Chapter

Improvement of Abiotic Stress Tolerance in Plants with the Application of Nanoparticles

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Abstract

Plants are under the threat of climatic changes and there is a reduction in productivity and deterioration in quality. The application of nanoparticles is one of the recent approaches to improve plant yield and quality traits. A number of nanoparticles, such as zinc nanoparticles (ZnO NPs), iron nanoparticles (Fe_2O_3 NPs), silicon nanoparticles (SiO_2 NPs), cerium nanoparticles (CeO_2 NPs), silver nanoparticles (Ag NPs), titanium dioxide nanoparticles (TiO_2 NPs), and carbon nanoparticles (C NPs), have been reported in different plant species to play a role to improve the plant physiology and metabolic pathways under environmental stresses. Crop plants readily absorb the nanoparticles through the cellular machinery of different tissues and organs to take part in metabolic and growth processes. Nanoparticles promote the activity of a range of antioxidant enzymes, including catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD), in plant species, which in turn improve the growth and development under stressful conditions. The present review focuses on the mode of action and signaling of nanoparticles to the plant systems and their positive impact on growth, development, and ROS scavenging potential. The appropriate elucidation on mechanisms of nanoparticles in plants leads to better growth and yields under stress conditions, which will ultimately lead to increased agricultural production.

Keywords: agriculture, climatic challenges, crop development, food security, nanotechnology

1. Introduction

Population of the globe is rising and is predicted to reach almost 9.6 billion by the year 2050. Sustained growth of 70–100% in global agricultural and food production is essential to feed the growing population [1]. The area under cultivation may shrink over time due to the increasing nonagricultural uses of the land and urbanization, making it difficult to increase agricultural production [2]. Plants are constantly exposed to environmental changes during their life cycle. Deteriorating soil health conditions inevitably have a detrimental impact on plant development and productivity [3]. Billions of dollars worth of crops are being destroyed each year due to abiotic stresses, such as salinity and drought. Prior to the advent of efficient selection techniques, conventional breeding was used to maintain agricultural productivity, but its effectiveness was constrained by the diversity of stress tolerance traits [2]. Determining innovative solutions to reduce abiotic stress challenges and maintain food security is therefore urgently required under these deteriorating environmental conditions [1] as most promising approach currently available is nanotechnology.

To improve abiotic stress tolerance in agricultural biosystems, Eric Drexler initially coined the term "Nanotechnology" [4]. It deals with the study of nanostructures that possess diverse physicochemical properties and biochemical activities that are dependent on their surface-to-volume ratio [5]. Different physical, chemical, and biological processes can be used to manufacture nanoparticles (NPs), and they can interact with plants in a variety of ways [6]. Crop plants readily absorb NPs, which can enter the cells and play crucial roles in metabolic and growth processes [7]. There is a surge in the use of nanobiotechnology tools in agricultural production that has the potential to boost plant metabolism since NPs promote plant growth, development, and yield to withstand environmental stresses [8]. Additionally, it has been observed that NPs promote the activity of a range of antioxidant enzymes, including catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD) [9]. Extensive research revealed that NPs are crucial for plants dealing with abiotic stress conditions [10].

Nanobiotechnology will improve plant functions that will help them cope with environmental challenges [11]. Therefore, this technology is strongly encouraged due to the rising global food demand as well as the potential for positive effects on the economy and ecology [12]. Despite its extraordinary potential in the enhancement of agricultural productivity and improvement in abiotic stress tolerance, the wider application of nanotechnology at the field level is limited in agriculture. In this review article, updates on the positive effects of nanotechnology for the improvement of abiotic stresses in crops have been discussed in detail.

2. Role of nanoparticles in salinity stress

Salinity has a negative impact on crops in various physiological and biochemical processes that decrease crop production drastically [13]. Water scarcity in the soil causes low osmotic potential and ionic toxicity of Cl^- and Na^+ in plant cells [14]. It is also seen that salt stress results in decreased concentration of photosynthetic pigments, reduced stomatal flow, lack of efficiency of photosystem II, and increased production of ROS.

2.1 Zinc nanoparticles (ZnO NPs)

Salt stress causes chlorophyll concentration leads to membrane disintegration and the rate of photosynthesis is significantly decreased. It also causes injury in thylakoid and grana that results in limited starch content [15]. Lupine (*Luminus termis*) was protected in saline conditions by priming with ZnO NPs, which enhanced the photosynthetic pigments, antioxidant responses, and growth [16]. ZnO NPs treatment also increased the antioxidant enzymes in *Zea mays* [17]. When *Abelmoschus esculentus* was treated with ZnO NPs, it increased the SOD and CAT activities and photosynthetic pigment [18]. Canola (*Brassica napus*) plant treated with ZnO NPs, alleviated the harmful effects of salt by upregulating the osmolyte biosynthesis, ionic regulation, and antioxidant system under saline conditions [19]. *Gossypium hirsutum* plants treated with ZnO NPs enhanced the contents of carotenoids, chlorophyll a and b, and total chlorophyll under salt stress conditions [20, 21]. When salt-stressed citrus plants (*Citrus reticulata*) were treated with ZnO NPs, it results in decreased accumulation of total soluble sugars and proline contents that help in the osmoregulation of plants and maintain the growth rate of treated plants [22].

2.2 Iron nanoparticles (Fe_2O_3 NPs)

Iron oxide nanoparticles are a rich source of Fe for plants. When peppermint was exposed to Fe_2O_3 NPs, proline content, and lipid peroxidation were decreased significantly in saline soil. Antioxidant enzyme activities (guaiacol peroxidase, CAT, and SOD) declined in plants. They also increased the potassium, zinc, calcium, iron, leaf dry and fresh weight, and phosphorus [23]. Grape softwood showed a prominent increase in protein content and reduced production of hydrogen peroxide, proline, and antioxidant enzyme activities when treated with potassium silicate and Fe_2O_3 NPs [24]. Under salt stress, the application of Fe_2O_3 NPs on *Helianthus annuus* increased the activities of POD and CAT [25]. Ajowan (*Trachyspermum ammi*) was treated with Fe_2O_3 NPs under saline conditions increased antioxidant activities, osmolyte synthesis, and maintained Na+/ K+ ratio. These adaptations help plants to improve leaf pigments, seed yield, membrane stability, and shoot and root growth [9].

2.3 Silicon nanoparticles (SiO_2 NPs)

SiO_2 NPs are used to help plants by forming a layer in cell walls and maintaining yield. In squash and tomato plants, the antioxidant system is enhanced and seed germination increases due to SiO_2 NPs under salt stress [26]. In Basil plants, silica nanoparticles have shown promising results related to morphological and physiological traits under salt stress [27]. SiO_2 NPs increased the seedling growth of lentils and seed germination and improved the defense mechanism of plants in saline conditions [28]. They help plants to cope up with salt stress by increasing the fresh weight in maize [29]. Under salt stress, the application of SiO_2 NPs on soybean decreased toxic ROS production and Na + level in leaves [30]. Wheat cultivars treated with SiO_2 NPs improved biological antioxidant levels and seedling growth under salt stress [31]. Application of SiO_2 NPs on the strawberry plant in saline conditions increased the photosynthetic pigment and maintained the carotenoid and chlorophyll content, decreasing the effect on epicuticular wax [32].

2.4 Cerium nanoparticles (CeO_2 NPs)

They can be used as fertilizer to stimulate the growth of roots, enhance the antioxidant enzyme activities, and to prevent membrane leakage and peroxidation [33]. Moreover, CeO_2 NPs help to preserve cell wall and chloroplast structure [34]. Activation of CeO_2 NPs as antioxidants depends upon the pH of surroundings, sub-cellular localization, surface charge, concentration, and particle size. CeO_2 NPs increased the growth in *Dracocephalum Moldavica* (a herbaceous plant also called Moldavian balm), by regulating nonenzymatic and enzymatic defense mechanisms under saline conditions [35]. *Brassica Napus* plants treated with CeO_2 NPs have efficient chloroplast and biomass under salt stress [36]. Anatomical changes, such as low accumulation of Na + in roots and high Na + flow toward shoots have also been reported [37].

2.5 Silver nanoparticles Ag NPs

Silver nanoparticles enhanced the sodium, potassium, and chloride to regulate the osmolality level in treated plants under salt stress conditions. The stability of Ag NPs can be easily controlled in aquatic environments as compared to soil conditions [38]. Priming of seeds was carried out with Ag NPs to enhance the seed germination in wheat and the development of tomato plants [39]. The combined effect of Ag NPs with NaCl reduced the thiobarbituric acid reactive substances, electrolyte leakage, and hydrogen peroxide to control the oxidative damage in plants that is linked with the overproduction of ROS [40]. *Triticum aestivum* treated with Ag NPs increased the fresh and dry biomass under saline conditions [41]. Seeds of *Pennisetum glaucum* treated with Ag NPs improved the growth, proline, and relative water content (RWC) and decreased the oxidative damage by increasing the antioxidant enzyme activities under saline conditions [42].

2.6 Titanium dioxide nanoparticles (TiO_2 NPs)

Titanium is a transition element and the 9th most abundant element that contributes 0.33% of the earth's outer layer [43]. It improves photosynthesis and chlorophyll pigments in plants by altering antioxidant enzyme activities [44]. Titanium has an integral role in plants' tolerance under stressful conditions [45]. *Dracocephalum moldavica* plants were treated with TiO_2 NPs improved plant growth, and proline content and increased enzymatic activities, soluble sugars, and amino acids under salinity stress [46].

Type of NPs	Plant species	Physiological responses of plants under salt stress	References
Zinc NPs (ZNO NPs)	*Luminus termis*	Enhanced photosynthetic pigments, antioxidant responses, and growth.	[16]
	Zea mays	Increased antioxidant enzymes and improved salinity tolerance.	[17]
	Abelmoschus esculentus	Increased the activities of CAT and SOD and photosynthetic pigments and decreased the accumulation of soluble sugar and proline content.	[18]
	Brassica napus	Ionic regulation, osmolyte synthesis, and upregulated oxidative defense system.	[19]
	Gossypium hirsutum	Enhanced content of carotenoids and chlorophyll a & b.	[20]
	Citrus reticulata	Decreased accumulation of total soluble sugars and proline contents, osmoprotectants.	[22]
Iron NPs (Fe_2O_3 NPs)	*Mentha piperita*	Decreasing lipid peroxidation and increase in leaf dry and fresh weight, potassium, calcium, iron, phosphorus, and zinc contents.	[23]
	Grape softwood	Increased protein content and reduced production of hydrogen peroxide, proline, and antioxidant enzymes.	[24]
	Helianthus annuus	Increased antioxidant activities.	[25]
	Trachyspermum ammi	Improved osmolyte synthesis, antioxidant activities, and improved Na+/ K+ ratio.	[9]

Type of NPs	Plant species	Physiological responses of plants under salt stress	References
Silicon NPs (SiO_2 NPs)	Tomato and squash	Increased ROS and seed germination. Maintained vitamin C concentration and chlorophyll content.	[26]
	Ocimum basilicum	Increasing proline accumulation, antioxidant responses, leaf dry and fresh weight, and chlorophyll content.	[27]
	Zea mays	Boosting defense mechanism by ROS.	[29]
	Glycine max	Decreased ROS, lipid peroxidation, and Na^+, increased antioxidant activities and K^+ content.	[30]
	Triticum aestivum	Improved chlorophyll content and seed germination.	[31]
	Fragaria ananassa	Maintained carotenoid and chlorophyll content, and decreased the effect on epicuticular wax.	[32]
Chitosan	*Zea mays*	Increasing chlorophyll content, growth, photosystem II, and enhanced nitric oxide bioactivity.	[53]
Cerium NPs (CeO_2 NPs)	*Glycine max*	Rubisco carboxylase activity stimulates growth and increased photosynthesis.	[33]
	Dracocephalum Moldavica	Increased enzymatic and nonenzymatic defense system.	[35]
	Brassica napus	Efficient chloroplast and increase in biomass.	[36]
Silver NPs (Ag NPs)	*Solanum lycopersicum*	Increased germination with seed priming.	[39]
	Triticum aestivum	Enhanced dry and fresh biomass of plants. Increased the activity of CAT and decreased the activity of POD, and increased the accumulation of soluble sugar and proline content.	[41]
	Pennisetum glaucum	Improved proline and RWC, decreased oxidative damage by increasing the antioxidant enzyme activities.	[42]
Titanium dioxide NPs (TiO_2NPs)	*Dracocephalum moldavica*	Increased seedling growth, dry and fresh weight, root and shoot length. Increased antioxidant activity.	[46]
Carbon NPs (C NPs)	*Brassica napus*	Reestablishing ion homeostasis and redox balance.	[49]
	Ocimum basilicum	Increased enzymatic and nonenzymatic defense system, increased carotenoid, and chlorophyll content.	[50]
	Sophora alopecuroides	Increased proline content in roots and leaves, photosystem II activity, soluble sugar in leaves, and membrane integrity was maintained.	[51]
	Triticum aetivum	Enhanced phosphorus and potassium contents in root and phosphorus content in the shoot. Increased activity of antioxidant enzymes. Improved chlorophyll content, free ascorbic acid, amino acid, and soluble sugars.	[52]

Table 1.
Effect of nanoparticles on plants under salinity stress.

2.7 Carbon nanoparticles (C NPs)

Carbon nanoparticles have distinctive properties, including morphologically small surface area and better chemical reactivity [47]. They help in increasing seed germination and crop production under salt stress [48]. Application of C NPs on *Brassica* *napus* increased the NaCl stress tolerance in the plant by reestablishing ion homeostasis and redox balance [49]. When *Ocimum basilicum* was treated with C NPs increased enzymatic and nonenzymatic defense systems, and increased carotenoid and chlorophyll content [50]. Proline content in roots and leaves, photosystem II activity, soluble sugar in leaves were increased, and membrane integrity was maintained due to an increase in unsaturated fatty acid in *Sophora alopecuroides* C NPs treated plants under salt stress [51]. Application of C NPs on *Triticum aetivum* plants under saline conditions enhanced phosphorus and potassium content in roots and phosphorus content in shoot and increased the activity of antioxidant enzymes and improved the chlorophyll content, free ascorbic acid, amino acid, and soluble sugars [52]. **Table 1** consists of the reports of different scientists who studied the effects of the treatment of different nanoparticles on different plant species and their responses to physiological levels under salt stress.

3. Role of NPS in drought tolerance

Water crisis is one of the several issues that have been afflicted by climate change and global warming. Water is crucial for plant vitality as it has a role in the transportation of nutrients. Therefore, water deficit results in drought stress, which harshly affects the survival of plants and reduces agricultural production [54]. Therefore, a key solution in relation to sustainable agriculture is the identification of resistant crop varieties or improving drought tolerance in plants. Crop management and coping with various environmental challenges are possible by the new features of nanotechnology. The negative impacts of a restricted water supply on agriculture have been attempted to be reduced utilizing nano-materials. Farmers may be able to identify the effects of stress on plants at an early stage by using nano-sensors in global positioning systems that produce satellite photographs of fields [55]. Crop production in drought-prone locations may rise if soils have been given better water-retention capabilities [56]. Using nanoparticle-based plant modifications, conventional technologies may be used to improve crop plants by increasing the capacity of food crops to retain water, and nanoparticles improve the effectiveness of water consumption in the plants [57].

3.1 Silicon nanoparticles (SNPs)

Only a few studies have documented the biological activity of silica, an element that makes up a major portion of the Earth's crust and is found as silicon [58]. The tolerance of Hawthorn (*Crataegus* sp.) plants to drought stress is increased by applying various concentrations of silica nanoparticles [59]. The findings indicated that pretreating SNPs had a favorable impact on the photosynthetic metrics, RWC, malondialdehyde, membrane electrolyte leakage, as well as the levels of carbohydrate and proline. Two *Sorghum bicolor* cultivars treated with silicon demonstrated enhanced drought tolerance by reducing their shoot-to-root ratio, which may have indicated enhanced root development and retention of photosynthetic rate. This suggests that increasing plant water uptake efficiency will increase resistance to drought [60]. Using sodium silicate at 1.0 mM enabled the reduction of the effects of drought stress on wheat [61]. Although the precise process is unknown but silicon helps stressed plants to boost shoot growth, preserve RWC, and chlorophyll content, and reduce the membrane lipid peroxidation.

3.2 Zinc nanoparticles (ZnO NPs)

Application of Zn plays a role in increasing the radical growth and seed viability along with the establishment of germinated seeds, especially in Zinc deficient areas. Soybean seeds subjected to water stress showed that nano-zinc oxide has improved seed germination [62]. A composite of ZnO, B_2O_3, and CuO NPs reduced the effects of drought stress on soybean [63] and increased grain production and shoot growth by 36 and 33%, respectively, and improved nitrate and phosphorus uptake. By boosting the activity of the antioxidant enzymes SOD and CAT in wheat, ZnO NPs improved drought resistance. Zn and Cu NPs also increased the antioxidative enzyme activity, decreased lipid peroxidation, stabilized the photosynthetic pigments with increased RWC, and enhanced drought tolerance in wheat [64]. CuO and ZnO NPs modified the root morphology of plants colonized by *Triticum aestivum*, a beneficial pseudomonad, altering the plants to withstand drought [65]. CuO NPs boosted the production of lateral roots in wheat seedlings, and ZnO NPs stimulated the growth of extended root hairs proximal to the root tip. Drought stress severely affected eggplant development and production [66]. Exogenous ZnO NPs with 50 and 100 ppm, boosted the RWC and membrane stability index, improved stem and leaf morphology and better photosynthesis in water-stressed eggplant and yield rose by 12.2 and 22.6%, respectively.

3.3 Iron nanoparticles (Fe_2O_3 NPs)

Iron is a key micronutrient that is essential for plant growth and development and its reduction causes chlorosis in plants [67]. Thus, iron absorption in plants experiencing drought stress may play a crucial role in their ability to withstand drought [68]. Fe_2O_3 NPs applied topically to *Carthamus tinctorius* leaves, reduced the negative effects of drought stress while simultaneously promoting yield, growth, and development metrics [69]. Plants under drought stress have a substantial impact of Fe_2O_3 NPs on the number and weight of seeds, number of bolls yield, and oil percentage in cotton. Drought stress in sunflower was significantly reduced by the application of maghemite nanoparticles (a member of iron oxide) [70]. The activity of zerovalent (nZVI) iron nanoparticles is hypothesized to activate the proton pump ATPase (H+ -ATPase) of the plasma membrane in leaves of *Arabidopsis thaliana* plants, which in turn contributes to their ability to withstand drought by increasing the stomatal aperture [71]. They retained the drought sensitivity and boosted CO_2 uptake, the rate of the stomatal opening was accelerated, which in turn increased the plant biomass and chlorophyll content [72].

3.4 Titanium nanoparticles (titanium dioxide TiO_2 & anatase titanium dioxide $AnTiO_2$)

Wheat seed gluten and starch contents have responded favorably for using TiO_2 NPs foliar applications and improved plant height, seed and ear numbers, ear weight, gluten and starch content, yield, biomass, and harvest index under drought stress [73]. Enhanced photosynthesis and increased the maize plant's capacity to absorb light under water deficit [74]. Applying nanoparticles and Gibberellic acid to basil plants effectively enhanced the rate of photosynthesis, enhancing their tolerance to drought stress [75]. Various doses and sizes (10–25 nm) of $AnTiO_2$NP on the flax plant under water-scarce conditions responded favorably for growth, development, hydrogen peroxide (H_2O_2), malondialdehyde content, seed oil production, protein content, and photosynthetic pigments [76]. The effects of TiO_2 NP on onion seedlings have also been documented as they boosted SOD activity. TiO_2 NP concentrations of 40 and 50 mg/ml, lowered the CAT and POD activities and secretion of amylase was reduced. However, seed germination and seedling growth were reduced at higher concentration of TiO_2 NPs, whereas the effect was enhanced at lower concentration [77].

Type of NPs	**Plant species**	**Physiological responses of plants under drought stress**	**References**
Silicon NPs (SiO_2NPs)	*Crataegus* sp.	Positive effects on photosynthesis, malondialdehyde, RWC, membrane electrolyte leakage, chlorophyll, carotenoid, carbohydrate, and proline content.	[59]
	Sorghum bicolor	Reduced shoot-to-root ratio, improved root growth and the maintenance of photosynthetic rate, augmentation of water uptake efficiency, increase in leaf area index and leaf weight.	[40]
	Triticum aestivum	Improved shoot growth, increased the leaf chlorophyll content, maintained leaf water potential in stressed plants, reduced membrane lipid peroxidation.	[61]
Zinc NPs (ZnO NPs)	*Glycine max*	Increased germination, radical growth and seed viability, shoot growth and grain yield, and uptake of N and P.	[62, 63]
	Triticum aestivum	Increased antioxidant enzymes, reduced lipid peroxidation, stabilized the photosynthetic pigments, proliferation of elongated root hairs, and increased water stress tolerant gene expression.	[64]
	Solanum melongena	Increased RWC and MSI, improved stem and leaf anatomy, photosynthetic efficiency, growth, and yield.	[66]
Iron NPs (Fe_2O_3 NPs)	*Carthamus tinctorius*	Improved crop yield at the flowering stage and enhanced oil percentage.	[69]
	Arabidopsis thaliana	Enhanced plasma membrane proton pump ATPase activity, plant biomass, chlorophyll content, and CO_2 assimilation.	[71, 72]
Titanium NPs (Titanium dioxide TiO_2	*Triticum aestivum*	Enhancement in seed gluten and starch contents, plant height, seed number, and biomass.	[73]
	Zea mays	Improved sunlight absorbance, synthesis of photosynthetic pigments, and photosynthesis.	[74]
	Ocimum basilicum	Increased plant drought resistance and improve photosynthetic mechanism.	[75]
	Linum usitatissimum	Increased chlorophyll and carotenoids, enhancing flax development and yield, declining malondialdehyde and H_2O_2 content.	[76]
	Allium cepa	Increased SOD activity, seed germination, and seedling growth.	[77]
Silver NPs (Ag NPs)	*Lens culinaris*	Increased germination rate, root length, root fresh, and dry weight.	[68]
Cerium Oxide NPs (CeO_2 NPs)	*Sorghum bicolor*	Enhanced catalytic scavenging of ROS, reduced O_2^- (41%), H_2O_2 (36%), increased yield, pollen germination, and CO_2 absorption.	[80]

Table 2.
Effects of nanoparticles on plants under drought stress.

3.5 Silver nanoparticles (Ag NPs)

Developing drought-tolerant cultivars and reducing drought stress is essential for maintaining food security [78]. Only a small amount of historical literature focused on the interaction between drought and Ag NPs. Diminishing the detrimental impacts of drought stress on *Lens culinaris* has been credited to the application of Ag NPs [68]. The study indicated that varying PEG and Ag NPs concentrations had a significant impact on seed germination, root length, and biomass. Hence, Ag NPs could help to reduce water stress that affects plant development and productivity [79].

3.6 Cerium oxide nanoparticles (CeO_2 NPs)

Cerium oxide NPs could help *Sorghum bicolor* to cope with drought stress by inducing oxidative stress by catalytically neutralizing ROS and maintaining the photosynthetic activity and grain yield [80]. The foliar spray of nanoceria dramatically decreased free radicals (H_2O_2 and superoxide) under drought conditions, for instance, by 36 and 41%, respectively. ROS-scavenging enzymes were shown to be more active in plants exposed to drought: POD (54%), SOD (94%), and CAT (117%). The rate of pollen germination, carbon absorption, and seed output per plant was improved by 38, 31, and 31%, respectively. Different reports summarizing the effects of a number of nanoparticles on different plant species and their physiological responses under drought stress are discussed in **Table 2**.

4. Nanoparticles and other environmental stresses

Titanium oxide nanoparticles play a substantial role in the mitigation of light stress in crops as they catalyze the oxidation-reduction reaction, which then forms superoxide anion radicals and hydroxides. Oxidative stress is induced by ultraviolet (UV) light and has a negative impression on the growth of the plant. UV-B produces H_2O_2 and superoxide radicals and enhanced the leakage of electrolytes and lipid peroxidation, which leads to reduce the photosynthesis rate and normal leaf structure is also deteriorated [81]. In wheat plants, Silicon NPs increase antioxidant activities for the regulation of oxidative stress after UV-B exposure [82]. Herbicides are used to control weeds in agroecosystems. A methyl viologen herbicide, Paraquat is used extensively to control weeds in rice. Multiwall carbon nanotubes can modulate the toxicity of Paraquat [50], which promotes lateral root growth and photosynthesis in *Arabidopsis* and protect against the toxicity of Paraquat by lowering its bioavailability and promoting the oxidative-stress-related protein expression and photosynthesis. Therefore, the NPs can modulate abiotic stress-induced responses in plant growth at different levels. However, their physiochemical, electrical, optical, and biological properties are crucial [83]. Plants' tolerance to low temperature in green beans is increased by the exogenous application of Ag NPs [84] as they are used to reduce the oxidative stress in wheat.

5. Effect of nanoparticles on antioxidant and molecular mechanism of plants

Nanoparticles have an impact on plants' antioxidant system at the molecular level as they increase the capability of plants to tolerate oxidative stress. When *Brassica*

Type of nanoparticles	Plant species	Impact on antioxidant system and ROS	References
Zinc NPs (ZnO NPs)	*Solanum lycopersicum*	Decreased malondialdehyde content and increased SOD, CAT, POD, and APX activities under salinity stress.	[91]
Silver NPs (Ag NPs)	*Pennisetum glaucum*	Significant increase in proline content, antioxidant enzyme activities, flavonoid contents, and phenolics.	[42]
Titanium NPs (Titanium dioxide TiO_2	*Spinacia oleracea*	Enhance antioxidant stress tolerance.	[92]
	Glycine max	Enhance antioxidant enzyme activities contribute to reduction in hydrogen peroxide and malondialdehyde content under salinity.	[45]
Silicon NPs (SiO_2NPs)	*Coriandrum sativum*	Reduce the detrimental impact of Pb under lead stress by altering vitamin C, antioxidant enzyme activation, and flavonoids and increase plant capabilities to endure abiotic stresses.	[93]
Cerium oxide NPs (CeO_2 NPs)	*Phaseolus vulgaris*	Scavenge ROS in isolated chloroplasts protect plant photosynthesis from detrimental effects Of ROS accumulation during abiotic stresses.	[87]

Table 3.
Effect of nanoparticles on plants for ROS and antioxidant system.

juncea plant was treated with silver NPs, antioxidant enzyme activities (CAT, ascorbate peroxidase APX and guaiacol peroxidase) were increased which reduced the ROS [78]. The antioxidant system of *Spirodela polyrhiza* plants was activated when copper NPs were used to induce the activity of CAT, POD, and SOD. Moreover, ROS level also increased remarkably because of malondialdehyde and glutathione [85]. When seedlings of *Brassica juncea* were treated with gold NPs, the activity of antioxidant enzymes (guaiacol peroxidase, CAT, glutathione reductase, and APX) was significantly increased, in addition to the accumulation of the higher amount of proline and hydrogen peroxide. The activity of glutathione reductase was maximum at 200 ppm and the activity of other antioxidant enzymes, such as APX and guaiacol peroxidase, were also increased at 400 ppm of gold NPs treated plants [86]. When roots of kidney beans were exposed to CeO_2 NPs for a longer time, then antioxidant enzymes' activities were reduced and soluble protein was increased. While leaves treated with CeO_2 NPs showed increased activity of guaiacol peroxidase [87]. Plants exposed to ZnO NPs increase the Zn and SOD antioxidant enzyme minimizing the effect of oxidative stress [88].

The molecular mechanism of plants can be studied by using the model plant species. *Arabidopsis thaliana* treated with AgNPs gene expression analysis done by RT-PCR and cDNA microarray analyzed for transcriptome behavior [89] showed 281 upregulated genes associated with metal and oxidative stress and 80 downregulated genes associated with hormonal stimuli and plant defense system. The effect of AgNPs on rice has also been studied and some responsive proteins were associated with transcription, oxidative stress, protein degradation, cell division, calcium signaling and regulation, and apoptosis [90]. Hence, the effect of different nanoparticles on different plant species for the functioning of ROS and antioxidant enzymes has been briefed in **Table 3**.

6. Mechanism of nanoparticle (NPs) absorption in plants

Absorption and translocation of NPs in plants are one of the latest disciplines of study. The most commonly used NPs to enhance abiotic stress tolerance in plants are metal-based (MB) and carbon-based (CB). Among MB, the most widely studied nanomaterials are metal and metal oxides, such as copper, silver, titanium, iron, and zinc; while the most explored CB nanomaterials are carbon nanotubes (CNTs), fullerene (C_{70}), and fullerol ($C_{60}(OH)_{20}$) [94]. The impact of NPs on plants is determined by a number of variables, including availability, uptake, translocation, and accumulation. The plant cell wall restricts the entry of foreign elements; therefore, effective techniques are needed to introduce advantageous NPs and make them available to plants.

Different factors like size, chemical content, and plant species affect the entry of NPs, which is further influenced by their stability, transport and absorption, toxicity, and accumulation [95]. Particle size, surface charge, and the hydrophobicity of the plant surface all play important roles in their absorption [96]. Additionally, the absorption rate and translocation in plants are directly correlated to the structure of the nanomaterial utilized [97]. All of these elements highlight the requirement for developing and enhancing laboratory techniques to comprehend the NPs physicochemical qualities [98] as they undergo biotransformation in the soil, which has a direct impact on their toxicity and bioavailability. Foliar spraying or incubating isolated cells, roots, pollen, seeds, and protoplast with NPs, direct injection, irrigation of plants with NPs, delivery by biolistic, and hydroponic treatment have all been employed in previous research to make NPs available to the plant cells [99]. Bioaccumulation defines the uptake of NPs by plant roots and travels through apoplastic and symplastic routes to the cortex and pericycle [100].

Nanoparticles entered through the stomata, cuticle, stigma, trichomes, wounds, and lenticels and move through the phloem. They reach the xylem and phloem through the root tip meristem, where the Casparian strips continue to the shoot but have not fully developed. Endocytosis allows NPs to enter cells even when the cell wall, cell membrane, and Casparian strips block their uptake and transport. Additionally, transporters like aquaporins and carrier proteins facilitate their easier entry into cells [101]. The capacity of roots to absorb nutrients can change if NPs accumulate on the surface of the roots. Parenchymatic intercellular gaps in seeds enable NPs to be directly absorbed before being diffused into the cotyledon. Stomata allow for the internalization of NPs larger than 10 nm, which are then delivered to the plant's vascular system *via* apoplastic and symplastic pathways. Once internalized, NPs move through vascular systems carried by phloem alongside sugar flow, move-in both the directions, and eventually build up in organs that could serve as sap-sinks [102]. The apoplastic pathway has been extensively described to enhance the transfer of water nutrients and nonessential metal complexes. Leaf shape and chemical composition of surface waxes limits the entry of NPs through leaf [103]. Hence, to ensure the NPs' effective absorption in plants, it is crucial to consider their size, concentration, and physiological environment.

7. Mechanism of translocation and accumulation of NPs in plants

Mechanism of NPs translocation in different plant cells and organelles has been clarified [96]. Plant cell wall serves as a barrier that manages NPs uptake and establishes solubilization needed to enable their translocation. NPs with a size range of 40–50 nm can easily pass through the cell wall [104]. Composition of NPs affects their mobility through cell membrane or cell wall and also encourages their adsorption to radical exudates. Positively charged NPs have better adherence to cell walls. Their coating and morphology have a big impact on how they behave inside plants and the rhizosphere [105] After penetration through cells, they go through the shoots [101] and roots are transmitted to various aerial tissues and the seeds [6]. Gold NPs were only collected in the shoots of *Oryza sativa* when used with *Cucurbita pepo*, *Raphanus raphanistrum*, and other plant species. Positively charged gold nanoparticles tend to be quickly absorbed by plant roots [106]. The entry of NPs into the cell is facilitated by capillary action and osmotic pressure [95]. Membrane proteins of NPs, including as receptors and transporters, are altered as a result of their interaction with the outermost layer.

Negatively charged gold nanoparticles are easily translocated from plant roots to shoots. The most stable are SiO_2 and TiO_2, as they remain present in plant tissues after their uptake. When *Zea mays* is exposed to ZnO NPs hydroponically, most of them are accumulated in its roots and shoots. It is explained by the maximal NPs dissolution in the rhizosphere, which produces the zinc ions and enhances its absorption and translocation in the plant [107]. Soil-grown wheat has also been observed for this perseverance.

Different processes have been identified by the translocation of CeO_2 and ZnO NPs into *Glycine max* [108]. CuO NPs have been shown to be capable of moving from *Zea mays* roots to shoots and vice versa. TiO_2 NPs with a diameter of 140 nm or larger may translocate in *Triticum aestivum* roots [103]. The data of different reports about accumulation of different NPs in different plant tissues have been summarized in **Table 4**.

Type of nanoparticles	Plant species	Conc (mg/l *mg/kg)	Accumulation (mg/kg)		References
			Roots	Shoots	
Copper NPs	*Oryza sativa*	1000	1544.1	17.27	[109]
	Lactuca sativa	250	3773	—	[110]
	Vigna radiate	125	—	18.46	[111]
	Brassica juncea	1500	190.4	—	[112]
	Cajanus cajan	20	5.82	19.06	[113]
	Phaseolus vulgaris	100	800	—	[114]
Silver NPs	*Glycin max*	4000	2102	11.35	[108]
	Oryza sativa	1000	20	5	[115]
	Solanum lycopersicum	250	—	50	[116]
Zinc NPs	*Solanum lycopersicum*	1000	—	250	[117]
	Zea mays	100	10	30	[107]
Titanium NPs	*Solanum lycopersicum*	1000	—	250	[117]
Magnesium NPs	*Zea mays*	1000	103	131	[118]

Table 4.
Accumulation of nanoparticles in different plant species' tissues.

8. Conclusion and prospective

Various abiotic factors are damaging the plants in terms of growth and development leading to a reduction in yield and deteriorating the quality. Applications of NPs have been proven very protective as they stimulate germination, growth, and improve yield. They increase tolerance in plants as they enhance the uptake of water and nutrients. They are capable to metabolize starch reserves in plant cells. They stimulate the process of photosynthesis and alter levels of phytochromes and modulate oxidative stress.

Although various studies suggest the beneficial roles of NPs in plants but the molecular basis of the actual mechanism is still unknown. Further elucidation on this mechanism may generate the smart NPs for the production of crops sustainable to the environment. In addition, their interaction with signaling molecules is also required to be explored. The economic stability of the use of NPs in agriculture is important as silver and gold nanoparticles costs very expensive. Understanding their mode of action, toxicity limits, signaling, and translocation; hence cheaper NPs may be used as an alternative.

Conflict of interest

The authors declare no conflict of interest.

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