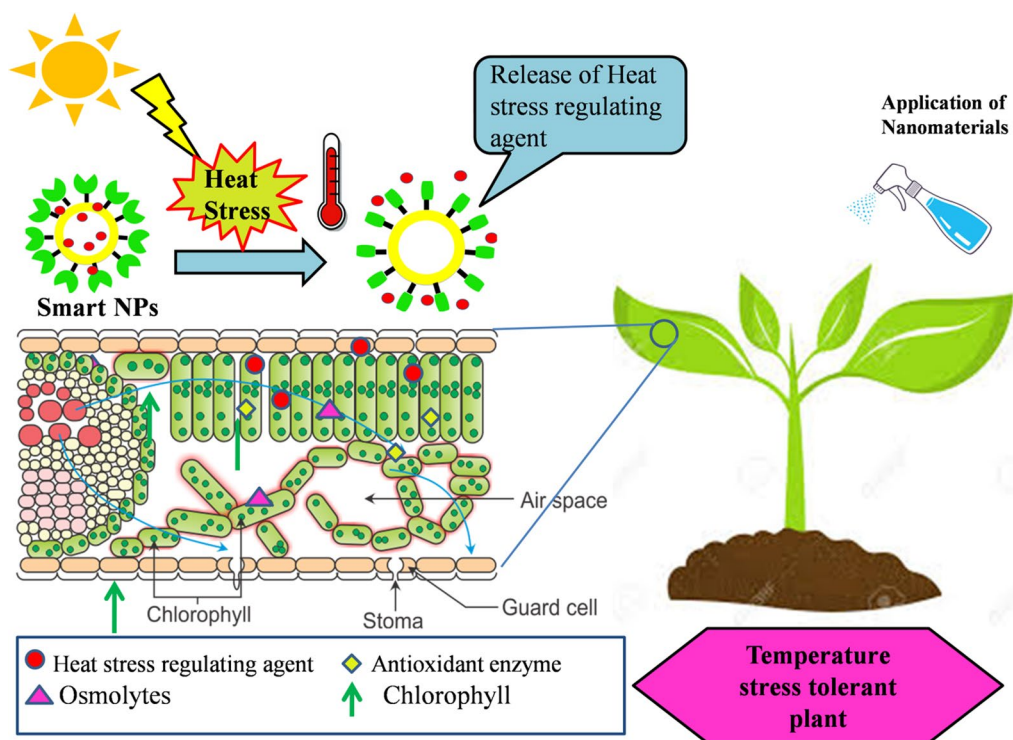


Fig. 4 When nanoparticles are applied to plants under temperature or heat stress, 1. Nano-polymers on temperature elevation release the heat stress-regulating agents inside of the plants 2. Plants exhibit modifications like: Enhanced antioxidant enzyme activity, enhanced osmolyte content, increased chlorophyll content, increased seeds per pod and pods per plant to overcome high temperature stress

processes like seed germination, cell division and maturity, root formation, and flowering. GA also enhances the tolerance to environmental stresses like chilling, drought, and salt. GA ultimately sustained the growth, nutrient contents, and yield (Iftikhar et al. 2019).

Abscisic acid (ABA) is a well-known stress phytohormone. ABA levels in plants indicate stress levels under a variety of abiotic stress conditions. ABA interacts with the *cis*- and *trans*-acting regulatory elements of responsive promoters of the gene involved in stress response. A number of transcription factors are involved in the regulation of ABA expression. ABA is stable at high temperatures and thus provides protection against cell dehydration. In response to NPs, ABA increases freezing, chilling, drought, and salt tolerance in numerous plant species (Vishwakarma et al. 2017) (Table 1).

Salicylic acid (SA) is an endogenous hormone present in plants. It regulates the biochemical and physiological processes when plants are exposed to extreme stress conditions. The cold tolerance of maize seedlings was improved by the application of exogenous salicylic acid. SA elevates antioxidant enzymes such as POD and SOD to eliminate ROS in plant cells. A large number of ROS causes the cell membrane to release all extracellular contents, ultimately causing cell death (Yan et al. 2023). The

SA levels were diminished in the apices at low ZnO NPs concentrations, whereas the SA profiles were delayed in the roots of the *Arabidopsis* plant (Vankova et al. 2017) (Table 2).

Synergetic effect of nanoparticles and PGPR

Plant show adaptation against different stresses. There are different varieties of plant available to cope with stresses such as drought-tolerant varieties or genetically engineered crops. These varieties are not economically feasible as well as have ethical and environmental concerns. To overcome this problem nanoparticles have shown promise (Azmat et al. 2022). Recent studies by Rukhsar-Ul-Haq et al. (2023) showed application of ZnONPs increased fresh and dry weight of shoot and root, chlorophyll "a" and chlorophyll "b" and triggered the antioxidant defense system in wheat plant. Multiple studies have proved efficiency of PGPR to alleviate different stress in plants (Rashid et al. 2022). Combination of PGPR and nanoparticles have given added benefits and increased crop yields (Muhammad et al. 2022). Azmal et al. (2022) discovered that plant growth-promoting rhizobacteria (PGPR) and green synthesised zinc oxide nanoparticles (ZnO-NPs) using fruit extract of Papaya protect wheat against heat and drought stress

Table 1 Plant response to nanoparticles under temperature stress

Plants	NP	Size	Conc	Stress	Major effect	References
Physiological modifications caused by nanoparticles						
Tomato	TiO ₂	16.04 nm	50, 100 and 200 mg/l	Heat stress	Regulated photosystem II, increases conductance to H ₂ O, and transpiration rate	Qi et al. (2013)
Wheat	Se	65-88 nm	20-40 mg/l	Heat stress	Increased carotenoids, chlorophyll, transpiration, stomata's conductance and net photosynthesis	El-Saadony et al. (2021)
Chrysanthemum	Se	-	50, 100, 150 and 200 mg/l	Heat stress	Improved plant growth and flower quality	Sellem et al. 2020
Sorghum	Se	10-40 nm	10 mg/l	Heat stress	Increased pollen germination, seed set percentage, seed yield & photosynthetic rate	Djanaguiraman et al. 2018a, b
Sugarcane	SiO ₂ , ZnO, Se & graphene nanoribbons	5-250 nm	1.5, 50 & 300 mg/l	Cold stress	Maximizes photochemical efficiency of PSII & photo-oxidizable PSI	Elsheery et al. 2020
Mungbean	ZnO	20-30 nm	0, 15, 30, 45, 60 mg/l	Heat stress	Increased carotenoids, chlorophyll	Kareem et al. (2022a)
Green beans	Ag	~10 nm	0.25, 1.25 and 2.5 mg/l	Cold stress	Increased chlorophyll activity, gas exchange parameters & grain yield	Prazak et al. 2020
Cotton	SiO ₂	-	50, 100, 200 mg/l	Cold stress	Increase in plant height, fresh and dry weight, and photosynthesis	Liang et al. 2023
Morphological modifications caused by nanoparticles						
Wheat	Ag	34 nm	25, 50, 75 and 100 mg/l	Heat stress	Improved chlorophyll a,b, & total chlorophyll; increased stomatal conductance, transpiration; and reduced malondialdehyde and abscisic acid	Iqbal et al. 2019
Anatomical modifications caused by nanoparticles						
Alfalfa	ZnO	10-20 nm	90 mg/l	Heat stress	Increase in plant fresh and dry weight, root and shoot length, leaf area, leaf number, leaf fresh weight	Kareem et al. 2022b
Postii	MWCNTs	Diameter 5-15 nm and length 50 µm	0, 10, 50, 100 and 200 mg/l	Heat stress	Ultrastructural changes to chloroplast, mitochondria, and cell wall	Zhao et al. 2021a, b
Wheat	Si	-	1.5 and 1.66 mM	Heat stress	Slowed stomatal closure, reduced mesophyll cell and chloroplast damage	Younis et al. 2020
Responses at the molecular levels						
Wheat	SINPs	-	-	Heat stress	Overexpression of TaPIP1 & TaNIP2	Younis et al. 2020
<i>Arabidopsis thaliana</i>	ZnO	20 nm	0, 0.1, 0.5 and 1 µg/mL	Heat stress	Overexpression of TaPIP1 The alleviation of TGS-GUS (-glucuronidase) Genes	Wu & Wang 2020

Table 1 (continued)

Plants	NP	Size	Conc	Stress	Major effect	References
Chickpea	TiO ₂		0 and 5 mg/l	Cold stress	Upregulation of the genes encoding RUBISCO, Chlorophyll a/b binding proteins, and Phosphoenolpyruvate Carboxylase (PEPC)	Hasanpour et al. 2015
Rice	ZnO	3 nm	25,50,100 mg/l	Cold stress	Induced the expression of genes related to the CAT, SOD, and POD antioxidative system & OsZIP52	Song et al. 2021
Modulation of antioxidant response						
Chickpea	TiO ₂	–	5 mg/l	Cold stress(ROS)	Decrease in H ₂ O ₂ content, increased Rubisco activity	(Hasanpour et al. 2015)
Chickpea	TiO ₂	7–40 nm	5 ppm	Cold stress(ROS)	Improved membrane damage caused by reducing H ₂ O ₂ content	(Mohammadi et al. 2013)
Licorice	TiO ₂	10–25 nm	2, 5 ppm	Cold stress(ROS)	Decreased H ₂ O ₂ content, increased total protein and osmolyte content	(Kardavan Ghabel, Karamian et al. 2020)
Arabidopsis	Ag NP	45 ± 5 nm	100 µM	ROS	Increased ROS accumulation, enhanced root growth	(Syu et al. 2014)
Wheat sorghum	Se NP	10–40 nm	10 mg/l	High temp stress	Improved pollen germination and maintains the lipid bilayer and fluidity by facilitating higher levels of unsaturated phospholipids	(Djanaguiraman et al. 2018a, b)
Peanut	Ag,Cu and Ag/Cu	190, 225 and 53 nm	500, 750, and 1000 ppm	ROS	Different NP doses induces stress enzymes CAT and POD	(Santos-Espinoza et al. 2020)
Wheat	Zn NP Fe NP	80 nm 53 nm	0.25–1 ppm	High temp stress	Increase in antioxidant enzyme activities	(Hassan et al. 2018)
Wheat	SINP	10–100 nm	10 µM	UV-B stress	H ₂ O ₂ enhanced, APX and SOD inhibited while CAT and NO was stimulated	(Tripathi et al. 2017a, b)
Wheat	ZnO TiO ₂	25 nm	1.5 and 10 ppm	High temp stress	Activities of SOD and GPX increased more than CAT	Thakur, Sourbh et al. 2021
Banana	Chitosan	< 100 nm	0,100,200,400 mg/l	Cold stress	Decreased levels of reactive oxygen species (ROS) and malondialdehyde (MDA), as well as an accumulation of soluble carbohydrates, proline, and amino acids	Wang et al. 2021

Table 2 Role of nanoparticles in Regulation of Biosynthesis of Phytohormones in plants under stress

Plants	Nanoparticles	Phytohormone	Major effect	References
Wheat	CuO	Auxin/IAA	Root hair proliferation and shortening of the zones of division and elongation	(Adams et al. 2017)
Arabidopsis	CuO	IAA	Accumulation of IAA in root tip cells and primary root elongation	(Yuan et al. 2013)
Arabidopsis	ZnO	IAA	Inhibition of IAA in the apices where as high doses in the roots	(Vankova et al. 2017)
Arachis hypogaea L	Ag/Cu	IAA	Decrease in IAA levels with different doses of Ag and Cu	(Santos-Espinoza et al. 2020)
Arabidopsis	ZnO	Cytokinins	Accumulation of <i>cis</i> -zeatin with higher ZnO levels	(Vankova et al. 2017)
Pepper plants	AgNP	Cytokinins	Affected the development by decreasing both plant height and biomass	(Vinković et al. 2017)
Wheat	ZnO	GA	Increased GA content reduced Zn accumulation and decrease in toxicity caused due to ROS	(Iftikhar et al. 2019)
Red pepper	AgNP	Auxin/ABA	Decreased levels of auxin/ABA	(El-Saadony et al. 2022)
Arabidopsis	ZnO	ABA	Increased ABA levels in apices and leaves	(Vankova et al. 2017)
Arabidopsis	AgNP	ABA/Auxin	Induces genes responsible for ABA and auxin signalling	(Syu et al. 2014)
Arabidopsis	AgNP	Ethylene	Inhibit ethylene perception	(Syu et al. 2014)
Arabidopsis	ZnO	Salicylic acid	Diminished levels in apices with low Zn-NP	(Vankova et al. 2017)

at a concentration of 10 ppm. ZnO-NPs combined with *Pseudomonas sp.* Produces more proline, antioxidant enzymes and abscisic acid, which protect the plants from all stress groups. Redondo-Gomez et al. (2022) investigated the use of isolated PGPR consortia from halophytes to improve strawberry growth and flowering performance under saline, elevated CO₂ and temperature conditions and discovered that the presence of

salt had a positive effect on plant growth in high CO₂ and elevated temperature conditions. Although, there are few reports on temperature stress because this is a relatively new area of research, there are numerous studies demonstrating the synergistic effect of PGPR and nanoparticles in overcoming other abiotic stresses. Different studies have been reported on this topic are summarized in the Table 3.

Table 3 Synergetic effect of nanoparticles and PGPR in stress alleviation

Sr.no	Nanoparticle	PGPR	Plant	Effect on Plant	Stress alleviated	Reference
1	Zn	<i>Pseudomonas sp.</i>	Wheat	Production of high proline, antioxidant enzymes and abscisic acid	Heat and Drought	Azmat et al. 2022
2	Mo	<i>Bacillus sp.</i> strain ZH16	Wheat	Promote indole-3-acetic acid synthesis, phosphate solubilization and ACC deaminase activity	arsenic (As) contamination	Ahmed et al. 2022
3	ZnO	PGPR mixed Biofertilizer	Maize	Enhanced fresh and dry biomass, relative water content, protein content, soluble sugars, proline content, enzymatic antioxidant defense mechanisms including activities of catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), superoxide dismutase (SOD), and malondialdehyde (MDA) content	Arsenic resistance	Khan et al. 2022a, b
4	ZnO	Biofertilizer	Safflower	Increased the plant productivity, percent water content, and osmolyte levels. improved the activities of antioxidant enzymes	Salinity	Asmin et al. 2021
5	ZnO	<i>Bacillus subtilis</i> , <i>Lactobacillus casei</i> , <i>Bacillus pumilus</i>	Tomato	Changed in the expression of SOD and GPx encoding genes	Salinity	Hosseinpour et al. 2020
5	ZnO	<i>Azospirillum brasilense</i>	Wheat	Triggered nitrogen metabolism, chlorophyll synthesis and membrane integrity	Drought	Muhammad et al. 2022

Temperature smart engineered nanomaterials to cope up with temperature stress

High and varying temperature leads to morphological, physiological and biochemical changes in plants, which affect plant growth and development and decrease yield. The adverse effects of heat stress can be reduced by developing crop plants with improved thermo-tolerance using various genetic approaches. Recently, the use of nanoparticles to improve plant growth and yield after heat stress has been reported. The small size of NPs allows its better penetration into targeted tissues. They can easily pass through the cellular membrane and associate themselves with biomolecules and cellular structures. The high surface area of NPs helps in carrying higher concentration of compounds and contributes towards their slow as well as steady release at the site of action. Nanoparticles can be engineered to give novel properties which can be useful in drug delivery. Biocompatible temperature-responsive polymeric materials can be added to make temperature smart nanoparticles which can help in delivery of drug by small variations in temperatures (Karimi et al. 2016). Few researchers have synthesized and applied temperature smart nanoparticle to make heat resistant plants.

Zhang et al. 2023 synthesized a temperature-responsive poly[2-(2-bromoisobutyryloxy)-ethyl methacrylate-graft-poly(acrylic acid)-block-poly(N-isopropyl acrylamide)] P[BiBEM-g-(PAA-b-PNIPAm)] bottlebrush polymer that can inoculate plants to confer resistance to heat stress for extended periods of time by releasing the heat stress-regulating agents inside of the plants in response to elevated temperatures. Zhang et al. 2020 developed poly(acrylic acid)-block-poly(N-isopropyl acrylamide) (PAA-b-PNIPAm) star polymers with varying block ratios for temperature programmed release of a model antimicrobial agent (Crystal Violet) under relevant pH and heat stress in plants. Djanaguiraman et al. 2018a, b proved role of selenium nanoparticles in grain sorghum. They showed that Se-NPs can move from root to shoot of sorghum plants. Foliar spray of Se-NPs during the booting stage of sorghum grown under HT stimulated the antioxidant defense system by enhancing antioxidant enzymes activity. Se-NPs facilitated higher levels of unsaturated phospholipids. Se-NPs under heat stress improved the pollen germination percentage, leading to a significantly increased seed yield.

Kareem et al 2022a, b showed exogenous foliar application of nano-ZnO significantly up-streamed the production of antioxidants and osmolytes to attenuate the shocks of heat stress in mung bean. Foliar-applied nano-ZnO raised not only the chlorophyll contents and gas exchange attributes, but also the seeds per pod (SPP) and pods per plant (PPP), which results in the better grain yield under heat stress. ZnO nanoparticles prevented the

heat stress-mediated membrane damage, lipid peroxidation and oxidative stress by stimulating antioxidant systems and enhancing osmolyte contents in alfalfa plants (Kareem et al 2022a, b). Magnetite and Zinc Oxide nanoparticles have shown to alleviate heat Stress in Wheat Plants (Hasan et al. 2018; Kausar et al. 2023).

Phytotoxic effect of nanoparticles

Many studies have been performed to demonstrate the effects of nanoparticles (NPs) on terrestrial plants, including agricultural plants, annual herbs, grasses, and flowering plants. NPs have shown both positive and negative effects on plant physiology and morphology. Phytotoxicity due to nanoparticles refers to the harmful effects nanoparticles on plants. Nanoparticles, have shown varying degrees of phytotoxic effects on plants. They can affect seed germination, cellular metabolism, root and shoot growth, biomass production, and genetic material integrity (Parthasarathi 2011; Yadav et al. 2014; Choudhury et al. 2016) Various NPs like silver, titanium dioxide, and zinc oxide have been found to inhibit root elongation significantly (Bajaj et al. 2023; Konotop et al. 2014). Additionally, nanoparticles can induce oxidative stress, alter cellular structures, and affect gene expression in plants, leading to phytotoxicity (Wu et al. 2012; Madanayake et al. 2021; Gowtham et al. 2024).

The size, shape, surface coating, and chemical composition of NPs play crucial roles in determining their level of toxicity. Phytotoxicity may also depend on environmental factors and the physical and chemical nature of the plant species (Ruttkey-Nedecky et al. 2017). Additionally, the toxicity of NPs is influenced by their concentration, with higher concentrations often resulting in more pronounced effects (Verma et al. 2021). Some nanoparticles remain adhered to the plant surface, while others are transported inside the vascular system of plants. Phytotoxicity tests are typically carried out during seed germination and seedling growth stages, revealing a wide variation in the phytotoxicity caused by different NPs (Table 4). Essential metal nanoparticles such as Zn, Cu, Fe, Mn, and their oxides are frequently studied due to their importance as essential nutrients for plants and their relatively low toxicity across a wide concentration range.

Besides, having direct effect on plants, Nanoparticles can prove toxic to plants in number of ways. For instance, NPs may have an impact on soil health and nutrient cycling through interactions with soil microorganisms. These interactions underscore the interdependence of aboveground and belowground ecosystem components by potentially having indirect effects on plant growth and health (Zhang et al. 2015; Hussain et al. 2023). Moreover, the functioning of

Table 4 Phytotoxic effects of Nanoparticles

Nanoparticle	Concentration	Phytotoxicity effect	References
AgNP	50 ppm	Inhibit seed germination, inhibit seedling growth, affect mass and length of roots and shoots	Budhani et al. 2019 Yan et al. 2019 Rastogi et al. 2019
ZnO	50 µg/ml	Affect Plant growth, rigidity of roots, and root cell viability Showed cytotoxic and genotoxic effects in the root meristems by affecting the cell membrane integrity, metabolic activity, reactive oxygen species accumulation, DNA damage, chromosome aberrations and cell cycle progression	Hossai et al. 2016 Sun et al. 2019
CuO	10 g/l	Inhibit the growth by affecting the shoot and root elongations, maximal quantum yield of photosystem II, and transpiration rate	Rajput et al. 2018
MWCNTs	500 mg/l	Differentially regulates the expression of genes important for maintaining cellular ROS homeostasis	Yang et al. 2023
Fe ₂ O ₃	100 mg/l	Decreased root elongations	Kumar et al. 2015
TiO ₂	100 mg/100 ml	Reduction in CO ₂ fixation, transpiration rate and stomatal conductance	Teszák et al. 2018
CeO ₂	500 mg/l	Destroy chloroplasts and vascular bundles	Nhan et al. 2015
La ₂ O ₃	≥ 10 mg/l	Decreased shoot, root biomass and root length	Liu et al. 2018

ecosystems, soil fertility, and plant communities may all be impacted over time by persistent exposure to NPs. Concerns regarding the health of humans and animals are raised by the possibility of NPs bioaccumulating and biomagnifying in the food chain (Karimi et al. 2018; Uddin et al. 2020).

To reduce phytotoxicity caused by nanoparticles, various strategies have been explored. One approach involves utilizing designed nanomaterials through different application methods like solution, seed priming, and spraying, which enhances plant resilience to metal stress (Bajaj et al. 2023). Green synthesis of nanoparticles, such as silver nanoparticles (AgNPs) from *Aloe vera* leaf extract, has been shown to effectively mitigate phytotoxicity compared to chemically synthesized AgNPs, promoting germination and growth in plants (Anju et al. 2022). Additionally, the use of biocompatible and non-phytotoxic cellulose acetate nanoparticles has been proposed as a promising solution for agricultural applications, as they do not induce phytotoxic, cytotoxic, or genotoxic effects, making them environmentally friendly (Lima et al. 2022). Furthermore, silver nanoparticles (AgNPs) have demonstrated phytostabilization properties, reducing toxic metal accumulation in plants while enhancing antioxidant activity and promoting plant health (Adejumo et al. 2023). By employing these strategies, it is possible to address and overcome phytotoxicity associated with nanoparticles in plants. Proactive mitigation strategies are required to ensure the safe use of emerging nanomaterials and applications in agriculture, while also minimising potential risks to the health of plants and the environment. Our understanding of nanoparticle-plant interactions will grow as a result of the identification of

knowledge gaps and the prioritising of future research directions, which will also inform risk assessment and management techniques.

Conclusion and future prospects

There are many ways in which nanotechnology in agriculture may have a fundamental impact on a variety of global predicaments, including addressing the impact of climate change and enhancing nutrient bioavailability in plants. The agricultural sector benefits from both targeting specific nanotechnology approaches and non-targeting specific nanotechnology approaches. It is through the interactions between plants and nanoparticles that real hope can be found for achieving agricultural sustainability, specifically in terms of onsite pathogen detection, crop improvement, and agriculture efficiency. The findings pertaining to nutritional elements containing NPs (i.e., Fe, Cu, Se, and Co) have demonstrated substantial scientific evidence of their efficacy in improving the plant's micronutrients, which has been reflected in improved growth parameters and notable improvements at the physiological level (i.e., chlorophyll and carotenoids, photosynthetic activity, metabolic pathways, and transpiration rate). Both inorganic and organic nanoparticles have shown promise in treating temperature stress in plants. The use of inorganic nanoparticles, have been studied extensively; however, the use of organic nanoparticles have not received as much attention. Despite the limited number of reports documenting the effectiveness of organic nanoparticles in alleviating temperature stress in plants, their unique properties and potential benefits warrant further investigation. In recent studies of nanoparticles, not only have different pathways and biomolecule interactions been examined, but also its effect on

different genes and the risks associated with their use in plants. Even though the beneficial effect of nanoparticles in abiotic stress tolerance is well established, the majority of these studies are still in the laboratory. The widespread use of nanoparticles has raised concerns about their possible negative environmental effects as well as the potential for nanoparticle buildup in edible plant parts. Consequently, specialized research is required to develop suitable evaluation methodologies to assess the effects of nanoparticles on abiotic ecosystem components. In order to commercialize nanotechnology from the lab to the agricultural fields, future research should focus on designing NPs that are reasonably priced, nontoxic, ecologically safe, and self-degradable.

Abbreviations

ABA	Abscisic acid
AgNP	Silver nanoparticles
AgNPs	Silver nanoparticles
APX	Ascorbate peroxidase
AuNPs	Gold nanoparticles
CAT	Catalase
CeO ₂	Cerium oxide
CKs	Cytokinins
Co	Cobalt
CO ₂	Carbon dioxide
CuO	Copper oxide
Fe ₂ O ₃	Iron oxide
Fv/Fm	Ratio of variable and maximal fluorescence
GA	Gibberlic acid
GNRs	Graphenenanoribbons
GPx	Glutathione peroxidase
H ₂ O	Water
H ₂ O ₂	Hydrogen peroxide
HS	Heat stress
HSP	Heat shock proteins
IAA	Indole acetic acid
K ₂ SiO ₂	Potassium silicate
La ₂ O ₃	Lanthanum oxide
MAPK	Mitogen activated protein kinase
MDA	Malondialdehyde
Mn	Manganese
MWCNTs	Multi-walled carbon nanotubes
NO	Nitric oxide
NPQ	Nanophotochemical quenching
NPs	Nanoparticles
PbNPs	Platinum nanoparticles
PEPC	Phosphoenol pyruvate carboxylase
PGPR	Plant growth-promoting rhizobacteria
Pm	Maximum photo-oxidizable PSI
POD	Peroxidase
PPP	Pods per plant
PS I & PS II	Photosystem I & II
ROS	Reactive oxygen species
RT-PCR	Reverse transcriptase polymerase chain reaction
SA	Salicylic acid
SAMK	Sympathomedullary pathway kinases
SeNPs	Selenium nanoparticles
SiO ₂	Silicon oxide
SOD	Superoxide dismutase
SPP	Seed per pod
TaNIP2	<i>Triticum aestivum</i> Nodulin 20-like intrinsic protein
TaPIP1	<i>Triticum aestivum</i> Plasma membrane intrinsic protein

TGS	Transcriptional gene silencing
TGS	Transcriptional gene silencing glucuronidase
TiO ₂	Titanium dioxide
ZnO	Zinc oxide
P[BiBEM-g-(PAA-b-PNIPAm)]	Poly[2-(2-bromoisobutyryloxy)-ethyl methacrylate-graft-poly(acrylic acid)-block-poly(N-isopropyl acrylamide)]
PAA-b-PNIPAm	(Acrylic acid)-block-poly(N-isopropyl acrylamide)

Author contributions

A.K.S and M.S. conceptualized the manuscript. A.K.S., M.S., S.B.A., and P.B. wrote the manuscript. A.K.S., M.S., S.B.A., P.K., and M.K.S., collaborated on composing and revising the content. A.K.S., M.S., and M.K.S. played a pivotal role in thoroughly reviewing the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding

This research received no external funding.

Availability of data and materials

No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

The authors gave their consent for publication of the research results.

Competing interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential competing interests.

Received: 11 December 2023 Accepted: 22 May 2024

Published online: 24 June 2024

References

- Adams J, Wright M, Wagner H, Valiente J, Britt D, Anderson A. Cu from dissolution of CuO nanoparticles signals changes in root morphology. *Plant Physiol Biochem*. 2017;110:108–17. <https://doi.org/10.1016/j.plaphy.2016.08.005>.
- Adejumo AL, Azeez L, Kolawole TO, Aremu HK, Adedotun IS, Oladeji RD, Abdullah M. Silver nanoparticles strengthen Zea mays against toxic metal-related phytotoxicity via enhanced metal phytostabilization and improved antioxidant responses. *Int J Phytoremed*. 2023;25(12):1676–86.
- Ahmad Z, Tahseen S, Wasi A, Ganie IB, Shahzad A, Emamverdian A, Ding Y. Nanotechnological interventions in agriculture. *Nanomaterials*. 2022;12(15):2667.
- Ahmad W, Coffman L, Weerasooriya AD, Crawford K, Khan AL. The silicon regulates microbiome diversity and plant defenses during cold stress in *Glycine max* L. *Front Plant Sci*. 2024;14:1280251.
- Ahmed T, Noman M, Rizwan M, Ali S, Ijaz U, Nazir MM, Li B. Green molybdenum nanoparticles-mediated bio-stimulation of *Bacillus sp.* strain ZH16 improved the wheat growth by managing in planta nutrients supply, ionic homeostasis and arsenic accumulation. *J Hazard Mater*. 2022;423:127024.
- Akter N, Rafiqul Islam M. Heat stress effects and management in wheat. A review. *Agron Sustain Dev*. 2017;37:1–17.
- Ali S, Mehmood A, Khan N. Uptake, translocation, and consequences of nanomaterials on plant growth and stress adaptation. *J Nanomater*. 2021;2021:1–17.

- Al-Khayri JM, Rashmi R, Surya Ulhas R, Sudheer WN, Banadka A, Nagella P, Aldaej MI, Rezk AAS, Shehata WF, Almaghasla MI. The role of nanoparticles in response of plants to abiotic stress at physiological, biochemical, and molecular levels. *Plants*. 2023;12(2):292. <https://doi.org/10.3390/plants12020292>.
- Alnaddaf LM, Al-Khayri JM, Jain SM. Introduction: impact of nanotechnology on plant cell biology. In: Al-Khayri JM, Alnaddaf LM, Jain SM, editors. *Nanomaterial interactions with plant cellular mechanisms and macromolecules and agricultural implications*. Cham: Springer International Publishing; 2023. p. 1–15.
- Amini S, Maali-Amiri R, Mohammadi R, Shahandashti S-SK. cDNA-AFLP analysis of transcripts induced in chickpea plants by TiO₂ nanoparticles during cold stress. *Plant Physiol Biochem*. 2017;111:39–49.
- Anju TR. Phytotoxicity of silver nanoparticles on growth of cicer arietinum L: a sustainable alternative using green synthesis. *ECS Trans*. 2022;107(1):799.
- Arumugam V, Vasudevan V. Impact of metal oxide nanoparticles against heavy metal stress in plants. In: Xinghui L, Periakaruppan R, Dhanasekaran S, editors. *Nanomaterial oxides in horticulture and agronomy*. Cambridge: Academic Press; 2023. p. 177–202.
- Arya SS, Tanwar N, Lenka SK. Prospects of nano-and peptide-carriers to deliver CRISPR cargos in plants to edit across and beyond central dogma. *Nanotechnol Environ Eng*. 2021;6(2):22.
- Aslani F, Bagheri S, Julkapli NM, Juraimi AS, Hashemi FSG, Baghdadi A. Effects of engineered nanomaterials on plants growth: an overview. *Sci World J*. 2014. <https://doi.org/10.1155/2014/641759>.
- Avellan A, Simonin M, McGivney E, Bossa N, Spielman-Sun E, Rocca JD, Lowry GV. Gold nanoparticle biodissolution by a freshwater macrophyte and its associated microbiome. *Nat Nanotechnol*. 2018;13(11):1072–7.
- Avellan A, Yun J, Morais BP, Clement ET, Rodrigues SM, Lowry GV. Critical review: role of inorganic nanoparticle properties on their foliar uptake and in planta translocation. *Environ Sci Technol*. 2021;55(20):13417–31.
- Azmat A, Tanveer Y, Yasmin H, Hassan MN, Shahzad A, Reddy M, Ahmad A. Coactive role of zinc oxide nanoparticles and plant growth promoting rhizobacteria for mitigation of synchronized effects of heat and drought stress in wheat plants. *Chemosphere*. 2022;297:133982. <https://doi.org/10.1016/j.chemosphere.2022>.
- Bajaj T, Alim H, Ali A, Patel N. Phytotoxicity responses and defence mechanisms of heavy metal and metal-based nanoparticles. In: Husen A, editor. *Nanomaterials and nanocomposites exposures to plants: response, interaction, phytotoxicity and defense mechanisms*. Singapore: Springer Nature Singapore; 2023. p. 59–96.
- Banerjee K, Pramanik P, Maity A, Joshi DC, Wani SH, Krishnan P. Methods of using nanomaterials to plant systems and their delivery to plants (mode of entry, uptake, translocation, accumulation, biotransformation and barriers). In: Ghorbanpour M, Wani SH, editors. *Advances in phytonanotechnology*. Cambridge: Academic Press; 2019. p. 123–52.
- Bañon S, Fernandez J, Franco J, Torrecillas A, Alarcón J, Sánchez-Blanco M. Effects of water stress and night temperature preconditioning on water relations and morphological and anatomical changes of *Lotus creticus* plants. *Sci Hortic*. 2004;101:333–42.
- Bhatla SC, Lal MA. *Mechanisms of water and solute transport. In plant physiology, development and metabolism*. Singapore: Springer Nature Singapore; 2023. p. 51–73.
- Budhani S, Egboluche NP, Arslan Z, Yu H, Deng H. Phytotoxic effect of silver nanoparticles on seed germination and growth of terrestrial plants. *J Environ Sci Health C Environ Carcinog Ecotoxicol Rev*. 2019;37(4):330–55. <https://doi.org/10.1080/10590501.2019.1676600>.
- Choudhury R, Majumder M, Roy DN, Basumallick S, Misra TK. Phytotoxicity of Ag nanoparticles prepared by biogenic and chemical methods. *Int Nano Letters*. 2016;6:153–9.
- Chouhan N. *Silver nanoparticles: synthesis, characterization and applications*. London: IntechOpen; 2018. p. 36–57.
- Djanaguiraman M, Belliraj N, Bossmann SH, Prasad PV. High-temperature stress alleviation by selenium nanoparticle treatment in grain sorghum. *ACS Omega*. 2018a;3(3):2479–91.
- Djanaguiraman M, Belliraj N, Bossmann SH, Prasad PV. High-temperature stress alleviation by selenium nanoparticle treatment in grain sorghum. *ACS Omega*. 2018b;3(3):2479–91. <https://doi.org/10.1021/acsomega.7b01934>.
- Doran PM. *Biotechnology of hairy root systems*. Berlin Heidelberg: Springer-Verlag; 2013. <https://doi.org/10.1007/978-3-642-39019-7>.
- El-Saadony MT, Saad AM, Najjar AA, Alzahrani SO, Alkhatib FM, Shafi ME, Hassan MAA. The use of biological selenium nanoparticles to suppress *Triticum aestivum* L. crown and root rot diseases induced by *Fusarium* species and improve yield under drought and heat stress. *Saudi J Biol Sci*. 2021. <https://doi.org/10.1016/j.sjbs.2021.04.043>.
- El-Saadony MT, Saad AM, Soliman SM, Salem HM, Desoky ES, Babalghith AO, El-Tahan AM, Ibrahim OM, Ebrahim AAM, Abd El-Mageed TA, Elrys AS, Elbadawi AA, El-Tarabily KA, AbuQamar SF. Role of nanoparticles in enhancing crop tolerance to abiotic stress: a comprehensive review. *Front Plant Sci*. 2022. <https://doi.org/10.3389/fpls.2022.946717>.
- Elsheery NI, Sunoj VSJ, Wen Y, Zhu JJ, Muralidharan G, Cao KF. Foliar application of nanoparticles mitigates the chilling effect on photosynthesis and photoprotection in sugarcane. *Plant Physiol Biochem*. 2020;149:50–60. <https://doi.org/10.1016/j.plaphy.2020.01.035>.
- Farooq A, Khan I, Shehzad J, Hasan M, Mustafa G. Proteomic insights to decipher nanoparticle uptake, translocation, and intercellular mechanisms in plants. *Environ Sci Pollut Res*. 2024. <https://doi.org/10.1007/s11356-024-32121-7>.
- Geisler-Lee J, Wang Q, Yao Y, Zhang W, Geisler M, Li K, Huang Y, Chen Y, Kolmakov A, Ma X. Phytotoxicity, accumulation and transport of silver nanoparticles by *Arabidopsis thaliana*. *Nanotoxicology*. 2012;7:323–37. <https://doi.org/10.3109/17435390.2012.658094>.
- Geisler-Lee J, Brooks M, Gerfen JR, Wang Q, Fotis C, Sparer A, Ma X, Berg RH, Geisler M. Reproductive toxicity and life history study of silver nanoparticle effect, uptake and transport in *Arabidopsis thaliana*. *Nanomaterials*. 2014;4:301–18. <https://doi.org/10.3390/nano4020301>.
- Gowtham HG, Shilpa N, Singh SB, Aiyaz M, Abhilash MR, Nataraj K, Murali M. Toxicological effects of nanoparticles in plants: mechanisms involved at morphological, physiological, biochemical and molecular levels. *Plant Physiol Biochem*. 2024;210:108604.
- Guo S, Wang J, Sun H, Wu J, Xu J, Sun J. Foliar uptake and in-leaf translocation of micro (nano) plastics and their interaction with epicuticular wax. *Environ Sci Nano*. 2023;10(4):1126–37.
- Haghighi M, Abolghasemi RJA, da Silva T. Low and high temperature stress affect the growth characteristics of tomato in hydroponic culture with Se and nano-Se amendment. *Sci Hortic*. 2014;178:231–40.
- Hartikainen H, Xue T, Piironen V. Selenium as an antioxidant and prooxidant in ryegrass. *Plant Soil*. 2000;225:193–200.
- 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(6):779–87. <https://doi.org/10.1134/s1021443715060096>.
- Hasanuzzaman M, Nahar K, Alam M, Roychowdhury R, Fujita M. Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. *Int J Mol Sci*. 2013;14(5):9643–84. <https://doi.org/10.3390/ijms14059643>.
- Hasanuzzaman M, Nahar K, Fujita M. Silicon and selenium: two vital trace elements that confer abiotic stress tolerance to plants. *Emerging technologies and management of crop stress tolerance*. Amsterdam: Elsevier; 2014. p. 377–422.
- Hassan NS, Salah El Din TA, Hendawey MH, Borai IH, Mahdi AA. Magnetite and zinc oxide nanoparticles alleviated heat stress in wheat plants. *Curr Nanomater*. 2018;3(1):32–43. <https://doi.org/10.2174/2405461503666180619160923>.
- Hedhly A, Hormaza JI, Herrero M. Global warming and sexual plant reproduction. *Trends Plant Sci*. 2009;14(1):30–6.
- Hong J, Wang C, Wagner DC, Gardea-Torresdey JL, He F, Rico CM. Foliar application of nanoparticles: mechanisms of absorption, transfer, and multiple impacts. *Environ Sci Nano*. 2021;8(5):1196–210.
- Hossain Z, Mustafa G, Sakata K, Komatsu S. Insights into the proteomic response of soybean towards Al₂O₃, ZnO, and Ag nanoparticles stress. *J Hazard Mater*. 2016;304:291–305.
- Hosseinpour A, Haliloglu K, Tolga Cinisli K, Ozkan G, Ozturk HI, Pour-Aboughadareh A, Poccai P. Application of zinc oxide nanoparticles and plant growth promoting bacteria reduces genetic impairment under salt stress in tomato (*Solanum lycopersicum* L. Linda). *Agriculture*. 2020;10(11):521.

- Hu P, An J, Faulkner MM, Wu H, Li Z, Tian X, Giraldo JP. Nanoparticle charge and size control foliar delivery efficiency to plant cells and organelles. *ACS Nano*. 2020a;14(7):7970–86.
- Hu S, Ding Y, Zhu C. Sensitivity and responses of chloroplasts to heat stress in plants. *Front Plant Sci*. 2020b;11:375.
- Hubbard JD, Lui A, Landry MP. Multiscale and multidisciplinary approach to understanding nanoparticle transport in plants. *Curr Opin Chem Eng*. 2020;30:135–43.
- Hussain M, Zahra N, Lang T, Zain M, Raza M, Shakoor N, Zhou H. Integrating nanotechnology with plant microbiome for next-generation crop health. *Plant Physiol Biochem*. 2023;196:703–11.
- Iftikhar A, Ali S, Yasmeen T, Arif MS, Zubair M, Rizwan M, Alhathloul HAS, Alayafi AA, Soliman MH. Effect of gibberellic acid on growth, photosynthesis and antioxidant defense system of wheat under zinc oxide nanoparticle stress. *Environ Pollut*. 2019;254:113109. <https://doi.org/10.1016/j.envpol.2019.113109>.
- Iqbal M, Raja NI, 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(2):387–95.
- KardavanGhabel V, Karamian R. Effects of TiO₂ nanoparticles and spermine on antioxidant responses of *Glycyrrhizaglabra* L. to cold stress. *Acta BotanicaCroatica*. 2020;79(2):137–47. <https://doi.org/10.37427/botcro-2020-025>.
- Kareem HA, Saleem MF, Saleem S, Rather SA, Wani SH, Siddiqui MH, Alamri S, Kumar R, Gaikwad NB, Guo Z, Niu J, Wang Q. Zinc oxide nanoparticles interplay with physiological and biochemical attributes in terminal heat stress alleviation in mungbean (*Vigna radiate* L.). *Front Plant Sci*. 2022a;13:842349. <https://doi.org/10.3389/fpls.2022.842349>.
- Kareem HA, Hassan MU, Zain M, Irshad A, Shakoor N, Saleem S, Wang Q. Nanosized zinc oxide (n-ZnO) particles pretreatment to alfalfa seedlings alleviate heat-induced morpho-physiological and ultrastructural damages. *Environ Pollut*. 2022b;303:119069.
- Karimi M, Sahandi Zangabad P, Ghasemi A, Amiri M, Bahrami M, Malekzad H, Ghahramanzadeh Asl H, Mahdieh Z, Bozorgomid M, Ghasemi A, Rahmani Taji Boyuk MR, Hamblin MR. Temperature-responsive smart nanocarriers for delivery of therapeutic agents: applications and recent advances. *ACS Appl Mater Interfaces*. 2016;8(33):21107–33. <https://doi.org/10.1021/acsami.6b00371>.
- Karimi M, Sadeghi R, Kokini J. Human exposure to nanoparticles through trophic transfer and the biosafety concerns that nanoparticle-contaminated foods pose to consumers. *Trends Food Sci Technol*. 2018;75:129–45.
- Kausar A, Hussain S, Javed T, Zafar S, Anwar S, Hussain S, Saqib M. Zinc oxide nanoparticles as potential hallmarks for enhancing drought stress tolerance in wheat seedlings. *Plant Physiol Biochem*. 2023;195:341–50.
- Khalid MF, Iqbal Khan R, Jawaid MZ, Shafiqat W, Hussain S, Ahmed T, Rizwan M, Ercisli S, Pop OL, Alina Marc R. Nanoparticles: the plant saviour under abiotic stresses. *Nanomaterials*. 2022;12:3915. <https://doi.org/10.3390/nano12213915>.
- Khan I, Awan SA, Rizwan M, Hassan ZU, Akram MA, Tariq R, Xie W. Nanoparticle's uptake and translocation mechanisms in plants via seed priming, foliar treatment, and root exposure: a review. *Environ Sci Pollut Res*. 2022a. <https://doi.org/10.1007/s11356-022-23945-2>.
- Khan MA, Yasmin H, Shah ZA, Rinklebe J, Alyemeni MN, Ahmad P. Co application of biofertilizer and zinc oxide nanoparticles upregulate protective mechanism culminating improved arsenic resistance in maize. *Chemosphere*. 2022b;294:133796.
- Khodakovskaya MV, de Silva K, Nedosekin DA, Dervishi E, Biris AS, Shashkov EV. Complex genetic, photothermal, and photoacoustic analysis of nanoparticle-plant interactions. *Proc Natl Acad Sci U S A*. 2011;108:1028–33.
- Konotop YO, Kovalenko MS, Ulynets VZ, Meleshko AO, Batsmanova LM, Taran NY. Phytotoxicity of colloidal solutions of metal-containing nanoparticles. *Cytol Genet*. 2014;48:99–102.
- Kumar V, Wani SH, editors. Heat stress tolerance in plants: physiological, molecular and genetic perspectives. Hoboken: John Wiley & Sons; 2020.
- Kumar S, Patra AK, Datta SC, Rosin KG, Purakayastha TJ. Phytotoxicity of nanoparticles to seed germination of plants. *Int J Adv Res*. 2015;3(3):854–65.
- Larue C, Veronesi G, Flank AM, Surble S, Herlin-Boime N, Carrière M. Comparative uptake and impact of TiO₂ nanoparticles in wheat and rapeseed. *J Toxicol Environ Health A*. 2012;75:722–34. <https://doi.org/10.1080/15287394.2012.689800>.
- Larue C, Castillo-Michel H, Sobanska S, Cécillon L, Bureau S, Barthès V, Ouedane L, Carrière M, Sarret G. Foliar exposure of the crop *Lactuca sativa* to silver nanoparticles: evidence for internalization and changes in Ag speciation. *J Hazard Mater*. 2014;264:98–106. <https://doi.org/10.1016/j.jhazmat.2013.10.053>.
- Lew TTS, Wong MH, Kwak SY, Sinclair R, Koman VB, Strano MS. Rational design principles for the transport and subcellular distribution of nanomaterials into plant protoplasts. *Small*. 2018;14(44):1802086.
- Liang Y, Liu H, Fu Y, Li P, Li S, Gao Y. Regulatory effects of silicon nanoparticles on the growth and photosynthesis of cotton seedlings under salt and low-temperature dual stress. *BMC Plant Biol*. 2023;23(1):504.
- Lima RG, Maranni M, Araujo LO, Maciel BM, Canassa T, Caires AR, Cena C. Preparation and phytotoxicity evaluation of cellulose acetate nanoparticles. *Polymers*. 2022;14(22):5022.
- Liu Y, Xu L, Dai Y. Phytotoxic effects of lanthanum oxide nanoparticles on Maize (*Zea mays* L.). *IOP Conf Ser Earth Environ Sci*. 2018;113(1):012020.
- Liu J, Zhang R, Xu X, Fowler JC, Miller TE, Dong T. Effect of summer warming on growth, photosynthesis and water status in female and male *Populus cathayana*: implications for sex-specific drought and heat tolerances. *Tree Physiol*. 2020;40(9):1178–91.
- López-Valdez F, Miranda-Arámula M, Ríos-Cortés AM, Fernández-Luqueño F, De-la-Luz V. Nanofertilizers and their controlled delivery of nutrients. *Agric Nanobiotechnol Mod Agric Sustain Future*. 2018. https://doi.org/10.1007/978-3-319-96719-6_3.
- Madanayake NH, Adassooriya NM. Phytotoxicity of nanomaterials in agriculture. *Open Biotechnol J*. 2021;15(1):109.
- Millán-Chiu BE, del Pilar Rodríguez-Torres M, Loske AM. Nanotoxicology in plants. In: Patra JK, Fraceto LF, Das G, Campos EVR, editors. Green nanoparticles: synthesis and biomedical applications. Cham: Springer International Publishing; 2020. p. 43–76.
- Mohammadi R, Maali-Amiri R, Abbasi A. Effect of TiO₂ nanoparticles on chickpea response to cold stress. *Biol Trace Elem Res*. 2013;152(3):403–10. <https://doi.org/10.1007/s12011-013-9631-x>.
- Muhammad F, Raza MAS, Iqbal R, Zulfiqar F, Aslam MU, Yong JWH, Ibrahim MA. Ameliorating drought effects in wheat using an exclusive or co-applied rhizobacteria and ZnO nanoparticles. *Biology*. 2022;11(11):1564.
- Nag S, Ghosh S, Dey A, Majhi S, Mondal A, Mishra A, Ahmad F. 3 method-sinplant for nanotechnology stress. In: Chen JT, editor. Advanced nanotechnology in plants: methods and applications. Boca Raton: CRC Press; 2024.
- Nair R, Varghese SH, Nair BG, Maekawa T, Yoshida Y, Kumar DS. Nanoparticulate material delivery to plants. *Plant Sci*. 2010a;179(3):154–63.
- Nair RM, Whittall A, Hughes SJ, Craig AD, Revell DK, Miller SM, Powell T, Auricht GC. Variation in coumarin content of *Mellilotus* species grown in South Australia. *N Z J Agric Res*. 2010b;53:201–13. <https://doi.org/10.1080/00288233.2010.495743>.
- Nejatizadeh F. Effect of silver nanoparticles on salt tolerance of *Satureja hortensis* L. during in vitro and in vivo germination tests. *Heliyon*. 2021;7(2):e05981.
- Nhan L, Ma C, Rui Y, et al. Phytotoxic mechanism of nanoparticles: destruction of chloroplasts and vascular bundles and alteration of nutrient absorption. *Sci Rep*. 2015;5:11618. <https://doi.org/10.1038/srep11618>.
- Omar RA, Talreja N, Ashfaq M, Chauhan D. Nanostructure-based smart fertilizers and their interaction with plants. In: Abd-Elsalam KA, Alghuthaymi MA, editors. Nanofertilizers for sustainable agroecosystems: recent advances and future trends. Cham: Springer Nature Switzerland; 2023. p. 399–430.
- Parthasarathi T. Phytotoxicity of nanoparticles in agricultural crops. In International Conference on Green technology and environmental Conservation (GTEC-2011). IEEE. 2011; 51–60.
- Pérez-de-Luque A. Interaction of nanomaterials with plants: what do we need for real applications in agriculture? *Front Environ Sci*. 2017;5:12.
- Pražak R, Świącilo A, Krzepińko A, Michałek S, Arczewska M. Impact of Ag nanoparticles on seed germination and seedling growth of green beans in normal and chill temperatures. *Agriculture*. 2020;10(8):312.
- Qi M, Liu Y, Li T. Nano-TiO₂ improves the photosynthesis of tomato leaves under mild heat stress. *Biol Trace Elem Res*. 2013;156:323–8.
- Rajput V, Minkina T, Fedorenko A, et al. Toxicity of copper oxide nanoparticles on spring barley (*Hordeum sativum distichum*). *Sci Total Environ*. 2018;645:1103–13.

- Raliya R, Biswas P, Tarafdar JC. TiO₂ nanoparticle biosynthesis and its physiological effect on mung bean (*Vigna radiata* L.). *Biotechnol Rep*. 2015;5:22–6. <https://doi.org/10.1016/j.btre.2014.10.009>.
- Ramírez Anguiano AC, Velasco Ramírez AP, Zamudio Ojeda A, Jiménez Torres HD, Velázquez Juárez G, Velázquez López JM, Velasco Ramírez SF. Effects of nanomaterials/nanocomposites on trace element uptake and phytotoxicity. In: Husen A, editor. *Nanomaterials and nanocomposites exposures to plants: response, interaction, phytotoxicity and defense mechanisms*. Singapore: Springer Nature Singapore; 2023. p. 127–56.
- Rani S, Kumari N, Sharma V. Uptake, translocation, transformation and physiological effects of nanoparticles in plants. *Arch Agron Soil Sci*. 2023;69(9):1579–99.
- Rashid U, Yasmin H, Hassan MN, et al. Drought-tolerant *Bacillus megaterium* isolated from semi-arid conditions induces systemic tolerance of wheat under drought conditions. *Plant Cell Rep*. 2022;41:549–69. <https://doi.org/10.1007/s00299-020-02640-x>.
- Rastogi A, Zivcak M, Tripathi DK, Yadav S, Kalaji HM, Brestic M. Phytotoxic effect of silver nanoparticles in *Triticum aestivum*: Improper regulation of photosystem I activity as the reason for oxidative damage in the chloroplast. *Photosynthetica*. 2019;57(1):209–16.
- Rehman A, Khan S, Sun F, Peng Z, Feng K, Wang N, Li H. Exploring the nanowonders: unveiling the role of Nanoparticles in enhancing salinity and drought tolerance in plants. *Front Plant Sci*. 2024;14:1324176.
- Rodríguez M, Canales E, Borrás-Hidalgo O. Molecular aspects of abiotic stress in plants. *Biotechnol Appl*. 2005;22:1–10.
- Ruttkey-Nedecky B, Krystofova O, Nejdil L, Adam V. Nanoparticles based on essential metals and their phytotoxicity. *J Nanobiotechnol*. 2017;15(1):1–19.
- Saeed F, Chaudhry UK, Raza A, Charagh S, Baksh A, Bohra A, Varshney RK. Developing future heat-resilient vegetable crops. *Funct Integr Genomics*. 2023;23(1):47.
- Santos-Espinoza AM, González-Mendoza D, Ruiz-Valdiviezo VM, Luján-Hidalgo MC, Jonapa-Hernández F, Valdez-Salas B, Gutiérrez-Miceli FA. Changes in the physiological and biochemical state of peanut plants (*Arachis hypogaea* L.) induced by exposure to green metallic nanoparticles. *Int J Phytomed*. 2020. <https://doi.org/10.1080/15226514.2020.1856037>.
- Schulze E-D, Beck E, Müller-Hohenstein K. *Plant ecology*. Berlin: Springer; 2005.
- Schwab F, Zhai G, Kern M, Turner A, Schnoor JL, Wiesner MR. Barriers, pathways and processes for uptake, translocation and accumulation of nanomaterials in plants—Critical review. *Nanotoxicology*. 2016a;10(3):257–78.
- Schwab F, Zhai G, Kern M, Turner A, Schnoor JL, Wiesner MR. Barriers, pathways and processes for uptake, translocation and accumulation of nanomaterials in plants—Critical review. *Nanotoxicology*. 2016b;10:257–78. <https://doi.org/10.3109/17435390.2015.1048326>.
- Seliem MK, Hafez Y, El-Ramady H. Using Nano-selenium in reducing the negative effects of high temperature stress on *Chrysanthemum morifolium* Ramat. *J Sustain Agric Sci*. 2020;46(3):47–60. <https://doi.org/10.21608/jsas.2020.23905.1203>.
- Singh S, Kapoor D, Khasnabis S, Singh J, Ramamurthy PC. Mechanism and kinetics of adsorption and removal of heavy metals from wastewater using nanomaterials. *Environ Chem Lett*. 2021;19(3):2351–81.
- Singla R, Kumari A, Yadav SK. Impact of nanomaterials on plant physiology and functions. In: Husen A, Iqbal M, editors. *Nanomaterials and plant potential*. Cham: Springer International Publishing; 2019. p. 349–77.
- Song Y, Chen Q, Ci D, Shao X, Zhang D. Effects of high temperature on photosynthesis and related gene expression in poplar. *BMC Plant Biol*. 2014;14:111.
- Song Y, Jiang M, Zhang H, Li R. Zinc oxide nanoparticles alleviate chilling stress in rice (*Oryza sativa* L.) by regulating antioxidative system and chilling response transcription factors. *Molecules*. 2021;26:2196. <https://doi.org/10.3390/molecules26082196>.
- Sun Z, Xiong T, Zhang T, Wang N, Chen D, Li S. Influences of zinc oxide nanoparticles on *Allium cepa* root cells and the primary cause of phytotoxicity. *Ecotoxicology*. 2019;28(2):175–88.
- Syu YY, Hung JH, Chen JC, Chuang HW. October). Impacts of size and shape of silver nanoparticles on *Arabidopsis* plant growth and gene expression. *Plant Physiol Biochem*. 2014;83:57–64. <https://doi.org/10.1016/j.plaphy.2014.07.010>.
- Taran N, Storozhenko V, Svetlova N, Batsmanova L, Shvartau V, Kovalenko M. Effect of zinc and copper nanoparticles on drought resistance of wheat seedlings. *Nanoscale Res Lett*. 2017;12:1–6.
- Teszák P, Kocsis M, Scarpellini A, Jakab G, Kőrösi L. Foliar exposure of grapevine (*Vitis vinifera* L.) to TiO₂ nanoparticles under field conditions: Photosynthetic response and flavonol profile. *Photosynthetica*. 2018;56(4):1378–86.
- Thakur S, Asthir B, Kaur G, Kalia A, Sharma A. Zinc oxide and titanium dioxide nanoparticles influence heat stress tolerance mediated by antioxidant defense system in wheat. *Cereal Res Commun*. 2021;50(3):385–96. <https://doi.org/10.1007/s42976-021-00190-w>.
- Tripathi DK, Singh S, Singh S, Pandey R, Singh VP, Sharma NC, Chauhan DK. An overview on manufactured nanoparticles in plants: uptake, translocation, accumulation and phytotoxicity. *Plant Physiol Biochem*. 2017a;110:2–12.
- Tripathi DK, Singh S, Singh VP, Prasad SM, Dubey NK, Chauhan DK. Silicon nanoparticles more effectively alleviated UV-B stress than silicon in wheat (*Triticum aestivum*) seedlings. *Plant Physiol Biochem*. 2017b;110:70–81. <https://doi.org/10.1016/j.plaphy.2016.06.026>.
- Uddin MN, Desai F, Asmatulu E. Engineered nanomaterials in the environment: bioaccumulation, biomagnification and biotransformation. *Environ Chem Lett*. 2020;18(4):1073–83.
- Uzu G, Sobanska S, Sarret G, Munoz M, Dumat C. Foliar lead uptake by lettuce exposed to atmospheric fallouts. *Environ Sci Technol*. 2010;44:1036–42. <https://doi.org/10.1021/es902190u>.
- Vankova R, Landa P, Podlipna R, Dobrev PI, Prerostova S, Langhansova L, Gaudinova A, Motkova K, Knirsch V, Vanek T. September). ZnO nanoparticle effects on hormonal pools in *Arabidopsis thaliana*. *Sci Total Environ*. 2017;593–594:535–42. <https://doi.org/10.1016/j.scitotenv.2017.03.160>.
- Verma DK, Patel S, Kushwah KS. Effects of nanoparticles on seed germination, growth, phytotoxicity and crop improvement. *Agric Rev*. 2021;42(1):1–11. <https://doi.org/10.18805/ag.R-1964>.
- Vinković T, Novák O, Strnad M, Goessler W, Jurašić DD, Paradiković N, Vrčec IV. July). Cytokinin response in pepper plants (*Capsicum annuum* L.) exposed to silver nanoparticles. *Environ Res*. 2017;156:10–8. <https://doi.org/10.1016/j.envres.2017.03.015>.
- Vishwakarma K, Upadhyay N, Kumar N, Yadav G, Singh J, Mishra RK, Kumar V, Verma R, Upadhyay RG, Pandey M, Sharma S. Abscisic acid signaling and abiotic stress tolerance in plants: a review on current knowledge and future prospects. *Front Plant Sci*. 2017. <https://doi.org/10.3389/fpls.2017.00161>.
- Wahid A. Physiological implications of metabolites biosynthesis in net assimilation and heat stress tolerance of sugarcane (*Saccharum officinarum*) sprouts. *J Plant Res*. 2007;120:219–28.
- Wang Z, Xie X, Zhao J, Liu X, Feng W, White JC, Xing B. Xylem- and phloem-based transport of CuO nanoparticles in maize (*Zea mays* L.). *Environ Sci Technol*. 2012;46(8):4434–41.
- Wang JW, Grandio EG, Newkirk GM, Demirel GS, Butrus S, Giraldo JP, Landry MP. Nanoparticle-mediated genetic engineering of plants. *Mol Plant*. 2019a;12(8):1037–40.
- Wang Y, Zhang Y, Zhang Q, Cui Y, Xiang J, Chen H, Hu G, Chen Y, Wang X, Zhu D, et al. Comparative transcriptome analysis of panicle development under heat stress in two rice (*Oryza sativa* L.) cultivars differing in heat tolerance. *PeerJ*. 2019b;7:e7595.
- Wang A, Li J, Al-Huqail AA, Al-Harbi MS, Ali EF, Wang J, Eissa MA. Mechanisms of chitosan nanoparticles in the regulation of cold stress resistance in banana plants. *Nanomaterials*. 2021;11(10):2670.
- Wong MH, Misra RP, Giraldo JP, Kwak SY, Son Y, Landry MP, Swan JW, Blankschtein D, Strano MS. Lipid exchange envelope penetration (LEEP) of nanoparticles for plant engineering: a universal localization mechanism. *Nano Lett*. 2016;16:1161–72. <https://doi.org/10.1021/acs.nanolett.5b04467>.
- Wu H, Li Z. Nano-enabled agriculture: How do nanoparticles cross barriers in plants? *Plant Commun*. 2022;3(6):100346.
- Wu J, Wang T. Synergistic effect of zinc oxide nanoparticles and heat stress on the alleviation of transcriptional gene silencing in *Arabidopsis thaliana*. *Bull Environ Contam Toxicol*. 2020;104:49–56. <https://doi.org/10.1007/s00128-019-02749-0>.
- Wu SG, Huang L, Head J, Chen DR, Kong IC, Tang YJ. Phytotoxicity of metal oxide nanoparticles is related to both dissolved metals ions and adsorption of particles on seed surfaces. *J Pet Environ Biotechnol*. 2012;3(4):126.

- Yadav T, Mungray AA, Mungray AK. Fabricated nanoparticles: current status and potential phytotoxic threats. *Rev Environ Contam Toxicol* Vol. 2014;221–230:83–110.
- Yan A, Chen Z. Impacts of silver nanoparticles on plants: a focus on the phytotoxicity and underlying mechanism. *Int J Mol Sci*. 2019;20(5):1003. <https://doi.org/10.3390/ijms20051003>.
- Yan H, Hao L, Chen H, Zhou X, Ji H, Zhou H. Salicylic acid functionalized zein for improving plant stress resistance and as a nanopesticide carrier with enhanced anti-photolysis ability. *J Nanobiotechnol*. 2023. <https://doi.org/10.1186/s12951-023-01777-7>.
- Yang S, Yin R, Wang C, Yang Y, Wang J. Phytotoxicity of zinc oxide nanoparticles and multi-walled carbon nanotubes, alone or in combination, on *Arabidopsis thaliana* and their mutual effects on oxidative homeostasis. *PLoS ONE*. 2023;18(2):e0281756.
- Yashveer S, Redhu NS, Singh V, Sangwan S, Laxman HV, Tokas J, Sindhu A. Nanoparticles in agriculture: characterization, uptake and role in mitigating heat stress. *Nat Resour Hum Health*. 2022;2:160–81.
- Yasmin H, Mazher J, Azmat A, Nosheen A, Naz R, Hassan MN, Ahmad P. Combined application of zinc oxide nanoparticles and biofertilizer to induce salt resistance in safflower by regulating ion homeostasis and antioxidant defence responses. *Ecotoxicol Environ Saf*. 2021;218:112262.
- Younis A, Khattab H, Emam M. Impacts of silicon and silicon nanoparticles on leaf ultrastructure and tap1 and tap2 gene expression in heat stressed wheat seedlings. *Biol Plant*. 2020;64:343–52.
- Yuan HM, Liu WC, Jin Y, Lu YT. Role of ROS and auxin in plant response to metal-mediated stress. *Plant Signal Behav*. 2013;8(7):e24671. <https://doi.org/10.4161/psb.24671>.
- Zhai G, Walters KS, Peate DW, Alvarez PJ, Schnoor JL. Transport of gold nanoparticles through plasmodesmata and precipitation of gold ions in woody poplar. *Environ Sci Technol Lett*. 2014;1:146–51. <https://doi.org/10.1021/ez400202b>.
- Zhang HY, Su WH. Classification, uptake, translocation, and detection methods of nanoparticles in crop plants: a review. *Environ Sci Nano*. 2024. <https://doi.org/10.1039/D4EN00059E>.
- Zhang D, Hua T, Xiao F, Chen C, Gersberg RM, Liu Y, Tan SK. Phytotoxicity and bioaccumulation of ZnO nanoparticles in *Schoenoplectus tabernaemontani*. *Chemosphere*. 2015;120:211–9.
- Zhang Y, Yan J, Avellan A, Gao X, Matyjaszewski K, Tilton RD, Lowry GV. Temperature and pH responsive star polymers as nano-carriers with potential for in vivo agrochemical delivery. *ACS Nano*. 2020;14(9):10954–65. <https://doi.org/10.1021/acsnano.0c03140>.
- Zhang Y, Fu L, Martinez MR, Sun H, Nava V, Yan J, Lowry GV. Temperature-responsive bottlebrush polymers deliver a stress-regulating agent in vivo for prolonged plant heat stress mitigation. *ACS Sustain Chem Eng*. 2023;11(8):3346–58.
- Zhao L, Peng B, Hernandez-Viezcas JA, Rico C, Sun Y, Peralta-Videa JR. Stress response and tolerance of Zea mays to CeO₂ nanoparticles: cross talk among H₂O₂, heat shock protein and lipid peroxidation. *ACS Nano*. 2012a;6:9615–22.
- Zhao L, Peralta-Videa JR, Ren M, Varela-Ramirez A, Li C, Hernandez-Viezcas JA, Aguilera RJ, Gardea-Torresdey JL. Transport of Zn in a sandy loam soil treated with ZnO NPs and uptake by corn plants: electron microprobe and confocal microscopy studies. *Chem Eng J*. 2012b;184:1–8. <https://doi.org/10.1016/j.cej.2012.01.041>.
- Zhao D, Wang X, Cheng Z, Tang Y, Tao J. Multi-walled carbon nanotubes prevent high temperature-induced damage by activating the ascorbate-glutathione cycle in *Paeonia ostii* T. Hong et J. X. Zhang. *Ecotoxicol Environ Saf*. 2021a;227:112948. <https://doi.org/10.1016/j.ecoenv.2021.112948>.
- Zhao J, Lu Z, Wang L, Jin B. Plant responses to heat stress: physiology, transcription, noncoding RNAs, and epigenetics. *Int J Mol Sci*. 2021b;22:117. <https://doi.org/10.3390/ijms22010117>.
- Zhu J, Li J, Shen Y, Liu S, Zeng N, Zhan X, Xing B. Mechanism of zinc oxide nanoparticle entry into wheat seedling leaves. *Environ Sci Nano*. 2020;7(12):3901–13.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.