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Research review paper

## Threats and opportunities of plant pathogenic bacteria

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## ABSTRACT

Plant pathogenic bacteria can have devastating effects on plant productivity and yield. Nevertheless, because these often soil-dwelling bacteria have evolved to interact with eukaryotes, they generally exhibit a strong adaptivity, a versatile metabolism, and ingenious mechanisms tailored to modify the development of their hosts. Consequently, besides being a threat for agricultural practices, phytopathogens may also represent opportunities for plant production or be useful for specific biotechnological applications. Here, we illustrate this idea by reviewing the pathogenic strategies and the (potential) uses of five very different (hemi)biotrophic plant pathogenic bacteria: *Agrobacterium tumefaciens*, *A. rhizogenes*, *Rhodococcus fascians*, scab-inducing *Streptomyces* spp., and *Pseudomonas syringae*.

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### 1. Introduction

The activities of microorganisms are tightly interwoven with plant production and agricultural efficiency. The beneficial effect of soil

microbes, especially fungi and bacteria, is accomplished either in a direct or an indirect fashion (Khan et al., 2009). The most general, yet widely recognized advantage of the soil microbial population on improvement of soil quality lies in their capacity to decompose organic matter thereby releasing valuable nitrogen and carbon sources (Hättenschwiler et al., 2011). However, loose or intimate microbial associations in the plant's rhizosphere, the thin layer of soil directly into contact with the plant root, have an enormous impact on plant health and productivity as well. Plant growth promoting rhizobacteria directly stimulate plant growth through the secretion of plant growth regulators, such as auxin, cytokinins, and gibberellins (Tsavkelova et al., 2006), by increasing the bioavailability of micronutrients, such as phosphorus and iron (Francis et al., 2010; Rodríguez et al., 2006), by providing nitrogen via associative nitrogen fixation (Hayat et al., 2010), and/or by inducing systemic resistance (De Vleeschauwer and Höfte, 2009; Lugtenberg and Kamilova, 2009). Plant growth promoting rhizobacteria can also indirectly improve plant performance by sequestering hazardous compounds from the soil, such as heavy metals and hydrocarbons (Auger et al., 2013; Dhal et al., 2013; Khan et al., 2013), and by acting as antagonists of plant pathogens via mechanisms as diverse as competitive niche occupancy, production of antibiotics, and interference with pathogen signaling and virulence (Badri et al., 2009; Beneduzi et al., 2012; Haas and Défago, 2005; Lin et al., 2012). The importance of these latter capabilities of beneficial microbes is exemplified by the existence of natural suppressive soils which are typically loaded with pathogens, but in which plants can flourish and remain disease-free (Mazzola, 2004). Much more specialized are symbiotic interactions, leading for instance to the formation of nodules inhabited by rhizobia or actinobacteria that fix atmospheric nitrogen and deliver it as ammonia to the plant; in return the plant provides the bacteria with carbon derived from photosynthates (Pawlowski and Demchenko, 2012; Seipke et al., 2012; Terpolilli et al., 2012). The usefulness of microbial biofertilizers as an alternative for chemical fertilization to improve soil quality and increase soil fertility and crop production in sustainable agriculture is becoming widely appreciated and applied (Malusá et al., 2012; Wu et al., 2005).

Of course, when one considers the relation between microbes and agricultural performance, phytopathogens and their destructive outcome on crops are not to be neglected. Without a doubt, plant diseases inflicted by fungi, bacteria, and other microorganisms, have a major impact on yield and throughout history have caused social dramas

such as massive famines (Fisher et al., 2012; Jackson et al., 2011). However, besides their detrimental effect, particular phytopathogens have a proven positive side as well. Indeed, when we consider the top 10 plant pathogenic bacteria in molecular plant pathology (according to Mansfield et al., 2012), and browse through the full collection of published patent applications from over 90 countries using a quick search in Espacenet ([www.epo.org/espacenet](http://www.epo.org/espacenet)), an elaborate list of opportunities is revealed for these pathogens (Table 1). For this review, we selected five diverse bacterial (hemi)biotrophic plant pathogens, based on our personal expertise and interest. We give a short overview of the symptoms they cause (Fig. 1) and how they establish disease and impact plant performance, and refer to recent reviews for more detailed information. At the same time we highlight different aspects of these bacteria and show that they are or have the potential to be of use for a more productive, eco-friendly and sustainable plant production or for other interesting biotechnological applications.

## 2. *Agrobacterium tumefaciens* and *A. rhizogenes*

### 2.1. Crown gall and hairy root cause important economic losses

The neoplastic diseases known as crown gall (Fig. 1A) and hairy root (Fig. 1B) were first described at the beginning of the 20th century (Smith and Townsend, 1907; Stewart et al., 1900) and the causative agents were identified as the common soil dwelling *Agrobacterium tumefaciens* (Smith et al., 1911) and *A. rhizogenes* (Ricker et al., 1930), two members of the same genus that belongs to the Rhizobiaceae ( $\alpha$ -Proteobacteria). Both bacteria exhibit a very broad host range of mostly woody and herbaceous dicotyledonous plants, with over 600 species covering almost 100 families susceptible to *A. tumefaciens* (De Cleene and De Ley, 1976) and over 260 plant species belonging to over 60 families responsive to *A. rhizogenes* (De Cleene and De Ley, 1981; Porter and Flores, 1991). Plants infected with *A. tumefaciens* typically develop tumorous outgrowths at wound sites on their roots and crown, whereas in *A. rhizogenes*-infected plants there is a massive proliferation of roots carrying numerous adventitious roots that resemble fine hairs (Gelvin, 1990). By now, three other pathogenic *Agrobacterium* species have been identified which have a more restricted host range: *A. vitis* causes galls mainly on grapes (Burr and Otten, 1999), *A. larrymoori* is pathogenic on *Ficus* (Bouzar and Jones, 2001), and *A. rubi* inflicts cane gall disease on *Rubus* (Holmes and Roberts, 1981). Because

**Table 1**  
Patent applications on positive uses of the top 10 bacterial plant pathogens in molecular biology (according to Mansfield et al., 2012) and additional phytopathogens selected based on personal expertise and interest; data obtained from [www.epo.org/espacenet](http://www.epo.org/espacenet).

	1 <sup>a</sup>	2 <sup>a</sup>	3 <sup>a</sup>	4 <sup>a</sup>	5 <sup>a</sup>	6 <sup>a</sup>	7 <sup>a</sup>	8 <sup>a</sup>	9 <sup>a</sup>	10 <sup>a</sup>	11 <sup>a</sup>	12 <sup>a</sup>	13 <sup>a</sup>
Total number of patents	114	62	453	82	211	15	52	12	3	13	160	14	22
Number of patents on:													
Bacterial metabolite production <sup>b</sup>	18			4	92		2	1			2	4	1
Biocontrol	11	1			8		2			2			
Bioremediation	3		6								1	2	
Protein/enzyme production	2		17	6	8				2	1		2	1
Bioconversion	3		16	1	13						1	4	
Ice nucleation	12				8								
Improvement of plant development	4		5		2		4				1	1	
Improvement of biotic/abiotic stress resistance	9		1	1	5	1	4						
Biosensor/bioassay			4								1		
Improvement of transformation methods/efficiency			198										
Generation of transgenic plants/fungi with novel properties <sup>c</sup>			159								44		
Use of hairy roots <sup>d</sup>												70	

<sup>a</sup> 1, *Pseudomonas syringae*; 2, *Ralstonia solanacearum*; 3, *Agrobacterium tumefaciens*; 4, *Xanthomonas oryzae*; 5, *Xanthomonas campestris*; 6, *Xanthomonas axonopodis*; 7, *Erwinia amylovora*; 8, *Xylella fastidiosa*; 9, *Dickeya*; 10, *Pectobacterium carotovorum*; 11, *Agrobacterium rhizogenes*; 12, *Rhodococcus fascians*; 13, *Streptomyces scabies* and *S. turgidiscabies*.

<sup>b</sup> Including secondary metabolites, polysaccharides (such as levan, alginate, xanthan, ...), phytohormones, gulonic and citric acid, amides, and nucleotides.

<sup>c</sup> Including bioremediation, bioconversion, better resistance against biotic/abiotic stress, altered plant morphology, modified flowering time, and production of secondary metabolites, enzymes or vaccines.

<sup>d</sup> Including bioremediation and production of secondary metabolites, proteins and mycorrhiza.

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