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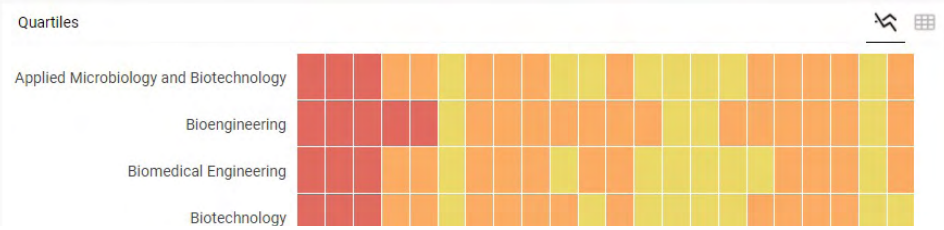

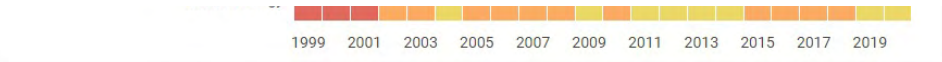

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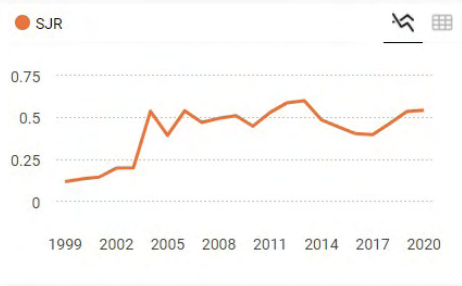

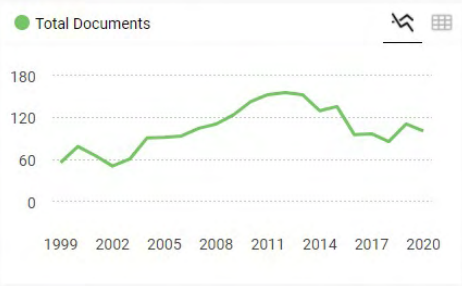

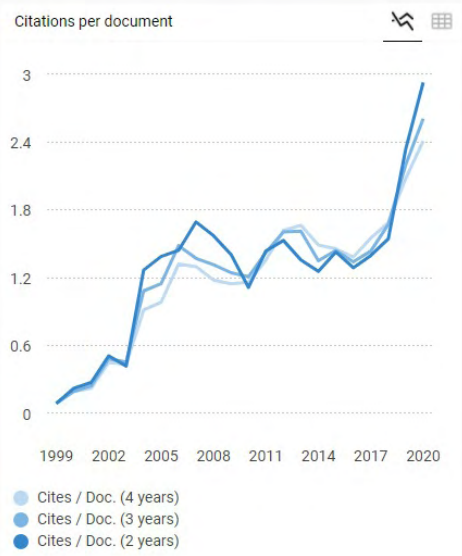

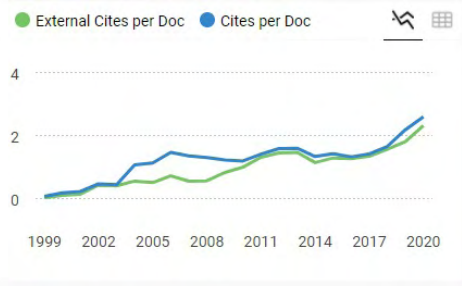

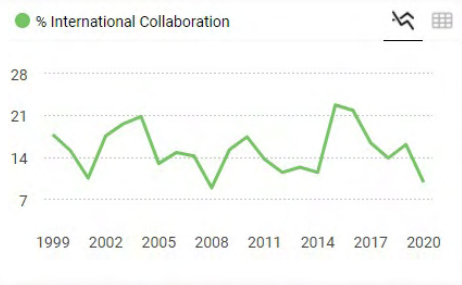

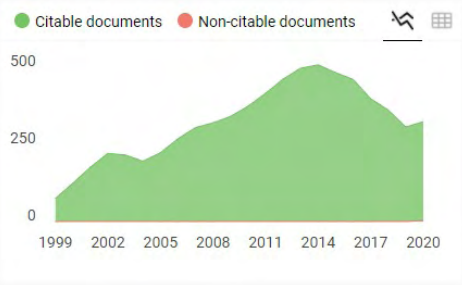

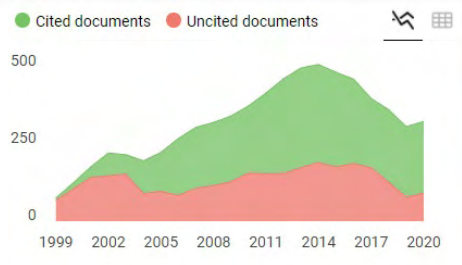

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RESEARCH PAPER

Genomic Characterization of a Newly Isolated Rhizobacteria *Sphingomonas panacis* Reveals Plant Growth Promoting Effect to Rice

Yeon-Ju Kim, Jaewon Lim, Johan Sukweenadhi, Ji Woong Seok, Sang-Won Lee, Jong Chan Park, Assiya Taizhanova, Donghyuk Kim, and Deok Chun Yang

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Abstract This article reports the full genome sequence of *Sphingomonas panacis* DCY99^T (=KCTC 42347^T =JCM30806^T), which is a Gram-negative rod-shaped, non-spore forming, motile bacterium isolated from rusty ginseng root in South Korea. A draft genome of *S. panacis* DCY99^T and a single circular plasmid were generated using the PacBio platform. Antagonistic activity experiment showed *S. panacis* DCY99^T has the plant growth promoting effect. Thus, the genome sequence of *S. panacis* DCY99^T may contribute to biotechnological application of the genus *Sphingomonas* in agriculture.

Keywords: *Sphingomonas panacis*, genome, plant growth promoting rhizobacteria (PGPR), systemic resistance, *Xanthomonas oryzae*

Yeon-Ju Kim[†*], Jaewon Lim[†], Johan Sukweenadhi, Sang-Won Lee, Jong Chan Park, Assiya Taizhanova, Deok Chun Yang
Graduate School of Biotechnology, College of Life Science, Kyung Hee University, Yongin 17104, Korea
Tel: +82-31-201-2645; Fax: +82-31-204-8116
E-mail: yeonjukim@khu.ac.kr

Jaewon Lim, Assiya Taizhanova, Donghyuk Kim[*]
School of Energy and Chemical Engineering, Ulsan National Institute of Science and Technology (UNIST), Ulsan 44919, Korea
Tel: +82-52-217-2945; Fax: +82-52-217-3009
E-mail: dkim@unist.ac.kr

Ji Woong Seok
Lab Genomics Co. Ltd, Seongnam 13487, Korea

Donghyuk Kim
School of Biological Sciences, Ulsan National Institute of Science and Technology (UNIST), Ulsan 44919, Korea

Donghyuk Kim
Korean Genomics Industrialization and Commercialization Center, Ulsan National Institute of Science and Technology (UNIST), Ulsan 44919, Korea

[†]These authors contributed equally.

1. Introduction

The genus *Sphingomonas* was first identified by Yabuuchi *et al*. [1]. *Sphingomonas* is classified within the family *Sphingomonadaceae*, the order *Sphingomonadales* and the a-4 group of the class *Alpha-proteobacteria*. Takeuchi *et al*. proposed the genus *Sphingomonas sensu stricto* and three new genera, *Sphingobium*, *Novosphingobium*, and *Sphingopyxis*, on the basis of phylogenetic and chemotaxonomic analyses [2,3]. Species in the genus *Sphingomonas* are diverse and can adapt to various environments such as bacterial growth plates [4], bulk/sea/waste water [5-7], alpine soil [8], spacecrafts [9], and arctic-lichen [10].

Members of the genus *Sphingomonas* are traditionally known as degraders well adapted for the bioremediation of polycyclic aromatic hydrocarbons [8,9,11,12]. Many strains of this genus can produce exopolysaccharides such as sphingans [13] and welan [13-16]. Some members of this group have been described as plant growth-promoting bacteria [17-20].

Panax ginseng C. A. Meyer is one of the most widely used herbal medicinal plants in Korea. *Sphingomonas* species were detected on the root surface of rusty ginseng by culture-dependent and culture-independent methods combined with metagenome analysis. The isolated novel strains *Sphingomonas panacis* DCY99^T and *S. panaciterrae* DCY91 showed antagonist activity against the severe ginseng pathogen *Ilyonectria* and also elicited systemic resistance in rice to its pathogen, *Xanthomonas oryzae.* Here we report the whole genome sequence and circular mega plasmid of strain *S. panacis* isolated from rusty ginseng root. The genome sequence of *S. panacis* DCY99^T provides a better understanding of its genetic background for more effective utilization of this strain.

2. Materials and Methods

2.1. Isolation and culture conditions

S. panacis DCY99^T was isolated from soil of a ginseng field in Hwacheon province, Republic of Korea by serial dilution method. *S. panacis* DCY99^T (KCTC 42347^T= JCM 30806^T) was grown in DSMZ medium 1 (Nutrient Agar) at 28°C.

2.2. Genome sequencing and assembly

The genomic DNA was isolated using JetFlex Genomic DNA purification kit (ThermoFisher). The extracted DNA was used to generate 20 kb SMRTbell^{TM} template libraries. Genome sequencing was performed at DNA Link, Inc. using the Pacific Biosciences RSII sequencing method. A draft genome of *S. panacis* DCY99^T was generated using *de novo* Hierarchical Genome Assembly Process (HGAP) implemented within the analysis pipeline SMRT Analysis 2.2 (Pacific Biosciences, CA, USA).

The draft genome sequence has been deposited in the NCBI (BioProject PRJNA308882), Genbank IDs are CP014168 for the main chromosome and CP014169 for the plasmid.

2.3. Gene annotation

Open reading frames (ORFs) were predicted using Glimmer 3.02 and predicted genes were annotated using Blastall 2.2.26. tRNA and rRNA genes were identified by tRNAscan-SE version 1.3 and RNAmmer version 1.2. Protein coding genes were also analyzed with the Clusters of Orthologous Groups of proteins (COGs) database.

2.4. Phylogenetic tree analysis

21 *Sphingomonas* strains with genomic sequences were selected for a phylogenetic tree analysis. The phylogenetic tree was constructed by using 16S rRNA gene sequences with Clustal Omega (https://www.ebi.ac.uk/Tools/msa/clustalo/) [21].

2.5. Comparative genomic analysis

NCBI BLAST alignment tool (blastn) was used to align multiple genome sequences. BLAST was performed using default parameters and an e-value of 10, mismatch penalty of -3, and matching reward of 1. The genome and plasmid were visualized by the comparison using the Artemis software and ACT.

2.6. Antagonistic activity experiment

The top agar method was used to determine the *in vitro* antagonistic activity of the *Sphingomonas* strains towards *Xoo* PXO99Az. The size of the halo zone is used as an efficiency of antagonistic activity. *Xoo* PXO61 was used as a negative control. The i*n vivo* antagonistic activity was measured following. *Xoo* PXO99Az strain was grown on peptone sucrose agar (1% peptone, 1% sucrose, 0.1% glutamic acid, and 1.5% bacto agar, pH 7.5, PSA) containing cephalexin (15 mg/L) for 3 days, suspended in distilled water at approximately 1.0 × 109 CFU/ml and then inoculated using the clipping method. *S. panaciterrae* DCY91 and *S. panacis* DCY99 were streaked on TSA medium. All 3 strains incubated at 28°C for 3 days. After incubation, strains were harvested and suspended in distilled water when the optical density at 600 nm reached 2.0. The tips of TP309 leaves were clipped, and the leaves were placed in the bacterial solutions and allowed to soak for 24 h. Lesion development was monitored for two weeks. Three different samples were measured as biological replicates.

3. Results and Discussion

3.1. Classification and features

The type strain, *S. panacis* DCY99^T was isolated from soil of a ginseng field in Hwacheon province, Republic of Korea by serial dilution method. The results of metal tolerating capability of *S. panacis* DCY99^T are corresponding to the its sampling origin (rusty ginseng roots). There was a significant amount of heavy metals accumulated in the rusty surface of ginseng. Classification and general features of *S. panacis* DCY99^T were described in Table 1. The previous result showed that *S. panacis* DCY99^T is Gram-negative, aerobic, non-spore forming, motile, rod shaped, oxidase and catalase positive [19]. The overall shape of *S. panacis* DCY99^T was analyzed with scanning electron microscope *S. panacis* (Fig. 1A). Colonies are circular, entire, low convex, smooth, opaque, light yellow, and 0.1-1.0 mm in diameter after growth on nutrient agar (NA) plates for 1 day. The bacteria grow optimally at 25-30°C and pH 6.0-6.5. Phylogenetic tree analysis with 16S rRNA gene sequences highlighted the taxonomic position of *S. panacis* DCY99^T and *S. panaciterrae* DCY91^T within the genus *Sphingomonas* (Fig. 1B). The isoprenoid quinone detected was ubiquinone Q-10 and *sym*-homospermidine as the major polyamine. The major polar lipids were sphingoglycolipid, diphosphatidylglycerol, phosphatidylethanolamine, phosphatidylglycerol and phosphatidylcholine. The major fatty acids were $C_{14:0}$2OH, $C_{16:0}$ and summered feature 8 ($C_{18:1}$ ω7*c*:$C_{18:1}$ ω6*c*). The novel species *Sphingomonas panacis* DCY99^T was registered as the type strain (=JCM 30806^T =KCTC 42347^T).

3.2. Growth conditions and genomic DNA preparation

S. panacis DCY99^T was selected for genome sequencing because this species produces compounds that protect plants from biotic stress and has growth-promoting activity in rice

Table 1. Classification and general features of *S. panacis* DCY99^T

MIGS ID	Property	Term	Evidence
	Classification	Domain Bacteria	TAS
		Phylum *Proteobacteria*	TAS
		Class *Alphaproteobacteria*	TAS
		Order *Sphingomonadales*	TAS
		Family *Sphingomonadaceae*	TAS
		Genus *Sphingomonas*	TAS
		Species *Sphingomonas panacis*	TAS
		Strain DCY99^T	TAS [19]
	Gram stain	Negative	IDA
	Cell shape	Rod	IDA
	Motility	Motile	IDA
	Sporulation	No spore production	IDA
	Temperature range	10-37°C	IDA
	Optimum temperature	25°C	IDA
	pH range; Optimum	5.5-7.5; 6.0-6.5	IDA
	Carbon source	Glucose, arabinose, mannose, others	TAS [19]
MIGS-6	Habitat	Mountain cultured rusty *Panax ginseng* C.A. Meyer root	IDA
MIGS-6.3	Salinity	0.5-4.5% NaCl	IDA
MIGS-22	Oxygen requirement	Aerobic	IDA
MIGS-15	Biotic relationship	Free-living	IDA
MIGS-14	Pathogenicity	Non-pathogenic	NAS
MIGS-13	Source material identifiers	KCTC 42347^T, JCM 30806^T	TAS [19]
MIGS-4	Geographic location	South Korea: Gangwon province	IDA
MIGS-5	Sample collection	April 2013	IDA
MIGS-4.1	Latitude	38.153 N	IDA
MIGS-4.2	Longitude	127.770 W	IDA
MIGS-4.4	Altitude	461 m	IDA

*Evidence codes - IDA Inferred from Direct Assay, TAS, Traceable Author Statement (*i.e*., a direct report exists in the literature), NAS Non-traceable Author Statement (*i.e*., not directly observed for the living, isolated sample, but based on a generally accepted property for the species, or anecdotal evidence). These evidence codes are from the Gene Ontology project [24].

and *Panax ginseng* C. A. Meyer. *S. panacis* DCY99^T (KCTC 42347^T= JCM 30806^T) was grown in DSMZ medium 1 (Nutrient Agar) at 28°C. DNA was isolated from 0.5-1 g of cell paste using the JetFlex Genomic purification kit as recommended by the manufacturer. A draft genome of *S. panacis* DCY99^T was generated using the PacBio platform following the manufacturer's instructions.

3.3. Genome sequencing and assembly

A total of 96,529 reads with an average length of 10,519 bp were generated and assembled using the *de novo* Hierarchical Genome Assembly Process (HGAP) implemented within the analysis pipeline SMRT Analysis 2.2 (Pacific Biosciences, CA, USA) (Table S1). Ambiguous bases and inserted/deleted regions between PacBio assembled and preassembled draft sequences were corrected manually by using consensus sequences for final assembly. Long reads were selected as seed sequences for constructing preassemblies, while short reads were mapped to the seeds using BLASTR software for alignment, which corrected errors in the long reads and thus increased the accuracy rating of bases. The sequencing run yielded 1,015,409,853 filtered sub-read bases and a total of 85,634,367 preassembled bases were used for deep sequencing. tRNA and rRNA genes were identified by tRNAscan-SE version 1.3 [22] and RNAmmer version 1.2 [23]. Open reading frames (ORFs) were predicted using Glimmer 3.02 and predicted genes were annotated using Blastall 2.2.26. Protein coding genes were annotated to The Clusters of Orthologous Groups of proteins (COGs) database [24]. Artemis software was used for data management and ACT was used for genome and plasmid visualization [25]. Sequencing project information was summarized (Table 1). The draft genome consisted of a single circular chromosome of 5,003,808 bp with a GC content of 65.66%, which is characteristic of most *Sphingomonas* strains (60 to 68%). A total of 4,800 genes were predicted to be encoded by the genome (Table S2). There was a single circular plasmid of 319,133 bp with a GC content of 62.71% (Table S3).

The draft genome sequence has been deposited in the

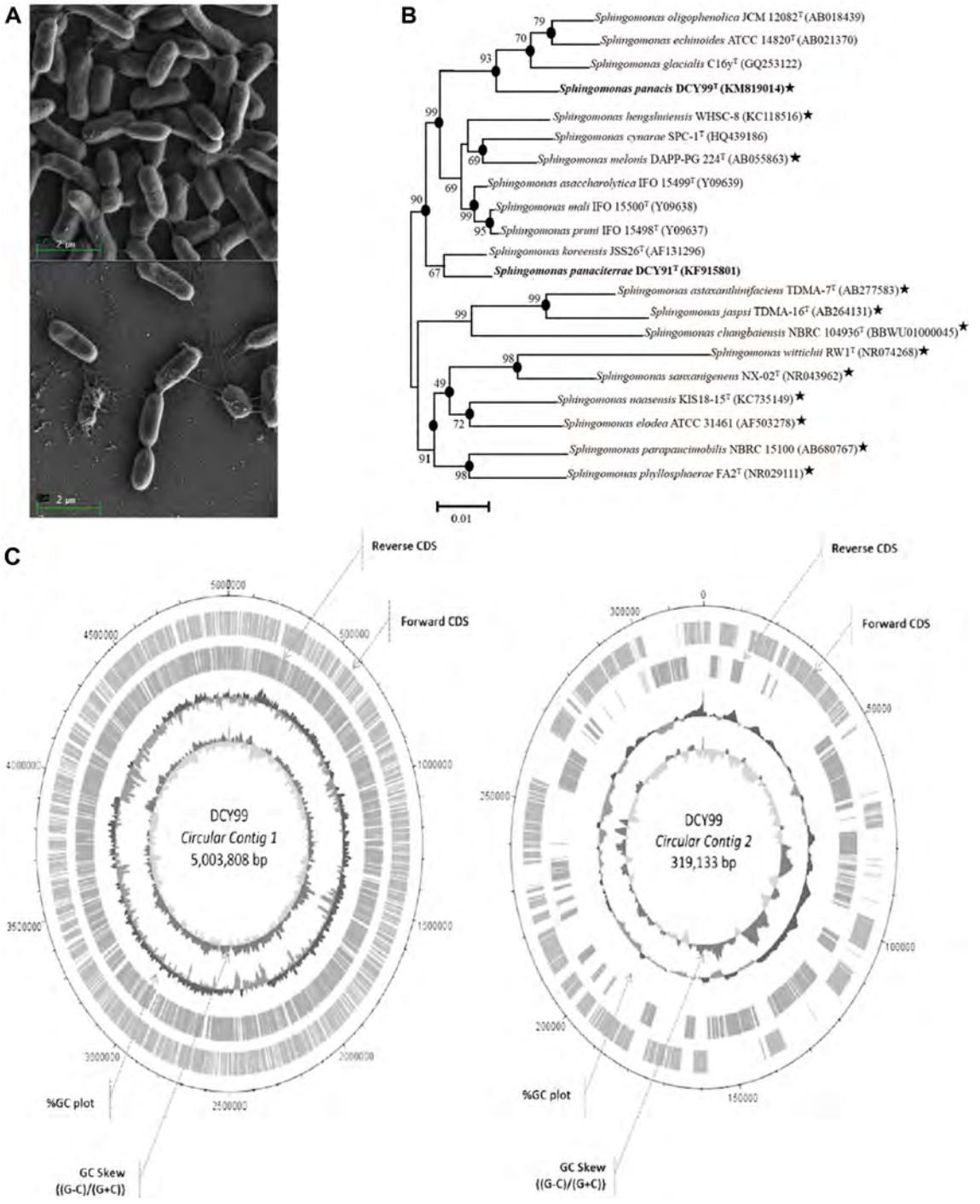

Fig. 1. Morphological and genomic characterization of a newly sequenced *S. panacis* DCY99^T. (A) Scanning electron microscope photos of *S. panacis* DCY99^T. (B) Phylogenetic tree analysis with 16S rRNA gene sequences highlights the taxonomic positions of *S. panacis* DCY99^T and *S. panaciterrae* DCY91 in the genus *Sphingomonas*. GenBank accession numbers are indicated in parentheses. Filled circles indicate that the corresponding nodes were also recovered in the tree generated with the neighbor-joining and maximum-parsimony algorithms. Stars indicate strains for which draft whole genome sequences are available. Bar, 0.01 substitutions per nucleotide position. (C) Graphical circular map and genetic features of *S. panacis* DCY99^T. The genomic features of *S. panacis* DCY99^T for the main chromosome (Contig 1) and the plasmid (Contig 2) are shown. From outside to the center: Genes on the forward strand, genes on the reverse strand, G+C content, and GC skew.

NCBI (BioProject PRJNA308882). The genome can be found under BioSample SAMN04417200, and the Genbank ID is CP014168 for the genome and CP014169 for the plasmid, respectively.

Table 2. Genome statistics.

Feature category	Genomic feature	Percentile
Genome size (bp)	5,003,808	100.00
DNA coding (bp)	4,376,256	87.46
DNA G+C (bp)	3,285,696	65.66
DNA scaffolds	2	-
Total genes	4,872	100.00
Protein coding genes	4,722	96.92
RNA genes	62	12.73
Pseudo genes	88	18.06
Genes in internal clusters	1,274	26.15
Genes with function prediction	4,431	90.95
Genes assigned to COGs	3,378	69.34
Genes with Pfam domains	2,039	41.85
Genes with signal peptides	600	12.32
Genes with transmembrane helices	889	18.25
CRIPSR repeats	2	-

3.4. Genome annotation

The deposited sequences that both CP014168 and CP014169 were annotated by the NCBI using the Prokaryotic Genome Annotation Pipeline. Genome annotation revealed 4,872 coding sequences (Table 2). The circular visualization of the genome annotation for the main chromosome and the plasmid is presented (Fig. 1C). The COG functional analysis of the genomic DNA of strain *S. panacis* DCY99^T was also performed (Fig. S1). Interestingly, genes for indole-3-acetic acid synthesis are present in the genome of *S. panacis* DCY99^T. These genes corroborate that these *S. panacis* strains could promote plant growth and elicit systemic resistance. Protein coding genes were annotated to The Clusters of Orthologous Groups of proteins was presented in Table S2 and S3. The genome annotation and the sequences of genes can be used for applications, such as developing detection kits for plant growth promoting bacteria or plant pathogens [26].

3.5. Insights from the genome sequence

Genome analysis showed that *S. panacis* DCY99^T contained many genes encoding oxidoreductases, chaperones proteins, and metal transporters. The genes encode the enzymes for the synthesis of the nucleotide sugars (UDP-Glc and UDP-GlcA) from Glc-1-phosphate such as *pgmG* and *ugpG* were found, indicating its ability to produce extracellular polysaccharide sphingans. Several important quorum sensing factor, such as *rsh* and *luxR* were also present on the genome. These genes presumably allow this strain to cope with different environmental stresses. *S. panacis* DCY99^T might have the potential for application in industrial biotechnology as a producer of miscellaneous hydrolases.

3.6. Comparative genomic analysis

NCBI BLAST alignment tool (blastn) was used to align multiple genome sequences. BLAST was performed using default parameters and an e-value of 10, mismatch penalty of -3, and matching reward of 1. The genome and plasmid were visualized by the comparison using the Artemis software and ACT. The genome of *S. panacis* DCY99^T was compared with *S. wittichii* RW1, *S. melonis* FR1, and *S. sanxanigenens* NX02, respectively (Fig. 2A). The principal features of the plasmid sequences for bacteria of the genus *Sphingomonas* were compared (Fig. 2B) Comparison of the genomic sequences available for bacteria within the genus *Sphingomonas* were summarized in Table S4. Principal features and comparison of the plasmid sequences available for bacteria in the genus *Sphingomonas* also was presented in Table S5.

3.7. *Sphingomonas* enhances resistance to bacterial leaf blight

Two *Sphingomonas* strains were tested against the rice

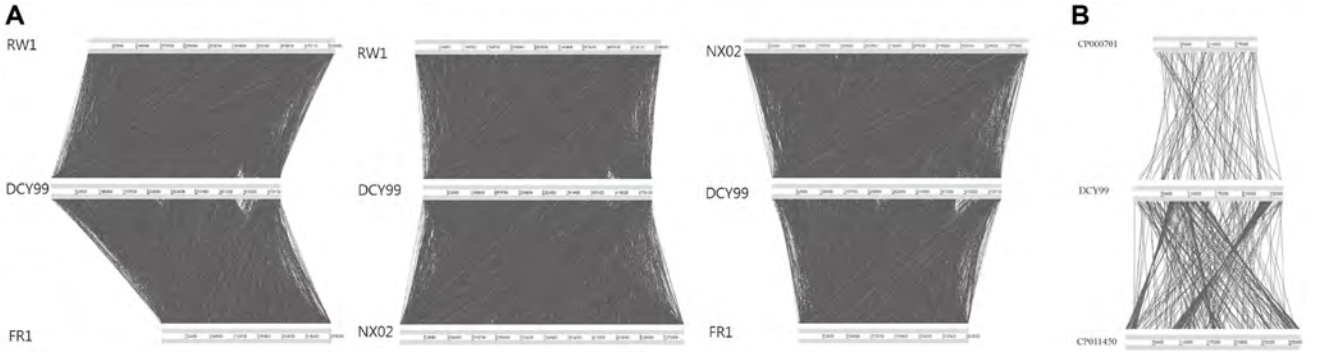

Fig. 2. Comparative genomic analysis for multiple *Sphingomonas* strains. (A) Genomic sequence comparison analysis for the main chromosomes of *S. panacis* DCY99^T, *S. wittichii* RW1, *S. melonis* FR1, and *S. sanxanigenes* NX02. (B) Genomic sequence comparison analysis for the plasmids of *S. wittichii* RW1 (CP000701) and *S. sanxanigenens* NX02 (CP011450).

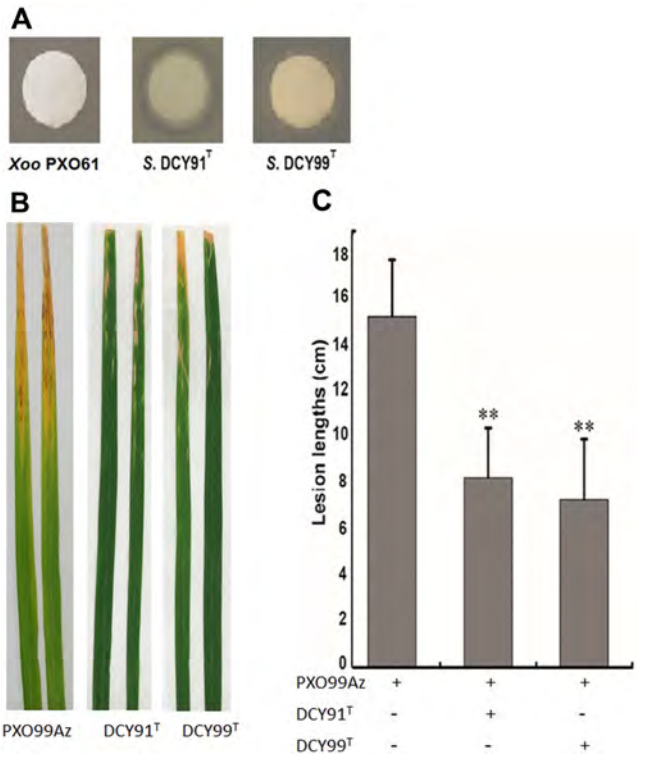

Fig. 3. Evaluation of the antagonistic activity of *Sphingomonas* against *Xoo* PXO99Az. (A) *In vitro* antagonistic test against *Xoo* PXO99Az. Growth of three bacterial strains, namely *Xoo* PXO61, *S. panaciterrae* DCY91, and *S. panacis* DCY99^T, on TSA medium containing *Xoo* PXO99Az was monitored. Eighteen biological replicates were performed. All experiments were repeated three times. (B) Lesion development of two *Sphingomonas* strain feeding lines and wild-type TP309 inoculated with *Xoo* PXO99Az. Photograph of rice leaves 14 days after inoculation. (C) Lesion lengths of rice leaves measured 14 days after inoculation. All experiments were repeated three times and the error bars indicate means ± SD (n = 9). At least three biological replicates were performed. Asterisk indicates $p < 0.01$ (Duncan test). Different letters above bars indicate statistically significant differences as determined by one-way analysis of variance (ANOVA), $p < 0.01$.

pathogenic bacteria *Xoo* PXO99Az. The top agar method was used to determine the antagonistic activity of the *Sphingomonas* strains towards *Xoo* PXO99Az. Presence of a halo zone around a disc was taken as evidence of antagonistic activity (Fig. 3A). *S. panaciterrae* DCY91^T had an antagonistic effect on *Xoo* PXO99Az as evidenced by a clear halo zone (2.537 ± 0.474 mm). The strain *S. panacis* DCY99^T had a greater antibacterial effect on *Xoo* PXO99Az (5.722 ± 0.521 mm) than *S. panaciterrae* DCY91^T. In contrast, the negative control *Xoo* PXO61 did not have significant antagonistic activity toward *Xoo* PXO99Az.

S. panaciterrae DCY91^T and *S. panacis* DCY99^T were streaked on TSA medium and incubated at 28°C for 3 days. After incubation, strains were harvested and suspended in distilled water when the optical density at 600 nm reached 2.0. The tips of TP309 leaves were clipped, and the leaves were placed in the bacterial solutions and allowed to soak for 24 h. *Xoo* PXO99Az strain was grown on peptone sucrose agar (1% peptone, 1% sucrose, 0.1% glutamic acid, and 1.5% bacto agar, pH 7.5, PSA) containing cephalexin (15 mg/L) for 3 days, suspended in distilled water at approximately 1.0×10^9 CFU/ml and then inoculated using the clipping method. Lesion development was monitored for two weeks. Three different samples were measured as biological replicates. Lesion lengths on rice leaves (TP309) inoculated with two strains (*S. panaciterrae* DCY91 and *S. panacis* DCY99^T) were 46 to 53% lower than rice leaves not inoculated with *Sphingomonas* (Fig. 3B, Fig. 3C). These data support that the enhanced resistance seen in TP309 was caused by the antagonistic effects of *Sphingomonas* against bacterial leaf blight.

4. Conclusion

This is the first report describing the genome sequence of *S. panacis* DCY99^T. The genome size of strain *S. panacis* DCY99^T (5.0 Mb) is smaller than that of other sequenced members of the genus *Sphingomonas*, including *S. sanxanigenens* NX02 (6.58Mb) and *S. wittichii* RW1 (5.92Mb). Strain *S. panacis* DCY99^T has a G+C content (65.66%) higher than that of *S. paucimobilis* EPA505 (63.9%). Antagonistic activity experiment showed *S. panacis* DCY99^T has the plant growth promoting effect. Thus, the genome sequence of *S. panacis* DCY99^T may contribute to biotechnological application of the genus *Sphingomonas* in agriculture.

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