

Plant growth-promoting root-colonizing bacterial endophytes

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ABSTRACT

The development of an environmentally friendly agricultural system as opposed to conventional methods using chemical fertilizers and pesticides for improved crop productivity is a promising aspect of modern agricultural biotechnology. Current research has focused on using free-living microbes that can colonize the plant endosphere as a means of enhancing crop productivity. In the plant rhizosphere, the complex root matrix facilitates microbe-microbe, microbe-plant, and soil-microbe interactions in establishing microbial communities, which precede endophytic colonization of the plant by some of these microbes. Endophytic microbes play an important role in plant growth promotion, as they employ direct or indirect mechanisms to facilitate plant growth by producing phytohormones and various secondary metabolites. The roles of endophytic microbes in sustaining plant growth under biotic and abiotic stresses through these mechanisms can provide insights into their envisaged putative functions in establishing host plant interactions for maximum use in the agricultural sector as an ecofriendly alternative tool to improve crop yield. In addition, a better understanding of endophytic bacteria functions in agriculture, medicine, biotechnology, and industry may enable scientists to unlock several opportunities by exploring valuable endophytic bioproducts in the recent application as bioinoculants, biostimulants, and environmental safety in pollution control and phytoremediation. Furthermore, the genomic insights into endosphere biology can provide detail structural diversity and functional profiling of endophytic microbiome for possible recommendations in future agriculture as a source of the organic amendment. Hence, this review emphasis on the root-colonizing endophytic bacteria and their importance in modern agricultural biotechnology.

1. Introduction

Agricultural intensification is an important condition for the food security of the population of the world (Jayne et al., 2019; Adeleke and Babalola, 2020b). However, the use of chemical fertilizers to improve soil fertility and increase crop yields poses a threat to both ecosystems and human health. For example, human diseases, in some cases, have been linked to the consumption of foods grown with chemical fertilizers (Babalola, 2010). Against this background, the use of biofertilizers consisting of bacteria that are naturally associated with plant roots may be a useful and promising alternative to the widespread application of agricultural chemicals. Biofertilizer application may be utilized in the agricultural bioeconomy to maximally ensure food production, and incorporation into the crop-breeding programs (Uzoh and Babalola, 2018; Fasusi et al., 2021). In recent times, the potential of crop microbiomes for food security has been the focus of many researchers using the current state-of-art technology in understanding the biological functions of plant microbiome to enhance plant growth and control of

plant diseases (Cordovez et al., 2019). The symbiotic association that exists between mycorrhizal and rhizobacteria in the root of leguminous plants enables them to establish cooperation with the host plants to overcome nutrients (nitrogen, phosphorus, potassium, etc.) deficiency in the soil and reduction of nitrogen fertilizer usage on farmlands (Oldroyd and Leyser, 2020). Some plant microbes, such as *Rhizobium*, *Bacillus*, *Azospirillum*, *Pantoea*, *Streptomyces*, *Flavobacterium*, and *Pseudomonas*, fix nitrogen to the soil by forming symbioses with the plant root, thus enhancing symbiotic efficiency in shaping plant-bacteria interactions (Remans et al., 2008). Isolation and identification of endophytic bacteria associated with bananas in Kenya and their potential use in developing biofertilizers for sustainable banana production have been reported (Ngamau et al., 2012). Also, Vargas-Díaz et al. (2019) have evaluated the use of endophytic bacteria from the root nodules of soybean and their potential as biofertilizers. Biofertilizer use in agriculture is considered safe and environmentally friendly and can replace agrochemicals (chemical fertilizers and pesticides) without any negative impacts on the ecosystem (Glick, 2020; Fasusi et al., 2021).

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To further create insights into the potential of indigenous crop microbiomes for sustainable agriculture, a new framework for the next green revolution has been proposed to serve as an ecological model in unifying the principles of endophytic research (Chen et al., 2021b). Adopting this approach can help understand plant-bacteria co-evolution with promises for a desirable selection of beneficial microbes to improved yield under drought stress (Tank and Saraf, 2010). Notably, a Raman-Stable Isotope Probing (Raman-SIP) and SynComs framework to validate the functions of plant microbiome under different conditions for sustainable agriculture with novel insights for future studies have recently been documented on beneficial biome (Chen et al., 2021b).

To this above premise, three-step have been suggested, which include; (i) labeling the wild-relative-crop-associated microbes with $^{15}\text{N}_2$ and using Raman-SIP to probe N_2 -fixing bacteria based on the $^{15}\text{N}_2$ -induced Raman shifts in carbon-nitrogen (C–N) bonds of cytochrome c (cyt c), which suggest how nitrogen fixation activity of endophytic bacteria based on C–N shifts can be determined (Cui et al., 2018), (ii) sorting, purification, and inoculation of endophytic bacteria representative based on their diversity and N_2 fixation. Consequently, there is a need to take into consideration, the priority effects on crops when inoculating with SynComs in combined form (Carlström et al., 2019). Also, growing crops in a clay-based medium that contain soluble organic nitrogen ammonium, or nitrate amended with or without SynComs is fundamental. In step 3, the selection of most copious or combined strains can further be tested under field conditions.

Despite the prospect of these frameworks in plant beneficial biome studies, several limitations surrounding their use have been highlighted in the previous study by Chen et al. (2021b), thus suggesting a future solution to improve the developed Raman hardware and software to facilitate the detection of endophytic bacterial cells of interest from the downstream procedures. The use of Raman-SIP to unraveled endosphere processes in bridging the gap between single-strain and community-level plant-microbe interactions has been documented (O'Banion et al., 2020). Authors proposed that through biotechnological advancement, Raman-SIP will be a powerful tool to unravel the potential of endophytic microbiome in agriculture sustainably.

Endophytic microbes are often referred to as endosphere colonizers that complete their life cycle within the tissues of plants without causing harm to the host plants (Santoyo et al., 2016; Adeleke and Babalola, 2020a, 2020b). The functioning of bacteria within plant tissues relies on their ability to colonize a complex root matrix and adapt to different environmental conditions (Banik et al., 2019). Plant adaptation to harsh environments can increase microbial survival in the endosphere. To this premise, the positive influence of endophytic bacteria in boosting the stress response in plants to environmental stressors can underlie their potential role in formulating bioinoculants (Orozco-Mosqueda et al., 2021). Based on the prediction of oxidative and nitrosative stress genes in diverse endophytic bacteria, such as *Stenotrophomonas indicatrix*, *Bradyrhizobium diazoefficiens*, *Leifonia* sp., and *Enterobacter cloacae*, it has been recommended that these microbes can stimulate the induction of resistance in plants to environmental stressors (Battu and Ulagathan, 2020; Li et al., 2020; Shastry et al., 2020; Adeleke et al., 2021b). Factors, such as drought, salinity, humidity, temperature, pathogen, and soil type have all been shown to influence the microbial population and functioning in plants (Adeleke and Babalola, 2020a; Igiehon et al., 2021). Also, the influence of plant type, genotype, developmental stage, geographical location, and soil type on bacterial diversity and survival has been reported (Chen et al., 2019b). Wemheuer et al. (2017) examined the influence of agricultural practices on the diversity of endophytic bacterial communities in the aerial parts of *Dactylis glomerata*, *Festuca rubra*, and *Lolium perenne* over two consecutive years using 16 S rRNA gene amplicon sequencing.

The application of plant growth-promoting endophytic bacteria (PGPEB) to improve plant growth in drought-prone regions and nutrient-limiting soils have been investigated under greenhouse and field experimental trials (Banik et al., 2019). For example, the effect of

co-inoculation of plant growth-promoting *Bradyrhizobium* and *Azospirillum* on soybean germination under drought stress has been investigated to enhance soybean yield under greenhouse experiments (Silva et al., 2019). Similarly, Dubey et al. (2021) reported bioprospecting the endophytic bacteria *Bacillus cereus*, *Pseudomonas* sp., and *P. oitidis* in enhancing soybean yield under drought stress. Hence, harnessing these bacteria should help circumvent some environmental stressors influencing plant performance.

The abundance of rhizobacteria below ground shares some functions with the root endophytic bacteria. There is direct infiltration of some rhizosphere bacteria from the external root zone into the internal tissue to become endophytes (Nwachukwu et al., 2021). Endophytic bacteria can be linked to signal networking models and secretion of plant metabolic compounds which facilitate microbial communication in and out of the root tissues (Soldan et al., 2019). Bacterial endophytes primarily penetrate plant roots vertically or horizontally by seed inoculation, cell injury, or cracks (Banhara et al., 2015). Many bacteria regarded as root endophytes have been reported to originate from the rhizosphere (Aloo et al., 2019).

An insight into the functioning of a few endophytic bacteria has been elaborated using a metagenomics approach (Akinsanya et al., 2015; Mashiane et al., 2017; Fadji et al., 2020). According to Akinsanya et al. (2015), a total of 175 bacterial species from the leaf, 211 from the root, and 148 from the stem were reported, revealing diverse endophytic bacteria in the plant root compared to the stem and leaf. A study by Fadji et al. (2020), reported major endophytic bacterial phyla, such as Firmicutes, Bacteroidetes, Actinobacteria, Proteobacteria, Acidobacteria, Chloroflexi, Verrucomicrobia, Tenericutes, Planctomycetes, Cyanobacteria, and Chlorobi in maize cultivated on organic fertilizer, inorganic and non-fertilizer soils. Furthermore, a diverse bacteria community structure in the tissues of *Pseudowintera colorata* (Mountain horopito or pepper tree) growing in sub-alpine regions of New Zealand has been reported to influence plant growth upon inoculating *P. colorata* seedlings and antagonism against four different phytopathogenic fungi (Purushotham et al., 2020). Maropola et al. (2015) documented the relative abundance of major bacterial lineages recovered from composite samples of sorghum root and stem tissues subsequently showing their role in enhancing sorghum yield. Several other studies have identified agriculturally important endophytic bacteria from the leaves and seeds of plants (Bilal et al., 2018; Rahman et al., 2018). Seed endophytes have been reported to exert beneficial effects on the next generation of the host plant, for example, plant protection against pathogens, releasing seeds from dormancy, seedling growth promotion, and enhanced seed germination (Khalaf and Raizada, 2018; Rahman et al., 2018). These attributes can be the reason why beneficial seed endophytes are often transferred from one generation to the other (Frank et al., 2017). Diverse seed endophytic bacteria phyla and genera have been reported (Truyens et al., 2015; Frank et al., 2017). Consequently, the identification of major endophytic bacterial phyla, Proteobacteria, and Firmicutes and genera, *Bacillus*, *Pantoea*, *Pseudomonas*, *Stenotrophomonas*, etc. with varied ecological functions, ranging from beneficial plant-microbe cooperation to antibiosis activity against plant pathogens have been reported in maize (Mashiane et al., 2018). Additionally, Bulgari et al. (2014) reported an endophytic bacterial community in grapevine leaves with identifiable genera, *Sphingomonas*, *Burkholderia*, *Pantoea*, and *Methylobacterium*. According to Lopez-Velasco et al. (2013), the abundance of the bacterial phyla Proteobacteria was discovered in the seed and leaf endophytes of spinach (*Spinacia oleracea*).

Despite the advancement of metagenomics in identifying some non-culturable microbes, there remains a need for further study of these microorganisms for possible use in agriculture. Therefore, this review is focused on bacterial endophytes associated with plant roots and endeavors to provide up-to-date information on their diversity and agricultural importance. In the sections below, the following shall be discussed (i) root-colonizing potential of endophytic bacteria and their

mechanism of action (ii) plant-endophyte interactions (iii) endophytic bacteria as a source of bioinoculants, and (iv) genomic insights into root endophytic bacteria communities.

2. Overview of plant root-colonizing endophytic bacteria and their mechanism of action

Endophytic bacteria colonizing plant roots can be isolated directly from surface-sterilized tissues. The mechanisms used by endophytic bacteria in plant growth promotion include nitrogen fixation, plant growth stimulation via phytohormone synthesis and modulation, siderophore production, induction of systemic resistance, and synthesis of bioactive compounds against phytopathogens (Ngoma et al., 2014). The plant growth-promoting potential of endophytic bacteria, for example, to produce IAA, has contributed to the growth regulation and developmental processes in plants, which include tissue differentiation, cell division, and elongation, apical dominance, and responses to light, gravity, and pathogens (Babalola and Glick, 2012). Also, ACC deaminase production by endophytic bacteria plays a major role in lowering plant ethylene levels, thus stimulating plant growth (Glick et al., 2007). The highlights of various PGPEB inhabiting the roots of different plants, mechanisms used by these bacteria, and the effects of these relationships are presented in Table 1. The presence of special organelles, such as fimbriae or pili in bacteria cells can enhance their attachment to the root matrix and subsequently the absorption of soil nutrients for plant use (Kandel et al., 2017).

Because of the high accumulation of nutrient and exudate secretions in the endo-rhizosphere compartments, the root zone is a hotspot predominated by large numbers of endophytic microbes and other plant growth-promoting bacteria (Tsunoda and van Dam, 2017; Glick, 2020). High bacterial diversity in the root endosphere compared to the stems and leaves of plants has been documented (Zhang et al., 2017). Organic compounds, such as amino acids, vitamins, and carbohydrates released from plant roots can act as signaling molecules for root-associated microbes to attach to the root surfaces in forming biofilms (Muzzamal et al., 2012). The colonization strategies employed by endophytic bacteria and root nodule bacteria are presented in Fig. 1. Elucidation of the bacterial community across plant organs has revealed their structural dynamic in natural environments (Brijesh Singh et al., 2019). Different vascular plants growing in different climatic zones, such as tropical, temperate, cold, and polar harbor one or more bacterial endophytes, but are less explored (Acuña-Rodríguez et al., 2020). Nevertheless, focusing on endosphere research will make information available on PGPEB across different climatic regions. For example, findings on endophytic bacteria from plant species growing in the glacier forefront, rock sides, stream banks, and snow patch communities have been documented and suggested to have promise for use in sustainable agriculture (Zheng et al., 2016). Furthermore, the predominance of bacterial communities in the roots of different Mediterranean wild legumes growing in tropical regions has been reported (Muresu et al., 2019). Some of the identifiable PGPEB include *Hedysarum carnosum*, *H. spinosissimum*, *Ornithopus compressus*, *Rhizobium sulae*, *Pseudomonas* sp., *Microbacterium* sp., *Microbacterium* sp., and *Pantoea agglomerans* (Muresu et al., 2019).

Based on the conservative biodiversity of the endophytic community, many hypotheses have been proposed for further investigation into the bacterial community structure of vascular plants in tropical, temperate, and other regions (Nandini et al., 2018). Many authors have reported endophytic bacterial phyla, for example, Actinobacteria, Bacteroidetes, Firmicutes, Acidobacteria, and Proteobacteria from plants growing in the Arctic, cold, tropical, polar, temperate, tropics, and cold regions (Nissinen et al., 2012; Park et al., 2013; Miguel et al., 2016; Firrincieli et al., 2020). To this end, additional research studying bacterial diversity across different climatic conditions would help elaborate their potential for various agricultural and industrial applications.

3. Plant-endophyte interactions in promoting plant growth

Plants harbor diverse bacterial communities and their cooperation contributes to the physiological functions of the host plants (Adeleke and Babalola, 2021). In a natural environment, the interdependent cooperation between endophytic bacteria and host plants depends on the nutrient bioavailability and colonization potential within the plant tissues. Some examples of identifiable endophytic bacteria genera include *Pseudomonas brenneri*, *Ewingella Americana*, *Pantoea agglomerans*, *Bacillus cereus*, and *Pseudomonas otitidis* (Babalola et al., 2021; Dubey et al., 2021; Rana et al., 2021).

Many PGPEB has been identified and their application in improving crop yields has been aimed at ensuring agricultural sustainability (Babalola et al., 2007; Adedeji et al., 2020). For example, *Rhizobacter* spp. and other nitrogen fixers have been employed in agricultural management (Etesami, 2018). PGPEB colonizes the root endosphere and may benefit plants either by direct or indirect means (Glick, 2012). Directly, endophytic bacteria enhance plant growth by nitrogen fixation, modulation of plant hormone levels (auxin, cytokinin, ethylene, and gibberellin), phosphate, iron and potassium solubilization, secondary metabolite synthesis, antibiosis activities against plant pathogens, and boosting plant responses to abiotic stresses (Rajini et al., 2020). Some examples of phosphate solubilizing bacterial genera, such as *Pseudomonas*, *Burkholderia*, *Paraburkholderia*, *Novosphingobium*, and *Ochrobactrum* have been reported to enhance the biomass yield of Chinese seedlings based on their multifunctional attributes (Chen et al., 2021a). The use of root endophytic bacteria in developing bioinoculants has shown success and their application in modern agricultural practices is promising (Afzal et al., 2019). Several plant growth-promoting bacteria have been studied (Santoyo et al., 2016; Mamphogoro et al., 2020; Imade and Babalola, 2021; Orozco-Mosqueda et al., 2021). Therefore, harnessing these bacteria in organic farming to enhance agricultural productivity can help avert future food challenges. Also, the application of these bacteria in the bioremediation process of environmental pollutants, heavy metals, xenobiotics as well as in the production of antibiotics, siderophores, enzymes, and induction of systemic resistance against pathogens has been documented (Glick, 2003, 2010; Glick and Stearns, 2011; Kong and Glick, 2017b; Etesami and Maheshwari, 2018). Based on the multifaceted roles of endophytic bacteria toward agricultural sustainability, additional research would help maximize their potential in sustainable plant health for improved crop yield.

The use of *Bradyrhizobium diazoefficiens* and *Azospirillum* spp. as inoculants to enhance crop yield and productivity on a commercial scale by farmers growing soybean, corn, and wheat in Argentina and Mexico has been documented (Cassán et al., 2020). *Rhizobium*-based-biofertilizers via seed inoculation are widely used in organic farming (Woldemeskel et al., 2018). The cooperation of PGPEB with plant roots can be achieved naturally or by inoculation. However, to confirm the efficacy of microorganisms on plant growth, it is necessary to re-isolate them after inoculation from the same inoculated plants. Interestingly, endophytic bacteria can be engineered in developing biopesticides as biocontrol agents against plant pathogens (Fadiji and Babalola, 2020b). Endosphere engineering can further be achieved through the information gained from metagenomics studies.

The mechanisms displayed by microbial endophytes vary, based on their type and source. Understanding the mechanisms used by endophytes is important, as differences in their ability to modulate plant hormone levels and other metabolites can be measured under laboratory conditions (Ambreetha et al., 2018). The bioinoculant application and effect of endophyte application on root development for nutrient absorption in tomato, corn, cotton, and sorghum have been documented (Lin et al., 2018).

The mechanisms employed by endophytic bacteria in enhancing agricultural productivity are summarized in Fig. 2. The direct mechanisms employed by PGPEB, include nitrogen fixation, synthesis of the phytohormones auxin, cytokinin, gibberellin, and abscisic acid

Table 1
Some plant-associated bacterial endophytes and their mechanisms of action.

Host plant	Endophytic bacteria	Mechanisms	Effects	References
Soybean	<i>Bradyrhizobium japonicum</i>	IAA production, nitrogen fixation	Increased root and shoot dry weight, and nitrogen content	Subramanian et al. (2015)
Arabidopsis	<i>Serratia proteamaculans</i>	IAA synthesis, ACC deaminase, acetoin, 2,3-butanediol synthesis	Improved root and shoot development	Taghavi et al. (2009)
	<i>Paraburkholderia phytofirmans</i>	IAA production, induction of salt tolerance	Enhanced tolerance to stress, increase root and shoot weight, chlorophyll content	(Zúñiga et al., 2013; Ledger et al., 2016)
Tomato	<i>Pseudomonas fluorens</i> and <i>P. migulae</i>	Induction of heat stress response; ACC deaminase, IAA production	Enhanced stress tolerance	(Ali et al., 2014a; Issa et al., 2018)
	<i>Bacillus pumilis</i> , <i>B. licheniformis</i> , <i>B. megaterium</i> , <i>B. cereus</i> , <i>Serratia marcescens</i>	IAA production, secondary metabolite synthesis, antibiosis, siderophore production, phosphate solubilization,	Increase root and shoot length, weight, and the number of secondary roots	Amarean et al. (2012)
Wheat	<i>Paraburkholderia phytofirmans</i>	Solubilization and recovery of nitrogen, phosphorus, and potassium	Enhanced root biomass, plant height, and chlorophyll content	Aziz et al. (2020)
	<i>Bacillus cabrialesii</i>	Biocontrol activity	Phytopathogen control	de los Santos Villalobos et al. (2019)
Onion	<i>Bacillus subtilis</i> , <i>Bacillus megaterium</i>	Biocontrol activity	Suppressed fungal pathogen mycelial growth	Pan et al. (2015)
	<i>Burkholderia phytofirmans</i>	ACC deaminase synthesis, IAA production	Enhanced plant vigor and resistance to biotic and abiotic stresses	Weilharter et al. (2011)
Sunflower	<i>Stentrophomonas indicatrix</i>	IAA synthesis, phosphate solubilization, siderophore production, secondary metabolite synthesis	Enhanced root number, root length, seed number, shoot length	Adeleke et al. (2021b)
Groundnut	<i>Chryseobacterium indologenes</i> , <i>Enterobacter cloacae</i> , <i>Klebsiella pneumoniae</i> , <i>Pseudomonas aeruginosa</i> , <i>Enterobacter ludwigii</i>	Nitrogen fixation, IAA and ACC deaminase production, siderophore production, phosphate solubilization	Increased root and shoot length and weight	Dhole et al. (2016)
Millet	<i>Bacillus amyloliquefaciens</i> , <i>B. subtilis</i> , <i>B. cereus</i>	Zinc, potassium and phosphate solubilization, siderophore production, antibiosis against <i>Fusarium solani</i> , <i>Rhizoctonia solani</i> , and <i>Sclerotium rolfsii</i> , protease, amylase, lipase, chitinase, pectinase production	Enhance root length, weight, percent disease index, and disease over control	Kushwaha et al. (2020)
Cotton	<i>Pantoea</i> spp, <i>Empedobacter</i> spp, <i>Enterobacter</i> spp, <i>Rhizobium</i> spp, <i>Klebsiella</i> spp.	Biocontrol activity, siderophore and IAA production, protease, chitinase, cellulose, pectinase production	Enhanced shoot and root length, germination, and vigor index	(Li et al., 2010, 2012)
Potato	<i>Klebsiella oxytoca</i> , <i>Pseudomonas marginalis</i> , <i>P. viridilivida</i> , <i>Bacillus endophyticus</i> , <i>B. atrophaeus/subtilis</i>	Amylase, cellulase, protease, and phosphatase production, biocontrol against plant fungal pathogens	Suppressed fungal pathogen mycelial growth	Boiu-sicuia et al. (2017)
Hopbush	<i>Burkholderia vietnamiensis</i>	Nitrogen fixation	Enhanced yield biomass	Shinjo et al. (2018)
Peanut	<i>Streptomyces alboniger</i> , <i>Bacillus idriensis</i> , <i>Pseudomonas taiwanensis</i> , <i>P. geniculata</i>	Ammonia production, hydrogen cyanide, and siderophore production, phosphate solubilization, ACC deaminase, IAA production, cellulase, protease, pectinase, chitinase	Enhanced root length	Afzal et al. (2017)
	<i>Bacillus velesensis</i>	Siderophore production, phosphate solubilization	Inhibition of fungal pathogen mycelial growth, seedling height, seedling dry weight, root length, and root dry weight	Chen et al. (2019a)
Sugarcane	<i>Gluconacetobacter diazotrophicus</i>	IAA synthesis, nitrogen fixation	Enhanced biomass yield	Bertalan et al. (2009)
	<i>Kosakonia radicincitans</i>	Nitrogen fixation, secondary metabolite synthesis, siderophore production, IAA biosynthesis	Enhanced root length and plant weight	Beracochea et al. (2019)
Rice	<i>Pantoea ananatis</i>	IAA and siderophore production	Increased plant growth and crop yield	Megías et al. (2016)
Poplar	<i>Stentrophomonas maltophilia</i> , <i>Pseudomonas putida</i>	ACC deaminase, IAA synthesis	Improved root and shoot development	Taghavi et al. (2009)
Cape periwinkle	<i>Achromobacter xylosoxidans</i>	ACC deaminase	Increased germination percentage and root weight under saline conditions	(Karthikeyan et al., 2012; Wu et al., 2021)

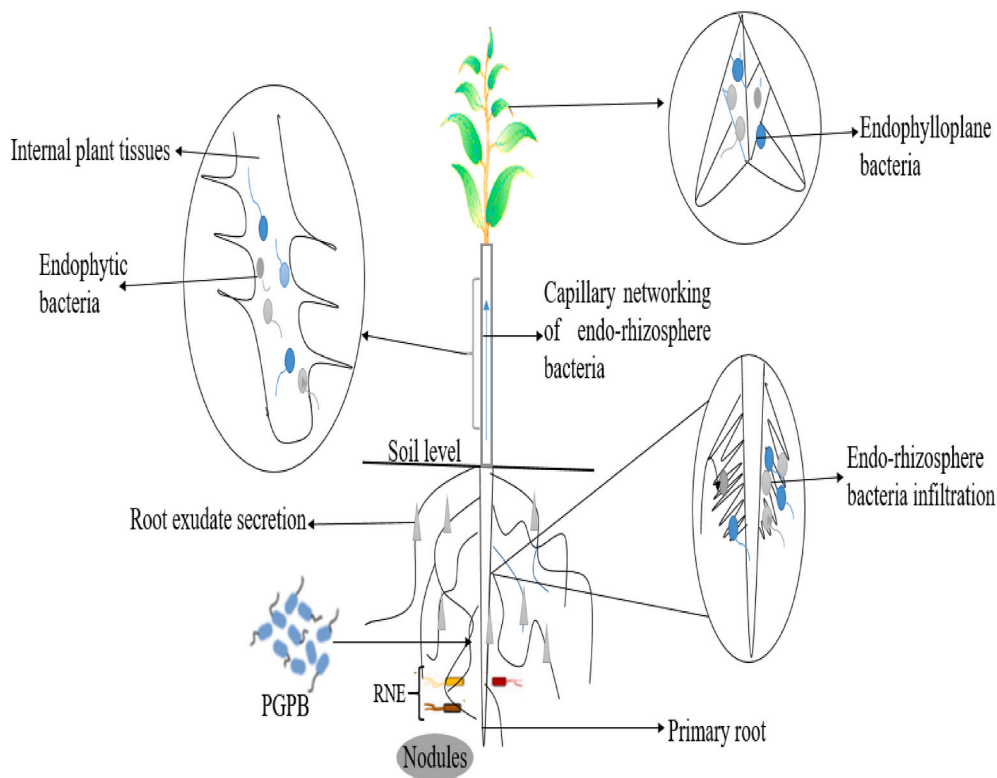


Fig. 1. Bacterial dynamics and root nodules containing endophytes. Key: RNE – root-nodule endophytes.

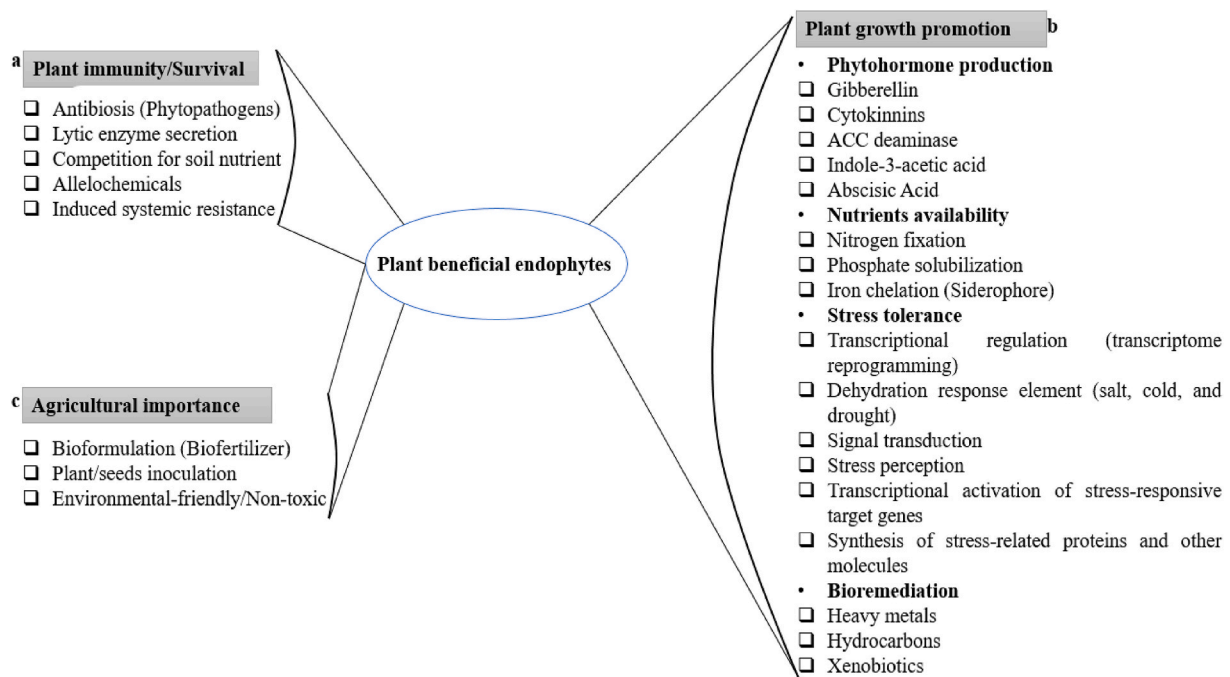


Fig. 2. Mechanisms used by PGPEB and agricultural importance. a - plant immunity/survival, b - plant growth promotion, c - agricultural importance.

(Maheshwari et al., 2019). Also, lowering of ethylene by the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase and the solubilization of minerals (zinc, iron, phosphorus, sulfur, and potassium) and the increased survival under stress conditions, such as drought and soil salinity (Dubey et al., 2021). Also, the ability of PGPEB to produce organic acids, enzymes, antimicrobial compounds such as antibiotics and cyanide, induce systemic resistance and produce siderophores all

promote plant growth indirectly (Santoyo et al., 2016). The enzyme ACC deaminase is one of the key attributes of endophytic bacteria in stimulating plant growth under high concentrations of toxic metals (Gamalero and Glick, 2012; Kong and Glick, 2017b; Pandey and Gupta, 2019). These abiotic stressors are of particular agricultural importance in less than favorable soils or climate conditions. Some endophytic bacteria can modulate root-bacteria and bacteria-bacteria interactions due to their

ability to fix nitrogen in the soil and the major group of bacteria found in this category are rhizobia inhabiting the nodules of plants (See Fig. 1). The α - and β -rhizobia, such as *Rhizobium tropici* and *Cupriavidus taiwanensis* colonizing root nodules of *Phaseolus vulgaris* and *Mimosa pudica* have been identified as nitrogen-fixing bacteria (Bomfeti et al., 2011). 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase-producing endophytic bacterium, *Pseudomonas fluorescens*, however, can lower ethylene levels in plants and this has been shown to play an important role in facilitating the nodulation process of α - and β -rhizobia (Nascimento et al., 2019). Furthermore, endophytic bacteria can indirectly enhance plant growth by stimulating plant responses or producing secondary metabolites against phytopathogens (Santoyo et al., 2012). One such indirect technique is the induction of systemic responses (ISR) which can be achieved through specific plant response pathways e.g., the jasmonic acid (JA) pathway (van Loon and Glick, 2004; Asghari et al., 2020). Stimulation of plant defense responses through signaling pathways in endophytic bacteria has been reported by Montejano-Ramírez et al. (2020). The authors investigated the antifungal compound (N, N-dimethyl hexadecyl amine) produced by the facultative endophytic bacterium *Arthrobacter agilis*. This compound modulates the expression of genes involved in low-response, defense, and iron concentrations in *Medicago truncatula* infected with phytopathogens, such as *Botrytis cinerea*, and *Pseudomonas syringae* without involving the JA pathway.

Additionally, the compound IAA produced by endophytic bacteria can directly contribute to plant physiological functions, such as growth promotion, lateral root formation, increase in biomass yield in terms of below and aboveground parameters, and chlorophyll pigmentation (Santoyo et al., 2016). Subsequently, to further discuss the direct and indirect mechanisms of PGPEB and their bioprospecting in agricultural biotechnology, we recommend a few recently published review articles and books (Adeleke and Babalola, 2021; Eid et al., 2021; Wu et al., 2021). These mechanisms help in understanding the coexistence between endosphere bacterial communities and host plants.

4. Plant root endophytes and bioinoculant synthesis

Roots are specialized organs that provide mechanical support to plants in the uptake of nutrients from the soil (Ahkami et al., 2017). The plant supporting tissue (xylem and phloem) in the roots can facilitate the absorption and movement of nutrients and water directly from the soil to the stem and other parts of the plant (Feng et al., 2019). The ability of root-associated endophytic bacteria to produce IAA can enhance root development, thus contributing to plant nutrition in absorbing nutrients from the soil (Adedeji and Babalola, 2020). Injury to plant roots allows free release of root exudates containing fixed carbon in the form of polysaccharide mucilage to the soil environment and these compounds can serve as a chemoattractant and source of energy to the microorganisms around the root (Adeleke and Babalola, 2021). Like soils, plant roots harbor a consortium of bacteria in the endosphere compartments (Wang et al., 2019). The root architectural system and rhizodeposition of nutrients can modulate the activities of root endophytic bacteria in the endo-rhizosphere regions. Regardless of the plant regions colonized by endophytes, they may exhibit similar functions in crop breeding (Hashem et al., 2019).

The root systems serve as an excellent source of nutrients for endophytic bacteria and form an interface for plant-bacterial interactions in a given ecotone. Excessive rhizodeposition of root exudates containing metabolite compounds, such as terpenoid, phenol, alkaloids, proteins, and peptides have been reported to influence belowground bacterial diversity (Imade and Babalola, 2021). Apart from the roots of plants, endophytic bacteria also colonize other parts of the plants. For example, the identification of endophytic bacteria colonizing the leaves and stem of plants has been reported (Cao et al., 2004; Akinsanya et al., 2015; Mahlangu and Serepa-Dlamini, 2018; Zakaria and Aziz, 2018). The bacterial populations found in various plant organs often share similar

functions but are different in terms of abundance and diversity (Bergna et al., 2018). The plant growth-promoting bacteria found in the root nodules of leguminous plants can function in fixing atmospheric nitrogen for plant use (Naik et al., 2019).

Many bacterial endophytes can be cultured and can be directly applied to crops either by spraying, seed, or root inoculation. Also, endophytic microbes can be used to combat phytopathogens as an alternative to pesticides and insecticides (Fadji and Babalola, 2020a). Bacterial root colonization is determined by bacteria strain, host genotype, soil pH, soil type, drought, salinity, root architecture, soil nutrients, etc. The pattern of bacterial colonization in the root endosphere differs from one bacterium to another. Endophytic bacteria may enter plant tissue via roots, stems, leaves, flowers, and cotyledons (Ambele et al., 2020). Findings have shown different entry modes and colonization patterns of different endophytic strains (Omomowo and Babalola, 2019; Fouda et al., 2021). The secretion of lytic enzymes, cell wall degrading enzymes, and cellulases by endophytic bacterial strains can facilitate the entry of a bacterial strain by hydrolyzing the external covering of plant cells (Toghueo and Boyom, 2021). A study by Reinhold-Hurek et al. (2006) revealed the colonization potential of the endophytic bacterium *Azoarcus* sp. in the root endosphere was due to endoglucanase biosynthesis and the presence of the *eglA* gene. Similar reports have been documented by Suzuki et al. (2005) on the biosynthesis of a nonspecific wax-degrading enzyme by *Streptomyces galbus*, which enhances the colonization of the Rhododendron endosphere by this bacterium. The colonization pattern of endophytic bacteria, such as *Paraburkholderia phytofirmans*, and *Ralstonia solanacearum* by attachment, and invasion of the root regions through the exodermis layer have been reported to facilitate subsequent bacterial entry and survival, and use of plant nutrients as a source of carbon (Afzal et al., 2019). In addition, all of the mechanisms for the successful establishment of bacteria as endophytes rely on their ability to utilize certain metabolites secreted from plants.

Biofertilization in agriculture is considered safe and environmentally friendly. The use of bacterial endophytes as bioinoculant has the potential to immensely contribute to crop production since these organisms exhibit a strong affinity for their host plants (Mahanty et al., 2017). Intensive agriculture using chemical fertilizer in large amounts has no doubt resulted in a manifold increase in the productivity of farm commodities, but the adverse effect of these chemicals are visible to soil structure, endo-rhizosphere biodiversity, water bodies, persistent in the food chain, and human health (Ngwira et al., 2013). Hence, organic farming using organic fertilizer in enhancing biodiversity can be instrumental in enhancing biodiversity as the best substitute for chemical fertilizer. To successfully achieve this, the real potential of organic agriculture on biodiversity requires a stronger shift to a systems approach, based on an improved understanding of ecosystem functions (Akanmu et al., 2021). Therefore, incorporation of organic fertilizer, such as compost, manure, animal waste, and biofertilizers into the soil can play a major role in improving soil fertility by supplying micro-and-macro-nutrients as major plant nutrients, which favor healthy root growth (Fasusi et al., 2021). In addition, organic fertilizers increase microbial activity in the endo-rhizosphere region, which helps free up other nutrients in addition to those provided by the fertilizer. Subsequently, soil amended with biofertilizers can enhance nutrient availability to crop plants and boost plant and soil health for higher crop yields sustainably (Mahanty et al., 2017).

Furthermore, for effective production of bioinoculants on a commercial scale, selection of appropriate carrier and bacterial strains is required. In addition, bacteria in the plant endosphere can be difficult to isolate due to the complex environment in which they are found. Nevertheless, findings into diverse bacterial community structures in the roots of soybean, corn, sorghum, tomatoes, millet, wheat, and cherry have been reported using 16 S rRNA gene amplicon sequencing (Berg et al., 2015). Furthermore, employing metagenomics techniques in evaluating unculturable endophytic bacteria should provide additional

opportunities to harness PGPEB for use in agriculture and further studies.

5. Genomic insights into root endophytic bacteria communities

Genomic insights into endosphere biology have significantly increased our understanding of root endophytic bacteria and their functioning in plant growth promotion and crop protection (Adeleke et al., 2021b). Diverse approaches in assessing endophytic bacterial communities have been documented in the literature. Hence, it is important to adopt appropriate techniques in studying bacterial endophytes inhabiting the root endosphere. In this regard, the two approaches widely adopted include culture-dependent and culture-independent techniques. Culture-dependent approaches include direct culturing of relevant bacteria while culture-independent approaches include shotgun metagenomics, proteomics, metabolomics, and meta-transcriptomics (Maropola et al., 2015; Selvin et al., 2019). The section below provides a brief overview of the metagenomics of endophytes. To isolate endophytic bacteria from plant organs such as leaves, roots, and stems, surface sterilization of the plant tissue is important before plating on appropriate media. Culture-dependent methods have been widely employed due to their low cost, ease of performance, and effectiveness in obtaining pure bacterial cultures for further characterization of bacteria morphology, phylogeny, physiology, and biochemistry (Pei et al., 2017).

It is often difficult to assess diverse bacteria communities in the plant endosphere due to the varied growth parameters required for culturing them. For instance, the growth of oligotrophic endophytic bacteria on solid media is often outcompeted by the copiotrophic endophytes due to their ability to utilize nutrients in synthesizing antibiotics (Okunishi et al., 2005). To successfully isolate endophytic bacteria from the plant endosphere, the procedures involved are (i) surface sterilization of plant tissue using disinfectants such as 3% hypochlorite, 70% ethanol, a combination of mercury chloride and ethanol. These disinfectants are used to remove unwanted or contaminating microbes from the plant surfaces. The efficient use of Tween 20 or Tween 80 to reduce the surface tension of solvents has also been used (Romero et al., 2014). Depending on the plant material, sterilization time with ethanol and hypochlorite is usually from 30 s to 10 min. Furthermore, the samples are typically rinsed several times with distilled water to remove the chlorinated compounds that may later induce mutagenesis and cell death. Alternatively, sodium thiosulfate has been reported to decrease the damaging effects of hypochlorite on bacterial cells, suggesting its suitability in preparing gnotobiotic models (Miché and Balandreau, 2001). Following an appropriate sterilization procedure helps to prevent the penetration of the disinfectant into the plant endosphere and the removal of epiphytic microbes. A sterility check is usually performed by plating the last rinse of water on appropriate bacteriological solid media, such as nutrient agar.

Copiotrophic endophytic are a group of endophytes that require a nutrient-rich medium for growth. This notwithstanding, endophytic bacteria are often referred to as oligotrophs that require specific media for growth. For example, the use of nutrient agar for culturing endophytic bacteria from *Aloe vera* has been reported (Youssef et al., 2016). Growing bacterial endophytes in a rich and minimal medium may be influenced by the media nutrient composition. Hence, devising innovative culture approaches will help obtain sufficient data from uncultivable endophytic microbes in future research.

Recent research is focused on the metagenomics approach in studying bacterial communities of the root endosphere. Employing metagenomics is promising because it helps to identify the role of bacterial endophytes in various plant biological processes, including nitrification, phytoremediation, biodegradation, plant growth promotion, and suppression of phytopathogens (Li et al., 2018). Culture-independent techniques first begin with the collection of healthy plant materials, washing these tissues with distilled water,

surface sterilization, DNA extraction from the sterilized plant tissues, and, finally, sequencing either the 16 S rRNA gene amplicon or shotgun metagenome to determine bacteria taxonomy. The metagenomics and functional profiling of diverse bacterial endophytes in plants, such as maize, rice, sorghum, and cowpea have been investigated by several researchers (Maropola et al., 2015; Kunda et al., 2018; de Araujo et al., 2019; Fadji et al., 2020). The specific functions of maize inhabiting endophytes, which include nitrogen metabolism, stress response, potassium, and phosphorus metabolism, iron acquisition, and metabolism have been reported by Fadji et al. (2020). Based on the putative functions of these bacteria, the authors have recommended the use of culture-dependent methods in identifying these bacteria for further exploration in sustainable agricultural systems.

Metagenomic techniques are promising without bias compared to culture-dependent methods in culturing prokaryotes, but with limitations, among which are, the extra cost of depleting host DNA for sequencing, the presence of plant DNA, the low efficiency of endophytic DNA extraction or amplification of the 16 S rRNA. Small amounts of bacterial DNA sometimes result after DNA extraction (Bulgarelli et al., 2013). These limitations might be the reasons why limited success has been recorded using shotgun metagenome sequencing to investigate endosphere bacterial communities in plants. Hong et al. (2019) performed a metagenomic analysis of the bacterial endophyte community structure and functions in *Panax ginseng* at different ages and identified important putative genes involved in iron acquisition and metabolism, metabolite metabolism, stress response, nitrogen fixation, and siderophore production which might contribute to bacterial functions in plants. Similarly, Tian et al. (2015) employed a metagenomics approach in studying endophytic bacterial communities and functions in tomatoes and found that they possess secondary metabolite genes which suggest that they may suppress nematode infection in tomato roots.

The genetic composition of bacteria in the root endosphere may differ from the bacterial genetic composition in the whole plant, but with similar structural diversity and metabolic activities (Stefan et al., 2018). Genetic analysis of many plant-associated microbes has revealed the structural composition and functions of the bacterial community in the endo-rhizosphere compartments (Beckers et al., 2017). The use of next-generation sequencing in the identification of bacteria genera associated with the roots of plants have been reported, which include maize (Potshangbam et al., 2017), sorghum (Correa-Galeote et al., 2018), millet (Manjunatha et al., 2019), and soybean (Yang et al., 2018). Similarly, several methods have been employed in the identification of novel genes from bacteria colonizing the root endosphere and a few of the specific functional genes have been revealed in field experimental studies (Afzal et al., 2019). For example, the identification of multiple genes responsible for plant growth promotion in endophytic *Bacillus toyonensis* COPE52 and *B. thuringiensis* CR71 which upon inoculation under greenhouse conditions has been reported to enhance the yield of blueberry (*Vaccinium* spp.) and cucumber (*Cucumis sativus*) (Contreras-Pérez et al., 2019; Flores et al., 2020). Also, a bioinformatics study by Ali et al. (2014b) reported a set of functional genes involved in determining the endophytic behavior of *Burkholderia* spp. Hence, prediction of plant growth-promoting genes involved in the synthesis of IAA (*dha* and *trp*), enzyme production (*lon*, *amy*, and *pul*), phosphate solubilization (*ppx* and *pho*), bacterial attachment (*flg*, *flh*, *fli*, and *mot*), biological control by secreting volatile compounds (i.e., acetoin, 2,3-butanediol (*ilv*), biofilms (*efp*, *hfq*, *bcs*, *yhj*, and *crp*), plant protection against oxidative and nitrosative stress (*sod*, *kat*, *bsa*, and *grx*), siderophores (*fbp*, *fitu*, and *fet*), cytokinin biosynthesis (*mia*), and ammonia production (*nad*) in the bacterial genome can be inferred to confirm the activities of these bacteria through inoculation experiments (Zaferanloo et al., 2013; Adeleke et al., 2021a; Singh et al., 2021). Furthermore, molecular analysis of endophytic bacteria from plant roots can enable scientists to determine genomic sequences that reveal important functions of these microbes via online analytical software.

Research into diverse bacterial communities in some plants using

culture-dependent methods has been reported (Puri et al., 2018), however, only a very small portion (1%) of the microbial population in these samples has been identified. The use of a metagenomics approach in studying endophytic bacteria is relatively new and has not yet been fully explored. Several hypotheses exist regarding the use of metagenomic analysis of root-associated endophytic bacteria. A metagenomic study of a transgenic *Bacillus thuringiensis* (Bt) cry maize cultivar and its isogenic parental line (i.e., a non-Bt maize cultivar) revealed that the most dominant Proteobacteria in the Bt maize endosphere were similar to those in the non-Bt maize cultivar (Mashiane et al., 2017). While this phenomenon appears universal, the challenges associated with the use of culture-independent techniques in culturing endophytic bacteria have caused some technical difficulties. Therefore, employing a metagenomics approach in studying diverse endophytic bacterial communities would help scientists to develop bioinoculants that can be applied in the field for improved crop production. For instance, based on the functional traits of some identifiable bacteria endophytes, a field experiment performed by Hungria et al. (2010) using singularly or combined applied endophytic *Azospirillum brasilense* and *A. lipoferum* as bioinoculants found that these strains contributed significantly to the yield of maize and wheat in Brazil.

6. Conclusion and future prospects

Endospheric communities are groups of microorganisms colonizing the internal tissues of plants without causing any deleterious effects to the host plants. Understanding the mechanisms employed by PGPEB in plant growth promotion is fundamentally important and this can be conventionally investigated *in vitro*. Endophyte interdependence with their host plants contributes to their effectiveness under different environmental conditions. On a commercial scale, harnessing endophytic products as an alternative to chemical fertilizers is suggested for developing eco-friendly approaches to agriculture. Many identifiable root-associated bacteria have been isolated and studied with great promises in agriculture and many of them are still under investigation. Most endophytic bacteria have not been cultured, thus limiting their use in agricultural biotechnology. It is, therefore, necessary to devise appropriate measures to achieve this by employing 16 S rRNA gene amplicon sequencing or shotgun metagenomics. The use of metagenomics techniques is promising to unveil structural diversity and novel functional information of nonculturable root-colonizing bacteria. A correlation between root bacterial endophytes and metagenomic insights into the functioning of these bacteria will help understand their functional attributes and ensure endosphere competence.

The metagenomic approach of studying root endosphere bacterial communities is a promising area of research that is currently being used to analyze bacterial metagenomes from plant roots based on diversity, functions, and metabolic pathways. Metagenomics can reveal novel aspects of root endophytes. Several molecular techniques can be employed in the characterization of bacterial genes such as characterizing and understanding nitrogen fixation genes. Some culturable bacterial endophytes have been isolated, identified, and characterized with this and other traits such as siderophores genes, ACC deaminase genes, and phosphate-solubilizing genes.

This review has focused on the relevance of root-endophyte bacteria that promote plant growth and soil health for improved crop yield. The benefits of these bacteria in crop production are multiple as they can be employed in the synthesis of bioinoculants that can be substituted for agrochemicals. Nevertheless, this area requires additional research on the use of biofertilizers in developing eco-friendly agriculture. Finally, the application of metagenomics in understanding root endophytic bacteria has been studied with success in determining their structural diversity, functional, and metabolic pathways. Promisingly, biotechnological advancement using modern analytical methods in determining endophytes and their metabolites can be adopted for research relating to plant-microbe interactions. For instance, stable isotope probing (SIP)

combined nanoscale secondary ion mass spectrometry techniques (NanoSIMS) combined with advanced Raman spectroscopy-based single cell-based methods can be employed in the study of plant-endophyte-interactions *in situ*, and biological functions in the removal of complex pollutants from the contaminated soil. Hence, the concept of this biotechnological advancement in establishing a strong plant-microbial framework may create insights for future endosphere research with promises in solving agricultural problems.

Authors' contributions

B.S.A and O.O.B had the idea for the article and suggested the review topic; B.S.A performed the literature search and wrote the first draft; O. O.B and B.R.G made substantial technical and intellectual contributions to the structure of the various drafts of the manuscript. All authors approved the article for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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