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Review

Plant growth-promoting bacteria in the rhizo- and endosphere of plants: Their role, colonization, mechanisms involved and prospects for utilization

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ABSTRACT

In both managed and natural ecosystems, beneficial plant-associated bacteria play a key role in supporting and/or increasing plant health and growth. Plant growth-promoting bacteria (PGPB) can be applied in agricultural production or for the phytoremediation of pollutants. However, because of their capacity to confer plant beneficial effects, efficient colonization of the plant environment is of utmost importance. The majority of plant-associated bacteria derives from the soil environment. They may migrate to the rhizosphere and subsequently the rhizoplane of their hosts before they are able to show beneficial effects. Some rhizoplane colonizing bacteria can also penetrate plant roots, and some strains may move to aerial plant parts, with a decreasing bacterial density in comparison to rhizosphere or root colonizing populations. A better understanding on colonization processes has been obtained mostly by microscopic visualisation as well as by analysing the characteristics of mutants carrying disfunctional genes potentially involved in colonization. In this review we describe the individual steps of plant colonization and survey the known mechanisms responsible for rhizosphere and endophytic competence. The understanding of colonization processes is important to better predict how bacteria interact with plants and whether they are likely to establish themselves in the plant environment after field application as biofertilisers or biocontrol agents.

1. Introduction

Since the elaboration of the rhizosphere concept by Lorenz Hiltner in 1904, many studies have reported that the soil environment attached to the root system is a hot spot of microbial abundance and activity due to the presence of root exudates and rhizodeposits (Hiltner, 1904; Smalla et al., 2006; Hartmann et al., 2008). Some rhizosphere microorganisms may be neutral or deleterious in regard to plant growth, whereas other microbes support their hosts (reviewed in Welbaum et al., 2004; Raaijmakers et al., 2008). Such plant growth-promoting bacteria (PGPB; Bashan and Holguin, 1998) or plant growth-promoting rhizobacteria (PGPR; Kloepper and Schroth, 1978) can stimulate plant growth, increase yield, reduce pathogen infection, as well as reduce biotic or abiotic plant stress, without conferring pathogenicity (Welbaum et al., 2004; van Loon and Bakker, 2005; Lugtenberg and Kamilova, 2009). Plant beneficial microorganisms are of interest for application in agriculture either as biofertilisers or as pesticides as well as for phytoremediation applications (reviewed in Sturz et al., 2000; Berg, 2009; Lugtenberg and Kamilova, 2009; Weyens et al., 2009). However, in many cases PGPB fail to induce the desired effects when applied in the field. This might be due to insufficient rhizosphere and/or plant colonization, which is as an important step required for exhibiting beneficial effects (Lugtenberg et al., 2001). Therefore, not only mechanisms responsible for plant growth promotion have to be investigated, but also a thorough understanding of all steps involved in plant colonization by PGPB is required to improve the efficiency and reliability of inoculant strains.

The rhizosphere is well known to host a variety of PGPB. In addition, some rhizosphere colonizers can enter plants as already postulated by Galippe in 1887 (Galippe, 1887). For a long time this was not recognized, although di Vestea (1888) confirmed Galippe's work. Other researchers at that time including Pasteur, Chamberland and Fernbach considered healthy plants to be free of microorganisms (reviewed in Smith, 1911). In the last decade it has been repeatedly demonstrated that the plant interior is colonized by a range of endophytes mostly deriving from the rhizosphere and many of them have been reported to improve plant growth or

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health (reviewed in Sturz and Nowak, 2000; Hardoim et al., 2008). Following rhizosphere colonization endophytes may colonize various plant organs (James et al., 2002; Compant et al., 2005b, 2008a). However, distinct microbial communities have been found in various plant organs such as roots, stem, leaves, flowers as well as fruits and seeds or even during plant development (Sessitsch et al., 2002; Berg et al., 2005b; Okunishi et al., 2005) indicating different capacities of bacterial strains to colonize various plant compartments.

In addition to understanding the mechanisms of the interaction between plants and microorganisms, colonization mechanisms and strategies represent an important aspect of the interaction. Successful colonization of a PGPB inoculant strain is a requirement to promote plant growth or health. In this paper we review the current understanding of the plant colonization process by bacteria including rhizosphere and subsequent endosphere colonization.

2. Rhizosphere and rhizoplane colonization

Since the 1980's, many studies have focused on the colonization by beneficial bacteria in the rhizosphere, i.e. the soil compartment, which influenced by rhizodeposits. Generally, approx. 10^7–10^9 CFU culturable rhizosphere bacteria g^{-1} of rhizosphere soil have been found (Benizri et al., 2001), whereas population densities in the rhizoplane range from 10^5–10^7 CFU g^{-1} of fresh weight (Benizri et al., 2001; Bais et al., 2006). By using gnotobiotic conditions and with the help of microscopic tools, which allow the detection of *gfp*- or *gusA*-labelled strains or of strains by immunomarkers or by fluorescence *in situ* hybridization, it has been demonstrated that bacterial cells first colonize the rhizosphere following soil inoculation (Gamalero et al., 2003). Then, bacterial cells have been visualized as single cells attached to the root surfaces, and subsequently as doublets on the rhizodermis, forming a string of bacteria (Fig. 1; Hansen et al., 1997). Colonization may then occur on the whole surface of some rhizodermal cells (Fig. 1) and bacteria can even establish as microcolonies or biofilms (Benizri et al., 2001). Rhizoplane colonization has been studied not only by using *in vitro* grown plants but also with plants grown in natural soil (Fig. 1), which is characterized by a high microbial diversity. Before being able to confer any plant beneficial effects, (inoculated) PGPB need to be rhizosphere and/or rhizoplane competent (Compant et al., 2005a), *i.e.* they have to be able to colonize the rhizosphere and/or the rhizoplane during an extended period characterized by strong microbial competition (Whipps, 2001). Many factors can be involved in rhizosphere and rhizoplane competence by PGPB. However, both in gnotobiotic systems and in natural soil, it is important to note that the root system is not colonized in a uniform manner. Different population densities were reported for the diverse root zones. This has been well described by Gamalero et al. (2004) with *Pseudomonas fluorescens* strain A6RI and tomato roots, where the distribution and density of the inoculant strain varied according to the root zone. Non-uniform bacterial colonization along the root can be explained by different factors such as varying root exudation patterns, bacterial quorum sensing effects as well as many others, which are summarized in Table 1 and described below in greater detail.

2.1. Chemotaxis towards root exudates

Rhizosphere and rhizoplane colonization has been described to be linked to root exudation (Lugtenberg and Dekkers, 1999). Carbon fixed by plant photosynthesis is known to be partly translocated into the root zone and released as root exudates (Bais et al., 2006). Various carbohydrates, amino acids, organic acids, as well as other compounds, which provide a source of nutrients for root-associated bacteria, are released in the rhizosphere (Walker et al., 2003). Microorganisms are known to be chemoattracted and move towards exudates, allowing them to colonize and multiply both in the rhizosphere and the rhizoplane (Lugtenberg and Kamilova, 2009). A mutant of a plant growth-promoting *P. fluorescens* strain, which lacked the *cheA* gene responsible for chemotaxis showed reduced movement towards root exudates (or specific exudate components) in the tomato rhizosphere and also decreased root colonization (de Weert et al., 2002). In addition, genes known to be involved in recognition and chemotaxis to plant root exudates are involved. Mark et al. (2005) studied the transcriptomic response of *Pseudomonas aeruginosa* strain PAO1 to exudates of two cultivars of sugarbeet. This strain is an opportunistic human pathogen but was

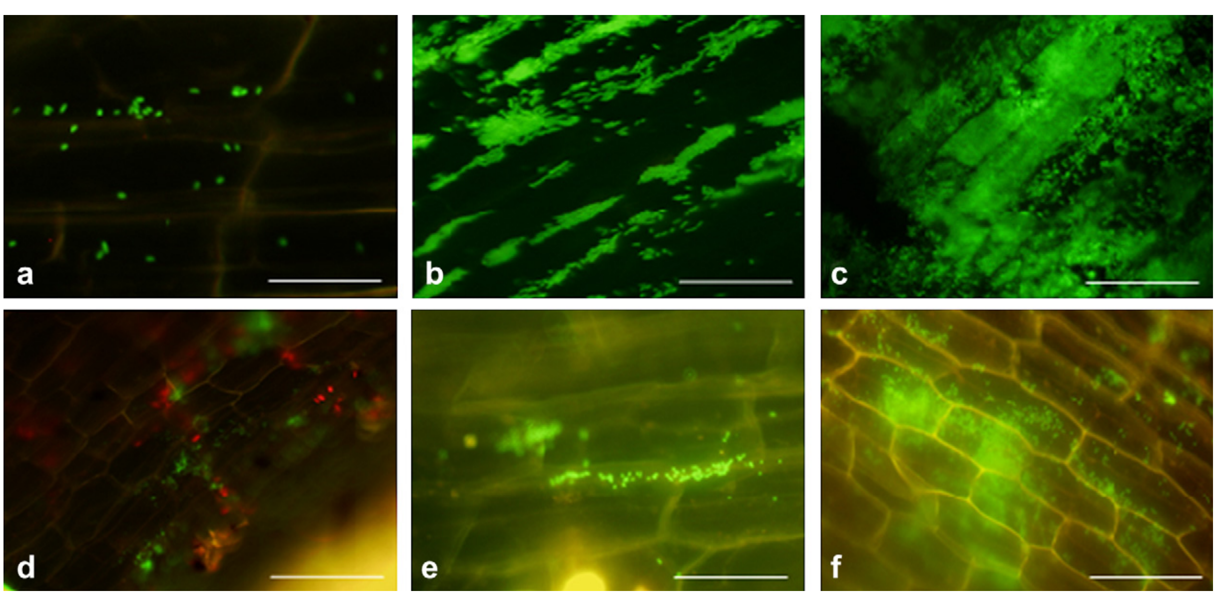

Fig. 1. Rhizoplane colonization under gnotobiotic (a–c) or non sterile conditions (d–f) of a beneficial bacteria, *Burkholderia phytofirmans* strain PsJN, tagged with *gfp* showing (a and d) single bacterial cells attached to the root surfaces of grapevine, (b and e) lines of bacteria or (c and f) bacteria colonizing the whole outline of some rhizodermal cells. Scale bars: (a) 15 μm, (b–d) 30 μm, (e) 15 μm and (f) 40 μm. Pictures by S. Compant.