Bacteria-Inducing Legume Nodules Involved in the Improvement of Plant Growth, Health and Nutrition

4

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Abstract

Bacteria-inducing legume nodules are known as rhizobia and belong to the class *Alphaproteobacteria* and *Betaproteobacteria*. They promote the growth and nutrition of their respective legume hosts through atmospheric nitrogen fixation which takes place in the nodules induced in their roots or stems. In addition, rhizobia have other plant growth-promoting mechanisms, mainly solubilization of phosphate and production of indoleacetic acid, ACC deaminase and siderophores. Some of these mechanisms have been reported for strains of rhizobia which are also able to promote the growth of several nonlegumes, such as cereals, oilseeds and vegetables. Less studied are the mechanisms that have the rhizobia to promote the plant health; however, these bacteria are able to exert biocontrol of some phytopathogens and to induce the plant resistance. In this chapter, we revised the available data about the ability of the legume nodule-inducing bacteria for improving the plant growth, health and nutrition of both legumes and nonlegumes. These data showed that rhizobia meet all the requirements of sustainable agriculture to be used as bio-inoculants allowing the total or partial replacement of chemicals used for fertilization or protection of crops.

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4.1 Introduction

Currently, two of the main challenges of global agriculture are the achievement of a sustainable crop production and the protection of natural environments. The increase of the world population requires an increase in food production but using agronomic practices that preserve the environment. In order to achieve these aims, the Food and Agriculture Organization of the United Nations (FAO) has proposed to declare the year 2020 as the International Year of Plant Health (IYPH 2020). Obtaining healthier plants implies the protection of the world plant resources from pests (https://www.ippc.int/en/iyph/). According to FAO expectations, healthier plants allow us to obtain higher crop yields avoiding diversity losses, to reduce the hunger and poverty and to achieve a safer trade, a higher economic development and a sustainable health. All of these aims are included in the goals of the Agenda 2030 for Sustainable Development, launched by the United Nations in September of the year 2015 (https://www.un.org/sustainabledevelopment/sustainable-development-goals/).

The increase in crop production that is necessary for the eradication of hunger and malnutrition in the world requires agronomic practices that are not just limited to the control of pests. The fertilization of crops, to date mainly based on the application of chemical fertilizers, is also essential to increase their productivity and get an adequate amount of food for the ever-growing world's population. Moreover, consumers currently also increasingly demand healthy and safe foods, which go beyond the obtaining of healthier plants themselves. It is hard to combine agronomic sustainable practices with the obtaining of safer and healthier plants because the current agronomic practices need to be changed. These changes involve the total or partial replacement of chemical fertilizers and pesticides by biofertilizers and biopesticides in order to protect the health of all living beings and also to preserve the environment.

Biofertilizers and biopesticides are mainly constituted by microorganisms which exert a positive effect on the growth, nutrition and health of the plants (Berg 2009; Berendsen et al. 2012; Abhilash et al. 2016; Vejan et al. 2016; Berg et al. 2017), and they are key factors for plant growth and protection (Berg et al. 2017). The plant microbiome, either rhizospheric or endospheric, is a determinant of the plant health, growth and nutrition (Berendsen et al. 2012; Gaiero et al. 2013; Santoyo et al. 2016; Berg et al. 2017). However, many species of bacteria present in the plant microbiome are opportunistic human pathogens (Mendes et al. 2013) and, despite some of them are plant growth promoters, they cannot be used as biofertilizers or biopesticides (Menéndez et al. 2016).

Within the plant beneficial bacteria that are also safe for human health, we can highlight the rhizobia, a diverse group of bacteria able to induce nodules in roots or stems of legumes where they carry out the nitrogen fixation (Velázquez et al. 2017b).

After their use as inoculants for more than one century, the rhizobia have proven to be non-pathogenic for humans, animals and plants. Moreover, they are able to improve plant growth and nutrition and to produce compounds, such as siderophores, involved in the biological control of plant pathogens (Gopalakrishnan et al., 2015; Vargas et al. 2017; Velázquez et al. 2017a).

In the present chapter, we revise the current knowledge about the plant growth mechanisms presented by strains belonging to different genera of rhizobia, as well as the effects of their inoculation on different plants from the point of view of their health, growth and nutrition.

4.2 Diversity of Bacteria-Inducing Legume Nodules

The existence of nodules in the roots of legumes was first reported in the seventeenth century by Malpighi, but it was at the end of the nineteenth century when Beijerinck (1888) isolated for the first time a bacterium from nodules of *Vicia*, which was initially named *Bacillus radicicola*. Later, this bacterium was renamed as *Rhizobium leguminosarum* (Frank 1889) and, until now, the bacteria nodulating legumes are generically called rhizobia. The rhizobia currently form a complex group of bacteria which belong to different phyla, classes, orders, families, and genera (Fig. 4.1) and are able to establish nitrogen-fixing symbioses with different legumes around the world.

The species nodulating legumes described before the year 2017 were recorded by Velázquez et al. (2017b) and those described from this year to date are listed in Table 4.1.

Most of rhizobia reported to date belong to the class *Alphaproteobacteria* within the phylum *Proteobacteria* and nodulate legumes from the subfamily Papilionoideae. They are distributed in several families of the order *Rhizobiales* (Velázquez et al. 2017b), and most of them belong to the genus *Rhizobium*, included in the family *Rhizobiaceae* (Conn, 1938) together with the old genera *Allorhizobium* (de Lajudie et al. 1998) and *Ensifer* (previously named *Sinorhizobium*) (Judicial Commission of the International Committee on Systematic of Prokaryotes, 2008) and the new genera *Neorhizobium* (Mousavi et al. 2014) and *Pararhizobium* (Mousavi et al. 2015).

All these mentioned genera contain species which present rapid growth on media containing mannitol as carbon source, whereas the genera *Bradyrhizobium* (Jordan, 1982) and *Azorhizobium* (Dreyfus et al. 1988) contain slow-growing species. They were included into the families *Bradyrhizobiaceae* (Garrity et al. 2005), whose correct name is *Nitrobacteraceae* (Validation list 107, 2016), and *Hyphomicrobiaceae* (Babudieri 1950; Skerman et al. 1980), respectively. Following the criteria of the growth rate in yeast mannitol agar (Vincent 1970), a new genus named *Mesorhizobium*, with an intermediate growth rate between the genera *Rhizobium* and *Bradyrhizobium*, was split from genus *Rhizobium* by Jarvis et al. (1997). The genus *Mesorhizobium* belongs to the family *Phyllobacteriaceae* (Mergaert and Swings 2005; Validation list No.107 2006).

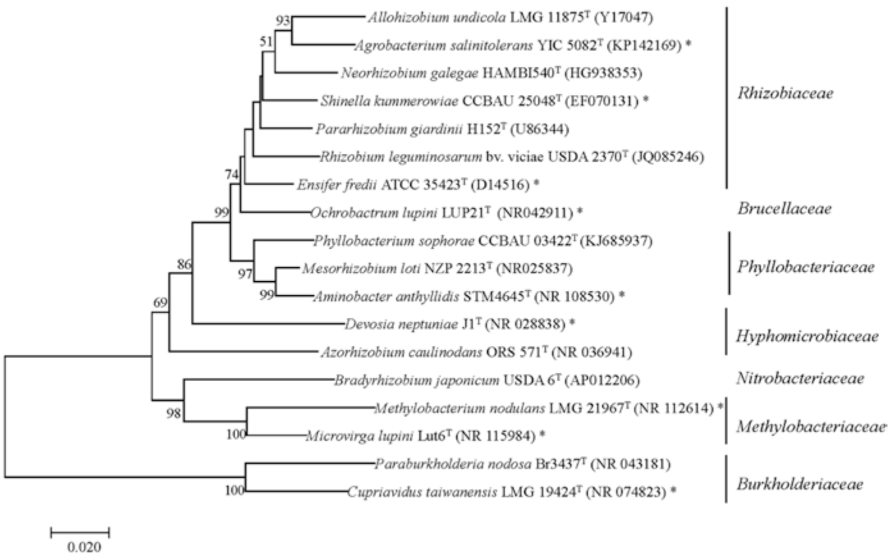

Fig. 4.1 Neighbour-joining phylogenetic tree based on nearly complete 16S rRNA gene sequences of type strains of 18 type species inducing legume nodules distributed in 7 families within the order *Rhizobiales*. The significance of each branch is indicated by a percentage of a bootstrap value calculated for 1000 subsets. Bar, 2 nt substitutions by 100 nt. Evolutionary analyses were conducted in MEGA7 software. Asterisks show the type strains of species that nodulate legumes, when the type species of the genus is not the one with this ability

Also, several species of non-classic rhizobial genera belonging to the *Alphaproteobacteria* have been reported as legume-nodulating bacteria (Velázquez et al. 2017b). Some of these genera belong to families that also contain classic rhizobia, such as *Phyllobacterium* (Valverde et al. 2005; Jiao et al. 2015) and *Aminobacter* (Maynaud et al. 2012) from the family *Phyllobacteriaceae*; *Shinella* (Lin et al. 2008) and *Agrobacterium* (Yan et al. 2017) from the family *Rhizobiaceae* and *Devosia* (Rivas et al. 2002) from the family *Hyphomicrobiaceae*. Other genera belong to families that classically did not include rhizobia, such as *Methylobacterium* (Sy et al. 2001) and *Microvirga* (Ardley et al. 2012; Radl et al. 2014) from the family *Methylobacteriaceae* and *Ochrobactrum* from the family *Brucellaceae* (Trujillo et al. 2005; Zurdo-Piñeiro et al. 2007).

Since the year 2000, several species belonging to two genera from *Betaproteobacteria* have also been reported as being able to induce nodules in several legumes (Velázquez et al. 2017b). When the first nodulating strains of *Betaproteobacteria* were reported, they were included in species of the genera *Burkholderia* and *Ralstonia* (Moulin et al. 2001; Chen et al. 2003), but they are currently included in the genera *Paraburkholderia* (Sawana et al. 2014; Dobritsa and Samadpour, 2016) and *Cupriavidus* (Vandamme and Coenye 2004) in both cases belonging to the family *Burkholderiaceae* (Velázquez et al. 2017b).

Table 4.1 Recently described species of rhizobia able to nodulate legumes

Species	Host legume or nodulated legumes	References
Order *Rhizobiales*, family *Rhizobiaceae*		
Genus *Rhizobium*		
R. hidalgonense	*Phaseolus vulgaris*	Yan et al. (2017a, b)
R. esperanzae	*Phaseolus vulgaris*	Cordeiro et al. (2017)
R. hedysari	*Hedysarum multijugum*	Xu et al. (2017)
Genus *Ensifer*		
E. shofinae	*Glycine max*	Chen et al. (2017)
Genus *Agrobacterium*		
A. salinitolerans	*Sesbania cannabina*	Yan et al. (2017)
Order *Rhizobiales*, family *Phyllobacteriaceae*		
Genus *Mesorhizobium*		
M. delmotii	*Anthyllis vulneraria*	Mohamad et al. (2017)
M. prunaredense	*Anthyllis vulneraria*	Mohamad et al. (2017)
M. helmanticense	*Lotus corniculatus*	Marcos-García et al. (2017)
M. zhangyense	*Thermopsis lanceolata*	Xu et al. (2018)
M. wenxiniae	*Cicer arietinum*	Zhang et al. (2018)
M. sanjuanii	*Lotus tenuis*	Sannazzaro et al. (2018)
Order *Rhizobiales*, family *Nitrobacteriaceae* (‘*Bradyrhizobiaceae*’)		
Genus *Bradyrhizobium*		
B. centrolobii	*Centrolobium paraense*	Michel et al. (2017)
B. macuxiense	*Centrolobium paraense*	Michel et al. (2017)
B. brasilense	*Vigna unguiculata*, *Macroptilium atropurpureum*	Martins da Costa et al. (2017)
B. sacchari	*Vigna unguiculata*, *Macroptilium atropurpureum*, *Cajanus cajan*	de Matos et al. (2017)
B. mercantei	*Deguelia costata*	Helene et al. (2017)
B. cajanii	*Cajanus cajan*	Araújo et al. (2017)
B. forestalis	*Inga* sp., *Swartzia* sp.	Martins da Costa et al. (2018)
B. algeriense	*Retama sphaerocarpa*	Ahnia et al. (2018)
B. ripae	*Indigofera rautanenii*, *Chamaecrista biensis*, *Vigna unguiculata*	Bünger et al. (2018)
B. shewense	*Erythrina brucei*	Aserse et al. (2017)
Order *Burkholderiales*, family *Burkholderiaceae*		
Genus *Paraburkholderia*		
P. piptadeniae	*Piptadenia gonoacantha*	Bournaud et al. (2017)
P. ribeironis	*Piptadenia gonoacantha*	Bournaud et al. (2017)

4.3 Plant Growth-Promoting Mechanisms

The bacteria able to induce legume nodules present direct and indirect mechanisms of plant growth promotion. The direct mechanisms include nitrogen fixation, phosphate solubilization and production of phytohormones and ACC deaminase, while the indirect mechanisms include production of siderophores, which can be also considered a direct mechanism because it enhances the Fe uptake by plants (García-Fraile et al. 2012; Suárez-Moreno et al. 2012; Laranjo et al. 2014; Das et al. 2017; Gopalakrishnan et al. 2015; Patil et al., 2017; Vargas et al. 2017; Velázquez et al. 2017a).

Nitrogen fixation was the first-studied plant growth-promoting mechanism of rhizobia since Hellriegel and Wilfarth at the end of the nineteenth century established that legume nodules are the responsible for nitrogen fixation (Hellriegel and Wilfarth 1888). From this time to date, many research works have focused on this ability in order to select the most effective rhizobial strains to be used as legume inoculants (Catroux et al. 2001; Checcucci et al. 2017). Nevertheless, the classic alpha rhizobia are specialized in the symbiotic nitrogen fixation with legumes (Remigi et al. 2016), and then, improvement of plant growth via nitrogen fixation is limited to these plants.

Phosphate solubilization is the second plant growth-promoting mechanism involved in nutrient mobilization presented by rhizobia (Rodríguez and Fraga, 1999; Thakur et al. 2014). Within them, the most active phosphate solubilizers in vitro are the species included into the genus *Mesorhizobium* (Peix et al. 2001; Rivas et al. 2006; Verma et al. 2013; Imen et al. 2015; Wdowiak-Wróbel and Małek 2016; Brígido et al. 2017), although this mechanism is also presented by strains of *Rhizobium* (Chabot et al. 1996; Antoun et al. 1998; Alikhani et al. 2007; Abril et al. 2007; Sridevi et al. 2007; Flores-Félix et al. 2013; Dahale et al. 2016; Othman and Tamimi 2016; Jiménez-Gómez et al. 2018), *Ensifer* (formerly *Sinorhizobium*) (Ormeño et al. 2007; Villar-Igea et al. 2007) and *Bradyrhizobium* (Boiero et al. 2007).

Also within the direct mechanisms, one of the most widely analysed is the production of the phytohormone indoleacetic acid (IAA), which is widely extended among rhizobial species nodulating legumes, such as those from the genus *Rhizobium* (Datta and Basu 2000; Bhattacharjee et al. 2012; García-Fraile et al. 2012; Kumar and Ram 2012; Flores-Félix et al. 2013; Jiménez-Gómez et al. 2018), *Allorhizobium* (Ghosh et al. 2015), *Ensifer* (formerly *Sinorhizobium*) (Bianco and Defez 2009; Dubey et al. 2010), *Mesorhizobium* (Wdowiak-Wróbel and Małek 2016; Vieira et al. 2017) and *Bradyrhizobium* (Boiero et al. 2007).

The production of aminocyclopropane-1-carboxylate (ACC) deaminase, responsible for the cleavage of the ethylene precursor ACC into ammonia and α-ketobutyrate, has been reported in different species of rhizobia from different genera (Nascimento et al. 2014, 2018), such as *Rhizobium* (Ma et al. 2003; Duan et al. 2009), *Allorhizobium* (Ghosh et al. 2015), *Ensifer* (formerly *Sinorhizobium*) (Ma et al. 2004; Kong et al. 2015), *Mesorhizobium* (Nascimento et al. 2012) and *Bradyrhizobium* (Rangel et al. 2017), and in nodulating species of *Methylobacterium* (Ekimova et al. 2018).

Different genera of rhizobia have been reported to produce siderophores (Carson et al. 2000; García-Fraile et al. 2012; Gopalakrishnan et al., 2015; Vargas et al. 2017; Velázquez et al. 2017), for example, *Rhizobium* (Patel et al. 1988; Carson et al. 1992; Wright et al. 2013; Jiménez-Gómez et al. 2018), *Mesorhizobium* (Berraho et al. 1997; Datta and Chakrabartty 2014; Wdowiak-Wróbel and Małek 2016; Brígido et al. 2017; Demissie et al. 2018), *Bradyrhizobium* (Nambiar and Sivaramakrishnan

1987; Lesueur et al. 1993; Abd-Alla 1998; Khandelwal et al. 2002; Boiero et al. 2007), *Allorhizobium* (Ghosh et al. 2015) and *Ensifer* (Lynch et al. 2001).

Some of these plant growth-promoting mechanisms have also been reported for several strains of *Paraburkholderia* and *Cupriavidus* from *Betaproteobacteria*, among which we must highlight the ability to fix nitrogen in symbiosis with several legumes (Remigi et al. 2016). Moreover, some species of *Paraburkholderia* have been shown to be able to produce indoleacetic acid, siderophores or ACC deaminase (Suárez-Moreno et al. 2012). Concretely, the species *Paraburkholderia tuberum* solubilizes phosphate and produces siderophores (Angus et al. 2013).

4.4 Growth Promotion of Legumes and Nonlegumes

The growth promotion of legumes by rhizobia via nitrogen fixation has been widely studied (Gopalakrishnan et al., 2015; Vargas et al. 2017; Velázquez et al. 2017b), and the inoculation with rhizobia of some legumes, such as soybean, has been performed for several decades in America with increases in the production, overall in South American countries (Leggett et al. 2017; Vargas et al. 2017). Moreover, increases in the production of other legumes, such as *Phaseolus vulgaris* and *Cajanus cajan,* have been obtained after the inoculation with *Rhizobium* and *Bradyrhizobium* strains, respectively (Mulas et al. 2011; Araújo et al. 2015; Koskey et al. 2017; Barros et al. 2018; Samago et al. 2018; Wolde-Meskel et al. 2018; Yanni et al. 2018).

It has also been reported that the co-inoculation of different rhizobial strains can improve the yield of legumes such as common bean (de Oliveira Longatti et al. 2013; Diez-Mendez et al. 2015; da Conceição Jesus et al. 2018). In the same line, the co-inoculation with rhizobia and other bacteria increased the nitrogen content on soybean (Subramanian et al. 2015) and improved the growth of chickpea (Verma et al. 2012; Yadav and Verma 2014; Prasanna et al. 2017), galega (Egamberdieva et al. 2010), lentil (Khanna and Sharma 2011), soybean (Hungria et al. 2013; Nimnoi et al. 2014; Htwe et al. 2018), peanut (Vicario et al. 2016) and mungbean (Kaur and Khanna 2016; Tarafder et al. 2016; Qureshi et al. 2011).

The co-inoculation of rhizobia and arbuscular mycorrhiza increases the nitrogen fixation in common bean (Tajini et al. 2011) and soybean (Meng et al. 2015), the nitrogen content on chickpea (Tavasolee et al. 2011) and pigeon pea (Bhattacharjee and Sharma 2012) and the productivity of pea (Shinde and Thakur 2016), cowpea (Haro et al. 2018), soybean (Hemmat Jou and Besalatpour 2018), *Styloshantes* (Crespo Flores et al. 2014), faba bean in alkaline soils (Abd-Alla et al. 2014; Hemid et al. 2014) and garden pea in acidic soils (Bai et al. 2017). Dual inoculations of rhizobia and arbuscular mycorrhiza also increase the grain protein content in chickpea under moderate water deficit (Oliveira et al. 2017).

In the last decades, also the study of the effect of rhizobial inoculation on the legume growth under different stresses is gaining interest, and several works have been performed in different legumes (Naveed et al. 2017). Drought and salt stresses are major limiting factors to plant productivity; nevertheless, inoculation with selected strains of rhizobia able to survive, grow and effectively nodulate legumes under these stress conditions can improve their productivity, quality and drought stress response (Faghire et al. 2012; Aamir et al. 2013; El-Akhal et al. 2013; Sharma et al. 2013; Bertrand et al. 2015; Staudinger et al. 2016; Yanni et al. 2016; Wang et al. 2016; Defez et al. 2017; Egamberdieva et al. 2017; Oliveira et al. 2017).

Several works also reported that the co-inoculation of different rhizobial strains (Ali et al. 2017; Ullah et al. 2017) and that of rhizobia and other bacteria or arbuscular mycorrhizal fungi can be a strategy to mitigate salt or drought stress (Ahmad et al. 2011a, b, 2012, 2013; Soliman et al. 2012; Martínez et al. 2015; Cerezini et al. 2016; Egamberdieva et al. 2016a, b; Ren et al. 2016; Zhu et al. 2016; da Piedade Melo et al. 2017; Fukami et al. 2017; Oliveira et al. 2017). Moreover, the co-inoculation of rhizobia and other bacteria can alleviate other stresses, such as copper stress (Challougui et al. 2015; Fatnassi et al. 2015).

Concerning the promotion of growth of nonlegumes, although the first works were carried out in the 1990s (Chabot et al. 1996; Yanni et al. 1997), most works have been carried out after the year 2000 (Velázquez et al. 2017a). Several of these works focused on the growth promotion of cereals by *Rhizobium* in rice (Yanni et al. 2001; Yanni and Dazzo 2010; Bhattacharjee et al. 2012; Granada et al. 2014), maize (Gutiérrez-Zamora and Martínez-Romero 2001; Shing et al. 2013) and wheat (Yanni et al. 2016) and by *Mesorhizobium* strains in barley (Peix et al. 2001). Although there are few reports to date, co-inoculation with rhizobia and other bacteria also increases the growth of some cereals, such as rice (Hasan et al. 2014; Tan et al. 2015).

Several works also showed that rhizobial inoculation also increased the growth of oil-containing plants such as canola and sunflowers, with high interest for human nutrition (McKevith 2005) and biodiesel production (Pimentel and Patzek 2005, Ge et al. 2017). The promotion of growth and the nitrogen uptake increase were reported by Alami et al. (2000) after the inoculation of a strain from the genus *Rhizobium* in sunflower plantlets. The inoculation with strains of the genus *Rhizobium* enhances the root growth of canola plants (Noel et al. 1996) and, under salinity stress conditions, treatments with different rhizobial strains increase the plant height and the dry weight of canola shoots and, moreover, the leaf area and relative water content (Saghafi et al. 2018).

In addition, the ability of rhizobia to promote the growth of fresh vegetables has been studied by several authors, dating also the first works in the 1990s (Chabot et al. 1996; Antoun et al. 1998). Nevertheless, most studies have been carried out in the recent years showing that *Rhizobium* strains are able to promote the growth and quality of tomato and pepper (García-Fraile et al. 2012), lettuce and carrots (Flores-Félix et al. 2013), strawberries (Flores-Félix et al. 2015, 2018), arugula (Rubio-Canalejas et al. 2016) and spinach (Jiménez-Gómez et al. 2018). The high potential of rhizobia to promote the growth of vegetables, together with the high safety level of these bacteria, highlights the need to perform more studies about the effect of different rhizobial species on the growth of other freshly consumed vegetables.

4.5 Biocontrol Mechanisms

The mechanisms of biocontrol presented by bacteria nodulating legumes have been less studied than those involved in plant growth promotion. Nevertheless, for some strains belonging to several rhizobial genera and species, different biocontrol mechanisms have been reported, including mycoparasitism, production of antibiotics and bacteriocins, antifungal metabolites, such as hydrocyanic acid (HCN), and phytoalexins, as well as the induction of systemic resistance in plants (Deshwal et al. 2003b; Das et al. 2017).

Concerning mycoparasitism, in 1978, it was reported that *Bradyrhizobium japonicum* colonized growing hyphal tips of *Phytophthora megasperma* being observed inside the hyphae. A decrease in the symptoms was observed with the application of *B. japonicum* to the soil after soybean planting suggesting that saprophytic soil rhizobia may reduce *Phytophthora* root rot by parasitizing hyphae of the fungus (Tu 1978). Also, Antoun et al. (1978) showed that strains of *Ensifer meliloti* (*Sinorhizobium meliloti*) were effective against *Fusarium oxysporum* in lucerne plants.

After this date, several works reported the in vitro inhibition of several fungi by strains of different rhizobial genera. For example, some *Bradyrhizobium* strains inhibit the mycelial growth and sclerotial formation and germination of *Sclerotium rolfsii* (Balasundaran and Sarbhoy 1988) and *Rhizoctonia solani* (Kelemu et al. 1995). In the same line, different fast-growing rhizobial strains are able to inhibit the growth of *Phytophtora cinnamomi* (Malajczuk et al. 1984), *Sclerotium rolfsii* (Balasundaran and Sarbhoy 1988), *Fusarium*, *Pythium* and *Rhizoctonia* (Ozkoc and Deliveli 2001).

In 1978, the production of bacteriocins by *Rhizobium trifolii* strains (currently *R. leguminosarum*) was reported, which were dominant in mixed cultures and were growing in peat, suggesting that they have advantages for competition (Schwinghamer and Brockwell 1978). Also, bacteriocin production by *Rhizobium japonicum* (currently *B. japonicum*) was also reported, although in this case, the producing strains were less competitive than the nonproducing ones (Gross and Vidaver 1978). More recently, the production of bacteriocins has been reported for other strains from *Rhizobium* (Hafeez et al. 2005; Ansari and Rao 2014), *Bradyrhizobium* (Hafeez et al. 2005) and several rhizobial strains nodulating mothbean, clusterbean and mungbean (Mondal et al. 2017). In addition, the genome of a bacteriocin-producing strain of *B. japonicum* has been sequenced, obtaining a better understanding of this molecule (Kohlmeier et al. 2015).

The production of peptide antibiotics active against other rhizobial strains, such as trifolitoxin, has also been reported for *R. leguminosarum* sv. *trifolii* (Triplett and Barta 1987) and *Rhizobium etli* (Robleto et al. 1997, 1998). The rhizobitoxine produced by *B. japonicum* (Minamisawa 1989) and *Bradyrhizobium elkanii* (Yuhashi et al. 2000) reduces the mycelial growth of *Macrophomina phaseolina* (Chakraborty and Purkayastha 1984). More recently, the analysis of the genetic region encoding a novel rhizobiocin produced by *R. leguminosarum* sv. *viciae* has been reported (Venter et al. 2001).

New genome sequences of rhizobia have shown the presence of bioclusters coding for secondary metabolites, such as the HCN, an antifungal metabolite produced by some rhizobia, although the abundance of strains producing this compound among rhizobia is low to date. For example, Antoun et al. (1998) reported the HCN production in three strains of *R. leguminosarum*, Arfaoui et al. (2006) in six strains of rhizobia-nodulating chickpea, Chandra et al. (2007) in a strain of *Mesorhizobium loti* and Priyanka and Wati (2017) in two strains of rhizobia isolated from *Vigna* nodules.

The production of siderophores, in addition to being a plant growth-promoting mechanism, is also a biocontrol mechanism because these compounds have high affinity for ferric iron-forming complexes which remove this ion from the rhizosphere preventing the growth and plant colonization by pathogenic microorganisms (Saha et al. 2016). Several types of siderophores are produced by different rhizobial species and genera (Das et al. 2017), and we recently found that *Rhizobium laguerreae* produced carboxylate-type siderophores (Jiménez-Gómez et al. 2018).

Induced systemic resistance is a plant defence mechanism against different types of pathogens which is elicited by several rhizobial strains alone (Elbadry et al. 2006) or combined with other bacteria (Dutta et al. 2008), endophytic fungi or arbuscular mycorrhiza (AM) (Martinuz et al. 2012; Gao et al. 2018a, b). The *Rhizobium etli* lipopolysaccharides have been shown to be agents inducing systemic resistance to infection by the cyst nematode *Globodera pallida* in potato roots (Reitz et al. 2000) and those of *R. leguminosarum* against the parasitic plant *Orobanche crenata* in pea (Mabrouk et al. 2016).

Rhizobial strains are also able to induce the production of some phytoalexins in plants treated with fungal pathogens, as occurred in the case of pea infected with *Fusarium solani* and inoculated with *R. leguminosarum* (Chakraborty and Chakraborty 1989), in the case of chickpea infected with *Fusarium oxysporum* and inoculated with rhizobia nodulating this legume (Arfaoui et al. 2007) and in the case of lucerne infected with *Phoma medicaginis* and treated with *Ensifer medicae* (*Sinorhizobium medicae*) and the AM *Funneliformis mosseae* (Gao et al. 2018a, b).

As occurred in the case of the plant growth-promoting mechanisms, those involved in the biocontrol of plant pathogens have been more studied in species of the classic rhizobial genera than in those of the new genus *Paraburkholderia*. Nevertheless, recent studies have been performed in legume-nodulating species of the genus *Paraburkholderia*, showing that three species of this genus showed antifungal activity (Eberl and Vandamme 2016). Therefore, also in this case, more studies should be performed to understand the biocontrol mechanisms in legume-nodulating species of this last genus.

4.6 Biocontrol of Phytopathogens from Legumes and Nonlegumes

Concerning the direct biocontrol of phytopathogens by rhizobia in plant assays, there are few studies to date (Das et al. 2017). Nevertheless, some studies showed the potential of rhizobial strains for the inhibition of some pathogenic fungi, such as *Macrophomina phaseolina* (Omar and Abd-Alla, 1998; Siddiqui et al. 2000; Arora et al. 2001; Deshwal et al. 2003a; Al-Ani et al. 2012), *Fusarium solani* (Omar and Abd-Alla, 1998; Rakib et al. 2012), *Fusarium oxysporum* (Arfaoui et al. 2006; Kumar et al. 2011), *Rhizoctonia solani* (Omar and Abd-Alla, 1998; Hemissi et al. 2011) and *Phytium* sp. (Bardin *et al.*, 2004) .

The co-inoculation of strains from *Rhizobium* and *Glomus* increased the biocontrol of the *Fusarium* wilt of chickpea (Singh et al. 2010) and the *Fusarium* root rot of *Phaseolus vulgaris* (Dar et al. 1997), also protecting *Vicia faba* plants against *Botrytis fabae* (Rabie 1998). The co-inoculations of *Rhizobium* and *Trichoderma* have been also shown to reduce the damping-off and root rot diseases in several legumes (Shaban and El-Bramawy 2011) and the incidence of collar rot disease caused by *Sclerotium rolfsii* in groundnut (Ganesan et al. 2007). In the same way, the co-inoculation of *Ensifer* (*Sinorhizobium*) and *Pseudomonas* significantly reduced *Fusarium* wilt in pigeon pea (Kumar et al. 2010).

Other studies showed a reduction in galling and nematode multiplication of Meloidogyne incognita in chickpea when the plants were inoculated with a strain of rhizobia nodulating this legume (Akhtar and Siddiqui 2008). The dual inoculation of *Rhizobium* and other *Pseudomonas* strains in lentils also controlled *Meloidogyne javanica* (Siddiqui et al. 2007). The co-inoculation of *Rhizobium* with *Pseudomonas* or *Bacillus* strains decreases the wilting of *Fusarium oxysporum* in lentils inoculated with this pathogen (Akhtar et al. 2010) and that of *Rhizobium* or *Bradyrhizobium* with *Bacillus* improved the bean root rot control in common bean and peanut, respectively (Estevez de Jensen et al. 2002; Yuttavanichakul et al. 2012).

The co-inoculation with rhizobia and arbuscular mycorrhiza could control soybean red crown rot in acidic soils (Gao et al. 2012). The co-inoculation of tomato with *Rhizobium etli* and the arbuscular mycorrhiza *Glomus intraradicis* leads to a 60% reduction in the galling by *Meloidogyne incognita* (Reimann et al. 2008). The tripartite inoculation of *Rhizobium* with *Glomus* and *Pseudomonas* also controlled the root rot disease in chickpea caused by *Meloidogyne incognita* and *M. phaseolina* (Akhtar and Siddiqui 2008).

The co-inoculation with *Rhizobium* and *Trichoderma* of faba bean plants has been shown to reduce 57%, on average, the incidence of chocolate spot disease produced by *Botrytis fabae* and increasing 23%, on average, of the yield of faba bean (Saber et al. 2009). Moreover, the dual inoculation of these microorganisms reduced the stem rot incidence promoting the growth of the groundnut (Ganesan et al. 2007), as well as the incidence of the damping-off and root rot in several legumes such as *Vicia, Cicer* and *Lupinus* (Shaban et al. 2011).

Although all these studies showed that rhizobia are promising bacteria to control different plant pathogens through different mechanisms, this ability has been poorly studied to date. Therefore, also taking into account the ability of these bacteria to improve the plant growth of legumes and nonlegumes and, especially, their safety as biofertilizers for human health, the effects of rhizobia on plant health should be further studied.

4.7 Conclusions

Bacteria-inducing legume nodules, commonly called rhizobia, are mainly known to produce beneficial effects on legumes via atmospheric nitrogen fixation. However, they are also able to promote the growth of other economically valuable crops, such as cereals, oleaginous plants or horticultural crops through other plant growth-promoting mechanisms, such as solubilization of phosphate and production of indoleacetic acid, among others. Since this group of bacteria is considered safe for human, animal and plant health and for the environment, they are good candidates for the formulation of biofertilizers. The ability of rhizobia to produce compounds involved in biocontrol and to induce systemic resistance in plants also makes them good candidates as biocontrollers, although research in this field is still limited. Thus, further studies are necessary to be performed in order to include rhizobia in the formulation of biopesticides.

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