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Review article

Endophytic bacteria: a possible path towards a sustainable agriculture

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Highlights

- Endophytic bacteria promote plant growth through eco-friendly mechanisms
- A patent search revealed market interest focused on China, USA, Canada, and Brazil
- Bioinoculants and biopesticides were dominant technologies for corn, soy, and sugarcane
- New strains and formulations were protected for seed coating and spraying

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Nitrogen fixation;
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Biological control;
Technological development.

Abstract: Endophytic bacteria are a promising tool in the development of a sustainable agriculture. Their biological mechanisms of atmospheric nitrogen fixation, phosphate solubilization, production of phytohormones and inhibition of plant pathogens and pests promote plant growth avoiding the need for chemical fertilizers and control agents. A patent search was carried out in the Derwent Innovations Index database to assess the panorama of technological development related to the use of endophytic bacteria in three important agricultural crops, i.e., corn, soybean, and sugarcane. The rank of patent publications by country was leaded by China, USA, Canada, and Brazil, and among these countries, China, USA, and Brazil lead the worldwide production of grains. Several new bacterial strains were protected as bioinoculants or biopesticides. Formulations containing endophytic bacteria were mostly intended for seed coating or spraying and acted directly in the control of pests and diseases, as well as in increasing resistance to environmental stress. In many cases, they acted in promoting the growth of plants producing hormones that regulate or increase nutrient uptake.

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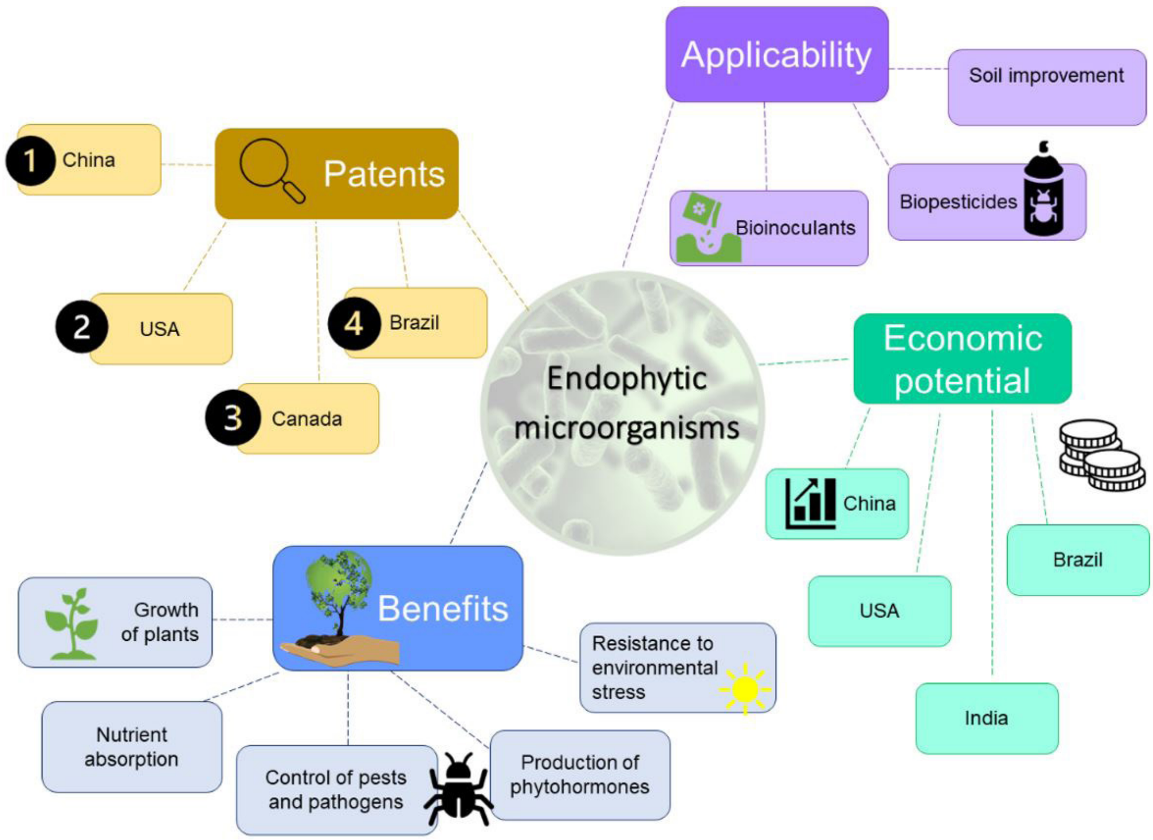
Graphical abstract



Introduction

The global population has doubled in the last 50 years, and the current world population of 7.6 billion is expected to increase to more than 9 billion by 2050, substantially increasing the demand for agricultural products by at least 70% (United Nations, 2019). This demand, associated to the reduction of arable land due to urban development, land degradation, and global climate change (Matsumoto et al., 2021) requires an increase in agricultural productivity without significant increases in land, water or fertilizer use, as they are all becoming limited and pose additional threats to the environment (Prasad et al., 2019).

The current approaches used in agriculture to promote plant growth and production rely heavily on the use of chemical fertilizers. However, their long-term use can bring harmful effects to the environment (Ullah et al., 2019), causing groundwater contamination, eutrophication, loss of soil fertility, soil pollution, reduced biodiversity and increased emissions of greenhouse gases (Prasad et al., 2019; Woźniak et al., 2019).

This scenario indicates the urgent need to find sustainable alternatives to increase crop production with environmental sustainability (Woźniak et al., 2019). Several alternatives have already been proposed and documented in the literature, and the use of plant growth-promoting bacteria (PGPB) emerges as a promising solution for sustainable and environmentally friendly agriculture (ALKahtani et al., 2020; Degrassi & Carpentieri-Pipolo, 2020; Hamid et al., 2021; Ullah et al., 2019).

PGPB are present in soil ecosystems, closely associated with higher plants, being classified as epiphytes or endophytes (Martínez-Viveros et al., 2010). Epiphytes are bacteria that colonize the rhizosphere (zone of interaction between the root and soil) and phyllosphere (the aerial part of the plant), while endophytic bacteria are those that can be found colonizing the endosphere (inner part of the plant) of a healthy plant, without causing any apparent damage or pathogenic symptoms to their host plant (Bandara et al., 2006; Gautam et al., 2016). Both epiphytes or endophytes use the same plant growth-promoting mechanisms (Glick, 2012; Santoyo et al., 2016). However, endophytic bacteria have been considered greater providers of beneficial effects to the host plant than many epiphytic bacteria for the following reasons: (i) endophytic bacteria live inside the plant and have greater contact with plant cells and therefore are more ready to exert a direct beneficial effect on the plant; and (ii) endophytic bacteria are not subject to competition for nutrients as normally occurs in the rhizophore and, therefore, end up having greater efficiency than epiphytic bacteria in promoting plant growth (Afzal et al., 2019; Santoyo et al., 2016).

Endophytic microorganisms are classified as obligate or facultative endophytes (Egamberdieva & Ahmad, 2018).

Obligate endophytes spend their entire life cycle within the host, unable to live outside plant tissues, depend on the host plant for survival, and disseminate through seeds or vegetative plant tissue (Frank et al., 2017; Kumar & Khapre, 2017). Obligate endophytes are not culturable or are more difficult to cultivate in the laboratory, as they require more specific conditions for their growth (Maela & Serepa-dlamini, 2019). On the other hand, facultative endophytes have a free life. They colonize plants opportunistically, that is, they can live outside the plant for part of their life (Singh et al., 2016).

Facultative endophytes are the category that helps to improve plant growth, development, and health. They enter plant tissues from the root through fissures formed at the junction of secondary roots or wounds caused by microbial phytopathogens or nematodes, as well as through flowers, stems, cotyledons via stomata (natural openings), wounds or fissures (Fadiji & Babalola, 2020; Herlina et al., 2017; Setiawati et al., 2018), remaining there or becoming systemic by transport or active migration through the conductive elements (Lodewyckx et al., 2002; Mengistu, 2020). In addition, facultative endophytes enter plants via the secretion of plant cell wall degrading enzymes, such as endoglucanases, pectinases, and cellulases, capable of loosening and degrading the cellulose fiber and, therefore, assisting in the entry and colonization of the host plant (Verma et al., 2021). Successful colonization by endophytes is affected by different factors, including plant genotype, plant tissue type, microbial taxon and environmental conditions (Singh et al., 2017).

Plants and endophytic microorganisms have a mutualistic interaction. Endophytes profit from nutrients made available by plants, including photosynthates (Guo et al., 2017); in return, the endophytic microorganisms improve the acquisition of plant nutrients from the environment, such as nitrogen, iron, and phosphorus (Kandel et al., 2017), e.g., through biological nitrogen fixation (Suhandono et al., 2016), phosphate solubilization (Krishnamoorthy et al., 2020), and siderophores production (ALKahtani et al., 2020). They also help in the synthesis of phytohormones such as auxins, gibberellins, and cytokinins (Aslam et al., 2018), prevent pathogenic infections by producing antifungal and antibacterial compounds (Ullah et al., 2019), and produce 1-aminocyclopropane-1-carboxylate (ACC) which minimizes the ethylene level of the plant induced by biotic or abiotic stress (Degrassi & Carpentieri-Pipolo, 2020). Endophytic bacteria have also been reported to trigger a latent disease defense mechanism called induced systemic resistance (ISR), which provides a higher level of protection to a broad range of phytopathogens (ALKahtani et al., 2020).

Endophytic bacteria are present in almost all plants and have been isolated from tissues of various plants, such as maize, wheat, soybean, onion, cucumber, and cauliflower (Aslam et al., 2018; Woźniak et al., 2019). Endophytic bacteria commonly found in plant tissues belong to the genera *Enterobacter*, *Arthrobacter*, *Bacillus*, *Flavobacterium*, *Burkholderia*, *Pseudomonas*, *Serratia*, *Stenotrophomonas*, *Micrococcus*, *Pantoea*, *Microbacterium*, *Klebsiella*, and *Herbaspirillum* (Nair & Padmavathy, 2014; Ullah et al., 2019; Woźniak et al., 2019).

Due to their plant growth promoting and disease control properties, many studies have suggested the use of endophytic bacteria in the form of bioinoculants in agriculture. There are many reports in the literature on the isolation of endophytic bacteria from roots, stems, leaves, seeds of different plant species and their agricultural applications (Rana et al., 2020). The number of registered patents is increasing, related to the application of endophytic bacteria as bioinoculants in agriculture, demonstrating their great contribution to the development of a sustainable agriculture (Krishnamoorthy et al., 2020; Ullah et al., 2019).

Atmospheric N_2 fixation

Nitrogen is the most important and limiting macronutrient for plant growth and development. It is an unlimited resource, highly abundant in the atmosphere, accounting for approximately 78% of the atmospheric gases, and mainly present in the diatomic form (N_2). Plants cannot use atmospheric N_2 directly, as they only uptake nitrate (NO_3^-) or ammonium (NH_4^+) as inorganic nitrogen sources and amino acids under particular conditions of soil composition. Therefore, regardless of the huge abundance of atmospheric N_2, the plant-available nitrogen is commonly deficient in agricultural soils (CTAHR, 2021).

The great demand for nitrogen in agriculture has been met with the use of nitrogen-rich fertilizers, such as ammonia, urea, and ammonium nitrate, produced by chemical processes. The use of nitrogen-rich fertilizers is inevitable to meet the growing demand for food, however, the prolonged use of these fertilizers can cause serious environmental damage, including (i) increase of nitrous oxide (N_2O) emission, one of the greenhouse gases; (ii) accumulation of nitrate in groundwater, which can cause various negative effects on human health; (iii) death of certain plant species; (iv) promotion of the growth of non-native grasses; and (v) eutrophication and nutrients imbalance causing the depletion of other important minerals in the soil, such as magnesium, calcium, and phosphorus, which can cause proliferation of toxic elements such as aluminum that harm plants, fish, and aquatic organisms (Liu et al., 2014).

An alternative to reduce the excessive use of nitrogen-rich fertilizers in agricultural practices, without harming crop productivity, is the use of endophytic diazotrophic bacteria. These bacteria are able to supply nitrogen to their host plants through the biological nitrogen fixation (BNF) mechanism (Poza-Carrión et al., 2014; Santi et al., 2015). BNF consists of the conversion of atmospheric nitrogen (N_2) into ammonia (NH_3) through the use of a highly specialized enzyme complex called nitrogenase encoded by the *nif* genes (Liu et al., 2020). Nitrogenase is a highly conserved protein present in all N_2 fixing bacteria, widely used as a molecular marker for the identification and characterization of diazotrophic bacteria.

Diazotrophic bacteria can be found living freely in soils and water, in the rhizosphere and phyllosphere, and in plant tissues, in symbiotic association with legumes and actinorhizal plants (e.g., *Frankia* spp.), fungi, woody plants, and terrestrial plants (Diagne et al., 2013). These diazotrophic bacteria include the genera *Rhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Sinorhizobium*, *Mesorhizobium* (Oliveira et al., 2020), *Enterobacter*, *Klebsiella*, *Serratia*, and *Pantoea*, involved in nitrogen fixation and growth promotion of several crops worldwide (Singh et al., 2021).

The presence of endophytic diazotrophic bacteria in sugarcane was discovered and described for the first time by the Brazilian researchers Döbereiner and Ruschel (Martins et al., 2020). Since the discovery of endophytic diazotrophic bacteria in sugarcane tissues, other important crops such as rice, wheat, corn, sorghum, and canola have been studied and postulated to receive significant amounts of fixed nitrogen in this way (Pankievicz et al., 2021; Setiawati et al., 2018). *Azospirillum brasilense* is the most studied species in association with cereals. Bacteria of the genus *Azospirillum*, in addition to other contributions through biological nitrogen fixation, are also considered potent plant growth promoters, as they can produce plant hormones (e.g., indole-3-acetic acid), solubilize phosphates and act as biocontrol agents against phytopathogens (Breda et al., 2020). While in sugarcane, the genera *Herbaspirillum, Burkholderia* (Carvalho et al., 2014), *Gluconacetobacter*, and *Azospirillum*, especially *Azospirillum amazonense* (Oliveira et al., 2004), are the best characterized endophytic diazotrophic bacteria. Studies suggest that these bacteria can act as a nitrogen biofertilizers for several important crops besides sugarcane (Medina-Cordoba et al., 2021; Nunes Oliveira et al., 2017).

More recent studies have focused their attention on testing other plant growth-promoting characteristics of endophytic diazotrophic bacteria including phytohormones production, phosphate solubilization, defense against phytopathogens and tolerance to abiotic stresses, in addition to the nitrogen fixation activity (Higdon et al., 2020; Rodrigues et al., 2016; Singh et al., 2021). This indicates the emerging concern of researchers in developing bacterial inoculants that can increase plant growth through a variety of mechanisms in order to reduce the dependence on agrochemicals.

Phosphate solubilization

Phosphorus is the second most important macronutrient for plant growth and development, after nitrogen, and represents about 0.2% to 0.8% of the plant's dry weight (Alori et al., 2017). It is an essential macronutrient that can limit the growth of plants (Matos et al., 2017), being a component of nucleic acids, adenosine triphosphate (ATP), and phospholipids (Kalayu, 2019; Sharon et al., 2016). In the plant, phosphorus is involved in the process of root development, stem strengthening, flower and seed formation, and promotion of crop maturity (Bononi et al., 2020; Sharon et al., 2016).

The level of phosphorus in the soil is around 0.05% (w/w), but a considerable part, 95 to 99%, is in the form of mineral (insoluble) salts, such as dicalcium and tricalcium phosphate, hydroxyapatite and phosphate rocks; therefore, only 0.1% is available for plants to support their growth (Alori et al., 2017; Zhu et al., 2011). Plants are only able to absorb considerable amounts of orthophosphate ions ($H_2PO_4^-$ or HPO_4^{2-} and PO_4^{3-}) from the soil. Therefore, the lower availability of phosphate in the soil certainly harms the agricultural productivity.

The challenge of phosphorus deficiency in agricultural soil is usually remediated by the application of phosphorus fertilizers. However, almost 70 to 90% of the applied phosphorus is rapidly immobilized by Ca^{2+}, Al^{3+} and Fe^{3+} cations and becomes unavailable to plants (de Abreu et al., 2017; Ouattara et al., 2019). Phosphorus speciation is mainly governed by the pH value of soil, in neutral to alkaline soils there is a predominance of Ca^{2+} cations that form a complex of calcium phosphate ($Ca_3(PO_4)_2$), while in acidic soils there is a predominance of Al^{3+} and Fe^{3+} cations that rapidly immobilize phosphorus to form aluminum phosphate ($AlPO_4$) and ferrous phosphate ($FePO_4$).

The immobilization of phosphorus by cations to form mineral salts decreases the efficiency of fertilization and the profitability of the crop, resulting in economic losses and environmental problems such as deterioration of soil quality (Arora & Singh, 2016). When phosphate fertilizers are used extensively for long periods, increased concentrations of phosphorus can be found in water, as a result of the transport of phosphorus-laden soil particles in lakes and surface waters (Emami et al., 2019). In addition, most commercial phosphorus fertilizers contain toxic elements such as lead (Pb), fluorine (F), arsenic (As), cadmium (Cd), mercury (Hg), and chromium (Cr), along with radionuclides such as Ra-226, Th-232, Pb-210, Po-210, and U-238 (Emami et al., 2019, 2020; Hegedűs et al., 2017).

Such environmental concerns and the rapid immobilization of phosphorus in soils have led scientists to search for environmentally friendly and economically viable alternatives to improve agricultural production (Matos et al., 2017). Among the alternatives, the use of endophytic bacteria has gained considerable attention. Several studies have reported the great potential of endophytic bacteria to solubilize phosphate and therefore increase soil fertility, plant nutrition, and growth (Ouattara et al., 2019). They increase the bioavailability of phosphorus through the solubilization of phosphorus containing minerals, using mechanisms that include the production of extracellular phosphatases, the secretion of organic acids, and the release of complexes or compounds such as organic acid anions, protons, and siderophores that chelate Ca^{2+}, Al^{3+}, and Fe^{3+} cations involved in the immobilization of phosphorus to form insoluble phytates (Arora & Singh, 2016; Emami et al., 2020; Nannipieri et al., 2011; Sharon et al., 2016). Endophytic bacteria with phosphate solubilization activity include the genera *Arthrobacter, Pseudomonas, Bacillus, Rhizobium, Burkholderia, Enterobacter, Erwinia, Paenibacillus, Lysinibacillus, Mesorhizobium, Microbacterium, Serratia* and *Flavobacterium*. Among them, the genera *Rhizobium*, *Pseudomonas*, and *Bacillus* are the most frequently reported (Arora & Singh, 2016; de Abreu et al., 2017; Matos et al., 2017; Prasad et al., 2019).

Production of phytohormones

Phytohormones or plant hormones are organic substances with no nutritional function, acting as signaling or regulatory molecules capable of influencing and/or controlling some physical, biochemical, and morphological characteristics of the plant, at different stages of its development, at very low concentrations (Fu et al., 2015; Gaspar et al., 2003;

Pařízková et al., 2017; Sauer et al., 2013). The synthesis of phytohormones can occur in any organ of the plant, then these hormones are transported to other organs (Aziz et al., 2015), and their influencing action on plant growth and development, as well as the mediation of the plant resistance to abiotic stresses, may be far away from their synthesis sites or in the same organ where they were synthesized (Gaspar et al., 2003; Xu et al., 2018).

There are five categories of phytohormones, namely auxins, cytokinins, abscisic acid, gibberellins, and ethylene (Halmann, 1990). However, some other categories of phytohormones may also be included such as brassinosteroids, jasmonic acid, and salicylates (Gray, 2004; Halmann, 1990; Sauer et al., 2013; Shi et al., 2017). Among the mentioned phytohormones, the benefits in plant growth and development are attributed to the production of the phytohormones auxin (indole-3-acetic acid or IAA, the most common natural auxin), cytokinins, and gibberellins, while the increased stress tolerance is often explained by an induction of systemic resistance involving abscisic acid, ethylene, salicylates, and jasmonic acid (Xu et al., 2018).

Among phytohormones, auxins, especially IAA, is considered the main contributor to plant growth and development (Zhao, 2010), being involved in various processes of regulation of plant growth and development. IAA acts in cell division (Teale et al., 2006), cell elongation (Sauer et al., 2013), cell differentiation (Sugawara et al., 2015; Tsavkelova et al., 2006), response to directional stimuli (tropic response), and mediation of resistance to stress conditions (Xu et al., 2018). In addition, it plays a significant role in stimulating root initiation (Nutaratat et al., 2016), root elongation, root hair formation, and branching (Ali & Vora, 2014; Grossmann, 2010; Halmann, 1990). The improvement in root surface area therefore has a positive effect on nutrients and water uptake and causes overall plant growth and development (Hagaggi & Mohamed, 2020).

In addition to being produced by plants, IAA is also synthesized by endophytic bacteria (Gomes et al., 2017). They synthesize IAA mainly via tryptophan-dependent pathways, where the amino acid L-tryptophan is the main precursor (Spaepen and Vanderleyden 2011; Herlina et al. 2017). There are several tryptophan dependent IAA synthesis pathways, which are usually named after the intermediate, such as the indole-3-acetonitrile (IAN) pathway, indole-3-acetamide (IAM) pathway, indole-3-pyruvic acid (IPyA) pathway, tryptamine (TAM) pathway, and indol-3-acetylaldehyde (IAAld) pathway (Li et al., 2018; Senthil et al., 2010; Spaepen et al., 2007). The tryptophan-independent pathway has been identified in some microorganisms, but tryptophan remains the most common and major precursor of IAA biosynthesis by microorganisms.

Prominent IAA-producing endophytic bacterial genera include *Pseudomonas*, *Bacillus*, *Azotobacter*, *Klebsiella*, *Burkholderia*, *Bradyrhizobium*, *Enterobacter*, *Rhizobium*, *Streptomyces*, *Azospirillum*, *Pantoea*, *Lysobacter*, and *Herbaspirillum* (Kumar et al., 2017). Although plants naturally synthesize IAA for growth, they respond positively to exogenous IAA applied during certain stages of growth (Egamberdieva et al., 2017). Bacterial IAA is non-toxic to plants over a wide range of concentrations and is effective in promoting the growth and development of various plant species when applied at certain development stages in optimal concentration (Bhutani et al., 2018; Khan et al., 2016; Ribeiro et al., 2018; Shi et al., 2009; Xin et al., 2009). Numerous bacterial endophytes have been reported to promote plant growth by their ability to biosynthesize IAA (Hagaggi & Mohamed, 2020).

Indirect plant growth promotion

Several studies have reported that endophytic bacteria have the ability to indirectly promote plant growth, inhibiting the growth of phytopathogens and plant pests. Endophytic bacteria of the genera *Arthrobacter*, *Actinobacteria*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Paenibacillus*, *Micrococcus*, *Pantoea*, *Pseudomonas*, *Rhizobium*, *Serratia*, and *Streptomyces* have already been screened and exploited as biocontrol agents against various plant pathogens (Jacob et al., 2020). Among them, *Bacillus* and *Pseudomonas* are the genera most frequently reported as biocontrol agents in several plants, such as pepper, tomato, potato, cassava, and wheat (Afzal et al., 2019; Amna et al., 2020; Meliah et al., 2021). *Bacillus* strains have been documented as the most potent microorganisms for the formulation of biocontrol products due to their ability to form endospores, resistant to extreme environmental conditions including heat, drought, salinity and heavy metals, allowing them to trigger defense responses in host plants even under unfavorable conditions (Kushwaha et al., 2020; Wang et al., 2020b).

The biocontrol activity of *Bacillus* spp. against pathogenic fungi is well documented in the literature. *Bacillus subtilis*, an important biocontrol agent used in agriculture, exhibits direct and indirect biocontrol mechanisms, the first represented by the synthesis of compounds that allow the defense of the plant, like hormones, antioxidants, and enzymes, and the second characterized by the promotion of plant growth and induction of acquired systemic resistance. *B. subtilis* is especially effective in alleviating biotic stress in plants (Hashem et al., 2019). *B. subtilis* and *Bacillus amyloliquefaciens* demonstrated efficient inhibitory activity against *Phytophthora sojae*, a soil-borne pathogen resistant to control agents that results in great reductions of soybean yield (Liu et al., 2019). Torres et al. (2020) reported that *Bacillus velezensis* promoted the growth of various horticultural crops such as tomato, pepper, pumpkin, and cucumber plants, and showed antifungal activity *in vitro* against various phytopathogens such as *Alternaria alternata*, *Fusarium oxysporum*, *Monilinia fructicola*, *Magnaporthe oryzae*, *Thanatephorus cucumeris*, and *Sclerotinia sclerotiorum*. Ferreira et al. (2021) reported that cassava endophytic bacteria, *B. velezensis* isolate 21Y and *Bacillus aryabhattai* isolates 4W and 23Y, inhibited the *in vitro* and *in vivo* growth of *Phytopythium* sp., a pathogen that causes the soft root rot of cassava. Kushwaha et al. (2020) demonstrated that *B. amyloliquefaciens* EPP90, an endophytic *Bacillus* from pearl millet (*Pennisetum glaucum*), has antagonistic activity against phytopathogenic fungi. Amna et al. (2020) reported, in *in vivo* experiments, that *Bacillus xiamenensis* PM14 inhibited the growth of six phytopathogenic fungi, including *Colletotrichum falcatum*, *Fusarium moniliforme*, *F. oxysporum*, *Macrophomina phaseolina*, *Rhizoctonia solani*, and *Pythium splendens*, and in greenhouse experiments, that the inoculation of *B. xiamenensis* PM14 to sugarcane plants suppressed sugarcane red rot disease symptoms and enhanced plant growth. Cheffi Azabou et al. (2020) reported *B. velezensis* OEE1 as an efficient biocontrol agent against *Verticillium* wilt of olive and a potential plant growth-promoter. One possible mechanism of indirect plant growth promotion and biocontrol is the synthesis of hydrolytic enzymes, such as chitinases, cellulases, ß-1,3-glucanases, lipases, pectinases, and proteases that can destroy phytopathogenic fungi and, therefore, protect the plant from biotic stress (Aktuganov et al., 2008; Caulier et al., 2019; Figueiredo et al., 2016; Glick, 2012; Jacob et al., 2020; Palaniyandi et al., 2013).

The ability of *Bacillus* spp. to act as a biocontrol agent against plant pests has also been reported. Ramalakshmi et al. (2020) reported the suppression of the root-knot nematode *Meloidogyne incognita* by *Bacillus thuringiensis*, and Zhou et al. (2021) reported the inhibition of the invasion, development, and reproduction of the soybean cyst nematode *Heterodera glycines* in soybean by *Bacillus megaterium* strain Sneb207. Insecticidal activity against pests has been reported for *B. thuringiensis* against *Lepidoptera* (Chakrabarty et al., 2020). In addition to its efficiency as a biocontrol agent, *Bacillus* spp. are also recognized for promoting plant growth and tolerance to abiotic stresses such as extreme temperatures, salinity, drought, and heavy metals.

Endophytic bacteria also have the ability to indirectly promote plant growth through the production of siderophores (iron chelators), that reduce iron availability to phytopathogens thus inhibiting their growth (Afzal et al., 2019). In addition, endophytic bacteria can use the ISR mechanism in host plants against pathogenic fungi, bacteria, viruses, nematodes, and pests. The ISR prepares the plant's defense mechanisms, thus protecting the unexposed parts of the plant against future pathogenic attacks (Afzal et al., 2019; Lacava et al., 2007; Ryan et al., 2008). Normally, endophytic bacteria can initiate ISR using pathways mediated by salicylic acid, jasmonic acid, and ethylene (Yanti et al., 2019). Salicylic acid signaling positively regulates plant defense against biotrophic plant pathogenic fungi, whereas jasmonic acid and ethylene pathways are commonly required for resistance to necrotrophic plant pathogenic fungi and pests (Wang et al., 2020a). However, endophytic bacteria can use distinct plant defense signaling pathways, depending on the type of phytopathogen invader, that is, the same bacterium could use different pathways to confer resistance to different pathogens (Afzal et al., 2019).

Panorama of technological development based on patent applications

A patent search was carried out to assess the panorama of technological development related to the use of endophytic bacteria in important agricultural crops: corn, soybean, and sugarcane. The bacterial genera were selected based on Afzal et al. (2019). The search was run in the Derwent Innovations Index database, using the following terms in the "Topic": (endophyt* OR *Acetobacter* OR *Achromobacter* OR *Agrobacterium* OR *Arthrobacter* OR *Bacillus* OR *Burkholderia* OR *Corynebacterium* OR *Curtobacterium* OR *Enterobacter* OR *Erwinia* OR *Gluconacetobacter* OR *Herbaspirillum* OR *Klebsiella* OR *Microbacterium* OR *Micrococcus* OR *Pantoea* OR *Paenibacillus* OR *Phyllobacterium* OR *Providencia* OR *Pseudomonas* OR *Rhizobium* OR *Serratia*) AND (sugar$cane OR soy* OR corn OR maize), associated to the International Patent Classification code A01P-021/00 (Plant growth regulators).

Although studies with endophytes began decades ago, the first patent publication, related to the use of these microorganisms in agriculture, dates from 2003, initially published by the World Intellectual Property Organization (WIPO), followed by publications in the United States, Australia, the European Patent Office (EPO), India, Canada, and Germany. The patent document entitled "New sulfur-oxidizing plant growth-promoting Rhizobacteria, e.g., RAY12 (*Achromobacter piechaudii*), RAY28 (*Agrobacterium tumefaciens*) or RAY132 (*Stenotrophomonas maltophilia*), useful for enhancing canola performance", described the use of the strains as biocontrol agents or as biofungicides, that is, when in contact with plants, growth-promoting bacteria were able to oxidize sulfur to provide sulfate to the plants. Consequently, the characteristics involved with growth were significantly improved, as were biomass, seed weight, macro and micronutrient absorption, among others (Banerjee et al., 2003).

The patent search for the period of 2016–2021 resulted in 401 patent documents, from which 172 were in fact related to the use of endophytic bacteria in the cultivation of corn, soybean, and sugarcane. An in-depth analysis of these documents was carried out to identify the recent technologies and the distribution of patent publications among countries. Results can be seen in Figure 1.

According to the map shown in Figure 1, China leads the rank of patent publications with 115 documents, followed by USA with 19, Canada with 16 and, fourthly, Brazil with ten documents. The search also found four documents originally published by the WIPO, two by the EPO, two in the Republic of Korea and in Mexico, and one document in Philippines, Australia, and Taiwan.

A recent publication shows that China has a long-term plan to modernize domestic agriculture with a focus on innovations, land reform and food security protection, maintaining much of agricultural production in its own territory and controlling global trade through large conglomerates. This long-term plan may justify the search for ways to reduce costs and improve agricultural efficiency (Seixas & Contini, 2018).

Another study conducted by the Brazilian Agricultural Research Corporation (Embrapa) in 2020 showed that Brazil occupies the fourth position in the global rank of grain producers, behind China, the United States, and India. Having produced 239 million tons and exported 123 million tons, Brazil accounts for 7.8% of the world's grain production (Guaraldo, 2020). Despite the large volume of production, when compared to China and USA, Brazil shows a low level of technological development regarding endophytic microorganisms. Among the ten patent publications found in the Brazilian domain none was originally applied in Brazil. When a search was performed in the Brazilian National Institute of Industrial Property (INPI) using the translated term for "endophyte", seven documents were found between

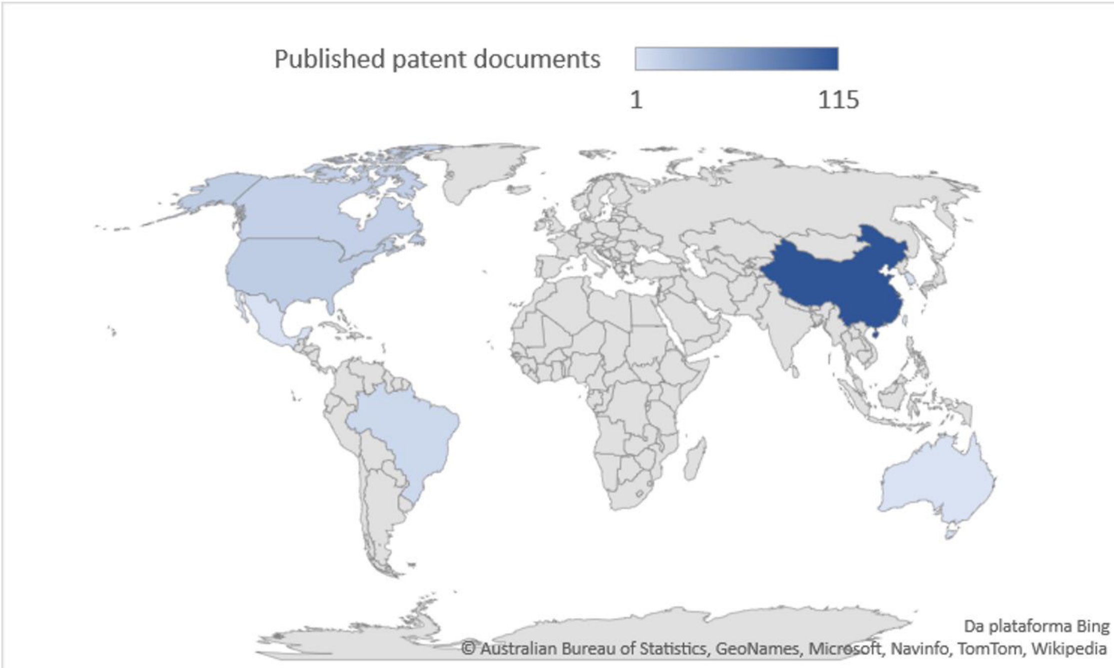


Figure 1. Number of published patent documents by country, between 2016 and 2021, related to the use of endophytic bacteria in the cultivation of corn, soybean, and sugarcane. Additionally, there were four publications by the World Intellectual Property Organization (WIPO, WO) and two by the European Patent Office (EP). Source of data: Derwent Innovations Index; search performed on October 6th, 2021.

2016 and 2019, related to the use of endophytes as biocontrol agents and plant growth promoters, and two of them were originally applied in Brazil.

According to the search results, formulations of bioinoculants or biopesticides containing endophytic microorganisms are mostly intended for seed coating or spraying and act directly in the control of pests and diseases, as well as in increasing resistance to environmental stress. In many cases, they act in promoting the growth of plants producing hormones that regulate or increase nutrient uptake (Parnell et al., 2019; Wei et al., 2021; White & Caraballo, 2019; Xun et al., 2021).

New strains such as *Microbacterium trichothecenolyticum* (WO2019217255-A1), *Bacillus proteolyticus* (CN112899206-A), *Paenibacillus amylolyticus* KY15 (CN110257293-A), *B. aryabhattai* strain J5 (CN105985922-A), and *Enterobacter* LY6 (CN105838750-A), were discovered as efficient producers of IAA. These strains also act in the capture, transport, and disposal of soil nutrients, and prevent or treat possible plant diseases (Cai et al., 2016; Hou et al., 2016; Kang & Wang, 2019; Parnell et al., 2019; Wei et al., 2021). Meanwhile, some bioproduct compositions focus, for example, on nitrogen fixation by the plant (WO20191422199-A1) and in the capture of carbon dioxide from the atmosphere, so photosynthetic processes are increased, thus improving growth, shoot and leaf size, rooting, plant stress resistance, and nitrogen use effectiveness (WO2019084324-A1) (Avidov et al., 2019; Harman et al., 2019). In general, the technologies aimed at increasing the quality and efficiency of agricultural production since, in addition to these benefits, there were significant reductions in the amount of pesticides used during cultivation, directly impacting the cost of production (Li et al., 2017).

Conclusion

Endophytic bacteria, through their mechanisms of atmospheric nitrogen fixation, phosphate solubilization, production of phytohormones, and inhibition of plant pathogens and pests, are a promising tool in the development of a sustainable, eco-friendly agriculture. Their use promotes plant growth reducing the demand for chemical fertilizers and pest control agents. In this segment, a panorama of technological development was designed focused on three important commodities, namely corn, soybean, and sugarcane. The rank of patent publications by country was leaded by China, USA, Canada, and Brazil. Several new bacterial strains were protected as bioinoculants or biopesticides. Formulations containing endophytic bacteria were mostly intended for seed coating or spraying and acted directly in the control of pests and diseases, as well as in increasing resistance to environmental stress. In many cases, they acted in promoting the growth of plants producing hormones that regulate or increase nutrient uptake.

Conflict of interests

The authors declare that there are no conflicts of interest.

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