

Fostering nanoscience's strategies: A new frontier in sustainable crop improvement for abiotic stress tolerance

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ABSTRACT

Advanced nano-engineering is a convenient technology to attain food security and ensure sustainable agricultural yield and productivity. In addition to addressing the yield barrier, the application of nanoscience emphasizes its potential through innovations such as precision farming, site-targeted delivery of agrochemicals, disease control, and mitigation of environmental stresses in plants. Abiotic stresses negatively influence growth and yield of plants by affecting the physiological, biochemical, and molecular aspects of plants. As seen in recent years, such precedents in plants can be significantly alleviated through the implementation of nanoparticles. The application of nanoparticles helps in understanding the appropriate mechanisms in plants against abiotic stresses and enhances those responses more effectively. Biochemical and physiological adaptations stimulated by nanoparticles include the activation of the antioxidative defense system, stress regulatory gene expressions, stimulation of crucial biochemical pathways, and hormonal regulations. Considering the potential advantages of nanomaterials to date, their full implementation is yet to be a reality in the agricultural sector, largely limited due to concerns regarding the uptake, translocation, bioavailability, and eco-toxicity of nanoparticles. Understanding the underlying mechanisms and responses induced by nanoparticles through molecular approaches is critical in assessing nanomaterials' biological potential. The present review addresses the possible scope of nanotechnology to counter abiotic stress in economically important crops, and their influence on development, growth, absorption, and translocation in plants. Here, an attempt is made to provide an elucidative framework on recent findings related to nanoparticle-induced stress tolerance in plants through a comprehensive insight into molecular mechanisms and biochemical responses that may help to meet the need for adaptive measures in crops during abiotic stress conditions.

1. Introduction

1.1. Agriculture: Modern Strategies

Due to the indispensable role of agriculture in fulfilling global food demand, it is understandable that it is regarded as the foundation of a nation's expanding economy. But the concurrent adversities due to increasing global temperature, shrinkage of cultivable lands, excessive usage of fertilizers and pesticides, attack by phytopathogens, and several other environmental factors disadvantageously influence the agricultural sector (Baweja et al., 2020). Apart from these, one daunting challenge is meeting the nutrition requirements of the rising population which demands an elevation in agricultural productivity by 60–100% by the next 30 years (Monteiro et al., 2021). In a recent report by the United Nations, the world population is projected to reach 8.5 billion by

2030 and 9.7 billion by 2050, a 26% increase from the current population with India being projected to be the most populous country by 2023 (United Nations, Department of Economic and Social Affairs, Population Division, 2022). Thus, these situations advocate an urgent need for better food security and increased crop production which are mostly reliant on ecological biodiversity and the advent of innovative techniques to counter the issues. Green plants in general including those in the agricultural sector remain exposed to numerous abiotic stresses throughout their lives. Based on the phase of development, the duration, and the severity of stress, plants have developed an intrinsic well-concerted adaptive response at the physiological, morphological, and biochemical levels to deal with different stresses (Rouached et al., 2015). Various metabolic and biochemical pathways are involved in response and adaptation such as polyamines and some signaling pathways against key abiotic stresses (Rangan et al., 2014). But most

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frequently, these regulations fail to effectively counter the stresses imposed by an unpredictable climate, water deficit, heavy metal toxicity, and salinity stress, which severely hamper plant yield and productivity (Salvi et al., 2021).

Various agronomic practices such as the use of agrochemicals, and plant breeding along with various technological advancements have brought about significant improvisation in the agricultural sector in dealing with different stresses (Tariq et al., 2021). Genetic manipulation of stress signaling pathways has been broadly investigated to elevate plant productivity (Matsui et al., 2014; Mazzucotelli et al., 2008). Genetic modification of plants has been implemented to increase yield and productivity while increasing resilience towards various biotic and abiotic stresses. Traditional genetic engineering is done mostly via the tissue culture technique, which is time-consuming, and not an easily feasible process, particularly for plants like cotton. While pollen transformation by different physical methods is an efficient method in comparison, problems such as a lower success rate and loss of pollen viability remain prevalent (Zhang et al., 2019). Additionally, genetically modified crops have concerns regarding food security and need a longer time to be tested and approved for commercial implementation, particularly in India (Kadam et al., 2014).

In the current scenario, applying chemical fertilizers is extensively practiced for increased crop yield and defense against pathogen attacks. However, the excessive and non-targeted use of fertilizers negatively impacts soil-nutrient homeostasis and ends up further contributing to the elevation of global temperatures (Rodrigues et al., 2017; Chugh et al., 2021). Less than half of the fertilizer is utilized by the plants as most macronutrients are insoluble in soil (Cole et al., 2016). A significant quantity of these agrochemicals as a result over-accumulates in the soil and leaches unto water bodies which incur harmful consequences on related biota, soil health, and widespread economic losses (Sharma et al., 2019). Hence, sustainable approaches with precision-based innovations need to intervene for better nutrient efficiency and improve the functional value of plants.

1.2. Nanotechnology: background and present scenario

Nanotechnology is the interdisciplinary science that deals with matters at the nanoscale, known as nanoparticles, which are defined as clusters of atoms or molecules with sizes in the 1–100 nm range (Potocnik, 2011). Over the last decade, several studies have been conducted emphasizing the implementation of nanotechnology in plant growth and development for advancement in the agriculture division (Shang et al., 2019). Nanotechnology, now considered the next big thing, was conceptualized in a talk titled “There’s Plenty of Room at the Bottom” by physicist Richard Feynman in 1959 and much later defined by Prof. Norio Taniguchi (Taniguchi, 1974). The concept only became practical with the advent of the scanning tunneling microscope in 1981. By the sheer quality of their unique size, nanoparticles possess remarkable characteristics that differ from the laws of applied quantum physics making them suitable to be tuned for wider applications (Maurice, Hochella, 2008). Unique surface functionalization, surface-to-volume ratio, porosity, higher zeta potential, high surface tension, hydrophobicity, and hydrophilicity allow nanoparticles to exhibit increased reactivity, controlled kinetics, and highly targeted site-specific applications (Solanki et al., 2015; Saxena et al., 2020). Nanotechnology offers innovative solutions to overcome the adversities including abiotic stresses faced in the agri-food sector with the ability to enhance efficiency in nutrient management, disease prevention, stress tolerance, and improvement of key physiological properties (Khan et al., 2022). Recently, nanomaterials have been highly used in food packaging and smart delivery systems for agrochemicals (Shang et al., 2019). The unique properties of nanoparticles can remarkably enhance the effectiveness and sensitivity of biosensors which can help against pathogen attacks by viruses and infectious particles and in monitoring plant growth and soil condition (Chen et al., 2016).

1.3. Agriculture in the age of nanotechnology

Modern agriculture has adopted a sustainable approach to transforming into precision farming using cutting-edge nanomaterials. For example, the nanoencapsulation used as an alternative to fertilizers is based on the slow and controlled release of active compounds over a period of time to achieve maximum biological competency without any disadvantages to the surrounding ecosystem or loss due to microbial degradation (Ghormade et al., 2011). In genetic engineering, nanoparticle-assisted delivery systems have been used to create novel crop varieties resilient to insects (Backgrounder, 2010). One of the primary objectives of nanotechnology is to improve plant traits against various biotic and abiotic stresses (González Guzmán et al., 2022). Improved photosynthetic efficiency, high chlorophyll content, increased root surface area, stomatal efficiency, enhanced antioxidant enzymatic activity, immobilization, and co-precipitation of toxic metal ions all these enhance the adaptations by the plant to withstand the abiotic stresses (Liang et al., 2007). Nanoparticles, due to their small size, have complex and uncertain interactions with different biomolecules and ionic particulates which is proposed to provide them the properties to combat adversities to the plants while improving their growth and ensuring protection (Khan et al., 2019). As these peculiar characteristics of nanoparticles are gaining worldwide attention faster, there need to be comprehensive risk assessments including cyto- and phytotoxicity studies for acceptance and application in the agricultural sector (Barrena et al., 2009). The current review is concentrated on the potential of nanoparticles, the mechanisms associated with them, and their influence on plants in mitigating different abiotic stresses for sustainable agriculture practices.

2. Source, synthesis, and delivery

With the emergence of nanotechnology in recent few years, nanoparticles, and their immense potential due to some unique properties have been realized through their broad spectrum of applications in several fields (Mitchell et al., 2021). However, nanoparticles are not novel to nature as important constituents of the atmosphere, soils, oceans, and biota are comprised of these. Combustion products in forest fires, ocean spray, volcanic ash, and cosmic dust often lead to the natural origin of nanoparticles (Hochella, 2008). Engineered nanoparticles which are being increasingly synthesized through bottom-up and bottom-down approaches are primarily influenced by their controllable size-shape, bioactivity, and bioavailability. Fundamentally, the synthesis of metal and metal oxide nanoparticles require the reduction of metal salts by using reducing agents derived from various sources. For example, over the last few years, microbes like bacteria and fungi have been shown to provide extracellular and intracellular means of metal nanoparticle synthesis with the former getting more attention for its lack of need for downstream processing. An array of protocols using bacterial biomass, supernatant, and derived components for biological nanoparticle synthesis have been elucidated in recent literature (Singh et al., 2016). Microorganisms possessing various reductase enzymes can aggregate and detoxify heavy metals via the reduction of metal salts to MNPs with lesser polydispersity and narrow size distribution (Gadd and Griffiths, 1977). While the synthesis of nanoparticles using microbes provides an alternative to conventional pathways, green synthesis using plant products has been proving to be increasingly advantageous in comparison due to the presence of broad variability of biomolecules including proteins, effective enzymes, and secondary phytochemicals, while using water, as the reducing medium (Singh et al., 2016). Moreover, the selective and progressive adsorption of biomolecules by nanoparticles through contact with complex biological fluids forms a layer that’s able to interact with biological systems with added efficiency over bare phyto-NPs (Monopoli et al., 2012). Influential factors like temperature, time, pH, and concentration significantly affect the physical properties of nanoparticles (Patra, Baek,

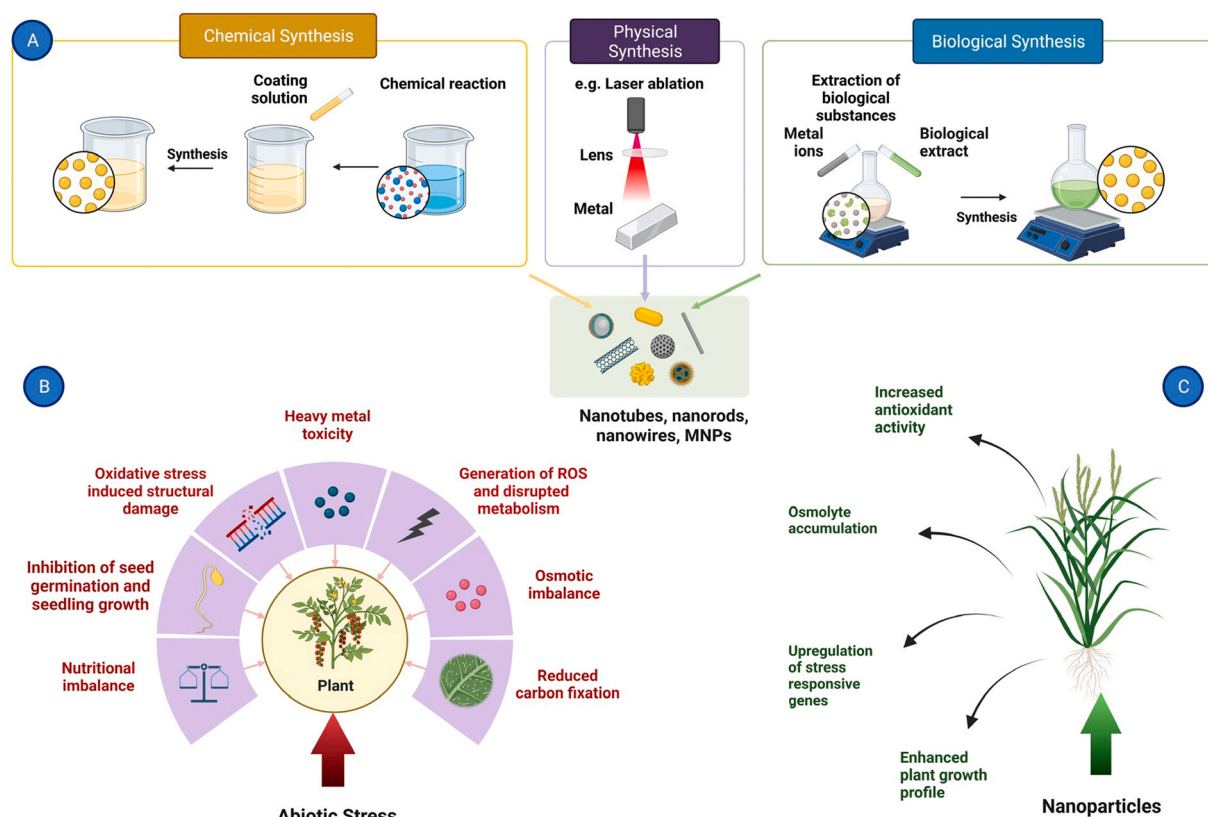


Fig. 1. General impact of nanoparticles to improve the alleviating ability of plants against different stress conditions. A. Different routes of nanoparticle synthesis B. Abiotic stress-induced unfavorable impacts on plant C. Improved physiological and morphological features in the plant through the application of nanoparticles Created with BioRender.com.

2014). Changes in pH can cause alteration in morphology and yield of NPs as it leads to variation in charge of plant secondary metabolites, which potentially impact both their reduction and binding ability during the synthesis of nanoparticles (Dikshit et al., 2021). Similarly, at elevated temperatures, the enzymes accountable for nanoparticle synthesis may be more active (Sanket, Das, 2021). (Fig. 1).

Plant micro-morphology and physiological nature are critical for effective nanoparticle delivery inside plant tissues. In general, nanoparticles can be introduced through plant surfaces, e.g., leaf, root, and stem (Horejs, 2021). Although the entry of NPs into the conductive system (xylem, phloem) is decided based on the complex structural features of the cuticle, epidermis, and endodermis (Ali et al., 2021b). The penetration through leaves occurs through a stomatal opening which based on the aperture allows NP entry while open, even though their response to be either closed or open relies on factors such as CO₂ concentrations, light intensity, moisture, temperature, and plant-dependent position of stomata (Su et al., 2019b). In leaves, cuticle is present as the primary barrier, preventing nanoparticles to a limit of less than 5 nm in size. While NPs bigger than 10 nm traverse via stomata, and their translocation is believed to be happening via symplastic and apoplastic routes (Ali et al., 2021a). Another point of entry for NP uptake into the plant system is through the roots. Root endodermis, preferably passage cells are pivotal to NP penetration and transport inside the plant. Moreover, the site of emergence for secondary roots, along with disrupted roots, might serve as operative nanoparticle entry points (Su et al., 2019c). In the vascular system the sap flow rate occurring in the xylem, phloem, cell wall interstices, and hydrostatic pressure gradient, created in narrow-sized flow channels, determine the transport velocity of nanoparticles to long distant sites inside the plant body (Wu and Li, 2022).

3. Uptake and translocation

While foliar and root application are known to be the most common methods for nanoparticle implementation, plant barrier tissues, the immediate surroundings (e.g., the rhizosphere around the roots, falling of rainwater on leaves) hamper the uptake of nanoparticles, leaving most of the applied NPs to be deposited on the outer layer (Su et al., 2019a). Aside from the direct correlation of NP's size to its absorption which makes its penetration feasible through stomata or cell wall pores, their size also defines their successive translocation into cells or organelles, bioaccumulation, toxicity, and kinetics of translocation (Tripathi et al., 2017a). The waxy cuticle is reported as the primary obstacle against NPs moving into substrate tissue as in higher plants, leaves are guarded against unregulated exchange of other solutes and loss of water (Pollard et al., 2008). The pathways available for the absorption of solutes across the cuticle are namely the lipophilic pathway for non-polar solutes where they get across via permeation and diffusion while solutes polar in nature travel over aqueous pores in the hydrophilic pathway with size in the range of 0.6–4.8 nm (Yashveer et al., 2022). However, a number of studies have informed foliar uptake and aggregation of NPs greater than 5 nm. The transfer of NPs in the range of 10–50 nm is favored through the symplastic route, which is interconnected by adjacent cell plasmodesmata (Shukla et al., 2016). The property of apparent negative charge of cell wall, makes the charge on nanoparticles, to be a direct influence on the attachment of NP to the cell surface. Following the particle size and charge, the hydrophobicity on the plant surface has a crucial part in uptake and translocation process (Kaphle et al., 2017). Furthermore, hydrophobic NPs have shown excellent infiltration across the cuticle (Lv et al., 2015), though it is unclear whether they effectively translocate beyond the cuticle

Besides the formulation of NPs, another crucial aspect that has an impact on uptake is the concentration of NPs. High NP concentrations may result in to accumulation of NPs on the surface of plant structures, limiting their absorption and translocation (Rajput et al., 2020). NPs coming through the stomatal pathway into the leaf apoplast may undertake long distance translocation through the endothelial system. Internalized NPs are translocated alongside with the flow of sugar via phloem sieve tubes. Thus, nanoparticles can travel bidirectionally and aggregate in various organs to varying extents where those structures act as effective sinks for the sap. Whereas, due to the non-circulatory nature of the vascular system, the particles moving downstream in the phloem cannot circulate back to their initial location via xylem (Corredor et al., 2009). Therefore, for the movement of nanoparticles from leaves to root, the phloem pathway is the only likely route in the absorption of NPs. In a study, authors investigated the foliar absorption of four metal oxide NPs in watermelon in the 24–47 nm range, they observed smaller NPs utilize the stomatal pathway to move into watermelon leaves and the finding of metal in the roots and shoots implied that NPs translocated first to shoot and eventually into the root via the phloem sieve tubes (Wang et al., 2013). The stomatal abundance is another factor that can cause higher and more efficient uptake of nanoparticles relying on the disparity in the stomatal density, their position, and the environmental factors governing the opening of these pores (Su et al., 2019a)

Nanoparticles absorbed through the root surface, prior to moving into the endodermis, traverse through epidermis, exodermis, and even the cortex. Passive integration through the apoplast of the endodermis must occur prior to nanoparticles reaching the stele (Judy, 2013). According to reports, the small NPs (3–5 nm range) can directly cross through the epidermis to enter into roots, as well as penetrate the roots using capillary forces and osmotic pressure, and due to the semi-permeable nature and smaller pores, constrain the large NPs (Mittal et al., 2020). A few NPs have the ability to induce pores in epidermis of the cell wall, facilitating the entry (Lin and Xing, 2008; Judy, 2013). The Casparian strip is impervious to both water and dissolved minerals as well as metal NPs, acting as the ultimate apoplastic-barrier between the outside and the xylem-phloem system (Aubert et al., 2012). However, under certain circumstances, NPs can enter the vascular tissues by avoiding the casparian strip through lateral root junction where the casparian strip is discontinued because lateral roots can pierce through the epidermal layer during differentiation and reach the exterior of vascular cylinder (Peng et al., 2015). Experimental evidence of this route reported accumulation of 30 nm ZnO NPs inside the associated xylem cylinder and at the lateral root junction of corn plant with the aid of μ -XRF, TEM, and fluorescence monitoring (Lv et al., 2015). Additionally, a recent analysis revealed that CeO₂-NPs penetrated roots of kidney beans at the point of secondary root emergence through openings in the casparian strip (Majumdar et al., 2014). Consequently, the lateral root formation induces new absorptive surfaces, providing metal NPs with potential pathways into the stele. NPs that are not internalized get aggregated on the Casparian strip, while NPs that have entered the xylem are transported to the shoots and then returned through the phloem (Zhang et al., 2011).

Particle size, morphology, surface functionalization, plant species, phase of growth, root integrity, and exposure conditions are some of the variables that affect the uptake of nanoparticles in plant (Lv et al., 2019a). In addition, the basic structure of nanoparticles is useful in assessing their influence on NP absorption, transport, and accumulation within plant parts (Larue et al., 2012). Surface charge is an additional factor that influences the absorption and translocation of nanoparticles in roots. Studies have demonstrated the accumulation of positively charged nanoparticles while negatively charged nanoparticles could easily translocate into vascular tissues (Lv et al., 2019b). The formation of nano-coronas on the surfaces of positively charged NPs by coatings of root exudates (negatively charged) can sometimes alter the surface charges of the NPs which can facilitate their translocation through the

vascular system like negatively charged NPs (Avellan et al., 2017). Another important factor is that the sizes of NPs in the rhizosphere differ greatly from their original sizes, as well as being highly dynamic and widely distributed (Lv et al., 2019c). The size, surface charge, and structure of NPs are further influenced by the different root exudates that are secreted by various plants at various developmental stages. As a result, it is tough to predict how plant species and stages of growth will affect NP uptake by roots (Keller et al., 2017). Whereas, as root damage increases, the physiological barrier against NPs becomes vulnerable and NPs may more easily penetrate the root through transpiration and other metabolic functions (Wang et al., 2013). According to the literature, endocytosis is the most feasible transmembrane pathway for NPs (Manzanares and Ceña, 2020). Plant cell endocytosis is comparatively less common than animal cell. However, endocytosis pathways are implicated in recent reports on NP internalization. Onelli et al. (2008) ascertained the connection of both clathrin-independent and clathrin-dependent pathways in the engulfment of AuNPs into protoplasts of tobacco plants. It's imperative to introduce NPs with higher stability to encounter the dynamic physiological environments. (Fig. 2).

4. Role of nanoparticles in growth and development of plant

4.1. Role of nanoparticles on germination of seed

Nanoparticles can boost the quality and yield of the crop when given at optimum concentration to the plant (Kole et al., 2013). NPs affect plant growth by imparting beneficial impacts of NPs on germination of seed, plant development and yield, stability of plant growth regulators (PGR), and resistance against disease (Ahmad et al., 2022). Plant production and development are based on seed germination. Natural germination requires patience and yield is not particularly high. However, treated seeds have achieved great germination rates, making nanotechnology a powerful tool to enhance both yield and germination (Shukla et al., 2019). The exact mechanism by which the germination rate is improved using nanoparticle treatments is still unknown. It may be ascribed that water retention and seed absorption are improved by nanoparticle treatments that dramatically increase seed germination and plant growth (Khodakovskaya et al., 2009). In an experiment, when tomato seeds were incubated for two days in a medium containing carbon nanotube, the moisture content of the seeds increased by 19% compared to untreated seeds. These results suggested that C-nanotubes might be responsible for creating microspheres (Sanborn et al. 2018) and aquaporins in the seed coverings that favor seed germination (Khodakovskaya et al., 2009). Zheng et al. (2005) demonstrated that nano TiO₂ enhanced the uptake of water by seed and thus accelerated spinach (*Spinacia oleracea*) seed germination. Feizi et al. (2011) analyzed the impacts of nTiO₂ and bulk TiO₂ on seedling growth and seed germination of wheat. The experimental findings suggested that wheat seeds at 10 ppm nano-sized TiO₂ concentration showed 0.89 days mean germination time compared to 1.35 days in nontreated seeds. Bulk TiO₂ at the same concentration, on the other hand had no effect on mean generation time. Bala et al. (2014) mentioned the potency of biocompatible and biodegradable HA (hydroxyapatite) nanorods on seed vitality chickpea plants. The maximum plant growth rate (more than twice that of the control) was seen at 1 mg/mL hydroxyapatite nanorods. The seed germination rate was also improved in the presence of HAP nanorods. Wheat and barley plants treated with Fe₃O₄ nanoparticles at the seedling stage demonstrated significantly high germination rates, in addition to longer root and coleoptile lengths (Serpoush et al., 2022). Kavitha et al. (2022) studied the influence of biosynthesized copper oxide NPs on the germination rate, seedling length, and mitotic index of *Vigna radiata* (green gram), and *Trigonella foenum-graecum* (fenugreek). Seed germination in both plants demonstrated no significant difference at lower concentrations but observable difference on upper concentrations (100–500 mg/L). This shows that the seed germination was not impacted by low CuO-NP concentrations. The

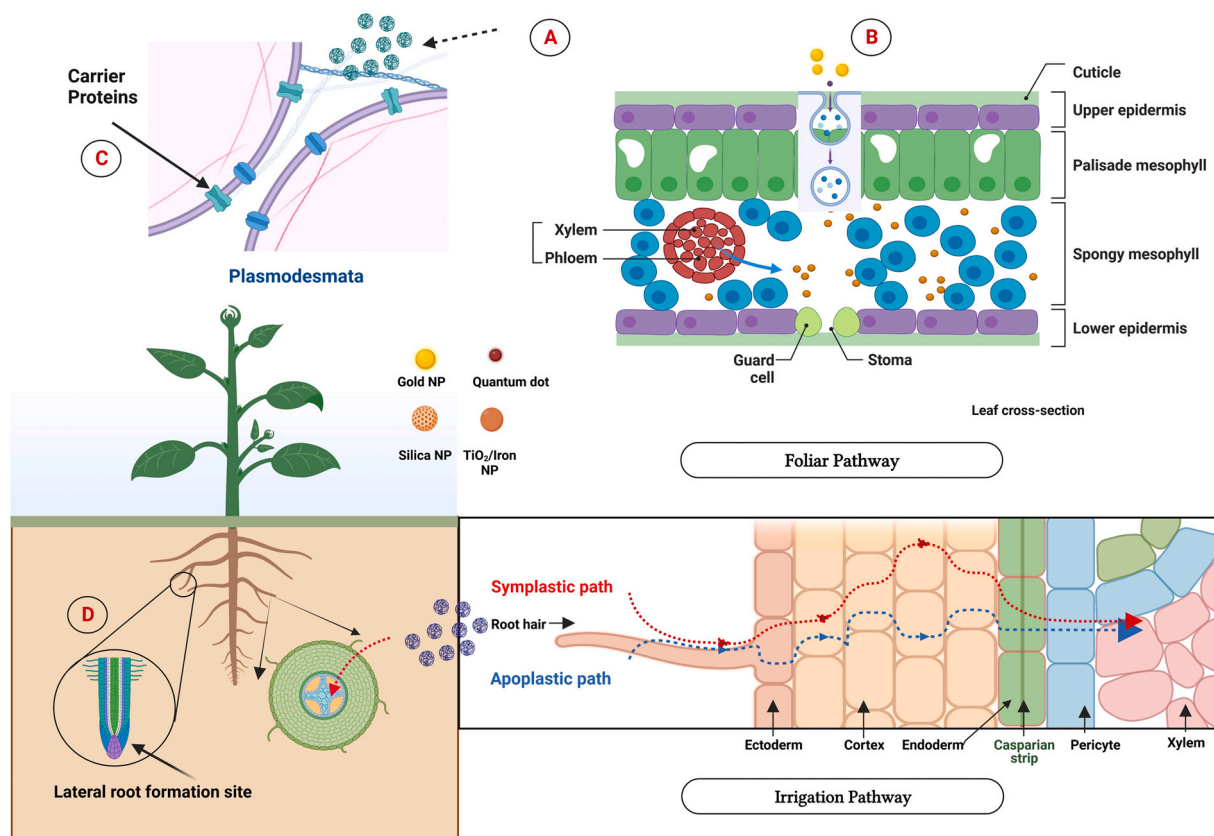


Fig. 2. Schematic representation of possible nanoparticle translocation route via root and foliar pathways; A) through plasmodesmata B) Through cuticle via pore formation C) by carrier proteins D) through the passage formed during lateral root formation Created with **BioRender.com**.

results suggest that higher CuO-NP concentrations have detrimental effects on the germination and cytophysiology of both plants. Mung beans, chickpeas, barley, and wheat seed germination studies in the presence of natural biomass and carbon-dots derived from plastic waste revealed a dose-responsive impact (250–5000 mg/l), such as lengthening of the root and coleoptile. The synthesized C-dots, being small in size and having a high surface area, offer better seed coat penetration and more nutritious content to plants (Chauhan et al. 2022).

4.2. Role of nanoparticles on development and yield of plant

The principle of little investment and the highest possible revenue and quality of the product underlies the implementation of nanobiotechnology in the agriculture sector (Cicek and Nadaroglu, 2015). Sheykhabglou et al. (2010) looked into the effect of nFe₃O₄ on the quality and yield of soybeans. They concluded from their research that nano-iron oxide at 0.75 g/L concentration increased the dry weight of the leaf and pod and that 0.5 g/L nano-iron oxide produced the maximum crop yield, which was 48% higher than the control. In a study, Wang et al. (2012) investigated stem length, root growth, seed germination, and impacts on plant biomass to assess the effect of oxidized multi-walled C-nanotubes (o-MWCNTs) on wheat plant physiology. According to the study, after being exposed to the o-MWCNT medium for a week, the plants showed faster root growth and increased biomass than the control samples. The cell length of the root region was increased by up to 1.4 times for the o-MWCNT medium (80 mg/mL) treated wheat seedlings and treatment significantly increased dehydrogenase activity in the seedlings. These results imply that o-MWCNT may dramatically boost dehydrogenase activity and stimulate cell elongation in the root system, leading to rapid root growth and greater biomass generation. Zn is a micronutrient that modulates the gene expression implicated in carbohydrate metabolism, plant stress tolerance,

and the synthesis of proteins, auxin, chlorophyll, and pollen (Hänsch and Mendel, 2009). Zn deficiency leads to growth inhibition, leaf chlorosis, and yield reduction in major plants (Broadley et al., 2007). The application of ZnNPs to promote plant yield and development has proved to be an effective strategy in many crops, e.g., *Pisum sativum* L. (Ahmed et al., 2022), *Triticum aestivum* L. (Lalarukh et al., 2022), chickpea mung and *Cicer arietinum* (Dhoke et al., 2011). ZnO nanoparticles synthesized through a green synthesis approach using leaf extract of *Vernonia cinerea* exhibited positive effects on the morphology and physiology of tomato seedlings at the recommended 50 mg/L dose concentration (Azim et al., 2022). ZnO nanoparticles are converted into Zn²⁺ ions inside the plant cell, which regulate carbonic anhydrase activity for CO₂ fixation and serve as a cofactor for catalase and SOD to shield the plant from oxidative damage (Raliya et al. 2016). Foliar applications of (Cu)-, (Fe)-, and (N)-doped TiO₂-NPs on cowpea (*Vigna unguiculata*) as nano fertilizer were observed. In response to treatments, morphological investigations found appreciable lengthening of the plant and increments in fresh and dry weights. Growth-stimulating hormone and photosynthetic pigment content built up, whereas lipid peroxidation and hydrogen peroxide levels declined. In contrast to soluble carbohydrates, the number of amino acids and soluble proteins improved in the treated crops. Additionally, treated cowpea plants contained more nitrogen, phosphate, and potassium compared to untreated plants (Kamal and Mogazy, 2021). TiO₂ nanoparticles prepared by green synthesis when applied in combination with calcium phosphate in wheat plants exhibited positive physiochemical attributes along with high biomass (Mustafa et al., 2021). The combination accelerated the antioxidant enzyme activities and the uptake of nutrients by plants ultimately resulting in their growth. Similarly, TiO₂ nanoparticles together with SiO₂ enhanced nitrate reductase activity to improve nitrogen absorption ability and water uptake by crops (Rico et al., 2013). TiO₂-NPs have been found to encourage chloroplast activity,

chlorophyll, and carotene synthesis resulting in the growth and development of plants. (Xuming et al., 2008). Copper NPs priming maize plants displayed higher yield as well as growth (van Nguyen et al., 2021b).

4.3. Role of nanoparticles on stability of plant growth regulators

Plant growth regulators (PGRs) are hormones that are crucial for boosting crop quality and productivity in agriculture (Rademacher, 2015). Auxin, gibberellins, cytokinin, and ethylene are among the most common natural and synthetic PGRs (Pereira et al., 2017). In various stages of plant growth, these substances are employed in low concentrations to operate at the cellular level. PGRs' deterioration, when exposed to external variables like light and heat, is the main barrier to their use. PGR/nanomaterial combinations have been shown to be more stable and environmentally friendly (Grillo et al., 2016). Nanoparticles may regulate the biosynthesis or signaling pathway of a particular plant hormone (Verma et al., 2016; Rasool, 2022). However, the NP-mediated plant development response relies on various parameters, including the type of nanoparticle, plant species, and the environmental factors (Tripathi et al., 2022). Chitosan nanoparticles containing thiamine stimulated IAA production and were used as a growth stimulator in chickpea seedlings (Muthukrishnan et al., 2019). Chandra et al. (2015) observed that chitosan nanoparticle application increased the concentration of nitric oxide (NO), a crucial signaling molecule implicated in plant development and defense. Copper oxide (CuO) nanoparticles at 75 and 150 mg/L induced positive effects on nutritional quality, yield, and auxin content in *Oryza sativa* L. and weedy grains (Deng et al. 2022). Indole acetic acid applied in combination with AgNPs improved the growth of *Daucus carota* L. (Faiz et al. 2022). To boost the bioavailability and effectiveness of auxin for higher agricultural yields and nutritional quality, Korpayev et al. (2021) applied silver and chitosan nanoparticles. There are reports on the advancement of nanocarrier frameworks for the controlled and stable release of plant growth hormones like gibberellic acid (Pereira et al., 2017; Yang et al., 2018), nitric oxide (Oliveira et al., 2016), brassinosteroid (Quiñones et al., 2010).

4.4. Role of nanoparticles on resistance against plant diseases

Plant pathogens, ranging from the simplest viroid to more diverse pathogens such as bacteria, fungi, nematodes, and oomycetes, induce a number of diseases in plants and are primary factors of substantial agriculture loss around the world (Syed Ab Rahman et al. 2018; Kamle et al. 2020). In addition to providing nutrients to plants, nanoparticles could also be effective against most of pathogenic micro-organisms. Thus, their application could play a dual role in increasing agricultural productivity via increasing resistance to the disease. Rexlin et al. (2022) addressed the problem of low agricultural productivity by employing biocompatible, comparatively non-toxic, and biodegradable ZnO NPs to enhance the quality and yield of the cluster bean seeds and pods. ZnO NPs treated the Zn deficiency in plants and exhibited exceptional diverse antibacterial and antifungal activity which is evident from the literature that reactive oxygen species and Zn ions released from ZnO NPs inactivate bacterial the cell wall and possess high antimicrobial activity (Rexlin et al., 2022; Kamaruzaman et al., 2022). In studies on tomato, carrot, and *Phalaenopsis* orchids, it has been found that silica (Si), promotes development and physical resistance in plants. (Vendrame et al., 2010; Andrade et al., 2013; Elsherbiny and Taher, 2018). The epidermal accumulation of silica may change cell wall integrity or increase the expression of disease-resistant genes in plants (Sukma et al. 2017). The interplay of SiNPs with the cell wall develops an extra layer of cuticle, which prevents pathogen entry inside the plant cell and mediates disease resistance in varied crops (Asgari et al., 2018; Goswami et al., 2022). El-Shetehy et al. (2020) showed that SiO₂ NPs induced dose-dependent acquired resistance in *Arabidopsis* plants.

Copper nanoparticles were found effective in the treatment of *Fusarium* wilt and had a positive influence on growth in tomato plants. The copper nanoparticles, in particular functioned as fungicides at a 0.5 mg/mL concentration. The plant growth was promoted as Cu-NPS acted as a source of micronutrients in cases of soil copper deficiency and principally raised total chlorophyll in the plant (Lopez-Lima et al., 2021). The management of plant diseases today makes extensive use of nano-copper and silicon (Singh et al., 2021). The tolerance of tomato plants against the *C. michiganensis* bacterium is anticipated to increase with their combined use (Cumplido-Nájera et al., 2019). Abdelkhalek and Al-Askar (2020) biosynthesized ZnO Nps employing an aqueous leaf extract of *Mentha spicata* and evaluated their antiviral activity against the tobacco mosaic virus (TMV). Green Synthesized ZnO-NPs mediated plant systemic resistance against TMV. The curative and protective effects of ZnO-NPs against TMV and PVY viruses in the tobacco plant were stated by (Cai et al., 2019). Copper-chitosan nanoparticles (CuChNp) were investigated to curb blast disease in finger millet. CuChNp dramatically boosted the defensive enzymes in finger millet, which led to an 89% increase in yield and 75% protection against *Pyricularia grisea*-caused blast disease (Sathiyabama and Manikandan, 2018). Downy mildew is a dreadful disease of pearl millet caused by *Sclerospora graminicola*, which leads to worldwide yield and economic losses (Dang and Panwar, 2004). The studies have shown that the management of disease with the intervention of various nanoparticles resulted in growth promotion and enhanced grain yield (Nandini et al., 2017; Rashad et al., 2021). In a study, tomato plants developed systemic resistance against bacterial wilt disease with magnesium oxide nanoparticle treatments. Following treatment with MgO NP, the expression of genes for systemic resistance-related GluA, ethylene inducible Osm, salicylic acid inducible PR1, jasmonic acid inducible LoxA, and jasmonate was boosted in the hypocotyls and roots of tomato plants (Imada et al. 2016). Chun and Chandrasekaran (2019) investigated the possibility of applying chitosan (CS) and chitosan nanoparticles (CNPs) to tomato plants to limit the wilt infection brought on by *Fusarium*. The finding documented the upregulated expression of pathogenesis related (PR) genes. The most noteworthy up-regulated 4.5-fold expression of SOD was shown at 48 hpi.

5. Role of nanoparticles in alleviating abiotic stress

In addition to having an influence on growth and development, NPs can ameliorate the deleterious effects of several key abiotic stresses encountered by plants (El-Saadony et al., 2022). These ever-increasing abiotic factors include salinity, drought, heavy metal-induced toxicity, water logging, and heat stress. Exposure to these abiotic factors leads to significant limitations in plant productivity and yield (El-Saadony et al., 2022). By activating particular genes and accumulating osmolytes, increasing phytonutrients, and producing photopigments, NPs aid in the mitigation of such stresses (Kumar et al., 2019). One of the inevitable symptoms of these abiotic stresses is the generation of reactive oxygen species due to the limitation in oxygen supply inside the plant cell (Kumari et al., 2022). While plants possess enzyme machinery to counter the oxidative stresses imposed by the environment, frequently the stress overcomes the plant defense mechanism to bring about serious consequences at physiological and molecular levels (Khan et al., 2021). However, due to their extremely small size, NPs have some unique features that set them apart from their bulk counterparts, which further reveals new avenues in many fields of application (Kumar et al., 2020). From previous studies, it has been demonstrated that the implementation of nanoparticles against these stresses has further amplified the plant's intrinsic pool of antioxidant enzymes (catalase, SOD, and peroxidase) (Khan and Upadhyaya, 2019). Recently, studies where these NPs act as nanoenzymes that can penetrate cell walls and scavenge ROS, have attracted much interest (Liu et al., 2021).

Over the past years, several key effects on plant physiology and adaptations against these stresses have been explored and identified.

For instance, osmotic stress is interconnected with these abiotic stresses, which eventually can disrupt ion distribution and cellular homeostasis (Moglianetti et al., 2016). Heat stress can have detrimental consequences, including degradation in the number of chlorophylls, disruption of photosystem II, disruption of electron flow, and attenuation in carbon fixation, which cumulatively interfere with the photosynthetic process (Hussain et al., 2021). Salinity stress induces a cascade of physiological, molecular, and biochemical alterations that directly affect the development of plants (Khan and Hemalatha, 2016). Some of the common effects of salt stress on plants include decreased soil osmotic potential and increased ionic stress (specific ionic toxicity) (Verslues et al., 2006). Whereas, drought stress results in a loss of turgidity in plants. Protoplasmic dehydration increases, which causes irreversible complications in cellular metabolism (Sagadevan et al., 2002). Turgor loss disrupts cellular metabolism, membrane integrity, and protein structure, as well as reducing leaf size, ion accumulation, and photosynthesis product yield (Cruz De Carvalho, 2008). Water-logged soil creates a hypoxic condition in roots due to the depletion of oxygen levels as water molecules take up the air space in the soil which affects the exchange of gases in the rhizosphere. The generation of oxidative stress has been documented for all the abiotic stresses.

There is sufficient evidence that NP treatment has resulted in numerous morphological and biochemical changes in response to most abiotic stresses (Rajput et al., 2021). The use of nanoparticles improves the photosynthetic rate, protection of chloroplasts, O_2 evolution, chlorophyll formation, and total chlorophyll content (Morteza et al., 2013). The application of TiO_2 NP reportedly enhanced chlorophyll concentration, net photosynthesis, water conductivity, and rate of transpiration in wheat and tomato plants. (Qi et al., 2013; Mahmoodzadeh et al., 2013). TiO_2 possesses photocatalytic properties; it protects chloroplasts, increases the quantity of light-harvesting complexes (LHCs), and increases O_2 evolution (Kongkanand et al., 2008). According to earlier studies, NPs influence the ability of plants to tolerate salinity stress by changing the levels of hormones, gene expression, defense mechanisms, antioxidant enzyme activity, and ion homeostasis (Zahra et al., 2021; Zulfiqar and Ashraf, 2021a). These effects may differ based on the size, shape, and concentration of NPs used, along with environmental conditions and plant species. (Etesami et al., 2021). At low concentrations of TiO_2 nanoparticles, seedling growth, and seed germination in onions were improved, while at higher concentrations, the effect was reversed (Laware, 2014). Abiotic stresses decrease photosynthesis by generating and aggregating ROS in the photosynthetic system. Wu et al., (2017) demonstrated that using CeO_2 NPs safeguards carbon dioxide assimilation and PSII quantum yield by scavenging ROS caused due to various stresses. Adaptations such as enhanced photosynthetic rate, reduced transpiration, and improved nutrient absorption help the plant effectively alleviate abiotic stresses. SiO_2 -NPs application in cucumber improved chlorophyll fluorescence, gas exchange, and carbonic anhydrase activity, all of which helped speed up photosynthesis (Alsaedi et al. 2017; Ahmad et al., 2019). NPs have been described as "magic bullets" due to their ability to improve physiological activities such as photosynthesis and nitrogen metabolism, seed germination, total chlorophyll content, carbohydrate and protein content, and eventually crop production (Siddiqui et al. 2015). AgNPs were reported to be significant for osmotic regulation in *Lathyrus sativus* L. under saline conditions; AgNP treatment lowers the harmful consequences of salinity stress in plants by revamping germination percentage, improving root to shoot length, and increasing the fresh and dry weight of seedlings (Hojjat, 2016). Copper nanoparticles applied to maize in arid settings improved plant biomass, chlorophyll, anthocyanin, carotenoid, and leaf water content (van Nguyen et al., 2021b). In canola plants (*Brassica napus*), $nCeO_2$ causes a shorter apoplastic barrier in the root, which in turn results in increased Na^+ transfer to shoots and reduced Na^+ buildup (Rossi et al., 2017a). Furthermore, by reducing the uptake of specific ions or by exchanging them, abiotic stresses can disrupt ionic homeostasis within cells

(Ahmad et al., 2019). For instance, under salinity stress, potassium or calcium ions get substituted by sodium ions. These ions predominantly induce cytosolic toxicity, which interferes with different physiological functions including signaling, nutrient translocation, and the process of photosynthesis (Tanveer and Shabala, 2018). The high K^+ to Na^+ ratio, which is altered by salt stress, has been shown to be a crucial determinant of stress tolerance and can be enhanced by application of NPs (Syta et al., 2018). The most promising ROS scavengers have been identified as nanoceria (CeNP); nanoceria may scavenge ROS and safeguard photosynthetic activities during abiotic stress (Rico et al., 2013).

The molecular and biochemical characteristics of the plant, as well as morpho-physiological parameters, are all improved by the use of nanoparticles (El-Badri et al., 2021). Differential gene expression has been studied in model plants as well as diverse crops to evaluate the effect of NPs at the molecular level. The application of NP can improve various biochemical parameters, causing improved biochemical characteristics along with higher crop yields (Arora et al., 2012). NPs have also been shown to have improved osmolyte concentration and antioxidant properties under abiotic stresses (Banerjee and Kole, 2016; Kalteh et al., 2018; Abdoli et al., 2020; Moradbeygi et al., 2020a). Moreover, NPs promote N-metabolism and enhanced levels of chlorophyll and proteins (Mishra et al., 2014; Alsaedi et al., 2017). Together, these studies demonstrated that NPs could boost agricultural productivity and stress management. For instance, treatment with Fe_3O_4 NPs (2000 mg/L) improved nodulation and nitrogen fixation in common beans, resulting in improved symbiotic performance (de Souza-Torres et al., 2021). A study where impact of SeNP on wheat plants triggered an increase in expression of heat shock factor A4A (HSFA4A) at 10 mg/l concentration, via promotion of certain signaling routes, was reported by Safari et al. (2018). The majority of gene expression studies on NP exposure found altered expression of stress tolerance-related genes, photosynthesis-related genes, and antioxidant enzyme genes (Hou et al. 2019). Genes linked to salinity stress, water stress, and oxidative stress were upregulated in an Arabidopsis plant transcriptome profiling study after being exposed to TiO_2 (2–5 ppm), and ZnO (15–60 mg/l). (Ltaief et al., 2021). Kaveh et al. (2013) reported upregulation of genes implicated in oxidative and heavy metal stress in *Arabidopsis thaliana* upon AgNP application. Proteomic analysis revealed that rice plants exposed to AgNPs increased proteins involved in ROS scavenging, regulation of genes, breakdown of proteins, calcium signaling, cell division, and programmed cell death (PCD) (Mirzajani et al., 2013). Aside from these NPs can induce direct transportation of DNA fragments into plant cells to modify the metabolic processes (Giraldo et al., 2014). Under stress, NPs enhance the antioxidant system's ability to scavenge free-radicals by altering the expressions of microRNAs and regulating various enzymes along with metabolic and morpho-physiological attributes (Siddiqi and Husen, 2016; Kambe et al. 2021).

6. Molecular responses triggered by nanoparticles during abiotic stress response

The biological functions of a plant are the result of processes occurring at the molecular level. Gene expression and the interaction of numerous biomolecules influence the mechanisms related to defense against various biotic and abiotic stresses. Certainly, the stresses interfere with the molecular mechanisms of plants on cellular and genetic levels, making the evaluation of the effect of nanoparticles more important through understanding molecular responses that significantly influence plant growth and development. The most crucial physiological process in plants, photosynthesis, is vulnerable to abiotic stresses like high NaCl levels or heat (Dubey, 2018). Chlorophyll is susceptible to high temperatures, the disruption of which leads to decreased photosynthesis (Faseela et al., 2020). Closing of stomata for better utilization of relative water content is an early adaptation of plants to heat

Table 1
Nanoparticle-induced potential in biochemical and physiological aspects of plants under key abiotic stresses.

S. No.	Type of NPs	NPs Treatment	Plant Species	Abiotic Stress	Outcomes	References
1	AgNP	1 mgL ⁻¹	<i>Triticum aestivum</i> L.	Salinity stress	Enhanced germination and growth of wheat seedlings	(Abou-Zeid and Ismail, 2018)
2	AgNP	25–100 mgL ⁻¹	<i>T. aestivum</i> L.	Heat Stress	enhanced levels of chlorophyll and balanced levels of relative water content (RWC)	(Iqbal et al., 2019)
3	AgNP	0, 10, 20, 30, 40 µg mL ⁻¹	<i>Lens culinaris Medic</i>	Drought Stress	Improvement in shoot length, fresh weight, germination percentage	(Hojjat, 2016)
4	AgNP	10, 20, 30 mM/L	<i>Thymus vulgaris</i> and <i>Thymus daenensis</i>	Salinity Stress	Improved shoot, and root length, enhancement of germination rate and seed vigor	(Ghavam, 2018)
5	AgNP	2, 5, 10 mM	<i>Triticum aestivum</i> L.	Salinity Stress	enhanced CAT & POD activities and improved conc. of proline, soluble sugars, MDA and H ₂ O ₂	(Mohamed et al., 2017)
6	AgNP & IAA		<i>Daucus carota</i> L.	Metal (Cd) Stress	Detoxified ROS, enhanced phenol synthesizing and oxidizing enzymes, and boosted plant growth	(Faiz et al., 2022)
7	SeNP	10, 50, 100 mgL ⁻¹	<i>Sorghum bicolor</i> L.	Heat Stress	enhanced pollen germination percentage and increased levels of unsaturated phospholipids as well as improved antioxidant activity	(Djanaguiraman et al., 2018)
8	AgNP	0, 50, 100 mgL ⁻¹	<i>Thymus vulgaris</i> L.	UV-B Stress	Alleviated yield, leaf photosynthetic pigments, leaf dry weight, and composition of essential oils	(Azadi et al., 2021)
9	TiO ₂ NP	0.01–0.03%	<i>T. aestivum</i> L.	Water deficit Stress	Improved agronomic traits, starch contents, and seed gluten	(Jaberzadeh et al., 2013)
10	TiO ₂ NP	0, 2, 5, and 10ppm	<i>Cicer arietinum</i> L.	Cold Stress	alleviated MDA and electrolyte leakage index (ELI)	(Mohammadi et al., 2013)
11	TiO ₂ NP	0.01–0.03%	<i>Vicia faba</i>	Salinity Stress	Significant improvement in levels of proline, amino acids, soluble sugars, and activity of antioxidant machinery	(Abdel Latef et al., 2018)
12	TiO ₂ NP		<i>Spinacia oleracea</i>	Heat Stress	improves chlorophyll, total nitrogen, ammonium, oxygen, and protein content as well as dry and fresh weight	(Yang et al., 2007)
13	Se, Si, and Cu NPs	200, 1000 mgL ⁻¹ SINPs; 10, 50 mgL ⁻¹ SeNPs; 100, 500 mgL ⁻¹ Cu NPs	<i>Capsicum annuum</i>	Salinity Stress	improved phytochemical content in fruits increased AXO, POD, CAT, and PAL activities as well as improved lycopene, and chlorophyll	(González-García et al. 2021)
14	SiO ₂ NPs	2.5 mM ⁻¹	<i>Oryza sativa</i>	Heavy metal stress	mitigation of heavy metal-induced toxicity through promoting growth via lessened bio-concentration and translocation	(Wang et al., 2016)
15	ZnO NP	1000 ppm	<i>Trigonella foenum-graecum</i>	Salt Stress	Improved SOD activity; elevated trigonelline content (osmotic regulator)	(Noohpisheh et al., 2020)
16	ZnO	30 mgL ⁻¹	<i>Vigna radiata</i> L.	Heat Stress	Alleviated chlorophyll content with upregulated antioxidants and osmoprotectants (LP, GB, and TSP) prevented oxidative damage	(Kareem et al., 2022a, 2022b)
17	Cu NP	52, 69.4, and 86.8 µM	<i>Zea mays</i>	Drought Stress	Higher chlorophyll content, and leaf water status, and contribute to enhancing plant growth and biomass with increased ROS scavenging activity	(van Nguyen et al., 2021a, 2021b)
18	Fe ₃ O ₄ NP	5–120 mgL ⁻¹	<i>Setaria italica</i>	Drought Stress	soluble sugar content of seedlings, chlorophyll content as well as overall plant biomass showed improvement	(Sreelakshmi et al., 2021)
19	Fe ₃ O ₄ NP	60 ppm	<i>Dracocephalum moldavica</i> L.	Salinity Stress	improved antioxidant defense, and improved rosmarinic acid synthase (RAS) and tyrosine aminotransferase (TAT) gene expression	(Moradbeygi et al., 2020a, 2020b)
20	CeO ₂ NP	500 mg.Kg ⁻¹ dry sand	<i>Brassica napus</i> L.	Salinity Stress	Improved photosynthesis and shortened apoplastic barriers in roots allow for increased Na ⁺ translocation to shoots and decreased Na ⁺ accumulation.	(Rossi et al., 2017a, 2017b)
21	Si NP	200 mg.kg ⁻¹	<i>Cucumis sativus</i> L.	Salinity Stress	Balancing nutrient uptake such as high Si and K ⁺ content in leaf and root respectively helped in regulating ionic homeostasis and stomatal opening	(Alsaedi et al., 2019)
22	Si NP	10 µM	<i>Triticum aestivum</i>	Water deficit stress	ROS-induced oxidative damage may have been counterbalanced through NO-induced activation of the antioxidant system	(Tripathi et al., 2017b)
23	TiO ₂ NP	SiO ₂ - 400, 800, 1600 and 3200 ppm; TiO ₂ - 25, 50, 100 and 200 ppm	<i>Gossypium barbadense</i> L.	Drought Stress	Proline content, total soluble proteins, phenolics content, total free AAs, CAT, POD, and SOD activities were all enhanced.	(Shallan et al., 2016)
24	SiO ₂ NPs	0, 5, 10 and 20 ppm	<i>Sorghum bicolor</i> L.	Water Stress	Increased seed germination percentage alleviation of water deficit affected length of root and shoot, as well as seedling weight	(Alzandi, 2019)
25	Al ₂ O ₃ NP	5, 30–60, and 135 nm	<i>Glycine max</i> L.	Flooding stress	Increased ribosomal proteins, modulate the activities of tricarboxylic acid cycle, the glutathione-ascorbate pathway, along with membrane permeability.	(Mustafa and Komatsu, 2016)

(continued on next page)

Table 1 (continued)

S. No.	Type of NPs	NPs Treatment	Plant Species	Abiotic Stress	Outcomes	References
26	AuNP	300 ppm	<i>T. aestivum</i>	Salinity Stress	improves nitrogen assimilation, nitric oxide synthesis, chlorophyll content, and ionic balance	(Wahid et al., 2022)
27	Mn ₃ O ₄ NP	1, 5 mg	<i>Cucumis sativus</i> L.	Salt Stress	improved biomass, net photosynthesis, and photosynthetic pigment content, change in metabolomes	(Lu et al., 2020)

stress (Tan et al., 2011). In a report, foliar application of ZnO-NPs substantially improved heat stress-induced declines in rate of photosynthesis, stomatal conductance, intracellular carbon dioxide concentration, and chlorophyll contents in the Mungbean plant (Kareem et al., 2022a). Heat stress-triggered disruption of chlorophyll negatively correlates with sucrose biosynthesis that causes decreased biosynthesis of osmoprotectants (TSP, GB, and LP) which is mitigated by nano-ZnO application with increased photosynthesis and hence increased biosynthesis of sucrose and overall improvement of chlorophyll contents (Kareem et al., 2022b). Also, Zn has a central role in biomembrane stability and act as a cofactor of SOD enzyme and can enhance the activity of antioxidants implicated in the amelioration of heat stress-mediated oxidative damage (Faizan et al., 2020). (Table 1).

Earlier literature has shown the impact of NPs to be concentration-dependent where they're normally effective at low concentrations (Cox et al., 2016). The signaling network in plants promotes plant defense and subsequent molecular responses. One such response is the influx of calcium ions into the cytosol which interact with calcium-binding proteins to trigger alterations in gene expressions relevant to adaptation against abiotic stresses (Khan et al., 2012; Ali et al., 2020). NPs have shown the property of binding to calcium ion receptors on Ca²⁺ channels and stimulating the cascade of gene activation and cellular metabolism against stress signals (Boudsocq and Sheen, 2013; Almutairi, 2016). In a proteomic analysis, AgNPs were shown to aggregate some protein precursors that were involved in Ca²⁺ regulation and signaling, oxidative stress tolerance, cell division, and programmed cell death (Mirzajani et al., 2014).

Chilling stress negatively influences plant photosynthesis. Stomatal limitations under chilling stress result in photoinhibition of photosystems (PS I & PS II) followed by oxidative damage to DNA, proteins, and lipids via accumulation of ROS in the thylakoid membrane (Allakhverdiev, 2011). Moreover, photodamage to the lipid bilayer of the thylakoid membrane induces the disruption of the photosynthetic apparatus caused by increased membrane fluidity (Havaux et al., 2000). Foliar treatment with NPs (nSiO₂, nSe, and nZnO) in sugarcane under chilling tension has revealed significant improvement in photosynthesis via maintenance of Fv/Fm; the maximum photochemical efficiency of PS II, photosynthetic gas exchange, and Pm: maximum photo-oxidizable P700 (Elsheery et al., 2020). Moreover, an increase in light-harvesting pigments and subsequent enhancement of nonphotochemical quenching of PS II in seedlings treated with NPs indicate the amelioration capacity of NPs in stress tolerance (Lima Neto et al., 2017). SiO₂NP had better Fv/Fm and Pm values than other NPs in this study (Elsheery et al., 2020). ZnO-NPs application in rice showed efficient regulation of the antioxidant system along with NP-induced gene expression of chilling-response transcription factors such as OsMYB30, OsMYB4, and OsbZIP52 (Song et al. 2021). Similarly, exposure to TiO₂ NP can increase the transcription rate of chilling stress-affected Rubisco (CaLRubisco, CaSRubisco) and chlorophyll-binding protein genes (Hasanpour et al., 2015). Nanoceria (CeO₂ NP), the biological activity of which is the occurrence of the Ce³⁺/Ce⁴⁺ redox couple on its surface, was reported to increase the quantum yield of PS II, rate of Rubisco carboxylation, and carbon assimilation in leaves (Korsvik et al., 2007; Heckert et al., 2008).

The positive impact of ZnO-NPs under salinity stress shows a significant alteration in stress-induced gene expression by downregulating some genes (SKRD2, MYC, and MPK4) and upregulating some (MYC, ARP, and MPK) in rapeseed plants (Hezaveh et al., 2019). Under salinity stress, an increased NaCl concentration can induce osmotic shock due to ion toxicity. It has been reported that Zn NP can alleviate salt stress by regulating increased biosynthesis of compatible solutes and through ionic regulation (Farouk, Al-Amri, 2019; Zulfiqar and Ashraf, 2021b). Under saline conditions, the complex LHC trimers and monomers were upregulated by silicon supplementation, while salinity stress-induced reductions in cytochrome b6/f and the ATP-synthase complex were also improved (Muneer et al., 2014). Additionally, silicon

has also been shown to trigger the gene expressions related to biosynthesis of abscisic acid (OsZEP, OsNCED, OsZEP), auxin, nitric oxide, and expression of a protein (OSHMA3) implicated in the influx of salt into the vacuole to alleviate the undesirable impacts of salt stress (Siddiqui et al., 2020; Tripathi and Rai, 2022; Tripathi and Vishwakarma, 2021). Exposure to salinity stress induces increased efflux of K^+ in leaf mesophyll cells through ROS-activated nonselective cation channels (ROS-NSCC). The application of cerium oxide NP has been shown to enhance the K^+ retention in mesophyll cells because of increased OH^- scavenging activity (Wu et al., 2018). Ion homeostasis is a key salinity tolerance trait in plants. An et al. (2020) demonstrated that priming seeds with CeO_2 -NPs (poly-acrylic acid coated) can improve cotton plant root morphology during salt stress by modifying essential molecular mechanisms. They reported increased expression of antioxidant genes and down-regulation of Ca^{2+} transporter CAX1 genes which enhance cytosolic calcium ion level, conserving the important stress signaling pathway. Application of Se-NPs in strawberry plants enhanced salinity tolerance through reduction in H_2O_2 content and lipid-peroxidation as well as accumulation of vital stress signaling molecules (indole-3-acetic acid and abscisic acid) (Zahedi et al., 2019).

The application of nanoparticles has also been quite effective in the mitigation of drought stress in crops. A study of seed pre-treatment with Cu and Zn colloidal NPs under drought conditions demonstrated improved antioxidative equilibrium and improved levels of key photosynthetic pigments. The effect of NPs decreased the accumulation of thiobarbituric acid reactive substances (TBARS) as well as enhanced activities of superoxide dismutase (SOD) and Catalase (CAT) in leaves which is indicative of reduced oxidative stress. Whereas, changing the Chl a/Chl b ratio and enhanced carotenoid content of leaves showed plant resistance against drought under the influence of NPs (Taran et al., 2017). Biosynthesized magnetite (Fe_3O_4) NPs were seen to be effective in alleviation of drought stress by enhancing quantum yield efficiency of PSII ($\Delta F/F_m'$) and electron transport rate (ETR) thereby strengthening the LH-complex when applied at lower concentration (Bisht et al., 2022). It has been demonstrated that photosynthesis can be significantly improved by nano SiO_2 treatment. Increased carbonic anhydrase activity, improved overall photochemical efficiency by increasing opening degree of reaction centers in PSII, and reduced antenna dissipation were induced by nano- SiO_2 (Xie et al., 2012). A parallel outcome has also been shown in tomato plant by improving carbonic anhydrase activity through ZnO application (Faizan et al., 2017). Introduction of *A. thaliana* to zero-valent iron NP triggered H^+ -ATPase activity in cell membrane causing overexpression of *AHA2* gene that is crucial for stomatal opening and drought response (Kim et al., 2015). TiO_2 NP due to its photocatalytic activity is the most studied nanoparticle as it can accelerate light energy transport and transformation in chloroplast via activation of a redox reaction in *A. thaliana* (Mingyu et al., 2007). Ze et al. (2010) reported, TiO_2 -NP can significantly promote upregulation of the LHCII-b gene and increase absorption peak intensity and higher LHCII content, which can influence the dissemination of light energy from PS I to PS II, oxygen evolution, and photolysis of water.

The foliar application of ZnO NP can act as a source of zinc in various plant parts and affect underlying metabolic activities including abiotic stress tolerance (Li et al., 2019). The effect of ZnO-NP on wheat under simultaneous water deficit stress and cadmium stress has been reported. The resultant higher Zn content in the plant induced decreased uptake and accumulation of Cd, by inactivating its transporter in the cell as both Zn and Cd share the same transporter (Adrees et al., 2021). Si-NP can protect plant cells against Cr toxicity by upregulating the antioxidant defense system and decreasing Cr (VI) accumulation (Tripathi et al., 2015). The rice plant being a Si-accumulator, prevents the entry of heavy metals by depositing higher Si content in the cell wall (Bhat et al., 2019). SeNP also positively impacts Cadmium stress-induced physiological stress by inhibiting expression of glycolate oxidases and NADPH oxidases, thereby minimizing membrane lipid damage (Qi et al., 2021). Arsenate-induced stress in maize cultivars was

reported to be alleviated by treatment with SiNPs which efficiently counter balanced the ROS-induced damage by reducing Arsenate accumulation and enhancing constituents of the AsA-GSH cycle (ascorbate-glutathione cycle) (Tripathi et al., 2016).

Recently discovered microRNA (miRNA), which is known to have a significant impact on plant physiology regulation, has also been linked to adaptation to abiotic and biotic stress. miRNA are small, single-stranded, noncoding post-transcriptional regulators of target gene expressions, thereby helping plants to counter any changing environment (Sun et al., 2018). An investigation demonstrated the upregulation of miR159a and miR156a in barley seedlings upon application of ZnO-NP (Plaksenkova et al., 2020), while another study revealed the down-regulation of these two miRNAs in maize (Adhikari et al., 2020). miR156 and miR159 are the most studied miRNAs as they are shown to be implicated in plant adaptation to drought, hypoxia, pathogen, and NP toxicity. In wild emmer wheat, 13 differentially regulated miRNAs were seen under shock drought stress (Kantar et al., 2010). Nano- TiO_2 might regulate plant metabolism via the expression of specific miRNAs (Boykov et al., 2019). Nevertheless, comprehensive knowledge of miRNA regulatory mechanisms and their complexity is still limited and requires more field studies to understand the impact of nanomaterials on them.

7. Conclusion and outlook

Following a thorough review of the existing literature, it is well established that NPs can significantly improve plant growth and development by alleviating numerous abiotic stresses. Considering the biostimulant potential of NPs, a basic understanding of how they work and affect plant metabolism is essential. The true potential of NPs in predicaments of the agricultural sector can be further realized through extensive studies of physiological, molecular, and biochemical impacts on plants. However, the implementation of NPs towards sustainable agriculture is still at the juvenile stage owing to the limitations of knowledge regarding the specific target of NP inside the plant cell, biomolecular interactions, and environmental risk assessments. Currently, one of the noteworthy advantages of NP application is its ability to mitigate the deleterious effects of released chemical products from bulk mineral fertilizers through target-specific and precision farming technology. Moreover, a few approaches can be suggested in light of possible avenues to boost the implementation of NPs as followings: i) critical observations concerning specific dosage, exposure duration, application route, translocation, and accumulation are important for strategic applications; ii) assessment and understanding of secondary effects, including the fate of NPs in the environment and the potential bioaccumulation along the food chain, would help widen the application against various concerns about NP toxicity; iii) the yet to be explored study regarding the distribution of NPs at subcellular level, i.e. nucleus and other organelles could answer the underlying mechanism of increased plant tolerance to stress; iv) It would be fascinating to conduct studies on the impact of NPs on proteomics, and the findings may improve our understanding of the mechanisms underlying NP-induced stress mitigation through comparative studies in both stressed and non-stressed plants; v) the need for further examinations on specific concentration ranges of various NPs linked with bio stimulation along with more investigations at metabolomic, genomic and proteomic levels; vi) furthermore, the wide implementation of the biogenic synthesis route is required to scale up the synthesis as well as decrease cost of NPs; vii) the development of comprehensive databases and collaboration at international level for legislation and regulation are essential for the successful exploitation of nanotechnology. Moreover, the design and synthesis of multifunctional nanocomposites in the coming years could very well further amplify the prospect of NP application in agriculture to its full potential. Taken together, well designed, carefully assessed, and extensive field testing are essential to enhancing the feasibility of nanoparticle implementation in the mitigation of abiotic stress.

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