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❀ **Among the many bacteria present on and around the root, *Pseudomonas* bacteria are (among) the best root colonizers and therefore very suitable to apply for beneficial purposes. In this chapter, we discuss the possibilities to use such bacteria for the following purposes: fertilization of the plant, stimulation of plant growth and yield, reduction of plant stress, and reduction of plant diseases.**

❀ **Key words:** antibiosis, anti-fungal metabolite, biocontrol, biofertilizer, biofilm, competition for nutrients and niches, *Fusarium oxysporum* f. sp. *radicis-lycopersici*, induced systemic resistance, phytostimulator, predation and parasitism, *Pseudomonas*, rhizoremediation, rhizosphere, root colonization, root exudate, stress control, tomato foot and root rot

BENEFICIAL RHIZOSPHERE PSEUDOMONADS

INTRODUCTION

The rhizosphere is defined as the volume of soil influenced by the root (Hiltner, 1904). The rhizosphere is a place where many (micro- and macro-) organisms live, meet and often fight (Lugtenberg and Bloemberg, 2004; Lynch, 1990; Pinton, Varanini and Nannipieri, 2007). They compete for nutrients and niches under strongly varying, and still rather obscure, conditions. They also have to defend themselves against enemies and unfavorable conditions. And all these processes usually happen in the complex substrate soil or in artificial substrates such as stonewool. Bacteria, viruses, fungi and protozoa all have developed their own strategies for attack and survival.

Scientists are trying to manipulate the rhizosphere in such a way that it becomes more advantageous for mankind, usually by forcing the plant of their choice to perform better. To do this successfully, we need to know the players and to understand their interactions with each other and with the growth substrate. Moreover, also the effects of abiotic factors should be taken into account.

The analysis of all these interactions requires a strong interdisciplinary approach and a large set of tools. In the rhizosphere, bacteria are often present as microcolonies or biofilms. Some micro-organisms cooperate with each other. Other organisms attack their competitors, using a variety of strategies. When the victim is our enemy, we call the winners beneficial microbes. When the victim is a friend, we call the winners pathogens. It therefore is not surprising that beneficial and pathogenic microbes use overlapping interaction traits.

For microbes, the rhizosphere contains more nutrients than bulk soil does. This so-called "rhizosphere effect "is caused by exudation of nutrients from the root. Of the total carbon fixed by the plant, up to thirty percent can be released by the root in the form of so-called root exudate (Lugtenberg et al., 2001). This results in a 10- to 100-fold higher bacterial concentration in the rhizosphere than in bulk soil. In soil, the concentration of culturable bacteria, which include opportunistic human pathogens (Berg et al., 2005; Egamberdiyeva et al., 2007) is approximately 10^8 cfu's/g of soil. The unculturable bacterial population is estimated to be 10- to 100-fold higher. Furthermore, several eukaryotes such as fungi, protozoa and nematodes are present in the rhizosphere.

Pure root exudate is a poor medium, allowing growth of *Pseudomonas* bacteria to a level of 10^7 to 10^8 CFUs/ml. The same bacteria easily reach over 10^9 CFUs/ml in a rich laboratory medium. It is therefore conceivable that the physiology of bacteria in the rhizosphere differs from that in the laboratory.

In contrast to soil, new stonewool is practically sterile. After extraction of one new stonewool plug, of 0.6 gram in weight, with 6 ml phosphate buffered saline and subsequent incubation of 0.1 ml of this extract on a King's medium B plate, no growth was observed (F. Kamilova, unpublished).

Stonewool does not contain nutrients at all. In this substrate, which is often used for growth of vegetable crops such as tomato, paprika and sweet pepper, plants receive plant nutrient solution **(PNS)** which contains all required chemical elements except carbon. Carbon is solely derived from exudate. As far as we know,

the major root exudate carbon sources for the mentioned plant are organic acids (mainly citric, malic, lactic and succinic acid), sugars (mainly glucose, xylose and fructose) and amino acids (mainly glutamic and aspartic acids) (Kamilova et al., 2006-a; Lugtenberg et al., 1999-b; Lugtenberg et al., 2001; Simons et al., 1997). Macromolecules are also present in root exudate, but are more difficult to utilize than the mentioned small molecules. The pH of root exudate is 5.5 (Kamilova et al., 2006-a).

Because this review is based on a lecture in which the work in our laboratory on the biocontrol of tomato foot and root rot **(TFRR)** was reported, we focus mainly on the activities of *Pseudomonas* biocontrol bacteria and the pathogenic fungus *Fusarium oxysporum* f. sp. *radicis-lycopersici* **(Forl)** in the tomato rhizosphere.

ROOT COLONIZATION AND BIOFILM FORMATION

After coating of *Pseudomonas* biocontrol bacteria on seeds, and subsequent growth of the plant in soil infested with spores of the pathogenic fungus Forl, microscopy has shown that bacteria (Chin-A-Woeng et al., 1997; Bolwerk et al., 2003) as well as hyphae (Lagopodi et al., 2002), are present on the root mainly between root epithelial cells. These sites, as well as places where lateral roots appear, are supposed to be the sites where exudate is secreted or lost from the root. Several days after the beginning of colonization, bacteria form denser micro-colonies or biofilms (Bloemberg t al., 1997; Chin-A-Woeng et al., 1997; Costerton et al., 1995). These colonized areas never occupy more than 15 percent of the root surface (Rovira, 1956). The rest of the root surface remains empty, presumably because of lack of nutrients. The bacteria in a biofilm are covered by a mucigel layer, presumably of plant origin (Chin-A-Woeng et al., 1997). When biocontrol *Pseudomonas* bacteria as well as hyphae of Forl are present, the bacteria also colonize the hyphae (Lagopodi et al., 2002; Bolwerk et al., 2004; Bloemberg et al., 2004; Bolwerk and Lugtenberg, 2006).

In our laborarory, the process of root colonization has been studied in some detail because root colonization is often the limiting factor for biocontrol (Weller, 1988). A collection of mutants of *P. fluorescens* WCS365 was screened against the wild type strain by coating a 1:1 mixture on seeds which were sown in a gnotobiotic system. After one week of germination and plant growth, one cm root tip of the ten cm long root was inspected for the ratio of CFUs in which the two strains were present (Simons et al., 1996). A mutant which was loosing in colonization, is a potential colonization mutant. In order to avoid mutants with a general growth defect, potential colonization mutants were screened for growth in competition with the wild type in laboratory media. Only mutants which grew as well as the wild type were considered to be competitive colonization mutants. Practically all of these were also defective in colonization when their kanamycin resistant derivatives were tested in soil. In addition, colonization appeared not to be a host plant-specific process: mutants impaired in colonization of tomato roots were also defective in colonization of roots of other plants.

From the mutant work it appeared that there are many competitive colonization traits. Most of the work has been reviewed (Lugtenberg and Dekkers, 1999-a; Lugtenberg et al., 2001; Chin-A-Woeng et al., 2004-b). These traits include a high growth rate in root exudate, chemotaxis towards exudate components, attachment to the root, the O-antigen of lipopolysaccharide, regulation of putrescine uptake, and synthesis of amino acids, vitamin B1 and uracil. Moreover, colony phase variation plays a role in competitive colonization (Achouak et al., 2004; Dekkers et al., 1998; Van de Broek et al., 2003; Van de Broek et al., 2005-a; Van de Broek et al., 2005-b). The most likely explanation is that phase I bacteria, which grow slower than phase II bacteria, can stop producing antibiotics and exo-enzymes, thereby saving energy for faster growth, when the conditions require so (Van de Broek et al., 2005-a). Also the type III secretion system **(TTSS)**, described to be injecting proteins into eukaryotic cells, is involved in colonization. The latter fact is interpreted in the sense that, before the needle evolved to a flagellum and a protein-delivering injection needle, the prototype TTSS was a simple needle which was injected by the bacterium into the plant as a pipeline through which nutrients from the eukaryote could be delivered into the bacterium (De Weert et al., 2007).

WEAPONS IN THE RHIZOSPHERE

Anti-fungal compounds produced by biocontrol pseudomonads include the classical antibiotics 2,4-diacetyl phloroglucinol (Bangera and Tomashow, 1999), phenazines (Chin-A-Woeng et al., 2003-a), pyrrolnitrin, pyoluteorin (Nowak-Thompson et al., 1999) , (Haas and Defago, 2005) . More recently, a novel antibiotic has been added to the weapon repertoire, namely 2-hexyl-5-propyl resorcinol (Cazorla et al., 2006). The study of cyclic lipopeptides as anti-fungal metabolites **(AFMs)** has become very popular in the past decade (De Bruyn et al., 2007; De Souza et al., 2003; Koch et al., 2002; Nielsen et al., 1999; Nielsen et al., 2000; Nielsen et al., 2002; Stanghellini and Tomlinson, 1987).

The fungal cell wall is rich in glucans, chitin and protein. Therefore enzymes that degrade fungal cell wall components can play important roles in biocontrol of fungal diseases (Harman et al., 2004).

FOOD CONSUMPTION IN THE RHIZOSPHERE

Many components present in root exudate have been identified (Uren, 2007; Lugtenberg et al., 2001; Kamilova et al., 2006-a). It should be noted that this information is probably far from complete since the components which

will be found depend on the approaches used to find them. A good example is that putrescine was only found after a gene impaired in a colonization mutant suggested its presence (Kuiper et al., 2001-b).

Root exudate is collected from sterile plants growing on filter paper or in a small volume of aqueous solution in order to prevent too much dilution. It should be noted that the composition of this exudate will differ from that in nature since in the latter case exudate components will be consumed by the indigenous microflora and by the plant. Also, the presence of microbes influences the exudation pattern of the root (Meharg and Killham, 1995; Kamilova et al, 2006-b).

We asked the question of how bacteria sense the presence of nutrients. Chemotaxis assays (De Weert et al., 2002) of *P. fluorescens* WCS365 to known tomato root exudate components (Lugtenberg et al., 2001) have shown that amino acids are the strongest chemo-attractants, followed by organic acids. Sugars are inactive (de Weert et al., 2002). If the measured concentrations of these chemoattractants in exudate are taken into account, it is most likely that in the rhizosphere citric and malic acid are the most important attractants for *Pseudomonas* bacteria to reach the rhizosphere (de Weert et al., 2002).

The most important chemoattractant for the attraction of *Pseudomonas* bacteria to Forl hyphae is fusaric acid, a secondary metabolite produced by most Fusarium strains. Chemoattraction towards fusaric acid was shown (de Weert et al., 2003) by using a series of Forls which produce different levels of this compound (Notz et al., 2002) and confirmed by re-using the pure compound (de Weert et al., 2003).

Kamilova et al. (2006-b) analyzed root exudates after interactions of the root with (i) the biocontrol strain *P. fluorescens* WCS365, (ii) the pathogenic fungus Forl, and (iii) both bacterium and fungus. It appeared that the presence of the bacterium alone results in the strong decrease of succinic acid. The fungus alone results in a decrease of citric acid but in an increase of the succinic acid concentration. When both are present, under biocontrol conditions, succinic acid decreases and citric acid remains constant. It should be noted that these data is difficult to interpret since it is not known how the presence of the microbes influences exudation and which metabolites are used by the plant.

WAR BETWEEN ORGANISMS IN THE RHIZOSPHERE

N-acyl homoserine lactones **(AHLs)** are signal molecules which are not only involved in the quorum-dependant production of (some of) their own antibiotics (Chin-A-Woeng et al., 2002; Dubern et al., 2006-b) and exo-enzymes, but also play a role in the interactions between rhizosphere micro-organisms (Bassler, 1999). In the following, we will give a number of examples of competition between microbes in the rhizosphere.

Some rhizobacteria produce enzymes which degrade AHLs. This can be done by hydrolysis of the lactone ring by an AHL-lactonase (Dong et al., 2000; Dong et al., 2001) or by breaking the amide ring using a AHL-acylase (Lin et al., 2003). Degradation of AHLs results in the inhibition of all AHL-dependant processes such as synthesis of some antibiotics such as PCN, production of exo-enzymes including some virulence factors (see Signal interference), and DNA transfer by a certain form of conjugation (Piper et al., 1993; Zhang et al., 1993). DNA transfer occurs very frequently in the rhizosphere (van Elsas et al., 1988). We have proposed that biofilms of bacteria covered by a mucoid layer are excellent niches for quorum-sensing dependant DNA transfer (Chin-A-Woeng et al., 1997).

The interaction between *Pseudomonas* bacteria and Forl hyphae is an example of competition in the rhizosphere that is partly understood at the molecular level. Based on laboratory experiments, we assume that the following processes occur. 1. *Pseudomonas* senses fusaric acid (De Weert et al., 2003) secreted by Forl (Notz et al., 2002) and swims towards the hyphae and colonizes them (De Weert et al., 2003). 2. Once it is present in sufficient numbers, it starts to produce the anti-fungal compound PCN (Chin-A-Woeng et al., 1998) in an AHL-dependent way (Chin-A-Woeng et al., 2001). 3. However, if fusaric acid is present in a sufficiently high concentration, this fungal metabolite stops the synthesis of AHL and therefore indirectly of PCN (van Rij et al., 2005). The outcome of this interaction between these two microbes will therefore be strongly dependant on the concentrations in which they are present and on the speed with which they react on each other.

Fusaric acid uses a different strategy to inhibit the synthesis of another AFM (anti-fungal metabolite), 2,4-diacetyl phloroglucinol **(Phl)**, of *P. fluorescens* strain CHAO-1. In this case, fusaric acid inhibits AFM synthesis at the level of the *phlA* promoter (Schnider-Keel et al., 2000). It should be noted that strain CHAO-1 does not produce AHL, but another, not yet identified, signal molecule.

Fusarium is also able to degrade an antibiotic directly. For example, some Fusarium strains degrade Phl (Schouten et al., 2003).

MANAGING RHIZOSPHERE PROCESSES

Mankind has realized long ago the potential of rhizosphere microbes for applications (Lugtenberg and Kamilova, 2004). The nitrogen-fixing capacity of *Rhizobium* bacteria was already applied in the end of the 19th century (Spaink et al., 1998). **Biofertilization** is the general name for the generation of nutrients for plants by microbes. This term also includes the generation of soluble phosphate from polymeric phosphate. Biofertilization will be extensively described in other chapters. **Rhizoremediation** (Kuiper et al., 2004-b) is the use of rhizosphere microbes for the degradation of pollutants. Many bacteria are known to degrade

environmental pollutants. However, upon their application in soil, these microbes stop degrading the pollutants due to lack of energy. By selecting bacteria which combine the abilities of pollutant degradation and utilization of the best food source in soil, namely root exudate, this problem can be overcome (Kuiper et al., 2001-a; Kuiper et al., 2002). **Phytostimulation** is the use of microbes to stimulate growth of plants. The molecular basis of this phenomenon usually is the production of the root growth hormone auxin from tryptophan secreted by the plant in root exudate. One of the bacteria able to stimulate root growth is *P. fluorescens* WCS365, which stimulates growth of radish but not tomato, cucumber and sweet pepper. Radish exudate contains at least ten times more tryptophan than the exudates of the other mentioned plants. See for example Kamilova et al. (2006-a). **Stress control** is the reduction of plant stress by microbes. The best studied form is the reduction of levels of the plant stress hormone ethylene by microbes which take up the ethylene precursor 1-aminocyclopropane-1-carboxylate **(ACC)** and convert it to 2-oxobutanoate and NH_3, using the enzyme ACC deaminase (Glick et al., 1994). By reducing ethylene levels in such a way, microbes have been described to make plants more resistant to stress from heavy metals (such as Cd2+ and Ni 2+; Belimovet al., 2007) and from polyaromatic hydrocarbons, to salt stress and to drought. **Biocontrol** of plant diseases is the use of organisms to decrease plant disease. Excellent reviews are available (Haas and Defago, 2005; Tomashow and Weller, 1996). Many plant diseases are caused by fungi. In our laboratory we have studied the disease TFRR caused by the fungus Forl. For recent reviews the reader is referred to Bloemberg and Lugtenberg (2001) and Chin-A-Woeng et al. (2003-b). In the following we will describe mechanisms used for the control of this disease by *Pseudomonas* bacteria in some detail.

MECHANISM OF BIOCONTROL

1. **Antibiosis.** Most described biocontrol products are based on bacteria which have been prescreened on being antagonistic on agar plates against the target pathogen(s) (Dowling and O'Gara, 1994). The percentage antagonistic isolates varies with the source, from approximately one to thirty percent. The only way to show that the AFM is required for biocontrol is to isolate mutants in one of the structural genes for the biosynthesis of the antibiotic and test whether such a mutant is impaired in biocontrol. This was for example the case for *Pseudomonas chlororaphis* strain PCL1391, which produces PCN (Chin-A-Woeng et al., 1998). In addition it appeared that extensive root colonization was also required, presumably as the delivery system for the AFM (Chin-A-Woeng et al., 2000).

A good example of why mutant analysis is strictly required to prove the involvement of an AFM is biocontrol of TFRR by *Collimonas fungivorans*. This fungus eater has many chitinolytic activities. Nevertheless, its mechanism of biocontrol action is rather competition for nutrients and niches than the expected mechanism predation and parasitism (Kamilova et al., 2007).

2. **Induced systemic resistance** (ISR). Some bacteria are able to trigger the plant to a fast and intensive defense reaction upon exposure to a range of widely different pathogens (van Peer et al., 1991; Wei et al., 1991; for a recent review, see van Loon and Bakker (2007). By applying biocontrol agent and pathogen at different sites on the plant one can show that the defense works systemically. P.fluorescens WCS417R (van Wees et al., 2000; van Loon and Bakker, 2007) and *Pseudomonas fluorescens* WCS365 (Kamilova et al., 2005) have been shown to act through ISR. Extensive colonization of the whole root system is not required as was shown for *P. fluorescens* WCS365 (Dekkers et al., 2000). The mechanism of ISR has been studied for *P. fluorescens* WCS417R, using Arabidopsis mutants. It was concluded that ISR is dependent on jasmonic acid and ethylene signalling in the plant (van Wees et al., 2000; van Loon and Bakker, 2007). It is not known whether all bacteria that use ISR as their mechanism of biocontrol use the same mechanism. A number of components which can be involved in inducing ISR have been identified as reviewed by van Loon and Bakker (2007). They include the O-antigen of lipopolysaccharide (Dow et al., 2000), flagella, Phl, siderophores (Audenaert et al., 2002, salicylic acid (De Meijer et al., 1999) and cyclic lipopeptides (Ongena et al., 2007). The volatile 2,3 butanediol, produced by *Bacillus subtilis* GB03, also induces ISR (Ryu et al., 2004). ISR has been compared (Lugtenberg and Leveau, 2007) with innate immunity in animals (Nuerberger and Brunner, 2002).

3. **Competition for nutrients and niches** (CNN). This mechanism, by which the biocontrol agent out competes the pathogen on the root, by being a more efficient user of exudate nutrients and faster in occupying the available root niches, has been proposed in the literature for decades but experimental proof was provided only recently. Kamilova et al. (2005) used crude mixtures of rhizosphere bacteria for inoculation of sterile seeds. The seeds were sawn in a gnotobiotic sand-PNS system and, after growth for one week, the one cm root tip, supposedly containing the most aggressive competitive colonizers, was removed and its bacteria were used for a new cycle of enrichment for excellent colonizers. After three cycles, most individual root tip isolates appeared to compete for the root tip as good as or even better than our model colonizer *P. fluorescens* WCS365. Most of these isolates appeared to be able to control TFRR. Two isolates, *P. fluorescens* PCL1751 (Kamilova et al., 2005) and *P. putida* PCL1760 (Validov et al., 2007), were studied in more detail. Using mutants impaired in motility and in the uptake of dicarboxylic acids (which represent more than 30 % of the root exudate carbon) it was shown that the strains use CNN as their mechanism of action for controlling TFRR.

OTHER ASPECTS OF BIOCONTROL.

It is likely that a good biocontrol agent has to use a combination of mechanisms, since the contribution of most mechanisms depends on the growth conditions. For example, antibiotic production is regulated in a very complex way (Chin-A-Woeng et al., 2001; Girard et al., 2006-a; Girard et al., 2006-b). The level of antibiotic produced depends heavily on the environmental conditions (Duffy and Defago, 1997; Duffy and Defago, 1999; Dubern and Bloemberg, 2006-a; van Rij et al., 2004). In a gnotobiotic sand system even a non-PCN — producing mutant of *P. chlororaphis* strain PCL1391 can control TFRR (Bolwerk and Lugtenberg, 2006). This is probably due to the absence of indigenous bacteria and the bacterial mutant apparently out competes Forl by CNN.

Biocontrol agents with different mechanisms of action vary enormously in the ease with which they can be isolated. No selection is possible for organisms acting through ISR. In the future, when the molecular basis of ISR is known better, it may be possible to pre-screen for an ISR-specific trait or enzyme. Several screening tests exist to isolate bacteria which degrade AHLs. Microbes which produce AFMs or fungal cell wall degrading enzymes can easily be screened for using antagonistic plate assays. Of all known mechanisms, the isolation of microbes using CNN (Kamilova et al., 2005; Validov et al., 2007) is superior in simplicity since the procedure is mainly based on selection.

Before a biocontrol product can be marketed, it has to be registered. Production of antibiotics is a severe disadvantage. It must also be expected that the registration of a product using signal interference will be problematic since such a product would also inactivate natural beneficial rhizosphere organisms that use AHLs for their beneficial activity. For example, *P. chlororaphis* strain PCL1391 would loose its beneficial activity because it is based on AHL-dependant PCN production. We expect that registration will be easiest for products that use ISR or CNN as their major mechanisms.

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Ризосферные псевдомонады, полезные для растений

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❀ **РЕЗЮМЕ: Среди большого числа бактерий, присутствующих на поверхности и в ризосфере корня, бактерии псевдомонады являются наилучшими колонизаторами корней, и поэтому могут иметь практическое применение. В этой статье обсуждаются возможности использования таких бактерии для следующих целей: использование в качестве удобрения для растений, стимулирование роста и урожайности растений, повышение устойчивости к стрессам и болезням.**

❀ **КЛЮЧЕВЫЕ СЛОВА:** антагонизм, антигрибные метаболиты, биорегулирование, биоудобрение, биоплёнка, конкуренция за питательные вещества и ниши, Fusarium oxysporum f. sp. radicis — lycopersici, системная индуцированная устойчивость, фитостимулятор, хищничество и паразитизм, Pseudomonas, ризоремедиация, ризосфера, корневая колонизация, корневой экссудат, регуляция стресса, фузариоз томата и корневая гниль.