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Pseudomonas prosekii isolated in Antarctica inhibits plant-pathogenic strains of *Pseudomonas viridiflava* and *Pseudomonas fluorescens*

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Abstract

Pseudomonas-caused plant diseases are present worldwide and affect most of the major lineages of higher plants which, as a consequence, may result in significant economic losses. Despite the use of bacteriocins produced by rhizosphere and soil bacteria has been nowadays considered as novel crop protection approach, antagonistic interactions of cold-adapted isolates toward agriculturally important phytopathogenic bacteria have not been studied yet. In this study, we tested inhibition activity of Antarctic *Pseudomonas* spp. against phytopathogenic pseudomonads. Four Antarctic stains (*P. prosekii* CCM 8878, CCM 8879, and CCM 8881 and *Pseudomonas* sp. CCM 8880) inhibited several phytopathogenic strains of *P. viridiflava* and *P. fluorescens.* Based on inhibition zone character and previous genome research we suggest that L-pyocin activity was responsible for this effect against *P. viridiflava* strains and that tailocin inhibited *P. fluorescens* isolate.

Key words: pyocin, *Pseudomonas*, phytopathogen, tailocin, antimicrobial agents, James Ross Island

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Introduction

Pseudomonas is an ubiquitous bacterial genus with wide metabolic plasticity resulting in colonization of various abiotic and biotic environments. A considerable number of species could inhabit terrestrial and aquatic environments, even the extreme ones, or could be associated with plants, invertebrate or human hosts (Palleroni 2015). The phytopathogenic *Pseudomonas* spp. cause plants diseases ranging from necrotic lesions and spots of stems, leaves or fruits to tissue macerations causing rots, blights, cankers, hyperplasias (*i.e.*, production of galls or scabs), and vascular

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infections resulting in wilts. *Pseudomonas*-caused plant diseases are worldwide spread and affect most of the major lineages of higher plants (Smith et al. 2009), having large economic impact. On the other hand, several *Pseudomonas* strains could be used as agricultural inoculants for plant growth promotion, defense priming and protection against other pathogens (Hu et al. 2021, Flury et al. 2016, Loper et al. 2012). For example, plant growth promoting strain *P. syringae* pv. syringae 260-02 controls colonization by plant pathogenic *P. syringae* pv. tomato DC3000, fungus *Botrytis cinerea* or *Cymbidium Ringspot Virus* (Passera et al. 2019). In competition interactions, pseudomonads produce various secondary metabolites, such as narrow spectra proteinaceous toxins called bacteriocins (Majeed et al. 2011, Oluyombo et al. 2019).

Bacteriocins produced by *Pseudomonas* spp. are referred as pyocins (Michel-Briand and Baysse 2002). Pyocin group varies in size, cytotoxic activity, immunity mechanisms, and killing spectrum (Ghequire and De Mot 2014). Soluble pyocins encompass colicin-like, microcin-like and L-type pyocins which are characterized by low molecular weight. Colicin-like pyocins (S-type and M-type) exhibit modular organization containing domains responsible for receptor-binding, translocation, and killing by nuclease or pore forming activity (Barreteau et al. 2012, Michel-Briand and Baysse 2002). Microcin inhibiting DNA gyrase has been identified in several *Pseudomonas* spp. (Metelev et al. 2013). L-type pyocins harbor tandem lectin domains targeting the cell envelope (Ghequire et al. 2018, McCaughey et al. 2014). Tailocins, high-molecular-weight (HMW) pyocins, are represented by myophage (R-type) and siphophage (F-type) tail-like structures (Nakayama et al. 2000) and their bactericidal activity is caused by the depolarization of the cytoplasmatic membrane (Michel-Briand and Baysse 2002). Pyocin production has been reported for diverse pseudomonads, *in silico* analyses revealed widespread occurrence of pyocin genes across various *Pseudomonas* spp. (Ghequire and De Mot 2014, Loper et al. 2012).

Our previous research confirmed production of both tailocins and soluble pyocins by *Pseudomonas* spp. collected in James Ross Island, Antarctica (Snopková et al. 2018, 2021). The aim of the present study was to assess a pyocin-based inhibition effect of Antarctic *Pseudomonas* spp. against agricultural important plant-pathogenic *Pseudomonas* spp.

Material and Methods

Bacterial strains and cultivation conditions

Pseudomonas spp. strains used throughout this study were collected from the northern part of the James Ross Island, Antarctica, belonging to the North-east Antarctic Peninsula region (according to classification by Terauds and Lee (2016). Soil and vegetable dwelling strains were obtained from to the vicinity of the Johann Gregor Mendel Station (63° 48′ 02″ S, 57° 52′ 57″ W) during the austral summer season of years 2007–9. All strains were maintained in the Czech Collection of Microorganisms (Brno, Czech Republic). The strains were subjected to direct cross inhibitory assay, the result of which was published recently by Snopková et al. (2021) together with detailed strain characteristics.

Phytopathogens causing severe disease of agriculturally important plants (*Pseudomonas viridiflava, P. putida, P. fulva, P. marginalis, P. fluorescens, P. tolaasii*) were provided by the Collection of Phytopathogenic Bacteria (Prague, Czech Republic). The isolates were causative or suspicious agents of plant diseases, several isolates were epiphytic and saprophytic bacteria connected to other phytopathogens or exhibited ice nucleation activity. The strains were isolated mainly from vegetable plants (potato, parsley, clover, cabbage, and apricot) or grape wine, less frequently from *Amaryllis* sp. or trees (horsechestnut, ornamental tree) in the Czech Republic or the Netherlands. Further information about phytopathogenic strains are listed in Table 1.

Bacteria were grown in a Tryptone Yeast (TY) agar (8 g/l casein, 5 g/l yeast extract, 5 g/l sodium chloride, pH 7.5; HiMedia, Mumbai, India) at 25°C or 30°C.

Species	**Strain**	**Source**	**Pathogenicity**	**Year$_{iso}$**
P. viridiflava	VURV-B 025	horsechestnut, NL	virulent strain	2010
P. putida	VURV-B 051	potato, CZ	blight brown lesion on stem	2010
P. putida	VURV-B 052	potato, CZ	bacterial soft rot disease	2010
P. viridiflava	VURV-B 069	parsley, CZ	CA of soft rot disease	2011
P. viridiflava	VURV-B 070	parsley, CZ	CA of soft rot disease	2011
P. viridiflava	VURV-B 071	parsley, CZ	CA of soft rot disease	2011
P. putida	VURV-B 073	parsley, CZ	CA of soft rot disease	2011
P. putida	VURV-B 074	parsley, CZ	CA of soft rot disease	2011
P. putida	VURV-B 088	potato, CZ	CA of soft rot disease	2011
P. putida	VURV-B 099	parsley, CZ	soft rot symptoms	2012
P. viridiflava	VURV-B 102	clover, CZ	soft rot symptoms	2013
P. fulva	VURV-B 150	ornamental tree, CZ	epiphytic bacteria	2006
P. marginalis	VURV-B 161	cabbage, CZ	epiphytic bacteria	2006
P. fluorescens	VURV-B 168	grape wine, CZ	epiphytic bacteria, opportunistic pathogen	2006
P. viridiflava	VURV-B 169	grape wine, CZ	saprophyt accompanying CA of crown gall	2006
P. fluorescens	VURV-B 171	grape wine, CZ	INA bacterium	2006
P. tolaasii	VURV-B 172	grape wine, CZ	saprophyt accompanying c. a. of crown gall	2006
P. fluorescens	VURV-B 195	grape wine, CZ	INA bacterium (-4.5°C)	2007
P. marginalis	VURV-B 203	apricot, CZ	dark brown lesion in stone	2014
P. marginalis	VURV-B 204	apricot, CZ	dark brown lesion in stone	2014
P. fluorescens	VURV-B 231	tomato, CZ	saprophyt accompanying different CA	2005
P. fluorescens	VURV-B 232	Amaryllis, import from NL	saprophyt accompanying CA of soft rot	2005
P. fluorescens	VURV-B 233	tomato, CZ	saprophyt accompanying different CA	2005

Table 1. List of phytopathogenic strains tested. *Legend*: NL – Netherlands, CZ – Czech Republic, CA – causal agent, INA – ice nucleation active strain, Year$_{iso}$ – Year of isolation. Strains susceptible to antimicrobial agents produced by Antarctic *Pseudomonas* spp. are in grey.

Antimicrobial activity detection

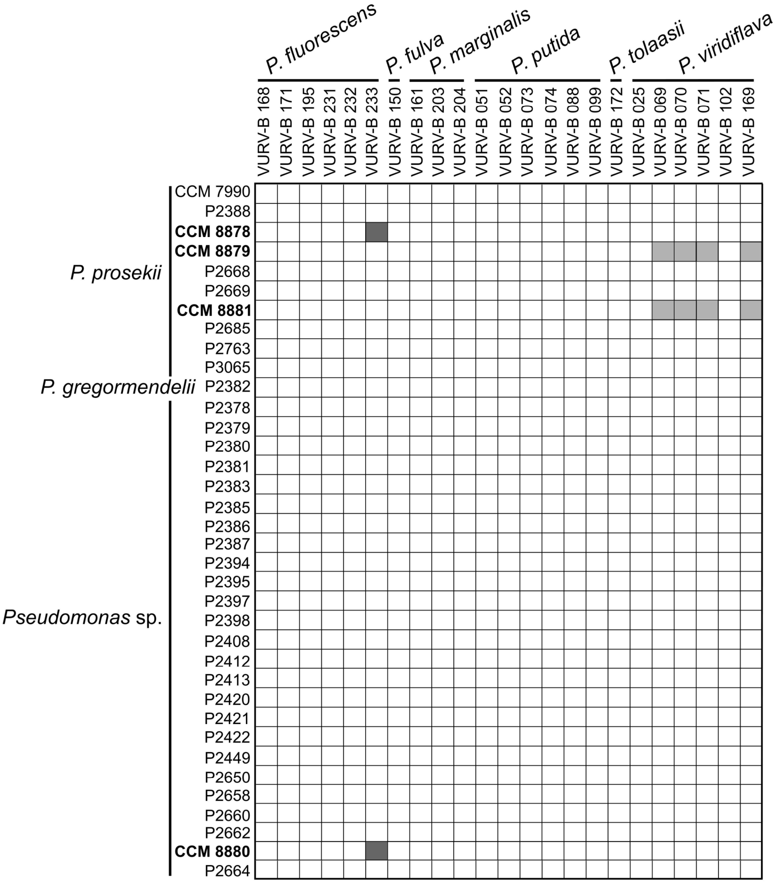
The overlay spot plate assay (Micenková et al. 2014) was used for the detection of bacteriocin-like inhibition of phytopathogens by Antarctic *Pseudomonas* spp. The tested strains were inoculated on the TY agar supplemented with mitomycin C (final concentration 5 µg/ml) and the plates were incubated at 4°C for 7 days in chamber refrigerator. Tested strain (potentially bacteriocin producer) was killed by chloroform vapors (30-min exposure) and overlayed with soft TY medium (0.6% of agar; wt./vol.) containing 10^8 cells of the phytopathogen culture. The plates were subsequently cultivated at 30°C for 24h. All combination of potential producers and phytopathogens were assessed. All samples were independently tested in replicates of two.

Identification of tailocins (R-, F-type pyocins) and/or soluble pyocins (S-type, L-type, M-type or microcin) were based on whether a small zone (1–2 mm, typical for tailocins) or large diffuse zone (> 3 mm, soluble pyocin production) was observed (Fyfe et al. 1984, Grinter et al. 2012).

Results and Discussion

Altogether, 756 individual tests covering 36 producers and 21 indicator strains were performed (in two replications). A total of 4 strains, namely *P. prosekii* CCM 8878, CCM 8879, and CCM 8881 and *Pseudomonas* sp. CCM 8880, exhibited antagonistic activity against plant-pathogenic *Pseudomonas* spp., *see* Fig. 1.

Pseudomonas prosekii CCM 8879 and CCM 8881 were able to inhibit 4 strains of *P. viridiflava* (VURV-B 069, 070, 071, and 169) which caused soft rot symptoms. *P. viridiflava* is a multihost phytopathogen infecting important agricultural crops, *e.g.* tomato (*Solanum lycopersicum*), melon (*Cucumis melo*) or eggplant (*Solanum melongena*). Production of pectinolytic enzymes might be pointed out as an underlying biochemical mechanism since it leads to soft rot symptoms and stem necrosis (Goumans and Chatzaki 1998, Sarris et al. 2012). All inhibition zones were wide (ranging from 4 to 20 mm), with the blurry edges so based on this observation, on inducibility by mitomoycin C and on presence of pyocin genes in the genomes of the producers, we speculate that inhibition was mediated by soluble pyocins. In both genomes, gene for L-type pyocin was detected, and an additional gene for S9-type pyocin was found in the strain CCM 8881 (Snopková et al. 2021). Based on similar inhibition spectra, we suggest that the observed antagonisms towards *P. viridiflava* were caused by L-type pyocins. Both pyocin types (L and S9) are relatively rare among *Pseudomonas* spp.; with occurrence lower than 5% of non-aeruginosa pseudomonads (Ghequire and De Mot 2014). Harboring of L-pyocin genes is significantly associated with soil-dwelling or plant-associated isolates (Ghequire et al. 2018, Grinter et al. 2012, Parret et al. 2005). Genes encoding L-pyocin could be harbored as a cargo gene in tailocin or prophage clusters and therefore horizontally disseminated (Ghequire et al. 2015). On the other hand, S9 pyocins were predicted *in silico* in several *Pseudomonas* spp., mainly in the *P. fluorescens* clade (Ghequire and De Mot 2014). Sharp et al. (2017) speculated that pyocin S9 forms a separate group beside other pyocins. The C-terminal domain of S9 pyocins has an HNH motif and DNase activity similar domains of pyocins S1 or S2 whereas the N-terminal domain is disordered and exhibit great variability in size and amino acid composition (Ghequire and De Mot 2014).



		P. fluorescens						P. fulva	P. marginalis			P. putida						P. tolaasii	P. viridiflava					
		VURV-B 168	VURV-B 171	VURV-B 195	VURV-B 231	VURV-B 232	VURV-B 233	VURV-B 150	VURV-B 161	VURV-B 203	VURV-B 204	VURV-B 051	VURV-B 052	VURV-B 073	VURV-B 074	VURV-B 088	VURV-B 099	VURV-B 172	VURV-B 025	VURV-B 069	VURV-B 070	VURV-B 071	VURV-B 102	VURV-B 169
P. prosekii	CCM 7990																							
	P2388																							
	CCM 8878						▓																	
	CCM 8879																			░	░	░		░
	P2668																							
	P2669																							
	CCM 8881																			░	░	░		░
	P2685																							
	P2763																							
	P3065																							
P. gregormendelii	P2382																							
Pseudomonas sp.	P2378																							
	P2379																							
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	P2658																							
	P2660																							
	P2662																							
	CCM 8880						▓																	
	P2664																							

Fig. 1. Inhibitory activity of Antarctic *Pseudomonas* on phytopathogenic strains. Each row represents the inhibitory activity of Antarctic *Pseudomonas* strain (*i.e.*, potential producer), and each column shows susceptibility of the phytopathogenic strain (*i.e.*, indicator). Light grey boxes indicate inhibition interaction mediated by soluble antimicrobials, dark grey boxes by particle antimicrobials. Antimicrobial producers are shown in bold.

Strains CCM 8878 and CCM 8880 inhibited only one of the 21 tested strains, *P. fluorescens* CPPB-233. *P. fluorescens* encompasses mainly saprophytes and root-associated strains, less frequently plant pathogens (Schroth et al. 2006). Further, many strains belong to the Plant Growth Promoting Rhizobacteria (PGPR) enhancing plant growth and reduce severity of various diseases (Ganeshan and Manoj Kumar 2005). Both inhibition zones were narrow (about 1 mm) which can be attributed to HMW pyocin (tailocin) production. Tailocins were detected in both strains in the previous study using electron micrographs (*see* Fig. 2). Gene mining analysis revealed corresponding gene clusters (Snopková et al. 2021). Strain CCM 8880 contained also a gene for soluble pyocin from S9 group but character of the inhibition zone corresponded rather to the high-molecular pyocin production. Based on the classification developed by Ghequire et al. (2015), the R-type tailocin produced by CCM 8878 belongs to the Rp3 group (with homology to *Vibrio parahaemolyticus* VP882 phage and *Halomonas aquamarina* phage_HAP-1). The R-tailocin of CCM 8880 belongs to the Rp4 group (with homology to Mu-like "*Shigella flexneri*" phage). Both clusters were located in a hot spot *mutS-cinA*, and both contain also few cargo genes, mainly toxins (Snopková et al. 2021). Recent studies focused on bacterial interactions suggest that tailocin production could be an important factor shaping plant or soil microbiome resulting in reduction of species diversity (Dorosky et al. 2017, Ghequire et al. 2015, Hockett et al. 2015), but no study on interaction among phytopathogens has been performed.

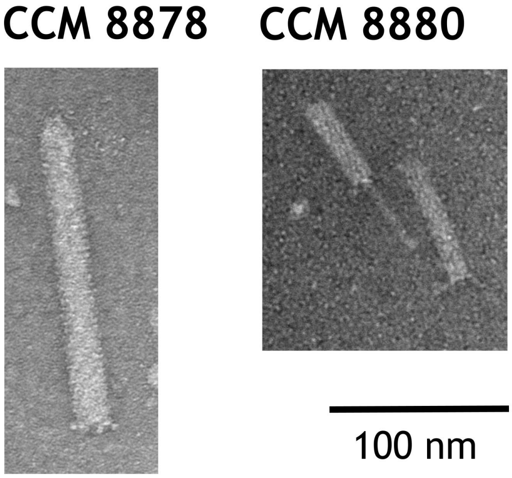

Fig. 2. Tailocin produced by *P. prosekii* CCM 8878 and *Pseudomonas* spp. CCM 8880. Electron micrographs adopted from Snopkova et al. 2021 (study contained detailed methodology for TEM). Scale bar represents 100 nm.

Phytopathogens are annually responsible for considerable losses due to the disease and spoilage of crops (Strange and Scott 2005). Commercially used metal-based bactericides have been applied in agriculture to control plant pathogenic bacteria, but these compounds bring several disadvantages, such as *e.g.*; phytotoxicity, non-specificity, and risk of resistance development. Pristine Antarctic environment could be a source of new antimicrobials equipped by activity at low temperature. Several studies have shown that bacteriocins are effective against phytopathogenic bacteria; tailocin produced by *P. fluorescens* SF4c antagonizes several phytopathogenic *Pseudomonas* spp. and *Xanthomonas* spp. (Fernandez et al. 2017, Príncipe et al. 2018). Putidacin L1 (producer strain *P. putida BW11M1*) exhibited cytotoxic activity against number of phytopathogenic pseudomonad species (Parret et al. 2003), and bacteriocin (producer *P. syringae* pv. ciccaronei) might be used in the prevention of olive knot disease (Lavermicocca et al. 2002). Nevertheless, the use of bacteriocins as biocontrol agents in plants is yet limited due to our insufficient knowledge about bacteriocin inhibition spectra, inhibition kinetics and their other interaction with plant-associated microbiome which request further research.

Conclusion

Our study confirmed a high potential of Antarctic pseudomonads in control of economically important plant disease. Three out of four inhibition interactions were mediated by recently described Antarctic species *P. prosekii* producing L-type pyocin or tailocin.

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