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

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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 gram-negative. 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 nitrogen-fixing 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

(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 bio-fertilizer 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/fastqc/) 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 to be done by using the 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, and CMB393. The Comprehensive Antibiotic 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*, including CRISPR-associated RAMP Cmr1-4, CRISPR-associated protein Csd1 family, CRISPR-associated 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 macrolide-specific 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 toxic compounds. Ribosome protection 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 gene), LimA 23S ribosomal methyltransferase, and fexA (florfenicol-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 matching region. LimA 23S 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

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%

Table 3: Important gene classes annotated in this study.

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

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 *al*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

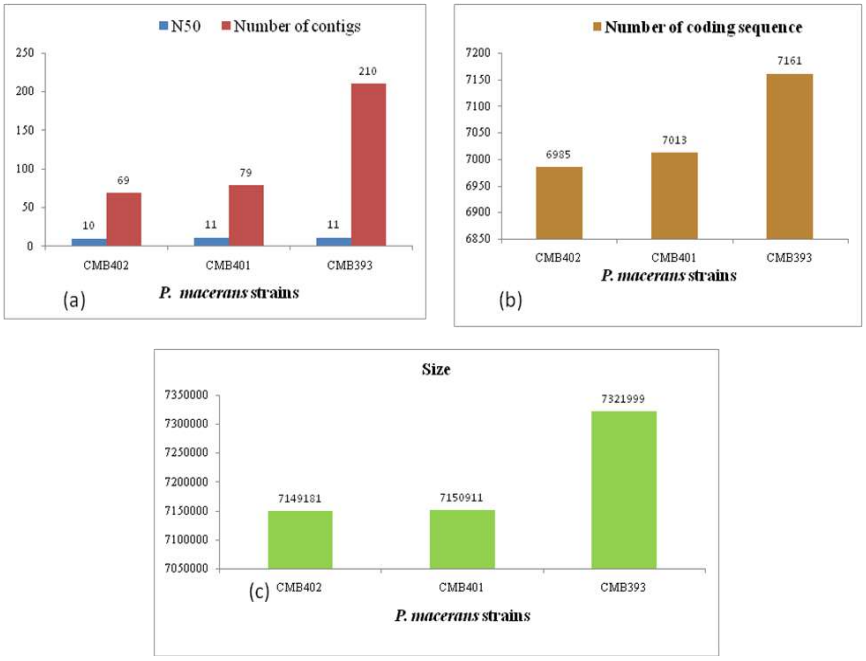

Fig. 1. General characteristics from genome annotation of *P. Macerans* strains a) L50 and Number of contigs b) Number of coding sequence c) Size.

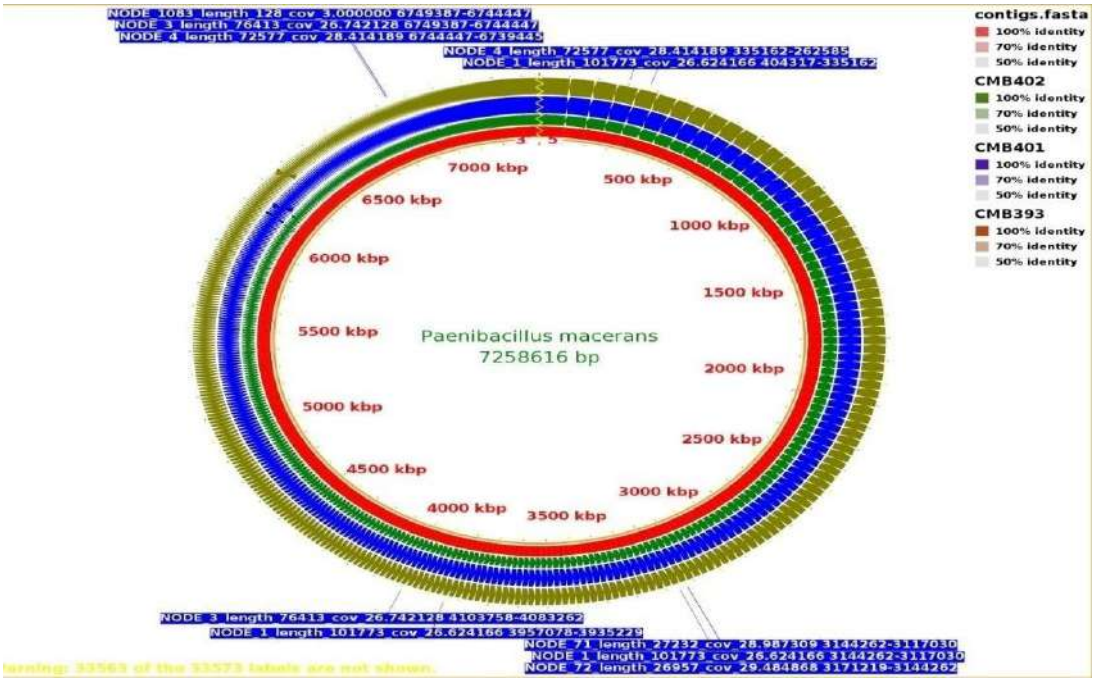

Fig.2. Comparative genome analysis of contigs.fasta-3CT49 (Reference sequence) against CMB402, CMB401 and CMB393 strains of *P. macerans* with 100, 70 and 50% identity using BRIG.

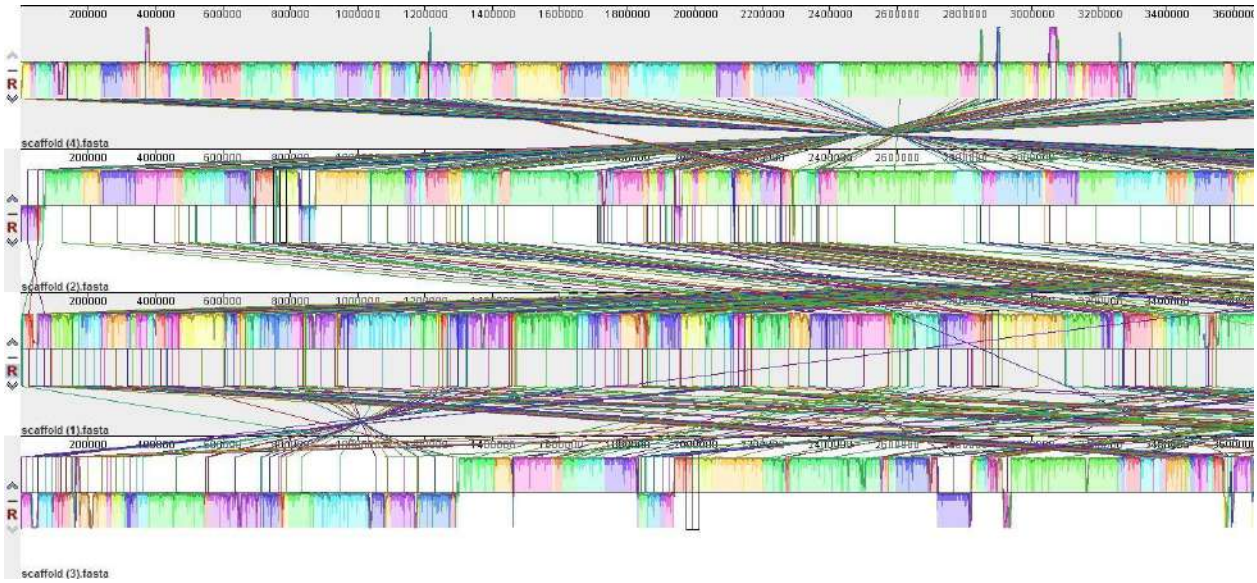

Fig. 3. Alignment and comparison of genome sequence of CMB402, CMB401 and CMB393 *P. macerans* strain with 3CT49 using MAUVE.

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.

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Conflict of Interest. None.

REFERENCES

Alikhan, N. F., Petty, N. K., Ben Zakour, N. L. and Beatson, S. A. (2011). BLAST Ring Image Generator (BRIG): simple prokaryote genome comparisons. *BMC Genomics*, *12*, 1471- 2164.

Andrews, S. (2010). Fast QC: a quality control tool for high throughout sequence data. *Babraham Bioinformatics*.

Arndt, D., Grant, J., Marcu, A., Sajed, T., Pon, A., Liang, Y. and Wishart, D. S. (2016). PHASTER: a better, faster version of the PHAST phage search tool. *Nucleic Acids Research*, *44*, 16-21.

Ash, C., Priest, F. and Collins, M. D. (1993). Molecular identification of rRNA group 3 bacilli (Ash, Farrow, Wallbanks Collins) using a PCR Probe test. *Antonie Van Leeuwenhoek*, *64*, 253-260.

Aziz. R. K., Bartels, D., Best, A. A., DeJongh, M., Disz, T., Edwards, R. A., Formsma, K., Gerdes, S., Glass, E. M. and Kubal, M. (2008). The RAST Server: rapid annotations using subsystems technology. *BMC Genomics*, *9*, 75.

Bankevich, A., Nurk, S., Gurevich, A. A., Dvorkin, M., Kulikov, A. S., Lesin, V. M., Nikolenko, S. I., Pham, S., Prjibelski, A. D., Pyshkin, A. V., Sirotkin, A. V., Vyahhi, N., Tesler, G., Alekseyev, M. A. and Pevzner, P. A. (2012). SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. Journal of *Computational Biology*, *19*(5), 455–477.

Boratyn, G. Z. M., Camacho, C., Cooper, P. S., Coulouris, G., Fong, A., Ma, N., Madden, T. L., Matten, W. T., McGinnis, S. D., Merezhuk, Y., Raytselis, Y., Sayers, E. W., Tao, T., Ye, J. and Zaretskaya, I. (2013). BLAST – a more efficient report with usability improvements. *Nucleic Acids Research*, *41*, 29-33.

Bosi, E., Donati, B., Galardini, M., Brunetti, S., Sagot, M. F., Lió, P., Crescenzi, P., Fani, R. and Fondi, M. (2015). MeDuSa: a multi-draft based scaffolder. *Bioinformatics, 31*(15), 2443-2451.

Brindavathy, R. and Shenbagavalli, S. (2021). Formulation of New Growth Medium and Fermentation Conditions for *Paenibacillus mucilaginous*, a Potassium Releasing Bacterial Stain (KRB-9). *Biological Forum – An International Journal, 13*(3b), 225-229.

Choudhuri, S. (2014). Additional Bioinformatic Analyses involving nucleic acid sequences. *Bioinformatics for Beginners*, 157-181.

Daligault, H. E., Davenport, K. W., Minogue, T. D., Lilly, K. A. B., Broomall, S. M., Bruce, D. C., Chain, P. S., Coyne, S. R., Frey, K. G., Gibbons, H. S., Jaissle, J., Korolena, G. I., Ladver, J. T., Lo, C. C., Munk, C., Palacios, G. F., Redden, C. L., Rosenzweig, C. N., Scholz, M. B. and Johnson, S. L. (2014). Twenty Whole Genome *Bacillus* sp. Assemblies. *Genome Announcements*, *2*(5), e00158-14.

Darling, A. E., Miklos, I. and Ragan, M. A. (2010). Dynamics of Genome Rearrangement in Bacterial populations. *PLoS Genetics 4*(7), e1000128.

Darling, A. C. E., Mau, B., Blattner, F. R. and Perna, N. T. (2004). Mauve - Multiple Alignment of Conserved Genomic Sequence with Rearrangements. *Genome Research*, *14*, 1394-1403.

Das, S. N., Dutta, S., Kondreddy, A., Chilukoti, N., Pullabhotla, S.V.S.R.N. and Vadlamudi, S. (2010). Plant growth-promoting chitinolytic *Paenibacillus elgii* responds positively to tobacco root exudates. *Journal of Plant Growth Regulation*, *29*, 409–418.

Gnirke, A., Melnikov, A., Maguire, J., Rogov, P., LeProust, E.M., Brockman, W., Fennell, T., Giannoukos, G., Fisher, S., Russ, C., Gabriel, S., Jaffe, B. D., Lander, E. S. and Nusbaum, C. (2009). Solution hybrid selection with ultra-long oligonucleotides for massively parallel targeted sequencing. *Nature Biotechnology*, *27*(2), 182-189.

Grady, E. N., Donald, J. M., Liu, L., Richman, A. and Yuan, Z. C. (2016). Current knowledge & perspectives of Paenibacillus : a review. *Microbial Cell Factories*, *15*(1), 203.

Hong, Y. Y., Ma, Y. C., Zhou, Y. G., Gao, F., Liu, H. C. and Chen, S. F. (2009). *Paenibacillus sonchi* sp. Nov., a nitrogen – fixing species isolated from the rhizosphere of Sonchusoleraceus. *International Journal of Systematic and Evolutionary Microbiology*, *59*(11), 2656-2661.

Hu, X., Chen, J. and Guo, J. (2006). Two phosphate & potassium solubilizing bacteria isolated from Tianmu Mountain, Zhejiang, China. *World Journal of Microbiology and Biotechnology*, *22*, 983-990.

Jin, H. J., Lv, J. and Chen, S. F. (2011). *Paenibacillus sophorae* sp. Nov., a nitrogen – fixing species isolated from the rhizosphere of *Sophora japonica*. *International Journal of Systematic and Evolutionary Microbiology*, *61*(4), 767-771.

Kehrenberg, C. and Schwarz, S. (2004). Fex A, a Novel Staphylococcus lentus gene encoding resistance to florfenicol and chloramphenicol. *Antimicrobial Agents Chemotherapy*, *48*(2), 615-618.

Khan, N., Mishra, A., Chauhan, P.S., Sharma, Y.K., Nautiyal, C.S. (2012). *Paenibacillus lentimorbus* enhance growth of chickpea (*Cicer arietinum* L.) in chromium - amended soil. *Antonie Leeuwenhoek 101*(2), 453-459.

Li, J. Y., Gao, T. T. and Wang, Q. (2020). Comparative & functional Analyses of two sequenced *P. polymyxa* genomes provides insights into their potential genes related to plant growth promoting features & biocontrol mechanisms. *Frontiers in Genetics*, *11*, 564939.

Li, Y., Zhang, J., Gong, Z., Xu, W. and Mou, Z. (2019). *Gcd* Gene Diversity of Quinoprotein Glucose Dehydrogenase in the Sediment of Sancha Lake and Its Response to the Environment. *International Journal of Environmental Research and Public Health*, *16*(1), 1.

Marra, L. M., Sousa Soares, C. R. F., de Oliveira, S. M., Ferreira, P. A. A., Soares, B. L. and de Carvalho, R. F. (2012). Biological nitrogen fixation and phosphate solubilization by bacteria isolated from tropical soils. *Plant Soil*, *357*, 289–307.

McArthur, A. G., Waglechner, N., Nizam, F., Yan, A., Azad, M. A. and Baylay, A. J. (2013). The comprehensive antibiotic resistance database. *Antimicrobial Agents Chemotherapy*, *57*, 3348–3357.

Navarro, Y. E., Hernandez, N. E., Morales, M. J., Jan, J. J., Martinez, R. E., Hernandez, R. C. and Rodriguez (2012). Isolation and characterization of nitrogen fixing heterotrophic bacteria from the rhizosphere of pioneer plants growing on mine tailings. *Applied Soil Ecology*, *62*, 52-60.

Olajide, A. M., Chen, S. and Pointe, G. L. (2020). Draft Genome Sequences of Five Paenibacillus species of Dairy Origin. *Microbiology Resource Announcements*, *9*, e00971-20.

Pasari, N., Gupta, M., Eqbal, D. and Yazdani, S. S. (2019). Genome analysis of *Paenibacillus polymyxa* A18 gives insights into the features associated with its adaptation to the termite gut environment. *Scientific Reports*, *9*, 6091.

Pandya, M., Rajput, M. and Rajkumar, S. (2015). Exploring plant growth promoting potential of non rhizobial root nodules endophytes of *Vigna radiata*. *Microbiology*, *84*, 80–89.

Rehman, M., Jyoti, S. Y., Regon, P., Kakati, S., Mishra P. K. and Tanti B. (2023). Comparative Genomics Analyses of some selected Pseudomonas strains having Biocontrol, Plant Growth Promoting and Bioremediation activities using Bioinformatic Tools. *Biological Forum – An International Journal*, *15*(6), 1-16.

Seemann, T. (2013). Barrnap 0.7: rapid ribosomal RNA prediction.

Seldin, L. (2011). Paenibacillus, nitrogen fixation & soil fertility. In: Logrn NA, De Vos P, eds. Endospore–forming Soil Bacteria. *Soil Biology*, *27*, 287-307.

Sharma, S. B., Sayyed, R. Z., Trivedi, M. H. and Gobi, T. A. (2013). Phoshphate Solubilizing Microbes : sustainable approach for managing Phosphorus deficiency in agricultural soils. *Springer Plus*, *2*, 587.

Stamereilers, C., Wong, S. and Tsourkas, P. K. (2021). Characterization of CRISPR Spacer and Protospacer Sequences in Paenibacillus larvae and Its Bacteriophages *Viruses*, *13*, 459.

Wang, Y., Shi, Y., Li, B., Shan, C., Ibrahim, M., Jabeen, A., Xie, G. and Sun, G. (2012). Phosphate solubilization of *P. polymyxa* & *P. macerans* from mucorrhizal & non – mycorrhizal cucumber plant. *African Journal of Microbiology Research*, *6*(21), 4567-4573.

Wang, X. and Wood, T. K. (2016). Cryptic prophages as targets for drug development. *Drug Resistance Updates*, *27*, 30–38.

Wen, Y., Wu, X., Teng, Y., Qian, C., Zhan, Z. and Zhao, Y. (2011). Identification & analysis of the gene cluster involved in biosynthesis of paenibactin, a catecholate siderophore produced by *P. elgii* B69. *Environmental Microbiology*, *13*, 2726-2737.

Xie, J. B., Du, Z., Bai, L., Tian, C., Zhang, Y., Xie, J.Y., Wang, T., Liu, X., Chen, X., Cheng, Q., Chen, S. and Li, J. (2014). Comparative genomic analysis of N_2- fixing and non-N_2 fixing *Paenibacillus* spp.: organization, evolution and expression of the nitrogen fixation genes. *PLoS Genetics*, *10*, e1004231.

Yadav, J., Verma, J. P. and Tiwari, K. N. (2010). Effect of plant growth promoting Rhizobacteria on seed germination and plant growth Chickpea (*Cicer arietinum* L.) under in Vitro conditions, *2*(2), 15-18.

Zheng, B., Zhang, F., Dong, H., Chai, L., Shu, F., Yi, S., Wang, Z., Cui, Q., Dong, H., Zhang, Z., Hou, D., Yang, J. and She, Y. (2016). Draft genome sequence of *Paenibacillus* sp. strain A2. *Standard Genomic Science*, *26*, 11, 9.

Zhou, Liang, Y., Lynch, K.H., Dennis, J. J. and Wishart, D. S. (2011). PHAST: a fast phage search tool. *Nucleic Acids Research*, *39*, 347–352.

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