High-Quality Complete Genome Resource of Tomato Rhizosphere Strain *Pseudomonas donghuensis* P482, a Representative of a Species with Biocontrol Activity Against Plant Pathogens

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Abstract

Strain P482 was isolated from a tomato rhizosphere and classified as *Pseudomonas donghuensis*. The *P. donghuensis* species was first established in 2015 and currently consists of only four strains: P482, HYS^T, SVBP6, and 22G5. *P. donghuensis* strains antagonize plant pathogens, including bacteria, fungi, and oomycetes, and, therefore, are of high interest regarding their biological control potential to combat plant diseases. The antimicrobial activity of *P. donghuensis* P482 is based on the production of iron-scavenging compound 7-hydroxytropolone, antifungal volatile organic compounds, and as-yet-unidentified secondary metabolites. Here, we report a complete genome resource for *P. donghuensis* strain P482. The genome consists of a single chromosome (5,656,185 bp) with 5,258 open reading frames (5,158 protein-coding genes, 74 transfer RNAs, 22 ribosomal RNAs, 3 noncoding RNAs, and 1 transfer-messenger RNA) and no plasmid. We believe that information on the first high-quality, complete genome of *P. donghuensis* will provide resources for analyses targeting the biological control potential of this species and understanding the traits essential for plant–microbe interaction.

Genome Announcement

Pseudomonas spp. constitute a group of *Gammaproteobacteria* known for their ability to adapt to various environments, metabolize multiple carbon sources, and produce a remarkable array of secondary metabolites (Gross and Loper 2009). Although the genus contains pathogens such as *Pseudomonas aeruginosa*, *P. entomophila*, or *P. syringe*, most *Pseudomonas* spp. are harmless dwellers or beneficial organisms (Peix et al. 2018). Many representatives of the genus promote plant growth or protect their hosts from the harmful activity of plant pathogens, placing them within the group of the plant-growth-promoting rhizobacteria (PGPR) (Lugtenberg and Kamilova 2009). Significantly, the mechanism of PGPR

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Keywords

7-hydroxytropolone, biological control, complete genome, genomics, PGPR, *Pseudomonas donghuensis*

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*The e-Xtra logo stands for “electronic extra” and indicates that two supplementary files are published online.

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Table 1. Strains of *Pseudomonas donghuensis* and the level of assembly of available genomic data

Strain ^a	Strain isolation source	Assembly level (number of contigs)	GenBank accession	Total sequence length	G+C (%)	ANI (%) ^{b,c}	Reference (genome)
P482	Rhizosphere of tomato, Poland	Complete (1)	CP071706	5,656,185	62.36	99.47 ^c	This study
	–	WGS (69)	JHTS000000000.1	5,623,997	62.38	99.47	Krzyzanowska et al. 2014
HYS ^T	Lake water, China	WGS (231)	AJJP000000000.1	5,646,028	62.42	100	Gao et al. 2012
SVBP6	Bulk soil of an agricultural plot, Argentina	WGS (43)	NWCB000000000.1	5,701,342	62.37	99.45	Agaras et al. 2018
22G5	Rhizosphere of weeds, China	WGS (3185)	RWIB000000000.1	6,546,541	60.74	99.41	Tao et al. 2020

^a Superscript T indicates type strain for the species.

^b ANI was calculated against type strain HYS^T using ChunLab's online Average Nucleotide Identity (ANI) calculator (Yoon et al. 2017).

^c ANI calculated for the complete chromosome of P482 and the draft version from 2014 equaled 99.98%.

activity of pseudomonads can differ depending on a species or even a particular strain—a feature related to the high versatility of genome size and content among *Pseudomonas* spp. (Loper et al. 2012; Silby et al. 2011). Due to their PGPR properties, the plant-beneficial *Pseudomonas* spp. are of high interest in application as biological plant-protection agents in integrated farming (Mercado-Blanco 2015).

In our previous studies, we isolated the P482 strain from the rhizosphere of a tomato plant grown in a garden in Gdynia, Poland (Krzyzanowska et al. 2012). Strain P482 inhibits the growth of bacterial plant pathogens of the soft rot *Pectobacteriaceae* (former pectinolytic *Erwinia* spp.) group, as well as *P. syringae*, and it attenuates disease symptoms caused by these pathogens on plant tissues (Golanowska et al. 2012; Krzyzanowska et al. 2012). Moreover, volatile organic compounds (VOCs) produced by P482 can inhibit the growth of fungal pathogens *Rhizoctonia solani*, *Fusarium culmorum*, and *Verticillium dahliae* and oomycete *Pythium ultimum* (Ossowicki et al. 2017). The phylogenetic studies revealed that the strain belongs to *Pseudomonas donghuensis*—a species represented exclusively at that time by one strain: HYS^T (Krzyzanowska et al. 2016). Currently, the *P. donghuensis* species consists of four strains: P482, HYS^T, SVBP6, and 22G5 (Agaras et al. 2018; Gao et al. 2015; Krzyzanowska et al. 2016; Tao et al. 2020), all of which were shown to have potential to antagonize plant pathogens (Agaras et al. 2015; Krzyzanowska et al. 2012; Tao et al. 2020; Yu et al. 2014). The antimicrobial properties of *P. donghuensis* strains are attributed mainly, but not exclusively, to the production of antimicrobial and iron-scavenging compound 7-hydroxytropolone (7-HT). 7-HT is not a typical metabolite of *Pseudomonas* spp. The *nfs* gene cluster necessary for its production has, thus far, been detected in *P. donghuensis* (Krzyzanowska et al. 2016; Muzio et al. 2020; Tao et al. 2020; Yu et al. 2014) and two closely related species, *P. qingdaonensis* and *P. wadenswilerensis* (Muzio et al. 2020). Prior to detection of 7-HT in *P. donghuensis*, the production of this metabolite was reported in *P. lindbergii* ATCC31099 (Korth et al. 1981) and *Streptomyces neyagawaensis* (Kirst et al. 1982). In the latter, it was studied for its ability to decrease microbial resistance to aminoglycoside antibiotics by the inhibition of aminoglycoside adenylyltransferase (Allen et al. 1982). Nonetheless, P482 is also known to produce antifungal VOCs such as dimethyl disulfide, S-methyl thioacetate, and dimethyl trisulfide (Ossowicki et al. 2017). Moreover, as we have recently unveiled, its genome harbors gene clusters involved in the synthesis of as-yet-unidentified secondary metabolites (Matuszewska et al. 2021).

Until now, none of the *P. donghuensis* genomes has been delivered in the complete (closed) form. Herein, for the first time, we provide a complete, high-quality genome sequence of *P. donghuensis* strain P482.

Draft genome of strain P482 was released in 2014 (Krzyzanowska et al. 2014). At that time, the quality of data and the available software did not allow the assembly of reads into a single molecule, resulting in 69 contigs. Sequencing of genomes of the three other representatives of *P. donghuensis* also did not yield a closed chromosome (Table 1). In this study, to refine the genomic sequence of *P. donghuensis* P482, the strain was cultured for 48 h on

Fig. 1. Order and orientation of genome content in the complete chromosome of *Pseudomonas donghuensis* P482 (this study) in relation to the superseded draft genome from 2014. Analysis was performed using progressiveMauve. Each color block represents a region of the complete genome of P482 that aligned to the WGS version. Sequences within the blocks are presumed to be free from internal genomic rearrangements. Placement of the blocks below the centerline indicates that a particular region aligns in the reverse complement orientation. Red vertical lines in the draft version represent contig borders. Stars indicate the genomic location of the homolog of the *nfs* gene cluster encoding the production of 7-hydroxytropolone an important antimicrobial compound produced by the strains of *P. donghuensis*.

lysogeny broth agar medium. Isolation of DNA and sequencing was performed at Oligo.pl (Institute of Biochemistry and Biophysics, Polish Academy of Sciences, Warsaw, Poland). Genome sequencing was performed using two sequencing platforms: Illumina MiSeq (69× coverage) and Oxford Nanopore GridION (109× coverage). Hybrid assembly of quality filtered reads was performed using Unicycler 0.4.8 (Wick et al. 2017). The remaining ambiguities and sequence errors were verified by PCR and Sanger sequencing. The resulting high-quality complete genome of strain P482 contains one circular chromosome of 5,656,185 bp with an average G+C content of 62.36%. No plasmid was detected. The sequence was annotated using the NCBI Prokaryotic Genome Annotation Pipeline, version March 2021 (Li et al. 2021). The genome was found to contain 5,258 open reading frames (ORFs), among which are 5,158 coding sequences (CDSs), 74 transfer RNAs, 22 ribosomal RNAs, 3 noncoding RNAs, and 1 transfer-messenger RNA.

New annotation performed for the complete genome provides us with the advantage of up-to-date annotation of protein functions. However, studies referring to the four-digit locus tags in the draft genome of P482 have already been published (Krzyżanowska et al. 2016; Matuszewska et al. 2021; Ossowicki et al. 2017). To avoid confusion regarding the designations of genes, we performed cross-mapping of CDSs between the draft and the newly annotated complete genome reported in this study. The mapping was performed at the protein level using BLASTP 2.11.0+ (Altschul et al. 1997) (Supplementary File S1). The threshold for successful mapping was set to E-value ≤ 0.001 and identity $\geq 96\%$. As a result, locus tags for 4,942 protein coding genes (95.8%) were transferred from the draft to the complete genome. Proteins encoded by 4,433 mapped CDSs showed an identity of 100% between versions, 487 showed identity of 99%, and 22 showed identity between 96 to 98%. All remaining genes, including nonprotein-coding genes, were designated with new five-digit locus tags.

Comparison of the refined sequence of *P. donghuensis* P482 with the draft revealed that the complete chromosome contains 32,188 base pairs more than the draft. The order and orientation of genome content in the chromosome in relation to the succeeded WGS assembly is depicted in Figure 1. The analysis was performed using progressiveMauve (Darling et al. 2010). The same program revealed 519 single-nucleotide polymorphisms (single-base changes) between the complete genome and the draft (Supplementary File S2). The cross-mapping of loci revealed 188 protein-coding sequences from the draft that could not be mapped to the complete chromosome of P482 (Supplementary File S3). Most of the unmapped genes encoded either hypothetical or putative proteins (92% in total) and only four (2.1%) of the remaining entries could be assigned function by Kyoto Encyclopedia of Genes and Genomes (KEGG) using BlastKOALA (Kanehisa et al. 2016). In contrast, 118 protein-coding sequences present in the new annotation of the closed genome could not be mapped to the draft (Supplementary File S4). Of this set, 11 entries (13%) were assigned a

KEGG KO identifier. Among the latter were such genes as *recC*, *recD*, and *pqqA*. The differences in detected ORFs between the complete genome and the draft resulted from the differences in the sequence, the fact that some ORFs were not identified in the draft due to its fragmentation into 69 contigs, as well as from applying another, more up-to-date engine to annotate the genome of P482.

In our previous study, the draft genome sequence of P482 was analyzed for the presence of genes encoding the production of secondary metabolites using antiSMASH 2.0 (Blin et al. 2013). The program revealed the presence of 23 gene clusters, including 5 with any suggestion of their function (2 nonribosomal peptide synthases, 1 Bacteriocin, and 2 Other) and 18 putative clusters, 1 of which was found to contain the *nfs* genes required to produce 7-HT (Krzyżanowska et al. 2016). Here, we analyzed the complete genome of P482 with antiSMASH 6.0 beta (Blin et al. 2021) in a similar setting, allowing the most extended search. The updated version of antiSMASH found genomic regions resembling those involved in the synthesis of metabolites such as pseudopyronine (62%), aryl polyen VI (40%), fragin (37%), lipopolysaccharides (27 and 5%), O-antigens (19 and 14%), pyoverdine (17, 11, and 6%), lan-kacidin C (13%), and chejuenolide (7%). Interestingly, however, the putative clusters predicted by antiSMASH 6.0 did not contain a region now known to encode the synthesis of 7-HT.

Pseudomonads developed high-affinity iron uptake systems based on TonB-dependent outer membrane receptors recognizing iron-siderophores (or iron-xenosiderophores) or heme as the iron-loaded ligands (Cornelis 2010). The analysis of the P482 genome revealed the presence of 43 genes coding for TonB-dependent receptors, among which 21 have been annotated as the TonB-dependent siderophore receptors and 3 as the TonB-dependent hemoglobin/transferrin/lactoferrin family receptors. Possessing multiple Ton-B-dependent receptors may give these bacteria an advantage in colonizing an ecological niche (e.g., plant rhizosphere or soil) and increase their competitiveness in an iron-poor environment.

The complete genome of P482 was investigated for the presence of prophage sequences using Prophage Hunter (Song et al. 2019). The analysis resulted in discovering a single putatively intact (active) prophage genome of 57,737 bp, located between positions 2,812,547 and 2,870,283. This prophage genome was shown to contain genes vital for temperate bacteriophages. These included: integrase, regulators governing switch between lytic and lysogenic life cycle, genes coding for holin and lysin, and structural proteins. According to PHASTER (Zhou et al. 2011), this prophage is phylogenetically the most similar to *Pseudomonas* phage YMC/01/01/P52_PAE_BP (Jeon et al. 2012). Furthermore, the presence of structural genes in the prophage genome was verified by VirFam (Lopes et al. 2014). It allowed classification of the prophage into order *Caudovirales* and the family *Siphoviridae*.

Data Availability

The genome resource for *P. donghuensis* P482 described in this study was deposited in GenBank under accession number CP071706.

Author-Recommended Internet Resources

Average Nucleotide Identity (ANI) calculator: <https://www.ezbiocloud.net/tools/ani>

Prophage Hunter: <https://pro-hunter.genomics.cn>

VirFam: <http://biodev.cea.fr/virfam/>

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