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RESEARCH ARTICLE

Genomic insights into the antifungal and plant growth-promoting traits of *Pseudomonas plecoglossicida* NAN2 isolated from the rice rhizosphere

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Abstract

Plant growth promoting rhizobacteria (PGPRs) are beneficial microorganisms that inhabit the rhizosphere and enhance plant growth through various mechanisms. In this study, a PGPR strain designated NAN2 was isolated from the rice rhizosphere and demonstrated multiple plant growth-promoting traits, including the production of hydrogen cyanide (HCN), ammonia, indole-3-acetic acid (IAA), phosphate solubilization and antifungal activity against *Magnaporthe oryzae*. Complete genome sequencing and annotation of strain NAN2 revealed a genome size of 5356785 base pairs (bp) with a GC content of 62 %, comprising 227 contigs, 4807 coding sequences (CDSs) and a total of 4960 genes. Notably, the genome contains a nonribosomal peptide synthetase (NRPS) gene cluster associated with the biosynthesis of rhizomides (A, B and C). These results suggest that NAN2 has strong potential as an environmentally resilient biocontrol agent that can protect plants from invasive diseases. To our knowledge, this is the first genomic analysis of *Pseudomonas plecoglossicida* NAN2 isolated from rice fields, providing valuable insights into its biocontrol capabilities and plant growth promoting (PGP) properties.

Keywords: antifungal activity; *Magnaporthe oryzae*; PGPR; *Pseudomonas plecoglossicida*; root colonization; whole genome analysis

Introduction

Rice, the staple food for more than 50 % of the world's population, plays a crucial role in global food security. However, rice is highly susceptible to phytopathogens, resulting in significant annual economic losses (1, 2). Fungal pathogens can produce mycotoxins, which facilitate the initial establishment and spread of infection, eventually leading to the colonization and spread of the entire host (3, 4). Synthetic fungicides are commonly used to manage rice blast disease; however, their usage is declining because of the shift toward sustainable food production (5). Biocontrol agents offer a more cost-effective, targeted and environmentally sustainable alternative to conventional methods (6, 7). The primary fungal pathogens affecting rice include *Bipolaris oryzae, Colletotrichum gloeosporioides, Fusarium fujikuroi, F. oxysporum, F. solani, Magnaporthe oryzae* and *Rhizoctonia solani* (8). Rice blast disease, caused by *M. oryzae* posess a substantial threat to rice production, leading to annual yield losses ranging from 10 % to 35 % (9-11). Various microorganisms have been reported to be associated with plant microbiomes and function as biocontrol agents against phytopathogens by producing antifungal lipopeptides, antimicrobial chemicals and enzymes (12-15). PGPR have gained widespread recognition as a sustainable and eco-friendly approach for controlling plant diseases and increasing crop productivity (16-20). The concept of PGPR was first introduced by Kloepper and Schroth (21). The rhizosphere of plants contains a variety of PGPR, including *Acinetobacter, Azotobacter, Azotofixans, Azospirillum, Bacillus, Klebsiella, Paenibacillus, Pseudomonas* and *Rhizobium* (22).

The genus Pseudomonas, belonging to the *Pseudomonadaceae* family, is categorized into ten groups based on rRNA-DNA hybridization. *Pseudomonas* species employ antagonistic mechanisms such as induced systemic resistance (ISR) and the production of cell wall degrading enzymes and antibiotics to establish and maintain a beneficial relationship with the host plants (23). *P. plecoglossicida* is a gram-negative, rod-shaped, motile bacterium within the *P. putida* group (24). Research has demonstrated that *P. plecoglossicida* has significant potential for improving crop productivity and soil fertility in organic farming systems (25). This study focused on *P. plecoglossicida* strain NAN2 and investigated its PGP and biocontrol capabilities. We performed genome sequencing to uncover the genetic basis of these traits, providing insights into their potential application in sustainable agricultural practices.

Materials and Methods

Isolation of rhizobacteria from rice rhizosphere

A total 10 rhizosphere soil samples were collected from rice (*Oryza sativa* L.) fields located in the Chengalpattu District of Tamil Nadu, India. The samples were taken at a depth of 5-10 cm, targeting the root zone region. For microbial isolation 0.2 g of soil sample was suspended in 20 mL of sterile water in a 50 mL tube and vortexed for 5 minutes. A 1 mL aliquot was serially diluted, up to 10^6 in sterile water, 100 µL from each dilution was spread onto nutrient agar (NA) plates. The plates were incubated at 37 °C for 24 hr.

Plant-growth promoting traits

The bacteria were streaked onto nutrient agar enriched with glycine (4.4 g/L). Permeable filter paper soaked with 2 % Na_2CO_3 dissolved in 0.5 % picric acid was placed on the inner surface of the Petri dish lids and incubated at 37 °C. After 72 hr, the colour of the petri dishes was monitored and the colour of the filter paper changed from yellow to orange-brown, indicating HCN production (26).

A pure culture was inoculated in 5 mL of peptone water and incubated for 4 days at 37 °C. After incubation, 1 mL of Nessler's reagent was added to the peptone water. The development of a yellow colour indicated ammonia formation (27).

Bacteria were grown in a nutrient broth containing tryptophan (0.5 g/L) at 37 °C for 72 hr in an incubator shaker. After centrifugation, the supernatant was mixed with 1 mL of Salkowski reagent (1.5 mL of 0.5 M $FeCl_3.6H_2O$ in 80 mL of 60 % H_2SO_4) and incubated at room temperature for 30 min. The development of a pink colour indicated the presence of IAA (28).

A single bacterial colony was spotted onto Pikovskaya agar plates and incubated at 37 °C for 7 days. Clear zones around the culture indicated phosphate solubilization (29).

Fungal spores were spread onto potato dextrose agar (PDA) and a bacterial colony was placed at the center of the plate. The plates were incubated at 28 °C for 3 days, during which a zone of clearance around the bacterial colony indicated inhibition of fungal growth.

SEM analysis of bacterial-fungal interaction

Small agar fragments were collected from the fungal inhibition zone and placed on aluminium foil. The samples were treated with 2.5 % glutaraldehyde for 4 hr, washed with ethanol, dried and sputter-coated with chromium (Cr). The prepared samples were then examined using an LEO 1450 VP scanning electron microscope (ZEISS, Ramsey, New Jersey, USA) and photographed (30).

Root colonization

Dehusked rice seeds were surface sterilized with 0.1 % mercuric chloride for 3 min and then rinsed with sterile water (31). After drying, the seeds were transferred to Murashige and Skoog (MS) media and incubated under a 16 h light/ 8h dark cycle for 14 days (32). The bacterial cultures were centrifuged at 10000 rpm for 5 min and the bacterial pellet was diluted to 1 × 10^7 CFU/mL in MS broth. The roots of the rice seedlings were then soaked in the bacterial suspension for 1 hr, while those in the control group were dipped in MS broth only. The plants were incubated in a growth chamber for 7 days, after which the roots were washed, fixed with 2.5 % glutaraldehyde, dehydrated with ethanol and dried. Bacterial colonization of the roots was observed using SEM (31).

Molecular characterization

A single bacterial colony was diluted in 10 µL of distilled water and used as a template for polymerase chain reaction (PCR). 16S rRNA gene amplification was performed in a 40 µL reaction volume, containing 0.5 µL forward primer (fD1:5'-AGAGTTTGATCCTGGCTCAG-3'), 0.5 µL of reverse primer (rP2: 5'-ACGGCTACCTTGTTACGACTT-3'), 20 µL of Ampliqon 2X master mix, 1 µL of template DNA and 18 µL of nuclease-free water (33). PCR reactions were carried out using a thermal cycler (Applied Biosystems) with the following parameters: initial denaturation at 95 °C for 5 min, followed by 30 cycles of denaturation at 95 °C for 30 sec, annealing at 58 °C for 30 sec and extension at 72 °C for 1 min 30 sec and a final extension at 72 °C for 4 min. The PCR product was visualized on a 1 % agarose gel and purified using the Qiagen PCR purification kit. The bacterial species was identified by comparing the obtained nucleotide sequences with those available in the National Center for Biotechnology Information (NCBI) database using the basic local alignment search tool (BLAST) (34).

Complete genome analysis

NAN2 strain was inoculated in Luria Bertani (LB) broth and incubated overnight at 37 °C at 150 rpm with shaking. Genomic DNA was extracted using the blood and tissue kit (Qiagen, Germany). The DNA was quantified using the NanoDrop 2000 (Thermo Scientific, USA) and the DNA was processed for genome sequencing in Illumina NovaSeq 6000 (35). The raw data quality was assessed using FastQC v.0.11.9 and preprocessing was performed with Fastp v.0.20.1 (36, 37). The completeness of the genome and the contamination rate were evaluated using CheckM (38). Genome annotation was carried out using Prokka (39). A circular genome representation was generated using CG viewer and CRISPR finder was used to identify CRISPR-Cas arrays (40, 41). Orthologous group cluster analysis was performed using eggNOG-mapper v1 to categorize the proteins in the genome (42). Protein functions were annotated by aligning sequences with the Kyoto Encyclopedia of genes and genomes (KEGG) database using BlastKOALA (43). Gene clusters responsible for secondary metabolite production were identified using antiSMASH (antibiotics and secondary metabolite analysis shell) (44). Plant growth-promoting traits (PGPT) were predicted using PGPT-Pred in PLaBAse v1.01 (45).

Results

Isolation of potential rhizobacteria from the rice rhizosphere

A total of 36 bacterial isolates were obtained from the rice rhizosphere in this study. Among them, NAN2's strain exhibited significant plant growth promoting roles, including production HCN, ammonia, IAA and phosphate solubilization. Additionally, NAN2 exhibited strong antifungal activity against *M. oryzae* (Fig. 1). These traits highlight NAN2 potential as a promising

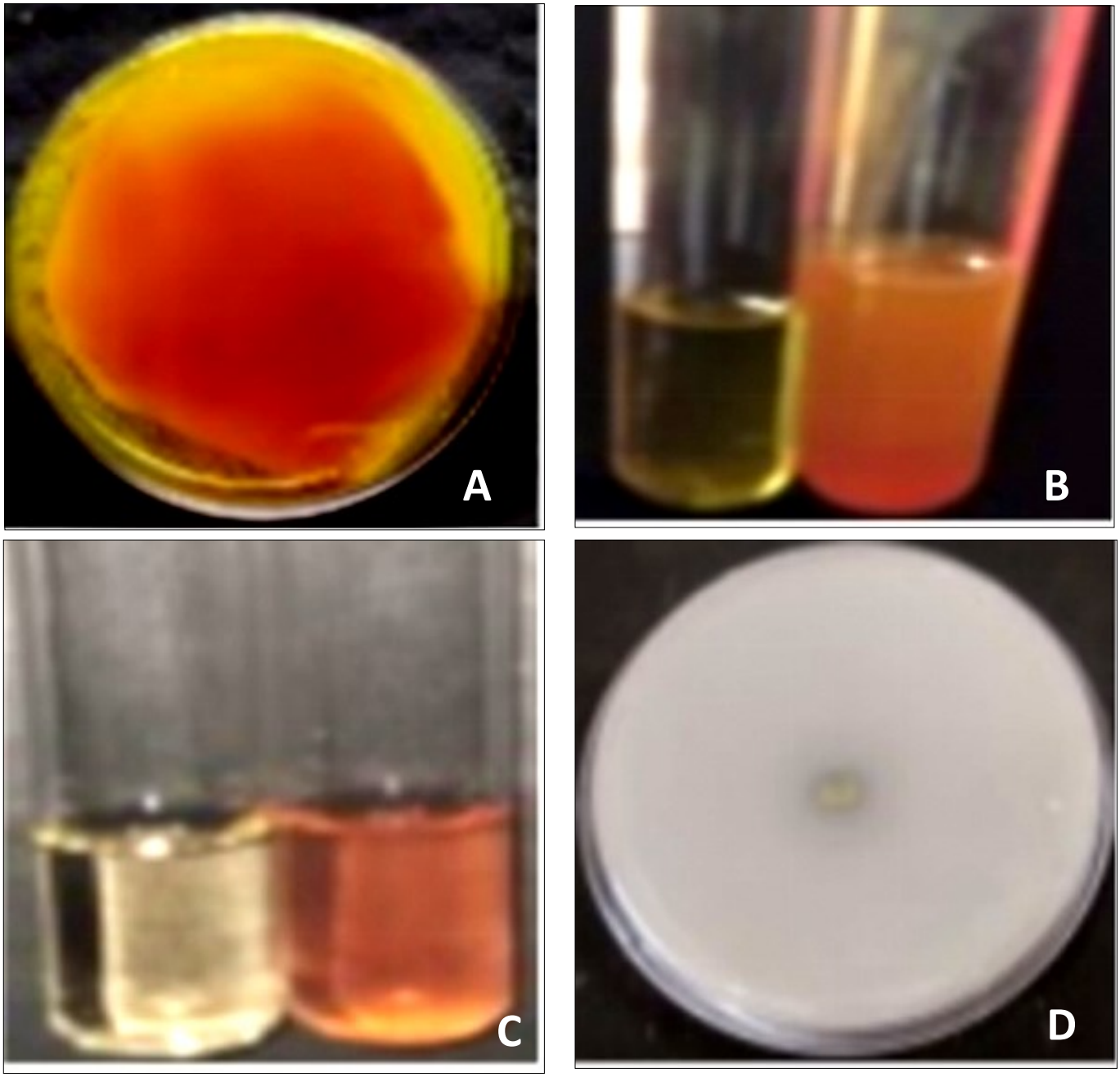


Fig. 1. Plant growth promoting properties of *P. plecoglossicida* NAN2 (**A**) hydrogen cyanide production (**B**) ammonia production (**C**) indole-3-acetic acid production and (**D**) phosphate solubilization.

biocontrol and PGP agent. HCN production was verified by a colour change in the filter paper from yellow to orange brown. Ammonia production was confirmed in peptone water, as evidenced by a colour change from brown to yellow. IAA production was detected by culturing the bacteria in nutrient broth supplemented with L-tryptophan. After incubation, the culture supernatant was mixed with Salkowski's reagent and the development of a pink colour indicates the presence of IAA production. The phosphate solubilization ability of the NAN2 was assessed using a halo zone formation assay on Pikovskaya's agar medium.

Antifungal activity

A dual culture assay on PDA agar revealed that strain NAN2 exhibits strong antifungal activity against *M. oryzae,* as indicated by a significant zone of inhibition (35 mm in diameter) surrounding the bacterial colony after 3 days of incubation (Fig. 2A).

SEM observation of fungal inhibition by NAN2

To investigate the antifungal effects of *P. plecoglossicida* NAN2 on *M. oryzae*, fungal hyphae exposed to the bacterial strain were analyzed through SEM (Fig. 2B, C). SEM images revealed significant structural alterations in *M. oryzae* hyphae treated with the NAN2 strain compared with those in the untreated control fungi. In the control group, fungal hyphae exhibited smooth, intact well organized structures and characteristics of healthy fungal growth. In contrast, hyphae exposed to the NAN2 strain showed severe morphological changes including surface shrinkage and wrinkling, indicating the loss of cellular integrity and dehydration. Hyphal disruption, fragmentation and distortion of hyphal structures suggest potential interference with cell wall integrity, possibly due to bacterial secondary metabolites. SEM analysis revealed an abnormal growth pattern of *M. oryzae* in the presence of the NAN2 strain, characterized by structural disintegration and hyphal deformation.

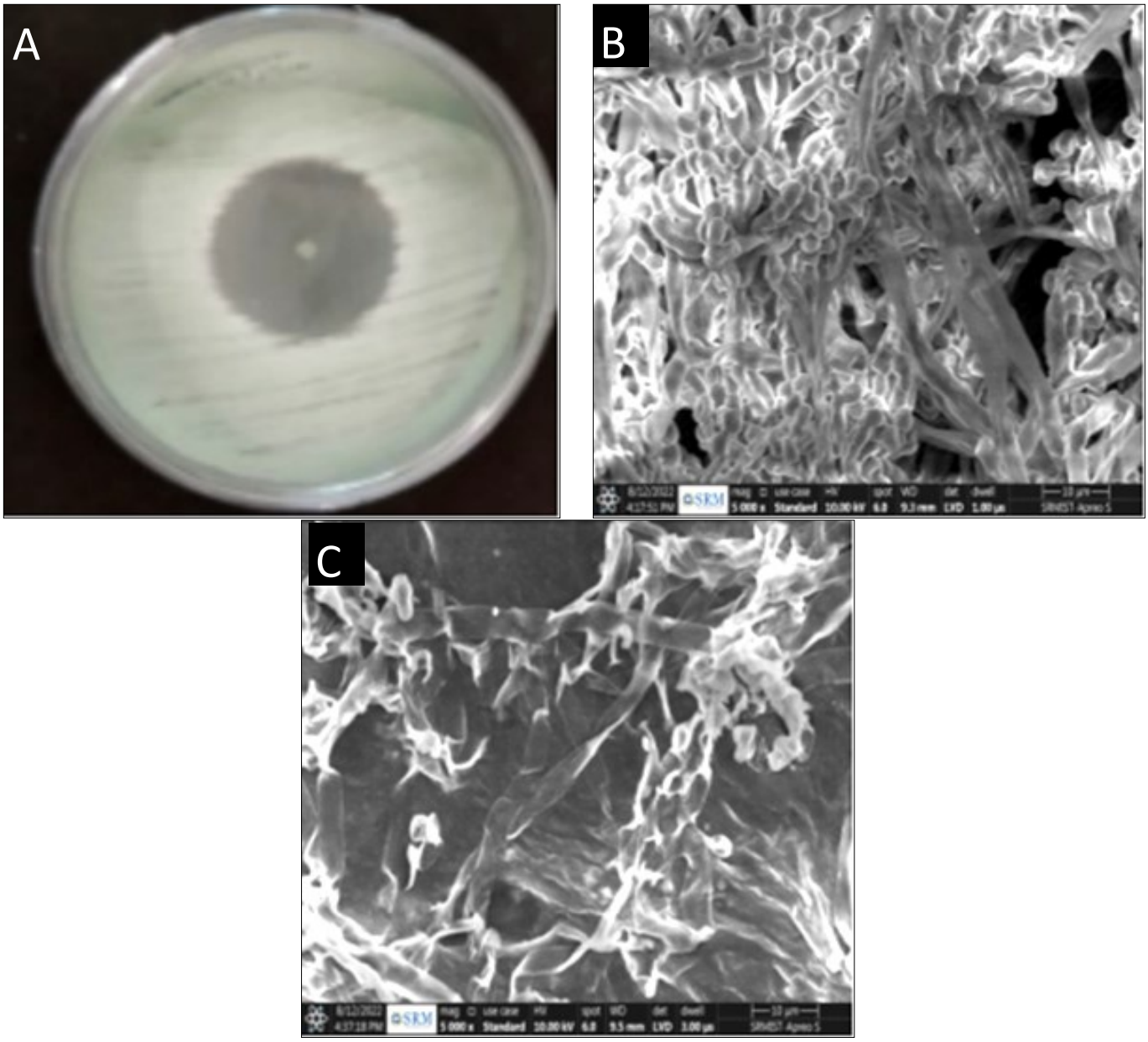


Fig. 2. (**A**) Zone of inhibition against *M. oryzae*. Scanning electron microscopy (SEM) analysis of bacteria inhibition of *M. oryzae* growth; (**B**) healthy growth of *M. oryzae* and (**C**) abnormal pathogen growth due to interaction with *P. plecoglossicida* NAN2 on PDA medium after 3 days.

Root colonization

SEM analysis of rice seedlings treated with *P. plecoglossicida* NAN2 revealed dense and uniform bacterial colonization on the root surface (Fig. 3). The bacterial cells adhered to the root epidermal cells, formed structured microcolonies spread along the root hairs and rhizoplane. In contrast, the control group showed an absence of bacterial colonization, with smooth and uncolonized root surfaces. The uniform colonization pattern suggests that NAN2 effectively establishes itself in the rhizosphere, likely through mechanisms such as biofilm formation, which enhance bacterial attachment and persistence on root surfaces. The root surface adhesion facilitated by bacterial exopolysaccharides, cell surface proteins and plant microbial interactions, possibly mediated by root exudates that attract and support bacterial growth. Effective root colonization enhances nutrient availability, including phosphate solubilization, the production of the phytohormone auxin which promotes root growth development and biocontrol activity, providing protection against root associated pathogens.

Molecular identification

The amplified 16S rRNA gene product was approximately 1500 base pairs (bp) in size (Fig. 4). BLAST analysis of the sequence fragment revealed 99.93 % identity to *P. plecoglossicida* NyZ12 (GenBank accession no. CP010359), confirming the taxonomic identity of the NAN2. This molecular confirmation supports the classification of NAN2 as a PGPR, reinforcing its potential application in sustainable agriculture.

Genome analysis

The complete genome of *P. plecoglossicida* NAN2 consists of 5356785 bp with a GC content of 62 %. The assembled genome contains 227 contigs-encoding 4807 coding sequences (CDS), 4960 genes, 68 miscRNAs, 11 rRNAs, 73 tRNAs, 1 tmRNA and 1792 hypothetical proteins. Additionally, genome analysis identified one CRISPRs array, two *Cas* genes and one *Cas* cluster (Fig. 5A). Clusters of orthologous groups (COG), categories in *P. plecoglossicida* NAN2 (Fig. 5B). The most represented categories are amino acid metabolism, transcription and inorganic metabolism.

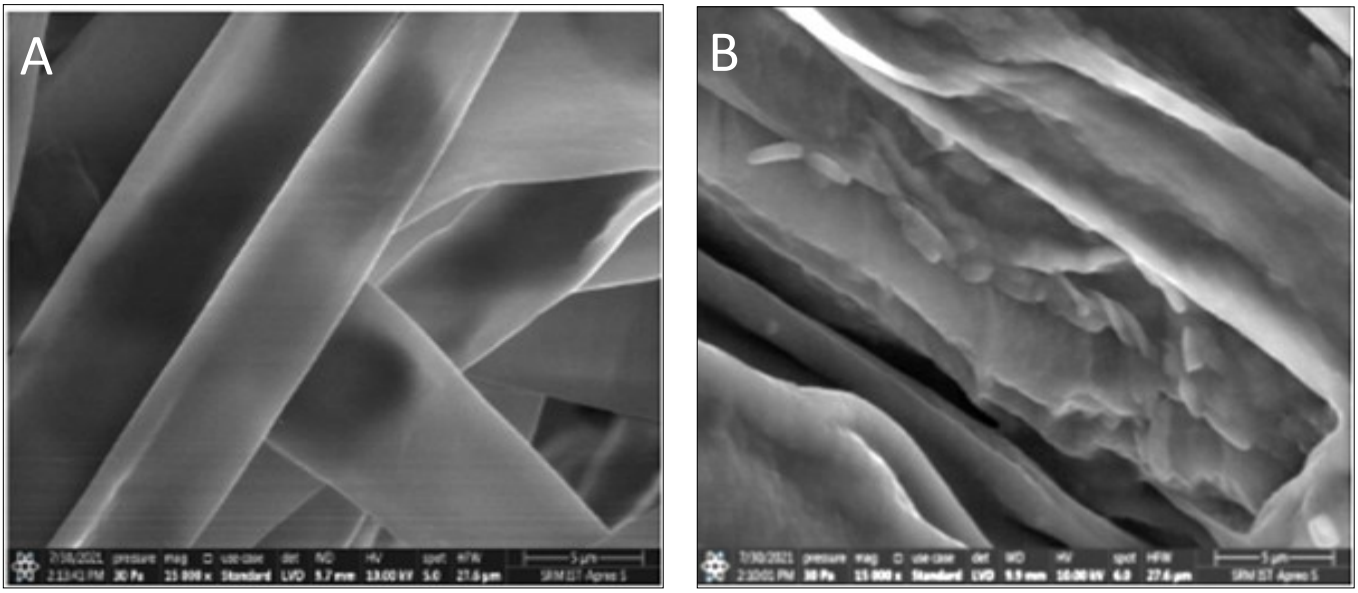


Fig. 3. Root colonization by *P. plecoglossicida* NAN2. (**A**) untreated rice rhizosphere showing no visible colonization on the root surface and (**B**) roots treated with *P. plecoglossicida* NAN2 exhibit extensive colonization, with bacterial cells adhering to the root surface.

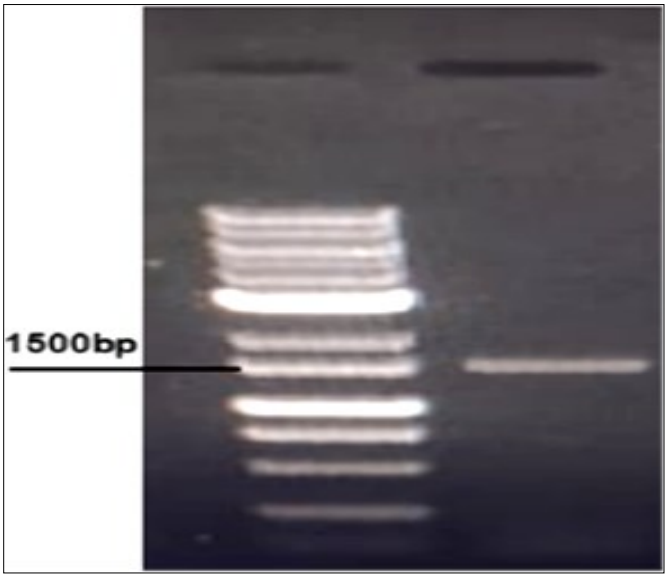
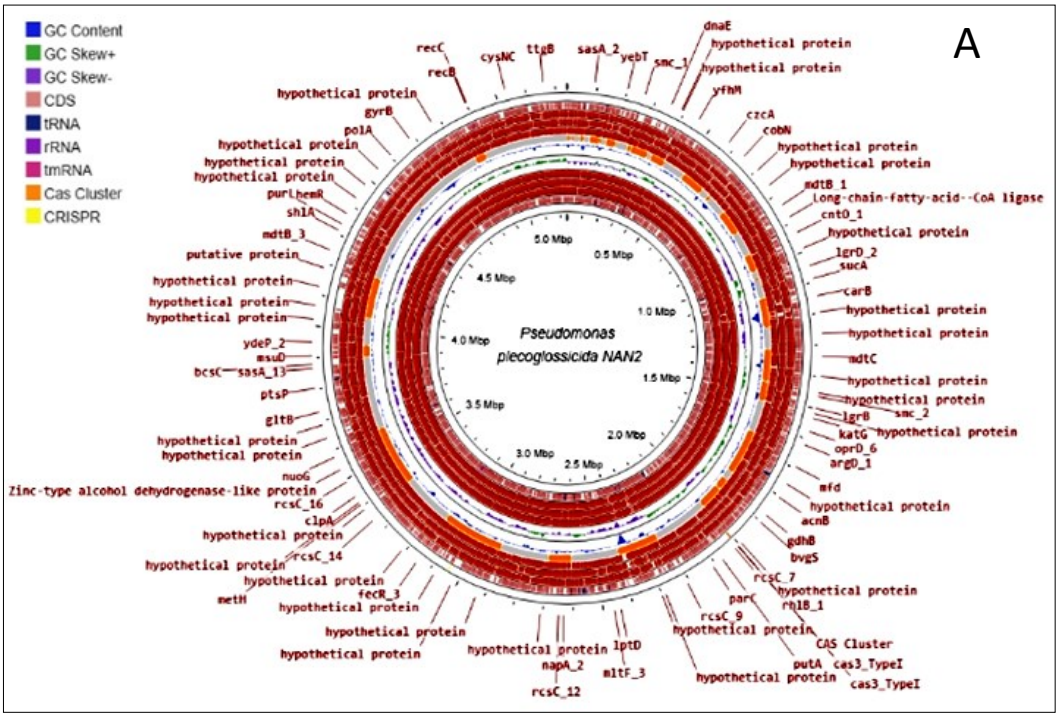


Fig. 4. 16S rRNA gene amplification. Lane 1: 1kb DNA ladder; Lane 2: amplified 16S rRNA gene of *P. plecoglossicida* NAN2.



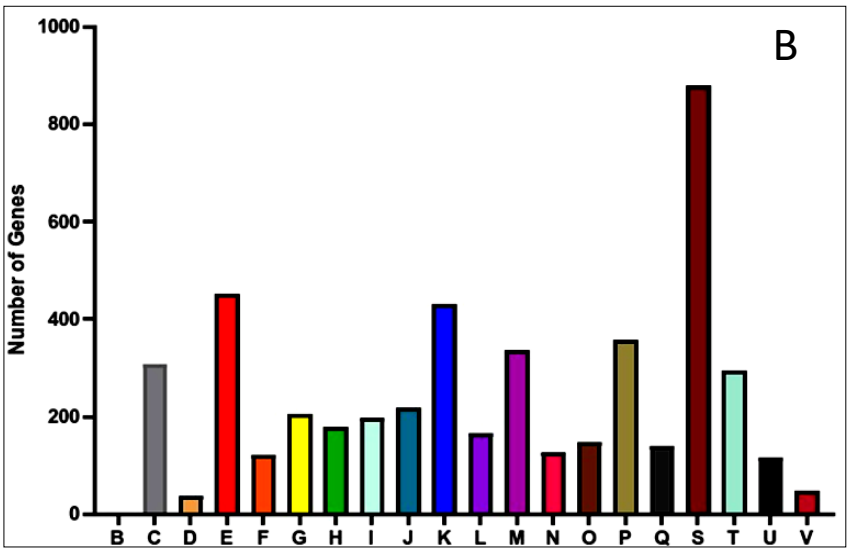


Fig. 5. Genomic and functional attributes of *P. plecoglossicida* NAN2. (**A**) circular genome map of NAN2, showing features, including GC content, GC Skew+, GC Skew-, coding sequences (CDS), tRNA, rRNA, tmRNA and the presence of *Cas* clusters and CRISPR regions. (**B**) the functional annotation of NAN2 genome highlights genes categorized under the clusters of orthologous groups (COG) classification. Chromatin structure and dynamics (**B**); energy production and conversion (**C**); cell cycle control, cell division, chromosome partitioning (**D**); amino acid transport and metabolism (**E**); nucleotide transport and metabolism (**F**); carbohydrate transport and metabolism (**G**); coenzyme transport and metabolism (**H**); lipid transport and metabolism (**I**); translation, ribosomal structure and biogenesis (**J**); transcription (**K**); replication, recombination and repair (**L**); cell wall, membrane, envelope biogenesis (**M**); cell motility (**N**); posttranslational modification, protein turnover, chaperones (**O**); inorganic transport and metabolism (**P**); secondary metabolites biosynthesis, transport and catabolism (**Q**); function unknown (**S**); signal transduction mechanisms (**T**); intracellular trafficking, secretion and vesicular transport (**U**) and defense mechanisms (**V**).

Functional analysis

KEGG analysis of the NAN2 genome revealed the presence of several genes associated with xenobiotic biodegradation and metabolism, distributed across 18 pathways (Fig. 6A). These include genes involved in the degradation of benzoate (23 genes), aminobenzoate (5 genes), fluorobenzoate (6 genes), chloroalkane and chloroalkene (4 genes), chlorocyclohexane and chlorobenzene (3 genes), toluene (2 genes), xylene (5 genes), nitrotoluene (2 genes), ethylbenzene degradation (1 gene), styrene (7 genes), atrazine (3 genes), caprolactam (2 genes), dioxin (1 gene), naphthalene (3 genes) and polycyclic aromatic hydrocarbon (2 genes). Additional pathways include metabolism of xenobiotics by cytochrome P450 (4 genes), drug metabolism - cytochrome P450 (5 genes) and drug metabolism - other enzymes (10 genes). The presence of genes encoding enzymes for these pathways suggests that *P. plecoglossicida* NAN2 can efficiently degrade these compounds, potentially mitigating their environmental impact.

Prediction of secondary metabolite biosynthesis gene clusters

Secondary metabolite biosynthetic gene clusters (BGCs) were identified using antiSMASH (Table 1). The predicted secondary metabolites include pyoverdine SMX-1, Pf-5 pyoverdine, rhizomides (A, B and C), 4,5-didehydro-acaterin/acaterin, lankacidin C, Pf-5 pyoverdine and APE Vf. Notably, highly similar gene clusters encoding NRPS were linked to the production of rhizomide, underscoring the potential of NAN2 as a biocontrol agent.

Genes related to potential plant-growth promotion

Genome annotation analysis using PGPT-Pred programs identified key genes associated with plant growth promotion (Fig. 6B). PGPT-Pred analysis indicated genes involved in plant colonization (24 %), competitive exclusion (21 %), biocontrol (21 %), biofertilization (13 %), phytohormone (11 %), bioremediation (8 %) and plant immune response simulation (1 %).

Data availability

Raw reads were deposited in the sequence read archive (SRA) under accession number PRJNA1196091.

Table 1. Biosynthetic gene clusters identified in the genome of *P. plecoglossicida* NAN2 associated with the production of secondary metabolites.

Region	Type	From	To	Most similar known cluster	Secondary metabolites	Similarity
Region 49.1	NRP metallophore, NRPS, NRP S-like	1	49791	NRP	Pyoverdine SMX-1	38 %
Region 54.1	NRPS	28273	76437	NRP	Pf-5 pyoverdine	8 %
Region 58.1	NAGGN	8936	23901			
Region 60.1	NRPS-like	1	2789	NRP	Rhizomide (A/ B/ C)	100 %
Region 62.1	Hserlactone, b utyrolactone, t hiopeptide	120676	163020	Other	4,5 didehydroac aterin / acaterin	66 %
Region 64.1	Redox cofactor	54223	76382	lankacidin C	NRP + polyketide	13 %
Region 66.1	NRPS-like	1	23757			
Region 66.2	Ranthipeptide	34418	55848	Pf-5 pyoverdine	NRP	7 %
Region 71.1	Arylpolyene	88184	131791	APE Vf	Other	35 %
Region 72.1	RiPP-like	22619	34808			

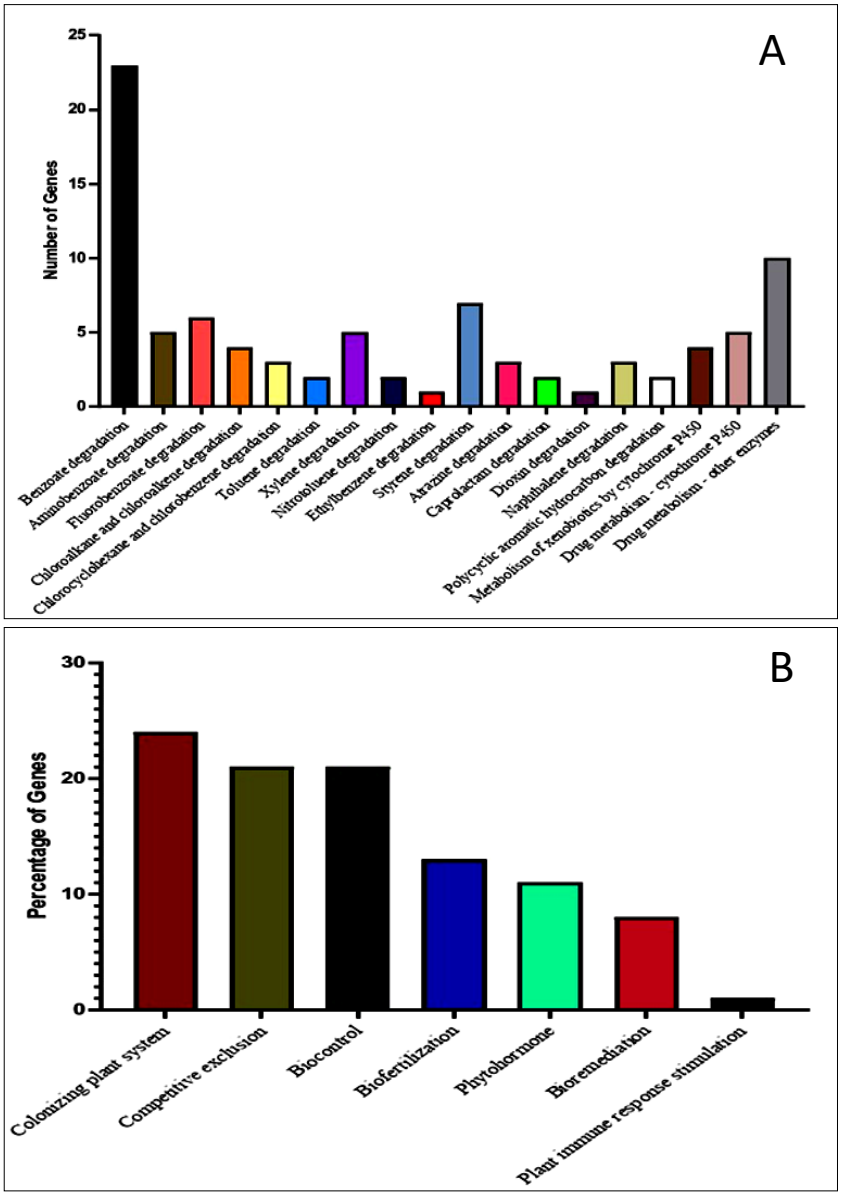


Fig. 6. Functional gene distribution in *P. plecoglossicida* NAN2. (**A**) genes involved in xenobiotic degradation pathways. (**B**) percentage of genes related to plant growth promoting traits. The presence of these genes' underscores NAN2 capability to enhance plant growth, improve nutrient uptake and support plant resilience under environmental stress conditions.

Discussions

The isolation and characterization of microorganisms with biocontrol activity against phytopathogens are important due to their potential as eco-friendly alternatives to chemical pesticides. Numerous rhizobacteria, such as *Bacillus subtilis, P. fluorescens, P. aeruginosa, Stenotrophomonas maltophilia, Burkholderia* spp., have been shown to enhance plant defense mechanisms against various phytopathogens while promoting plant growth, thus contributing to improved crop production (46). In this study, we report the isolation and complete genome analysis of the *P. plecoglossicida* strain NAN2, which has demonstrated multiple plant growth-promoting traits. NAN2 was isolated from the rice rhizosphere and exhibited the production of HCN, ammonia, phytohormone, phosphate solubilization and antifungal activity against *M. oryzae*. A previous study has reported that *P. plecoglossicida* SRI-156 exhibited plant growth-promoting traits and acted as a biocontrol agent against *Macrophomina phaseolina* (47). However, to our knowledge this is the first report of *P. plecoglossicida* NAN2 exhibiting fungal inhibition against *M. oryzae*.

SEM revealed abnormal growth of *M. oryzae* in the presence of the NAN2 strain, characterized by deformed hyphae, disrupted surface structure. This observation aligns with similar finding, which noted morphological alterations in the mycelia of *Lasiodiplodia theobromae* during its interaction with *Bacillus amyloliquefaciens* (30). The results of this study suggest that *P. plecoglossicida* NAN2 possesses both antifungal and plant growth-promoting properties, making it a promising candidate for the biocontrol of prevalent fungal pathogens.

PGPR play crucial roles in plant health by colonizing surfaces or internal tissues, facilitating nutrient recycling, promoting growth and inhibiting pathogen development (48, 49). In this study, strain NAN2 successfully colonized the root surfaces of rice plants, as visualized by SEM, which detected the accumulation of bacterial cell clumps and biofilm-like structures. Similar observation was reported earlier regarding the colonization of maize roots by *P. geniculata* MF-84 (50). The CRISPR-Cas system plays a critical role in bacterial defense, enabling sequence-specific resistance against invading genetic material (51). The presence of these elements highlights the potential resilience of the bacterial strain in dynamic

environments, making them promising candidates for biocontrol. Moreover, antiSMASH analysis of NAN2 genome revealed significant similarity to secondary metabolite gene clusters, including those encoding rhizomide A, B and C which are synthesized by nonribosomal peptide synthetase gene clusters. A previous study showed that rhizomides exhibit antimicrobial activity against *Bacillus subtilis, Staphylococcus aureus* and *Pseudoperonospora cubensis* (52).

Conclusion

In the present study, we investigated *P. plecoglossicida* NAN2, a PGPR isolated from the rice rhizosphere. Using a comprehensive approach involving characterization and whole-genome sequencing, we explored its growth-promoting mechanisms. Our results confirmed that *P. plecoglossicida* NAN2 enhances plant growth through multiple traits, including the production of HCN, ammonia, IAA, phosphate solubilization and antifungal activity against *M. oryzae*. Furthermore, genomic analysis revealed a strong genetic potential for its role as a PGPR, reinforcing its promise as a biofertilizer to enhance crop growth and development.

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Authors' contributions

NK conducted the experiments, performed genome analysis and contributed to writing of the original draft. GG participated in the investigation, genome analysis and writing of the original draft, as well as reviewing and editing the manuscript. IS conducted the experiments, participated in the investigation and genome analysis, contributed to writing the original draft, conceptualized the study, supervised the work and participated in manuscript review and editing. All authors read and approved the manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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