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Review

Rhizobia: A Promising Source of Plant Growth-Promoting Molecules and Their Non-Legume Interactions: Examining Applications and Mechanisms

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Abstract: For over a century, the scientific community has had a comprehensive understanding of how rhizobia can promote the growth of legumes by forming nitrogen fixing nodules. Despite this knowledge, the interaction of rhizobia with non-legumes has remained largely ignored as a subject of study until more recent decades. In the last few years, research has shown that rhizobia can also associate with non-legume roots, which ultimately leads to the stimulation of growth through diverse direct and indirect mechanisms. For example, rhizobia can enhance growth through phytohormones production, the improvement of plant nutrient uptake, such as the solubilization of precipitated phosphorus, the production of siderophores to address iron needs, and also the reduction of ethylene levels through the ACC deaminase enzyme to cope with drought stress. Additionally, rhizobia can improve, indirectly, non-legume growth through biocontrol of pathogens and the induction of systemic resistance in the host plant. It can also increase root adherence to soil by releasing exopolysaccharides, which regulate water and soil nutrient movement. The objective of this review is to assess and analyze the existing knowledge and information regarding the mechanisms through which rhizobia promote the growth of non-legumes. By conducting a comprehensive analysis of these findings, we aim to gain new insights into the development of *Rhizobium*/non-legume interactions.

Keywords: *Rhizobium*; PGPR; legumes; non-legumes; symbiosis; biofertilizers

Citation: Fahde, S.; Boughribil, S.; Sijilmassi, B.; Amri, A. Rhizobia: A Promising Source of Plant Growth-Promoting Molecules and Their Non-Legume Interactions: Examining Applications and Mechanisms. *Agriculture* **2023**, *13*, 1279. https://doi.org/10.3390/agriculture13071279

Academic Editors: Tibor Szili-Kovács and Tünde Takács

Received: 8 May 2023
Revised: 7 June 2023
Accepted: 13 June 2023
Published: 21 June 2023

1. Introduction

For sustainable agriculture, it is essential to efficiently utilize and manage available resources to ensure its long-term viability. This includes proper utilization of the soil, water, and other natural resources for a balanced system, as well as efficient management practices that ensure the good utilization of these resources [1]. This type of resource management not only supports the longevity of the agricultural system, but also helps to conserve and preserve the environment for future generations. Incorporating microbial inoculants as biofertilizers is a financially advantageous and ecological friendly method that aims to decrease dependence on external inputs while enhancing the quality and quantity of internal resources [2]. Thus, symbiotic interactions between plant roots and bacteria have growth stimulating effects and are of great interest, as many studies have shown their beneficial effects upon inoculation [3,4]. The use of rhizobia with non-legume plants is a relatively new area of research that aims at exploring the potential benefits of establishing symbiotic relationships between non-legume plants and these groups of soil bacteria. The idea behind the use of rhizobia with non-legume plants is to extend the benefits of rhizobia to a wider range of crops, which could help to improve soil fertility, increase crop yields, and come up with a synergetic effect with synthetic fertilizers [1].

It has been established that the positive impact of rhizobia on non-leguminous plant growth is achieved through a combination of direct and indirect mechanisms [2,5]. Direct mechanisms include the synthesis of phytohormones and vitamins, inhibition of plant ethylene synthesis, improvement of nutrient uptake (such as the solubilization of inorganic phosphorus, and mineralization of organic phosphorus), and enhancement of stress resistance. Indirect mechanisms, on the other hand, encompass the reduction or prevention of harmful effects caused by pathogenic microorganisms, largely through the synthesis of antibiotics and/or fungicidal compounds, competition for nutrients (such as through siderophore production), and induction of systemic resistance to pathogens. Furthermore, rhizobia can contribute to the indirect growth of non-leguminous crops through interactions with other beneficial microorganisms [6].

In recent years, many studies have been investigating the use of rhizobia in relation to crops, such as rice [7,8], maize [9,10], barley [11], sunflower [12], radishes [6], among others. The results of these studies have shown that some non-legume plants can interact with rhizobia and benefit from their plant growth promotion activities. However, much more research is needed to fully understand the potential benefits and drawbacks of such relationships, as well as to focus on the development of rhizobial strains that possess the ability to enhance crop productivity across diverse environmental conditions.

2. Plant Growth-Promoting Rhizobia Diversity and Ecology

The use of chemical fertilizers to enrich soil with nutrients in high-input cropping systems is often deemed a necessity to achieving optimal crop yields. However, their efficiency is hindered by factors, such as volatilization, denitrification, leaching, and conversion into forms that plants cannot utilize. It is well known that prolonged use of chemical fertilizers can negatively impact soil ecology, harm the environment, degrade soil fertility, and have detrimental effects on human health [13]. Considering the limitations and negative consequences associated with prolonged use of chemical fertilizers, alternative approaches, such as biofertilizers, have gained significant attention in recent years [14]. Biofertilizers offer a more sustainable and environmentally friendly solution for enriching soil with nutrients in high-input cropping systems. Unlike chemical fertilizers, biofertilizers consist of beneficial microorganisms that promote nutrient availability and uptake by plants while improving soil health and fertility [15]. Accordingly, PGP Rhizobia biofertilizers are considered a highly promising means of reducing reliance on agrochemicals, including fertilizers and pesticides [16].

Plant Growth Promoting Rhizobacteria, usually referred as PGPR, are beneficial bacteria that colonize plant root systems and enhance their growth and health [17]. PGPR are a diverse group of bacteria that have beneficial effects on plant growth and health by improving nutrient uptake, the suppression of plant pathogens, and promoting stress tolerance [18].

According to the level of interaction they have with plant root cells, PGPRs can be divided into two groups: intracellular plant growth promoting rhizobacteria (iPGPR) that live inside plant tissue, as well as extracellular plant growth-promoting rhizobacteria (ePGPR) that live in the soil surrounding plant roots [19]. Endophytic PGPR can colonize the plant tissue and provide benefits to the plant, such as increased resistance to abiotic stress and biotic stress, improved nutrient uptake, and growth promotion. They are known to produce growth-promoting compounds, such as indole acetic acid (IAA), gibberellins (GA3), and enzymes, such as phytase and protease, which can help in nutrient acquisition. Rhizosphere PGPRs, on the other hand, interact with the plant roots, and they can provide benefits to the plant, such as improving soil structure, nutrient uptake, and plant growth. They can compete with pathogens for space and nutrients, reducing the ability of pathogens to infect the plant. They can also act as biocontrol agents by producing antibiotics or other compounds that inhibit the growth of pathogens [20,21].

Numerous soil microbes from various genera have been identified as highly efficient PGPR [22]. Among these, the most commonly utilized genera are *Pseudomonas*, *Agrobac-*

terium, *Arthrobacter*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Flavobacterium*, *Micrococcous*, and *Serratia*, which are classified within the ePGPRs [23]. Whilst the iPGPR encompass a variety of microorganisms that can symbiotically fix atmospheric nitrogen with higher plants. *Frankia* is one of the known and well-studied species. Endophytes are a diverse group of soil bacteria, such as *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, and *Rhizobium* [17,24].

PGPR have been found to be highly effective in the remediation of sites contaminated with pesticides and hydrocarbons [25,26]. Hence, PGPRs play a significant role in various biotic processes within the soil by promoting nutrient cycling and contributing to sustainable crop production [27].

The commercialization of PGPRs as biofertilizers is a relatively new field, but it is growing rapidly. Several PGPRs bacterial strains are commercially available as formulated products (such as Kodiak® [28], Serenade® [29] Bio-YIELD® [30]) [15,30]. The commercialization of PGPRs biofertilizers is driven by an increasing demand for sustainable farming practices, as well as by the need to improve crop yields in a changing climate [31,32]. PGPRs biofertilizers are seen as a more environmentally friendly substitute for chemical fertilizers, and they can also help to reduce the need for pesticides [15,30].

3. Characteristics of Rhizobia

Rhizobia are a diverse group of bacteria found in soil that play an important role in the global nitrogen cycle. They can form symbiotic relationships with specific plant species, mainly legumes, resulting in natural nitrogen fixation, which enables the bacteria to convert atmospheric nitrogen into a form that can be used by plants. In return, the plant host provides rhizobia with a source of carbon. This process is called symbiotic nitrogen fixation [33].

Rhizobia are Gram-negative bacteria, belonging to the phylum Proteobacteria. Specifically, they are classified into Alpha and Betaproteobacteria subclasses [34,35]. The exact number of species in Rhizobia is not fixed, as new species are continually being discovered and described. The genus *Rhizobium* alone contains over 150 known species, and the other genera within the Rhizobiaceae family contain multiple species, as well. In addition, there are also many uncharacterized and uncultivated species that have been detected in different environments [36].

The family Rhizobiaceae encompasses a variety of bacterial genera, such as *Bradyrhizobium*, *Azorhizobium*, *Mesorhizobium*, *Ensifer* (*Sinorhizobium*), *Neorhizobium*, *Pararhizobium*, and *Allorhizobium* [37], which are characterized by their ability to establish intracellular, N_2-fixing infections in many different types of plant hosts. This feature is intricate and often closely co-evolved with the specific plant hosts they reside in [38].

Additionally, rhizobia have the capability to form a non-specific associative relationship with roots of other plants (non-legumes) without creating nodules. These associative interactions between plant roots and bacteria have growth-promoting effects and are of great significance, as many crops exhibit an improvement in yield upon inoculation [2].

The symbiotic relationship between rhizobia and legumes is a complex process that involves a series of molecular interactions between the bacteria and the host plant [37]. The process of plant infection by rhizobia includes several steps, such as recognition and attachment of the bacteria to the host plant's root hairs through the production of chemical signals called Nod factors, penetration into root hair cells, differentiation into an infection form called bacteroid [39], formation of nodules, and maintenance of the symbiotic relationship. Nodules are specialized structures that allow the rhizobia to fix atmospheric nitrogen and provide it to the plant in exchange for carbohydrates and other nutrients [40,41]. Many common crop legumes and model plants, including *Medicago* spp., pea, *Lotus japonicus*, bean, and soybean, experience this type of infection [42,43]. However, it is important to note that the process may vary among different Rhizobia species and host plants [44–47].

Rhizobia have been shown to stimulate root growth, protect plants from soil-borne pathogens, enhance stress tolerance, and induce systemic resistance. This is achieved through mechanisms, such as solubilizing minerals and producing plant growth hormones, such as auxin, gibberellin, and cytokinin. Along with their N_2-fixing abilities with legumes, rhizobia also act as plant growth-promoting rhizobacteria (PGPR) and can reduce disease susceptibility. Research is increasingly focusing on the role of rhizobia in managing biotic and abiotic stresses [48–51], with mechanisms including phytohormone production, reducing ethylene levels in roots through ACC deaminase, and releasing compounds that promote induced systemic tolerance (IST) [37,49,52].

However, the composition of the root microbiome can be affected by host plants, but rhizobia have to compete with a multitude of bacteria for root colonization and with other compatible rhizobial strains for nodulation. Competitiveness is a complicated trait that is affected by various abiotic factors, such as soil pH or nutrient availability, and biotic factors, such as host–symbiont association, plant- or strain-intrinsic factors, the production of exopolysaccharide, and catabolic capacity in rhizobia for diverse substrates (e.g., myo-inositol, glycerol, arabinose, homoserine, or erythritol) [33].

4. Role of Rhizobia as PGPR and Mechanism of Action

4.1. Direct Mechanism

4.1.1. N_2 Fixation

Nitrogen is a limiting factor for plant growth and development. It is an essential component of many bio-molecules and constituent of chlorophyll, which plays a crucial role in plant physiological processes [53].

The direct assimilation of nitrogen by plants cannot be possible due to its inert gaseous form [54]. Even if the organic form of nitrogen in soil represents 90%, it cannot be assimilated by plants [55]. This accessibility problem made the use of industrial N fertilizers essential for enhancing plant productivity. However, with all the environmental issues we encounter, using biological methods could be an important alternative to replace the intensive use of chemical fertilizers [54].

Biological Nitrogen Fixation (BNF) is accomplished by diazotrophs, which can be free-living microorganisms, such as *Acetobacter* spp., *Azospirillum* spp., *Azotobacter* spp., *Bacillus* spp., *Citrobacter* spp., *Clostridium* spp., *Enterobacter* spp., *Klebsiella* spp., *Pseudomonas* spp., *Serratia* spp., or *Streptomyces* spp., or it can also be accomplished by symbiotic microorganisms interacting with some dicotyedonous species (actinorhizal plants), such as *Frankia* spp., some cereal grass-associated microorganisms, e.g., *Azospirillum* spp., *Herbaspirillum* spp., and *Azoarcus* spp., or also rhizobia entering in interaction with legumes [56].

Rhizobia have been recognized for their ability to decrease annual nitrogen inputs from various food crops globally, estimated at 53 million tonnes [57].

The nitrogen fixation ability by rhizobia is principally performed by *nif* (genes encoding for components of the nitrogenase), *fix* (genes for symbiotic nitrogen fixation), and *nod* (genes for nodulation) genes through the conversion of atmospheric nitrogen N_2 to ammonia by the action of the nitrogenase enzyme [53,55].

This association is initiated by the secretion of root substances, called flavonoids, inducing the expression of rhizobial *nodD* genes, which control the transcription of additional nodulation genes, e.g., *nod*, *nol*, and *noe*. Eventually, serial gene clusters contribute to N_2 fixation as shown in Figure 1, starting with *nifHDK*, controlling the nitrogenase, *nifA*, *fixA*, *fixLJ*, and *fixK* as transcriptional regulators, and various other genes involved in nitrogen fixation [54].

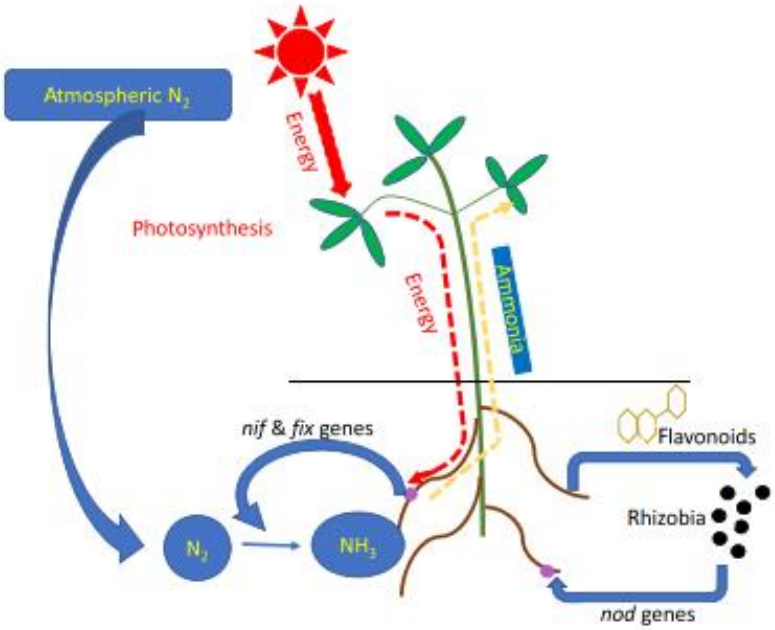

Figure 1. Schematic illustration of the symbiotic N_2 fixing process in legumes, resulting from the interaction with rhizobia [53].

Rhizobium–legume association can also be beneficial for non-legumes, such as cereals grown in mixed intercropping, or also crops rotated with symbiotic legumes through a direct transfer of N_2 fixed by rhizobia [58]. Antoun et al. [6] experimentally inoculated radish with *Bradyrhizobium japonicum*, generating a 15% increase in the plant dry matter. Furthermore, Vargas et al. [24] studied the nitrogen-fixing activity through the acetylene reduction assay in wild rice (*Oryza breviligulata*) inoculated with *Bradyrhizobia*.

Similar studies on the rhizobia association with non-legumes in order to increase their plant-host range have been carried out. *Rhizobium* infection and symbiotic recognition in the soil is mainly controlled by root hairs and most specifically the Nod factor signals secreted by the bacteria. These signals induce the inclination of root hairs, which facilitate the entrance of rhizobia into nearly all legumes.

Dent and Cocking [1] studied the control of *Rhizobium* infection in *Trifolium repens* (white clover), which is a non-host to *Rhizobium*, using the enzymatic degradation of root hair's cell wall. Therefore, the inoculation of white clover with *Rhizobium* 101/u or *R. loti* and a mixture of cellulase-pectolyase enzyme alongside polyethylene glycol allowed the formation of N_2-fixing nodules.

Identical enzyme treatment has been studied on oilseed rape, which induced the formation of nodules [1]. However, nitrogenase activity remained significantly low because rhizobia exclusively invaded deceased cells, and their ability to fix nitrogen was inhibited by the presence of oxygen [1,59].

4.1.2. Phosphate Solubilization

After nitrogen, phosphorus is considered as the second limiting macronutrient for plant growth and development [60]. It has the main role in plant's molecular biology, and it does not just enter in the formation of macromolecules, such as DNA, RNA, ATP, but also in cell division, the formation of new tissue, and energy transfers by plants [61].

Despite its abundant presence in soils, phosphorus accessibility is relatively limited due to the fact that the majority of phosphorus in soils exists in insoluble forms (inorganic bound, fixed or labile, or organic bound) [62].

It has been found by Vargas et al. [24] that only less than 5% of soil phosphorus is available for uptake by plants [24]. The only two chemical forms of (P) that can be absorbed by plants are monobasic (HPO^{4-}) and dibasic (HPO_4^{2-}) ions [21].

One of the most important PGPR traits is their ability to convert phosphates from insoluble to soluble forms. Microbes that are considered as the most efficient phosphate solubilizers are rhizobia, including *R. leguminosarum*, *R. meliloti*, *M. mediterraneum*, *Bradyrhizobium* sp., and *B. japonicum* [54], along with *Bacillus*, *Pseudomonas*, and some fungi, such as *Aspergillus* and *Penicillium* [63].

Numerous mechanisms of action are involved in the P solubilization activity of PGPR (Figure 2), and these depend on the type of P available on soil, regarding whether it is organic or inorganic P.

1. Inorganic P solubilization mechanisms
    - Organic Acid Production
      The production of organic acid is considered as the initial mechanism to be used in order to solubilize inorganic phosphorus [64]. This phenomenon depends mostly on the soil's pH.
      Phosphate Solubilizing Microbes (PSM) produce, during their growth, some organic acids that have the potential to decrease the soil's pH. This acidification enables the solubilization of rock phosphate [64].
      It has been established that the acids produced by PSM are mainly glycolic (monocarbocyclic hydroxy acids), 2-keto gluconic (monocarboxylic), acetic acids, malic (dicarboxylic hydroxy acids), oxalic acid, citric acid, and succinic acid (dicarboxylic acid). However, in the midst of all these acids, gluconic acid has been found to be the lead acid to be used in the P solubilization mechanism [44,64].
    - Inorganic Acid Production
      Inorganic acids do not appear to be as effective as organic acids for the solubilization of P. Nitrifying and sulfur-oxidizing bacteria generate inorganic acids during the oxidation of nitrogenous or inorganic sulfur compounds. These inorganic acids then interact with insoluble phosphate compounds, transforming them into soluble variants [64].
    - Chelation
      Fulvic, humic, and 2-keto gluconic acids are some known acids that play the role of chelators of substances, such as aluminum, calcium, and iron cations, which facilitate the inorganic phosphorus solubilization. These acids are liberated all along the processes of plant debris degradation by microorganisms [64].
      Besides the previously mentioned inorganic P solubilization mechanisms, there are other mechanisms, such as mineral P solubilization through proton (H^+) extrusion. This process effectively lowers the pH of the environment without requiring the release of acids [63]. Furthermore, microorganisms that produce exopolysaccharides have the ability to form complexes with metals, resulting in the solubilization of metal phosphates [64].
2. Organic P Solubilization Mechanisms

Organic P immobilization can be achieved by multiple microbial enzymes, such as phytase, phosphohydrolase, and phosphonatase. These enzymes provoke the lysis of many organic O compounds present freely in soil. Hence, the release of phosphate ions that are ready for the assimilation occurs [64].

4.1.3. Phytohormones Production/Regulation (Plant Growth Regulators)

Plant hormones, also known as phytohormones, are natural organic compounds produced by plants, and they play the role of chemical messengers that influence plant growth and its interaction with the environment.

These plant growth regulators (PGR) could be produced in some specific parts of the plant, and then they are transported to different organs, where they can influence many physiological, biochemical, and morphological processes [16].

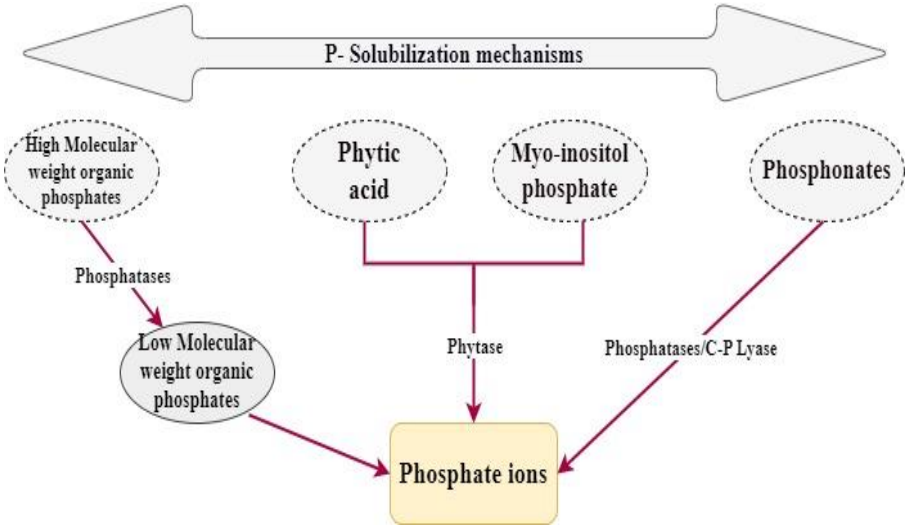

Figure 2. Mechanism of phosphate solubilization by microorganisms.

It has been proved by many studies that phytohormone production by several bacteria is one of the most interesting and important mechanisms of plant growth promotion by bacteria [49,65,66].

There are five main groups of hormones: auxins, gibberellins, cytokinins, ethylene, and abscisic acid [67].

- Auxins

Auxins are powerful molecules that are consistently synthesized by plants [56]. They are known as key regulators of cell division stimulation and elongation [24], as well as abiotic stress control [56].

It is well known that PGPR play major role in the enhancement of the plant physiology, differentiation, expansion, and cell division by their ability to produce auxins and, particularly, Indole Acetic Acid (IAA) [56]. Over 80% of rhizosphere bacteria, such as *Azospirillum*, *Pseudomonas*, *Klebsiella*, *Rhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Paenibacillus*, and *Bacillus*, actively produce and release auxins [24,68].

IAA produced by PGPR is a signaling molecule included in the bacteria's physiology, with a main role in direct plant growth promotion [61], which is performed by controlling the root initiation and morphogenesis, cell elongation and differentiation, flowering, apical dominance, and many more plant development processes [16].

The IAA produced by rhizobacteria has the biggest effect on the roots. It was observed that the post-inoculation by PGPR improved the plant's nutrition and soil exchanges [20]. The amount of IAA produced by rhizobia depends on the plant flavonoids and phenolic acids released in the rhizosphere, such as protocatechuic acid, 4-hydroxybenzaldehyde, and p-coumaric acid [37].

Rhizobia producing IAA might include several pathways of IAA biosynthesis [20]. Therefore, the bacterial effect on the plant is mainly influenced according to the pathway chosen [30]. It is known that the main precursor for IAA production is tryptophan. Tryptophan-dependent pathways are identified as five different routes, such as indo-3-pyruvate (IPyA), tryptophan side-chain oxidase (TSO), indole-3-acetamide (IAM), which is related to pathogenic bacteria, tryptamine (TAM), and indole-3-acetonitrile (IAN) [63].

Tryptophan-independent pathways are still less known. However, it has been reported that *Azospirillum brasilense* is capable of producing 10% of IAA using tryptophan-dependent pathways, while 90% of IAA is produced without including the tryptophan as precursor [20]. Additionally, in spite of the fact that the tryptophan production was blocked, maize mutants showed a high level of IAA produced, which confirmed the tryptophan-independent path [24].

The production of IAA by rhizobia is regulated by specific genes. The biosynthesis of IAA in rhizobia primarily involves the indole-3-pyruvate pathway (IPyA), which has been identified in *Bradyrhizobium*, *Rhizobium*, and *Azospirillum* [66,69].

For a start, the tryptophan is converted by the enzyme aminotransferase into IpyA (transamination), and then it is decarboxylated through the indole-3-pyruvate decarboxylase (IPDC) to indole-3-acetaldehyde (IAAld), which is eventually oxidized into IAA [66]. The key enzyme (IPDC) is regulated by the gene *ipdc* that has been characterized in *Azospirillum lipoferum* [69].

The second important and well-known pathway is the indole-3-acetamide pathway, which consists of two steps, where the tryptophan is first converted to IAM by the action of the enzyme tryptophan-2-monoxygenase, then, the enzyme IAM hydrolase takes place and converts IAM to IAA [69].

The genes encoding for the two enzymes are, respectively, *iaaM* and *iaaH*, and they were identified in *Rhizobium* sp. and *Bradyrhizobium* sp. [66].

- Cytokinins

Cytokinins stimulate cell division and enlargement, shoot and root elongation, root hair formation, leaf expansion, and chlorophyll accumulation during plant development [70]. Moreover, recent studies have found that, in addition to the plant growth promotion and nutrient optimization by cytokinins, they can also be involved in plant defense responses and in delaying leaf senescence [71].

Cytokinins are purine derivatives, and the most abundant CKs are adenine-type, with a replacement in the N6 position, either with an isoprenoid or with an aromatic side chain [20]. Some of the well-known CKs are trans-zeatin (6-(4-hydroxy-3-methyl-trans-2-butenylamino) purine), i6Ade (6-(3-methyl-2-butenylamino) purine), dihydrozeatin (6-(4-hydroxy-3-methyl-butylamino) purine), and cis-zeatin (6-(4-hydroxy3-methyl-cis-2-butenylamino) purine) [72].

Compared to the auxins, cytokinins are usually present in small amounts, and their production by PGPR was less identified due to the limitations of their quantification methods [73].

In spite of their identification restrictions, it has been found that CKs can be released by almost 90% of the rhizospheric microorganisms cultured in vitro [54]. When tested in-vitro, several plants associated microorganisms, e.g., *Rhizobium* sp., *Azotobacter* sp., *Pantoea agglomerans*, *Rhodospirillum rubrum*, *Pseudomonas fluorescens*, *Bacillus subtilis*, and *Paenibacillus polymyxa*, showed the production of cytokinin, together with some other growth promoting substances [30].

Additionally, Nieto and Frankenberger [74] have found that *Azotobacter chroococcum* produce some CK's precursors, particularly isopentyl alcohol (IA) and adenine (ADE), when cultivated under controlled field conditions, and they convey crop growth and development [16].

Furthermore, some reports concluded that *Rhizobium* strains (*Rhizobium leguminosarum*) are some of the most efficient cytokinin producers [54]. Kisiala et al. [75] have confirmed the production of different types of CKs, including CK-nucleotides (CK-NT), ribosides (CK-RB), methyl-thiol CK (CK-MET), and free bases (CK-FB) by strains of *Sinorhizobium* sp. and *Mesorhizobium loti*. However, the CK-FB was found to be the most biologically active form among all the other cytokinin, despite CK-MET being the predominant type of rhizobial CK [75].

- Gibberellins

Gibberellins encompass a vast category of phytohormones, consisting of 136 distinct molecules. Among these, one hundred and twenty-eight are derived from plants, seven are derived from fungi, while a mere four gibberellins (GA1, GA3, GA4, GA20) have been attributed to bacterial sources [20].

Just as with the auxins and cytokinins, gibberellins are a group of phytohormones that is associated with many plant mechanisms, namely, seed germination, flowering, seed

dormancy regulation, ripening of fruit, root growth promotion, and abundance of root hair. However, to date, there is no known function for gibberellins in fungi and bacteria [56].

Gibberellins are composed of a complex tetracarbocyclic diterpenes molecules that consist of a skeleton of 19–20 carbon atoms as a common structure [20].

The exact mechanism of gibberellic acid (GA) synthesis within nodules is complex and can vary, depending on the specific host plant and associated symbiotic microorganisms. In general, the synthesis of GA within nodules involves a series of enzymatic reactions (Figure 3).

Gibberellins production has been confirmed in diverse bacterial genera, e.g., *Azospirillum* sp., *Rhizobium* sp., *Acetobacter diazotrophicus*, and *Bacillus* sp., using quite a few physiochemical methods, namely, Gas Chromatography–Mass Spectroscopy (GC–MS), High-Performance Thin-Layer Chromatography (HPTLC), and High-Performance Liquid Chromatography (HPLC), in order to detect and quantify the levels of gibberellins [20].

Researchers have reported the presence of the gene cluster included in the biosynthesis of gibberellins, most commonly known as cytochrome p450, in *Bradyrhizobium japonicum* [76] and *Rhizobium* NGR234 [75]. Additionally, Lucas et al. [77] have proved the presence of GA synthetic genes in numerous species, for instance, *Bradyrhizobium japonicum*, *Mesorhizobium loti*, *Rhizobium elti*, and *Sinorhizobium fredii*.

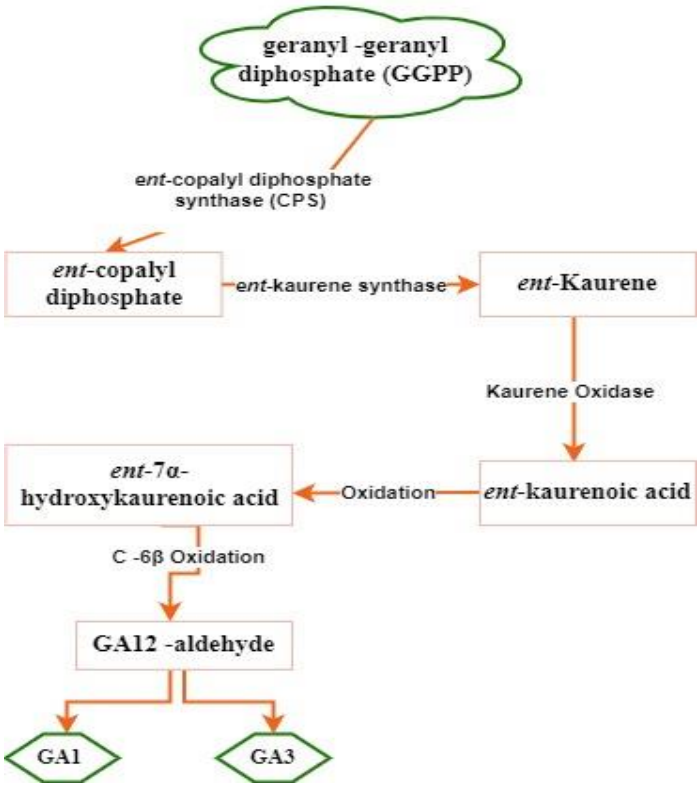

Figure 3. GA synthesis mechanism in nodules of *Mesorhizobium loti* through an enzymatic synthesis pathway [77].

Just as with the previous phytohormones, gibberellins produced by PGPRs are considered as stimulators of plant growth and development. As reported by Lucas et al. [78], the increase in GA3 levels in roots and boosting their growth has been related to *Azospirillum* strain inoculation in maize roots.

Moreover, studies concluded on the action of gibberellins in alleviating abiotic stress, particularly for their role in plant thermotolerance [56]. Under conditions of high temperature, *Bacillus tequilensis* strain SSBO7, associated with soybean, released GA1, GA3, GA5, GA8, GA19, GA24, and GA53, and, as a consequence, shoot length and biomass were improved [79].

- Abscisic acid

Abscisic acid is a terpene hormone class that consists of three isoprene units, also called sesquiterpenes. Abscisic acid acts especially as a plant growth inhibitor. For instance, ABA plays an essential role in senescence processes, inducing seed dormancy, stomatal closure, and stimulating proteins storage inside the seeds during dormancy [54]. The importance of ABA in the rhizosphere appeared under abiotic stress, such as drought stress and freezing temperatures. Its production is accentuated under these conditions in order to regulate plant capacity to survive in harsh environment [56].

The production of abscisic acid is carried out in several parts of the plant, primarily in the leaves, stems, seeds and fruits, as well as partially in the chloroplast [56]. However, its production seems to be different from one plant organ to another and during certain specific phases (ABA).

Abscisic acid has been detected using TLC or radio-immunoassay as a product of many PGPRs, mainly *Rhizobium* sp., *B. japonicum*, *Azospirillum* sp., *Achromobacter xylosoxidans*, *Bacillus pumilus*, and *Lysinibacillus halotolerans* [80,81].

Boiero et al. [81] have found that *B. japonicum*, commonly used in Canada, the USA, and South America for soybean and non-legume inoculations, has the ability to produce ABA when quantified with a physiochemical methodology in pure cultures.

- Ethylene

Just as with all other plant regulators, ethylene is also considered as an essential phytohormone for plant growth and development. Out of all phytohormones, ethylene is the only one in the gaseous state [62].

At low concentrations, ethylene plays a role in plant growth by regulating many physiological responses in plant, including seed germination stimulation, adventitious roots and root hair promotion, as well as breaking seed dormancy [56]. However, high ethylene concentrations provoke the inhibition of the root elongation process, premature senescence, and abscission. Moreover, the nodules' formation process in leguminous plants, along with symbiotic N_2 fixation, are inhibited [16].

In addition to its plant growth regulator role, ethylene is also known as a stress hormone, and it is synthetized by plants under either biotic or abiotic stress, including drought, salinity, flooding, temperature gradients, or also in response to pathogen interactions [56].

Ethylene could be produced by many bacterial species along with the aminocyclopropane-1-carboxylate (ACC) deaminase, which is the direct precursor of ethylene biosynthesis in plants, and consequently, plant growth promoting rhizobacteria play a key role in adjusting/lowering the levels of ethylene in plants [73].

Some rhizobia are able to produce ACC deaminase, hydrolyze ACC, and thus generate ammonia and alpha-ketobutyrate as final products, which can be used eventually as source of carbon and nitrogen [54].

It has been proved that many Rhizobial strains, such as *R. leguminosarum* bv. *viciae*, *S. meliloti*, *R. gallicum*, *B. elkani*, *B. japonicum*, *M. loti*, *R. japonicum*, and *R. hedysari* have the ability to produce ACC deaminase [54].

Contesto et al. [82] studied the plant growth promoting activity of strains of *R. leguminosarum* bv. *viciae* and *M. loti* and have confirmed their ability to increase the number of lateral roots in *Arabidopsis thaliana* through adjusting ethylene levels in the infection area.

Additionally, research has revealed that the presence of ACC deaminase, which is encoded by the *acdS* gene and regulated by the *nif* promoter, enhances the nodulation capacity of *Mesorhizobium* strain on chickpea. This association can be directly attributed to the involvement of the *nif* gene in the nitrogen fixation process [54,63].

4.1.4. Siderophores Production

Iron is a crucial micronutrient for all life forms and also is abundant in the lithosphere, being the fourth most common element in earth crust by weight [56]. In plants, iron is indispensable for chlorophyll synthesis and biosynthesis, it is involved in DNA synthesis,

and it has a key role in electron transport, redox reaction, detoxification of oxygen radicals, and many more biochemical processes [30].

Despite its huge abundance, iron is not accessible to plants due to its presence under insoluble forms of hydroxides [$Fe(OH)_3$] and oxyhydroxides [FeO(OH)] [83], while the plant root tends to absorb iron under its reduced form (ferrous Fe^{2+}) [62].

Siderophores released by several rhizobacteria play key roles in overcoming this situation and increase the iron accessibility for plants. Siderophores are of low molecular weight (400–1000 Da), water soluble, and iron chelating molecules with high affinity for the ferric form Fe^{3+} (Kd = 10^{-20}–10^{-50}) [71]. These siderophores have a high affinity, which facilitates the sequestration and transportation of iron into the cells and, thus, enhances plant growth [54]. Microbial siderophores, which are regulated by a specific *sid* gene [63], belong mainly to four classes, viz. carboxylates, hydroxamates, phenol catecholates, and pyoverdines, depending on their structure, iron correlating functional groups, and types of ligands [30]. Moreover, there are some siderophores called mixed siderophores, which result from a combination of structures of two main classes, as depicted in Figure 4 [68].

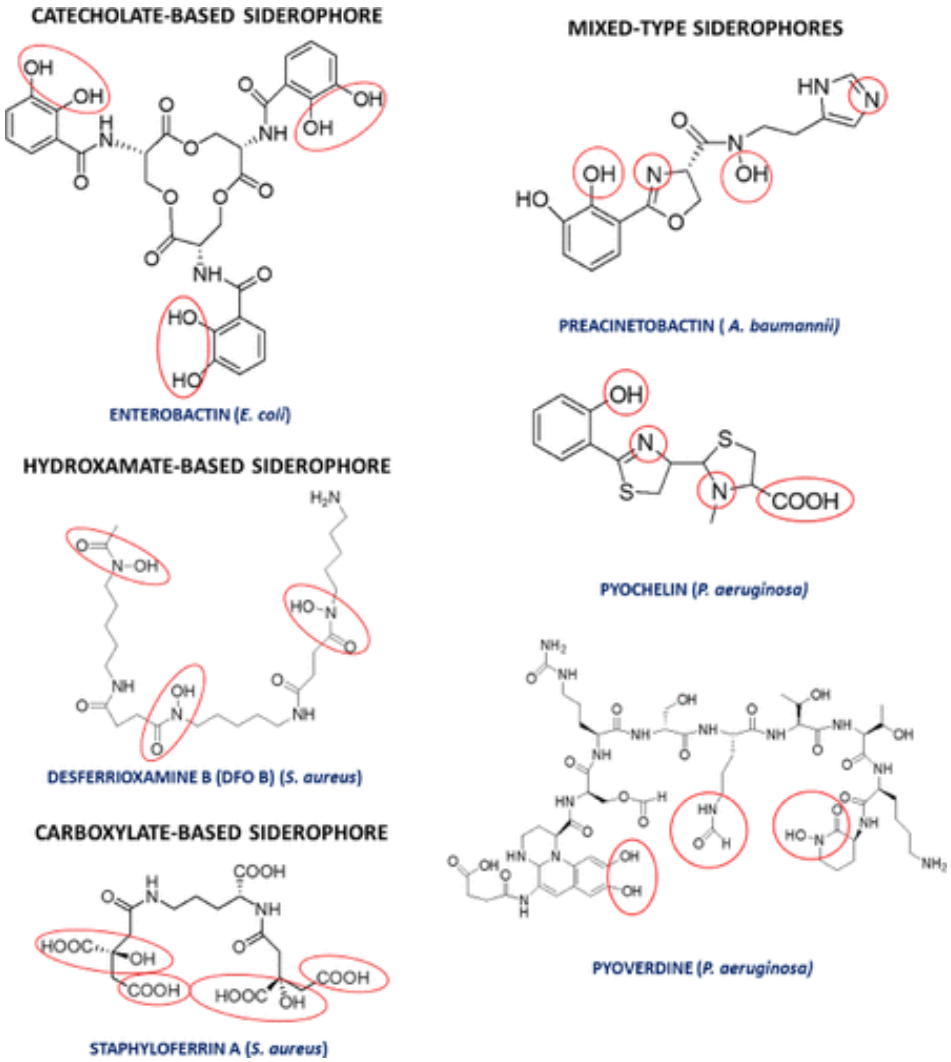

Figure 4. Classification of siderophores based on their chemical structures. The metal-binding subunits are circled in red. Reprinted with permission from Kircheva, Nikoleta, and Todor Dudev. "Gallium as an antibacterial agent: a DFT/SMD study of the Ga^{3+}/Fe^{3+} competition for binding bacterial siderophores". Inorganic Chemistry 59.9 (2020): 6242–6254. Copyright 2023 American Chemical Society [84].

Rhizobial siderophores have been considered mainly as chelators that enhance iron nutrition and plant growth. Siderophore-producing bacteria are identified as efficient biocontrol agents (BCAs), and they have been involved indirectly in the inhibition of pathogen development through their Fe^{3+} ion-binding ability, which limits iron availability to plant pathogens and fungi that are not able to assimilate the iron–siderophore complex, thus preventing their growth [20,85].

Many reports have demonstrated the successful inhibition of plant pathogens by rhizobia that produce siderophores. Ten strains of *Bradyrhizobium* nodulating peanut (*Arachis hypogaea*) were evaluated by Deshwal et al. (2003), and three of them were able to produce siderophores. Additionally, all three strains of *Bradyrhizobium* effectively inhibited the radial growth of the fungus in vitro.

In another study, Omar and Abd-Alla [86] found a similar result after evaluating 20 *Bradyrhizobium* and *Rhizobium* isolates against *Fusarium solani*, *M. phaseolina*, and *R. solani*. The antagonistic activity against the fungi has been shown by all the isolates both in the iron-rich and iron-deficient media. In this case, the potential of siderophores' production seems to function more as a competitive advantage. This enables PGPR to effectively establish colonization within the rhizosphere, emphasizing factors other than a direct iron deprivation mechanism.

Moreover, siderophores can also improve plant growth in contaminated soils. In the iron uptake process, several heavy metals, such as aluminum, cadmium, copper, lead, and zinc, as well as with radionuclides, including uranium, can interfere and cause a toxic effect [87]. Siderophores have binding ability and form a complex siderophore–metal, which increases the concentration of soluble metal. Consequently, bacterial siderophores help to alleviate the stresses imposed on plants by heavy metal-contaminated soils [30].

Roy and Chakrabartty [88] studied the production of siderophores by *Rhizobium* sp. under high concentration of Al^{3+}. Apart from enhancing iron availability, siderophores produced by rhizobia also have the capability to form complexes with Al^{3+}, thereby mitigating its toxicity. Rogers et al. [89] observed analogous findings that demonstrated the efficacy of vicibactin, a hydroxamate siderophore, produced by *R. leguminosarum* bv. *viciae*, in alleviating aluminum toxicity. The complex has the potential to be transported into the bacterial cytoplasm. Nevertheless, it is unlikely to cause toxicity within the intracellular environment, as aluminum cannot be released from the complex through reduction. Furthermore, the complex accumulates as a non-toxic molecule, and, even if it is released, Al^{3+} will precipitate as $Al(OH)_3$ at the slightly alkaline pH of the cytoplasm [89,90].

4.2. Indirect Mechanism

4.2.1. Antibiotics Synthesis

PGPRs play a vital role in plant protection. One of the fundamental methods of PGPR as biocontrol agents is the production of antibiotics. Antibiotics are antagonistic compounds produced by microorganisms against phytopathogens [91].

Antibiotics synthetized by PGPR comprise a diverse group of low-molecular-weight organic substances that negatively impact the growth or metabolic activities of other microorganisms. They are also considered to have antiviral, cytotoxic, insecticidal, anthelmintic, and phytotoxic effects and are produced due to the interaction between microorganisms in order to survive under competition or predation [85].

For biological control, the widely known antibiotics are 2,4 diacetylphloglucinol (DAPG), phenazine, pyoluteorin, pyrrolnitrin, tropolone, tensin, oomycin A, cyclic lipopeptides (all of which are diffusible), and hydrogen cyanide (HCN, which is volatile) [91].

Numerous microorganisms are able to produce different extracellular metabolites with inhibitory actions even at low concentrations, in particular, PGPR (*Bacillus* sp.) participate in the suppression of phytopathogenic microorganisms by producing several antibiotics, such as mycosubtilin, bacillomycin D surfactin, and fengycin, while antibiotics produced by fluorescent *Pseudomonas* include pyoluteorin, phenazines, viscosin, and massetolide A [92].

Many studies have proved the role of antibiotics produced by rhizobia in phytopathogen control. *R. leguminosarun* bv. *trifolii* T24 has been reported to release the peptide antibiotic trifolitoxin (TFX) [93]. In another study, Chakraborty and Purkayastha [94] showed the effective suppression of *M. phaseolina* infecting soybean by the direct action of antibiotic rhizobitoxine produced by *Bradyrhizobium japonicum*. *Rhizobium* sp. strains ORN 24 and ORN 83 were considered as bacteriocin producers, with antagonistic activities against *Pseudomonas savastanoi*, which is responsible for olive knot disease [24]. Moreover, the growth and yield of *Brassica campestris* were observed to be enhanced by the presence of *Mesorhizobium loti MP6*, a bacterial strain isolated from the root nodules of *Mimosa pudica*. Moreover, *Mesorhizobium loti MP6* isolate demonstrated significant antagonistic properties against *Sclerotinia sclerotiorum*, a pathogen known for inducing white rot in Brassica campestris. Importantly, a prolonged incubation period resulted in a remarkable 75% inhibition of *S. sclerotiorum* growth.

Antibiotic production is closely related to the metabolic status of the cell, which is also linked to nutrient availability, as well as environmental stimuli, including minerals, pH, temperature, and trace elements, particularly zinc levels (Zn), which may influence the genetic stability of bacteria, which can impact their capacity to synthetize secondary metabolites [62]. The mechanism of action of bacterial antibiotics is to cause membrane damages by inhibiting the synthesis of pathogen cell walls, which consequently influence the cell membrane structures [30]. For instance, *Rhizobium* spp., *Azospirillum* spp., *Klebsiella pneumoniae*, *Yersinia* spp., and *Frankia* spp. were found to possess a pectinolytic ability [56].

In addition to the use of microbial antagonists against phytopathogens in agricultural crops as an alternative to chemical pesticides [20], certain antibiotics that are synthesized by PGPR are now being investigated for their potential applications in experimental pharmaceuticals. This emerging area of research holds promise in discovering new compounds to combat the issues arising from multidrug-resistant pathogenic bacteria [62].

4.2.2. Induction of Systemic Resistance

Including their plant growth promoting ability, PGPR are also capable of enhancing the defensive system in their host plant against a wide range of phytopathogens—for instance, fungi, pathogenic bacteria, viruses, or, also, in some cases, insects and nematodes, naturally existing in soil [62,85].

Plant-induced resistance is classified into two major phenomena, Systemic Acquired Resistance (SAR) and Induced Systemic Resistance (ISR), which can be distinguished based on the nature of the stimulant, as well as the regulatory mechanism implicated [30].

- Systemic Acquired Resistance (SAR)

Systemic Acquired Resistance (SAR) is a defense mechanism that can be induced by the presence of a broad range of either pathogenic or non-pathogenic microorganisms or even chemicals accumulated in the rhizosphere, including salicylic acid (SA), 2,6-dichloro-isonicotinic acid (INA), and S-methyl ester (BTH) [61]. Various genes encoding for pathogenic-related proteins (chitinase and glucanase) are involved in salicylic acid signal transduction [30].

- Induced Systemic Resistance (ISR)

Instead of requiring the pathogenic-related proteins or salicylic acid accumulation, ISR depends on jasmonic acid (JA) and ethylene signaling pathways [30]. Similar to SAR, the ISR defense mechanism is also induced against several types of elicitors. However, it does not generate noticeable symptoms on the PGPR host plant [62].

Many studies have reported the ability to induce systemic resistance in plants by rhizobial species, such as *R. etli*, *R. leguminosarum* bv. *phaseoli*, and *R. leguminosarum* bv. *trifolii* [54]. Díaz-Valle et al. [18] studied the inoculation of common bean with *Rhizobium etli* which as a result stimulated the plant resistance to infection by *Pseudomonas syringae pv. phaseolicola* through the activation of defense related genes.

Elbadry et al. [95] inoculated Faba bean (*Vicia faba* L.) with *Pseudomonas fluorescens* FB11 and *Rhizobium leguminosarum* bv. *viceae* FBG05 to study their systemic resistance induction to bean yellow mosaic potyvirus (BYMV). A significant drop in virus concentration, as well as a remarkable decrease in the Percent Disease Incident (PDI), were proved in the inoculated plants. The association of PGPR strains with *Rhizobium* evaluated by Dutta et al. [96] showed an optimistic result. When inoculated with a mixture of PGPR *B. cereus* or *P. aeruginosa* and *Rhizobium*, pigeon pea (*Cajanus cajan*) showed a high resistance level when exposed to the pathogenic *Fusarium udum* compared to the individual elicitor and the non-inoculated control.

4.2.3. Production of Cell Wall-Degrading Enzymes

Among the biocontrol mechanisms most used against soil borne pathogens, there is the production of cell wall-degrading enzymes [20]. The release of lytic enzymes, such as β-1,3-glucanase, proteases, chitinases, lipase, or cellulase, result in the suppression of pathogens' growth and activities by degrading their cell wall [83].

A variety of PGPR are known for their ability to produce cell wall-degrading enzymes. For instance, *Paenibacillus* spp. and *Streptomyces* spp. strains were able to inhibit the development of *Fusarium oxysporum* through the production of β-1,3-glucanase [56]. Moreover, it is known that the pectinolytic activity is generally related to phytopathogenic bacteria. However, some non-pathogenic *Rhizobium* species were also found to degrade pectin [58]. Furthermore, Kumar et al. [97] reported that *Sinorhizobium fredii* KCC5 and *Pseudomonas fluorescens* LPK2 were able to produce β-1,3-glucanase and chitinase, which caused the growth inhibition of *Fusarium udum*.

4.2.4. Production of Hydrogen Cyanide (HCN)

Hydrogen cyanide is a secondary metabolite produced by many microorganisms, and it is a volatile compound that is known for its antimicrobial role and disease inhibition [98]. In association with glycine (main precursor of HCN), HCN synthetase enzyme forms HCN. The latter most likely acts as an inhibitor of electron transport, which eventually causes the suppression of the energy supply chain and consequently affects microorganisms' growth [99].

Several bacterial genera have shown cyanogenesis ability (cyanide production), for instance, *Rhizobium*, *Bacillus*, *Alcaligenes*, *Pseudomonas*, and *Aeromonas* [76]. However, fluorescent *Pseudomonas* is preponderantly identified as an HCN producer [100].

5. Examples of Successful Application of Rhizobia as Biofertilizer

The global growth population and increasing food demand are some important challenges that face the agricultural sector. Farmers all over the world need to continuously increase crop production, either by increasing the amount of land used for agriculture or by improving productivity on existing fields through irrigation, the use of cutting-edge techniques, such as precision farming, or the use of chemical fertilizers for a speedy rise in crop production [76]. However, the continuous use of chemical fertilizers causes ecological and health damage, such as soil contamination and water pollution, which in turn pose a threat to essential organic matter and reduces important soil nutrients [61].

In order to overcome this problem, scientific communities have introduced microbe-based fertilizers as cost-effective and eco-friendly alternatives. Due in large part to the negative effects of using chemical inorganic fertilizers, the use of biofertilizers in agriculture has recently gained significant attention from the research community and is now widely recognized as an environment-friendly practice [76].

Biofertilizers are recognized as products that are formulated using living microorganisms, either bacteria, fungi, or algae, that improve soil nutrient availability in plants [70]. The chosen microorganism can be used alone or in combination with other living cultures. The key advantage of biofertilizers is their direct application to seeds, plant surfaces, or

soil, where they can colonize the rhizosphere or inside of the plant, thus enhancing the supply of essential elements to the host plant [72].

Microorganisms that promote host–plant development through the inhibition of phytopathogens are considered as biopesticides. Consequently, some PGPRs represent both aspects, biofertilizers and biopesticides [101].

There are many different formulations of bacterial biofertilizers on the market. They can be found as granular powder or fluid-bed granules. In whatever way, the bioformulation of these bacterial inoculants should be appropriate for soil and plant tissue application [20]. In this regard, the use of bio-nanotechnologies may open up new possibilities for the creation of carrier-based microbial inoculants. Furthermore, nano-formulations use can increase biofertilizers' stability against high temperatures, desiccation, or also UV inactivation [102].

The most indicated use of biofertilizers in legumes is inoculation with *Rhizobium* spp. It has been present in the market since 1896, when Nobbe and Hiltner acquired a U.S patent associated with the utilization of pure cultures of rhizobia. They commercialized their patented culture under the name of "Nitragin" [103,104].

Strains of *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium*, and *Sinorhizobium* were considered as powerful PGPR for their role as biofertilizers [101]. In another study, it was found that *Rhizobium* (*R. etli* bv. *Phaseoli*, *R. leguminosarum* bv. *Trifolii*) and *Sinorhizobium* sp. improved corn growth, plant height, and grain yield of maize in several agroecological fields [16].

The evaluation of *Bradyrhizobium diazoefficiens*-based bio-inoculants confirmed their capacity to amplify soybean production, irrespective of the carrier material employed. Both liquid and peat-based bio-inoculants demonstrated the capability to augment nodulation and yield of soybean, surpassing the outcomes observed in the control group [105].

Ismail et al. [106], have developed a *Rhizobium* liquid biofertilizer technology. This has been reported to improve crop yields of green gram, black gram, pigeon pea and chickpea, soybean, and groundnut by 10 to 28%.

Under drought stress, *Faba bean* was inoculated with *R. leguminosarum* bv. *viciae* (F46) to study its impact [107]. The increase in growth parameters, including root dry weight, total N content, and relative water content, was notable. Additionally, inoculation with *Rhizobium* under water deficit significantly enhanced water use in chickpea [108].

In a study conducted by Chaintruel et al. [109], it was found that rice plants bio-inoculated with *Bradyrhizobium* exhibited a 20% increase in total biomass. Additionally, Hussain et al. [110] reported significant improvements in yield (43%), biomass (18%), and grain size (25%) in rice that was inoculated with *R. leguminosarum*.

In the field experiments conducted by Egamberdiyeva et al. [111], it was observed that all the treatments employed had a positive impact on the cotton yield when compared to the control group. Notably, the highest increase in cotton yield was observed after applying PSB *Rhizobium meliloti* URM1, resulting in a substantial improvement of up to 77% (equivalent to 285.7 g per plant).

The use of other supplements (e.g., fungicides, nutrients, and fertilizers) that could weaken the viability or efficiency of rhizobia is one of the main difficulties facing the application of *Rhizobium* inoculants [39]. To overcome this matter, the co-inoculation with a microbial consortium, rather than a specific species, has been widely reported to have a better result [112]. Consortia are defined as a mix of bacteria or fungi in order to ensure a wide range of applications and soil conditions [39]. As an example, Figueiredo et al. [113] reported that the co-inoculation with *Rhizobium* and another PGPR in common bean reduced the impact of drought stress and improved nodulation and nitrogen content. Moreover, the co-inoculation with *Bacillus* and *Rhizobium* strains can enhance bean, pigeon pea, and soybean nodule development and root structure [39].

6. Conclusions and Future Perspectives

To summarize, the urgency for refining the process of nitrogen delivery to cereal and non-leguminous crops is imperative for the progression of sustainable agriculture. This encompasses not just reducing pollution from ammonia, nitrates, and nitrous oxide, but also guaranteeing food security with a healthy environment. The integration of rhizobia into non-legume crops has demonstrated potential in enhancing plant growth, soil fertility, and overall crop yield. This is due to the ability of rhizobia to fix nitrogen in soil, which is a crucial element for plant development. Additionally, the symbiotic relationship established between rhizobia and the host plant's roots results in improved plant health, increased root growth, and enhanced stress tolerance.

However, it is important to be cautious about the potential risks related to the inoculation process, such as the possibility of rhizobia to negatively affect the host plant or to compete with native populations. To mitigate these risks, it is important to carefully choose a suitable rhizobia strain for the targeted crop, evaluate the conditions under which the inoculation will occur, monitor the process, and make adjustments as necessary to ensure long-term success.

In conclusion, the inoculation of rhizobia into non-legume crops has great promise in advancing agriculture by improving crop growth and soil fertility. By being mindful of the potential risks and benefits, it is possible to fully reap the benefits of this innovative technology and promote sustainable agriculture practices for the future.

Author Contributions: Conceptualization, S.F. and B.S.; validation, A.A., B.S. and S.B.; resources, A.A.; data curation, S.F.; writing—original draft preparation, S.F.; writing—review and editing, S.F. and S.B.; supervision, S.B., B.S. and A.A.; project administration and funding acquisition, A.A. and S.B. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Genetic Resources Section at ICARDA.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The original contributions presented in the study are included in the article. Further inquiries can be directed to the corresponding author.

Acknowledgments: We wish to thank the International Center for Agricultural Research in the Dry Areas (ICARDA) for allowing access to microbiology laboratory and the National Center for Scientific and Technical research (CNRST) for the financial support under the framework of the Research Excellence Scholarship Program.

Conflicts of Interest: The authors declare no conflict of interest.

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