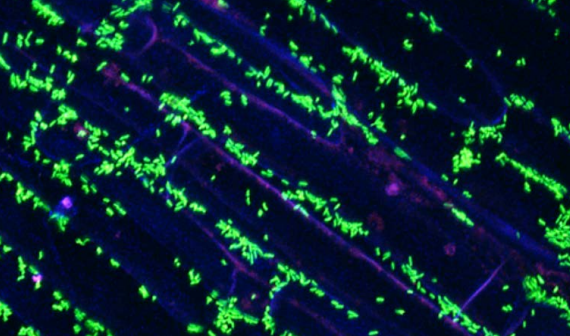# The use of *Pseudomonas spp.* as bacterial biocontrol agents to control plant disease

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1 Introduction

Bacteria have their origin in marine environments. They split into a group of land-adapted bacteria, the Terrabacteria, and a group that remained in water, the Hydrobacteria, about 3 billion years ago. The genus *Pseudomonas* belongs to the *Gammaproteobacteria*, a class of bacteria that emerged from

the Hydrobacteria 1.75 billion years ago (Battistuzzi and Hedges, 2009). The *Pseudomonas* genus diverged well before the colonization of land by plants. The evolutionary history of the *Pseudomonas* genus is founded on hundreds of millions of years spent mostly in aquatic habitats in the absence of higher plants (Morris et al., 2013). *Pseudomonas* is now one of the most ubiquitous genera in the world. *Pseudomonas* bacteria are inhabitants of sea, freshwater and soil-related environments. Many species live in association with plants and animals, mostly as saprophytes, but some are pathogenic for plants or animals. *Pseudomonas* bacteria have useful applications in biotechnology, plant growth promotion, bioremediation and biocontrol (Peix et al., 2009).

This chapter will focus on beneficial plant-associated *Pseudomonas* strains with the capacity to control plant diseases. There is an extensive literature on this topic with thousands of papers. Most *Pseudomonas* biocontrol agents have been isolated from soil, the rhizosphere of plants or from water. They are good root colonizers and well known for their capacity to control soilborne pathogens. Some strains can also protect against leaf pathogens by inducing systemic resistance in plants. They usually do not survive well on above-ground parts of plants, except for a few *Pseudomonas* biocontrol strains from the *P. syringae* group. This review will start with recent advances in *Pseudomonas* taxonomy and a summary of its most important biocontrol traits. An overview will then be given of the most important *Pseudomonas* groups and subgroups harboring biocontrol strains. Examples of well-characterized and representative biocontrol strains will show the links between the phylogeny, ecology and biocontrol traits. The chapter concludes by reviewing commercially available biocontrol strains.

2 *Pseudomonas* taxonomy

The genus *Pseudomonas* is diverse and complex and is currently divided into various phylogenetic groups with more than 220 described species. New species are being described constantly. A good overview of the historical evolution of *Pseudomonas* taxonomy and species described up to 2009 is given by Peix et al. (2009). The same authors have published an update of about 70 new species described from 2009 until 2018 (Peix et al., 2018). Species and phylogenetic groups have been delineated based on multi locus sequence analysis (MLSA) using the genes 16S rDNA, *gyrB, rpoB* and *rpoD* (Gomila et al., 2015; Lalucat et al., 2020; Mulet et al., 2010) and whole-genome sequences (Garrido-Sanz et al., 2016; Hesse et al., 2018). The 16S rRNA gene allows differentiation of the genus *Pseudomonas* but is not at the species level. Particularly useful for species discrimination are the *rpoD, gyrB* and *rpoB* genes. The *rpoD* gene is most discriminative for species delineation, followed by *gyrB*, and by the *rpoB* which is the least discriminative of these markers (Mulet

et al., 2010). The taxonomy of *Pseudomonas* is constantly evolving and major breakthroughs have been made by the availability of *rpoD*, MLSA and whole-genome sequences of the species type strains (Girard et al., 2020b; Hesse et al., 2018; Lalucat et al., 2020).

The main phylogenetic groups defined by the 4-gene MLSA are to a large extent consistent with the groupings in genomics analyses. This means that new *Pseudomonas* isolates can easily be taxonomically positioned by sequencing these four genes (Garrido-Sanz et al., 2016) or just the *rpoD* gene (Girard et al., 2020b). Lalucat et al. (2020) have presented a complete MLSA-based phylogenetic tree using 216 *Pseudomonas* species. They distinguish three main lineages represented by the species:

- *P. aeruginosa*;
- *P. fluorescens*; and
- *P. pertucinogena*.

The *P. fluorescens* lineage comprises five phylogenetic groups:

- *P. fluorescens*;
- *P. asplenii*;
- *P. lutea*;
- *P. syringae*; and
- *P. putida*.

The *P. aeruginosa* lineage comprises eight phylogenetic groups:

- *P. straminea*;
- *P. anguilliseptica*;
- *P. oryzihabitans*;
- *P. stutzeri*;
- *P. oleovorans*;
- *P. resinovorans*;
- *P. aeruginosa*;
- *P. linyingensis*; and
- the genus *Azotobacter*.

The *P. fluorescens* group is further divided into eight subgroups:

- *P. fluorescens*;
- *P. gessardii*;
- *P. fragi*;
- *P. mandelii*;

- *P. koreensis*;
- *P. jessenii*;
- *P. corrugata*; and
- *P. chlororaphis*.

Hesse et al. (2018) constructed a phylogeny of 166 type strains within the *Pseudomonas* genus based on protein sequences of 100 single-copy orthologous genes and found 13 groups of *Pseudomonas*. In their protein-based phylogeny, the *P. fluorescens* group is composed of 10 subgroups since they distinguish the *P. protegens* subgroup from the *P. chlororaphis* subgroup and, in their phylogeny, *P. asplenii* is clustered within the *P. fluorescens* group. *P. chlororaphis* and *P. protegens* will be considered as two separate subgroups since their biocontrol traits are clearly different.

3 Plant-beneficial *Pseudomonas* strains

Plant-beneficial effects of *Pseudomonas* bacteria have been extensively studied and the most important findings are summarized in a number of comprehensive reviews. Many *Pseudomonas* strains can promote plant growth directly in the absence of pathogens by increasing the availability and uptake of mineral nutrients via phosphate solubilization, by enhancing root growth via the production or manipulation of phytohormones, or by enhancing tolerance to abiotic stress. Aspects of plant growth promotion have been reviewed elsewhere and will not be further discussed here (Berg, 2009; Dimkpa et al., 2009; Hayat et al., 2010; Lugtenberg and Kamilova, 2009; Ma et al., 2016; Ngumbi and Kloepper, 2016; Rajkumar et al., 2017).

The most important mechanisms of disease suppression by *Pseudomonas* biocontrol agents include:

- competition for nutrients or space (Kamilova et al., 2005);
- antibiosis (Haas and Défago, 2005; Raaijmakers et al., 2002; Raaijmakers and Mazzola, 2012); and
- induced systemic resistance (Bakker et al., 2007; De Vleesschauwer and Höfte, 2009; Pieterse et al., 2014).

A hallmark paper on *Pseudomonas* biocontrol that gives a good introduction to the subject has been published by Haas and Défago (2005). Weller (2007) has given an overview of 30 years of biocontrol research using *Pseudomonas* to control soilborne pathogens. Many good reviews have also appeared in books. A comprehensive overview of the older literature can be found in Thomashow and Weller (1996). More recent reviews have been published by Mercado-Blanco (2015) and Olorunleke et al. (2015b). Reviews about more specific aspects of *Pseudomonas* biocontrol will be cited later in the chapter.

The *P. fluorescens, P. putida, P. syringae* and *P. aeruginosa* groups harbor biocontrol strains. Within the *P. fluorescens* group, *P. chlororaphis*, *P. protegens* and *P. corrugata* subgroups, the so-called CPC cluster are especially rich in biocontrol agents and biocontrol properties (Vacheron et al., 2016). The *P. fluorescens*, *P. mandelii*, *P. jessenii* and *P. koreensis* subgroups, the so-called FMJK cluster, have fewer biocontrol properties but are enriched in phytostimulatory properties such as plant hormone modulation and plant nutrition (Vacheron et al., 2016).

It should be noted that biocontrol agents are not properly taxonomically determined in many published studies. Identification is based only on the 16S rDNA gene which does not have enough resolution to discriminate between subgroups or species. Many species that are described in the literature as *P. fluorescens* actually belong to other or undescribed species. Misidentification is a common problem even for publicly available genomes (Tran et al., 2017). In their analysis of 166 genomes of type strains and 1224 additional genomes of *Pseudomonas* spp. Hesse et al. (2018) identified 350 distinct clusters. They found that 189 clusters potentially represent novel species of *Pseudomonas*. Many of these clusters are singletons consisting of only one strain of *Pseudomonas*. These data show the tremendous diversity in *Pseudomonas* and we can expect the description of many new species in the coming years. Thanks to whole-genome sequencing and major advances made in *Pseudomonas* taxonomy, mainly in the *P. fluorescens* group, it is becoming increasingly clear that there is a strong link between phylogeny and biocontrol phenotypes (Garrido-Sanz et al., 2016). Researchers are urged to identify their *Pseudomonas* biocontrol strains properly by sequencing at least the *rpoD* gene to determine to which *Pseudomonas* group or subgroup they belong.

4 Secondary metabolite production in *Pseudomonas* biocontrol strains

Secondary metabolite production in *Pseudomonas* has been reviewed extensively. A comprehensive overview of the biosynthesis, chemistry and biological significance of *Pseudomonas* secondary metabolites is provided by Gross and Loper (2009). The literature about secondary metabolites involved in biocontrol is summarized in Haas and Défago (2005), Mishra and Arora (2018), Olorunleke et al. (2015b), and Raaijmakers and Mazzola (2012). It has become evident that only a limited number of bioactive compounds play a clear role in biocontrol of plant diseases:

- hydrogen cyanide (HCN);
- 2,4-diacetylphloroglucinol (DAPG);
- phenazines;

- pyrrolnitrin;
- pyoluteorin;
- 2-hexyl-5-propyl-alkylresorcinol;
- siderophores; and
- (cyclic) lipopeptides.

These compounds are usually produced by specific phylogenetic groups or subgroups within the *Pseudomonas* genus (Table 1) and are briefly discussed below.

4.1 Phenazines

Phenazines are redox-active nitrogen-containing tricyclic pigments that are produced by *Pseudomonas* and some other Gram-negative *Proteobacteria* (Mavrodi et al., 2006). More than 100 different phenazine structures have been described but biocontrol strains produce phenazine-1-carboxylic acid (PCA, lemon yellow), phenazine-1-carboxamide (PCN, green), 2-hydroxyphenazine (2-OH-PHZ, brick-red) or 2-hydroxyphenazine-1-carboxylic acid (2-OH-PCA, orange). Pyocyanin (PYO), a blue phenazine pigment, is only found in *P. aeruginosa* where it contributes to infection in mammalians (Price-Whelan et al., 2006).

The core phenazine biosynthesis genes are clustered and highly conserved. A seven-gene locus, named *phzABCDEFG* is responsible for the synthesis of PCA, which starts from chorismic acid, a product from the shikimate pathway. Phenazine diversity results from modification of PCA with dedicated enzymes such as PhzO (modifies PCA into 2-OH-PCA), PhzH (modifies PCA into PCN), PhzS (modifies PCA into 1-OH-PCA) and PhzM (modifies PCA into pyocyanin together with PhzS). In all phenazine-producing *Pseudomonas* strains, phenazine production is regulated by quorum sensing and also requires a functional GacS/GacA two-component signal transduction system. More details about phenazine biosynthesis can be found in Biessy and Filion (2018), Gross and Loper (2009) and Mavrodi et al. (2006).

Phenazines display broad-spectrum activity against fungal, oomycete and bacterial pathogens (Biessy and Filion, 2018), but can also trigger induced systemic resistance (ISR) in various plants (Ma et al., 2016b; De Vleesschauwer and Höfte, 2009). Phenazines have a physiological role in biofilm formation and iron reduction (Mavrodi et al., 2013). Phenazines are typically produced by *Pseudomonas* strains that belong to *P. aeruginosa*, or the *chlororaphis* and *fluorescens* subgroups within the *P. fluorescens* group (Table 1). Extensive information about microbial phenazines can be found in Chincholkar and Thomashow (2013).

Table 1 Examples of secondary metabolites produced by specific taxonomic groups and subgroups within the genus *Pseudomonas* (see text for references)

Taxonomic group/subgroup	Antibiotics	Biosurfactants	Siderophores
P. aeruginosa	HCN, phenazines (PYO, PCA, PCN), PLT	Rhamnolipids	pyoverdine, pyochelin
P. chlororaphis	HCN, phenazines (PCA, 2-OH-PCA, PCN), PRN, HPR	Viscosin group	pyoverdine, achromobactin
P. protegens	HCN, DAPG, PRN, PLT,	Orfamide group, sessilin	pyoverdine, enantio-pyochelin
P. corrugata	HCN, DAPG	Mycin/Peptin group, corrugatin	Pyoverdine, achromobactin, corrugatin
P. koreensis	HCN	Amphisin group, Bananamide group, cocoyamide/gacamide	pyoverdine
P. mandelii	HCN	Mycin/Peptin group	pyoverdine
P. gessardii			pyoverdine, (thio)quinolobactin
P. fluorescens	phenazines (PCA)	Viscosin group, Orfamide group	pyoverdine, pseudomonin
P. putida	HCN	WLIP, xantholysin, entolysin, putisolvin	pyoverdine
P. syringae	HCN	Mycin/Peptin group	pyoverdine, achromobactin

Abbreviations: Antibiotics: DAPG: 2,4-diacetylphloroglucinol, HCN: hydrogen cyanide, HPR: 2-hexyl-5-propyl-alkylresorcinol, PCA: phenazines-1-carboxylate, PCN: phenazines-1-carboxamide, 2-OH-PCA: 2-hydroxyphenazine-1-carboxylic acid, PLT: pyoluteorin, PRN: pyrrolnitrin, PYO: pyocyanine, Lipopeptides: Mycin: Syringomycin group lipopeptides, Peptin: Corpeptin, Sclerosin and Syringopeptin group lipopeptides.

4.2 2,4-diacetylphloroglucinol (DAPG)

DAPG is a polyketide antibiotic that is produced by *Pseudomonas* strains that predominantly belong to the *P. protegens* and *P. corrugata* subgroups (Table 1) and a few isolated strains in other taxonomic groups (Almario et al., 2017). It plays a key role in the biocontrol of root and seedling diseases and is active against fungi, oomycetes, nematodes and bacteria. The compound is phytotoxic at high concentrations. DAPG- producing *Pseudomonas* strains have typically been isolated from soils suppressive to take-all, an important wheat root disease caused by *Gaeumannomyces graminis* var. *tritici* (Weller et al., 2007). The DAPG gene cluster is highly conserved and comprises nine genes involved in biosynthesis (*phlACB* and *phlD*), efflux (*phlEI*), degradation (*phlG*) and regulation (*phlH* and *phlF*). The biosynthesis starts from three molecules of malonyl CoA. PhlD is a type III polyketide synthase responsible for the biosynthesis of phloroglucinol. Besides its role in direct antibiosis, the compound can induce systemic resistance in *Arabidopsis* to the downy mildew pathogen *Hyaloperonospora parasitica* (Iavicoli et al., 2003), *Pseudomonas syringae* pv. *tomato* (Weller et al., 2012) and *Botrytis cinerea* (Chae et al., 2020) by triggering jasmonate- and ethylene-mediated defense responses. DAPG can promote amino acid exudation from plant roots by blocking amino acid influx (Phillips et al., 2004) and stimulates root branching in tomato by interacting with the auxin-dependent signaling pathway (Brazelton et al., 2008).

4.3 Pyoluteorin

Pyoluteorin is a hybrid non-ribosomal peptide synthetase/polyketide synthase product consisting of a resorcinol ring attached to a dichlorinated pyrrole moiety. Pyoluteorin is produced by *Pseudomonas* strains belonging to the *P. protegens* subgroup (Ramette et al., 2011) and a few *P. aeruginosa* isolates (Hu et al., 2005). The antibiotic has not been reported in genera other than *Pseudomonas*. Pyoluteorin suppresses seedling damping-off diseases caused by the oomycete pathogen *Pythium ultimum* in cotton and cress (Howell and Stipanovic, 1980; Maurhofer et al., 1994b).

The pyoluteorin biosynthetic gene cluster was first described in *P. protegens* Pf-5. It encompasses 17 genes and contains structural genes (*pltABCDEFGLM*) and genes involved in efflux (*pltIJKNOP*) and regulation (*pltZ* and *pltR*) (Gross and Loper, 2009). The cluster is only present in *Pseudomonas* strains that also have *phlD*, either as part of the DAPG operon, as is the case in *P. protegens* or associated with the pyoluteorin gene cluster in *P. aeruginosa* strains. Nanomolar concentrations of phloroglucinol, the precursor of DAPG that is synthesized by PhlD are required for pyoluteorin production, while micromolar concentrations of phloroglucinol inhibit pyoluteorin production

(Kidarsa et al., 2011). Phloroglucinol is transformed by a halogenase encoded in the pyoluteorin gene cluster by *pltM* into chlorinated derivatives that induce expression of pyoluteorin biosynthetic genes via PltR (Yan et al., 2017).

4.4 Pyrrolnitrin

Pyrrolnitrin is a chlorinated phenylpyrrol derived from tryptophan with a broad-spectrum activity against Ascomycete and Basidiomycete fungi (Ligon et al., 2000). Pyrrolnitrin is produced by various bacterial genera, including *Pseudomonas, Burkholderia, Serratia* and *Myxococcus*. The four-gene pyrrolnitrin biosynthetic gene cluster *prnABCD* was first described in *P. chlororaphis* subsp. *aurantiaca* BL915 (previously identified as *P. fluorescens* and *P. aurantiaca*) (Hill et al., 1994; Kirner et al., 1998) and is highly conserved in pyrrolnitrin-producing strains. The cluster is found in *Pseudomonas* biocontrol strains that belong to the *P. protegens* and *P. chlororaphis* subgroup. *Pseudomonas* strains may have obtained this cluster by horizontal gene transfer (Costa et al., 2009). The compound has been used as a lead structure in the development of a new class of agricultural fungicides, the phenylpyrroles (Nyfeler and Ackermann, 1992). The phenylpyrrole fungicides, Fenpiclonil and Fludioxonil, are registered against multiple fungal crop diseases for seed or foliar treatment (Kilani and Fillinger, 2016).

4.5 2-hexyl-5-propyl-alkylresorcinol (HPR)

2-hexyl-5-propyl-alkylresorcinol (HPR) is structurally related to DAPG but the biosynthesis pathway is completely different. The compound is derived from octanoic acid. The biosynthetic gene cluster for HPR was first elucidated in *P. chlororaphis* subsp. *aurantiaca* BL915 and is composed of three biosynthetic genes *darABC* and two regulatory genes *darS* and *darR* (Nowak-Thompson et al., 2003). The biosynthetic gene cluster is present in various biocontrol strains belonging to the *P. chlororaphis* subgroup (Biessy et al., 2019; Calderón et al., 2013). HPR has antifungal and antibacterial activity.

4.6 Hydrogen cyanide (HCN)

Hydrogen cyanide (HCN) is a respiratory poison that inhibits cytochrome c oxidase, the terminal component of the respiratory chain, in many organisms. In prokaryotes, HCN production seems to be restricted to the *Proteobacteria* and to certain cyanobacteria (Blumer and Haas, 2000a). Within the genus *Pseudomonas* known HCN producers can be found in the *P. aeruginosa* group and in various subgroups of the *P. fluorescens* group. Virtually all DAPG producers in the *P. corrugata* and *P. protegens* subgroup also produce HCN and this trait is also common in the *P. chlororaphis* subgroup (Table 1).

A cluster of three genes, *hcnABC*, is responsible for HCN production from the metabolic precursor glycine (Laville et al., 1998). The *hcnABC* cluster appears to be ancestral in *Pseudomonas* strains associated with roots (Frapolli et al., 2012). Cyanogenesis in *Pseudomonas* is regulated by the GacA/GacS signal transduction system (Sonnleitner et al., 2009) and by the anaerobic regulator ANR and is stimulated by iron (Blumer and Haas, 2000b). HCN production by *P. protegens* CHA0 accounts for the suppression of tobacco black root rot caused by *Thielaviopsis basicola* and iron sufficiency is important for both HCN production and disease suppression (Voisard et al., 1989). HCN production by *Pseudomonas* has also been implicated in the suppression of root-knot nematodes (Siddiqui et al., 2006), aphids (Kang et al., 2019), termites (Devi and Kothamasi, 2009) and other insects (Flury et al., 2017). HCN, together with DAPG is also responsible for the biocontrol activity of *P. brassicacearum* LBUM300 against bacterial canker of tomato caused by *Clavibacter michiganensis* subsp. *michiganensis* (Lanteigne et al., 2012; Paulin et al., 2017).

4.7 Biosurfactants

Pseudomonas strains produce two types of biosurfactants:

- rhamnolipids; and
- nonribosomal lipopeptides.

Rhamnolipids are glycolipids typically produced by *P. aeruginosa* and their role in biocontrol has been summarized in D'aes et al. (2010), Olorunleke et al. (2015b) and Crouzet et al. (2020). Lipopeptides are produced by strains in various *Pseudomonas* groups and subgroups (Table 2). They are comprised of an oligopeptide composed of 8–25 amino acids that are N-terminally acylated with a fatty acid. They are produced by nonribosomal peptide synthetases. The vast majority of *Pseudomonas* lipopeptides is not linear but displays a macrolactone ring that contains 4–9 amino acids.

Pseudomonas CLPs have been classified in at least 15 different groups (Table 2) and their biosynthesis, structures and biological functions have been reviewed recently (Geudens and Martins, 2018; Götze and Stallforth, 2020). A complete overview of all described *Pseudomonas* lipopeptides to date can be found in Götze and Stallforth (2020). Many new structures have been unraveled in recent years and their identification is greatly facilitated by genome mining (Paterson et al., 2017). They play a role in swarming motility, biofilm formation, environmental adaptation, nutrient availability, root colonization and biocontrol (D'aes et al., 2010; Olorunleke et al., 2015b; Raaijmakers et al., 2010).

Table 2 Lipopeptides produced by *Pseudomonas* biocontrol strains

Group	AA[1]	Phylogenetic group/subgroup	CLPs involved in biocontrol	Reference
Bananamides	8:6	*P. koreensis* SG	bananamide D-F	Omoboye et al., 2019a
Corrugatin	8	*P. corrugata* SG		
Viscosin	9:7	*P. fluorescens* SG, *P. chlororaphis* SG, *P. putida* G	viscosin, viscosinamide, WLIP, massetolide, pseudodesmin	Omoboye et al., 2019b; Oni et al., 2020a; Thrane et al., 2000; Tran et al., 2007
Syringomycin	9:9	*P. syringae* G, *P. corrugata* SG, *P. mandelii* SG	syringomycin, cormycin, thanamycin, nunamycin	Bull et al., 1998; Michelsen et al., 2015a; Van Der Voort et al., 2015
Orfamide	10:8	*P. protegens* SG, *P. fluorescens* SG	orfamide, poaeamide	Ma et al., 2016a; Zachow et al., 2015
Amphisin	11:9	*P. koreensis* SG	lokisin, rhizoamide	Omoboye et al., 2019b, Hultberg et al., 2010a
Cocoyamide	11:5	*P. koreensis* SG	cocoyamide/gacamide	Jahanshah et al., 2019; Oni et al., 2019a
Putisolvin	12:4	*P. putida* G	putisolvin I, II, III, IV	Kuiper et al., 2003
Entolysin	14:5	*P. putida* G	entolysin	Omoboye et al., 2019b; Oni et al., 2019a; Vallet-Gely et al., 2010a
Xantholysin	14:8	*P. putida* G	xantholysin	Omoboye et al., 2019b; Oni et al., 2019a
Tolaasin	18:5	*P. protegens* SG	sessilin	D'aes et al., 2014; Olorunleke et al., 2015a
Fuscopeptin	19:5	*P. asplenii* SG		
Jessenipeptin	19:5	*P. asplenii* SG		
Corpeptin	22:5	*P. corrugata* SG, *P. mandelii* SG	corpeptin, thanapeptin, nunapeptin	Michelsen et al., 2015a; Van Der Voort et al., 2015
Sclerosin	22	*P. corrugata* SG	sclerosin	Berry et al., 2012a
Syringopeptin (SP22)	22:8	*P. syringae* G		
Syringopeptin (SP25)	25:8	*P. syringae* G		

[1]AA: amino acid, the first figure indicates the number of AA in the peptide chain, the second figure the number of AA in the macrolactone ring.

4.8 Strain-specific bio-active molecules

In addition, various strain-specific bio-active metabolites are only produced by a limited number of *Pseudomonas* bacteria. Gene clusters carrying the biosynthetic genes for these metabolites have most likely been obtained by horizontal gene transfer. Examples are:

- rhizoxins;
- promysalin;
- sessilin; and
- L-furanomycin.

Rhizoxins, produced by a few strains from the *P. protegens* subgroup (Loper et al., 2008; Takeuchi et al., 2015) and *P. chlororaphis* MA342 (Ligon et al., 2000) have activity against fungi and oomycetes. Sessilin is an antifungal cyclic lipopeptide (CLP) that appears to be unique to the biocontrol strain *Pseudomonas* sp. CMR12a (D'aes et al., 2014). Promysalin is a salicylic acid-containing antibiotic produced by *P. putida* RW10S1 (Li et al., 2011) with activity against Gram-positive and Gram-negative bacteria (Kaduskar et al., 2017). L-furanomycin is a non-proteinogenic amino acid found in *P. fluorescens* SBW25 that selectively inhibits Gram-negative plant pathogenic bacteria (Trippe et al., 2013).

4.9 Siderophores

Siderophores are implicated in biocontrol activity by competition for iron, direct antagonism or induced systemic resistance. Most *Pseudomonas* strains produce the fluorescent compound pyoverdine (Meyer, 2000) and about 100 distinct pyoverdines have been identified which are structurally divided into four groups. In addition, many *Pseudomonas* strains produce other siderophores in addition to pyoverdine with a lower affinity for ferric iron than pyoverdine. Their chemical structures are diverse and include pyochelin and enantio-pyochelin, achromobactin, pseudomonine, corrugatin and (thio)quinolobactin (Cornelis, 2010; Schalk et al., 2020).

4.10 Insect toxins

Pseudomonas biocontrol strains that belong to the *P. protegens* and *P. chlororaphis* subgroup interact with insects and produce the insecticidal Fit toxin. This is a large protein toxin related to the insect toxin Mcf of *Photorhabdus* and *Xenorhabdus* spp., bacterial symbionts that live in the intestines of entomophagous nematodes. Fit-toxin producers have oral and injectable insecticidal activity against Lepidoptera larvae. The fit locus comprises eight genes, *fitABCDEFG* and the Fit toxin is the product of *fitD*. The other gene

products are involved in transport and regulation (Flury et al., 2017, 2016; Péchy-Tarr et al., 2008; Ruffner et al., 2015, 2012).

4.11 Regulation of secondary metabolites

Regulation of secondary metabolites in *Pseudomonas* is complex and will not be discussed in detail in this review. Excellent overviews of antibiotic regulation are provided by Haas and Keel (2003) and Sonnleitner and Haas (2011). Most antibiotics with a role in biocontrol are produced only when the GacS/GacA two-component system is active. This regulatory system is widely conserved in Gram-negative bacteria and regulates biocontrol traits or pathogenicity factors post-transcriptionally. Mutations in *gacS* or *gacA* abolish biocontrol activity in the majority of biocontrol *Pseudomonas* strains. A good introduction can be found in Haas and Défago (2005). On interaction with bacterial signal molecules, which are presumably intermediates of the Krebs cycle (Takeuchi et al., 2009), GacS is autophosphorylated and a phosphate residue is transferred to GacA. This activates the transcription of small RNA genes. These RNAs bind to small proteins that function as post-transcriptional repressors of biocontrol genes. This relieves the translational repression exerted by these proteins at or near the ribosome-binding sites of the target mRNA (Sonnleitner and Haas, 2011).

Spontaneous mutants in *gacA* or *gacS* contribute to the genetic instability of some *Pseudomonas* strains, which is obviously a problem in biocontrol. Particular strains that produce a large number of secondary metabolites accumulate a high proportion of Gac$^-$ mutants in culture (Yan et al., 2018). Colony variants that exhibit a Gac$^-$ phenotype are easy to recognize because they have an increased colony size, are more flat and more fluorescent due to overproduction of pyoverdine (Duffy and Defago, 2000).

5 Secretion systems that play a role in biocontrol

5.1 Type III secretion systems

Many Gram-negative bacteria can interact with diverse eukaryotic hosts via a type III secretion system. This is a protein secretion system that originates from the bacterial flagellar system and spans the two membranes in Gram-negative bacteria. Through this system so-called effector proteins can be secreted directly in the cytoplasm of the host. The type III secretion system plays a role in both parasitic and mutualistic interactions and is found in various *Pseudomonas* biocontrol strains.

T3SS genes are present in *Pseudomonas* biocontrol strains belonging to the *P. fluorescens* and *P. corrugata* subgroups and are enriched in the rhizosphere as compared to corresponding bulk soil. T3SS is involved in interactions with phytopathogens, mycorrhizal fungi and predators (Nazir et al., 2017). Most

Pseudomonas bacteria contain a T3SS that belongs to the Hrp1 family, but some strains also have an additional T3SS that belongs to the SPI-1 family. SPI-1 type T3SS was first identified in *P. fluorescens* F113, a well-studied biocontrol strain of the *P. corrugata* subgroup and enhances resistance to amoeboid grazing (Barret et al., 2013). The Hrp1-type T3SS of *P. fluorescens* strain KD targets the oomycete pathogen *Pythium ultimum,* promoting cucumber protection (Rezzonico et al., 2005). The role of the T3SS in other beneficial *Pseudomonas* bacteria remains elusive, but it was suggested that effectors delivered via this system may suppress host immunity to facilitate root colonization (Yu et al., 2019).

5.2 Type VI secretion systems

Another secretion system that is commonly found in commensal, symbiotic and pathogenic plant-associated bacteria is the type VI secretion system. This secretion system is used to inject toxic effectors in eukaryotic and prokaryotic cells and is involved in interbacterial competition. T6SS clusters are widely distributed in the genus *Pseudomonas* and especially enriched in the *P. putida* group (Bernal et al., 2018). The biocontrol strain *P. putida* KT2440 contains three T6SSs and various T6SS effectors and the systems are used to outcompete various phytopathogenic bacteria in vitro and in planta (Bernal et al., 2017).

6 *Pseudomonas* biocontrol strains: *Pseudomonas protegens* subgroup

Pseudomonas protegens was formally described by Ramette et al. (2011) and comprises isolates that produce the secondary metabolites DAPG and pyoluteorin. Most *P. protegens* strains also produce HCN, pyrrolnitrin, the CLP orfamide and two siderophores: pyoverdine and enantio-pyochelin. The species has insecticidal activity (Flury et al., 2016) and some isolates contain additional gene clusters encoding rhizoxin analogues (Loper et al., 2008) and toxoflavin (Philmus et al., 2015). Isolates belonging to this species have been obtained from the rhizosphere of tobacco, cotton, wheat (Ramette et al., 2011), canola (Zhang et al., 2020b), tomato, cucumber and shepherd's purse (Takeuchi et al., 2014). They have also been found on the phyllosphere of lemon (Michavila et al., 2017) and wheat (Levy et al., 1992), in stored rice grains (Jeong et al., 2018), on lamb's lettuce in hydroponics (Moruzzi et al., 2017), in recycled irrigation water (Yang and Hong, 2020) and on brown macroalga in the Baltic sea (Heiman et al., 2020). Recently it was shown that *P. protegens* can also survive in insects (Flury et al., 2019).

Much of our knowledge about *P. protegens* comes from two of the best-studied biocontrol strains: *P. protegens* Pf-5 and *P. protegens* CHA0. Both strains have become models and many biocontrol traits in *Pseudomonas* were first

discovered in these strains. Also our knowledge about the complex regulation of secondary metabolites in *Pseudomonas* biocontrol strains was largely obtained from these two strains (Haas and Défago, 2005; Haas and Keel, 2003).

P. protegens Pf-5 was obtained from cotton roots in Texas and suppresses *Rhizoctonia solani* and *Pythium ultimum* on cotton (Howell and Stipanovic, 1980, 1979). It also controls a variety of other diseases such as fungal diseases on wheat (Pfender et al., 1993) and turfgrass (Rodriguez and Pfender, 1997), Fusarium crown and root rot of tomato (Sharifi-Tehrani et al., 1998) and seed piece decay of potato (Xu and Gross, 1986) (see Table 3). *P. protegens* Pf-5 was the first biocontrol strain of which the whole genome was sequenced (Paulsen et al., 2005). Pf-5 produces the typical *P. protegens* antibiotics HCN, DAPG, pyrrolnitrin and pyoluteorin (Loper et al., 2007). The CLP orfamide was first discovered in *P. protegens* Pf-5 by a combination of genome sequence analysis and isotope-guided fractionation (Gross et al., 2007). Further genome mining revealed the capacity to produce two additional antibiotics: rhizoxin (Loper et al., 2008) and toxoflavin (Philmus et al., 2015).

Rhizoxin is a polyketide macrolide with antifungal, phytotoxic and antitumor properties and binds to ß-tubulin. Rhizoxin-producing endosymbionts have been found in the rice-pathogenic fungus *Rhizopus microspores*. Rhizoxin is the causative agent of rice seedling blight and inhibits mitosis in seedling roots. Rhizoxin biosynthesis genes were first described from the *Rhizopus* endosymbiont *Burkholderia rhizoxina* (Partida-Martinez and Hertweck, 2007) and they are orthologous to the biosynthesis genes found in *P. protegens* Pf-5. The main rhizoxin produced by Pf-5 inhibits the growth of the plant pathogenic fungus *Fusarium oxysporum* (Brendel et al., 2007).

Toxoflavin has antibiotic activity against bacteria and fungi and is phytotoxic against a broad range of monocot and dicot plants. The compound is produced by the plant pathogenic bacteria *Burkholderia glumae* and *B. gladioli* and is a key virulence factor. The toxoflavin gene cluster in Pf-5 shows substantial differences with the *tox* genes from *Burkholderia*. The Pf-5 strain produces trace amounts of toxoflavin with antibiotic activity against various plant pathogenic bacteria (Philmus et al., 2015).

P. protegens CHA0 was isolated from the roots of 7-week-old tobacco plants grown in soil from Morens, Switzerland, with natural suppressiveness to black root rot caused by *Thielaviopsis basicola* (Stutz et al., 1986). Since then, it was shown that strain CHA0 can protect many crop plants including wheat, cucumber, sugar beet, cotton, flax, corn and cress from oomycete and fungal pathogens (Voisard et al., 1994) (Table 3). In addition, *P. protegens* CHA0 can induce systemic resistance to *Hyaloperonospora* in *Arabidopsis* (Iavicoli et al., 2003), root-knot nematodes in tomato (Siddiqui and Shaukat, 2003), *Tobacco Necrosis Virus* in tobacco (Maurhofer et al., 1994a) and *Banana Bunchy Top Virus* in banana (Kavino et al., 2008). Biocontrol traits of *P. protegens* CHA0

Table 3 Selected *P. protegens* group biocontrol strains

Strain	Origin	Activity	Metabolites	Genome sequence	References
P. protegens					
CHA0	black root rot suppressive soil, Switzerland	Tb, TNV, tobacco; Pu, cucumber, wheat and cress; Gg, wheat; Mj and Mp, tomato; BBT, banana; Ha, Arabidopis, insecticidal activity	**DAPG, FIT, HCN, PLT, PRN PCH, PVD, ORF**	Jousset et al., 2014; Smits et al., 2019	Flury et al., 2017, 2016; Kavino et al., 2008; Keel et al., 1992; Maurhofer et al., 1994a; Siddiqui et al., 2006;Stutz et al., 1986; Voisard et al., 1994
Pf-5	cotton rhizosphere, Texas, USA	Rs, cotton; Pu, cotton; Pt, wheat straw; Sh and Dp, turfgrass; Fo, tomato; Pc, potato; insecticidal activity	**DAPG, FIT, HCN, PLT, PRN, PCH, PVD, ORF, RZX, TXF**	Loper et al., 2007; Paulsen et al., 2005	Howell and Stipanovic, 1980, 1979; Pfender et al., 1993; Rangel et al., 2016; Rodriguez and Pfender, 1997; Xu and Gross, 1986
Pf4	roots from hydroponic lamb's lettuce plants, Italy	Rs, lamb's lettuce,	FIT, HCN, ORF, PLT, PVD, PRN, RZX	Polano et al., 2019	Moruzzi et al., 2017; Polano et al., 2019
Cab57	rhizosphere of shepherd's purse, Japan	Pu, cucumber	DAPG, FIT, HCN, PLT, PRN, ORF, PCH, PVD, FIT	Takeuchi et al., 2014	Takeuchi and Someya, 2019
PF	Wheat leaves, Oklahoma, USA	Zt, wheat, insecticidal activity	**DAPG**, HCN, PRN, PLT, RZX, **FIT**	Flury et al., 2016	Levy et al., 1992
Related to *P. protegens*					
CMR12a	rhizosphere of red cocoyam, Cameroon	Pm, cocoyam; Rs, bean and cabbage, Po, rice; Bo, rice; insecticidal activity	**PCA, PCN, SES, ORF, FIT**, HCN	Biessy et al., 2019	D'aes et al., 2014, 2011; Flury et al., 2016; Ma et al., 2017; Z. Ma et al., 2016b; Oni et al., 2019b; Perneel et al., 2007

CMR5c	rhizosphere of red cocoyam, Cameroon	Pm, cocoyam, insecticidal activity	DAPG, **FIT,** HCN, ORF, PCA, PCH, PCN, PLT, PRN,	Biessy et al., 2019	Biessy et al., 2019; Flury et al., 2016; Perneel et al., 2007
OS17	rhizosphere of rice, Japan	Pu, cucumber	DAPG, FIT, HCN, PCH, **RZX**	Takeuchi et al., 2015	Takeuchi et al., 2015

Abbreviations: Pathogens: *BBT: Banana Bunchy Top Virus, Bo: Bipolaris oryzae, Dp: Drechslera poae: Fo: Fusarium oxysporum, Gg: Gaeumannomyces graminis var. tritici, Ma: Macrophomina phaseolina, Mj: Meloidogyne javanica, Pm: Pythium myriotylum, Po: Pyricularia oryzae, Pu: Pythium ultimum, Pst: Pseudomonas syringae pv. tomato; Pt: Pyrenophora tritici-repentis, Rs: Rhizoctonia solani, Sh: Sclerotinia homeocarpa, Tb: Thielaviopsis baticola, TNV: Tobacco Necrosis Virus, Zt: Zymoseptoria tritici.* Metabolites: DAPG: 2,4- diacetylphloroglucinol, HCN: hydrogen cyanide, FIT: insecticidal toxin, ORF: orfamide, PCA: phenazines-1-carboxylate, PCH: pyochelin, PCN: phenazines-1-carboxamide; PLT: pyoluteorin, PRN: pyrrolnitrin, RZX: rhizoxin, TXF: toxoflavin. For metabolites in bold a role in biocontrol has been shown.

have been investigated in great detail. The strain produces the antibiotics HCN, DAPG, pyrrolnitrin, pyoluteorin (Haas and Défago, 2005), orfamide-type CLPs (Ma et al., 2016a), the siderophores pyoverdine and enantio-pyochelin (Youard et al., 2007), and various traits involved in insect toxicity (Flury et al., 2017, 2016). Mutant analysis has revealed that suppression of the different plant diseases involves different mechanisms. HCN and DAPG are involved in black root rot control, DAPG, but not HCN is needed for take-all control, while pyoluteorin is responsible for *Pythium* control (Voisard et al., 1994). Determinants that trigger ISR include DAPG and pyoverdine (De Vleesschauwer and Höfte, 2009).

In nutrient-rich cultures both *P. protegens* Pf-5 and *P. protegens* CHA0 readily accumulate Gac⁻ mutations that completely abolish their biocontrol capacities (Bull et al., 2001; Duffy and Defago, 2000; Yan et al., 2018). Cultures of mutants of *P. protegens* Pf-5 unable to produce pyoluteorin or orfamide accumulated a smaller number of Gac⁻ mutants. Pyoluteorin biosynthesis, but not pyoluteorin itself, contributed significantly to accumulation of Gac⁻ mutants. However, few of these mutants accumulated in the presence of the competitor *Bacillus subtilis* (Yan et al., 2018).

Other *P. protegens* biocontrol strains have been obtained from North America, Europe and Japan and examples are given in Table 3. *P. protegens* CAB 57 originates from the rhizosphere of shepherd's purse in Japan and is active against *P. ultimum* in cucumber (Takeuchi et al., 2014). At least in Japan *P. protegens* strains do not seem to be very common. In a screen of 2800 *Pseudomonas* isolates from the rhizosphere of various plants in Japan, only 5 isolates belonged to the *P. protegens* subgroup (Takeuchi and Someya, 2019). *P. protegens* bacteria were not prevalent either in a collection of 698 *Pseudomonas* isolates from the maize rhizosphere in France and Switzerland (Vacheron et al., 2016). Their high level of effectiveness in short-term greenhouse trials may be counterbalanced by lower rhizosphere competitiveness and survival under field conditions. This suggests a trade-off between rhizosphere prevalence and the ability to produce a large number of plant-beneficial properties (Vacheron et al., 2016).

The *Pseudomonas* strain Os17 isolated from the rhizosphere of rice belongs to the *P. protegens* subgroup but is clearly different from the species *P. protegens*. This strain contains the biosynthetic gene clusters for HCN, DAPG, rhizoxin, pyoverdine and enantio-pyochelin, but gene clusters for pyrrolnitrin, pyoluteorin and orfamide are absent. The strain suppresses damping-off and root rot caused by *P. ultimum* on cucumber. Mutant analysis revealed that rhizoxin is important in *Pythium* biocontrol (Takeuchi et al., 2015).

Pseudomonas sp. CMR12a and CMR5c have been obtained from the rhizosphere of red cocoyam in Cameroon and have antagonistic activity against *Pythium myriotylum*, the causal agent of the destructive cocoyam root rot disease (Perneel et al., 2007). They belong to the *P. protegens* group, but

are clearly different from the core *P. protegens* strains (Biessy et al., 2019; Flury et al., 2016). In terms of biocontrol traits they have characteristics of both *P. protegens* and *P. chlororaphis*. Both strains produce the phenazines PCA and PCN, metabolites that are typically produced by *P. chlororaphis* group strains. CMR5c also has the typical *P. protegens* biosynthetic gene clusters for DAPG, PLT and PRN (Biessy et al., 2019; Flury et al., 2016; Perneel et al., 2007).

Both strains produce orfamide-type CLPs (Ma et al., 2016a). In addition, CMR12a produces an unusual CLP, sessilin, which is closely related to tolaasin, a CLP produced by the mushroom pathogen *P. tolaasii* (D'aes et al., 2014). Analysis of their whole genome has revealed that the phenazine biosynthetic gene cluster in both strains is located on a genomic island. In case of CMR12a, this genomic island also contains the sessilin biosynthetic gene cluster which is absent in CMR5c.

Recently, various isolates closely related to CMR12a were found on the root of tissue-cultured derived cocoyam plantlets that had been grown for 2 or 4 weeks in the cocoyam root rot suppressive soil from Boteva, Cameroon. Some of these isolates did not carry the genomic island and did not produce phenazines or sessilin. Intriguingly, these isolates hardly colonized the roots of 8-week-old cocoyam plantlets, indicating that these strains are associated with young cocoyam plantlets only (Omoboye, 2019).

Biocontrol activity of *Pseudomonas* sp. CMR12a has been studied in detail. The strain controls damping-off disease on Chinese cabbage caused by *R. solani* AG 2-1 and root rot disease on bean caused by *R. solani* AG 4-HI. In cabbage, phenazines alone were sufficient to suppress *Rhizoctonia* damping-off, whereas co-production of sessilins and orfamides was required in the absence of phenazines. To suppress *R. solani* on bean, co-production of phenazines, sessilins and orfamides appeared to be important (Olorunleke et al., 2015a). All three metabolites are involved in the suppression of *P. myriotylum* on cocoyam (Oni et al., 2019b). The strain induces resistance to fungal pathogens in rice and bean. Phenazines are solely involved in ISR against the rice blast fungus *P. oryzae*, while phenazines, orfamide and sessilin can trigger ISR in bean against web blight disease caused by *R. solani* AG 2-2 (Ma et al., 2016b). Orfamide at high concentrations is responsible for ISR in rice against the brown spot pathogen *Bipolaris oryzae* (Teleomorph: *Cochliobolus miyabeanus*), but is not effective against the rice blast pathogen *Pyricularia oryzae* (Ma et al., 2017).

The insecticidal activity of *P. protegens* subgroup strains, including *P. protegens* Pf-5, *P. protegens* CHA0, *Pseudomonas* sp. CMR12a and *Pseudomonas* sp. CMR5c, has intensively been studied but will not be further discussed here. Virulence factors that contribute to insect pathogenicity include the Fit toxin, HCN, cyclic lipopeptides, rhizoxins and secreted lytic enzymes (Flury et al., 2017, 2016; Rangel et al., 2016). In addition the T6SS contributes

to insect pathogenicity of *P. protegens* in oral infection assays (Vacheron et al., 2019).

7 *Pseudomonas* biocontrol strains: *Pseudomonas chlororaphis* subgroup

P. chlororaphis isolates have been obtained from soil and the rhizosphere of crops such as tomato, potato, maize, radish, beet, alfalfa, soja and clover (Biessy et al., 2019); the stem of sugarcane (Mehnaz et al., 2009); and roots of avocado (Cazorla et al., 2006). The species is divided in four subspecies: *aureofaciens*, *aurantiaca*, *chlororaphis* (Peix et al., 2007) and *piscium*. *P. chlororaphis* subsp. *piscium* was proposed to accommodate two isolates from the intestines of perch and rainbow trout (Burr et al., 2010), but various rhizosphere isolates also cluster in this subspecies (Biessy et al., 2019). Secondary metabolite production in the *P. chlororaphis* subgroup has been studied by Biessy et al. (2019).

All *P. chlororaphis* isolates produce PCA and HCN, but the subspecies differ in the type of phenazines produced and in the production of other secondary metabolites. The subspecies *aureofaciens* and *aurantiaca* produce 2-OH-PCA, the *piscium* subspecies produces PCN, while isolates belonging to the *chlororaphis* subspecies produce either PCN or 2-OH-PCA. All subspecies, except subsp. *piscium* also produce pyrrolnitrin and HPR. NRPS clusters for the production of lipopeptides from the Viscosin group are commonly found in the subspecies *piscium*, *aurantiaca* and *chlororaphis*, but not in the subspecies *aureofaciens*. Many *P. chlororaphis* strains produce two siderophores, pyoverdine and achromobactin. More details can be found in Biessy et al. (2019).

Biocontrol activities of *P. chlororaphis* isolates have been studied extensively and various commercially available biopesticides belong to this species (see Table 6). The biocontrol capacities of *P. chlororaphis* have been reviewed by Anderson and Kim (2020, 2018). *P. chlororaphis* isolates directly control fungi, nematodes, oomycetes and aphids and can induce resistance to fungal and bacterial leaf pathogens. Metabolites involved in biological control activity include phenazines, HCN, pyrrolnitrin, HPR and 2,3-butanediol (Table 4). Well-studied strains include *P. chlororaphis* subsp. *aureofaciens* O6, *P. chlororaphis* subsp. *piscium* PCL1391, *P. chlororaphis* 30-84 and *P. chlororaphis* PCL1606. These and other strains are listed in Table 4.

The role of phenazines in biocontrol has been studied in various *P. chlororaphis* strains. PCA is involved in the suppression of take-all disease of wheat as was shown for *P. chlororaphis* 30-84 (Pierson and Thomashow, 1992). PCN is clearly more effective than PCA in the biocontrol activity against *F. oxysporum* f. sp. *radicis-lycopersici* in tomato. *P. chlororaphis* PCL1391 was active in this pathosystem in contrast to PCA-producing strains such as *P. chlororaphis* 30-84 (Chin-A-Woeng et al., 1998). This has been explained by the fact that PCN is still

Table 4 Selected *P. chlororaphis* group biocontrol strains

Strain	Origin	Activity	Biocontrol metabolites	Genome sequence	References
O6 (subsp. *aurofaciens*)	soil, Utah, USA	Pc and Pstb, tobacco; Cc, cucumber; TMV, tobacco; rkn, tomato, aphids	**BTD, HCN**, PCA, 2-OH-PCA, PRN, HPR	Loper et al., 2012	Han et al., 2006; Kang et al., 2019, 2018; Kim et al., 2004; Lee et al., 2011; Park et al., 2012
PCL1391 (subsp. *piscium*)	rhizosphere tomato, Spain	Fo, tomato; Fo, watermelon; Cl, bean	**PCN**, PCA, HCN, CLP of the Viscosin group	Biessy et al., 2019	Bardas et al., 2009; Biessy et al., 2019; Chin-A-Woeng et al., 1998; Tziros et al., 2007
PCL1606	rhizosphere avocado, Spain	Dn, avocado; Fo, tomato	**HPR**, PRN, HCN	Calderón et al., 2015	Arrebola et al., 2019; Calderón et al., 2015; Cazorla et al., 2006
30-84	wheat rhizosphere, Washington, USA	Gg, wheat	**PCA, 2-OH-PCA,** PRN, HCN, HPR	Loper et al., 2012	Pierson and Thomashow, 1992
Pb-St2	sugarcane stem, Pakistan	Cf, sugarcane	PCA, 2-OH-PCA, PRN, HCN, HPR, WLIP	Mehnaz et al., 2014	Mehnaz et al., 2013, 2009
JD-37	potato rhizosphere, Shanghai, China	Bm, maize	PHZ, PRN, HCN,	Jiang et al., 2014	Fang et al., 2013
R47	potato rhizosphere, Zurich, Switzerland	Pi, potato	PCA, 2-OH-PCA, PRN, HCN, HPR	De Vrieze et al., 2020	De Vrieze et al., 2020; Hunziker et al., 2015
G05	Pepper rhizosphere, China	Fg, wheat; Fo, cucumber	**PRN, PCA**		Chi et al., 2017; Huang et al., 2018

Abbreviations: Pathogens: *Bm: Bipolaris maydis, Cc: Corynespora cassicola, Cf: Colletotrichum falcatum, Cl: Colletotrichum lindemuthianum, Dn: Dematophora necatrix, Fg: Fusarium graminearum, Fo: Fusarium oxysporum, Gg: Gaeumannomycis graminis var. tritici, Pi: Phytophthora infestans, Pc: Pectobacterium carotovorum, Pstb: Pseudomonas syringae pv. tobacco;* rkn: root knot nematodes. Metabolites: BTD: 2,3-butanediol, HCN: hydrogen cyanide, PCA: phenazines-1-carboxylate, 2-OH-PCA; PRN: pyrrolnitrin, HPR: 2-hexyl-5-propyl-alkylresorcinol. For metabolites in bold a role in biocontrol has been shown.

active at a pH of 5.7 and higher, while the antagonistic activity of PCA drastically decreases at this pH because the anionic form of PCA will predominate. This means that PCA-producing bacteria are most active at acidic pH.

P. chloraphis Pcho10 was obtained from *Fusarium* spp.-infested wheat heads in China. This strain strongly reduced *F. graminearum* infections on wheat heads in growth chamber and field conditions and predominantly produces PCN. PCN appeared to be the major compound responsible for activity against *F. graminearum* (Hu et al., 2014). In case of *P. chloraphis* G05 (Table 4), PCA contributed to the ability to suppress *F. oxysporum* on cucumber (Chi et al., 2017), but pyrrolnitrin rather than PCA was essential to control *Fusarium* head blight on wheat caused by *F. graminearum* (Huang et al., 2018).

P. chloraphis O6 is known to induce systemic resistance to bacterial and fungal pathogens and stimulates aerial growth. The strain produces the volatile 2, 3-butanediol, a metabolite also known from *Bacillus* spp. The compound is responsible for aerial growth stimulation and ISR against *P. carotovorum* (Han et al., 2006). Genes involved in 2,3-butanediol biosynthesis are also present in the genomes of other *P. chloraphis* strains (Biessy et al., 2019). In this strain HCN production is involved in nematicidal (Kang et al., 2018; Lee et al., 2011) and aphicidal activity (Kang et al., 2019).

The role of HPR in biocontrol has been investigated in *P. chloraphis* PCL1606. This isolate was obtained from a screening of rhizosphere bacteria obtained from healthy avocado roots for in vitro antagonism against *Dematophora necatrix* (teleomorph: *Rosellinia necatrix*), the causal agent of white root rot on avocado and various other fruit trees and crops (Cazorla et al., 2006). In contrast to other *P. chloraphis* biocontrol strains, PCL1606 does not produce phenazines. The *dar* genes, responsible for HPR production in PCL1606, are highly homologous to the *dar* genes present in *P. chloraphis* subsp. *aurantiaca* BL915. Mutants in HPR are impaired in antagonistic activity in an avocado-*D. necatrix* and a tomato-*F. oxysporum* f. sp. *radicis-lycopersici* pathosystem (Calderón et al., 2013). The HPR biosynthetic gene cluster is present in various other *P. chloraphis* biocontrol strains including *P. chloraphis* 30-84 and *P. chloraphis* O6 (Calderón et al., 2013). Biessy et al. (2019) showed that the HPR biosynthetic cluster is present in the subspecies *aureofaciens*, *aurantiaca* and *chloraphis*, but not in the subspecies *piscium*. HPR plays a key role in biofilm production in *P. chloraphis* PCL1606 (Calderón et al., 2019).

8 *Pseudomonas* biocontrol strains: *Pseudomonas corrugata* subgroup

The *Pseudomonas corrugata* subgroup as defined by Garrido-Sanz et al. (2016) and Hesse et al. (2018) comprises the plant pathogenic species *P. corrugata* and *P. mediterranea* and plant beneficial isolates that are classified as *P.*

brassicacearum, *P. kilonenis* or *P. thivervalensis*. This group is called the 'bcm clade' (Melnyk et al., 2019). *P. corrugata* and *P. mediterranea* are closely related and both cause stem pith necrosis on tomato and pepper. *P. corrugata* has also been reported on chrysanthemum and geranium (Catara, 2007). The line between plant-pathogenic and beneficial isolates in this subgroup is very thin (Gislason and de Kievit, 2020).

P. corrugata strains have been isolated from soil and from the rhizosphere of non-diseased plants in various countries (see Catara (2007) for an overview). These strains show activity against a wide range of soilborne fungal, bacterial and oomycete pathogens and postharvest fungal pathogens on fruits. Some *P. corrugata* strains have been patented for biocontrol. *P. corrugata* produces the antimicrobial and phytotoxic CLPs corpeptin A and corpeptin B with 22 amino acid residues, and cormycin, with 9 AA residues (Emanuele et al., 1998; Strano et al., 2015). Pith necrosis symptoms are strongly reduced in mutants unable to produce these compounds. Biocontrol activity in *P. corrugata* and *P. mediterranea* is mediated by these CLPs and volatiles such as HCN (Strano et al., 2017). *P. corrugata and P. mediterranea* strains do not produce the fluorescent siderophore, pyoverdine (Gislason and de Kievit, 2020).

Beneficial isolates within the *P. corrugata* subgroup have been classified as:

- *P. brassicacearium*
- *P. kilonensis*
- *P. thivervalensis*

P. brassicacearum and *P. thivervalensis* were first described by Achouak et al. (2000), while the species *P. kilonensis* was delineated in 2001 (Sikorski et al., 2001). These three species are closely related and it has been suggested that *P. kilonensis* should be considered as a junior synonym of *P. brassicacearum* (Tran et al., 2017). These species generate pyoverdine in contrast to *P. corrugata* and *P. mediterranea*. *P. brassicacearum*-like organisms are frequently found in soils that are disease-suppressive against take-all caused by *G. graminis* var. *tritici* in wheat. Isolates also have been obtained from agricultural soil or rhizosphere of other crops such as canola, potato, strawberry and tomato. They usually show excellent biocontrol capabilities. Many isolates that belong to these species produce the antibiotic DAPG.

Well-studied DAPG-producing strains in the *P. corrugata* subgroup include *Pseudomonas fluorescens* F113 (also called *P. kilonensis* F113), which was originally isolated from the root hairs of a sugar beet plant in Ireland (Shanahan et al., 1992) and *Pseudomonas fluorescens* Q2-87 (originally called *P. aureofaciens* Q2-87) obtained from wheat roots in a suppressive soil in Washington (Harrison et al., 1993). The species name of both isolates is in need of revision since they clearly belong to the *P. corrugata* subgroup (Garrido-Sanz

et al., 2016). *Pseudomonas* strain Q2-87 produces DAPG and HCN but only DAPG contributes to its in vitro biocontrol activity against *G. graminis* var. *tritici* (Vincent et al., 1991).

Pseudomonas strain F113 is an excellent rhizosphere colonizer with biocontrol activity against various bacteria, fungi and nematodes including *P. carotovorum* (Cronin et al., 1997a), *F. oxysporum* (Barahona et al., 2011), *P. ultimum* (Fenton et al., 1992) and *Globodera* spp. (Cronin et al., 1997b). Biocontrol activity in this strain is strongly linked to the production of DAPG (Redondo-Nieto et al., 2013). The capacity to produce DAPG is lost in the pathogenic species, *P. corrugata* and *P. mediterranea*, probably because this compound can elicit ISR in plants (Almario et al., 2017).

A subset of *P. brassicacearum* strains does not produce DAPG but contain lipopeptide-encoding NRPS gene clusters located on a genomic island, which has been called the LPQ island by Melnyk et al. (2019). These lipopeptides are very similar to cormycin and corpeptins produced by *P. corrugata*. However, unlike corpeptin, which is a cyclic lipopeptide, sclerosin produced by *P. brassicacearum* DF41 is linear (Berry et al., 2012). *P. brassicacearum* DF41 isolated from canola root tips in Canada (Savchuk and Fernando, 2004) can protect canola against *Sclerotinia sclerotium* which is due to the production of sclerosin (Berry et al., 2010).

Pseudomonas sp. SH-C52 produces lipopeptides that have been characterized as thanapeptin and thanamycin. *Pseudomonas* sp. SH-52 has been found in soils with natural suppressiveness to the fungal pathogen *R. solani* (Mendes et al., 2011). Thanamycin is implicated in the antagonistic activity of SH-52 against *Sclerotium rolfsii* on groundnut (Le et al., 2012) and shows activity against various other fungi in vitro. Thanapeptin is active against oomycetes. Besides thanamycin and thanapeptin, this strain produces a 2-amino acid lipopeptide, brabantamide, with activity against Gram-positive bacteria and oomycetes (Van Der Voort et al., 2015).

SH-52 is closely related to *P. mediterranea* and *P. corrugata* and, like these species, lacks the capacity to produce pyoverdine, but has the biosynthetic gene clusters for the siderophores, achromobactin and corrugatin. Various other *Pseudomonas* strains of the *P. corrugata* group have biosynthetic gene clusters for thanamycin or thanapeptin-like CLPs. More information about lipopeptide production in the *P. corrugata* subgroup can be found in Girard et al. (2020a). Gislason and de Kievit (2020) have mined the genomes of 21 *P. brassicacearum* strains for regions associated with plant beneficial traits and pathogenicity. They found a negative correlation between DAPG and lipopeptide production; strains that produce lipopeptides do not produce DAPG. Selected biocontrol strains belonging to the *P. corrugata* subgroup are listed in Table 5.

Table 5 Selected *P. corrugata* group biocontrol strains

Strain	Origin	Activity	Metabolites	Genome sequence	References
Q2-87	wheat rhizosphere of TAS soil, Washington, USA	Gg, wheat; Pst, *Arabidopsis*	DAPG, HCN, PVD	Loper et al., 2012	Harrison et al., 1993; Weller et al., 2012
F113	root hairs of sugar beet, Ireland	Pc, Fo, Pu, *Globodera* sp.	DAPG, HCN, PVD	Redondo-Nieto et al., 2012	Barahona et al., 2011; Cronin et al., 1997b, 1997a; Fenton et al., 1992; Shanahan et al., 1992
Q8r1-96	wheat rhizosphere of TAS soil, Washington, USA	Gg, wheat	DAPG, HCN, PVD	Loper et al., 2012	
DF41	canola root tips, Canada	Ss, canola	Sclerosin, HCN	Loewen et al., 2014	Berry et al., 2012, 2010; Savchuk and Fernando, 2004
SH-C52	*R. solani* suppressive soil, the Netherlands	Rs, sugar beet	ACH, COR, BRB, HCN, THM, THP	Van Der Voort et al., 2015	Le et al., 2012; Mendes et al., 2011; Van Der Voort et al., 2015

Abbreviations: Pathogens: *Fo*: *Fusarium oxysporum*, *Gg*: *Gaeumannomyces graminis* var. *tritici*, *Pc*: *Pectobacterium carotovorum*, *Pst*: *Pseudomonas syringae* pv. *tomato*, *Pu*: *Pythium ultimum*, *Rs*: *Rhizoctonia solani*, *Ss*: *Sclerotinia sclerotiorum*. Metabolites: ACH: achromobactin, BRB: brabantamide, COR: corrugatin, DAPG: di-acetyl-phloroglucinol, HCN: hydrogen cyanide, THM: thanamycin, THP: thanapeptin. TAS: take-all suppressive.

9 *Pseudomonas* biocontrol strains: *Pseudomonas fluorescens* subgroup

P. fluorescens forms a large subgroup within the *P. fluorescens* group. At least 20 described type species cluster within this group but many genomes that fall within this subgroup are distinct from the type species. Various well-known and intensively studied biocontrol strains belong to this subgroup. These include two of the so-called Dutch strains that were isolated in the 1980s at the Dutch Phytopathological Laboratory 'Willy Commelin Scholten', WCS374 obtained from the rhizosphere of potato (Geels and Schippers, 1983) and WCS417 from the rhizosphere of wheat grown in a field suppressive to take-all disease (Lamers et al., 1988). These strains have intensively been studied for their plant-growth-promoting and biocontrol abilities. Whole-genome sequencing has clarified their taxonomic position (Berendsen et al., 2015). WCS417 belongs to the species *P. simiae*. WCS374 is closely related to the biocontrol strains *Pseudomonas* sp. A506 isolated from the pear phyllosphere in California, USA (Stockwell and Stack, 2007) and *Pseudomonas* sp. SS101 from the rhizosphere of wheat in the Netherlands (de Souza et al., 2003). It has been proposed to group these strains under the new species name *P. defensor* with WCS374 as the type strain.

P. simiae* WCS417 has intensively been studied for its capacity to trigger induced systemic resistance in *Arabidopsis*, grapevine, radish, banana, bean, carnation and tomato. *P. defensor* WCS374 does not trigger ISR in *Arabidopsis* or grapevine, but is able to do so in Eucalypt, radish and rice (reviewed by De Vleesschauwer and Höfte, 2009). Biocontrol activity of these strains is linked to siderophore-mediated competition for iron by pyoverdines. Pyoverdines have also been implicated in the capacity of these strains to elicit ISR, reviewed by Lemanceau et al. (2009). The strains produce bacteriocins, but no antibiotics or CLPs. In addition, the genomes of both strains contain two T6SS loci. Both *P. simiae* WCS417 and *P. defensor* WCS374 possess a type III secretion system and putative effectors have been identified by genome mining (Berendsen et al., 2015). Highly similar T3SS clusters to WCS374 have been found in A506 and SS101 (Stringlis et al., 2019). These T3SS gene clusters are quite distinct from T3SS clusters in phytopathogenic *Pseudomonas* bacteria. Unlike pathogenic bacteria that contain a T3SS cluster, these strains do not trigger a hypersensitive response in tobacco leaves. The presence of T3SS in beneficial rhizosphere bacteria suggests a possible involvement in the suppression of root immune responses, facilitating root colonization.

According to Hesse et al. (2018), another strain that belongs to the same clique group as *P. simiae* WCS417 is *P. fluorescens* PICF7, an endophyte of olive roots and an effective biocontrol agent against *Verticillium* wilt of olive. A cysteine auxotrophic mutant of PICF7 had a reduced root colonization

capacity and lost full biocontrol efficacy in olive but was not impaired in the inner colonization of olive root tissues. Swimming motility and pyoverdine production were not involved in endophytic colonization and biocontrol (Maldonado-Gonzalez et al., 2015).

Specific strains within the *P. fluorescens* subgroup are known to produce CLPs that belong to the Viscosin group (viscosin, massetolide, WLIP, viscosinamide) (Oni et al., 2020a). Well-studied strains in this aspect include the massetolide producer *P. fluorescens (lactis)* SS101 and the viscosin-producer *P. fluorescens* SBW25.

P. fluorescens (lactis) SS101 is a plant growth-promoting bacterium and has biocontrol activities against *Pythium intermedium* root rot of flower bulbs (de Souza et al., 2003), tomato late blight caused by *P. infestans* (Tran et al., 2007), *P. syringae* pv. *tomato* and *Spodoptera exigua* on *Arabidopsis*. Massetolide production is involved in the control of *Pythium* root rot on flower bulbs (de Souza et al., 2003) and *P. infestans* on tomato. Massetolide mutants of *P. fluorescens* SS101 were significantly less effective in biocontrol against *P. infestans* on tomato and had an impaired capacity to colonize tomato roots (Tran et al., 2007). Key mechanisms that are linked to growth promotion and ISR against *P. syringae* pv. *tomato* in *Arabidopsis* include modulation of sulfur assimilation, auxin biosynthesis and transport, steroid biosynthesis and carbohydrate metabolism (Cheng et al., 2017).

P. fluorescens SBW25 was originally isolated from the leaf surface of a sugar beet plant grown at the University farm, Wytham in Oxford, UK. *P. fluorescens* SBW25 has extensively been used as a model organism to investigate biofilm formation, experimental evolution and adaptation, plant colonization, plant growth promotion and biocontrol. The strain can colonize the roots and leaves of a wide variety of plants and shows biocontrol activity against *Rhizoctonia* and *Pythium* (Naseby et al., 2001) and triggers ISR in *Arabidopsis thaliana* against *P. syringae* pv. *tomato* (Preston et al., 2003). The strain possesses a rhizosphere-induced type III protein secretion system (Preston et al., 2001). It produces the CLP viscosin which plays a role in swarming motility, biofilm formation and causes lysis of *P. infestans* zoospores (De Bruijn et al., 2007). Another secreted metabolite is L-furanomycin, a non-proteinogenic amino acid with antibacterial activity against several plant pathogens, including *Erwinia amylovora*, *P. syringae* and *Dickeya dadantii* (Trippe et al., 2013).

The endophyte *P. poae* strain RE*1-1-14 was isolated from the internal part of sugar beet roots and is an antagonist of *R. solani*, the causal agent of damping-off and root rot disease of sugar beet. The strain produces the CLP poaeamide, a structurally new member of the Orfamide group. Poaeamide inhibited mycelial growth of *R. solani* and various oomycetes in vitro, and was essential for swarming motility, while a poaemide-deficient mutant colonized the plants at higher densities (Zachow et al., 2015).

Various strains within the *P. fluorescens* subgroup produce the phenazine PCA. Taxonomically, they are associated with the species *P. synxantha*, *P. libanensis*, *P. orientalis* and *P. aridus*. *P. aridus* is a provisionally named species and has not been formally described (Biessy et al., 2019; Parejko et al., 2013). Most of these strains have been obtained from the rhizosphere of dryland wheat in the USA (Mavrodi et al., 2012a,b). All strains produce a T3SS. These strains do not produce other antibiotics or HCN, but some of them have NRPS gene clusters encoding CLPs that based on predictions belong to the Viscosin or Orfamide group. A well-characterized biocontrol strain that belongs to this subgroup is *P. fluorescens* 2–79. The strain was isolated in 1979 from the roots of wheat plants grown in a take-all suppressive soil in Washington state, USA, and is a strong biocontrol agent suppressing *G. graminis* var. tritici in vitro and in planta (Nesemann et al., 2015).

10 *Pseudomonas* biocontrol strains: *Pseudomonas koreensis* subgroup

P. koreensis was first described as a new species by Kwon et al. (2003). The species was obtained from a Korean agricultural soil with low pH and is able to grow at 4°C. Mulet et al. (2010) created the *P. koreensis* subgroup based on partial sequencing of the four housekeeping genes *16S rRNA, gyrB, rpoB* and *rpoD*. Type strains that belong to this subgroup include *P. moraviensis*, *P. granadensis*, *P. helmanticensis* and *P. baetica* (Hesse et al., 2018). *P. fluorescens* Pf0-1, a Gac-deficient model strain of *Pseudomonas* behavior in soil (Seaton et al., 2013), is also a member of the *P. koreensis* subgroup.

Many *P. koreensis*-like organisms are found in tropical regions. Lopes et al. (2018) analyzed the fluorescent *Pseudomonas* population from a low pH Brazilian soil (pH = 5) under sugarcane cultivation. They found that 55 of the 74 isolates belonged to the *P. fluorescens* group and of these 37 (67%) associated to the *P. koreensis* subgroup. In research on the cocoyam rhizosphere in the disease suppressive soil of Boteva in Cameroon (pH = 5.15), it was found that 55% of the *Pseudomonas* isolates belonged to the *P. fluorescens* group. Within this group 84% were members of the *P. koreensis* subgroup (Oni et al., 2020b). Intriguingly, 58% of these isolates produce CLPs that belong to various families.

A great number of isolates produce the newly described CLP cocoyamide, which contains a peptide tail of 11 amino acids. This CLP appears identical to gacamide, a CLP that was recently described in *P. fluorescens* Pf0-1 complemented for GacA (Jahanshah et al., 2019). Other CLPs produced by these isolates are bananamide, lokisin and rhizoamide (Oni et al., 2020b). Lokisin and rhizoamide belong to the amphisin group of CLPs (Table 2). *Pseudomonas* spp. COW3 and COW 65 from the cocoyam rhizosphere produces novel variants of bananamide termed bananamide D, E, F and G (Omoboye et al., 2019a). These compounds

display antagonistic activity against the oomycete pathogen *P. myriotylum* and inhibit appressoria formation in the blast fungus *Pyricularia oryzae*. The lokisin producer *Pseudomonas* sp. COR10 and a crude extract containing lokisin induced systemic resistance to *P. oryzae* in rice (Omoboye et al., 2019b).

CLP production appears to be a very common trait within the *P. koreensis* subgroup (Oni et al., 2020b; Stringlis et al., 2018). Virtually all *P. koreensis* isolates from the sugarcane rhizosphere in Brazil are predicted to produce CLPs. *P. granadensis* LMG27940, isolated from a soil sample in Granada, Spain produces the CLP MDN-0066, a compound very closely related to bananamides (Cautain et al., 2015). *Pseudomonas* sp. BW11P2, isolated from the banana rhizoplane in the tropical wetlands of Galgadera, Sri Lanka, produces bananamide A-C (Nguyen et al., 2016). Other putative bananamide producers (predicted by genome mining only) originate from cotton in South Korea and soybean roots in Mississippi, USA (Omoboye et al., 2019a).

P. koreensis 2.74 (CBS 125413) was isolated from the filter skin of a slow filter used in a closed hydroponic system in which tomato was cultivated in Sweden. This strain produces the CLP lokisin and a crude extract of this CLP has a protective effect against *P. ultimum* on tomato (Hultberg et al., 2010a). These authors also showed that *P. koreensis* 2.74 and the CLP could significantly reduce potato late blight caused by *Phytophthora infestans* in a detached-leaf assay (Hultberg et al., 2010b).

P. koreensis RU47 obtained from a take-all suppressive soil in the UK, shows biocontrol effects against *R. solani* AG1-1B in lettuce and *R. solani* AG3 in potato under growth chamber and field conditions (Adesina et al., 2009; Schreiter et al., 2018). The in vitro antagonistic activity of RU47 against *R. solani* AG1-1B is weak, but the strain consistently suppressed the pathogen on lettuce in four independent greenhouse experiments. Other *Pseudomonas* strains with strong in vitro antagonism were inconsistent in the four experiments (Adesina et al., 2009). This example shows that many interesting *Pseudomonas* biocontrol strains are missed if initial screening is based on in vitro antagonism. This is especially true for CLP producers, since they usually do not show clear inhibition zones in vitro. Genome mining revealed that RU47 produces HCN, extracellular enzymes and an amphisin-type CLP that is yet to be characterized (Kuzmanović et al., 2018).

11 *Pseudomonas* biocontrol strains: *Pseudomonas mandelii* subgroup and *Pseudomonas gessardii* subgroup

11.1 Pseudomonas mandelii *subgroup*

P. mandelii originates from mineral water and was first described by Verhille et al. (1999). Other species that belong to this subgroup include

P. frederiksbergensis, *P. lini*, *P. migulae*, *P. proseki* and *P. arsenicoxydans*. These species are typically found in extreme or polluted environments. *P. prosekii* is a recently described species comprising psychrotolerant strains isolated from James Ross Island close to the Antarctic Peninsula (Kosina et al., 2013; Snopkova et al., 2020). *P. migulae* strains have been found in mineral water, oil-contaminated rhizosphere of *Galega orientalis* in Finland (Jussila et al., 2006) and in soil samples in a selenium mining area in southwest China (Li et al., 2015). The type strain of *P. arsenicoxydans* is an arsenite-oxidizing bacterium isolated from sediment samples from the Camarones Valley in the Atacama Desert in Chile (Campos et al., 2010). *P. lini* has been isolated from the rhizosphere of jujube, a drought-tolerant plant perennial fruit tree that is cultivated in arid and semiarid regions (Zhang et al., 2020a). Tellurite-resistant and tellurite-reducing *P. lini* strains were found in Antarctica (Arenas et al., 2014).

Biocontrol strains in the *mandelii* subgroup include *Pseudomonas* sp. PICF141 obtained from the rhizosphere of olive in a commercial nursery in Cordoba, Spain (Gomez-Lama Cabanas et al., 2018) and *Pseudomonas* sp. In5 originating from a potato soil in Greenland suppressive to *R. solani* AG3 (Michelsen et al., 2015b; Michelsen and Stougaard, 2011).

Pseudomonas sp. In5 is closely related to *P. frederiksbergensis* (Girard et al., 2020a) and produces the CLPs nunamycin and nunapeptin (Michelsen et al., 2015b). *P. frederiksbergensis* 39A2 and *P. frederiksbergensis* 38F7, both obtained from Wyoming soil in the USA in 2008 (South et al., 2020) are predicted to also produce the same CLPs (Girard et al., 2020a), reinforcing the close relatedness of these strains. Nunapeptin contains a 22 amino acid peptide similar to corpeptin produced by *P. corrugata*, sclerosin produced by *P. brassicacearum* DF41 and thanapeptin produced by *Pseudomonas* sp. SH-52. All these strains co-produce a second CLP with 9 amino acid peptide, which is nunamycin in case of *Pseudomonas* sp. In5. The presence of nunamycin has also been predicted in the two *P. frederiksbergensis* strains. A crude extract which contains both nunamycin and nunapeptin possessed strong antimicrobial activity against the basidiomycete *R. solani* AG3 and the oomycete *P. aphanidermatum* (Michelsen et al., 2015a). Recently it was shown that fungal-associated molecules, rather than plant signal molecules, positively regulate nunamycin and nunapeptin synthesis in *Pseudomonas* sp. In5 (Christiansen et al., 2020).

Pseudomonas sp. PICF141 is most closely related to *P. lini* in the P. *mandelii* subgroup and shows biocontrol activity against defoliating pathotypes of *Verticillium dahlia* on 5-month-old olive plants. Gene clusters for the production of HCN, 2,3-butanediol, fusaricidin, amphisin and the insecticidal Fit toxin were detected in the genome of PICF141 (Gomez-Lama Cabanas et al., 2018). Fusaricidin is a potent depsipeptide antibiotic produced by *Paenibacillus*

polymyxa. It remains to be proven that these compounds are actually produced by *Pseudomonas* sp. PICF141.

11.2 Pseudomonas gessardii *subgroup*

The unusual siderophore, thioquinolobactin, was first described by Matthijs et al. (2007) and Mossialos et al. (2000) in *P. fluorescens* ATCC 17400, a psychrophilic organism isolated from hen's egg (Stanier et al., 1966). This strain shows a strong in vitro antagonism against the oomycete *Pythium debaryanum*. The antagonism is repressed by iron and lost in a mutant impaired in thioquinolobactin production (Matthijs et al., 2007). More recently, the gene cluster encoding this siderophore was found in *Pseudomonas* sp. DTU12.1, a strain obtained from leaf-covered soil in Denmark with bioactivity against *Xanthomonas campestris* and *P. carotovorum*.

Genome mining revealed that the cluster is also present in three other *Pseudomonas* strains, *Pseudomonas* sp. O6C 162, *P. brenneri* BIGb2073 and *P. fluorescens* PS834 (Sazinas et al., 2019). In *Pseudomonas* sp. 06C 126, a strain from Lake Erie (central basin), the quinolobactin gene cluster contributes to the growth inhibition of oomycete plant pathogens (Wagner et al., 2018) and *P. aeruginosa* isolates from cystic fibrosis patients (Chatterjee et al., 2017). Based on *rpoD* sequencing and ANIb values, all these strains clustered closely together and belong to the same species (Sazinas et al., 2019). They are most related to the type strain of *P. proteolytica* (LMG 22170) in the *P. gessardi* subgroup (Hesse et al., 2018). The type strain of *P. proteolytica* was isolated from cyanobacterial mat samples from a pond in Antarctica (Reddy et al., 2004).

12 *Pseudomonas* biocontrol strains: *Pseudomonas putida* group

P. putida is ubiquitous and abundant in temperate soils and waters. Microorganisms belonging to this group are commonly found in polluted soil. *P. putida* is characterized by its physiological robustness, metabolic versatility and high tolerance to stress (Volke et al., 2020). *P. putida* isolates can use natural and man-made toxic organic compounds as a source of carbon and energy and have been studied intensively for their role in the biodegradation of environmental pollutants. *P. putida* is also routinely used as a host in industrial biocatalysis. Readers are referred to the recent review of Kivisaar (2020) for more information about these aspects. The *P. putida* group includes also clinical isolates. They have been detected in human secretions and tissues in hospitals and *P. putida* infections can be fatal in severely ill or immune-compromised patients (Ogura et al., 2019).

The *P. putida* group includes a variety of species and is taxonomically and phylogenetically poorly described. Unlike the *P. fluorescens* group, no subgroups have formally been described and the group is clearly in need of taxonomic revision. Yonezuka et al. (2017) subjected 59 clinical and non-clinical strains of the *P. putida* group to phylogenetic analysis based on ANI analysis. Based on a 95% threshold, they were classified into 26 species and included nine strain clusters and 17 singletons. A MLSA analysis based on nine housekeeping genes agreed with the ANI analysis. Their results indicate a mixed distribution of clinical and non-clinical isolates suggesting that some limited genes are responsible for pathogenicity.

Many *P. putida* strains are excellent colonizers of plant roots and promote their growth. Plant growth promotion is due to their ability to secrete phytohormones such as indole acetic acid that promote root elongation. Many isolates can solubilize phosphates and have the ability to induce systemic resistance or stress tolerance in plants. Inhibition of fungal growth is mainly through the production of siderophores. Isolates of the *P. putida* group do not usually produce the archetypical *Pseudomonas* biocontrol antibiotics such as phenazines, DAPG, pyoluteorin or pyrrolnitrin. But their genomes contain orphan gene clusters with uncharacterized NPRS or hybrid NRPS/PKS orthologs.

Production of CLPs is a common feature and include WLIP (Oni et al., 2020a, 2019b; Rokni-Zadeh et al., 2013), xantholysin (Li et al., 2013a,b; Oni et al., 2019b), entolysin (Oni et al., 2020b; Vallet-Gely et al., 2010) and putisolvin (Kuiper et al., 2003; Oni et al., 2020b, 2019b). WLIP and entolysin can induce systemic resistance to *Pyricularia oryzae* in rice (Omoboye et al., 2019b). Putisolvin-producing *P. putida* strains were enriched in the cocoyam rhizosphere from soils in Nigeria and Cameroon conducive to the cocoyam root rot disease caused by *P. myriotylum* (Oni et al., 2020b) and in the rhizosphere of black pepper in Vietnam (Le et al., 2012). They appear to abound in harsh or contaminated environments where CLP diversity is low, but their role in biocontrol is marginal. Xantholysin can inhibit appressoria formation in *P. oryzae* (Omoboye et al., 2019b) and shows strong insecticidal activity against aphids (Lim et al., 2017).

Various *P. putida* biocontrol strains have been reported in the literature, but often their taxonomic position has only been determined by sequencing the 16S rDNA which is not reliable in differentiating *Pseudomonas* groups, subgroups or species. As an example, *Pseudomonas* CMR12a and CMR5c were initially classified as *P. putida* strains based on their 16S rDNA sequence (Perneel et al., 2007), but turned out to belong to the *P. protegens* group based on MLSA and whole-genome sequencing (Biessy et al., 2019; Flury et al., 2016).

The best-characterized strain in the *P. putida* group is *P. putida* KT2440, a metabolically versatile strain with a remarkable ability to survive in marginal and polluted soil and a workhorse for *Pseudomonas* research and

biotechnological applications (Timmis, 2002). The strain is used as a model organism in biodegradation studies. It was the first *Pseudomonas* strain for which the genome was sequenced in 2002 (Belda et al., 2016; Nelson et al., 2002). *P. putida* KT2440 is also an efficient colonizer of the spermosphere and rhizosphere of plants (Molina et al., 2000). The strain induces systemic resistance to *P. syringae* pv. *tomato* in *Arabidopsis* and an extracellular haemperoxidase was found to be important for both root colonization and induction of ISR (Matilla et al., 2010). *P. putida* KT2240 has three T6SS gene clusters and 10 potential T6SS effectors. *P. putida* KT2440 outcompetes various Gram-negative phytopathogenic bacteria including *P. syringae*, *X. campestris, P. carotovorum* and *A. tumefaciens*. This destruction appears to be dependent on the K1-T6SS (Bernal et al., 2017).

Another well-studied plant-growth-promoting and biocontrol strain is *P. putida* WCS358, one of the Dutch strains from the 'Willie Commelin Scholten' collection. WCS358 produces a pyoverdine-type siderophore PVD358 that can be used by very few other *Pseudomonas* strains, while the strain has a large number of pyoverdine receptors. As such it is able to utilize pyoverdines by a wide range of other *Pseudomonas* strains. WCS358 was originally isolated from the rhizosphere of potato (Geels and Schippers, 1983) and can suppress soilborne plant diseases by siderophore-mediated competition for iron (reviewed by Lemanceau et al. (2009)). WCS358 can induce systemic resistance in *Arabidopsis* against *P. syringae* pv. *tomato* and *F. oxysporum* f. sp. *raphani* (Van Wees et al., 1997)*;* in bean against *Colletotrichum lindemuthianum* and *B. cinerea*; and in tomato against *B. cinerea*. Multiple microbe-associated molecular patterns of WCS358 including PVD358, LPS-containing cell walls and flagella induced resistance in *Arabidopsis*, while in bean and tomato, flagella were not effective, whereas PVD358 and LPS-containing cell walls did induce resistance (Meziane et al., 2005). The taxonomic position of this strain within the *P. putida* group has been elucidated (Berendsen et al., 2015) and the species name *P. capeferrum* was proposed because the plant protective effects of this strain are linked to siderophore production.

Recently, a new bioactive metabolite has been discovered in *P. donguensis* SVBP6, an isolate from an agricultural plot in Argentina with broad-spectrum antifungal activity (Agaras et al., 2018; Muzio et al., 2020). The compound was identified as 7-hydroxytropolone, a compound with a seven-membered non-benzenoid aromatic ring. The biosynthetic gene cluster was identified by Tn5 mutagenesis and harbors 15 genes encoding metabolic enzyme functions, a putative efflux transport system and transcriptional regulators. Genome mining revealed that 15 strains among all *Pseudomonas* genomes available at the Pseudomonas Genome Database harbor this gene cluster (Muzio et al., 2020). They are representatives of *P. donghuensis* (8 strains), *P. qingdaonensis* (7 strains) and *P. wadenswilerensis* (1 strain). These species were recently described

(Frasson et al., 2017; Gao et al., 2015; Wang et al., 2019), are closely related and belong to the *P. putida* group. The 7-hydroxytropolone genomic region is associated with antibacterial activity against the black leg and soft rot pathogens *Dickeya solani* and *P. carotovorum* subsp. *brasiliense* in *P. donghuensis* P482 (Krzyzanowska et al., 2016). *P. donguensis* P482 is a tomato rhizosphere isolate from Poland with antibacterial and antifungal activity (Krzyzanowska et al., 2014, 2012). *P. donguensis* HYS, the type strain of the newly established *donguensis* species, was isolated from water of East Lake in Wuhan, China. In this strain 7-hydroxytropolone is used as an iron scavenger (Jiang et al., 2016).

13 *Pseudomonas* biocontrol strains: *Pseudomonas syringae* group and *Pseudomonas aeruginosa* group

13.1 Pseudomonas syringae *group*

The *P. syringae* group is a phylogenetic complex of strains from agricultural and environmental habitats. They are commonly isolated from diseased plants and many organisms that belong to this group are plant pathogens. They can also be found as saprophytes in environments linked to the water cycle such as freshwater, epilithic biofilms, snowpacks, precipitation and wild alpine plants (Morris et al., 2013). The *P. syringae* group contains 15 validly described species, 62 pathovars defined by pathogenic characters, 9 genomospecies defined by DNA-DNA hybridization (Gardan et al., 1999), and 13 phylogroups defined by MLSA (Berge et al., 2014). Based on a combination of methods (3-gene MLSA, amino acid sequences of 139 monocopy genes and average nucleotide identities based on BLAST (ANIb) calculated for 139 genomes), Gomila et al. (2017) distinguished 19 phylogenomic species distributed within 6 phylogenomic branches within the *P. syringae* group.

A few *P. syringae* biocontrol stains have been described. They probably all belong to Genomospecies 1 as defined by Gardan et al. (1999), phylogroup 2 as described by Berge et al. (2014) or phylogenomic branch I as defined by Gomila et al. (2017). The best-studied *P. syringae* biocontrol strains are ESC-10 and ESC-11 (also known as strain L-59-66), isolated from apple fruits (Stockwell and Stack, 2007) and leaves (Janisiewicz and Marchi, 1992), respectively. Both strains have been developed in commercial products Bio-Save 10 and Bio-Save 11 which have been registered in 1995 and are commercially available in the USA (Table 6). The strains are effective biocontrol agents against various postharvest diseases on apple, pear and citrus. Strain ESC-10 produces a hypersensitive response on tobacco and is a weakly virulent pathogen of citrus. Strain ESC-11 is not a pathogen and does not produce a hypersensitive response (Smilanick et al., 1996). Strain ESC-10 is superior for the protection of citrus from green and blue molds, while strain ESC-11 is superior to control postharvest pathogens on apples and pears (Bull et al., 1997). In vitro, both

strains produce the CLP syringomycin. Purified syringomycin E inhibited *P. digitatum* spore germination at about 5 µg/mL but about 100 µg syringomycin E per wound was needed to control green mold on lemon to an extent equal to that provided by the biocontrol strains ESC-10 and ESC-11 (Bull et al., 1998). Strain ESC-10 reduced Rhizopus rot on peach caused by *Rhizopus stolonifera* to levels comparable with that of dichloran and iprodione (Northover and Zhou, 2002).

The *P. syringae* strains MA-4 and NSA-6, obtained from the phyllosphere of apple in Canada, also effectively controlled Rhizopus rot on peach. These strains were also effective against brown rot on peach caused by *Monilinia fructicola* and the activity was significantly improved by adding 0.5% CaCl$_2$ to the soak solution (Zhou et al., 1999). According to Zhou et al. (1999) MA-4 and NSA-6 can also control apple scab, caused by *Venturia inaequalis* on apple.

P. *syringae* pv. *syringae* 22d/93 isolated from the phyllosphere of soybean in Jena, Germany (Völksch et al., 1996), is a strong antagonist of *P. syringae* pv. *glycinea*, the causal agent of bacterial blight of soybean. Antagonism has been demonstrated in vitro and in planta under greenhouse and field conditions (May et al., 1997; Völksch and May, 2001). The cyclic lipopeptides, syringomycin and syringopeptin, are produced but have no activity against *P. syringae* pv. *glycinea* (Braun et al., 2010). The rare amino acid 3-methylarginine selectively inhibits *P. syringae* pv. *glycinea* in vitro and the toxin probably acts as an inhibitor of the arginine biosynthesis pathway or an arginine-dependent pathway (Braun et al., 2010). Purified 3-methylarginine suppressed the growth of the pathogen in planta. Mutant analysis revealed that none of these compounds is required for antagonistic activity in planta when the pathogen was applied to artificial wounds (Braun et al., 2010). The strain produces two siderophores, pyoverdine and achromobactin, that play an essential role in leaf colonization but are not directly implicated in biocontrol (Wensing et al., 2010).

13.2 Pseudomonas aeruginosa *group*

Pseudomonas aeruginosa is an ubiquitous organism with minimal requirements for survival that is commonly found in water, soil, animal hosts and associated with plants (Botzenhart and Döring, 1993; Hardalo and Edberg, 1997). *P. aeruginosa* is best known as an opportunistic pathogen of humans. It can cause severe problems in patients hospitalized with cancer, AIDS, cystic fibrosis and severe burns. The bacterium can invade any tissue in which the immune system is compromised (Moradali et al., 2017). *P. aeruginosa* has also been found in association with various other organisms such as nematodes, insects (Mahajan-Miklos et al., 2000) and amoebae (Pukatzki et al., 2002). *P. aeruginosa* has many secondary metabolites in common with biocontrol *Pseudomonas* strains and produces phenazine antibiotics, HCN, the siderophores pyoverdine and

Table 6 Commercially available bioprotectants based on *Pseudomonas* in Europe and the USA

Biocontrol strain	Commercial Name	Company	Usage	Crop/Applications	Pathogen
P. chlororaphis MA342	Cedomon	BioAGri, Sweden; Koppert, The Netherlands	Fungicide	Seed-dressing in field-grown cereals (barley, oats, triticale, wheat)	Seedborne pathogens
	Cerall	BioAGri, Sweden; Koppert, The Netherlands	Fungicide	Seed-dressing in wheat, rye and triticale	Seedborne pathogens
	Cedress	BioAGri, Sweden; Koppert, The Netherlands	Fungicide	Seed-dressing in carrots and pea	*Ascochyta* on pea and *Acrothecium carotae* on carrots
P. aureofaciens strain Tx-1	Spot-Less	Turf Science Laboratories Inc., CA, USA	Fungicide	Lawn and grass management, recreational and ornamental lawns	*Sclerotinia homeocarpa, Colletotrichum spp.,, P. aphanidermatum, Michrodochium nivale, Pyricularia grisea*
P. chlororaphis AFS009	Howler	AFS009 Plant Protection Inc., NC, USA	Fungicide	Fruits, vegetables, ornamentals, hydroponic crops, beans, peas, peanut, trees, turf, home and garden use	*Rhizoctonia, Pythium, Fusarium, Phytophthora, Sclerotinia, Colletotrichum, Botrytis*
	Zio	SePRO	Fungicide	Turfgrass, ornamental plants, vegetable and fruit transplants	
P. fluorescens A506	Blightban, Frostban B	Nufarm Americas, USA	Bactericide, frost prevention	Fruit trees, strawberry, tomato, potato	Frost-forming and russet inducing bacteria, *E. amylovora*
Pseudomonas sp. DSMZ 13134	Proradix	SP Sourcon Padena, Germany	Fungicide, plant growth regulator	Potato	*R. solani, Helminthosporium solani*

P. syringae strain ESC-10	Bio-save 10LP, 10NT	Jet Harvest Solutions, FL, USA	ungicide	Postharvest: apples, pears, citrus, potato	*P. digitatum, P. italicum, Geotrichum candidum, B. cinerea, Mucor piriformis, Fusarium sambucinum, H. solani*
P. syringae strain ESC-11	Bio-save 11LP, 11NT	Jet Harvest Solutions, FL, USA	Fungicide	Postharvest: apple, pear, potato, sweet potato,	*P. expansum, B. cinerea, M., Fusarium sambucinum, H. solani, Rhizopus stolonifer*
P. fluorescens CL145A	Zequanox	Marrone Bio Innovations	Molluscicide	Water	Zebra and quagga mussels
P. fluorescens D7	D7	Verdesian Life Sciences, NC, USA	Herbicide	Wheat, barley, triticale, oats, rangeland	downy brome, medusahead, Japanese brome, jointed goatgrass

pyochelin, and rhamnolipid-type biosurfactants. Phenazines produced by *P. aeruginosa* are pyocyanin, a blue pigment, but some strains can also produce 1-OH-PHZ, PCA and PCN (Mavrodi et al., 2006). Hence, it is not a surprise that they are able to inhibit a wide range of plant pathogens by the secretion of antimicrobial compounds or by inducing systemic resistance. *P. aeruginosa* is commonly found in the rhizosphere or as an endophyte of plants, especially in tropical regions. Antagonistic plant-associated *P. aeruginosa* strains have, for instance, been isolated from chickpea (Anjaiah et al., 1998), chilli pepper (Paul et al., 2013), black pepper (Kumar et al., 2013), rice (Yasmin et al., 2017), cotton (Yasmin et al., 2014), ginger (Jasim et al., 2014), tomato (Kumar et al., 2009) and cocoyam (Oni et al., 2020b).

Well-studied *P. aeruginosa* biocontrol strains include PNA1, isolated from chickpea roots in India (Anjaiah et al., 1998), 7NSK2, isolated from the rhizosphere of barley in Belgium (Iswandi et al., 1987) and M18 from the rhizosphere of sweet melon in Shanghai, China (Hu et al., 2005).

P. aeruginosa 7NSK2 produces pyocanin and the siderophores, pyoverdine and pyochelin. Pyoverdine and pyochelin are involved in suppression of *Pythium*-damping-off of tomato (Buysens et al., 1996). ISR against *B. cinerea* in tomato is mediated by pyocyanin and pyochelin (Audenaert et al., 2002), while pyocyanin triggers ISR against *P. oryzae* in rice, but enhances susceptibility to *R. solani* (De Vleesschauwer et al., 2006). *P. aeruginosa* PNA1 produces rhamnolipids, PCA and PCN. Phenazines contributed to the suppression of Fusarium wilt caused by *F. oxysporum* f. sp. *ciceris* in chickpea (Anjaiah et al., 1998) and *Fusarium udum* in pigeonpea (Anjaiah et al., 2003). Phenazines and rhamnolipids acted synergistically in the control of *Pythium splendens* on bean and *P. myriotylum* on cocoyam (Perneel et al., 2008). Ginger is also susceptible to *P. myriotylum* and an endophytic PCA-producing *P. aeruginosa* isolate obtained from the ginger rhizome gave protection against the pathogen (Jasim et al., 2014).

P. aeruginosa M18 can effectively control *Mycosphaerella melonis* on sweat melon plants (Wu et al., 2011) and has strong activity against various fungal, oomycete and bacterial pathogens (Xu and Liu, 2013). The strain predominantly produces PCA rather than pyocyanin especially at 28°C (Huang et al., 2009). In addition it produces pyoluteorin, an antibiotic that is commonly found in *P. protegens* isolates but not in *P. aeruginosa* (Huang et al., 2004). Interestingly, PCA is negatively regulated and pyoluteorin is positively regulated by the global regular GacA (Ge et al., 2004). Expression and regulation of PCA in this strain has been studied in great detail and a high-yielding engineered strain has been constructed (Du et al., 2013) and the fermentation was optimized using surface response methodology (Li et al., 2008). PCA produced by the engineered *P. aeruginosa* M18 strain has been developed in a biopesticide called Shenqinmeisu that was approved in China in 2011 for the control of

various fungal and microbial diseases of fruits, vegetables, rice, wheat, potatoes and other crops (Xu and Liu, 2013).

14 Commercial *Pseudomonas*-based bioprotectants

Despite the overwhelming literature on *Pseudomonas* biocontrol, few *Pseudomonas*-based products are commercialized as bioprotectants (Table 6). In Europe, only *P. chlororaphis* MA342 and *Pseudomonas* sp. DSMZ 13134 are registered and sold in various European countries under the commercial names Cedomon, Cerall, Cedress and Proradix.

P. chlororaphis MA342 was isolated from roots of wild crowberry (*Empetrum nigrum* L.) in Sweden (Hökeberg et al., 1997) and included in the EU list of approved active substances in 2004. It is used as a seed treatment on cereals (wheat, rye, triticale), carrot and pea to protect against seedborne pathogens and against foliar and ear pathogens in cereals (EFSA, 2017; Johnsson et al., 1998). It is a good spermosphere, but poor rhizosphere and phyllosphere colonizer. The strain is known to produce 2,3-deepoxy-2,3-didehydro-rhizoxin (DDR). Cerall is a ready-to-use water-based formulation for seed treatment. Cedomon is an oil-based formulation used in barley and oat. Cedress is a flowable suspension for seed treatment of carrots and peas.

It should be noted that the taxonomic identification of MA342 as *P. chlororaphis* is questionable. The strain has not properly been identified and based on 16S rRNA sequence analysis, the strain most probably does not belong to the species *P. chlororaphis*. The production of the metabolite DDR has become an issue for the renewal of the approval of *P. chlororaphis* MA342 as an active substance because of potential genotoxic effects (Hernandez-Jerez et al., 2020).

Field trials in Sweden (Johnsson et al., 1998), Finland (Lötjönen and Torniainen, 2005) and Lithuania (Liatukas et al., 2019) have revealed that *P. chlororaphis* MA 342 can effectively control seedborne cereal pathogens that are present on the seed or near the seed coat such as *Pyrenophora* spp., but does not control seedborne pathogens like the loose smut *Ustilago nuda* that are located in the seed embryo. There is no effect either against soilborne diseases or leaf diseases. Average yield increases in spring barley range between 2% and 5%, but there are strong differences between cultivars. In field trials in Lithuania, seeds of the cultivar 'Alisa DS' were effectively sanitized by the use of Cedomon, leading to yield increases of 5–15%, while this was not observed on the cultivar 'Luoke' (Liatukas et al., 2019). Field experiments in Finland have revealed that Cedomon could control net blotch (*Pyrenophora tera*) in barley nearly as well as chemical products and increased yield with 200–300 kg. Barley life stripe (*Pyrenophora graminae*) was decreased with 40–80%. There was no effect against loose smut (*Ustilago nuda*) of barley or Fusarium.

Seed dressing treatments with Cedomon did not increase the yield of oat compared to untreated controls (Lötjönen and Torniainen, 2005).

Pseudomonas sp. DSMZ 13134 was isolated from the roots of lettuce (EFSA, 2012) in a search for biocontrol agents against *P. ultimum*. The taxonomic position of this strain is uncertain and it is not clear which metabolites it can produce. Its modes of action include competition for space, induced systemic resistance and stimulation of root growth. The strain was included in the EU list of approved active substances in 2013 (EU, 2013). The Proradix product is a wettable powder that is approved for tuber treatment of potato prior to planting against black scurf (*R. solani)* and silver scurf (*Helminthosporium solani)*. The product controls black scurf on potato with an efficacy of 28–40% and silver scurf with an average efficacy of 46% (Moszczynska et al., 2015; CTGB, 2014). In field trials with barley in Germany seed inoculation with Proradix increased yields with 4–19% (Fröhlich et al., 2012).

P. chlororaphis-based products commercially sold in the USA are Spot-Less, Howler and Zio. Howler and Zio are biofungicides containing *P. chlororaphis* strain AFS009 (PC code 006800, registered 2017) to control various oomycete and fungal pathogens on many different crops (EPA, 2017a,b). AgBiome selected the strain after screening a library of more than 60 000 microorganisms. Both products are wettable powders that should be mixed with water and can be applied as a foliar spray, soil drench, in furrow spray, transplant spray or dip, cuttings or bare root dip, or in hydroponic or chemigation application. The products can also be mixed with potting mix or applied dry in furrow. Zio is marketed to the turf and ornamental sector by SePRO. Howler is marketed for use on specialty crops. According to AgBiome, modes of action of *P. chlororaphis* strain AFS009 include production of antibiotics and cell wall degrading enzymes, competition and induced resistance, but further details could not be found.

Spot-less is based on *P. chlororaphis subsp. aureofaciens* Tx-1 (PC code 006473, registered 1999) (Hardebeck et al., 2004; Powell et al., 2000) and is registered for use in turf grass against dollar spot (*Sclerotinia homoeocarpa*), anthracnose (*Colletotrichum* spp.), *Pythium,* pink snow mold (*Microdochium nivale*) and grey leaf spot *(Pyricularia grisea)* (EPA, 2006). The product is a fermented culture of *P. aureofaciens* Tx-1 following 12–14 h of culture in the BioJect® Fermentation and Injection System. The culture is diluted with water and injected into a sprinkler irrigation system. The strain is known to produce PCA. In field trials it was shown that PCA provided significantly better management of dollar spot on creeping bentgrass than untreated plots. Results were comparable to management provided by chlorothalonil (Powell et al., 2000). Field studies carried out at West Lafayette, Indiana in 1998 and 1999 revealed that Tx-1 marginally controls dollar spot, only when disease pressure is low. In combination with fungicides and under low disease pressure, Tx-1

could increase the dollar spot control of fungicides by 37% and increased the duration of control by 2.6 days (Hardebeck et al., 2004). Repeated inoculation with TX-1 resulted in the establishment of the strain in the rhizosphere of turfgrass with a minimal impact on the indigenous bacterial community. The strain also was capable of overwintering. Low activity of TX-1 in the field may be explained by limited PCA production in situ (Sigler et al., 2001).

P. syringae-derived products sold in the USA are the Bio-Save products based on *P. syringae* ESC-10 (PC code 006441, registered 1994) and ESC-11 (PC code 006451, registered 1996) that are used for the control of postharvest pathogens on fruits, potato and sweet potato that have been discussed above. The active ingredients were registered in 1990 and 1996, respectively. Their history has extensively been reviewed by Stockwell and Stack (2007). ESC-10 reduces green and blue mold on lemon with 80–99% effectiveness and on orange with 40–59% effectiveness. ECS-11 gives excellent control of blue mold and grey mold on apple and pear, but host-specific effects are observed for control of postharvest diseases on pear. Both products can be used in combination with fungicides and are very useful to control fungicide-resistant pathogen populations. Their use in the USA is widely adopted (Stockwell and Stack, 2007).

P. fluorescens A506 (PC code 006438, registered 1992) is the active ingredient in Frostban B (Blightban) (EPA, 2017c). The product is used to suppress frost damage on various crops and to suppress fire blight caused by *E. amylovora*. The primary mechanism in fire blight control is competitive exclusion. The commercial product is composed of lyophilized cells of the bacterium that need to be diluted in water. A506 is reviewed by Stockwell and Stack (2007). In non-inoculated orchards in California, *P. fluorescens* A506 could reduce the incidence of fire blight by 50–80%, fruit russet by 30–50% and frost injury by 40–50% (Lindow et al., 1996; Lindow and Suslow, 2003). The strain did not provide significant control in inoculated experimental orchards in Oregon (Stockwell et al., 2010).

Other *Pseudomonas* strains have been registered in the USA (*P. syringae* 724RS, *P. fluorescens* 1629RS, *P. chlororaphis* 63-28) but they are not, or no longer, commercially available. Anderson and Kim (2018) list various bioprotectants based on *P. chlororaphis* O6 that are registered by HyunNong Inc. in South Korea. These include NematoKill against root-knot nematodes, ItaEpi against aphids and three products that are used as microbial fertilizer. However, additional information about these products could not be found.

Bioprotectants or biofertilizers based on various strains of *P. chlororaphis* are commercially available in Russia and listed by Maksimov et al. (2011) with the trade names Pseudobacterin-2, Agat-25K, Helen and Binoram. AGAT-25 is used to control roots rots, mildew, septoriose, brown rust, ear fusariosis, cercosporiosis and pseudoperonosporosis, while Pseudobacterin-2 is used to

control root rots (Kabaluk et al., 2010). The active ingredient in Pseudobacterin-2 is *P. aureofaciens* BS1393, a strain obtained from the rhizosphere of barley. Trials in cereals, vegetables and oilseed crops have indicated that Pseudobacterin-2 can reduce disease severity by 65–88%, resulting in a 20–25% yield increase (Thomashow, 2013).

Various *Pseudomonas*-based bioprotectants are registered for commercial use in India. They are all called *P. fluorescens* and have different formulations and accession numbers. A strain with accession number MTCC 5176 is registered to control loose smut on wheat. Strain IPL/PS-01 (accession number MTCC 5727) is available in different formulations to control bacterial leaf blight on rice, and soilborne diseases on tomato. Strain IIHR-PF-2 (accession number ITCCB0034) is approved to control root rot and wilt diseases on tomato, brinjal, carrot and okra. A strain with accession number MTCC 2539 is approved for late leaf spot control on groundnut. Strain TNAU (accession number ITCC BE 0005) is used on groundnut, rice, chili seedlings, tomato and cotton. Strain BIL-331 (accession number MTCC 5866) is approved to control various diseases on rice (Government of India, 2020). The taxonomic status, origin and mode of action of these strains are unclear.

Table 6 lists two other applications of *Pseudomonas* biocontrol. *P. fluorescens* D7 (PC code 16418, registered 2014) is the active ingredient in D7, a product approved in 2014 for use as a herbicide in cereals. D7 is a freeze-dried powder that is dissolved in water and applied as a spray solution to the soil surface. It is used for preemergence applications. Zequanox contains killed cells of *P. fluorescens* CL145A and is registered for control of quagga and zebra mussels in limited open-water environments and in cooling and service water systems for industrial facilities. It was shown that dead *P. fluorescens* CL145A cells achieved the same percentage mussel mortality as live cells and that the mode of action is intoxication (Molloy et al., 2013).

It is not entirely clear why so few *Pseudomonas* strains are commercialized. Possible bottlenecks are inconsistency in field performance, genetic instability, poor shelf life in comparison with spore-forming biocontrol agents, and costs and difficulty of registration (Berg, 2009; Mark et al., 2006; Tabassum et al., 2017). A lot of progress has been made in recent years in the formulation of non-sporulating bacteria (Berninger et al., 2018) and poor shelf life should probably no longer be a major issue. Inconsistency in field performance is, however, a key problem. Good performance in specific trials is often not translated in consistent and effective control in diverse field situations. This can be due to external factors such as soil or climatic conditions, but is also driven by intrinsic traits of the biocontrol agent, such as variable production of secondary metabolites or poor host colonization (Mark et al., 2006). Host-specific responses to bioprotectants are observed, which could in part be driven by quantitative and qualitative differences in plant exudates.

Microbiome studies have revealed that plant species, cultivars and soil type are key drivers of rhizosphere microbiome composition and functioning. A series of elegant studies by the Raaijmakers' group using bean as a model have shown that plant domestication and resistance breeding caused changes in root architecture and altered root exudates. This in turn changed rhizosphere microbiome composition and functioning (Mendes et al., 2019, 2017; Mendes and Mendes, 2018; Pérez- Jaramillo et al., 2016). Specific root exudates may be needed to stimulate *Pseudomonas* colonization and the in situ production of bio-active molecules. The regulation of secondary metabolites in *Pseudomonas* spp. is complex and may require specific nutrients and environmental stimuli or the presence of other microorganisms as was recently shown for *Pseudomonas* sp. In5 (Christiansen et al., 2020). A second major hurdle in the commercialization of microbial biopesticides is the slow, difficult and costly registration process, especially in Europe. These aspects have recently been reviewed (Frederiks and Wesseler, 2018; Scheepmaker et al., 2019).

15 Conclusion

Recently an ever-increasing number of high-quality *Pseudomonas* whole-genome sequences has become available, and insights in the taxonomy of *Pseudomonas* have greatly advanced. Genome mining and the division of the vastly heterogeneous genus *Pseudomonas* in phylogenomic groups and subgroups have clarified the relationship between phenotypic characteristics and phylogeny. Well-known *Pseudomonas* biocontrol strains that have been studied for many years can now be positioned in their correct phylogenetic (sub)group.

Based on their activity, three types of *Pseudomonas* biocontrol strains can be distinguished. The first type comprises the CPC (*chlororaphis, protegens, corrugata* subgroups) cluster defined by Vacheron et al. (2016) and *P. aeruginosa*. CPC isolates produce an arsenal of secondary metabolites, including antibiotics with antagonistic properties such as pyrrolnitrin, DAPG, phenazines and HCN. They have broad-spectrum activity against soilborne pathogens and many strains can induce systemic resistance to foliar pathogens. This cluster has received considerable attention in the past.

CPC strains are readily picked up in in vitro screens for biocontrol strains because of their clear antagonism on plate and broad-spectrum antimicrobial activity. However, several disadvantages come with the production of multiple bioactive compounds, as evidenced in the *P. protegens* group. *P. protegens* strains are prone to *gac* mutations, some of their metabolites are phytotoxic, and they are outcompeted by other bacteria in the rhizosphere of field-grown plants. This may explain why they have not been commercialized.

P. chlororaphis strains are genetically more stable (Yan et al., 2018), and most strains do not produce potential phytotoxic compounds. They are preferred by biopesticide companies. It is striking that a *P. chlororaphis* strain was selected in the 60 000 strain-screen by Agbiome. To my knowledge, there are no commercial biopesticides containing *Pseudomonas* strains from the *P. corrugata* group although Salavida, a product from Sourcon Padena, based on *P. brassicacearum* 3Re-27, is commercialized as a biostimulant in Germany (Berg, 2009). *P. aeruginosa* strains with biocontrol properties also belong to this division. Their spectrum of metabolites is rather similar to *P. chlororaphis* subgroup isolates. The fact that they are opportunistic human pathogens precludes their commercialization, but they are a source of bioactive compounds such as phenazines and rhamnolipids.

A second type is found in the *P. putida* group and the *P. fluorescens*, *P. koreensis*, *P. mandelii* and *P. gessardii* subgroups in the *P. fluorescens* group. Vacheron et al. (2016) has termed *P. fluorescens*, *P. koreensis*, *P. mandelii* and *P. jessenii* the FMJK cluster. It was found that FMJK and *P. putida* are predominantly present in the maize rhizosphere and have fewer biocontrol traits, but more phytostimulatory properties than CPC strains (Vacheron et al., 2016). These (sub)groups harbor many plant growth-promoting *Pseudomonas* strains. An example is *P. jessenii* UW4, an ACC deaminase-producing strain that promotes plant growth in the presence of different environmental stresses, such as flooding, heavy metals, cold, high concentrations of salt and the phytopathogenic bacterium *Agrobacterium* (Duan et al., 2013).

Biocontrol strains from the second type do not produce the archetypical *Pseudomonas* antibiotics. Their biocontrol capacities predominantly depend on siderophores or a diverse arsenal of CLPs. CLPs have interesting antimicrobial and resistance-inducing properties. It has been hypothesized that their large diversity is driven by microbial competition in the rhizosphere (Oni et al., 2020a). An enrichment in CLP production is also seen in a subset of isolates closely related to the plant pathogenic *P. corrugata* and *P. mediterranea* in the *P. corrugata* subgroup. Other traits remain to be investigated such as the targets and roles of the effector proteins secreted by the T3SS and T6SS machinery and the function of strain-specific orphan gene clusters. This second type has significant potential because these strains are often competitive root colonizers and adapted to harsh conditions. The fact that they usually do not produce antibiotics will also facilitate the registration process in case of commercialization.

The third type encompasses biocontrol strains adapted to above-ground plant parts. They predominantly belong to the *P. syringae* group and have antagonistic activities against aerial pathogens. *P. fluorescens* A506 also belongs to this type. Their main mode of action is probably competition. Commercial biofungicides based on *P. syringae* and *P. fluorescens* A506

are already on the market for 30 years to control postharvest and bacterial pathogens.

Despite the overwhelming literature on *Pseudomonas* biocontrol, only few *Pseudomonas* strains are commercialized. This is mainly due to inconsistent field performance, which can be explained by poor adaptation to environmental conditions, suboptimal formulation, and host-specific responses to microorganisms. In addition, the expensive, tedious and time-consuming registration procedure, especially in Europe, hampers the introduction of new microbial bioprotectants.

16 Where to look for further information

16.1 Pseudomonas *biocontrol*

Haas and Défago, 2005; Mercado-Blanco, 2015; Olorunleke et al., 2015b; Müller and Behrendt, 2021

16.2 Pseudomonas *taxonomy*

Garrido-Sanz et al., 2017; Girard et al., 2020b; Gomila et al., 2015; Hesse et al., 2018; Lalucat et al., 2020; Mulet et al., 2010

16.3 Secondary metabolites in Pseudomonas

Gross and Loper, 2009

16.4 Phenazines

Biessy and Filion, 2018; Mavrodi et al., 2013, 2006; Chincholkar and Thomashow, 2013

16.5 Lipopeptides

Geudens and Martins, 2018; Götze and Stallforth, 2020; Raaijmakers et al., 2010

16.6 Whole genomes of Pseudomonas

Pseudomonas genome DB https://www.pseudomonas.com/

16.7 Whole genome comparisons of Pseudomonas *biocontrol strains*

Biessy et al., 2019; Garrido-Sanz et al., 2016; Loper et al., 2012

16.8 Formulation

Berninger et al., 2018

17 Acknowledgements

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