Original Research Article

Rhizospheric bacteria with potential benefits in agriculture
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ABSTRACT

Rhizobacteria are a vast and very diverse group of bacteria that live in the vicinity of roots. They develop beneficial, neutral, and even detrimental relationships, although the latter to a lesser extent. The interactions between bacteria and plant roots have played a determining role in the adaptation and productivity of plant species over time. Several studies show that rhizobacteria have improved plant growth, production, and health, both directly through mechanisms that include the assimilation of vital nutrients such as nitrogen fixation, phosphorus and potassium solubilization, and phytostimulation through the production of various phytohormones) and indirectly (by affecting the growth of important pathogens, activating plant immunity, and improving problems caused by abiotic stress). Due to their metabolic diversity, rhizobacteria could contribute positively to the improvement of agricultural productivity and the solution of environmental problems caused by the methods used in current agriculture. Several genera, such as Acidithiobacillus, Aminobacter, Arthrobacter, Azarcus, Azospirillum, Azotobacter, Bacillus, Burkholderia, Clostridium, Enterobacter, Gluconoacetobacter, Pseudomonas, Serratia, and Sphingomonas, have demonstrated their enormous growth-promoting capacity. This review provides a focus on the mechanisms by which rhizobacteria enhance plant growth, their contribution to sustainable agriculture, and their commercialization, a field that continues to grow steadily.

Keywords: plant growth promoting bacteria; biological nitrogen fixation; rhizosphere; phosphate solubilization

1. Introduction

Agricultural productivity has increased incredibly in the last forty years, thanks to technologies developed during the green revolution and the expansion of the use of land, water, and other natural resources[1]. However, this modern farming process has included the indiscriminate use of pesticides and fertilizers (nitrogen and phosphorus), which has resulted in various environmental problems caused by the pollution of these natural resources[2]. On the other hand, according to FAO[1] agriculture will face a great challenge since, by 2050, it will have to produce almost 50% more food, fodder, and biofuel than it produced in 2012, due to a trend in population increase. In addition, the high variability of temperature, rainfall, droughts and floods, pests, and diseases resistant to different chemical compounds that have been abused in their use will be important factors that will damage crop yields. The above poses great challenges for agriculture, which has to look for systems that allow optimal food production with cost reduction and conservation of natural resources in the long term[3].
Nature is a key point in the solution of these problems. Over time, plants and microorganisms have co-evolved and developed diverse relationships that have conferred adaptive advantages in diverse habitats on earth\textsuperscript{[4,5]}. First, plants, because of their ability to convert solar energy into chemical energy, have positioned themselves at the top of trophic chains, providing other organisms, such as rhizobacteria, with food (photosynthates and secondary metabolites), an ideal place to inhabit, and an essential element in the metabolism of cellular aerobic respiration (oxygen)\textsuperscript{[6]}. While rhizobacteria incredibly improve growth, health, and adaptability against different biotic and abiotic stress conditions in plants\textsuperscript{[6,7]}. 

In recent years, research on the understanding of plant-microorganism interactions has been encouraged to replace agrochemicals (fertilizers and pesticides) with highly effective products that contribute to improved plant productivity and are also environmentally friendly\textsuperscript{[2]}.

2. Rhizobacteria

Rhizobacteria are bacteria that inhabit the rhizosphere, an area of soil attached to the root and extending a few millimeters from the surface of the root system. This zone is characterized by the unique and dynamic interaction of biogeochemical processes occurring between plant roots and soil microorganisms, which are highly influenced by root exudates\textsuperscript{[8]}. In addition, it harbors a large number of microorganisms that generally stimulate plant growth and reduce the incidence of diseases\textsuperscript{[7]}. This bacterial group has also been assigned the name \textit{Plant Growth Promoting Rhizobacteria} (PGPR)\textsuperscript{[9]}.

In the process of establishing relationships with rhizobacteria, plants invest up to 20\% of the carbon sources obtained during photosynthesis, in exchange for the improvement of root architecture, nutrient uptake, and stimulation of the plant immune system carried out by PGPR\textsuperscript{[6]}. One of the best-known examples of such benefits is found in the case of \textit{Rhizobium} bacteria\textsuperscript{[6]}.

The impact of rhizobacteria is highly influenced by root exudates, which also play an important role in signaling and recognition processes between plants and microorganisms\textsuperscript{[10]}. The mechanisms of attraction of the bacteria to the rhizosphere of their host are mediated by a specific bacterial chemotaxis towards particular plant exudates; likewise, good adhesion and colonization on the root surface are factors that can influence the functionality of the associative symbiosis\textsuperscript{[7,10]} (\textbf{Figure 1}).

\textbf{Figure 1.} Mechanisms of action of PGPR.
3. Direct mechanisms in the promotion of plant growth

3.1. Biological nitrogen fixation (BNF)

Nitrogen (N) is one of the vital nutrients for plant growth and productivity. This element is present in amino acids inherent in proteins, amides, chlorophyll, hormones, nucleotides, vitamins, alkaloids, and nucleic acids\[11\]. A common feature of microorganisms involved in FBN is the presence of nitrogenase enzymes, which reduce atmospheric nitrogen into the assimilable ion NH\(_4^+\). Enzymatic activity is generally susceptible to the concentration of oxygen in the medium; therefore, microorganisms have adopted adaptive mechanisms such as respiratory protection, conformational protection, and cellular compartmentalization\[12\].

On land, N\(_2\) constitutes approximately 78% of the gases in the atmosphere; however, this form is not assimilable by plants. Nitrogen-fixing organisms are generally classified into symbiotic, fixing bacteria in which members of the family Rhizobiaceae and the genus Frankia are found\[11\] and free-living, associative, and endophytic non-symbiotics, such as cyanobacteria (Anabaena, Nostoc), Azospirillum, Azotobacter, Gluconoacetobacter diazotrophicus, Azocarbus\[13\], Paraburkholderia\[14\].

3.2. Phosphate solubilization

Phosphorus (P) is the second-most important nutrient involved in plant growth and productivity. This element is essential in cell division, signal transduction, macromolecular biosynthesis, photosynthesis, and plant respiration, with energy acquisition, storage, and use being one of its main functions\[15\]. Unlike nitrogen, phosphorus is not available in the atmosphere, so its main source is more limited as it comes mainly from primary and secondary minerals present in the soil. Another problem is that this element is usually found in lower concentrations than other elements, ranging from 0.001 to 1 mg L\(^{-1}\)\[16\], further decreasing its availability to plants. Phosphorus in soil is usually found in three categories: (I) as an inorganic compound forming complexes with aluminum (Al), iron (Fe), manganese (Mn), and calcium (Ca); (II) organic compounds, such as humus, inositol, phytic acid, phytin, sugar phosphates, nucleotides, phosphoproteins, phosphonates, and phospholipids; and (III) as organic and inorganic compounds associated with living cell matter\[17\]. However, plants only take up phosphate in monobasic form (H\(_2\)PO\(_4^-\)) and dibasic form (HPO\(_4^{2-}\))\[18\].

Some rhizobacteria have the ability to solubilize phosphates from inorganic or organic compounds using different pathways. For example, the activity of enzymes such as non-specific phosphatases, phytases, phosphonatases, and C-P lyases has been reported\[7,18\], which solubilize phosphorus from organic compounds in the soil. Likewise, one of the most studied mechanisms is the obtaining of this element compound by rhizobacteria through the release of organic acids such as gluconic or 2-ketogluconic acid, capable of chelating the bioavailable phosphorus in the soil using its hydroxyl and carboxyl radicals. The production of these acids can be variable and depends on root exudates\[7,11,19\]. Thus, phosphate-solubilizing rhizobacteria represent an alternative to improving the application of chemical phosphate fertilizers and agricultural productivity, as they have the ability to provide available forms of phosphorus to plants\[20\].

3.3. Potassium solubilization

Potassium (K) is the third essential macronutrient needed in plant growth, so its limitation significantly affects crop production\[21,22\]. In plants, K plays a very important role in processes such as photosynthesis, in which it regulates stomatal opening and closing and therefore CO\(_2\) absorption, and has also been found to be involved in enzyme activation, protein synthesis, maintenance of cell turgor, reduction of respiration, transport of sugars, and nitrogen absorption, thus being vital for better plant development\[23\]. K deficiency generates plants with poorly developed roots, a low growth rate, and low seed production, which is reflected in lower
yield\textsuperscript{[24]}. Potassium deficiencies are not usually the same as nitrogen or phosphorus deficiencies; however, inadequate application, runoff, leaching, and soil erosion are often serious problems\textsuperscript{[23]}.

Recently, rhizobacteria have been identified with the ability to solubilize minerals such as K, which can contribute to resource conservation and thus increase productivity\textsuperscript{[21]}. Likewise, the positive effects of rhizobacteria on K availability in soil\textsuperscript{[25]} and K uptake in crops such as maize\textsuperscript{[26]}, tobacco\textsuperscript{[27]} and wheat\textsuperscript{[28]} have been previously reported. The main mechanisms related to mineral potassium solubilization include the production of organic acids such as oxalic acid, tartaric acid, gluconic acid, 2-ketogluconic acid, citric acid, malic acid, succinic acid, propionic acid, glycolic acid, malonic acid, fumaric acid, and proton production\textsuperscript{[29]}. Some genera, such as \textit{Acidithiobacillus}, \textit{Aminobacter}, \textit{Arthrobacter}, \textit{Bacillus}, \textit{Burkholderia}, \textit{Cladosporium}, \textit{Enterobacter}, \textit{Paenibacillus}, and \textit{Sphingomonas}, have been reported as potassium-solubilizing rhizobacteria\textsuperscript{[30]}.

3.4. Production of phytohormones

Phytohormones are organic molecules that, in small concentrations (<1 mM), regulate the expression of genes involved in plant growth and development. These can be synthesized in different locations of the plant, and their action varies according to environmental changes that modify the gene expression of the organism, so they have a prominent impact on plant development and productivity\textsuperscript{[22,31]}. Some rhizobacteria have the ability to produce phytohormones, being one of the most studied mechanisms associated with the promotion of plant growth, such as \textit{B. amyloliquefaciens} in potato crop\textsuperscript{[32]}, \textit{Azospirillum} and \textit{Klebsiella} in corn crops\textsuperscript{[33]}, \textit{Bacillus}, \textit{Lysinibacillus}, \textit{Arthrobacter}, and \textit{Rahnella} in \textit{Eucalyptus nitens} plantations\textsuperscript{[34]}. Some of the groups influenced by rhizobacteria include auxins, cytokinins, gibberellins, abscisic acid, ethylene, and jasmonic acid\textsuperscript{[35,36]}. These molecules influence plant physiology by increasing root volume, host plant root respiration rate, and proton flux in the root membrane, causing an increase in the uptake of soluble nutrients and minerals\textsuperscript{[37]}.

3.5. Auxins

Auxins are a very important type of phytohormone in plants; they influence various developmental events such as cell division, elongation, apical dominance, adventitious root formation, and phototropism\textsuperscript{[36,38]}. One of the most well-known auxins produced by rhizobacteria is indole-3-acetic acid (IAA)\textsuperscript{[39]}. AIA released by rhizobacteria mainly affects the root system, increasing its size, weight, branching number, and surface area in contact with the soil. All these changes lead to an increase in their ability to explore the soil for nutrient exchange, thus improving plant nutrition and growth capacity. In addition, this auxin has been found to act as an important molecule in plant-microorganism signaling and interaction\textsuperscript{[40]}. Likewise, the ability of rhizobacteria to modulate and tolerate abiotic stress using this phytohormone has been demonstrated\textsuperscript{[36]}.

Rhizobacteria use L-tryptophan that is secreted into the rhizosphere to synthesize IAA, mainly through the indole-3-pyruvic acid (IPyA) pathway. Some genera, such as \textit{Azospirillum}, \textit{Rhizobium}, and \textit{Bradyrhizobium}, synthesize the hormone through this pathway\textsuperscript{[41]}.

3.6. Cytokinins

Cytokinins are another important group of phytohormones; their structure is generally derived from adenine, where the N6 position of adenine is substituted with an isoprenoid, such as in zeatin, or an aromatic side chain, such as in kinetin. These types of hormones promote processes such as cell division and differentiation, an increase in root area through adventitious root formation, leaf formation, and the prevention of senescence\textsuperscript{[7,42]}. 
In the early 1970s, Phillips and Torrey\textsuperscript{[43]} reported a cytokinin-like substance in culture filtrates of *Rhizobium leguminosarum* and *Bradyrhizobium japonicum*, which was later identified as zeatin. At present, more than 30 different plant growth-promoting cytokinin compounds produced by plant-associated microorganisms have been found, such as zeatin, isopentenyladenine, and dihydroxizatin, among others. Likewise, a large number of species producing this phytohormone have been reported, such as *Arthrobacter giacomelloi*, *Azospirillum brasilense*, *Bradyrhizobium japonicum*, *Bacillus licheniformis*, *Paenibacillus polymyxa*, *Pseudomonas fluorescens*, and *Rhizobium leguminosarum*, among others\textsuperscript{[44,45]}.

### 3.7. Gibberellins

Gibberellins are a group of phytohormones consisting of about 136 molecules with different structures that regulate plant growth in various metabolic processes, including seed germination, stem elongation, flowering, fruit formation, and plant height\textsuperscript{[41]}. Gibberellins interact with other phytohormones, leading to important responses that mediate stress tolerance\textsuperscript{[36]}. The ability to stimulate plant growth and development under various abiotic stress conditions has also been reported\textsuperscript{[46]}. In addition, gibberellins induce efficient ion uptake within the plant, which enhances growth and maintains plant metabolism under normal and stress conditions\textsuperscript{[47]}.

Gibberellins produced by PGPRs promote plant growth and increase yields\textsuperscript{[48]}. Currently, activity by several gibberellin-producing PGPR species has been reported, such as: *Azotobacter* spp., *Bacillus pumilus*, *B. licheniformis*, *Herbaspirillum seropedicea*, *Leifsonia xyli*, *Pseudomonas* spp., *Rhizobium meliloti* and *R. phaseoli* which have been used to induce germination in seeds\textsuperscript{[7]}.

### 3.8. Abscisic acid

Abscisic acid (ABA) is a phytohormone with a sesquiterpenoid structure that plays a very important role in plant physiology, mainly in adaptive responses to biotic and abiotic stresses\textsuperscript{[36,49,50]}. ABA is involved in processes such as seed dormancy and organ abscission. Likewise, it has been reported that, under abiotic stress conditions, ABA up-regulates the expression of stress-responsive genes, leading to improved performance in tolerance responses\textsuperscript{[51,52]}. Furthermore, during drought, ABA has been found to function as an anti-transpirant as it induces stomatal closure to minimize water loss through transpiration\textsuperscript{[49]}. Similarly, it has been reported that ABA can control root growth and water content under drought stress conditions\textsuperscript{[36]}. Its exogenous application can ameliorate the effects caused by stresses, such as salinity, drought and cold stress, as well as wounding\textsuperscript{[36,53]}.

The study related to ABA-producing rhizobacteria and their metabolism has been a bit more limited compared to that of other phytohormones, however, there are some species such as: *Azospirillum brasilense*, *Arthrobacter koereensis*, *Bacillus amyloliquefaciens*, *B. licheniformis* that have demonstrated the ability to produce this phytohormone\textsuperscript{[36,52]}, counteracting the negative effects caused by biotic and abiotic stresses.

### 3.9. Exopolysaccharide and biofilm production

A wide variety of rhizobacteria possess the ability to release exopolysaccharides (EPS) and form biofilms in the root\textsuperscript{[54]}. Thus, rhizobacterial communities form complex structures of microbial cells adhering to the root surface, which are surrounded by an extracellular polymeric matrix (biofilms)\textsuperscript{[55,56]}. Rhizobacteria within the biofilm significantly protect plants from external stress, because they maintain greater adherence to surfaces, improving the soil aggregation state of the rhizosphere, which increases the availability of water and nutrients, likewise, the microbial density increases, which improves plant growth\textsuperscript{[54,57]}. In addition, rhizobacterial exopolysaccharides function as signal molecules that activate the defense response during the process of pathogen infection. Some EPS bind cations, including Na\textsuperscript{+}, suggesting a role in mitigating salinity...
stress by reducing the Na$^+$ content available for plant consumption$^{[56]}$. Some PGPRs such as *Rhizobium leguminosarum*, *Azotobacter vinelandii*, *Bacillus drentensis*, *Enterobacter cloacae*, *Agrobacterium* sp., *Xanthomonas* sp. and *Rhizobium* sp. release exopolysaccharides$^{[22,58]}$. The application of EPS-producing PGPRs represent a promising measure to combat drought and salinity stress, thereby increasing global food security$^{[59]}$.

4. Indirect mechanisms in the promotion of plant growth

4.1. Stress drivers

Stress is defined as any factor that negatively influences plant development$^{[60]}$. Plants are sessile organisms and are frequently subjected to various types of stresses such as: high temperatures, cold, drought, salinity, alkalinity, UV radiation, and pathogen infection. These factors are often unpredictable and come to significantly impair agricultural productivity$^{[22]}$. In the face of the present climate change, the aforementioned problems represent a challenge in the improvement of agricultural sustainability and production. In the following, mention is made of the participation of PGPRs and their role in stress management.

4.2. ACC deaminase

Ethylene is an essential metabolite for the growth and senescence of leaves, flowers, and fruits. This hormone, which is produced endogenously and at optimal levels, is important for inducing physiological changes in plants as it functions as a signal molecule that activates transcription of various genes that influence progression, reproductive success, and organ longevity, thus regulating plant lifespan$^{[61]}$. However, under stress conditions such as those generated by salinity, drought, heavy metals, and pathogenicity, endogenous ethylene levels are deliberately increased, causing defoliation, inhibition of cell elongation, senescence, and other cellular processes that negatively affect plant development$^{[44,62,63]}$. Therefore, alternatives have been sought to help counteract and decrease stress in plants caused by unpredictable environmental changes.

The direct precursor in the synthesis of ethylene in plants is ACC (1-aminocyclopropane-1-carboxylate acid). Rhizobacteria, with the ability to produce the enzyme ACC deaminase, facilitate and help plant growth and development under stress conditions as they decrease ethylene levels by metabolizing the precursor into a source of carbon (alpha-ketobutyrate) and nitrogen (ammonia), which they use as food$^{[7,64]}$. In addition, it has been found that in some legumes, this can increase the number of nodules, producing changes in root architecture and promoting the development of lateral roots$^{[65]}$.

Currently, bacterial strains exhibiting ACC deaminase have been identified in a wide range of genera, such as *Achromobacter*, *Alcaligenes*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Rhizobium*, *Rhodococcus*, *Enterobacter*, *Klebsiella*, *Methyllobacterium*, *Mesorhizobium*, *Pseudomonas*, and *Sinorhizobium$^{[7,66]}$.

4.3. Osmoprotectants

Under drought stress conditions, many rhizobacteria produce molecules that function as osmoprotectants (glutamate, trehalose, proline, glycine betaine (GB), proline betaine, ectoine etc.), maintaining fluid balance in cells and stimulating plant growth under unfavorable conditions. Some rhizobacterial species, such as *Bacillus polymyxa*, *Pseudomonas jessenii*, *Pseudomonas syxantha*, *Azospirillum lipoferum*, and *Arthrobacter nitroguajacolicus*, have been able to enhance plant growth under water stress conditions through the accumulation of free amino acids such as proline and soluble sugars$^{[67]}$.

Some strains, such as *Bacillus subtilis*, *Klebsiella variicola*, *Pseudomonas fluorescens*, and *Raoultella planticola*, have shown the ability to enhance the biosynthesis and accumulation of cholines, a precursor in
GB metabolism, resulting in increased accumulation of this compound, thus improving relative leaf water content and dry weight[67].

4.4. Heat shock proteins

High temperatures (>40 °C) are a major problem affecting the production of many crops worldwide[68]. It promotes protein denaturation and aggregation, causing serious problems in plants. Some rhizobacteria, such as Bacillus subtilis, have the ability to induce thermotolerance in plants by synthesizing high-molecular-weight proteins (8–90 kDa), known as heat shock proteins (HSPs: Heat Shock Proteins). The main function of HSPs is the protection of other proteins that are affected by high temperatures[69].

HSPs are constituted by chaperones (such as GroEL, DnaK, DnaJ, GroES, ClpB, ClpA, ClpX, small heat shock proteins (sHSPs), and proteases). Chaperones are involved in the proper folding of proteins that are denatured, whereas proteases are responsible for the degradation of proteins that are irreversibly damaged. The activity of such chaperones is essential for cell survival during heat shock and for subsequent recovery[70].

4.5. Induced systemic resistance (ISR)

Some rhizobacteria increase the defensive capacity of plants for prolonged periods, a mechanism known as ISR (induced systemic resistance)[71]. This response keeps the whole plant on alert and is induced in distant or unaffected parts[72]. The ISR response is dependent on jasmonic acid and ethylene signaling in the plant. Accumulation of these molecules coordinates at the systemic level the activation and enhancement of defense capabilities such as cell wall strengthening, production of antimicrobial phytoalexins, peroxidase, chitinase, β-1,3-glucanase, phenylalanine ammonium lyase, pathogenesis-related proteins and biosurfactant production[73]. During interaction with the plant, rhizobacteria release cellular structures such as: lipopolysaccharides (LPS), flagella, salicylic acid, siderophores, cyclic lipopeptides, among others, which induce ISR[7,74]. Induction of ISR by rhizobacteria is a useful tool to reduce diseases caused by pathogens.

5. Biocontrol mechanisms (antagonism)

Some PGPRs naturally eliminate phytopathogens (bacteria, fungi, weeds and insects) by producing various secondary metabolites that are excreted locally or near the plant surface[75]. The molecules released by these microorganisms are biodegradable and are needed in small quantities, unlike some agrochemicals that are resistant to degradation and are applied in large quantities to agricultural crops[7]. Some of the main inhibitory compounds produced by some rhizobacteria are presented below (Table 1).

<table>
<thead>
<tr>
<th>Rhizobacteria</th>
<th>Plant</th>
<th>Conditions</th>
<th>Results</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pseudomonas gessardii BLP141, P. fluorescens A506 and P. fluorescens LMG 2189</td>
<td>Sunflower (Helianthus annuus)</td>
<td>Greenhouse</td>
<td>Improved plant growth, physiology, yield and antioxidant activities, as well as proline accumulation.</td>
<td>Saleem et al.[76]</td>
</tr>
<tr>
<td>Bacillus sp. JS</td>
<td>Tobacco (Nicotiana tabacum ‘Xanthi’) and Lettuce (Lactuca sativa ‘Crispa’)</td>
<td>In vitro</td>
<td>Fresh weight and shoot length increased.</td>
<td>Kim et al.[77]</td>
</tr>
<tr>
<td>Klebsiella sp. Br1, Klebsiella pneumoniae Fr1, Bacillus pumilus S1r1, B. subtilis and Acinetobacter sp. S3r2</td>
<td>Corn (Zea mays L.)</td>
<td>Greenhouse</td>
<td>It increased top and root dry biomass and total nitrogen content.</td>
<td>Kuan et al.[78]</td>
</tr>
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</table>
Table 1. (Continued).

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<thead>
<tr>
<th>Rhizobacteria</th>
<th>Plant</th>
<th>Conditions</th>
<th>Results</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>P luteola IMPCA244, O anthropi IMP311, Aeromonas salmonicida N264, Burkholderia cepacia N172, P. fluorescens N50 and S. maltophilia</td>
<td>Sugar cane (Saccharum officinarum)</td>
<td>Greenhouse</td>
<td>Plant height (27.75%), stem diameter (30.75%), number of tillers (38.5%), leaf area (49%), and aerial and root dry matter weight increased.</td>
<td>Morgado González et al.[79]</td>
</tr>
<tr>
<td>Pseudomonas putida, Azospirillum, Azotobacter</td>
<td>Artichoke (Cynara scolymus)</td>
<td>In vitro</td>
<td>Shoot length, shoot weight and germination time increased.</td>
<td>Jahanian et al.[80]</td>
</tr>
<tr>
<td>Pseudomonas sp.</td>
<td>Soybeans and wheat</td>
<td>Field</td>
<td>Increased soil enzymatic activities, total productivity and nutrient uptake.</td>
<td>Sharma et al.[81]</td>
</tr>
<tr>
<td>Bradyrhizobium sp., Pseudomonas sp., Ochrobactrum cytisi</td>
<td>Lupinus luteus</td>
<td>Field</td>
<td>Both biomass and nitrogen content increased.</td>
<td>Dary et al.[82]</td>
</tr>
<tr>
<td>Pseudomonas putida strain R-168, P. fluorescens strain R-93, P. putida DSM291, Azospirillum lipferum DSM 1691, A. brasiliense DSM 1690</td>
<td>Corn (Zea mays L.)</td>
<td>Field</td>
<td>Plant height, seed weight, number of seeds, and leaf area increased.</td>
<td>Gholami et al.[83]</td>
</tr>
<tr>
<td>Azospirillum amazonense</td>
<td>Rice (Oryza sativa L.)</td>
<td>Greenhouse</td>
<td>It increased grain dry matter accumulation (7%–11.6%), panicle number (3%–18.6%) and nitrogen accumulation at grain maturity (3.518%–5%).</td>
<td>Rodrigues et al.[84]</td>
</tr>
<tr>
<td>Pseudomonas sp.</td>
<td>Rice (Oryza sativa), maize (Zea mays)</td>
<td>In vitro</td>
<td>They showed ability to control root fungal pathogens.</td>
<td>Lawongsa et al.[85]</td>
</tr>
<tr>
<td>Azospirillum brasiliense Sp245</td>
<td>Bean (Phaseolus vulgaris)</td>
<td>Greenhouse</td>
<td>Increased root growth.</td>
<td>Remans et al.[86]</td>
</tr>
<tr>
<td>Bacillus subtilis, Pseudomonas aeruginosa</td>
<td>Solanum lycopersicum, Abelmoschus esculentus, Amaranthus sp.</td>
<td>Greenhouse</td>
<td>Dry biomass increased by 31% for Solanum lycopersicum, 36% for Abelmoschus esculentus and 83% for Amaranthus sp.</td>
<td>Adesemoye et al.[87]</td>
</tr>
<tr>
<td>Pseudomonas jessenii PS06, Mesorhizobium ciceri C-2/2</td>
<td>Cicer arietinum</td>
<td>Greenhouse</td>
<td>The co-inoculation treatment increased seed yield (52% more than the control) and nodule fresh weight.</td>
<td>Valverde et al.[88]</td>
</tr>
<tr>
<td>Azotobacter chroococcus HKN-5, Bacillus megaterium</td>
<td>Brassica juncea</td>
<td>Greenhouse</td>
<td>It protected the plant from metal toxicity and stimulated plant growth.</td>
<td>Wu et al.[89]</td>
</tr>
</tbody>
</table>

5.1. Antibiotics

Many rhizobacteria secrete molecules that eliminate or decrease the growth of some phytopathogens by inhibiting cell wall synthesis, structural destabilization of the cell membrane, or inhibition of translation in phytopathogens, among others[90]. Antibiotic production is one of the most studied biocontrol strategies of rhizobacteria and includes a wide variety of antibiotics (amphisin, 2,4-diacetylphloroglucinol (DAPG), oomycin-A, phenazine, pyrrolutecorin, pyrrolnitrin, tensin, oligomycin-A, kanosamine, zwittermicin-A, and xanthobaccin)[91].

Some genera of antibiotic-producing rhizobacteria correspond to Burkholderia[92], Streptomyces[93], Bacillus, Pseudomonas, and Stenotrophomonas[91].

5.2. Siderophore production

Iron (Fe) is an essential element for virtually all living things in important cellular functions such as DNA synthesis, respiration, and free radical detoxification[94]. For microorganisms, the availability of this element
is critical to the success or failure of their colonization of a given environment. To solve this problem, many organisms, such as rhizobacteria, secrete low-molecular-weight molecules (0.5 to 1.0 kDa) called siderophores which specifically act as chelating agents to sequester iron in the presence of other metals and reduce it to Fe\(^{2+}\), a much more soluble and usable form for their nutrition\[^{62}\]. PGPRs with the ability to produce siderophores gain competitive advantages in root colonization, competition for the ecological niche, and inhibition of the growth of phytopathogenic fungi due to the low concentration of Fe\(^{3+}\) available in soils\[^{73}\].

5.3. Volatile organic compounds (VOCs)

VOCs are diverse molecules of low molecular weight (300 g mol\(^{-1}\)), among which are aldehydes, alcohols, ketones, hydrocarbons, indoles, fatty acid derivatives, terpenes, and jasmonates\[^{95}\]. Recently, about 846 different VOCs produced by 350 bacterial species have been reported, among which the most representative are acetoin and 2,3-butanediol\[^{96}\]. A large number of rhizobacterial genera, such as Pseudomonas, Bacillus, Arthrobacter, Stenotrophomonas, and Serratia, have demonstrated the ability to produce volatile organic compounds that positively affect plant growth\[^{22}\].

6. Conclusions

Rhizobacteria represent a biotechnological alternative in agriculture, mainly due to the large number of molecular mechanisms that allow improving yield and plant health. Inoculants based on rhizobacteria are a biotechnological alternative in sustainable agriculture that can increase yields and reduce production costs in agricultural practice. Likewise, rhizobacteria can help reduce the use of chemical fertilizers, pesticides, and artificial regulators that have negative effects on natural ecosystems and contribute to more environmentally friendly agriculture. More research is needed to understand the mechanisms of phytostimulation in different environmental conditions and different crops, as well as to find strains that can be controlled in different scenarios.

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Conflict of interest

The authors declare no conflict of interest.

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