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Role of allelochemicals in plant growth promoting rhizobacteria for biocontrol of phytopathogens☆

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ABSTRACT

Soil borne fungal diseases pose serious constraints on agro-productivity. Biological control is non-hazardous strategy to control plant pathogens and improve crop productivity. PGPR (plant growth promoting rhizobacteria) have long been used as plant disease control agents. PGPR produced a wide range of secondary compounds that may act as signals—that is, allelochemicals that include metabolites, siderophores, antibiotics, volatile metabolites, enzymes and others. Their mode of action and molecular mechanisms provide a great awareness for their application for crop disease management. The present review highlights the role of PGPR strains, specifically referring to allelochemicals produced and molecular mechanisms. Further research to fine tune combinations of allelochemicals, plant-microbe–pathogen interaction will ultimately lead to better disease control.

1. Introduction

Plant diseases cause economical loss of billions of dollars by reducing crop yield, lower produce quality and contaminating food grain with toxic chemicals (Guo et al., 2013). The endless variety and complexity of the many diseases of plants caused by fungi have led to the development of a correspondingly large number of fungicides; unfortunately several plant pathogens have developed resistance to certain fungicides (Agrios, 2005). Another approach is to apply genetically resistant cultivars, but this is not viable after a few years (Fry, 2008).

Nowadays, allelopathicals are being explored and research is ongoing in field crop production for integrated disease management. Allelochemistry, the production and release of toxic chemicals produced by one species that affect a receiving susceptible species, has been the subject of diverse groups of scientific community. Allelopathy defined as chemically elicited interactions between plants or pathogens is mediated by secondary metabolites type of compounds (Seigler, 1996). Allelopathy word is composed of two Latin words where “alleles” mean ‘each other’ and “pathos” mean ‘to suffer’, respectively. ‘Novel weapons hypothesis’ was first proposed by Callaway and Aschehoug (1996) for plant species stated that “Exotic plants might release allelochemical compounds that are novel species in the new range contributing to its invasive success”. This basic hypothesis can be also applied to microbial communities as reported by Inderjit and van der Putten (2010). Allelopathy involves the synthesis of bioactive compounds known as “allelochemicals” which play a vital role as natural pesticides and can resolve problems like pest biotypes, health defects, soil and environment pollution resulting in climate change caused by the indiscriminate use of synthetic agrochemicals (Barazani and Friedman, 2001; Farooq et al., 2011).

The rich microbial diversity provides a seemingly endless resource for this purpose. Rhizobacteria are most widely studied as plant growth-promoting bacteria (PGPB), associated with plant rhizosphere and are present in all agriecosystems (Kloepper and Schroth, 1978). Antagonistic bacteria are considered ideal biological control agents (BCA) because of the rapid growth, easy handling, and aggressive colonization of the rhizosphere (Weller, 1988). The use of PGPR specifically as biocontrol agents of soil borne fungal plant pathogens as an alternative or complementary strategy to physical and chemical disease management have been investigated for over a century (Berg and Smalla 2009; Haas and Defago, 2005). PGPR indirectly enhance plant growth via suppression of phytopathogens by producing chemicals that inhibit the growth of plant pathogens. Siderophores, antibiotics, biocidal volatiles, lytic enzymes and detoxification enzymes are all examples of allelochemicals produced by soil microbes (Fig. 1). Siderophores chelate available iron from the soil; antibiotics discourage bacterial colonization; lytic enzymes degrade many organic compounds including chitin (fungal cell walls); detoxification enzymes prevent damage from pathogenic toxins. Production of volatiles such as hydrogen cyanide, suppress the growth of fungal pathogens;

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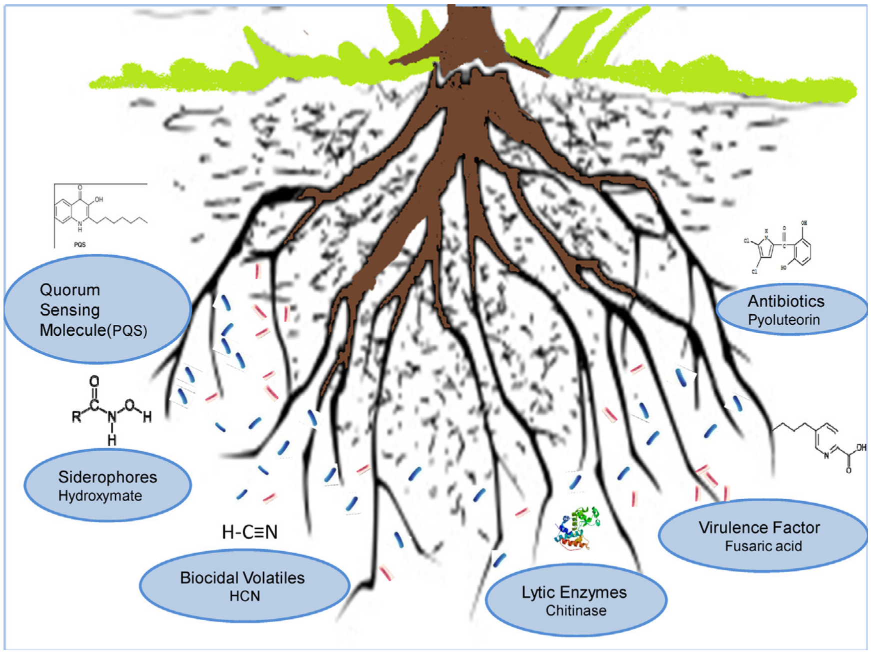

Fig. 1. Basic mechanisms of allelochemicals from rhizobacteria.

the ability to successfully compete with pathogens for nutrients or specific niches on the root; and the ability to induce systemic resistance (ISR) (Compant et al., 2005). The allelopathic effect is highly dependent on environmental conditions such as water, nutrition, bacterial density, soil structure, and texture (Barazani and Friedman, 2001).

The secondary metabolites of BCA like antibiotics are unique and have the advantage due to their mode of action over the chemical fungicides (Jayaprakashvel and Mathivanan, 2011). Siderphore production by PGPR under iron limiting conditions can promote plant growth by directly supplying iron for plant utilization and by removing iron from surrounding environment for the growth of phytopathogens thereby reducing their competitiveness (Tank et al., 2012). PGPR strains cause enzymatic digestion or deformation of cell wall components of fungal pathogens by the enzymes chitinase, β-1,3-glucanase, proteases, etc. is one of the significant mechanisms of biocontrol of soil borne pathogens (Aeron et al., 2011). The presence of endophyte such as *Rhizobium etli* (Martinuz et al., 2012) discourages nematode parasitism through induced resistance and activating ethylene and jasmonic acid pathways in the tomato plant. These hormone pathways increase the plant's resistance to colonization by phytopathogenic organisms. *Bacillus thuringenesis* been successfully used for many years to control larvae of moths, beetles and flies that cause damage to crop roots. *Pseudomonas* inhibits the growth of virulent bacteria by producing antibiotics after colonizing root systems. The pathway for the anitbiotic synthesis is not well described but might be similar to other two-component signaling systems that regulate antibiotic production (Whipps, 2001). Although biocontrol activity of microorganisms involving synthesis of allelochemicals has been studied extensively with free-living rhizobacteria, similar mechanisms apply to endophytic bacteria (Lodewyckx et al., 2002), since they can also synthesize metabolites with antagonistic activity toward plant pathogens (Chen et al., 1995). For example, Castillo et al. (2002) demonstrated that munumbicins, antibiotics produced by the endophytic bacterium *Streptomyces* sp. strain NRRL 30562 isolated from *Kennedia nigriscans*, can inhibit in vitro growth of phytopathogenic fungi, *P. ultimum*, and *F. oxysporum*. Subsequently, it has been reported that certain endophytic bacteria isolated from field-grown potato plants can reduce the in vitro growth of *Streptomyces scabies* and *Xanthomonas campestris* through production of siderophore and antibiotic compounds (Sessitsch et al., 2004). Interestingly, the ability to inhibit pathogen growth by endophytic bacteria, isolated from potato tubers, decreases as the bacteria colonize the host plant's interior, suggesting that bacterial adaptation to this habitat occurs within their host and may be tissue type and tissue site specific (Sturz et al., 1999). Aino et al. (1997) have also reported that the endophytic *P. fluorescens* strain FPT 9601 can synthesize DAPG and deposit DAPG crystals around and in the roots of tomato, thus demonstrating that endophyte can produce antibiotics in plants.

Bacteria in root zone are important in changing the properties of plants and soil agroecosystems. Plants selectively release root exudates and leachates to sustain certain rhizobacteria. These bacteria produce enzymes and metabolites which enhance the availability of minerals and nutrients, improve nitrogen fixation, induce plant disease resistance, and improve plant health. Beneficial interactions stimulate crop yields and improve plant health (Sturz and Christie, 2003). The selection of bioantagonistic microorganisms, other than to take into account the direct effect on pathogen development, must consider conditions in agro ecosystems where the bioantagonist should act, i.e. salinity and pH of soils and different temperature, among others.

This review surveys the state of art focusing on mode of actions of allelochemicals from PGPR and their use for the biocontrol of plant diseases.

2. Allelochemicals present in PGPR

Allelochemicals are associated with BCAs and are used in plant disease control that can be categorized based on various modes of action. Types of allelochemicals associated with PGPR strains and involved with disease management are shown in Table 1.

2.1. Siderophores

Iron is an essential growth element for all living organisms. The scarcity of bioavailable iron in soil habitats and on plant