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Review

Importance of Lactic Acid Bacteria as an Emerging Group of Plant Growth-Promoting Rhizobacteria in Sustainable Agroecosystems

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Abstract: Increasing awareness of the problems caused by synthetic agrochemicals, such as chemical fertilizers, pesticides, and herbicides, makes it crucial to discover substitute approaches that can guarantee competitive plant production and protect the environment while maintaining the natural balance in agroecosystems. One of the leading alternatives is utilizing rhizobacterial strains named plant growth-promoting rhizobacteria (PGPR). The utilization of PGPR-based biofertilizers for advancement in the sustainability of farming productions has received considerable critical attention all over the world because of their contribution to not only improving plant growth but also inducing biotic and abiotic stress tolerance. This review updates the aforementioned eco-friendly strategy in sustainable agroecosystems and provides new insights into the phytostimulation and bioprotection ability of lactic acid bacteria (LAB), an emerging taxon of PGPR. In this regard, the ability of LAB to synthesize metabolites, including organic acids, phenolic acids and their flavonoid derivatives, phytohormones, and antimicrobial substrates, is presented. The use of LAB provides a bridge between PGPR and environmentally friendly crop productivity, which can lead to sustainable production systems by reducing the use of agrochemicals, improving soil quality, and minimizing environmental pollution. All the beneficial aspects of LAB need to be addressed by future research to plan systematic methodologies for their use and/or to combine the use of PGPR along with other organic or inorganic inputs in sustainable production systems.

Keywords: biofertilization; bioprotection; plant growth-promoting rhizobacteria; phytostimulation

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1. Introduction

Supplying adequate agrifood products and byproducts, the demand for which has increased as the global population rises, requires diverse strategies, including (i) incrementing the cultivation area and (ii) improving the production per unit area. However, although the first approach (e.g., land use change) increased production, the conversion of natural landforms into farming land led to an environmental challenge through land degradation [1–3]. This problem has become increasingly important in the Mediterranean basin, which demonstrates obvious movements of degradation, especially in areas where climate changes and meteorological conditions contribute extremely to it [4]. As an alternative strategy, the application of agrochemicals (e.g., artificial fertilizers, herbicides, etc.) and intensive farming management practices to increase crop production has brought the major disadvantage of the increasing contamination of agricultural products and the environment [5,6]. Moreover, the strong demand for agrochemicals from domestic and global markets has driven up their prices and caused economic challenges in the agricultural sector [7].

One of the most significant current discussions is a reconsideration of technologies to boost plant production, focusing on alternative strategies, mainly the application of beneficial biological approaches and bio-based products. The application of beneficial microbial consortia, mainly plant growth-promoting rhizobacteria (PGPR), has become one of the most widely used biological alternatives in sustainable agriculture. Such beneficial rhizobacteria can be considered plant biostimulants, which, according to Regulation (EU) No. 2019/1009 of the European Parliament [8], can be used as fertilizing products to promote the plant nutritional value, increase the nutrient locked-up availability in the rhizosphere/soil, and improve plant tolerance against abiotic and biotic stresses [9]. Moreover, the presented sustainable alternatives of agrochemicals receive considerable critical attention in fulfilling part of the United Nations Sustainable Development Goal 15, including how microbial-based biofertilization can promote the sustainable use of agroecosystems and preserve farmlands from degradation.

Recently, investigators have attempted to evaluate the potential of identified PGPR and their mechanisms of action as agents of biofertilization, phytostimulation, bioremediation, and bioprotection (Figure 1). Table 1 presents an overview of some identified PGPR and their functional attributes, as further discussed in Sections 2 and 3.

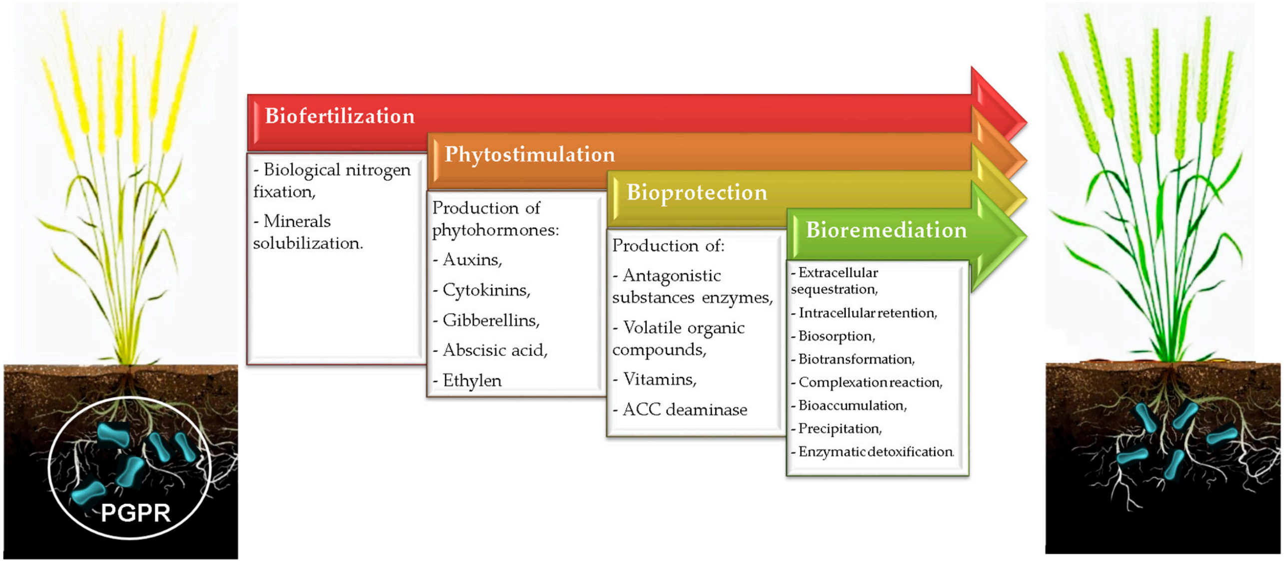

Figure 1. Potential roles of PGPR in agroecosystems.

Table 1. Some identified PGPR and their mechanisms as the agents of biofertilization, phytostimulation, bioremediation, and bioprotection.

PGPR Strain	Mode of Action	Plant (PGPR Isolated from and/or Affected by PGPR)	Reference
Providencia rettgeri (Strain RFFL-I; Accession No. MK618564.1)	- Phosphate solubilization - Production of exopolysaccharides, HCN, siderophores, and IAA - Enzyme activities (e.g., phosphatase, cellulase, pectinase, and chitinase)	Barley	Ferioun et al. [10]
Azospirillum spp. (Strain YM 249; Accession No. LN833443 and strain Gr 22; Accession No. LN833448)	- Nitrogen biological fixation - Phosphate solubilization - IAA production	Potato	Naqqash et al. [11]
Bacillus cereus (Accession No. AJ276351.1)	- Production of cytokinins and IAA	Walnut	Liu et al. [12]
Bacillus spp. (Accession No. OM978377; OM978378; OM978375; OM978380)	- Phosphate solubilization - IAA production	Tomato	Kouam et al. [13]

Table 1. *Cont.*

PGPR Strain	Mode of Action	Plant (PGPR Isolated from and/or Affected by PGPR)	Reference
Azospirillum brasilense (commercial inoculant)	- Nitrogen biological fixation - IAA production	Maize	Hungria et al. [14]
Azotobacter vinelandii ATCC 12837	- Nitrogen fixation - Production of siderophores, IAA, GA3, HCN, and vitamins	Tomato	Conde-Avila et al. [15]
Pseudomonas aeruginosa, *P. putida*, *P. cepacia*, *P. fluorescens*	- Phosphate solubilization - Production of siderophores, IAA, and HCN	-	Deshwal and Kumar, [16]
Acinetobacter pittii (Accession No. MT974044), *Acinetobacter oleivorans* (Accession No. MT974043), *Acinetobacter calcoaceticus* (Accession No. MT974039), *Comamonas testosteroni* (Accession No. MT974042),	- Phosphate solubilization - Potassium solubilization - Zinc solubilization - Biological nitrogen fixation - IAA production	Durum wheat	Yaghoubi et al. [17]
Lactococcus lactis (Genome accession No. JADBCD000000000), *Enterococcus faecium* (Genome accession No. JADBCB000000000), *Bacillus velezensis* FUA2155, *Bacillus amyloliquefaciens* Fad 82	- Phosphate and potassium solubilization - Antifungal activity	Wheat	Strafella et al. [18]
Enterobacter asburiae *Pseudomonas koreensis P. linii*	- Phosphate solubilization - Production of siderophores and IAA	Melon	Murgese et al. [19]
Enterobacter sp. (Accession No. KX209145) *Pseudomonas* sp. (Accession No. KX290125) *Azotobacter chroococcum* (Accession No. KX209144) *Rhizobium* sp. (Accession No. KX209152) *Staphylococcus* sp. (Accession No. KX209174)	- Phosphate solubilization - Production of siderophores and IAA - Enzyme activity (ferric-chelate reductase)	Barley, tomato, and cucumber	Scagliola et al. [20]
Bacillus tequilensis *Variovorax paradoxus* *Acidovorax facilis* *Leucobacter aridicollis* *Streptomyces fimicarius* *Pseudomonas nitroreducens*	- Phosphate solubilization - Production of siderophores and IAA - Nitrogenase and 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity	Sugarcane	Solanki et al. [21]
Pseudomonas sp. (Accession No. GU550663)	- Heavy metal phytoremediation - Production of siderophores and IAA	Thyme leaf, sandwort, and brown mustard	Ma et al. [22]
Pantoea ananatis, *Enterobacter* sp. (commercial inoculant)	- Phosphate and potassium solubilization	Rice	Bakhshandeh et al. [23]
Bacillus cereus, *B. megaterium* (commercial inoculant)	- Potassium solubilization	Soybean	Bakhshandeh et al. [23]

Table 1. *Cont.*

PGPR Strain	Mode of Action	Plant (PGPR Isolated from and/or Affected by PGPR)	Reference
Pantoea agglomerans (Accession No. KT804413), *Rahnella aquatilis* (Accession No. KM977991), *Pseudomonas orientalis* (Accession No. KJ529081)	- Potassium solubilization - IAA production	Rice	Yaghoubi et al. [24]
Bacillus licheniformis (Strain MSB29; Accession No. KF803996), *Pseudomonas azotoformans* (Strain HSS-1; Accession No. KJ816640)	- Potassium solubilization - IAA production	Rice, banana, maize, sorghum, and wheat	Saha et al. [25]
Burkholderia cenocepacia	- Phosphate solubilization	Tobacco	Liu et al. [26]
Agrobacterium tumefaciens (Accession No. KX209151) *Rhizobium* sp. (Accession No. KX209189)	- Zinc solubilization	Barley and tomato	Yaghoubi et al. [27]
Enterobacter asburiae (Strain BFD160; Accession No. KX290147), *Pseudomonas koreensis* (Strain TFD26; Accession No. KX290158), *Pseudomonas lini* (Strain BFS112; Accession No. KX290180)	- Mineral solubilization	Cucumber	Scagliola et al. [28]
Pseudomonas putida P. fluorescens Azospirillum lipoferum	- Zinc and iron solubilization - IAA production	Rice	Sharma et al. [29]
Rhizobium sp.	- Nitrogenase activity - IAA production	Rice	Purwanto et al. [30]
Micrococcus yunnanensis YIM 65004, *Stenotrophomonas chelatiphaga* LPM-5	- Siderophore production	Canola and maize	Ghavami et al. [31]
Bacillus amyloliquefaciens RWL-1 (Accession No. HQ840415)	- Biostimulation (gibberellin production)	Rice	Shahzad et al. [32]
Lactobacillus acidophilus	- Biocontrol (antimicrobial) - IAA production	Banana, cotton, maize, and wheat	Mohite [33]
Pseudomonas fluorescens CHA0, *Rhizobium leguminosarum* bv. *phaseoli*	- Biopesticede (to control root-knot nematode, *Meloidogyne javanica*)	Chickpea, bean, lentil, and pea	Tabatabaei and Saeedizadeh [34]
Bacillus subtilis GB03; FZB24, *B. amyloliquefaciens* IN937a, *B. pumilus* SE34	- Biodegradation of pesticides in contaminated soil	-	Myresiotis et al. [35]
Azospirillum lipoferum A. brasilense	- Biodegradation of crude oil in soil	Wheat	Parewa et al. [36]
Pseudomonas aeruginosa (Accession No. KP717554), *Alcaligenes feacalis* (Accession No. KP717561), *Bacillus subtilis* (Accession No. KP717559)	- Protection of plants against the toxic effects of heavy metals (Ni, Cr, and Cd)	Brown mustard	Aka and Babalola [37]
B. lentus A05, *Pseudomonas aeruginosa* A08	- Bioherbicide	*Ageratum conyzoides* weed	Rakian et al. [38]

Table 1. *Cont.*

PGPR Strain	Mode of Action	Plant (PGPR Isolated from and/or Affected by PGPR)	Reference
Pseudomonas fluorescens CHA0^T	- Biosynthesis of the antibiotics (2,4-diacetylphloroglucinol, phenazine-1-carboxylic acid, pyoluteorin, and pyrrolnitrin)	Wheat	Müller et al. [39]
Streptomyces rochei IDWR19, *S. carpinensis* IDWR53, *S. thermolilacinus* IDWR81	- Biocontrol (antifungal) - Enzyme production (e.g., chitinase, cellulase, and phytase)	Wheat	Jog et al. [40]
Bacillus megaterium	- Ethylene inhibition - Phosphate solubilization - Phytohormones (ABA) production	Tomato	Porcel et al. [41]
Bacillus sonorensis	- Bioprotection (Chitinase production) - Phosphate solubilization - Production of HCN, IAA, and ACC deaminase	Sweet and chili peppers	Thilagar et al. [42]
Ochrobactrum sp. (Accession No. JQ514559)	- Biodegradation of chlorpyirfos - Phosphate solubilization - Production of HCN and IAA	Rice	Abraham and Silambarasan [43]
Sinorhizobium meliloti 1021	- Vitamins (biotin) production	Alfalfa	Hofmann et al. [44]
Sinorhizobium meliloti 1021	- Vitamins (riboflavin and lumichrome) production	Alfalfa	Phillips et al. [45]

Among the most potentially beneficial rhizobacteria, lactic acid bacteria (LAB) are suggested as a new promising group of PGPR. However, their functions in agroecosystems, including their role as biofertilizers, biocontrol agents against pathogens, and biostimulants in plant production, have received far too little attention, apart from intensive studies on their traditional role in food processing sectors. Understanding the functional attributes of LAB and their mechanisms is important to use them as a potential way to improve soil health and sustainable plant production. Therefore, this review aims to update the recognized potential of PGPR, mainly LAB, and to reveal their mechanisms of action via which they impact agroecosystems by securing their sustainability.

2. Functional Attributes of PGPR and Their Mechanisms

2.1. Phytostimulation

Bacterial phytohormone production is one of the important studied traits in the plant–microorganism relationship because plant growth and development are directly dependent on phytohormone levels. To date, nine categories of plant hormones have been recognized: auxins (mainly in the form of 3-indol acetic acid (IAA)), gibberellins (GAs), cytokinins (CKs), ethylene (ETH), abscisic acid (ABA), brassinosteroids (BRs), salicylic acid (SA), jasmonic acid (JA), and strigolactones (SLs) [46].

2.2. Biofertilization

Atmospheric nitrogen can be converted to plant-absorbable forms (NH_4^+) by PGPR with biological nitrogen-fixing (diazotrophy) ability [18]. Nitrogen-fixing bacteria (NFB) are categorized into two main groups including (i) symbiotic bacteria associated with leguminous plants (e.g., *Rhizobium*) and nonleguminous plants (e.g., *Frankia genus* and *Azospirillum* species associated with some dicotyledonous species and cereal grasses, respectively) and (ii) nonsymbiotic free-living bacteria (e.g., cyanobacteria and some genera, including *Azotobacter*, *Arthrobacter*, *Beijerinckia*, *Pseudomonas*, and *Diazotrophicus*) [47].

Phosphate solubilizing bacteria (PSB) are among the known PGPR, with a notable capability in solubilizing insoluble complexes of P in soil and making them available to plants using various mechanisms [48,49]. Typically, PSB affect a soil's biological and physicochemical characteristics, particularly through the release of various organic acids that lead to the chelation of mineral ions and decrease the environmental pH, providing soluble forms of P into the soil [5]. Moreover, the secretion of some enzymes (e.g., phytases and phosphatases) by PSB into the soil can lead to the breaking down of complex organic P forms by catalyzing the mineralization process [49].

The application of potassium solubilizing bacteria (KSB) was proposed as one of the sustainable efficient practices in plant production by transforming insoluble K from feldspar and aluminosilicate minerals into available K and improving the K uptake by plants [24,50]. Various mechanisms are used by KSB, such as the synthesis of organic acids (e.g., oxalic acid, citric acid, succinic acid, tartaric acid, and α-ketogluconic acid), which can affect the dissolution of K-containing minerals by decreasing the pH of the environment as well as by attaching the polysaccharides to the mineral surface [51,52]. The complexation of metal ions (e.g., Fe^{2+}, Al^{3+}, and Ca^{2+}) and proton supply are other mechanisms of KSB to enhance the dissolution of K compounds [52].

It has been reported that zinc (Zn) deficiency can be addressed by applying a type of PGPR known as zinc solubilizing bacteria (ZSB), which can mobilize Zn complexes and solubilize insoluble Zn forms in the soil, including ZnO, $ZnCO_3$, and $Zn_3(PO_4)_2$, through various mechanisms [27]. These PGPR exude organic acids and phenolic and flavonoid compounds in the rhizosphere, resulting in the sequestration of Zn cations, lowering the pH of the rhizosphere and, consequently, increasing the soluble form of Zn and the ratio of Zn^{2+} to organic Zn ligands [53]. In fact, Zn absorption is mainly affected by soil pH, in which Zn easily adsorbs on cation exchange places at high pH levels while being replaced by $CaCl_2$ at low pH levels [27].

On the other hand, it has also been suggested that the high Zn mobilization in soils in the presence of high levels of low molecular weight organic acids, phenolics, siderophores, and other bacterial metabolites mostly depends on the complexing capacity of these metabolites compared to their ability to acidify the rhizosphere [53,54]. Such complexing capacity is raised at high levels of soil pH due to the high concentration of deprotonated carboxylic and phenolic moieties, which are more potent Lewis bases in reacting with metal cations. Moreover, some organic molecules possessing more than one acidic moiety (e.g., citric acid) show a greater complexing capacity at high pH levels and, therefore, can form polydentate complexes with cations possessing more than one positive charge, such as Fe^{3+} and Zn^{2+}, when all the acidic functional groups are consecutively deprotonated [17,54].

Several studies have clearly shown the favorable effects of PGPR on nutrient uptake and plant production. For instance, Bakhshandeh et al. [52] reported an increment in P and K uptake by rice plants, influenced by three PGPR strains (*Pantoea ananatis*, *Rahnella aquatilis*, and *Enterobacter* sp.), of up to 35–77% in leaves, 17–53% in stems, and 25–75% in roots, as well as plant height (+11–15%) and biomass (+27–65%), depending on the PGPR strain. Moreover, some researchers have documented that the application of PGPR treatment promoted plant growth by improving leaf photosynthetic efficiency by up to 19, 12, 12, 16, and 20% in durum wheat [55], rice [56], eggplant [57], cucumber, and pepper [58], respectively, compared to nontreated control plants, which could lead to higher CO_2 assimilation [59] and enhanced grain yield [56].

2.3. Bioprotection

Several enzymes synthesized by PGPR have a critical function in protecting a plant from stress and pathogens [60]. Some of them, including chitinases, cellulases, and glucanases, could be labeled as biopesticides since they hinder plant pathogen growth by hydrolyzing polysaccharides and fibrillar materials of the cell wall of pathogenic fungi [60,61]. In this regard, Saraf et al. [62] reported that enzyme synthesis (e.g., proteases, chitinase, and β-1,3-glucanase) by PGPR strains can be considered an important strategy to control soil-borne pathogens through enzymatic degradation or deformation of their cell wall.

Another effective mechanism of PGPR is the synthesis of volatile organic compounds (VOCs), which makes them able to interact with plants and other soil microorganisms by causing systemic resistance to disease and pathogens and promoting plant development [63,64]. In fact, some characteristics of these secondary metabolites, such as low molecular weight (<300 g mol^{-1}), high vapor pressure (>0.01 kPa), and low boiling point, enable them to volatilize and act as the agents of cell signaling [63,65]. Nearly 846 different potential VOCs produced by soil bacteria have been identified [58], the most important of which is N,N-dimethylhexadecylamine (DMHDA), a plant protector against pathogens (e.g., *Botrytis cinerea* and *Phytophthora cinnamomi*), and dimethyl disulfide (DMSD), an elicitor of plant defense as well as a plant growth stimulator by increasing the status of sulfur nutrition in plants [49,63].

Plants can usually produce enough vitamins (e.g., biotin, riboflavin, niacin, thiamin, and pantothenate) for their development and provide them to soil microorganisms through root exudates as main nutritive compounds for their survival and development; on the other hand, unhealthy and stressed plants may suffer from vitamin deficiency [5,66]. In this context, some PGPR, especially *Bacillus* sp. and *Rhizobium* sp., have great potential to synthesize vitamins, such as pantothenic acid, thiamine, riboflavin, pyrroloquinoline quinone, and biotin, and can contribute to their supply to plants [66,67]. The main functions of vitamins are (i) to act as cofactors in various metabolic pathways, (ii) to facilitate the synthesis of vital metabolites for plants and microbes, (iii) to induce resistance to pathogens, (iv) to promote plant growth and productivity, and (v) to participate in energy transformation in the plant from reserved compounds [67].

Harnessing the antagonistic activity of PGPR has already been suggested as an effective approach to control plant pathogens and inhibit the metabolic activities of various microorganisms through antibiotics [66,68]. In addition to the direct antipathogenic potential of PGPR, they also act as the determinative agents to trigger induced systemic resistance (ISR) in plants and promote plant growth through antifeedant, anthelminthic, phytotoxic, antioxidant, cytotoxic, and antitumor activities in insects and mammals [69]. Among them, diacetylphloroglucinol (2,4-DAPG) synthesized by *Pseudomonas* sp. [70,71], phenazine by *Pseudomonas* sp. [72], lipopeptides (e.g., iturin, fengycin, and bacillomycin) and polyketide by *Bacillus* sp. [73], phenazione-1-carboxylic acid (PCA) by *Pseudomonas fluorescens* [74], and circulin and colistin by *Bacillus subtilis* [75] are the most efficient low molecular weight extracellular metabolites that have been extensively studied.

One of the potent biological approaches of PGPR strains is the ability to synthesize 1-aminocyclopropane-1-carboxylate deaminase (ACCD), which can regulate plant growth and induce stress tolerance by decreasing ethylene levels [76]. ACCD, as one of the major enzymes in the intermediate precursor of ethylene production in plants, is responsible for the conversion of ACC to a-ketobutyrate and ammonium [77,78]. The interactions between plants and ACCD-producing PGPR can modify plant defense reactions to a wide range of environmental stresses (e.g., salinity, flooding, high temperature, drought, phytopathogens, and heavy metal contamination) by the degradation of ACC enzymes and decreasing ACC levels in root and leaf tissues [77,79].

2.4. Soil Bioremediation

Recently, PGPR have come to the forefront because of their environmental cleanup ability (bioremediation) as a substitute approach to chemical and physical traditional techniques in eliminating (or controlling) pollutants in soils [80]. Although some organic compounds can endure in soil for a long time, they can be degraded by aerobic PGPR or even dechlorinated and mineralized by anaerobic bacteria [81,82]. For instance, polychlorinated biphenyls (PCBs), as a group of well-known organic contaminants, can be oxidized in aerobic bioremediation processes, where some genera of PGPR (e.g., *Bacillus*, *Pseudomonas*, *Rhodococcus*, and *Achromobacter*) can utilize the biphenyl (a vital primary substrate that supports PCB cometabolism) using several enzymes, such as dehydrogenases, dioxygenases, hydrolases, hydratases, and aldolases [82,83].

In anaerobic degradation processes, organic compounds are broken down by anaerobic bacterial strains to release the energy required for their metabolic processes. In this process, reductive dechlorination or dehalorespiration in contaminated soils replaces the normal bacterial respiration using aryl halides as electron acceptors for their respiration, resulting in the formation of less toxic and more biodegradable compounds [84].

Soil microbes serve various mechanisms for reducing the toxicity for plants and themselves, including intracellular retention, extracellular sequestration, biosorption, biotransformation, bioaccumulation, complexation reaction, precipitation, and enzymatic detoxification (oxidation and reduction) of toxic metals [85–87], whose efficiency depends on the great variability among the toxicity levels of heavy metals. Among them, the most effective mechanism of PGPR strains is the decline in ROS production through the production of some specific enzymatic and nonenzymatic antioxidants (e.g., hydrolases, dioxygenases, hydratases, dehydrogenases, and aldolases), which can preserve plants from ROS-induced oxidative damage [49,60].

3. Lactic Acid Bacteria (LAB): An Emerging Group of PGPR

3.1. Soil- and Plant-Associated LAB

Diverse genera of beneficial rhizobacteria have already been proposed as PGPR, with *Bacillus* and *Pseudomonas* being the predominant genera [88]. Nevertheless, metagenomic analyses of plant and rhizosphere microbiomes have resulted in the identification of an emerging group of PGPR, namely, lactic acid bacteria (LAB), which are barely detectable in the plant–soil ecosystem due to their low abundance [18,89]. LAB are known as microaerophilic, Gram-positive, cytochrome-deficient, and nonsporulating bacteria that are also involved in food and silage fermentation as well as soil health; however, some of them are recognized as human pathogens [90,91]. Despite intensive investigations into the conventional function of LAB in the food processing industry, too little attention has been given to their other functions, such as acting as biofertilizers, biocontrol agents, and biostimulants in plant growth. Furthermore, little is known about LAB due to the difficulty of isolating them by plating serial dilutions of rhizospheric soil samples since enrichment methods using selective culture media have been largely ignored [18,92,93]. Despite their low relative abundances, LAB have been isolated from the rhizosphere in some studies, which has consequently led to their introduction as a crucial component of sustainable agricultural approaches as environmentally sustainable and efficient strategies to control pests and diseases and enhance crop yield [93–95].

It has been stated that root exudates, including amino acids, carbohydrates, enzymes, organic acids, phenols, and flavonoids, account for a considerable proportion (5–21%) of photosynthetically fixed carbon in plants, which can change the soil environment and, consequently, shape microbial communities [96]. Although such a carbohydrate-rich rhizosphere is ideal for LAB, a quick breakdown of organic acids in the rhizosphere has been proposed as a limiting factor in the capability of LAB to acidify soil to their benefit, thus preventing LAB from being the predominant taxon in agricultural soils [97]. Moreover, recent research on the efficient transfer of LAB from the rhizosphere and phyllosphere to the plant endosphere [98] provided an interesting strategy to assess their roles in plant growth and production. In fact, LAB also constitute a small fraction of the epiphyte [99,100] and endophyte populations of plant microbiota [100,101]. Among the plant-associated LAB, there are some well-known generalist taxa, including *Lactiplantibacillus plantarum*, *Lactococcus lactis*, *Leuconostoc* spp., *Weissella* spp., and *Enterococcus* spp., and some specialist taxa, such as *Fructilactobacillus florum* and *Fructobacillus* spp., that have been discovered relatively recently [102]. However, the consequences of LAB on plant physiology still need to be fully deciphered. Overall, the genomic diversity in LAB is mainly due to the particular pressure applied by each plant niche [103,104].

3.2. Biofertilization and Bioremediation Effects of LAB

The ability of LAB to synthesize metabolites, including organic acids, phenolic acids and their flavonoid derivatives, phytohormones, and antimicrobial substrates, has already been reported [19,105–107]. LAB have been reported to have a high capacity to solubilize insoluble forms of phosphate [19,108,109] and potassium [18], to biologically fix nitrogen [110], and to produce iron-chelating compounds [111] and siderophores [112]. They are also involved in soil biochemical cycles through regulating soil organic matter content and detoxifying hazardous chemicals [111]. Heavy metal biosorption mechanisms of LAB have been previously reported, involving bacterial surface-associated functional groups, including carboxyl, hydroxyl, and phosphate [111,113]. Previous studies on food technology outlined the critical role of LAB in breaking down organic macromolecules and indigestible polysaccharides and converting disfavored flavor compounds [114].

In addition, it has already been suggested that shifts in the microbiome in response to environmental changes may imply the plasticity of the available microbial genetic pool in aiding plant adaptation to environmental stress [115,116]. Accordingly, the finding of a rich diversity of LAB in the rhizosphere of plants grown in deserts [93,97] can confirm the role of LAB in improving the tolerance of associated plants. It can also be assumed that LAB conferring a specific stress tolerance can be derived from holobionts thriving under similar stress conditions. Improved tolerance of LAB-treated plants to abiotic stresses has been correlated with changes in plant metabolic responses related to proline content, phenolic acids, and antioxidant enzymes [97,117]. Such reported findings can support the assumption that LAB are effective as biofertilizers by increasing nutrient bioavailability and as biostimulants to stimulate plant growth or seed germination by alleviating diverse environmental stresses [97,118,119]. The beneficial outcomes of the application of LAB treatment in several plant species have been summarized in Table 2. A scheme of the biofertilization, bioprotection, and biodegradation potential of LAB is shown in Figure 2.

Table 2. Beneficial effects of lactic acid bacteria in agroecosystems.

LAB Species	Experimental Condition	Summary of Results	Reference
Lactiplantibacillus plantarum	Pot	Commercial inoculants of *L. plantarum* reduced eight potato pathogen infestations, including *Pectobacterium carotovorum*, *Streptomyces scabiei*, *Alternaria solani*, *A. tenuissima*, *A. alternata*, *Phoma exigua*, *Rhizoctonia solani*, and *Colletotrichum coccode.*	Steglińska et al. [120]
		Improving cucumber plant growth indirectly through organic acid (succinic and lactic acid) production and increasing the bioavailability of mineral nutrients in the soil in comparison with the commercial inoculants of *L. plantarum*.	Kang et al. [121]
	Field	Reducing the Fusarium head blight index in wheat plants via the synthesis of organic acids and plantaricin in response to *L. plantarum* SLG17 application.	Baffoni et al. [122]
		Increasing the percentage of germination rate and improving the length of shoot and roots of tomato in response to inoculation with *L. plantarum* ONU12.	Limanska et al. [123]
		L. plantarum JCM1149 showed antibacterial activity and suppressed soft rot caused by *Pectobacterium carotovorum* subsp. carotovorum in cabbage, onion, potato, tomato, and radish.	Tsuda et al. [124]
	In vitro	The *L. plantarum* MF042018 strain's ability as a reassuring biosorbent for removing heavy metals from industrial wastewater is approved.	Ameen et al. [113]
		Adopting an energy-efficient defense strategy and efficient partitioning of carbon fluxes between primary and secondary metabolites to relieve salt-caused oxidative damage in plants treated with *L. plantarum* ATCC 9019.	Phoboo et al. [117]

Table 2. *Cont.*

LAB Species	Experimental Condition	Summary of Results	Reference
Lactococcus lactis (Genome accession No. JADBCD000000000), *Enterococcus faecium* (Genome accession No. JADBCB000000000)	In vitro	Showing a high level of antifungal activity and solubilization efficiency of phosphate and potassium despite no ability of phytohormone production.	Strafella et al. [18]
Lacticaseibacillus paracasei	Field and pot	Improving seed germination rate and growth of tomato. Inducing tolerance against infection by pathogen (*Ralstonia solanacearum*) in seedlings.	Konappa et al. [125]
Lactococcus lactis	Field	Improving the basil plants' tolerance against a pathogen (*Alternaria* sp.).	Ghosh et al. [126]
Lactobacillus amylovorus FST 2.11; DSM 20522 (-)	Field and pot	Revealing the favorable effect on the expression of some defense-related marker genes and transcription factors in barley plants upon Fusarium head blight.	Byrne et al. [127]
Enterococcus sp. CL2 (accession No. KJ124182.1), *Enterococcus casseliflavus* ZZUA83 (accession No. LC119138.1)	In vitro	Showing high ability in phosphate solubilization and IAA production.	Mussa et al. [109]
Weissella paramesenteroides CE.3.6 *Liquorilactobacillus sucicola* BGGO7-28	In vitro	Inhibiting the growth of *Penicillium digitatum* as a pathogen agent in citrus fruits.	Ma et al. [128]
Lactobacillus spp.	Pot	Causing systemic acquired resistance (SAR) in tomato plants by changing the morphology, resulting in resistance to fungal pathogens.	Hamed et al. [129]
Lactobacillus spp. *Sporolactobacillus* sp.	Field and in vitro	Showing antifungal activities and controlling some important plant pathogenic fungi, such as *Fusarium verticillioides*, *Penicillium sp.*, and *Verticillium dahlia in maize.*	Kharazian et al. [130]
Levilactobacillus brevis JJ2P, *Lactobacillus reuteri* R2	In vitro	Inhibition of *Zymoseptoria tritici* in wheat seedlings and reducing the growth of wheat leaf blotch.	Lynch et al. [131]
Pediococcus pentosaceus LB44, *Weissella confusa* LM85	In vitro	Effective antibacterial potential against a broad spectrum of Gram-positive and Gram-negative bacteria.	Kaur and Tiwari [132]

3.3. Bioprotection Effects of LAB

LAB have also received considerable attention for their capability to synthesize antifungal metabolites (e.g., diketopiperazines, hydroxy derivatives of unsaturated fatty acids, and 3-phenyllactic acid), antibacterial (e.g., bacteriocins and bacteriocin-like substances), and general antimicrobial metabolites (e.g., hydrogen peroxide, organic acids, pyrrolidone-5-carboxylic acid, diacetyl, and reuterin) [133–135]. In addition to direct antagonism against pathogens, LAB can affect the plant response to pathogens by causing systemic acquired resistance (SAR) and enhancing plant innate immunity [97]. Mao et al. [136] observed that the antibacterial activity of *Lacti plantarum* DY-6 was dependent on the production of acetic acid, lactic acid, caprylic acid, propionic acid, and decyl acid. On the other hand, Magnusson et al. [137] observed that the ability to synthesize lactic acid in the bacterial strains without antimicrobial activity was in the same range or even higher than those possessing antimicrobial activity, while the amount of acetic acid corresponded to that normally detected in the culture medium used for assessment tests. Therefore, they concluded that the antimicrobial activity of *Lacti. plantarum*, *Latilactobacillus sakei*, *Loigolactobacillus coryniformis*, and *Pediococcus. pentosaceus* against *Aspergillus* sp., *Fusarium* sp., and *Penicillium* sp. was due to the synthesis of other metabolites [137]. Through an HPLC analysis of antagonistic bacteria supernatants, they detected two antifungal cyclic dipeptides, cyclo (Phe-Pro) and cyclo (Phe-4-OH-Pro), whose structures were similar to those found in *Lacti. plantarum* by Ström et al. [138]. Axel et al. [139] found that chemical acidification has no effect on mold inhibition in food, so it is more plausible that the antagonistic activity of LAB depends on the synergistic action between organic acids and other active compounds [140]. The production of bacteriocins by soil- and plant-associated LAB is rare but not excluded, as it was observed that the treatments of cell-free supernatants with organic solvents, surfactants, H_2O_2, high temperature, and different pH do not affect their antimicrobial activity [132]. Yanagida et al. [141] were the first to report the production of bacteriocins by *Ligilactobacillus animalis* C060203 and *Enterococcus durans* C102901, which exhibited strong antibacterial activity against *Lati. sakei* JCM 1157^T. The defeat of antibacterial potential in response to proteinase K treatment confirmed the proteinaceous nature of antimicrobial compounds. A comparative genomic analysis between LAB isolated from plant/soil ecosystems and those isolated from dairy products, nondomestic animals, and human isolates revealed that plant/soil LAB are enriched in genes involved in bacteriocin synthesis, suggesting a probable role in plant fitness [18]. This finding confirms that LAB are a natural farm of antimicrobial metabolites [133] and can be used in agronomic fields to prevent or relieve disease sustainably.

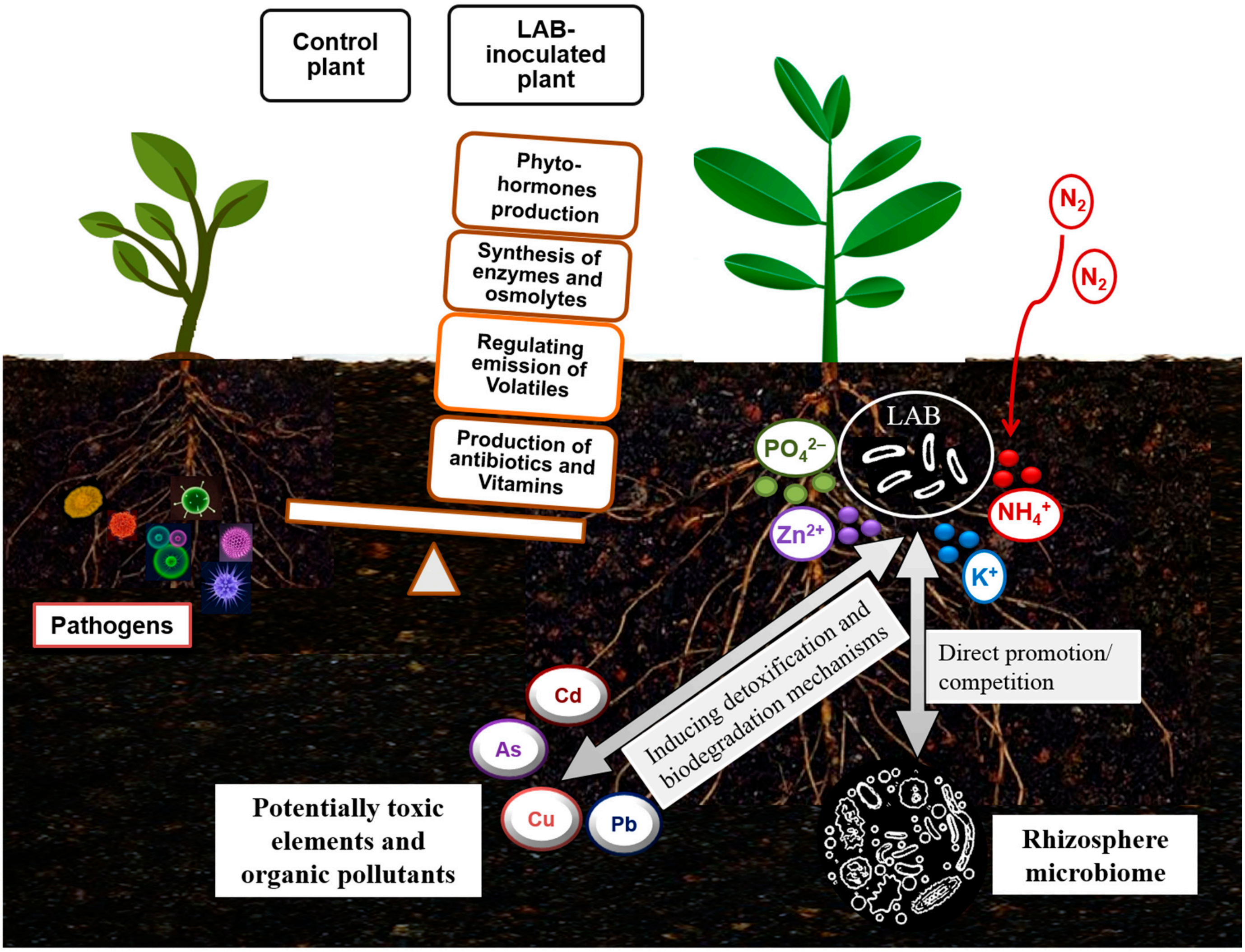

Figure 2. Schematic portrayal of the biofertilization, bioprotection, and biodegradation potential of lactic acid bacteria.

4. Concluding Remarks and Future Perspectives

This review updates the eco-friendly approaches of PGPR application in sustainable agroecosystems as well as provides new insights into the direct or indirect mechanisms of action of these beneficial rhizobacteria involved in biological nitrogen fixation, the solubilization of insoluble minerals, biological control of soil-borne pathogens, stimulation of phytohormone synthesis (e.g., auxins, cytokinins, gibberellins, etc.) in plants, the promotion of enzyme activity involved in reactive oxygen species (ROS)-scavenging, and the biosynthesis of 1-amino cyclopropane-1-carboxylate deaminase (ACC deaminase), hydrogen cyanide, antibiotics, siderophore, and volatile organic compounds. Consequently, these mechanisms provide a bridge between PGPR, mainly LAB, and environmentally friendly crop productivity, which leads to sustainable production systems by reducing agrochemical use, improving soil quality, and minimizing environmental pollution. All these beneficial aspects of LAB need to be addressed in future research to plan methodologies to utilize them and/or to combine the use of these PGPR along with other organic or inorganic inputs in sustainable production systems.

Further work is needed to investigate the environmental sensitivity of LAB to determine how limiting they can be in widespread use. Moreover, a research question that could be asked includes how the competition of LAB with indigenous microorganisms can affect their survival in soils after inoculation. Satisfactory results can be achieved by keeping the bacterial load of the inoculum constant over time. Therefore, future research should focus on the development of efficient microbial formulations that are compatible with conventional techniques, including seed disinfection and pesticide use, to be efficient under various field conditions and soil types and be safe for humans, animals, and plants. Solid and liquid carriers that support the growth and longer viability of microorganisms as alternatives to expensive lyophilization processes have been identified, but each microorganism requires specific growth conditions, and the path to a solution that suits each of them is still a long one.

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