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REVIEW ARTICLE

Nanomaterial based drought mitigation in crops is through antioxidant defense system

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Abstract

Drought stress significantly impacts crop productivity by affecting the growth and development of plants. Studies have shown that drought stress induces oxidative damage, and the use of antioxidant molecules or nanoparticle (NPs) possessing antioxidant properties may decrease the negative effects of oxidative stress. So far, antioxidants like ascorbic acid, glutathione, proline, and glycine betaine have been studied in detail, but there is limited information available on the effect of NPs in decreasing drought induced oxidative damage. When plants are subjected to drought stress conditions, their ability to scavenge reactive oxygen species (ROS) decreases leading to an increase in ROS that can damage membranes, proteins, and lipids. Nonenzymatic antioxidants, such as tocopherols, ascorbate, glutathione, phenols, and carotenoids, along with enzymatic antioxidants such as superoxide dismutase, catalase, and ascorbate peroxidise, can strengthen the plant defense against ROS. Nanoparticles possessing antioxidant properties can mimic antioxidant enzymes, activate, and alter gene expression levels, leading to reduced ROS levels because of their increased surface area and presence of free electrons on their surface. This review discusses the effects of drought stress on crops, the synthesis, and unique properties of NPs, and the various traits improved by NPs possessing antioxidant properties to mitigate drought stress in plants.

Keywords

antioxidant machinery; drought stress; nanoparticles; reactive oxygen species

Introduction

Crops encounter different abiotic stresses, such as high temperature, drought, flooding, salinity, and heavy metal stress, during their life cycle, which affect them at various stages of growth. The most serious of all the abiotic stresses is drought. A shortage of rainfall below the required normal range in a specific region is termed as drought. The impact of drought on crops depends more on the distribution pattern rather than the total rainfall in a season. Drought is a recurring climatic phenomenon that varies in space, time, and intensity. A monsoon year is termed a drought year when the rainfall received is 15% less than normal. In India, during the period 1901-2015, the years 1965, 1972, 2002, and 2009 were extremely dry. More than 30% of the area under cultivation in India experiences drought if the total rainfall received during the southwest monsoon is less than 15% (1). An analysis of rainfall patterns during the northeast monsoon in South India from 1901-2015 indicated that the probability of moderate and severe drought is around 6-10% and 3-6%, respectively. The IPCC's Sixth Assessment Report on Climate Change forecasts a decline in the yield of coarse cereals, like wheat and rice, by 9% by 2050.

According to the United Nations estimate, the global population of 7.6 billion will increase to 8.6 billion in 2030, 9.8 billion in 2050, and 11.2 billion in 2100 (2). Even if fertility rates continue to fall, the upward trend in population size is anticipated to continue, with about 83 million people added to the world's population each year. The FAO estimates that increasing global food production and nearly doubling agricultural output in emerging nations will be necessary to feed a population of 9.1 billion in 2050 (3). As the global population increases, the challenge of sustaining crop yield becomes even more critical, especially under climate change induced water scarcity.

From the above, it is clear that the enhanced threat to crop production by environmental odds will be manifested in the form of drought stress of higher frequency and magnitude. Hence, it is important to improve the resilience of the crops to climate change through targeted breeding. The dividends from traditional approaches to achieving this task are diminishing, as they place an empirical emphasis on crop yield and less on traits contributing to stress tolerance. This gap can be bridged with novel approaches, such as the utilization of nanotechnology-based solutions. Nanotechnology, a cutting-edge approach, holds promise for mitigating the impacts of drought on crops. This review emphasizes the effects of drought stress on crops, its associated mechanisms of tolerance, and the role of NPs in alleviating drought stress.

Effect of drought stress and mechanism of tolerance

The impact of drought stress on crops is diverse, extending from morphological to molecular levels, and is prominent across all phenological stages. Also, the effects of drought stress depend on its severity, duration, and timing of the stress. Poor seed germination and seedling establishment are the primary consequences of drought stress. In crops like pea (*Pisum sativum* L.), alfalfa (*Medicago sativa* L.), and rice (*Oryza sativa* L.), drought stress during seed germination and seedling growth stage has been shown to decrease germination potential (4). In order to escape the adverse impact of drought, certain plants complete their life cycle during periods of optimum moisture availability. The ability of the plants to complete their life cycle before the onset of drought stress by altering the vegetative and reproductive growth in response to water availability through rapid development and developmental plasticity is defined as drought escape. Rapid development involves rapid growth and production of seeds before the depletion of soil moisture (5). Drought adversely affects cell division, enlargement, and differentiation. The allocation of photosynthates and metabolites needed for cell division is also decreased under drought stress. A lower shoot to root ratio observed in cowpea under drought indicates that plants invest more resources in root development compared to aboveground biomass to survive water stress (6). Cell elongation is affected by a reduction in turgor pressure due to inhibition in the flow of water to the surrounding cells from the xylem vessels under drought (7). Thus, reduction in cell division and cell enlargement of root tissue under drought stress leads to susceptibility to drought.

Plants exposed to drought exhibit significantly decreased leaf water potential, relative water content (RWC), and transpiration rate, resulting in increased leaf temperature. Water-use efficiency (WUE), the ratio between the dry matter produced and the total water consumed at the whole plant level, was increased under drought stress compared to well-watered conditions in cowpea when the stress was imposed during flowering stage (8). However, in potato (*Solanum tuberosum* L.), drought stress at the early vegetative stage significantly decreased WUE, resulting in reduced plant growth and dry matter accumulation (9). This suggests that crop growth stages affect drought stress impact on the WUE efficiency. Plants maintaining sufficient tissue water content or water potential under low soil and atmosphere water potential, through increased water uptake from the soil (water spenders) and decreased transpiration rate (water savers) fall under the drought avoidance category. Water spenders maintain higher tissue water content under drought stress through deeper roots, root length, and hydraulic conductance. Water savers sustain effective water usage under drought stress with the help of increased stomatal and cuticular resistance and alterations in leaf area, anatomy, and orientation, thereby reducing water loss (10).

Accumulation of osmotically active substances in the cytosol to maintain the turgor pressure of the cell is called osmotic adjustment (11). Drought tolerant plants maintain the cell turgor and volume under low leaf water potential or drought stress, leading to continued metabolic activity through increased osmotic adjustment, antioxidant enzyme activity, and epicuticular wax deposition. Maintenance of the plasticity of roots and shoot architecture is essential, as it contributes to drought tolerance at the canopy level. Rapid ground cover significantly enhances the efficient water usage by plants, with a notable reduction in loss of water due to direct evaporation. This is possible through shoot structural traits supported by tolerance mechanisms at the cellular level.

Photosynthesis during water stress conditions can be impaired by both stomatal and non-stomatal limitations. Under drought stress, non-stomatal limitation to photosynthesis is higher than stomatal limitation under mild drought stress. However, under severe drought stress, stomatal limitation overrides the non-stomatal limitation. Evidence suggests that the decline in canopy photosynthesis of the central part of Amazon evergreen forests by 28% during the dry season is due to the stomatal closing in the canopy (12). Overall, drought stress damages the photosynthetic machinery and reduces the stomatal conductance, leading to reduced crop yield.

Among several detrimental effects caused by drought stress, ROS generation is a major problem. Under normal state, ROS are constantly produced in plants, and plants possess effective scavenging strategies to maintain ROS at non-damaging levels. Even though ROS production occurs under normal conditions, it is much more aggravated under drought stress. During water deficit conditions, the ability of plants to scavenge ROS is reduced, resulting in an increase in highly reactive oxygen species. This leads to severe membrane damage, denaturation of proteins, peroxidation of lipids, and eventually programmed cell death (13). Drought can cause the generation of various ROS, including non-radical forms of ROS like singlet oxygen ($^1O_2$) and hydrogen peroxide (H_2O_2), as well as free radicals such as superoxide ($O_2^{\bullet-}$), hydroxyl radicals ($OH^\bullet$), perhydroxy radical ($HO_2^\bullet$), and alkoxy radicals ($RO^\bullet$). Among the known ROS, the most reactive chemical species are the hydroxyl radicals ($OH^\bullet$) (13). ROS generation takes place in different parts of the cell, including chloroplast, mitochondria, peroxisomes, plasma membrane, and even the cell wall under both stress and non-stress conditions. Excessive ROS generation under drought stress is detrimental to plants. Preserving cellular redox balance by overexpression of antioxidant enzyme activity under drought conditions is another tolerance mechanism, as it helps maintain cell membrane integrity. The following section will elaborate on the inbuilt enzymatic and non-enzymatic antioxidant machinery of plants.

Antioxidant machinery of plants

A substance that functions as an oxidizing agent during the redox reaction and has one or more unpaired electrons is called an oxidant. Through a chemical reaction involving the transfer of electrons, oxidants cause the formation of free radicals. An antioxidant is any compound that delays or inhibits the oxidation process. The antioxidant machinery of plants consists of both enzymatic and non-enzymatic components.

Catalase (CAT), guaiacol peroxidase (GPX), ascorbate peroxidase (APX), superoxide dismutase (SOD), glutathione reductase (GR), and dehydroascorbate reductase (DHAR) are the primary enzymes that make up the plant antioxidant enzymatic machinery. Ascorbate and thiols (GSSG or GSH) are important antioxidants with low molecular weight. ROS and peroxy radicals are neutralized by CAT and GPX, and the dismutation of O_2^- to H_2O_2 is mediated by SOD (14). Halliwell-Asada pathway involves the regulation of ROS and is mediated by the APOX, DHAR, and GR. The H_2O_2 produced by SOD is immediately reduced to H_2O by APOX. Ascorbate is replenished by the DHAR and is used by APOX to reduce H_2O_2 (15). Plants employ a wide range of non-enzymatic antioxidants along with antioxidant enzymes, working together to safeguard them from ROS stress.

The constituents of the non-enzymatic machinery include tocopherols, ascorbate, ascorbic acid, reduced glutathione, phenols, and carotenoids. Plants produce tocopherols, which are found in the chloroplast and function as membrane stabilizers while providing protection against drought. Lipid-soluble vitamin E, also known as α-tocopherol, assists in the removal of lipid peroxides and neutralize O_2^- and OH^- or $^1O_2$, which are extremely harmful to biomolecules (16). Much like vitamin E, ascorbate detoxifies $^1O_2$, OH^-, and O_2 radicals, as it can function as an electron donor. The application of exogenous ascorbate and GSH improves overall resistance to drought stress by enhancing antioxidant defences, helping plants to scavenge ROS (17). Phenols are secondary metabolites with a wide range of functions in the plant life cycle. Phenols, such as flavonoids found in the vacuole and the apoplast, serve as effective antioxidants *in vitro*. By donating either protons or electrons, phenols are involved in the quenching of hydrogen peroxide. Studies have shown that plants possessing higher flavonoid content have higher antioxidant capacity (18). Carotenoids are lipophilic isoprenoids, primarily found in leaves, flowers, and fruits. The most well-known types are β-carotene, lycopene, and zeaxanthin. Carotenoids are involved in the photoprotection of chlorophyll and have an auxiliary function in photosynthesis by absorbing light. Similar to tocopherols, ascorbate, and GSH, carotenoids scavenge the $^1O_2$ and peroxyl radicals produced in the chloroplast and lipid peroxidation process respectively (13). Phenols and ascorbate nullify the ROS effects by acting as electron donors, while carotenoids absorb excess light under high irradiance, thereby protecting the photosynthetic machinery of plants.

Even though plants have inbuilt tolerance mechanisms and antioxidant systems to overcome drought stress, yield losses are inevitable, which demands the adoption of other methods to improve plant performance. These can be grouped into conventional methods utilizing the phytohormones and nutrients and novel methods employing NPs mediated drought stress alleviation.

Mitigating drought stress using plant growth regulators

Abscisic acid

Endogenous and exogenously applied hormones alter the metabolism of plants under drought conditions when used at lower concentrations. Abscisic acid (ABA), a sesquiterpene compound, is synthesized from zeaxanthin, a process involving two cell organelles: plastids and cytoplasm. ABA plays a prominent role under drought stress. Osmotic stress induced during drought is found to enhance ABA production, causing essential physiological changes, such as root development, to cope with the reduced availability of water prevailing under drought. ABA triggers the synthesis of H_2O_2 in guard cells by NADPH oxidase, and H_2O_2 in turn, helps in stomatal closure, which reduces transpirational water loss (19). ABA induced stomatal closure helps plants minimize the transpiration rate that takes place *via* alterations in ion fluxes in guard cells surrounding the stomatal pore. Under drought stress, plants exhibit markedly elevated ABA levels, altered transcription rate of genes, and induction of ABA synthesis enzymes. Both ABA-dependent and ABA-independent pathways have led to an upregulation of the transcript levels of different ABA biosynthesis genes, including zeaxanthin epoxidase (ZEP/ABA1), abscisic acid aldehyde oxidase (AAO3), 9-cis-epoxycarotenoid dioxygenase (NCED3) under drought stress conditions (20). Zeaxanthin epoxidase is crucial for the synthesis of ABA, and plants that overexpress ZEP showed more growth during drought conditions. AtZEP-overexpressing plants not only showed increased de novo ABA production but also significantly increased expression of the endogenous stress-responsive genes such as RD29A (21). The other enzymes AAO3 and NCED are involved in the final oxidation reaction, converting ABA aldehyde to ABA and interacting with other transcription factors, such as WRKY DNA-binding proteins 57 (WRKY57), Arabidopsis NAC domain-containing protein 2 (ANAC2) respectively (22). It is clear that both ABA-dependent and ABA-independent pathways prepare the plant for survival under drought stress.

Auxin, cytokinin and ethylene

Many physiological and developmental processes in plants are influenced by auxin. Significant progress has recently been made in understanding the role of auxin under drought stress. When applied exogenously at the silk emergence stage in maize, auxin helped plants maintain photosynthetic quantum efficiency and postponed the onset of senescence (23). Priming seeds with auxin has been reported to mitigate drought stress effects in wheatgrass by enhancing the antioxidant enzyme activity such as SOD, CAT, and POD (24). Similar reports suggest that gibberellic acid (GA) protects plants from oxidative damage by maintaining chlorophyll levels and RWC in crops (25). Drought stressed sorghum plants, with the application of GA, showed improvement in several morphological and biochemical traits, such as germination percentage, dry weight of seedlings, and catalase and ascorbate peroxidase activities (26). Foliar application of cytokinin significantly improved photosynthetic rate, chlorophyll content, and several antioxidant enzymes, such as SOD, CAT, and APX, along with yield in wheat under drought conditions (27). Ethylene acts as an important hormone in responding to environmental stress factors. Ethylene insensitive mutants performed poorly under drought stress when comparing with the wild type plants which had higher expression of the PC5S1 gene and compatible solutes in *Arabidopsis* (28). Similar studies in maize under drought indicated that downregulation of aminocyclopropane-1-carboxylic acid synthase (ACC synthase), a key enzyme in the ethylene biosynthetic pathway, resulted in higher yield compared to wild type plants (29). It is evident from the above references that phytohormones play a major role in enhancing the survival rate of plants under drought stress.

Non-conventional plant growth regulators

Other plant growth regulators such as potassium (K), triacontanol, mepiquat chloride, brassinosteroids, and salicylic acid, are also used to counterbalance the negative impacts of drought stress. In maize under drought stress, K treatment improved root growth and stem elongation as well as leaf water potential, osmotic potential, and turgor potential (30). Triacontanol treatment under drought stress in strawberry plants improved water use efficiency and gas exchange parameters, such as photosynthetic rate and stomatal conductance (31). Mepiquat chloride treatment in soybean plants under drought conditions significantly increased the activities of antioxidant enzymes, such as SOD, POD (32). Other plant growth regulating substances, such as polyamines, salicylic acid, brassinosteroids, glycine betaine, and nitric oxide (NO) increased drought stress tolerance in rice by lowering the levels of H_2O_2 (33). It is clear that the application of phytohormones, whether used for seed priming or applied exogenously, plays a crucial role in safeguarding plants from drought stress. Phytohormones achieve this by triggering molecular-level responses, such as activating antioxidant enzymes and upregulating genes associated with proline synthesis and drought tolerance.

Mitigating drought using nanoparticles

Definition

Materials that exist at the nanoscale are called nanomaterials. The term nanoscale is a commonly accepted terminology that primarily refers to materials possessing at least one dimension less than 100 nm (34). Nanomaterials can be further divided into categories based on their general shape into 0D, 1D, 2D, or 3D. There are distinct classes of NPs such as carbon-based NPs, metal NPs, ceramic NPs, semiconductor NPs, polymeric NPs, and lipid-based NPs.

Nanoparticles have been used more recently to minimize the negative consequences of drought stress. Nanoparticles at lower concentrations have proven to be beneficial, and the mitigating role of NPs depends on the shape, size, and dosage of the NPs applied (35). Numerous studies have documented how NPs protect plant germination, development, reproduction, and yield from drought stress.

Synthesis of nanoparticles

Nanoparticles can be synthesized through different methods, which can generally be classified into top-down approach as invented by Norio Taniguchi in 1974, a method to extract atomic-scale materials from bulk materials and bottom-up approach involves the synthesis of NPs from their atomic and molecular constituents, including biological and chemical methods (Fig. 1). The top-down methods include techniques such as ball milling, in which the kinetic energy of the moving ball is transferred to the material being milled, leading to the fragmentation of the milled material (36); sputtering, where atoms from the target material intended for deposition are ejected as a result of ion bombardment (37); and laser application. The bottom-up methods involve solid state, liquid state, gas phase methods, as well as synthesis from bacteria, algae, fungus, yeast, and plants (38) (Fig. 2).

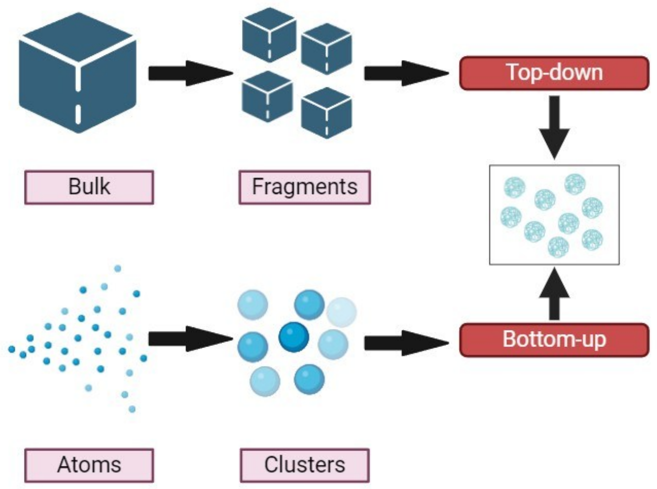

Fig. 1. Top-down and bottom-up approaches for nanoparticle synthesis.

Special features of nanoparticles

A few metal oxide nanomaterials are naturally endowed with physicochemical characteristics that enable them to imitate an antioxidant molecule and scavenge reactive N and oxygen species, which has been demonstrated to be efficacious against damages posed by oxidative stress. Prominent antioxidant properties, including SOD, CAT, and oxidase mimicking activities, have been shown by both metallic and non-metallic NPs such as cerium oxide (CeO_2), magnetite, iron, copper oxide, and carbon-based particles such as buckyballs, respectively (39). The capacity to transition between several oxidation states helps metallic NPs in conferring antioxidative properties, and the antioxidant property is determined by the composition, nature, size, and surface charge of NPs (40). Antioxidant activity is increased when different phytochemicals are combined or incorporated into single or bimetallic combinational NPs (41). Nanoparticles of silicon (Si), silver (Ag), and oxides of cerium, zinc (Zn), copper (Cu), titanium (Ti), and iron (Fe) have been found to increase photosynthetic rates, RWC, and lower the levels of malondialdehyde (MDA) (42).

Traits improved by nanoparticles under drought stress

This section focuses on several traits improved by NPs treatments, which help plants withstand the negative

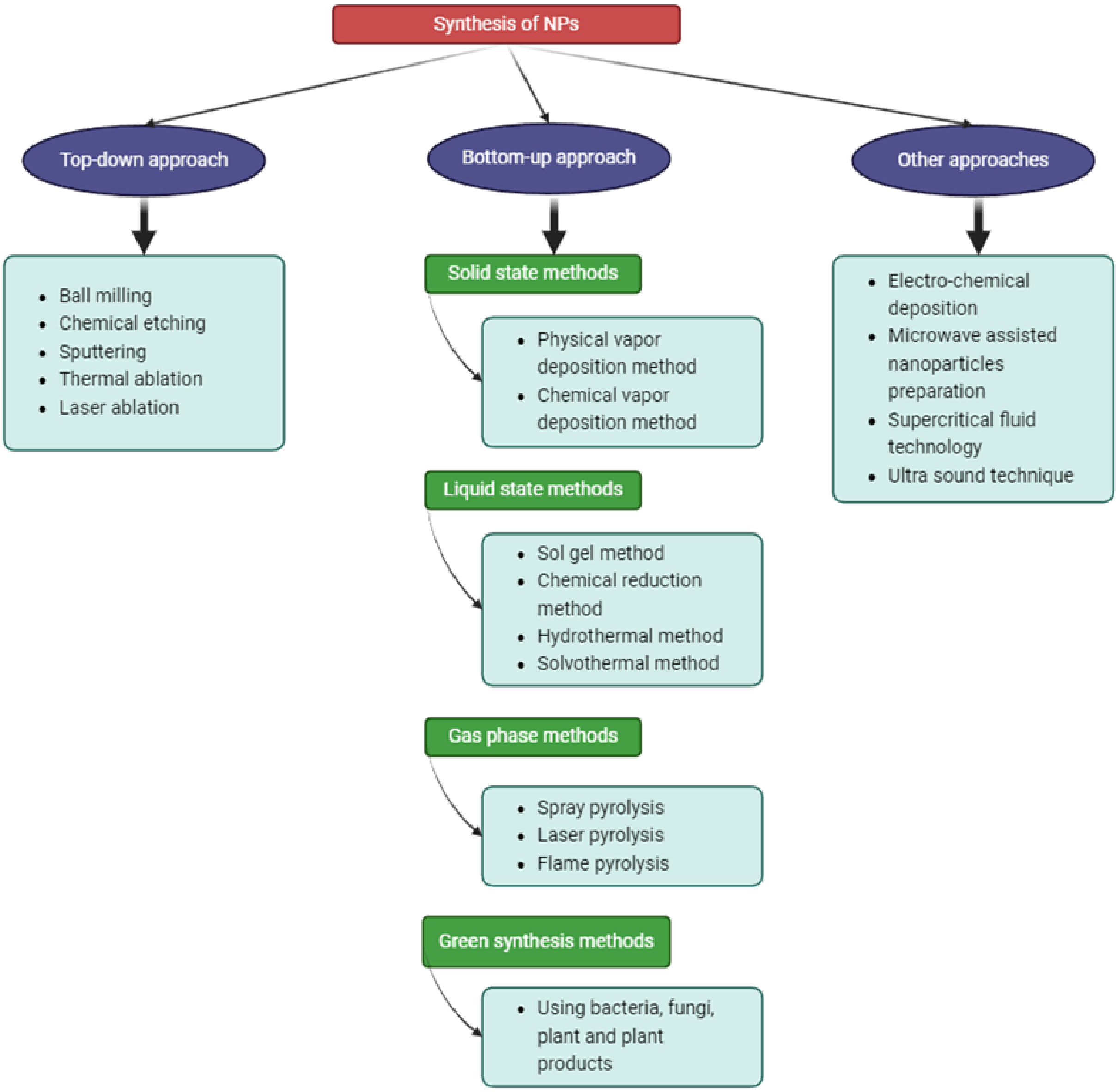

Fig. 2. Various methods currently utilized for the synthesis of nanoparticles.

impacts of drought stress.

Morphological traits

Nanosilica has been recognized for its beneficial effects in enhancing resilience to various abiotic stresses through enhanced WUE by deeper root growth, maintenance of turgidity, increased photosynthesis rate, and higher activity of antioxidant enzymes (43). The growth of chickpea under drought stress was enhanced through the application of TiO_2 NPs, leading to increased RWC and reduced damage caused by ROS due to higher activity of antioxidants and nutrient absorption (44). In wheat, selenium NPs (SeNP) has been shown to improve plant height, shoot, and root length, fresh and dry weight of shoot and root, leaf area, and number of leaves in both normal and drought stress conditions (45). Optimal growth and development under drought stress hinge on the meticulous maintenance of metabolic processes. Nanoparticles contribute to achieving this state by supporting and stabilizing these essential processes, helping plants to withstand the drought.

Physiological traits

Under drought stress, normal physiological processes such as nutrient uptake from the soil, and photosynthesis are impaired. Nanoparticles play a crucial role in mitigating these effects by helping to preserve and stabilize these physiological functions. The reduced mobility of nutrients in the soil, coupled with elevated soil pH and decreased levels of soil organic matter, significantly impairs plants' ability to absorb nutrients during drought conditions. Zinc oxide NPs have been demonstrated to enhance the uptake of nutrients, including nitrogen (N), phosphorus (P), and K, under drought stress (46). Additionally, SiNP treatment promoted the absorption of nutrients such as N, K, Cu, Mn, and Si in maize and improved photosynthetic rate, and stomatal conductance under drought conditions (47). In comparison to untreated pomegranate trees under drought stress, trees treated with SeNPs showed high nutrient content of magnesium (Mg), P, calcium (Ca) and higher levels of photosynthetic pigments (48). Overall, the application of ZnO, SiNPs and SeNPs may be utilized as a promising strategy to improve plant performance under drought stress.

Drought stress limits photosynthesis by reducing the biosynthesis of chlorophyll and other photosynthetic pigments, thereby inhibiting plant growth (49). Copper, zinc, and silver NPs mitigated drought stress impacts on wheat by maintaining the chlorophyll content and chlorophyll stability index in leaves (50). The use of Fe NPs activated the plasma membrane H^+-ATPase, facilitated stomatal opening, increased chlorophyll content, and enhanced CO_2 assimilation in *Arabidopsis thaliana* during water stress (51) (Fig. 3).

Photo System II (PS-II) efficiency and metabolic activities resulting from the exogenous application of ZnO NPs, are attributed to the maintenance of membrane integrity and plant water status under drought in brinjal (52). Calcium NPs, when applied at 100 mg L^{-1}, have a positive effect on PSII efficiency, gas exchange parameters, and chlorophyll content under drought conditions in rapeseed (53). The main role of NPs in improving physiological traits under drought stress lies in the maintenance of PS-II efficiency, increasing the performance of the photosynthetic machinery.

Biochemical traits

One of the important reasons for using NPs in the alleviation of drought stress is that they can effectively scavenge the ROS produced in drought and can improve the metabolism of plants. Foliar application with CeNPs significantly increased the antioxidant enzyme activity and lowered the H_2O_2 and MDA content under drought stress

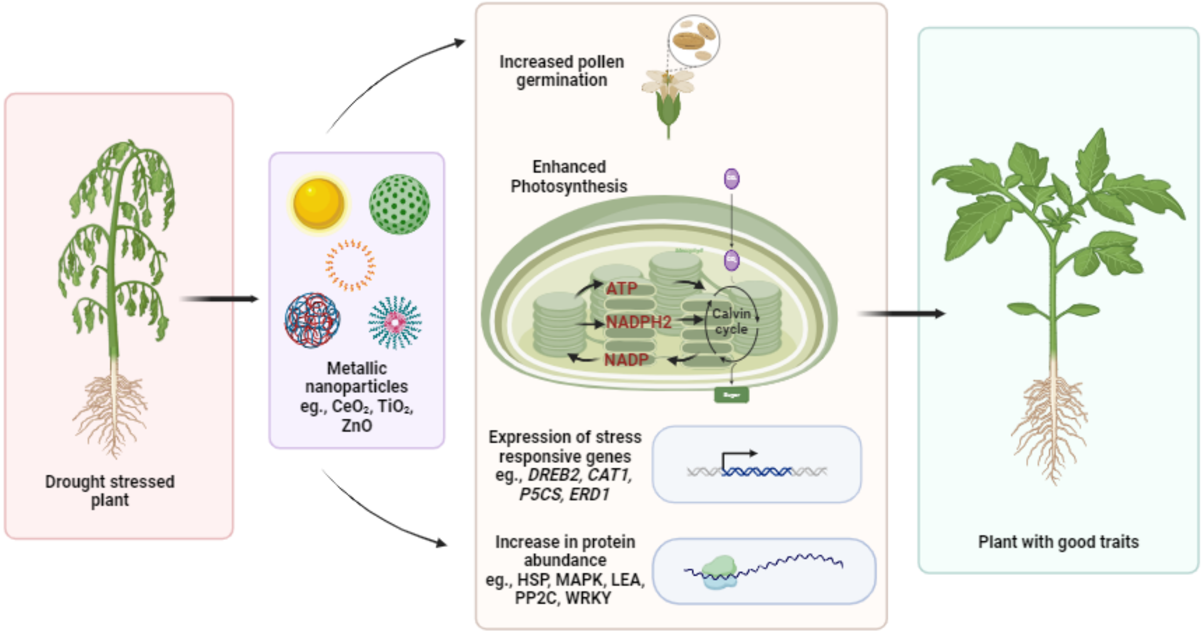

Fig. 3. Nanoparticles confer plants with beneficial traits by positively influencing several morphological, physiological, and biochemical traits (CeO_2 - Cerium Oxide, TiO_2 - Titanium Dioxide, ZnO - Zinc Oxide, ATP - Adenosine Triphosphate, $NADPH_2$- Nicotinamide Adenine Dinucleotide Phosphate (reduced), NADP - Nicotinamide Adenine Dinucleotide Phosphate, DREB2 - Dehydration Responsive Element-Binding Protein 2, CAT1 - Catalase 1, P5CS - Δ1-Pyrroline-5-Carboxylate Synthetase, ERD1 - Early Responsive to Dehydration 1, HSP - Heat Shock Protein, MAPK - Mitogen-Activated Protein Kinase, LEA - Late Embryogenesis Abundant, WRKY - WRKY Transcription Factor, PP2C - Protein Phosphatase 2C).

conditions compared to control conditions in wheat (54). Under drought conditions during the booting stage, foliar-sprayed nanoceria (10 mg L^{-1}) effectively decreased levels of hydrogen peroxide (36%) and superoxide radical (41%) in leaves as well as cell membrane lipid peroxidation (37%) in sorghum (55).

Zinc oxide NPs boosted the activity of antioxidant enzymes in crops such as tomato and wheat (SOD and CAT), improving drought tolerance (56, 57). Silicon NPs have been involved in accumulating osmolytes and induce antioxidative defense, mitigating the adverse effects of drought stress in barley (58). In drought conditions, TiO_2 treated sweet corn exhibited increased activities of SOD, APX, and CAT enzymes in leaves, along with elevated proline content (59) which enhanced antioxidant defense system contributing to the plant's ability to withstand and survive under drought stress.

Applying SeNPs under drought stress circumstances has been shown to counteract oxidative stress by increasing the transcription of stress responsive genes and proteins and maintaining ROS levels within normal limits. When subjected to drought stress, foliar application of SeNPs decreased oxidative stress, and reduced H_2O_2 and MDA contents in crops such as soybean (60) and wheat (61). The aforementioned research unequivocally demonstrates that during drought stress, NPs such as CeO_2, Se, and ZnO act as antioxidants to counteract the harmful effects of ROS (Fig. 4).

Yield and yield attributes

Several factors that contribute to yield reduction in plants under drought stress include a reduction in leaf area and the early transition of plants to the reproductive stage. Silicon dioxide treatment has been shown to improve grain yield and yield traits, such as thousand-grain weight, in wheat under drought stress. In addition, other traits that contribute to yield improvement such as biomass were also improved (62). Cu NPs were found to improve seed number as well as the mean dry weight of seeds under both well-watered and water stress regimes. In a study conducted to analyze the effect of Cu and Ag NPs, Cu NPs improved the number of spikelets per spike, grains per spike, and yield under a lower concentration of 3 mg L^{-1}. However, the same concentration negatively impacted the yield in the case of Ag NPs under drought conditions (50). This indicates that different NPs improve yield components in a dosage-dependent manner. Improved thousand-grain weight in barley treated with soil applied chitosan NPs, compared to foliar application under terminal drought, has also been reported (63). This highlights the variation in the effectiveness of NPs in improving yield traits depending on the method of application. Through the improvement of numerous morphological, physiological, and biochemical traits, NPs demonstrate a great deal of promise in increasing crop yield under drought stress.

Nanoparticles mediated molecular responses under drought

The application of SiO_2 NPs in maize under drought

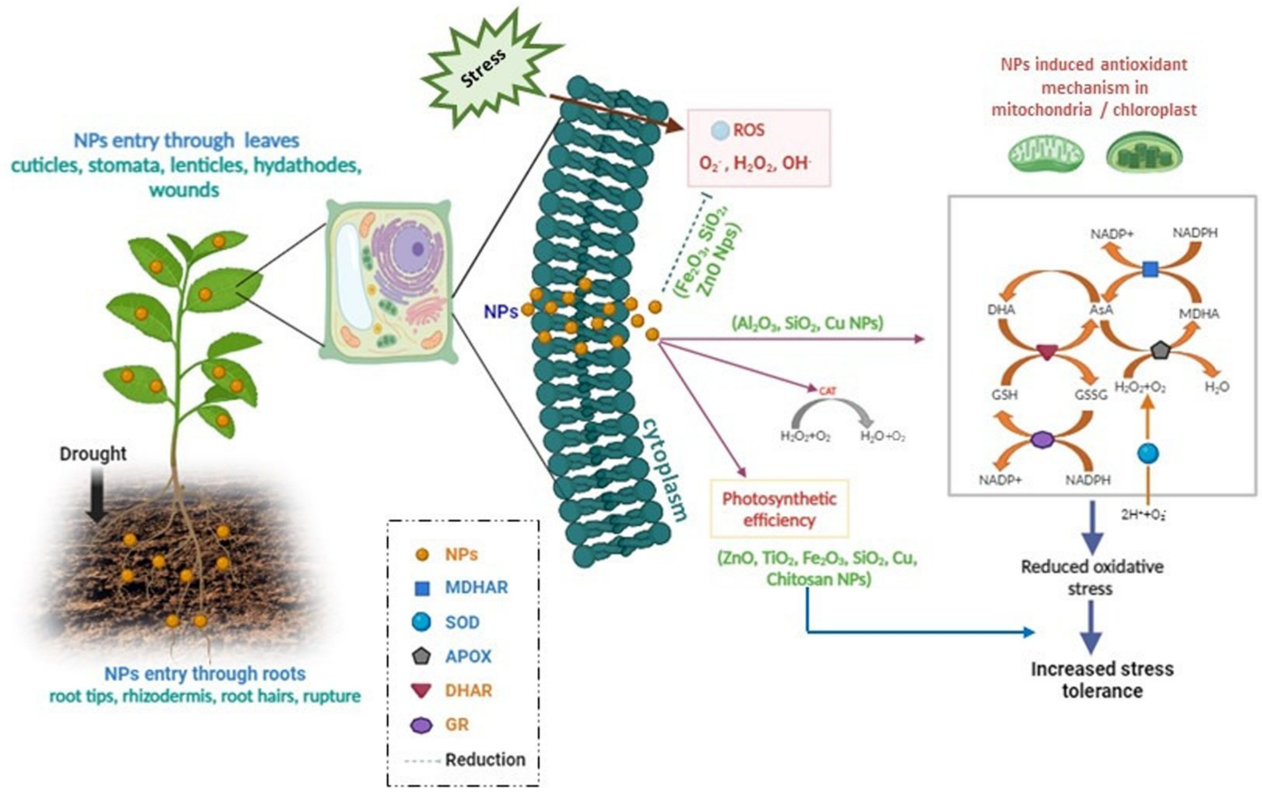

Fig. 4. Nanoparticles mitigate oxidative damage in plants by reducing reactive oxygen species levels and enhancing antioxidant enzyme activity (Al_2O_2 - Aluminum Oxide, APOX - Ascorbate Peroxidase, AsA - Ascorbic Acid, Cu - Copper, DHA - Dehydroascorbic Acid, DHAR - Dehydroascorbate Reductase, Fe_2O_2 - Iron(II) Oxide, GSH - Reduced Glutathione, GSSG - Oxidized Glutathione, GR - Glutathione Reductase, H_2O - Water, H_2O_2 - Hydrogen Peroxide, MDHA - Monodehydroascorbate, MDHAR - Monodehydroascorbate Reductase, NPs - Nanoparticles, $NADP^+$ - Nicotinamide Adenine Dinucleotide Phosphate (oxidized), NADPH - Nicotinamide Adenine Dinucleotide Phosphate (reduced), O_2 - Molecular Oxygen, $O_2^{\cdot-}$ - Superoxide, $OH^{\cdot}$ - Hydroxyl Radicals, SOD - Superoxide Dismutase, SiO_2 - Silicon Dioxide, TiO_2 - Titanium Dioxide, ZnO - Zinc Oxide).

conditions led to higher expression of the D2 protein (psbD) which is a crucial component within the plastid, forming the core of photosystem II that is needed for maintaining the thylakoid membrane integrity and ensuring efficient photosynthesis. Silicon dioxide NP treated plants also had reduced expression of aquaporin genes (AQPs) and osmotin like proteins (OSM-34) suggesting improved membrane integrity and RWC compared to untreated plants under drought stress conditions (64). Specific genes associated with drought tolerance were upregulated in NP treated soybean, with the variation in the response depending on the type of NP used. Fe, Cu, Co, and ZnO NPs all were found to be involved in positively modifying the gene expression pattern of RD20A (responsive to dehydration), DREB2 (dehydration responsive element-binding), ERD1 (early responsive to dehydration 1), FDL19 (flowering locus D 19), NAC11, WRKY27, MYB118, and MYB174 (myeloblastosis) towards protecting the plants from water deficit stress (65).

The application of ZnO NPs led to increase the transcript levels of genes associated with drought tolerance in the roots of wheat plants. In roots of drought stressed plants treated with ZnO NPs, the gene expression of DHN (dehydrins), DREB, bZIP (basic leucine zipper), and NAC was significantly higher compared to non-ZnO-treated plants, with fold changes of 5.36, 16.04, 1.92, and 7.27, respectively. Similarly, in leaf tissues, the relative transcript abundance of these genes was also elevated, with fold changes of 3.12, 4.33, 3.59, and 3.79, respectively. Additionally, under drought stress transcripts of antioxidant genes such as SOD, APX, and CAT and proline biosynthetic genes such as P5CS (pyrroline-5-carboxylate synthase) and BADH (betaine aldehyde dehydrogenase) was notably increased (66).

Furthermore, chitosan NPs (CS-NPs) enhance plant physiological responses and mitigates the adverse effects of abiotic stresses by triggering stress transduction pathways (67). Chitosan NPs enhanced the antioxidant capacity of Catharanthus roseus plants by upregulation of genes such as peroxidase 1 (PRX1) cultivated under drought stress (68).

In summary, the use of NPs resulted in elevated gene expression, leading to enhanced hormonal signaling, secondary metabolite synthesis, and antioxidant activity, ultimately improving plant tolerance to drought stress. However, there remains a lack of comprehensive investigation into the expression of NP-induced activation genes, necessitating further research to elucidate the mechanisms underlying the augmentation of drought tolerance following increased gene expression after NP application.

Conclusion

The potential of NPs to enhance drought tolerance in agriculture has gained significant attention, particularly in seed germination and key metabolic processes like those involving gibberellins and abscisic acids. While NPs show promising effects in protecting the photosynthetic apparatus, improving nutrient absorption, and influencing stomata movements during stress, further research is needed to understand their roles in these physiological functions fully. Exploring the synergy between NPs and microbes to improve drought tolerance offers a new research avenue. Despite progress, most NPs studies are still confined to lab environments, raising concerns about accumulation in edible plants and environmental impacts. The mechanisms behind NPs remain underexplored, especially their molecular role in regulating stress-responsive genes. Therefore, focused research is essential to bridge knowledge gaps and ensure safe, efficient use of NPs in sustainable agriculture.

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Authors' Contributions

LJ contributed to the drafting and editing of the manuscript. SA and DM were involved in manuscript editing. RR, KR, PSM, and AK also provided support in editing.

Compliance with Ethical Standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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