

# Which specificity in cooperation between phytostimulating rhizobacteria and plants?

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Received 16 May 2012; accepted 17 August 2012

Available online 7 September 2012

## Abstract

Plant growth-promoting rhizobacteria (PGPR) are found in association with a large range of host plants. Although the subject of plant host specificity has been well studied in parasitic and mutualistic interactions, the question of whether phytostimulating rhizobacteria efficiently interact only with a specific host remains poorly discussed. This review presents elements suggesting the existence of specificity in three-step establishment of associative symbiosis between phytostimulating rhizobacteria and plants: bacterial attraction by the host plant, bacterial colonization of roots, and functioning of associative symbiosis.

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**Keywords:** Adherence; Cooperation; Chemotaxis; Plant growth-promoting rhizobacteria; Plant genotype; Host specificity

## 1. Introduction

Strategies of adaptation strongly influence the survival of both partners in plant–microbe interactions. Whatever the strategy, host specificity appears to be a fundamental concept in understanding coevolutionary processes leading to these complex and intimate interactions (Kirzinger and Stavrindes, 2012). Defined on the basis of host range, host specificity is inversely proportional to the number of host species with which a given microorganism is able to interact (Poulin and Keeney, 2008). In the case of parasitic strategies, host range is controlled by the gene-for-gene concept: this involves recognition by the plant, through resistance proteins, of avirulence products emitted by a bacterial pathogen (Fig. 1) (Skamnioti and Ridout, 2005). In mutualistic strategies such as

symbioses between legumes and rhizobia, specificity is defined at the molecular level and relies essentially on signalling events taking place between bacteria and host plants: (i) bacterial perception of plant compounds (flavonoids) that triggers synthesis of bacterial Nod factors; and (ii) perception of Nod factors by specific plant receptor kinases that leads to dedifferentiation of cells located in the cortex and ultimately to nodule formation (Fig. 1) (Masson-Boivin et al., 2009).

In addition to mutualistic intimate interactions, plant growth-promoting rhizobacteria (PGPR) can establish associative symbiosis (cooperation) with plants (Vessey, 2003). For more than fifty years, PGPR have been known to stimulate growth of numerous host plants, including crops and legumes. In turn, they benefit from root exudates. PGPR are usually separated into distinct groups according to their beneficial activities towards plants: (i) phytostimulating rhizobacteria that enhance plant growth directly by providing nutrients and/or phytohormones; (ii) mycorrhiza and root nodule symbiosis helper rhizobacteria, which positively affect functioning of plant–microbe mutualistic interactions; and (iii) biocontrol rhizobacteria that protect plants from pathogens through

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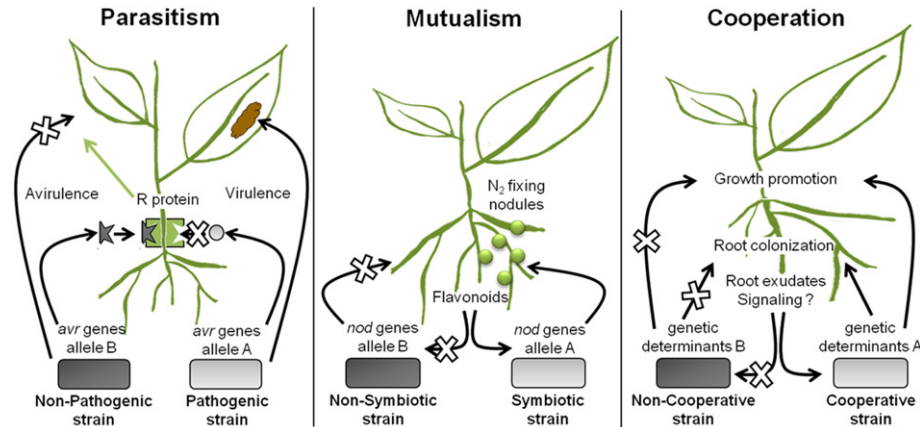


Fig. 1. Overview of mechanisms controlling host specificity in parasitic, mutualistic and cooperative interactions. Grey tones show differences between bacterial genotypes. Parasitism: host range is controlled by the gene-for-gene concept involving recognition of avirulence products (grey symbols) of a bacterial pathogen by resistance proteins (R proteins, green rectangles) of the plant. Mutualism: in model symbiosis between legumes and rhizobia, specificity relies essentially on signalling: bacterial perception of plant flavonoids that triggers the synthesis of bacterial Nod factors and perception of Nod factors by specific plant receptor kinases that leads to the formation of  $N_2$ -fixing nodules (green circles). Cooperation: propensity to colonize and therefore stimulate growth of a restricted group of plants might involve mechanisms implicated in host recognition and root colonization, as well as tight control of bacterial plant beneficial properties.

production of antimicrobial compounds or by stimulating plant resistance (for reviews see Frey-Klett et al., 2007, 2011; Saharan and Nehra, 2011). However, this categorization is simplistic, as PGPR act on plants through a combination of plant growth and plant health-improving mechanisms (Bashan and de-Bashan, 2010). Because of their potential use as bio-fertilizers and biopesticides, their mechanisms of action have been extensively studied in model bacteria such as *Azospirillum* spp. and *Pseudomonas* spp. (Vessey, 2003). The plant genotype shapes PGPR communities both in terms of population size and composition (Bouffaud et al., 2011; Haichar et al., 2008; Hartmann et al., 2009). In addition, plant growth-promoting effects of PGPR have been shown to depend both on host plant genotypes and bacterial strains for a wide range of phytostimulating rhizobacteria (Moutia et al., 2010; Chanway et al., 1988; Gyaneshwar et al., 2002; Pedraza et al., 2010). However, host specificity is difficult to establish in the case of phytostimulating PGPR because the outcome of plant–PGPR interaction relies on quantification and statistical analyses of plant growth parameters.

In the case of PGPR, host specificity appears to be controlled either by strain-specific bacterial adaptation towards non-specific traits of the host plant or by non-specific bacterial adaptation towards genotype-specific traits of the host plant. Thus, a propensity to colonize and therefore stimulate growth of a restricted group of plants might involve mechanisms implicated in host recognition and root colonization, as well as tight control of bacterial beneficial properties by plant compounds (Fig. 1) (Smith and Goodman, 1999; Berg and Smalla, 2009; Kloepper, 1996). To our knowledge, this genotype-dependent specificity in PGPR–plant cooperation has been mainly discussed in the case of biocontrol and mycorrhiza helper PGPR, but less so when considering phytostimulating rhizobacteria (Frey-Klett et al., 2007; Smith and Goodman, 1999; Berg and Smalla, 2009).

In this context, the following review focuses on phytostimulating rhizobacteria belonging to the genera *Azoarcus*,

*Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Gluconobacter*, *Herbaspirillum*, *Klebsiella* and *Pseudomonas*. The highlight will be placed on mechanisms leading to specificity in the three-step establishment of associative symbiosis between bacteria and host plants: (i) attraction of bacteria from the surrounding soil to the rhizosphere; (ii) attachment to the root surface; and finally, (iii) functioning of associative symbiosis that becomes effective.

## 2. The specific attraction of rhizobacteria towards roots depends on bacterial and plant genotypes

Root exudates play a key role in mediating plant–microbe interactions (Bais et al., 2006). In particular, bacterial chemotaxis towards exuded compounds is an important trait for root colonization and plant-driven selection of microorganisms (de Weert et al., 2002; Hartmann et al., 2009). As such, quantitative and qualitative variations in root exudate composition have been observed at the plant genotype level (Erro et al., 2009; Kumar et al., 2007), and bacterial strain-dependent chemotaxis towards a particular compound is an essential feature when considering host specificity in PGPR–plant interactions (Hardoim et al., 2008).

Chemotactic behaviour of PGPR has been studied both with crude exudates and with specific exuded compounds that can serve as carbon sources or signalling compounds, like flavonoids. Discrepancies in chemotaxis were reported for *Azotobacter* spp., *Azospirillum brasilense*, *Bacillus pumilus* and *Corynebacterium flavescens* (Bacilio-Jiménez, 2003; Kumar et al., 2007). Indeed, among 9 *Azotobacter* spp. strains tested, two were preferentially attracted by wheat exudates and 7 others by cotton exudates; the observed differences have been attributed to plant-specific variations in the energy yield of exuded organic acids (Kumar et al., 2007). Similarly, chemotactic effects of rice root exudates were shown to be stronger on rice endophytes (*C. flavescens* and *B. pumilus*) and rice root-surface-isolated *Bacillus* sp. than on maize-isolated

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