

Potential innovations from the application of beneficial soil microbes to promote sustainable crop production

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Abstract. Crop productivity may be significantly inhibited by factors, such as increased temperature, soil erosion, pathogen and pest attacks, and drought and salt stresses, mostly resulting from global climate change. However, microorganisms that are found in the rhizosphere can aid in the mobilization of essential soil nutrients, facilitate plant growth, and reduce abiotic and biotic stresses of plants. Soil microbes accomplish these beneficial functions via several mechanisms. Here, an elaborate description of the molecular mechanisms of plant growth-promotion by soil microbes and the potential of these organisms to be used as biofertilizers and biopesticides to improve plant health is provided. In addition, the possible revolution that could be realized by the synergism of these beneficial microbes with nanotechnology is discussed. While the use of biofertilizers to enhance plant growth has been demonstrated to be a beneficial phenomenon, this approach has often failed to yield the desired result in field applications. However, identifying microbial species with beneficial attributes and combining them with nanotechnology tools like nanoencapsulation and biosensors could lead to the formulation of important agriproducts (nanobiopesticides and nanobiofertilizers) that will ensure sustained

delivery of the agriproducts and facilitate early detection and proper management of plant pests and diseases. It is anticipated that precision farming will improve agricultural sustainability by increasing crop production for the steadily increasing world population.

Keywords: biofertilizers, secondary metabolites, nanoencapsulation, quorum sensing, volatile organic compounds, sustainable agriculture.

Introduction

The world population continues to increase with predictions that it will reach 8 billion by 2025 and up to 9 billion by 2050, requiring a large increase in food production to meet the nutritional demand of the growing population (McCarthy *et al.*, 2018; Meybeck *et al.*, 2018; Tripathi *et al.*, 2019). Modern agriculture is challenged with inadequate/insufficient supply of nutrients for plant growth, insects and pest attacks, and drought and salt stresses. Another important issue affecting agricultural productivity is soil erosion in which nutrients from topsoil are washed into deeper soil layers. Also, the contamination of soils by heavy metals and chemicals from the excessive use of synthetic fertilizers, which eventually end up in water bodies, makes it difficult to access good drinking water (McCarthy *et al.*, 2018; Osman, 2018). Ironically, in an effort to increase agricultural productivity, farmers have resorted to the excessive use of synthetic fertilizers to boost the nutrient composition of soils (Shabbir *et al.*, 2019).

To ensure the maintenance of sustainable agriculture, an increase in crop productivity is necessary. This can be achieved by the provision of essential nutrients, including nitrogen (N), phosphorus (P), and potassium (K) in the soil for plant use. Furthermore, certain traits like better nutritional value, drought and salt tolerance, disease resistance, and heavy metal resistance are required by food crops to boost their productivity. Sustainable agriculture is achievable because certain soil microbial communities, often known as plant growth-promoting microbes (PGPM), assist plants in making the afore-mentioned attributes available for plant use. The consequences of using soil microbial biomass are an increase in water use efficiency as well as the nutrient uptake capacity of plants (Schütz *et al.*, 2018). These microbial communities colonize the plant rhizosphere and favor plant growth. They are also essential in the improvement of plant growth, health, and yield without contaminating the environment (Odelade & Babalola, 2019).

The past few decades have seen the application and commercialization of some plant growth-promoting bacteria (PGPB) strains, including those of *Bacillus*, *Streptomyces*, *Pseudomonas*, *Klebsiella*, *Serratia*, *Azotobacter*, *Enterobacter*, *Variovorax*, and *Azospirillum* as biofertilizers (Alori & Babalola, 2018; Reed *et al.*, 2013). Certain fungi, including arbuscular mycorrhizal fungi (AMF), *Trichoderma* (*T. viride*, *T. harzianum*, *T. polysporum*, and *T. koningii*), *Aspergillus niger*, *A. fumigatus*, *Saccharomyces* sp. and algae (microalgae) have also been used as biofertilizers for improvement in crop growth (Abbey *et al.*, 2019; Kamal *et al.*, 2018; Win *et al.*, 2018). Despite this progress, their universal application in the agricultural sector represents only a very small fraction of agricultural practice because of the inconsistency in the growth of plants following inoculation with PGPM (Maçik *et al.*, 2020). To effectively enhance plant growth, PGPM must be environmentally friendly, exhibit high rhizosphere competence, interact well with other rhizosphere microbes, and tolerate environmental conditions like oxidizing agents, UV radiation, and heat (Alori & Babalola, 2018; Babalola, 2010). To facilitate a large increase in agricultural yield and food production PGPM possessing the above-mentioned qualities are greatly needed.

Recent advancements in PGPM formulations have incorporated technologies such as biosensors and nanoencapsulation, which are essential for developing biofertilizers and biopesticides (Gouda *et al.*, 2018). The incorporation of microbes with plant growth-promoting traits and nanotechnology in the development of new formulations of biofertilizers can both promote crop productivity and enhance agricultural sustainability. This review discussed the various strategies employed by PGPM to enhance plant growth, improve soil fertility, and control agricultural pests. It also explored the innovative agricultural products that nanobiotechnology can introduce, which will increase crop production and promote agricultural sustainability in a changing climate.

Importance of soil microbes on plant growth and health

The rhizosphere microbiome, defined as the entire genome of the microbial communities in the roots surrounding soils, performs important roles in plants including facilitating the production of metabolites, uptake of nutrients, as well as tolerance to both abiotic and biotic stresses (Chukwuneme *et al.*, 2020). Plants living within an ecosystem exist as colonies, rather than as individual entities. They live along with the plant microbiota (bacteria, fungi, viruses, protists, nematodes), working together to influence plant growth and productivity (Glick & Gamalero, 2021). The current methods of culturing microbes have only been able to culture about 1% of microorganisms in the soil, thereby underestimating

the microbial diversity of rhizosphere and soil microbiomes (Devi & Soni, 2020). The rhizosphere microbiome is composed of beneficial microorganisms, including the free-living bacteria that facilitate plant growth known as plant growth-promoting bacteria, the nitrogen fixers, biocontrol agents, and the mycorrhizal fungi (Ajilogba *et al.*, 2013; Gouda *et al.*, 2018). This microbial habitat is also inhabited by microbes that exert deleterious effects on plant growth, i.e., pathogenic microbes (Orozco-Mosqueda *et al.*, 2018). The use of modern sequencing technologies has expedited the identification of a large number of soil microbes, most importantly, bacteria dwelling in the rhizosphere plant microbiome (Mohanram & Kumar, 2019). The rhizosphere microbiome is dominated by Proteobacteria, Firmicutes, Bacteroidetes, Acidobacteria, Actinobacteria, Planctomycetes, Chloroflexi, Verrucomicrobia, Cyanobacteria, Gemmatimonadetes, Ascomycota, Basidiomycota, Glomeromycota and ectomycorrhizal fungi (Trivedi *et al.*, 2020). The interactions between plant roots and the rhizosphere microbes enable plants to cope with environmental disturbances by identifying and reacting to external stimuli, leading to specific modifications in plant growth and development (Mohanram & Kumar, 2019). Plant health is highly reliant on the ecological services of microbes that act in association with the plant, which includes protecting the plant against disease pathogens, tolerance to environmental stresses and biofertilization.

Soil microbiome aiding in plant nutrient acquisition

In recent studies, nitrogen-fixing free-living rhizospheric and endophytic microbes of the genera *Azotobacter*, *Azospirillum*, *Achromobacter*, *Bradyrhizobium*, *Pseudomonas*, *Burkholderia*, *Bacillus*, Mycorrhizal fungi, *Trichoderma*, and *Aspergillus* have shown positive effects on crops by increasing above and below ground biomasses (Abbey *et al.*, 2019; Igiehon & Babalola, 2018a; Igiehon & Babalola, 2018b; Kamal *et al.*, 2018). The soil microbiome also consists of several microbes that aid in the solubilization of inorganic phosphates for plant use (Babalola, 2010). These microbes include those from the bacterial genera *Aerobacter*, *Alcaligenes*, *Pseudomonas*, and *Bacillus* and those from the fungi genera *Fusarium*, *Penicillium*, *Chaetomium*, *Aspergillus*, and *Cephalosporium* (Moharana *et al.*, 2018). In the soil, inorganic phosphates are often complexed with metal ions including Fe^{3+} , Al^{3+} , and Ca^{2+} and can be solubilized into hydroxyl ions (OH^-) or organic acids released by phosphate solubilizing bacteria (Etesami *et al.*, 2021; Mohanram & Kumar, 2019). Phosphate solubilizing microbes often secrete various phosphatase enzymes that aid in mineralizing organic P from the soil. In addition, they secrete protons and organic acid anions like malate, citrate, and oxalate that assists in solubilizing inorganic P (Moharana *et al.*, 2018).

Rijavec and Lapanje (2016) proposed that hydrogen cyanide (HCN) increases the availability of P indirectly by metal chelation.

Some microbes in the rhizosphere microbiome with sequestering capabilities participate in the uptake of trace elements like zinc (Zn) and Fe, whose low concentration in the soil may result in a decrease in crop yields (Kumar *et al.*, 2017). An abundance of Fe exists in the soil. However, the majority of this nutrient occurs in forms that are not readily accessible to plants. Rhizosphere bacteria like *Plantibacter*, *Streptomyces*, *Pseudomonas*, *Curtobacterium*, and *Stenotrophomonas* have been shown to mobilize Zn by acidifying the medium through the production of gluconic acid (Costerousse *et al.*, 2018). Their roles also include the release of organic acid anions known as siderophores that chelate and transport ferric ion (Fe^{3+}) to plant cell surfaces, where they are reduced to ferrous ion (Fe^{2+}) (Sabur, 2019). Siderophores also act to deprive pathogenic microbes of Fe, thereby curtailing their growth (Babalola, 2010). Some common microbial siderophores include pyoverdine, achromobactin, citrate, ferrioxamines, pyochelin, enterobactin, ferrichromes, and yersiniabactin (Aznar & Dellagi, 2015). The promotion of iron nutrition through siderophores has been successful in dicotyledonous and gramineous plant species by fluorescent *Pseudomonads* (Orr & Nelson, 2018). It has also been shown that certain Zn mobilizing bacterial strains increase the uptake of Zn by plants, and as a consequence increase the yields of many crops like wheat, soybean (Bhatt & Maheshwari, 2020), and rice (Vaid *et al.*, 2020). The mechanisms used by these bacteria in the mobilization of Zn in the root microbiome of plants are not especially clear. However, their mode of action is analogous to the phosphate solubilizing microbes and Fe mobilizers, which include the use of organic acids and chelating agents.

Plant growth-promoting microbes can reduce the inorganic fertilizer requirement of various plants by facilitating nutrient acquisition. The study of Ye *et al.* (2020) demonstrated that 75% of inorganic fertilizer application combined with bioorganic fertilizer increased the yields of tomato plants to the same extent as those plants treated with 100% inorganic fertilizer application. In another study, soil nutrient status and the growth of wheat plants were improved by the combined application of bacterial consortia with 75% of the (previously determined) optimal amount of chemical fertilizer (Wang *et al.*, 2020). The results showed that inoculation of wheat plants with bacterial consortia resulted in increased N, P, and K contents by 97.7, 96.4, and 42.1%, respectively. According to the authors, plant height, fresh and dry weight, tiller counts, and N, P, and K contents of soils were the same in the treatment with combined PGPB and 75% fertilizer and that with 100% fertilizer treatment.

Similarly, the combination of nitrogen-fixing and phosphate-solubilizing bacterial strains with a half dose of urea (nitrogen) and di-ammonium phosphate (DAP, phosphorus) fertilizers enhanced the growth and yield of *Brassica juncea* plants (Maheshwari *et al.*, 2010). Also, the addition of urea and DAP granules with a mixture of *Bacillus* sp. KAP6 slurry and compost improved the nutrient use efficiency (NUE), photosynthetic rate, growth, and yield of wheat (Ahmad *et al.*, 2017). Moreover, the nutritional quality of organic fertilizers, such as farmyard manure and composts, can be improved by inoculation with beneficial microbial strains. For instance, the application of an integrated organo-mineral fertilizer composed of farmyard manure and compost, inoculated with a microbial consortium consisting of several phosphorus-solubilizing bacteria, i.e., *Azotobacter*, and *Rhizobium* sp., in soybean and fenugreek fields resulted in increased nutrient content, yield, and biomass of the plants (Biswas & Anusuya, 2014). The combined application of biogas slurry, humic acid, arbuscular mycorrhizal fungi (AMF), *B. ciculans*, and *Azotobacter chroococum* on maize seeds resulted in increased growth, yield, and nutrient uptake of the plants as well as increased microbial activity by improving the levels of mycorrhizal colonization, increasing the dehydrogenase and phosphatase enzymes, and bacterial count (Gao *et al.*, 2020).

Plant productivity enhancement is another function of the rhizosphere microbiome. The organisms in the plant rhizosphere help to decompose organic matter, which eventually results in a positive increment in soil fertility. Some bacterial species, including *Cellulomonas* sp., *Sporocytophaga* sp., *Pseudomonas* sp., *Streptomyces* sp., *Cytophaga* sp., and *Chryseobacterium gleum*, can degrade plant biomass and, as a result, release nutrients for plants to absorb (Ahmed *et al.*, 2018). Thus, rhizosphere microbes can facilitate plant growth even in soils with inadequate nutrients.

Signaling events in the plant microbiome

Soil microbiome and production of plant hormones

The major drivers in the regulation of plant growth and development are phytohormones, which also participate in molecular signaling in reaction to abiotic conditions that either curtail plant growth or develop into poisonous substances when uncontrolled (Caddell *et al.*, 2019). Several microbes have been recognized to release hormones for uptake by plant roots. Several other groups have been manipulated in such a way as to maintain hormonal balance in plants for growth promotion and stress response. Many PGPM are capable of producing auxins that strongly promote root architecture and growth (Duca *et al.*, 2014; Kour *et al.*, 2019; Subrahmanyam *et al.*, 2020). Indole-3-acetic acid (IAA) is

the most widely used and studied auxin produced by PGPM (Afzal *et al.*, 2015). The role played by external IAA depends on the levels of internal IAA in plants. Therefore, when the IAA concentration in plants is high, the application of microbial IAA may cause positive, negative, or even neutral effects on plant growth (Wenz *et al.*, 2019). In a study, auxin-producing PGPB were reported to induce transcriptional changes in defense, hormone biosynthesis, and genes that were related to the cell wall of the plant (Kandaswamy *et al.*, 2019). These organisms have also been reported to induce longer roots (Tsukanova *et al.*, 2017), increase root weight, and reduce stomatal density and size (Llorente *et al.*, 2016). They also aid in the activation of genes involved in auxin response that enhance plant growth (Ruzzi & Aroca, 2015).

Moreover, in salt affected soils, the application of halotolerant PGPM typically give a much improved stimulatory effect, because they produce higher IAA under salinity conditions to significantly facilitate the growth of plants (Zhao *et al.*, 2016). Furthermore, Fukami *et al.* (2018) showed that through leaf spraying of hormonal mixtures of bacterial cultures of *A. brasilense* maize growth could be improved. A study by Zhou *et al.* (2017) demonstrated that the microbial strains *Planococcus rifietoensis*, *Micrococcus yunnanensis*, and *Variovorax paradoxus*, with multiple PGP capabilities isolated from halophytes planted in high salt environments, improved the tolerance of sugar beet plants exposed to salt stress by improving the plant photosynthetic capability, seed germination, and biomass. The inoculation of halotolerant IAA-producing bacterial strains, *Brachybacterium saurashtrense* strain JG-06, *Brevibacterium casei* strain JG-08, and *Haererohalobacter* strain JG-11 from *Salicornia brachiata* improved *Arachis hypogaea* growth under salt stress by increasing root and shoot length, dry root and shoot weight, total biomass, and plant height (Zhou *et al.*, 2017). The results of these experiments indicated the presence of reduced proline and soluble sugar contents as well as enhanced amino acid, auxin, and total protein content in inoculated *Arachis hypogaea* plants compared to uninoculated plants under salt stressed conditions (Zhou *et al.*, 2017).

Several PGPM have been reported to produce the phytohormones, gibberellins, and cytokinins (Backer *et al.*, 2018; Gupta *et al.*, 2015), even though their mechanisms of production and synthesis are still poorly understood (Frankenberger Jr & Arshad, 2020). Plant growth-promoting microbes can support the production of large amounts of gibberellins, resulting in improved shoot growth in plants (Gouda *et al.*, 2018). These hormones can alter the architecture of plant roots by interacting with auxins (Gouda *et al.*, 2018). The production of root exudates by plants could also be a result of cytokinin production by PGPM, which significantly increases the plant-associated microbial communities (Olanrewaju *et al.*, 2019).

Another plant hormone whose level is modulated by PGPM is ethylene. This hormone is gaseous, often active at concentrations of about 0.05 ml per liter. This stress hormone is often activated when plants are exposed to either abiotic or biotic stress. Ethylene buildup as a consequence of stress may either contribute to an increase in plant tolerance to stress (low levels of ethylene) or aggravate the stress reaction symptoms and aging in plants (high levels of ethylene) (Backer *et al.*, 2018). The function of ethylene production by PGPM has been examined in both stressed and unstressed environments, while most of the studies have reported the stimulation of plant growth to a greater extent under stressed conditions, such as salt stress and water deficit (Forni *et al.*, 2017; Gepstein & Glick, 2013; Rubin *et al.*, 2017). Some PGPM in the plant rhizosphere produce the enzyme, 1-aminocyclopropane-1-carboxylase (ACC) deaminase, which decreases the production of ethylene in plants (Bakka & Challabathula, 2020; Glick *et al.*, 2007). Numerous studies have reported improved tolerance to abiotic and biotic stresses by inoculating plants with ACC deaminase producing PGPM. This group of microorganisms helps to regulate plant ethylene levels, so as not to get to the levels where they become unfavorable to plant growth (Afridi *et al.*, 2019; Khan *et al.*, 2020).

Soil microbes and the production of volatile organic compounds (VOCs) and secondary metabolites

Some plant-associate microorganisms produce various secondary metabolites and VOCs that can increase plant growth and their ability to withstand stress. For example, polyamines are essential for modifying the physiological properties of plants and providing defense against environmental stressors. The bacterium, *B. megaterium* BOFC15 releases the polyamine spermidine, which causes the production of polyamine in the plant *Arabidopsis*, bringing about an increase in biomass production, higher photosynthetic capacity, and a change in the root architecture. The results obtained showed that the addition of polyethylene glycol (PEG) induced water-deficit conditions, the inoculated plants displayed greater tolerance to drought stress and abscisic acid (ABA) content (Zhou *et al.*, 2016). Hydrogen cyanide production by some PGPM facilitates the control of pathogenic microbes in the rhizosphere (Suresh & Abraham, 2019). The production of VOCs by PGPM may enhance plant growth by increasing shoot biomass and improving stress resistance in plants (Etesami, 2020).

Soil microbes and quorum sensing (QS) molecules

Often, the interactions in the plant rhizosphere occur when plants communicate with microbes in the form of signals to recruit beneficial organisms for their growth and maintenance. In this regard, the plants release roots exudates

consisting of a carbon source, which only the microbes of interest can recognize and respond to. The secretion of root exudates in the plant rhizosphere enables the plant to have control over its inhabiting microbes (Berendsen *et al.*, 2012). Also, the tunable and diverse nature of the chemical composition of plant root exudates help plants to select and recruit the microbes they desire. Quorum sensing (QS), also known as auto-inducers is a form of inter- and intra-species signaling in the rhizosphere that allows soil microbes to communicate and interact with one another by the detection, production, and release of chemical signals (Bukhat *et al.*, 2020; Seneviratne *et al.*, 2017).

Cell to cell communication via QS occurs when PGPM colonize plant roots after receiving a cognate signal. This interaction is subsequently accompanied by alteration of gene expression due to the density of the microbial communities (Helman & Chernin, 2015; Hong *et al.*, 2012). The QS signals control several microbial phenotypes including rhizosphere competence, virulence, the production of secondary metabolites and hydrolytic enzymes, conjugation, biofilm formation, adhesion, motility, coordination of microbial activities in the rhizosphere, and microbial population density (An *et al.*, 2014; Chu *et al.*, 2011).

Recently, plants have started to respond to QS signal molecules used by soil microbes. Plant growth can be enhanced as a result of the release of QS signal molecules, which alters both plants immune responses as well as hormone profiles (Hartmann *et al.*, 2014). One of the key signaling molecules used for communication among microbes for QS are the *N*-Acyl homoserine lactones (AHLs). Many soil organisms have been reported to produce and respond to QS signaling molecules including those from the bacterial genera: *Pseudomonas*, *Bacillus*, *Burkholderia*, *Ochrobacterium*, *Ralstonia*, *Erwinia*, and *Serratia* (Imran *et al.*, 2014; Li *et al.*, 2015). Studies have reported the roles of AHLs in promoting the growth of plant species including *Hordeum vulgare*, *Vigna radiata*, *Medicago truncatula*, and *Arabidopsis thaliana*. In these plant species, AHLs were reported to have enhanced the formation of root hairs and adventitious roots, root branching, number of nodules, and lateral root hair primordia, and also induced lateral root growth and elongation of roots (Chagas *et al.*, 2018; Ortíz-Castro *et al.*, 2009; Ortíz-Castro & López-Bucio, 2019; Rosier *et al.*, 2018). Furthermore, AHLs may increase a plant's ability to obtain water and nutrients from soil by improving transpiration rates and stomatal conductance (Ortíz-Castro *et al.*, 2009). *N*-Acyl homoserine lactones also regulate gene expression responsible for stress response, regulation of metabolism, the development of roots, balancing of hormones, stimulation of plant defense, and activation of host symbiotic interactions (Ali *et al.*, 2016; Hassan *et al.*, 2016; Imran *et al.*, 2014; Schikora *et al.*, 2016). Another important type of QS signaling molecule is the diffusible-signal factor (DSF; also known as *cis*2 unsaturated fatty acids) that is produced by

certain Gram-negative bacteria including *Burkholderia* sp. and *Stenotrophomona smaltophilia* (Ryan *et al.*, 2015). Antibiotics are also important QS signaling molecules produced by bacteria that may play significant roles in inter and intra-species signaling at very low and non-inhibitory concentrations (Andersson & Hughes, 2014). The various mechanisms of plant growth enhancement by PGPM are illustrated in Fig. 1.

Improvement of stress tolerance by PGPM

Conventional means of imparting stress tolerance in plants including genetic engineering and breeding have major drawbacks. For instance, the process of breeding requires the allocation of huge capital and time. On the other hand, the issue of public acceptance in some countries (especially in Europe) limits the process of genetic engineering. This has resulted in increased importance in the role played by beneficial microbes in the management of plant stress as well as in the development of climate-resilient agriculture.

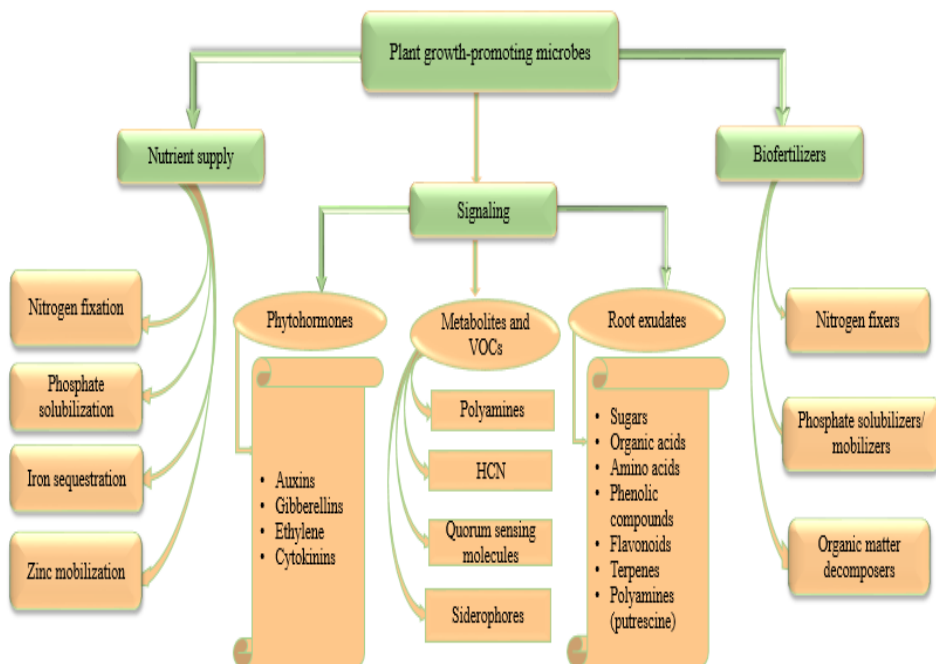


Figure 1. Mechanisms of growth enhancement by plant growth-promoting microbes.

Abiotic stress responses in the rhizosphere microbiome

The potential of soil microbes to mitigate abiotic stressor of plants have been highlighted in many studies. Prudent *et al.* (2015) reported that the use of the small peptide bacteriocin thuricin 17 produced by the bacterium *B. thuringiensis* NEB17 on soybean plants under drought-stressed conditions led to an adjustment in the root structures, increased biomass of the plant's roots and nodules, total nitrogen content, root ABA, and root length. The findings of Chukwuneme *et al.* (2020) on drought tolerance confirmed an improvement in plant dry root and shoot weights, root and shoot length, number of leaves, and the chlorophyll contents of plants inoculated with *S. pseudovenezuelae* and *A. arilaitensis* compared to uninoculated plants. Plants can also cope with flooding stress through the help of beneficial microbes. The ACC deaminase producing *Streptomyces* sp. GMKU 336 inoculated in mung bean (*Vigna radiata*) plant led to increases in plant height, biomass, adventitious roots, leaf area, chlorophyll content, leaf color, and also decreased the plant ethylene level under conditions of flood (Jaemsaeng *et al.*, 2018). Moreover, salt stress in plants can be managed by the activity of ACC deaminase (Cheng *et al.*, 2007; Mayak *et al.*, 2004). Under *in vitro* and greenhouse conditions, the ACC deaminase producing *Bacillus* strains, *Bacillus safensis* NBRI 12 M, *B. subtilis* NBRI 33 N, and *B. subtilis* NBRI 28B enhanced tolerance to salt stress by decreasing the level of stress ethylene in maize plants (Misra & Chauhan, 2020).

Host immunity and protection of plants from pathogens

Many soil microbes have biocontrol effects on plants protecting them from pathogen attacks. They do this by competing for space and nutrients and by producing hydrolytic enzymes or antibiotics (Glick, 2020; Verma *et al.*, 2019). These microbes produce antimicrobial metabolites, such as butyrolactones, ammonia, oligomycin A, pyoluterin, phenazine-1-carboxylic acid (PCA), pyrrolnitrin, etc. (Mohanram & Kumar, 2019; Patel *et al.*, 2020). In a study by Meyer *et al.* (2016), it was found that *P. fluorescens* suppressed the soil pathogens *Fusarium oxysporum* and *Meloidogyne incognita* by producing the antibiotic 2,4-diacetylphloroglucinol (DAPG). Several rhizosphere microbes with biocontrol ability produce multiple antibiotics with differing magnitudes of antimicrobial activity. Fluorescent *Pseudomonas* strains isolated from plant roots, identified as *Pseudomonas protegens* and *P. chlororaphis*, exhibited the presence of multiple antibiotics biosynthetic genes (Someya *et al.*, 2020). From the above-mentioned study, 4 antibiotic genes were observed in *P. protegens*, including genes encoding hydrogen cyanide (HCN), pyoluteorin, pyrrolnitrin, and 2,4-diacetylphloroglucinol whereas, 3 antibiotic genes, including those encoding pyrrolnitrin, HCN, and

phenazine, were found in *Pseudomonas chlororaphis*. These bacterial strains observed to have antibiotics biosynthesis genes also exhibited antimicrobial activity against the fungal pathogen *Rhizoctonia solani* that caused damping-off disease in cabbage plants. The spray application of chitinase and β -1-3-glucanase-producing microbial consortia (*Penicillium* sp. *B. subtilis* and *B. velezensis*) around the rhizosphere of banana plantlets under greenhouse conditions resulted in 60% reduction in disease severity of both *Alternaria* sp. and *F. oxysporum* (Win *et al.*, 2021).

An experiment with different *B. amyloliquefaciens* strains showed an increase in the production of fengycins and iturins (both antimicrobial lipopeptides) as a response mechanism to the plant pathogens, *Botrytis cinerea* and *F. oxysporum* (Cawoy *et al.*, 2015). The production, *in situ*, of secondary metabolites by *B. amyloliquefaciens* FZB42 in the lettuce rhizosphere revealed the presence of the lipopolypeptides surfactin, bacillomycin D, and fengycin that acted against *Rhizoctonia solani* (Chowdhury *et al.*, 2015). The study reported an increased production of bacillomycin and surfactin by the bacterium in the presence of *R. solani*, which was attributed to the effect of antibiosis and the recognition of the FZB42 response to fungal attack. In addition, some rhizosphere bacteria known as bacterial iron chelators are capable of restricting the growth of pathogenic microbes by sequestering the available iron in the soil, thereby making iron less available to pathogenic microbes. Zhu *et al.* (2020) reported that the siderophore-producing *B. subtilis* IBCBF-4 significantly controlled the proliferation of the fungal infection, *Fusarium wilt* of watermelon plants, caused by the pathogen *F. oxysporum*.

Certain microorganisms are capable of reducing diseases in plants by the activation of a resistance mechanism known as microbial-mediated induced systemic resistance (ISR). These microbes can protect plants from pathogenic attacks by triggering molecular and biochemical defense responses inside the plant (Khan *et al.*, 2019). The elicitation of ISR by PGPM is capable of activating the genes associated with pathogenesis, which are controlled by phytohormone signaling pathways as well as proteins that attack plant pathogens (NA *et al.*, 2020; Wilkinson *et al.*, 2019). Microbe-associated molecular elicitors and signal compounds from bacteria, including chitin oligomers, have been reported to regulate the induction of ISR in plants. The cell-surface factors of pathogens like the O-antigen of lipopolysaccharides and flagellins trigger ISR while the analogs of jasmonic and salicylic acids are responsible for triggering ethylene to stimulate non-expresser pathogenesis-related gene 1 (NPR1) that controls systemic acquired resistance (SAR) in plants (Nadarajah, 2017). A graphical representation of the different methods of stress tolerance in plants facilitated by PGPR is shown in Fig. 2.

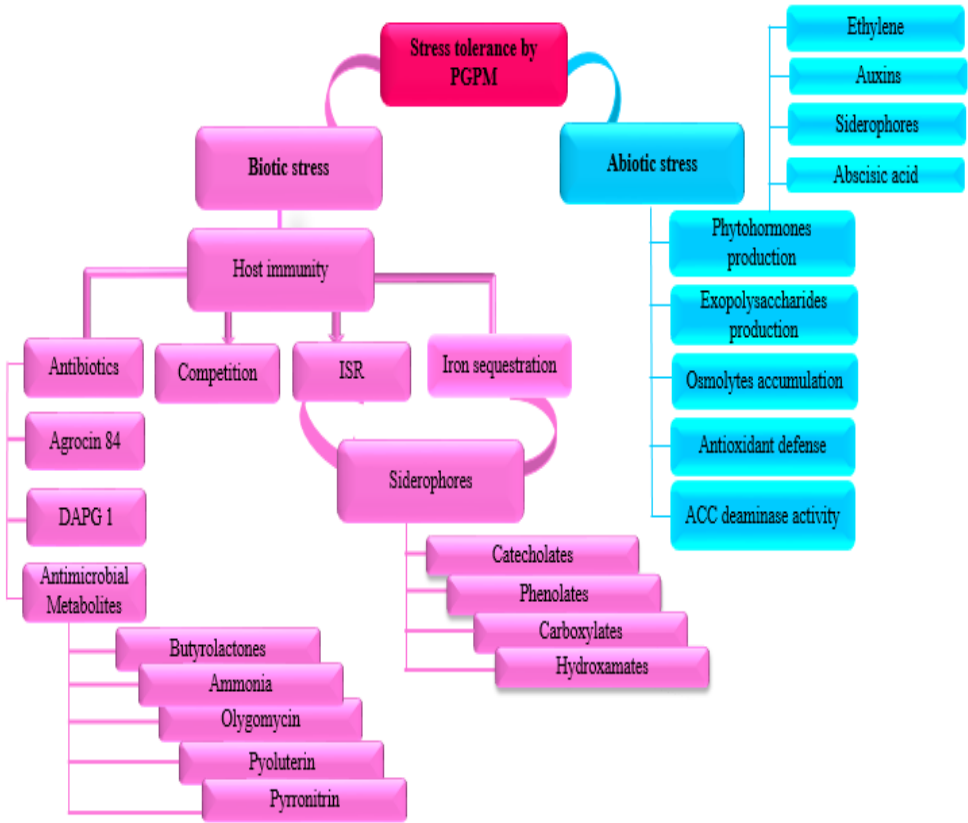


Figure 2. Methods of plant stress tolerance by plant growth-promoting microbes.

Precision agriculture by incorporating PGPM and nanotechnology

Although significant progress has been made in agricultural sector in recent decades, the sector continues to face multiple challenges regarding food crop production sufficient for the constantly increasing world population. Climate change has contributed to a decrease in agricultural products due to increased evapotranspiration rates, temperatures, rainfall intensity, drought, and spread of plant diseases. Plant growth-promoting microbes has successfully been applied as inoculants to growth crop production. However, effective crop improvement by PGPM is determined by factors, such as weather conditions, climate, soil characteristics, and microbial activities in bulk soils (Mukherjee,

2019). Moreover, the effectiveness of PGPM in promoting plant growth can be limited by disease infestation, weeds, and herbicide application. Recent advancements in agriculture have involved the development and use of modern technologies, such as biosensors, nanomaterials, and nanofertilizers. Nanotechnology has achieved great success in various scientific fields, including chemistry, material sciences, physics, medicine, and pharmacy. Considering these achievements, nanotechnology has the potential to improve agriculture and aid in the realization of precision agriculture. Therefore, integrating PGPM with nanotechnology can help to achieve a greater agricultural productivity and address some of the most persistent challenges facing agriculture.

Nanotechnology in biofertilizers production

Success in the application of biofertilizers in agriculture depends on how they were prepared, the method used in the application process, and the storage system used (Duhan *et al.*, 2017). The major pitfall of fertilizers of microbial origins is inconsistency in their performances when applied to different fields, whereas, factors such as sensitivity to temperature, short shelf-life, storage, and dehydration can dramatically affect the field performance of biofertilizers. The use of polymeric nanoparticles as coats on prepared biofertilizers to produce biofertilizer formulations that are desiccation-resistant has been reported (Eleni & Krokida, 2017). An example is a water-in-oil emulsion, a method that is used to disperse and distribute microbes in liquid formulations to the intended sites (Acharya & Pal, 2020). This method helps microbes that dehydrate easily and thereby aids in the improvement of cell viability. Upon application of the polymeric coated nanoparticles, the core ingredient (biofertilizer) is slowly released into the targeted sites (soils) without the contents being inactivated.

Gold and silver nanoparticles may be effective in enhancing the growth of horticultural crops such as peas and legumes (Zulfiqar *et al.*, 2019). Under *in vitro* conditions, these nanoparticles, in combination with natural biofertilizers like *Paenibacillus elgi*, *P. fluorescens*, and *Bacillus subtilis*, have been successfully used to promote plant growth. The advantage of nanobiofertilizers over other fertilizers is that they are needed in very low amounts and are relatively inexpensive. For instance, a liter of nanobiofertilizer is sufficient for application on several hectares of crop grown lands. When the effects of gold nanoparticles on PGPB, including *P. putida*, *P. elgii*, *P. fluorescens*, and *B. subtilis* were examined, the findings revealed a significant increase in plant growth for *P. elgii*, *P. fluorescens*, and *B. subtilis*, while no impact was observed for *P. putida* (Shukla *et al.*, 2015).

Improving plant-microbe interactions through nanotechnology

As discussed, quorum sensing molecules released by various soil microbes play important roles in plant health by aiding in the alleviation of plant stresses, stimulating plant defense systems, and producing antibiotics. Quorum sensing microbes or the molecules that they produce may be very useful resources in agriculture e.g., to formulate and commercialize products from QS signal molecules that stimulate plant growth or to commercialize the microbes that produce QS signal molecules for use in agriculture. The processes that could be adopted for the identification of these molecules have previously been described (Antar *et al.*, 2021; Gray & Smith, 2005). However, it is important that further research be conducted to determine whether the use of microbes that produce these signals will be better for applications in fields or the direct use of the signal molecules. If the signal molecules are used directly, then the problem of inoculum viability is eliminated. On the other hand, the application of microbes that produce these signals will ensure the long-lasting secretion of these molecules in the environment compared to when the signal molecules were used (Antar *et al.*, 2021). To ensure the persistence of signal molecules applied in soils for plant growth enhancement, signal molecules could be encapsulated to allow their slow release into the environment. It is also important to optimize the concentration of QS signal molecules during product formulation. When larger concentrations of genistein were applied to soybean, improved growth and nodulation were observed in the plants while the stress of suboptimal root zone temperatures was minimal (Zhang & Smith, 1995).

Nanobiotechnology for controlling insect pests of plants

Nanotechnology is a promising tool for the control and management of insect pests of crop plants. Das *et al.* (2019) studied the effects of zinc oxide, aluminum oxide, and titanium dioxide nanoparticles application in the management of rice weevil (*Sitophilus oryzae*). Iron nanoparticles developed using extracts from *Eucalyptus* plant displayed antifeedant activity against diamondback moth (*Plutella xylostella*), indicating that the *Eucalyptus* plant extract acted in synergy with the iron nanoparticles (Chhipa & Kaushik, 2015). *Bacillus thuringiensis* synthesized ZnO nanoparticles (*Bt*-ZnO) acted against pulse beetles (*Callosobruchus maculatus*) and reduced their hatchability and productiveness. *Bt*-ZnO also decreased the activities of the gut digestive enzymes of this pest including the glutathione S-transferase, α -amylase, α -glucosidase, and cysteine protease (Malaikozhundan *et al.*, 2017). Nanoparticles prepared with a cell-free supernatant from *Photobacterium luminescens* were used against the cotton insect pests, *Aphis gossypii* and *Tetranychus macfarlanei*.

Results revealed a lower 50% lethal concentration (LC₅₀) of the cell-free supernatant nanoparticle than the normal cell-free supernatant (Kulkarni *et al.*, 2017). The effectiveness of the formulation was attributed to the multistage process involved in the preparation of the nanoparticles, indicating that the methods of delivery of nanoparticles is a vital factor that should be considered when formulating the products. Nanoencapsulation of biopesticides protects the active substances against unfavorable environmental conditions while ensuring a targeted and controlled release of the substances to the target pests (Rodríguez *et al.*, 2016). Unlike conventional agrochemicals, nanoencapsulation of pesticides enables the chemicals to be properly absorbed by plants because they are gradually and continuously released into the soil, and because their effect on pests is more long-lasting and persistent (Djiwanti & Kaushik, 2019; Duhan *et al.*, 2017; Eleni & Krokida, 2017). Therefore, nanobiotechnology presents an innovative system of controlling insect pests, providing an opportunity for increased plant production.

Bioherbicide production through nanotechnology

The major threat facing agricultural production, which substantially reduces crop production, are weeds. Weed pests compete with crop plants for available nutrients. Traditional methods of controlling weeds have been effective; however, the challenges of their use in agriculture include huge time consumption, soil pollution, reduction in soil fertility, and destruction of cultivated plants. The application of a specific herbicide for a long time causes the weed to develop resistance to that particular herbicide. In addition, damages are inflicted on succeeding crops due to continuous and prolonged use of herbicides, which leaves residues in soil. Recently, an ecofriendly approach of weed control, involving the use of microbes or other biotic agents to decrease the impact, reproductive capability, vigor, and density of weeds in an agricultural environment has emerged (Kremer, 2019). The products resulting from this approach, known as bioherbicides (for biocontrol of weeds) is effective in the control and suppression of economically important and persistent weeds. Bioherbicides also efficiently control herbicide-resistant weeds resulting from long-term use of conventional herbicides on plants (Abbas *et al.*, 2018; Hershenhorn *et al.*, 2016). The main constraint towards successful commercialization of bioherbicides is ensuring that the appropriate formulation is available and the method of application is convenient enough to allow a uniform distribution of the biological agent at the targeted site (Hershenhorn *et al.*, 2016).

The control of weeds using nanotechnology is still at its early stage of development. Here, we employ ideas from other studies on nanoformulations to suggest the possibilities of applying nanotechnology in the development of bioherbicides. Viruses are naturally occurring nanoparticles with an outer and a core coating. The size of the viral protein coats of DNA or RNA plant viruses ranges from 10 – 1000 nm, making them suitable as vectors for transmitting substances that are disease-inducible in weeds (Pérez-de-Luque & Hermosín, 2013). The tobacco mild green mosaic virus (TMGMV) is an example of a bioherbicide that was patented for use in the biological control of perennial pasture weed, tropical soda apple (*Solanum viarum*) in the United States (Charudattan & Hiebert, 2007). This virus is extremely effective and could serve as a template for the discovery and formulation of similar biological agents (Charudattan, 2010).

The use of microbial metabolites and other biological products to develop effective bioherbicides has become the focus of researchers in search of alternative means of weed control for sustainable agriculture (Duke *et al.*, 2014; Radhakrishnan *et al.*, 2018). The development of resistance in weeds previously exposed to herbicides could be overcome by the use of microbial metabolites (Duke *et al.*, 2014). However, only a few microbial metabolites are currently being studied for their potential as biochemical bioherbicides. The future development of biochemically formulated bioherbicides needs to mimic the currently developed nanoformulations that enhance the slow or controlled release of agrochemicals into target weeds. Biochemically formulated nanobioherbicides could increase biocontrol because nanoparticles have a large surface area, therefore, only a small quantity of bioherbicide will be needed. This will reduce costs, as a smaller package will contain a higher concentration of the bioherbicide (Pallavi *et al.*, 2017). The small nature of the particles reduces to a large extent, their susceptibility to environmental conditions, such as UV radiation, heat, and desiccation resulting from application, delivery, and storage (Kremer, 2019). The effectiveness of the metabolites of *Photorhabdus luminescens*, an endosymbiotic bacterium that colonizes the parasitic nematode *Heterorhabditis indica*, which acts against arthropod pests of crops, was improved using nanotechnology (Kulkarni *et al.*, 2017). The formulation was prepared using a cell-free supernatant of the bacterium cultures and mixed with gum arabic, which served as a binder. The formulated product was sprayed onto target insects, resulting in a rapid and high rate of death of the pests due to the greater penetration power of the particle that carries the toxins into the insects (Kulkarni *et al.*, 2017). The foliar application of *F. oxysporum* metabolites coated with chitosan nanoparticles on the weed, *Ninidam theenjan* resulted in leaf necrosis, indicating the possibility of the nanobioformulation to effectively control agricultural economically

important weeds (Namasivayam *et al.*, 2015). Notwithstanding the above-mentioned preliminary results, it is important that additional studies be conducted to demonstrate the efficacy of this formulation in field conditions.

Microencapsulation of biological agents, which assures the intactness of the natural phytotoxic metabolites of microbes with herbicidal attributes (Rojas-Sánchez *et al.*, 2022), is promising for potentially effective nanobioherbicides. The nanocapsules are usually organic polymers, in the form of shells carrying the bioherbicide, which open to release their contents under specific conditions such as a change in pH (Pérez-de-Luque & Hermosín, 2013). The encapsulation of biopesticides is an attractive approach for controlling agricultural pests because it makes them efficient, stable, and safe to use (Nuruzzaman *et al.*, 2016). This approach could also be adapted for the formulation of biological agents that can be applied on agricultural weeds. The successful use of nanobiotechnology has the potential to dramatically alter the area of agricultural pest management including the management of agricultural weeds.

Production of biofungicides using nanotechnology

Most of the losses in agricultural production result from fungal attacks on crop plants. Globally, approximately \$45 billion in crop productivity is lost yearly due to pathogenic fungi (Fernandez Acero *et al.*, 2011). However, an increase in agricultural production may be achieved if plant pathogenic fungi are effectively managed (Fisher *et al.*, 2012). While several fungicides are commercially available, their application impacts negatively on plants. Fungicides may inhibit photosynthesis, which decreases plant growth and yield (Geetha, 2019; Petit *et al.*, 2012). Also, conventional fungicides form residues; cause the development of resistance by pathogens, and several health problems to man, animals, plants, and microbial communities (Aguilar-Marcelino *et al.*, 2021; Panth *et al.*, 2020). Nanobiotechnology has helped to increase the nutrient-use efficiency of plants through the application of nanoformulations of fertilizers and overcoming the barriers in yield and nutritional quality of plants (Abd-Elsalam *et al.*, 2019). Besides the use of OMICs tool in understanding the mechanisms of host-parasite interactions, nanobiotechnology can assist in investigating and managing diseases and plant pests. The antifungal activities of nanobiofungicides towards many pathogenic fungi have been tested (Ingle *et al.*, 2014; Singh *et al.*, 2015; Yadav *et al.*, 2015). It is expected that, in the near future, the production of nanobiofungicides, with better solubility, specificity, and stable dispersal, will be available for the control of plant diseases. Silver nanoparticles (AgNPs) have potentially significant impact in their use in agriculture (Krishnaraj *et al.*, 2012). The control of *B. sorokiniana* infection that causes spot blotch disease in wheat was investigated using biosynthesized AgNPs. The study, which was conducted both *in vitro*-and,

in a greenhouse, revealed strong antifungal activity against *B. sorokiniana* and its infection on the wheat plant. The antifungal activity of biosynthesized AgNPs from a cell-free extract of *Penicillium chrysogenum* was also tested against *Trichophyton rubrum*, which resulted in a large antifungal effect against the pathogen (Pereira *et al.*, 2014). Another study investigated the biocontrol of *Sclerotium rolfsii*, the cause of collar rot of chickpea, by AgNPs synthesized from pelleted *Stenotrophomonas* sp. BHU-S7. In this case, it was reported that the biosynthesized AgNPs exhibited inhibitory effects on the pathogenic propagules by reducing their germination and eliminating their ability to cause disease in the plant (Mishra *et al.*, 2017; Mishra *et al.*, 2014). Sustainable agriculture requires a reduced use of agrochemicals to ensure environmental safety. Nanobiofungicides have shown their ability to be used in the control of plant diseases, enhancement of plant growth, and antifungal activity. For optimum performance, nanobiofungicides can be encapsulated to ensure better penetration and a slow and sustained release of the active ingredients. This technology can provide an efficient, cheap, and ecofriendly means of controlling agricultural pests and ensures less environmental contamination and safe handling.

Benefits of nanobiotechnology in the production of agricultural products

The use of nanoformulations ensures a slow and controlled release of phytotoxic metabolites or the microbes attached to a non-carrier into the target pests. This system reduces the loss of the active ingredients in the formulation by ensuring they stay within the roots or aerial parts of the plant (Fadiji *et al.*, 2022b). The non-carrier will also protect the formulated agriproduct from degradation (Hershenhorn *et al.*, 2016). The mode of delivery of the products helps to ensure environmental safety by reducing environmental toxicity. The products obtained are soluble, highly specific, and stable in dispersal.

The use of nanobiosensors in agriculture

The development of smart biosensors that detect the presence of nutrients and contaminants can greatly affect precision farming. Precision farming uses highly efficient global positioning systems (GPS), computers, and remote sensing devices to identify the nature and locations of problems, measure environmental conditions of a certain location, and use resources with maximum efficiency (Gouda *et al.*, 2018). This type of farming has a long-sought objective of reducing the input of fertilizers, herbicides, and pesticides while improving crop yields through the observation of environmental variables and the application of directed action (Bhattacharyya *et al.*, 2016).

In agriculture, nanobiosensors can be used to detect a range of agricultural inputs like fertilizers, pesticides, herbicides, and soil characteristics including pH and moisture content. They enhance sustainable agriculture because an increase in agricultural productivity can be achieved with biosensors. Smart biosensors as a key component of precision farming ensure better management of fertilizers, reduce the cost of inputs, and are ecofriendly, therefore improving productivity. Through precision farming, smart application systems based on nanosensors can aid in the management of raw materials such as nutrients, agrochemicals, and water (Anjum & Pradhan, 2018; Duhan *et al.*, 2017; Fadiji *et al.*, 2022b). For increments in crop productivity, monitoring of agricultural contaminants, and assessing their impacts on plant health, metal oxide nanoparticles such as the electrochemically controlled single-walled carbon nanotubes (SWCNTs) can be used (Deshpande, 2019). Nanosensors can be applied to spot the incidence of plant pathogens as well as the level of soil nutrients (Kaushal & Wani, 2017). The use of nanobiosensors in agriculture and food industries enables prompt, real time, and site-specific sensing of pathogens in plants and food products, real time crop monitoring, and predicting the field and environmental conditions, thus ensuring food safety (Singhal & Rana, 2019).

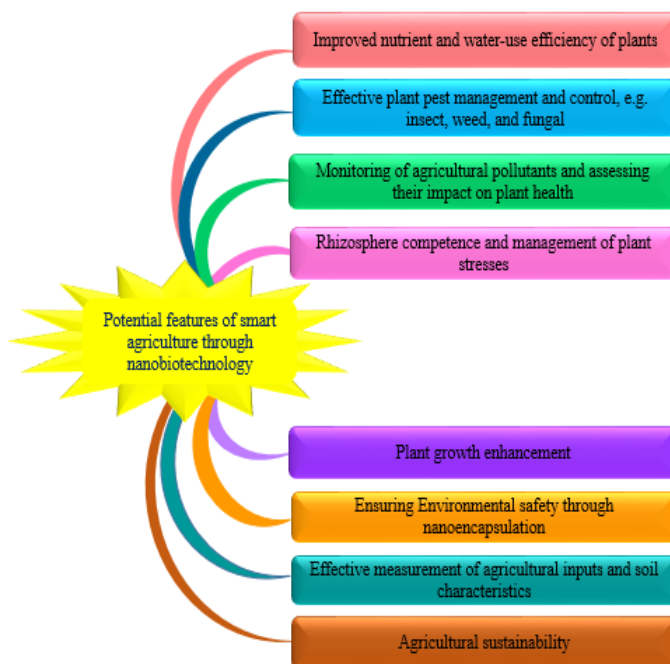


Figure 3. Potential benefits of the application of nanobiotechnology in agriculture.

Nanosensors, such as quantum dots (QDs), are used to sense the presence of pathogens. For instance, the sensor, based on fluorescence resonance energy transfer, can sense a disease affecting lime known as witches' broom, caused by *Candidatus Phytoplasma aurantifolia* (*Ca. P. aurantifolia*). The developed immunosensor exhibited 100% sensitivity and specificity with a detection limit of 5 ca of *P. aurantifolia* per μL (Rad *et al.*, 2012). Several microorganisms have been successfully used to synthesize cadmium quantum dots (Yadav *et al.*, 2015). *Fusarium oxysporum* in combination with tritellurium dichloride (Te_3Cl_2) and cadmium dichloride (CdCl_2) was used in the biosynthesis of fluorescent cadmium telluride (CdTe) quantum dots (Alghuthaymi *et al.*, 2015). The presence of deltamethrin in vegetable and fruit samples was detected using the biosensors, highly fluorescent silica nanospheres embedded with CdTe, and water-soluble CdTe quantum dots (Arora, 2018; Ojha *et al.*, 2018). Fig. 3 shows the different features of nanobiotechnology in agriculture.

Major concerns about the use of nanotechnology in agriculture

Although the combination of nanotechnology and plant growth-promoting microbes present a promising approach to curb the growth of many economically important weeds, extensive research needs to be performed to determine host specificity and to ascertain how compatible these nanoparticles are with other microbial agents. Some nanoparticles could have detrimental effects on soil microbial processes and communities (Eivazi *et al.*, 2018), therefore, before considering the adoption of this approach, it is necessary to determine the activity of nanoparticles in the food chain and the environment.

Impacts of nanotechnology on microbial diversity

Microbial communities can serve as models to ascertain the environmental impacts of nanoparticles. Therefore, determining the effects of nanoparticles on the diversity of soil microbial communities is essential. Using different quantitative and qualitative parameters such as metabolic fingerprinting, fatty acid methyl ester analyses, and colony forming units, the short-term effects of gold, silica, copper, and palladium nanoparticles on soil microbial communities were evaluated and it was found that the influence of the nanoparticles on microbial diversity was statistically insignificant (Shah & Belozerova, 2009). Simonin and Richaume (2015) reported that organic nanoparticles including carbon nanotubes and fullerenes exhibited lower toxicity at >250 mg/kg of soil to microbial communities compared to metal and metal oxide nanoparticles

whose toxicity level was 1 mg/kg of soil. The effect of silver sulfide nanoparticles on soil microbiota, particularly those that take part in nitrification processes, was evaluated using metagenomics (Doolette *et al.*, 2016). In this study, a combination of methods including 16S rRNA amplicon sequencing, quantitative PCR, and bacterial sensitivity distribution were used, and a different method to determine the toxicity thresholds of silver nanoparticles on specific members of a microbial community was suggested. One limitation of the study was soil specificity, implying that the method needs to be standardized for each soil type.

In another study, a decline was observed in bacterial communities involved in the fixation of atmospheric nitrogen and the oxidation of methane after these communities were exposed to zinc oxide (ZnO) and titanium oxide (TiO₂) nanoparticles. However, the nanoparticles reacted positively with the bacterial taxa involved in the breakdown of biopolymers and organic contaminants (Ge *et al.*, 2012). Maruyama *et al.* (2016) reported that herbicides, such as imazapyr and imazapic, encapsulated with chitosan/tripolyphosphate (Ch/Tpp) and alginate/chitosan (Alg/Ch), affect bacterial diversity. The study revealed that the microbial profiles of soils treated with encapsulated nanoparticles were different from those treated with only herbicides. The effect of encapsulated and non-encapsulated herbicides on bacterial communities was ascertained using bacterial genes involved in nitrogen cycling viz., nitrification, denitrification, and nitrogen fixation. Encapsulation with Alg/Ch increased the proportion of bacteria that contain nitrate reductase genes, while increases in the proportion of nitrogen-fixing bacteria were observed in Ch/Tpp encapsulated treatments due to the presence of nitrogenase reductase genes.

The mechanism of interaction between soil microbes and nanoparticles involves the direct absorption of nanoparticles by microbes where the nanoparticles immediately penetrate the microbial cells, affecting cytoplasm conductivity when the nanoparticle size is ~50 nm (Samanta & Mandal, 2017; Singh *et al.*, 2019). Most metal and metal oxide nanoparticles exhibit antimicrobial activity through mechanisms such as accumulation of ROS, formation of pores in microbial cell membranes, DNA damage, endocytosis, release of metal ions, membrane attachment and cell growth inhibition (Abd-Elsalam *et al.*, 2019; Singh *et al.*, 2019). The interaction of nanoparticles with microbial diversity may interfere with the mechanisms of plant nutrition in several ways. However, studies have demonstrated a positive interaction between carbon nanotubes and the communities of microarthropods beneath turf grass (Bai *et al.*, 2017). In this study, the effect of three types of carbon nanomaterials namely, carbon nanotubes (CNTs), graphene, and graphene oxide on soil microarthropod communities was studied, with the results suggesting that carbon nanoparticles increased all soil microarthropods.

Recommendation and prospects

Developing novel PGPB strains capable of being used as biofertilizers, biopesticides, and biofungicides is possible by genetic manipulation of such strains (Gouda *et al.*, 2018). The process of improving agricultural productivity with soil microorganisms can be a cost-effective, environmentally friendly, and sustainable tool that both increases plant productivity and manages stresses in plants. Nanotechnology and nano-based products are currently used to improve agricultural productivity in several countries including China, France, the United States, Germany, Switzerland, South Korea, and Japan (Gouda *et al.*, 2018; Mukherjee *et al.*, 2019). In sub-Saharan Africa, this technology is still very new and its use is limited to very few crops, partly due to lack of awareness of this technology by farmers or lack of support from the government. Therefore, increasing efforts towards commercializing nanobioproducts, ensuring their availability at affordable prices, and enabling easy access to farmers should be encouraged. In this way, farmers will embrace and incorporate the technology into agricultural practice for the purpose of improving plant growth, crop yield, and ensuring agricultural sustainability.

Agglomeration, the tendency of grouping together to form large particles is a major issue that raises serious concerns that may result from the use of nanoparticles. In producing nanoparticles, post-synthetic methods, including the use of surface modifiers and chemicals are used to inhibit particle aggregation. Such practices can negatively impact the toxicity and safety of the nanomaterial (Hegde *et al.*, 2016), which makes it imperative to perform ecotoxicity studies to ascertain the effect of edaphic factors on the bioavailability as well as the natural mechanisms of nanoparticle uptake. There is also a need to assess the impact of engineered nanomaterials in agriculture (Fadiji *et al.*, 2022a), as the human abdomen is its end destination. Increased bioaccumulation of nanoparticles in the food chain may be detrimental to the environment (Gardea-Torresdey *et al.*, 2014; Ma *et al.*, 2018). The most important task is determining the right concentration at which engineered nanoparticles can be applied without inflicting harm and to ascertain at what concentrations they can become toxic to plants, the environment, and man. Nanoparticles applied to the soil can interact with soil microbial communities, thereby affecting the soil ecosystem, the sequestration of carbon, and soil microbial dynamics. Other functions in the soil, including mycorrhizal associations, organic matter decomposition, and the transformation of nitrogen can also be affected due to the application of engineered nanoparticles on soils. However, published literature on the interaction of nanoparticles with soil microbiota and transmission of nanoparticles from plants to man is limited. Therefore, additional knowledge is needed on the interaction

of plant microbiomes with nanoparticles as well as the safety of food and agricultural products that originate from plants grown in soils where nano-based products were applied.

Conclusion

The practice of agriculture has been an important aspect of human lives for thousands of years as it provides a means of sustenance to humankind. However, the exploitation of global resources by human activities has severely reduced agricultural productivity, resulting in a search for better ways to improve agricultural yields to satisfy the increasing human demand for food. Plant growth-promoting microbes have been shown to be effective in improving plant growth by providing nutrients, acting as biofertilizers, biopesticides, controlling pathogenic attacks on plants, and recycling of nutrients. They have also played major roles in managing and controlling abiotic stresses like drought, high salt, pesticide and heavy metal pollution, cold, and flooding. For decades, farmers have relied heavily on the use of chemical-based fertilizers and pesticides that have resulted in the distribution of chemicals that are ultimately detrimental to human lives. These chemicals are not just poisonous upon consumption by humans but often exhibit adverse effects on soil microorganisms and the environment (Baweja *et al.*, 2020). The modifications resulting from the spread of these chemicals can change the present plant-microbe interactions existing in the soil by modifying the biogeochemical cycles as well as microbial biology. A crucial step towards the development of sustainable agriculture that will aid the improvement of soil fertility, crop productivity, balanced nutrient cycling, and plant stress tolerance would be through the application of modern tools and practices that incorporate PGPM. Signal compounds, such as phytohormones (auxins, cytokinins, and gibberellins), quorum sensing molecules (including AHLs, DSFs, antibiotics, pheromones, peptides, tyrosol, and γ -butyrolactone) and various secondary metabolites may improve plant growth and health by ensuring the availability of nutrients and their acquisition by plants, decreasing the effects of abiotic stresses, as well as suppressing certain plant biotic stresses. Moreover, selecting the appropriate microbes for plant growth enhancement and the incorporation of technologies that bring together the applications of nanotechnology, biotechnology, and agro-biotechnology facilitate the development of novel products with potential to increase production in agriculture. Certain soil microbes can produce QS signal molecules that improve plant growth and yield, and so could play significant roles in marginal land reclamation and sustainable agriculture, especially now that agricultural land is expected to be lost as a result of the growing global

urbanization. In addition, the use of nanobiosensors in agriculture could encourage innovative farming practices, as they aid in the management of nutrients, water, and fertilizers. They also control plant stresses (biotic and abiotic) and detect the presence of pollutants in the soil. However, the commercialization of nano-derived products for agricultural use requires a thorough assessment of its impacts on soil, microbial community, plants, and human endeavors to prevent any unwanted side effects.

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