Pseudomonas and other Microbes in Disease-Suppressive Soils

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Abstract Soil-borne phytopathogens cause extensive damage to cultivated plants worldwide, resulting in yield loss worth billions of Euros each year. Soil fumigation is the most effective chemical treatment but is too expensive for many crops, and fumigants like methyl bromide are being phased out for environmental reasons. In this context, much is to be learned from disease-suppressive soils, where susceptible plants are protected from soil-borne pathogens by the indigenous microbiota, because these microbial interactions may be exploited to design sustainable crop protection strategies for ordinary farm soils. However, our knowledge of plant-protecting microorganisms and biocontrol mechanisms involved in soil suppressiveness remain very fragmented, as most knowledge on disease suppressive soils comes from studies restricted to individual plant-protecting microbial populations, mostly fluorescent *Pseudomonas* species. The phenomenon of disease suppressiveness remains therefore poorly understood, even in the most studied cases such as suppressiveness to wheat take-all.

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We reviewed the respective biocontrol contributions of fluorescent pseudomonads and other plant-protecting microorganisms in disease-suppressive soils. The ability to inhibit soil-borne pathogens and to protect plants occurs both in *Pseudomonas* and non-*Pseudomonas* microorganisms, including diverse bacteria and fungi, and both play important roles in soil suppressiveness. In *Pseudomonas*, antibiosis and competition were shown to be important mechanisms of pathogen suppression, though direct effects on plant, e.g. induced systemic resistance, phytohormone interference and plant-growth promotion, were also reported. These types of mechanisms occur also in non-*Pseudomonas* biocontrol microbes, some of them also displaying hyperparasitism in certain types of suppressive soils.

This review shows that in suppressive soils where *Pseudomonas* play an important role, the roles of non-*Pseudomonas* microorganisms were often neglected, and *vice versa*. Yet, *Pseudomonas* and other microorganisms may interact with each other in the rhizosphere and with the plant, and some recent studies indicate that disease suppressiveness is an emerging soil property that can typically result from these multiple interactions. In conclusion, we propose that a parallel assessment of *Pseudomonas* and non-*Pseudomonas* microorganisms in suppressive soils, e.g. using microarrays or metagenomics, may bring a better understanding of disease suppressiveness.

Keywords Biocontrol • Disease-suppressive soil • Plant pathogen • *Pseudomonas* • Rhizosphere

1 Introduction

Crop plants are faced with a wide range of bioagressors, including pests, parasites and pathogens (Agrios 1997). Among them, phytoparasitic microorganisms are responsible for hundreds of billons Euros in crop loss worldwide. Many of them infect plant shoots and may be managed via chemical control. However, microorganisms affecting crop health and yield may also reside inside agricultural soils, where they infect the plant via the root. These soil-borne phytoparasitic microorganisms can be harder to control by chemical means, because they are physically protected by soil particles. Soil fumigation is the most effective chemical treatment but is expensive, has adverse effects on beneficial microbes involved in soil fertility and quality, and may cause other environmental problems in relation to global change.

Soils harbour a wide range of phytoparasitic microorganisms, including pathogenic fungi, oomycetes, nematodes and bacteria (Raaijmakers et al. 2009), and these phytoparasites may cause extensive damage to crops (Agrios 1997). However, the survival, infectivity and/or pathogenicity of plant-parasitic microorganisms in soil is generally reduced due to competition and other negative interactions exerted by the rest of the microbial community, and this common soil property is referred to as general disease suppression (Cook and Baker 1983). In addition to general disease suppression, certain soils exhibit specific disease suppression towards a particular parasite (Haas and Défago 2005). In these soils, disease incidence in presence of virulent

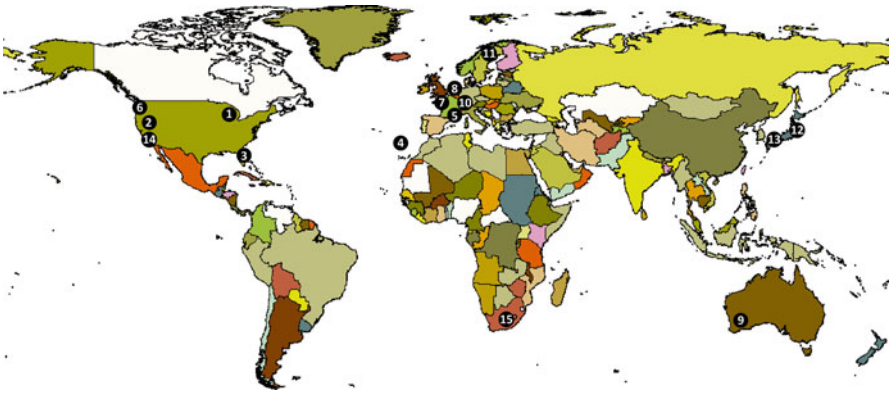

Fig. 1 Countries with emblematic case studies of soils with specific suppression towards soil-borne phytoparasites. **1** *Streptomyces scabiei* (potato scab); **2–5** *Fusarium oxysporum* (Fusarium wilt of watermelon, banana and flax); **6–9** *Gaeumannomyces graminis* var. *tritici* (wheat take-all); **10** *Thielaviopsis basicola* (black root rot of tobacco); **11–12** *Plasmodiophora brassicae* (clubroot disease of cabbage); **13** *Ralstonia solanacearum* (tomato wilt); **14** *Heterodera schachtii* (endoparasitic nematode; damage to sugarbeet roots); **15** *Xiphinema elongatum* and *Paratrichodorus minor* (ectoparasitic nematodes; damage to sugarcane roots)

pathogen, susceptible plant and pathogen-favorable environmental conditions is much lower than expected, unlike in disease-conducive soils (i.e. allowing plant infection and spread of the disease; Baker and Cook 1974; Weller et al. 2002; Mazzola 2002; Borneman and Becker 2007; Janvier et al. 2007). The microbial basis of suppressiveness has been shown in experiments where this property was eliminated by soil sterilization/pasteurisation, and acquired by conducive or sterilized/pasteurised suppressive soil following the addition of small amount of suppressive soil (Baker and Cook 1974; Weller et al. 2002; Mazzola 2002; Haas and Défago 2005).

The focus of this review is on specific disease suppressiveness, which has been documented for several phytoparasitic bacteria (Becker et al. 1997; Shiomi et al. 1999), nematodes (Rimé et al. 2003; Borneman and Becker 2007), oomycetes (Persson et al. 1999; Murakami et al. 2000) and especially fungi (Stutz et al. 1986; Weller et al. 2002; Janvier et al. 2007). Soils specifically suppressive towards a pathogen occur worldwide (Fig. 1). They were originally defined by Baker and Cook (1974) as soils in which the pathogen does not establish, establishes but causes no or little disease, or causes disease that subsequently diminishes with continuous culture of the crop. The definition comprises two recognized types of specific suppressiveness, i.e. natural (long-standing) suppressiveness and suppressiveness induced by monoculture. Induced disease suppressiveness develops as a result of crop monoculture, and is well documented especially for take-all disease of wheat (caused by the fungus *Gaeumannomyces graminis* var. *tritici*), potato scab (caused by the actinobacterium *Streptomyces scabiei*), Rhizoctonia root rot of wheat and cauliflower (caused by *Rhizoctonia solani*) and damage caused by the cereal-cyst nematode *Heterodera avenae* (Kerry 1982; Roget 1995; Weller et al. 2002; Postma et al. 2010). Often, repeated growth of a same crop favours the pathogen, and disease severity increases year after year. In the case of induced

disease suppressive soils, however, rhizosphere populations of plant-protecting microorganisms build up after a few years, and they lead then to disease suppressiveness, which explains why this phase is often referred to as disease decline (Weller et al. 2002). Induced disease suppressiveness lasts as long as the monoculture is not interrupted using a non-host plant. In contrast, natural disease suppressiveness does not require monoculture (Haas and Défago 2005), although it is likely that the extent of disease suppression may be influenced by past conditions of crop rotation (Ramette et al. 2003a). It has been extensively studied for several soil-borne diseases, such as *Thielaviopsis basicola*-mediated black root rot (Stutz et al. 1986) and Fusarium wilt caused by *Fusarium oxysporum* (Alabouvette 1986). Although microrganisms play the key role in disease suppressiveness, soil physicochemical properties may also contribute to the phenomenon (especially in the case of natural disease suppressiveness, e.g. Höper et al. 1995). Indeed, soil factors such as pH and clay mineral composition may favour the establishement of plant-protecting populations or expression of plant-beneficial traits (Höper et al. 1995; Keel et al. 1992; Ramette et al. 2006).

In a majority of studies, the assessment of disease-suppressive soils has focused on the role of the fluorescent *Pseudomonas* spp. (Lemanceau et al. 2006), especially in a context of antibiosis (Haas and Défago 2005; Weller 2007), without considering the potential role of other microorganisms in specific disease suppression. This is particularly the case for soil suppressiveness to take-all or black root rot disease. However, it is likely that non-pseudomonads contribute also to disease suppression in many cases (Rimé et al. 2003; Ramette et al. 2006; Borneman and Becker 2007). In a smaller number of studies, other plant-protecting microorganisms have been considered, e.g. *Bacillus*, *Streptomyces*, *Pasteuria penetrans*, *Trichoderma* or non-pathogenic *Fusarium oxysporum* (Weller et al. 2002; Janvier et al. 2007), but typically without parallel analysis of fluorescent *Pseudomonas* populations.

Both *Pseudomonas* and non-*Pseudomonas* microorganisms display a range of biocontrol traits that are likely to be involved in specific suppression. This review therefore aims at assessing current knowledge on the biocontrol properties and respective role of fluorescent pseudomonads versus non-*Pseudomonas* microorganisms in specific disease suppressiveness of soils. We believe that this is a prerequisite for understanding the phenomenon of specific disease suppressiveness with its implications for sustainable soil management and prospecting for suppressive soils and novel biocontrol microorganisms.

2 Role of Fluorescent *Pseudomonas* in Disease-Suppressive Soils

2.1 Modes of Action of Fluorescent Pseudomonas

2.1.1 Antibiosis

Several modes of plant protection are known for fluorescent pseudomonads (Fig. 2; Couillerot et al. 2009). The main one documented is antagonism mediated by the production of secondary antimicrobial metabolites, noticeably 2,4-diacetylphloroglucinol

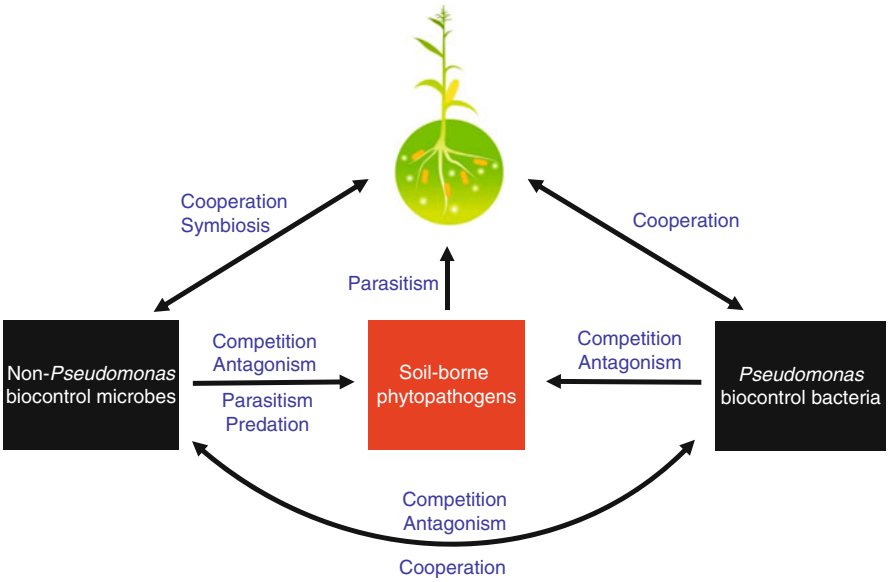

Fig. 2 Interplay between *Pseudomonas* and non-*Pseudomonas* biocontrol microorganisms and protection of plant roots from soil-borne phytopathogens (Modified from Couillerot et al. 2009)

(DAPG), phenazines, and hydrogen cyanide (Chin-A-Woeng et al. 2000; Raaijmakers et al. 2002; Haas and Défago 2005; Weller 2007). Antimicrobial metabolites also include pyrrolnitrin, pyoluteorin, lipopeptides and others, but they have been comparatively less studied. Only fragmented information is available on the mode of action of these compounds. In phytopathogenic fungi and oomycetes, DAPG can target the cell membrane, phenazines and pyrrolnitrin the electron transport chain, while hydrogen cyanide affects copper-containing cytochrome c oxidases (Haas and Défago 2005; Raaijmakers et al. 2009; Schouten et al. 2008). Evidence for the implication of antimicrobial secondary metabolites in biological control has been obtained using mainly two different approaches. First, non-producing mutants protected less than the corresponding parental strains, which has been shown for instance in the case of DAPG (Fenton et al. 1992; Keel et al. 1992), hydrogen cyanide (Voisard et al. 1989), pyoluteorin (Maurhofer et al. 1994) and phenazines (Thomashow and Weller 1988). However, the loss of the ability to produce a given metabolite is compensated in certain strains by excess production of another metabolite (Haas and Keel 2003), which complicates data interpretation. Second, the introduction into non-producing wild-type strains of genes conferring the ability to produce antimicrobial secondary metabolites conferred (or enhanced) plant protection ability (Fenton et al. 1992; Timms-Wilson et al. 2000). Similarly, the development by genetic means of overproducing derivatives could also result in improved biocontrol (Haas and Keel 2003; Mark et al. 2006).

Quantification of antimicrobial secondary metabolites in the rhizosphere is tricky. DAPG has been detected at levels up to 250 ng/g root in bulk samples from the wheat rhizosphere (Raaijmakers et al. 1999), but it is likely that the

actual concentration faced locally by pathogens in root surface micro-habitats is higher. Concentrations needed for *in vitro* inhibition of phytopathogenic bacteria, oomycetes, fungi and nematodes vary according to the target, from a few μg/ml to more than 100 μg/ml (Keel et al. 1992; de Souza and Raaijmakers 2003), and biocontrol pseudomonads are more effective against highly-sensitive pathogenic strains than less sensitive ones (Mazzola et al. 1995). Often, pseudomonads with plant-protection ability can produce more than one antimicrobial secondary metabolite (Raaijmakers et al. 2002; Haas and Keel 2003), certain compounds being more effective in some pathosystems than in others. Parallel analysis of the plant-protection efficacy of several biocontrol pseudomonads indicated that strains producing hydrogen cyanide protected better than the others in a pea-*Pythium ultimum* pathosystem (Ellis et al. 2000), whereas strains producing DAPG protected better overall than non-producing strains in cucumber-*P. ultimum* and tomato-*F. oxysporum* f. sp. *radicis-lycopersici* pathosystems (Sharifi-Tehrani et al. 1998). In the latter pathosystems, the ability to produce DAPG was more influential than the one to produce hydrogen cyanide when a much larger collection of biocontrol pseudomonads was used (Rezzonico et al. 2007).

The role of antimicrobial metabolites of *Pseudomonas* in antagonism is in fact difficult to ascertain, because these compounds can have multiple effects. Indeed, they may inhibit non-pathogens as well (Keel et al. 1992; Walsh et al. 2003), which in turn might interfere with phytopathogens. Furthermore, certain antimicrobial metabolites may have a direct impact on plant physiology. For instance, DAPG can modify root system architecture (Brazelton et al. 2008) and stimulate root exudation of amino acids (Phillips et al. 2004), which in turn affects perhaps the rhizosphere microbial community including phytopathogens, and it triggers an induced systemic response in the plant (see below). In addition to biocontrol functions, the ability to produce secondary antimicrobial metabolites may also contribute to ecological fitness, as shown for DAPG on potato (Cronin et al. 1997b) (but not on sugarbeet; Carroll et al. 1995) and phenazine on wheat (Mazzola et al. 1992). It has been hypothesized that certain genes encoding antimicrobial secondary metabolites in the fluorescent *Pseudomonas* spp. noticeably *phlD* (DAPG synthesis) could have been acquired from the plant, where perhaps they were also involved in plant defense functions (Cook et al. 1995; Ramette et al. 2001).

2.1.2 Other Biocontrol Mechanisms

Certain fluorescent pseudomonads may antagonize phytopathogens via the production of lytic enzymes or effectors (Raaijmakers et al. 2009). Data are scarce on the possible role of cell wall-degrading extracellular lytic enzymes e.g. β-1,3-glucanase and chitinase in *Pseudomonas* antagonism (Lim et al. 1991), and they seem to play a minor role in the plant-protection ability of pseudomonads (Sharifi-Tehrani et al. 1998). Another type of antagonistic interaction, in which pathogen virulence is targeted, implicates putative effectors. Indeed, mutation of type III protein secretion gene *hrcV* lowered the ability of *P. fluorescens* KD to reduce both polygalacturonase

activity in *Pythium ultimum* and Pythium damping-off of cucumber (Rezzonico et al. 2005). Type III secretion system genes are a basic feature of many biocontrol pseudomonads (Preston et al. 2001; Mazurier et al. 2004), but in *P. fluorescens* KD they may have been acquired horizontally in more recent time, apparently from pathogenic *Pseudomonas syringae* (Rezzonico et al. 2004).

In addition to antagonism, competition by pseudomonads is thought to contribute to pathogen control (Fig. 2), although to a lesser extent than antagonism (Haas and Défago 2005). Competition may take place for nutrients (Kamilova et al. 2005), especially organic carbon and/or iron (Lemanceau et al. 1992; Paulitz et al. 1992; Duijff et al. 1993). Besides conferring protection from disease (noticeably Pythium damping-off and Fusarium wilt), competition is also important for successful establishment of biocontrol pseudomonads in the rhizosphere (Moënne-Loccoz et al. 1996) and expression of antagonistic traits (Chin-A-Woeng et al. 2000).

Even if biocontrol fluorescent pseudomonads are effective at inhibiting phytopathogens, direct effects on the plant are also documented (Fig. 2), noticeably induced systemic resistance (ISR; Pieterse et al. 2003). During ISR, several plant defence mechanisms are activated and the plant resists better to a range of pathogens (van Loon 2007). ISR can be triggered by different surface constituents of *Pseudomonas* cells, such as the O-antigenic sidechain of lipopolysaccharides and flagella (Pieterse et al. 2003), and by metabolites released by these bacteria, e.g. the siderophore pyoverdine (Maurhofer et al. 1994), a benzylamine derivative (Ongena et al. 2007), and the antimicrobial metabolite DAPG (Iavicoli et al. 2003).

In addition to ISR, certain pseudomonads can also act on the plant by phytohormone interference, as follows. Ethylene levels in roots may be influenced by bacterial deamination of its precursor 1-aminocyclopropane-1-carboxylate (ACC), which is thought to diminish the quantity of plant ACC left for ethylene synthesis (Glick et al. 1998). This can contribute to plant health by promoting growth and alleviating stress (Glick 2005). Transfer of the ACC deaminase locus into *Pseudomonas protegens* CHA0 (previously *P. fluorescens* CHA0; Ramette et al. 2011) enhanced biocontrol of Pythium damping-off of cucumber (Wang et al. 2000). Unlike strain CHA0, a large range of biocontrol pseudomonads display ACC deaminase activity (Blaha et al. 2006), but whether this trait actually contributes to biocontrol in any of these strains remains to be established. Phytohormone interference may also result from production of the phytohormone indole-3-acetic acid (IAA), a trait occurring in many plant-beneficial pseudomonads including several biocontrol strains (Kamilova et al. 2005). Certain IAA-producing pseudomonads can stimulate root growth (Lippmann et al. 1995; Patten and Glick 2002), and overproduction of IAA has the potential to enhance plant growth promotion effects (Dubeikovsky et al. 1993; Beyeler et al. 1999). However, spontaneous or controlled mutations that reduced IAA synthesis ability or genetic modifications enhancing this ability did not have a significant impact on the biocontrol efficacy of pseudomonads (Oberhansli et al. 1991; Beyeler et al. 1999; Suzuki et al. 2003).

Finally, a few plant growth-promoting pseudomonads are thought to act on the plant by enhancing nutrient availability, noticeably via nitrogen fixation for

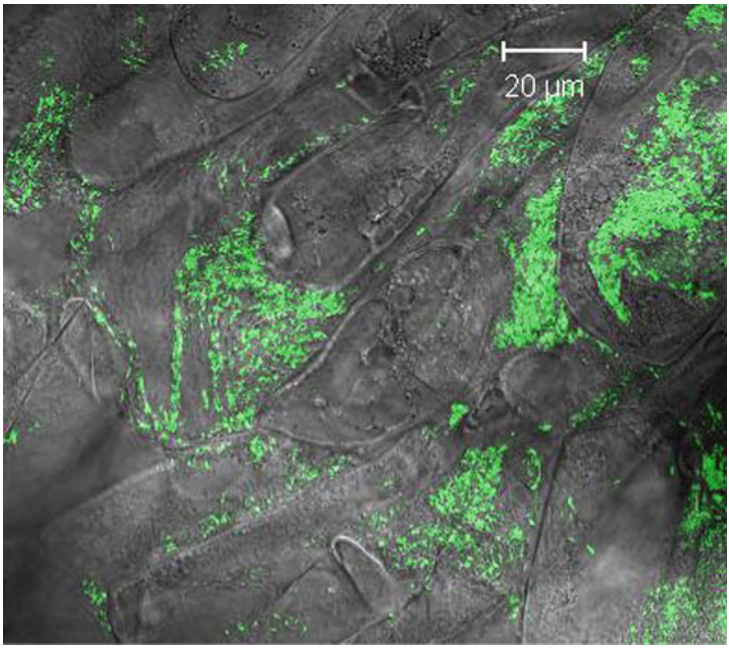

Fig. 3 Colonization of wheat roots by the biocontrol strain *Pseudomonas protegens* CHA0 labelled with a P_{lac}-*egfp* plasmid fusion, which makes the cells green (they appear in light grey when printed in black and white) via the expression of autofluorescent green protein EGFP. Plants were grown under gnotobiotic conditions and roots assessed by confocal laser scanning microscopy. Results show that *P. protegens* CHA0 colonized roots extensively. It was found as a combination of individual cells and cell patches, forming discontinued biofilms prevalent in the intercellular spaces between epidermal cells (Source: C. Prigent-Combaret)

P. stutzeri strains and relatives (Mirza et al. 2006) or phosphate solubilization (Rodriguez and Fraga 1999; Peix et al. 2003). However, its significance in terms of plant protection from disease is unknown.

2.2 Prevalence and Biogeography of Pseudomonas in Soil

Fluorescent pseudomonads are often found at rather high population levels in bulk soil (e.g. 10^6 CFU/g soil; Troxler et al. 1997a) and the rhizosphere ($10^{5–7}$ CFU/g root; Troxler et al. 1997b), where they may represent 0.1–1% of the total culturable bacterial community (Haas and Défago 2005). These population levels are in accordance with estimates obtained using quantitative PCR (Johnsen et al. 1999) and are consistent with their high root-colonization ability (Fig. 3). Certain types of fluorescent pseudomonads have been monitored in greater detail, especially those producing DAPG. The latter may represent 10–15% of all culturable fluorescent pseudomonads from the rhizosphere (Picard et al. 2004), and from less than 1%

(McSpadden Gardener and Weller 2001) to up to 30% of all culturable fluorescent pseudomonads in certain suppressive soils (Ramette et al. 2003b). The prevalence of *phlD*$^+$ isolates in the rhizosphere depends on plant genotype and growth stage (Picard et al. 2004).

Soil fluorescent pseudomonads display a cosmopolitan distribution worldwide when considering broad groups of strains defined by restriction of 16S rRNA gene *rrs* (Cho and Tiedje 2000). At (almost) strain level, however, endemism was evidenced when assessing isolates from large geographic distances (based on BOX-PCR clusters; Cho and Tiedje 2000) as well as within a same field (based on RAPD markers; Moënne-Loccoz et al. 2001). The same may apply to the case of plant-protecting pseudomonads based on analysis of strains producing DAPG (Wang et al. 2001; Ramette et al. 2006) and/or HCN (Ramette et al. 2003b), in that they have been documented across several continents, climatic regions and soil types, yet with a rather endemic distribution (except pyoluteorin-producing DAPG$^+$ strains; Wang et al. 2001) when considering strain properties and/or population structure (Ramette et al. 2006; Weller et al. 2007). In addition, the genetic diversity of *phlD*$^+$ *Pseudomonas* populations from a given site may fluctuate with plant genotype and development (Picard et al. 2004).

2.3 *Suppressive Soils Where Plant Protection Is Attributed Mainly to Pseudomonas*

2.3.1 *Pseudomonas* and Take-All Suppressive Soils

Soil suppressiveness to take-all disease is largely attributed to antagonistic root-colonizing fluorescent pseudomonads (Smiley 1979; Sarniguet and Lucas 1992; Weller et al. 2002), especially those producing antimicrobial compounds such as phenazines or DAPG (reviewed by Weller et al. 2007). Work in Washington State and elsewhere showed that rhizosphere DAPG$^+$ pseudomonads were recovered at higher levels in take-all decline soils (i.e. at or above the threshold population density of 10^5 CFU/g root necessary for disease suppression) than in conducive soils (Raaijmakers and Weller 1998), where they remained below this threshold, both in greenhouse experiment (Raaijmakers and Weller 1998) and in the field (Weller et al. 2007). The amount of DAPG recovered from the rhizosphere of wheat was proportional to cell number of inoculated DAPG$^+$ *P. fluorescens* Q2-87, and accordingly DAPG was detected in the rhizosphere of plants colonized by indigenous DAPG$^+$ pseudomonads in take-all-suppressive soil but not in conducive soil (Raaijmakers et al. 1999).

Wheat monoculture is thought to enrich selectively for certain types of antagonistic *Pseudomonas* during take-all decline (Chapon et al. 2002; Weller et al. 2007). Comparison of neighboring fields under crop rotation of wheat or flax monoculture showed that DAPG$^+$ pseudomonads were enriched in the two monoculture soils, but that distinct *Pseudomonas* genotypes predominated on wheat versus flax roots

(Landa et al. 2006). In western France, the decline of wheat take-all correlated with changes in the prevalence of two major *Pseudomonas* (sub)populations (Sanguin et al. 2008). Evidence was also obtained for parallel modifications in the genetic structure of the *G. graminis* var. *tritici* population, leading to predominance of less aggressive genotypes once suppressiveness was reached (Lebreton et al. 2004). The relation between antagonistic pseudomonads and *G. graminis* var. *tritici* is complex, as multiple changes in gene expression take place in the bacterium when it is in presence of the pathogen (Barret et al. 2009).

When DAPG$^+$ isolates from take-all decline soil were tested, inoculation into conducive soil resulted in take-all suppression (Raaijmakers and Weller 1998), whereas DAPG-deficient *Pseudomonas* mutants displayed reduced biocontrol. In addition, the DAPG$^+$ strain *P. fluorescens* Q2-87 controlled DAPG-sensitive strains but not DAPG-tolerant strains of *G. graminis* var. *tritici* (Mazzola et al. 1995).

2.3.2 *Pseudomonas* and Black Root Rot Suppressive Soils

Natural soil suppressiveness to *T. basicola*-mediated black root rot of tobacco is thought to result from antagonistic effects of root-colonizing fluorescent pseudomonads, especially strains producing DAPG and/or HCN (Stutz et al. 1986; Voisard et al. 1989; Keel et al. 1992). DAPG$^+$ strains isolated from black root rot suppressive soil inhibited *T. basicola in vitro*, and one of them (*P. protegens* CHA0) protected tobacco from the pathogen when inoculated to a conducive soil (Stutz et al. 1986). The percentage of root-associated DAPG$^+$ pseudomonads among the total culturable fluorescent *Pseudomonas* spp. was higher for suppressive versus conducive soils (Ramette et al. 2003a), but the difference was not extensive and fluctuated from one sampling to the next. In addition, the number of culturable *phlD*$^+$ rhizosphere pseudomonads was comparable or even sometimes higher with black root rot conducive soils than in suppressive counterparts (Ramette et al. 2003a; Frapolli et al. 2010).

Analysis of *phlD*$^+$ rhizosphere isolates from black root rot suppressive and conducive soils indicated that their population structure depended more on field location than soil suppressiveness status (Ramette et al. 2006), but as many as a quarter of *phlD* DGGE bands and one third of *phlD* alleles identified by band sequencing were only found in suppressive soils (Frapolli et al. 2010). Whether these differences in *phlD*$^+$ *Pseudomonas* population structure are important for disease suppression remains to be determined, but results raise the possibility that suppressiveness could require particular consortia of DAPG$^+$ pseudomonads interacting with one another (Haas and Défago 2005).

In the Swiss region of Morens, black root rot suppressive soils are developed on morainic deposits and conducive soils on molasse sandstone (Stutz et al. 1989). Although both types of soil display very similar physicochemical properties, they differ in clay mineralogy. Indeed, vermiculite (which releases iron during weathering) is prevalent in suppressive soils and illite (of lower iron content) in conducive soils (Stutz et al. 1989). Iron availability is important for production of biocontrol

metabolites such as HCN by Morens isolate *P. protegens* CHA0 (Keel et al. 1992), and DAPG$^+$ HCN$^+$ pseudomonads from conducive soils did protect tobacco from black root rot when inoculated in artificial vermiculitic soil (Ramette et al. 2006), pointing to the importance of gene expression conditions specific to suppressive soils.

3 Role of Non-*Pseudomonas* Microorganisms in Disease-Suppressive Soils

3.1 Non-Pseudomonas Microorganisms with Plant Protecting Abilities

A large number of studies have documented the ability of non-*Pseudomonas* microorganisms to protect plants from soil-borne disease when used as inoculants (Fig. 2). These biocontrol microorganisms include Gram-negative and Gram-positive bacteria, as well as oomycetes and fungi (Table 1). Bacteriophages were also considered for their biocontrol properties (Goodridge 2004), but they are out of the scope of this review. Biocontrol Gram-negative bacteria (*Proteobacteria*) are mainly documented in the eight families *Pseudomonadaceae*, *Xanthomonadaceae*, *Enterobacteriaceae* (*Gammaproteobacteria*), *Burkholderiaceae*, *Comamonadaceae* (*Betaproteobacteria*), *Rhizobacteriaceae*, *Rhodospirillaceae* and *Acetobacteraceae* (*Alphaproteobacteria*). Biocontrol Gram-positive bacteria belong to the *Firmicutes* (genera *Bacillus*, *Pasteuria* and *Paenibacillus*) or the *Actinobacteria* (genera *Streptomyces*, *Rhodococcus*, *Cellulomonas*, *Kocuria*, *Actinoplanes* and *Nocardioides*). Most plant-protecting fungi are documented among the mitosporic *Ascomycetes*, e.g. non-pathogenic *Fusarium*, *Coniothyrium*, *Phoma*, *Arthrobotrys* and especially *Gliocladium* and *Trichoderma* (Howell 2003), as well as several arbuscular mycorrhizal fungi (the *Glomeromycota* genus *Glomus*). A smaller number of reports are available on biocontrol *Basidiomycetes* (e.g. binucleate *Rhizoctonia*) and oomycetes (particularly non-pathogenic *Pythium*). Nevertheless, knowledge on the biogeography, diversity and mode of action of non-*Pseudomonas* biocontrol microorganisms is often fragmented. In addition, there is rather limited information on their possible role in soil disease suppressiveness (Mazzola 2002; Borneman and Becker 2007; Janvier et al. 2007).

3.2 Modes of Action of Non-Pseudomonas Plant-Beneficial Microorganisms

3.2.1 Antibiosis

Antimicrobial secondary metabolites that can affect plant pathogens are produced by a wide range of non-*Pseudomonas* microorganisms from the *Proteobacteria*, *Firmicutes*, *Actinobacteria* and *Ascomycetes* (Table 1). Among *Gammaproteobacteria*,

Table 1 Some recent examples of fungal, oomycete and non-*Pseudomonas* bacterial strains that suppressed plant pathogens in pot and/or field experiments

Taxonomic affiliation of strain	Species	Strain	Pathosystem	Experimental conditions	Antimicrobials	Other mode of action	Reference
Bacteria							
Alphaproteobacteria							
Rhizobacteriaceae	*Agrobacterium vitis*	F2/5	*Agrobacterium tumefaciens* on grapevine	Greenhouse		Bacteriocin	Burr and Reid (1994)
Acetobacteraceae	*Gluconacetobacter diazotrophicus*	35–47	*Meloidogyne incognita* on cotton	Field		Ammonia and volatile fatty acids	Bansal et al. (2005)
Betaproteobacteria							
Burkholderiaceae	*Burkholderia cepacia*	BC11	*Rhizoctonia solani* damping-off of cotton	Gnotobiotic system	Lipopeptide AFC-BC11		Kang et al. (1998)
		5.5B	*Rhizoctonia solani* stem rot of poinsettia	Greenhouse	Pyrrolnitrin		Hwang and Benson (2002)
	Burkholderia ambifaria	BC-F	*Pythium ultimum* damping-off of cucumber and soybean	Pot experiment (soilless mix)		unknown	Li et al. (2002)
Comamonadaceae	*Comamonas acidovorans*	HF42	*Magnaporthe poae* summer patch of Kentucky bluegrass	Field		unknown	Thompson et al. (1998)
	Delftia tsuruhatensis	HR4	*Pyricularia oryzae* rice blast, *Xanthomonas oryzae* rice bacterial blight, *Rhizoctonia solani* rice sheath blight	Greenhouse		unknown	Han et al. (2005b)

Gammaproteobacteria							
Pseudomonadaceae	*Azotobacter armeniacus*	RC2	*Fusarium verticillioides* root rot of maize	Greenhouse	unknown	unknown	Cavaglieri et al. (2004)
Xanthomonadaceae	*Lysobacter enzymogenes*	C3	*Bipolaris sorokiniana* leaf spot of tall fescue	Greenhouse		ISR, lytic enzymes	Kilic-Ekici and Yuen (2003)
	Stenotrophomonas maltophilia	34 S1	*Magnaporthe poae* summer patch of Kentucky bluegrass	Pot experiment		Chitinase	Kobayashi et al. (1995, 2002)
		PD3533	*Ralstonia solanacearum* potato brown rot	Greenhouse		unknown	Messiha et al. (2007)
Enterobacteriaceae	*Enterobacter cloacae*	EcCT-501R3	*Pythium ultimum* on cotton seedlings	Pot experiment		Competition for seed exudates	van Dijk and Nelson (2000)
	Pantoea agglomerans	Eh252	*Erwinia amylovora* fire blight of pear	Orchand	mccEh252	unknown	Stockwell et al. (2002) and Anderson et al. (2004)
	Pantoea dispersa	SB1403	*Xanthomonas alibilineans* leaf scald disease of sugar cane	Pot experiment		Albicidin hydrolysis	Zhang and Birch (1997a, b)
	Serratia plymuthica	R1GC4	*Pythium ultimum* in cucumber	Pot experiment		ISR	Benhamou et al. (2000)

(continued)

Table 1 (continued)

Taxonomic affiliation of strain	Species	Strain	Pathosystem	Experimental conditions	Antimicrobials	Other mode of action	Reference
		A21-4	*Phytophthora capsici* blight of pepper	Greenhouse	Macrocyclic lactone A21-4		Shen et al. (2007)
		IC14	*Botrytis cinerea* gray mold and *Sclerotinia sclerotinum* white mold of cucumber	Greenhouse	Pyrrolnitrin	Enzymes, siderophores	Kamensky et al. (2003)
	Rahnella aquatilis	HX2	*Agrobacterium tumefaciens* in grapevine	3-year field experiment	unknown	unknown	Chen et al. (2007)
Firmicutes							
Paenibacillaceae	*Paenibacillus polymyxa*	18191	*Botrytis cinerea* grey mold of strawberry	Field	unknown	unknown	Helbig (2001)
		E681	*Fusarium oxysporum* and *Rhizoctonia solani* damping-off of sesame	Greenhouse and field	unknown	unknown	Ryu et al. (2006)
Bacillaceae	*Bacillus* sp.	Sunhua	*Streptomyces scabiei* potato scab	Pot experiment	Iturin A, macrolactin A		Han et al. (2005a)
		CRS7	*Botrytis cinerea* gray mold of chickenpea	Prophylactic foliar spray application in greenhouse		Chitinase	Kishore et al. (2005)
	Bacillus thuringiensis	COT1	*Pectobacterium carotovorum* potato soft rot	Gnotobiotic system		AHL-lactonase	Dong et al. (2004)
	Bacillus subtilis	RB14	*Rhizoctonia solani* damping-off of tomato	Pot experiment	Iturin A, surfactin		Asaka and Shoda (1996)

		BS 107	*Pectobacterium carotovorum* potato soft rot	Gnotobiotic system	unknown		Sharga and Lyon (1998)
		GBO3 (Kodiac)	*Fusarium solani* f. sp. *phaseoli* dry bean root rot	Field		unknown	Estevez de Jensen et al. (2002)
		CE1	*Fusarium verticillioides* root rot of maize	Greenhouse		unknown	Cavaglieri et al. (2005)
	Bacillus pumilus	SE34	*Phytophthora infestans* late blight of tomato	Greenhouse		ISR	Yan et al. (2002)
	Bacillus amyloliquefaciens	RC-2	*Colleotrichum dematidum* mulberry anthracose	Culture filtrate tested in greenhouse	Iturins		Yoshida et al. (2001) and Hiradate et al. (2002)
Alicyclobacillaceae	*Pasteuria penetrans*	P-20	*Meloidogyne arenaria* damage on peanut	Microplot field experiment		Parasitism	Chen et al. (1996)
Actinobacteria							
Micromonosporaceae	*Actinoplanes* sp.	25844	*Pythium ulimum* damping-off of table beets	Field		Parasitism	Khan et al. (1997)
Streptomycetaceae	*Streptomyces violaceusniger*	YCED-9	*Pythium ultimum* damping-off of lettuce	Greenhouse	Guanidylfungin A, nigericin, geldanamycin	β-1,3-glucanase, chitinase	Crawford et al. (1993) and Trejo-Estrada et al. (1998)

(continued)

Table 1 (continued)

Taxonomic affiliation of strain	Species	Strain	Pathosystem	Experimental conditions	Antimicrobials	Other mode of action	Reference
	Streptomyces lydicus	WYEC108	*Pythium ultimum* damping-off of pea	Greenhouse		Mycoparasitism	Crawford et al. (1993) and Yuan and Crawford (1995)
	Streptomyces sp.	CR-43	*Meloidogyne incognita* root galling of tomato, *Pratylenchus penetrans* black root rot of strawberry	Greenhouse and field		unknown	Dicklow et al. (1993)
		A15, A20, A22, STL	*Macrophomina phaseolina* charcoal stem rot of melon	Greenhouse	unknown	unknown	Etebarian (2006)
		AMG-P1	*Phytophthora infestans* tomato late blight	Greenhouse	Paromomycin		Lee et al. (2005)
		201	*Fusarial wilt* of *Brassicaceae*	Pot experiment	2-methylheptyl isonicotinate		Bordoloi et al. (2002)
		96 and 63	*Pratylenchus penetrans* in roots of alfalfa	Pot experiment		unknown	Samac and Kinkel (2001)
	Streptomyces diastochromogenes	PonSSII	*Streptomyces scabiei* potato scab	4-year field-pot experiment	unknown	Competition	Liu et al. (1995), Lorang et al. (1995), and Neeno-Eckwall et al. (2001)

	Streptomyces scabiei	PonR	*Streptomyces scabiei* potato scab	4-year field-pot experiment	unknown	Competition	Liu et al. (1995), Lorang et al. (1995), and Neeno-Eckwall et al. (2001)
		PonSSII, GS93-23, 15	*Phytophthora medicaginis* root rot of alfalfa	Field	unknown		Xiao et al. (2002)
		Di-944	*Rhizoctonia solani* damping-off of tomato	Greenhouse	unknown	unknown	Sabaratnam and Traquair (2002)
	Streptomyces argenteolus	EN60	*Gaeumanomyces graminis* var. *tritici* take-all of wheat	Field	unknown		Coombs et al. (2004)
	Streptomyces caviscabies	EN23, EN28, EN35	*Gaeumanomyces graminis var. tritici* take-all of wheat	Field	unknown		Coombs et al. (2004)
	Streptomyces galilaeus	EN4, EN39	*Gaeumanomyces graminis var. tritici* take-all of wheat	Field	unknown		Coombs et al. (2004)
Nocardioidaceae	*Nocardioides albus*	EN47	*Gaeumanomyces graminis var. tritici* take-all of wheat	Field	unknown		Coombs et al. (2004)

(continued)

Table 1 (continued)

Taxonomic affiliation of strain	Species	Strain	Pathosystem	Experimental conditions	Antimicrobials	Other mode of action	Reference
Fungi							
Ascomycetes	*Trichoderma harzianum*	T39	*Sphaerotheca fusca* powdery mildew on cucumber	Greenhouse		ISR	Elad et al. (1998)
		2413	*Phytophthora capsicii* root rot of pepper	Pot experiment and field		Mycoparasitism	Ezziyyani et al. (2007)
		T-203	Root galling of tomato caused by *Meloidogyne javanica*	Greenhouse		Protease	Sharon et al. (2001)
		T-203	*Pseudomonas syringae* pv. *lachrymans* in cucumber	Hydroponic system		Induced resistance	Yedidia et al. (2003)
	Trichoderma virens	Gv29-8	*Pseudomonas syringae* pv. *lachrymans* in cucumber	Hydroponic system		Induced resistance	Viterbo et al. (2007)
	Coniothyrium minitans	LRC 2137	*Sclerotinia sclerotiorum* alfalfa blossom blight	Field		Mycoparasitism	Li et al. (2005)
	Verticillium biguttatum	M73	*Rhizoctonia solani* sclerotia formation on potato	Field		Mycoparasitism?	Jager and Velvis (1986)
	Phoma sp.	GS8-1, GS8-2	*Colletotrichum orbiculare* in cucumber	Pot experiment (soilless mix)		ISR	Meera et al. (1995)
	Arthrobotrys oligospora	ORS 18692 S7, ORS 18692 S5	*Meloidogyne mayaguensis* on tomato	Pot experiment and field		Predation	Duponnois et al. (1995)

	Fusarium oxysporum	Fo47	Fusarium wilt of tomato	Hydroponic system, pot experiment (soilless mix)	Competition, ISR	Fuchs et al. (1997) and Larkin and Fravel (1999)
	Dactylella oviparasitica	50	*Heterodera schachtii* on beet	Greenhouse	Parasitism	Olatinwo et al. (2006)
Basidiomycetes	binucleate *Rhizoctonia*	P9023	*Rhizoctonia solani* stem rot in poinsettia	Pot experiment	ISR	Hwang and Benson (2003)
Chromista						
Oomycetes	*Pythium nunn*	P9023	Sweet orange and azalea root rots caused by different *Phytophthora* species	Pot experiment	Mycoparasitism	Fang and Tsao (1994)

Pantoea (previously *Enterobacter*) *agglomerans* may produce pyrrolnitrin (Chernin et al. 1996), *Serratia* pyrrolnitrin (Kamensky et al. 2003), prodigiosin (Kalbe et al. 1996), chlorinated macrolides (Shen et al. 2007) and surfactants (Roberts et al. 2007), *Stenotrophomonas* and *Lysobacter* the macrocyclic lactams xanthobaccins (Islam et al. 2005) and maltophilin (Jakobi et al. 1996; Li et al. 2008). Within the *Betaproteobacteria*, species from the *Burkholderia cepacia* complex are well known for synthesis of pyrrolnitrin (Cartwright et al. 1995; El-Banna and Winkelmann 1998), phenazines (Cartwright et al. 1995) and lipopeptide AFC-11 (Kang et al. 1998). Antimicrobials affecting phytopathogens are much less documented in the other proteobacterial subdivisions. In the *Alphaproteobacteria*, *Azospirillum brasilense* may release phenylacetic acid (Somers et al. 2005) and *Rhizobium* hydrogen cyanide (Antoun et al. 1998). Among the *Deltaproteobacteria*, *Myxococcus fulvus* may produce pyrrolnitrin (Gerth et al. 1982) and other myxobacteria (e.g. *Sorangium*, *Chondromyces*) a range of antimicrobials (Reichenbach 2001).

The *Firmicutes* produce a variety of antimicrobials that can affect phytopathogens, particularly non-ribosomally synthesized peptides and lipopeptides (Donadio et al. 2007). Thus, *Paenibacillus* may produce polymyxins, fusaricidins, gasaverin and saltavalin (Pichard et al. 1995; Kajimura and Kaneda 1996), and *Bacillus* several amphiphilic cyclic lipopeptides from the iturin, fengycin and surfactin families (Asaka and Shoda 1996; Touré et al. 2004), the macrolide macrolactin A (Han et al. 2005a), and (noticeably in the well-studied biocontrol strain *B. cereus* UW85) the aminopolyol zwittermycin A (Silo-Suh et al. 1994) and kanosamine (Milner et al. 1996). *Actinobacteria* are well known for production of a very wide range of antimicrobial metabolites, and many of them are used as antibiotics in medical and veterinary contexts. However, several antimicrobials from the *Actinobacteria* (generally not used against animal or human pathogens) are active against plant pathogens. In *Streptomyces*, they include the polyketide geldanamycin, the polyether nigericin, the polyene-like compounds guanidylfungin A (all three documented in the biocontrol strain *Streptomyces violaceusniger* YCED-9; Trejo-Estrada et al. 1998) and faerifungin (in *Streptomyces griseus*; Smith et al. 1990), the aminoglycoside paromomycin (Lee et al. 2005), the macrolide oligomycin A (Kim et al. 1999), as well as 1-propanone,1-(4-chlorophenyl) and 2-methylheptyl isonicotinate (Bordoloi et al. 2002; Ezziyyani et al. 2007).

Among *Ascomycetes*, antimicrobials relevant for plant protection are best documented in *Trichoderma* and include gliovirin (Stipanovic and Howell 1982), gliotoxin (Lumsden et al. 1992) and (lipo)peptaibol peptides (Szekeres et al. 2005; Xiao-Yan et al. 2006). Terreic acid and butyrolactons are reported in *Aspergillus terreus* (Cazar et al. 2005).

Although a wide range of phytopathogen-inhibiting metabolites are known in many non-*Pseudomonas* microorganisms, the contribution of a given compound to plant protection is often not established, especially for biocontrol strains producing several of them. The importance of antibiosis in biological control was evidenced by gene deletion (and in some cases, gene complementation) for iturin A produced by *B. subtilis* (biocontrol of *Rhizoctonia solani*-mediated damping-off of cotton; Asaka and Shoda 1996), zwittermycin A produced by *B. cereus* (biocontrol of

Phytophthora medicaginins-mediated damping-off of alfalfa; Silo-Suh et al. 1994), pyrrolnitrin (biocontrol of Rhizoctonia stem rot of poinsettia; Hwang and Benson 2002) and AFC-BC11 (biocontrol of *Rhizoctonia solani*-mediated damping-off of tomato; Kang et al. 1998) produced by *B. cepacia*, and Eh252 produced by *Pantoea agglomerans* (biocontrol of *Erwinia amylovora*-mediated fire blight of pear; Stockwell et al. 2002). The mode of action is documented for only some of these antimicrobial metabolites. Lipopeptides (e.g. iturins, fengycins and surfactins from *Bacillus*) act on cell membranes as surfactants (Deleu et al. 1999), lipopeptaibols (produced by *Trichoderma*) form tunnels in cytoplasmic membrane (Cosette et al. 1999), nigericin acts on membrane as an ionophore exchanging K^+ for H^+ (Bergen and Bates 1984), aminoglycosides (produced by *Streptomyces* spp.) affect prokaryotic and mitochondrial translation (Recht et al. 1999), while oligomycin inhibits mitochondrial ATPase (John and Nagley 1986).

3.2.2 Other Biocontrol Mechanisms

As in the case of *Pseudomonas*, antagonism in non-*Pseudomonas* biocontrol agents is not restricted to production of antimicrobial metabolites, as it can also be mediated by lytic enzymes that act against pathogen cell wall or virulence factors (enzymes and signal molecules). A variety of cell wall-degrading chitinases, glucanases, proteases and lyzozymes are produced by plant-protecting bacteria, such as in the *Proteobacteria Lysobacter* (Palumbo et al. 2005), *Pantoea agglomerans* (Chernin et al. 1995), *Serratia* (Kalbe et al. 1996) and *Gluconacetobacter diazotrophicus* (Pinon et al. 2002), the *Firmicutes Bacillus* (Leelasuphakul et al. 2006), *Brevibacillus* (Huang et al. 2005) and *Paenibacillus* (Budi et al. 2000), the *Actinobacteria Streptomyces* (Trejo-Estrada et al. 1998), as well as several fungi such as *Trichoderma* biocontrol strains (Metcalf and Wilson 2001; Djonovic et al. 2007). In contrast to *Pseudomonas*, production of cell wall-degrading extracellular lytic enzymes seems to be one of the major modes of action of many non-*Pseudomonas* biocontrol strains against phytopathogens. Their chitinases act on several fungal (Chernin et al. 1995; Metcalf and Wilson 2001) and nematode phytoparasites (Cronin et al. 1997a; Kishore et al. 2005), their β-1,3- and β-1,6-glucanases on the oomycete *Pythium ultimum* (Palumbo et al. 2005; Djonovic et al. 2007), their lysozyme-like enzymes on the *Proteobacteria Xanthomonas albilineans* (Pinon et al. 2002), and their proteases on phytoparasitic nematodes (Sharon et al. 2001; Huang et al. 2005; Lian et al. 2007), oomycetes (Dunne et al. 1997) and fungi (De Marco and Felix 2002).

Certain enzymes operate instead on the pathogen enzymes or toxins, resulting in lower disease severity (Elad and Kapat 1999; Zhang and Birch 1997a, b), although this is mainly documented for shoot pathogens. Others interfere with pathogen signalization, such as the lactonase AiiA from *Bacillus* sp. 240B1, which cleaves *N*-acylhomoserine lactone quorum sensing signals of *Pectobacterium carotovorum*, thus decreasing production of extracellular enzymes by the pathogen and the extent of soft rot disease on potato and other plants (Dong et al. 2000). *N*-Acylhomoserine

lactone degradation has been found in other soil bacteria (Uroz et al. 2005; Yoon et al. 2006; Medina-Martinez et al. 2007) and may play a role in biocontrol of bacterial phytopathogens (Dong et al. 2004).

Like their *Pseudomonas* counterparts, non-*Pseudomonas* biocontrol agents compete with plant pathogens for space and nutrients. Competition for root colonization sites is documented for non-pathogenic *F. oxysporum* (against pathogenic *F. oxysporum*; Eparvier and Alabouvette 1994) and arbuscular mycorrhizal fungi (against fungal, oomycete and nematode pathogens; Azcón-Aguilar and Barea 1996). Competition for carbon and nitrogen usually concerns biocontrol microorganisms closely related to the pathogen e.g. non-pathogenic *F. oxysporum* (for suppression of Fusarium wilt; Lemanceau et al. 1993) or *Streptomyces* (for suppression of potato scab; Neeno-Eckwall et al. 2001), but sometimes also microorganisms that are unrelated e.g. the fungi *Trichoderma* (Howell 2003) and *Collimonas* (Kamilova et al. 2007), as well as *Enterobacter cloacae* (van Dijk and Nelson 1998, 2000). Siderophores were found in several biocontrol strains from e.g. *Enterobacter* (Loper et al. 1993), *Serratia* (Kamensky et al. 2003) and *Burkholderia* (Bevivino et al. 1998), but competition with phytopathogen for iron has not been evidenced.

Certain non-*Pseudomonas* biocontrol agents can act on phytopathogens via hyperparasitism (Fig. 2), a mode of action not documented with *Pseudomonas* counterparts. The *Firmicute Pasteuria penetrans* is an obligate (hyper)parasite of root-knot nematodes (Siddiqui and Mahmood 1999). It occurs worldwide and displays a wide host range (Siddiqui and Mahmood 1999), but individual *P. penetrans* isolates seem to be mainly adapted to one or a few nematode species (Dutky and Sayre 1978) or even nematode strains (Duponnois et al. 2000). Among hyperparasitic fungi, the mitosporic *Ascomycete Dactylella oviparasitica* may survive saprophytically and sporulate in soil (Stirling and Mankau 1979), and it parasites fourth stage juveniles, females, and eggs of different nematodes, including *Heterodera schachtii* (Borneman and Becker 2007). A related phenomenon occurs with predation of phytoparasitic *Meloidogyne* spp. by the fungus *Arthrobotrys oligospora* (Duponnois et al. 1995). Mycoparasitic *Trichoderma* penetrate and disrupt the mycelium of phytopathogenic fungi and oomycetes (Chet et al. 1981; Gupta et al. 1999) whereas *Acremonium* targets oospores of *Pythium ultimum* (Khan et al. 1997). Mycoparastism was also reported in oomycetes *Pythium oligandrum* and *Pythium nunn*, which may penetrate mycelia of plant-pathogenic *Pythium* species as well as of certain fungi (Lifshitz et al. 1984; Berry et al. 1993).

Many non-*Pseudomonas* strains may enhance plant health by acting directly on plant physiology and growth (Fig. 2). The induction of resistance in the plant is documented in the case of bacteria, e.g. *Bacillus pumilus* (Yan et al. 2002) and *Serratia* (Press et al. 1997; Benhamou et al. 2000), and fungi, e.g. *Trichoderma* (Yedidia et al. 2000), *Phoma* (Meera et al. 1995), *F. oxysporum* (Fuchs et al. 1997) and binucleate *Rhizoctonia* (Hwang and Benson 2003). Only few studies, however, focused on molecular mechanisms involved (inducers implicated, possible involvement of salicylate/jasmonate/ethylene, pathogenesis-related protein production in plant), so the knowledge about induced resistance mediated by non-*Pseudomonas* microorganisms remains fragmented. In *Trichoderma virens*, an 18-mer peptaibol

was shown to trigger ISR (Viterbo et al. 2007). *T. harzianum* induced resistance in cucumber, which was accompanied by production of typical pathogenesis-related (PR) proteins such as chitinases and ß-1,3-glucanases (Yedidia et al. 2000). ISR in cucumber, mediated by *S. marcescens*, is independent from the salicylic acid pathway (Press et al. 1997).

Production of phytohormones corresponding to cytokinins, gibberellins and auxins has been shown in a large range of plant-beneficial *Proteobacteria*, such as *Azospirillum* (Dobbelaere et al. 1999), *Phyllobacterium* (Larcher et al. 2003), and *Herbaspirillum* (Bastián et al. 1998), as well as *Firmicutes* such as *Paenibacillus* (Timmusk et al. 1999) and *Bacillus* (Gutierrez-Manero et al. 2001). This can result in enhanced plant development and growth (Dobbelaere et al. 1999; Larcher et al. 2003). ACC deaminase activity has been reported in various plant-beneficial strains from the *Alphaproteobacteria* (*Azospirillum*, *Mesorhizobium*, *Bradyrhizobium*, etc.), *Betaproteobacteria* (*Burkholderia*, etc.) and *Gammaproteobacteria* (*Enterobacter*, etc.) (Shah et al. 1998; Glick 2005; Blaha et al. 2006), but evidence for a role of this trait in biological control is lacking in the case of non-*Pseudomonas* microorganisms.

Various plant growth-promoting properties, such as symbiotic (by nodulating bacteria *Rhizobium* and *Frankia*; Mylona et al. 1995) and associative nitrogen fixation (by endophytic or rhizosphere bacteria from *Alpha-*, *Beta-*, *Gammaproteobacteria*, *Firmicutes* and *Cyanobacteria*; Ghosh and Saha 1993; Kennedy et al. 2004), nitrogen mineralization (Griffiths and Robinson 1992), phosphorus solubilization (by several *Proteobacteria*, *Firmicutes*, and *Actinobacteria*, as well as *Trichoderma* and *Aspergillus*; Banik and Dey 1982; Altomare et al. 1999; Rodriguez and Fraga 1999) and enhanced mineral uptake (by arbuscular mycorrhizal fungi, George et al. 1995) are extensively documented. These properties are considered as important for plant vigor and health, with the potential to help plants to overcome disease, but direct experimental evidence is often missing (Bally and Elmerich 2007). However, several plant growth-promoting microorganisms display biocontrol effects, for example *Gluconacetobacter diazotrophicus* (against *Meloidogyne incognita* in cotton; Bansal et al. 2005), *Azospirillum brasilense* (against *Rhizoctonia* spp. in *Prunus*; Russo et al. 2008), *Burkholderia cepacia* (against *Fusarium* spp. in maize; Bevivino et al. 1998) or *Delftia tsuruhatensis* (against rice blast, rice bacterial blight and rice sheath; Han et al. 2005b), but their biocontrol properties have been generally less studied than their plant growth-promoting traits.

3.2.3 Conclusion

The distribution of plant-protecting traits in non-*Pseudomonas* microorganisms is rather contrasted, regardless of whether bacteria or fungi are considered. Some of these traits are rather widespread, such as the synthesis of particular types of lytic enzymes involved in antagonism, or bacterial constituents triggering induced resistance (Neilands 1995; van Loon 2007). Other traits are restricted to a limited number of genera, such as the ability to produce pyrrolnitrin in *Proteobacteria* including

certain pseudomonads (de Souza and Raaijmakers 2003) or to certain species within a particular genus, as illustrated by the case of the antifungal metabolite zwittermycin A in *Bacillus cereus* (Stabb et al. 1994). In many cases, however, plant-beneficial properties are not found in all members of the species but rather in selected strains or groups of strains (Berg 2000).

As for pseudomonads, certain non-*Pseudomonas* species are comprised of both biocontrol strains and pathogens, e.g. *F. oxysporum* (Fravel et al. 2003; Bolwerk et al. 2005) and *S. scabiei* (Liu et al. 1995). In addition, some traits contributing to plant-beneficial effects can occur both in biocontrol strains and in deleterious or pathogenic strains. This is for instance the case for ACC deaminase activity (Blaha et al. 2006), auxin production (Spaepen et al. 2007) and synthesis of hydrogen cyanide (Schippers et al. 1990). The unexpected distribution of several plant-beneficial traits is sometimes related to the fact that the corresponding genes may have been subjected to horizontal gene transfer (de Souza and Raaijmakers 2003; Hopwood 2003; Hontzeas et al. 2005; Blaha et al. 2006).

3.3 Suppressive Soils Where Plant Protection Is Mainly Attributed to Non-Pseudomonas Microorganisms

Plant protection by non-*Pseudomonas* microorganisms is documented for several types of suppressive soils. These microorganisms include bacteria (mostly *Firmicutes* and *Actinobacteria*), fungi and nematodes. In contrast, disease suppressiveness due to bacteriophages has not been evidenced so far. Plant protection effects often stem from negative interactions with the pathogen, which are implemented by avirulent strains of the same species (e.g. soils suppressive to Fusarium wilt) and/or genus (e.g. soils suppressive to potato scab), or hyperparasitic microorganisms (for certain soils suppressive to nematodes). Some of the best understood cases are presented below.

3.3.1 Non-*Pseudomonas* Microorganisms and Potato Scab Suppressive Soils

While potato scab is caused by *Streptomyces scabiei* strains that produce the phytotoxin thaxtomin (Kinkel et al. 1998), potato scab suppressiveness, which is induced by potato monoculture, is attributed to non-pathogenic strains from *Streptomyces scabiei*, *Streptomyces diastatochromogenes* or *Streptomyces albogriseolus* (Liu et al. 1995; Lorang et al. 1995). The pathogenic and non-pathogenic strains are genetically close. They could not be separated by repetitive intergenic DNA fingerprinting (rep-PCR; Sadowsky et al. 1996), but were distinguished based on fatty acids profiling (Kinkel et al. 1998). The introduction of two biocontrol *Streptomyces* strains into infested soil negatively affected the population size of pathogenic strains, with no impact on the whole microbial community (as assessed with PLFA; Bowers et al. 1996). This correlated with a reduction of potato scab incidence.

Experiments with spontaneous non-inhibitory mutants of *Streptomyces* biocontrol strains and spontaneous pathogen mutants resistant to at least one antimicrobial produced by the biocontrol strains revealed that both antibiosis and competition contributed to suppression of pathogenic strains (Schottel et al. 2001; Neeno-Eckwall et al. 2001). The composition of the *Streptomyces* soil subcommunity can be modified according to the type of organic soil amendment, suggesting that the biocontrol potential of suppressive indigenous strains could be enhanced via appropriate choice of farming practices (Schlatter et al. 2009). So far, the assessment of potato scab suppressive soils has focused on biocontrol *Streptomyces* strains, and the potential role of non-*Streptomyces* microorganisms (including *Pseudomonas*) in these soils has been neglected.

3.3.2 Non-*Pseudomonas* Microorganisms and Fusarium Wilt Suppressive Soils

Soil suppressiveness to Fusarium wilt implicates non-pathogenic strains of *F. oxysporum*. In soils from southern France naturally suppressive to the disease, competition was identified as an important mode of action of non-pathogenic *F. oxysporum* against pathogenic *F. oxysporum* strains (Alabouvette 1986). The establishment of a *Pueraria* cover crop in an oil palm grove increased the size of the *F. oxysporum* population in soil (without changing its genetic structure) and the level of soil suppressiveness to Fusarium wilt of oil palm, strengthening the competition hypothesis (Abadie et al. 1998). In the case of Fusarium wilt suppressiveness induced by monoculture, which is documented for certain watermelon cultivars, protection by non-pathogenic *F. oxysporum* strains is attributed to induced resistance in host plant (Larkin et al. 1996). Indeed, the possibility of induced resistance was shown for a non-pathogenic *F. oxysporum* strain using tomato in split-root and other systems (Fuchs et al. 1997). The dose of non-pathogenic strain necessary for tomato protection differed according to its main mode of action, i.e. high for strains effective at competing with the pathogen and low for strains whose main mode of action was induced resistance (Larkin and Fravel 1999).

So far, non-pathogenic *F. oxysporum* strains cannot be distinguished from pathogenic ones unless plant inoculation tests are performed, which complicates monitoring of their dynamics in soil. There is a high intraspecies diversity in *F. oxysporum*, but pathogenic strains did not form a separated clade based on molecular phylogeny (Baayen et al. 2000). High diversity was also found within natural populations of *F. oxysporum* (Steinberg et al. 1997). Indigenous field populations of *F. oxysporum* remained stable for years and differed across fields of different geographical locations in France (Edel et al. 2001), which is compatible with a functional implication of these microorganisms in long-standing disease suppressiveness.

Interestingly, antagonistic properties of certain non-pathogenic *F. oxysporum* strains may depend on their bacterial ectosymbionts (e.g. *Serratia, Bacillus* and *Achromobacter*), which are attached to the hyphae. For instance, *F. oxysporum* strain MSA 35 (isolated from an Italian suppressive soil) lost its antagonistic

properties and even became pathogenic when it was cured of its ectosymbionts (Minerdi et al. 2008). The original strain produced volatile compounds that repressed the expression of virulence genes in the pathogenic strain tested while the cured strain did not, showing a new potential long-distance mechanism of *F. oxysporum* antagonism mediated by volatile compounds (Minerdi et al. 2009).

The importance of certain soil abiotic properties, e.g. smectite clay, soluble sodium, sodium adsorption ratio and soil aggregate stability, has been shown for several Fusarium wilt suppressive soils (Stotzky and Martin 1963; Höper et al. 1995; Domínguez et al. 2001, 2003). It is likely that these properties may influence antagonistic populations and gene expression, but this has not been clearly shown so far.

3.3.3 Non-*Pseudomonas* Microorganisms and Rhizoctonia Suppressive Soils

Though a non-pathogenic *Rhizoctonia* strain could be used for biocontrol of Rhizoctonia rot in a pot experiment (Hwang and Benson 2003), the potential role of indigenous non-pathogenic *Rhizoctonia* spp. in Rhizoctonia suppressive soils is unknown. In the case of Rhizoctonia damping-off of radish, soil suppressiveness was induced by repeated culture of radish and was attributed to *T. harzianum*. Hyperparasitism was suggested as the mode of action by which *T. harzianum* suppressed *R. solani* (Chet et al. 1981). In addition, suppressiveness to Rhizoctonia potato rot correlated with the extent of *Bacillus* genetic diversity, raising the possibility that these bacteria could also play a part (Garbeva et al. 2006), while on cauliflower suppressiveness correlated with the abundance of *Lysobacter* (Postma et al. 2010).

3.3.4 Non-*Pseudomonas* Microorganisms and Soils Suppressive to Endoparasitic Nematodes

Soil suppressiveness towards the endoparasitic nematodes *Heterodera schachtii* or *Meloidogyne* spp. was shown to be associated with nematode-parasitic microorganisms. In the case of soils suppressive to the beet cyst nematode *H. schachtii* (which may be induced by monoculture), suppressiveness could be transferred to a conducive soil using solely nematode cysts isolated from a suppressive soil (Westphal and Becker 1999, 2000). rRNA gene analysis of microorganisms associated with these cysts identified *Rhizobium*-like bacteria and the fungus *Dactylella oviparasitica*, which were consistently associated with highly-suppressive soils (Yin et al. 2003a, b). *D. oviparasitica* can parasite eggs of *H. schachtii*, and one *D. oviparasitica* strain protected Swiss chard against the nematode when inoculated to conducive soil (Olatinwo et al. 2006). Other microorganisms that can act on *H. schachtii*, e.g. *Bacillus megaterium* and *F. oxysporum*, were isolated from nematode cysts or beet roots in suppressive soils, but their importance in suppressiveness is debated (Jorgenson 1970; Neipp and Becker 1999; Yin et al. 2003a).

Soil suppressiveness towards root-knot-causing *Meloidogyne* spp. is induced by monoculture, and is associated with hyperparasitim by *Pasteuria penetrans.*

The *Firmicute P. penetrans* is an obligate nematode parasite. Its endospores adhere to second-stage juveniles and germinate, the germ tube penetrating the cuticle (Sayre and Wergin 1977), and it is also found in mature females (Weibelzahl-Fulton et al. 1996). *P. penetrans* sporulates within the nematode and prevents its reproduction (Sayre and Wergin 1977).

3.3.5 Non-*Pseudomonas* Microorganisms and Soils Suppressive to Ectoparasitic Nematodes

In the case of sugarcane monoculture soils suppressive to ectoparasitic nematodes, such as *Xiphinema elongatum* and *Paratrichodorus minor*, no hyperparasite has been identified so far. Rather, soil suppressiveness was associated with a higher soil content in weak ectoparasitic nematodes, especially *Helicotylenchus dihystera* (Rimé et al. 2003), whose competitive interactions with the more aggressive ectonematodes limit the ability of the latter to parasite roots (Spaull and Cadet 1990; Mateille et al. 2008). In addition, sandy soils suppressive and conducive to ectoparasitic nematodes from the same South African region differed in sugarcane rhizobacterial community structure (Rimé et al. 2003), indicating a possible beneficial role for root bacteria. Interestingly, *Burkholderia tropica* correlated positively with the less pathogenic species *Pratylenchus zeae* (endoparasite) and *H. dihystera*, and negatively with aggressive *X. elongatum*, and it was hypothesized that the rhizobacterium could be one factor influencing the composition of the ectonematode community towards a lower prevalence of aggressive species (Omarjee et al. 2008).

3.3.6 Conclusion

Several non-*Pseudomonas* microorganisms play a major role in different suppressive soils, the most studied ones being the *Firmicute Pasteuria*, the *Actinobacteria Streptomyces*, and the mitosporic *Ascomycetes Fusarium*, *Dactyllela* and (to a lesser extent) *Trichoderma*. A substantial amount of information is available on their possible mode(s) of action, e.g. antibiosis, competition, induced resistance or parasitism, but relatively few detailed studies have targeted the implementation of these modes of action in suppressive soils. In comparison with *Pseudomonas*, less is known about root colonization by non-*Pseudomonas* biocontrol strains, their population levels in soil necessary to achieve suppressiveness, and their diversity within and between suppressive soils. Furthermore, it is striking to note that most information on the role of non-*Pseudomonas* microorganisms originates from suppressive soils for which the ecology and role of *Pseudomonas* biocontrol strains is poorly documented or unknown. Similarly, it appears that the potential role of non-*Pseudomonas* microorganisms remains neglected in suppressive soils where plant protection by fluorescent pseudomonads has been extensively studied (Lemanceau et al. 2006), e.g. take-all decline soils and soils suppressive to *T. basicola*-mediated black root rot. This limits our ability to compare and contrast the relative importance of *Pseudomonas* versus non-*Pseudomonas* microorganisms in soil suppressiveness.

4 Interactions Between *Pseudomonas* and Non-*Pseudomonas* Microorganisms

4.1 Interactions Between Pseudomonas and Non-Pseudomonas Microorganisms from Biocontrol Studies

Pseudomonas and non-*Pseudomonas* biocontrol microorganisms are present in the same rhizosphere environment, where they have coevolved with the plant, its guild of phytoparasites, and perhaps also with one another. On this basis, it is likely that multiple rhizosphere interactions take place between *Pseudomonas* and non-*Pseudomonas* biocontrol microorganisms (Couillerot et al. 2009). Some of these interactions may be indirect, as plant-associated microorganisms may influence plant development and behaviour, which in turn will determine ecological conditions for the other plant-beneficial populations in the rhizosphere (Fig. 2). This is documented for *Pseudomonas* strains and/or metabolites (especially DAPG), in terms of root system architecture and plant growth (Patten and Glick 2002; Brazelton et al. 2008), plant physiology (Iavicoli et al. 2003) and root exsudation (Phillips et al. 2004). Similar effects are also known with non-*Pseudomonas* plant-beneficial microorganisms (Heulin et al. 1987; Dobbelaere et al. 1999).

The direct interactions between *Pseudomonas* and non-*Pseudomonas* plant-beneficial microorganisms may range from antagonism and competition to cooperation (Fig. 2; Couillerot et al. 2009). On one hand, rhizosphere incompatibility was shown for some *Pseudomonas* and non-*Pseudomonas* strains (e.g. *Bradyrhizobium*; Siddiqui and Ehteshamul-Haque 2001). In addition, various root bacteria were inhibited *in vitro* by the *Pseudomonas* metabolites DAPG and/or pyoluteorin (Natsch et al. 1998). Certain pseudomonads may inhibit *T. harzianum* (de Boer et al. 2007), a fungal species playing an important role in disease suppression, and compound(s) produced by biocontrol *P. protegens* CHA0 reduced expression of chitinase genes *nag1* and *ech42* in *T. atroviride* (Lutz et al. 2004). Similarly, *P. fluorescens* A506 produced a protease that cleaved an antimicrobial metabolite of *P. agglomerans* Eh252 involved in *Erwinia amylovora* antagonism (Anderson et al. 2004), but it is not known whether this metabolite is also active against root pathogens.

On the other hand, positive effects may also take place. *P. fluorescens* F113 can stimulate mycelial growth of the symbiotic fungus *Glomus mosseae* and mycorrhization of tomato roots (Barea et al. 1998). Combining *Pseudomonas* and non-*Pseudomonas* microorganisms with complementary modes of action lead often to enhanced biological control (Mazzola 2002), as shown using wild-type strains and mutants. This was for instance the case for proteolytic *Stenotrophomonas maltophilia* W81 and DAPG-producing *P. fluorescens* F113 against *Pythium*-mediated damping-off of sugarbeet (Dunne et al. 1997), as well as non-pathogenic *F. oxysporum* Fo47 and iron-competing *Pseudomonas putida* WCS358 against Fusarium wilt of flax (Duijff et al. 1993), although combining *Pseudomonas* and non-pathogenic

Fusarium did not lead to improved tomato protection from Fusarium wilt (Larkin and Fravel 1998). Co-inoculation of *Pseudomonas alcaligenes* with *Glomus intraradices* and *Bacillus pumilus* improved control of a chickpea root-rot disease complex caused by the root-knot nematode *Meloidogyne incognita* and the root-rot fungus *Macrophomina phaseolina* (Sayeed and Siddiqui 2008), but the biocontrol mechanisms involved were not determined. DAPG$^+$ *P. protegens* CHA0 and *Trichoderma atroviride* P1 displayed enhanced expression of respectively DAPG biosynthetic gene *phlA* (in presence of P1 culture filtrate) and chitinase gene *nag1* (in presence of DAPG) (Lutz et al. 2004), illustrating the potential of molecular interactions between *Pseudomonas* and non-*Pseudomonas* biocontrol microorganisms. The importance of such interactions is also illustrated by the observation that certain soil bacteria (including one *Pseudomonas* strain related to *P. koreensis*) unable alone to interfere with growth of fungal phytopathogens did inhibit the latter when they were used in combination (presumably via antibiosis), which also means that their potential role in soil suppressiveness could have been easily overlooked in previous investigations (de Boer et al. 2007).

4.2 Interactions Between Pseudomonas and Non-Pseudomonas Microorganisms in Suppressive Soils

The significance of microbial interactions between *Pseudomonas* and non-*Pseudomonas* microorganisms in suppressive soils is very poorly documented. The only clear example of such interaction is from a French soil suppressive to Fusarium wilt. Here, plant protection implicated both non-pathogenic *F. oxysporum* and fluorescent *Pseudomonas* spp., and competition between non-pathogenic and pathogenic *F. oxysporum* strains was enhanced following iron sequestration effects mediated by *Pseudomonas* siderophores (Lemanceau and Alabouvette 1991). The remaining studies focused either on *Pseudomonas* or non-*Pseudomonas,* or assessed both but without considering the significance of their interactions for disease suppression (reviewed below in Sects. 4.3 and 4.4).

4.3 Importance of Pseudomonas in Suppressive Soils Where the Suppression Is Attributed Mainly to Non-Pseudomonas Microorganisms

4.3.1 *Pseudomonas* and Rhizoctonia Suppressive Soils

Suppression of *Rhizoctonia* and *Pythium* damage to apple in orchard replant soils was induced by repeated culture of wheat, which also changed the population structure of fluorescent pseudomonads towards a higher prevalence of *Pseudomonas putida* (Mazzola and Gu 2000). In addition, a correlation was found between the

ability of wheat cultivars to recruit antagonistic pseudomonads and the efficacy of replant disease control (Mazzola 2002). These results pointed to fluorescent pseudomonads as a likely factor accounting for (at least part of) disease suppressiveness. Similarly, suppressiveness to *Rhizoctonia solani* AG3-mediated potato rot might implicate antagonistic *Pseudomonas* populations (Garbeva et al. 2006). Antagonistic pseudomonads were also recovered from soils suppressive to *Rhizoctonia solani* AG 2-1 in cauliflower, but their abundance (in contrast to that of antagonistic *Lysobacter*) did not correlate with soil suppressiveness level (Postma et al. 2010).

4.3.2 *Pseudomonas* and Fusarium Wilt Suppressive Soils

Fluorescent pseudomonads have been extensively considered in relation to Fusarium wilt control, especially in California (Scher and Baker 1982) and southern France (Alabouvette 1986), and competition for iron (Scher and Baker 1982) and phenazine production (Mazurier et al. 2009) were identified as mechanisms by which these bacteria suppressed the disease in these soils. ISR is also an important mode of action of biocontrol pseudomonads against *F. oxysporum* (Lemanceau and Alabouvette 1991, 1993), but evidence for a role of ISR in soil suppressiveness is lacking. On greenhouse tomato, *Pseudomonas* isolates were not as effective as non-pathogenic isolates of *F. oxysporum* and *F. solani* collected from a Fusarium wilt-suppressive soil (Larkin and Fravel 1998).

Antagonistic DAPG$^+$ pseudomonads have been isolated from Fusarium wilt suppressive soils from different continents (Wang et al. 2001), and they reached significant population levels on pea roots in a pea-monoculture soil suppressive to Fusarium wilt in Washington State (Landa et al. 2002). The analogy with the case of monoculture-induced take-all decline of wheat suggests that a similar phenomenon, resulting in pea protection by DAPG$^+$ pseudomonads, might take place in this Fusarium wilt suppressive soil. At another location, culturable fluorescent pseudomonads were recovered in higher numbers from the watermelon rhizosphere after monoculture induction of Fusarium wilt suppressiveness, but only non-pathogenic *F. oxysporum* strains seemed able to play a major role in this case (Larkin et al. 1996).

4.3.3 *Pseudomonas* and Soils Suppressive to Ectoparasitic Nematodes

In South African sandy soils suppressive or conducive to damage caused by ectoparasitic nematodes, fluorescent pseudomonads were recovered at levels below 10^4 CFU/g rhizosphere soil (Rimé et al. 2003). Therefore, it is very unlikely that these bacteria could play a significant role in the suppressiveness of these soils. The production of DAPG can affect phytoparasitic *Globodera* (Cronin et al. 1997c) but DAPG$^+$ pseudomonads have not been considered so far in soils suppressive to such nematodes.

4.4 *Importance of Non-Pseudomonas Microorganisms in Suppressive Soils Where the Suppression Is Attributed Mainly to Pseudomonas*

4.4.1 Non-*Pseudomonas* Microorganisms and Take-All Suppressive Soils

In take-all decline soils, the potential role of non-*Pseudomonas* microorganisms has been considered, and a rather wide range of bacteria and fungi have been proposed as being implicated in suppressiveness (reviewed by Weller et al. 2002). Certain studies pointed at a possible role of *Trichoderma*, especially *T. koningii*, in take-all suppressive soils (Simon and Sivasithamparam 1989; Duffy et al. 1997). A *T. koningii* strain affecting *G. graminis* var. *tritici* probably via mycoparasitism and antibiosis was isolated from a take-all suppressive soil in Australia (Simon and Sivasithamparam 1989), but little was done since to assess the ecological role of *T. koningii* in soil suppressiveness to take-all. Similarly, a fungal isolate from *Phialophora* originating from a take-all suppressive field protected wheat in conducive soil (Mathre et al. 1998), but its significance in take-all decline remains unknown.

In western France, the bacterial rhizosphere community of field-grown wheat at the start of wheat monoculture, during take-all outbreak and after take-all decline was assessed using a 16S rRNA gene-based taxonomic microarray (Sanguin et al. 2009). Changes in rhizobacterial community composition were evidenced during disease, as found elsewhere with *rrs* T-RFLP (McSpadden Gardener and Weller 2001). Significant differences were also observed when comparing the disease and the suppressive stages. Indeed, a wide range of bacterial taxa were less prevalent, i.e. *Bacteroidetes*, *Flavobacteria*, *Verrucomicrobia* and *Actinobacteria*, or more prevalent, i.e. *Planctomycetes*, *Nitrospira*, *Acidobacteria*, *Chloroflexi*, *Alphaproteobacteria* (including *Azospirillum*) and *Betaproteobacteria*, in the suppressive stage than in the disease stage. Similarly, differences in rhizobacterial community structure were observed by T-RFLP during the decline of barley take-all (Schreiner et al. 2010). Whether these taxa actually contribute to suppressiveness remains to be shown, but it is interesting to note that at least some of them are known to contain strains that display biocontrol or plant growth-promoting properties.

4.4.2 Non-*Pseudomonas* Microorganisms and Black Root Rot Suppressive Soils

For Swiss soils of Morens, in which black root rot is controlled, a possible functional role of non-pathogenic *T. basicola* strains in suppressiveness was discounted in early work (Stutz et al. 1986). However, the hypothesis of Ramette et al. (2006) that suppressiveness could also result from the contribution of non-*Pseudomonas* microorganisms was strengthened by 16S rRNA gene-based microarray observations

that differences in rhizobacterial community composition were rather extensive in terms of abundance of a wide range of bacterial taxa between suppressive and conducive soils (Kyselková et al. 2009). Taxa associated with suppressiveness included *Alphaproteobacteria* (*Sphingomonadaceae*, *Gluconacetobacter* and *Azospirillum*), *Betaproteobacteria* (*Nitrosospira*/*Nitrosovibrio*, *Comamonas*, various *Burkholderia* species and *Herbaspirillum seropedicae*), *Gammaproteobacteria* (e.g. *Xanthomonadaceae* and *Stenotrophomonas*/*Xanthomonas*), *Deltaproteobacteria* (*Polyangiaceae*), *Actinobacteria* (*Agromyces* and *Collinsella*), *Firmicutes* (*Paenibacillus alginolyticus*), *Cyanobacteria* (*Lyngbia*), and *Acidobacteria*. The role of these taxa in black root rot suppression will be important to assess. The wheat take-all study of Sanguin et al. (2009) was performed using the same metho dology but with a smaller probe set, limiting possibilities of comparison. Yet, certain taxa (i.e. *Acidobacteria* and *Azospirillum*) were associated with disease suppressiveness in both types of suppressive soils.

5 Outlook

Soil suppressiveness to disease is not completely understood, in part because individual phytoprotecting populations have been studied rather in isolation from the rest of the rhizosphere community. Indeed, biocontrol capacities of microorganisms cannot always be predicted from the knowledge of their behaviour under simplified conditions (Kamilova et al. 2007). On one hand, the plant-protecting effects of certain biocontrol microorganisms was largely mediated by the impact they had on composition and functioning of the microbial community, whose members, in turn, were responsible for disease suppression (Ramos et al. 2003). On the other hand, even though plant protection in suppressive soils may result mainly from the contribution of one or a few prominent microbial groups, functional redundancy may be important and it could be also that interactions with the rest of the microbial community may influence significantly root colonization and expression of biocontrol traits in the former (McSpadden Gardener and Weller 2001; Weller et al. 2002).

It is likely that new ecogenomic approaches ('omics') assessing the relative importance of all community members and the *in situ* expression of microbial genes and functions implicated in plant protection will help reach a better comprehension of the mechanisms behind soil suppressiveness. Microbial community analysis carried out on soils of contrasted suppressiveness levels is a promising approach to identify taxa more prevalent or more active in suppressive situations, which represent candidate plant-protecting microbes (Borneman and Becker 2007; Benítez and McSpadden Gardener 2009). With this type of approach, it is likely that parallel changes in the prevalence of (antagonistic) *Pseudomonas* populations may correlate with other changes in rhizobacterial community composition, as already found in certain types of suppressive soils (McSpadden Gardener and Weller 2001; Hjort et al. 2007; Kyselková et al. 2009; Sanguin et al. 2009; Schreiner et al. 2010). In addition, metagenomic analyses (using microarrays or deep sequencing) of

suppressive soils in combination with clever experimental set-ups may be useful to reveal novel biocontrol microorganisms and novel genes involved in plant protection (van Elsas et al. 2008; Hjort et al. 2010) while metaproteomics and metabolomics are promising for identifying molecular effectors.

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