Abiotic Stress in Plants

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Abiotic stress in plants is a crucial issue worldwide, especially heavy-metal contaminants, salinity, and drought. These stresses may raise a lot of issues such as the generation of reactive oxygen species, membrane damage, loss of photosynthetic efficiency, etc. that could alter crop growth and developments by affecting biochemical, physiological, and molecular processes, causing a significant loss in productivity. To overcome the impact of these abiotic stressors, many strategies could be considered to support plant growth including the use of nanoparticles (NPs). However, the majority of studies have focused on understanding the toxicity of NPs on aquatic flora and fauna, and relatively less attention has been paid to the topic of the beneficial role of NPs in plants stress response, growth, and development. More scientific attention is required to understand the behavior of NPs on crops under these stress conditions.

Keywords: abiotic stresses ; environmental contaminants ; heavy metals ; nanoparticles ; soil

1. Introduction

In the current scenario, population explosion has emerged as one of the major challenges, especially for sustainable food production, in feeding the growing population [1]. The world population may reach up to 10.9 billion by 2100 and will lead to an increase in demand for food by nearly 50%. To achieve the “Zero Hunger” goal, which is one of the goals of sustainable development of the UN to be achieved by 2030, there is an urgent need for revolutionizing conventional agricultural practices. Such changes can be achieved by employing eco-friendly and sustainable innovations [1][2][3][4].

Plants are unable to move physically from their location to prevent the consequences of environmental stress such as abiotic stresses. Among different abiotic stresses, heavy metal (HM) contamination, soil salinity, and drought stress are described to limit the crop productivity by multiple orders of magnitude [5][6][7]. These changes under abiotic stress trigger perturbations in the metabolism of plants, thereby facilitating reorganization of the metabolic network in order to keep the vital metabolic processes active [8][9][10][11][12].

Soil pollutants, especially HMs and metalloids such as Cr, Cd, Ni, Zn, As, and Hg, are identified as the most commonly detected contaminants [13][14]. The increased release of HMs in the terrestrial environment has been documented to severely affect the productivity of cultivated areas [15][16]. Furthermore, most of the metal contaminants eventually find their way into the terrestrial and aquatic environment, thereby directly or indirectly affecting human health and the associated ecosystems [17][18]. Additionally, there are ample chances of accumulation of HMs in plants exposed to contaminated areas [19].

Salinity and drought stresses are devastating stresses that are reported to limit the economic yield of several crops via inducing biochemical and physiological perturbations [20][21][22]. These stresses confine the plant productivity and growth due to osmotic stress, nutritional imbalance, and oxidative stress [23]. The salt stress results in the accumulation of sodium (Na^+) and chloride (Cl^-) ions in the cytosol, eventually causing considerable damage to the cell [24]. Drought stress is known to induce stomatal closure, to inhibit photosynthesis, to reduce the leaf area, to reduce the biomass and growth, to decrease the water potential, to increase the amount of osmolytes, and to induce the generation of reactive oxygen species (ROS) [25]. Abiotic stress triggers perturbation in the metabolism of plants, thereby facilitating reorganization of the metabolic networks in order to keep the vital processes active [8][9][10][11][12]. Thus, the onset of abiotic environmental stressors because of immobile nature of plants eventually leads to reduced crop productivity.

Numerous stress management strategies have been developed by researchers in recent decades. Among them, nanotechnology is one of the emerging strategies that has been anticipated to improve crop productivity [2][3]. Nevertheless, most of the research focusing on nanoparticles (NPs) currently is concentrated on their toxicity [4][26][27][28][29]. Relatively fewer publications are available regarding the role of NPs in crop protection, especially under various abiotic stress conditions [8][30][31].

Nanoparticles may be described as materials with diameters between 1 to 100 nm in at least one dimension [32]. Metal and metal-based NPs show various physiochemical features that are different from their native bulk compounds. The application of NPs has gained widespread popularity in agriculture and allied sectors including various other fields, i.e., the chemical, optical, biomedical, pharmaceutical, food, and textile industries [33][34]. Different NPs for field applications such as nano-agrochemicals have been used to increase agricultural productivity. Some of them include phosphorous NPs ($Ca_5(PO_4)_3OH$), calcium NPs ($CaCO_3$), Mg NPs, ZnO NPs, Fe_2O_3 NPs, TiO_2 NPs, Ag NPs ($AgNO_3$), Mn NPs ($MnSO_4$), Cu NPs (CuO), Mo NPs, SiO_4 and AlO_4 CNTs (carbon nanotubes), and a complex of Chitosan with Zn or Cu [4][35].

Nanoparticles as soil-improving agents, nano-fertilizers, nano-pesticides, growth stimulators, and nano-sensors for controlling various agricultural factors in the farm [36] have been utilized for improving crop yield. It has gained popular acceptance for its potential application in the smart and controlled delivery of pesticides and herbicides and in the sustained-release of fertilizer formulations. Additionally, the contribution of NPs in the alleviation of abiotic stress-induced toxicity in plants is of immense agricultural importance. The intervention of nanotechnology has demonstrated effectiveness not only in the removal of non-degradable metals, but also in the detoxification of slowly degrading contaminants [37]. The past decades have substantially received tremendous contribution about NPs improving plant growth and soil characteristics, particularly in the management of marginal soils affected by HM contamination [38][39]. In a recent study, the contents of chlorophyll (a and b) and carotenoids were noticeably enhanced by magnetic NP treatment to *Hordeum vulgare*, apart from the positive impacts on the genes of photosystems [40]. Likewise, the negative impacts of drought and salinity stress have also been mitigated by the use of NPs [41][42].

In order to obtain in-depth knowledge on field applications of NPs, the present review aimed to discuss the challenges of different abiotic stresses causing substantial changes in crops at the morphological, anatomical, biochemical, and physiological levels and the possible roles and mechanisms of NPs for mitigating the negative consequences of abiotic stresses to improve the agricultural productivity.

2. Alleviation of Heavy Metal Toxicity in Plants Using Nanoparticles

Excessive release of HMs in the environment by an exponential rise in anthropogenic activities and industrial processing is of great concern [43][44]. The risks of HM contamination in cultivated fields and aquatic environments due to the indiscriminate addition of various agro-fertilizers are of considerable concern [45][46]. The abundance of HMs in a given environmental matrix beyond certain limits exerts toxicity because of accumulation and genotoxic, carcinogenic, and mutagenic behaviors [46][47][48][49].

The HMs and metalloids associated with the environmental and human health concerns include Cu, Zn, Cd, Cr, Pb, As, and Hg [50][51]. Therefore, it is imperative to develop innovative and economical technologies for the successful elimination of HMs from contaminated sites. However, the characteristic toxicity at low concentrations, slow removal using conventional approaches, and non-biodegradable attributes of HMs [49][52][53][54] are the important factors imposing restrictions in successful detoxification from contaminated sites. The fabrication of effective and eco-friendly NPs for successful employment in managing widespread contamination of hazardous HMs has received much popularity [55]. Among the different metal and non-metal-based NPs, generally, those with an environmentally friendly nature, cost-effectiveness, and ease of availability are preferred for application in environmental clean-up programs as well as in the alleviation of toxicity [56].

The contribution of myriads of NPs in overcoming the challenges of HM-induced toxicity has been presented by various researchers worldwide (Table 1). In general, it has been observed that NPs minimize the uptake of HMs by modifying the expression of genes responsible for metal uptake and by reducing HM bioaccumulation. Furthermore, NP treatment improves the physiological and biochemical parameters of the plants such as enhancing the synthesis of defense enzymes (SOD, POX, CAT, APX, etc.); augmenting nutrient uptake; decreasing the loss of electrolytes; improving pigments and soluble proteins; reducing peroxidation; and causing rise in the levels of proline, glutathione, and phyto-chelatins. These attributes are primarily responsible for the overall increase in the tolerance of the crops and may vary slightly according to different plant species.

Table 1. Applications of NPs in the mitigation of HMs stress by altering the morphophysiological responses of plants.

Nanoparticles	Plants	Germination and Morphological Responses	Physiological Responses	References
Si (10 μM)	*Pisum sativum* L.	Presence of Si NPs improved the growth in presence of Cr	Si NPs minimized the Cr storage, enhanced the synthesis of defense enzymes and augmented nutrient uptake	[57]
ZnO (25 mg/L)	*Leucaena leucocephala*	Application of NPs induced seedling growth	ZnO NPs amendment improved pigments and soluble proteins, reduced peroxidation; there was rise in the antioxidant defense enzymes	[58]
Fe_3O_4	*Triticum aestivum* L.	Fe_3O_4 NP treatment minimized the inhibitory action of HMs	Fe_3O_4 NPs supplementation improved the level of superoxide dismutase and peroxidase	[59]
Si (19, 48, and 202 nm)	*Oryza sativa* L.	Si NPs enhanced the number of cultured cells and decreased proportionally with the rise in NP size; the treatment maintained the cellular integrity in the presence of metals	Si NPs amendment caused altered expression of genes responsible for reduced metal uptake	[60]
ZnO (0, 50, 75, and 100 mg/L)	*Zea mays* L.	Treatment caused rise in plant length, leaf number, and biomass	ZnO NPs application enhanced chlorophyll content, gas exchange characteristics, and antioxidant enzymes; addition led to reduced content of Cd in root and shoot	[61]
ZnO (0, 25, 50, 75, and 100 mg/L) and Fe NPs (0, 5, 10, 15, and 20 mg/L)	*T. aestivum* L.	Treatment induced plant growth, dry weight, and grains under Cd stress	Addition of NPs decreased the loss of electrolyte and activity of superoxide dismutase and peroxidase along with diminished Cd accumulation	[62]
Si	*Glycine max* L.	Si NPs minimized the growth inhibitory action of Hg	Incorporation of Si NPs improved the chlorophyll content and reduced the Hg content in root and shoot	[63]
Mel-Au (200 μM)	*O. sativa* L.	—	Application of Mel-Au NPs caused reduction of Cd level in root and shoot, improved chlorophyll content and raised the activity of antioxidant enzymes	[64]
Fe (25 and 50 mg/L)	*O. sativa* L.	Treatment of Fe NPs improved plant length and dry weight	Fe NPs application caused rise in the level of proline, glutathione and phyto-chelatins; Fe NPs addition led to improved defense enzymes and glyoxalase machinery	[19]
ZnO (10–100 mg/L)	*O. sativa* L.	Amendment of ZnO increased the growth of seedlings	Treatment facilitated reduced accumulation of arsenic in root and shoot together with rise in phytochelatin level	[65]
Cu (25, 50, and 100 mg kg^{-1} of soil)	*T. aestivum* L.	Rise in plant height and shoot dry weight	Increase in N and P content; reduced Cd transport, rise in the level of vital ions and antioxidant pool	[66]
Cu (0, 25, 50, and 100 mg kg^{-1} of soil)	*T. aestivum* L.	Improved biomass and growth	Reduced Cr availability; increase in nutrient uptake; rise in antioxidant content	[67]
Fe_2O_3 (0, 25, 50, and 100 mg kg^{-1} soil)	*O. sativa* L.	Improved fresh and dry biomass; increased height	Augmented detoxifying enzymes, photosynthetic potential, and nutrient uptake attributes; reduced formation of ROS, lowered expression of genes supporting the transport of Cd; restricted Cd mobilization in upper plant parts	[68]
Fe_2O_3 (25, 50, and 100 mg kg^{-1} soil)	*T. aestivum* L.	Rise in plant fresh and dry biomass; increase in plant length	Reduced Cd transport; enhanced N, P, and K content; increased antioxidants and pigment content	[69]
TiO_2 (0, 100, and 250 mg/L soil)	*Z. mays*	Foliar application improved shoot and root dry weight	Reduced accumulation of Cd; increased activities of antioxidant enzymes	[70]

Nanoparticles	Plants	Germination and Morphological Responses	Physiological Responses	References
SiO_2 (30 and 50 nm)	*G. max*	Improved seedling fresh weight	Improved chlorophyll content; lowered accumulation of Hg in root	[63]
Au (200 μM)	*O. sativa L.*	—	Reduced level of Cd in root and leaves by 33 and 46.2%, respectively; improvement in antioxidant defense enzyme; restricted expression of genes associated with metal transport	[64]
Si (0, 25, 50, and 100 mg/kg soil)	*T. aestivum L.*	Improved plant height	Improved chlorophyll; photosynthesis; diminished Cd content in tissues;	[64]
ZnO (0, 50, and 100 mg L^{-1})	*G. max*	Improved root and shoot growth	Reduced arsenic concentration in root and shoot; improved photosynthesis, water loss, photochemical yield; raised antioxidative defense enzymes	[71]
Ti (0.1 to 0.25%)	*Vigna radiata L.*	Augmented radicle length and biomass	Decline in the level of ROS and lipid peroxidation; upregulation of genes related with antioxidative enzymes	[72]
Se and Si (5, 10, and 20 mg L^{-1})	*O. sativa L.*	—	Lowered accrual of Cd and Pb; improved yield	[73]

3. Alleviation of Salinity Stress in Plant Using Nanoparticles

Salinity has emerged as a global concern due to steady increases in salt-affected land throughout the world [74]. For example, it is straddling from the Indo-Gangetic plain to the Great Hungarian Plain, Russia, Israel, China, and the United States of America [75][76]. The extent of salinity-affected areas is expected to cover about 50% of total agricultural land by 2050. Salinity stress causes various detrimental effects to plants' physiological, biochemical, and molecular features and reduces productivity [77]. These impacts and their consequences induced by salinity stress in plants are shown in Figure 1.

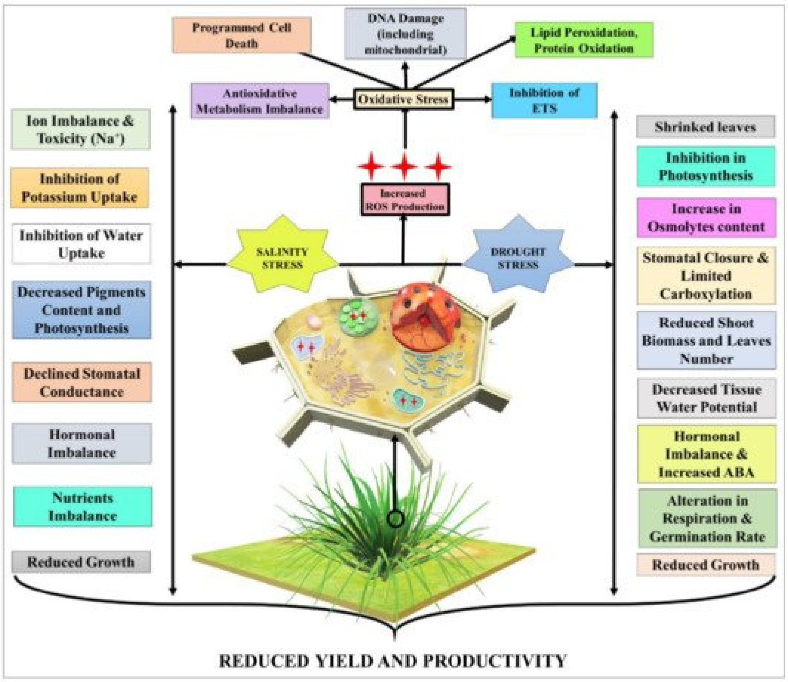

Figure 1. Salinity and drought stress-mediated responses in the plants; ETS: electron transport system.

Nanoparticles can help the plant under salt stress by regulating ion balance; reducing the Na^+ ion toxicity; increasing the uptake of K^+; activating the antioxidative defense system; increasing the contents of the pigment, compatible solutes; and increasing stomatal conductance. In salinity-stressed *T. aestivum* L., the application of magnetite NPs improved chlorophyll contents and antioxidative enzymes along with the amelioration of various polypeptide chains, which are reported to be linked with salinity stress tolerance [78]. Nano-SiO_2 improved the growth of *G. max* under salt stress by raising the level of leaf K^+ and biological antioxidant activities [79]. Similarly, in salt-stressed *T. aestivum* L. cultivars, nano-SiO_2 was found to improve seed germination and growth [80].

The application of Zn NPs to salt-stressed *Brassica napus* plants alleviated the salinity-induced detrimental impacts by upregulating the antioxidative mechanism, osmolyte biosynthesis, and ionic control [81]. In *Solanum lycopersicum*, Cu NPs applied to the leaves mitigated salinity stress by improving growth and the Na^+/K^+ ratio. Moreover, Cu NPs improved the level of glutathione, polyphenols, and vitamin C content as compared to the control. Additionally, the activities of APX, GPX, and SOD were also modulated, thereby improving the overall plant's normal growth and development [82]. In addition, seed priming with ZnO NPs (60 mg/L) ameliorated the detrimental consequence induced by the NaCl treatment in *Lupinus termis* via increasing the pigments, osmoregulation, and regulation of the contents of stress-associated metabolites. In another study, the seed priming of *T. aestivum* L. with Ag NPs was also proven to be an adequate salinity stress management strategy [83].

Recently, a study depicted that the exogenous application of salicylic acid+nano-Fe_2O_3 to *Trachyspermum ammi* L. alleviated salinity stress to a considerable extent via increasing K^+ uptake, K^+/Na^+ ratio; iron content; activities of various antioxidative enzymes *viz*. SOD, catalase (CAT), peroxidase (POD), and phenol peroxidase (PPO); and the contents of the compatible solutes. These modifications collectively led to the improvement in membrane stability index, leaf water content, pigments, and growth of the plants (Table 2) [84].

Table 2. Applications of NPs in salinity stress mitigation by altering the morphophysiological responses of plants.

Nanoparticles	Plants	Germination and Morphological Responses	Physiological Responses	References
Ag (0, 2, 5, and 10 mM)	*Triticum aestivum* L.	Seed priming with Ag NPs significantly augmented the fresh and dry biomass of salinity stressed wheat plants at all doses compared to the control.	Ag NPs increased the activities of vital antioxidative enzymes whilst declined the contents of stress indicators, i.e., MDA and H_2O_2 in wheat leaves as compared to salt stressed plants.	[83]
Zn-, B-, Si-, and Zeolite NPs	*Solanum tuberosum* L., Diamont cultivar	Application of individual and binary treatment of NPs improved plant height, shoot dry weight, number of stems per plant, and tuber yield as compared to the control.	NP treatment increased leaf relative water content, leaf photosynthetic rate, leaf stomatal conductance, and chlorophyll content in comparison to the control; improved nutrients contents, leaf proline content, and leaf gibberellic acid level; and enhanced the contents of protein adn carbohydrates, and antioxidative enzymes' activities.	[85]
Fe (0, 0.08, and 0.8 ppm), and potassium silicate (0, 1, and 2 mM)	*Vitis vinifera*	—	Application of NPs significantly increased the total protein content, activities of antioxidative enzymes (POD, CAT, and SOD), and hydrogen peroxide, while reduced proline content.	[86]
Fe (0.0, 0.08, and 0.8 ppm)	*Fragaria ananassa*	Application of Fe NPs (at higher concentrations) increased root dry weight and dry weight of the explants.	Fe NPs improved the contents of photosynthetic pigments and total soluble carbohydrate, membrane stability index, and relative water content of salinity-stressed plants.	[87]
N–Na_2SiO_3 (400 ppm)	*S. tuberosum* L.	Foliar spraying of N–Na_2SiO_3 restored the tuber number per plant and tuber yield along with improved water use efficiency and tuber dry matter percentage under salinity stress.	Application of N–Na_2SiO_3 exerted positive impacts on the quantum yield of PS II, carotenoids content, and DPPH radical scavenging activity in salinity stressed plants.	[88]
SiO_2 (0, 50, 100, and 150 mg/L)	*Musa acuminata*	All doses of SiO_2 NPs improved the number of shoots and shoot length of banana.	Application of SiO_2 NPs increased chlorophyll content, lowered electrolyte leakage, reduced MDA content, and altered the content of phenolic compounds	[89]
CNPs (0.3% and 90–110 nm)	*Lactuca sativa*	The salinity-induced deleterious effects on germination and associated parameters were alleviated by the exposure of C NPs, e.g., treatment of C NPs for 2 h significantly improved the germination rate in some varieties.	—	[90]

Nanoparticles	Plants	Germination and Morphological Responses	Physiological Responses	References
ZnO (0, 1000, and 3000 ppm)	*Trigonella foenum-graecum*	—	Interaction of NaCl and ZnO was recorded to reverse the salinity induced consequences (L-proline, protein, MDA, aldehydes, sugars, H_2O_2, and antioxidative enzymes) in both cultivars, but the results were more apparent in case cv. Ardestanian than cv. Mashhadian.	[91]
ZnO (10, 50, and 100 mg/L)	*Lycopersicon esculentum*	Foliar spraying of ZnO NPs increased shoot length and root length, biomass, and leaf area.	Increased chlorophyll content and photosynthetic attributes, protein content, and activities of antioxidative enzymes (POX, SOD, and CAT) in salinity-stressed tomato plants.	[92]
TiO_2, (40, 60, and 80 ppm)	*Zea mays* L.	Seed priming with TiO_2 positively impacted the germination (germination percentage, germination energy, and seedling vigor index) and seedling growth (lengths of root and shoot, fresh, and dry weight) and reduced the mean emergence time.	Results showed the enhancement in potassium ion concentration, relative water content, contents of total phenolic and proline contents; increased SOD, CAT, and PAL activities; and decreased sodium ion concentration, membrane electrolyte leakage, and MDA content.	[53]

4. Alleviation of Drought Stress in Plants Using Nanoparticles

Drought stress is reported to have severe consequences for crops, including reduced leaf area, reduced growth, limited carboxylation, decreased water potential, hormonal imbalance, and oxidative stress [93][94]. It is frequently associated with high temperature due to increased water loss through evapotranspiration. Owing to this reason, plants reduce the leaf water and turgor pressure. These consequences are also associated with the stomatal closure, which in turn decelerates the plant's metabolism and ceases vital enzymatic reactions. In addition, the severe water shortages eventually contribute to stunted crop growth and finally death [95][96].

An insight into the morphophysiological responses and consequences of plants against drought stress is presented in Figure 1. The key factors under drought stress are the severity and duration of the stress, which could be directly correlated with drought stress-induced loss in crop productivity and economic yield [97]. Furthermore, salinity combined with drought stress led to a decrease in water potential, but the osmotic potential decreased more significantly [98].

Applications of NPs to drought stress plants have been observed to improve photosynthetic rate, stomatal conductance, relative water content, and ameliorated cell membrane damage by lowering the contents of stress metabolites and electrolyte leakage. Furthermore, increases in osmolyte contents, carotenoid content, chlorophyll content, protein content, and phenolic substances (i.e., rosmarinic acid and chlorogenic acid) and improved activities of antioxidant enzymes such as CAT, SOD, and POX have also been found as a general mechanism in overcoming and mitigating drought stress.

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