

Biological Forum – An International Journal

16(12): 98-105(2024)

ISSN No. (Print): 0975-1130 ISSN No. (Online): 2249-3239

The Genomic Landscape of Plant Growth-promoting Rhizobacterium Paenibacillus macerans Strains

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(Received: 16 September 2024; Revised: 18 October 2024; Accepted: 11 November 2024; Published: 14 December 2024) (Published by Research Trend)

ABSTRACT: *Paenibacillus macerans* is a plant growth-promoting rhizobacterium (PGPR) that promotes plant growth, improves soil fertility, and suppresses plant diseases, while also possessing beneficial traits for DNA metabolism, virulence, disease and defence. Despite its potential, *Paenibacillus macerans* remains understudied, with limited comprehensive genomic information available. This study utilizes draft genome sequence data of *Paenibacillus macerans* strains CMB402, CMB401, and CMB393 to investigate their genomic characteristics and comparative analysis with reference sequence 3CT49. The results show that CMB402 exhibits a higher GC content, a higher N50 value, and a lower number of contigs compared to the other two strains. Notably, CMB402, CMB401 harbors three and CMB393 with two antibiotic-resistance genes with similar values and 7285 annotated genes, including those involved in DNA metabolism, virulence, disease and defence. Comparative analysis reveals that CMB402 has undergone fewer genome rearrangements than CMB401 and CMB393. This study provides valuable insights into the metabolic capabilities of *Paenibacillus macerans*, including antibiotic resistance, and virulence, which can be useful for biologists studying plant metabolism and stress responses.

Keywords: *Paenibacillus macerans*, Comparative genome analysis, Antibiotic resistance gene, Prophage, Virulence.

INTRODUCTION

Paenibacillus macerans is a gram-variable bacterium, with rods that are either gram-positive or gramnegative. The name Paenibacillus derived from the Latin word paene which means almost a Bacillus (Ash et al., 1993). Pseudomonas, Rhizobium and Bacillus genus are among the foremost phosphate solubilizers. This genus mostly is plant growth-promoting rhizobacteria which help plants for providing resistance to particular diseases and in agricultural productivity (Seldin, 2011). It also act as a PGPR due to deleterious effect of microorganisms (Yadav et al., 2010). It is also involved in phosphate solubilization because of the presence of the gcd (glucose dehydrogenase) gene which involves the oxidation of glucose into gluconic acid (Li et al., 2019) and iron acquisition (Wen et al., 2011). Many species of Paenibacillus which almost include *P. mucilaginous* (R. Brindavathy and Shenbagavalli S. 2021, Hu et al., 2006), P. elgii (Das et al., 2010), P. kribbensis (Marra et al., 2012), P. xylanilyticus (Pandya et al., 2015), P. peoriae (Xie et

al., 2014), P. polymyxa and P. macerans (Wang et al., 2012) showed the phosphate solubilization activity. Members of the genus Paenibacillus are capable of nitrogen fixation for those plant species which are tolerant to heavy metals and grow in extreme environments (Navarro et al., 2012). It is a nitrogenfixing bacteria but it also has a drawback in that, by repeated sub-culturing it loses its activity as compared to phosphate solubilizing fungi (Sharma et al., 2013). Another study showed that it is paraphyletic, this genus currently comprises around 200 species and can produce a variety of biocidal substances and further nitrogen-fixing ability determined by 15 N2 fixing assays used to estimate nitrogenase activity (Grady et al., 2016). Many species of Paenibacillus which almost include P. azotofixans, P. polymyxa, P. macerans, P. odorifer, P. graminis, P. sabinae, P. zanthoxyli, P. peoriae, P. brasilensis etc. showed the nitrogenase activity (Hong et al., 2009; Jin et al., 2011). The genome of this species has a nif gene operon at almost 10.5 kb region which also includes nine genes and that particular nif gene operon involves in nitrogen fixation

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(Xie et al., 2014). P. macerans ATCC8244 strain is predominantly involved in nitrogen fixation (Daligault et al., 2014). For comparison and visualization of prokaryote genomes, Mauve and BRIG were used which can visualize or display the presence, absence or variations among different strains of bacteria as well as display the custom graph and annotation (Alikhan et al., 2011). Currently, genomic sequences of P. macerans ATCC8244 (GenBank accession number-NZ KN125580) have been completed (Daligault et al. 2014). To advance our understanding of the genome used those strains of P. macerans that were not yet analyzed and whose genomic characterization was not conducted yet. Therefore, in this study, a comparative genome analysis of three P. macerans strains, CMB402, CMB401 and CMB393 was done, to identify common genes in these strains and further investigated the antibiotic-resistant gene, prophages and plasmid which is followed by annotation analysis and this study lays a foundation of using these strains as a biofertilizer in agriculture and plays an important role in biomedical sectors as well. Similarly, as the comparative genomic study of 14 Pseudomonas shows the biocontrol, bioremediation and PGPR activities by using P. fluorescens as the reference strain by using EDGAR 2.0 and Mauve 2.3.1 softwares (Rehman et al., 2023).

The genomic landscape of *P. macerans* is complex and diverse, with various strains exhibiting different characteristics and abilities. In this study, we aimed to explore the genomic diversity of *P. macerans* by comparing the genomes of three *P. macerans* strains, CMB402, CMB401 and CMB393, we aimed to identify common genes and investigate their antibiotic-resistant genes, prophages and plasmids. Our study provides a comprehensive understanding of the genomic landscape of *P. macerans* and lays the foundation for the use of these strains as bio-fertilizers in agriculture and their potential applications in biomedical sectors.

MATERIALS AND METHODS

Data collection, pre-processing and genome assembly. Raw data for selected bacterial strains (CMB402, CMB401 and CMB393) were downloaded from the European Nucleotide Archive site (ENA) (http://www.ebi.ac.uk/ena) (Table 1). Raw reads of genome sequences of P. macerans CMB 402, CMB 401 and CMB 393 were accustomed to FastQC Version 0.12.0 (Andrews, 2010)(https://www.bioinformatics.babraham.ac.uk/projects/fa stqc/) which gives a preliminary report into data quality. Raw reads are converted into filtered sequences using NGSQC Toolkit (http://www.nipgr.res.in/ngsqctoolkit.html). After trimming the reads, the low-quality reads were removed. Finally, High Quality (HQ) reads and QC statistics area units are generated within the output folder. After getting filtered files, genome assembly has done bv using the to be SPAdes tool (http://bioinf.spbau.ru/spades) (Bankevich et al., 2012). The Barrnap tool version Barrnap: 0.9 is employed to predict the placement of rRNA genes in genomes (Seemann, 2013; Boratyn *et al.*, 2013). MeDuSa (http://combo.dbe.unifi.it/medusa) is employed for generating scaffolds from contigs (Bosi *et al.*, 2015). For annotation of sequence, RAST (Rapid Annotation Subsystem Technology) (Aziz *et al.*, 2008) is utilized. Once the annotation is completed, genomes are downloaded in an extremely variety of formats or viewed online.

Prediction of prophage in *P. macerans.* Phaster is used for rapid identification and annotation of prophage in *P. macerans* CMB402, CMB401 and CMB393. has three input options; upload a nucleotide sequence file in fasta format. Download the complete set of results in a zipped folder or view them in three files (A summary file, a detailed file, and an interactive genome viewer) through which the results can be analyzed (Arndt *et al.*, 2016; Zhou *et al.*, 2011).

Identification of plasmids associated with antimicrobial resistance and prediction of antibiotic resistance genes. Plasmid Finder, a web-based tool, was used to identify and characterize whole plasmid sequence data from P. macerans CMB402, CMB401, CMB393. Comprehensive Antibiotic and The Resistance Database (CARD) was used to predict genes that confer resistance to antibiotics in P. macerans CMB402, CMB401, and CMB393. The Resistance Gene Identifier (RGI) code was employed to predict genes based on similarity and SNP models (McArthur et al., 2013).

Comparative Genome Analysis. BRIG (Alikhan *et al.*, 2011) was used to visualize the genomic order of *P. macerans* CMB402, CMB401, CMB393, and 3CT49 as a circular image, enabling the comparison of multiple organism sequences without arbitrary limits on the number of genomes compared. Mauve (Darling *et al.*, 2010) was used to align sequences in different species that evolve from common ancestral sequences and xenologous regions of sequences that have undergone local and large-scale changes in *P. macerans* CMB402, CMB401, CMB393 with 3CT49 strain.

RESULTS AND DISCUSSION

Genome assembly characteristics and annotations. The *de novo* assembly of the genome can be evaluated using a variety of factors, including the number of scaffolds and contigs available, their sizes, the proportion of reads that can be assembled, and the contig N50 value, which is frequently used to measure and evaluate the quality of assembly (Choudhuri, 2014). From our analysis, the P. macerans CMB402 strain had a high-quality draft assembly compared to the CMB401 and CMB393 strains, as it had a high N50 value of 159,232. The GC percentages of P. macerans CMB402, CMB401, and CMB393 were 52.88%, 52.87%, and 52.75%, respectively, and their genome sizes were 7,142,881 bp, 7,144,711 bp, and 7,319,099 bp, respectively. Regions with 50-60% GC content obtained the most coverage, while regions with high (70-80%) or low (30-40%) GC content received considerably less coverage (Gnirke et al., 2009). The P. macerans ATCC strain has a GC content of 53% and a genome size of 7,331,450 bp, which is almost similar to

this study (Daligault et al., 2014). P. macerans CMB402 has a higher GC percentage of 52.88, which showed higher coverage and better data quality (Table 2).

The contigs were then assembled into scaffolds, resulting in increased N50 values of 278,921 bp for P. macerans CMB402, 227,313 bp for P. macerans CMB401, and 228,196 bp for P. macerans CMB393 (Fig. 1a). Paenibacillus macerans 3CT49 has 108 contigs, 6,340 coding sequences, and 120 RNAs (Olajide et al., 2020). In contrast, P. macerans CMB402 has 69 contigs, 6,985 coding sequences, and 99 RNAs. Strain CMB401 has 79 contigs, 7,013 coding sequences, and 97 RNAs, while strain CMB393 has 210 contigs, 7,161 coding sequences, and 96 RNAs (Figure 1a, b). Based on genome assembly and structural genome annotation, it is noted that P. macerans CMB402 has the highest N50 value of contigs and scaffolds, a lower number of contigs, and a higher percentage of GC content compared to P. macerans CMB401, CMB393, and 3CT49 (Fig. 1a, b, c). This suggests that if the number of contigs is lower, the N50 stats value will increase.

Annotated genes in DNA metabolism, virulence, and antibiotic resistance in P. macerans. The annotated genes involved in DNA metabolism and virulence, disease, and defense in P. macerans were identified and characterized. CRISPR sequences were found in the genomes of three different strains of P. macerans, **CRISPR**-associated RAMP including Cmr1-4, CRISPR-associated protein Csd1 family, CRISPRassociated protein Cas2, and CRISPR-associated protein Cas1. The number of CRISPR arrays varied among the strains, with P. macerans CMB402 and CMB401 having 10 CRISPR arrays and CMB393 having 17 CRISPR arrays. In comparison, Paenibacillus larvae DSM25430 strain had 7 CRISPR arrays (Stamereilers et al., 2021). Based on CRISPR array accumulation, P. macerans CMB393 was found to be the best strain, having a higher number of CRISPR arrays compared to P. macerans CMB402, CMB401, and Paenibacillus larvae DSM25430 strain. Genes involved in virulence, disease, and defense was also annotated in P. macerans CMB402, CMB401, and CMB393 strains. These genes included macrolidespecific efflux protein MacA, acriflavin resistance protein, and multi-antimicrobial extrusion protein (Na(+)/drug antibiotic family of MDR efflux pumps) categorized under multidrug resistance efflux pumps. Chromate transport protein ChrA, copper translocating p-type ATPase, cadmium efflux system accessory proteins, copper-zinc-cadmium, and transcriptional regulator MerR family were involved in resistance to Ribosome protection toxic compounds. type tetracycline resistance group 2, translation elongation factor G, and fosfomycin resistance protein FosB were involved in resistance to antibiotics (Table 3). P. macerans was also found to accommodate metal resistance genes, including ChrA and MerR, which provided cadmium, zinc, and copper resistance. According to Khan et al. (2012), Paenibacillus species have been reported to support the growth of plants in heavy metal-contaminated sites.

Antibiotic resistance genes were identified in P. macerans CMB402, CMB401, and CMB393 strains. In P. macerans CMB402 and CMB401, three antibiotic resistance genes were found: vanI (vancomycin resistance LimA 23S ribosomal gene), methyltransferase, (florfenicoland fexA chloramphenicol resistance gene). Alteration in the target sites of antibiotics, such as vanI, was a common mechanism of resistance, with 69.1% identity of the LimA 23S matching region. ribosomal methyltransferase had 84.97% identity of the matching region. In P. macerans CMB393, only two antibiotic resistance genes were found: LimA 23S ribosomal methyltransferase and vanI (vancomycin resistance gene). LimA 23S ribosomal methyltransferase had 86.01% identity of the matching region, and vanI had 68.22% identity of the matching region (Table 4). The Comprehensive Antibiotic Resistance Database's Resistance Gene Identifier (RGI) was used to investigate the putative antimicrobial resistance genes in genomic sequences (McArthur et al., 2013). According to Pasari et al. (2019), fosfomycin, vancomycin, tetracycline, and many more antibiotic resistance genes were identified in Paenibacillus polymyxa A18. In staphylococci, the fexA gene codes for the florfenicol efflux protein (Kehrenberg et al., 2004).

Genomic Analysis of P. macerans Strains. Prophage regions were identified in the genomes of P. macerans CMB402, CMB401, and CMB393. In P. macerans CMB402, six prophage regions were found, with four incomplete regions having a score of less than 70 and two intact regions (region 3 and region 5) with a score of 150. The presence of intact prophages in CMB402 may provide a competitive advantage over CMB401 and CMB393 strains, as they can release free phages that can infect and kill competing phage-susceptible cells. In P. macerans CMB401, five prophages were found, with three incomplete regions and two intact regions (region 1 and region 5) with a score of 150. In contrast, P. macerans CMB393 had three incomplete prophages with a score of 20. Prophages can fill up to 20% of bacterial chromosomes and provide novel roles to their hosts, serving as a key source of new genes for bacteria (Wang et al., 2016).

BRIG was used to visualize the comparative genome analysis of P. macerans CMB402, CMB401, and CMB393 against the simulated draft genome of 3CT49. The image shows the similarity between the central reference sequence (contigs.fasta) and other sequences as a set of concentric rings. The colored rings represent the BLAST comparisons of CMB402, CMB401, and CMB393 against the 3CT49 genome, with 100% identity indicated by colored rings and gaps (white color) representing less than 50% identity (Fig. 2). A similar study showed that Paenibacillus species A2 had similarity with Paenibacillus elgii B69 (Zheng et al., 2016).

Mauve software was used to align the genomes of P. macerans 3CT49, CMB402, CMB401 and CMB393. The alignment shows inverted regions in CMB401 and CMB393 as blocks below the genome's center line. The colored blocks in the first genome are associated with

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similarly colored blocks in the other genomes, indicating homologous regions. The boundaries of the colored blocks usually indicate the breakpoints of genome rearrangement, unless sequence has been gained or lost in the breakpoint region. The image shows the linear comparison between the genome sequences of CMB402, CMB401, CMB393, and 3CT49 (Fig. 3). Mauve aligns genomes in the same way despite the input order by detecting multi-MUMs in subsets of the genomes (Darling *et al.*, 2004). Similarly, Due to complexity of *Pseudomonas* genome by using

DGAR 2.0 and Mauve 2.3.1 researcher have shown evolutionary relationship in terms of gene order (Rehman *et al.*, 2023). The complete genome sequences of the sequenced strains were compared using Mauve to determine the evolutionary gap between them and various *Paenibacillus polymyxa* strains (Li *et al.*, 2020). The analysis showed that CMB401 and CMB393 genomes have undergone more genome rearrangements and showed more deletions and inversions than CMB402, which further helps in evolutionary study.

Table 1: Raw Reads for genomic analysis.

Strains of Paenibacillus macerans	CMB402	CMB401	CMB393	
Forward raw reads	SRR11410548_1.fastq	SRR11410549_1.fastq	SRR11410553_1.fastq	
Reverse raw reads	SRR11410548_2.fastq	SRR11410549_2.fastq	SRR11410553_2.fastq	

Table 2: Values for assembly validation.

Strain	CMB402	CMB401	CMB393
Total Sequences	196	213	263
Total Bases	7142881	7144711	7319099
Min sequence length	128	128	128
Max sequence length	374120	696080	437958
N50 length	159232	150671	144293
(A+T)s	47.12%	47.13%	47.25%
(G+C)s	52.88%	52.87%	52.75%

Category	Subsystem	Gene / Enzyme				
Virulence, Disease and Defence		Macrolide specific efflux protein MacA				
	Multidrug resistance efflux	Acriflavin resistance protein				
	pumps	Multi antimicrobial extrusion protein (Na(+) / drug antibiotic family of				
		MDR efflux pumps				
	Resistance to chromium	Chromate transport protein ChrA				
	compounds					
	Cadmium resistance	Cadmium efflux system accessory protein				
	Fosfomycin resistance	Fosfomycin resistance protein FosB				
	Copper homeostasis	Copper translocating P-type ATPase				
	Copper – Zinc – Cadmium	Copper – Zinc – Cadmium resistance protein				
	resistance	Transcriptional regulator, MerR family				
DNA metabolism	CRISD Cmr Cluster	CRISPR – associated RAMP Cmr3				
	CRISP CIIII Cluster	CRISPR – associated RAMP Cmr6				
	CRISPRs	CRISPR – associated protein, Csd1 family				
	CRISPRs	CRISPR – associated protein Cas2				

Table 3: Important gene classes annotated in this study.

Table 4: Antibiotic resistance genes within strain CMB402, CMB401 and CMB393.

Antibiotic resistance genes within strain CMB402							
RGI Criteria	ARO Term	Detection Criteria	AMR Gene family	Drug Class	Resistance Mechanism	% Identity of Matching Region	% Length of Reference Sequence
Strict	Vanl	Protein Homolog	Glycopeptide resistance gene cluster, van ligase	Glycopeptide antibiotic	Antibiotic target <i>al</i> teration	69.1%	98.56
Strict	LlmA 23S ribosomal RNA methyltransferase	Protein Homolog	LlmA 23S ribosomal RNA methyltransferase	Lincosamide antibiotic	Antibiotic target alteration	84.97%	106.27
Strict	fexA	Protein Homolog	Major facilitator superfamily (MSF) antibiotic efflux pump	Phenicol antibiotic	Antibiotic target alteration	68.58%	98.32
Antibiotic resistance genes within strain CMB401							
Strict	Vanl	Protein Homolog	Glycopeptide resistance gene cluster, van ligase	Glycopeptide antibiotic	Antibiotic target alteration	69.1%	98.56
Strict	LlmA 23S ribosomal RNA methyltransferase	Protein Homolog	LlmA 23S ribosomal RNA methyltransferase	Lincosamide antibiotic	Antibiotic target alteration	84.97%	106.27

Strict	fexA	Protein Homolog	Major facilitator superfamily (MSF) antibiotic efflux pump	Phenicol antibiotic	Antibiotic target alteration	68.58%	98.32
Antibiotic resistance genes within strain CMB393							
Strict	Vanl	Protein Homolog	Glycopeptide resistance gene cluster, van ligase	Glycopeptide antibiotic	Antibiotic target alteration	68.22	98.56
Strict	LlmA 23S ribosomal RNA methyltransferase	Protein Homolog	LlmA 23S ribosomal RNA methyltransferase	Lincosamide antibiotic	Antibiotic target alteration	86.01	106.27



Fig. 1. General characteristics from genome annotation of *P. Macerans* strains a) L50 and Number of contigs b) Number of coding sequence c) Size.

P. macerans strains



Fig.2. Comparative genome analysis of contigs.fasta-3CT49 (Reference sequence) against CMB402, CMB401 and CMB393 strains of *P. macerans* with 100, 70 and 50% identity using BRIG.



Fig. 3. Alignment and comparison of genome sequence of CMB402, CMB401 and CMB393 *P. macerans* strain with 3CT49 using MAUVE.

CONCLUSIONS

In summary, the present study has elucidated the genomic characteristics of P. macerans strains CMB402, CMB401, and CMB393, providing valuable insights into their genetic makeup and potential applications. The findings of this study suggest that *P*. macerans strain CMB402 is a promising candidate for agricultural and bioremediation applications, owing to its possession of genes related to phosphate solubilization, nitrogen metabolism, and antibiotic resistance. Furthermore, the high-quality draft assembly and intact prophages of CMB402 indicate its potential for genetic stability and adaptability. While P. macerans CMB393 exhibits a robust defensive system, as evidenced by its 17 CRISPR array-encoded genes, CMB402's overall genomic characteristics make it an attractive candidate for further research and development. Collectively, these findings contribute to our understanding of the genetic diversity of P. macerans and highlight the potential of this species for various biotechnological applications.

FUTURE SCOPE

In comparative genome analysis of *P. macerans* strain, CMB402 is showing higher potential as compared to other strains and besides having phosphate solubilization and nitrogen metabolism related genes it can be screened for bioremediation application which makes CMB402 as a potential candidate in agriculture productivity.

Acknowledgement. The authors would like to extend their sincere gratitude to all individuals who contributed to this project, either directly or indirectly. We are also thankful to Bionivid Technology Pvt. Ltd. for their technical support throughout the project. A Special thanks to Dr. A.T. Vivek, NIPGR, New Delhi for data analysis. We would like to express our heartfelt appreciation to the Director, Institute of Agricultural Sciences, Banaras Hindu University, for support to complete this research work. Conflict of Interest. None.

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How to cite this article: Verma K., Srivashtav V., Singh A., Prasad R. and Kumar S. (2024). The Genomic Landscape of Plant Growth-promoting Rhizobacterium *Paenibacillus macerans* Strains. *Biological Forum – An International Journal, 16*(12): 98-105.