Chapter 15
Actinobacteria and Their Role as Plant Probiotics

Esther Menendez and Lorena Carro

Abstract *Actinobacteria* is one of the largest phyla within the domain *Bacteria*. This phylum comprises more than 400 genera heterogeneously distributed in up to 50 families, 20 orders and 6 classes, being composed with very diverse groups of microorganisms. Members included within this phylum were recovered from a wide range of aquatic and terrestrial environments and also from a huge number of higher organisms, including plants. *Actinobacteria* inhabiting soils and plants are well known as producers of bioactive molecules and as biocontrol agents, possessing antimicrobial activities mostly against pathogenic fungi and/or bacteria. Moreover, some of them have the capacity to exert beneficial effects on plant growth and development via different plant growth-promoting mechanisms, i.e., phytohormones biosynthesis, siderophore production, and phosphate solubilization, among others. The available genomic data revealed that members belonging to this phylum have a huge potential as Plant Probiotic *Actinobacteria*. A plethora of studies reported the isolation and identification of plant endophytic actinobacteria possessing those features and also their performance under controlled conditions. However, few studies show the effects of the inoculation of these actinobacteria on real field conditions. In this chapter, we will provide an overview of the available data on the *Actinobacteria* displaying plant growth-promoting features, particularly in the ones that already had applications in agriculture. Together with a correct taxonomic classification, we will present evidence that the Plant Probiotic *Actinobacteria* should be considered as a source of bacterial candidates that will be important for a future sustainable agriculture.

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15.1 Introduction

The *Actinobacteria* is a phylum of Gram-positive bacteria and one of the largest taxonomic units within the domain *Bacteria* (Barka et al. 2015). The majority of the *Actinobacteria* are free-living organisms, being well known for their ubiquitous presence in soil and aquatic habitats and their contribution to organic material recycling. Between these bacteria, we found indeed some of the most well-known producers of antibiotics, exemplified by the genera *Streptomyces, Micromonospora* and *Actinomadura* (Raja and Prabakarana 2011). The *Actinobacteria* establishes close relationships with their environment and the organisms of their surroundings, with key molecular exchanges that allow their coexistence. Within the phylum, we found pathogenic bacteria for humans (*Mycobacteria*, *Nocardia*, or *Tropheryma*), for plants (*Streptomyces scabiei*, which cause scab in potatoes), and for animals (*Corynebacterium, Mycobacteria*). However, beneficial actinobacteria are also found for all these organisms, *Bifidobacterium* being well known for their implication in human and animal health, *Pseudonocardia* for the protection of ant's gardens, or *Frankia* for their symbiotic relationship with actinorhizal plants. New studies on bacterial communities have shown that *Actinobacteria* composition is related to plant health (Wang et al. 2017), inducing a new interest in the study of *Actinobacteria*'s role as plant endophytes. This is clearly remarkable in the number of new species described from plant tissues in the last 10 years (Table 15.1), with more than ten new species published on the *International Journal of Systematic and Evolutionary Microbiology* only in the last 3 months (August–October 2018). High numbers of actinobacterial taxa found in healthy plant tissues have compelled us to think that these microorganisms have the capacity to improve plant health and could act as plant probiotics.

The FAO/WHO Expert Consultation Report defines Probiotics as "live microorganisms which when administered in adequate amounts confer a health benefit on the host" (Hill et al. 2014). Consequently, plant probiotics should be defined as "live microorganisms which when administered in adequate amounts confer a health benefit on the plant". Between the actinobacteria, *Frankia* genus could be considered the first and most studied plant probiotic actinobacteria. This genus has been studied for more than a century due to its ability to fix atmospheric nitrogen, which is exchanged with the plants with which it establishes symbioses (Beijerinck 1901; Carro et al. 2015). Presence of *Frankia* strains has been also related to improvements in stress tolerance, as high salinity concentration (Ngom et al. 2016) or soil degradation (Diagne et al. 2013). Nevertheless, many other genera have been included in the list of Plant Probiotic *Actinobacteria* in the last years, exemplified by *Streptomyces*, which have been shown to improve plant vegetative growth and to induce and contribute to plant defense from pathogen attacks (Conn et al. 2008); by *Micromonospora*, which are able to improve plant growth and the tripartite symbioses with rhizobia in legumes (Carro 2010; Martínez-Hidalgo et al. 2014); or by *Arthrobacter*, which are able to increase iron-stress resistance (Sharma et al. 2016). Most of the actinobacteria tested as plant probiotic bacteria have been directly

Table 15.1 A selection of new *Actinobacteria* species described from plant tissues in the last 10 years

Genus	Species	Plant	References
Actinocorallia	*A. populi*	*Populus adenopoda*	Li et al. (2018c)
Actinomadura	*A. barringtoniae*	*Barringtonia acutangula*	Rachniyom et al. (2018)
Actinomycetospora	*A. callitridis*	*Pinus sp.*	Kaewkla and Franco (2018)
	A. endophytica	*Podochilus microphyllus*	Sakdapetsiri et al. (2018)
Amnibacterium	*A. endophyticum*	*Aegiceras corniculatum*	Li et al. (2018d)
Arthrobacter	*A. endophyticus*	*Salsola affinis*	Wang et al. (2015)
Brachybacterium	*B. endophyticum*	*Scutellaria baicalensis*	Tuo et al. (2018)
Frankia	*F. canadensis*	*Alnus incana*	Normand et al. (2018)
	F. torreyi	*Comptonia peregrina*	Nouioui et al. (2018a)
	F. irregularis	*Casuarina equisetifolia*	Nouioui et al. (2018b)
Glycomyces	*G. anabasis*	*Anabasis aphylla*	Zhang et al. (2018)
Jiangella	*J. alba*	*Maytenus austroyunnanensis*	Qin et al. (2009)
Kocuria	*K. arsenatis*	*Prosopis laegivata*	Roman-Ponce et al. (2016)
Kribella	*K. podocarpi*	*Podocarpus latifolius*	Curtis et al. (2018)
Marmoricola	*M. endophyticus*	*Thespesia populnea*	Jiang et al. (2017)
Micromonospora	*M. luetiviridens* *M. luteifusca* *M. noduli* *M. phytophila* *M. pisi* *M. ureilytica* *M. vinacea*	*Pisum sativum*	Garcia et al. (2010), Carro et al. (2016a, b, 2018b), Carro and Nouiuoi (2017)
	M. zeae	*Zea mays*	Shen et al. (2014)
	M. costi	*Costus speciosus*	Thawai (2015)
	M. globae	*Globba winitii*	Kuncharoen et al. (2018)
	M. oryzae	*Oryza sativa*	Kittiwongwattana et al. (2015)
	M. parathelypteridis	*Parathelypteris beddomei*	Zhao et al. (2017)
	M. sonneratiae	*Sonneratia apetala*	Li et al. (2013)
	M. taraxaci	*Taraxacum mongolicum*	Zhao et al. (2014)
	M. terminaliae	*Terminalia mucronata*	Kaewkla et al. (2017)
	M. tulbaghiae	*Tulbaghia violacea*	Kirby and Meyers (2010)
	M. violae	*Viola philippica*	Zhang et al. (2014)

(continued)

Table 15.1 (continued)

Genus	Species	Plant	References
Naumannella	*N. huperziae*	*Huperzia serrata*	Sun et al. (2017)
Nesterenkonia	*N. endophytica*	*Glycyrrhiza uralensis*	Li et al. (2018a)
Nocardioides	*Z. zeicaulis*	*Zea mays*	Kämpfer et al. (2016)
Phytoactinopolyspora	*P. endophytica*	*Glycyrrhiza uralensis*	Li et al. (2015)
Solirubrobacter	*S. phytolaccae*	*Phytolacca acinosa*	Wei et al. (2014)
Streptomyces	*S. dioscori*	*Dioscorea bulbifera*	Wang et al. (2018a)
	S. alni	*Alnus nepalensis*	Liu et al. (2009)
	S. populi	*Populus adenopoda*	Wang et al. (2018b)
	S. geranii	*Geranium carolinianum*	Li et al. (2018b)
	S. ginkgonis	*Ginkgo biloba*	Yan et al. (2018)

inoculated on plants, in most of the cases to evaluate the protection against some pathogenic microorganisms. However, contrary to other bacteria, many of them have not been tested for the general characteristic evaluated to determine a plant growth-promoting bacteria (PGPB): nitrogen fixation capacity, phosphate solubilization, production of plant hormones (IAA, ACC desaminase), etc. In this chapter, an overview of *Actinobacteria* known as plant growth promoters will be given, with emphasis on their taxonomic position and their use in agriculture.

15.2 Current Taxonomy of *Actinobacteria*: Classic and NGS-Based Classification

The taxonomic status of a strain, according to the polyphasic taxonomy, is determined by both phenotypic and genotypic characterization. A combination of chemotaxonomic analysis and other phenotypic features (tolerance tests, enzyme production, ability to metabolize carbon and nitrogen sources) together with other genetic traits of the taxon (16S rRNA phylogeny, GC content, DNA–DNA hybridization) was classically used for new actinobacteria species descriptions (Carro and Nouiuoi 2017). The use of multilocus sequences analyses (MLSA) greatly improved the relationships between these new isolates (Carro et al. 2012) and the upstream taxa, as exemplified by the analysis done by Adekambi et al. (2011). Lately, the new sequencing technologies developed and its availability for the vast majority of researchers have introduced new methods for phylogenomic reconstructions, allowing a better classification regarding higher taxa never seen before. Specifically, the works developed by Sen et al. (2014) for the class *Actinobacteria* and Nouioui et al. (2018c) for the whole phylum have greatly rearranged their respective status.

The phylum *Actinobacteria* was first described by Cavalier-Smith (2002) and include six classes: *Acidimicrobiia* (Norris 2012), *Actinobacteria* (Stackebrandt et al. 1997), *Coriobacteriia* (König 2012), *Nitriliruptoria* (Ludwig et al. 2012), *Rubrobacteria* (Suzuki 2012) and *Thermoleophilia* (Suzuki and Whitman 2012). From these classes, 450 genera are unequally distributed, the majority of them (418) being within the class *Actinobacteria*. Endophytic bacteria have been described only in the class *Actinobacteria* and in the class *Rubrobacteria*. This latter class just comprises one plant-associated species, *Solirubrobacter phytolaccae* (Wei et al. 2014).

After last reclassification based of whole-genome sequences (Nouioui et al. 2018c), the class *Actinobacteria* comprises 20 orders: *Acidothermales*, *Actinomycetales, Bifidobacteriales, Catenulisporales, Corynebacteriales, Cryptosporangiales, Frankiales, Geodermatophilales, Glycomycetales, Jiangellales, Kineosporiales, Micrococcales, Micromonosporales, Nakamurellales, Nitriliruptorales, Propionibacteriales, Pseudonocardiales, Sporichthyales, Streptomycetales* and *Streptosporangiales*. Most of these orders contain endophytic strains; only in six of them, no plant related strains have been isolated (*Acidothermales*, *Actinomycetales, Bifidobacteriales, Catenulisporales, Nitriliruptorales* and *Sporichthyales*). Strains belonging to those orders are related to human samples or extreme habitats. All the other orders contain genera in which some or most of their species have been described as plant endophytes (isolated from within the plant tissues). Among them, the most important genera of plant pathogens are mainly found in the order *Corynebacteriales*, including *Corynebacterium*, *Nocardia*, and *Rhodococcus*; in the order *Micrococcales*, including *Clavibacter*, *Curtobacterium*, *Leifsonia*, and *Rathayibacter*; and in the order *Streptomycetales*, including some species of the genus *Streptomyces*, such as the phytotoxin-producer *S. scabies* (Lozi 1994). Although several species of these genera have been found to be pathogenic, in most cases other species within the same genus have been described as nonpathogenic endophytes or even plant growth-promoting bacteria, i.e., the strain BMG51109 of *Nocardia* (Ghodhbane-Gtari et al. 2018) or the strain SK68 of *Streptomyces* (Damodharan et al. 2018). Although not an exact distribution between pathogen and PGPB could be established between the genera of *Actinobacteria*, some relationships could be observed mainly due to these double functions of some genera (Fig. 15.1). Most of the pathogens appear in genera from the family *Microbacteriaceae* of the order *Micrococcales*, while *Frankiales*, *Jiangellales* or *Micromonosporales* include mainly PGPB or asymptomatic endophytic strains.

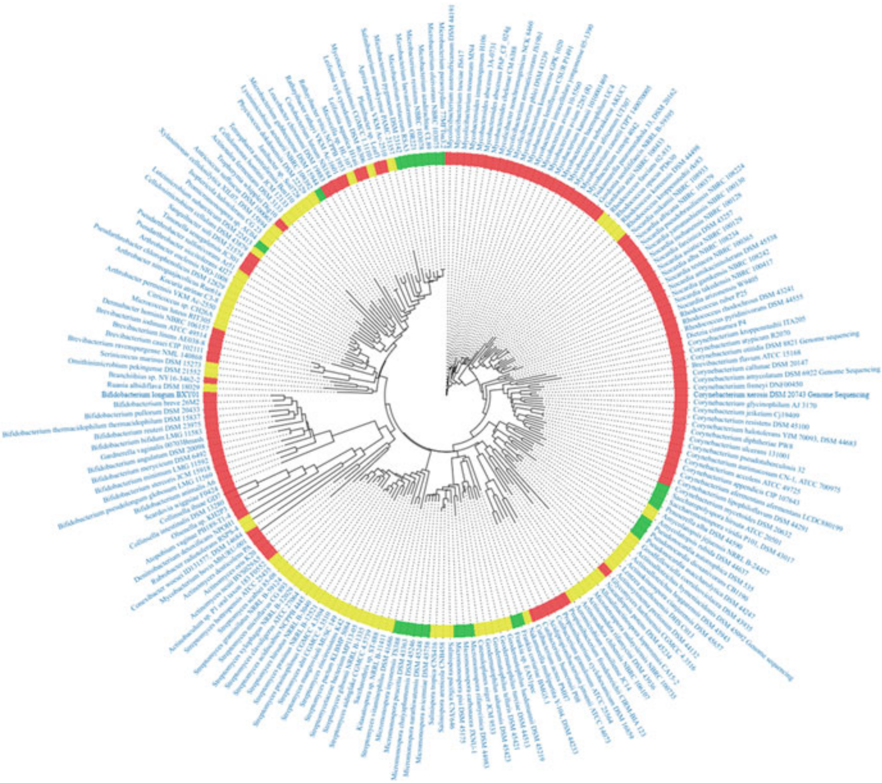

Fig. 15.1 Phylogenetic distance tree of selected *Actinobacteria* genus generated by distance tree tool of IMG 3.2. Groups are based on most abundant species found for a genus as beneficial endophytes (green), clinical samples, plant pathogens (red) and other sources, including soil and rhizosphere (yellow)

15.3 Genomes Data Mining of PGP Traits on *Actinobacteria*

New technologies have encouraged the research of genes from plant endophytes related to their abilities for plant growth promotion, generating full sets of candidate genes to be further analyzed due to their potential. Trujillo et al. (2014) and Carro et al. (2018a) identified some of these genes in several species of the genus *Micromonospora*, including genes related to plant hormones production, phosphate solubilization, or siderophores production, among the most common ones, and also genes related to the biosynthesis of trehalases or other degrading enzymes (amylases, cellulases, chitinases, pectinases, and xylanases), among the most interesting ones for biotechnological applications.

Most of the plant endophyte genomes have been shown to harbor a whole set of genes for central carbohydrate metabolism that could be related to the utilization of root exudates as energy source (Kang et al. 2016). Other frequently found genes include the ones related to nutrient deficiencies, oxidative stress, drought tolerance, as well as secretion mechanisms and signaling (Trujillo et al. 2015). Genes related to biosynthesis pathways of plant growth modulators, such as auxins and cytokinins, are generally found in most plant probiotic bacteria, which combined with others related to degradation of ethylene through 1-amino-cyclopropane-1-carboxylic acid deaminase generate further improvements of plant status under stress conditions. Some genes that contribute to efficient colonization and competitiveness are also important in first steps of interactions (Francis et al. 2016).

Genome analysis has also put in evidence the importance of actinobacteria as secondary metabolites producers and its possible use in agriculture for biological control. The production of several peptides and antibiotics observed in actinobacteria probiotics could be used to defend the host plant against pathogens (Paterson et al. 2017; Remali et al. 2017). The mechanism of biocontrol also involved induction of plant defense response by, for example, the upregulation of PR10a, NPR1, PAL, and LOX2 genes in colonized plants by *Streptomyces* (Patel et al. 2018).

15.4 Applications of Plant Probiotic *Actinobacteria* in Agriculture

The members of the phylum *Actinobacteria* have a huge and well-appreciated range of biotechnological applications. As we have seen before, the metabolic potential and the biological significance of several groups of actinobacteria are well known, which are of paramount importance in the biotech industries, mostly related to biomedicine (Golinska et al. 2015; Barka et al. 2015; Passari et al. 2017). Actinobacteria associated with plants, namely endophytic actinobacteria, have been studied for its application in agriculture (Palaniyandi et al. 2013), mainly in biocontrol and suppression of plant diseases and, in some cases, in plant growth promotion (Ganapathy and Natesan 2018; Singh and Dubey 2018) (Table 15.2). However, studies showing the effects of Plant Probiotic *Actinobacteria* on crop yields are still scarce (Viaene et al. 2016; Araujo et al. 2017). Some of those works are enumerated in Table 15.3.

Among *Actinobacteria*, the streptomycetes are one of the most abundant bacterial groups in soils, accounting for up to 10% of the total microbiome (Janssen 2006). The genus *Streptomyces* is the most studied genus within the phylum *Actinobacteria*, not only due to its uncountable properties but also because of the versatility of the species within this genus (Viaene et al. 2016).

The vast majority of the studies about the potential of *Streptomyces* strains as plant growth promoters and biocontrollers present effects under in vitro controlled conditions due to its innate ability to produce secondary metabolites (including antibiotic and antimicrobial compounds). Strains belonging to different species of the genus *Streptomyces* isolated from wheat rhizosphere and root endosphere

Table 15.2 List of genera from the phylum *Actinobacteria* with confirmed plant growth promotion potential

Actinobacteria	Plant host	References
Actinoplanes	*Cucumis sativus*	El-Tarabily et al. (2009)
Agromyces	*Oryza sativa*	Bal et al. (2013)
Arthrobacter	*Triticum aestivum*	Upadhyay et al. (2012)
	Brassica *Hordeum vulgare* Weed	Kim et al. (2011)
Curtobacterium	Weeds	Kim et al. (2011)
	Hordeum vulgare	Cardinale et al. (2015)
Frankia	*Atriplex cordobensis* *Colletia hystrix* *Trevoa trinervis* *Talguenea quinquenervia* *Retanilla ephedra*	Fabri et al. (1996)
Kocuria	*Vitis vinifera*	Salomon et al. (2016)
	Prosopis laegivata	Roman-Ponce et al. (2016)
Microbacterium	*Hordeum vulgare*	Cardinale et al. (2015)
	Oryza sativa	Bal et al. (2013), Banik et al. (2016)
	Saccharum officinarum	Lin et al. (2012)
	Arabidopsis thaliana	Schwachtje et al. (2012)
	Vitis vinifera	Salomon et al. (2016)
	Brassica Weeds	Kim et al. (2011)
Microbispora	*Pisum sativum*	Misk and Franco (2011)
Micromonospora	*Medicago sativa*	Martínez-Hidalgo et al. (2014)
	Lupinus angustifolia	Trujillo et al. (2010, 2015)
	Discaria trinervis	Solans (2007)
Nocardia	*Casuarina glauca*	Ghodhbane-Gtari et al. (2018)
Streptomyces	*Aristida pungens* *Cleome arabica* *Solanum nigrum* *Panicum turgidum* *Astragallus armatus* *Peganum harmala* *Hammada scoparia* *Euphorbia helioscopia*	Goudjal et al. (2014)
	Triticum aestivum *Solanum lycopersicum*	Anwar et al. (2016)
	Triticum aestivum	Jog et al. (2014)
	Discaria trinervis	Solans (2007)
Rhodococcus	*Oryza sativa*	Bertani et al. (2016)
	Hordeum vulgare Weeds	Kim et al. (2011)

Table 15.3 Plant Probiotic *Actinobacteria* with known effects on plant performance and development in field and greenhouse conditions

Actinobacterial taxa	Origin	PGP traits	Plant host and cultivation conditions	Effects caused on crops	References
Streptomyces	Chickpea rhizosphere	Antifungal activity Hydrolytic enzymes IAA HCN Siderophores	Chickpea/ Greenhouse and field	Increase of plant biomass and grain yield	Alekhya and Gopalakrishnan (2017)
Micromonospora	Nodules of naturally-occurring *Medicago sativa* plants	Hydrolytic enzymes IAA	Alfalfa/ Greenhouse	Increases in plant biomass and essential microelements	Martínez-Hidalgo et al. (2014)
Arthrobacter sp	Rapeseed roots	P solubilization AHL-like molecules	Rapeseed/ Field	Higher yields and weight per 1000 seeds	Valetti et al. (2018)
Streptomyces *Microbispora*	Whole roots of *Lens esculentus*, *Cicer arietinum*, *Pisum sativum*, *Vicia faba* and *Triticum vulgare*	Antimicrobial activity Siderophores P solubilization HCN	Chickpea/ Greenhouse	Bioprotection against *Phytophtora* and improved plant development	Misk and Franco (2011)
Actinoplanes campanulatus, *Micromonospora chalcea*, *Streptomyces spiralis*	Cucumber roots	Antagonistic activities Plant growth regulators (PGRs)	Cucumber/ Greenhouse	Reduced damping-off disease of cucumber seedlings (Table 3) and root and crown rots of mature cucumber, reduced damping-off disease of cucumber seedlings (Table 3) and root and crown rots of mature cucumber Reduced disease incidence Increased plant development and production	El-Tarabily et al. (2009)

(continued)

Table 15.3 (continued)

Actinobacterial taxa	Origin	PGP traits	Plant host and cultivation conditions	Effects caused on crops	References
Streptomyces griseus/ Micromonospora aurantiaca related strains	Mine soil	Antimicrobial activity, Siderophores P solubiliza-tion IAA	Wheat/ Greenhouse	Increase dry weight of wheat plants infected with *Pythium*	Hamdali et al. (2008a, b)
Arthrobacter woluwensis	Rhizospheric soil	IAA ABA Siderophores Halotolerance Organic acids	Soybean/ Greenhouse	Increase on plant length and biomass and higher levels of chlorophyll (SPAD) under saline stress	Khan et al. (2018)
Streptomyces spp.	*Vitis vinifera* rhizosphere/ endosphere	Antifungal activity	Grapevine/ Field	Reduced disease in grafted *Vitis* plants	Alvarez-Pérez et al. (2017)
Streptomyces	Wheat anthers	Antifungal activity	Wheat/ Greenhouse and field	Reduction of disease incidence	Palazzini et al. (2007, 2017)
Arthrobacter spp.	Burned holm oak rhizosphere	IAA Hydrolytic enzymes Siderophores	Alfalfa and pepper/ Greenhouse	Increase of plant biomass	Fernández-González et al. (2017)
Streptomyces spp.	Roots of native plants from India	IAA Siderophore Ammonia production	Wheat/Field	Increase of grain yield and plant biomass	Yandigeri et al. (2012)

showed several activities, such as chitinase and phytase activities, as well as phosphorous solubilization. These strains are also able to produce different compounds, such as IAA, siderophores, organic acids and antifungal metabolites (Jog et al. 2014). Wheat plants in growth chamber (lab-controlled conditions) inoculated with *Streptomyces* strains showed higher plant biomass, number of lateral roots and branches, and nutritional content (essential elements) in comparison with uninoculated control plants (Jog et al. 2014).

In tomato plants, Palaniyandi et al. (2014) isolated a *Streptomyces* strain, called PGPA39, from an agricultural soil, which possess ACC deaminase, biosynthesize IAA and solubilize phosphate. This strain was also halotolerant. Spores of this strain were mixed in sterilized soil and sown with tomato plants, alleviating stress in those plants and showing higher plant biomass and root development than that of noninoculated salt-stressed tomato control plants.

As shown, there are several species and strains belonging to this genus that have plant growth potential, but there are few reports regarding studies showing improvements in crop yields under real field conditions (Viaene et al. 2016; Araujo et al. 2017) (Table 15.3).

Alekhya and Gopalakrishnan (2017) performed a screening of actinobacteria isolated from chickpea rhizosphere to find strains with antagonistic potential. Seven strains belonging to different species of the genus *Streptomyces* and displaying several PGP traits (broad spectrum antifungal activity, hydrolytic enzymes, IAA and HCN biosynthesis and siderophore production) were selected and tested under greenhouse conditions and also, in a field assay. Under greenhouse conditions, inoculated chickpea plants exhibit an increase in shoot weight (up to 84%), root weight (up to 57%), pod number (up to 102%) and pod weight (up to 84%). At harvest time, field assays also showed better performance of chickpea plants inoculated with the selected *Streptomyces* strains: seed number (up to 22%), stover yield (up to 86%), grain yield (up to 17%) and total dry matter (up to 51%).

Studies on grafted *Vitis vinifera* plants showed also the beneficial effects of *Streptomyces* strains under field real conditions (Alvarez-Pérez et al. 2017). In this work, several actinobacterial strains were isolated from young grapevine plants rhizosphere and endosphere. The isolates displayed in vitro antifungal activity, which was confirmed in field assays conducted in three experimental open-root field nurseries of grafted plants. The presence of phytopathogenic fungi affecting grafted *Vitis* plants was dramatically reduced (Alvarez-Pérez et al. 2017).

In cereals, there are also some examples of studies confirming the PGP potential of *Streptomyces* strains under field conditions. Yandigeri et al. (2012) isolated several *Streptomyces* strains from roots of 5 different native plants from India. Those isolates produce IAA, ammonia and siderophores. Three of these strains were tested in wheat plants in a field assay under drought conditions. Their findings revealed that the strains were drought-tolerant and improved seedling vigor after inoculation. At harvest time, wheat plants had higher biomass and there was a significative increase in grain yields.

With the aim of identifying good biocontrol agents, Palazzini and colleagues isolated several strains from wheat anthers and later identified one of them as a good biocontrol strain, *Streptomyces* sp RC87B (Palazzini et al. 2007). This strain presented antifungal activities, particularly against *Fusarium graminearum sensu stricto* under in vitro and in a greenhouse assay using a wheat cultivar that is susceptible to *Fusarium* infections. Ten years later, a study using the same strains confirmed that this potential can also be translated to field conditions. Wheat susceptible to *Fusarium* infection experienced a reduction of disease incidence (Palazzini et al. 2017).

Not only *Streptomyces* but also other actinobacterial genera, i.e., *Micromonospora, Microbispora, Microbacterium, Actinoplanes*, or *Arthrobacter*, were also tested alone or in combination with other bacterial members such as rhizobia or other actinobacteria, mostly under lab-controlled conditions or greenhouse assays, even that there are some of these studies that involved field trials.

Co-inoculation of leguminous plants with actinobacteria and rhizobial strains produced beneficial effects in those plants, increasing the nodule number, symbiotic efficiency and the plant biomass in most of the cases. *Micromonospora* strains, able to produce hydrolytic enzymes and IAA, alone and in combination with *Ensifer (Sinorhizobium)* strains produced significative increases in shoot and root dry weights and shoot C, N, P and K elements in *Medicago sativa* plants under in vitro and greenhouse conditions (Martínez-Hidalgo et al. 2014).

A study involving a set of field trials with soybean plants showed that the co-inoculation of *Bradyrhizobium japonicum* USDA110 with a strain of *Streptomyces* leads to an enhancement of nitrogen fixation and the production of a higher plant biomass and grain yield (Soe et al. 2012).

Misk and Franco (2011) co-inoculated two strains of *Mesorhizobium ciceri* and different biocontrol-tested *Streptomyces* spp. on chickpea plants under greenhouse conditions. Some of those *Streptomyces* strains suppressed the incidence of *Phytophthora* root rot disease and, in combination with both mesorhizobial strains, also enhanced vegetative growth. Interestingly, these authors also identified a non-streptomycete strain belonging to the genus *Microbispora*, which showed biocontrol and PGP traits; sadly, this strain was not tested in the greenhouse assays.

Interestingly, there is a study reporting the beneficial effects of a triple inoculation of three actinobacterial strains, closely related to the species *Actinoplanes campanulatus*, *Micromonospora chalcea* and *Streptomyces spiralis*, on cucumber plants affected with damping-off disease produced by the phytopathogenic oomycete *Pythium*. The three isolates produced the highest level of growth promotion when together (El-Tarabily et al. 2009). Moreover, all three actinomycete strains, alone and in combination, significantly increased root and shoot production in the presence or absence of *Pythium aphanidermatum* in comparison with the untreated control.

Arthrobacter is another genus that is cited frequently as potential plant growth promoter and as bioremediation agent in agriculture. Khan et al. (2018) identified a rhizospheric strain of *Arthrobacter woluwensis*, strain AK1, which showed ABA and IAA production under saline conditions. This halotolerant strain mitigated salt stress and promoted rice growth under in vitro conditions and also promoted soybean growth under greenhouse conditions.

In a search for phosphate solubilizers, Valetti et al. (2018) isolated an *Arthobacter* strain that significatively increased the yield of rapeseed crops when compared with the yield produced by the negative control plots (no fertilized and non-inoculated). Interestingly, the harvest index derived from the *Arthrobacter* sp. LRCP-11 is superior to the one derived from the negative control and fertilized uninoculated treatment.

Furthermore, there is a recent study discussing the potential role of the genus *Arthrobacter* in burned forests (Fernández-González et al. 2017). These authors performed a metagenomic analysis of the holm oak rhizosphere of undisturbed and burned oak forests. *Actinobacteria* was the most abundant phyla in both cases but is more abundant in the burned one. The genus *Arthrobacter* was one of the genera in burned rhizospheres, showing a significant increase in abundance with respect to other genera of *Actinobacteria*. Isolates from this genus displayed hydrolytic enzyme activities and IAA production and some of them lead to the significant increase of alfalfa and pepper vegetative growth under greenhouse conditions.

15.5 Conclusions and Futures Perspectives

The use of *Actinobacteria* as plant probiotics is still in a very early stage compared with the use and application of other PGP bacteria. However, the high number of new species described having a close relationship with plants, including endophytic and rhizosphere actinobacteria, as well as the importance of these microorganisms revealed by plant microbiomes, make them a very interesting alternative to solve agricultural problems. These microorganisms have an excellent potential for plant protection due to its ability to produce inhibitory compounds that will not allow the development of plant pathogens, as well as inducing the natural defense systems of the plants, even from an early stage of development. The sequencing and further analysis of complete or nearly complete genomes have also evidenced the potential of the *Actinobacteria*. Future studies will help in the discovery of new molecules implicated in plant–endophyte symbiotic interactions. The actinobacteria are also soil microorganisms, a feature that will help in their permanence for a long period of time in this unpleasant environment. Until now, the application of these micro-organisms in real agricultural conditions has been limited; however, the limitations of the use of pesticides and chemical fertilizers in several worldwide countries and the global acceptance of the use of Plant Probiotic Bacteria as a "Green" alternative will encourage the use of these Plant Probiotic *Actinobacteria* in real crop production.

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