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Plant growth-promoting rhizobacteria: A biofertilization alternative for sustainable agriculture

Alejandro Moreno Reséndez*, Verónica García Mendoza, José Luis Reyes Carrillo, Jesús Vásquez Arroyo, Pedro Cano Ríos

Universidad Autónoma Agraria Antonio Narro, Torreón 27059, México

*** Corresponding author:** Alejandro Moreno Reséndez, alejamorsa@hotmail.com

ABSTRACT

Modern agriculture faces new challenges in integrating ecological and molecular approaches to achieve higher crop yields and minimize environmental impacts. In order to generate higher yields, synthetic fertilizer doses per unit area have been significantly increased, which can cause pollution, damage to health, and loss of soil fertility, becoming one of the most important concerns in agricultural production. To improve production without the use of synthetic fertilizers, research has been directed towards the development of new biotechnologies, leading to a growing interest in beneficial soil microorganisms that can promote plant growth and, in some cases, prevent infections of plant tissue by pathogens. The interactions of plant growth-promoting rhizobacteria (PGPR) with the biotic environment of plants and microorganisms are very complex and use different mechanisms of action to promote plant growth. These mechanisms are grouped into: 1) biofertilization; 2) phytostimulation; and 3) biocontrol. Inoculation of crops with PGRP substantially reduces the use of synthetic fertilizers and negative impacts on the soil, increases crop yields, and contributes to the producer's economy and the population's food supply. This review describes the basic aspects inherent to the interaction between CVPGRs and plant species, focusing on the benefits that CVPGRs bring to agricultural activity.

Keywords: biotic activity; biocontrolp; inoculation; microorganisms; rhizosphere

1. Introduction

Agriculture is the main sector of economic growth in developing countries[1], including Mexico. However, in contemporary production systems, most crops are very demanding with respect to fertilizer demand[2]. In relation to this demand, it has been estimated that by 2018, there will be a global consumption of 200.5 × 106 tons of N-P_2O_5-K_2O[3]. On the other hand, every day there is more evidence that the continuous application of nitrogen fertilizers can cause negative impacts on agro-ecosystems, such as nitrate leaching, contamination of water resources, and gaseous emissions, causing irreparable damage to the environment[4] and posing a potential risk to humanity[5]. The above makes it evident that there are several problems that demand ongoing attention from researchers. Specifically, a promising method to reduce the use of synthetic fertilizers in agriculture is the application of PVGRs as microbial inoculants[1]. The use of PVGRs as biofertilizers is a sustainable option to promote the availability of nutrients, plant growth, and yields[4]. In view of the above, we describe the elements inherent to the interaction between PVGRs and plant species, focusing on the effects

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they cause to agricultural crops through their root systems.

2. Plant growth promoting rhizobacteria

The expression Plant Growth Promoting Rhizobacteria (PGPR) was coined by J. W. Kloepper and M. N. Schroth in 1978 to describe bacteria that inhabit the rhizosphere and positively affect plant development[6]. These bacteria have the ability to actively colonize the root system to promote and/or improve its growth and yield[7]. RPCVs account for about 2%–5% of rhizospheric bacteria[8]. The acronym RPCVs refers to all bacteria that are capable of enhancing plant growth through one or more mechanisms. The following genera of bacteria have been reported as RPCV: Agrobacterium, Arthrobacter, Azoarcus, Azospirillum, Azotobacter, Bacillus, Burkholderia, Caulobacter, Chromobacterium, Enterobacter, Erwinia, Flavobacterium, Klebsiella, Micrococcus, Pantoea, Pseudomonas, Rhizobium, and Serratia[9].

RPCVs exert beneficial effects on plants through direct and indirect mechanisms, or a combination of both[10,11]. Direct mechanisms occur when bacteria synthesize metabolites that facilitate plants, or when plants increase the availability of different nutritive elements required for their metabolism and to improve their nutrition process[12]. Among the direct mechanisms, the following stand out: nitrogen (N) fixation; the synthesis of phytohormones, vitamins, and enzymes; the solubilization of inorganic phosphorus (P) and the mineralization of organic phosphate; the oxidation of sulfides; the increase in root permeability; the production of nitrites; the accumulation of nitrates; the reduction of heavy metal toxicity and ACC deaminase enzyme activity; the secretion of siderophores; the reduction of ethylene levels in soils; and increased root permeability[13].

Indirect mechanisms are characterized by the reduction or elimination of phytopathogenic microorganisms, either through the production of antimicrobial substances or antibiotics, lytic enzymes or a combination of these; by competition for nutrients or space in the ecological niche, as well as by stimulation of the plant's natural defenses through biocontrol mechanisms; the induction of systemic resistance (IRS) to a broad spectrum of pathogenic organisms and the production of siderophores, as a mechanism to sequester available Fe in soils and thus limit the development and presence of these phytopathogens; production of antibiotics and hydrogen cyanides that impact on phytopathogens; hydrolysis of molecules such as fusaric acid generated by them to release 1-3-glucanase, which inhibits the development of the fungal wall of fungi such as Phytium ultimum and Rhizoctonia solani[13].

One of the limitations of PVGRs is that the beneficial effect they promote on a given plant species is not the same for other plants. In this regard, Xu et al.[14] point out that the combined use of biocontrol agents should generally not be recommended in practice without a clear understanding of their main control mechanisms and their relative competitiveness. To avoid the above, to date there are a number of reports that clarify the type of RPCV, their effect, and the crops where they can be applied; see examples in **Table 1**.

Table 1. Plant growth-promoting rhizobacteria, effects and crops where they have been evaluated.

RPCV	Effect	Crops
Azospirillum spp, *Azotobacter* spp, *Bacillus* spp, *Burkholderia* spp, *Gluconacetobacter* spp, *Herbaspirillum* spp.	Biofertilization fixed N_2	Corn, rice, wheat, sorghum, sugar cane.
Bacillis spp, *Pseudomonas* spp, *Streptomyces* spp, *Paenibacillus* spp, *Enterobacter* spp, *Azospirillum* spp.	Biocontrol (diseases, pathogens and insects)	Tomato, tobacco, cucumber, bell bell pepper, peanut, alfalfa, chickpea, bean, plum.
Methylobacterium spp, *Bacullus* spp, *Alcaligenes* spp, *Pseudomonas* spp, *Variovorax* spp, *Enterobacter* spp, *Azospirillum* spp, *Rhizobium* spp, *Klebsiella* spp.	Elongation, growth	Turnip, carnation, canola, soybeans, beans, corn, beans, peas.
Aeromonas spp., *Agrobacterium* spp, *Alcaligenes* spp, *Azospirillum* spp, *Bradyrhzobium* spp, *Comamonas* spp, *Enterobacter* spp, *Rhizobium* spp, *Paenibacillus* spp, *Pseudomonas* spp, *Bacillus* spp.	Phytohormone producers [3-indole-acetic acid (IAA), cytokinins, gibberellins].	Rice, lettuce, wheat, soybean, radish, rapeseed, alder.

Source: Parray et al.[11].

Root colonization

An essential step for RPCVs to efficiently carry out biological control and promote plant growth is undoubtedly the colonization of their root system[15]. Key elements for efficient colonization include, among others, the ability of microorganisms to: a) survive after inoculation; b) grow in the spermosphere (region surrounding the seed) in response to the production of exudates by the seed; c) attach to the surface of the first roots; and d) colonize the entire root system[15,16]. For example, Labra-Cardón et al.[6] point out that colonization in the spermosphere of Cyperus elegans (Cyperaceae) and Echinochloa polystachya (Poaceae) seeds was an important event to promote the growth of the seedlings obtained.

Root colonization by endophytic microorganisms includes four stages: 1) attraction; 2) recognition; 3) adhesion; and 4) invasion, which are affected by biotic and abiotic factors[16]. In addition, seed colonization is the first step in the process itself. Microorganisms that settle on seeds during germination can grow and colonize the roots to their full extent. Seed colonization during the impregnation or immersion phase has a significant effect on plant growth[15].

Colonization ability is a key factor in the prevention and treatment of fungal diseases because host plants are closely related to biofilm formation; strong colonization leads to proper biofilm formation[17]. Better crop results depend on proper colonization of bacteria in the rhizosphere; applying the correct inoculation technique to seeds will result in a higher germination percentage as well as crop productivity, in addition to increasing its resistance to stress[18].

Adriano et al.[19] point out that when biofertilizers are applied to seeds, plant surfaces, or soils, they colonize the rhizosphere or the interior of plants and favor their growth. They also promote the development of plant defense mechanisms and generate adverse environments for pathogenic organisms. For example, P. fluorescens, a natural soil inhabitant, is predominantly numerous in the rhizosphere microflora of many plant species and is the first to colonize young roots. Many of these organisms suppress diseases in plants, protecting roots and seeds from infection by pathogens present in the soil[20].

3. Mechanisms used by the RPCV that affect plant species

The following sections describe the mechanisms of action of the CVERs, through which they favor an increase in agricultural productivity in different regions, from a sustainable approach.

3.1. Biofertilization

Among the processes that affect the development and production of plant species, nutrition is considered essential. This is because crops are demanding with respect to appropriate mineral nutrition levels, a requirement that is due to their production volumes per unit area[21]. In this sense, soil fertility improvement has been one of the strategies commonly used to increase agricultural production. However, over time, it has become evident that the use of synthetic fertilizers has not proved to be the expected panacea, since of the total fertilizers applied, only 10%–40% are assimilated by plants[22] and furthermore, because the loss of soil fertility in intensive systems has forced producers to increase the use of these fertilizers to maintain their production, at the cost of increased production costs and environmental impacts[23]. On the other hand, as a consequence of the rising cost of synthetic fertilizers, the scarce natural reserves of some minerals, and the large energy consumption for their production, the use of biological alternatives has been promoted, not only as a necessity in agricultural production but also in scientific agriculture today and in the future, without affecting the environment in addition to economic feasibility[24]. Thus, in the early 1990s, new concepts and practices inherent to plant nutrition were developed, conditioned by the growing concern for the environment worldwide. Research in this field of knowledge was oriented towards the use of nutrition that included fertilization alternatives with less dependence on polluting inputs[25]. In other words, new technologies should be focused on maintaining and preserving the sustainability of the production system through the rational exploitation of natural resources and the application of relevant measures to preserve the environment[26]. In this sense, the inhibition and agronomic management of microorganisms with biofertilizing properties became rational technologies and emerged as innovative and promising practices for agricultural activity.

Biofertilizers are understood as all those products that contain live microorganisms with the capacity to colonize the rhizosphere or the interior of plants, which, when applied to the soil and/or plants through inoculation, can live associated with or in symbiosis with the plant species and help them in their nutrition and protection, with the aim of partially or totally replacing the application of synthetic fertilizers and reducing their polluting effect[27]. Unlike synthetic and organic fertilizers, biofertilizers do not directly supply any nutrients to crops, and these are bioproducts, mainly made from bacteria. Armenta Bojórquez et al.[25], describe that the microorganisms used in biofertilizers are grouped into those that: (a) have the capacity to synthesize substances that promote plant growth through various processes such as atmospheric N_2 fixation, solubilization of inorganic Fe and P, increased tolerance to drought stress, salinity, toxic metals, and excess pesticides; (b) are able to diminish or prevent the effects of pathogenic organisms; and (c) fulfill both functions to promote growth and inhibit the effects of pathogens, e.g., Bacillus subtilis produces auxins to promote tomato growth and induces systemic resistance against F. oxysporum, responsible for root wilt and rot.

Inoculation of biofertilizers containing rhizospheric bacteria has led to significant increases in the productivity of agricultural crops[25]. This is due to the fact that bacteria associated with plant species have the capacity to produce or generate growth regulators, and approximately 80% of these are auxin producers. In quantitative terms, the most important auxin is indole acetic acid (IAA), which is responsible for increasing both the root system and the absorption of nutrients[26]. As a complement, and with respect to the role played by bacteria, and of which there are myriad research reports, Mishra and Dash[27] elaborated a list of advantages and disadvantages inherent to the use of biofertilizers, which are described below:

Advantages

- The supply of nutrients is more balanced, which helps maintain plant health.
- They help to increase the biological activity of the soil, thus improving the mobilization of nutrients and the decomposition of toxic substances.
- Increase soil structure, favoring better root growth.
- They increase the organic matter (OM) content of the soil, thereby improving cation exchange capacity, increasing moisture retention, promoting aggregate formation, and buffering sudden changes against acidity, alkalinity, salinity, pesticides, and toxic heavy metals.
- They gradually or slowly release nutrients and contribute to the soil's residual organic N and P reserves, reducing N losses through leaching and P fixation, and can also supply micronutrients.
- They favor the growth of earthworms and beneficial microorganisms.
- They help suppress diseases and parasites transmitted by native soil organisms.

Disadvantages

- Compared to synthetic fertilizers, they have a reduced content of nutrients, which requires the use of large volumes to cover the nutrient demand during crop growth.
- The rate of release of nutrients is too slow to meet plant requirements, so nutrient deficiencies may occur in plants.

- Primary macroelements may not be in sufficient quantities in organic fertilizers to support maximum crop growth.

An additional disadvantage is that in several countries, preferably in rural areas, the use of biofertilizers has been hindered or delayed, largely due to the idiosyncrasies of their inhabitants, since the basic reluctance to use bacteria as beneficial microorganisms is due to the fact that these, in these regions, are still associated with human and animal diseases[26].

3.2. Atmospheric nitrogen fixation

Biological nitrogen fixation (BNF) is limited to prokaryotes that possess, unlike the plant, a nitrogenase enzyme complex, which consists of two proteins, dinitrogenase and dinitrogenase reductase. Both contain Fe in their structure, and furthermore, dinitrogenase contains Mo[28], which catalyzes the reduction of atmospheric N into ammonia[29]. This process is explained, in general terms, by Equation (1). Lopez and Boronat[30] describe this equation, noting that the microbiological activation of atmospheric N_2 generates ammonia, which ionizes to the ammonium cation (NH_4^+) via ATP hydrolysis and the transfer of reducing power coupled to an electronic transport chain. Bacteria that fix atmospheric N into biologically usable ammonium are called diazotrophs. Diazotrophic organisms include a wide range of archaea and bacteria that colonize diverse plant species in a wide variety of ecosystems[29].

$$N_2 + 8H^+ + 8e^- + 16ATP \rightarrow 2NH_3^+ + 16ADP + 16P_i + H_2 \quad (1)$$

Among the symbiotic rhizospheric N-fixing prokaryotic rhizobial bacteria in association with legumes are the rhizobia group, e.g., Rhizobium, Bradyrhizobium, Sinorhizobium, Azorhizobium, Mesorhizobium, and Allorhizobium, and Frankia strains, belonging to the genus Streptomicetaceae, filamentous sporulating bacteria associated with actinorrhizal plants, especially genera Alnus and Casuarina[15,29]. For more than a century, symbiosis between bacteria of the genus Rhizobium and legumes has been considered the most efficient way to fix atmospheric N, making it available to plants. However, in recent decades, the study of GNF by associative, free-living, or asymbiotic bacteria, a process discovered in 1901 by Martinus Willem Beijerinck, has gained more attention by researchers with the purpose of finding alternatives to the growing demand for synthetic fertilizers[31].

Under normal conditions, N-fixing microorganisms benefit from this element without excreting nitrogen compounds. But upon their death and after their decomposition, N will be available to plants, generating an average of 25 kg Nha^{-1} per year on the continents. This process is then sufficient to maintain the reserves and recover the losses of these compounds in the ecosystem[15]. Finally, due to the importance of the FBN process, regardless of whether it is by symbiosis or asymbiotically, Neyra et al.[32] describe that the incorporation of this element promotes the stimulation of microbial processes during the decomposition of OM and the recycling of essential nutritional elements within productive agricultural systems, as well as in those considered sustainable agro-ecosystems. They also mention that it is necessary to continue with the study of the growth-promoting capacity of Rhizobium because sustainable agriculture demands improving the efficiency of the FBN process through the use of competitive bacteria capable of extending the advantage of symbiosis to other non-leguminous plant species.

3.3. Phosphate solubilization

P is the most important mineral element after N; its deficiency crucially limits plant growth[33]. As for N, it can nowadays be asserted that some PGR, specifically phosphate solubilizing bacteria (PSB), solubilize insoluble phosphates in soils and make them available to plants[34] and these, in turn, provide them with carbon compounds that are metabolized for microbial growth, while root exudates and plant detritus provide the energetic substrate that favors their solubilizing activity. BSF constitutes 1%–50% (**Table 2**) of the total microbial population in soils[33]. It is also necessary to highlight that some microorganisms that solubilize soil phosphates can also present other plant growth-promoting activities such as the production of AIA, gibberellic acid, hydrogen cyanide (HCN), cytokinins, ethylene, asymbiotic N fixation, and resistance to soil pathogenic organisms[33].

Table 2. Main phosphate solubilizing bacterial genera.

BSF		
Achromobacter	**Erwinia**	**Rahnella**
Acinetobacter	Flavobacterium	Ralstonia
Aereobacter	Gordonia	Rhodobacter
Agrobacterium	Kitasatospora	Rhodococcus
Arthrobacter	Klebsiella	Serratia
Bacillus	Mesorhizobium	Sinorhizobium
Bradyrhizobium	Micrococcus	Streptomyces
Burkholderia	Mycobacterium	Streptosporangium
Chryseobacterium	Pantoea	Thiobacillus
Delftia	Phyllobacterium	Yarowia
Enterobacter	Pseudomonas	

BSF = Phosphate solubilizing bacteria; Source: Beltran[33].

The bacterial genera presented in **Table 2** belong to the BSF group, and they solubilize phosphates due to their capacity to produce organic acids, among which the following acids stand out: acetic, adipic, citric, formic, fumaric, glycolic, gluconic, indolacetic, lactic, malic, malonic, oxalic, propionic, succinic, and 2-ketogluconic[33,34]. The most frequently reported phosphate solubilizers are gluconic and 2-ketogluconic[35].

Most of the organic acids produced by BSPs are aliphatic, i.e., they are non-aromatic acids[35]. These acids modify the pH, causing the dissolution of insoluble phosphates in soils[34]. In addition to having a direct action on acidification, chelation, precipitation, and oxide reduction reactions in the rhizosphere, they form complexes with metals, solubilize metals, and participate in their transport. The solubilization of minerals may be due to these acids lowering the pH and, moreover, to the formation of stable complexes with cations such as Ca^{+2}, Mg^{+2}, Fe^{+3}, and Al^{+3}. The effect of organic acids also affects phosphates incorporated into the soil through synthetic fertilizers, reducing the precipitation of these phosphates by Fe and Al[35].

In soils, the solubilization of phosphate by organic acids depends on the pH and mineralogy of the soil. This process is carried out by two mechanisms: (a) an acid exchange, for example, H^+- ions from citrate are exchanged for P bound to the surface of $Al(OH)_3$ or $Fe(OH)_3$ crystals, reducing them and releasing P; and (b) the other, which depends on the concentration of organic acids produced by BSF; the amount and type of organic acids released depend on the type of microorganisms. The quenching effect of these acids on solubilization consists in that through their hydroxyl and carboxyl groups they sequester the cations attached to the phosphate, converting it to soluble forms[22,33].

BSF is also capable of mineralizing insoluble organic phosphate through the excretion of extracellular enzymes such as phosphatases, catalysts of phosphate ester hydrolysis, phytases, and C-P lyases. It should be noted that solubilization and mineralization mechanisms can coexist within the same BSF. Inoculation with BSF increases P availability in the rhizosphere and its uptake by the plant[36]. A 50% reduction in P fertilizer application could be achieved by the combined use of P-solubilizing microorganisms and RPCV without affecting yield[37]. On the other hand, the introduction of overexpressed genes in rhizosphere bacteria to solubilize phosphates and improve the ability of microorganisms as inoculants has attracted the attention of researchers. To date, the bases of the genetics of mineral phosphate solubilization are not clearly established, because although it is known that the generation of organic acids is the main mechanism to carry out this process, it could be assumed that any gene involved in the synthesis of organic acids could have some effect on this characteristic, called the solubilizing phenotype. In relation to the above, it has been evidenced that the ability of some Gram-negative bacteria to dissolve calcium phosphates—the solubilizing phenotype—is the result of the periplasmic oxidation of glucose to gluconic acid by the glucose dehydrogenase quinoprotein (G-DH) pathway, a component of the direct glucose oxidation pathway[33].

Finally, Beltrán[33] highlights that, although there are efforts to understand P solubilization at the molecular scale, the mechanism used by different BSFs requires further research. In addition to the above, despite the advantages that genetic modification of microorganisms can bring, their release into the environment remains controversial; some nations encourage the management of genetically modified organisms, while others prohibit it and require labeling of products containing genetically modified ingredients. Despite this controversy, there is scientific evidence that, following the appropriate regulations, genetically modified microorganisms could, in the near future, be used without risk in agricultural activities.

3.4. Production of siderophores: Iron chelation

Siderophores are small molecules produced by microorganisms under Fe-limiting conditions that increase their entry into the microbial cell[38]. Commonly, bacteria acquire Fe by secreting low-molecular-weight Fe chelates, called siderophores, which are in constant association with Fe complexes[11,39]. In addition to their low molecular weight, these compounds are soluble in aqueous solutions at neutral pH and can be fluorescent or not[40].

Various organisms synthesize small molecules, non-ribosomal peptides, with high affinity for Fe^{+3} that act specifically as chelating agents to sequester Fe in the presence of other metals and cause its reduction to F^{+2}, which is a much more soluble and usable form for the nutrition of these organisms[10]. The sequestration of Fe by microorganisms under scarce conditions develops as follows: once Fe is sequestered from the surrounding medium, the siderophore-Fe complex is recognized by specific receptors of the microbial membrane, and once inside the cells, it is deposited in a specific site by a process involving a ligand exchange that may or may not be preceded by Fe reduction or hydrolysis of the siderophore[41]. The presence of siderophores would represent a great advantage for microorganisms since they could acquire Fe from the surrounding medium more easily than the rest of their competitors[40].

Siderophores are divided into three main families depending on the characteristic functional group: hydroxamates, catecholates, and carboxylates[42]. To date, more than 500 siderophores are known, and the chemical structures of 270 of them have already been determined[10]. Siderophores produced by heavy metal-resistant isolates have been implicated in the biological control of diseases such as vascular wilt caused by Fusarium oxysporum and pea nut stem rot caused by Rhizoctonia solani[43].

RPCV have developed several strategies, both to survive and adapt to their environment and to provide the plant with Fe. One of these strategies is the production of siderophores[39]. For example, several species of the genera Pseudomonas, Bacillus, and Enterobacter have been evaluated and reported as biocontrol agents against plant pathogens. Under Fe stress conditions, these strains produce siderophores that chelate available Fe and deprive the respective phytopathogens of this element, thus restricting their proliferation and root colonization[44].

3.5. Extracellular polysaccharide production

The ability to produce, secrete, or exude polysaccharides is another of the multiple benefits that RPCVs possess[8]. These exudates include polysaccharides: structural, intracellular, and extracellular—or exopolysaccharides (EPS)[15], which are mainly composed of carbohydrates, forming homo or heteropolymers and may contain organic and inorganic substituents. These products offer advantages such as the great versatility of microorganisms to synthesize neutral or negatively charged polysaccharides from renewable sources under controlled conditions and the possibility of genetic manipulation, with which it may be possible to obtain products with better functional properties and even higher quality[45]. The main contribution of rhizospheric microorganisms to soil stability is associated with the production of EPS. These products are found in the form of hydrated gels around the cells and constitute the interface between the microorganisms and their immediate environment[15].

The production of high levels of EPS by certain bacteria allows plants to better withstand adverse environments[46]. In the rhizosphere, EPS produced by rhizobacteria enters the soil aggregates and alters their porosity. Therefore, porosity, which is directly related to the transfer of water from the soil to the roots, is partially controlled by bacterial activity. They also help to: maintain the water film required for photosynthetic activity and plant growth; improve the soil aeration process and infiltration; and cover and protect roots against attack by phytopathogens[15]. Under salt stress conditions, EPSs make cations available in the root zone, thus contributing to reducing the salinity of the rhizosphere. Bacterial EPS under soil-water stress conditions can limit or postpone the desiccation of the medium. Conversely, in cases of excess water (rain, flooding), EPS contributes to preventing the dispersion of clay soils[15].

3.6. Production of plant growth promoting substances

These substances are signaling molecules that act as chemical messengers that influence the ability of plants to respond to their environment[37]. They regulate the expression of genes involved in plant growth and development, which are synthesized in different plant structures, and their action varies depending on environmental changes that modify the organism's gene expression[47] and are generally effective in small concentrations[37]. It has been established that they are also involved in catabolic repression, pathways, and regulation of biofilm formation. Moreover, these molecules exhibit specific effects on plant physiology, such as increasing root volume, increasing the rate of respiration of the host plant root, and increasing the flow of protons in the root membrane; consequently, the absorption of soluble mineral elements is favored[47]. However, although it is known that phytohormones regulate plant development and physiology, as well as immunity, their production by microorganisms has not been considered a biological control mechanism; for example, it has been identified that P. fluorescens G20-18 has the ability to efficiently control P. syringae infection in the Arabidopsis model, allowing the maintenance of tissue integrity and, ultimately, biomass yield[20].

Molina-Romero et al.[47], have established that RPCVs have the capacity to produce more than one type of growth-promoting substance. Within these five groups, the following stand out: 1) auxins (AIA); 2) gibberellins; 3) ethylene; 4) cytokinins; and 5) abscisic acid (ABA), and of these, the first four are involved in phytostimulation by rhizobacteria[37]. Sarma and Saikia[48] emphasize that phytostimulation is considered to be the most studied mechanism of RPCVs. The phenomenon of phytostimulation is particularly given by the manipulation of the complex and balanced network of hormones or similar compounds that directly influence plant growth or stimulate plant root formation. For example, many Azospirillum species produce auxins, cytokinins, and gibberellins, which stimulate root development, leading to significant increases in agricultural yields[41].

4. Biocontrol or antagonism mechanisms

The deleterious microbes that inhabit the rhizosphere cause diseases and sometimes lead to the complete loss of crops[49]. Different microorganisms have been used for the biological control of these diseases: various RPCVs as biocontrol agents naturally eliminate phytopathogens by producing secondary metabolites, which, in addition to being excreted locally or near the plant surface, are biodegradable molecules and are not required in high quantities, unlike pesticides that are resistant to degradation and are applied in large quantities to maintain plant health[47].

Some VSRs have the ability to prevent the development of soil-borne diseases in plants by keeping the level of deleterious microbes below the threshold[49]. These RPCVs produce antibiotics, antimicrobial volatile organic compounds (VOCs), and hydrolytic enzymes, siderophores, or bacteriocins. On the one hand, they can stimulate resistance, systemic or induced, in plants against different phytopathogens, or on the other hand, eliminate such organisms[49]. Specifically, several molecules produced by Gram-negative antagonistic bacteria capable of exerting biocontrol against pathogens causing root diseases have been characterized, among which are hydrocyanic and phenazine-1-carboxylic acids, pyoluteorin, pyrrolnitrin, cyclic lipopeptides, and diacetylphloro-glucinol[47].

Deleterious rhizobacteria are known to be a group of saprophytic, non-parasitic pathogens that excrete exopolysaccharides and chemicals in the form of cyanide, phytohormones, siderophores, and phytotoxins that can negatively affect plant metabolism. Recently, this group of microorganisms has been used as a biological weed control agent[50]. As an example, de los Santos-Villalobos et al.[39], highlight that siderophores produced by Burkholderia cepacia XXVI, isolated from mango orchards, proved to be an alternative biocontrol of the fungus Colletotrichum gloeosporioides causing anthracnose in this crop.

The efficacy of bacterial biocontrol agents is strictly associated with their ability to actively colonize the ecological niches occupied by plant pathogens; to reach these niches, bacteria move in the environment thanks to external appendages, such as flagella[51]. On the other hand, some aerobic spore-forming bacteria possess advantages that make them suitable candidates for use as biocontrol agents; e.g., species of the genus Bacillus are able to produce spores that allow them to resist adverse environmental conditions, in addition to favoring easy formulation and storage of commercial products[49]. Biocontrol activity should be considered a mode of behavior dependent on the prevailing conditions rather than an inherent property of a bacterial strain[52]. Recently, the development of molecular techniques has enabled the construction of genetic recognition tools to analyze and study bacterial behavior within the soil microbial community[53]. For example, Gopalakrishnan et al.[54], obtained seven bacterial isolates (SRI-156, SRI-158, SRI-178, SRI-211, SRI-229, SRI-305, and SRI-360) from the rhizosphere of an intensive rice (Oryza sativa) system with potential for both plant growth promotion and biocontrol of charcoal rot of sorghum, caused by Macrophomina phaseolina, and concluded that the selected bacterial strains produced siderophores, indoleacetic acid (except SRI-305), hydrogen cyanide (except SRI-158 and SRI-305), and phosphate solubilization (except SRI-360).

4.1. Antibiotic production

Antibiosis is probably the best-known and perhaps most important mechanism used by RPCVs to limit pathogen invasion in plants. It consists of inhibiting the development of phytopathogenic microorganisms through the production of secondary meta-bolites[55], or the secretion of broad-spectrum molecules[47]. The latter authors highlight that these metabolites act through mechanisms of action such as: a) inhibition of cell wall synthesis; b) structural destabilization of the cell membrane; and c) inhibition of the formation of the translation initiation complex of phyto-pathogenic organisms. In addition, Raaijmakers and Mazzola[56] note that antibiotics comprise a chemically heterogeneous group of low-molecular-weight organic compounds produced by microorganisms that are detrimental to the growth or metabolic activities of other microorganisms, generally acting on several vital processes of these, including cell wall biosynthesis and DNA, RNA, and protein synthesis. Examples of antibiotic-producing PCVRs include the genera Burkholderia and Streptomyces ces[47].

Bacteria that reduce the incidence or severity of plant diseases are referred to as biological control agents, while those that exhibit antagonistic activity towards a pathogen are defined as antagonists. The following rhizospheric environment and antagonistic activities can be highlighted: 1) synthesis of hydrolytic enzymes, such as chitinases, glucanases, proteases, and lipases, which can lyse pathogenic fungal cells; 2) competition for nutritive elements and adequate colonization of niches on the root surface; 3) regulation of plant ethylene levels through the enzyme ACC-desaminase, which can act to modulate the ethylene level in a plant in response to stress imposed by infection; and 4) production of siderophores and antibiotics[57]. RPCVs, as biocontrol agents, are isolated and introduced in an optimal amount into the rhizosphere to control the development of plant diseases[49]. For example, P. fluorescens generates phenazines and pyrrolnitrin, which are broad-spectrum antibiotics[58].

4.2. Production of lytic enzymes

A great variety of microorganisms produce different enzymes that act against other microorganisms present in their habitat, which can act as phytopathogens, causing economic losses in crops such as rice, wheat, and soybeans, among others[40]. Due to this characteristic, various RPCV strains have the ability to degrade the cell walls of certain microorganisms through the production of hy-drolitic enzymes, such as β-glucanases, cellulases, dehydrogenases, exo and endo-polygalacturonases, phosphatases, hy-drolases, lipases, pectinolyases, proteases, and chitinases, which act primarily against fungi[15,47]. Tejera-Hernández et al.[40] point out that B. subtilis produces these metabolites with the capacity to counteract the effects of the fungus F. oxysporum.

Among the rhizobacteria that produce these enzymes are B. altitudinis, B. amyloliquefaciens, B. cereus, and B. subtilis[47]. These bacteria utilize various mechanisms that can inhibit fungal pathogens, including competition for nutrients, the production of antifungal lipopeptides, or the production of lytic enzymes such as chitinases, which can degrade the fungal cell wall, as a means to prevent the spread of fungal hyphae[59]. The antifungal activity of microorganisms is due to their ability to generate lipopeptides and glycopeptides; examples of these are rhamnolipids and surfactin produced by P. aeruginosa and B. subtilis, respectively, which allow them to solubilize the main components of microbial cell membranes, in addition to giving them a better chance of survival in habitats with high competition for nutrients[60]. This antifungal activity allows RPCVs to protect the plant against biotic stress by eliminating pathogens[18].

4.3. Synthesis of hydrogen cyanide and volatile compounds

The antagonistic activity of RPCVs also works through the production of volatile compounds[50]. These compounds play a primary role in pathogen control, in contrast to antibiotics, which can only prevent pathogens from infecting plants. Additionally, these compounds can spread over long distances and create a bacteriostatic microenvironment around antagonistic communities[49]. The best-known volatile compound is hydrogen cyanide (HCC). The main group of RPCVs used as biological control agents is the genus Pseudomonas, which are considered the most common producers of cyanide, in addition to having a wide application in biotechnological processes and being of great importance for agroindustries[50].

As complementary examples, the bacteria P. fluorescens strain F113rif (F113) is a biocontrol agent isolated from the rhizosphere of sugar beet (Beta vulgaris var. altissima) capable of suppressing the disease produced by the oomycete Pythium ultimum. The biocontrol capacity of this strain has been related to the production of secondary metabolites, among which stand out: siderophores, diacetyl-floro-glucinol (DAPG), CNH, and an extracellular protein[61]. For their part, B. methylotrophicus bacteria presented the greatest antagonistic effects against phytopathogens, due to their ability to produce antibiotics and/or volatile organic compounds such as CNH, which inhibits the growth of phytopathogenic fungi and exerts deleterious effects on their growth in vitro[62]. Another significant effect of the CNH-producing CVRs is that their incorporation into the rhizosphere of the weed reduces its growth parameters, with little or no effect on plant species of economic interest; this practice turns out to be a low-cost and environmentally friendly alternative for weed biocontrol, against the application of herbicides and synthetic compounds, which are harmful to the environment. In addition, the incorporation of these rhizobacteria offers several advantages, such as a shift in the balance of competition between weed and crop—in favor of the crop and against the weed; greater selectivity; lower resistance; and the introduction of agricultural practices that are sustainable[50]. Regardless of the benefits already described, the role of cyanide production is contradictory, as it may be associated with deleterious rhizobacteria as well as beneficial bacteria[63].

5. Induced and acquired systemic resistance

Like all living beings, plants possess genes that encode to generate various chemical weapons—small exogenous molecules called inducers—which are extremely efficient, constituting defense mechanisms that protect them against the attack of pathogenic organisms, either by diminishing or preventing such attacks. This biological phenomenon has been called resistance[64]. Systemic resistance is a physiological state that enhances defensive capacity and is elicited by specific environmental stimuli. Innate plant defenses are enhanced toward subsequent biotic challenges. This enhanced state of resistance is effective against a wide range of pathogens, including plant parasites and insect herbivores[65]. The mechanism of induced resistance involves two phenomena: induced systemic resistance (ISR) and acquired resistance (ASR), which, although distinct, are phenotypically similar[65]. The ISR is associated with the ability of the PVGRs to promote plant growth and protect against pathogen attack, and the ASR is associated with the responses of plant species to the presence or attack of pathogens[66]. The similarity of both resistances is based on the fact that plants, after being exposed to an inducing agent, activate defense mechanisms both at the point of infection and in other regions (systemic resistance), in a more or less generalized way, and their difference lies in the nature of the elicitor molecule present in the inducer and the signaling pathways. When the latter are triggered by a biotic agent, they can depend on both salicylic acid (AS), associated with the accumulation of pathogenesis-related proteins (PRP), and jasmonic acid (jasmonate) and ethylene, which are not associated; in this case, the accumulation of PRP is known as RSA, while if the inducer is of abiotic type and only follows the pathway of jasmonic acid and ethylene, then it corresponds to RSI[64,65].

RSI can be induced by a wide variety of microorganisms, including Gram-positive bacteria such as B. altitudinis, B. amyloliquefaciens, B. cereus, B. mycoide, B. pasteuri, B. pumilus, B. sphaericus, or Gram-negative bacteria belonging to the genus Pseudomonas, e.g., P. fluorescens, P. putida, P. aeruginosa, and Enterobacteria such as Serratia e.g., S. marcesens, S. plymuthica, as well as Pantoea agglomerans, through the generation of diverse metabolites, among which stand out: AS, lipopolysaccharides (LPS), siderophores, cyclic lipo-peptides, 2,4-diacetylphloroglucinol, homoserine lactones, and volatile compounds such as acetoin and 2,3-butanediol[47].

Saharan and Nehra[63] note that, triggered by local infection, plants respond with an AS-dependent signaling cascade that leads to systemic expression of broad-spectrum and long-lasting disease resistance that is effective against fungi, bacteria, and viruses. After infection, endogenous AS levels increase locally and systemically, and AS levels increase in the phloem before RSI occurs. They further state that AS is synthesized in response to infection, both locally and systemically; consequently, new AS production in uninfected plant parts may contribute accordingly to the systemic expression of RSI. On the other hand, Camarena-Gutiérrez and de la Torre-Almaráz[67] point out that if plants survive an initial attack by pathogenic organisms or if protection is generated after: a) an attack by herbivorous arthropods or b) mechanical damage or contact with some synthetic chemicals, they can protect themselves against subsequent attacks by homologous pathogens even when the plants do not possess genes that determine cultivar-specific resistance, thus becoming immune. This ability of cells to repel subsequent attacks, which is dispersed throughout the plant, corresponds to the ASR. The ASR has four peculiar characteristics: 1) it is effective against a broad spectrum of pathogenic organisms, depending on the plant species treated; 2) it is long-lasting; 3) it is dispersed in plants, mainly in the apical direction; and 4) it moves to the grafted buds. These last two characteristics strongly suggest that the signals established by the ASR are translocated throughout the plant. The timing and degree of ASR protection depend on the plant species and the inducer, because some effectors induce ASR in some species and not in others[66]. Additionally, over time, its strength and stability can be affected by climatic conditions and nutrition[67].

An essential aspect of ASR is that the first infection caused by a pathogen generates a necrotic lesion, which can be the result of programmed cell death after pathogen recognition in an incompatible interaction (where a hypersensitive response was generated) or of cell death originated by the action of the pathogen in a compatible interaction[67]. The sequence of events that favor ASR starts locally; that is, in cells adjacent to the hypersensitive response, cell wall thickening is observed by the incorporation of structural proteins or lignin, the deposition of callose, and the induction of phytoalexin synthesis[67].

ASR has a very interesting practical aspect. In agriculture, it can be induced by infecting the plant to be protected, using first an avirulent or virulent strain whose response to infection should produce a large necrosis. Alternatively, plants can be sprayed with either Gram-positive or Gram-negative bacterial culture filtrates or, even better, with one of the identified signal products, such as AS. Since these substances are biologically decomposed and the spectrum of pathogens that can be repelled is very broad, their application in systemic response release has good potential for plant protection. Intensive research on ASR, in particular its molecular genetics, will soon show that it can be successfully applied, perhaps in combination with other protection measures[67].

6. Areas of opportunity inherent to the RPCVs

Based on the review, analysis, and interpretation of the publications cited in this document, it is suggested that the research activities related to the CVS should focus on the following topics, since it is estimated that these will provide more and better knowledge on the development of agricultural crops and their production in an environmentally friendly manner:

Since a large part of the deterioration of agroecosystems is due to the irrational use of agrochemicals to control pests, diseases, and weeds, there is a continuous demand for alternatives that promote the use of products of ecological origin that minimize their impact and reduce environmental contamination. From a sustainable point of view, it is necessary to study the potential of PGR in the improvement of economically and socially important crops, with the consequent preservation of the environment.

Soil microorganisms are of great importance for sustaining life on Earth. The study of their diversity is vital and transcendent, since they are part of numerous complex and dynamic communities, and to understand their function as well as the changes that occur in these communities in response to different factors and environmental perturbations in specific niches, it is essential to identify and quantify each of the members of these communities.

One of the permanent challenges, due to the myriad of microorganisms present in the microbial rhizosphere, of which it is estimated that a large part remains to be identified and characterized, and given the relevance that the development of agricultural production with a sustainable approach has acquired, is to continue to determine the functional role of this population in the diverse ecosystems of the Earth. This will make it possible to answer questions such as: Which species of microorganisms not yet identified could have biotechnological relevance?

There is a need to continue gathering information to understand in greater detail the mechanisms of plant resistance and their relationship with the application of PVPRs.

Due to the limitations of synthetic fertilizers, both for their use of non-renewable natural resources for their production and for their residual effect on the environment, and organic fertilizers or manures for their reduced content of nutrients, the study of the RPCV, with a broad spectrum of colonization of plant species, will help these microorganisms be used as effective biofertilizers or phytostimulants in the agricultural sector, seeking to improve the processes of nutrition and crop resistance to drought, salinity, and high temperatures, in order to increase yields, given the need for satisfaction demanded by the growing world population in the primary production sector.

7. Conclusion

Because several experts point out that it is necessary to further elucidate the mechanisms described in this document through which the CPGRs increase the growth and yields of plant species, Strengthening the integral knowledge of the rhizosphere has been, is, and will continue to be essential for the understanding of a myriad of aspects, processes, and phenomena that are pillars of agricultural and environmental sustainability. In addition, having a more complete description of soil microbial diversity will allow us to broaden our knowledge of its role in the biogeochemical cycles of the elements essential for plant development.

Conflict of interest

The authors declare no conflict of interest.

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