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Use of Plant Growth-Promoting Rhizobacteria in Maize and Sugarcane: Characteristics and Applications

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Free-living bacteria that actively colonize plant roots and provide positive effects on plant development are called plant-growth promoting. Plant growth-promoting bacteria can promote plant growth and use their own metabolism to solubilize phosphates, produce hormones and fix nitrogen, and they can directly affect plant metabolism. PGPR also increase plant absorption of water and nutrients, improving root development and increasing plant enzymatic activity; moreover, PGPR can promote other microorganisms as part of a synergistic effect to improve their effects on plants, promoting plant growth or suppressing pathogens. Many studies have shown several benefits of the use of PGPR in maize and sugarcane crops. These bacteria are an excellent alternative to farmers to reduce chemical fertilization and pesticide input without promoting the environment impact and yield-reducing. The present review is an effort to elucidate the concept of rhizobacteria in the current scenario and their underlying mechanisms of plant growth promotion with recent updates. The latest paradigms of a wide range of applications of these beneficial rhizobacteria in both crops maize and sugarcane have been presented explicitly to garner broad perspectives regarding their functioning and applicability. The results from several studies have shown that the utilization of PGPR in maize and sugarcane is the great alternative to farmers face the challenge the modern agriculture.

Keywords: plant-growth-promoting, *Saccharum* spp., *Zea mays*, rhizosphere, yield

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INTRODUCTION

This review focuses on plant growth-promoting rhizobacteria that are beneficial for the plant. Some beneficials do so by promoting plant growth directly, i.e., in the absence of pathogens. Others do this indirectly by protecting the plant against soil- borne diseases, most of which are caused by fungi.

The use of PGPR is one potential way to decrease negative environmental impact resulting from continued use of chemical fertilizers, pesticides and herbicides. This term was first defined by Kloepper and Schroth (1978) to describe soil bacteria that colonize the rhizosphere of plants, growing in, on or around plant tissues that stimulate plant growth by several mechanisms. Since that time, research activities aimed at understanding how these bacteria perform their positive (or negative) effect have steadily increased and many studies have been published on these microorganisms (Vessey, 2003; Lugtenberg and Kamilova, 2009; Perez-Montano et al., 2014).

Increasing crop production to meet the demands of consumer markets and the growing world population relies on the use of a large amount of chemical fertilizers and pesticides, which are often overused in soil (Kumar et al., 2017). The use of chemical fertilizers in crop production provides an average yield increase of approximately 50% compared to production without their use; however, chemical fertilization practices ignore the biological potential of roots or the rhizosphere by increasing nutrient mobilization and acquisition and decreasing the interactions between plants and rhizospheric microorganisms (Meena et al., 2017). Many studies have demonstrated the abilities of plant growth-promoting microorganisms to increase plant nutritional status and reduce the use of pesticides (Aloo et al., 2019).

Plant growth-promoting rhizobacteria is an excellent alternative to farmers face the new challenges of modern agriculture as serious environmental and social problems emerged as a consequence of industrialization of agriculture provoked by necessity to increase a great amount of food to the general population. Currently, it is urgent to maintain high productivity impacting the environment as little as possible (Pérez-Montaño et al., 2013).

There are two mechanisms used by PGPR to promote plant growth. Each mechanism contains several parameters related to plant growth. The direct mechanism contains the parameters production of phytohormones Cassán et al. (2009) such as auxins (Khalid et al., 2004b); siderophores (Yu et al., 2019); phosphorous solubilization Krey et al. (2013), or nitrogen-fixing (Riggs et al., 2001). Indirect mechanism is related to biocontrol, by mean of antagonistic activity against phytopathogenic microorganisms inducing plant systemic resistance responses, interfering in the bacterial quorum sensing (QS) systems, etc. Some reports show PGPR may use more than one of these mechanisms for accomplishing plant growth enhancement (Bashan and Holguin, 1997; Ahmad et al., 2016).

In this review we begin with a description of how bacteria live on the root, which nutrients are available, and how the bacteria colonize the root. Competitive rhizosphere colonization is crucial for many mechanisms of action of plant-beneficial bacteria. Which bacterial traits are important for root colonization when bacteria compete with each other and with other organisms. We describe various mechanisms used by specialized beneficial rhizobacteria to positively influence plant growth. These mechanisms were classified as direct mechanisms and indirect mechanisms. The direct mechanisms approached in this review were phytohormone production, biological nitrogen fixation, phosphorus solubilization, potassium solubilization. The indirect mechanisms approached were production of antibiotics, induced systemic resistance, production of siderophores, rhizoremediation, and stress control and interference with the quorum sensing system. This review brings in **Tables 1**, **2** the most important studies related to the use of these bacteria in maize and sugarcane production, respectively. Finally, this review also brings in **Figure 1** that shows the benefits to plants from host-PGPR interactions, **Figure 2**, direct mechanisms that benefit plant growth, and in **Figure 3**, indirect mechanisms that benefit plant growth.

MICROBES IN THE RHIZOSPHERE

For the plant growth-promoting rhizobacteria colonize the rhizosphere two-step selection process by which the bacterial microbiota of roots is differentiated from the surrounding soil biome are necessary. One potential molecular mechanism underlying the formation of a distinctive rhizosphere microbiota from soil biomes is rhizodeposition. This process refers to intertwined plant developmental and secretory activities in the root system. Rhizodermis cells secrete a wide range of compounds, including organic acid ions, inorganic ions, phytosiderophores, sugars, vitamins, amino acids, purines, and nucleosides, and the root cap produces polysaccharide mucilage (Dakora and Phillips, 2002). Rhizodeposition appears to fuel an initial substrate-driven community shift in the rhizosphere, which converges with host genotype–dependent finetuning of microbiota profiles in the selection of root endophyte assemblages (Bulgarelli et al., 2013). To exert their beneficial effects, bacteria usually must colonize the root surface efficiently (Lugtenberg and Kamilova, 2009). The substrate-driven selection also underlies the establishment of phyllosphere communities but takes place solely at the immediate leaf surface. Both the leaf and root microbiota contain bacteria that provide indirect pathogen protection, but root microbiota members appear to serve additional host functions through the acquisition of nutrients from the soil for plant growth. Thus, the plant microbiota emerges as a fundamental trait that includes mutualism enabled through diverse biochemical mechanisms, as revealed by studies on plant growth–promoting and plant health–promoting bacteria (Bulgarelli et al., 2013).

MECHANISMS USED BY PGPR

Direct Mechanisms

The direct action of plant growth-promoting microorganisms involves soil improvements and the production of substances needed for plant growth, which improves fertility by mobilizing soil minerals (Naik et al., 2019). These improvements include the supply of growth regulators and essential minerals such as potassium, phosphorous and (Tabassum et al., 2017).

Phytohormone Production

Phytohormones are responsible for plant growth development and allow plants to tolerate different stress conditions (Shaterian et al., 2005). Some rhizobacteria are able to produce phytohormones, including cytokinins, auxins, gibberellins, ethylene, and abscisic acid (ABA), which play a role in different growth processes in plants, including cell multiplication, which results in increased cell and root expansion (Glick, 2014; Kaur et al., 2016). However, the production of ABA by rhizobacteria is considered an indirect way of promoting plant growth (Belimov et al., 2014).

Auxins

Auxins influence many aspects of plant development (Halliday et al., 2009; Grossmann, 2010). The most essential (and well-known) is indole-3-acetic acid (IAA), which is produced by

TABLE 1 | Bacteria specie, abilities, experiment condition, and results promoted by the application of many plant growth- promoting rhizobacteria in maize crop.

Rhizobacteria/Consortium (maize)	Abilities	Condition	Results	References
Lysinibacillus sphaericus (T19)	BNF and IAA production	Field	Increased productivity	Breedt et al., 2017
A. brasilense Az39, *Bradyrhizobium japonicum* E109 (individual experiments and consortia)	Phytohormone production	Growth chamber	Increase in promoting seed germination and early seedling development (use of isolated or combined species)	Cassán et al., 2009
B. pumilus S1r1	BNF	Greenhouse	Higher corncob productivity (up to 30.9%)	Kuan et al., 2016
A. brasilense and *P. fluorescens*	IAA production and phosphate solubilization	Field	Higher grain yield	Di Salvo et al., 2018
P. fluorescens F113	Nutrient acquisition	Greenhouse	Addition of N, K, Ca, Mg, and Mn equal to 40, 49, 60, 100, and 141%, respectively, in the shoots	Rocha et al., 2019
Enterobacter cloacae	ACC deaminase production	Greenhouse	Increases of 60, 73, 43, 69, 76, and 42%, respectively, in grain production, photosynthetic rate, stomatal conductance, chlorophyll A, total chlorophyll and carotenoids	Danish et al., 2020
B. subtilis and *A. brasilense*	Phosphate solubilization	Field	Higher grain yield	Pereira et al., 2020
Chryseobacterium sp. NGB-29 and *Flavobacterium* sp. O NGB-31	BNF and production of large amounts of IAA	Greenhouse	Increased growth parameters	Youseif, 2018
Ralstonia eutropha 1C2 and *Chryseobacterium humi* ECP37	Zn bioavailability in the soil	Greenhouse	Increased biomass and Zn accumulation and availability in plants	Moreira et al., 2019
Pseudomonas aurantiaca SR1	Production of phytohormones, antibiotics, and siderophores	Field	Increased productivity, length, and shoot and root dry weight	Rosas et al., 2009
B. subtilis 320	Phosphate solubilization and phytohormone production	Field	Increase in productivity and P in the shoots	Lobo et al., 2019
Burkholderia cepacia	Biocontrol and phosphate solubilization	Greenhouse	Increased leaf area, length, and shoot and root dry weight	Zhao et al., 2014
Pseudomonas tolaasii 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
Pseudomonas kilonensis F113 and *Pseudomonas protegens* CHA0	Phosphate solubilization and biocontrol	Field	Increase in leaf yield, height, and length	Alori et al., 2019
Enterobacter cloacae PGLO9	Phosphate solubilization	Greenhouse	Longer root length, shoot length, and increased shoot and root biomass	Verma et al., 2018

different microorganisms and this hormone, in plants, plays an essential role in cell division, fruit development and leaves senescence (McSteen, 2010). IAA stimulates the development of many parts of the plants such as roots, leaves, and flowers (Phillips et al., 2011). In dicotyledons, IAA induces the formation of lateral roots, while in monocotyledons, it induces the formation of adventitious roots (McSteen, 2010).

Plant development is affected by IAA in both favorable and harmful ways and many bacteria have the ability to synthesize IAA, including beneficial bacteria and phytopathogens (Duca et al., 2014). More than 80% of bacteria isolated from the rhizosphere are IAA producer (Patten and Glick, 1996; Khalid et al., 2004a). IAA is responsible by part of the communication and signaling system between plants and rhizospheric bacteria (Spaepen et al., 2007).

The tryptophan is the main precursor for the synthesis of IAA and the addition of this amino acid to culture media results in increased production in all cases (Spaepen et al., 2007). Tryptophan biosynthesis starts from metabolic nodes in a five-step reaction encoded by *trp* genes (Merino et al., 2008).

The pathways of tryptophan-dependent include indole-3-acetamide, indole-3-pyruvate, indole-3-acetonitrile pathways and tryptamine (Spaepen et al., 2007), although some intermediaries may differ most pathways show similarity to those described in plants (Patten and Glick, 1996; Woodward and Bartel, 2005). IAA synthesis pathways have been identified using several biochemical and genetic methods; however, a small set of genes and enzymes involved in these pathways have been characterized (Spaepen and Vanderleyden, 2011).

The interaction between IAA concentration and plant growth correlation is not linear, and plants should have optimal levels of endogenous IAA for optimal development (Duca et al., 2014). Excessive amounts of IAA can promote harmful effects on plants, decreasing root growth (Duca et al., 2014). Therefore, to

TABLE 2 | Bacteria specie, abilities, experiment condition, and results promoted by the application of many plant growth- promoting rhizobacteria in sugarcane.

Rhizobacteria/Consortium (sugarcane)	Abilities	Condition	Results	References
A. brasilense + *B. subtilis*	Phosphate solubilization	Field	Increased yield, dry matter, total P accumulation, and reduced fertilization by 75%	Rosa et al., 2020
B. pumilus	Production of IAA and enzymes (endoglucanases and xylanases)	Pot	Increase in dry matter and number and diameter of tillers	Santos et al., 2018
B. subtilis (BSSC11) and *Bacillus megaterium* (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
P. koreensis and *P. entomophila*	BNF, production of phytohormones, and biocontrol capacity	Growth chamber	Improvement of plant growth and development	Li et al., 2017
Escherichia sp. (VRE34)	Antagonism to phytopathogens, IAA production, P solubilization, and BNF	Greenhouse	Increase in plant height, stem diameter, and number of leaves	Patel et al., 2019
Burkholderia gladioli TNCSF 021	P solubilization	Pot	Increase in leaf chlorophyll, N content, and total biomass	Muthukumarasamy et al., 2017
Bacillus altitudinis and *Bacillus velezensis*	Biological control	Greenhouse	Increase in dry weight, surface area, and total root length	Liu et al., 2018
Bacillus xiamenensis 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
Azotobacter sp. (AZS3), *P. fluorescens* (Ps5), and *Bacillus* sp. (Bc1)	Production of IAA, siderophores and hydrogen cyanide; phosphate solubilization; and antifungal activity	Pot	Increased dry weight of roots and shoots and shoot height	Ahmad et al., 2016
P. fluorescens	Antifungal activity and induced systemic resistance	Field	Improved vegetative germination and productivity	Viswanathan and Samiyappan, 2002
A. brasilense	Nitrogenase activity	Field	Increase in length, diameter, and Brix value	Lopes et al., 2012
B. subtilis NH-160	Production of IAA, phosphate solubilization, and antifungal activity	Greenhouse	Inhibition of red rot infection	Hassan et al., 2010
Azospirillum spp.	Tolerance to water stress	Pot	Increase in root dry matter	Moutia et al., 2010

stimulate plant growth using IAA it must be carefully regulated to avoid inhibitory effects caused by overdosing (Duca et al., 2014). In this context, plants have many mechanisms of neutralization to control excess IAA, such as amino acids production (Sitbon et al., 1992). However, plants are not always able to carry out neutralization and are sometimes harmed by excess IAA (Duca et al., 2014).

Aeromonas punctata (Iqbal and Hasnain, 2013), *Azospirillum brasilense* (Camilios-Neto et al., 2014), *Bacillus subtilis* (Tahir et al., 2017), and *Burkholderia phytofirmans* (Poupin et al., 2016) are some bacterial species that efficiently synthesize IAA.

Cytokinins

Cytokinins are responsible for the formation of shoots, inhibition of root elongation, and the improvement of cell division and root development; cytokinins are also a type of growth regulator (Porcel et al., 2014; Jha and Saraf, 2015). In particular, they are mandatory for the progression of the cell cycle (Schaller et al., 2015). Furthermore, the balance between auxins and cytokinins determines the function of the meristem, the architecture of the root system, the formation of lateral organs of shoots and the development of reproductive organs (Schaller et al., 2015). Cytokinins can regulate chloroplast biogenesis and chlorophyll biosynthesis (Cortleven and Schmulling, 2015), and they are related to development of plant resistance to abiotic stressors and biotic (Grosskinsky et al., 2011; O'Brien and Benkova, 2013).

Rhizobacteria can produce several types of cytokines, of which zeatin and kinetin are the most abundant (O'Brien and Benkova, 2013). Rhizobacteria are able to synthesize zeatin in two different ways: directly and indirectly. The direct pathway involves the synthesis of dimethylalyl diphosphate and isopentenyl adenosine monophosphate, while the indirect pathway involves *cis*-zeatin that contains tRNA to release cytokinins (Tabassum et al., 2017).

Several *Paenibacillus polymyxa, Azotobacter* species., *Rhizobium* species., *B. subtilis, Rhodospirillum rubrum*, *Pseudomonas fluorescens, Pantoea agglomerans*, strains are capable of producing cytokines (de Salamone et al., 2001; Glick, 2012).

Gibberellins

Gibberellins are another essential class of phytohormones released by rhizobacteria; these compounds are responsible for different processes in higher plants, such as seed germination, stem elongation and fruiting, the flowering process (Saleem

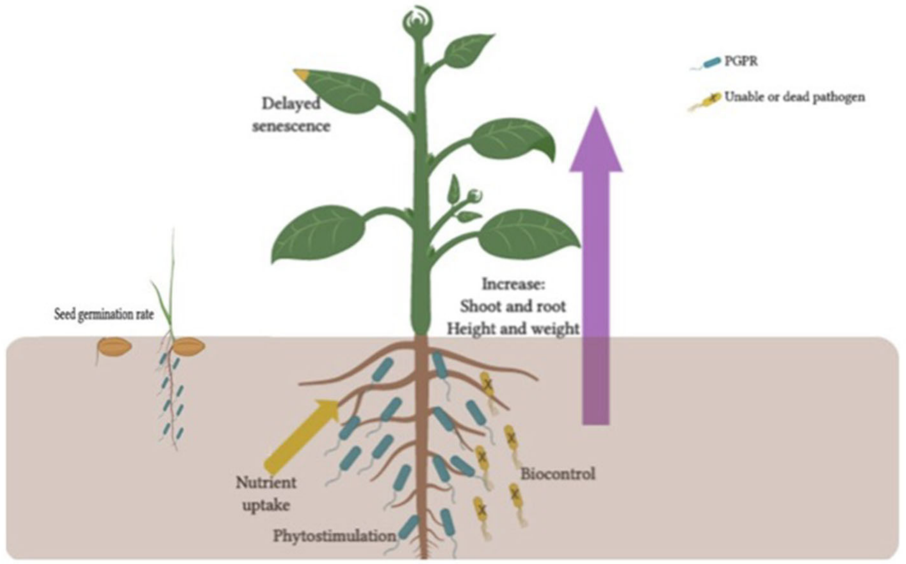

FIGURE 1 | Benefits to plants from host-PGPR interactions. These benefits have been shown to include in sees germination rate, root growth, yield, leaf area, chlorophyll content, nutrient uptake, protein content, hydraulic activity, tolerance to abiotic stress, shoot and root weights and heights, bio-control, and delayed senescence.

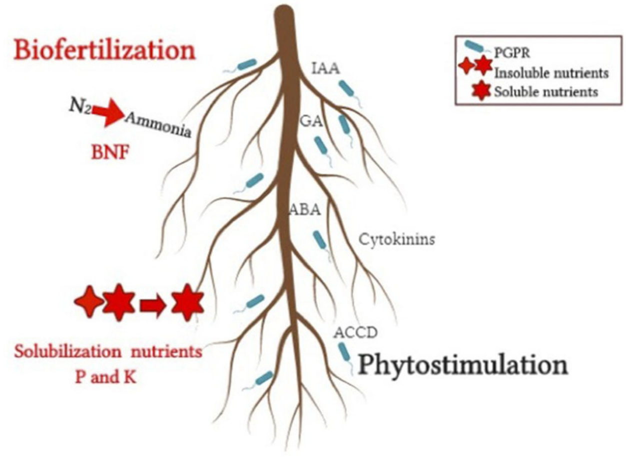

FIGURE 2 | Direct mechanisms that benefit plant growth from host-PGPR interactions. Biofertilization, nutrients solubilization, and phytostimulation.

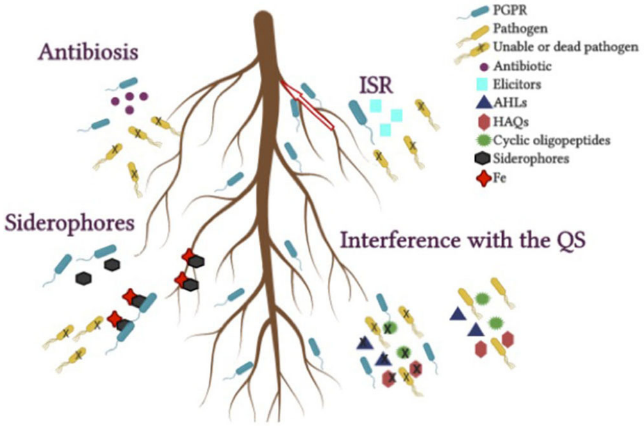

FIGURE 3 | Indirect mechanisms that benefit plant growth from host-PGPR interactions. Antibiosis, siderophores, interference with the quorum sensing (QS), induced systemic resistance (ISR).

et al., 2015). Gibberellins positively regulate cell division and elongation, stimulating the growth of the hypocotyl and stem, and they have a positive effect on root and leaf meristem size (Martínez et al., 2018). Gibberellin can promote xylem increase and shoot growth and can also decrease root growth (Guo et al., 2015; Wang et al., 2015).

Studies have shown that some plants with gibberellin-producing bacteria in their rhizospheres exhibit better growth rates (Poupin et al., 2013; Vacheron et al., 2013). Some gibberellin-producing bacterial species include *Bacillus amyloliquefaciens* (Shahzad et al., 2016), *Enterococcus faecium* (Wang et al., 2015), *Sphingomonas* spp. (Khan et al., 2014), and *Bacillus pumilus* (Joo et al., 2004).

Ethylene

At low concentrations, ethylene has been proven to be potentially active in fruit and leaf maturation, seed germination, leaf senescence, flower wilting, flower initiation, root elongation and branching, nodule formation, and leaf abscission (Reid, 1988). At relatively high concentrations, ethylene can be toxic to plants, causing defoliation, root growth inhibition and premature senescence (Vacheron et al., 2013). When plants experience various stresses, such as infection, flooding, drought, and even the presence of potentially toxic metals, they produce ethylene precursors, that is, 1-aminocyclopropane-1-carboxylate (ACC) (Reid, 1988; Li et al., 2005; Liu et al., 2013).

ACC deaminase (ACCD) is an enzyme synthesized by some rhizobacteria; this enzyme can benefit plants due to its action in reducing ACC levels, transform it into ammonia and α-ketobutyrate (Belimov et al., 2001). This breakage allows to regulate the adverse effects of excess ethylene, reducing its levels. Therefore, rhizobacteria capable of producing ACCD are beneficial for plants growing under stress conditions, such as high salinity (Mayak et al., 2004) drought (Sandhya et al., 2010), and the presence of potentially toxic metals (Belimov et al., 2001), regulating plant ACC levels and reducing the levels of ethylene to non-toxic levels.

Azotobacter spp. (Dubey et al., 2012; Farajzadeh et al., 2012), *Bacillus* spp. (Belimov et al., 2001), and *Pseudomonas* spp. (Sandhya et al., 2010; Kamran et al., 2016) are several species known for their production of ACCD.

Abscisic Acid

Abscisic acid (ABA) is a phytohormone related in mediating stomatal opening (Mansfield et al., 1990; Maksimov et al., 2011) and also various plant aspects including development and growth in the absence of stress (Cheng et al., 2002). Abscisic acid is a molecule produced by plants, higher fungi, algae, and bacteria (Zeevaart, 1999).

Water stress stimulates high levels of ABA biosynthesis in plants, which causes partial stomatal closure as an adaptive response to conserve water (Dodd, 2007). ABA can also affect the inhibition of seed germination, the of induction of plant senescence and the abscission of fruits and leaves (Munemasa et al., 2015; Sah et al., 2016).

ABA has the abilities to reduce plant growth, even though a certain amount of ABA is required for growth, since this hormone regulates stomatal opening and, therefore, CO_2 absorption and loss of water (Pospisilova, 2003). Some PGPR can reduce ABA levels in host plants and indirectly increase plant growth (Belimov et al., 2014); these positive effects depend on endogenous ABA levels in the host plant (Vacheron et al., 2015).

Many rhizobacteria produce ABA in culture media and mediate the ABA status of plants (Dodd et al., 2010). *Achromobacter xylosoxidans* (Forchetti et al., 2007; Sgroy et al., 2009), *A. brasilense* (Cohen et al., 2009), *Bacillus licheniformis*, *B. subtilis*, *Brevibacterium halotolerans*, and *Pseudomonas putida* (Sgroy et al., 2009) are some of these rhizobacteria.

Biological Nitrogen Fixation

Nitrogen (N) is the most limiting nutrient for plant development and can be assimilated from the soil in the form of ammonia, nitrate and nitrite (Gopalakrishnan et al., 2017). These N forms are not abundant in most soils, and chemical N fertilizer used in agriculture is often lost because of rain or by mineral leaching of nitrogen fertilizer (Perez-Montano et al., 2014).

Under these circumstances, bacteria play a fundamental role because some bacteria can perform biological nitrogen fixation (BNF) and N-fixing microorganisms are classified into two groups: symbiotic microorganisms and free-living microorganisms (Gopalakrishnan et al., 2017). BNF is carried out by a specific gene product called *nif*, which, together with other structural genes, participates in protein iron activation, electron transfer biosynthesis of the molybdenum iron cofactor and many other regulatory processes required for enzyme synthesis and activity (Reed et al., 2011).

Bacteria that perform symbiosis, such as *Rhizobium* and *Bradyrhizobium*, act by forming nodules on the roots of plant species such as soybean, pea, peanut, and alfalfa, converting N_2 into ammonia, which can be used by the plant as a source of N (Murray, 2011).

Inside plant cells, rhizobia undergo a differentiation process that generates the specialized form for N fixation—the bacteroid (Olanrewaju et al., 2017). One or more bacteroids then become surrounded by parts of the plant cell membrane to form a so-called symbiosome (Madigan and Martinko, 2006). When the symbiosome is formed do the bacteroids convert atmospheric N through the enzyme nitrogenase into ammonia, in return, the plant provides organic acids (for bacteroids to produce energy) and provides an appropriate microenvironment for the action of nitrogenase, thus establishing a symbiotic relationship with bacteria (Madigan and Martinko, 2006; Olanrewaju et al., 2017).

Free-living bacteria are able to interact with roots; they live close to them so that the nitrogen fixed by these bacteria can be easily absorbed by plants and so that they the bacteria feed on root exudates (amino acids, peptides, proteins, enzymes, vitamins, and hormones) (Tabassum et al., 2017).

Some examples of free-living N-fixing bacteria include *Azotobacter*, *Paenibacillus,* *Burkholderia*, *Bacillus* and *Azospirillum*, *Herbaspirillum* (Huang et al., 2012; Anand et al., 2013; Angus et al., 2013; Habibi et al., 2014; Geddes et al., 2015; Goswami et al., 2016).

Phosphorus Solubilization

Phosphorus (P) is another essential nutrient for plants and plays an important role in nearly all major metabolic processes, including, signal transduction, energy transfer, respiration, photosynthesis, macromolecular biosynthesis (Anand et al., 2016). Although the P reserve in soils is large, it is present mainly in the form of insoluble compounds that cannot be absorbed by plants, limiting their growth. Plants absorb phosphate only in the form of monobasic ($H_2PO_4{}^-$) and dibasic ions (HPO_4^{-2}) (Perez-Montano et al., 2014).

Microorganisms play an important role in P transformation in the soil, including the P solubilization required for plant growth (Rodriguez and Fraga, 1999).

The ability to solubilize and mineralize P by phosphate-solubilizing bacteria is an important characteristic (Oteino et al., 2015). Several low-molecular-weight organic acids synthesized by various soil bacteria are capable of solubilizing inorganic P (Sharma et al., 2013). Members of the genera *Arthrobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Microbacterium*, *Pseudomonas*, *Erwinia*, *Rhizobium*, *Mesorhizobium*, *Flavobacterium*, *Rhodococcus,* and *Serratia* have the ability to solubilize phosphates (Oteino et al., 2015).

The phosphate solubilization is based on the secretion of organic acids by microorganisms due to sugar metabolism and organisms living in the rhizosphere use sugars from root exudates (Goswami et al., 2014). The acids released by microorganisms act as good chelators of divalent Ca^{2+} ions that follow the release of phosphates from insoluble compounds. Many phosphate-solubilizing microorganisms lower the pH of media by secreting organic acids such as acetic acid, lactic acid, malic acid, succinic acid, tartaric acid, gluconic acid, 2-ketogluconic acid, oxalic acid and citric acid (Rodriguez and Fraga, 1999; Patel et al., 2015).

Organic P solubilization is also called organic P mineralization and plays an essential role in the phosphorus cycling of an agricultural system (Khan et al., 2007). P can be released from organic compounds in the soil by enzymes such as non-specific acid phosphatases, phytases, phosphonatases and C-P lyases (Sharma et al., 2013).

Potassium Solubilization

Potassium (K) is the third most important macronutrient required for plant growth and this element plays a vital role in various plant physiological and metabolic processes (Zhao et al., 2001), including photosynthesis (Wang et al., 2012), plant growth, metabolism, assimilation, sugar accumulation, and plant growth and development (Sparks and Huang, 1985). Since more than 90% of K is present in the form of insoluble minerals of rock and silicate, the soluble K concentration is generally very low in soils (Parmar and Sindhu, 2013).

K-solubilizing bacteria, such as *Acidothiobacillus* spp., *Bacillus edaphicus*, *Bacillus mucilaginosus*, *Pseudomonas* spp., *Burkholderia* spp., and *Paenibacillus* spp., have been reported for their action of solubilizing K into assimilable forms from K minerals in the soil (Liu et al., 2012).

As in the case of P solubilization, the main mechanism of K solubilization is the production of organic acids, inorganic acids and protons (the acidolysis mechanism) (Sheng et al., 2008; Parmar and Sindhu, 2013; Maurya et al., 2014; Meena et al., 2015), which are capable of converting insoluble K (mica, muscovite, and feldspar biotite) into soluble forms of K that are easily absorbed by plants (Hu et al., 2006; Mo and Lian, 2011).

Several organic acids involved in the solubilization of insoluble K, tartaric acid, succinic acid, α-ketogluconic acid, citric acid, and oxalic acid are the most important ones released by K-solubilizing bacteria (Meena et al., 2014).

Indirect Mechanisms

The indirect action of microorganisms to promote plant growth includes the production of biocontrol agents that inactivate or kill pathogens, providing a healthy environment for plants (Naik et al., 2019).

Antibiosis, competition, production of lytic enzymes (chitinases and glucanases) with the ability to hydrolyze fungal cell walls are considered indirect mechanisms of growth promotion (Bhattacharyya and Jha, 2012). Bacteria can also indirectly improve plant growth by suppressing pathogens and increasing plant innate immunity against pathogens (Tabassum et al., 2017).

Production of Antibiotics

Antibiotics are low-molecular-weight toxins produced by the bacterial community are able to eliminate or reduce the growth of other microorganisms (Bakker et al., 2013). Both antibiotics and toxins have been identified as being produced by certain rhizospheric bacteria (Nakkeeran et al., 2013). These include amphysines, phenazines, 2-4-diacetylfloroglucinol, pioluteorin, pyrrolnitrin, hydrogen cyanide (HCN), oomycins, polymyxin, circulin, colistin, tensin, tropolone, and cyclic lipopeptides (Maksimov et al., 2011; Pandya and Saraf, 2014; Wani and Khan, 2014; Sherathia et al., 2016).

Bacteria can produce only a single antibiotic substance, while others can secrete several substances (Reimer and Bode, 2014; Majed et al., 2016). The availability of nutrients and environmental stimuli within proximity strongly affect the synthesis of antibiotics (Choudhary et al., 2007).

Rhizobacteria of the genus *Bacillus* are the most important for the production of antibiotics (Jayaprakashvel and Mathivanan, 2011). *B. amyloliquefaciens* and *B. subtilis* are described as producers of a wide variety of antibacterial and antifungal antibiotics, including subtilin, bacillisin, and emicobacillin (Leclere et al., 2005; Chang et al., 2007).

Induced Systemic Resistance (ISR)

ISR is described as an enhanced defensive capability of plants in response to various pathogens induced by beneficial microorganisms present in the rhizosphere (Conrath et al., 2015), a phenomenon in which the interaction of some microorganisms with roots results in plant resistance to some pathogenic bacteria, viruses, and fungi (Lugtenberg and Kamilova, 2009). ISR can also be triggered by specific environmental stimuli that lead to the upregulation of plants' innate defenses against biotic challenge and this heightened state of alert allows plants to respond faster and stronger against subsequent attack by pathogens (Van Loon, 1997).

ISR is stimulated by non-pathogenic microorganisms; ISR begins in the roots and extends to the shoots (Solano et al., 2008), initiates the defense mechanisms of plants and protects unexposed parts of plants against future pathogenic attacks by microorganisms and insects. This defense response depends on the signaling of ethylene and jasmonic acid in the plant (van Loon, 2007; Pieterse et al., 2012).

ISR has been reported to be one of the mechanisms by which PGPR can reduce the occurrence of some plant diseases, modulating the physical and biochemical properties of host plants and consequently promoting plant growth (Pieterse et al., 2014).

Some of the defense mechanisms produced via ISR in plants include reinforcement of cell walls (Ahn et al., 2007), production of secondary metabolites (Choudhary et al., 2007) and accumulation of defense-related enzymes, such as chitinases, glucanases, peroxidase, phenylalanine ammonia-lyase and polyphenol oxidase (Bhattacharyya and Jha, 2012).

P. fluorescens (Pieterse et al., 1996), *Burkholderia phytofirmans* (Compant et al., 2005), *B. pumilus* (Benhamou et al., 1996), *Bacillus cereus* (Conn et al., 2008), *Rhizobium leguminosarum*, *P.*

putida and *Serratia marcescens* (Bhattacharyya and Jha, 2012) are examples of rhizobacteria that undergo ISR.

Production of Siderophores

Iron, which is one of the most abundant elements on Earth, is not available for direct assimilation by plants and microorganisms because, in nature, it occurs mainly as Fe^{3+} and is generally present in the form of insoluble hydroxides and oxy-hydroxides (Rajkumar et al., 2010).

To obtain iron for their growth and development, some bacteria synthesize low-molecular-weight iron-chelating molecules called siderophores (Shaikh and Sayyed, 2015; Mhlongo et al., 2018). Siderophore-producing bacteria can stimulate plant growth directly, improving plant Fe nutrition, or indirectly, inhibiting the activity of plant pathogens in the rhizosphere, which in turn limits their Fe availability (Ma et al., 2011).

Pathogen suppression caused by the production of siderophores occurs by restricting the survival of pathogens by inhibiting iron nutrition by chelating available iron (Chaiharn et al., 2009). In other words, solubilization and the competitive acquisition of iron under limiting conditions reduces the availability of iron to other soil inhabitants, subsequently limiting their growth (Haas and Defago, 2005).

In addition to iron, there is evidence indicating that siderophores form stable compounds with other potentially toxic metals, such as Al, Cd, Cu, Pb, and Zn (Gururani et al., 2013). This phenomenon is advantageous for alleviating plant stress caused by potentially toxic metals present in polluted soils Ahemad and Kibret (2014) and is not solely due to the increased availability of mineral nutrients for plants (Babu et al., 2013).

Bacterial siderophores can be classified into four main classes based on the type of ligand and basic characteristics of the functional groups associated with iron. The main classes include catecholates, carboxylate, and hydroxamates (Crowley, 2006).

Several bacterial species are capable of producing siderophores, including, *Azospirillum* (Banik et al., 2016), *Dickeya* (Sandy and Butler, 2011), *Klebsiella* (Zhang et al., 2017; Bailey et al., 2018), *Nocardia* (Hoshino et al., 2011; Soutar and Stavrinides, 2018), *Pantoea* (Burbank et al., 2015), *Pseudomonas* (Baune et al., 2017; Deori et al., 2018; Pourbabaee et al., 2018), *Azotobacter* (Romero-Perdomo et al., 2017), *Paenibacillus* (Liu et al., 2017), *Bacillus* (Kesaulya et al., 2018; Pourbabaee et al., 2018), *Serratia* (Lee et al., 2017) and *Streptomyces* (Schutze et al., 2015; Gáll et al., 2016; Goudjal et al., 2016).

Rhizoremediation and Stress Control

Plants are often exposed to various environmental stresses, and plant growth is sometimes inhibited by a large number of biotic (insects, bacteria, fungi, and viruses) and abiotic (radiation, salinity, temperature, flood, drought, and contaminants,) stresses, resulting in highly negative impacts on survival and plant biomass (Islam et al., 2016).

Phytoremediation uses plants and microorganisms to remove, destroy or scavenge toxic metals from contaminated environments in an efficient and economical way (Ma et al., 2011).

Most potential metals are toxic to plants, but bacteria are capable of neutralizing metal toxicity, linking it to negatively charged functional groups throughout the cell wall, which provides interactions with positive ions, in particular metal ions—a phenomenon called metal biosorption (Syed and Chinthala, 2015). Microbial species with considerable resistance to metals showed immobilization of toxic metals or reducing its concentration when added to contaminated soils by reducing their toxicity to the plant or crop (Wani and Khan, 2014).

Interference With the Quorum Sensing System

Many bacteria rely on chemical communication to recognize the environment and retrieve information about population density. Consequently, multiple molecules are released, which synchronize the expression of genes, coordinate behavior through a process called quorum sensing (QS) and determine the relationships with eukaryotic species (Ortiz-Castro and Lopez-Bucio, 2019). QS is considered a social trait of bacteria (Whiteley et al., 2017).

Communication between cells is mediated by small molecules of diffusible signals called self-inducers (Fuqua et al., 1994). Generally, signaling mediated by self-inducers occurs at high population densities because microorganisms act in communities where there are advantages for the entire population of cells, simulating a multicellular organism (Ganin et al., 2009; Bai and Rai, 2011).

While N-acyl-hemoserine-lactones (AHLs) and occasionally 4-hydroxy-2-alkylquinolones (HAQs) are often found in gram-negative bacteria, gram-positive bacteria mainly use cyclic oligopeptides. AHLs are the most common self-inducing molecules that regulate the expression of genes involved in the production of virulence factors or biofilm formation in various plant pathogens (Quiñones et al., 2005). Many plants are capable of producing molecules that specifically interfere with QS systems of bacteria associated with plants, and in any case, depending on whether the bacterium is detected as a pathogen or as a beneficial microorganism, the molecule improves or inhibits QS-regulated phenotypes (Pérez-Montaño et al., 2013).

PGPR Used in Maize

Maize (*Zea mays* L.), which is a member of the Poaceae family, is one of the most important cereal crop species in the world and serves as a staple food for many populations (Rouf Shah et al., 2016). According to the International Grains Council (2019), global maize consumption is expected to reach new peaks in the coming years (projection until 2024), and the use of maize for animal feed is expected to increase during the same period.

Maize is among the three most important crop species in the world, providing almost half of the daily energy to organisms in Africa and the Americas (FAOSTAT Food Balance Sheets, 2020). The demand for maize in response to growing populations will require marked increases in the production, sustainability, and resilience of maize-based agricultural systems (Shiferaw et al., 2011).

To maintain increases in maize productivity, an increase in the amount of fertilizers will be necessary, resulting in both an increase in production costs and a greater negative impact on the environment. Many beneficial effects of plant growth-promoting rhizobacteria on crop growth and yield have been well-documented. Breedt et al. (2017) found an increase yield ranging from 24 to 34% using *Paenibacillus alvei*, *B. safensis*, *B. pumilus*, and *Brevundimonas vesicularis.* Cassán et al. (2009) assessed the effect of the mixture of *A. brasilense* with *Bradyrhizobium japonicum* and verified the increase of seeds germination rate, and early development. Kuan et al. (2016) reported that plant growth-promoting bacteria may provide a biological alternative to fix atmospheric N_2 and delay N remobilization in maize plant to increase crop yield based on an understanding that plant-N remobilization is directly correlated to its plant senescence promoting high ear up to 30.9% with reduced fertilizer-N input. Di Salvo et al. (2018) reported that PGPR used as inoculants of cereal crops including maize can improve their growth and grain yield. The crops responses to inoculation are complex because are defined by plant-microorganisms interactions, many of them still unknown. Thus, it is necessary to improve the knowledge about the microbial ecology of the rhizosphere of crops under different agricultural practices.

Several bacteria that have the ability to produce IAA and have positive effects on shoot and root weight and nutrient uptake on maize plants. Besides, activities like phosphorus solubilization, or even other non-evaluated PGPR traits that stimulate plant growth (Lobo et al., 2019).

The bioprotective role of PGPR on maize crops has also been studied. The toxigenic fungus *Fusarium* is one of the significant genera associated with maize. Some PGPR such as *Bacillus amyloliquefaciens* and *Microbacterium oleovorans* were able to protect maize against *Fusarium verticillioides* when applied in the form of seed coatings (Pereira et al., 2011). Interestingly, some PGPR species have appeared to promote plant growth by acting as both biofertilizers and as biocontrol agents. For instance, strains of *B. cepacia* have been observed with biocontrol characteristics against *Fusarium* spp. Simultaneously, they can also stimulate the growth of maize under iron-poor conditions via siderophore production (Bevivino et al., 1998).

PGPR Used in Sugarcane

Sugarcane (a hybrid of *Saccharum* species) is one of the oldest and most valuable crop species in the world due to the vast benefits associated with its industrial use. Sugarcane is grown in tropical and subtropical regions (Chhabra et al., 2016) and is mainly used to supply raw materials to the sugar industry for the production of sugar (Zhao and Li, 2015). In addition, sugarcane also has global importance due to the benefits associated with the production of biofuel and biogas (Hoang et al., 2015).

New technologies developed in all production sectors have allowed extending the period of sugarcane planting and, consequently, more efficient use of labor and inputs, thus increasing the sustainability and competitiveness of the sugar and alcohol industries (Oliveira et al., 2012).

Among the various techniques available, PGPR stand out for their environmental and economic gains, which can reduce the amount of fertilizers needed, optimizing sugarcane production.

One of the most limitations for sugarcane production is the poor and inadequate fertile soil which fail to meet the nutritional and growth requirements and hence unable to achieve high production (Caione et al., 2015). Phosphorus (P) is the most critical element with high interaction with soil Raj and Antil (2011) required in a small amount by sugarcane in comparison of N and K, but still plays an essential role in the development of tillering and root system and greatly influence the longevity (Kingston, 2013).

The low availability of phosphorus is due to low P in the source material, clay absorption and its precipitation with oxides and hydroxides of iron and aluminum (Caione et al., 2015). As consequence of it, a great amount of P fertilizers is applied in sugarcane production promoting high production cost. Furthermore, phosphate fertilizers are produced by rock phosphate and the phosphate source worldwide are not renewable (Sattari et al., 2012).

Around 10–30% of the phosphorus fertilizer applied in the first year is absorbed by the roots of cane crop whereas an intensive amount accumulates in the soil as fixed P, not available to plants (Syers et al., 2008). Therefore, is urgent to find alternatives to reduce the use of phosphate fertilizers. Since every day looking to a more sustainable agriculture combined with increase in yield and economically practicable.

The use of plant growth-promoting rhizobacteria (PGPR) is a promising alternative in sugarcane production with low environmental impact to increase the efficiency of the use of mineral fertilizers including phosphate, providing high cost-effective yields (Spolaor et al., 2016).

Several field and greenhouse studies with phosphate fertilizer in sugarcane (Calheiros et al., 2012; Caione et al., 2015; Albuquerque et al., 2016; Borges et al., 2019).

Rosa et al. (2020) evaluated the effect of inoculation with three PGPR species and five P doses in sugarcane and reported that the inoculation can play a fundamental role in cultivation, generating great benefits to the crop and saving fertilizers cost for the producers. These results revealed a combination of *Azospirillum brasilense* and *Bacillus subtilis* allied to the low cost of P_2O_5 was the best fertilizers management in the sugarcane which is meaningful production practice of sugarcane.

Santos et al. (2018) reported that the use of *B. subtilis* together with by-products can improve soil fertility parameters and decrease adverse effects associated with vinasse fertilization, in addition to providing shoot and root growth and providing collective synergy for high yield of sugarcane production with environmental benefits. Moura et al. (2018) have shown that the use of *Azospirillum* in sugarcane crop improved root system leading to better water and nutrient uptake that in turn may influence yield positively. This report showed that the significant interaction of cultivar x water regime x *Azospirillum* inoculation suggests a complex interplay of these factors, likewise, involving indigenous plant auxin pool. Li et al. (2017) isolated *Pseudomonas* sp associated with sugarcane rhizosphere and verified useful activity the isolate such as phosphate solubilization, siderophore production, ACC deaminase activity, and IAA production, as well as N_2 fixing activity and diseases management. These features are measured as important PGP traits and have been found to be effective in improving the growth and nitrogen content of sugarcane plants. The association of PGPR in sugarcane production may be an eminent development biofertilizer application, for sustainable crops production, in reducing environmental pollution and in biological agri-business. (Muthukumarasamy et al., 2017) verified that the association between diazotrophic P and K solubilizing *Rosneateles terrae* and *Burkholderia gladioli* with sugarcane were able to increase the leaf chlorophyll, N content and total biomass and encourage the farmers to use PGPR to improve N, K, and K availability in the soil.

CONCLUSIONS AND PERSPECTIVES

This review has focused on a heterogeneous group of microorganisms found in the rhizosphere. These microorganisms live in association with roots, can stimulate plant growth and can reduce the incidence of diseases. Among the large number of PGPR, the most studied genera include *Azospirillum*, *Bacillus,* and *Pseudomonas*. The important role that PGPR play in agriculture is proven by the large number of publications on this topic to date. The exact mechanisms used by PGPR are not yet fully known, although some characteristics of these bacteria can be used to promote plant development. In addition, for these growth-promoting characteristics to have an effect on plants, bacteria need to be rhizosphere competent and must be able to survive in rhizospheric soil, where communities can be affected by a large number of factors, such as soil characteristics, plant genotype, and agricultural practices, that together determine the presence and predominance of certain microbial groups. Growth promotion of maize and sugarcane could be optimized with appropriate combinations of PGPR, environmental conditions and plant genotypes. In this sense, additional efforts must be made in the development of good inoculants and production systems that allow reducing the amount of chemical fertilizers and insecticides used to increase soil fertility and crop productivity.

AUTHOR CONTRIBUTIONS

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

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