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Synergistic relationship of endophyte-nanomaterials to alleviate abiotic stress in plants

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Plant responses to abiotic stresses through diverse mechanisms and strategic measures in utilizing nanomaterials have positively impacted crop productivity. Stress can cause membrane depletion, reactive oxygen species formation, cell toxicity and death, and reduction in plant growth. However, nanomaterials can mitigate some of the negative impacts of abiotic stresses and enhance crop yield. Some endophytic microbes can synthesize nanomaterials, which can maintain and enhance plant health and growth *via* nitrogen fixation, siderophore production, phytohormones synthesis, and enzyme production without any pathological effects. Nanoparticle-synthesizing endophytes also help boost plant biochemical and physiological functions by ameliorating the impact of abiotic stresses. The increase in the use and implementation of nano-growth enhancers from beneficial microbes, such as nano-biofertilizers, nano-pesticides, nano-herbicides, and nano-fungicides are considered safe and eco-friendly in ensuring sustainable agriculture and reduction of agrochemical usage. Promisingly, nanotechnology concepts in agriculture aim to sustain plant health and protect plants from oxidative stresses through the activation of anti-oxidative enzymes. The mechanisms and the use of nanomaterials to relieve abiotic plant stress still require further discussion in the literature. Therefore, this review is focused on endophytic microbes, the induction of abiotic stress tolerance in plants, and the use of nanomaterials to relieve abiotic plant stresses.

KEYWORDS

environmental stressors, food security, plant health management, soil-plant microbe interactions, sustainable development goal 2, zero hunger

Introduction

The environmental problems linked to climate abiotic-induced stresses pose serious threats and ecological pressures on soils and plant health, limiting crop productivity (Varshney et al., 2011). Thus, the need to devise a problem-solving approach to enhance crop yield under stress becomes imperative. The biotic factors, such as bacterial and fungal pathogens, insect and nematode pests as well as abiotic factors such as temperature, salinity, drought, flooding, heavy metals, and pH cause a large number of modifications in plant biochemical and physiological processes (Kumar et al., 2019). The approaches to mitigate these stresses in crops should be targeted to maximally address the food supply and demand of the world population. Over time, the use of chemical fertilizers to improve crop productivity has been employed, but with profound detrimental effects on the ecosystems (Adeleke and Babalola, 2022). Hence, developing modern technology remains important to ensure Sustainable Development Goals (SDGs) without any significant negative impact on the ecosystem.

Nanotechnological approaches have been employed in agriculture, industry, and medicine (Audah, 2019; Elemike et al., 2019; Zulfiqar et al., 2019). Nanoparticles (NPs), are characterized by sizes ranging from 1 to 100 nm in diameter, various physical, chemical features, biochemical activity, and increased reactivity (Dutta and Sugumaran, 2021). Different methods have been employed in the synthesis of NPs, which include inert gas condensation, physical ball milling, biological and chemical processes (Aboyewa et al., 2021). The biological means of synthesizing NPs can be achieved by harnessing some endophytic microbes, such as bacteria and fungi (Ahmad F. et al., 2012; Eid et al., 2021). Some examples of NPs produced by endophytic microbes include titanium, platinum, cadmium, gold, zirconium, selenium, magnetite, usnic acid, gold-silver alloy, uraninite, tellurium, and palladium (Aboyewa et al., 2021). NPs from endophytic fungi have been reported to play an important role in plant disease management due to the presence of NP-assisted genes (Sonawane et al., 2022).

Endophytic microbes are microbes inhabiting the internal tissues of plants, which can be beneficial or pathogenic (Adeleke and Babalola, 2022). The beneficial types help ensure sustainable plant and soil health under a variety of stresses including drought stress (Premachandra et al., 2020). Some of these microbes also possess the ability to synthesize nanomaterials, which can be exploited in maintaining plant health without any pathological effects (Sonawane et al., 2022). Promisingly, NP-synthesizing endophytic microbes can help boost plant physiological functions and can be used as bioinoculants in developing eco-friendly agriculture. Nevertheless, information on the actual mechanisms and the use of nanomaterials to relieve abiotic plant stresses have not been fully discussed in the literature. Depending on the type, application and use, various NPs of carbon-based, metallic and non-metallic and organic polymers

have been developed (Kumar et al., 2021; Fadiji et al., 2022b). The use and implementation of known nano-growth enhancers, nano-biofertilizers, nano-pesticides, nano-herbicides, and nano-fungicides are on the increase in modern agricultural systems (Imade et al., 2022; Sonawane et al., 2022). Based on experience to date, this approach is considered safe, eco-friendly for improved soil nutrition and crop yield.

Plants are prone to different environmental stressors, such as ultraviolet light, drought, flooding, salinity, temperature extremes (low or high), and the presence of heavy metals (Chaudhary et al., 2021c). All of these factors can induce oxidative stress causing membrane depletion, reactive oxygen species formation, cell toxicity and death, which cause a reduction in plant growth (Thomas and Puthur, 2017; Hasanuzzaman et al., 2019). Regardless of the nature of the abiotic stress, NPs may be involved in plant cellular metabolism, growth, and stress protection (Ajillogba et al., 2021). Also, some NPs exhibit the ability to modify the expression of genes involved in electron transport, energy transport, cell biosynthesis, and cell organization under stress conditions (Pandey, 2018; Sonawane et al., 2022). Thus, many studies have validated the multifunctional attributes of NPs in crop improvement (Abd-Alla et al., 2019; Chavan and Nadanathangam, 2019; Kibbey and Strevett, 2019).

Notwithstanding the positive attributes of NPs, information on the mechanisms of how NPs alleviate stresses and how endophytic microbes induce plant stress tolerance are still required. Consequently, this review addresses the role of endophytic microbes in inducing abiotic stress tolerance in plants, and the use of nanomaterials to relieve abiotic plant stresses.

Microbe-nanomaterial interactions

Biological activities through alterations in the function and structure of bacteria can be unveiled using modern and advanced nano-technological processes (Chaudhary et al., 2021b). Recent methods are being used to assess the surface chemistry, structural form of NPs and their effects on biocidal activities (Noukelag et al., 2022; Rehman et al., 2022). Examples of ecofriendly nano-sized agents include a variety of phyto/zooplankton, fungal spores, bacteria, and other microorganisms. NPs react differently with microbes, which shows that the microbial cell surfaces can differ substantially in their reactivity and attraction (Gangadoo et al., 2022). Silica NPs react effectively with microorganisms of different groups (Wang et al., 2020). For instance, bacteria and microalgae are smaller with less reactive attributes compared to fungal spores. A comprehensive mechanism showing the harmful effect of metallic nano-sized particles on bacteria cells is still required. In addition, there is a need for special attention to the structural alteration of bacterial cells using *in vitro* studies.

The continuous upsurge in the cases of fungal infections in immunocompromised patients, which require urgent medical treatment has caught the attention of most researchers. Meanwhile, the need for an ecofriendly measure for treating mycoses and identification of the source of infection has prompted researchers toward the use of metallic NPs (Singh et al., 2019; Soliman et al., 2021). Several studies have assessed the antifungal effects of NPs (Khattoon et al., 2018; Ahmadpour et al., 2021; Sadek et al., 2022). A study by Masoumizadeh et al. (2022) reported the effect of AgNPs on fungal pathogens, *Candida spp.* Also, the findings of Santhoshkumar et al. (2019) on the toxicological and antidermatophytic activity of AgNPs synthesized using leaf extract of *Passiflora caerulea* revealed the maximum antifungal activities against dermatophyte, *Trichophyton rubrum*.

Nanomaterial-microbial compatibility

Bacteria and NPs

Plasmolysis of bacteria is a slaying event that involves the breakdown of cytoplasmic components and morphological reduction of cytoplasm due to the loss of intracellular components and plasma membrane contraction from the cell wall. It has been reported that metallic NPs induce pleiotrophic effect on bacteria cells. Nanomaterials bind with bacteria proteins (thiol moieties) hindering their activities, forming an attachment with the cell membrane and causing cell death. Consequently, altering cell permeability by obstructing the activities of electrons in cells and obstructing respiration (Radzig et al., 2013; Mohanty et al., 2014). ROS generated as a result also inhibits respiratory enzymes. Oxidized DNA precursors result in DNA lesions (Park et al., 2009).

Advances in the cell to the non-cell formation, the reaction against resistant, persistent strains and swarming motility have encouraged researchers about bacterial genes encoding guanine nucleotide exchange factors. NPs enhance the activities and response of genes encoding guanine nucleotide exchange factors, which gives scientists better insights into improved NPs applications as antibacterial agents. Because of these highlighted responses, several studies have been conducted to verify the expression of bacterial genes to nano-sized particles (Khati et al., 2018). Exposure to metallic NPs revealed consistent gene patterns using transcriptional analytical methods such as RT qPCR or microarray. For instance, when *E. coli* was subjected to AgNPs, it exhibited a distinctive expression in gene functions, such as homeostasis of iron, silver and copper, which regulate the oxidative balance via the use of microarray experiment and its features to metabolize sulfur (Nagy et al., 2011; McQuillan and Shaw, 2014). In other studies, researchers assessed alterations in gene expression of bacteria subjected to the treatment with

carbon NPs. A study by Kang et al. (2008) showed the leakage of cellular material, disrupted membrane, reduced viability and metabolism of *E. coli* when subjected to single-walled nanotubes. In another study by Pelletier et al. (2010) using microarray, *E. coli* was exposed to cerium oxide NPs, the NPs upregulated several oxidoreductases sowing depletion in iron deficiency, oxidation stress and cellular respiration. Yang et al. (2012b) exposed *Pseudomonas aeruginosa* to quantum dots and genes controlling metal efflux transporters and oxidative stress were upregulated.

To check the compatibility of nanomaterials and bacterial cells, Dimkpa et al. (2012) showed that NPs could also affect microorganisms and plants by causing modifications in cellular levels of siderophores (pyoverdine) of plant growth-promoting bacterium (Dimkpa et al., 2012).

Fungi and NPs

Almost all NPs are capable of creating holes in the membrane of most fungal cells. The alteration in physiological traits of fungi releases biomolecules resulting in cell death. In a study by Kim et al. (2009), Kim and co. observed the reaction between AgNPS and *Candida albicans* and discovered membrane depolarization in *C. albicans*. Pits and pores were formed on the cell wall of the organism. This leads to the release of trehalose and glucose into the prepared suspension. The antifungal activity of AgNPs was also performed on other fungal species such as *Saccharomyces cerevisiae*, *Candida tropicalis*, *Phomopsis spp.*, *Penicillium expansum*, *Botrytis cinerea* and *Trichophyton rubrum* (He et al., 2011; Nasrollahi et al., 2011; Mallmann et al., 2015). The effect of Fe₃O₄NPs was tested against *Candida spp* and perforation of cell membranes was observed (Prucek et al., 2011). The cell wall and the membrane of *Cryptococcus neoformans* were also depleted when *C. neoformans* was exposed to AgNPs in a study by Ishida et al. (2013).

The use of *In silico* and mathematical modelling could help provide a better understanding of microbe-nanomaterial compatibility and interactions. Studies to experiment with the interaction between microbes and NPs are extremely important to unveil the details of these interactions. Meanwhile, bioinformatics tools are also needed to ensure statistical analysis and data curation about the future occurrences of microbial interaction with NPs (Singh et al., 2019; Adeleke et al., 2022).

Synergistic relationship: Endophyte-induced NPs

Recent developments required to ensure an ecofriendly interface for nanoscience studies have delivered exciting results by revealing multifaceted metal-based NPs with

numerous applications and functions (Baker et al., 2015a; Kumari et al., 2020). Ecofriendly biological resources viz. algae, fungi, bacteria and plants have been adopted to synthesize NPs, with each bio-factory having its pros and cons (Iravani et al., 2014; Rahman et al., 2019). Microorganisms are said to be an attractive option because of their dependable and unlimited metabolite production which are useful as reducing agents. In the case of plants, the disturbing plant diversity/species most times complicate the usage (because of selection problem) (Baker et al., 2015b). Even though microorganisms have been identified as the best option for the ecofriendly synthesis of NPs, the potential of endophytes remains under-explored. Adopting endophytes as reducing agents for the biosynthesis of nanomaterials opens new opportunities for the discovery of novel NPs with various applications (Rahman et al., 2019). Microorganisms (e.g., endophytes) remain the biological agents with harmless, clean and the most commercially available approach for NPs synthesis. That said, limitations faced by often synthesized endophyte NPs affect the stability of NPs because microbes are retarded overtime. With the variation in parameters such as substrate condition, synthesis condition, growth on media, pH, temperature and physicochemical parameters (stability, shape, and size) of NPs, which might change easily (Ovais et al., 2018).

The diverse endophytic microbes from different sources have been used in the synthesis of NPs. These include; the biosynthesis of AgNPs using *Bacillus cereus* isolated from *Adhatoda beddomei* and *Garcinia xanthocymus* as recapping agents to produce AgNPs with antibacterial properties (Sunkar and Nachiyar, 2012a; b). A study by Devi and Joshi (2015) also reported the use of *Cryptosporiopsis ericae* isolated from *Poteotilla fulgens* L. in the synthesis of NPs. The synthesized nanomaterial had an absorbance peak of ≈ 430 nm, spherical, and a diameter ranging between 2 nm and 16 nm. Rahi and Parmar (2014) and Singh et al. (2013) also synthesized AgNPs using *Penicillium* spp. isolated from the tissue of *Curcuma longa* and *Aloe vera* root. The synthesized NPs had a size range between 15 nm and 45 nm with immense antibacterial activity against antibiotic-resistant pathogens. Several studies have used endophytes as an ecofriendly route for the biosynthesis of multifunctional metal-based NPs. These include; Hulikere and Joshi (2019)—*Cladosporium cladosporoides*, Ramalingam et al. (2015)—*Cochliobolus lunatus*, Qian et al. (2013)—*Epicoccum nigrum*, Yashavantha Rao et al. (2016)—Endophytic bacterium EH419, Neethu et al. (2018)—*Penicillium polonicum* and Abdel-Aziz et al. (2018)—*Aspergillus* spp.

Impact of nanomaterials on microbial diversity and soil health

In natural ecosystems, microorganisms drive ecological processes (Chaudhary et al., 2022). These processes include;

anaerobic digestion, removal of nutrients in wastewater treatment, and biogeochemical cycling (Ahmed et al., 2012). On a single cell or population of microbes, antimicrobial activities and the potency of nanomaterials have been studied extensively elucidating their effects on the microbial community. As a result, there is an extensive understanding of the pros and cons associated with the ecotoxicity of NPs. Recently, scientists have studied the effect of nanomaterials on the community structure and functions of microorganisms in natural environments, such as water treatment facilities, marine, rivers and soils (Mohanty et al., 2014).

Effect of nanomaterials on microbial diversity

Microbial diversity in the soil plays a crucial role in nutrient cycling, plant diversity and agricultural output (Mohanty et al., 2014). Scientists have shown that important nanomaterials properties viz., aggregation, size, shape and charge, could be influenced by the environment (Lowry et al., 2012; Liu et al., 2014). NPs migrate at different levels in the soil matrix, and as such altering the microbial community structure in the soil. Also, the type of soil affects the impact of NPs. In a study by Frenk et al. (2013), the microbial community in clay and sandy soils were shown to respond differently to magnetite and copper oxide NPs. In a related study by Pawlett et al. (2013), a similar result was obtained from the reaction of microorganisms in the sandy soil to zero-valent iron nanomaterials. Herein, the microbial groups obtained from the combination of sandy soil and FeNPs were more susceptible than microbial communities in clay soil. Also, AgNPs were suspected to affect the community profile of freshwater microbial habitat in a study by Das et al. (2012). Both microbial biofilms and planktonic communities were influenced by nanomaterials as related in the study by Flemming and Wingender (2010) and Ding et al. (2014). Although, planktonic communities most times exhibit low tolerance to antimicrobial agents and toxic environments compared to their biofilm counterparts (Cao et al., 2012). For instance, the exposure of marine biofilm to AgNPs does not affect the community structure, succession and biofilm development of the community (Fabrega et al., 2011). However, apart from the reduction in microbial communities associated with a biofilm, the integrity of cells in a biofilm could be compromised because of its exposure to NPs (Battin et al., 2009).

In an engineered ecosystem using nanomaterials, most researchers adopt microbial communities associated with waste plants as model systems. Often, the impact of microbial communities and their community composition is of utmost interest to researchers. Meanwhile, most studies concentrate on the impact of NPs on commonly studied bioprocesses with the inclusion of methanogenesis, phosphorus and nitrogen removal. Even though most studies have reported the negative of

nanomaterials on microbial community structure (Liang et al., 2010; Ahmed and Rodrigues, 2013), some other studies showed that the microbial communities associated with sludge digester were not affected by nanomaterials (Nyberg et al., 2008; Yang et al., 2012a). This discrepancy could be associated with variations in the physical and chemical properties of nanomaterials and their complex reaction with several other materials from either organic or inorganic sources (Mohanty et al., 2014).

Impact of nanomaterials on microbial community functions

The effect of nanomaterials on microbial community functions is another important aspect of NPs-induced community variation yet to be explored. Some studies have further highlighted possible alterations in microbial functions induced by the exposure of the environment to nanomaterials. These include functions associated with nutrient removal and methanogenesis in wastewater treatment plants. In a study by Alvarez and Cervantes (2012), the process of methane production was significantly inhibited by nanomaterials such as Al₂O₃ and its toxicity was reduced when coated with humic acids. In a similar study, Yang et al. (2012a) reported the effect of AgNPs on methane production in landfill bioreactors at different concentrations.

Several studies viz., Masrahi et al. (2014), Liang et al. (2010), and Li et al. (2014) also reported nitrogen removal processes using nanomaterials such as TiO₂ and AgNPs. The negative impact of graphene oxide was also reported on wastewater treatment by removing nitrogen and phosphorus from waste materials (Ahmed and Rodrigues, 2013). To discuss the effect of nanomaterials on microbial diversity, structure and functions, organism-determined toxicity of nanomaterials is required i.e., each microorganism with susceptible nanomaterials because bacteria tolerate nanomaterials differently. For instance, Gram-positive bacteria react positively to single-walled carbon nanotubes by changing their membrane lipid composition. The mechanism of nanomaterials-microbe specificity is widely unknown and there is a need to further investigate the process (Jin et al., 2014; Mohanty et al., 2014).

Mechanisms of mitigating abiotic stress in plants

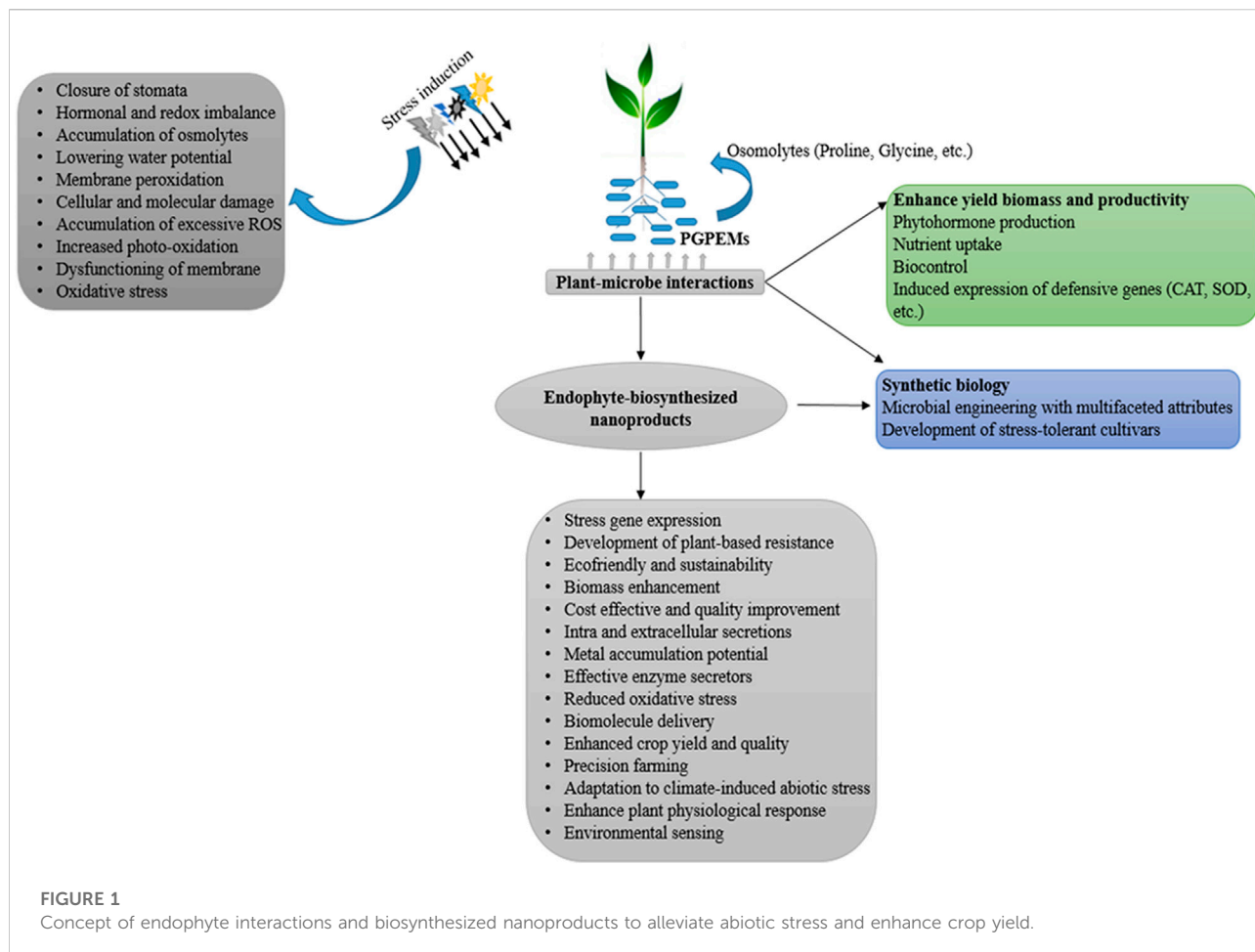
Abiotic stresses remain one of the most significant factors limiting the growth and yield of plant crops (Yadav, 2017). There is a need for plants to resist stressful edaphic and environmental conditions using either innate or induced biological mechanisms. For induced biological mechanisms to relieve the plant of unwanted stressors, an environmentally friendly method is

needed to avoid complications associated with the use of synthetic chemicals. In this regard, the use of endophytic microbes remains one of the more reliable methods to mitigate the effects of abiotic stresses. Microbes are ubiquitous in diverse natural environments and exhibit diverse metabolic responses to manage soil stressors (Meena et al., 2017; Akinola and Babalola, 2020; Akinola et al., 2021b). Due to the proximity between plants and microbes in the soil, the plant microbiome induces local and systemic mechanisms in crop plants to cope with continuous changes to the environment. This synergism (plant-microbe) in the agroecosystem induces complex mechanisms within the plant cellular system (Figure 1). Interestingly, the continuous change in climatic conditions has paved the way for a better understanding of plant cellular complexity; researchers are constantly ruminating on questions associated with the physiological, molecular, and biochemical processes related to plant-microbe interplay (Glick, 2020; Akanmu et al., 2021).

Because of the growing concern about climate change, it is important to explicitly explicate the synergy between plant-soil-microbe about protection against abiotic stressors. Understanding the changes in different abiotic stresses induced by either anthropogenic or natural means is crucial to reducing the negative effects of environmental stress as it impacts agricultural productivity (Jalil and Ansari, 2019). A report by the Food and Agriculture Organization (FAO) of the United Nations on the challenges limiting global food productivity argued that one of the major problems faced by the scientific community in the effort to increase crop production is unwanted abiotic stressors (FAO, 2009). As such, there is a need to address the challenges associated with plant growth sustainably. These include eco-friendly technological processes and the efficient use of bioproducts to address the constraints posed by environmental stresses (FAO, 2009).

Several abiotic factors can limit plant growth and development including low or high temperature, heavy metal toxicity, soil alkalinity or acidity, drought, flooding and salinity (Emamverdian et al., 2015; Pasala et al., 2016; Jalil and Ansari, 2019). Abnormal soil acidity can lead to nutrient deficiency in plants thereby reducing essential physiological attributes needed to improve plant growth and development (Jalil and Ansari, 2019; Akinola and Babalola, 2020). Similarly, salt treatment induces toxicity in plant tissues, leading to osmotic imbalance and stress which hinders plant growth. In addition, abiotic stressors increase the production of ROS and induce phytotoxicity by negatively impacting protein structure and functions (Baral and Izaguirre-Mayoral, 2017; Mukhtar et al., 2018; Komaresofla et al., 2019).

Naturally, plant cell organelles viz., chloroplasts, peroxisomes and mitochondria help in producing ROS, with hydrogen peroxide and oxygen radicals being produced in the mitochondria. Hydrogen peroxide and oxygen are produced in the chloroplast (Jalil and Ansari,



2019). Using peroxidase dismutase, the peroxides are transformed into hydrogen peroxide (H_2O_2). The oxidation process involved in the conversion of xanthine and hypoxanthine to uric acid is achieved in the peroxisomal matrix using xanthine oxidase to generate oxygen radicals (Halliwell and Gutteridge, 2015; Jalil and Ansari, 2019). These radicals destroy cell biomolecules, such as DNA, carbohydrates, lipids, and proteins, resulting in cell death.

Plants can rapidly acclimatize to an abrupt change in the environment, such as unwanted abiotic conditions. A shift in the soil condition alters plant metabolic equilibrium and causes plant cells to modify genetic and metabolic processes (Tuteja and Mahajan, 2007; Tuteja and Sopory, 2008; Simontacchi et al., 2015). Plants then activate defense mechanisms needed to relieve unwanted stress conditions, reprogramming metabolic processes within the plant cell, thus facilitating bio-physicochemical relief of abiotic stress conditions (Massad et al., 2012; Mickelbart et al., 2015; Yolcu et al., 2016).

Due to uncertainty surrounding the mechanism of action of metallic NPs, different hypothetical mechanisms were frequently mentioned in different studies. These include that:

- NPs aggregate and dissolve the cell membrane, resulting in the alteration of cell permeability and dissolution of the PMF—Proton motive force (McQuillan, 2010; Singh et al., 2019).
- ROS—Reactive oxygen species that help in the destruction of the cellular structure are produced by metallic NPs and ions (Singh et al., 2019).
- Absorption of metal ions by cells helps in the degradation of intracellular ATP and the disruption of DNA synthesis (Singh et al., 2019).

Oxidation reactions attributed to metallic ions in cells induce responses such as ROS—due to cell signal differentiation and cell death (Mueller et al., 2005). The integral components of ROS include peroxomonocarbonate ($HOOCO_2^-$), peroxy nitrate (O_2NOO^-), peroxy nitrite ($ONOO^-$), nitric compounds, hypochlorite and hypochlorous acids, peroxy (RO_2^-), and hydroperoxy (HO_2^-), and other oxygen-related compounds (Wu et al., 2014). With the catalysis of superoxidase dismutase (SOD), oxygen ions have a short lifespan due to instant reduction. NADPH—nicotinamide adenine

dinucleotide phosphate oxidase in the mitochondria induces lipid peroxidation of the cell membrane (Singh et al., 2019). SOD initiates the complete conversion of oxygen into hydrogen peroxide. Physiologically, different detoxifying enzymes *viz.*, glutathione peroxidase, catalase, SOD and antioxidants (flavonoids, vitamin E and ascorbic acids) modulate intracellular stages. Meanwhile, ROS activated by NPs of either CuO, ZnO or Ag plays a crucial role in genotoxicity. Oxidative stress degraded genetic materials are associated with different biological mechanisms *viz.*, mutagenesis. Stress activation due to oxidative species results in nanotoxicity and the accumulation of oxidative stress leading to DNA destruction (Fu et al., 2014). The destruction of DNA because of OS; involves the breakage of single and double-stranded sugar bases, the generation of basic sites and DNA-protein crosslinks. Closely, hydroxyl radicals cause rapid damage to cells, whereas, from a distance, less-reactive ROS may interact easily (Fu et al., 2014).

Microbe-induced abiotic stress tolerance

An adaptation used in the process of abiotic stress tolerance is often referred to as induced systemic tolerance/resistance (IST/ISR). The intrinsic genetic and metabolic potential of microbes contribute immensely to the relief of plants from abiotic stresses (Gopalakrishnan et al., 2015). The role of endosphere and rhizosphere inhabitants belonging to different genera *viz.*, *Cyanobacteria* (Singh et al., 2011), *Trichoderma* (Pandey et al., 2016; Igiehon and Babalola, 2021), *Burkholderia* (Naveed et al., 2014a; Naveed et al., 2014b), *Methylobacterium* (Meena et al., 2012), *Bradyrhizobium* (Tittabutr et al., 2013), *Enterobacter* (Sorty et al., 2016), *Bacillus* (Ashraf et al., 2004; Sorty et al., 2016), *Pantoea* (Sorty et al., 2016), *Rhizobium* (Igiehon and Babalola, 2021; Igiehon et al., 2021), *Azospirillum* (Omar et al., 2009), *Azotobacter*, and *Pseudomonas* (Ndeddy Aka and Babalola, 2016) have functional traits useful in improving plant growth under abiotic stresses. The functional role of *Trichoderma harzianum* in alleviating soil stresses through the upregulation of genes such as malonaldehyde, dehydrin, and aquaporin genes, has been reported by Pandey et al. (2016) on different serotypes of rice. Also, the synthesis of exopolysaccharides, antioxidants, protein defensins and phytohormones may be induced using plant growth-promoting rhizobacteria. Most of these functions are effective against drought and other abiotic stressors (Kaushal and Wani, 2016). Therefore, the effective productivity monitoring parameters, *viz.*, screening, selection and inoculation of stress-mitigating microbes, can be helpful as a viable option to increase crop productivity to solve the problem of a growing world population with insufficient food (Akinola and Babalola, 2021). *Trichoderma harzianum* inoculation enhances the oil content of *Brassica juncea* inhibited by salinity stress and improves the plant's physiological traits,

such as reducing sodium ion uptake, enhancing osmolyte synthesis, antioxidant accumulation, and facilitating the uptake of essential plant nutrients (Ahmad et al., 2015). Similarly, ACC deaminase production was shown to be responsible for the upregulation of monodehydroascorbate reductase in *B. juncea* (Brotman et al., 2013). Also, the addition of *Acinetobacter* sp. and *Pseudomonas* sp. have been used to increase the production of ACC deaminase and indole-3-acetic acid (IAA) in oat and barley grown in salinity-stressed soil (Chang et al., 2014). *Streptomyces* sp. strain PGPA39 has also been used to alleviate salinity stress in tomato plants (Palaniyandi et al., 2014). In *Arabidopsis*, wheat, and maize plants, *Burkholderia* sp., has been used to relieve plants and soil of salt and drought stresses (Naveed et al. (2014a); Naveed et al. (2014b); Pinedo et al. (2015)).

There are a large number of microorganisms within proximity to plant tissues and across the vicinity of plant roots because the plant root exudates provide diverse metabolites and nutrients which attract beneficial microorganisms. These metabolites are crucial to the microbial presence surrounding and attached to plants (Akinola et al., 2021a; Akinola and Babalola, 2021) with chemoattraction being associated with microbial movement toward these compounds (Meena et al., 2017). While utilizing these plant exudates, plant growth-beneficial microorganisms associated with the plant endosphere induce both direct and indirect mechanisms, such as biocontrol agents, phytostimulation, and biofertilization (Hayat et al., 2010; Akinola and Babalola, 2020).

Indirect mechanisms of plant growth promotion include the production of antimicrobial agents, hydrogen cyanide (HCN), and antibiotics, which exert antagonistic effects against plant pathogens. Direct mechanisms include nitrogen fixation, stimulation of plant hormone synthesis, solubilization of potassium and phosphorus, synthesis of siderophores which facilitate iron uptake, and sequestration of zinc and other micro- and macronutrients from the soil (Meena et al., 2017). In addition, many plant-associated microbes also induce systemic resistance against various phytopathogens triggered by plant secondary metabolites (Meena et al., 2017; Omomowo and Babalola, 2019). Apart from bacteria, mycorrhizal fungi are also good to plant growth promoters. These include both vesicular-arbuscular mycorrhiza (VAM) and other ectomycorrhizal fungi (Akinola and Babalola, 2021). These fungi use their extensive hyphal networking to increase plant nutrient uptake. For instance, in studies by Sun et al. (2010) and Baltruschat et al. (2008), an endophytic fungus—*Piriformospora indica* was used to improve drought and salinity tolerance in Chinese cabbage and barley, respectively. These processes were achieved by improving both physiological traits and the level of plant antioxidants. At some point, microbes activate systemic or local stress responses in plants under abiotic stress. In other instances, they activate direct

TABLE 1 Examples from the recent literature of the effect of plant growth-promoting microbes in the relief of plant stress.

Crop type	Adopted organism(s)			Stress	Inference	References
	Fungi	Bacteria	Archaea			
Wheat		<i>Bacillus pumilus</i> (FAB10)		Salinity	Enhanced wheat growth with improvement in photosynthesis, plant tissue proline content, and transpiration	Ansari et al. (2019)
Paddy plants		<i>Curtobacterium albidum</i> (SRV4)		Salinity	Improved plant proline content, membrane solubilization index, and photosynthetic pigment efficiency	Vimal et al. (2019)
Wheat		<i>Bacillus megaterium</i> + <i>B. licheniformis</i> + Fulvic acid		Alkalinity	Improved plant growth, reduction in soil cadmium, increase in organic matter	Li et al. (2019)
Guinea grass (<i>Megathyrsus maximus</i>)		<i>Bacillus</i> spp.		Drought	Increased accumulation of proline and glutathione reductase activity	Moreno-Galván et al. (2020)
Maize (<i>Zea mays</i> L.)		<i>Azotobacter salinestris</i> , <i>A. chroococum</i>		Drought	Increase in shoot dry weight, chlorophyll content, plant height and N, P, Fe concentration	Shirinbayan et al. (2019)
Lettuce <i>Latuca sativa</i>		<i>Curtobacterium herbarum</i> (CAH5)		Drought	Reduction in oxidative stress and lipid peroxidation	Silambarasan et al. (2019)
Common ice-plant (<i>Mesembryanthemum crystallinum</i> L.)		<i>Streptomyces diastaticus</i> WZ902 (LC390202), <i>Bacillus subtilis</i> subsp. <i>Inaquisorum</i> LM03-B (LC390203)		Salinity	Increased plant growth, and elongated roots. ACC deaminase activity, phosphorus solubilization, and siderophore production	Mahmood et al. (2019)
Sorghum and sudan grass seedlings on red mud	<i>Trichoderma asperellum</i> RM-28			Sodic/saline-Alkalinity	Decreased pH and EC of red mud, and improved plant chlorophyll content, growth, and oxidative stress	Anam et al. (2019)
<i>Salicornia</i> sp		<i>Staphylococcus</i> sp. (rhizosphere strain) + <i>Staph.</i> sp. (endophytic strain)		Salinity	Enhanced growth and high salt tolerance with both strains. Increased phosphate solubilization and IAA production	Komaresofla et al. (2019)
Thale cress <i>Arabidopsis thaliana</i>		<i>Pantoea stewartii</i> JZ2, <i>Bacillus</i> sp. JZ34, <i>Microbacterium barkeri</i> JZ37, <i>Arthrobacter</i> sp. JZ12, <i>Cellulomonas</i> sp. JZ18		Salinity	Endophytic bacteria from the desert help reduce Na ⁺ /K ⁺ ratio and increase plant shoot and root biomass	Eida et al. (2019)
Sulla carnosa		<i>Actinobacter</i> sp. (Br3) + <i>Pseudomonas putida</i> (Br18) + <i>Curtobacterium</i> sp. (Br20)		Salinity	Enhanced soluble sugar, oxidative enzyme activities, ameliorated induced soil salinity and increased plant growth	Hmaeid et al. (2019)
Wheat (<i>Triticum aestivum</i>)		1-aminocyclopropane-1-carboxylate dismutase (ACCD)-producing <i>Klebsiella</i> spp. (8IJA, 27IJA)		Salinity	Increase in plant biomass and superoxidase dismutase activity	Acuña et al. (2019)
Maize (<i>Zea mays</i> L.)	<i>Glomus tortuosum</i>			Salinity	Increased crop output, chlorophyll content, and rubisco activity	Xu et al. (2018)
Finger millet (<i>Eleusine coracana</i> L. Gaertn)		<i>Pseudomonas</i> spp.		Drought	Improved growth performance and foliar nutrient content and increased antioxidant properties	Chandra et al. (2018)

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TABLE 1 (Continued) Examples from the recent literature of the effect of plant growth-promoting microbes in the relief of plant stress.

Crop type	Adopted organism(s)			Stress	Inference	References
	Fungi	Bacteria	Archaea			
Ice plant (<i>Aizoaceae</i> spp.)		<i>Mesembryanthemum crystallinum</i>		Salinity	Increase in rubisco activity, crop output, and chlorophyll content	Zhang et al. (2018)
White clover (<i>Trifolium repens</i>)		<i>Azospirillum brasilense</i>		Salinity	Polyphenols and phenol production	Khalid et al. (2017)
Lettuce (<i>Lactuca sativa</i>)		<i>Curtobacterium herbarum</i> (CAH5)		Drought and Aluminium stress	Increased plant root and shoot growth, enhanced plant growth under 4-nitroaniline	Silambarasan and Vangnai (2017)
Maize (<i>Zea mays</i> L.)		<i>Pseudomonas putida</i> (FBKV2)		Drought	Increase in root length and dry biomass	Vurukonda et al. (2016)
Mung beans (<i>Vigna radiata</i>)		<i>Bacillus drentensis</i> , <i>Enterobacter cloacae</i>		Salinity	Increase in plant height, seed yield, dry biomass, chlorophyll content, water absorption rate, transpiration, and salt tolerance	Mahmood et al. (2016)
Tomato (<i>Solanum lycopersicum</i>)		<i>Arthrobacter</i> strains (TF1, TF7), <i>Bacillus megaterium</i> (TF2, TF3)		Salinity	Increase in seedling length, vigor index, dry weight, and tomato seed germination	Fan et al. (2016)
Maize (<i>Zea mays</i> L.)		<i>Chryseobacterium humi</i> ECP37 + <i>Pseudomonas reactans</i> EDP28		Salinity	Increased seedling and plant yield	Moreira et al. (2016)
Maize (<i>Zea mays</i> L.)	<i>Glomus etunicatum</i> +	<i>Methylobacterium oryzae</i> CBMB20			Improved crop yield after the <i>in vivo</i> application of organisms	Lee et al. (2015)
Garden thyme (<i>Thymus vulgaris</i>)		<i>Enterobacter</i> sp. + <i>Bacillus</i> sp. + <i>Bacillus thuringensis</i> + agrowaste		Drought	Optimal nutrition and better physiological traits compared to control	Armada et al. (2015a)
French lavender (<i>Lavandula dentate</i>), Common sage (<i>Salvia officinalis</i>), Lavender-cotton (<i>Santolina chamaecyparissus</i>)						
Maize (<i>Zea mays</i> L.)	Consortium of AMF	<i>Bacillus thuringensis</i>		Drought	Increased plant growth, photosynthesis efficiency, decreased oxidative damage to lipids, increased accumulation of proline and nutrient	Armada et al. (2015b)
Chicken pea (<i>Cicer arietinum</i>) cultivars BG-3629, BG-1003		<i>Pseudomonas putida</i>		Drought	Conferred drought tolerance by improving several biochemical and physiological parameters	Tiwari et al. (2016)
Mung beans (<i>Vigna radiata</i>)		<i>Pseudomonas putida</i> (SB21)		Acidity	The large increase in plant growth	Saluja et al. (2014)
Mung beans (<i>Vigna radiata</i>)		<i>Comamonas</i> spp. (SB20)		Alkalinity	Increase in plant yield after exposure to alkaline soil	Saluja et al. (2014)
White clover (<i>Trifolium repens</i>)	Arbuscular mycorrhiza fungi (AMF) +	Combination of any two of <i>Bacillus thuringensis</i> , <i>Rhizophagus intraradices</i> , <i>Pseudomonas putida</i>		Drought	Increased root and shoot weight with high superoxidase dismutase (SOD) activity	Ortiz et al. (2015)
Common bean (<i>Phaseolus vulgaris</i>)		<i>Pseudomonas fluorescens</i>		Salinity	Na ⁺ exclusion, proline production, increased SOD, catalase activity and shoot biomass	Younesi and Moradi (2014)

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TABLE 1 (Continued) Examples from the recent literature of the effect of plant growth-promoting microbes in the relief of plant stress.

Crop type	Adopted organism(s)			Stress	Inference	References
	Fungi	Bacteria	Archaea			
Barley (<i>Hordeum vulgare</i>), Oats (<i>Avena sativa</i>)		<i>Pseudomonas</i> sp., <i>Acinetobacter</i> spp.		Salinity	Increased IAA and ACC deaminase production	Chang et al. (2014)
Rice sensitive to salt (GJ-17)		<i>Bacillus pumilus</i> , <i>Pseudomonas</i> <i>pseudoalcaligenes</i>		Salinity	Increased SOD activity and reduced lipid peroxidase	Jha and Subramanian (2014)
Tomato (<i>Solanum</i> <i>lycopersicum</i>)		<i>Streptomyces</i> sp. (PGPA39)		Salinity	Phosphate solubilization, increased plant yield, IAA production, and ACC deaminase activity	Palaniyandi et al. (2014)
Mung beans (<i>Vigna radiata</i> L)		<i>Pseudomonas</i> sp. + <i>Rhizobium</i> sp		Salinity	Increased ACC deaminase activity and IAA production	Ahmad et al. (2013)
Wheat (<i>Triticum aestivum</i>)		<i>Serratia ficaria</i> , <i>Enterobacter</i> <i>cloacae</i> , <i>Pseudomonas</i> <i>fluorescens</i> , <i>P. putida</i>		Salinity	Improved nutrient uptake and enhanced plant growth	Nadeem et al. (2013)
Rice (<i>Oryza sativa</i>)		<i>Bacillus amyloliquefaciens</i> NBRISN13 (SN13)		Salinity	Increased colonization of osmoprotectant utilizing microbes to induce salt tolerance in rice	Nautiyal et al. (2013)
Wheat (<i>T. aestivum</i>)		<i>Halobacillus</i> spp <i>Bacillus</i> <i>halodenitrificans</i>		Salinity	Increase in dry weight and root length of the plant	Ramadoss et al. (2013)
Tomato (<i>Solanum</i> <i>lycopersicum</i>)		<i>Bacillus pumilis</i> , <i>Bacillus</i> <i>subtilis</i>		Salinity	High PGP traits, vigor index, and ability to tolerate saline soil	Damodaran et al. (2013)
Wheat (<i>T. aestivum</i>)		<i>Streptomyces</i> sp		Salinity	Increase in N, P, Fe, and Mn of the wheat shoots and alleviation of salt inhibition	Sadeghi et al. (2018)
Rice (<i>Oryza sativa</i>)		<i>Bacillus</i> sp., <i>Alcaligenes</i> sp., <i>Ochrobactrum</i> sp		Salinity	Increased germination, root, shoot growth, and chlorophyll content. ACC deaminase reduces ethylene production under salt stress	Bal et al. (2013)
Groundnut (<i>Arachis</i> <i>hypogaea</i> L.)		<i>Haererohalobacter</i> sp. (JG-11), <i>Bravibacterium casei</i> (JG-08), <i>Brachybacterium</i> <i>saurashtrense</i> (JG-06) <i>Raoultella planticola</i> Rs-2		Salinity	Increase in phosphorus, nitrogen content, High Ca ²⁺ and balanced K ⁺ /Na ⁺ ratio. ACC deaminase activity	Shukla et al. (2012)
Mung bean (<i>Vigna radiata</i>)		<i>Rhizobium phaseoli</i> + PGPR (<i>Pseudomonas fluorescens</i> (MK20), <i>P. syringae</i> MK1)		Salinity	ACC deaminase activity and high plant yield	Wu et al. (2012)
Mung bean (<i>Vigna radiata</i>)		<i>Rhizobium phaseoli</i> + PGPR (<i>Pseudomonas fluorescens</i> (MK20), <i>P. syringae</i> MK1)		Salinity	Increased efficiency of water use and ACC deaminase activity	Ahmad et al. (2012b)
Wheat (<i>T. aestivum</i>)		<i>Bacillus</i> sp. (SKU-3), <i>Paenibacillus</i> sp. (SKU-11)		Salinity	Exopolysaccharides produced by test organisms mitigate soil salinity	Upadhyay et al. (2011)
Sunflower treated with NaCl		<i>Pseudomonas fluorescens</i> biotype F, <i>P. fluorescens</i> CECT378 ^T		Salinity	Balanced K ⁺ /Na ⁺ ratio, siderophore, and IAA production	Shilev et al. (2012)
Wheat (<i>T. aestivum</i>)		<i>Pseudomonas extremorientalis</i> (TSAU6), <i>P. aureantiaca</i> (TSAU22), <i>P. extremorientalis</i> (TSAU20)		Salinity	Production of phytohormones such as gibberellin, auxin, zeatin, and alleviation of salinity inhibition	Egamberdieva (2009)
Soybean (<i>Glycine max</i>)		<i>P. putida</i> (62BN)		Acidity	Reduction in cadmium concentration and increased plant growth in acidic soil	Rani et al. (2009)
Soybean (<i>Glycine max</i>)		<i>P. monteilli</i> (97AN)		Alkalinity	Increased plant growth and amelioration of soil alkalinity	Rani et al. (2009)

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TABLE 1 (Continued) Examples from the recent literature of the effect of plant growth-promoting microbes in the relief of plant stress.

Crop type	Adopted organism(s)			Stress	Inference	References
	Fungi	Bacteria	Archaea			
Wheat seedling		Exopolysaccharides producing bacterial strains viz. <i>Aeromonas hydrophila/caviae</i> (MAS-765), <i>Bacillus insolitus</i> (MAS17), <i>Bacillus</i> sp. (MAS617, MAS620, MAS820)		Salinity	Increased physiological properties (root, shoot, and yield) in a saline environment and reduced Na ⁺ uptake by the plant	Ashraf et al. (2004)
Indian mustard (<i>Brassica juncea</i> L.) Barley (<i>Hordeum vulgare</i>)	<i>Trichoderma harzianum</i> <i>Piriformospora indica</i>			Salinity	An antioxidative defense system was used to mitigate the effect of NaCl on plant	Ahmad et al. (2015)
				Salinity	Microorganism induces desaturation of fatty acids in leaves, attenuated NaCl-induced lipid peroxidation and metabolic heat efflux useful in salt tolerance	Baltruschat et al. (2008)
<i>Arabidopsis thaliana</i>	<i>Trichoderma</i> spp.			Salinity	Activation of antioxidative compounds viz. ACC deaminase for tolerance against salt stress	Brotman et al. (2013)
Soybean (<i>Glycine max</i>)	AMF	<i>Rhizobium</i> spp		Drought	The synergy between AMF and <i>Rhizobium</i> spp. Relieve plants of drought stress by increasing the level of plant proline	Igjeon and Babalola (2021)
Rice (<i>Oryza sativa</i> L)		<i>Bacillus pumilus</i>		Salinity and heavy metal	The bacterium reduces the antioxidative activity of the plant due to the limited uptake of Na ⁺	Khan et al. (2016)
Rice (<i>Oryza sativa</i> L)	<i>Trichoderma harzianum</i> Th-56			Drought	<i>T. harzianum</i> modulates the activation of essential compounds such as lipid, peroxidase, SOD, and proline, needed to improve drought tolerance in rice	Pandey et al. (2016)
Micro Tom Tomato		<i>Streptomyces</i> sp. PGPA 39		Salinity	Reduction in leaf proline content increased chlorophyll content and plant biomass after inoculating the plant with <i>Streptomyces</i> sp	Palaniyandi et al. (2014)
<i>Piptatherum miliaceum</i> L. <i>Thymus vulgaris</i> Letc.	AMF	<i>Bacillus thuringensis</i>		Drought	Decreased stomatal conductance, electrolyte leakage, proline activity, increased water content, and nutrient uptake	Ortiz et al. (2015)
<i>Brassica juncea</i>		<i>Pseudomonas aeruginosa</i> , <i>Bacillus subtilis</i> , <i>Alcaligenes faecalis</i>		Heavy metal	Organisms reduce the uptake, toxic effect of heavy metals and also increase plant growth	Ndeddy Aka and Babalola (2016)
Maize (<i>Zea mays</i> L)		Endophytes <i>Burkholderia phytofirmans</i> (PsJN), <i>Enterobacter</i> sp. FD17		Drought	Endophytes relieve the effect of drought by increasing root-shoot biomass, chlorophyll content, photosynthesis, leaf area, and other physiological traits	Naveed et al. (2014b)
Wheat		<i>Burkholderia phytofirmans</i> PsJN		Drought	<i>B. phytofirmans</i> increases ionic balance, antioxidant level, nutrient uptake, and	Naveed et al. (2014a)

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TABLE 1 (Continued) Examples from the recent literature of the effect of plant growth-promoting microbes in the relief of plant stress.

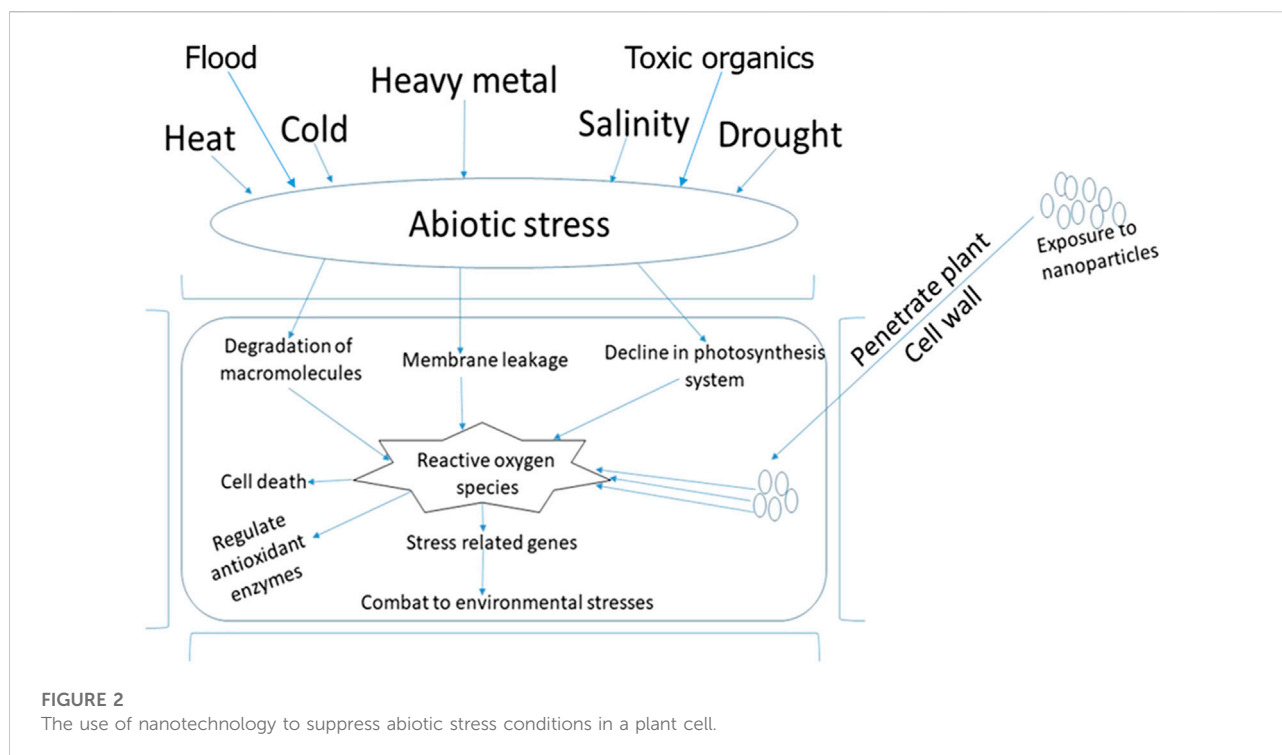
Crop type	Adopted organism(s)			Stress	Inference	References
	Fungi	Bacteria	Archaea			
Legume		<i>Bradyrhizobium</i> , <i>Rhizobacteria</i> containing stress-induced ACC deaminase		High temperature, Drought, and salinity	protein concentration in grains Synergism between used organisms mitigated different plant stressors by adjusting the expression of ACC deaminase to varying levels of stress conditions	Tittabutr et al. (2013)
Chinese cabbage	<i>Piriformospora indica</i>			Drought	Plastid-localized CAS proteins, drought-related genes and antioxidant enzymes were stimulated	Sun et al. (2010)
Rice (<i>Oryza sativa</i> L.)		<i>Pseudomonas putida</i> MTCC102		Nutrient deficiency	<i>P. putida</i> strain relieved the stress of iron deficiency	Sharma et al. (2013)
Rice (<i>Oryza sativa</i> L.)		<i>Pseudomonas</i> strains PF1, TDK1		Salinity	<i>Pseudomonas</i> strains relieved the plant of salt stress, increased physiological parameters, such as root and shoot length, dry weight, and plant height	Sen and Chandrasekhar (2014)
<i>Arabidopsis thaliana</i>		<i>Burkholderia phytofirmans</i> PsJN		Salinity	<i>B. phytofirmans</i> induces long-term transcriptional and metabolic changes in plants, suggesting the need to understand spatiotemporal mechanisms associated with the process	Pinedo et al. (2015)
Wheat (<i>Triticum aestivum</i> L.)		<i>Sinorhizobium</i> strains, <i>Rhizobium</i> sp., <i>Pseudomonas</i> sp., <i>Enterobacter</i> sp., <i>Acinetobacter</i> sp., <i>Bacillus</i> , <i>Pantoea</i> sp		Salinity	Plant growth-promoting bacteria isolated from halophytic weeds help germination and seedling wheat growth under saline stress	Sorty et al. (2016)
Chinese cabbage	<i>Piriformospora indica</i>			Drought	The upregulation of the expression level of drought-related genes, viz. RD290A, ANACO72, CBL1, and DREB2A in the leaves of Chinese cabbage help relieve plants of imposed drought stress	Sun et al. (2010)
Barley (<i>Hordeum vulgare</i> L.)		<i>Hartmannibacter diazotrophicus</i> E19 ^T		Salinity	<i>H. diazotrophicus</i> increased the root and shoot ratio of barley under salt stress. This growth promotion was associated with ACC-deaminase production	Suarez et al. (2015)

responses to support plant growth and development. This complex and multipronged action of soil microbes makes them a vital and viable choice for disease suppression and abiotic stress control in plants (Franken, 2012; Meena et al., 2017).

Several mechanisms have highlighted the enormous benefit of plant-associated microbiomes (Kushwaha et al., 2020; Glick and Gamalero, 2021; Adeleke and Babalola, 2022). The microbes

found in the plant root environment typically belong to the genera *Pseudomonas*, *Klebsiella*, *Aeromonas*, *Azotobacter*, *Enterobacter*, *Bacillus*, *Azospirillum*, and *Achromobacter* (Ortiz et al., 2015; Kaushal and Wani, 2016; Sorty et al., 2016; Babalola et al., 2021; Fasusi et al., 2021) (Table 1).

All rhizosphere and endosphere bacteria with the ability to maintain plant growth under different adverse soil conditions are referred to as plant growth-promoting bacteria (PGPB) (Agri



et al., 2022). There are other mechanisms plant microbes use to promote plant growth and development. IAA is produced to improve plant root development (Meena et al., 2017) where auxins initiate root growth and cell elongation. However, the high production of auxin may negatively affect root growth (Sorty et al., 2016; Akinola and Babalola, 2020). High auxin secretion also has drawbacks because of the increased ethylene production. In addition, the enzyme ACC deaminase is a key component in lowering the stress ethylene that results from both biotic and abiotic stress (Glick, 2004).

The mechanisms mentioned above have been reported in rhizosphere bacteria and fungi with enhanced phytohormones production for sustainable plant growth (Belimov et al., 2007; Ojuederie et al., 2019; Akinola et al., 2021c). Other studies have employed rhizobiomes to mitigate environmental stresses and improve the growth of crop plants in maize (Rojas-Tapias et al., 2012; Akinola et al., 2021a; Chaudhary A. et al., 2021), rice (Sharma et al., 2013), soybean (Sen and Chandrasekhar, 2014), and barley (Suarez et al., 2015).

The use of nanomaterials to relieve abiotic plant stresses

Plants possess several mechanisms needed to cope with unwanted soil conditions, including heat stress, drought, flooding, salinity, and chilling. Several researchers have studied molecular and cellular plant responses to abiotic stress

(Gepstein and Glick, 2013; Ali and Glick, 2019; Santoyo et al., 2021a). Primarily, plants respond to abiotic stress using methods, such as an increase in MAPK (mitogen-activated protein kinase), abscisic acid, ROS, increased intracellular messenger viz., polyphosphate, inositol and raised Ca^{2+} in the cytoplasm as shown in Figure 2.

Meanwhile, stress relief responses, such as regulation of the expression of specific stress genes, and the proteins involved in the protection from cellular damage are involved in the advanced level of plant response. In addition, secondary metabolites ensure physiological processes to reduce abiotic stress conditions by activating the biosynthesis of polyamines signal transduction, ROS-induced photosystem protection and stabilizing cellular structure (Oh et al., 2009; Jalil and Ansari, 2019).

In mitigating soil stresses, the plant cell wall helps in plant adaptation and guides against stress perception. Induced peroxidases modify plant cell walls, which bring together oxidative stress and ROS when in contact with plant stressors (Rouet et al., 2006; Daudi et al., 2012). When plants encounter oxidative stress, immediate defense responses, such as the regulation of gene expression, enzyme production, phenylpropanoid aggregation, and ROS are produced (Daudi et al., 2012; Jalil and Ansari, 2019).

Although plants develop various mechanisms to initiate responses against adverse conditions. Nevertheless, their responses may differ even among the same plant species. Consequently, augmentation of stress tolerance in plants and identification of tolerant plant material remains conservative and

ecofriendly methods towards sustainable agricultural practices and crop production (Akinola et al., 2022; Chaudhary et al., 2022). Nanoscience is an emerging multi-disciplinary area that involved the use of nanomaterials in different fields at the nano-level. The most promising application of nanoscience could be exploited in agroecosystem practices, food processing and packaging materials. In the current scenario, nanomaterials can be used as a tool to effectively promote plant growth and also ameliorate plant stressors (Saxena et al., 2016; Chaudhary et al., 2021b).

A lot has been done on the use of nanotechnological approaches to stress responses (Shabnam et al., 2014; Tripathi et al., 2015; Singh and Lee, 2016). The effect of NPs on sustainable plant growth and development is concentration-dependent, which also increases antioxidant enzyme activity. For example, in a study to assess the effect of TiO₂ NPs on onion seedlings, TiO₂ NPs increased the activity of the superoxidase dismutase enzyme (Laware and Raskar, 2014). Meanwhile, a drastic change in the physiological traits of the onion plant was noticed with an increased concentration of TiO₂ NPs (Laware and Raskar, 2014). Under these conditions, the activities of the catalase and amylase enzymes decreased at lower concentrations of TiO₂. In another study by Changmei et al. (2002), SiO₂ and TiO₂ NPs showed significant positive effects on the growth and sprouting of *Glycine max* seedlings.

Effect of NPs on heavy metal stressed plants

Contamination of the plant-soil environment by metallic ions is a severe menace to sustainable agricultural practices worldwide. Heavy metal stress increases plant toxicity, thus leading to retarded plant growth (Chibuike and Obiora, 2014; Jalil and Ansari, 2019). This happens due to decreased enzymatic activities induced by a continuous decrease in essential nutrients available in the soil (Sharma et al., 2012). Furthermore, heavy metal ions induce ROS production affecting the plant's physiological properties; viz., membrane permeability reduction, cell structure deformation, and degradation of available plant cell protein. To relieve the constraints attributed to heavy metal stress, plants induce defense mechanisms including the production of polyphosphates, organic acids, and metal chelates, which all reduce the influx of metal ions and activate the synthesis of antioxidants to lower ROS production. The activation of these defense mechanisms ensures resistance against heavy metal stress. Moreover, the use of synthesized NPs can reduce the burden of phytotoxicity induced by heavy metals on plants (Sharma et al., 2012; Gunjan and Zaidi, 2014; Tripathi et al., 2015).

Because of the small size and surface area of synthesized NPs, they can easily penetrate plant cells and retain a high affinity for metallic ions. In a study by Worms et al. (2012), it was reported

that quantum dots (i.e., the nanoparticles of a semiconductor) reduce Pb and Cu accessibility to plant cells. The report of Singh and Lee (2016) showed TiO₂ NPs reduce Cd toxicity and improve physiological traits, viz., plant growth, and photosynthetic rate. The study of Li and Huang (2014) with *Brassica juncea* revealed the effect of hydroxyapatite NPs in the relief of cadmium toxicity. Similarly, synthesized SiNPs helped to reduce chromium toxicity in peas (Tripathi et al., 2015). Shabnam et al. (2014) also discovered that the treatment of cowpea with AuNPs induces a reduction of Au ions to a nontoxic form by phenolic compounds of cowpea seeds (Table 2).

Effect of NPs on heat stress

Exposing a plant to an extreme temperature for a long period results in retarded plant growth and development. Heat stress reduces photosynthetic and chlorophyll content, membrane ion leakage, protein degradation, and lipid depletion. This is because an increase in ROS generation induces oxidative stress (Wahid, 2007; Karuppanapandian et al., 2011; Prasad et al., 2011). Haghghi et al. (2014) reported the effect of low concentrations SeNPs in reducing heat stress by stimulating the photosynthetic ability of plants, increasing hydration, and improving plant growth.

Anti-oxidative properties of the plant have also been improved at low SeNPs levels, while high concentrations of SeNPs induce oxidative stress (Haghghi et al., 2014). Plants induce the production of molecular chaperones and heat shock proteins during heat stress to resist oxidative stress (Hasanuzzaman et al., 2013; Hasanuzzaman et al., 2014).

Furthermore, carbon nanotubes, such as HSP90 have been used to upregulate genes involved in heat shock protein synthesis. A study by Zhao et al. (2012) showed that the exposure of maize to CeO₂NPs upregulates HSP70 and generates large amounts of hydrogen peroxide.

Effect of NPs on salinity stress

Salinity is an important abiotic stressor that deteriorates and limits the output of food crops. Owing to the susceptibility of most plants (i.e., lycophyte category) to salt stress, the majority of plant products are negatively affected, thereby reducing their economic value (Munns and Tester, 2008; Akinola and Babalola, 2020). Salinity stress hinders both physiological and biochemical processes associated with the sprouting of the plant.

Salinity causes one or more of the following: specific ionic toxicity, nutritional imbalance, and a reduced osmotic potential (Jalil and Ansari, 2019). In addition, some other critical physiological processes, such as lipid metabolism, protein synthesis, and photosynthesis, are often negatively affected (Parida and Das, 2005). The use of nano-based-fertilization

TABLE 2 Some recent reports of the effect of nanotechnology in alleviating plant stressors.

Nanoparticle	Characterization	Plant stress	Size of the nanoparticle	Test plant	Inference	References
CuNPs	SEM, XRD	Drought	30 nm–40 nm	Maize (<i>Zea mays</i> L.)	CuNPs increased carotenoid, chlorophyll, and anthocyanin levels in maize grown under drought stress. Also, reactive oxygen species (ROS) decreased as a result of the activities of scavenging enzymes	Van Nguyen et al. (2022)
MgNPs	SEM, XRD	Lead-induced	≈20 nm	<i>Daucus carota</i>	MgNPs help to detoxify ROS to mitigate Pb-induced stress and improve plant growth and nutrient uptake	Faiz et al. (2022)
Chitosan-Selenium NPs (Cs-SeNPs)	XRD, SEM, TEM	Salinity	≈50 nm	Bitter melon (<i>Momordica charantia</i>)	Cs-SeNPs alleviated the effect of salinity stress by reducing Na ⁺ aggregation, MDA and H ₂ O ₂ oxidants and increased relative water content, K ⁺ , proline concentration and antioxidant enzyme activity in plant	Sheikhalipour et al. (2021)
CeNPs	XRD, SEM	Salinity	10 nm	Rice (<i>Oryza sativa</i> L.)	CeNPs enhanced nitric oxide production by activating the transcription of <i>NIA2</i> -encoding nitrate reductase and controlling dephosphorylation of its protein which resulted in NO production and plant tolerance to salt	Zhou et al. (2021)
FeNPs	FTIR, XRD, SEM, TEM, EDS	Drought and Cadmium toxicity	18 nm–94 nm	Rice (<i>Oryza sativa</i> L.)	FeNPs decreased ROS and improved plant biomass, nutrient acquisition, photosynthesis efficiency, and other plant physiological traits. More also, Cd transporter genes (<i>OsLCT1</i> , <i>OsHMA2</i> , <i>OsHMA3</i>) were curtailed in FeNPs-treated rice plant	Ahmed et al. (2021)
SiNPs	XRD, SEM, TEM	Salinity	< 50 nm	Lentil (<i>Lens culinaris</i> Medik.)	SiNPs improved the physiological traits viz. root length, shoot length, seedling fresh and dry weight of lentil under salinity stress	Sabaghnia and Janmohammadi (2015)
ZnNPs	SEM, XRD	Drought	10 nm–30 nm	Soybean (<i>Glycine max</i>) seeds	ZnNPs were effective on seedling growth in water stress conditions	Sedghi et al. (2013)
AgNPs + 2, 4-dichlorophenoxyacetic acid	XRD, SEM	Oxidative	10 nm–40 nm	<i>Vigna radiata</i> L.	The synergistic effect of AgNPs and 2, 4-dichlorophenoxyacetic acid inhibited senescence in plants under oxidative stress	Karuppanapandian et al. (2011)
TiNPs	SEM, XRD	Cold	7 nm–40 nm	<i>Cicer arietinum</i> L.	TiNPs increased cold tolerance via an improved redox status of plant	Mohammadi et al. (2013)
SiNPs	SEM, UV-Vis, XRD	Heavy metal	10 nm–30 nm	<i>Pisum sativum</i> L.	SiNPs protected plants against phytotoxicity induced by chromium and improved plant growth	Tripathi et al. (2015)
CeNPs	SEM, XRD	Heat shock and lipid peroxidation	10 nm ± 1 nm	<i>Zea mays</i> L.	Improved plant growth under heat shock	Zhao et al. (2012)
TiNPs	SEM, XRD, TEM	Heavy metal	< 100 nm	<i>Glycine max</i>	TiNPs increased Cd uptake and minimize stress induced by Cd on soybean	Singh and Lee (2016)

(Continued on following page)

TABLE 2 (Continued) Some recent reports of the effect of nanotechnology in alleviating plant stressors.

Nanoparticle	Characterization	Plant stress	Size of the nanoparticle	Test plant	Inference	References
SiNPs	XRD, SEM, TEM	Salinity	20 nm–30 nm	Basil (<i>Ocimum basilicum</i>)	Significantly increased the morphological and physiological traits of plants under salt stress	Kalteh et al. (2018)
Single-walled carbon nanotubes (SWNTs)	ICP-MS, SEM	Drought	10 nm–20 nm	<i>Arabidopsis thaliana</i>	Plant nanotubes augmented photosynthetic and biochemical sensing	Giraldo et al. (2014)
TiNPs	SEM, TEM	Drought	20 nm–30 nm	Wheat	TiNPs increased the agronomic traits of plants under drought stress	Jaberzadeh et al. (2013)
TiNPs	SEM, XRD	Cold	7 nm–40 nm	<i>Cicer arietinum</i> L.	TiNPs induced positive physiological effects on plant cells	Hasanpour et al. (2015)
SeNPs	XRD, SEM	High and low tempt	20 nm–30 nm	<i>Lycopersicon esculentum</i>	SeNPs helped to improve plant growth under high and low-temperature stress	Haghighi et al. (2014)
Hydroxyapatite (HAP) NPs	SEM, TEM	Heavy metal (Cd)	10 nm–40 nm	<i>Brassica chinensis</i> L. (bok choy)	HAPNP reduced Cd uptake and other effects of Cd-contaminated soil	Li and Huang (2014)
SiNPs	XRD, ICP-MS, SEM	Drought	10 nm–30 nm	Hawthorn (<i>Crataegus</i> sp.)	Increased plant biomass, xylem water potential, and malondialdehyde (MDA) content	Ashkavand et al. (2015)
SiNPs	TEM	Drought	10 nm–15 nm	Wheat grass (<i>Agropyron elongatum</i> L.)	SiO ₂ NPs significantly increased seed germination of tall wheat grass	Azimi et al. (2014)
TiNPs	TEM, SEM	Drought	≈21 nm	Onion (<i>Allium cepa</i>)	TiNPs enhanced seed germination and seedling growth. It also increased the activities of hydrolytic and antioxidant enzymes, amylase, protease, and SOD	Laware and Raskar (2014)
AgNPs	XRD, SEM	Salinity, cold, Heat and Drought	10 nm–30 nm	<i>A. thaliana</i>	AgNPs are a novel and eco-friendly method to control multiple abiotic stressors	Kohan-Baghkheirati and Geisler-Lee (2015)

Key (definition of abbreviations): SEM, scanning electron microscope, XRD—X-Ray Diffraction Crystallography, TEM, Transmission Electron Microscopy; FTIR, Fourier-Transform Infrared Spectroscopy; EDS, Energy Dispersive Spectroscopy, UV-Vis—Ultraviolet-Visible Infrared Spectrophotometry, ICP-MS, Inductively Coupled Plasma Mass Spectrometry; MDA, Malonaldehyde.

processes proffers solutions to relieve unwanted plant stresses and enhance the efficient use of plant resources. Less than 50% of applied chemical pesticides and fertilizers are used by the plant; the remainder often increases soil toxicity. This problem and many other growth-impeding factors may be effectively resolved using nanoscience (Martínez-Ballesta et al., 2016). For instance, the use of SiNPs and Si-fertilizer has a sustainable effect on the morphological and physiology of basil plants (*Ocimum basilicum*) under salinity stress. The results of this study suggested that the change in the physiological traits may be a result of tolerance induction in the basil plant, which helps to mitigate the effect of salt stress (Kalteh et al., 2018). Many other studies have shown that SiO₂NPs can relieve the effect of salinity stress. For example, Haghighi et al. (2014) and Sabaghnia and Janmohammadi (2015) showed the positive effects of SiNPs on *Lens culinaris* Medik. Under salinity stress, SiNPs was able to induce a significant increase in the

growth of *Lens culinaris* Medik seedlings and the germination of seeds. Introducing SiNPs not only enhances early seedling growth and seed germination but also improves other growth features associated with the plant under salinity stress. In the same study by Haghighi et al. (2014) on tomatoes, SiO₂NPs decreased ionic toxicity of the stressor leading to a substantial increase in the shoot, root fresh and dry weight of tomato plants under salt stress. Gao et al. (2006) showed the effect of SiO₂NPs on maize plants after long exposure to salinity stress. Applying SiO₂NPs enhanced the sprouting of the plant (Savvas et al., 2009), as shown in Table 2. The mechanism of action of silica nanoparticles reduces the Na⁺ ion concentration in the plant. As a result, limited Na⁺ ion is available for absorption by plant tissues. Since salinity stress increases Na⁺ ion uptake and osmotic potential, the process of contamination is reduced using SiO₂NPs because of this mechanism of action (Raven, 1983).

In addition, multi-walled carbon nanotubes (MCN) have been tested against salinity-stressed broccoli plants (Martínez-Ballesta et al., 2016). The MCN-treated plants exhibited increased assimilation of CO₂, aquaporin transduction, increased water uptake and modified the broccoli root plasma membrane which increased the sprouting of the plant.

Effect of NPs on chilling stress

Low temperatures can destroy plant cells because of ion leakage and permeability distortion of the plant cell membrane. This chilling stress leads to a reduction in plant growth and germination (Bhattacharya, 2022; Petruccioli et al., 2022) with tolerance to chilling varying between different plant species. The greater the damage to plant membranes, the more deleterious the effect of chilling stress on the plant (Rawat et al., 2020). In addition, photosynthesis and its biochemical components are greatly affected by chilling stress because low temperature damages the photosystems, inhibiting properties associated with light absorption, such as increasing Rubisco degradation, CO₂ assimilation, transpiration rate, and reducing the chlorophyll content (Jajoo and Mathur, 2021; Sherin et al., 2022). To ensure the relief of plants from chilling stress, NPs are used to enhance photosystem activities by inhibiting ROS production, increasing the activities of the chloroplast, and improving the production of Rubisco enzymes (Ayyaz et al., 2022; Chandel et al., 2022).

TiO₂NPs activate processes needed to enhance the synthesis of chlorophyll and the expression of the Rubisco binding protein gene, improve leaf pigment, antioxidant enzyme synthesis, and decrease the effect of chilling stress by reducing plant cell damage and ion leakage (Asadi and Cheniany, 2022; Sardar et al., 2022; Zare et al., 2022). Low-temperature stress upregulates the expression of *MeAPX2* and *ZnSOD/MeCu* genes, which increases glutathione reductase, dehydroascorbate reductase, and monodehydroascorbate activities that remove ROS. It also helps to reduce oxidative stress (Sonkar et al., 2021). The use of TiO₂NPs to reduce chilling stress has restructured plant biochemical physiognomies whenever plant cells are exposed to low-temperature environments (El-Gazzar et al., 2020; Elsheerya et al., 2020; Nasr et al., 2021).

Effect of NPs on drought stress

Soil drought is an abiotic stress limiting crop productivity in arid and semi-arid regions (Gamalero and Glick, 2022). Several studies have highlighted the effects of silicon NPs on drought-induced plant stress. For instance, SiNPs have been used to relieve the impact of drought stress on hawthorns (*Crataegus sp.*) (Ashkavand et al., 2015). The aforementioned study was conducted using different concentrations of SiNPs, depending

on the severity of the stress. Biochemical and physiological responses differ in plant seedlings based on the positive effect of SiNPs on carbohydrate contents, proline, leaf pigments, membrane leakage, water content, malondialdehyde, and photosynthetic parameters (Ashkavand et al., 2015). A study was conducted to test the effect of SiNPs on two different sorghum (*Sorghum bicolor* (L.) Moench) cultivars with different drought tolerance susceptibility patterns, maintaining the photosynthetic rate and reducing the root-to-shoot ratio. This showed that SiNPs was able to augment plant water uptake efficacy (Hattori et al., 2005). Also, a low concentration of sodium silicate was used to mitigate the effect of drought stress on wheat (Pei et al., 2010). The silicon content of the compound was able to maintain the leaf potential in water absorption, improve the leaf chlorophyll content, and enhance shoot growth. Although the mechanism of action of this compound is yet to be determined, silicon compounds have been reported to be involved in the reduction of plant membrane lipid peroxidation.

In soybean, ZnONPs have been reported to boost the resilience of soybean plants to drought stress (Sedghi et al., 2013). This study revealed that the application of ZnONPs helped in the germination of soybean in a drought-stressed plant; an effect attributed to the role of Zn in the improvement of seed viability and sprouting of plant seeds in Zn deficient areas (Degenhardt and Gimmler, 2000).

Iron is an essential nutrient needed for plant growth and development; an iron-deficient plant shows physiological change, viz., chlorosis and reduced metabolism (Jalil and Ansari, 2019). Micronutrients can be used to relieve the effects of drought stress in some plants. Davar et al. (2014) showed the impact of exogenous FeNPs in the flowering and fruiting stages of a plant under drought stress. In addition, to reduce the adverse effects of drought stress, TiO₂NPs have been applied to the leaves of wheat to improve agronomic and physiological features, such as gluten, starch, photosynthetic activities, biomass, harvest index, final yield and plant weight (Jaberzadeh et al., 2013).

Plant microbes in agriculture to address future food scarcity

Some bacteria and fungi can colonize the internal tissues of their host plants without causing any detrimental effects (Adeleke and Babalola, 2021b). Various bacterial and fungal endophytes produce plant growth traits, such as siderophores, nitrogen fixation, phosphate solubilization, antibiotic production and induced systemic resistance to various environmental stresses (Santoyo et al., 2016; Adeleke et al., 2021).

Plant roots absorb water and minerals from the soil, then translocate them to other plant parts (Liu et al., 2021). In addition, the plant produces copious amounts of exudates such as amino acids, organic acids, and sugars into the soil which are utilized by soil microbes and contribute to the

TABLE 3 Various endophytic microbes inhabiting crop plants and their functions.

Endophyte	Plant(s)	Functions	References
<i>Burkholderia seminalis</i> strain 869T2	<i>Arabidopsis</i> , loose-leaf lettuce, romaine lettuce, red-leaf lettuce, and Chinese amaranth	Plant growth promotion, auxin production, siderophore synthesis, and phosphate solubilization	Hwang et al. (2021)
<i>Cyanobacteria (Nostoc punctiforme</i> PCC 73102)	Rice (<i>Oryza sativa</i>)	When these organisms are inoculated into the roots of rice, they produce heterocysts and nitrogenase activity that contributes to plant growth under a limited nitrogen supply	Álvarez et al. (2020)
<i>Firmicutes</i>	Tomato (<i>Solanum lycopersicum</i>)	These endophytes dominate different cultivars of tomato promoting resistance against <i>Ralstonia solanacearum</i>	Sahu et al. (2020)
<i>Proteobacteria, Bacteroidetes, Firmicutes, Actinobacteria</i>	Sugarcane (<i>Saccharum officinarum</i>)	These organisms were isolated from sugarcane leaves, sheaths, and roots. They contributed to plant growth promotion	Teheran-Sierra et al. (2021)
<i>Klebsiella</i> MK2R2, <i>Bacillus</i> B2L2, <i>Enterobacter</i> E1S2	Maize (<i>Zea mays</i>)	These endophytic organisms have the potential to improve the growth of maize and nitrogen fertilization	Mowafy et al. (2021)
<i>Pseudomonas protegens</i> MP12	Grapevine (<i>Vitis vinifera</i>)	This organism colonizes inner grapevine tissues, and contributes to antifungal ability, preventing mycelial growth of certain grapevine phytopathogens	Andreolli et al. (2021)
<i>Rhizobium (Bacillus siamensis)</i>	Chickpea plants (<i>Cicer arietinum</i> L.)	This rhizobium had various PGP features including nitrogen fixation, phosphate solubilization, ACC deaminase, IAA production, synthesis of hydroxamate-type siderophores	Gorai et al. (2021)

microbial biomass in the root environment (Lyu et al., 2021). Also, seeds produce low molecular weight organic exudates into the surrounding soil during germination. Several endophytes have been reported to be present in the endosphere (He et al., 2021).

Endophytic relationships with the host plants can be symbiotic or pathogenic. Often, essential and uncommon organic substances are secreted by endophytes that assist in providing various functions, not only for soil health but also as a solution to plant stress challenges. Endophytes can often protect plants from phytopathogens and abiotic stresses (Table 3).

The impact of abiotic stressors on plant growth and soil health can be major or minor depending on the prevailing environmental conditions (Sachdev et al., 2021). Abiotic stresses negatively affect crop production and microbial diversity (Chouhan et al., 2021). Various mechanisms employed by endophytic microorganisms induce systemic resistance (ISR) or abiotic stress tolerance in plants (Gupta et al., 2021). Therefore, there is a need to restructure modern agricultural systems to include recent developments in endosphere biology (Santoyo et al., 2021b). Some studies have explained the role of endophytic bacteria in agricultural systems under abiotic stresses in combating future food scarcity. For instance, *B. amyloliquefaciens* RWL-1 producing ABA can enhance rice yield in soil with a high salt concentration (Ganie et al., 2021). This bacterium produces essential amino acids and salicylic acid which assist rice growth in salinity/drought conditions (Thepbandit et al., 2021). The endophytic fungus, *Bipolaris sp.*, produces gibberellins which contribute to the growth of *Glycine max* (Lubna et al., 2022). *Sphingomonas sp.* LK11 is an endophyte from leguminous plants that also

synthesizes gibberellins which enhance tomato growth and the plant chlorophyll content (Adeleke and Babalola, 2021a).

Various reports revealed the presence of IAA-producing endophytic bacteria (Rashid et al., 2012; Panigrahi et al., 2020; Turbat et al., 2020). *Burkholderia kururienensis* is an endophyte that stimulates the expression of IAA genes, especially in the roots of transgenic rice, thereby contributing to rice growth (Zhou et al., 2020).

Some endophytes are halotolerant, which can be isolated from the weed *Psoralea corylifolia* to assess their PGP activity in wheat. The growth of wheat plants can be improved with the aid of an extract from the bacterial isolates during the production of IAA under saline-stress conditions (Amini Hajiabadi et al., 2021). The identification of various strains embedded in weeds revealed various genera including *Acinetobacter*, *Enterobacter*, *Marinobacterium*, *Pseudomonas*, *Rhizobium*, and *Sinorhizobium* (AlSharari et al., 2022). The hormone cytokinin is also produced by some endophytic bacteria, according to Eid et al. (2021). *Pseudomonas resinovorans* and *Paenibacillus polymyxa* isolated from *Gynura procumbens* are good examples of endophytic bacteria producing cytokinin (Eid et al., 2021). From a bacterial culture, the obtained extracts were tested *in vitro* and inoculated into the cotyledon of cucumber to observe their cytokinin activity.

A strain of *Sinorhizobium meliloti* engineered to overproduce cytokinin by transferring the *Agrobacterium tumefaciens ipt* gene into the bacterium, and a strain of *Pseudomonas spp.*, that protected alfalfa plants from drought-stressed conditions (Oleńska et al., 2020), these two bacteria were inoculated together or separately, in the cultivation of sorghum (*Sorghum bicolor*). The results revealed that the two strains inoculated together reduced the requirement for chemical nitrogen fertilizer

TABLE 4 The biological activities of nanoparticle-synthesizing endophytic microbes against plant pathogens.

Endophytic organisms	Plant pathogens	Microbial activity	References
Silver (Ag) Nanoparticle			
<i>Alternaria alternate</i>	<i>Bacillus cereus</i> , <i>Klebsiella pneumoniae</i> , <i>Pseudomonas aeruginosa</i> , <i>E.coli</i> , <i>Staphylococcus aureus</i> , <i>Proteus mirabilis</i>	Antibacterial and antioxidant	Govindappa et al. (2022)
<i>Micromonospora</i> sp. SH121 (Mm-AgNPs)	<i>Bacillus cereus</i> , <i>Enterococcus faecalis</i> , <i>Enterococcus hirae</i> , <i>Escherichia coli</i> , <i>Klebsiella pneumoniae</i> , <i>Proteus vulgaris</i> , <i>Pseudomonas putida</i> , <i>Staphylococcus epidermidis</i> , <i>Streptococcus pneumoniae</i> , <i>Aspergillus flavus</i>	Antimicrobial, antibiofilm, and anticancer	Mazmancı et al. (2022)
<i>Streptomyces</i> species	Bacterial and fungal agents	Biosynthesis and Antibacterial	ALqahtani et al. (2022)
<i>Phoma</i> sp. (MN995524), <i>Chaetomium globosum</i> (MN995493), and <i>Chaetomium</i> sp. (MN995550)	<i>Klebsiella pneumoniae</i>	Antibacterial activities	Sonbol et al. (2022)
<i>Trichoderma atroviride</i>	Pathogenic bacteria and fungi	Antibacterial, anticandidal, and antifungal effects	Abdel-Azeem et al. (2020)
<i>Pseudomonas poae</i>	<i>Fusarium graminearum</i> head blight pathogen	Antifungal	Ibrahim et al. (2020)
<i>Rhizobium pusense</i> (MS-1), <i>Bacillus cereus</i> MS-2, <i>Bacillus flexus</i> (MS-3), <i>Methylophilus flavus</i> (MS-4), <i>Pseudomonas aeruginosa</i> (MS-5)	<i>Bacillus thuringiensis</i> , <i>Azotobacter chroococcum</i> (CL13), <i>Escherichia coli</i> , <i>Pseudomonas putida</i> (ECL5), <i>Bacillus licheniformis</i> (R-1), <i>Rhizobium</i> sp. (CV1)	Antibacterial activity	Singh et al. (2022b)
<i>Talaromyces purpureogenus</i>	<i>Listeria monocytogenes</i> , <i>Escherichia coli</i> , <i>Shigella dysenteriae</i> , <i>Salmonella typhi</i>	Antibacterial activity	Sharma et al. (2022)
<i>Serratia marcescens</i> , <i>Burkholderia cepacia</i>	<i>Aspergillus niger</i> , <i>A. fumigatus</i> , <i>Fusarium oxysporum</i> , <i>Pythium</i> sp., <i>Rosellinia</i> sp	Antifungal activity	Mittal et al. (2021)
<i>Terminalia arjuna</i>	<i>Escherichia coli</i> MTCC1687, <i>Pseudomonas aeruginosa</i> ATCC9027, <i>Staphylococcus aureus</i> ATCC6538	Antibacterial activity	Singh et al. (2022a)
<i>Penicillium cinnamopurpureum</i>	<i>Bacillus subtilis</i> (MTCC-121), <i>Pseudomonas aeruginosa</i> (MCC-3097), <i>Staphylococcus aureus</i> (MCC-2043), <i>Escherichia coli</i> (MCC-3099)	Antibacterial activity	Dinesh et al. (2022)
<i>Phoma glomerata</i> , <i>Phoma herbarium</i> , <i>Fusarium semitectum</i> , <i>Trichoderma</i> , <i>Candida albicans</i>	<i>Candida albicans</i> , <i>Pseudomonas aeruginosa</i> , <i>E. coli</i> , <i>Bipolaris sorokiniana</i> , <i>Magnaporthe grisea</i>	Antibacterial, antifungal, and insecticidal activity	Shinde et al. (2022)
Gold (Au) Nanoparticle			
<i>Phoma</i> sp	<i>Rhizoctonia solani</i> AG1-IA, <i>Xanthomonas oryzae</i>	Antifungal and antibacterial activity	Soltani Nejad et al. (2022)
<i>Pseudomonas aeruginosa</i>	<i>Vigna unguiculata</i>	Plant growth enhancement/promotion	Panichikkal and Krishnankutty, (2022)
<i>Aspergillus terreus</i>	<i>Fusarium oxysporum</i> , <i>Rhizoctonia solani</i>	Antimicrobial, antioxidant, and antifungal activity	Mishra et al. (2022)
<i>Alternaria alternate</i> , <i>Fusarium</i> species	Cervical carcinoma (HeLa), breast carcinoma (MCF-7), non-small cell lung carcinoma (H1975), hepatocellular carcinoma cell line (Hep G2)	Anticancer activity	Ravi et al. (2022)
<i>Aspergillus</i> sp., <i>Alternaria</i> sp	<i>Escherichia coli</i> , <i>Staphylococcus aureus</i>	Antibacterial, antifungal, and antitumor activities	Mostafa et al. (2022)
<i>Lysinibacillus odysey</i>	<i>Staphylococcus epidermidis</i> <i>Staphylococcus aureus</i> , <i>Streptococcus pyogenes</i> , <i>Enterococcus faecalis</i> , <i>Bacillus subtilis</i>	Dose-dependent antioxidant and antibacterial activity	Cherian et al. (2022)
Zinc-oxide (ZnO) nanoparticles			
<i>Aspergillus niger</i>	<i>Staphylococcus aureus</i>	Antibacterial activity	Abdelkader et al. (2022)
<i>Enterobacter hormaechei</i>	<i>Klebsiella pneumoniae</i> (ATCC: 4617), <i>Escherichia coli</i> (ATCC: 15224), <i>Pseudomonas aeruginosa</i> (ATCC: 9721), <i>Bacillus subtilis</i> (ATCC: 6633), <i>Staphylococcus epidermidis</i> (ATCC: 14990) <i>Aspergillus fumigatus</i> , <i>Aspergillus niger</i> , <i>Aspergillus flavus</i> , <i>Fusarium solani</i> , <i>Mucor mycosis</i>	Antifungal, antibacterial, and antioxidant potential	Saqib et al. (2022)
<i>Trichoderma viride</i>	<i>Staphylococcus aureus</i> , <i>Bacillus</i> spp., <i>Pseudomonas aeruginosa</i> , <i>Klebsiella</i> spp., <i>Acinetobacter baumannii</i> , <i>Candida albicans</i>	Antimicrobial and antioxidant activities	Kaur et al. (2022)

to a low level and significantly improved the cultivation of sorghum. The procedure also enhanced the colonization effectiveness of both bacteria in the roots of rice plants (Abbaszadeh-Dahaji et al., 2020). In summary, endophytes can play a major role in modulating phytohormone levels in plants, thereby contributing to plant growth and managing various stress conditions.

Symbiotic nitrogen fixation reduces atmospheric nitrogen by the action of the leguminous plants in association with nitrogen-fixing bacteria, increasing the plant's nutritional value (Rana et al., 2020). Several years ago, the only known nitrogen-fixing bacteria in legume nodules were rhizobia. However, numerous non-rhizobial bacterial species have been found in legume root nodules. Hanaka et al. (2021) reported how an endophytic bacteria isolated from the soybean, *Bacillus mojavensis*, exhibited biocontrol activity against the soybean pathogenic fungus, *Rhizoctonia solani*. These endophytic microorganisms have antagonistic activity against soil-borne pathogens and possess the ability to enhance the growth of soybean plants. The *B. mojavensis* strain produced ammonia, HCN, and siderophores. It also contributed to chitinase activity and solubilization of phosphate (Hanaka et al., 2021). The inoculation of this endophyte onto soybean seeds can help control various pathogens.

The introduction of nanotechnology in agriculture is a developing sector in agriculture despite several applications, and the true possibilities are yet to be obtained. Nanotechnology constitutes certain substances with unusual features that are revealed either as a result of the quantum confinement effects or the production of certain reactive surfaces that are at a nanoscale (Umapathy et al., 2022). The nanoscale degree when compared with the macroscopic level, reveals the properties of the material that are special as a result of the reduced size, shape of nanomaterials, and greater surface area-to-weight ratio. Nanomaterials or nanoparticles (NPs) have beneficial properties, with high reactivity, modified bioactivity, and surface effects (Bruchiel-Spanier et al., 2022). NPs are produced by either a single element like silver (Ag) or gold (Au) or by a mixture of elements, which are observed in those constituting oxides like titanium oxide (TiO₂), silicon oxide (SiO₂), and zinc oxide (ZnO) (Behl et al., 2022). Gold and silver NPs regarded as inorganic NPs, are relevant as a result of their application. Although, few studies have shown how the NPs are manufactured from endophytes (Fadiji et al., 2022a; Kaur et al., 2022; Saqib et al., 2022), thus suggesting possible means for continuous studies on endophytic nanoparticles.

Various approaches including biological, chemical, and physical approaches are made use of in the production of NP, yet, the process of biosynthesis is environmentally friendly, free of chemical derivatives that are hazardous to humans, animals, and the environment. These chemicals have been used recently to reduce the potential of applying chemicals in the biomedical and food processing industries. Several procedures involving

intracellular and extracellular for the biological synthesis of nanomaterials coexist in nature. In this field, the study is still understudied (Qian et al., 2022). The production of environmentally friendly, and non-toxic biological materials for manufacturing NPs would result in supporting the production of natural materials with the aid of living organisms (Fadiji et al., 2022a).

NPs produced from metal-based are manufactured by microorganisms through extracellular and intracellular mechanisms (Franco et al., 2022). The process of electrostatic induction takes place in metallic ions between negative and positive charges intracellularly in the cell wall of the microorganisms, followed by the decrease of the metal ions to their metallic form. Cell disruption is a constitutional prerequisite to acquiring pure NPs (Fadiji et al., 2022a). The biomass extracts from the cell, or culture supernatant when added to the solution of metals produce NPs outside the cell of the microorganisms (extracellularly) (Jadoun et al., 2022). Reductases are produced and liberated into the culture medium by cofactors, with microbial cells that execute this procedure. Endophytic microbes have been suggested as biofactories for the synthesis of metal-based NPs with agricultural and therapeutic applications. These microbes are embedded in plants intercellularly, producing a symbiotic link (Roy et al., 2022). The advantage confers on the plant by the endophytes is to improve health status *via* various mechanisms, like the release of antimicrobial (antibacterial and antifungal) compounds and the secretion of growth-promoting metabolites (Shahid et al., 2022).

In plant tissues, endophytic microbes accommodating them can produce nanoparticles, which are advantageous to the host plant by promoting plant growth or reducing the prevalence of diseases (Koné et al., 2022). Endophytes can resist metals occurring in the environment to alleviate toxicity and stress in the host plant, as well as improve their beneficial association and adaptation over other microbes inhabiting the ecosystem (Mathur and Ulanova, 2022). The potential of endophytes to take away metals can be applied to manufacture metal-based NPs *via* extracellular and intracellular processes (Table 4). Typical examples were obtained in the production of AgNPs, which have a spherical shape and a mean size of 22 nm–45 nm, which can be manufactured intracellularly employing the supernatant of Ag-resistant *Bacillus safensis* TEN12 (Ahmed et al., 2020). Zinc oxide (ZnO) NPs sized 2 nm–9 nm, were produced extracellularly by the zinc-tolerant endophyte *Curvularia geniculata* (Ahmed et al., 2020). Gürsoy et al. (2021) reported how gold nanoparticles (AuNPs) sized 20 nm–40 nm were produced intracellularly in the cell wall and cytoplasm of *Chlorella sorokiniana*. Cobalt oxide nanoparticles (CoONPs), which are spherical at 20 nm in diameter, were produced extracellularly by the *A. nidulans* that are CoO-tolerant (Ahmed et al., 2020). *Aspergillus nidulans* are endophytes, which reveal the potential of the CoO-tolerant produced spherical CoONPs with a diameter of 20 nm through an

extracellular tract (Fadji et al., 2022a). Endophytic microorganisms can produce some biological active materials with a broad gap of structural and biological potential, which can be employed to examine the health and promote plant growth and are significant in improving the sustainability of agriculture (Kumar and Nautiyal, 2022). Fungi and bacteria isolated from parts of plants can be cultured in the laboratory under the most desirable growth conditions to synthesize NPs with the needed characteristics for application in the agricultural sector (Elnahal et al., 2022).

Fate of NPs

The use of NPs for agroecosystem practices could be a very complicated matrix and information on the fate of nanomaterials in the soil is inadequate. After applying NPs to the soil, they are absorbed in the plant tissue directly. Such interaction could either increase or decrease the bioavailability and toxicity of NPs depending on the physicochemical properties of the soil. However, the potency of NPs is most dependent on the type of crop and the properties of the soil *viz.*, microbial community, clay content, ionic strength, pH, salinity, organic matter, etc., (Reddy et al., 2016; Thiagarajan and Ramasubbu, 2021).

Effect of microbial community

Plant endophyte and the microbial community helps in the transformation of NPs. They help to recycle nutrients, effectively decomposition of organic compounds and conserve soil quality. The introduction of nanomaterials could affect microbial inhabitation which invariably reduces plant productivity (Jacoby et al., 2017; Chavan et al., 2020). The effect of NPs on the rhizosphere bacteria of butter crunch lettuce was reported by Kibbey and Strevett (2019). NPs and rhizosphere bacteria react together *via* electrostatic interactions that affect the surface properties of bacteria, which disallow easy attachment to the root surfaces of the plant. They also reported that fluctuations in soil mineral nutrients (P, Fe, Mn, etc.) were a result of spiked biosolid amendment of soil with NPs, which affects soil microbial load. Withal, NPs were also reported to have affected the sequestration of plant nutrients and other agroecosystem processes as reported by Bellani et al. (2020).

At times, NPs may also inhibit the colonization of plant growth promoters when combined with other nutrients. This deleterious effect was reported by Liu et al. (2020). Here, the negative effect associated with the combination of TiO₂NPs with Cu₂ (OH)₂ CO₃ was reported. The synergy between TiO₂NPs and Cu₂ (OH)₂ CO₃ boosted photocatalytic disinfection processes that disabled the effect of microorganisms such as *Fusarium graminearum* and *E. coli* within a short time of application (Liu et al., 2020).

Effect of clay content

Another important component that determines the fate of NPs is the clay content of the soil. The high the clay content of the soil, the decreased mobility of NPs because both the physical straining and electrostatic interactions would be increased. However, the soil retention capacity depends mainly on the clay to NPs ratio. The higher the ratio, the better the soil retention capacity (Shah et al., 2016). Metals are easily retained in the soil when there is an increase in the clay content. And as such reduces the uptake of metallic ions by the plant. This simply indicates the low toxicity of metallic NPs (Larue et al., 2018; Thiagarajan and Ramasubbu, 2021).

Effect of natural organic matter

NOM influences the stability and aggregation of NPs within the soil. NOM includes mobile and reactive organic fractions *viz.* hydrocarbons, amino acids, hydrophilic acids, fatty acids, fulvic, and humic acids. NOM is produced through the disintegration of animal and plant remains in the soil. Sludge-amended soil and NOM have been reported to cover 10.9% and 8.9% of soil, respectively. Meanwhile, the physicochemical properties of NPs and features of proximal soil are usually influenced after the adsorption of NOM (Bakshi et al., 2019). A recent study by Zhang et al. (2020) showed the stability of TiO₂NPs when introduced to a paddy field with high organic matter. In another study that demonstrated the effect of a high concentration of NOM on the bioaccumulation of NPs, the ability of NOM to retrain NPs could be attributed to the change in the surface area of soil as a result of an increase in the concentration of NOM. The interaction of NPs with NOM alters the binding property of the soil to improve the steric repulsion between nanomaterials by aggregating and retaining them in the soil. Asides, the reaction of NPs and NOM depends greatly on their particle sizes through hydrophobic interaction (Lee et al., 2011).

Conclusion

Globally, crop improvement and productivity are faced with diverse abiotic stress challenges. To avert this problem, the use of nanomaterials from endophytic microbes has the potential to mitigate the effects of abiotic stresses affecting plants by stimulating plant defense mechanisms. Beneficial endophytic microbes as bioinoculants can be effectively harnessed for various ecological purposes such as abiotic stress reduction, nutrient absorption, enhancing photosynthesis, increasing plant growth parameters, and obviating agrochemical use. Additionally, the nanomaterial synthesizing endophytic microbes promise to improve crop productivity sustainably.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

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