



Multifaceted beneficial effects of rhizosphere microorganisms on plant health and productivity

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ABSTRACT

Plant growth promoting microorganisms (PGPM) and biological control agents (BCA) are shown to possess secondary beneficial effects that would increase their usefulness as bio-inoculants, regardless of the need for their primary function. Indeed, PGPM, such as *Rhizobium* and *Glomus* spp., can promote plant growth and productivity (primary effect) but have now been shown to also play a role in reducing disease (secondary effect). Conversely, BCA, such as *Trichoderma* and *Pseudomonas* spp., can control disease (primary effect) but have recently demonstrated stimulation of plant growth (secondary effect) in the absence of a pathogen. Further work shedding light onto the precise mode of action and ecophysiology of these microorganisms would assist with their timely and appropriate use and potentially unleash their full promise as beneficial rhizosphere bio-inoculants for improved growth and health of plants. The potential increased use of these microorganisms afforded by their multifaceted beneficial effects may further help in reducing problems associated with the use of synthetic chemicals in agriculture.

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1. Introduction

The principal goal of agriculture is the production of high quality, safe and affordable food for an ever-increasing worldwide population. Furthermore, agricultural growers and producers have the additional constraints of economic profitability and sustainability. With the increasing problems associated with the use of synthetic chemicals in agriculture (impacts on health and the environment, resistance development in plant pathogens and pests, etc.), there has been an ever-increasing interest in the use of native and non-native beneficial microorganisms to improve plant health and productivity while ensuring safety for human consumption and protection of the environment. In this context, many soilborne microorganisms have proved beneficial over the years and are now integrated into a wide variety of growing systems as part of integrated pest and productivity management practices (Antoun and Prévost, 2005).

In general, the rhizosphere harbors an extremely complex microbial community including saprophytes, epiphytes, endophytes, pathogens and beneficial microorganisms. In natural systems, these microbial communities tend to live in relative harmony where all populations generally balance each other out in their quest for food

and space (Bélanger and Avis, 2002). In “artificial” systems, i.e. agriculture, there is a modification in this natural balance that can drastically alter the microbial community and can lead to loss of beneficial microbes and/or ingress of plant pathogens that may have a devastating effect on plant productivity. In these cases, the integration of beneficial microorganisms into production systems can somewhat shift the balance of the microbial communities toward a population structure more conducive to increased plant health and productivity.

Beneficial rhizosphere organisms are generally classified into two broad groups based on their primary effects, i.e., their most well known beneficial effect on the plant: (i) microorganisms with direct effects on plant growth promotion [plant growth promoting microorganisms (PGPM)] and (ii) biological control agents (BCA) that indirectly assist with plant productivity through the control of plant pathogens. In addition to their primary effects on plant productivity and health, respectively, recent work has shown that these beneficial microorganisms possess secondary, i.e., more recently discovered effects that may bestow them increased interest for plant growers (Fig. 1) (Whipps, 2004; Vassilev et al., 2006). More specifically, PGPM have shown activities relating to biocontrol of soilborne pathogens. Conversely, BCA have demonstrated properties that directly promote plant growth. This review will focus on case studies of recent and some key earlier examples of the added interests of PGPM and BCA through their secondary beneficial effects.

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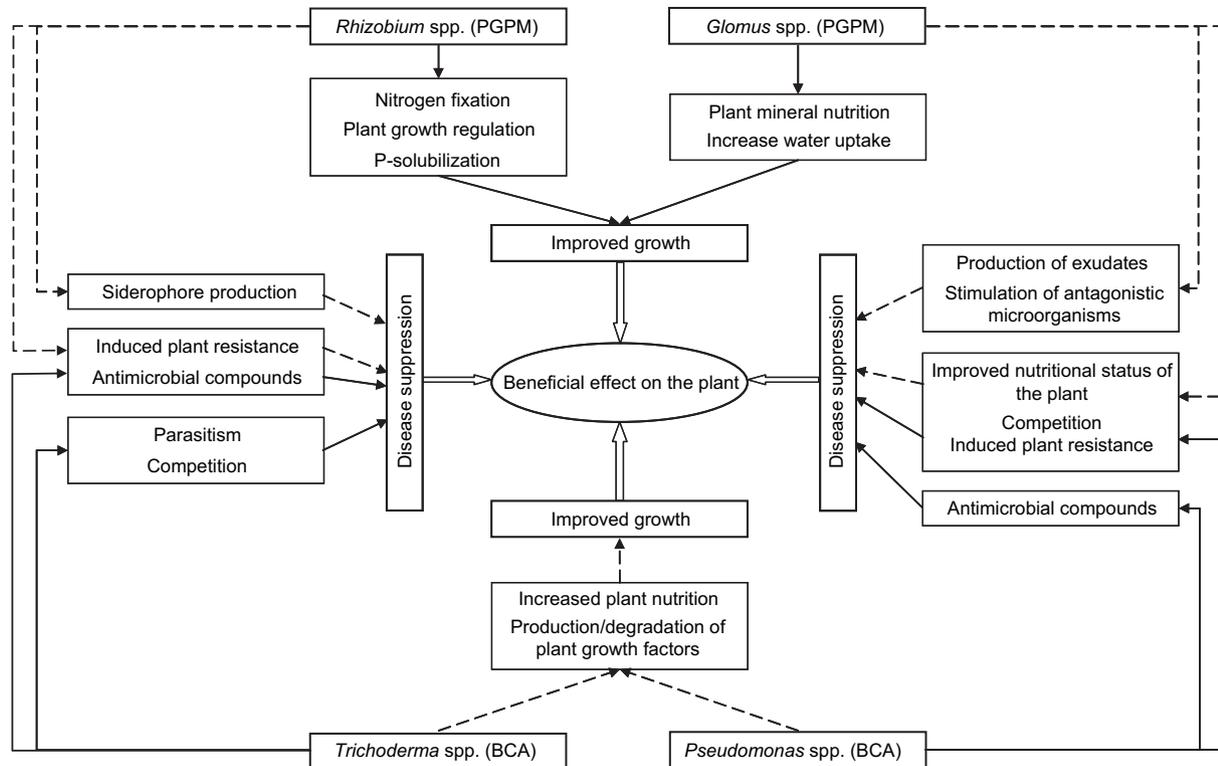


Fig. 1. Potential modes of action of plant growth promoting microorganisms (PGPM) and biological control agents (BCA) with primary and secondary beneficial effects on plants. Solid lines, primary effect; dash lines, secondary effect.

2. Plant growth promoting microorganisms (PGPM) with biocontrol activities

2.1. *Rhizobium* spp.

Rhizobia (including *Rhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Sinorhizobium*) are generally regarded as microbial symbiotic partners of legumes and are mainly known for their role in the formation of nitrogen-fixing nodules (Antoun and Prévost, 2005). In particular, *Rhizobium* spp. are a vast group of soilborne rhizobia with representatives that have proven plant growth promoting activities through nitrogen fixation. These bacteria can equally produce plant growth regulators and solubilize organic and inorganic phosphates that would have a role in their plant growth promoting activities (Antoun et al., 1998). In addition to their plant growth promoting effects, *Rhizobium* spp. have been increasingly associated with disease suppressive effects in the recent literature (Elbadry et al., 2006; Huang et al., 2007; Huang and Erickson, 2007; Siddiqui et al., 2007). Table 1 describes various *Rhizobium* spp. that have shown efficacy in reducing disease caused by fungi, bacteria, viruses, nematodes, and/or parasitic plants.

Disease suppression afforded by *Rhizobium* spp. has been linked to direct inhibition of pathogens development (through competition or antibiosis) as well as indirect inhibition through the stimulation of plant defense mechanisms (Fig. 1 and Table 2). Many *Rhizobium* spp. have been studied with regard to their potential mode of action in directly inhibiting plant pathogen growth, mainly with regard to the extracellular compounds they produce. Early work revealed that *Rhizobium* spp. have the potential to produce extracellular compounds (such as trifolitoxin) with direct antimicrobial activities (Breil et al., 1996) indicating that antibiosis may be part of their reported biocontrol efficacy. However, these compounds seem to be rather specific to other *Rhizobium* spp. suggesting that they would be more involved in limiting nodule

formation by competing *Rhizobium* strains rather than biocontrol (Triplett, 1990). Another trait of biocontrol by *Rhizobium* spp. is their ability to produce iron-chelating siderophores. These compounds would reduce or eliminate the available iron for other microorganisms in the same ecological niche and thus produce their antagonistic activity through competition. Antoun et al. (1998) determined that 181 of 196 tested *Rhizobium* spp. produced siderophores. Arora et al. (2001) determined that only siderophore-producing strains of *Rhizobium meliloti* (*Sinorhizobium meliloti*) were able to inhibit *Macrophomina phaseolina* in vitro. These strains were equally capable of increasing groundnut seed germination in the presence of *M. phaseolina*. Although siderophore production has been linked to biocontrol capabilities in other microorganisms, there is, to our knowledge, no direct evidence of siderophore production as a component of antagonism toward plant pathogens by *Rhizobium* spp.

Conversely, *Rhizobium* spp. have been studied more in depth where induced resistance (IR) is concerned. The presence of *Rhizobium* spp. would in this case indirectly stimulate the plant to activate its defense mechanisms when challenged with a pathogen through the production of plant defense compounds (phenolics, flavonoids or other phytoalexins, in particular). Rabie (1998) demonstrated that total and free phenolics increased significantly in *Botrytis fabae*-infected broad bean when the plant was pre-inoculated with *Rhizobium leguminosarum* bv. *viceae*. Elicitation of isoflavonoid phytoalexins by *Rhizobium* spp. has been associated with disease control in alfalfa and common bean (Dakora et al., 1993a, b; Dakora, 2003). *Rhizobium*-mediated induction of phenolics (particularly gallic, ferulic, tannic and cinnamic acids) was correlated with reduced sheath blight (*Rhizoctonia solani*) of rice (Mishra et al., 2006). *R. leguminosarum* strains induced high activity of peroxidase and phenylalanine ammonia lyase in peas that were parasitized by *Orobanche crenata* (Mabrouk et al., 2007). In the particular case of *Rhizobium etli*, lipopolysaccharide (LPS) has been

Table 1
Examples of disease reduction by *Rhizobium* spp

	Pathogen	Host-plant	Selected references
<i>R. etli</i>	<i>Globodera pallida</i>	Potato	Reitz et al. (2000)
	<i>Meloidogyne incognita</i>	Potato	Hallmann et al. (2001)
<i>R. leguminosarum</i> bv. <i>phaseoli</i>	<i>Fusarium solani</i>	Bean	Dar et al. (1997)
	<i>F. solani</i>	Okra, soybean, sunflower	Omar and Abd-Alla (1998)
	<i>Macrophomina phaseolina</i>	Okra, soybean, sunflower	Omar and Abd-Alla (1998)
	<i>Orobanchace crenata</i>	Pea	Mabrouk et al., 2007
	<i>Rhizoctonia solani</i>	Okra, soybean, sunflower	Omar and Abd-Alla (1998)
<i>R. leguminosarum</i> bv. <i>trifolii</i>	<i>Phytophthora clandestina</i>	Clover	Simpfendorfer et al. (1999)
<i>R. leguminosarum</i> bv. <i>viceae</i>	<i>Curtobacterium flaccumfaciens</i>	Bean	Huang et al. (2007)
	<i>Pythium</i> spp.	Bean	Huang and Erickson (2007)
	Yellow mosaic virus	Bean	Elbadry et al. (2006)
<i>R. tropici</i>	<i>Fusarium oxysporum</i> f. sp. <i>phaseoli</i>	Bean	Estevez de Jensen et al. (2002)
	<i>F. solani</i>	Bean	Estevez de Jensen et al. (2002)
	<i>R. solani</i>	Bean	Estevez de Jensen et al. (2002)
<i>Rhizobium</i> sp.	<i>M. incognita</i>	Lentil	Siddiqui et al. (2007)

implicated in induced systemic resistance (ISR) triggering. Reitz et al. (2000, 2002) showed that LPS from *R. etli* played a major role in the elicitation/triggering of ISR. Purified LPS was shown to induce systemic resistance and *R. etli* mutants that lacked part of the LPS were deficient in the ability to induce systemic resistance.

2.2. *Glomus* spp.

Arbuscular mycorrhizal (AM) fungi are obligate symbionts of more than 80% of terrestrial plants. In exchange for reduced carbon (St-Arnaud et al., 1996), AM fungi supply the plant with mineral nutrients (phosphorus, in particular) and increase water uptake (Selosse et al., 2006; Fig. 1). *Glomus* spp. have probably been the most extensively studied of the AM fungi and were shown to not only improve plant productivity through nutrient uptake, but to equally possess qualities that may assist their host-plant in staving off disease.

Whipps (2004) reviewed prospects for mycorrhizas in biocontrol of plant diseases and, of particular interest, listed examples

of the effects of *Glomus* spp. on plant diseases. In general, *Glomus* spp. symbiosis provided disease control in numerous root pathogen–plant combinations. However, *Glomus* spp. symbiosis was reported to stimulate foliar plant pathogens in all reports except for decreasing chocolate spot (*Botrytis fabae*) on broad bean (Rabie, 1998) and yellows disease (Phytoplasma) on tomato (Lingua et al., 2002). More recently, mycorrhization of tomato plants with *Glomus intraradices* (Fritz et al., 2006) and *Glomus fasciculatum* (de la Noval et al., 2007) was shown to reduce early blight disease in leaves infected with *Alternaria solani*. Liu et al. (2007) also reported a 4.4-fold decrease in *Xanthomonas campestris* pv. *alfalfae* populations in the leaves of alfalfa mycorrhized with *G. intraradices*. These reports suggest that inoculation with *Glomus* spp. has the potential to reduce disease both locally (at and around the site of mycorrhization) and at a distance (in adjacent non-mycorrhized roots and, in particular, in the shoots and leaves).

Considering the potential of *Glomus* spp. to reduce disease of both root and foliar pathogens, great strides have been accomplished in the study of the modes of action of *Glomus* spp. in biocontrol. The potential modes of action reported for these fungi include (i) direct pathogen growth alterations from AM fungi exudates, (ii) competition for food or space, (iii) improved nutritional status of the plant, (iv) modified root branching or root morphology of the host-plant, (v) development of an environment conducive to antagonistic microorganisms in the rhizosphere, and (vi) induced resistance (Fig. 1; Table 3).

According to the results obtained in an in vitro two-compartment Petri dish system, St-Arnaud et al. (1995) hypothesized that *G. intraradices* might stimulate the germination of *Fusarium oxysporum* f. sp. *chrysanthemi* propagules close to its mycelium but at a distance from the roots of plant, probably through the production of extramycelial excretions. This would induce a *suicide germination* of the pathogen through exhaustion or lysis of the germinating hyphae and could reduce pathogen inoculum in the soil. Norman and Hooker (2000) concluded that reduced sporulation of *Phytophthora fragariae* by exudates from *Glomus etunicatum* and *Glomus monospora* was part of the observed biocontrol activity. Although competition for photosynthates or carbon has been proposed as a mechanism of biocontrol by AM fungi, there is little or no evidence that this is a generalized mechanism of *Glomus* spp. (Azcón-Aguilar and Barea, 1996). In contrast, competition for infection sites or root space has been much more apparent as a biocontrol activity of *Glomus* spp. Indeed, *Glomus mosseae* reduced *Phytophthora parasitica* (Fusconi et al., 1999; Vigo et al., 2000) and *R. solani* (Morandi et al., 2002) infection loci in tomato and pea roots, respectively. However, Fillion et al. (2003) indicated that competition for infection sites was probably not implicated in the biocontrol

Table 2
Plant growth promoting *Rhizobium* spp. with biocontrol activities

	Potential mode of action			Selected references
	AC ^a	Sid ^b	IR ^c	
<i>R. etli</i>			×	Reitz et al. (2000, 2002)
<i>R. leguminosarum</i> bv. <i>phaseoli</i>		×	×	Antoun et al. (1998), Rabie (1998), Mishra et al. (2006)
<i>R. leguminosarum</i> bv. <i>trifolii</i>	×	×	×	Breil et al. (1993, 1996), Antoun et al. (1998), Mishra et al. (2006)
<i>R. leguminosarum</i> bv. <i>viceae</i>		×	×	Antoun et al. (1998), Mabrouk et al. (2007)
<i>R. meliloti</i> ^d		×	×	Antoun et al. (1998), Arora et al. (2001), Dakora et al. (1993a)

^a Production of antimicrobial compounds.

^b Siderophore production.

^c Induced resistance.

^d Now known as *Sinorhizobium meliloti* (Sawada et al., 2003).

Table 3
Plant growth promoting *Glomus* spp. with biocontrol activities

	Potential mode of action			Selected references
	DI ^a	Competition ^b	ILR/ISR ^c	
<i>G. etunicatum</i>	×		×	Norman and Hooker (2000), Yao et al. (2003)
<i>G. fasciculatum</i>			×	de la Noval et al. (2007), Hause et al. (2007)
<i>G. intraradices</i>	×		×	St-Arnaud et al. (1995), Fritz et al. (2006), Liu et al. (2007)
<i>G. monospora</i>	×			Norman and Hooker (2000)
<i>G. mosseae</i>		×	×	Fusconi et al. (1999), Vigo et al. (2000), Morandi et al. (2002), Pozo et al. (2002)

^a Direct inhibition or alteration of pathogen growth through exudate production (potentially including antibiosis).

^b Competition for infection sites.

^c Induced local and/or systemic resistance.

mechanisms of *G. intraradices* against *Fusarium solani* f. sp. *phaseoli*. Changes in root architecture as a result of *Glomus* symbiosis have also been proposed as a mechanism of control of disease through the reduction of potential infection sites by root pathogens (Norman et al., 1996; Fusconi et al., 1999). Furthermore, the improved nutritional status of the plant (phosphorus uptake in particular) has been recognized as a means by which *Glomus* spp. may assist the plant in staving off disease (Linderman, 1994; Karagiannidis et al., 2002). In the case of development of an environment conducive to antagonistic microorganisms in the rhizosphere, many authors have shown that *Glomus* spp. modify the root microbiota when mycorrhization is in place (reviewed by Whipps, 2004) and, therefore, hypothesized that antagonistic microorganisms may be stimulated or augmented thus providing biocontrol of soilborne organisms. For example, Filion et al. (1999) indicated that *G. intraradices* stimulated growth of *Pseudomonas chlororaphis* and conidial germination of *Trichoderma harzianum*, two microorganisms with known biocontrol capabilities. However, there have not been, to our knowledge, any direct links between increased disease protection and enhanced antagonistic activities of (potential) biocontrol agents afforded by *Glomus* spp.

On the other hand, plant defense mechanisms have been well studied in *Glomus*-mycorrhized plant and there is increasing evidence that local and systemic IR is part of the biocontrol activities of *Glomus* spp. against root and foliar pathogens. A recent review by Whipps (2004) indicated that the majority of classic plant defense responses occur during *Glomus* spp. mycorrhization including phenolic and phytoalexin production, formation of structural barriers, production of pathogenesis related (PR) proteins and enzymes associated with plant defense mechanisms. However, the author concluded that evidence of induced plant defense mechanisms by AM fungi was inconsistent and that ISR, i.e. plant resistance mechanisms in adjacent non-mycorrhized roots, shoots and leaves following inoculation with AM fungi, remains controversial. Conversely, other works on the effects of *Glomus* spp. on plant disease are linking disease decrease with local and systemic alterations in genes and gene products associated with disease resistance. Indeed, Pozo et al. (2002) used a split root experimental system that would indicate that *G. mosseae* could reduce disease symptoms of *P. parasitica* both locally and systemically (on neighboring non-mycorrhized roots). This bio-protective effect was correlated with localized and systemic qualitative differences in plant defense-related enzymes (chitinase, chitosanase, β -1,3-glucanase and superoxide dismutase). In potato plants, *G. etunicatum* reduced *R. solani* disease severity on roots and shoots (Yao et al., 2002), which was accompanied by an accumulation of rishitin and solavetivone, two potato phytoalexins that directly inhibit growth of *R. solani* in vitro (Yao et al., 2003). *G. intraradices* inoculation decreased *X. campestris* populations in the leaves of *Medicago truncatula* and was associated with an increase in stress and defense response transcripts, which accounted for 26% of all induced transcripts, in the shoots (Liu et al., 2007). Fritz et al. (2006) indicated that the protective effect of *G. intraradices* against early blight of tomato resembles ISR. de la Noval et al. (2007) used the same plant pathogen system to confirm that ISR was occurring in *G. fasciculatum*-mycorrhized tomato probably through a jasmonate-dependent signaling pathway that is known to be upregulated during mycorrhization and can lead to an enhanced defense status of the plant (Hause et al., 2007).

3. Biological control agents (BCA) with growth promoting activities

3.1. *Trichoderma* spp.

Of all the existing fungal BCA, *Trichoderma* spp. are probably the most studied for their effects on reducing plant diseases. Their

mode of action has been multifaceted including parasitism, competition, antibiosis, and/or induced resistance (Kubicek et al., 2001; Benítez et al., 2004; Harman et al., 2004) (Fig. 1). In addition to the effectiveness of *Trichoderma* spp. in controlling plant pathogens, many studies have shown the direct benefits of these fungi on plant growth and production.

In absence of pathogens, *T. harzianum* applications increased (i) germination of pepper seeds, (ii) emergence of seedlings of bean, radish, tomato, pepper, and cucumber, (iii) seedling length and leaf area in pepper, and (iv) dry weight of cucumber plants (Kleefeld and Chet, 1992). Multiple strains of *T. harzianum* and *Trichoderma viride* increase shoot fresh and dry weight and *T. harzianum* increased shoot to root ratio of lettuce (Ousley et al., 1994). In peas, three strains of *T. harzianum* increased fresh shoot weight, root weight and/or root length (Naseby et al., 2000). Vásquez et al. (2000) showed that *T. harzianum* increased shoot dry weight in corn. Yedidia et al. (2001) revealed that *T. harzianum* increased cucumber plant root area by 95%, root length by 75%, dry weight by 80%, shoot length by 45%, and leaf area by 80% when compared to the control. Using tobacco as a model system, Chacón et al. (2007) demonstrated significant increases in fresh weight, number of leaves, leaf area and root proliferation by *T. harzianum*. *Trichoderma atroviride* revealed a three-fold increase in both shoot and root dry weight of seedling (Gravel et al., 2006) and a significant increase in total and/or marketable fruit (Gravel et al., 2007) in healthy tomato plants.

With regard to the added secondary benefits of *Trichoderma* spp. on plant growth, two main mechanisms of action have been revealed in the past decade: (i) increased plant nutrition through solubilization and/or enhanced uptake of macro- and micro-nutrients and (ii) production of plant growth factors (Fig. 1; Table 4). These mechanisms are responsible for the so-called 'biofertilizer effect' of *Trichoderma*.

Harman (2000) and Harman et al. (2004) documented the abilities of *T. harzianum* to enhance nitrogen use efficiency in corn

Table 4
Biological control species of *Trichoderma* and *Pseudomonas* with plant growth promoting activities

	Potential plant growth promoting activities			Selected references
	Enhanced mineral uptake or solubilization	Plant growth regulators		
		IAA ^a	Cyt ^b	
<i>T. atroviride</i>		×		Gravel et al. (2007)
<i>T. harzianum</i>	×			Anusuya and Jayarajan (1998), Altomare et al. (1999), Harman (2000), Yedidia et al. (2001), Harman et al. (2004), Ögüt and Er (2006)
<i>T. viride</i>	×		×	Anusuya and Jayarajan (1998), Tsavkelova et al. (2006)
<i>P. chlororaphis</i>		×		Kang et al. (2006)
<i>P. fluorescens</i>	×	×		Das et al. (2003), Kang et al. (2006)
<i>P. putida</i>	×	×	×	de Freitas et al. (1993), Glick et al. (1997), Patten and Glick (2002), Mehnaz and Lazarovits (2006), Gravel et al. (2007)

^a Indole acetic acid regulation (production and/or degradation).

^b Cytokinin-like compounds.

^c Ethylene regulation through aminocyclopropane carboxylate deaminase activity.

but provided no insight into the specific mechanisms involved. Ögüt and Er (2006) showed that *T. harzianum* generally decreased Fe, Mn, Zn, and Cu in bean foliar biomass but significantly increased Cu in the seeds. In these same trials, *T. harzianum* also increased Mn accumulation in the seeds of wheat. In cucumber plants, inoculation with *T. harzianum* caused a significant increase in P, Cu, Fe, Zn, Mn and Na concentration in the roots, which was accompanied by a 25%, 30% and 70% increase in Zn, P, and Mn, respectively, in the shoots (Yedidia et al., 2001). Considering that the nutrients, P in particular, were available (soluble) in the culture substrate, increased uptake rather than increased solubilization was proposed as the plant growth promoting activity (Yedidia et al., 2001). In the case of the solubilization of insoluble or sparingly soluble minerals, Altomare et al. (1999) indicated that *T. harzianum* or its culture filtrates were able to solubilize Fe₂O₃, MnO₂, metallic Zn, and rock phosphorus in vitro through chelation and redox activity; acidification did not seem involved. Anusuya and Jayarajan (1998) demonstrated solubilization of P from both tricalcium phosphate and rock phosphate by *T. harzianum* and *T. viride*.

Although there has been little work devoted to the implication of plant growth factors in the *Trichoderma* plant growth promoting effect, recent work has demonstrated that cytokinin-like molecules, possibly kinetin, may be produced by *T. viride* (Tsavkelova et al., 2006). Of particular interest, *T. atroviride* has been shown to produce and degrade indole acetic acid (IAA), the most common plant auxin and to possibly possess aminocyclopropane carboxylic acid (ACC) deaminase activity that would control ethylene production (Gravel et al., 2007). The combined effect of IAA and ethylene regulation in the rhizosphere may well account for the increased growth of hydroponic tomatoes in the presence of *T. atroviride* (Gravel et al., 2007).

3.2. *Pseudomonas* spp.

Among biocontrol bacteria, *Pseudomonas* spp. have been broadly studied for their ability to reduce the development of various soilborne plant pathogens (Paulitz et al., 1992; Larkin and Fravel, 1998; Schisler et al., 2000; Carisse et al., 2003). Numerous modes of action for *Pseudomonas* spp. have been reported, including the production of different antimicrobial compounds (Howell and Stipanovic, 1980; de Freitas and Germida, 1991; Harris et al., 1997; Sharifi-Tehrani et al., 1998; Thrane et al., 2000), competition (Paulitz et al., 1992; Fukui et al., 1994; Mohamed and Caunter, 1995; Ellis et al., 1999) and induction of the plant defense mechanisms (Benhamou et al., 1996; Chen et al., 1998; Ongena et al., 2000, 2002; Ramamoorthy et al., 2002a, 2002b). In addition to their beneficial effect on the development of plants in the presence of pathogens, *Pseudomonas* spp. were also shown to improve plant growth in absence of pathogens.

In this regard, multiple strains of fluorescent pseudomonads have the ability to stimulate seed germination as well as shoot and root development of different crops, including chickpea, eggplant, soybean and tomato (Kloepper et al., 1988; Dileep Kumar, 1998). Among these pseudomonads, the plant growth promoting effect of biocontrol strains of *Pseudomonas fluorescens* has been recognized in numerous studies (Howie and Ehandi, 1983; Kloepper et al., 1988; Kurek and Jaroszuk-Sciset, 2003; Kang et al., 2006). A strain of *Pseudomonas putida*, which was shown to reduce damage caused by *Pythium ultimum* on tomato and to improve the growth of the infected plants (Gravel et al., 2006), was also shown to directly stimulate growth of healthy plants in a disease-free environment (Gravel et al., 2007). Other studies have also reported the stimulating effect of *P. putida* on the development of cucumber plants (Amer and Utkhede, 2000) and canola seedlings (Xie et al., 1996). Mehnaz and Lazarovits (2006) demonstrated an increase in

root and shoot weight of corn plants inoculated with a strain of *P. putida* known for its antagonistic activity against *Fusarium* sp. Also of interest, de Freitas and Germida (1991) described the plant growth promoting effect on winter wheat of the biocontrol bacteria *Pseudomonas cepacia* and *P. putida*. The growth stimulating effect of a strain of *P. chlororaphis*, primarily known as a systemic resistance inducer, has also been described on tobacco (Kang et al., 2006).

The direct plant growth promoting effect of biocontrol agents, such as *Pseudomonas* spp., in pathogen-free environments, is often associated with the following mechanisms: solubilization of insoluble P sources (Richardson, 2001) and/or regulation of the concentration of plant growth regulators either through their production or their degradation (Glick et al., 1998; Vessey, 2003) (Fig. 1; Table 4). Most likely, the growth promoting ability of bacteria from the genus *Pseudomonas* results from the synergic effect of more than one mode of action.

Solubilization of insoluble sources of P by plant growth promoters, including *Pseudomonas* spp., has been linked to growth stimulation (Goldstein, 1986). In this regard, Das et al. (2003) described the P solubilization ability of *P. fluorescens* strains whereas Mehnaz and Lazarovits (2006) have linked the PGPM activity of *P. putida* to the solubilization of organic P. The synthesis of organic acids by *Pseudomonas* spp. could be responsible, at least in part, for the solubilization of inorganic P sources (Banik and Dey, 1982; Illmer and Schinner, 1992).

Moreover, the production of IAA by bacteria, such as *Pseudomonas* spp., is often associated with their potential to stimulate plant growth (Xie et al., 1996; Antoun et al., 1998; Barazani and Friedman, 1999; Patten and Glick, 2002). Among others, Patten and Glick (2002) showed that the production of IAA by *P. putida* was closely linked to the optimal development of the root system in canola and mung bean. Other growth promoting strains of this bacterium were shown to synthesize IAA from tryptophan (de Freitas et al., 1993; Mehnaz and Lazarovits, 2006; Gravel et al., 2007). *P. fluorescens* and *P. chlororaphis*, two known biocontrol agents with growth promoting ability, were also shown to synthesize IAA (Kang et al., 2006).

The level of plant growth regulators in the vicinity and within the root system plays an important role in the growth promoting ability of a microorganism. The regulation of the concentration of such compounds by plant growth promoting bacteria has also been intensively studied (Glick et al., 1997, 1998). The degradation of IAA by *P. putida* has been reported by Leveau and Lindow (2005) to affect plant development. Other biodegradation activities in PGPR, through the action of ACC deaminase activity that hydrolyzes ACC into ammonia and α -ketobutyrate, prevent the synthesis of plant growth inhibiting levels of ethylene in the roots (Penrose et al., 2001). The reduction in the level of ACC in the rhizosphere through ACC deaminase activity increases the exudation of ACC by the plant to maintain equilibrium, reducing the potential synthesis of ethylene in the roots (Glick et al., 1998). ACC deaminase has previously been reported for *Pseudomonas* spp. and its activity has been associated with an increase in root elongation due to the reduced inhibition caused by ethylene (Glick et al., 1997; Wang et al., 2000; Safronova et al., 2006).

4. Future perspectives on the effective use of multifaceted beneficial effects of rhizosphere microorganisms

In the previous sections, case studies of *Rhizobium*, *Glomus*, *Trichoderma* and *Pseudomonas* spp. revealed that increasing knowledge on the secondary beneficial effects of PGPM and BCA are being uncovered and that this would most likely enhance the usefulness of these microorganisms regardless of their primary function in agricultural management practices. For example, the use of PGPM, such as *Rhizobium* or *Glomus*, regardless of the plant's

nutritional or growth status may well assist the plant in combating disease. Conversely, the use of BCA, such as *Trichoderma* or *Pseudomonas*, can stimulate plant growth regardless of pathogen presence.

However, there remain unknowns concerning the use of these microorganisms for their secondary beneficial effects. In particular, although the secondary beneficial effects of these microorganisms are known, this is not always the case for the precise modes of action. It is certain that further investigation into these modes of action would be necessary. With the advent of functional genomics and proteomics studies of these microorganisms (for *Trichoderma*, in particular; Marra et al., 2006; Woo et al., 2006; Chacón et al., 2007), work on genes and gene products should be able to more precisely determine these modes of action. This information could eventually assist with the timely and appropriate application of these organisms in agricultural management practices. Additional work on a more precise quantification of these secondary effects would also be useful. Few of the works cited in this review were directly testing these beneficial effects, which were often a 'by-product' of the experimental setup on the primary beneficial effect. A more focused experimental design that would test both growth promotion and disease control in presence and absence of a pathogen would help in elucidating the relative primary to secondary beneficial effects of these microorganisms. Future work aimed at elucidating the relative benefits of the primary and secondary effects should also include a cost/benefit analysis that would be able to assess the added value of the secondary effects.

It is also critical to realize that, whether these multifaceted beneficial organisms are to be used for their primary, secondary or both effects, there are general ecophysiological parameters that must be taken into account and properly evaluated to ensure constant efficacy of the bio-inoculation. For example, poor field survival is often a limitation of the effective use of these organisms. In this respect, inhospitable environmental conditions such as non-optimal temperature and humidity parameters may greatly hamper survival of the microorganism or at least reduce the expression of its beneficial effects (Paulitz and Bélanger, 2001). Unfortunately, environmental conditions that are conducive to the manifestation of beneficial effects remain largely unknown for these microorganisms and require further investigation. Furthermore, competitive displacement of beneficial microorganisms by endogenous or introduced rhizosphere microorganisms that occupy the same ecological niche may well affect the efficacy of the beneficial agent in vivo. Considering the proven primary and secondary beneficial effects of the aforementioned microorganisms, the addition of multiple microorganisms to a given system appears attractive. However, the possible competitiveness between these microorganisms must be taken into account. Various reports indicate that co-inoculation of beneficial organisms generally increased plant growth and/or decreased plant disease relative to single inoculation with a sole beneficial organism (e.g. Naseby et al., 2000; Dileep Kumar et al., 2001; Whipps, 2004; Chandanie et al., 2006; Raimam et al., 2007). Most of the effects of the individual microorganisms in co-inoculation are additive, although a synergistic effect has been reported in some cases (Ravnskov et al., 2006; Kohler et al., 2007). However, neutral or negative effects have been reported (Dar et al., 1997; Green et al., 1999; Whipps, 2004; Akköprü and Demir, 2005) indicating that the outcome of co-inoculation of these microorganisms on plant health and productivity should be determined on a case-by-case basis (Hodge, 2000; Siddiqui and Shaikat, 2002; Whipps, 2004). For example, the co-inoculation of *G. intraradices* with *T. harzianum* decreased *T. harzianum* populations and dry shoot weight in cucumber compared to inoculation with *T. harzianum* alone (Green et al., 1999). Ravnskov et al. (2006) demonstrated the mutual inhibition with co-inoculation of *G. intraradices* and the biocontrol agent

Clonostachys rosea although this did not impair their growth promotion of tomato. These results demonstrate that, from an ecophysiological standpoint, the interactions between beneficial organisms are poorly understood and further investigation into these processes would be necessary for obtaining optimal benefits to plant health and growth.

5. Conclusion

The present review on the secondary beneficial effects of rhizosphere microorganisms would indicate their immense potential as bio-inoculants, regardless of the need for their primary function. More precisely, PGPM will promote plant growth and productivity (primary effect) but could equally play a role in reducing disease (secondary effect) regardless of plant growth and nutritional status. Conversely, the use of BCA can control disease (primary effect) but could also stimulate plant growth (secondary effect) in the absence of pathogens. In specific circumstances, the secondary effect may well be the dominant benefit provided by these beneficial rhizosphere microorganisms.

Overall, beneficial microorganisms, such as those reviewed in this work, have demonstrated multifaceted beneficial effects pertaining to increased plant growth and health. However, more studies on the precise mode of action and the ecophysiology of these microorganisms in relation to other soilborne inhabitants may well help in the timely and appropriate use of these organisms. This could allow the release of their full potential as multifaceted beneficial bio-inoculants for improved growth and health of plants. The potential increased use of these microorganisms afforded by their multifaceted beneficial effect may further help in reducing problems associated with the use of synthetic chemicals in agriculture.

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