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Nanotoxicity: Generation of reactive oxygen species in plants

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ABSTRACT

Nanotechnology is most fascinating field in the modern scientific society, which plays multifunctional roles in different dimensions. Particles having size between 1 nm and 100 nm are called nanoparticles (NPs). NPs contain remarkable physical and chemical characteristics that enable them to perform variety of functions. The structural alteration of NPs (particle dimension, size, surface area, composition, and chemical properties) leads to malfunctioning in biological system resulting the generation of reactive oxygen species (ROS) in plants. In plants, ROS is defined as a "double-edged sword" due to its nature of reacting with the number of biomolecules causing an irreversible damage which leads cell death. The toxicity of NPs is one of the most important factors causing imbalance in the generation of ROS in plants. On the other hand, balance formation of ROS in plants has huge potential to ameliorate abiotic stress and enhanced crop productivity. This review has covered the phytotoxicity induced by NPs in the form of ROS and its role. Biostimulant for regulation of ROS under abiotic stress has also been discussed briefly.

1. INTRODUCTION

Nanotechnology is the most emerging field among the different branches of science including material science, chemistry, and biology [1]. The regular employment of nanotechnology for constructing nano-size products in the scientific field is rising [2]. In today's era, nanoparticles (NPs) have been an eye-catching part for researcher having distinctive characteristics, such as plasticity, better thermal conductivity, catalytic reactivity, and boosting the potency of metals and alloys [3,4], and three major classifications of NPs are seen, (1) organic, (2) inorganic, and (3) carbon-based [5]. Physical, chemical, and biological methodologies are involved in the amalgamation, synthesis and disintegration of NPs. Despite that, the first two methods are quite exclusive, complex and hazardous for the surroundings because of the deadly compounds used as reducing agents [6]. The biological process for synthesizing NPs is less time-consuming, less expensive, and requires less energy [7]. Biological, morphological, and biochemical procedure aid to produce metal-based NPs like, bacterial reduction of metals by distinct plant portions, i.e., root, stem, leaf, and flower. Currently, more than 1000 commercial products containing NPs are available in the market. Cu, Ag, and Zn-based NPs are the most popular antibacterial agents out of all the numerous types of NPs, and they are also frequently used in agriculture [8]. Zinc based NPs are among the most accepted NPs in the nanoindustry, and are produced 10–100 times more over the other. The increased use and regular release undoubtedly lead to Zn-based NPs accumulating in the ecosystem.

Since 2.7 million years ago, oxygen-evolving photosynthesis has been adding oxygen (O_2) to the Earth's decreasing atmosphere. Reactive oxygen species (ROS), a byproduct of various metabolic activities, took part in accomplishing metabolization activities [9,10]. These principle signaling molecules enable cells to react swiftly to novel physiological stimuli and programming of plants activities. Across plants whole life cycle, ROS perform imperative job in biotic and abiotic stress signaling, interaction and combination of ecological incentives, and stress-mediated network, thus participating in the establishment of security method and plant resistance [11]. Thus, the initiation of a network is mediated by stress, all of which contribute to the development of security measures and plant resistance. Various studies have shown to the exposure of different environmental stresses including abiotic and

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biotic may cause plants to produce free radical scavengers and oxygen derivatives [12,13]. Stress signal and enzymatic regulation improve through free radicals, consolidate redox state and induces imperative participation of osmolytes [14-16]. The presence and function of respiratory burst oxidase homologues and NADPH oxidase are strongly predicated on this production, which accounts for 1–2% of the total oxygen (O_2) usage in plants [17-19]. The products of oxidation are collectively referred to as ROS, and they mostly include the following radicals: Hydroxyl (OH), hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), perhydroxyl (HO_2), and anion radical (O_2^-) [20,21]. Both forms of ROS are produced in nature at low levels throughout a variety of aerobic metabolic activities, such as photorespiration in peroxisomes, chloroplast, and mitochondrial electron chain [22-24]. Increased ion toxicity causes an oxidative burst by the production of ROS. Although ROS does not work as a stress signal, they are the secondary messengers that signal fundamental cell functions such as apoptosis, necrosis, and cell proliferation, thus regulating various functions in plants.

There are several factors (heavy metal, salinity, temperature, and dryness) that are known to alter the equilibrium between ROS production and its scavenging. In these situations, a few key criteria, such as the severity, duration of the stress, growth alteration, and the rate at which plants adapt to difficult circumstances, largely determine a plant's capacity to tolerate [25]. Plants have developed a miscellaneous strategies to endure adverse environmental states like stress-responsive genes that encode their proteins needed for the initiation and control ROS to adapt to intriguing environmental conditions [26]. NPs activities due to the application of zinc oxide have been shown by [27] to conduct ROS scavenging capabilities, preventing oxidative damage in stressed plants. Numerous earlier kinds of research have demonstrated the use of NPs to lower ROS generation in plants under both natural and stressed environmental conditions [28-33]. Previous studies confirmed that NPs can regulate abiotic stress in various plant species by altering the hormonal levels, antioxidant enzymes activities, and gene expression in crop plants. Overall, scientists have concluded that minute concentration of NPs may start the ROS detoxification mechanism. Therefore, the inoculation of NPs has brightened the chance of crop cultivation in stressed crops. This article intended to increase our understanding of ROS production, signaling, and their function in plants to successfully handle abiotic stress. The impact and function of NPs in the ROS as well as the crosstalk between NPs and the ROS were discussed mainly focusing on the ROS as a biostimulant under abiotic stress.

2. ROS AND ITS ROLE IN PLANTS

ROS production, which are naturally occurring by-products of cellular oxidative metabolism, is essential for controlling cell survival, cellular damage, differentiation, cell signaling, and the production of substances that cause inflammation[Table 1] [34,35]. ROS produces free radicals produces including singlet oxygen ($^1O_2$), peroxyl (RO_2), carbonate (CO_3^-), alkoxyl (RO), superoxide (O^{2-}), hydroxyl (HO), hydroperoxyl (HO_2), and carbon dioxide radical (CO_2^-). The most persistent and prevalent ROS in plants is O^{2-}, OH, and $^1O_2$ [22]. This free oxygen is continuously produced through chloroplasts during the photosynthetic electron transport system (ETS) and is afterward eliminated by reduction and assimilation. In photosystem I and photorespiration, reduced components of the ETS reduce O_2 to a superoxide radical [36]. O_2 acts as a free radical with a reduced half-life because of superoxide dismutases (SODs) and eventually convert it to H_2O_2 rapidly [37]. Biologically relevant ROS also include non-radicals such as hypochlorous acid, nitric oxide, organic peroxides, peroxynitrite, peroxynitrate, peroxynitrous acid, H_2O_2, and ozone (O_3) [38]. H_2O_2, a non-radical ROS product conveys ROS-mediated aquaporin membranes with greater stability and firmness than free radicals [37].

Numerous experiments have exhibited that exposure to a variety of environmental biotic or abiotic stressors can induce plants to develop both non-radical moderately reactive oxygen derivatives and highly reactive oxygen-free radicals [13]. This generation persuades the attainability and operational ability of NADPH oxidases and respiratory burst oxidase homologues [19]. It represents <1–2% of the plant's overall O_2 consumption [39]. Plants have developed sophisticated immune systems that can perceive pathogen transmission and activate an effective immune response through two separate but interdependent immune response stratums [40]. Pattern recognition receptors, built with extracellular conserved microbial- or pathogen-associated molecular patterns induce immunity in the first layer. Nucleotide-binding leucine-rich repeat receptors mediate the second layer [41].

ROS generated under unmitigated environmental circumstances cannot induce cellular impairment due to the production of stress-responsive genes [39]. Based on multiple pieces of evidences, it has been hypothesized that this degree of ROS production is related to a limited natural role in the developmental processes mediated by phytohormones such as auxins and cytokinins [10]. Oxidative stress is produced due to the excess genesis of ROS due to biotic stress also [Figure 1] [42]. Redox homeostasis to maintain a balanced biomolecules state in plants depends on ROS. Even though salicylic acid (SA) is thought to be the main ROS regulator, the underlying processes are rarely explored [43]. SA is indispensable in biotic stress management for preventing microbial growth, fungal diseases, and viral infections during HR in different pathosystems, including tobacco mosaic virus [44,45]. However, both the pathosystems and the source of ROS have an impact on the mechanism of SA regulation and obstruct ROS signaling [46]. Treatment with SA in *Arabidopsis* caused the PRRs to be regulated, which in turn caused ROS generation that was most likely At RBOHD-dependent [47].

Several RBOHD isoforms promoters in *Arabidopsis* and rice containing SA-responsive cis-regulatory elements further validated the production [48]. However, under stressful environmental conditions, cellular ROS concentrations are excessively accelerated and reach levels that are greater than the antioxidant scavenging abilities that plants use to balance out excessive ROS generation [49]. This trait could lead to oxidative stress, protein, lipid, and nucleic acid damage in the membrane, eventually resulting cell death and dysfunction [42]. Increased ROS production is employed to increase the potency of damaging components in a genetically controlled process called abiotic stress-induced programmed cell death [50]. Natural stressors such as pathogen infection, heavy metals, heavy radiation, heat stress, salinity stress, and drought stress are just a few examples that could break the delicate balance between ROS creation and removal pathways [51]. Arsenic is one such hazardous metalloid that pollutes the environment and has severe effect on life on Earth. Arsenic is known to be harmful to plants and to induce a number of serious ailments in humans, even in trace amounts [52]. Studies show that the accumulation of As in cells increases the generation of ROS, such as O_2 and H_2O_2, which creates oxidative stress in plants and results in impaired cellular metabolism, reduced plant development, and decreased yield [53]. Numerous crucial factors, such as the duration and intensity of the stress, cellular metabolic status, the level of ROS in the cells, and antioxidant capacity, are frequently consistent with plants response mechanism to the oxidative stress caused by high ROS concentrations [39].

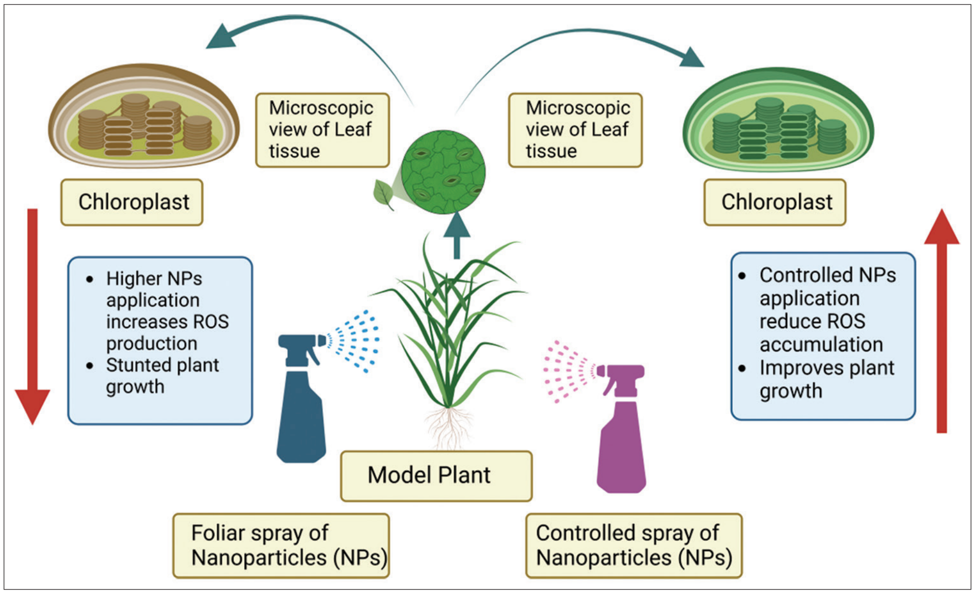

Figure 1: Schematic representation of reactive oxygen species generation in chloroplast.

Table 1: Effects of ROS compartmentalization under abiotic stress.

Different sites of ROS production and compatmentalization	Effects of ROS	References
Mitochondrial	Electron transport chain is reduced, aging of leaves, higher carbonized proteins, H_2O_2 formation, Lipid peroxidation	[91,92]
Chloroplast	Increase ROS production, electron leakage, singlet oxygen generation	[93]
Peroxisome	Intracellular H_2O_2, glycolate oxidation, cellular redox homeostasis, physiological disorder	[94]
Plasma membrane	NADPH oxidase production, superoxide anion radical formation, mechanosensitive Ca^{2+} channel production	[95]
Cell wall	Peroxidase enzyme, electron transfer, ROS signaling, influence abiotic stressor	[96]
Nucleus	Gene expression, molecular oxygen reduction, redox potential hamper,	[97]
Apoplastic region	Cell surface, enzyme produces ROS, stomatal closure, programmed cell death	[50]
Cytosolic area	Oxidation procedure, diffusion, transport and leakage in ROS condition, APX overexpression	[98,99]

ROS: Reactive oxygen species, APX: Ascorbate peroxidase

In plants ROS-scavengers and non-enzymatic antioxidants such as ascorbate (AA), glutathione (GSH), carotenoids, -tocopherol, prolines, flavonoids, and phenolic chemicals play a role. These antioxidant enzymes include dehydroascorbate reductase (DHAR), catalase (CAT), SOD, glutathione reductase (GR), guaiacol peroxidase (GPX), monodehydroascorbate reductase (MDHAR), ascorbate peroxidase (APX), and low molecular mass antioxidants [54]. It is widely established that increased antioxidant enzyme or non-enzymatic antioxidant activity reduces the severity of oxidative stress-related damage in response to novel environmental stimuli [51]. For instance, it was shown that several conventional types of rice plants exposed to drought stress had an overall increase in the antioxidant enzymes APX, SOD, GPX, CAT, and GR [55]. Cu stress to *Colobanthus quitensis* (Kunth) Bartl, made it feasible to cause the upregulation of AA, GSH, phenolics, phytochelatins (as GSH oligomers), and sugars as non-enzyme-based antioxidants [56]. Before translating into adequate responses, ROS signals are first detected and processed by plants. The extent of alteration or modulation of potential signaling targets including transcriptional regulators, protein kinases, and stress-induced proteins depends on the oxidizing behavior of ROS aggregates. The ability of ROS to oxidise thiol groups and methionine residues in the protein to influence the protein redox status is noteworthy [57]. Thio- and gluta-redoxins are proteins can control cellular redox conditions through their reciprocal activation/deactivation or reversible oxidation/reduction [58]. It has been discovered that ROS-driven redox perturbations can activate quick adaptive responses by mitochondrial/chloroplastic retrograde signaling [59]. In addition, ROS can facilitate the retrograde signaling pathway from the plastid to the nucleus [39]. Therefore, the nucleus can accommodate the H_2O_2 produced in plastids at the consequence of triggering the expression of defense genes [60].

Limited studies have explored the interactions between ROS and other secondary messengers acting as a signal transduction cascade including Ca^{2+} and antimicrobial family derived reactive nitrogen species (RNS) [61]. Elevated amounts of oxidative potential cause them to react with the messengers of NO to form (non-) radical RNS products such as nitroxyl anion (NO), nitrate (NO_3), nitrous acid (HNO_2), nitrosonium cation (NO^+), nitric dioxide (NO_2), and ONOO [62]. These NOx species play a natural role in plant development, metabolism, stress signaling, and stomatal closure [63]. Depending on the concentration and subcellular microcompartment type, the interaction of ROS and RNS with antioxidant enzymes can have either favorable or detrimental effects on plant cells [64].

3. NPS AND ROS

We scrutinized that the NPs contributed to oxidative stress by causing lipid peroxidation, a decrease in chlorophyll content, and the synthesis of GSSG [65]. Zn-based NPs persuaded free radicals development in *Triticum aestivum*, resulting in a rise MDA and down GSH amount and chlorophyll levels [66-68]. Kim *et al*. [69] demonstrated the toxic level of CuO-NPs on *Cucumis sativus* which exhibited a considerable enhancement of ROS. Oxidative stress caused by Cu-NPs has also been observed on *Vigna radiata* and *T. aestivum* grown on agar media and resulted in stunted seedling and shoot height [70]. The underlying mechanisms related to the generation of NP-generated ROS vary depending on the kind of NP, and the real cellular process relating to ROS production is yet unknown [34]. The higher formation of ROS by the stimulation of NPs exposure can induce oxidative stress and alter the all metabolic functioning of the plants and leads cell death and reduced growth [Figure 2]. Most of the NPs may incite the free-radicals facilitated toxicity through Fenton-type reactions (Huang *et al*., 2010). Since the primary result of NP-induced cellular harm or malfunction of cells is the result of ROS genesis [71]. Under biotic (fungal and bacterial) and abiotic (drought, salt, and cold) stress, (mitogen-activated protein kinase kinase kinase 1 [MEKK1]) and MAP3K are switch-on. MEKK1 is turn-on due to ROS formation. Production of ROS under different stresses start-up the MPK6 and MP3K cause diverse response.

Plants establish an antioxidant defense system to scavenge the excessive ROS to combat oxidative stress which performs as an adaptive response mechanism [72,73]. The cellular amount of ROS and physio-biochemical states are tightly controlled by diverse detoxifying enzymes, including CAT, glutathione peroxidase (GPX), SOD as well as a variety of antioxidants, including flavonoids, ascorbic acid, GSH, and Vitamin E. ROS is produced as intermediates under various physiobiochemical states [51,74]. In unfavorable conditions, ROS accumulations also enhance, and with the assistance of precise signal transduction pathways, they contribute to the plant's defense mechanism [42,75].

The increased amount of ROS genesis during stress conditions within the cell, membrane damage occurs along with DNA, RNA, and protein synthesis can result in cell death through oxidative stress [76,77]. As a result of changes in metabolic activity and as a subtype of the abiotic stress response signal transduction network, ROS are produced as the primary cause of ROS in abiotic stress [Figure 3] [78].

4. BIOSTIMULANT FOR REGULATION OF ROS IN PLANTS UNDER ABIOTIC STRESS

Plants under stress conditions especially under abiotic stress (salinity, drought, heat, water, metal, chilling, and temperature) faces various deteriorating conditions to survive. Plants had developed diverse internal mechanisms and defensive criteria to survive in the stressful conditions [79]. Some of them are immune stimulation, molecular metabolism, and especially biostimulant. Biostimulant promotes defense mechanisms, improve growth, yield, climate, and stress resilience [80]. Plant interaction with stimulants reveals reactions with enzymes, antioxidants, metabolic fluxes, and cellular physiology [81]. Crop health improvement through minimizing ROS production of various plants is performed by proper application of biostimulant [82]. Although more scientific ground is required for properly understanding the functions of biostimulant during stressful conditions, Yakhin *et al*. [83] suggested comparatively detailed information about the functions of biostimulant which help provide nutrients to plants, assimilation, soil health improvement, etc.

Salinity stress in lettuce is induced by improving reluctant metabolites like sterols, terpenes, etc. by using protein based biostimulant [84]. Tomato (*Solanum lycopersicum*) plants under salt stress were also observed using seaweed-based biostimulant, which accelerated proline and antioxidant contents in plants [85]. Vegetal biopolymer in melon under stress improves growth conditions, root growth, photosynthetic activity, and hormonal interaction [86]. Drought-resistant protein-based biostimulant derivatives in tomato mitigate oxidative stress; reduce hormonal imbalance, and excess level enzyme content [87]. Calcium-treated rice (*Oryza sativa*) plants stimulate MDA, LOX,

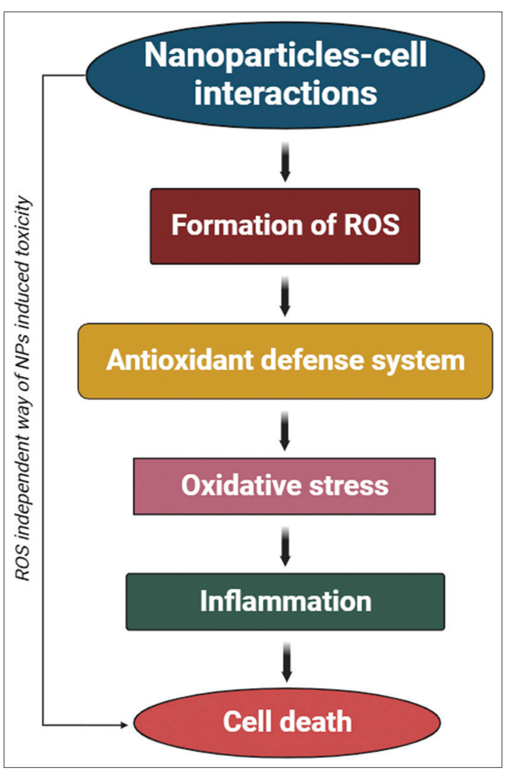

Figure 2: A schematic representation of nanoparticles-mediated reactive oxygen species generation leading to cell death.

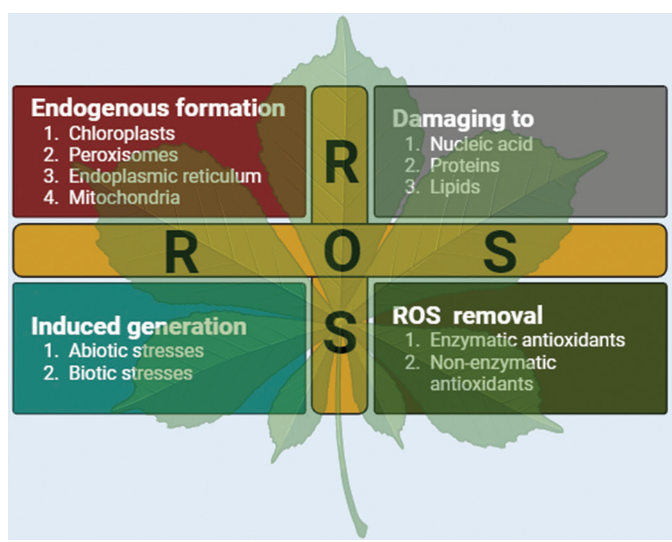

Figure 3: Schematic representation of reactive oxygen species formation, its effects and removal.

MDHAR, and GR contents tremendously where Mn-treated plants show reduced amount of MDA, DHA, improves SOD, MDHAR in rice [88]. Biochar application in *Brassica chinensis* and *Spinacia oleracea* lead to MDA reduction, APX increases internally [89]. GABA co-treatment in *Brassica juncea* L. cv. BARI Sharisha-11 contributed similarly to biochar treatment and accelerated enzymatic functions [90].

5. CONCLUSION AND FUTURE PERSPECTIVE

This review has summarized the wealth of data on the ROS generation due to higher accumulation of NPs. Elevated amount of NPs increased the level of MDA and lipid peroxidation which leads to oxidative stress. Enhancement of ROS leads in reduced morpho-physiological attributes and crop yield. NPs altered the polyunsaturated fatty acids, injured cell membrane accessibility and disturbed cell shape, harm protein and DNA, finally cell death. To decrease the formation of ROS is helpful in sustainable crop production and crop health. Biostimulant is helpful to control the production of ROS under abiotic stress conditions, increase defense performance, growth indices, crop yield, and abiotic stress resilience. In future, effects of NPs on the production of ROS under omics, metabolomics, and transcriptomics level could be explored.

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7. AUTHORS’ CONTRIBUTIONS

MF, PA, SH, and VDR: Conceptualization, SA and SHT: Investigation, AF and SHT: Resources, MF, ANY, and SA: Writing—original draft preparation, PA and SMA: Writing—review and editing, TM: Visualization, SH: Supervision.

8. CONFLICTS OF INTEREST

The authors report no financial or any other conflicts of interest in this work.

9. ETHICAL APPROVALS

This study does not involve experiments on animals or human subjects.

10. DATA AVAILABILITY

All the sources of data provided in this manuscript have duly been referred in the references which are freely available in public domain.

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