Impact of Nanoparticles on Plants under Drought Stress

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Drought is a chronic abiotic stress affecting crop growth and development, accounting for approximately 70% of the potential loss of global crop yield and productivity. Drought hinders agriculture and forestry worldwide, due to very little rainfall or significant differences in moisture. The current trends of global warming are causing a major impact on the moisture levels of the soil and the environment, and are increasing the intensity of droughts. Plants are subjected to various stresses during their growth, and the morphology of plants is affected at all stages of development due to drought stress, with productivity losses expected to reach 30% globally by 2025.

nanoparticles stress tolerance physiology molecular drought

1. Introduction

A variety of factors influence agricultural productivity, including the climate. Agriculture is fundamental to human welfare, and many organizations and others are concerned about the effects of climate change on agriculture. As a result of increasing annual temperatures, changing patterns of rainfall, floods, and dwindling water reserves, major agriculture crops are affected by climate change. The agricultural sector provides income and employment to almost half of the labor force and supplies raw materials to industry in developing and less developed countries. Global hunger and food insecurity are continuously increasing due to the phenomenal increase in global population and stagnant agricultural performance [1]. Climate change causes many biotic and abiotic stresses to plants which affect plant growth and cause declines in yield [2]. Different strategies have been adopted to overcome these negative effects of climate change, i.e., the use of tolerant genotypes, application of different plant growth regulators, and the use of organic fertilizers. Currently, nanotechnology is substantially contributing to this sector. Nanotechnology studies the various structures of matter on the scale of a billionth of a meter. A nanoparticle (NP) is a small molecular aggregate with an interfacial layer surrounding a diameter of 1 to 100 nanometers. Several critical properties of matter are fundamentally impacted by this interfacial layer at the nanoscale [3][4]. As a result of their small size, NPs have some unusual properties compared with bulk materials. Nanoparticles refer to organic materials rather than individual molecules. The fact that NPs link bulk materials to atomic or molecular structures cause them to be of high scientific interest. The various NPs used for the treatment of plants to overcome environmental challenges are: titanium dioxide (TiO_2), zinc (Zn), zinc oxide (ZnO), cesium (Ce), cobalt (Co), copper (Cu), copper oxide (CuO), selenium (Se) NPs, silver (Ag), silicon (Si), silicon oxide (SiO_2), iron oxide (FeO), calcium ($CaCO_3$), magnesium (Mg), magnesium oxide (MgO), manganese (Mn), and molybdenum (Mo) NPs; and aluminium oxide (AlO_4) and carbon nanotubes (CNTs).

To cope with environmental stress, plants have developed a wide range of efficient and comprehensive molecular programs to rapidly sense stressors and adapt accordingly [5]. Plants can enhance this response through the interaction of NPs with plants. Nanotechnology promises to increase crop yield by improving plant tolerance mechanisms under abiotic stress conditions [6]. Several studies have shown that NPs play a vital role in improving the tolerance of plants to abiotic stresses by modulating various physiological, biochemical, and molecular processes (**Figure 1**).

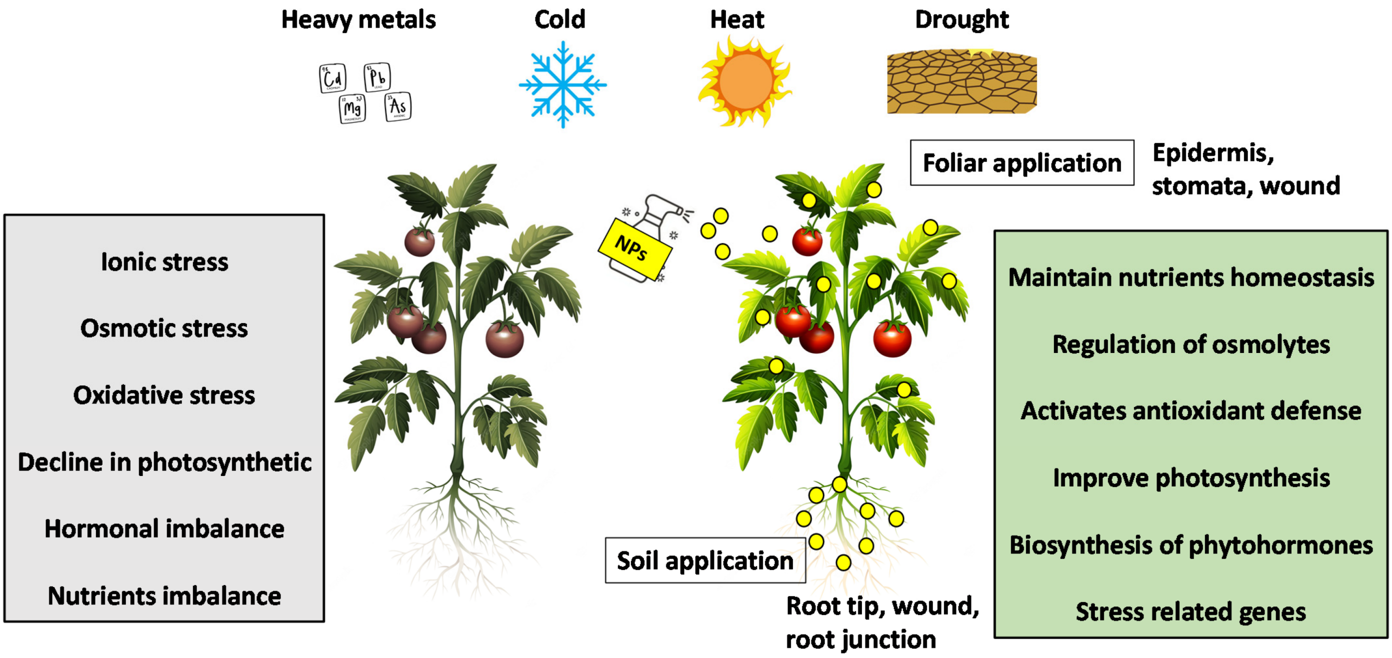

Figure 1. Mechanisms of NPs mitigate abiotic stresses in plants.

Crop growth and improvement can effectively be achieved in modern agriculture through nanotechnology. NPs can be used in the agricultural sector as nano-agrochemicals (nanobiocomposites, nanopesticides, nanofertilizers), agri-food production, nanobiosensors, agri-environment, organic agriculture, postharvest management, and plant genetic progress by NP-mediated gene transfer [7][8]. In recent years, the reliance on nanotechnology in different industries has been increasing due to its copious potential, sustainable, eco-friendly, and cost-effective applications. The use of nanopesticides and nanofertilizers has enhanced agricultural productivity, for example, urea-doped calcium phosphate nanofertilizers have helped commercial crops to obtain efficient nutrients from the soil, specifically urea; helped maintain crop growth and productivity; and helped to achieve sustainable agriculture [9][10][11]. Madusanka et al. [12] observed the slow release of nitrogen by using a urea-hydroxyapatite-montmorillonite nanohybrid composite. The use of hydroxyapatite nanoparticles significantly influenced the crop yield and germination attributes of tomato plants [13]. The range of applications of nanotechnology in the remediation of soil and water has increased food quality and production. Moreover, with nanotechnology being eco-friendly, its use has a significant benefit in reducing the harmful effects of chemicals used on crops, and the effects caused by agriculture on the environment [14]. NPs have been effective on seed and plant metabolisms by enhancing growth. The advantageous characteristics of NPs being small allows them to cross biological barriers in plants more efficiently and remediate plant stresses, such as salt stress and heat stress, and stress caused by heavy metals [15].

2. Drought Stress

Severe droughts are a major problem for agriculture in a changing climate, as water scarcity is predicted to become more common. Drought refers to the conditions where a plant's water demand cannot be fully met, such as where the transpiration water level of the plant exceeds the water absorbed by the root system, insufficient precipitation, a drop in the groundwater level, or water retention by soil particles [16]. Plants reduce water loss through adjustments in morphological anatomy, physiology and biochemistry to maintain their water status as a result of drought [17][18]. Drought stress leads to a reduction in cell enlargement as compared with affecting cell division. It affects plant growth by altering the functioning of various physiological and biochemical processes, i.e., photosynthesis, respiration, enzymatic activity, and nutrient metabolism [19]. The response of plants to drought stress varies at different tissue levels, depending on the intensity and duration of the stress, as well as plant species and growth stage. Understanding how plants respond to drought is very important and an essential part of improving the tolerance of crops to stress.

Different molecular, biochemical, physiological, morphological and ecological traits and processes are disrupted under drought stress conditions [20][21]. A deficit of water has adverse effects on plant yield and quality. Growth stage, age, plant species, drought severity, and duration are key factors affecting plant response to drought [22]. Plants die off under prolonged drought conditions [23]. Water scarcity in plants increases the concentration of the solute in the cytosol and extracellular matrices as a result of the reduction in plant cells' water potential and turgor, which leads to growth inhibition and reproductive failure. Wilting is caused by the accumulation of abscisic acid and compatible osmolytes [24][25]. Adverse influences are aggravated due to the overproduction of ROS and radical scavenging compounds such as ascorbate and glutathione [26][27]. Water stress in plants due to drought affects the stomatal functions and limits the gaseous exchange, decreasing the rate of transpiration and carbon assimilation [28]. In turn, the mechanisms of resistance of plants to drought vary. Therefore, plants can reduce resource utilization and regulate growth in response to adverse environmental conditions [29]. Signal transduction, a network at the molecular level, enhances these responses to drought stress [30]. Plant stomatal regulation by enhancing ion transport, transcription factor activity, and ABA signal transduction is also involved in the molecular mechanism of plant response [31]. In some changing environments, there is a need to enhance the resistance of plants against drought. To improve water use efficiency when the physical fitness of roots and leaves is insufficient to cope with certain drought molecular signals, plant enhancement may be conducted by including genes encoding regular proteins and signals by crosstalk, expressing many other genes according to different regulatory mechanisms [32]. To achieve future food demands, further advancement is required in enhancing drought tolerance in plants, and the adoption of economical and beneficial agricultural practices will be critical [33].

2.1. NPs Mitigate Drought Stress in Plants

NPs are known by their specific shape, tunable pore size, and high reactivity with enhanced surface area [34]. NPs are considered an effective and promising tool for regulating crop yield and overcoming current and future limitations of agricultural production by increasing the tolerance mechanisms in plants under abiotic stress conditions. The mitigating effect of NPs on drought stress is caused by inducing physiological and biochemical regulation, and regulating the expression of genes relating to drought response/tolerance. NPs enhance the photosynthetic activity of drought-induced plants, whereby the improvement of root growth, upregulation of aquaporins, altered intracellular water metabolism, accumulation of compatible solutes, and ionic homeostasis are the main mechanisms by which NPs alleviate osmotic stress caused by water deficiency. NPs reduce leaf water loss caused by the accumulation of ABA through stomatal closure, and ameliorate oxidative stress damage by reducing reactive oxygen species and activating antioxidant defense systems.

2.1.1. Physiological and Biochemical Aspect

Nanotechnology has the capability to enhance plant photosynthesis efficiency by altering the enzymatic activity involved in the C3 cycle, along with regulating photosynthetic pigments responsible for plant growth [35]. NPs have positive effects on plant germination and growth, however, their efficacy varies with their concentration and host plant. In sorghum plants under drought conditions, foliar spraying of nanowax increased seed yield in plants in comparison with spraying with water. TiO_2 NPs have many strong effects on the morphological, biochemical, and physiological properties of crops [36]. During the growth phase of cucumber plants, exogenous application of NPs promoted rubisco activase activity, chlorophyll formation, and photosynthetic rate, which led to an increase in plant dry mass [37]. It was further noted that foliar application of NPs could increase the seed yield of soybean, due to enhanced photosynthesis [38].

The impact of nano-TiO_2 varies with respect to changing environmental conditions, plant species, and different application doses. In this context, Mohammadi et al. [39] investigated the effects of nano-TiO_2 concentrations on the biochemical and morphophysiological properties of dragonhead plants. The TiO_2 increases the growth and essential oil in plants under water deficit stress. A formulation of nano-sized ZnO and CuO was used as a fertilizer. The results showed that at different NP doses, root growth was reduced, while contrarily, at other levels, Zn NPs expanded lateral root formation whereas Cu NPs induced proliferation and elongation of root hairs close to the roots of wheat seedlings under simulated drought stress [40]. These responses typically occur when the roots are colonized by a beneficial bacteria isolated from wheat roots grown in calcareous soils under dryland farming conditions.

It has been observed that ZnO and CuO NPs exhibited protection against drought stress in different plants [40]. This protection may be induced by the enhanced generation of lateral root hairs which resulted in proper water absorption. Enhanced cell wall lignification in mustard and Arabidopsis under CuO may alter water flow, thereby limiting cell wall elongation. The response of plants to drought stress is an increase in lignification. The disruption of water flow occurs due to the binding of copper ions to the pectin of the cell wall [41]. Some notable results were found in some studies, such as increased seed germination and antioxidant content after barley, soybean, and maize were treated with carbon nanotubes (CNTs) [42]. CNTs can induce root and shoot growth in wheat plants.

Various major efforts have been conducted over the past few decades to reduce the effects of drought stress on plant quality and productivity. The researchers further suggest that fullerenol (FNPs) NPs with molecular formula C60(OH)24 may help alleviate the effects of drought stress and provide additional water supply between plant cells. Precisely, nanofullerenols (FNPs) can enter the root and leaf tissues of plants, where they can bind water molecules in various parts of the cell. This water absorbing FNP activity further suggests that FNPs may be useful for plants [43][44]. The results of this study by Borišev et al. [43] further demonstrated that foliar application of nanofullerenol could alter intracellular water metabolism in drought-stressed plants. Under drought stress, the content of the permeate product proline in plant roots and leaves was significantly increased. These results further suggest that FNPs could also function as a binder for intracellular water, thereby generating additional water reserves, and allowing them to adapt to drought stress. Ag NPs are the most used NPs in research experiments [45].

In plants, NPs target the cellular organelles and release various contents [8], thus modulating the activity of antioxidants enzymes, i.e., SOD, CAT, and POD [46]. This effect was exhibited by incremented SOD activity in plants under TiO_2 NP application [47]. In agriculture, certain elements, along with oxides as NPs, have been used for incremental resistance against drought stress. Si NPs have been used extensively for ameliorating the negative impacts of various abiotic stresses including drought [48]. The improvement in growth, physio- and biochemical characteristics has been observed upon treatment with silica and ZnO NPs on different crops [34]. Similarly, Si NPs ameliorated drought stress on wheat plants [49]. Similarly, ZnO NPs reduced the negative impact of salinity and drought stress on plants [50]. It has been observed that excessive NP application led to a generation of oxidative stress, i.e., leading to cell cycle arrest, programmed cell death, protein regulation, and induction of antioxidant enzymes [51], whereas NP-treated plants exhibited significant reductions in MDA levels along with free radicals, i.e., H_2O_2 and O_2^-, under drought conditions. However, it was also observed that TiO_2 application enhanced antioxidant enzyme activities, i.e., POD and CAT, whereas MDA levels were reduced due to the induction of the plant's antioxidant system [26].

Under drought stress, the level of anthocyanin in plants exposed to CuO NPs continued to increase, and the level of proline was also shown to increase under drought stress. Wheat roots treated with CuO-treated NPs exhibited a greater accumulation of free radicals, consistent with plants responding to the challenge of NP-induced ROS bursts. Elevated ROS levels, further suggesting that drought stress triggers a consequence of elevated ABA, may lead to transcriptional changes that lead to tolerance. The amplification of various antioxidant enzymes (GR, SOD, GPX, APX, and CAT) in plants suggested that foliar application of fullerenol (FNPs) NPs with molecular formula C60(OH)24 might have some valuable effects on mitigating the oxidative effect of drought stress, which further depends on the concentration of NPs applied [42]. The exact mode of action and physiological mechanism of FNPs on plants needs to be further studied.

2.1.2. Molecular Aspect

Transcriptomic and proteomic approaches have deeply investigated the effects of NPs on different plant species at the molecular level. Morphological and physiological effects have been reported to largely depend on the dose used, as well as the type, size and shape of NPs [52][53]. Expression of the *P5CS* gene leads to increased plant tolerance to different environmental stress conditions, including biotic and abiotic stresses, since this gene encodes proline biosynthesis. *MAPK2*, a member of the *MAP* kinase gene family, plays an extremely important role in regulating phytohormones and antioxidant protection mechanisms in response to different stress environments [53] in combination with *Ca21* and ROS. *AREB/ABF* are transcriptional regulators necessary for the regulation of the *AREB* gene encoding abscisic acid, and are critical in stimulating resistance to stressful environments such as drought and salt stress [53][54]. Downregulation of the *ZFHD* gene reduces the negative effects of salt and drought stress and is controlled by the abscisic acid biosynthesis pathway. On the other hand, downregulation of the *TAS14* gene reduces osmotic pressure and enhances solute aggregation, including K1 and sugars, making plant species more resistant to drought and salt stress [53]. Application of Ag NPs (5 and 10 mg/L) to rape plants modulated the metabolic pathways of glucosinolate and phenolic related genes, which are also associated with biotic and abiotic stresses, and inhibited carotenoid genes [55]. Downregulation of the *ZFHD* gene reduces the negative effects of salt and drought stress and is controlled by the abscisic acid biosynthesis pathway. The use of Ag and Ag1 NPs on Arabidopsis plants resulted in overexpression of oxidative stress and metal response-related genes, and downregulation of ethylene and auxin-related genes [53]. Three of these genes overexpressed by Ag NPs are involved in the biosynthesis of thalianol, which is thought to contribute to a plant's antioxidant protection mechanism. The response of different NPs against drought stress conditions is summarized in **Table 1**.

Table 1. Impact of NPs on plants under drought stress.

NPs	Plant	Effect	Reference
ZnO	*Triticum aestivum* L.	Enhanced plant growth and mineral content in grains.	[56]
B NPs, SiO_2 NPs and Zn NPs	*Triticum aestivum* L.	Enhanced protein contents and mitigates drought stress.	[57]
ZnO NPs	*Zea mays* L.	Enhanced yield and ameliorated antioxidative behavior.	[58]
Nano-Cu NPs	*Zea mays* L.	Upgraded the protective mechanism of maize under drought conditions.	[59]
Nano-Si NPs	*Tanacetum parthenium* L.	Improved water and phosphorus absorbing capabilities and general growth.	[60]
ZnO NPs	*Solanum lycopersicum*	Enhanced ascorbic acid and free phenols conc. along with the ameliorated activity of antioxidative enzymes.	[61]
Cu, Fe and Zn NPs	*Glycine max* (L.) Merrill	Upregulated expression of drought-sensitive genes.	[38]

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