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Rhizobia as a Source of Plant Growth-Promoting Molecules: Potential Applications and Possible Operational Mechanisms

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The symbiotic interaction between rhizobia and legumes that leads to nodule formation is a complex chemical conversation involving plant release of *nod*-gene inducing signal molecules and bacterial secretion of lipo-chito-oligosaccharide nodulation factors. During this process, the rhizobia and their legume hosts can synthesize and release various phytohormones, such as IAA, lumichrome, riboflavin, lipo-chito-oligosaccharide Nod factors, rhizobitoxine, gibberellins, jasmonates, brassinosteroids, ethylene, cytokinins and the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase that can directly or indirectly stimulate plant growth. Whereas these attributes may promote plant adaptation to various edapho-climatic stresses including the limitations in nutrient elements required for plant growth promotion, tapping their full potential requires understanding of the mechanisms involved in their action. In this regard, several N₂-fixing rhizobia have been cited for plant growth promotion by solubilizing soil-bound P in the rhizosphere via the synthesis of gluconic acid under the control of pyrroloquinoline quinone (PQQ) genes, just as others are known for the synthesis and release of siderophores for enhanced Fe nutrition in plants, the chelation of heavy metals in the reclamation of contaminated soils, and as biocontrol agents against diseases. Some of these metabolites can enhance plant growth via the suppression of the deleterious effects of other antagonistic molecules, as exemplified by the reduction in the deleterious effect of ethylene by ACC deaminase synthesized by rhizobia. Although symbiotic rhizobia are capable of triggering biological outcomes with direct and indirect effects on plant mineral nutrition, insect pest and disease resistance, a greater understanding of the mechanisms involved remains a challenge in tapping the maximum benefits of the molecules involved. Rather than the effects of individual rhizobial or plant metabolites however, a deeper understanding of their synergistic interactions may be useful in alleviating the effects of multiple plant stress factors for increased growth and productivity.

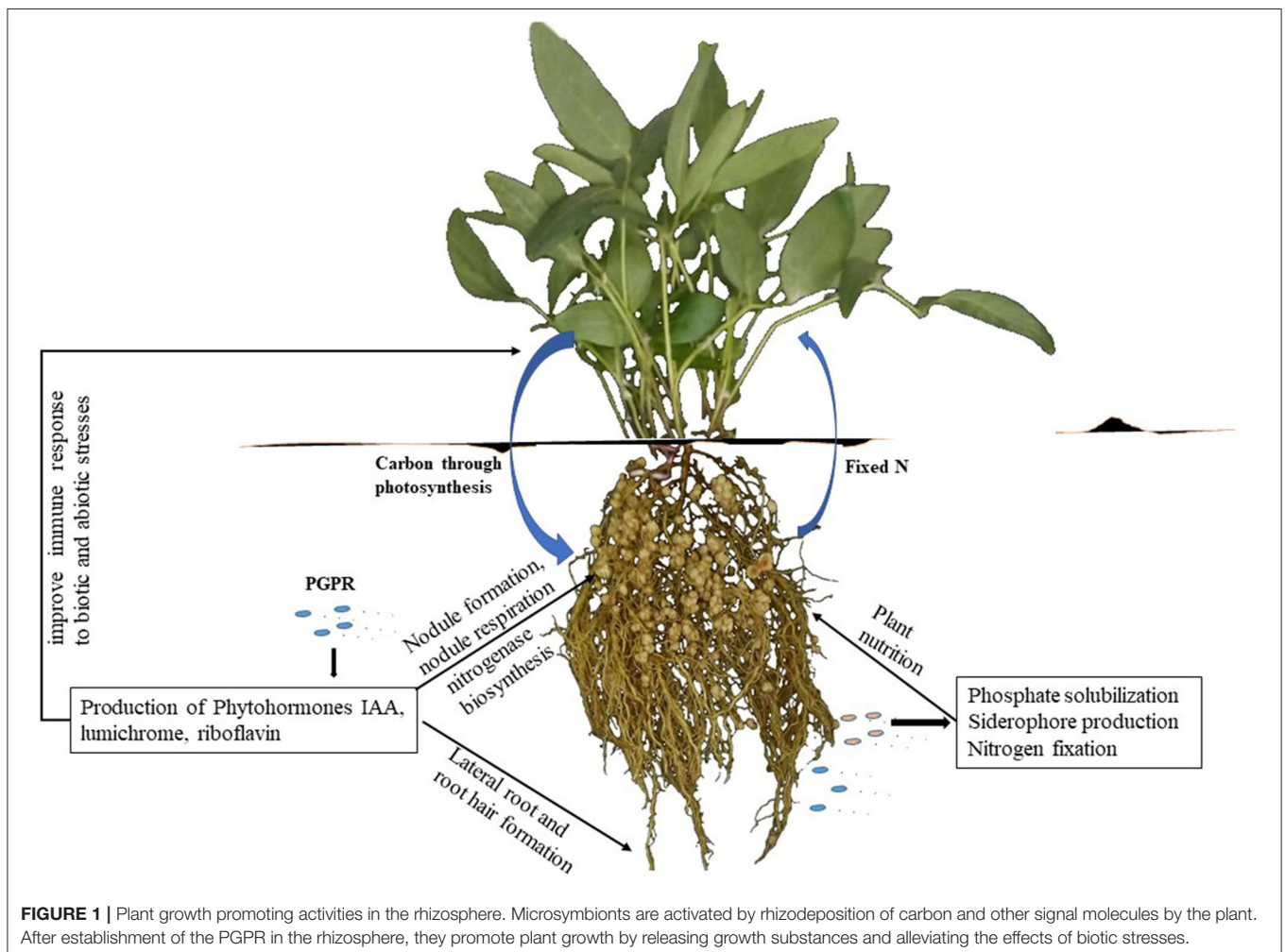
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INTRODUCTION

Nitrogen is an essential component of all amino acids and nucleic acids, thus making it an important plant nutrient element. Although the atmosphere consists of 78.1% N_2 gas, plants cannot use it unless it is converted into a usable form (Ferguson et al., 2010). Biological N_2 fixation (BNF) is a free source of N that can be exploited by resource-poor farmers for increased crop yields (Giller and Cadisch, 1995), making it one of the most important microbiological processes on earth; globally, $\sim 33\text{--}46$ Tg of N year⁻¹ is contributed by the legume-rhizobia symbiosis (Herridge, 2008). So far, 21 bacterial genera have been identified as nodule-forming microsymbionts (Wang et al., 2019a). These microsymbionts are distributed among major bacterial genera of the alpha-proteobacteria such as *Rhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Mesorhizobium*, *Ensifer* (*Sinorhizobium*), *Neorhizobium*, *Pararhizobium*, and *Allorhizobium*, collectively termed “rhizobia”, which can form symbiotic associations with diverse legumes. Similarly, species of the beta-rhizobia *Cupriavidus*, *Paraburkholderia*, and *Trinickia* can also form symbiotic relationships with members of the

Papilionoideae and *Caesalpinioideae* (LPWG, 2017; Sprent et al., 2017).

The formation of root nodules in symbiotic legumes involves a complex molecular signaling between the legume host and the rhizobial microsymbiont (Oldroyd et al., 2011). At the onset of nodule organogenesis, the rhizodeposition of flavonoid compounds from legume seed coats or root exudates induce the synthesis of NodD proteins which activate the transcription of genes needed to produce rhizobial lipo-chito oligosaccharide Nod factors (Andrews and Andrews, 2017). Upon perception of Nod factors by the plant, nodule organogenesis commences via the curling of the root hair tips leading to formation of an infection thread, mitotic division of root cortical cells, and consequently the formation of a nodule primordium (Oldroyd et al., 2011). Rhizobia penetrate the cortical cells via the infection thread and are eventually released into the nodule primordium housed in host-derived cells known as symbiosomes (Okubo et al., 2012). Rhizobia undergo differentiation into N_2 -fixing bacteroids which carry out the conversion of atmospheric N_2 into ammonia in a reaction catalyzed by the nitrogenase enzyme (Udvardi and Kahn, 1992). Whereas many rhizobia invade roots



via the infection thread, others utilize either “crack entry” or root epidermal cells as points of infection (González-Sama et al., 2004; Ardley et al., 2013; Bianco, 2014). When N₂ fixation commences, the bacteroids in root nodules supply the host legume with fixed N while receiving C compounds from host photosynthesis (Udvardi and Kahn, 1992).

Besides the provision of symbiotic N, some rhizobia also exhibit physiologically desirable traits such as the production of plant growth-promoting phytohormones, which include indole-3-acetic acids (IAA), cytokinins, gibberellins, riboflavin, lumichrome, Nod factors, etc (Table 1, Figure 1), all of which play diverse roles in enhancing plant growth and productivity (Dakora and Phillips, 2002; Berg, 2009). Thus, rhizobia confer several advantages on plants in addition to the provision of N from symbiotic interactions. The beneficial effects of rhizobia are mediated by the production of diverse

metabolites and enzymes that are directly or indirectly elicited by rhizobia and plants during nodule formation (Table 1). Of the plant growth-promoting molecules, the secretion of IAA, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, lumichrome, riboflavin and protons for phosphate solubilization have been suggested as important PGPR mechanisms underlying plant growth promotion (Figure 1) (Li et al., 2000; Matiru and Dakora, 2005; Gravel et al., 2007; Bal et al., 2013; Dakora et al., 2015). ACC deaminase is an enzyme that can decrease deleterious amounts of ethylene in higher plants, leading to increased productivity. Lumichrome and riboflavin are novel molecules from rhizobial exudates that are known to stimulate plant growth. On the other hand, IAA is an important member of the auxin family that is responsible for controlling plant physiological processes, including cell enlargement and division, tissue differentiation and light/gravity

TABLE 1 | Rhizobial metabolites and their functional roles in plant growth and development.

Rhizobial metabolite	Functional roles	References
Lipo-chito oligosaccharides (Nod factors)	*Stimulates seed germination Stimulates lateral root formation Induces the expression of flavonoid genes Regulates phytohormone biosynthesis and homeostasis in legumes Promotes root colonization by arbuscular mycorrhizal fungi Causes cell division and embryogenesis	Dakora, 2003; Prithiviraj et al., 2003; Kidaj et al., 2012
Riboflavin	*Increased bacterial root colonization and nodule occupancy Primed plant defense response Serves as vitamins for plants and bacteria Plant growth promotion	Yang et al., 2002; Dakora, 2003; Zhang et al., 2009; Angulo et al., 2013; Dakora et al., 2015
Lumichrome	Induces plant tolerance to drought through stomatal control Stimulates seedling growth Stimulates root CO ₂ production Promotes early tillering in sorghum plants	Dakora, 2003; Dakora et al., 2015
Nitrogenase-linked H ₂	Increases soil microbial population and carbon deposition	Dong and Layzell, 2001; Dakora, 2003
Indole-3-acetic acid (IAA)	*Promotes nodulation *Promotes root growth and plant development	Pii et al., 2007; Camerini et al., 2008; Spaepen et al., 2008; Stajković et al., 2011; Zúñiga et al., 2013
Cytokinin	Regulates nodule organogenesis Increases plant growth	Sturtevant and Taller, 1989; Ping and Boland, 2004; Giron et al., 2013; Gauthier-Coles et al., 2019
Gibberellin	Promotes nodulation in a dose-dependent manner Promotes seed germination and plant development	Bottini et al., 2004; Ferguson et al., 2005; Foo et al., 2016; McGuinness et al., 2019
Ethylene	Involved in plant defense response to pathogens Promotes plant growth	Dubois et al., 2018
Siderophore	Mobilizes of Fe for plant uptake Increases nodulation and N ₂ fixation Improves plant adaptation to pathogen and stress *Increased plant growth	Duhan et al., 1998; Arora et al., 2001; Katiyar and Goel, 2004; Rungin et al., 2012; Hao et al., 2014; Lebrazi and Fikri-Benbrahim, 2018
1-aminocyclopropane-1-carboxylate deaminase (ACC deaminase)	*Improves nodulation and plant growth via the regulation of ethylene production	Ma et al., 2003; Glick et al., 2007; Barnawal et al., 2014; Nascimento et al., 2019
Rhizobitoxine	Improves nodulation and plant growth via the regulation of ethylene production	Ma et al., 2003
Jasmonates	Has role in mycorrhizal and the legume-rhizobium symbiosis. Implicated in the autoregulation of nodulation in legumes. Improved plant response to drought stress	Hause and Schaarschmidt, 2009; Hettenhausen et al., 2015; Wang et al., 2019b
Brassinosteroids	*Regulates nodule number, probably through the regulation of ethylene production. Reported for plant growth promotion	Ferguson et al., 2005; Bartwal et al., 2013; Foo et al., 2016; McGuinness et al., 2019

NB: Superscript (*) before functional roles indicate experiments in which mutants for a particular trait were compared with wild-type, with one strain being negative for the trait. All other experiments either involved exogenous application of signal molecules, with or without gene expression studies.

responses (Teale et al., 2006; Shokri and Emtiazi, 2010) (Table 1).

Plant growth promoting rhizobacteria (PGPR) comprise a diverse group of bacteria that present growth benefits to plants through several mechanisms. The rhizosphere soil of plants tends to contain PGPR that are capable of releasing protons to solubilize soil-bound phosphorus for plant use, and are usually referred to as phosphorus-solubilizing bacteria (PSB) (Chaiarn and Lumyong, 2009). The detailed mechanisms by which microsymbionts alter plant growth have remained elusive. Nevertheless, efforts at identifying highly effective rhizobial strains that combine adaptation to their environment with plant-growth promoting traits could improve plant growth and inoculation response under field conditions. This review addresses the roles played by the secretion of siderophore, IAA, ACC deaminase, lumichrome, riboflavin and protons for P solubilization in plant growth promotion, especially during the legume-rhizobia symbiosis. The secretion of these molecules by non-rhizobial plant growth promoting bacteria leading to increased plant development is also discussed.

RHIZOBIAL SYMBIONTS AS PROMOTERS OF LEGUME PLANT GROWTH

Legumes that harbor efficient rhizobia in their root or stem nodules often meet their N requirements from N₂ fixation (Belane et al., 2011; Mohale et al., 2014). It is this symbiotic trait that gives legumes a superior survival advantage over their non-legume counterparts in N-depleted soils where other plant growth requirements are optimal. Nodulation and N₂ fixation in legumes are an interactive process which involve the action of rhizobial Nod factors; and during the process, some rhizobia may produce phytohormones such as IAA, gibberellic acid and cytokinins which present plant growth promoting effects (Bottini et al., 1989; Hayashi et al., 2014) (Table 1). Aside serving as signal molecules in the early stages of nodule formation, Nod factors isolated from *Rhizobium leguminosarum* were also found to increase seed germination, nodulation and plant growth in pea and vetch, as well as pod yield in pea (Kidaj et al., 2012). Similarly, Nod factors from *Bradyrhizobium japonicum* strain 532C increased germination and early plant growth in soybean and other non-leguminous crops; moreover, the parent culture of *Bradyrhizobium japonicum* strain 532C, but not its mutant deficient in Nod factor synthesis, was also found to induce similar growth effects on plants (Prithviraj et al., 2003). These observations clearly stress the multiple roles of rhizobial Nod factors as both signal molecules for nodulation and plant growth promoters in diverse crops. On the other hand, an IAA overproducing mutant of *Sinorhizobium meliloti* increased nodulation in *Medicago* sp. when compared to the parent strain, a report that stresses the involvement of this auxin in nodule formation aside its role in plant growth enhancement (Pii et al., 2007). Rhizobia can also increase nutrient availability in the root zone, especially N and P (Chebotar et al., 2001; Argaw, 2012), produce molecules that inhibit pathogens (Tavares et al., 2018), as well as alter rhizosphere chemistry involving

the regulation of ethylene levels (Nascimento et al., 2018). Moreover, aside the growth promoting effects of cytokinin from either plant or bacterial origin, they are also involved in the nodulation process of legumes as well as plant response to pathogens (Giron et al., 2013; Gauthier-Coles et al., 2019). In pea plants, deficiencies in gibberellins and brassinosteroids were associated with impaired nodulation, pointing to their significant role in the symbiotic process and subsequent plant growth (Ferguson et al., 2005; Foo et al., 2016). The significant roles of the legume-rhizobia symbiosis in enhancing plant growth and productivity has been demonstrated in several legumes including soybean (*Glycine max*), mung bean (*Vigna radiata*), chickpea (*Cicer arietinum*), common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*), Bambara groundnut (*Vigna subterranea*) and Kersting's groundnut (Dashti et al., 1998; Shaharoon et al., 2006; Chihaoui et al., 2015; Gyogluu et al., 2018; Mohammed et al., 2018; Abdiev et al., 2019; Dabo et al., 2019; Ibny et al., 2019). However, a major limitation to tapping the maximum benefit of the symbiosis is related to its susceptibility to diverse environmental stress factors. For example, even when rhizobial strains exhibit high N₂-fixing efficiency, their wider utilization in the field can be unpredictable, further hampering their adoption (Ulzen et al., 2016). Thus, tapping the maximum benefit of rhizobia for improved plant performance will require selection and/or engineering strains with multiple adaptive and plant growth promoting traits.

RHIZOBIAL PRODUCTION OF IAA AND N₂ FIXATION IN LEGUMES

Indole acetic acid (IAA) is an important member of the auxin family responsible for controlling plant physiological processes, including cell division and enlargement, tissue differentiation, and light/gravity response (Teale et al., 2006; Shokri and Emtiazi, 2010). Rhizobia together with other bacteria, fungi and algae are producers of auxins, especially IAA (Shokri and Emtiazi, 2010), a common by-product of L-tryptophan metabolism in several microorganisms, including rhizobia (Datta and Basu, 2000; Ghosh and Basu, 2006; Mandal et al., 2007). The level of IAA production can vary among rhizobial isolates; and endogenous phenolic acids such as protocatechuic acid, 4-hydroxybenzaldehyde and p-coumaric acid in root nodules could increase IAA synthesis by rhizobial isolates from *Vigna mungo* (Mandal et al., 2009). Microbes and plants can mutualistically benefit from each other, with the microbes releasing plant growth-promoting substances in return for photosynthate from the plant. For example, the N-fixed by bacteroids in root nodules is transported to the aerial parts of plants in exchange for the carbon compounds from photosynthesis (Udvardi and Kahn, 1992; Kaiser et al., 2015).

IAA production by cowpea-nodulating rhizobia from South Africa and Mozambique differed, with about 80% of the rhizobial symbionts producing from 0.64 to 56.46 µg/ml of IAA (Dabo et al., 2019). Similar variations in the levels of IAA synthesis were also reported for rhizobial symbionts of Bambara groundnut in South African and Malian soils (Ibny et al., 2019). However,

there is so far, no assessment of the relationship between rhizobial secretion of IAA and plant growth and/or grain yield. Nevertheless, Ali et al. (2008) showed that exogenous supply of IAA increased nitrogenase activity and leghemoglobin concentration in root nodules just as an engineered high IAA producing rhizobial strain showed significantly higher nitrogenase activity than the parent strain (Defez et al., 2019). Outside the legume symbiosis, bacterial production of IAA also presents growth promoting effects on non-legumes. In wheat for instance, root growth was reduced in plants treated with mutants of *Azospirillum brasilense* exhibiting low IAA synthesis than the wild-type (Spaepen et al., 2008). Moreover, whereas IAA synthesis is known for its plant-growth promoting effects, the mechanism seems to involve its degradation by bacteria; and was earlier demonstrated in *Arabidopsis thaliana* where an IAA degradation mutant of *Burkholderia phytofirmans* PsJN failed to increase root elongation when compared to the wild-type in the presence of exogenous IAA supply (Zúñiga et al., 2013).

IAA production by rhizobia is controlled by specific genes, and the overproduction of this auxin has been reported in several bacterial mutants, including that of *Ensifer (Sinorhizobium) meliloti* RD64 when compared to its wild type (Defez et al., 2019). The *fixJ* gene which works as a regulator to switch on the nitrogen fixation genes was highly expressed at 42 days of inoculation in the mutant of *Ensifer (Sinorhizobium) meliloti* RD64 leading to abundant FixJ protein which is regulated by *nifA*, *fixK1*, and *fixK* genes (Defez et al., 2019; Alemneh et al., 2020). Additionally, the IAA-overproducing *Ensifer meliloti* RD64 also showed an enhanced expression of the *fixNOQP1,2* operon genes (which code for haem-copper cbb3-type oxidases at 40 days after inoculation), with an upregulation of *gtA*, *icd*, and *sucA* genes (responsible for TCA cycle enzymes) in the bacteroids (Defez et al., 2019). The inoculation of soybean with IAA-producing bacteria also showed upregulation of the *otsA* gene, which encodes for trehalose 6-phosphate synthase, and plays a major role in nodule formation, nodule respiration and nitrogenase biosynthesis (Suárez et al., 2008; Bargaz et al., 2013). Moreover, IAA-producing rhizobia have also been shown to significantly increase free amino acids such as valine, alanine, aspartic acid and glutamic acids in host plants as well as photosynthetic products supplied to bacteroids in root nodules (Tsikou et al., 2013; Erice et al., 2014; Defez et al., 2019). These findings together suggest that IAA promotes an increase in nitrogen fixation via the upregulation of the genes involved in carbon transport to N₂-fixing bacteroids (Fisher, 1994; Defez et al., 2019).

BACTERIAL SECRETION OF SIDEROPHORES ENHANCES FE NUTRITION, PROMOTES PHYTOREMEDIATION AND CONTROLS PLANT PATHOGENS

Beyond the reduction of N₂ to NH₃ for direct use by plants in the synthesis of macromolecules such as chlorophyll, Rubisco

and nucleic acids, some rhizobial strains are known to improve the availability and uptake of iron via siderophore production. Iron is one of the essential elements required by plants for growth and is a component of critical macromolecules such as leghaemoglobin and nitrogenase, both required for the N₂ fixation process (Paudyal et al., 2007). As a result, a deficiency in Fe limits the efficiency of N₂ fixation through a reduction in nodule development and nitrogenase activity (Duhan et al., 1998; Stajković et al., 2011). Fe exists in soils as the divalent (Fe²⁺) and trivalent (Fe³⁺) cations, and its availability for plant uptake is governed by several factors including soil pH and the levels of other soil nutrients (Rajkumar et al., 2010). Whereas siderophores are known to have diverse chemical structures, most bacteria produce the catecholate-type while fungi together with some bacteria produce the hydroxamate-type siderophores (Carson et al., 2000; Schalk et al., 2011; Grobelak and Hiller, 2017). For example, bacteria isolated from the rhizoplane of *Arabidopsis thaliana* were shown to produce both catecholate and hydroxamate siderophores, which subsequently improved plant growth and phytoremediation by decreasing metal toxicity to plants (Grobelak and Hiller, 2017). Siderophores have a high affinity for Fe³⁺ where soil Fe is low and can reduce it to Fe²⁺ for uptake and utilization by legumes (Gopalakrishnan et al., 2015; Lebrazi and Fikri-Benbrahim, 2018). Identifying siderophore-producing rhizobia is therefore important for increased plant growth and crop yields, especially of nodulated legumes. Several species of rhizobia have been identified as siderophore producers with benefits beyond Fe³⁺ sequestration. Many of these rhizobia have been found to differ markedly in their secretion of siderophores, with consequences on host plant nodulation (Carson et al., 1992). For example, increased siderophore production by *Rhizobium* and *Bradyrhizobium* strains that nodulated pigeon pea revealed increases in nodule mass, shoot N and Fe content (Duhan et al., 1998). The co-inoculation of common bean with *Rhizobium phaseoli* and a siderophore-producing *Pseudomonas* sp. LG also resulted in greater N and P accumulation (Stajković et al., 2011). Although the mechanisms of growth promotion remain complex and elusive, several studies involving mutants also point to the plant growth promoting traits of siderophores. For example, a mutant of *Pseudomonas fluorescence* with greater capacity for siderophore synthesis was found to increase plant growth in mung bean over the wild-type counterpart (Katiyar and Goel, 2004). Similarly, a wild-type endophytic *Streptomyces* sp. GMKU 3100 markedly improved root and shoot growth in mung bean and rice when compared to its siderophore-deficient mutant (Rungin et al., 2012). To tap the benefits of this trait, siderophore-producing microsymbionts such as *Sinorhizobium meliloti*, *Rhizobium leguminosarum*, *Rhizobium leguminosarum* bv. *trifoli*, and *Bradyrhizobium japonicum* have been identified as potential strains for use as Fe-based biofertilizers for increased crop yields (Guerinot, 1991). In addition to enhancing Fe nutrition and promoting plant growth, siderophores have also been implicated in plant adaptation to high concentrations of heavy metals in agricultural soils. Apparently, bacterial siderophores can chelate heavy metals such as Al, Cd, Cu, Pb and Zn to form complexes that are not toxic to plants (Braud

et al., 2009; Schalk et al., 2011). Rhizobial siderophores are therefore important in the reclamation of contaminated soils for agricultural use. Although the legume-rhizobia symbiosis is sensitive to Al toxicity, siderophores can bind with Al ions and alleviate their toxic effect (Jaiswal et al., 2018), thus enhancing phytoremediation. So far, however, little is known about the chemistry of siderophores' interaction with heavy metals. Similarly, little attempt has been made to identify legume-rhizobia symbioses with efficiency in reclaiming contaminated soils associated with mining.

The genetics of siderophore production is rather complex. However, some genes involved in siderophore formation have been characterized. Rhizobia need iron for their own use in growth and symbiotic functioning, just as many proteins involved in the N₂ fixation process require iron for the synthesis of hemoglobin needed for transporting O₂ to respiring bacteroids. There are different types of siderophores. Rhizobia have the ability to produce a catechol siderophore to acquire iron under iron-poor conditions in the soil (Datta and Chakrabarty, 2014). The gene for rhizobactin 1021, a hydroxamate siderophore, was expressed under iron stress in *Sinorhizobium meliloti* (Lynch et al., 2001). Six genes (*rhbABCDEF*) needed in the biosynthesis of the siderophore have been identified and are located on an operon that is repressed under iron-replete conditions, while the gene *rhtA* encodes the outer membrane receptor protein for rhizobactin 1021 siderophore (Lynch et al., 2001). The transcription of both *rhbABCDEF* and *rhtA* genes is regulated by the product of the eighth gene in the cluster, namely *rhrA*, which has the characteristics of an AraC-type transcriptional activator (Lynch et al., 2001). According to McRose et al. (2018), some bacteria use quorum sensing (QS) to regulate siderophore production, including its concentration and ability to promote Fe uptake. In *B. japonicum* strain 61A152, a simple molecule such as citric acid can act as a siderophore (Guerinot et al., 1990), a finding confirmed by Siqueira et al. (2014) who showed that *B. japonicum* (Bj CPAC15), *B. diazoefficiens* strains Bd CPAC7, Bd USDA 110^T and Bj USDA 6^T all had three genes encoding citrate synthase enzyme. However, they also found genes related to the biosynthesis of catecholate siderophores in strains Bj CPAC 15 and Bd CPAC 7. So far, however, siderophores produced by rhizobia have been identified in only *S. meliloti*, *B. japonicum*, and *B. diazoefficiens* (Lynch et al., 2001; Siqueira et al., 2014). With the many new symbionts continuously being reported, it is important to also identify their siderophores, as a necessary step for their use as Fe biofertilizers. Furthermore, more studies are needed to ascertain the Fe-releasing efficiency of the different types of siderophores.

THE ROLE OF LUMICHROME AND RIBOFLAVIN IN PLANT GROWTH PROMOTION

Microorganisms such as rhizobia are crucial in the promotion of plant growth, as they can synthesize and release phytohormones that alter the rhizosphere chemistry in favor of plant growth

(Table 1). Rhizobial metabolites such as riboflavin and lumichrome are reportedly involved in chemical cross-talks leading to plant growth promotion, as well as improved immune response to biotic and abiotic stresses (Dakora et al., 2015; Kanazawa et al., 2020). As a result, soil microbes such as rhizobia and non-rhizobial bacteria have been used as inoculants because of these additional benefits. Exogenous application of lumichrome to both monocots and dicots yielded varied results, pointing to a dose-dependent beneficial outcome which is likely to be influenced by the type of plant species and the environment (Matiru and Dakora, 2005). Thus, any anticipated use of bacterial metabolites as plant growth promoters in cropping systems would require a better understanding of their operational mechanisms. Riboflavin released by rhizobia into the rhizosphere can promote microsymbiont colonization of root hairs, leading to greater and more effective nodulation and N₂ fixation. For example, mutants of *Sinorhizobium meliloti* containing additional copies of the *ribBA* genes were found to exhibit increased synthesis of riboflavin leading to greater root colonization in *Medicago sativa* (Yang et al., 2002). Conversely, a *Rhizobium leguminosarum ribN* mutant exhibited reduced nodule occupancy when compared to the wild-type, further pointing to the vital role of riboflavin in the establishment of the legume-rhizobia symbiosis (Angulo et al., 2013). Lumichrome, the degradation by-product of riboflavin, is also reported to promote plant growth through improved symbiotic and photosynthetic functioning in legumes (Table 1; Phillips et al., 1999; Matiru and Dakora, 2005). Although the genetic basis for the involvement of lumichrome on stomatal function is scanty, the study by Matiru and Dakora (2005) reported increases in leaf stomatal conductance and transpiration rates when compared to untreated plants, with rhizobial inoculation producing similar responses. Similarly, lumichrome treatment was reported to increase photosynthetic rates in corn and soybean when compared to untreated plants (Khan et al., 2008). At the molecular level, lumichrome can induce the expression of genes involved in cell differentiation and cell expansion leading to increased plant biomass accumulation (Pholo et al., 2018). Given their roles at different stages of the legume-rhizobia symbiosis, riboflavin and lumichrome released by rhizobia can maximize plant growth and increase crop productivity via several alterations in the plant's physiology, including enhanced symbiosis and photosynthetic functioning.

The genetic basis of plant growth promotion by lumichrome (chemically defined as 7,8 dimethylalloxazine) stems from its ability to induce the expression of genes responsible for cell growth and mitotic division, and appears to coordinate cell division and proliferation in developing leaves. Lumichrome is also reported to increase CO₂ concentration in the rhizosphere (Phillips et al., 1999) which is needed for the growth of N₂-fixing rhizobia and mycorrhizal fungi (Maier et al., 1979). Pholo et al. (2018) found that the enhancement of mitotic *CYCD*_{3,3}, *CYCA*_{1,1}, *SP*₁*L*₃, *RSW*₇, and *PDF*₁ transcripts in lumichrome-treated *Arabidopsis thaliana* plants resulted in high plant biomass from cell differentiation and cell expansion. Moreover, lumichrome also increased starch accumulation in soybean and tomato by increasing glyceraldehyde 3-phosphate

denhydrogenase (GAPDH) transcripts and NAD-dependent enzyme activity (Gouws et al., 2012). Additionally, lumichrome can also reduce the levels of gene expression associated with ethylene metabolism such as *Acc oxydase 1 (ACO1)*, and a C₂H₂ zinc finger protein, leading to a minimal effect of ethylene on plant growth. However, Pholo et al. (2018) found a synergistic ethylene-auxin cross-talk via a reciprocal over-expression of *ACO1* and *SAUR54* in which ethylene activated the auxin biosynthetic pathway and regulated *Arabidopsis* growth, in addition to suppressing the negative effects of methyl jasmonate (MeJa) on chlorophyll loss and decreases in Rubisco and photosynthesis (Pholo et al., 2018). For example, treating *Arabidopsis thaliana* or soybean with Methyl jasmonate caused a decrease in leaf photosynthetic rates due to impaired chlorophyll production (Jung, 2004; Anjum et al., 2011). Whereas, pre-incubation of *Bradyrhizobium japonicum* with jasmonates prior to inoculation led to enhanced nodulation and N₂ fixation in soybean (Mabood and Smith, 2005), the possible indirect inhibitory effect of jasmonate on symbiosis via reduced photosynthetic functioning remains to be determined.

ACC DEAMINASE-PRODUCING RHIZOBIAL BACTERIA

ACC (1-aminocyclopropane-1-carboxylic acid) deaminase is a known precursor of ethylene (Penrose and Glick, 2003) and is a plant growth-promoting enzyme (Table 1) that uses pyridoxal 5-phosphate (PLP) as substrate (Honma and Shimomura, 1978). ACC deaminase enzyme localized in the cytoplasm, is encoded by *acdS* gene (Honma and Shimomura, 1978; Jacobson et al., 1994). In *Mesorhizobium loti*, this *acdS* gene is located in the symbiotic island and is regulated by the *NifA2* gene (Nukui et al., 2006). When ACC produced by plants is exuded into the rhizosphere, rhizobacteria that express ACC deaminase activity take up the ACC and degrade it within the bacterial cytoplasm (Glick et al., 1998; Penrose and Glick, 2003). This enzyme is constitutively expressed during nodule initiation, and under stressed conditions in plant roots (Ligero et al., 1986; Spaink, 1997; Saleem et al., 2007). The plant exuded ACC is often used by bacteria as an N source; however, ACC deaminase can also degrade ACC to lower ethylene levels, especially in plants exposed to biotic and abiotic stresses, as well as during nodule initiation by legumes and rhizobia (Glick et al., 1998). Earlier studies have shown the harmful effect of ethylene in inhibiting nodule formation through interfering with root hair deformation, infection thread elongation into the inner cortex, calcium spiking and the proliferation of rhizobia in legumes such as *Pisum sativum*, *Trifolium repens*, and *Medicago sativa* (Goodlass and Smith, 1979; Peters and Crist-Estes, 1989; Lee and LaRue, 1992; Oldroyd et al., 2001; Tamimi and Timko, 2003; Lohar et al., 2009). However, co-inoculation of either *Rhizobium tropici* CIAT899 or *Cupriavidus taiwanensis* STM894 with the wild-type ACC deaminase-producing *Pseudomonas fluorescens* YsS6 was found to improve nodulation and plant growth in *Phaseolus vulgaris* and *Mimosa pudica*, respectively, when compared to its mutant defective in ACC deaminase

production (Nascimento et al., 2019). Ma et al. (2004) also found that an ACC deaminase-producing *Sinorhizobium meliloti* mutant elicited 40% more nodulation in *Medicago sativa* than the parent strain. Thus, the mechanism by which ACC deaminase-producing bacteria increase plant nodulation seems to involve the regulation of both ACC oxidase activity and ethylene synthesis, as observed in pea plants treated with ACC deaminase-producing *Arthrobacter protophormiae* (Barnawal et al., 2014). Furthermore, a *S. meliloti* strain harboring the *acdS* gene and co-inoculated with *P. putida* UW4 increased nodule number in *Medicago lupulina* when compared to inoculation with the wild type (Kong et al., 2015). The important plant growth promoting traits of these bacteria-produced molecules points to the need to bioprospect for rhizobial strains that possess such traits for increased symbiotic performance, plant growth promotion and increased grain yield.

The *PvACS* gene in *Phaseolus vulgaris* encodes ACC synthase which causes the formation of ethylene responsible for nodule senescence (Nascimento et al., 2018; Serova et al., 2018). The *PvGS(n-1)*, a gene controlling the transcription of glutamine synthetase and commonly found in senescent nodules, is needed for ammonium assimilation in legumes (Hungria and Kaschuk, 2014; da Silva et al., 2019). However, the expression of this gene was found to enhance nitrogenase activity and leghaemoglobin concentration, leading to delayed senescence which increased ammonia assimilation and N₂ fixation (Lara et al., 1983; Alemneh et al., 2020). Another enzyme, Uricase II, is needed in the metabolism of N-fixed for export as ureides from root nodules to shoots and tends to decline in senescent nodules (Papadopoulou et al., 1995; Capote-Mainez and Sánchez, 1997) as found for leghemoglobin, which is a physiological marker for nodule senescence. ACC deaminase-producing rhizobia can stimulate nodule formation and function and thus increase the amount of N₂-fixed needed for plant growth.

RHIZOBIA-AIDED ACQUISITION OF PHOSPHORUS BY NODULATED LEGUMES

To increase crop yields for meeting global food security would require major nutrient inputs, especially N and P. Plants take up P in the form of phosphate that comes from the 83% of the world's P reserves occurring as rock phosphate in only Morocco, China, South Africa and the USA (Vaccari, 2009). The world's vast 5.7 billion hectares of agricultural land are generally deficient in P that must be added as input to increase crop productivity (Mouazen and Kuang, 2016). In Africa, most smallholder farmers grow their crops with insufficient or no P input. However, plant growth-promoting bacteria and fungi can influence plant development directly or indirectly by facilitating the supply and uptake of mineral nutrients from the soil. Solubilization of unavailable soil P compounds by symbiotic rhizobia in the rhizosphere is one strategy for enhancing P availability for plant growth and yield (Marra et al., 2012). Although P is an important macronutrient for plant development, about 95 to 99% of the soil P occurs in insoluble form which is not useable by plants (Vassilev et al., 2001). Some rhizobial bacteria are however

capable of solubilizing unavailable soil P for plant uptake and growth. Aside plants, bacteroids in root nodules also require P for their metabolism; and the high-affinity phosphate transporter PstSCAB is known to promote the efficiency of the *Sinorhizobium fredii*-soybean symbiosis (Hu et al., 2018), just as the uptake of inorganic P leading to enhanced N₂ fixation during P starvation is facilitated by the *phoCDET* genes which encode the ABC-type transport system in *Sinorhizobium meliloti* (Bardin et al., 1996; Yuan et al., 2006). Thus, given the vital roles of P in both plant and bacterial metabolism, screening for P-solubilizing traits in N₂-fixing rhizobia can be a cheaper and useful strategy to ameliorate the negative effects of soil P stress on plants for improved crop yields and food security.

Immobilization of P can occur in inorganic and organic forms (Rodríguez and Fraga, 1999). During microbial P transformation, the carboxyl and hydroxyl ion containing organic acids release their protons and bind to cations (Bergkemper et al., 2016), thus lowering the pH (Richardson and Simpson, 2011). The acidification caused by microbial activity can result in the release of P ions by substitution with H⁺ (Rodríguez and Fraga, 1999; Richardson and Simpson, 2011). In low-P soils, rhizobia can solubilize soil-bound P in the rhizosphere through acidification by synthesizing gluconic acid under the control of pyrroloquinoline quinone (PQQ) genes (Yadav et al., 2020). Of all the organic acids, gluconic acid is most potent in P solubilization and the oxidation of glucose to gluconic acid by rhizobia is an important step in the solubilization of soil P (Richardson et al., 2011). Gene *gcd* in rhizobia encodes quinoprotein glucose dehydrogenase (PQQGDH), which is involved in the release of organic anions to solubilize inorganic P (Rodríguez et al., 2000). In addition to organic acids, inorganic acids and mycorrhizal fungi in soil can also enhance phosphorus solubilization (Alori et al., 2017). Whereas rhizobia are largely known for their N₂-fixing traits, mycorrhizal fungi are particularly known for their role in the acquisition of phosphorus and other nutrients required by plants (Bolan, 1991). A synergistic interaction was observed when faba bean was treated with *Rhizobium leguminosarum* bv. *viciae* and arbuscular mycorrhizal fungi which resulted in increased nodulation and nitrogenase activity probably through enhanced P acquisition by the mycorrhizal partner (Abd-Alla et al., 2014).

Rhizobia and other microbes harbour genes such as *phoD* and *phoA* which encode alkaline phosphatase, the *appA* gene which encodes phytase, and the *phn* gene which encodes C-P lyase enzymes that can convert soil organic-P into available P for plant uptake (Rodríguez et al., 2006). The organic P however occupies about 30–50% of the total soil P pool in forms such as inositol phosphate (soil phytate), phosphomonoesters, phosphodiester, phospholipids, nucleic acids, and phosphotriesters (Rodríguez and Fraga, 1999). The activity of microbial P-enzymes on the huge P reservoir in soils largely accounts for P supply to terrestrial plants. P assimilation under P-poor soil conditions is usually achieved using high-affinity P transporters, in contrast to P-rich soils where low-affinity P transporters are involved (Hsieh and Wanner, 2010). The expression of genes *phoU*, *phoR*, and *phoB* in soil microbes largely regulates the P-starvation response in cropping systems for increased use of external P sources (Eder

et al., 1996). However, information is lacking from a systems approach that links P status of the soil to plant and bacterial gene expression for P-enzyme formation/release for increased P availability, uptake and utilization. For example, what are the cues for low-P sensing in soil by plants and microbes, and what is the timeframe required for biological processes such gene expression to occur? And what are the regulatory mechanisms underlying the build-up of P pool in response to its demand by plants?

ROLE OF SYMBIOTIC RHIZOBIA IN PLANT DEFENSE

The successful induction of root nodules and their subsequent colonization by rhizobia require the production of rhizobial Nod factors that allow for their recognition by the host legume (Via et al., 2016). Aside their growth promoting effects, rhizobia have been implicated in processes leading to induced systemic resistance (ISR) in host plants which is governed by complex mechanisms; for example, inoculating common bean with *Rhizobium etli* led to enhanced resistance to infection by *Pseudomonas syringae* pv. *phaseolicola* via the accumulation of reactive oxygen species, increased callose production and the activation of defense related genes (Díaz-Valle and Alvarez-Venegas, 2019). The response of host plants to pathogen infection can include a molecular cross-talk between salicylic acid and jasmonates, both of which play key roles in the activation of plant defense related genes (Pieterse et al., 2012). Upon attack by insects for instance, intricate processes which include the synthesis of salicylic acid and jasmonates occur leading to the activation of genes responsible for plant defense (Hettenhausen et al., 2015; Wang et al., 2019b). Moreover, siderophores produced by symbiotic rhizobia and other microbes do not only enhance Fe nutrition for healthy plant growth and grain yield in legumes, but also serve as biocontrol agents against pathogens (Table 1). For example, siderophores produced by *Sinorhizobium meliloti* were shown to suppress *Macrophomina phaseolina*, the causal agent of charcoal rot in groundnut (Arora et al., 2001). Similarly, co-inoculation of groundnut with *Rhizobium* and *Trichoderma harzianum* successfully inhibited infection by *Sclerotium rolfsii*, the fungal pathogen that causes stem rot disease (Ganesan et al., 2007). A *Rhizobium* species was also found to protect soybean from root rot caused by *Phytophthora megasperma*, while a *Sinorhizobium* sp. inhibited plant infection by *Fusarium oxysporum* (Deshwal et al., 2003). Rhizobitoxine-producing strains of *Bradyrhizobium japonicum* were also able to successfully block infection of soybean by *Macrophomina phaseolina*, the causal pathogen of charcoal rot (Deshwal et al., 2003).

In addition to their roles as signal molecules in the legume-rhizobia symbiosis, rhizobial metabolites such as riboflavin and lumichrome, as well as vitamins which include thiamine, biotin, niacin and ascorbic acid have been implicated in legume plant defense against pathogens (Mehboob et al., 2009; Palacios et al., 2014). For instance, spraying riboflavin on tobacco and *Arabidopsis* caused resistance to *Peronospora parasitica*,

Pseudomonas syringae pv. tomato, the Tobacco mosaic virus and *Alternaria alternata* (Dong and Beer, 2000), possibly due to the expression of pathogenesis-related genes which induced systemic acquired resistance to the pathogens. In Arabidopsis, riboflavin was similarly found to induce the priming of plant defense response toward infection by *Pseudomonas syringae* pv. tomato and was linked to the expression of genes involved in plant defense responses (Zhang et al., 2009). Moreover, *Mesorhizobium loti* induced the expression of the Phenylalanine Ammonia lyase (*LjPAL1*) gene responsible for the synthesis of salicylic acid, and consequently altered the response of *Lotus japonicum* to infection by *Pseudomonas syringae* (Chen et al., 2017). Legumes are also reported to protect themselves against pathogens using isoflavonoids, phytoalexins and phytoanticipins (Dakora and Phillips, 1996). It is therefore possible that the health of a legume plant is dependent on a molecular cross-talk involving several defense molecules such as isoflavones, riboflavin, thiamine and other yet unknown molecules (Subramanian et al., 2004; Ahn et al., 2005; Yadav et al., 2020). In Arabidopsis for example, infection with *Sclerotinia sclerotium* increased the expression of the *IFS1* gene that codes for isoflavone synthase and highlights the involvement of isoflavones as plant defense molecules (Subramanian et al., 2004). Also, a thiamine treatment led to the accumulation of hydrogen peroxide (H₂O₂) and a build-up of lignin in roots of rice following infection with the root-knot nematode (*Meloidogyne graminicola*); this was associated with the increased transcription of the *OsPAL1* and *OsC4H* genes involved in the phenylpropanoid pathway (Huang et al., 2016). Clearly, plants have diverse ways of overcoming biotic and abiotic stress within their environments through the synthesis of novel molecules. For example, following the infection of Arabidopsis by *Pieris rapae*, one branch of the jasmonate signaling pathway regulated by the *MYC2* gene was expressed (Santino et al., 2013). Clearly, a lot remains to be unraveled regarding the complex chemical cross-talks involved in plant adaptation to disease infection and pathogen attack.

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CONCLUSIONS

Plant growth and productivity is dependent on multiple factors, which include mineral nutrition, resistance to insect pests and diseases. Fortunately, symbiotic rhizobia are capable of triggering biological pathways that cause outcomes with direct and indirect effects on plant growth promotion and protection. Studying the interlinkages of outcomes from the legume–rhizobia symbioses has the potential to identify microsymbionts for use as inoculants due to the multiplicity of functions that they elicit. For example, rhizobia can be identified that (i) produce greater symbiotic N for host plant growth and productivity (ii) elicit the synthesis of host-plant compounds for defense and increased plant growth, (iii) produce environmental cues that regulate stomatal function and (iv) emit vitamins as growth factors for plant defense and increased growth/productivity. Whereas, some of the outcomes triggered by rhizobia may be tied to their symbiotic interactions with legumes, the effects of some of the signal molecules produced often extends to non-legumes, thus indicating a wider distribution of these traits among diverse bacterial genera.

AUTHOR CONTRIBUTIONS

SJ and MM drafted the manuscript. FI produced the photo used in **Figure 1**. The photo was shot by her from her glasshouse studies. Some of the ideas in the manuscript are also from her Master's thesis. FD conceived the idea, edited, and approved the final version of the paper. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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