Pseudomonas Lipopeptides

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The Pseudomonas genus is ubiquitous and comprises species which are well known phytopathogens, such as *P. syringae*, or opportunistic human pathogens, such as *P. aeruginosa*, but also host members associated with water, soil and plant surfaces. Pseudomonas spp. are well adapted to growing in the rhizosphere and are well suited for biocontrol and growth promotion. Pseudomonas lipopeptides (Ps-LPs) play crucial roles in bacterial physiology, host–microbe interactions and plant disease control.

Pseudomonas fluorescens | lipopeptides | antimicrobial | plant-microbe interactions | direct antagonism | induced systemic resistance | secondary metabolites

1. Introduction

The *Pseudomonas* genus is ubiquitous and comprises species which are well known phytopathogens, such as *P. syringae*, or opportunistic human pathogens, such as *P. aeruginosa*, but also host members associated with water, soil and plant surfaces [1]. *Pseudomonas* spp. are well adapted to growing in the rhizosphere and are well suited for biocontrol and growth promotion [2]. Thus, the use of fluorescent *Pseudomonas* spp. as potential biopesticides has gained attention over the last decade. These bacteria are of particular interest because of their enormous metabolic versatility and wide adaptation across environmental gradients [3].

Based on phylogenomic and Multi Locus Sequence Analyses (MLSA), the *Pseudomonas* genus has been delineated into 453 species (https://lpsn.dsmz.de/genus/pseudomonas; accessed on 18 December 2021) which are distributed across three lineages (*P. fluorescens*, *P. aeruginosa* and *P. pertucinogena*), several groups (G) and subgroups (SG) [4][5][6][7][8]. Most biocontrol strains have been described within the *P. fluorescens* group comprising among others, the *P. fluorescens* SG, *P. koreensis* SG, *P. chlororaphis* SG, *P. jessenii* SG, *P. mandelii* SG and *P. corrugata* SG. Additionally, several biocontrol strains are positioned within the *P. putida* and *P. syringae* groups. These disease-suppressing pseudomonads were isolated from several sources ranging from the healthy plant rhizosphere [9][10][11], plant rhizosphere [12][13][14][15], phyllosphere [16][17], bulk soil [15] and suppressive soils [10][18]. The commonality among well-studied biocontrol strains is their capacity for secondary metabolite production including siderophores, lipopeptides (LPs), hydrogen cyanide, bacteriocins and certain antibiotics such as phenazines, 2,4-diacetylphloroglucinol (DAPG), pyrrolnitrin and pyoluteorin [3][19].

Examples of commercially available *Pseudomonas*-based bioprotectants include fungicides such as Cedomon and Cerall (*P. chlororaphis* MA342) both targeting seed-borne pathogens of cereals, Spot-Less (*P. aureofaciens* strain Tx-1) for management of fungal diseases on lawns and grasses, and Howler (*P. chlororaphis* AFS009) useful in the management of *Rhizoctonia*, *Pythium*, *Fusarium*, *Phytophthora*, *Colletotrichum* spp. in fruits, vegetables and ornamentals [19]. A detailed list of commercial bioprotectants based on *Pseudomonas* in Europe and USA, including their usage, and target crops/applications/pathogens have been enumerated in a recent review [19].

Lipopeptides are bacterial metabolites consisting of a peptide part attached to a fatty acid tail [1]. Most beneficial LPs are cyclized although linear LPs have also been described [20][21]. LPs have drawn remarkable interest because of their broad-spectrum antimicrobial and ecological functions. These multiple functions include biofilm formation and colonization of surfaces, quorum sensing, cell motility, soil remediation, anti-oomycete, antiviral, antifungal, antibacterial, herbicidal, insecticidal, antiprotozoal and anticancer properties [3][22][23][24][25][26][27].

2. Genome Comparison of Selected Lipopeptide-Producing *Pseudomonas* spp.

A previous study provided the phylogenomic analysis of the *Pseudomonas* genus based on the genomes of the type strains of 163 described species and compared these type strain genomes to those of 1223 Pseudomonas genomes in public databases [7]. Results showed that 400 of those 1223 genomes were distinct from any other type strain suggesting that the *Pseudomonas* genomic diversity had been grossly underrepresented by the type strains. Furthermore, a detailed comparative genome analysis of ten strains within the *Pseudomonas fluorescens* group highlighted the enormous diverseness of this group and the capacity of the variable genome to adapt individual strains to their distinct lifestyles and functional capacities [3]. Here, using the *P. fluorescens* Pf0-1 as a reference genome, and compared the genome of 32 lipopeptide-producing *Pseudomonas* strains affiliated with the *P. koreensis*, *P. fluorescens*, *P. mandelii*, *P. corrugata*, *P. asplenii*, *P. chlororaphis*, *P. protegens*, subgroups including the *P. putida* and *P. syringae* groups. By comparing the protein coding sequences (CDS) of reference to query genomes, a Blast Atlas was generated which showed the close relatedness of other members of the *P. koreensis* group (*P. fluorescens* MS80, *P. granadensis* LMG 27,940 and *P. kribbensis* 46-2) to the reference genome *P. fluorescens* Pf0-1 (**Figure 3**).

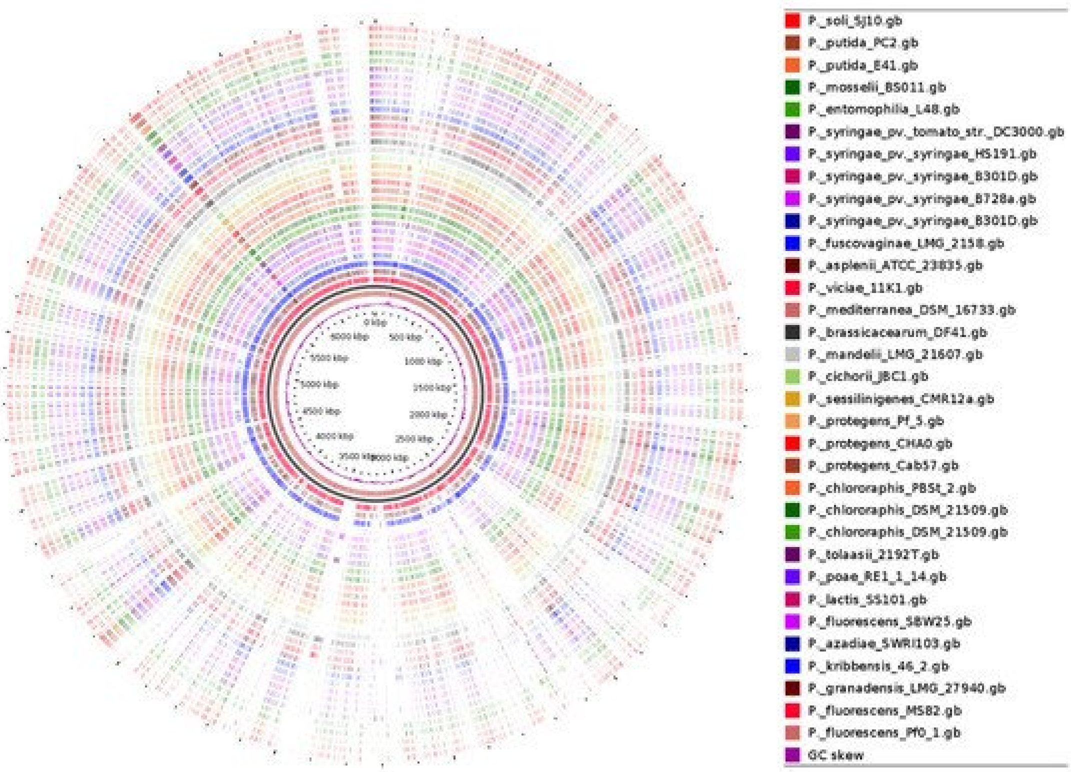

Figure 3. Comparative Genome Blast Atlas of 35 Lipopeptide-Producing *Pseudomonas* Strains. The BLAST Atlas analysis displays regions of the uploaded query files (34 genomes) where there are BLAST hits to the reference genome *P. fluorescens* Pf0-1). The GView Server was used [28].

3. Chemical Diversity of Beneficial *Pseudomonas* LPs

Most beneficial LPs have been predominantly characterized from strains affiliated with the *P. fluorescens* and *P. putida* group. The chemical diversity of *Pseudomonas* LPs has been detailed in two recent reviews [1][21]. **Table 1** shows the diversity of beneficial LPs and presents the discovery of similar LPs from diverse strains, countries, niches and environments. Not all LPs listed have been functionally characterized, however, the disease suppressive capacity of their producing strain(s) has been established on specific plant hosts thus indicating non-virulence. Clearly, the *P. koreensis* subgroup presents the highest diversity of LP families and individual members, including variants. This SG is characterized by at least six amphisin group members alongside the novel rhizoamide, the bananamide group comprising six variants and the cocoyamide/gacamide group. Moderate LP diversity is showcased by the *P. fluorescens* SG while the *P. protegens* SG comprises various orfamide variants A-H and the poaeamide LPs. Lastly, the *P. putida* group contains four described LP types: entolysin, putisolvin, xantholysin, WLIP and a novel 17AA LP named N8. **Figure 4** shows the chemical structures of representative biocontrol LPs that have been characterized.

Figure 4. Chemical structures of selected biologically active *Pseudomonas* Cyclic Lipopeptides. Bananamide D (Bananamide Group); WLIP (Viscosin Group); Thanamycin (Syringomycin Group); Lokisin (Amphisin Group); Cocoyamide; Putisolvin I; Entolysin A and Xantholysin A. Whenever the absolute configuration of the lipopeptides was reported in the literature, it is indicated by standard stereodescriptors. In case of WLIP, the 3D-structure was secured by x-ray [29] and can be viewed as entry CCDC 919,229 at The Cambridge Crystallographic Data Centre via www.ccdc.cam.ac.uk (accessed on 19 December 2021).

Table 1. Taxonomy of LP-producing Biocontrol Pseudomonads, their corresponding Molecules and Origin.

Taxonomy	Biocontrol Strains	Host/Origin	Country	LP Family	LP	Reference
P. fluorescens SG	SS101	Wheat rhizosphere	Netherlands	Viscosin	Massetolide	[30]
	SBW25	Sugarbeet phyllosphere	UK		Viscosin	[31]
	DR54	Sugarbeet rhizosphere	Denmark		Viscosinamide	[32][33]
	A2W4.9, U2W1.5	White cocoyam rhizosphere	Nigeria		Viscosinamide	[34]
	BRG100	Green foxtail rhizosphere	Canada		Pseudophomin	[35]
	RE*1-1-14	Internal part of soybean roots	Germany		Poaemide	[36][37]

Taxonomy	Biocontrol Strains	Host/Origin	Country	LP Family	LP	Reference
	NCPPB1311	Cultivated mushrooms	UK		WLIP	[38]
P. koreensis SG	DSS73	Sugarbeet rhizosphere	Denmark	Amphisin	Amphisin	[14][39]
	HKI0770	Forest soil	Forest soil		Anikasin	[40][41]
	CTS17	Sugarbeet rhizosphere	Denmark		Hodersin	[14][42]
	DSS41	Sugarbeet rhizosphere	Denmark		Lokisin	[43]
	2.74	Tomato hydroponics	Sweden		Lokisin	[44]
	S150	Tobacco rhizosphere	China		Lokisin	[45]
	COR10	Red cocoyam rhizosphere	Cameroon		Lokisin	[10]
	UCMA 17988	Raw bulk tank milk	France		Milkisin	[46]
	COW8	White cocoyam rhizosphere	Cameroon		Rhizoamide (N2—11:7) †	[11]
	96.578	Sugarbeet rhizosphere	Denmark		Tensin	[33][47]
	BW11P2	Banana rhizoplane	Sri Lanka	Bananamide	Bananamide I, II, III	[12][48]
	COW3, COW65	White cocoyam rhizosphere	Cameroon		Bananamide D, E, F, G	[10][49]
	COW5	White cocoyam rhizosphere	Cameroon	Cocoyamide	Cocoyamide A	[10]
	Pf0-1	Loam soil	USA		Gacamide A	[50][51]
P. protegens SG	CHA0	Tobacco roots	Switzerland	Orfamide	Orfamide	[52][53]

Taxonomy	Biocontrol Strains	Host/Origin	Country	LP Family	LP	Reference
	Pf-5	Cotton rhizosphere	USA		Orfamide	[54][55]
	CMR5c	Red cocoyam rhizosphere	Cameroon		Orfamide	[53]
	CMR12a	Red cocoyam rhizosphere	Cameroon		Orfamide, Sessilin	[56]
P. chlororaphis SG	COR52	Red cocoyam rhizosphere	Cameroon	Viscosin	Pseudodesmin	[34]
P. mandelii SG	In5	Suppressive potato soil	Greenland	Syringomycin	Nunamycin	[18]
	In5	Suppressive potato soil	Greenland	Syringopeptin	Nunapeptin	[18]
P. corrugata SG	SH-C52	Sugarbeet rhizosphere	Netherlands	Syringomycin	Thanamycin	[57]
	DF41	Canola root	Canada		Thanamycin - var1	[58][59]
	11K1	Bean rhizosphere	China		Brasmycin	[60]
	SH-C52	Sugarbeet rhizosphere	Netherlands	Syringopeptin	Thanapeptin	[57]
	DF41	Canola root	Canada		Sclerosin	[59]
	11K1	Bean rhizosphere	China		Braspeptin	[60]
P. putida G	BW11M1	Banana rhizoplane	Sri Lanka	Xantholysin	Xantholysin	[12][61]
	COR51	Red cocoyam rhizosphere	Cameroon		Xantholysin	[10]
	BS011	Rice rhizosphere	China		Xantholysin	[62]
	267	Black	Vietnam	Putisolvin	Putisolvin I, II	[63]

Taxonomy	Biocontrol Strains	Host/Origin	Country	LP Family	LP	Reference
		pepper				
	COR55	Red cocoyam rhizosphere	Cameroon		Putisolvin III, IV, V	[10][11]
	L48	Fly	Guadeloupe	Entolysin	Entolysin A, B	[64]
	COR5	Red cocoyam rhizosphere	Cameroon		Entolysin B	[10]
	RW10S2	Rice rhizosphere	Sri Lanka	Viscosin	WLIP	[65]
	COW10	White cocoyam rhizosphere	Cameroon		WLIP	[10]
	NSE1	White cocoyam rhizosphere	Nigeria		WLIP	[66]
	COR35	Red cocoyam rhizosphere	Cameroon	Unclassified	N8 (17:8) †	[11]
P. asplenii SG	COR33	Red cocoyam rhizosphere	Cameroon	Unclassified	N5 (13:8) †	[11]
	COR18	Red cocoyam rhizosphere	Cameroon		N5 (13:8), N7 †, Mycin LP †	[11]
Novel U2 SG	COR58	Red cocoyam rhizosphere	Cameroon	Unclassified	N4 (12:10) †	[10][11]

† novel LPs.

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