THE ROLE OF NANO-PARTICLES IN PLANT TOLERANCE AGAINST DROUGHT STRESS: REVIEW AND FUTURE PERSPECTIVE

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Abstract. Drought stress is a severe abiotic stress that causes huge yield losses globally. It adversely impacts crop growth and yield by negatively affecting plant functioning, nutrient acquisition, water uptake, and photosynthetic efficiency. Besides this, drought also causes oxidative and osmotic damage, severely reducing plant growth and development. Nanotechnology has emerged as an excellent field for mitigating abiotic stress in plants. Using nanoparticles (NPs) has shown promising results in mitigating the toxic impacts of abiotic stress in plants. Applying nanoparticles improves seed germination, seedling growth, nutrient and water uptake, osmolyte synthesis, and antioxidant activities, which protect plants against drought stress. They also protect the photosynthetic apparatus and cellular membranes, increase the expression of stress-responsive proteins, and bring ultra-structural changes in the plant body, which confers drought tolerance in plants. Therefore, this review discusses the different mechanisms mediated by NPs to induce drought tolerance in plants. This review also identified the different research gaps needed in future research programs. Therefore, the present review will guide readers in enhancing crop production using NPs under soaring drought intensity.
Keywords: *drought stress, antioxidants, gene expression, membrane stability, yield*

Introduction

Drought is a serious abiotic stress negatively affecting crop productivity, and leading to potential loss (about 70%) of agricultural productivity (Summy et al., 2020). Global change is characterized by elevated carbon dioxide in atmosphere, enhancing average temperature and more frequent extreme events including drought periods, heat waves (Feller, 2016). Plants are exposed to numerous external factors at the developmental stage, and plant morphological traits are significantly affected at all growth stages by drought (Summy et al., 2020). Drought stress attributed to water deficient which cannot meet plant water demands (Salehi-Lisar and Bakhshayeshan-Agdam, 2016). Plants respond to water deficit conditions through modification in morpho-physiology and alteration in biochemical processes to regulate water level (Khalid et al., 2021a; Chaudhry and Sidhu, 2022). Drought stress negatively affects plant growth by reducing cell enlargement and altering several physio-biochemical mechanisms, such as

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photosynthesis and respiration, enzymatic reaction, and cell metabolism (Jeyasri et al., 2021).

Drought stress significantly affected the morphological, molecular, and physio-biochemical processes of plants (Ortíz et al., 2015; Khalid et al., 2021b). It enhanced the extracellular and cytosolic solute concentration that reduces water potential and turgidity of cell, which inhibited growth. Water deficit conditions seriously disrupt the stomatal structure and functioning, hindering the gas exchange, which decreases the transpiration and carbon assimilation rate (Hussain et al., 2019a). In turn, plant tolerance mechanisms vary against drought stress. At a molecular level, cell signaling enhances stress responses in plants (Prakash et al., 2019; Zandalinas et al., 2020). Under adverse environments, there is an imperative requirement to improve plant tolerance against water deficit conditions. To achieve global food security in the future, additional progression is needed to enhance plants' drought tolerance and stress adaptation, besides the adoption of useful agricultural practices (Diatta et al., 2020).

Nanotechnology is a speedily emerging field that has showed promising results in improving plant stress tolerance under adverse conditions. Nanoparticles (NPs) is an efficient approach to improve crop productivity and overwhelming the current and future limitations by improving the tolerance mechanisms (Seleiman et al., 2020). The NPs mitigates drought stress by regulating the physio-biochemical process, and stress-related genes (Raza et al., 2023a). They also improve photosynthetic ability, root growth, up-regulates aquaporin genes, alter water metabolism, solutes accumulation, ion balance and decreases oxidative and osmotic damages (Khalid et al., 2022). The present review discusses the different mechanisms NPs mediate to induce plant drought tolerance. It summarizes the effects of NPs on physio-biochemical and molecular processes in plants under drought stress and their coping mechanism. It also highlights the knowledge gaps that should be filled for the promising future of NPs to mitigate drought stress.

Adverse effects of drought stress conditions on plant development

Climate change enhanced the drought stress events causing serious hazards to crop production by decreasing plant development (Narayanasamy et al., 2023; Raza et al. 2023b). Drought is accountable for approximately 50% of crop damage, and in various regions of the planet, drought event frequency and intensity are predicted to enhance, leading to serious yield losses (Rasheed et al., 2023; Wang et al., 2023; Zhao et al., 2023). The plant responds to stressful conditions depending on different factors, including stress duration and strength, and plant genetics and developmental stage (Salvi et al., 2021; Varshney et al., 2021). Earlier reports indicated that drought conditions adversely affected the all-growth stages, soil heterogeneousness, and nutrient mobilization as well as availability (Limousin et al., 2022; Riyazuddin et al., 2022; Yang and Qin, 2023). Water stress conditions decreased the plant biomass at the vegetative stage, which is related to critical switches of reproductive transition (Cooper and Messina, 2023). Furthermore, drought stress repressed important biochemical and photochemical mechanisms such as Rubisco activity, and stomatal conductance that reduced CO_2 exchange in leaves thereby affecting the carbon metabolism (Pandey et al., 2023; Yang and Qin, 2023).

Drought stress adversely affected the photosynthetic pigment-protein complex, decreasing photosystem efficacy and quantum yield of the electron transport chain (Gholami et al., 2022; Raza et al., 2023b; Yang and Qin, 2023); resultantly, water deprivation inhibited photosynthesis, decreasing plant height and biomass besides leading

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to senescence. Additionally, drought conditions disrupt the plant's relative water contents leading to osmotic stress leading to ion imbalance then serious membranes damage and disrupt the normal cellular functioning (Asghar et al., 2022; Cooper and Messina, 2023). Continues occurrence of drought stress leads to excess ROS generation, such as free reactive radical, singlet oxygen, and superoxide, which enhance lipid peroxidation that disrupts the cell metabolic processes through being detrimental to lipids, proteins, and macro-molecules functioning (Ayyaz et al., 2021; Pandey et al., 2023; Raza et al., 2023b). Water deprivation hampers the ionic uptake to the water transport system and aerial parts of plants by restricting the movement and availability of ions in the soil for plants (Plett et al., 2020). Drought stress indirectly affects the plant in several ways, consequently reducing the crop output (Cooper and Messina, 2023; Rasheed et al., 2023; Yang and Qin, 2023). Recently reported that water deficit conditions severely affected plants in the flowering stage, thereby leading to sterile pollen grains, disrupting the normal functioning of reproductive organs that limited crop production (Yang et al., 2021; Wu et al., 2022; Wang et al., 2023).

Plant's responses to encounter drought stress conditions

Plants have a specific requirement of water for normal developmental processes during their growth; however, under water deficit conditions, plants respond by various adapting strategies to cope with the stress conditions that can regulate the water balance (Abbas et al., 2023; Batool et al., 2023). Different types of plants exhibited different ways to respond to drought conditions, including a rapid life cycle before drought event, and water use efficiency and retention capacity (Du et al., 2020b), altering the hydraulic conductance of root, inducing the aquaporin-related gene transcription and production of dehydrins proteins (Gharibi et al., 2019; Tiwari et al., 2021). Plants adapted by osmotic adjustment and increase osmotic potential by accumulating the osmotic substances (glycine betaine, free amino acids, proline, soluble sugar, and protein) to shield proteins and membrane structure during the damaging effect of stress (Gilbert and Medina, 2016; Salvi et al., 2021; Kausar et al., 2023b).

Under drought stress, plants showed plasticity feedback by regulating transpiration rate, thereby enhancing transpiration and water transport (Bacher et al., 2021; Salvi et al., 2021). Moreover, plants respond by accumulating secondary metabolites, including flavonoids that improve drought adaptation by chaperones besides heat shock proteins (Baozhu et al., 2022). Plants remobilized the sugar-related metabolic processes through a sink-source relationship to cope with stress and improve the recovery to improve production (Correia et al., 2022). Additionally, different polyphenols, such as 4-coumaric acid, caffeic acid, anthocyanins, ferulic acid, cis-resveratrol-3-O-glucoside, kaempferol, catechin, rutin, quercetin and quecetin-3-O-glucoside, and kaempferol-3-O-glucoside, apigenin and chlorogenic acid, exhibited ROS scavenging capacity to reduced oxidative stress (Sharma et al., 2019; Takahashi et al., 2020).

Plants possess different complex signaling processes that induce antioxidative defense systems and phytohormonal signaling (Álvarez-Aragón et al., 2023). Previous reports suggested that plants activated their enzymatic antioxidative defense system including POD, SOD, CAT, and APX for free radicle scavenging to cope with stress (Batool et al., 2023). In addition, several hormones, including cytokinin, salicylic acid, ABA, brassinosteroids, auxin, jasmonates, and ethylene, synergistically work for stress signaling (Abbas et al., 2020; Mubarik et al., 2021). Especially, ABA has an imperative

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role during stress response besides regulating plant acclimatization to water deficiency (Mubarik et al., 2021). Water scarcity stimulated the ABA synthesis, which regulated the closure of stomata, reducing transportation losses besides inducing ABA-responsive factors to reduce cell dehydration (Saradadevi et al., 2017; Takahashi et al., 2020; Li et al., 2021). Interestingly, novel hormones such as peptides actively take part in plant vasculature activating drought-related factors in tissue-tissue interactions that inter-relate the stress signals (Saradadevi et al., 2017; Takahashi et al., 2019).

Plants exhibited several molecular responsive mechanisms to drought conditions via regulating stress-responsive genes (Raza et al., 2023b; Wang et al., 2023). Several differential genes respond to drought stress by their expression (Yang and Qin, 2023); for instance, the *CarMT* gene induced the antioxidant system, to increase stress tolerance in *A. Thaliana* under water deficit condition (Dubey et al., 2019). Whereas the expression of *ZmNAC111* induced accumulation of mRNA to cope with stress in *Zea mays* (Zhang et al., 2018). Different transcription factors, including the HD-ZIP gene family, played a dynamic role in plant acclimation against water stress by controlling physiochemical mechanisms (Sharif et al., 2021).

Previously found that hydraulic and Ca^{2+} signals, mRNAs, reactive species, and plant hormones are important in plant stress response (Kudla et al., 2018). Additionally, upon severe water deficit conditions, plants accumulated different branched-chain amino acids, including isoleucine, valine, and leucine besides methionine, lysine, and threonine (Pires et al., 2016). Furthermore, ABA-related mutant (*nced3*) accumulated higher branched chain amino acids and aminobutyric acid upon water deprivation (Urano et al., 2009). Previous studies found that the accumulation of plant acetate induced the jasmonic acid pathway to improve stress tolerance (Kim et al., 2017; Fàbregas and Fernie, 2019).

Role of nano-biotechnology in agricultural sector

Rapidly enhancing population needs higher food security and a sustainable agricultural industry (Farooq et al., 2022; Sonmez et al., 2023). Climate change, deficient arable land, and high pesticides, water, fertilizers, and agrochemical costs seriously threaten food security. Precision agriculture can overwhelm environmental limitations and improve agricultural production to guarantee food security worldwide (Jeger et al., 2021; Neme et al., 2021; Farooq et al., 2022). Recently, nanotechnology has emerged as a promising field in agricultural systems with its application as nanoparticles (NPs), nano-carriers, nano-fertilizers, nano-pesticides, nano-capsules, and nano-sensors (*Figure 1*); nevertheless, applied nano-materials should be flexible according to climatic fluctuation based on plant requirements and thus needs precision system for application of nanomaterials in agricultural field for food security (Usman et al., 2020; Zulfiqar and Ashraf, 2021; Vithanage et al., 2023).

Nano-porous materials could be designed to slowly water accumulating and distributing in water-deficient agricultural land (Ranjan et al., 2022). Admiringly, it can assist in delivering the appropriate precise amount of nutrients and pesticides in plants, reducing superfluous chemical usage and the environmental effects of mineral leaching (Usman et al., 2020; Hu and Xianyu, 2021). Nevertheless, there are challenges in smart and efficient designing and successful application could lead to providing safe and non-toxic nano-enabled agrochemicals applications that are marvelous eco-friendly solutions in advanced agriculture (Usman et al., 2020; Hu and Xianyu, 2021; Abdollahdokht et al., 2022). Moreover, the development of nano-material-based engineered genetic tools for

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targeted distribution of nanocarriers in crop development programs (Yan et al., 2022). However, nanotechnology considered a few negative aspects regarding polluting the natural environment, and food security (Jiang et al., 2021; Liu et al., 2021), which need future research to motivate growers and the community that it is a promising and innovative technology in agriculture to achieve sustainable and ecofriendly cultivation and address 21st century's challenges (*Fig. 1*).

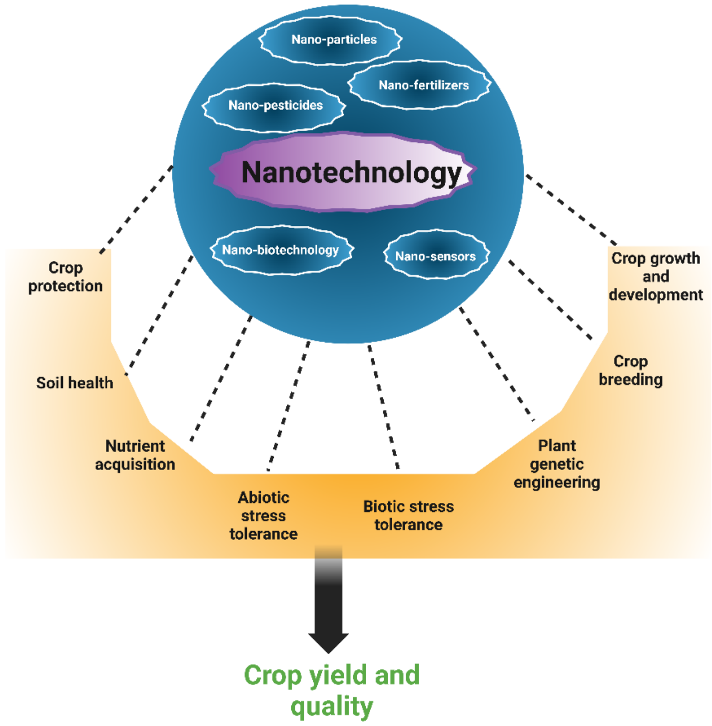

Figure 1. *Nanotechnology with different aspects in the agricultural field to improve crop production*

Nanoparticles improve plant health at diverse developmental stages under stress conditions

The plant responds for its survival to adverse environmental conditions according to stress intensity, duration, and growth stage (Liu et al., 2021). Non-conducive environment exerts unfavorable impacts on a plant's normal functioning during various developmental stages, whereas, exogenously applied stress modulators facilitate the plants for stress mitigations. Previous studies showed the growth stage-dependent plant response to different exogenous substances which can improve or delay growth traits (Kupke et al., 2021; Ostrowska et al., 2021; Ranjan et al., 2022). Likewise, the appropriate level of NPs lessens the hostile impact of environmental factors (drought and salt) (Zulfiqar and Ashraf, 2021; Abdelsalam et al., 2023). Different types of NPs (ZnO and Ag-NPs) stimulate antioxidative defense mechanisms in various plant tissues, alleviating the ROS and enhancing growth (Mahakham et al., 2017; Acharya et al., 2020; Waqas Mazhar et al., 2022). Moreover, NP-modulated stress mitigation significantly depends on their concentrations, plant types, and phenological stage (Usman et al., 2020; Hu and Xianyu, 2021). Generally, NPs-related plant stress responses during various growth stages under stress conditions are presented (*Fig. 2*).

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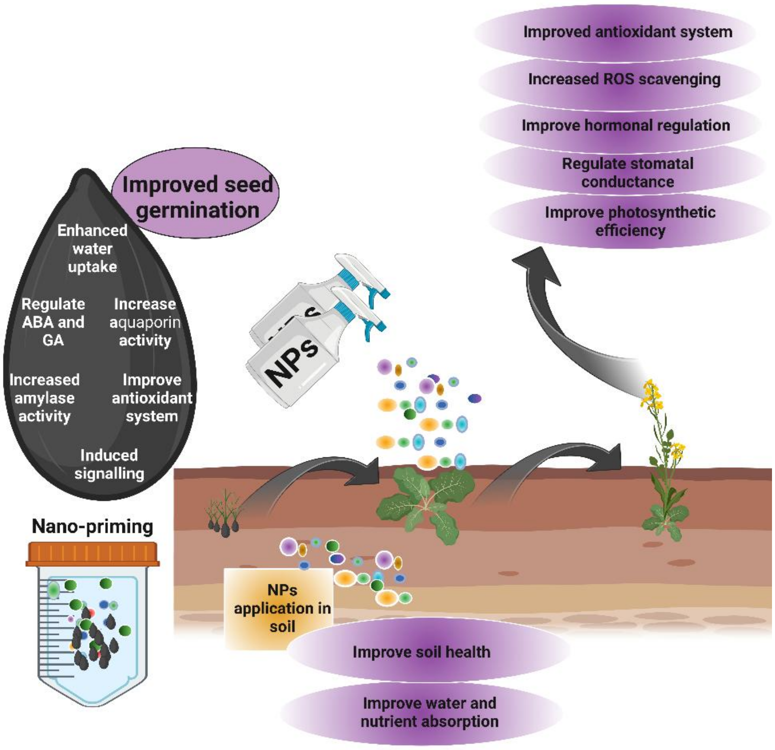

Figure 2. *A schematic description of NPs mediated mechanisms. Three common modes of NPs application nano-priming, foliar, and soil treatment are beneficial for plant and soil health through different physiochemical processes*

Nanoparticles mediated seed germination under drought stress conditions

NPs can modify metabolic mechanisms at the physio-biochemical level during the germination process (Li et al., 2021). Studies showed that NPs highly improved sprouting and seedling growth compared to bulk and ionic materials (Singh et al., 2020; Abbasi Khalaki et al., 2021; do Espirito Santo Pereira et al., 2021). Seed sprouting is a vital and sensitive initial growth period of a plant life cycle that involves metabolic adjustments to encounter environmental factors. NPs facilitate breaking seed dormancy through enhancing water and nutrient absorption, inducing enzymatic activity (proteases, peroxidases, catalases, amylase), and activating plant antioxidative mechanisms under external stimuli (Mahakham et al., 2017; Acharya et al., 2020), which enhanced seed vigor for seedling establishment. Metal nonmaterial has been widely used as seed priming treatment such as priming of Ag-NP of aged rice showed higher propagation and vigor of seedlings through inducing amylase enzyme activity, thereby, elevating soluble sugar concentration than untreated seeds (Mahakham et al., 2017). Priming of ZnO-NPs (25, 50, and 100 ppm) enhanced seed germinating ability by improving soluble sugar and proline levels of rapeseed seeds under 150 mM salt stress (El-Badri et al., 2021). Untargeted metabolomics analysis in Fe-NPs primed seedlings displayed the improvement in non-enzymatic antioxidants and jasmonate-related defense system, demonstrating the Fe-NPs potential in activating signaling pathways of *Citrullus lanatus* L. (Kasote et al., 2019).

Similarly, selenium and ZnO-NPs mediated the ABA and GA-related gene expression on seeds in the germination process under salinity conditions, enhancing their

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germination ability (El-Badri et al., 2021). In Rice, ZnO-NPs priming (25 ppm) leads to better plant development a yield competing with untreated seeds under drought through accumulating osmotic substances especially proline and antioxidative enzymes (Waqas Mazhar et al., 2022). NPs with TiO_2 (60 ppm) in maize seeds significantly enhances the seed germinating and vigor ability under salt stress modulated through higher antioxidative enzymatic efficiency (Shah et al., 2021).

NPs could reduce the damage to photosynthesis machinery and ultra-structural variation of cells upon unfavorable environmental cues by triggering H_2O_2 signaling and antioxidative system (Salam et al., 2022). Moreover, NPs enhanced the stress tolerance, as seed priming of 90 ppm concentration of multi-walled carbon nanotubes enhanced salt tolerance in *Vitis vinifera*, improved seed germination and seedling establishment, through decreasing malondialdehyde (MDA) level of lipid peroxidation and inducing the antioxidative system (Li et al., 2022). Similarly, NPs in broccoli seedlings improved the growth under salinity stress via increasing aquaporin transduction to enhance water uptake and CO_2 adjustment (Martínez-Ballesta et al., 2016). Above mentioned studies showed that NPs is an efficient environmentally friendly approach to elevate water absorption through nanopores, improving the antioxidative system, and starch hydrolysis thereby enhancing germination processes.

Nanoparticles mediated seedling growth under drought stress conditions

Nano foliar application on seedlings lessens the stress-related growth effects in parallel with the germination stage. Foliar spraying of ZnO NPs enhanced biomass through accelerating antioxidative defense systems to scavenge ROS and reduce MDA levels under drought conditions in cucumber seedlings (Ghani et al., 2022). Likewise, ZnO-NPs remarkably boosted growth-related traits (plant biomass, photosynthesis, and seed yield) in salt-treated wheat plants during vegetative and later growth stages (Adil et al., 2022). Additionally, different types of factors such as antibiotics, and TiO-NPs applied into the soil (50 ppm), enhanced nutrition value by improving grain nutrient acquisition of iron, protein, and sugar (31 to 42%) in *Triticum aestivum* (Amin et al., 2023). Conclusively, applying functionalized NPs under biotic and environmental factors is gaining consideration and various reports documented their promoting effects in different developmental processes responding to various stressful cues. For instance, functionalized graphene oxide-glycine betaine NPs with 50 ppm dose reduced the adversative impact of salt stress in *Ocimum basilicum* L. through promoting photosynthesis, membranous stability, oxidative and non-oxidative metabolite accumulation (Ganjavi et al., 2021). Besides, ZnO NPs amplified salt tolerance in *Sophora alopecuroides* through regulating carbon and nitrogen-related metabolism, and PSII activity for plant growth (Wan et al., 2020).

Nanoparticles mediated reproductive growth under drought stress conditions

Several environmental factors impact reproductive growth, a dynamic life period in flowering plants (Salehi et al., 2021). Previous studies showed vulnerability in vital reproductive processes, including the transition phase, inducing flowering, sporogenesis, and gametogenesis, to the external environment, resulting in male sterility and seed abortion during later stages of development (Du et al., 2020a; Salehi et al., 2021). Moreover, the appropriate usage of NPs can enhance the yield-related traits leading to higher seed yield and fruit quality. Likewise, foliar application of SiO_2 and TiO_2 NPs considerably enhanced seed weight and yield upon water deficit conditions in barley

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(Ghorbanian et al., 2017). Further, at full bloom and 1 month after salt stress, ZnO and Si NPs external spraying at concentrations of 50,150 ppm exert positive effects on plant development, nutrient absorption, carbon metabolism, proline status, and antioxidative enzymatic activity, thereby decreasing flower malformation and seed abortion, enhancing fruit yield and quality of *Mangifera indica* (Elsheery et al., 2020). Application of Fe-NPs in soil improved photosynthesis and reduced osmotic damage in wheat plants upon combined metal (cadmium) and water deficiency events, consequently increasing plant development and subsequent yield (Adrees et al., 2020). In the same way, micronutrient NPs (ZnO, B2O3, and CuO) soil treatment and foliar spraying three weeks later from germination improved wheat productivity by approximately 33-36% under water deficit conditions; moreover, the soil treatment was highly effective compared to foliar application (Dimkpa et al., 2017). However, additional investigation is needed to assess the effect of NPs on later plant growth stages upon unfavorable environmental stresses.

Taken together, NPs application mediate various molecular mechanisms during the germination of seeds, expansion in seedlings, and plant maturity by improving the oxidative stress-responsive gene expression, and accretion of proteins and metabolites to facilitate defense systems for stress tolerance, ensuring plants encounter different environmental factors by regulating key signaling molecules, such as H_2O_2 and responsible transcription factors. Still, the interrelated mechanism of NPs and reproductive stages of plants require further consideration by future investigation through different omics approaches besides phenotypical and agronomic-related traits under abiotic stresses.

Application of NPs to improve plant stress tolerance

Food security is a serious challenge of continuous population due to limited resources and drastic continuous global climate change. Climatic adversities lead to serious environmental unfavorable conditions which highly affected plant developmental mechanisms and crop production (Kumar et al., 2021; Wang et al., 2021; Farooq et al., 2022; Rivero et al., 2022). Subsequently, it is imperious to assist the better adaptation in plants via hormonal regulation, enzymatic defense systems induction, stress-responsive genes activation, dehydration damage evasion, and nutrient uptake and apprehension (Rivero et al., 2022; Cooper and Messina, 2023; Raza et al., 2023b). Recently various reports illustrated the imperative role of nanotechnology in improving crop productivity in adverse external cues, especially under drought and salt stress conditions (Usman et al., 2020; Jiang et al., 2021; Zulfiqar and Ashraf, 2021; Kandhol et al., 2022).

Drought stress management by NPs

On exposure to external environmental stimuli, drought conditions restricted plant development and yield (Varshney et al., 2021; Cooper and Messina, 2023; Raza et al., 2023b; Yang and Qin, 2023), whereas NPs mediate the improvement in unfavorable drought stress through activating physio-biochemical processes and regulating stress-responsive gene transcription (*Table 1*). Several types of NPs are recognized to confer stress tolerance and boost yield with lowered economic and nutritional damages upon water deficit conditions (Kandhol et al., 2022). Furthermore, the method of exogenous nanoparticle application significantly influences plant growth by modulating a range of physicochemical processes, ultimately boosting plant resilience. Among the most effective application methods, seed priming, foliar application, and soil treatment have been shown to improve stress tolerance in plants (*Fig. 3*).

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Table 1. *Nanoparticle applications with effective participation in stress amelioration in various species of plant*

NPs	Crops	Applied level	Treated mode	Ameliorative effects	References
ZnO-NPs	*Triticum aestivum*	1.7 mg/kg	soil	Improved plant development and mineral accumulation in grains	Dimkpa et al. (2020)
Fe_3O_4	*Fragaria ananassa*	0.0, 0.08, and 0.8 ppm	Medium	Induced defensive system before transplanting plant	Mozafari et al. (2018)
Ag NPs	*Crocus sativus* L.	55 and 110 ppm	Foliar	Modulating stress effects through inducing peroxidase, catalase, and ascorbic acid, and protecting photosynthetic apparatus	Sabertanha et al. (2018)
C NPs	*Zea mays*	0, 25 and 50 ppm	Seed priming	Mediated germination processes and photosynthetic efficacy	Shahriari et al. (2019)
ZnO NPs		100 mg L−1	Soil	Improved crop productivity via melatonin production and inducing antioxidative system under stress.	Sun et al. (2020a)
K NPs		0, 100 and 200 ppm	Foliar	Increased the level of nitrogen, potassium, copper, manganese, and silicon while reducing the hostile stress effects	Aqaei et al. (2020)
Cu NPs		52 (3.333 mg/L), 69.4 (4.444 mg/L) and 86.8 μM (5.556 mg/L)	Priming	Modulated the defensive system by reducing ROS levels under stress	Van Nguyen et al. (2022)
ZnO NPs		100 ppm	Soil	Enhanced carbon metabolism, and sugar related mechanisms, and antioxidative system induction to protect mitochondrial and chloroplast structure	Sun et al. (2020b)
Si NPs	*Tanacetum parthenium*	0, 1.5 and 3.0 mM)	Foliar	Enhanced water and phosphorus absorption.	Esmaili et al. (2021)
Cu NPs	*Triticum aestivum* L.	0, 3, 5 and 7 ppm	Foliar	Increased chlorophyll stability, leaf turgor, stomatal closure, nutrient absorption, and water efficiency	Ahmed et al. (2021)
ZnO NPs	*Solanum lycopersicum*	25 and 50 mg/L ZnO-NPs	Foliar	Improved ascorbic acid, free phenols contents, and regulate antioxidative enzyme activities	El-Zohri et al. (2021)
Fe_3O_4 NPs	*Setaria italica* L.	5, 10, 15, 20, 50, 90 and 120 ppm	Soil	Improved photosynthetic efficiency and accumulation of osmolyte	Sreelakshmi et al. (2021)
ZnO NPs	*Solanum melongena* L.	0, 50 and 100 ppm	Foliar	Increased photosynthetic efficiency and fruit nutrient besides water use efficiency	Semida et al. (2021)

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NPs	Crops	Applied level	Treated mode	Ameliorative effects	References
Cu, Fe, and Zn NPs	*Glycine max*	50 mg/L of Fe, ZnO, and Cu NPs and 0.05 mg/L	Seed soaking	Induced drought-responsive genes	Linh et al. (2020)
SiO_2 NPs	*Triticum aestivum* L.	150 ppm	Soil	Induced antioxidative enzymatic system	Akhtar et al. (2021)
Mn NPs	*Glycine max* L.	Nano-chelates of manganese with iron and zinc	Foliar	Enhanced micro-nutrient status and crop yield	Vaghar et al. (2021)
CaO NPs	*Onobrychis viciifolia* L.	0.5 and 1.5 ppm	Foliar	Modulated H2O2 denegation, and malondialdehyde with improving chlorophyll content and responsive gene expression	Ertuş and Yazıcılar (2023)
Se NPs	*T. aestivum*	10 ppm	Foliar	Enhanced photosynthetic capacity, and improved antioxidative enzymatic defense system	Omar et al. (2023)
ZnO NPs		50, 100 and 150 ppm	Foliar	Increased photosynthetic pigments and antioxidant defensive systems to avoid osmotic stress	Kausar et al. (2023a)
TiO_2 NPs	*Solanum lycopersicum*	100 ppm	Foliar	Enhanced relative water level and regulated proline and MDA	Çevik (2023)
CH NPs		60 and 90 ppm	Soil	Modulated stress-responsive gene expression	Mohamed and Abdel-Hakeem (2023)
B_2O_3 NPs	*Pisum sativum* L.	12.5, 25 and 50 ppm	Foliar	Boosted antioxidant defense system	Sutulienė et al. (2023)
ZnO NPs	*Coriandrum sativum* L.	100 ppm	Foliar	Increased photosynthetic efficacy, stomatal regulation, and secondary metabolite accumulation	Ahmed et al. (2022)
F_2O_3 NPs	*Vitis vinifera* L.	0.7 ppm	Foliar	Reduced MDA and ROS accumulation and improved defense system	Bidabadi et al. (2022)
Si NPs	*T. aestivum* L.	30, 60, 90 and 120 ppm	Foliar	Decreased ROS and MDA generation and improved defensive system	Boora et al. (2023)
ZnO and SiO_2 NPs	*S. tuberosum* L.	0, 50 and 100 ppm and 0, 25 and 50 ppm	Foliar	Improve gaseous conductance, and photosynthetic efficiency in leaves	Al-Selwey et al. (2023)
Mn_3O_4 NPs	*Z. mays* L.	500 ppm	Soil-root	Improved root structure, biomass, and protein content while reducing ROS and lipid peroxidation	Sun et al. (2023)
MS NPs	*A. thaliana* L.	0–5,000 ppm	Foliar	Improved root structure leaf area and vegetative biomass	Tran et al. (2023)

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NPs	Crops	Applied level	Treated mode	Ameliorative effects	References
SiO_2 NPs	*Crataegus rhipidophylla*	10, 50 and 100 mg L−1	Irrigation	Enhanced stomatal regulation, photosynthesis rate, water potential in vascular tissues	Ashkavand et al. (2015)
ZnO NPs	*Dracocephalum kotschyi* L.	10 and 20 ppm	Foliar	Improved photosynthetic processes, osmolyte, and antioxidant enzyme activity	Karimian and Samiei (2023)
ZnO and SiO_2 NPs	*Solanum tuberosum* L.	0, 50 and 100 ppm and 0, 25 and 50 ppm	Foliar	Enhanced tuber mass, ascorbic acid, soluble solutes, and starch accumulation	Seleiman et al. (2023)
Zn NPs	*Brassica rapa* L.	100, 500 and 1000 ppm	Foliar	Improved plant length, biomass, and defense system by accumulating secondary metabolites	Li et al. (2023)

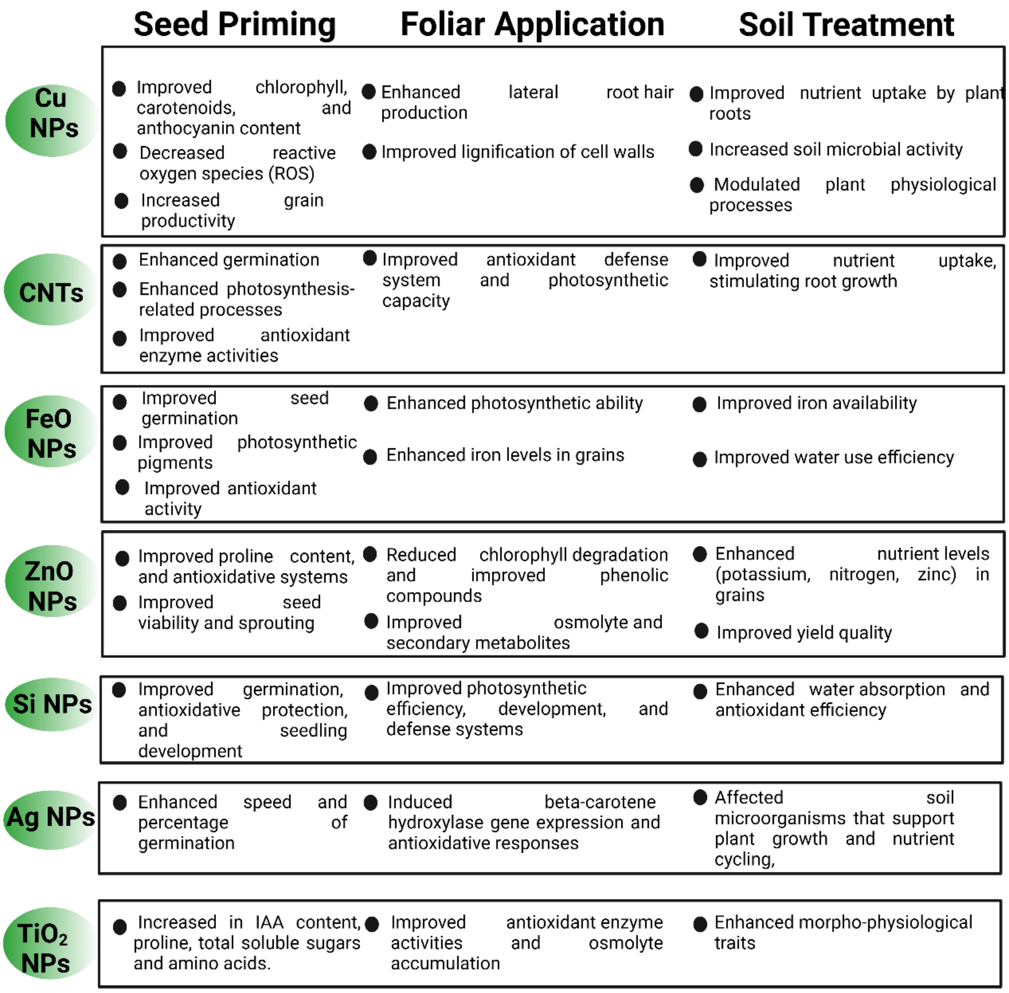

Figure 3. *Function of nanoparticles in enhancing plant stress tolerance through different application methods including seed priming, foliar application, and soil treatment*

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Nanoparticles application as seed priming

In maize plants upon drought stress, Cu-NPs seed priming improved chlorophyll, carotenoids, and anthocyanin contents with decreasing ROS, thereby increasing grain productivity (Nguyen et al., 2020). Cu-Zn-NPs primed wheat seeds alleviated the stress by enhancing antioxidative activities, improving water content, leaf area, and photosynthetic pigments, and reducing the synthesis of thiobarbituric acid under water deficiency (Taran et al., 2017). Seed priming (25 ppm) with NPs in maize enhanced the germination processes, and photosynthesis-related substances upon water deprivation (Shahriari et al., 2019). In soybean, NPs treated seeds showed higher seed germination, and plant biomass and length, besides antioxidant enzyme activities, thus regulating lipid peroxidation and H_2O_2 level upon drought stress (Sun et al., 2020c). Fe3O2-NPs priming improved wheat seed germination, photosynthetic pigment proline accumulation, and antioxidant enzymatic activity under water deficiency (Noor et al., 2022). ZnO-NPs primed rice seed showed lower stress effects with higher growth with enhancing proline content and improving anti-oxidant system supporting the plants to encounter drought conditions (Waqas Mazhar et al., 2022). Moreover, ZnO-NPs boost the soybean resilience of stress tolerance by the role of Zn in improving seed viability and sprouting (Degenhardt and Gimmler, 2000; Sedghi et al., 2013). Notably, the efficiency of NPs on germination of seeds and plant growth varies with applied concentration and host plant. Notably, higher seed germination and efficient antioxidant system was noted in NPs treated maize (Liu et al., 2016). Likewise, SiO_2-NPs improved stress adaptation by enhancing germination, anti-oxidative protective system, water absorption, amylase activity, and seedling development in *T. aestivum* under water deficiency (Akhtar et al., 2021).

Nanoparticles application as a soil treatment

Besides, Fe-NP treatment in soil seven days before sowing lessened osmotic stress and cadmium uptake and improved photosynthetic ability and Fe level of grains upon cadmium and water-limited conditions in wheat plants (Adrees et al., 2020). Furthermore, Si-NPs treatment in soil considerably enhanced photosynthetic-related pigments in *Hordeum vulgare* L. by mediating the vegetative growth and antioxidative enzymatic efficiency during the post-drought recovery period (Ghorbanpour et al., 2020). In addition, potassium-NPs supply into drought-affected soil in maize enhanced nutrient uptake, seed potassium, and nitrogen content, and shoot silicon, copper, and manganese contents, repressed adversative stress effects (Aqaei et al., 2020). The Si-NPs effects on two sorghum cultivars with contrasting stress tolerance showed that Si-NPs improved water absorption capacity (Hattori et al., 2005). In a particular fertilizer formulation of ZnO and CuO-NPs application at various NP dosages, root growth is differently affected, where, at specific Zn NPs level lateral root expanding during its formation while Cu NPs cause root hairs proliferation and elongation of close in wheat seedlings under drought stress, which could be due to valuable bacteria isolated from roots in calcareous soils under dryland (Yang et al., 2017). Likewise, under drought stress in wheat TiO_2-NPs soil treatment induced stress tolerance by enhancing morpho-physiological traits, osmolyte accumulation, membrane integrity, and chlorophyll level (Mustafa et al., 2021). Soil treatment with Cu-NPs (300 mg L^{-1}) improve water and nutrient retention capacity and fertility of soil along with better source to sink relationship under water deficit conditions, which mitigated the deleterious effects of drought stress (Raza et al., 2024).

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Nanoparticles treatment as a foliar application

Additionally, ZnO-NPs foliar treatment (50 and 100 ppm) after transplanting (30 and 45 days later) in *Solanum melongena* L. improved RWC and membrane integrity and regulated the structural variation in plant morphology of above-ground parts and photosynthetic machinery upon water stress conditions (Semida et al., 2021). Moreover, soil amendment with ZnO-NPs (1, 3, and 5 mg kg^{-1}) under drought conditions lessened the stress effects in sorghum and boosted grain yield by 22%–183% and improved the nutrient level in grain such as potassium was enhanced by 16–30% and nitrogen and zinc was increased by 94% (Dimkpa et al., 2019). Furthermore, exogenously applied ZnO-NPs (0.1% and 0.05%) in two-week-old moringa increased stress tolerance by reducing chlorophyll degradation and improving the antioxidative system and phenolic compounds under drought conditions (Foroutan et al., 2019). Foliar application of NPs (ZnO) working to preserved cellular integrity and water status, resulting in efficient PS-II and metabolic processes under drought conditions (Semida et al., 2021). ZnO NPs significantly improved the accumulation of phenolic compounds leading to higher antioxidant activity and lower MDA and ROS accumulation (El-Zohri et al., 2021). Moreover, 1% of nano-chitosan external application under drought stress on the 45th day of growing seedlings alleviated the stress effects in *Catharanthus roseus* through activating the alkaloid synthesis-related gene expression, improving osmolytes synthesis and antioxidative enzymatic activity of catalase and peroxidase enzymes, and decreasing lipid peroxidation and H_2O_2 level (Ali et al., 2021).

In Murashige and Skoog medium, FeO-NPs application alleviated the adverse effects of drought by enhancing photosynthesis efficiency, morpho-physiological development, proline concentration, sugar, and proteins with non-toxic effects in strawberry plants (Mozafari et al., 2018). Additionally, field experiments were conducted with foliar Si-NPs application at the 10 to 12-leaf stage of beet, to defend against water shortage exposure by enhancing development, through improving photosynthetic efficiency and defense system by alleviating leaf senescence (Namjoyan et al., 2020). In crocus corms, Ag-NPs application modulated the negative impact of stress by inducing the beta-carotene hydroxylase gene besides enhancing antioxidative responses (Sabertanha et al., 2017). *Tephrosia apollinea* plants treated with Ag-NPs showed a strong antioxidant defense system with elevated plant biomass and lower osmotic stress (Ali et al., 2019).

At different plant growth stages, foliar application of nano-Fe and Mn, improved crop productivity, and mending the dehydration-induced damage leads to stress tolerance in barley plants (Zahedi and Alipour, 2018). Also, foliar manganese nano-chelates treatment at V4 and 1 week later decreased the stress impact by improving leaf area, grain yield, dry weight, and nutrient intake in soybean during drought conditions (Vaghar et al., 2021). Besides, manganese nano-chelates foliar spray one week before and after irrigation enhanced photosynthetic pigment levels to decrease drought stress in *Vigna radiate* L. (Sanavi and Mohammad, 2018). In Calendula officinalis, potassium-NPs remarkably enhanced proline, glycine, betaine, and morpho-physiological characteristics under water deficiency (Erfani et al., 2022).

Under drought stress, TiO_2-NP at the 4 to 6 leaf stage and 14 days later in maize significantly enhanced grain production by increasing antioxidant enzymes activities of SOD, APX, and CAT and improved osmolyte accumulation in leaf (Karvar et al., 2021). Also, exogenously applied nitric oxide in wheat seedlings enhanced the defensive impact of TiO_2-NPs in stress tolerance, photosynthetic efficacy, and the antioxidant protective system under drought conditions (Faraji and Sepehri, 2020). Metal oxide NPs scavenge

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stress-induced radicles through osmolyte accumulation, increasing water regulation and oxidative responses (Alabdallah et al., 2021). Se-NPs application with 30 ppm at the trifoliate stage lessened drought stress and increased growth-related traits by improving stress tolerance in wheat crops (Ikram et al., 2020) ZnO-NPs improved drought tolerance through enhancing antioxidant activities, relative water content, and photosynthetic pigments besides decreasing stress-related proline level in soybean (Shirvani et al., 2024).

Upon drought exposure, foliar applied ZnO-NPs in cucumber seedlings improved osmolytes and secondary metabolites such as sugar, amino acids, and proline, and reduced MDA and ROS content (Ghani et al., 2022); moreover, a lower dose of sodium silicate mitigated drought stress in wheat plants (Pei et al., 2010). A previous study showed that silicon NPs lessened the drought effects in hawthorns (*Crataegus* sp.) by mediating physiochemical responses (Ashkavand et al., 2015). Iron is a crucial element required for normal developmental processes its shortage showed physiological aberrations (chlorosis and metabolic disturbances) (Jalil and Ansari, 2019); moreover, micronutrients also play an imperative role in lessening the drought stress effects in plants, for instance exogenously applied FeNPs on flowering and later growth stages provide stress resilience thus enhanced productivity (Davar Zareii et al., 2014). Likewise, TiO_2NPs foliar application in wheat improved physiological traits including photosynthetic activities, gluten, starch, biomass accumulation, harvest index, and ultimately crop productivity was increased (Jaberzadeh et al., 2013).

It improved photosynthetic efficacy through enzyme activity related to the C3 cycle besides photosynthetic pigments for plant development (Lowry et al., 2019). Whereas, foliar application of NPs improved yield than water spray in sorghum under drought stress. TiO_2 NPs improved plant biochemical and morpho-physiological properties (Djanaguiraman et al., 2018). In cucumber, exogenously applied NPs improved rubisco activase activity, and photosynthesis-related traits, leading to improved plant dry mass (Ghani et al., 2022); similarly, NPs increased the soybean yield by enhancing photosynthesis (Linh et al., 2020). TiO_2 NPs effect differs with altering environmental cues, plant types, and applied concentration. Nano-TiO_2 content on morphophysio-chemical traits of dragonhead plants (Mohammadi et al., 2016). The TiO_2 enhanced plant growth and essential oil under drought conditions.

ZnO and CuO NPs possess protecting properties encountering stress in many crops by enhancing lateral root hair production for efficient water uptake. CuO application improved the lignification of cellular walls in brassica and A. thaliana upon drought, and limited cell wall extension (Yang et al., 2017) (Nair and Chung, 2015). Furthermore, fullerenol NPs alleviated stress impact by water uptake and distribution in plant cells through NPs entry into roots and leaves where it interacts with molecules of water in different cell parts and alter intracellular water metabolism (Borišev et al., 2016; Verma et al., 2019).

A previous study reported that NPs target organelles and release different contents to modulate the antioxidative enzyme activities (Siddiqi and Husen, 2016); similarly plant SOD activity was improved with TiO_2 NP application (Ghasemlou et al., 2019). Additionally, Si NPs application ameliorated the adverse effects of abiotic stresses such as drought stress (Siddiqui et al., 2020), meanwhile ZnO NPs with silica improved plant development, and physiochemical traits have been noted upon stress (Seleiman et al., 2020). Besides, Si NPs decreased stress in wheat plants (Rizwan et al., 2019) and, ZnO NPs decreased salt and drought stress (Khan et al., 2020). In addition, excess NP application causes osmotic stress, leads to arresting cell cycle and programmed death, and

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promotes protein and antioxidative-related responses (Jalil and Ansari, 2019), while appropriate NPs application reduces MDA content with lower accumulation of free radicals under drought conditions. Nevertheless, TiO_2 improved the antioxidant system to reduce MDA (Ahmad et al., 2019).

Under water deficiency, CuO NPs enhanced anthocyanin and proline in plants, besides, CuO-treated NPs roots highly accumulated the free radicals, consistent with plant's responses to NP-regulated ROS cascade, which induced ABA signaling, which causes transcriptional changes for stress tolerance. Transcriptomic and proteomic studies comprehensively examined NPs effects on various crops at the molecular level. Morpho-physiological responses showed that NPs effects greatly depend on application dose, nature, size, and shape of NPs (Pérez-de-Luque, 2017; Pérez-Labrada et al., 2020). The P5CS gene expression encoding proline biosynthesis improved stress tolerance to external unfavorable environments, such as biotic and abiotic factors, since this; moreover, the MAP kinase gene family (MAPK2) regulated phytohormones and antioxidant mechanisms with Ca21 and ROS under stressful environments (Pérez-Labrada et al., 2020). Additionally, AREB/ABF as transcription factors regulating AREB gene encoding ABA to improve stress resilience against water deprivation and salinity conditions (Yoshida et al., 2015; Pérez-Labrada et al., 2020). Downregulation of the ZFHD gene decreases the adverse effects of salt and drought stress and is regulated by the ABA-related pathway; whereas, TAS14 gene downregulation decreases osmotic stress and improves osmolyte accumulation (K1 and sugar) to mediate stress tolerance (Pérez-Labrada et al., 2020). Ag NPs treatment with 5 and 10 mg/L controlled the glucosinolate and phenolic-related metabolic processes that are also related to biotic and abiotic stress responses, and repressed carotenoid genes in rapeseed plants (Thiruvengadam et al., 2015). The Ag NPs application in Arabidopsis leads to the over-expression of osmotic and metal-responsive genes, also induced by thalianol biosynthesis related, and downregulating the ethylene and auxin-related genes (Pérez-Labrada et al., 2020). Several reports documented the different types, doses, and effects of different NPs that successfully alleviated drought stress and improved key metabolic processes. However, NPs such as Mn-NPs and Cu-NPs are still in progress to find their action mechanisms for stress tolerance; therefore, deep insight is needed on the molecular level to ensure their effects in combating stress.

Conclusions

Climate Change is directly influencing agricultural crop productivity; moreover, concerns related to climatic issues are leading to a growing interest in stress tolerance-related strategies to encounter the intensity of deleterious weather events, including water stress. Drought stress negatively affects biochemical and photochemical mechanisms, resulting in decreasing plant biomass besides leaf senescence; additionally, it disrupts the plant's relative water contents leading to osmotic stress that seriously damages membranes and disrupts normal cellular functioning. It reduced plant biomass at the vegetative stage, which is related to critical switches of reproductive transition. Plants respond to drought stress through several physio-biochemical responses at cellular and whole-organism levels at the expense of their growth and development; therefore, it is urgent to use sustainable substitutes that facilitate plants for their survival and growth to encounter frequent and intense drought episodes. Nanotechnology is a promising, interdisciplinary, and revolutionary area in the current climate fluctuation scenario and it

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is presenting nanoscale matter with its potential in advanced agriculture worldwide. NPs displays several unique characteristics and properties compared to its bulk matter that have great potential in various fields including agriculture. Exogenous NPs application (seed, foliar, and soil application) is a hopeful practice to improve plant growth, crop yield, and soil health upon normal and stressed conditions. NPs contribute to several morphophysiological mechanisms such as germination, seedling growth, reproductive development, and overall plant yield that facilitate the plants against drought stress. It boosts the osmotic adjustment by a buildup of an antioxidative defense system under drought conditions; moreover, it is also used as fertilizer nanocarriers, improving soil health that leads to stress management with proper crop growth and ultimately crop yield.

The use of NPs has shown appreciable results in mitigating the toxic effects of drought stress. Nevertheless, more studies are needed to investigate the impacts on NPs under combined stress conditions. There are limited studies available about the uptake and movements of NPs in plants. Thus, it is essential to perform studies to determine the mechanism of NPs movement, uptake, and translocation within plants under drought stress. Further, diverse genomic and proteomic studies are also direly needed to study the behavior of NPs in soil-plant systems and their impacts on antioxidant defense systems. The use of NPs can pose health and environmental contamination problems due to their accumulation of edible plant parts. Thus, it is mandatory to know the impact of NPs on plants, and their risks on humans, and the environment. Biogenic NPs also show appreciable results to counter abiotic stress. Therefore, more studies are direly needed to develop biogenic NPs as they are less toxic and biodegradable. The nano-technology made significant progress in breeding and genetics, yet the transformation of exogenous DNA by CRISPR/Cas is a challenging task. Thus, modern techniques including nanostructures and nanogels must be used to improve the delivery of DNA to produce the genome editing crops. In literature, most studies are conducted in controlled conditions and there is a paucity of information about the impact of NPs under field conditions. Thus, extensive field studies are required to determine the impact of NPs in mitigating the toxic impacts of drought stress.

Despite the promising potential of nanoparticle in improving drought stress tolerance, various challenges still need clear understanding and deep insight. A primary issue is variation of nanoparticle uptake and bioavailability that is significantly affected by different factors such as particle size, surface charge, and plant species. Whereas, small nanomaterial tends to enter plant cells more easily, their uptake efficiency varies under different environmental conditions. In addition, nanoparticles translocation from roots to upper tissues (stems and leaves), remains inefficient in some cases, limiting their effectiveness in improving drought tolerance across the entire plant. Moreover, the ecological impacts of nano-materials, such as potential toxicity to non-target organisms and soil microbiota, are under-researched. To address these limitations, further investigation is required which focusing on field trials to evaluate the real-world applicability of nanotechnology and bio-safety studies to assess long-term environmental risks, ensuring that their use is effective and leads to sustainable agriculture.

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