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ORIGINAL ARTICLE

Complete genome sequence of the mango bacterial dry rot pathogen *Sphingomonas carotinifaciens* strain NY01

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Abstract

Mango bacterial dry rot has become an increasingly serious issue in the mango-producing regions of Guangdong, China, leading to dry and necrotic leaves and branches. Previous studies have shown that the pathogenic bacterium, strain NY01 was identifed as *Sphingomonas sanguinis* by morphological observation and 16S rRNA sequencing analysis. In order to further understand the pathogenic physiological and pathogenic mechanism of the pathogen, the whole genome sequence of the pathogen was analyzed on the PacBio RSII platform.The complete genome of strain NY01 consists of one chromosome (3,280,800 bp) and three plasmids (275,887 bp, 143,601 bp, and 37,326 bp), 59 transfer RNA (tRNA) sequences, and 12 rRNA sequences. The genome was found to comprise 3593 coding genes, of which 3426 were annotated with biological functions across various databases. Comparative genomic analysis found that the NY01 strain clustered closely together with *Sphingomonas carotinifaciens* DSM 27347 2020 (GCF_009789535.1), exhibiting an average nucleotide identity (ANI) of 97.18%, indicating a strong evolutionary relationship. This finding contrasts with prior 16S rRNA sequencing results, highlighting that 16S rRNA sequence analysis for genus identification of *Sphingomonas* should be regarded as a preliminary assessment and requires validation through whole genome sequencing. This conclusion serves as a caution for future identifications of *Sphingomonas* species. This study clarified the taxonomic status of the pathogenic bacteria and explored pathogenic factors, which can serve as a theoretical basis for understanding the occurrence and progression of the disease, as well as for implementing effective prevention and control measures.

Keywords Mango bacterial dry rot · Classification · *Sphingomonas carotinifaciens* · Genome · PacBio RSII sequencing

Introduction

Mangoes, which are rich in sugar, fatty acids, mineral elements, organic acids, amino acids, and vitamins, have gained immense popularity among consumers, leading to the rapid development growth of this industry (Mirza et al. 2021). Thriving in warm climates and intolerant to frost, mangoes are best suited for regions with distinct dry and wet seasons in tropical and subtropical monsoon climates. Currently, mangoes are cultivated in at least 80 countries and regions worldwide (Shah et al. 2010). However, with the rapid expansion of mango cultivation areas, mango diseases have become increasingly prominent. The rapid decline in mango yield and quality poses a significant threat to the mango industry, subsequently impacting the income of mango farmers (Shu et al. 2020; Shukla et al. 2020). Throughout the entire growth cycle, mangoes are susceptible to various diseases. It has been reported that there are over 60 types of infectious diseases affecting mangoes, involving more than 100 pathogens, including pathogenic fungi, bacteria, and nematodes (Krishna et al. 2007; Dofuor et al. 2023). The bacterial disease of mango trees has shown an increasing trend year by year. At present, the reported bacterial diseases include bacterial black spot, bacterial

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apical necrosis, bacterial dry rot and bacterial necrotic disease, etc. The pathogens involved include the genera *Xanthomonas* spp. (Ah-You et al. 2007; Pruvost et al. 2011), *Pseudomonas* spp. (Cazorla et al. 1998), and *Pantoea* spp. (Gutiérrez-Barranquero et al. 2019).

Between 2016 to 2017, our research team conducted a survey on mango diseases and pests in mango-producing regions, identifying a severe mango bacterial wilt disease affecting commercial mango orchards cultivating the Keitt cultivar in the Leizhou Peninsula region of Guangdong Province, China. Initially resembling symptoms of mango bacterial black spot, this disease progresses to leaf and branch drying and necrosis, distinguishing it from bacterial black spot and as mango bacterial dry rot. Through morphological observations and 16S rRNA sequencing analysis, the pathogenic bacterium strain NY01 was confirmed as *Sphingomonas sanguinis* (Liu et al. 2018). Subsequently, in 2019, the disease emerged in the Deshehari cultivar within the same mango region. Inoculation of strain NY01 into this variety resulted in similar symptoms observed in the field, leading to the conclusion that both cultivars are affected by the same pathogen. In order to prevent the further spread of the disease, the pathogenic strain NY01 underwent whole-genome sequencing at Guangzhou Genedenovo Biotechnology Co., Ltd., using third-generation sequencing technology. Genes related to virulence, carbohydrate metabolism, drug resistance, and antimicrobial activity were predicted and annotated using various databases, including GO, KEGG, COG, NR, and Swiss-Prot. The analysis of pathogenic factors, resistance genes, drug resistance genes, and metabolic pathways in the NY01 strain establishes a theoretical foundation for the prevention and control of mango diseases. This research approach aims to offer theoretical insights into the pathogenic mechanism, aiding in disease control and providing a basis for further studies on this issue.

Materials and methods

Pathogenicity testing of strain NY01 in the cultivated variety Deshehari

In 2019, the bacterial dry rot disease was broke out in the mango cultivated variety Deshehari, which is cultivated in Leizhou Peninsula, Guangdong Province, China. The pathogen strain NY01, isolated from the Keitt cultivar, was identified as *Sphingomonas sanguinis* by morphological observation and 16S rRNA sequencing analysis (Liu et al. 2018). One-year-old Deshehari mango seedlings grown in pots within a controlled glasshouse environment, were utilized for inoculation. For specific inoculation procedures, please refer to Liu et al. (2018). Strains of NY01 cultured on nutrient agar (NA) medium were employed for microscopic examination and genomic analysis.

Complete genome sequencing and analysis of the NY01 strain

To obtain more information about this pathogen and to explore the interaction mechanisms of the NY01 strain with mango, we sequenced the NY01 genome using the PacBio Sequel platform (Genedenovo Biotechnology Co., Ltd., Guangzhou, China). Highly accurate preassembled reads (99.999% accuracy) were obtained through low-quality filtering and correction. These reads were then utilized for genome assembly. The HGAP software was used for overlap assembly (Chin et al. 2013), and predictions for protein-coding genes of the NY01 strain were made using Glimmer 3.0 and GeneMarkS software (Besemer et al. 2001).

Functional genome annotation

To predict the open reading frames (ORFs), the NCBI prokaryotic genome annotation pipeline and Prokka (version 1.11) were used (Tatusova et al. 2016). Additionally, rRNAmmer software was employed for rRNA prediction (Lagesen et al. 2007), tRNAscan for tRNA prediction (Lowe and Eddy 1997), and Rfam for sRNA prediction. The predicted gene sequences were compared with various functional databases, including Nr, COG, KEGG, GO, and Swiss-Prot, using blast software to obtain protein functional annotation information (El-Gebali et al. 2019). Furthermore, comparisons and analyses with databases such as Pathogen-Host Interaction (PHI), Virulence Factor Database (VFDB), Antibiotic Resistance Gene Database (ARDB), and Carbohydrate-Active Enzymes Database (CAZyme) were conducted to identify potential pathogenesis-related genes (Alcock et al. 2020).

Phylogenetic and comparative genomic analysis

Genome-wide comparisons of NY01 strain and 7 *Sphingomona*s genome files downloaded from NCBI database were performed by OrthoMCL software to identify orthologous genes, and then Mafft software was used for sequence comparison of executive homologous genes of different strains (Chen et al. 2006; Katoh and Standley 2013). The phylogenetic tree based on conserved core single-copy orthologous genes was constructed by Neighbor-joining method with 1000 bootstrap replicates statistical support, using MEGA version X (Feng et al. 2017). The species boundary and genetic evolution distance of 8 strains were calculated by using PYANI software for ANI analysis. A heatmap based on ANI values

Table 1 The strain information from NCBI database

Strain name	RefSeq assembly	Abbreviation
S.sanguinis NBRC 13937	GCF_001591005.1	Ssa_ NBRC_13937
S.sanguinis VD7	GCF_037149935.1	Ssa_VD7
S. paucimobilis FDAARGOS_908	GCF_016027095.1	Spa_FDAAR-GOS_908
S. paucimobilis AIMST_S2	GCF_003314795.2	Spa_AIMST_ S2
S. carotinifaciens DSM 27347 2019	GCF_009789535.1	Sca_ DSM_27347-1
S. carotinifaciens DSM 27347 2020	GCF_009789535.1	Sca_ DSM_27347-2
S. ginsenosidimutans KACC_14949	GCF_002374835.1	Sgi_ KACC_14949
S. corticis 36D10-4-7	GCF_012035195.1	Spa_36D10-4-7

was generated by using the package heatmap in statistical sofware R (Table 1).

Results

Pathogenicity assessment of the strain NY01

Bacterial dry rot was documented in the mango cultivars ‘Deshehari’, with symptoms resembling those of mango bacterial black spot but progressing to desiccation and necrosis of leaves and branches (Fig. 1A). Following inoculation of one-year-old Deshehari seedlings, the NY01 pathogen induced symptoms consistent with those observed in the field, confirming that the pathogens affecting both cultivars are identical. The NY01 strain cultured on agar plates formed yellow, smooth, and opaque colonies (Fig. 1B) and exhibited a rod-shaped morphology with dimensions approximately 0.7 to 1.4 µm (Fig. 1C,D). Phylogenetic analysis of the 16S rDNA confirmed its identification as *Sphingomonas sanguinis* (Figure S1).

Genome assembly and prediction

After sequencing on the PacBio RSII platform, we obtained 1,431,240,431 base pairs (bp) of raw reads. Following the removal of sequence adapters, 1,377,777,999 bp of reads were retained. Quality control analysis revealed that the deduced genome of the NY01 strain consists of one chromosome (3,280,800 bp in size, GC content 67.42%; Fig. 2) and three plasmids: Ssp01, Ssp02, and Ssp03, with respective sizes of 275,887 bp, 143,601 bp, and 37,326 bp, and respective GC contents of 55.56%, 56.11%, and 58.16%. Gene prediction and annotation were carried out using HGAP software, resulting in a total of 3593 predicted genes with an average total length of 837,462 bp (Table 2, Supplementary material 1). Furthermore, 71 non-coding RNA sequences were predicted, including 59 transfer RNA (tRNA) sequences and 12 rRNA sequences. These predictions were made using the tRNAscan and rRNAmmer software programs, respectively (Table 3).

By utilizing online software programs such as CRISPR finder and Island Viewer4, the genome was predicted to contain three CRISPR loci and 25 GIs. These genetic islands are primarily associated with various biological functions, including cell flagella, intracellular regulation, transmembrane transport, transcription, and transport, suggesting potential associations with host-pathogen interactions (Supplementary material 2). Additionally, CRISPR finder online software was employed to predict CRISPR in the genome, leading to the identification of three CRISPR loci located on the chromosome, one of which was deemed reliable.

Gene annotation

The genome contained 3593 coding genes, among which 3426 genes with biological functions were annotated in multiple underlying databases (GO, KEGG, COG, NR and Swiss-Prot) (Supplementary material 1, Table 4). In COG database, 2992 genes were annotated, which were categorized into 21 classes

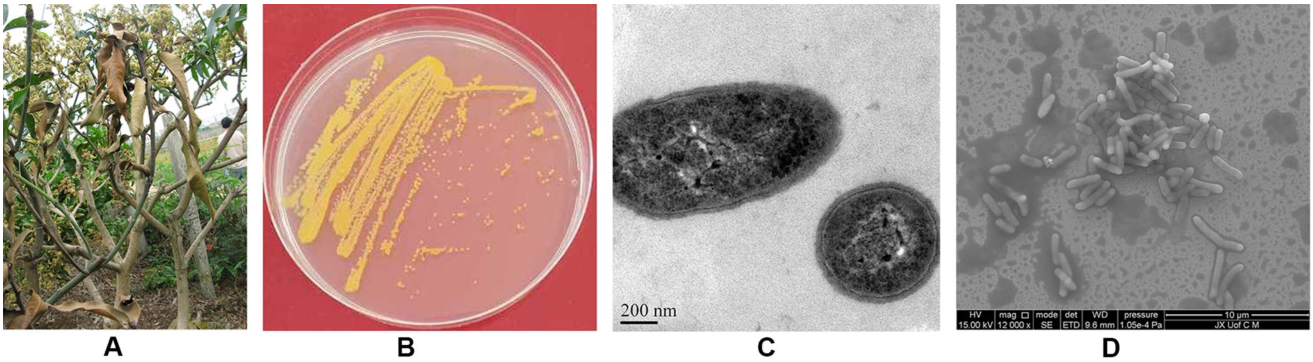


Fig. 1 Isolation and identified of *Sphingomonas* sp. strain NY01. **A** Representative leaves and branches of mango bacterial dry rot. **B** Strain morphology. **C–D** Cellular electron micrograph

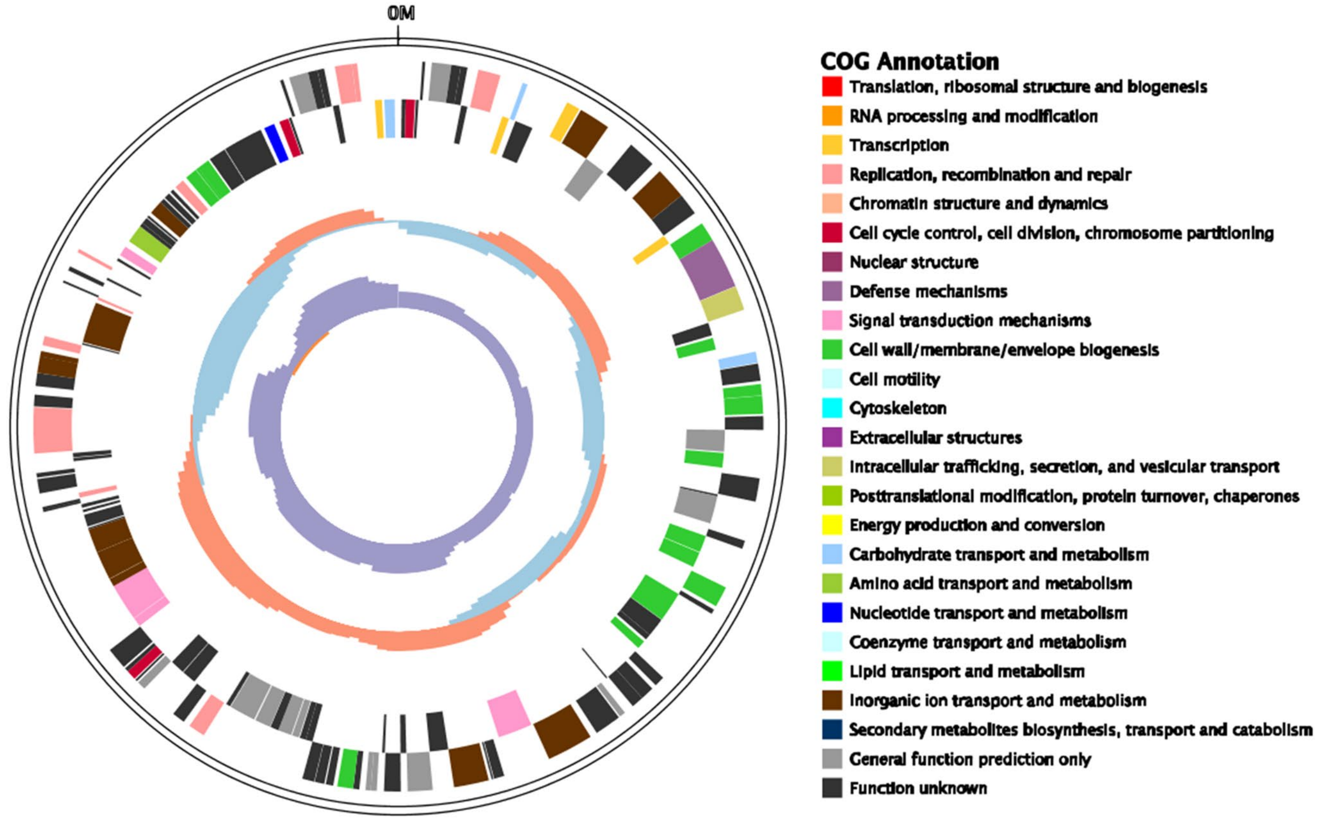


Fig. 2 Chromosome genome map of Strain. *Note* The second and third circles indicate the positive chain and negative chain genes, respectively. The fourth circle shows the ncRNA, with black representing tRNA and red representing rRNA. The fifth circle represents GC content, with red indicating values greater than the mean and blue indicating values less than the mean. The sixth circle represents GC offset, where purple indicates values greater than 0 and orange indicates values less than 0

Table 2 General features of the strain NY01 genome

Sample	Total length	GC content	Coding gene
Chr1	3280800	67.42%	3111
Ssp01	275887	65.56%	296
Ssp02	143601	64.11%	141
Ssp03	37326	58.16%	45

Table 3 Chromosomal non-coding RNA prediction

Type	Number	Average length(bp)	Total length	In genome(%)
23s rRNA	4	2821	11287	0.34
16s rRNA	4	1475	5900	0.18
tRNA	59	78	4606	0.14
5s rRNA	4	114	456	0.01

including general function predication only, function unknown, signal transduction mechanisms, and amino acid transport and metabolism. In KEGG database, 1018 genes were annotated, including 575 genes in metabolic pathway, accounting for 56% of the total annotation of KEGG. In GO database, 55 genes were annotated, which were mainly classified in cell, cell part, cellular processes and metabolic processes. There were 279 genes annotated in the PHI database, accounting for 8.14%

Table 4 Gene annotation result

Sample	Annotation method	genes with annotation	rate of annotated genes
Chr	Nr	2978	95%
	Swiss-Port	2023	65%
	COG	2303	74%
	KEGG	2631	84%
	GO	34	1%
Ssp01	Nr	282	95%
	Swiss-Port	149	50%
	COG	165	55%
	KEGG	94	31%
	GO	15	5%
Ssp02	Nr	130	92%
	Swiss-Port	61	43%
	COG	75	53%
	KEGG	41	29%
	GO	3	2%
Ssp03	Nr	36	80%
	Swiss-Port	16	35%
	COG	21	46%
	KEGG	9	20%
	GO	3	6%

of the total genome, which distributed in 9 modules including secretion system, toxin relate factions, exopolysaccharides, extracellular enzyme, antibiotic, pathogenitcity related factions, two-component system PdeK, synthesis/metabolism related enzymes, and unknown gene (Table 5). These genes play diverse functional roles in the interaction between pathogens and hosts, including cell wall synthesis, transport and metabolism, intracellular transport, replication and expression, signal transduction, and defense.

Proprietary database annotation

Through VFDB annotation, a total of 66 virulence genes were identified (Supplementary material 3). These genes encompass a diverse range of enzymatic proteins involved in various functions, such as flagella synthesis and motility, metabolism, intracellular transport, transcriptional regulation, and others. Upon comparison with the CARD database, NY01 exhibited the presence of 7 drug-resistant genes (Table 6). These genes encode for 6 homologous proteins and 1 rifampin-resistant variant protein. Through sequence alignment, a total of 486 carbohydrate-related enzymes were identified (Supplementary material 4). Among these enzymes, 424 were located on chromosomes, constituting 87% of all carbohydrate enzymes (Fig. 3). Additionally, 27 were found on Ssp01, another 26 on Ssp02, and 9 on Ssp03. The Glycoside Hydrolase (GH) family was the most abundant, representing 40% of all carbohydrate enzymes, followed by Glycosyl Transferases (GT), which comprised 35%.

Table 5 PHI annotation

Category	Chr	Ssp01	Ssp02	Ssp03
Type of secretion system	42	9	1	0
toxin relate factions	64	0	2	0
Exopolysaccharides	2	0	1	1
Extracellular enzyme	56	1	5	2
Antibiotic	11	0	0	0
pathogenitcity related factions	14	0	1	1
Two-component system PdeK	27	0	1	0
Synthesis/metabolism related enzymes	24	2	4	2
Unknown gene	6	0	0	0
In total	246	12	15	6

Table 6 Analysis of drug resistance genes

Model type	ARO name	ARO category
protein homolog model	resistance to elfamycin	gene involved in self-resistance to antibiotic
	farB	modulating antibiotic efflux
	farB	modulating antibiotic efflux
	acrB	antibiotic resistance gene cluster, cassette, or operon
	desR	determinant of macrolide resistance
	mfd	determinant of fluoroquinolone resistance
protein variant model	resistance to rifampicin	determinant of rifamycin resistance

Note Model type: RGI prediction type; ARO name: All ARO annotations by filtering thresholds; ARO category: Best annotation ARO classification of resistance genes

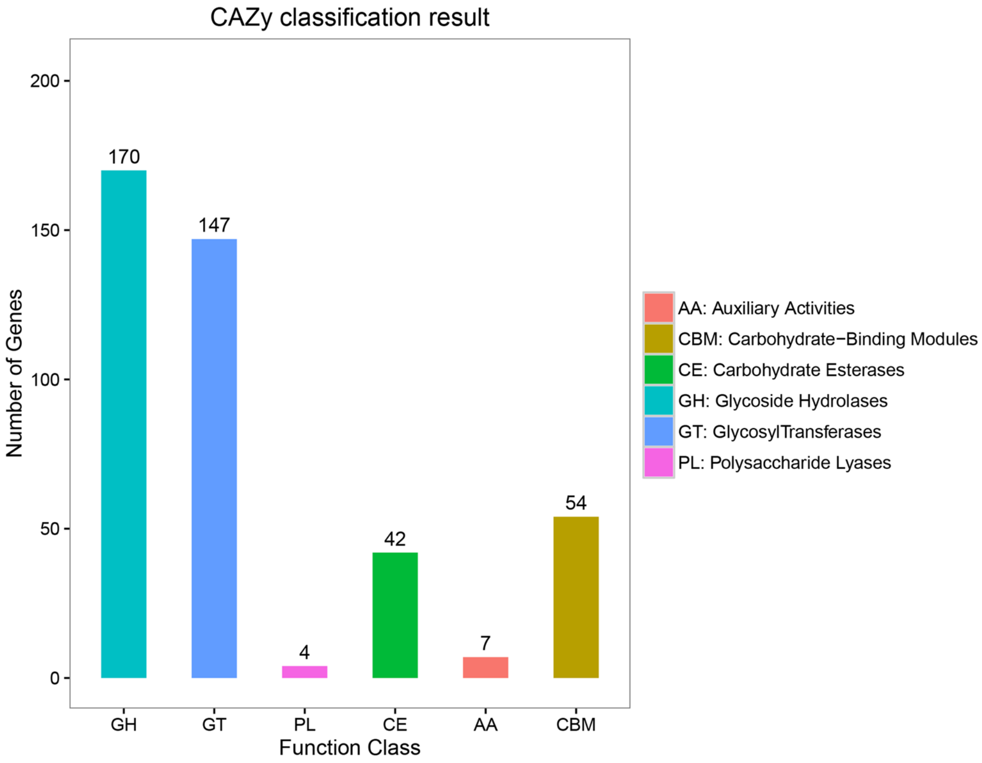


Fig. 3 Chromosome CAZy annotation

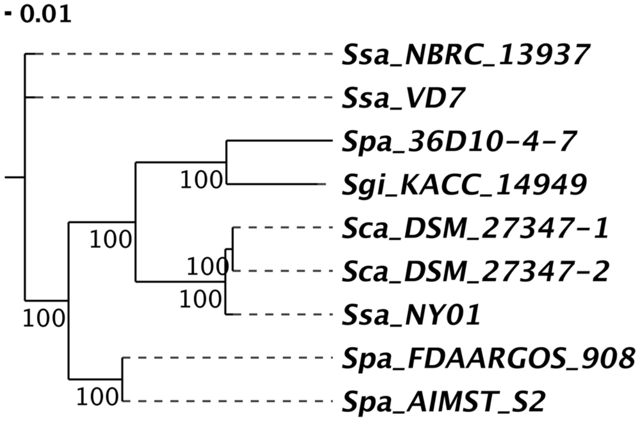


Fig. 4 Phylogenetic relationship of strain NY01 and the complete genomes of seven *Sphingomonas* strains downloaded from the NCBI database

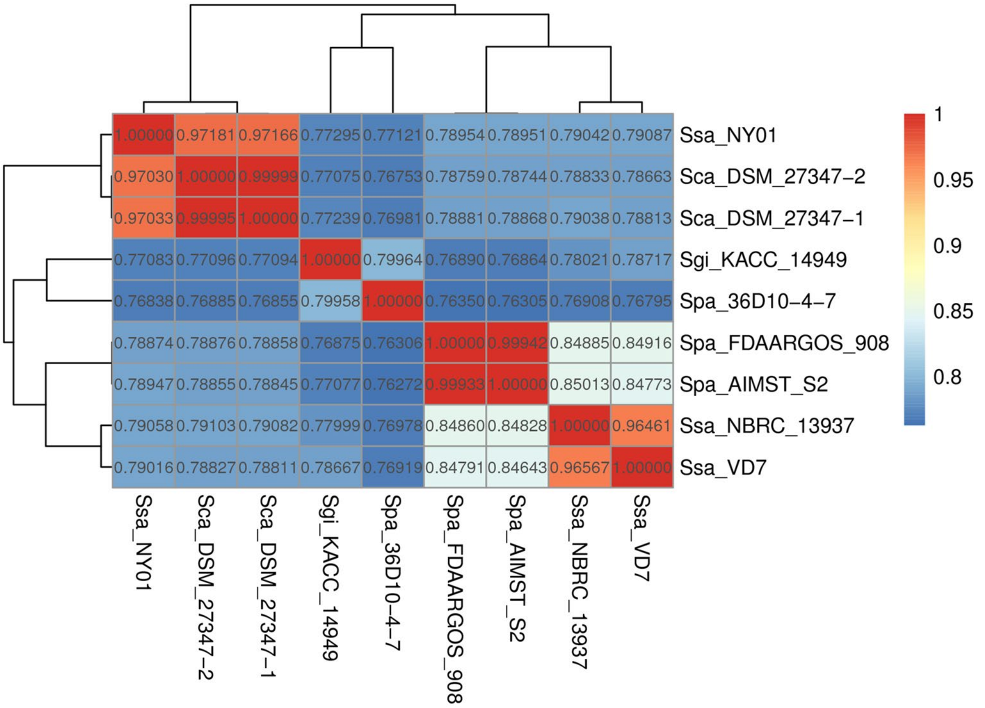
Comparative genomic analysis

A phylogenetic tree constructed based on conserved core single-copy orthologous gene alignment showed the clear lineage divergence, four terminal branches were clearly separated for eight *Sphingomonas*. The NY01 strain clustered together with *S. carotinifaciens* DSM 27347 2019 with a high bootstrap value support (100%), which suggested that they had a close evolutionary relationship (Fig. 4). To further confirm the evolutionary relationships, we conducted an ANI phylogenetic analysis on the two genomes to estimate the genomic divergence and relatedness between them. The results showed that the ANI values of the 8 *Sphingomonas* strains ranged from 76% to 97% (Fig. 5), with the strain NY01 and *S. carotinifaciens* DSM 27347 2019 having an ANI value of 97.18%, which was higher than the usual 95% similarity threshold used for species boundaries (Richter et al. 2009). Previous studies have shown that the pathogen was identified as *S. sanguinis* by morphological observation and 16S rRNA sequencing analysis (Liu et al. 2018). Therefore, the 16S rRNA sequencing identified strains may be errors, and whole genome sequencing is needed to improve its accuracy.

Discussion

The genus *Sphingomonas*, a member of the class Alphaproteobacteria, is widely distributed in various aquatic and terrestrial environments. This aerobic chemolithoautotrophic organism possesses the ability to degrade complex organic compounds (Asaf et al. 2020). *Sphingomonas* has attracted global attention from researchers due to its widespread distribution, robust metabolic capabilities, and multifunctional characteristics. Research has primarily focused on the biodegradation of organic pollutants such as polycyclic aromatic hydrocarbons in soil and water environments, as well as its impact on soil health and microbial communities (Zhou et al. 2016; Menon et al. 2019; Lamantia et al. 2022). Initially isolated by Japanese scholar Yabuuchi in 1990 from a clinical sample of a sailor's leg ulcer in a hospital (Yabuuchi et al. 1990), *Sphingomonas* has since been obtained from various environments, including forest soil

Fig. 5 Heatmap of 8 strains based on the average nucleotide identity (ANI) values between two *Sphingomonas* species



	Ssa_NY01	Sca_DSM_27347−2	Sca_DSM_27347−1	Sgi_KACC_14949	Spa_36D10−4−7	Spa_FDAARGOS_908	Spa_AIMST_S2	Ssa_NBRC_13937	Ssa_VD7
Ssa_NY01	1.00000	0.97181	0.97166	0.77295	0.77121	0.78954	0.78951	0.79042	0.79087
Sca_DSM_27347−2	0.97030	1.00000	0.99999	0.77075	0.76753	0.78759	0.78744	0.78833	0.78663
Sca_DSM_27347−1	0.97033	0.99995	1.00000	0.77239	0.76981	0.78881	0.78868	0.79038	0.78813
Sgi_KACC_14949	0.77083	0.77096	0.77094	1.00000	0.79964	0.76890	0.76864	0.78021	0.78717
Spa_36D10−4−7	0.76838	0.76885	0.76855	0.79958	1.00000	0.76350	0.76305	0.76908	0.76795
Spa_FDAARGOS_908	0.78874	0.78876	0.78858	0.76875	0.76306	1.00000	0.99942	0.84885	0.84916
Spa_AIMST_S2	0.78947	0.78855	0.78845	0.77077	0.76272	0.99933	1.00000	0.85013	0.84773
Ssa_NBRC_13937	0.79058	0.79103	0.79082	0.77999	0.76978	0.84860	0.84828	1.00000	0.96461
Ssa_VD7	0.79016	0.78827	0.78811	0.78667	0.76919	0.84791	0.84643	0.96567	1.00000

(Ko et al. 2017), garden soil (Akter et al. 2020), desert soil (Dong et al. 2022), mountain soil (Zhu et al. 2019), solar panel surfaces (Tanner et al. 2020), air (Xue et al. 2018), tap water (Choi et al. 2017), hospital environments (Pascale et al. 2013), international space station (Lombardino et al. 2022), plants (Lin et al. 2018) and animals.

Sphingomonas is associated with a range of diseases in the human body, causing inflammation and posing a serious threat to human health, including pneumonia, meningitis, endophthalmitis, septic arthritis, and myelitis (Rinawati et al. 2022; Alias et al. 2023; Janković et al. 2023). While there are reports suggesting that *Sphingomonas* belongs to endophytic bacteria in plants (Kim et al. 2022; Liang et al. 2024), it is rarely considered a pathogen (Liu et al. 2023). Identifying the specific species of the mango bacterial wilt pathogen can provide a theoretical basis for preventing the further spread of the disease and developing effective control strategies.

In spite of the phylogenetic divergence between *Sphingomonas* and *Pseudomonas*, they shared many major virulence factors, such as adherence, antiphagocytosis, iron uptake, proteases, and quorum sensing, including *flgG*, flgH, and xcpR (Saeb et al. 2014). The genes flgG and flgH encode flagella-associated proteins, which play vital roles as virulence factors for host cell invasion and biofilm formation. Meanwhile, xcpR encodes the type II secretion system that can transfer toxins outside the cell through its secretory pathway. These genes hold the potential to become key virulence genes in *Sphingomonas* species as pathogens. *S. carotinifaciens* has been rarely studied to date. Though the complete genome sequence of strain L9-754 T, an endophyte isolated from leaf tissues of Jatropha curcas, has been published, the key virulence factors and mechanism of action of this pathogen remain unclear (Li et al. 2021). In the present study, we have sequenced the complete genome of *S. carotinifaciens* strain NY01 isolated from mango. This will aid in improving our understanding of the genomic characteristics and pathogenic mechanism of the disease. Additionally, it will lay a theoretical foundation for the prevention and control of the disease in the future.

Conclusion

We have identified the pathogen responsible for mango bacterial dry rot and analyzed its pathogenic genes through whole-genome sequencing, offering valuable insights into the biological characteristics of the pathogen. Our research outcomes also contribute significant genetic resources for the future management of mango bacterial dry rot

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42161-025-01855-9.

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Data availability The complete genomic data of the strain NY01 is available in GenBank under the accession numbers CP101722, CP101723(Ssp1), CP101724(Ssp2), and CP101725(Ssp3).

Declarations

Conflict of interest The author(s) declare no conflict of interest.

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