



Application of Nanobiotechnology in Enabling Plants to Overcome Water-logging Stress: A Review

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ABSTRACT

Abiotic stresses adversely affect plant growth and ultimately crop productivity. Of these, water-logging is the most widespread and most commonly experienced stress factor. While water is essential for all plant growth and development processes, waterlogging is an obstacle to sustainable agriculture. Recent FAO reports indicate that universal crop production must be enhanced by 70% by 2050 in order to meet the growing demand for food by an estimated 2.3 billion people. As demand for food increases, there is an urgent need to identify environment-friendly strategies capable of being accepted and adopted widely to enhance crop yields and mitigate the effects of climate change. Nanotechnology as a science of manipulating materials at the nano-scale has significant potential to enhance agricultural productivity by nonconventional means. This technology has been gaining momentum lately as a possible solution to reduce the adverse effects associated with various stresses, particularly with waterlogging, to enhance future food security. This paper discusses the potential applications of nanoparticles to achieve sustainable crop productivity, together with their impact on the mechanism of tolerance to waterlogging stress.

Key words: Abiotic Stress, Crop productivity, Food security, Nanobiotechnology, Waterlogging.

Agriculture is the source of income for more than half of the population and thus the backbone of many developing countries (Anonymous, 2009; Ansari *et al.*, 2009). The current world population is nearly 8 billion and almost half of that live in Asia. While developing countries experience daily food shortages due to environmental factors; developed countries have food surplus, and their industries are thus striving for fresher and healthier food (Manjunatha *et al.*, 2016). Ecological factors have a significant contribution towards global food security since agriculture is also challenged by increasing incidents of adverse weather events (Bilan *et al.*, 2018; Ansari *et al.*, 2012). In short; the sustainability of food supply and safety is facing two major challenges: ever-increasing populations and climate change particularly affecting water availability (FAO, 2017). The solution to both these challenges is embracing new technologies to enhance crop yields and mitigate the effects of climate change. Waterlogging, defined as the soil condition where excess water limits the gas diffusion (Setter and Waters, 2003; Ansari *et al.*, 2013), is a major obstacle to sustainable agriculture, causing substantial yield losses. Waterlogging of agricultural areas may result due to intense and/or excessive rainfall over a long period, as well as local floods (Fukao *et al.*, 2019). While plants need water for growth and development, excess water generated during water logging is certainly harmful and can change the community structure (Ury *et al.*, 2020). Worldwide, almost 16% of the available fertile lands are affected by soil waterlogging and depending on the plant development, spring floods or heavy rainfall cause 40-80% yield loss (Ahsan *et al.*, 2007; Shaw *et al.*, 2013). Waterlogging caused almost two-thirds of all crop damage between 2006 and 2016 (FAO,

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2017). For instance, the excessive monsoon rains in Pakistan resulted in extensive waterlogging between 2010-2014, resulting in a loss of at least 11.10⁹ tons of cotton, maize, sugarcane and rice; yielding a total economic loss of over 16.10⁹ dollars (Rehman *et al.*, 2016). Furthermore, water-logged areas require additional actions, such as removing sediments, restoring physical and nutritional soil properties, reconstituting beneficial microbial activity in the

soil and, if the damage is fatal, replanting (Rey *et al.*, 2019; Singh and Nara, 2013), so that farming can be re-started. Annually the economic loss due to such crop damage is estimated to be billions of dollars, calling for urgent action to mitigate water-logging stress (Voeselek and Bailey-Serres, 2013; Pucciariello *et al.*, 2014). Stagnant waterlogged conditions significantly affect plant growth and development. The stress response level of plants grown on arable farmland or in a watery environment varies, and this regulates the distribution and quantity of vegetation (Blom and Voeselek, 2016). The different survival rates and stress tolerance observed in plants belonging to the same genus are important in waterlogging tolerance (Phukan *et al.*, 2016). The mechanism affecting the growth and development of plants under excess of water is still unresolved, as water is chemically harmless. However, the physical properties of water, with its ability to restrict free gas exchange, can affect plant growth and development (Phukan *et al.*, 2016).

Oxygen deficiency in waterlogged soils is relatively fast and can occur within a few hours depending on prevailing conditions (Nishiuchi *et al.*, 2012; Ansari *et al.*, 2015). The diffusion rate of oxygen in water is approximately 10^4 times slower than in air. This reduces O_2 flux by about 32×10^4 times when soil pores fill with water (Armstrong and Drew, 2002; Colmer and Flowers, 2008; Ansari *et al.*, 2016). The real cause of harm to plants in waterlogged soil is the slow diffusion of gas in the water. The rapid O_2 consumption by soil microorganisms, leads to insufficient oxygen uptake of subsoil tissues (Ozturk *et al.*, 2009). In addition to O_2 deficiency, CO_2 and ethylene concentrations are increased in the soil. Furthermore, other toxic substances such as iron, manganese and hydrogen sulfide, are produced under waterlogged conditions; causing serious damage to plants (Pampana *et al.*, 2016; Setter *et al.*, 2009; Ansari *et al.*, 2018). Thus, the growth and development of most

commercial crops are impeded under waterlogged conditions (Nishiuchi *et al.*, 2012).

Plants can build up different mechanisms to respond to negative conditions, while responses may differ even for the same species. Therefore, for sustainable agriculture and increased crop production, identification of naturally tolerant plants or increasing of stress tolerance of existing plants have important. In recent years, nanotechnology has emerged as a multi-disciplinary research area that offers significant opportunities to improve tools and technologies for research and transformation of the biological sciences (Fortina *et al.*, 2005; Saxena *et al.*, 2016; Manzer *et al.*, 2015; Ansari *et al.*, 2020) and nanobiotechnological practices for the mitigation of the adverse effects of water logging have attracted much research interest. The potential applications of nanotechnology in various agriculture sectors are given in Fig 1.

Thus, the objective of this the review is to explore the potential applications of various NPs in agriculture to achieve sustainable crop productivity, with particular emphasis on the benefits of the unique properties exhibited by a diverse range of nanoparticles and their impact on plant growth and especially on the mechanism of tolerance to water-logging stress.

Nanoparticles (NPs)

Nanoparticles (NPs) are very small molecular clusters ranging between 1-100 nm (Roco, 2003) in diameter. The most important difference of nanomaterials from other materials is their increased relative surface area and quantum effects. Their exceedingly small dimensions often result in diverse and unique physicochemical properties such as diverse particle morphology, large surface area, flexible pore size and increased reactivity, when compared to their bulk material counterparts (Nel *et al.*, 2006; Ansari *et al.*,

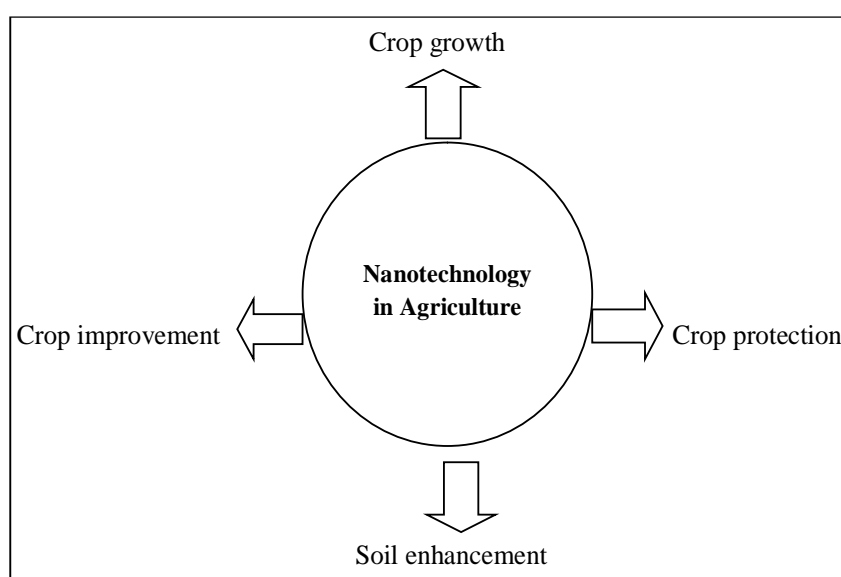


Fig 1: Nanotechnology applications in various agriculture sectors.

2019). As NPs generally exhibit a high surface to volume ratio and high surface energy, their chemical and biochemical reactivity are also relatively higher than to their bulk counterparts (Dubchak *et al.*, 2010).

Some important properties are summarized in (Fig 2). These include size, morphology, aspect ratio, hydrophobicity, surface area/roughness, surface contaminations /adsorption, solubility-release of toxic species, Reactive Oxygen Species (ROS) production capacity, competitive binding sites with receptor and dispersion/ aggregation, structure/composition (Somasundaran *et al.*, 2010; Ansari *et al.*, 2021b).

Nanoparticles can be synthesised by biological, chemical or physical means (Muruganatham *et al.*, 2018). There is substantial previous work on the synthesis of both metal (Ag, Au, Pd) and metal oxide (Fe_3O_4 , SiO_2 , TiO_2 , ZnO) nanomaterials. While chemical synthesis of NPs was initially popular, in the recent years, biosynthesis, also referred to as Green synthesis, of metallic NPs using plants or plants extract, has also become popular (Javad and Butt, 2018; Gude *et al.*, 2013). This is because plants contain a wide range of phytochemicals including alcohols, amines, phenolics, terpenoids, flavonoids, latex and enzyme cofactors which can play a role as stabilizing and reducing agents during the green synthesis of metal nanoparticles from metal salt solutions. Such green synthetic methods are popular because they are cost-effective, eco-friendly and provide a controlled synthesis with well-defined shape and size (Kumar and Yadav, 2009; Siddiqui *et al.*, 2014; Ahmed *et al.*, 2019).

Nanoparticles in agriculture and plant growth

NPs are used in agriculture to regulate the processes such as plant growth and development, increasing yields, and avoiding various stress factors (Saxena *et al.*, 2016). NPs are generally classified in agriculture as carbon nanomaterials (NMs), metal NPs and metal-oxide NPs.

Various types and compositions of NPs are available, and are selected by application areas rather than through

systematic studies. The most commonly used NPs in plant sciences are Ag, Au, Ti, Zn. Numerous studies have been carried out to identify the effects of different NPs on plant species, and to solve their mechanisms of action. The effects produced by these materials are believed to depend the NPs type, the species and the substrate (*i.e.*, culture medium, hydroponics or soil) of plant. However, there are often many inconsistencies between comparable studies and therefore, many problems covering the biological effects of nanoparticles cannot be solved (Manzer *et al.*, 2015; Ansari *et al.*, 2021a).

Role of carbon NMs in plant growth

Carbon NMs have unique chemical, electrical, mechanical and thermal properties. The most commonly used carbon-based nanomaterials are fullerene (C70), fullerol (C60 (OH) 20) and carbon nanotubes (single walled-SWCNT and multiwalled-MWCNT) (Verma *et al.*, 2018). It is known that Fullerene, fullerol and carbon nanotubes increase water holding capacity, biomass, fruit yield and secondary metabolite production in plants (Ahmed *et al.*, 2019). Scientists demonstrated the impact of NMs on germination, growth and development in order to increase agricultural applications.

In a study where different concentrations of fullerol were applied to bitter melon seeds, it was found that seed productivity, biomass, fruit number, water content and secondary metabolite content increased (Husen and Siddiqi, 2016). A study carried out with tomato revealed that when seeds exposed to MWCNTs, germination rate and biomass enhanced considerably (Khodakovskaya *et al.*, 2009).

Role of metal NPs in plant growth

A number of studies demonstrated that metal NPs raise plant growth and development. Au NPs may lead to an improvement in crop productivity, depending on the chlorophyll and sugar content, leaf area, number of leaves, plant height that (Gopinath *et al.*, 2014). Likewise, Au NPs

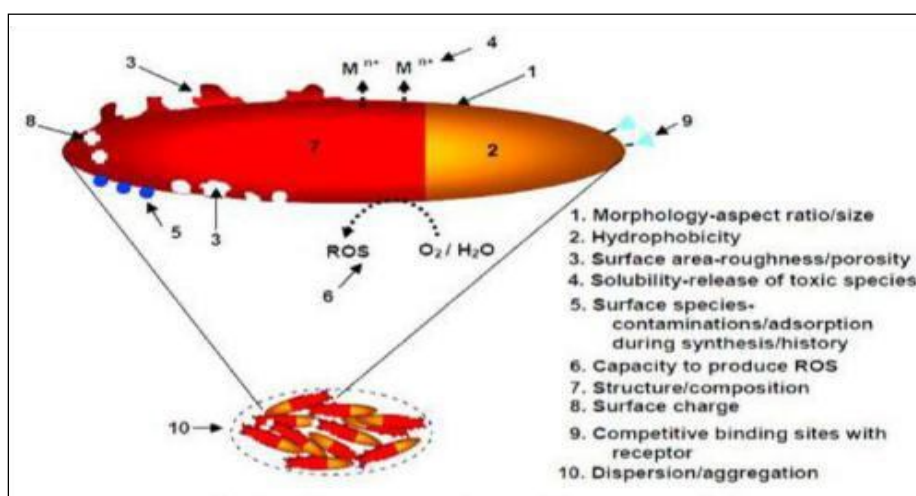


Fig 2: Various properties of the nanoparticles (Manjunatha *et al.*, 2016).

play a considerable role in seed germination and antioxidant defense system of *Arabidopsis thaliana* (Siddiqui *et al.*, 2014).

Silver nanoparticles have been reported to possess a wide range of applications including biological tagging in medicine, coatings on domestic products, in electronics, food packaging, medical drug delivery and pesticides (Kumar and Yadav, 2009; Siddiqui *et al.*, 2014). Silver nanoparticle treatments are also increasing in the agriculture mainly as crop improvement agents, where varied studies have shown that AgNPs have enhanced seed germination as well as growth and development in plants (Ahmed *et al.*, 2019). The effect of silver nanoparticles (AgNPs) on seven varieties of Mill tomatoes seed germination was investigated. This study demonstrated that seeds treated with five concentrations of AgNPs sprouted earlier than seeds germinated with deionized water (Gopinath *et al.*, 2014). Similarly, the effects of six different silver nanoparticle concentrations (*viz.* 0, 25, 50, 100, 200 and 400 ppm) on the growth and antioxidative enzymes of oriental mustard seedlings were studied, exhibiting that silver nanoparticles induced an increase in chlorophyll content, root and shoot length and antioxidant defence enzymes (Husen and Siddiqi, 2016).

The role of metal oxide NPs in plant growth

Favourable effects of metal oxide nanoparticles on plant growth and development including for example, nano-sized Titanium dioxide (TiO_2) [62], Zinc oxide (ZnO) (Saif *et al.*, 2014), and Ca nanoparticles (Reddy *et al.*, 2017) have been reported on plant growth and development.

Zheng *et al.*, (2019), showed enhanced spinach growth when Titanium Dioxide -NPs were applied to either the seeds or leaves. This was attributed to TiO_2 -NPs increasing the activities of several enzymes and supporting nitrate adsorption, accelerating the formation of inorganic nitrogen to organic nitrogen (Sebastian *et al.*, 2018).

TiO_2 NP stimulated plant growth and development when applied to seeds (Setter *et al.*, 2009). Increases in dry, fresh weight, chlorophyll content, Rubisco activity and photosynthetic rate were observed in *S. oleraceae* when exposed to anatase TiO_2 NPs (Verma *et al.*, 2018). Seed germination, plumule growth and radicle of canola seedlings were induced by TiO_2 NPs (Husen and Siddiqi, 2016). Enhanced plant growth was caused by promoting activities of Rubisco and chlorophyll formation (Khodakovskaya *et al.*, 2009).

It was noticed that the germination rate increased when sage seeds were exposed to TiO_2 nanoparticles (Sebastian *et al.*, 2018). Feizi *et al.* (2010) detected an increase in *Salvia's* germination rate when they exposed 21-day-old seeds to 60 mg.L^{-1} batch of nano-sized Titanium Dioxide. This application did not have any important effect on biomass or root-shoot elongation. The lowest average germination time was observed when 60 mg L^{-1} concentration was applied; and the average germination time did not improve at higher concentrations.

TiO_2 NPs are photocatalytic in nature and can perform an oxidation-reduction reaction to form hydroxide and superoxide anion radical when exposed to light (Villagarcia *et al.*, 2012).

Fe oxide NPs improved root length in pumpkin (Saif *et al.*, 2014), and the pod and leaf dry weight in soybean (Saxena *et al.*, 2014). According to Singh and Nara (2013), RuO_2 nanoparticles increased the germination rate and seedling growth of the oriental mustard.

Many studies have been undertaken in controlled aquatic environments so that a complete ecosystem and food chain could be represented and variations induced by high sensitivity to environmental factors could be eliminated. For example, Juhel *et al.*, (2015), examined the alumina effects NPs on the photosynthesis, growth and morphology of *Lemna minor*. Since Lemnaceae family is ideal in stress adaptation and / or toxicity studies; these plants are preferred for regulatory toxicity tests and ecotoxicological tests of chemicals. The hypothesis was that aluminium oxide NPs (alumina and Al_2O_3 -NP) could enhance *L. minor* growth, or based on published results demonstrating that Al NPs could improve the electron transfer efficiency of isolated photosynthetic reaction centres (Roco, 2018). They used engineered Al NPs to study basic mechanisms of the alumina NP-mediated growth stimulation and to investigate the effects on photosynthesis, growth and morphology.

Zinc (Zn), is an essential micronutrient for optimum plant growth and development, facilitating critical metabolic reactions in plants. Zn is required at low concentrations, so the presence of Zn at nano levels provides an appropriate amount of Zn distribution to the plant to be used by plants for growth and development. Therefore, ZnO may be conceived as bio-friendly as well as eco-friendly material that can be used as a green reagent for plants (Rehman *et al.*, 2016). Low concentrations of ZnO NPs are known to increase seed germination in wheat (Phukan *et al.*, 2016). Few studies have shown that suitable concentrations (1.5 mg/mL) of ZnO nanoparticles yielded increases in biomass production in *Cicer arietinum* as compared to ZnSO_4 treatment (Siddiqui *et al.*, 2014). *Cyamopsis tetragonoloba* subjected to ZnO NPs, showed increased chlorophyll content, root-shoot length, protein synthesis and biomass (Rey *et al.*, 2019).

Silicon (Si), being abundant in soil, is one of the most important nanoparticles and its role in plant growth, development and defence is acknowledged and well documented (Pampana *et al.*, 2016). Si NPs also demonstrated growth-promoting effect during the development stages in corn, particularly on seed germination, RWC, photosynthetic pigment, root and shoot elongation. Considerable increase in these features were observed when exposed to various concentrations of SiO_2 compared to the control group (Fortina *et al.*, 2015). Many other studies have investigated the effect of Silicon oxide nanoparticles on the germination and growth of plants. Some of them have shown that nano- SiO_2 particles were absorbed faster and better than micro-

SiO₂, H₄SiO₄, Na₂SiO₃. When applied on seeds and root of corn, were they could be instantly utilized by plants for their growth and development (Reddy *et al.*, 2017). No toxic consequences were found on plants when pear seedlings were irrigated with nano-SiO₂ high concentrations (Fortina *et al.*, 2015).

Thus, NPs have numerous positive impacts on plant growth and the effectiveness of NPs differs from plant to plant, depending on the concentrations used (Table 1). The role of nanoparticles is dependent on their size, surface area, reactivity, chemical composition and concentration level to which they respond positively (Thombre *et al.*, 2014). More work is required to understand the relationship between the identified growth response and the environment. This chapter discusses the role of NPs in promoting seed germination, photosynthesis and plant growth.

Role of nanoparticles on mitigating adverse environmental conditions

In addition to their role in growth and development, nanoparticles also play an important role in increasing various stress tolerances and reducing deleterious effects of heavy metals in the environment.

It was demonstrated that TiO₂ nanoparticles increased various stress tolerances (Drought, Salinity and water) by affecting different processes such as malondialdehyde (MDA) and superoxide radicals accumulation, and by simultaneously inducing activities of antioxidant defence enzymes such as

ascorbate peroxidase, catalase, guaiacol peroxidase and superoxide dismutase of Spinach (Rehman *et al.*, 2016).

González-Melendi *et al.* (2011) have shown, that carbon-coated iron NPs have potential use in plants as nano-device delivery systems. Their hypothesis was that NPs binding to agricultural chemicals (or other substances including pollutants) could reduce the contaminant amounts released to the environment, reducing the damage to plant tissues (Sebastian *et al.*, 2018). Their studies attempted to validate the hypothesis by providing a set of tools for the determination and analysis of carbon-coated Fe magnetic core shell nanoparticles applied to plants. The concentration of magnetic NPs in selected plant tissues was determined by the magnetic field gradients. This study revealed that NPs can be loaded with diverse substances before they are taken up by plants and can be concentrated into localized areas using magnets, providing evidence for the wide potential applications of magnetic NPs in agriculture (Thombre *et al.*, 2014).

Water logging stress

Among the abiotic stresses, alkalinity, drought, salinity, water-logging are the main factors that conduce to reduce crop growth and productivity (Pucciariello *et al.*, 2014). Heavy rains can result in fields flooding if appropriate drainage is not provided. Other effective causes are flooding of water in rivers and increased groundwater table. Besides, extreme irrigation also results upshots in temporary water-logging in plants. All of these conditions cause either hypoxia

Table 1: Role of different nanoparticles on growth and development in various plants.

| NPs | Optimum concentration | Plants | Consequences | Reference |
|------------------------------------|--|---|--|----------------------------------|
| Ag NPs | 10 to 30 µg.mL ⁻¹ | <i>Boswellia ovalifoliolata</i> | Increased germination rate and seedling growth | Savithramma <i>et al.</i> 2010 |
| Al NPs | 2000 mg.L ⁻¹ | <i>Raphanus sativus</i> , <i>Brassica napus</i> | Root growth improved | Lin and Xing, 2007 |
| Au NPs | 62, 100, 116 mg.L ⁻¹ | <i>Cucumis sativus</i> , <i>Lactuca sativa</i> | Significant enhancement in germination index | Barrena <i>et al.</i> 2012 |
| CeO ₂ NPs | 250 ppm | <i>Arabidopsis thaliana</i> | Biomass enhanced | Ansari <i>et al.</i> 2019 |
| CO ₃ O ₄ NPs | 5 g.L ⁻¹ | <i>R. sativus</i> | Increased root growth | Villagarcia <i>et al.</i> , 2012 |
| CuO NPs | 500 mg.kg ⁻¹ | <i>Triticum aestivum</i> | Biomass enhanced | Sebastian <i>et al.</i> , 2018 |
| CNTs | 40 µg.mL ⁻¹ | <i>Lycopersicon esculantum</i> | Increased germination and seedling growth | Fortina <i>et al.</i> , 2015 |
| GNPs | 10 µg.mL ⁻¹ | <i>A. thaliana</i> | Increased root-shoot elongation, early flowering | Kumar <i>et al.</i> , 2013 |
| Fe oxide NPs | 0.50- 0.75 g.L ⁻¹ | <i>Glycine max</i> | Improvement in quality and yield | Sheykhabglou <i>et al.</i> 2014 |
| Fe oxide NPs | 50 ppm | <i>Vigna radiata</i> | Biomass enhanced | Dhoke <i>et al.</i> 2010 |
| MWCNTs | 50 and 200 µg.mL ⁻¹ | <i>L. esculantum</i> | Improved germination rate and seedling growth | Khodakovskaya <i>et al.</i> 2009 |
| Nanoanatase TiO ₂ | 0.25% | <i>S. oleracea</i> | Enzyme activity stimulation | Reddy <i>et al.</i> 2017 |
| Ce oxide NPs | 500, 1000, 2000, 4000 mg.L ⁻¹ | <i>G. max</i> , <i>Zea mays</i> , <i>Medicago sativa</i> | Significantly increased root and stem | Lin <i>et al.</i> 2007 |
| ZnO NPs | 500 mg.L ⁻¹ | <i>G. max</i> | Root growth increased | Lin <i>et al.</i> 2007 |
| ZnO NPs | 1.5 ppm | <i>C. arietinum</i> | Dry weight increase | Bilan <i>et al.</i> 2018 |
| ZnO NPs | 1000 ppm | <i>Arachis hypogea</i> | Root and stem growth increase, high yield | Rehman <i>et al.</i> 2018 |

(partial anaerobiosis) or anoxia (full anaerobiosis) in the soil and air is expelled from the soil pores (Gopinath *et al.*, 2014).

Water logging not only causes an oxygen deficiency, which is dissipated 104 times less in water than in air (Gopinath *et al.*, 2014), it also produces toxic compounds that inhibit growth and eventually cause the death of plants. Anoxia and hypoxia cause suppression of breathing, a state of energy deficiency, and an increase in genes associated with abscisic acid and ethylene synthesis. These are important strategies in adaptation to waterlogging (Phukan *et al.*, 2016). Two of the other adaptable strategies are the nodal root formation in the air-water interphase and the aeranchymatous cell developments in the root cortex to ease diffusion of oxygen (Nishiuchi *et al.*, 2012).

Thus, in the efforts to minimize these adverse effects using nanoparticles, it is important to know if the observed effect in plants is increasing water-logging tolerance or decreasing the harmful effects of water-logging (Ahmad *et al.*, 2019). The study with saffron, an aromatic and medicinal plant species (Phukan *et al.*, 2016), demonstrated a decrease in the root length, number of roots, root biomass caused and leaf biomass raise by water-logging stress. When Ag NPs at concentrations of 40-80 ppm was applied to saffron corms, the adverse effects of water retention stress were alleviated.

Nanotechnological applications have a potential to reduce the waterlogging stress in plants. Recently, a number of studies have evaluated nanoparticle-mediated effects on plants under different stresses, as shown in Table 2 (Fortina *et al.*, 2005).

Plants strategies to cope with water logging

Under water-logging conditions plant roots are damaged due to lack of O₂. Consequently, water-logging decreases gas exchange between the plant and the atmosphere. In fact, when plants do not receive enough oxygen for respiration, they form aerenchyma in their roots which acts as an oxygen reservoir (Ahmad *et al.*, 2019). Longitudinal diffusion of oxygen to the root apex could be increased by induction of a barrier to radial O₂ loss (ROL) that reduces oxygen loss to the environment (Fig 3, 4). Moreover, this barrier can block the movement of toxins such as reduced metal ions, and gases such as methane and carbon dioxide, from the soil to the roots (Thombre *et al.*, 2014). The most important adaptation to flooded conditions is the formation of aerenchyma. It can occur in roots and shoots of plant species such as corn and rice.

An aerenchyma formation in plants

The aerenchyma formation is significant for the functioning and survival of plants faced with waterlogging. It provides the transfer of oxygen and aeration of gases (*i.e.* CO₂, CH₄) from roots to shoots (Prathna *et al.*, 2011). Aerenchyma forms as a result of exposure to various stress factors such as waterlogging, nutrient deficiencies and mechanical impedance in corn roots. Under waterlogged conditions, ethylene can accumulate in submerged tissue, inducing

genes involved in the aerenchyma formation (Sebastian *et al.*, 2018). The aerenchyma could be providing a photosynthetic advantage by collecting carbon dioxide from root respiration and transferring it to the leaf intercellular spaces in various species (Saif *et al.*, 2014).

Aerenchyma can be generated by one of two mechanisms: (i) schizogeny, (ii) lysigeny (i) Schizogenous aerenchyma, that improves by extremely regulated cell separation and differential cell enlargement, which forms spaces between cells without causing death of cells (*e.g.* *Rumex palustris*) and (ii) while lysogenous aerenchyma, which is formed by programmed cell death (PCD), creating gas spaces in the plants root cortical region (Saif *et al.*, 2014); for example, it was observed in maize (Reddy *et al.*, 2017), rice (Gopinath *et al.*, 2014), and wheat (Verma *et al.*, 2018).

Aerenchyma can be created by both mechanisms in many species like duck potatoes (Husen and Siddiqi, 2016). While lysogenous aerenchyma occurs in the cortex of the roots, it can occur in the cortex and pith cavity of the stems (Khodakovskaya *et al.*, 2009). Under normal growth conditions, lysigenous aerenchyma in most wetland plants might be developed mainly in their roots, *e.g.*, in for example, common rush and rice. Its formation is enhanced when the soil is full with water. Lysigenous aerenchyma is stimulated during waterlogging in the dryland plants, such as corn (Gopinath *et al.*, 2014) and its formation could be further increased during waterlogging (Fig 3) (Srinivasan and Saraswathi, 2010).

During the formation of aerenchyma in the root of rice, cells in the mid-cortex die first and then cell death radially spreads to other cortical cells (Lin and Xing, 2007). The epidermis, endodermis, exodermis and stele could be unaffected, demonstrating that lysigenous aerenchyma formation took place *via* closely controlled mechanisms (Saif *et al.*, 2014). However, root lysogenic aerenchyma of non-wetland species (barley, corn, wheat, *etc.*) may not occur in well-drained soils, indicating that insufficient aeration may have a stimulating effect (Khodakovskaya *et al.*, 2009).

Signalling mechanism of lysigenous aerenchyma formation

In maize and rice, ethylene, a hydrocarbon that could be diffuse inside and outside of plant tissues from both exogenous and endogenous reservoirs and which is also a gaseous plant hormone, plays a key role in hypoxic stress (Husen and Siddiqi, 2016). Ethylene promotes lysogenic aerenchyma formation (Khodakovskaya *et al.*, 2009). Ethylene is simply produced from methionine and is first converted to S-adenosylmethionine (AdoMet) through Sadenosylmethionine synthase. AdoMet is then converted to 1-aminocyclopropane-1-carboxylate (ACC) by ACC synthase (ACS). ACC oxidase (ACO) generates ethylene via oxidizing ACC in a reaction which is also produces carbon dioxide (CO₂) and hydrogen cyanide (HCN), respectively. Ethylene as a plant hormone is concerned with regulating processes of cell death (Husen and Siddiqi, 2016). Several of the adaptive growth responses take place in response to

Table 2: Effects of nanomaterials on various abiotic stresses in plants including Water-logging stress.

| Abiotic stress | Nanomaterials | Concentration | Plants | Stress responses | Reference |
|---------------------|--------------------------------------|--|-----------------------------|--|---------------------------------|
| Waterlogging stress | Ag | 40, 80, 120 ppm | <i>Crocus sativus</i> | Inhibition of ethylene signal, supporting root growth | Ahmed <i>et al.</i> 2019 |
| | Ag | 40, 80, 120 ppm | <i>G. max</i> | Decreasing cytotoxic formation with the side effects of glycolysis products, enhancing the abundance of the stress-related protein, increasing seedling growth. | Ahmed <i>et al.</i> 2019 |
| | Al ₂ O ₃ | 80 ppm | <i>G. max</i> | Arrangement of cell death, energy metabolism and enhanced growth. | Ahmed <i>et al.</i> 2019 |
| | SiO ₂ | 25 mM | <i>L. esculentum</i> | Seed germination, dry weight and root length increased at low concentrations, while seed germination was restricted at high concentrations. | Husen and Siddiqi, 2016 |
| Salinity stress | SiO ₂ | 25 mM | <i>Ocimum basilicum</i> | Enhanced fresh-dry weight, photosynthetic pigment and proline amounts | Kumar <i>et al.</i> 2016 |
| | SiO ₂ | 25 mM | <i>Cucurbita pepo</i> | Increased seed germination, seedling growth, photosynthesis, antioxidant enzyme activities, decreased chlorophyll degradation, electrolyte leakage, MDA and H ₂ O ₂ levels, and oxidative damage | Siddiqui and Al-Whaibi, 2014 |
| | SiO ₂ | 25 mM | <i>Solanum lycopersicum</i> | Up-regulated the four salt stress genes and down-regulated the six genes which alleviated the salinity effect on seed germination, fresh weight and root length | Ansari <i>et al.</i> , 2019 |
| | ZnO-Fe ₃ O ₄ | 30, 60, 90 mg.L ⁻¹ | <i>M. peregrina</i> | Decreased in Na ⁺ and Cl ⁻ amounts; increased in N, P, K ⁺ , Ca ²⁺ , Mg ²⁺ , Fe, Zn, carbohydrates, total chlorophyll, carotenoids, crude protein, proline, enzymatic and non-enzymatic antioxidant amounts | Somasundaran <i>et al.</i> 2012 |
| Drought stress | ZnO | 2 g.L ⁻¹ | <i>Helianthus annuus</i> | Increased in growth, chlorophyll content, CO ₂ assimilation, Fv/Fm, sub-stomatal CO ₂ content, activities of some antioxidant enzyme, proline amount, Zn content and decreased Na ⁺ content in leaves | Torabian <i>et al.</i> 2014 |
| | Si | | <i>Sorghum bicolor</i> | Enhanced leaf dry weight, leaf area index, root-shoot dry chlorophyll content | Ahmed <i>et al.</i> 2019 |
| | SiO ₂ | 0, 10, 50 and 100 mg.L ⁻¹ | <i>Crataegus</i> sp. | Enhanced xylem water potential, MDA content and biomass, photosynthesis and stomatal conductivity, nonsignificant effect on chlorophyll and carotenoid amount | Ahmed <i>et al.</i> 2019 |
| | TiO ₂ | 0, 10, 100, and 500 mg. L ⁻¹ | <i>Linum usitatissimum</i> | Increased chlorophyll and carotenoid content, decreased H ₂ O ₂ and MDA content, improved flax growth and yield | Ahmed <i>et al.</i> 2019 |
| | | 0%, 0.01% and 0.03% | <i>O. basilicum</i> | Alleviated the adverse effects of drought | Manjunatha <i>et al.</i> 2017 |
| | | 0.01, 0.02, and 0.03% | <i>T. aestivum</i> | Enhanced starch and gluten content, yield and growth | Javad <i>et al.</i> 2018 |
| | TiO ₂ or SiO ₂ | 25, 50, 100, 200 ppm or 400, 800, 1600, 3200 ppm | <i>Gossypium hirsutum</i> | Increased total free amino acid, proline, total phenolic, total soluble protein contents, total antioxidant capacity, CAT-POX-SOD activities, total reducing power | Mazar <i>et al.</i> 2016 |

ethylene that is accumulated in under submerge water tissues (Reddy *et al.*, 2017). This accumulation yields a reduction in diffusion from the plant to the wrap around water and simultaneous stimulation of the biosynthesis of this hormone during stress conditions (Khodakovskaya *et al.*, 2009). The roots of rice form lysigenous aerenchyma even under well-ventilated conditions (Srinivasan and Saraswathi, 2010). Corn roots promote the expression of the biosynthetic mechanism that results in increased ethylene production under hypoxic conditions (Ahmad *et al.*, 2019). The process of programmed cell death (PCD), that appears in the corn roots during the lysigenous aerenchyma formation, seems to be regulated through ethylene (Husen and Siddiqi, 2016). Surprisingly, the hypoxic treatment sharply enhanced production of ethylene in maize roots within few hours, for example; in 3 h as compared to under aerobic conditions. Exposure of corn roots to ethylene action inhibitors, such as silver ions, or biosynthesis inhibitors such as aminooxyacetic acid, aminoethoxyvinylglycine, and cobalt chlorethylene prevents the formation of aerenchyma in the hypoxic situation (Ahmad *et al.*, 2019). The 1-methylcyclopropene use, an ethylene inhibitor, in corn roots completely stops the formation of aerenchyma under hypoxic states (Husen and Siddiqi, 2016).

Lysigenous aerenchyma formation in the rice root could be enhanced more via ethylene treatment under aerated conditions, however, a reduction through application with an ethylene perception inhibitor, for example; Ag ions below stagnant (0.1% agar) deoxygenated a condition that mimics anoxic conditions (Husen and Siddiqi, 2016). In these days ethylene has been found to increase aerenchyma formation of root in a rice variety which is known as Calrose (Villagarcia *et al.*, 2012).

Cell wall degradation during lysigenous aerenchyma formation

Although there are many physiological studies on lysigenous aerenchyma formation, there is very little literature on the

genes that make for this formation. of late a study done by Rajhi *et al.* (2014) in maize roots exposed a gene related to the lysigenous aerenchyma formation by using a microarray investigation together with a laser microdissection technique. It was reported that under waterlogged conditions, calcium depending signalling genes encoding those are potentially known as calcineurin and calmodulin-like proteins was more modulated and simultaneously the expression levels of these two proteins were more prominent in the cortical cells, as compared to the stelar cells of roots of maize (Husen and Siddiqi, 2016). Interestingly, waterlogging also stimulates the expression of genes associated with the cell wall. Stimulation of the expressions of Ca^{2+} signalling and cell wall alteration associated genes is supposed to be inhibited *via* the treatment with 1-methylcyclopropene. These findings confirm the mechanisms of ethylene-arbitrated lysigenous aerenchyma formation (Fig 3) (Prathna *et al.*, 2011).

Radial oxygen loss (rol) barrier formation

During waterlogging conditions, internal aeration is supposed to be very essential for the root growth and development of plants. Moreover, in some wetland species a structural barrier that hinders O_2 outflow from the roots, basal part is known as a radial oxygen loss barrier (Prathna *et al.*, 2011). This radial oxygen loss barrier sharply reduces the oxygen-transported loss through the aerenchyma to the root tips and modifies root growth into anoxic soil. Interestingly, a few plant roots successfully develop the radial oxygen loss barrier during waterlogging conditions (Ahmad *et al.*, 2017). Moreover, the roots of some wetland plants may comprise well-developed aerenchyma that generally maintains a low resistance pathway for oxygen diffusion from the shoots to the roots (Nishiuchi *et al.*, 2012). Interestingly, a few wetland species also can form a barrier to radial oxygen loss (Phukan *et al.*, 2016). This radial oxygen loss barrier forms from the root basal parts and ultimately suppresses the oxygen transported loss through aerenchyma to the root apex.

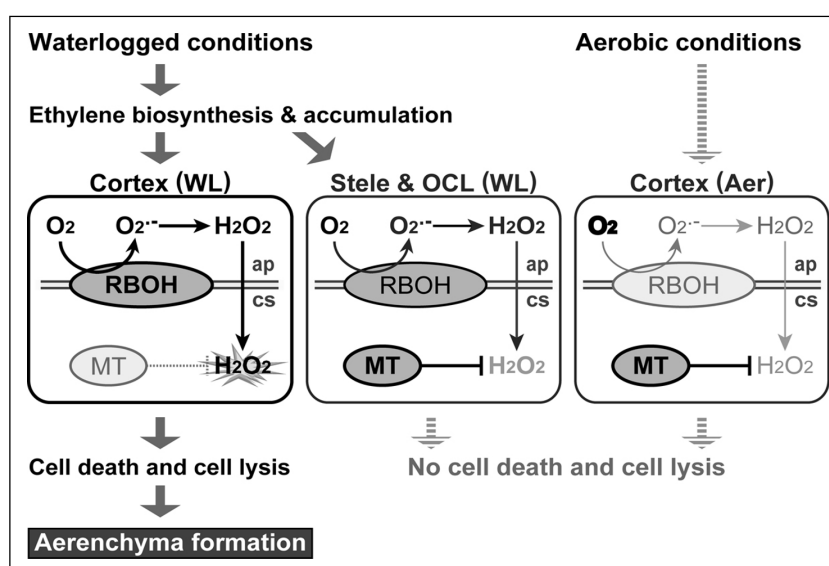


Fig 3: Lysigenous aerenchyma formation model.

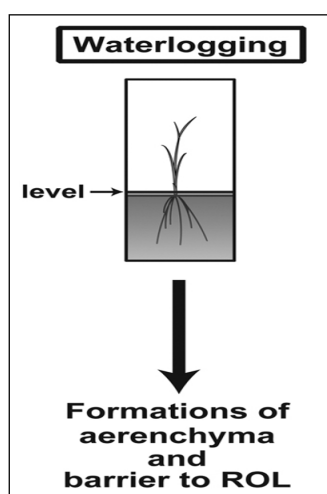


Fig 4: Adaptation strategies for excessive water (waterlogging) stress in plants.

CONCLUSIONS AND PROSPECTS

Globally, the sustainability of food supply and safety faces two major challenges: increasing human populations and the climate change, particularly affecting water availability.

Waterlogging, defined as the soil condition where excess water limits the gas diffusion, is one such environmental stress causing substantial yield losses. Waterlogging conditions hinder the internal aeration necessary for the growth and development of roots in plants. Although different mechanisms including aerenchyma formation and a barrier to radial oxygen loss have been discussed, more work also has to be done on the chemical and anatomical nature of the barrier to ROL barrier versus nutrient and water uptake, respectively.

In recent years, nanobiotechnology has been gaining momentum as a possible means for enhancing crop yields and mitigating the adverse effects of various environmental stresses. However, it is imperative to elucidate the exact mechanisms of the interactions of NPs with plants at both the molecular, genetic and cellular levels, so that these aforementioned favourable effects of nanoparticles can be fully exploited. Rigorous studies are required to understand the molecular, biochemical, and physiological mechanisms of plants in response to NP treatment as well as their influence on the gene expression regulation in plants regarding stress management, including the stress of waterlogging.

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Author contributions

The first draft of the manuscript was designed and written by Mohd Kafeel Ahmad Ansari and all authors commented and improved the initial versions of the manuscript. All authors read and approved the final manuscript.

Statements and Declarations

Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Conflict of interest

The authors declare no potential conflict of interest related to this study.

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