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The bacterial world inside the plant

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Sustainable agriculture requires the recruitment of bacterial agents to reduce the demand for mineral fertilizers and pesticides such as bacterial endophytes. Bacterial endophytes represent a potential alternative to the widespread use of synthetic fertilizers and pesticides in conventional agriculture practices. Endophytes are formed by complex microbial communities and microorganisms that colonize the plant interior for at least part of their life. Their functions range from mutualism to pathogenicity. Bacterial endophytes colonize plant tissues, and their composition and diversity depend on many factors, including the plant organ, physiological conditions, plant growth stage, and environmental conditions. The presence of endophytes influences several vital activities of the host plant. They can promote plant growth, elicit a defense response against pathogen attack, and lessen abiotic stress. Despite their potential, especially with regard to crop production and environmental sustainability, research remains sparse. This review provides an overview of the current research, including the concept of endophytes, endophytes in plant organs, endophyte colonization, nutrient efficiency use, endophytes and crop nutrition, inoculation with synergistic bacteria, the effect of inoculum concentration on plant root microbiota and synthetic communities. It also examines the practical opportunities and challenges when utilizing endophytes in the field of sustainable agriculture. Finally, it explores the importance of these associations with regard to the future of agriculture and the environment.

KEYWORDS

plant growth-promoting, endophytes, yield, SynComs, plant growth

Introduction

With a growing global population and limited land resources, agricultural intensification is essential for global food security (Jayne et al., 2019; Devika et al., 2021). However, the use of chemical fertilizer to improve crop yield has had a negative effect on soil quality (Adeleke et al., 2021). The consumption of some foods grown in fertilized fields treated with agrochemicals has been associated with human diseases (Babalola, 2010). Additionally, recent reports have shown that 52% of all fertile food-producing soils globally are now classified as degraded, which poses more new challenges for growing crops. Global food production is expected to decline by 12% over the next 25 years (UNCCD Brochure, 2012; Patel and Minocheherhomji, 2018). Therefore, it is imperative that we establish sustainable and non-hazardous agricultural practices.

Microbial communities in plants represent a potential solution to the decline in global food production. Plant growth and health are modulated by microbial communities that colonize their tissues. Although some microbes are detrimental and cause diseases, others may promote plant growth and tolerance to biotic and abiotic stresses by enhancing nutrient acquisition *via* many mechanisms (Brader et al., 2017).

The application of plant growth-promoting microorganisms (PGPs) may improve plant production under unfavorable conditions, with the potential to reduce the use of chemical fertilizers and pesticides. However, the current application of endophytes, especially in the field, faces a number of challenges. For example, microbial application may not completely replicate the effectiveness of chemical fertilizers (Sessitsch et al., 2019). In addition, PGP may fail to induce plant growth due to insufficient rhizosphere colonization (Lugtenberg et al., 2001). Many mechanisms that are related to plant growth promotion necessitate further investigation, including the steps involved in plant colonization by PGPs, plant–soil interactions of root endophytes, and microbes associated with all plant parts. Additionally, the interaction of microbes living within the same plant, how they modulate above- and belowground communities, and the involved processes all require further examination to improve the efficiency of the inoculant strain (Compant et al., 2016).

Currently, microbiome research has received tremendous attention due to several factors related to plant growth promotion. Usually, this research begins with screening different isolates for specific characteristics that are related to plant growth under controlled conditions, and then further evaluations are conducted under uncontrolled field conditions (Figure 1). Associations between endophytes and their hosts support health and plant growth (Sessitsch et al., 2019). Figure 2 shows a schematic representation comparing uninoculated and inoculated plants with bacterial endophytes.

Most plant-associated bacteria are derived from the soil environment (Compant et al., 2010). Microorganisms that live inside the plant are called endophytes. They consist of several microorganisms that spend either their full or partial life cycle colonizing plant tissues. However, the definition of “endophyte” has been modified over time (Hardoim et al., 2015). Endophytes may cause diseases or live as symbionts. They rely on many factors, including the environment, plant genotype, and microbiota (Brader et al., 2017). Hardoim et al. (2015) previously suggested that the term “endophyte” should refer to all microorganisms that colonize the plant tissues for either their whole lifetime or part of their lifetime. One study showed that some species of endophytes may be either pathogenic or beneficial. While most endophytes are innocuous toward select plant species, they may be pathogenic toward other plants (Fadji and Babalola, 2020). The pathogenicity shown by some endophytes may be attributed to environmental factors. Fluorescent pseudomonads may be pathogenic or beneficial to

most plants depending on the conditions. In the present review, the term “endophyte” refers to any microorganism, including pathogens, that can colonize the internal tissues of plants.

Endophytes in plant organs

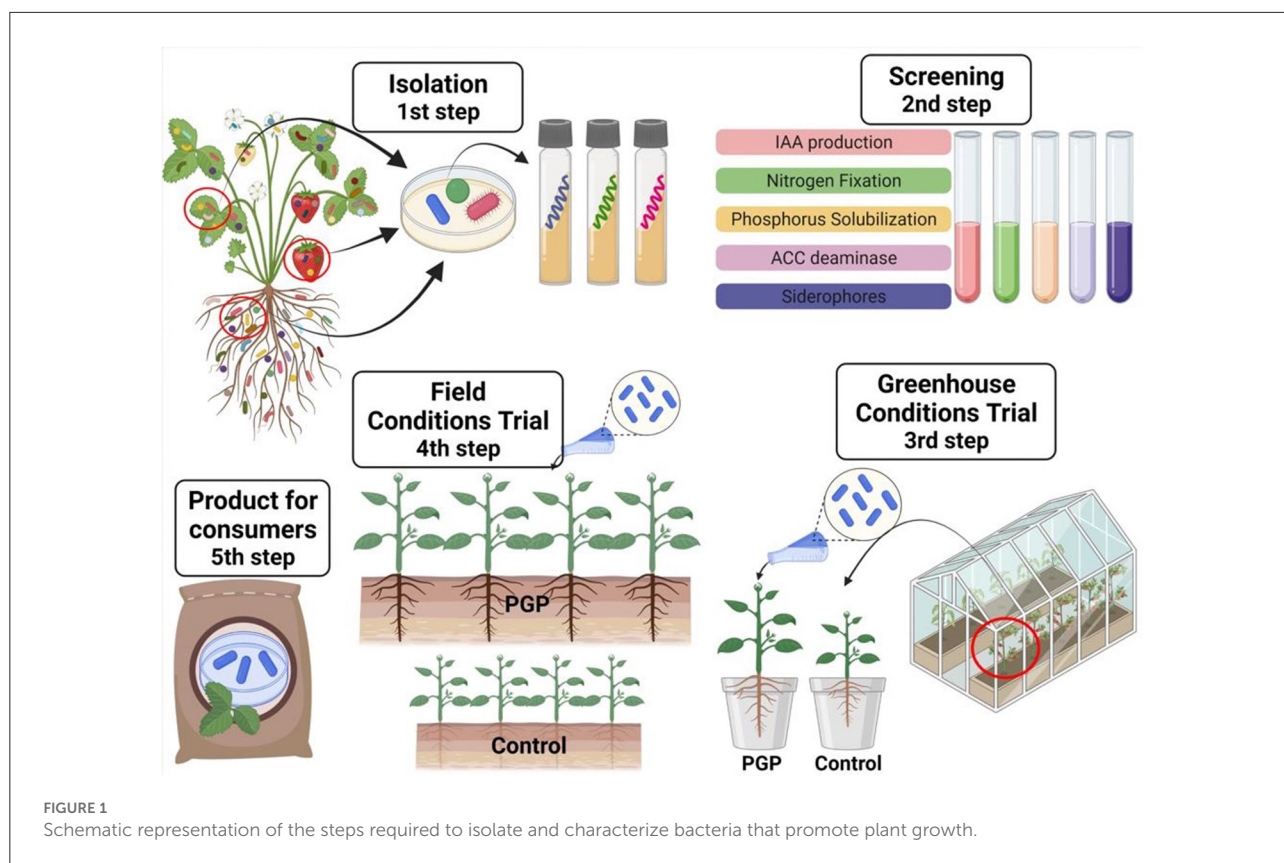
The best-characterized endophytes are associated with roots and leaves and live on or inside plant organs (Bulgarelli et al., 2013). Different plant organs house a wide range of microbiota that exert a strong influence on each compartment, such as flowers, fruits, and seeds (Compant et al., 2010). Different chemical compositions are found in roots, stems, leaves, fruits, and seeds, which promote the colonization of several bacterial communities responsible for plant growth, stress adaptation and defense (Hounsoume et al., 2008). The degree of colonization by microbiota is dependent on the different chemical compositions of each plant organ (Bulgarelli et al., 2013).

The microorganisms associated with plants are essential for seed germination and healthy crop development (Firdous et al., 2019). Plants that allow endophyte entrance, seed colonization, and vertical transmission for subsequent generations benefit from distinct advantages (Truyens et al., 2013). The majority of the microbial genera found in the microbiome are also found in the soil and play an essential role in conservation, germination, and seed development. A fascinating review by Samreen et al. (2021) addressed associated bacterial and fungal endophytes: diversity, life cycle, transmission, and application potential.

Typically, bacterial communities living in different organs of the same plant and in the rhizosphere soil possess similar characteristics, and each group of microbes is determined by the genetics of the plant host, growing conditions, and the interactions between the environment and individual plants (Wearn et al., 2012; Baldan et al., 2014). These results suggest that the plants attract endophytes that will provide certain compounds, hormones, and metabolites. However, chemotactic behavior alone does not fully explain endophyte host levels. Soil microorganisms may sense and respond to multiple chemoattractants simultaneously. The behavior of soil microorganisms may be influenced by abiotic and biotic environmental factors during the colonization of different plant organs. Chemoattractant or repellent molecules may be released in the field to modulate the actions of microorganisms, improving the growth of crop plants. With the identification of more chemoattractants, additional strategies may be used to guarantee endophyte colonization in different host plant organs (Tsai et al., 2020).

Endophyte colonization

The abundance and diversity of endophytes may be modulated by the plant immune system, thereby maintaining



an adequate bacterial population in different plant organs (Liu et al., 2017). High bacterial cell density can be detrimental to host organs. For instance, high cell density induces quorum-sensing regulated processes, such as virulence and pathogenicity, that are crucial for beneficial functions (Hartmann et al., 2014).

Bacterial taxa rely on the specific environment promoted by the plant compartment to determine their occurrence, abundance, and activities (Brader et al., 2017).

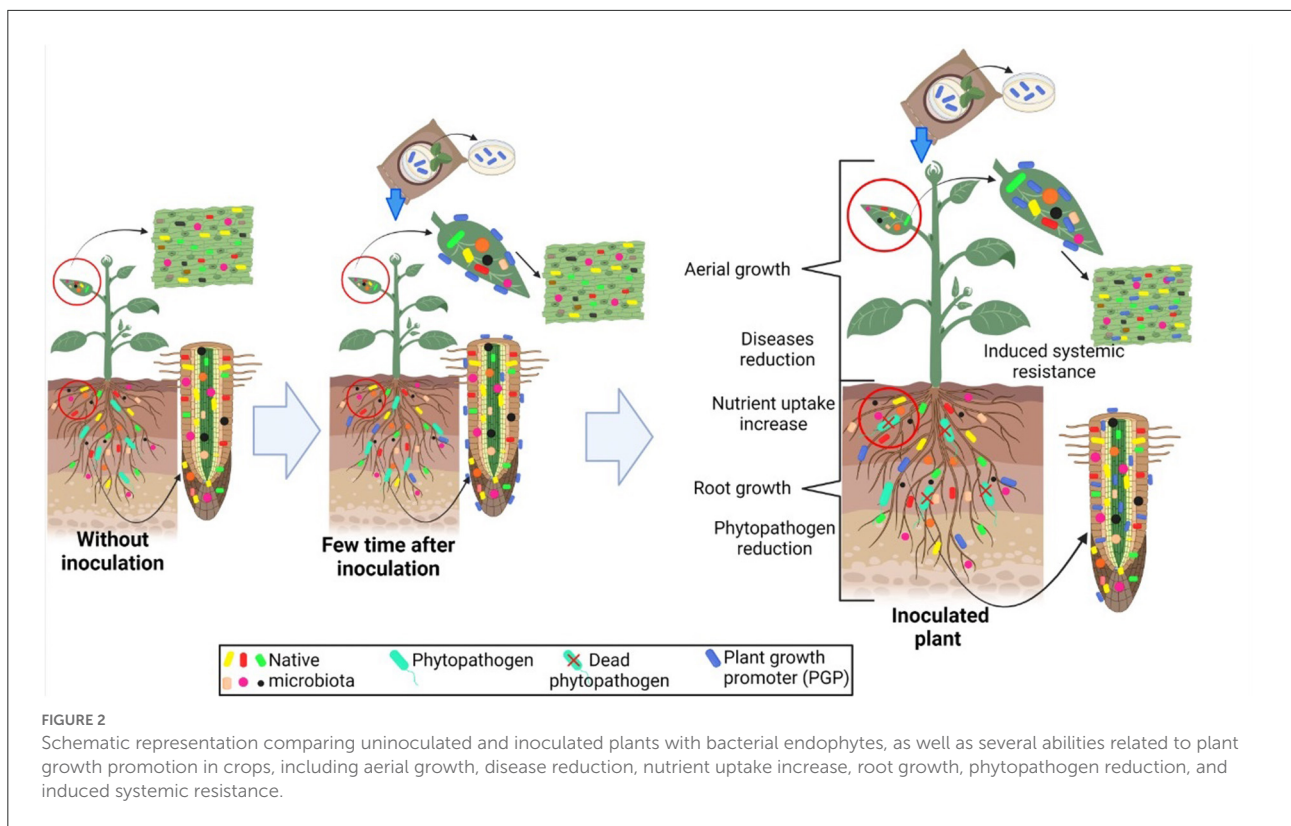
Typically, three classes of bacterial endophytes are mentioned. They include the following: endophytes that are not able to reproduce in the absence of plant tissue - these endophytes are spread from seed to seed; facultative endophytes - these endophytes typically live in the soil and opportunistically colonize the plant tissues; and passive endophytes - these endophytes do not typically occupy the plant tissues, but depending on the circumstances, they may colonize the tissues *via* wounds on the root hairs (Hardoim et al., 2015). In the soil environment, microorganisms that reach the rhizosphere are influenced by root exudates supporting the establishment and development of the microbial community (Lemanceau et al., 2017).

Plants have the ability to detect several environmental factors, such as the presence of beneficial microbes, nutrients, and hydric stress, including the presence of pathogens. Plant

exudation is modulated by a combination of these factors (Li et al., 2018).

Plants release approximately 10–40% of their fixed carbon made by photosynthesis through their roots in both inorganic and organic forms. The secretion and diffusion of these exudates are chemically diverse and include compounds such as cellulose, fatty acids, phenolics, nucleotides, putrescine, sterols, vitamins, organic acids and amino acids (Sasse et al., 2018). The bacteria must be able to colonize the rhizosphere using the available nutrients and compete with several microorganisms interacting with the plant genotype (Taulé et al., 2021).

The soil microbiome is modulated by the root environment, root exudates, and root morphology. In addition, bacterial endophytes become established in different plant organs (Rodríguez et al., 2018; Sasse et al., 2018). Several factors can shape endophyte colonization in the soil and inside the leaves, such as the plant genotype and environment (Vincent et al., 2018). The success of endophyte colonization within plant leaves can be influenced by competition with other endophytes and their capacity to face imposed challenges (Vacher et al., 2016). The competition for limited resources within communities of organisms determines each species' realized niche (Chase, 2003). The composition of the bacterial communities and their activities limit the species of bacterial endophytes that colonize the plant leaf (Van Bael et al., 2017).



Plants promote a favorable environment for endophyte colonization, and consequently, endophytes will compete with a colonizing pathogen (Ghazi et al., 2021). Kennedy (2010) demonstrated a reduction in pathogen colonization when the establishment of beneficial microbes occurred first. Berg and Raaijmakers (2018) verified that plant seeds may be home to several microbial endophytes whose composition is determined by the environment, agricultural practices and plant genotype.

Thus, some bacterial traits improve the bacterial interaction and colonization of the plant. Endophytic bacteria are great competitors due to their diverse ability to produce secondary metabolites that can reduce several pathogens, protect against predatory organisms, and guarantee their colonization in the plant (Taulé et al., 2021). Specific microbes can colonize plant seeds and are transmitted vertically to various generations (Shade et al., 2017). Additionally, microbes can be transmitted horizontally to different environments Figure 2.

Inoculation with synergistic bacteria

The inoculation with synergistic bacteria with plant growth-promoting abilities is becoming increasingly common. This practice has some advantages, such as an increase in the successful establishment of bacteria in the rhizosphere and in the condition of interaction with plants (Bulgarelli et al., 2013).

Some studies on the combination of PGPR have found that most of the microorganisms used in mixtures did not interfere negatively with each other (Kaur et al., 2015; Korir et al., 2017; Vandana et al., 2021). However, few reports indicate that certain mixtures of microbial strains do not show synergistic or at least comparable effects on plant growth promotion concerning the separate application of microorganisms (Felici et al., 2008; Lobo et al., 2022). These authors support the hypothesis that the co-presence of the two microorganisms may alter, directly or indirectly, the internal hormone content of the root, interfering with the normal morphogenesis of the root itself.

Effect of inoculum concentration on plant root microbiota

Under field conditions, PGPMs are applied in the form of formulated products, these new formulations have increased the concentration of microorganisms involved in the field. However, despite the advance in the use of inoculants in agriculture, few studies have evaluated the effect of inoculant concentration on plant growth promotion. Thus, this theme has become essential to define whether the increase in the concentration of microorganisms is an important aspect related to product efficiency or whether it is just an aspect of commercial advantage. Escobar Diaz et al. (2021) evaluated the effect of

B. subtilis concentration in cotton crop under field conditions and verified that the parameters that were favored by the highest inoculant concentrations were soil respiratory activity, phosphorus in root dry matter, nitrogen in shoot dry matter, and number of colonies forming units in roots and leaves. Concentrations did not affect nitrogen in root dry matter, phosphorus in shoot dry matter, and microbial biomass carbon. Interestingly, concentrations did not affect cotton fiber or seed yield. dos Santos et al. (2022) evaluated the effect of inoculant concentration based on *B. subtilis* on soybean crops and verified that *B. subtilis* inoculations did not affect the endophytic community of roots. Bueno et al. (2022) showed a strong tendency for the inoculant concentration to increase and the necessity of mineral fertilization dose for the plants to achieve the same development. The authors proposed that these high inoculum concentrations promoted an increase in the bacterial rhizospheric population, and as a consequence, more photosynthetic metabolites from the plants and more nutrients from the soil are needed. Thus, the need for mineral fertilization for plant growth must be increased. More studies are needed to understand better the effect of inoculum concentration on the microbiota.

Nutrient use efficiency

Global agriculture suffers a high economic pressure for food production. Thus, a significant number of chemical fertilizers are used annually. These chemical fertilizers use energy extracted from fossil fuels that are pollutant resources and spread gases related to the greenhouse effect. In addition, the indiscriminate use of chemical fertilizers neglects the principles of management and soil conservation, promoting damage to soil health and accelerating nutrient depletion, acidification, and erosion (Brevik, 2012; Sarkar et al., 2017). Moreover, the low use of organic fertilizers has worsened soil fertility (Sarkar et al., 2021a). Chemical fertilizer practices and cereal production worldwide have exacerbated the negative balance of nutrients in soil (Sanyal et al., 2014). Among agricultural crops, nutrient efficiency use is less than 50% in most agricultural regions (Baligar et al., 2001). Factors such as energy crises and reduction of nutrient efficiency form a great challenge for modern agriculture (Sarkar et al., 2021b). Some studies have demonstrated that the consumption of fossil fuels, changes in the climate scenario, soil degradation, and food security have resulted in a cyclical degradation process of natural resources, low productivity, and low nutrient efficiency use (Rakshit, 2019). Therefore, breaking this deleterious cycle is a necessary practice. Technology that promotes nutrient availability in the soil improves the nutrient supply to plants and enhances the plant's capacity to take up nutrients (Aloo et al., 2019).

To face this challenge, using plant growth-promoting microorganisms is an excellent strategy for reducing the use of

agrochemicals and the environmental impact without reducing crop yield. *Trichoderma harzianum*, *Pseudomonas fluorescens* and *Bacillus subtilis* have been used to increase macronutrient uptake (N, P, and K), root length, heading percentage, head diameter, head weight, and the total weight of red cabbage (Sarkar et al., 2021c). In another study, *Trichoderma harzianum*, *Pseudomonas fluorescens*, and *Bacillus subtilis* were applied singly and in combination with 75% of the recommended dose fertilizer (RDF). The authors verified that compatible microbes improved the nutrient composition and bioactive compounds of red cabbage, that the performance of the dual consortium was better than that of the triple consortium and that the reduced fertilizer dose (75% RDF) in combination with *Trichoderma* sp. and *Pseudomonas* sp. achieved the highest head yield (Sarkar and Rakshit, 2021). Cipriano et al. (2021) inoculated sugarcane with *Paraburkholderia caribensis*, *Kosakonia radicincitans*, *Paraburkholderia tropica*, *Pseudomonas fluorescens*, and *Herbaspirillum frisingense*. They showed that the nutrient-use efficiency increased by an average of 250–300% compared the treatments to the control. The integrated use of microbes for nutrient and disease management, along with organic manures and inorganic fertilizers, has been suggested as the most effective method to maintain healthy and sustainable soil while increasing crop productivity. Inoculation with these methods increased crop yields by ~10–15% under farm conditions (Kumar et al., 2021). The application of *B. subtilis* and *P. putida* increased the percentage of nitrogen by ~40% compared to the control (Mehrasa et al., 2022). *Bacillus* sp., *Pseudomonas* sp., *Staphylococcus* sp., *Paenibacillus* sp., *Stenotrophomonas* sp., *Sphingobacterium* sp., *Lysinibacillus* sp., *Advenella* sp., *Enterobacter* sp., *Variovorax* sp., and *Plantibacter* sp. were evaluated in wheat and increased phosphorus acquisition efficiency by 29.5% (Emami et al., 2020). The inoculation of *Herbaspirillum seropedica* in rice crops increased the shoot nutrient contents of N, P, K, Ca, Mg, and S by 120, 350, 430, 150, 110, and 300%, respectively (Ramos et al., 2020).

Sarkar et al. (2021b) have written a fascinating review concerning nutrient use efficiency. In this review, the author demonstrated that rhizosphere chemistry and other mechanisms of plant–microbial interactions will frame suitable strategies to harness the best ecosystem services, including improved resource use efficiency.

Endophytes and crop nutrition

Nitrogen (N) is essential for maintaining vital activities in the cell. It is an essential component of various important molecules responsible for maintaining cell functions. These molecules include adenosine triphosphate (ATP), nucleic acids, and chlorophyll (Werner and Newton, 2005). This nutrient, as well as oxygen, carbon, and hydrogen, is required in all

living biomass (Howarth et al., 2009). The process responsible for converting organic nitrogen to inorganic nitrogen, thereby enabling plant use, is a combination of nitrification and ammonification (Paul and Kumar, 2015). The bacterium Rhizobia is the most studied symbiotic N₂-fixing organism in agriculture (Shamseldin et al., 2017). Biological nitrogen fixation (BNF) is a process in which nitrogen is converted to ammonia by nitrogenase activity, thereby becoming available for microbe and plant assimilation (Wichern et al., 2008). The atmosphere is the principal major reservoir of nitrogen. However, for nitrogen to be absorbed by plants, it must first be fixed by bacteria.

Pseudomonas fluorescens has been used to reduce the amount of N fertilizer applied to wheat crops. The fungus *Trichoderma harzianum* promoted a 25% reduction in the nitrogen dose for the same crop. Duarah et al. (2011) reported a reduction in NPK fertilizer application using seeds inoculated with bacteria and verified a considerable enhancement in NUE.

Phosphorus is essential for plant growth and affects many biological processes. It is required in photosynthesis, signal transduction, molecule biosynthesis, and respiration processes. A tremendous quantity of phosphorus is present in soils in both organic and mineral forms. Nevertheless, the main factor limiting plant growth in different environments is its availability (Mitter et al., 2021). Soil microbes can mineralize phosphorus into plant-mineral forms through several mechanisms of mineralization and solubilization (Alori et al., 2017). Phosphate-solubilizing microbes (PSMs) utilize various mechanisms to produce and release different compounds that solubilize organic phosphorus immobilized in organic matter and inorganic P, such as tricalcium phosphate, rock phosphate, and hydroxyapatite. One such mechanism is the production of organic acids, CO₂, and hydroxyl ions (Wei et al., 2018).

Inoculation of wheat seeds with *P. fluorescens* and NPK fertilizer application at 25, 50, 75, and 100% resulted in enhanced P use efficiency, at 102, 56, 57, and 21%, respectively, when compared with corresponding uninoculated treatments in wheat field studies (Duarah et al., 2011). Seed priming with a conidial suspension of *T. harzianum* (1×10^8 spores/mL) significantly increased the P uptake by sunflower (*Helianthus annuus* L.) in a greenhouse study (Nagaraju et al., 2012).

Potassium (K) is another important element for plant growth. It is an essential nutrient in the cell cytoplasm and functions and is related to protein synthesis and photosynthesis. Potassium is the most abundant element on Earth and the second most abundant nutrient in the soil. However, the K present in the soil at approximately 98% is in a non-soluble form. Potassium is trapped within mica and feldspar minerals in the soil, such as muscovite and biotite. Another portion, approximately 1–2%, is adsorbed onto organic matter and clay. Some, 0.1–0.2%, is available in the soil solution and is directly taken up by the plants (Srivastava et al., 2021).

Seed treatment with *T. harzianum* isolates increased the uptake of K by 62% in sunflower grown in greenhouse

conditions (Nagaraju et al., 2012). Bacterial isolates (*Pseudomonas orientalis*, *Rahnella aquatilis*, and *Pantoea agglomerans*) isolated from Iranian soils containing mica and illite minerals proved their K solubilizing ability by augmenting K use efficiency in rice grown under pot conditions (Khanghahi et al., 2018).

Micronutrients are essential for plant growth and development. They participate in many critical enzymatic activities responsible for maintaining cell metabolism. Various studies have shown that micronutrient deficiencies decrease crop yield, mainly in crops under soil with low organic matter (Rashid and Ryan, 2004). Essential micronutrients are nickel, silicon, iron, copper, boron, and molybdenum (Castro et al., 2018; Shukla et al., 2018).

Synthetic communities

The endophytic community originates from bacteria of different sources, mainly soil and seeds. Bacteria from seeds play an important role in early plant stages (Verma et al., 2019). Interestingly, soil is also a source of bacteria during the later plant stages. The recruited bacteria must interact with natural microbiota to perform important functions related to plant development (Lemanceau et al., 2017).

Synthetic definition systems (SynComs) result from the core microbiome responsible for important functions in the microbial community, which acts as a substitute for the natural microbiome (Vorholt et al., 2017). Synthetic microbial communities (SynComs) have been constructed based on several combinations and interactions between plants and their microbiome and are based on various mechanisms that drive microbial communities in different aspects and environments (Vorholt et al., 2017). Information based on microbiome traits, such as microbe–microbe interactions, microbe–plant interactions, redundancy, dominance, and modularity, has been used to assemble these SynComs and optimize their effect on plant growth. Synthetic communities have also been constructed with respect to the important roles played by distinct strains from individual microbial cultures and in higher-complexity interaction networks. This experimental approach enables the inhibition, or specific removal (drop-out), of individual strains, populations, or functions and monitors the whole response of the system. Additionally, this approach allows us to know the individual strains and their prioritization. With the introduction of microorganisms into a preestablished community, their effects can also be evaluated (Vorholt et al., 2017).

Carlström et al. (2019) inoculated *Arabidopsis thaliana* with 62 native bacterial strains. They verified that some missing strains could interfere, to varying degrees, with specific niches already colonized by the natural microbiome. These results demonstrated that individual phyla, such as Actinobacteria and

Proteobacteria, may significantly influence the communities and microbial structure.

Specific and essential plant genes in the community can also be determined. The dynamics of the microbiome can be previously established and then applied using SynCom. This strategy could enable intelligent farming systems (Trivedi et al., 2020). Stochastic events may determine the presence of some microbes; however, substantial evidence has shown that core microorganisms are established according to plant conditions. These microbes are consistently related to the main taxonomic resolution (Müller et al., 2016). Variations due to plant genotype and environment modulate the microbiome composition. However, studies have shown that the establishment of these SynComs has been consistent throughout the years (Schlaeppli et al., 2014; Finkel et al., 2017).

The assemblage of core microbes could exert several benefits related to plant growth and health. However, it is almost impossible to predict whether a microbial consortia can become established in a place where a microbiome is already installed (Liu et al., 2019).

SynCom can reduce the incidence of diseases. It was built based on previously established microbiome characteristics and the analysis of culture collections (Liu et al., 2019). Niu et al. (2017) reported a reduction in diseases caused by *Fusarium verticillioides* after Syncom application. Interestingly, the severity of the disease was also significantly reduced.

The reductionist synthetic community approach can be used to improve disease suppressing efficacy. Nevertheless, it is necessary to know microbe–microbe interactions and plant–microbe interactions when constructing multiple-strain biological control consortia for assembly (Niu et al., 2020).

Sustainable agriculture

Food security concerns have led to agricultural intensification and widespread use of chemical fertilizers and pesticides to maximize production (Kumar et al., 2015). Therefore, the harmful effects of these chemicals on non-target organisms and the destabilization of the environment through pollution are expected to become higher than they are now (Yu et al., 2010). Endophytes produce several compounds that can be applied for the biocontrol of a wide range of plant diseases and pests (Shafi et al., 2017) and for plant production. The commercialization, formulation, and application of efficient PGP strains have been proposed as a potential solution for improving agricultural yields without the deleterious effects of synthetic fertilizers and pesticides (Glick, 2014).

Studies carried out under controlled conditions have shown promising results (Shafi et al., 2017). However, crops are grown under varying environmental conditions, which produces large differences and inconsistencies in terms of results (Kamilova et al., 2015).

Many researchers around the world are combining different techniques, including hybridization and techniques that are cultivation-independent, to improve the understanding of microbial strains and determine which are cultivable and uncultivable (Reinhold-Hurek and Hurek, 2011; Berg et al., 2014).

Studies showing how plants shape their microbiome, including ecological interactions in agricultural systems, have been crucial. In the context of climate change, soil pollution, and agricultural intensification, soil microorganisms have been intensely affected (Mitter et al., 2019).

The use of biofertilizers and their success as PGPs rely on selecting specific functions or microorganisms and developing new products to enhance the survival of inoculated strains (Mitter et al., 2021).

Bell et al. (2019) reported that due to the complexity of the microbiome, including genetic diversity and the heterogeneity of the soils, the production of different formulations could be an effective strategy for coping with varying environmental conditions. However, it is unrealistic and unfeasible to design specific biofertilizers for each specific field (Mitter et al., 2019).

New technologies should guarantee a higher number of viable cells during storage and application, and the use of carriers and additives that are cost-effective and easy to use is important to support the presence of endophytes in the product (Bashan et al., 2016; Mitter et al., 2019).

The development of new products requires continuous research and validation. The products should be evaluated against different environmental conditions, such as crop, climate, soil type and agricultural practices, to generate ranges of microbial products that could be utilized. This would result in a better understanding of their potentialities and feasible use for sustainable production. Table 1 shows the bacterial species, abilities, experimental conditions, and results promoted by the application in crops.

Limitations in the use of endophytes

There are numerous advantages to using endophytes for plant growth promotion, including the low cost of commercialization. However, their use is still not yet widespread because of inconsistent results over varying environmental conditions, plant genotypes and soils. Additionally, agricultural practices and recommendations already exist (Debnath et al., 2019).

To achieve the desired effects related to plant growth and health, microbial products need to overcome many challenges, such as the colonization rate, survival, and shelf life. Typically, endophyte studies have a limited number of variables, making it difficult to understand their performance more fully (Acharya et al., 2017).

TABLE 1 Bacterial species, abilities, experimental conditions, and results promoted by the application in crops.

Endophytes	Abilities	Condition	Results	References
<i>A. brasilense</i> + <i>B. subtilis</i>	Phosphate solubilization	Field	Increased yield, dry matter, total P accumulation, and reduced fertilization by 75%	Rosa et al., 2020
<i>Lysinibacillus sphaericus</i> (T19)	BNF and IAA production	Field	Increased productivity	Breedt et al., 2017
<i>B. pumilus</i>	Production of IAA and enzymes (endoglucanases and xylanases)	Pot	Increase in dry matter and number and diameter of tillers	Santos et al., 2018
<i>B. subtilis</i> (BSSC11) and <i>Bacillus megaterium</i> (BMSE7)	Phosphate solubilization and the production of siderophores, IAA, ammonia, and HCN	Field	Increase in root length, shoot length, and total dry matter	Chandra et al., 2018
<i>B. pumilus</i> S1r1	BNF	Greenhouse	Higher corn cob productivity (up to 30.9%)	Kuan et al., 2016
<i>Burkholderia gladioli</i> TNCSF	Phosphorus solubilization	Pot	Increase in leaf chlorophyll, N content, and total biomass	Muthukumarasamy et al., 2017
<i>Bacillus altitudinis</i> and <i>Bacillus velezensis</i>	Biological Control	Greenhouse	Increase in dry weight, surface area, and total root length	Liu et al., 2022
<i>Enterobacter cloacae</i>	ACC deaminase production	Greenhouse	Increases in grain production (60%), photosynthetic rate (73%), stomatal conductance (43%), chlorophyll A (69%), total chlorophyll (76%) and carotenoids (42%).	Danish et al., 2020
<i>Bacillus xiamenensis</i> PM14	Production of siderophores, IAA, amylase, pectinase, cellulase, chitinase, protease, and ACC deaminase and phosphate solubilization	Greenhouse	Increase in height, fresh weight, length, and root diameter and length	Xia et al., 2020
<i>B. subtilis</i> and <i>A. brasilense</i>	Phosphate solubilization	Field	Higher grain yield	Pereira et al., 2020
<i>Chryseobacterium</i> sp. NGB-29 and <i>Flavobacterium</i> sp. O NGB-31	BNF and production of large amounts of IAA	Greenhouse	Increased growth parameters	Youseif, 2018
<i>B. subtilis</i> 320	Phosphate solubilization and phytohormone production	Field	Increase in productivity and P in the shoots	Lobo et al., 2019
<i>Burkholderia cepacia</i>	Biocontrol and phosphate solubilization	Greenhouse	Increased leaf area, length, and shoot and root dry weight	Zhao et al., 2014
<i>Pseudomonas tolaasii</i> IEXb	Phosphate solubilization	Field	Increase in seedling emergence, shoot length, grain yield, 1,000-grain weight, total dry biomass, and P content in plants	Viruel et al., 2014
<i>Pseudomonas kilonensis</i> F113 and <i>Pseudomonas protegens</i>	Phosphate solubilization and biocontrol	Field	Increase in leaf yield, height, and length	Alori et al., 2019
<i>Enterobacter cloacae</i> PGLO9	Phosphate solubilization	Greenhouse	Longer root length, shoot length, and increased shoot and root biomass	Verma et al., 2018
<i>Azospirillum</i> , <i>Azotobacter</i> , <i>Pseudomonas</i> , <i>Bacillus</i> , <i>Klebsiella</i> , <i>Acetobacter</i> , <i>Burkholderia</i> , <i>Enterobacter</i> , and fungal species (<i>Aspergillus</i> , <i>Trichoderma</i> , <i>Fusarium</i> , <i>Penicillium</i> , <i>Glomus</i> ,	Improved nutrient use	Seed and soil	Improved plant growth, nutritional quality and plant protection	Sarkar et al., 2021a
<i>Bacillus thuringiensis</i> , <i>Trichoderma</i> spp.,	Pests control	Field	Reduction of phytopathogen	Sarkar et al., 2017

(Continued)

TABLE 1 Continued

Endophytes	Abilities	Condition	Results	References
<i>Trichoderma harzianum</i> , <i>Pseudomonas fluorescens</i> and <i>Bacillus subtilis</i>	Phosphorus and Potassium solubilization	Field	Increased macronutrient uptake (N, P, and K), root length, heading percentage, head diameter, head weight, and the total weight of red cabbage	Sarkar et al., 2021c
<i>Trichoderma harzianum</i> , <i>Pseudomonas fluorescens</i> , and <i>Bacillus subtilis</i>	Phosphorus and Potassium solubilization	Field	Reduced fertilizer dose (75% RDF) in combination with <i>Trichoderma</i> sp. and <i>Pseudomonas</i> sp. achieved the highest head yield	Sarkar and Rakshit, 2021
<i>Paraburkholderia caribensis</i> , <i>Kosakonia radicincitans</i> , <i>Paraburkholderia tropica</i> , <i>Pseudomonas fluorescens</i> , <i>Herbaspirillum frisingense</i>	Nitrogen fixation, phosphorus solubilization	Greenhouse	The endophytic strains promoted sugarcane seedlings growth mainly by improving nutrient efficiency.	Cipriano et al., 2021
<i>Rhizobium</i>	Nitrogen fixation	Field	Improved crop production	Kumar et al., 2021
<i>Bacillus subtilis</i> , <i>Pseudomonas Putida</i>	Nitrogen fixation	Field	Improved nitrogen by 40%	Mehrasa et al., 2022
<i>Bacillus</i> sp, <i>Pseudomonas</i> sp, <i>Staphylococcus</i> sp, <i>Paenibacillus</i> sp, <i>Stenotrophomonas</i> sp, <i>Sphingobacterium</i> sp, <i>Lysinibacillus</i> sp, <i>Advenella</i> sp, and <i>Enterobacter</i> sp, <i>Variovorax</i> sp, and <i>Plantibacter</i> sp	Phosphorus acquisition	Greenhouse	Improved phosphorus acquisition	Emami et al., 2020
<i>Herbaspirillum seropedica</i>	Shoot nutrient content	Greenhouse	Increased macronutrient in shoot	Ramos et al., 2020

Some endophytes show low rhizosphere competence due to competition with the original soil microbiota. Another aspect that can interfere with the success of endophyte colonization and, consequently, their ability to promote plant growth is the complexity of plant–microbe interactions (Fadji and Babalola, 2020).

Microbial endophytes can show high variability and low reproducibility with regard to their results as plant growth-promoting agents. The reasons for this may include variations in environmental conditions and the edaphic microbiome (Schütz et al., 2018).

Field trials have many uncontrolled aspects that are unable to be evaluated under greenhouse conditions. Additionally, biotic and abiotic factors can interfere with the success of endophytes (Batista and Singh, 2021). The endogenous microbiome may contain antagonistic microbes and competitors that can negatively affect the ability of endophytes to colonize the rhizosphere and endosphere, thus restricting plant growth (Ortas, 2003), and the efficiency of endophytes on agricultural crop production may be reduced (Mitter et al., 2021).

The success of endophyte utilization requires assessing their functionality, production methods and proper formulation. Another potential challenge in using endophytes is that some are

opportunistic pathogens for animals, other plants, and humans (Fadji and Babalola, 2020).

Future and perspectives

Endophytes have attracted attention due to their ability to promote plant growth through different functions and mechanisms, as shown in this review. Microbial endophytes isolated from different plants of agricultural interest play important roles in balancing plant physiology, making nutrients available in the plant, and phytostimulation. Despite recent advances in scientific understanding, many questions remain, including “How can evolutionary relationships and endophyte diversity be determined by metagenomics and bioinformatics tools to predict endophyte functions?” and “How can endophytes be used effectively to reduce production costs and environmental impacts?” Sustainable agriculture requires the reduction of inputs and self-contained functioning, both of which translate to more affordable and eco-friendly solutions. This review highlights the potential of biological-dependent tools, specifically endophytes, to help address global food production challenges. It is clear that there are currently large gaps in our understanding that

need to be filled before these tools can be applied to real world situations. Nevertheless, endophytes may be the key to the future of sustainable crop productivity and effective nutrient management.

Conclusion

Microbial endophytes are microorganisms that can colonize different plant tissues. First, this process relies on the specific interaction between the microorganisms from the rhizosphere and the plant host. This interaction may also be influenced by biotic and abiotic factors. Interestingly, these microorganisms have several abilities to promote plant growth, such as nitrogen fixation, phosphorus solubilization, phytohormone and siderophore production, phytopathogen control, and systemic resistance against diseases. These microorganisms are called plant growth-promoting endophytes and may be used in crops to reduce chemical fertilizers, insecticides, and fungicides. Thus, these microorganisms can be used to mitigate environmental impacts and production costs without yield reduction.

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Author contributions

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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