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Review

Effect of plant growth-promoting Rhizobacteria on plant hormone homeostasis

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ABSTRACT

Plant growth-promoting rhizobacteria (PGPR) includes a wide variety of bacterial strains from different taxonomic groups that inhabit plant roots and their rhizosphere. By bringing about complex changes in plant growth and development, PGPR can enhance both productivity of agricultural crops, and their pathogen resistance. Colonization by PGPR is associated with changes in plant metabolism, signaling and hormone homeostasis. Different PGPR strains can synthesize phytohormones, metabolize them, or affect plants' hormone synthesis and signal transduction. This review covers various mechanisms employed by PGPB to alter the homeostasis of the plant hormones auxin, ethylene, cytokinin, gibberellin, abscisic acid, jasmonic acid and salicylic acid.

Contents

1. Introduction

Plant growth-promoting rhizobacteria (PGPR) consist of the rhizosphere bacteria that can enhance plant growth and stress resistance by a wide variety of mechanisms (Glick, 2012). PGPR are currently intensively studied due to their properties which are of considerable value both for traditional and sustainable agriculture (Farrar et al., 2014). PGPR can enhance plant mineral nutrition *via* associated nitrogen fixation (Kuan et al., 2016), mobilization of phosphate in the soil (Chen et al., 2006; Mehta et al., 2015), siderophore production (Vansuyt et al., 2007; Zhou et al., 2016), stimulation of the mycorrhizal

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symbiosis development and modulation of root architecture (Navarro-Rodenas et al., 2016). PGPR can also activate plant pathogen resistance (Niu et al., 2011; Van de Mortel et al., 2012; Sharifi and Ryu, 2016), suppress pathogen growth (Ali et al., 2014; Saraf et al., 2014; Prasannakumar et al., 2015) and alleviate the inhibitory effects of abiotic stressors like drought (Lim and Kim, 2013), salinity (Kim et al., 2014) and heavy metal pollution (Gupta et al., 2002; Zhu et al., 2015). Because of growing public concern about the damaging effects of chemical fertilizers and pesticides, there is an increasing interest in improving our understanding of molecular mechanisms of interaction between plants and their rhizosphere microbial community.

It is well established that PGPR colonization is associated with profound changes in the host plant's development and hormone homeostasis. Phytohormones act as messengers to coordinate cellular activities and to regulate various cellular processes in plants, including abiotic stress responses and plant - pathogen interaction. PGPR colonization brings about many changes in plant development. These changes include, but are not limited to growth stimulation, modification of root and shoot architecture, and synthesis of secondary metabolites. As hormones regulate plant growth and development, the effects of colonization by PGPR are directly associated with changes in concentration, localizations and signaling of hormones (Dodd et al., 2010; Spaepen et al., 2014; Verbon and Liberman, 2016). In this review, we discuss various ways in which different PGPR strains affect host plant hormone homeostasis.

It should be noted that many physiological processes in the plant are regulated by complex interactions between several hormones rather than by the concentration of some particular hormone (O'Brien and Benkova, 2013; Naseem et al., 2015). Several recent studies have examined the complex effect of PGPR on the expression of plant genes, including the genes that play important roles in signaling, metabolism and degradation of phytohormones (Camilios-Neto et al., 2014; Lara-Chavez et al., 2015). Yet, there is still a lack of comprehensive analysis of the roles of plant hormones in PGPR - host plant interaction. Here we review the literature on the role of such phytohormones as auxin, ethylene, cytokinin, gibberellin, abscisic acid, salicylic acid and jasmonic acid in the interactions between PGPR and plants.

2. Auxin

Auxin is an important phytohormone that is vital for plant development and growth. It is required for cell cycle progression (Demeulenaere and Beeckman, 2014) and for the release of bud dormancy (Rios et al., 2014). It affects the size of the shoot and the root meristems, defines flower morphogenesis and position of the lateral organ primordia (Demeulenaere and Beeckman, 2014; Dresselhaus and Schneitz, 2014; Landrein and Vernoux, 2014). Auxin is necessary for gravitropism and phototropism of roots and shoots (Retzer et al., 2014) as well as for shadow avoidance (Ruzza et al., 2014). Auxin can also modulate plant associations both with pathogenic and symbiotic microorganisms, coordinating plant responses associated with the establishment and maintenance of plant – microorganism interactions. This subject has been well presented in several recent reviews (Grunewald et al., 2009; Ludwig-Muller, 2014; Liang Pin Ng et al., 2015; Boivin et al., 2016). Even though auxin research has a long history, new facts regarding its metabolism, reception and transport as well as its role within the plant are constantly emerging (Barbez et al., 2012; Sukumar et al., 2013; de Jong et al., 2014; Kumar et al., 2015; Niu et al., 2015). Since the majority of physiological processes in the plant are directly or indirectly associated with this phytohormone, it is not surprising that PGPR can affect the amount and localization of auxin, as well as the direction of auxin movement in the plant (Ahmed and Hasnain, 2014).

There are several locations of auxin synthesis in the plant (Ljung et al., 2005). The major synthetic activity is localized in the shoot apex from where auxin flows downwards to the root tip forming a concentration gradient (Taiz and Zeiger, 2002). Main root (MR) and lateral root (LR) meristems are also sources of auxin (Ljung et al., 2005). The local maximum concentration is found in the stem cells of the root meristem (Petersson et al., 2009). After reaching the root tip, the auxin flow direction is reversed and the hormone reaches the root pericycle. In the zones of the local auxin maximum concentrations, where the hormone concentration in pericycle reaches the necessary level, LRs primordia are formed (De Smet et al., 2007). As the MR grows, primordia leave the initiation zone. If the level of auxin is sufficient, the primordia develop into LRs and themselves become the sources of auxin (Ljung et al., 2005; De Smet et al., 2007; Lucas et al., 2008). The effect of exogenous IAA on the root system of *Arabidopsis thaliana* depends on its concentration; in the range of 1.0–5.0 nM it stimulates the growth of MR and LRs, up to 12.5 nM it inhibits LRs formation and at 25.0 nM it blocks growth of both the MR and LRs (Ivanchenko et al., 2010).

How can bacteria affect plant auxin homeostasis? First of all, directly by synthesizing auxin. There is abundant data indicating that different PGPR strains synthesize auxin in culture (Spaepen et al., 2007; Ahmed and Hasnain, 2014). However, the majority of these studies employ a cheap and accessible Salkowski reaction (Contesto et al., 2010; Iqbal and Hasnain, 2013) that is designed to estimate the amount of indole compounds in the solution (in this case, in the culture medium). Since this reaction is not specific for auxin, one cannot be entirely sure if the studied strain can indeed synthesize IAA or other biologically active auxins. In some cases the auxin synthesizing ability of certain PGPB was demonstrated with more advanced technics, such as GC–MS (Ali et al., 2009; Ali, 2015), HPLC (Júnior et al., 2011), and biotests (Tsavkelova et al., 2007). Auxin plays an important role in the establishment and maintenance of beneficial plant – PGPB interaction. For instance, auxin-producing PGPR strains *Aeromonas punctata* PNS-1, *Serratia marcescens* 90–166 and *Azospirillum brasilense* Sp245 stimulate growth and induce morphological changes in *A. thaliana* (Table 1) (Shi et al., 2010; Iqbal and Hasnain, 2013; Spaepen et al., 2014). In plants inoculated with these strains the level of endogenous auxin increases, as indicated by the elevated expression of DR5-GUS (Tables 2 and 3), a transgenic construct containing promoters of auxin-induced genes and the GUS reporter (Shi et al., 2010; Iqbal and Hasnain, 2013; Spaepen et al., 2014). Moreover, the mutant strain *Azospirillum brasilense* FAJ0009, incapable of auxin synthesis, does not induce any morphological changes in the host plant (Spaepen et al., 2014). At the same time, the auxin over-producing strain of *Burkholderia cepacia* have a greater stimulating effect on rice plants than both control strains and mutant strains with negligible auxin production (Singh et al., 2013). This evidence suggests that in these cases auxin synthesis may be the primary cause of the stimulatory effect of some PGPR strains on host plants. Interestingly, high concentrations of auxin synthesized by non-pathogenic strains of rhizobacteria such as *Enterobacter* sp. I-3 may have an inhibiting effect on plants (Park et al., 2015). Therefore, to achieve a stimulating effect on the host plant, the amount of the auxin produced by the strain should correspond with the optimum for a given species under given environmental conditions.

Can the PGPB-synthesized auxin be the primary cause underlying increased elongation of the root cells? An increased root growth in PGPR-colonized plants is routinely explained by the elevated auxin concentration (Contesto et al., 2010; Shi et al., 2010; Iqbal and Hasnain, 2013; Poupin et al., 2016). Alternatively, the enhanced root growth may depend on enhanced loosening of cell walls that accompanies PGPR colonization. Partial degradation of cell walls can promote more effective root colonization by PGPR (Beauregard et al., 2013). Components of the plant cell wall such as pectins, arabinogalactans and xylans are essential for the construction of the matrix exopolysaccharides that aid PGPR *Bacillus sp.* biofilm formation (Beauregard et al., 2013). Bacterial galactosidases split off galactose residues from xylans, pectins, arabinogalactans in the plant cell walls. Galactose is necessary for building polysaccharides of the biofilm matrix. Therefore, we cannot be