Plant-Associated *Rhodococcus* Species, for Better and for Worse

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Contents

Abstract *Rhodococcus fascians*, causative agent of the leafy gall syndrome, produces a mixture of cytokinins to modify the hormone landscape of its broad range of plant hosts leading to tissue deformations and developmental alterations. Recent developments indicate that the pathogenic nature of these bacteria is superimposed on its plant growth-promoting effect. In the last two decades, its unique position as the only species within the genus able to interact with plants has been overthrown. Indeed, Pistachio Bushy Top Syndrome is an emerging disease linked to the presence of two *Rhodococcus* species, *R. fascians* and *R. corynebacterioides*. Both bacteria would act synergistically to cause the symptoms, giving the prospect of virulence strategies that differ from those of the leafy gall inducers. Additionally, as a result of microbiome research, it is clear that many *Rhodococcus* species live in close association with plants, and several of them exhibit plant growth-promoting

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activities. Finally, genome analyses of a collection of *R. fascians* isolates imply that the taxonomic position of this group of bacteria within the genus will have to be reevaluated, and likely a new genus consisting of several species will be proposed soon.

1 Introduction

As illustrated by most chapters in this book, members of the genus *Rhodococcus* are renowned for their specialized metabolic capacities, and most are harmless, environmental, free-living organisms (Ceniceros et al. 2017). The genus, however, also comprises two pathogens: *R. equi*, the causative agent of pneumonia in foals leading to major losses worldwide in the equine industry (von Bargen and Haas 2009; Anastasi et al. 2016; MacArthur et al. 2017; Vázquez-Boland et al. this issue), and *R. fascians*, a plant pathogen causing the leafy gall syndrome mainly affecting ornamental production facilities all over the world (Depuydt et al. 2008b). Nevertheless, based on recent developments, the monopoly of *R. fascians* within the genus to interact with plants appears to be broken.

As a result of a growing environmental awareness, the use of agrochemicals to assure optimal crop yield is now considered less favorable, and considerable efforts are made toward more integrated agricultural approaches in which crop productivity and resilience against abiotic and biotic stress can be achieved with a reduced input. In that context, the use of biostimulants has gained a lot of attention, and the search for microorganisms that can stimulate plant productivity and protect crops from adverse conditions has become a major endeavor (Calvo et al. 2014). As an interesting side effect of these studies, a much broader view is obtained on the composition of rhizospheric and phyllospheric microbiomes, and it has become clear that diverse actinobacteria, including *Rhodococcus* species, readily associate with plants (Hamedi and Mohammadipanah 2015). Additionally, a novel disease termed Pistachio Bushy Top Syndrome has been reported which appears to be caused by two *Rhodococcus* species (Stamler et al. 2015a, 2015b).

Here, we summarize the latest progress on the *R. fascians* leafy gall pathology and provide an overview of the novel insights on the capacity of other *Rhodococcus* species to beneficially or detrimentally interact with plants.

2 *Rhodococcus fascians*, Causative Agent of the Leafy Gall Syndrome

2.1 Symptoms and Host Range

R. fascians, unlike most pathogens, is a genuine biotroph that does not truly damage its host but uses subtler strategies to infect plants. It was first recognized as a plant pathogen in 1936 as the causative agent of fasciation on pea (Brown 1927; Tilford 1936). However, on most hosts, fasciations are not induced, but rather the disease is apparent as a combination of several symptoms, including deformed leaves and flowers, swollen tissues due to secondary growth of vascular tissues, loss of apical dominance, excessive shoots, witches' brooms, and/or differentiated galls covered with small shoots, collectively called the leafy gall syndrome (Stes et al. 2011b, 2013; Dolzblasz et al. 2018). The host range of *R. fascians* has reached over 150 species across 50 plant families, including primarily herbaceous dicotyledonous plants and some monocots (Putnam and Miller 2007). The extensive host range of leafy gall-inducing *R. fascians* isolates illustrates that the virulence factors of these bacteria target widely conserved pathways in plants. Since typical symptoms associated with the leafy gall syndrome lead to disfigured plants, *R. fascians* has mainly been problematic in the ornamentals industry where plants are grown for their aesthetic value (Depuydt et al. 2008b).

2.2 The Trick-with-the-Cytokinin-Mix

The genome of the leafy gall-inducing model strain *R. fascians* D188 consists of three replicons: the circular chromosome, a circular plasmid pD188 encoding cadmium resistance and not involved in pathogenicity, and a conjugative linear virulence plasmid pFiD188 (Fig. 1). Over 25 years of research on the interaction between strain D188 and the model plants *Arabidopsis thaliana* and *Nicotiana tabacum* resulted in a molecular and developmental framework bringing together the pathways of microbe and plant that contribute to the disease (reviewed by Stes et al. 2011b, 2013).

In essence, key to symptom development is the bacterial production of an array of cytokinins via genes of the *fas* operon encoded on pFiD188 (Crespi et al. 1992; Francis et al. 2012; Pertry et al. 2009, 2010) and the concomitant modification of the hormone landscape of the infected plant (Depuydt et al. 2008a, 2009a; Stes et al. 2011a, 2012, 2015; Dhandapani et al. 2018). The interaction starts with the epiphytic colonization of the plant. During this phase, no symptoms are induced, but the bacteria secrete low levels of a mixture of cytokinins and of auxin produced via chromosomal pathways that stimulate the metabolism of the plant cells resulting in the release of nutrients to the benefit of bacterial colonization (Cornelis et al. 2001; Depuydt et al. 2009b; Dhandapani et al. 2017, 2018; Francis et al. 2016). As a

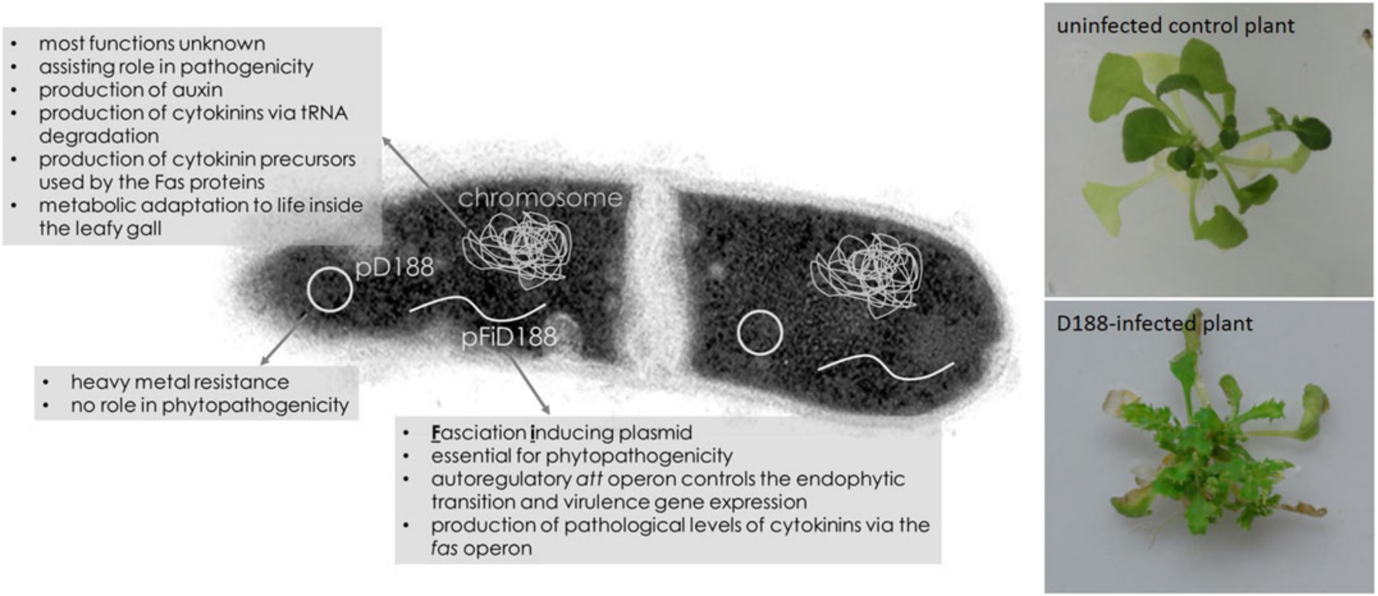

Fig. 1 Genome composition of the leafy gall-inducing model *R. fascians* strain D188 and symptoms on *Arabidopsis thaliana*

consequence of the shift in the primary metabolism of the plant upon perception of the bacteria (Depuydt et al. 2009b), a physiological change is triggered in the bacteria that will ultimately lead to the second phase of the interaction: the pathogenic endophytic phase. This phase is initiated by the production of an autoregulatory molecule encoded by the *att* locus located on pFiD188, establishing a positive regulatory loop resembling quorum sensing. The *att* system activates the transition to the endophytic phase possibly by stimulating the production of cell wall-degrading enzymes allowing active penetration of plant tissues and results in the production of higher pathological levels of a mixture of cytokinins encoded by the *fas* locus inducing the formation of an abundance of meristematic tissues in the plant that develop into shoots (Temmerman et al. 2000; Maes et al. 2001; Pertry et al. 2009; Fig. 1). The physiology of the symptomatic tissues is very different from uninfected plants, and the high concentration of meristematic cells leads to the provision of specific nutrients (Depuydt et al. 2009a, 2009b). These nutrients are believed to be metabolized via the glyoxylate shunt, since the bacteria require a functional malate synthase encoded by the chromosomal *vicA* gene for efficient survival inside the plant tissues (Vereecke et al. 2002). Hence, the success of the interaction with the host depends on the co-option of chromosomal and linear-plasmid-encoded functions, and eventually, through hormone secretion, the bacteria trigger the plant to provide it with a unique niche in terms of food and protection (Depuydt et al. 2009b; Dhandapani et al. 2017, 2018).

The virulence mechanism described above for *R. fascians* D188 is most likely similar for most other pathogenic leafy gall-inducing isolates because the *fas* and *att* genes are highly conserved (Creason et al. 2014a; Radhika et al. 2015). Nevertheless, the central position of cytokinins in the mode of action of the leafy gall inducers has been debated since their discovery because of the very low levels produced by in vitro-grown *R. fascians* cultures (Thimann and Sachs 1966; Eason et al. 1995; Pertry et al. 2009; Radhika et al. 2015). Even today, newcomers in the field question if cytokinins are essential for the leafy gall syndrome (Creason et al. 2014a; Savory et al. 2017), but until now, no valid alternative function for the *fas* operon has been proposed, and no other mode of action has been experimentally demonstrated (Vereecke, 2018). In contrast, there is a wealth of information that supports the indispensable role of *fas*-derived cytokinins in leafy gall formation:

1. The implication of cytokinins in symptom development has been recognized since 1966 (Klämbt et al. 1966; Helgeson and Leonard, 1966; Rathbone and Hall 1972; Scarbrough et al. 1973; Balázs and Sziráki 1974; Armstrong et al. 1976; Murai et al. 1980; Crespi et al. 1992; Eason et al. 1996; Dhandapani et al. 2017).
2. Mutations in the *fasA* and *fasD* genes render *R. fascians* nonpathogenic (Crespi et al. 1992, 1994; Pertry et al. 2009, 2010).
3. There is a 100% correlation between the presence of *fasD* and virulence (Eason et al. 1995, 1996; Stange et al. 1996; Nikolaeva et al. 2009; Creason et al. 2014a; Savory et al. 2017).

4. The biochemical activity of several Fas proteins in the production of cytokinins has been experimentally demonstrated (Crespi et al. 1992; Pertry et al. 2009, 2010; Radhika et al. 2015).
5. The cytokinins produced by *R. fascians* in culture are recovered in a higher amount in infected plants versus non-infected ones (Pertry et al. 2009, 2010; Radhika et al. 2015; Dhandapani et al. 2017).
6. *R. fascians*-infected plants activate cytokinin homeostasis mechanisms in the same way as if they were subjected to an excess of exogenous cytokinins (Depuydt et al. 2008a, 2009b; Motte et al. 2013).
7. The transcriptome of infected *Arabidopsis* and sweet pea plants clearly shows an enhanced cytokinin response (Depuydt et al. 2008a, 2009b; Dhandapani et al. 2017, 2018).

One challenging aspect of the trick-with-the-cytokinin-mix model was that the same mix of *fas*-dependent cytokinins was also detected in the supernatants of the plasmid-free strain D188-5. The cytokinin levels in this nonpathogenic derivative are much lower than those produced by the wild-type strain D188, and they are believed to result from tRNA degradation (Pertry et al. 2009, 2010). Because the bacteria cause symptoms only when the linear plasmid pFiD188 is present (Crespi et al. 1992), it was postulated that virulence does not depend on the exposure of the plant to one specific kind of cytokinin molecule but rather to particular concentrations and ratios of several of these plant growth regulators (Pertry et al. 2009, 2010). The higher pathological levels of cytokinins could only be produced through a co-option of chromosomal and linear plasmid genes (Francis et al. 2016). Although the cytokinin-mix production strategy used by *R. fascians* has been extended to plant-insect interactions (Giron and Glevarec 2014), Radhika et al. (2015) provided the missing link in the model. Indeed, the *mtr* genes encoding SAM-dependent methyltransferases and located upstream of the *fas* operon are involved in methylating the precursor of 2-iP used by FasD. These methylated cytokinins, which are not produced by plants, are resistant to plant cytokinin dehydrogenase-oxidases, are recognized by the plant cytokinin receptors, and have high morphogenic activities, most likely represent unique virulence-associated cytokinins (Radhika et al. 2015).

2.3 Epidemiology of Leafy Gall Disease in Ornamental Nurseries

As early as 1950, modes of spread of *R. fascians* within commercial nurseries of ornamental plants have been documented, and infield survival of up to 5 years in soil under favorable conditions has been reported (Baker 1950; Faivre-Amiot 1967; Oduro 1975; Miller et al. 1980), but overall information on the epidemiology of leafy gall-inducing *R. fascians* isolates remains scarce. Until recently, no in-depth information on the composition of the *R. fascians* populations on infected plants was available, and the relatedness between the bacteria on different plants within a nursery or between nurseries had not been studied. The phylogenetic relationship of 60 isolates collected from symptomatic tissues from single plants or from different plants in the same production facility was analyzed using a genomic epidemiological approach. The data showed that single nurseries could be infected by up to seven genotypes, that single plants could be colonized by at least three genotypes, and that different nurseries harbored highly related genotypes. Altogether, it could be concluded that the pathogens had been introduced in nurseries at multiple and independent occasions. Additionally, evidence was provided for point source outbreaks likely as a result of the acquisition of diseased plants from a common provider, but the presence of reservoir populations in some nurseries was apparent as well. When the linear plasmids of these isolates were compared, two major plasmid types could be distinguished, but the distribution of these plasmids indicated that plasmid exchange between genotypes occurred frequently. Additionally, the pathogenic isolates coexisted with nonpathogenic ones (Savory et al. 2017). Thus, as in other plant-associated bacteria, including *Pantoea agglomerans* (Weinthal et al. 2007), *Streptomyces scabies* (Zhang et al. 2016; Zhang and Loria 2017), *Pseudomonas syringae* (Monteil et al. 2016), and *Pseudomonas savastanoi* pv. *savastanoi* (Buonaurio et al. 2015), also in leafy gall-associated *Rhodococcus* species, the acquisition of a virulence plasmid drives pathogen evolution.

2.4 **Rhodococcus fascians*, a Troubled Species***

The taxonomic position of *R. fascians* has been troublesome since it was first isolated from diseased peas. At that time, the causative agent of the observed fasciations was named *Phytomonas fascians*, which was thought to be a specialized form of *Phytomonas (Agrobacterium) tumefaciens* (Tilford 1936). Few years later, the bacterium was renamed *Bacterium fascians*, because the generic name "*Phytomonas*" for plant pathogenic bacteria was no longer valid (Lacey 1939). Nonetheless, also this generic name led to persistent controversy, and based on post-fission movements of the bacteria and the presence of intracellular bodies, it was eventually recognized as *Corynebacterium fascians* (Dowson 1942). In the following years, it became apparent however that the leafy gall-inducing bacteria were more similar to *Rhodococcus* species than to *Corynebacterium*, and thus, more than 40 years later, in 1984, Goodfellow reclassified the pathogen as *Rhodococcus fascians* based on genetic, phenetic, and chemical characteristics (Goodfellow 1984). Now, as a consequence of the data obtained by (next-generation) sequencing techniques, once again doubt has been casted on the taxonomy of this microbe, and after 34 years, phylogenomic evidence suggests that the systematics of the genus *Rhodococcus* should be revised, and the *R. fascians* species likely belong to a distinct genus encompassing several species (Creason et al. 2014b; Sangal et al. 2016; Savory et al. 2017).

A strong indication that the genus *Rhodococcus* probably needs to be divided into more genera was based on 16S rRNA phylogenetic analysis of 217 actinomycete isolates, which revealed the occurrence of at least four *Rhodococcus* groups that were as phylogenetically distinct from each other as from *Nocardia* and *Gordonia* (Gürtler et al. 2004). However, an example that 16S rRNA-based classification is probably not sufficient to resolve the *Rhodococcus* genus is the inclusion into the species *R. fascians* of new isolates from diverse extreme environments unrelated to plants, such as Antarctic soils, marine waters, tidal flats, sediments contaminated with nuclear waste, polychlorinated dioxins, crude oil and hydrocarbons, deep glacier ice cores, and even carp intestines (Gürtler and Seviour 2010). Genome analysis of 19 isolates obtained from diseased ornamental plants, 2 isolates from a glacial ice core and 1 from permafrost, and 2 endophytes isolated from *Arabidopsis* indicated that these bacteria grouped into two clades representing up to seven different species (Creason et al. 2014b). Both clades contained pathogenic as well as nonpathogenic isolates. Even more, *Next Generation Systematics* based on the genome analysis of 100 rhodococcal strains and 15 representatives of related genera has provided a genomic framework that revealed seven distinct species-groups and three singletons (Sangal et al. 2016). Species-group E consisting of 28 genomes represents the *R. fascians* cluster which can be further subdivided in two subgroups corresponding to the two clades identified by Creason et al. (2014b). Subgroup E1 corresponds to clade II and would comprise two species, whereas subgroup E2, including the type strain and the model strain D188, corresponds to clade I and encompasses six predicted species (Sangal et al. 2016). Based on this information and as discussed by Sutcliffe and colleagues in this issue, a formal proposal of a new and hopefully final genus name for *R. fascians* is to be expected soon.

3 Pistachio Bushy Top Syndrome, a Novel *Rhodococcus*-Associated Disease

In 2011, a novel disease emerged on pistachio “UCB-1” rootstock trees, termed Pistachio Bushy Top Syndrome (PBTS) which significantly affected the pistachio industry in California, Arizona, and New Mexico, causing massive economic losses (Stamler et al. 2015a, 2015b). PBTS is characterized by stunted growth of the rootstock trees, the formation of additional shoots, the strongly reduced capacity of the rootstock to accept a *Pistacia vera* graft, the development of cracked tissue at graft junctions weakening the graft union, the emergence of ectopic shoots from gall-like tissue formed at lateral buds, and, most typically, a complete disturbance of regular root development (Stamler et al. 2015a, 2015b) (Fig. 2). The causative agents of PBTS were found to be two *Rhodococcus* species: *Rhodococcus* sp. strain 1 (PBTS1) genetically related to *R. corynebacterioides* and *Rhodococcus* sp. strain 2 (PBTS2) with high genetic similarity to *R. fascians* (Stamler et al. 2015b, 2016). Little information is available on the former bacterium, but it has been found as an endophyte in xylem of eggplant and leaves of *Arabidopsis* (Traw et al. 2007; Achari and Ramesh 2014). Concerning the *R. fascians* isolate, few woody plants were

Fig. 2 Typical symptoms associated with Pistachio Bushy Top Syndrome on "UCB-1" pistachio rootstock. (**a**) Loss of apical dominance leads to bushy top appearance; (**b**) deformed leaves; (**c**) deformed root system; (**d**) unsuccessful grafting attempts; (**e**) bark cracking at the graft union

shown to be sensitive to leafy gall-inducing *R. fascians* strains (Putnam and Miller 2007), but the Anacardiaceae or cashew family to which pistachio belongs is a new host of this bacterium. While the strategy utilized by the model strain *R. fascians*

D188 to cause leafy galls on the model plant *Arabidopsis* is largely understood and the major players involved in the initiation and maintenance of the symptoms have been identified, as summarized above, to date, virtually nothing is known on the pathogenic strategies deployed by the PBTS strains. Nevertheless, both isolates generated an amplicon with *fasD*-specific primers, and PBTS2 also generated an amplicon with *fasA*-specific primers, suggesting that cytokinins might play a role. Interestingly, while performing Koch's postulates, it appeared that both PBTS *Rhodococcus* strains work in synergism to alter plant development on clonal "UCB-1" pistachio (Stamler et al. 2015b).

Whereas the current knowledge on the mode of action of the PBTS *Rhodococcus* strains is still in its infancy (Stamler et al. 2015a, 2015b, 2016), Koch's postulates were clearly fulfilled. Still the diagnosis of PBTS1 and PBTS2 as outbreak strains of PBTS on pistachio has been challenged because the presence of the virulence genes could not be confirmed, and consequently, the PBTS isolates analyzed were not pathogenic. Hence, the hypothesis has been put forward that the PBTS *Rhodococcus* strains would actually be beneficial bacteria naturally associated with pistachio (Savory et al. 2017). In our opinion, it is premature to assume that leafy gall and PBTS inducers necessarily use the same virulence mechanism and that all aspects of the biology of both syndromes are shared. Additionally, concerning the epidemiology of PBTS, very strong conclusions were drawn based on the analysis of two single PBTS isolates, whereas the epidemiology of leafy gall inducers in ornamental orchards could only be revealed by studying 60 different isolates (Savory et al. 2017). One can only hope that good and integer science will resolve this issue in the future (Randall et al. 2018; Vereecke 2018).

4 Beneficial and Undefined Associations of *Rhodococcus* Species with Plants

The concept of plants serving as a habitat for complex microbial communities interacting with each other and with the plant host is now widely accepted and gaining more research interest as to how we can use these organismal interactions in plant growth and health management. The composition of the microbial communities interacting with different plant parts can vary greatly and reflects niche adaptation. Within these microbiomes, several *Rhodococcus* species, apart from the well-known plant pathogen *R. fascians* (discussed above), have recently been found living in close association with various plant parts. For example, *Rhodococcus* isolates were found as part of the rhizosphere of *Origanum vulgare* in a sub-Himalayan region (Bafana 2013), the phyllosphere of *Arabidopsis thaliana* plants (Bai et al. 2015; Ritpitakphong et al. 2016), and as an endophyte of leaves of *Cercidiphyllum japonicum* (Li et al. 2008) and stem tissues of *Artemisia annua* and *Sorghum bicolor* (Zhao et al. 2012; Maropola et al. 2015). Although the ecological role of most of these plant-associated *Rhodococcus* species remains to be discovered, a number of isolates have been shown to display plant growth-promoting properties and can confer resistance to plant pathogens.

4.1 Rhodococcus fascians *Beyond Leafy Gall Formation*

Recent work has shown that upon loss of its linear plasmid, the resulting nonpathogenic derivative D188-5 of *R. fascians* strain D188 can stimulate plant growth (Francis et al. 2016). This bacterium is very well equipped for an epiphytic lifestyle and likely acts as a phytostimulator mainly through the production of the plant hormones cytokinin and auxin (IAA) and the degradation of ethylene via 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Francis et al. 2016). The delicate interplay between cytokinin and auxin regulates meristem formation and development in both shoots and roots from early embryogenesis (Su et al. 2011), while ethylene inhibits shoot and root proliferation at high concentrations which generally occurs when the plant is under environmental stress (Sing et al. 2015). The fact that this plasmid-free, nonpathogenic derivative of D188 promotes plant growth suggests that pathogenic isolates may actually be plant growth-promoting bacteria gone astray. This reasoning is supported by the conservation of the plant growth-promoting determinants, especially the chromosomal genes involved in cytokinin and auxin metabolism, in strains covering both clades of the *R. fascians* species group discussed above (Francis et al. 2016). Additionally, plant growth-promoting activity has been attributed to other leafy gall-associated *R. fascians* strains (Savory et al. 2017), but the experimental data to support this conclusion were thought to be insufficient (Randall et al. 2018; Vereecke 2018).

The plant pathogen *R. fascians* was also identified as one of the dominant bacterial species on different cultivars of spring barley in combination with various other pathogenic and nonpathogenic bacteria, yeasts, and fungi (Newton et al. 2010) and as one of the *Rhodococcus* isolates in the rhizosphere of the nickel hyperaccumulator *Thlaspi goesingense* (Idris et al. 2004). The latter isolates displayed moderate to high siderophore production, and some also produced ACC deaminase (Idris et al. 2004). Although the later subjective synonym *R. luteus* (Klatte et al. 1994) was used, *R. fascians* was also isolated as a xylem-inhabiting bacterium from grape cultivars in Nova Scotia (Bell et al. 1995). Importantly, none of these hosts displayed disease symptoms suggesting that the pathogenic lifestyle of *R. fascians* might be strongly condition dependent.

4.2 *Plant-Associated* **Rhodococcus** *Species Have Plant Growth- Promoting Activities and Confer Plant Resistance to Pathogens*

Apart from the plant growth-promoting ability of the plasmid-free derivative of *R. fascians* D188 (Francis et al. 2016), several other *Rhodococcus* species were shown to stimulate plant growth and development. An isolate from postglacial clay and positive for ACC deaminase significantly increased the root biomass of pea plants in a pot experiment by 25% (Belimov et al. 2001). An endophytic species of tomato roots also tested positive for IAA production, synthesis of ACC deaminase, and had high siderophore activity (Abbamondi et al. 2016). Although not tested on plants, *Rhodococcus* aff. *qingshengii*, isolated from a polluted river in India, produced high levels of IAA (Hasuty et al. 2018). As part of its plant growth-promoting properties, *R. globerulus*, an endophyte of the medicinal plant *Plectranthus amboinicus*, was capable of phosphate solubilization making insoluble organic phosphorus available to plants. This trait opens up the possibility of using the isolate as a biofertilizer (Murugappan et al. 2017).

In a diversity study of the nodule microbiomes of *Lotus japonicus* and *Anthyllis vulneraria* in Sweden, two *Rhodococcus* isolates have been found with the ability to nodulate these two plants. These bacteria probably obtained this exceptional ability through horizontal gene transfer from other nodule-inhabiting bacteria, as their *nodA* gene was closely related to that of *Mesorhizobium loti* (Ampomah and Huss-Danell 2011). Moreover, it is speculated that the combined activity of the nitric oxide synthase of *Rhodococcus* isolate APG1, an endophyte of the aquatic fern *Azolla pinnata*, together with symbiotic *Arthrobacter* species could be beneficial to plants by providing nitrogen oxides for regulatory functions (Cohen and Yamasaki 2003; Cohen et al. 2004). *Rhodococcus* was also found as one of the main genera colonizing the shoot endosphere of a willow cultivar that is particularly well-suited for phytoremediation of heavy metal-contaminated soils. This property was attributed to the very diverse endophytic bacterial population among which a high number of metal-resistant plant growth-promoting bacteria, although for the identified *Rhodococcus* species no specific plant-stimulating properties were reported (Weyens et al. 2013).

Rhodococcus species themselves are commonly used for bioremediation due to their unique biochemical properties, such as biodegradation of hydrophobic natural compounds and xenobiotics, including polychlorinated biphenyls (PCB) (van der Geize and Dijkhuizen 2004; Larkin et al. 2005; Ceniceros et al. 2017; and further discussed in this volume). These bacteria are often found to live in close association with plants grown at such contaminated sites, and it is this unique plant—*Rhodococcus* combination that improves soil bioremediation (Leigh et al. 2006). *R. erythropolis* U23A, isolated from the rhizosphere of plants grown in PCB-contaminated soils, showed increased PCB degradation due to chemotaxis toward plant secondary metabolites (Toussaint et al. 2012; Pham et al. 2015). *R. erythropolis* strain CD 106 not only significantly increased the effectiveness of the phytoremediation of petroleum hydrocarbon-contaminated soil by 31.2% in combination with ryegrass but also increased the biomass of roots and shoots by 30–49%, respectively (Płociniczak et al. 2017). Also, plant growth inhibition by chromium, more specifically Cr^{6+}, can be alleviated by the psychrotroph *R. erythropolis* MTCC 7905 due to its ability to reduce Cr^{6+} to the nontoxic Cr^{3+} and several plant growth-promoting activities, such as ACC deaminase production, indole and siderophore production, although these latter activities decreased with increasing Cr^{6+} concentrations (Trivedi et al. 2007).

Finally, microbiome studies show that the natural inhabitants of plants such as leaf epi- and endophytic bacteria can confer resistance to plant pathogens. In that respect, *R. kyotonensis* and *R. corynebacterioides*, endophytes isolated from *Arabidopsis*, were shown to confer mild disease suppression against *Pseudomonas syringae* pv. tomato DC3000 (Hong et al. 2015), and another endophyte, *Rhodococcus* sp. KB6, significantly repressed black rot disease in sweet potato caused by *Ceratocystis fimbriata* (Hong et al. 2016). *R. erythropolis* can intercept and degrade the quorum-sensing signals produced by *Pectobacterium atrosepticum* and *P. carotovorum*, the causative agents of blackleg and soft rot disease in potato plants and tubers. These signals are important in the onset of virulence gene expression, and hence, degradation of the quorum-sensing N-acyl homoserine lactone signals limits disease development (Jafra et al. 2006; Cirou et al. 2007; Latour et al. 2013; Kwasiborski et al. 2015).

5 Concluding Remarks

Although the leafy gall-inducing model *R. fascians* strain D188 has been studied for over a quarter of a century, detailed information on the genes implicated in the pathogenicity is only available for the *fas* and the *att* operon. However, the linear plasmid, around 200 kb in size, is highly conserved in all other leafy gall inducers analyzed to date, suggesting that many other determinants encoded by the linear plasmid must be essential for a successful interaction with the plant host. Future experimentation will hopefully give more insight into the role of these other genes in the pathogenicity of *R. fascians*, and time will tell if the *fas* operon and the trick-with-the-cytokinin-mix are indeed determinative for leafy gall formation.

With the outbreak of PBTS on pistachio, the genus *Rhodococcus* acquired an additional pathogenic member, and with the expanding research on plant-associated microbiomes, it is clear that the capacity of members of this genus to interact with plants has been largely underestimated. Given that the genus *Rhodococcus* is renowned for its highly specialized metabolic capacities, the comparison of the genomes of all plant-interacting *Rhodococcus* species, beneficial and adverse, might reveal novel functions specifically utilized by this group of bacteria to interact with a plant host.

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