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Functional and Genomic Characterization of *Streptomyces albus* VCCM 22715 as an Antifungal Biocontrol and Plant Growth-Promoting Agent for *Panax vietnamensis*

Ngoc Tung Quach[1], Thi Hanh Nguyen Vu[1], Manh Van Le[1], Xuan Khoi Tran[1], Van The Nguyen[1], Cao Cuong Ngo[2], Thi Thanh Xuan Le[1] and Quyet-Tien Phi[1]*

[1]Institute of Biology, Vietnam Academy of Science and Technology, Hanoi, Vietnam.
[2]Joint Vietnamese - Russia Tropical Science and Technology Research Center, Hanoi, Vietnam.

Abstract

Panax vietnamensis Ha et Grushv. is a high-value endemic ginseng species and a rich source of biologically active ginsenosides. However, low productivity and high susceptibility to phytopathogens limit supply relative to demand. Here, we evaluated the efficacy of bacterial strain VCCM 22715 against phytopathogenic fungi and assessed its effects on the growth of *P. vietnamensis*. Among 61 strains, VCCM 22715 showed the strongest activity against *Rhizoctonia solani*, inhibiting mycelial growth by 80.1 ± 5.7%. An ethyl acetate extract also inhibited *R. solani* (52.8 ± 5.3%), *Magnaporthe oryzae* (73.5 ± 0.3%), and *Fusarium solani* (52.8 ± 5.3%). Based on phenotypic characterization and molecular analyses, the strain was identified as *Streptomyces albus* VCCM 22715. Notably, the strain produced 24.3 ± 2.5 µg/mL indole-3-acetic acid (IAA) and significantly increased plant height, root length, fresh weight, and dry weight of *P. vietnamensis* ($p < 0.05$). Whole-genome analysis revealed an 8.0 Mb linear chromosome with 73% GC content, 6,796 protein-coding sequences, and 16 secondary metabolite biosynthetic gene clusters. Key genes implicated in IAA biosynthesis were also detected. Collectively, these results indicate that *S. albus* VCCM 22715 is a promising biocontrol and plant growth-promoting agent for field-cultivated ginseng.

Keywords: Antifungal activity, Indole-3-acetic acid, *Panax vietnamensis*, *Streptomyces albus,* Whole-genome analysis

***Correspondence:** tienpq@ib.ac.vn

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INTRODUCTION

Medicinal crop production has traditionally relied heavily on agricultural chemicals, including inorganic fertilizers and pesticides.[1] The emergence of pest resistance to synthetic agrochemicals has contributed to antibiotic resistance in pathogens and has increased the need for new pesticides.[2,3] Consequently, alternatives to conventional agrochemicals are increasingly important for achieving sustainable agriculture.

One promising approach is the use of biostimulants derived from plant growth-promoting bacteria (PGPB). PGPB, including *Pseudomonas*, *Bacillus*, *Streptomyces*, and *Azospirillum*, can increase crop productivity, enhance resilience to abiotic stresses and phytopathogenic microbes, and reduce reliance on agrochemicals.[4] Among these, *Streptomyces* spp. are prolific producers of bioactive metabolites and account for approximately 75% of antibiotics and antifungal compounds on the global market.[5] *Streptomyces lydicus* and *Streptomyces griseoviridis* have been commercialized as the biofungicides Actinovate® and Mycostop®, respectively.[6] Strawberry fruit rot caused by *Botrytis cinerea*, *Mucor hiemalis*, *Rhizopus stolonifer*, and *Sclerotinia sclerotiorum* is suppressed by reveromycins A and B produced by *Streptomyces* sp. 3-10.[6] In addition, *Streptomyces* spp. can promote plant growth by traits such as nitrogen fixation, IAA production, and phosphorus and potassium solubilization, thereby increasing plant biomass and length.[7,8] For example, *Streptomyces albidoflavus* St-220 promotes the growth of *Salvia miltiorrhiza* seedlings under greenhouse conditions by solubilizing inorganic phosphate, fixing nitrogen, and producing IAA.[9] Accordingly, the discovery of new Streptomyces strains with plant growth-promoting and antifungal activities tailored to specific medicinal plants remains an active area of research and application.

Panax vietnamensis Ha et Grushv. is a valuable endemic species first discovered in Quang Nam and Kon Tum provinces, Vietnam.[10] Overharvesting, slow growth, and poor regeneration have pushed wild populations toward extinction.[11,12] In parallel, excessive use of chemical fertilizers and pesticides has raised concerns regarding phytochemical integrity and the accumulation of toxic compounds. Here, *Streptomyces albus* VCCM 22715 was screened for antifungal activity and identified to the species level. Broad-spectrum antifungal activity of its ethyl acetate extract was also assessed, and the effects of the strain on *P. vietnamensis* growth were evaluated under *in vivo* conditions. To elucidate the genetic basis of antifungal and plant growth-promoting properties, we performed genomic analysis.

MATERIALS AND METHODS

Screening of bacterial strains for antifungal activity

Sixty-one bacterial strains isolated from mangrove plants, together with the phytopathogenic fungus *Rhizoctonia solani*, were obtained from the VAST-Culture Collection of Microorganisms (Institute of Biology, Vietnam Academy of Science and Technology). Antifungal activity was screened using a plate confrontation assay as described previously.[13] Briefly, a 5 mm mycelial plug of *R. solani* was placed at the center of potato dextrose agar (PDA) plates (HiMedia, India). Test strains were inoculated at four equidistant points, each 25 mm from the plate center, and incubated for 5-7 days. Plates containing only *R. solani* served as the control. The percentage of fungal growth inhibition (GI) was calculated by comparing mycelial diameters in control and treated plates.[13]

Morphological characterization and 16S rRNA gene sequence analysis

The most active strain was cultured on ISP2 agar at 30 °C for 9 days to assess colony morphology, growth characteristics, pigmentation, and color as described previously.[14] Genomic DNA from strain VCCM 22715 was extracted using the G-spin™ Total DNA Extraction Mini Kit (Intron Bio). Molecular identification was performed by PCR amplification of the 16S rRNA gene, followed by agarose gel electrophoresis, purification, and Sanger sequencing. The sequence was trimmed using BioEdit v7.2.5 and compared with the National Center for Biotechnology Information (NCBI) database using BLAST. A phylogenetic tree was constructed in MEGA v11.0 using the neighbor-joining approach with maximum-likelihood-based analysis.

Preparation of ethyl acetate extract and evaluation of antifungal activity

VCCM 22715 was cultivated in potato dextrose broth (PDB; HiMedia, India) for 3 days at 30 °C as a seed culture and then inoculated into five 1,000 mL flasks, each containing 250 mL fresh PDB. After incubation for 8 days at 30 °C, cultures were pooled, centrifuged at 8,000 rpm for 20 min, and extracted three times with ethyl acetate. The organic phase was evaporated at 50 °C to obtain a brown crude extract. Immediately before each assay, fresh stock solutions were prepared and incorporated into PDA to final concentrations of 0, 100, or 150 µg/mL. A 5 mm mycelial plug of *Magnaporthe oryzae*, *Fusarium solani*, or *R. solani* was placed at the center of each plate. Plates containing 5% (v/v) dimethyl sulfoxide (DMSO) served as the solvent control. After 7 days at 30 °C, colony diameters were measured and growth inhibition (GI %) was calculated as described previously.[13] All assays were performed in triplicate, and data are presented as mean ± standard deviation (SD).

Determination of indole-3-acetic acid production

IAA production by VCCM 22715 was quantified as described previously.[3] The strain was grown in ISP2 medium supplemented with 100 µg/mL tryptophan and incubated at 30 °C for 3 days (triplicate cultures). Cultures were centrifuged at 10,000 rpm for 10 min, and 1.0 mL supernatant was mixed with 1.0 mL Salkowski reagent. The mixture was incubated in the dark at room temperature for 30 min, and absorbance at 530 nm was measured. IAA concentration was calculated using the standard curve equation ($y = 0.0065x + 0.0033$), generated from serial IAA standards (0, 5, 10, 20, 40, and 80 µg/mL).

Pot experiment

Pot experiments were performed in a greenhouse in Yen Bai Province, Vietnam, where the mean annual temperature in 2024 was approximately 19.6 °C. Each plastic pot contained approximately 1 kg UV-sterilized soil (neutral pH). Six-month-old ginseng plants were pre-cultivated in pots for 1 month before treatment. Treatments included non-inoculated controls and pots inoculated with *S. albus* VCCM 22715. For inoculation, *S. albus* VCCM 22715 was grown on PDA for 7 days at 30 °C to obtain spores, which were applied to each pot to a final density of 10^4 CFU/g soil. Six plants were treated weekly for 3 weeks with the VCCM 22715 spore suspension, whereas six control pots received sterile water. After 6 months, plants were harvested to assess growth parameters, including plant height, root length, fresh weight, and dry weight of each *P. vietnamensis* plant. Experiments were performed in triplicate, and data are presented as mean ± SD. Statistical analyses were conducted using GraphPad Prism 9.

Whole-genome sequencing and genome mining

Genomic DNA from VCCM 22715 was extracted using the G-spin™ Total DNA Extraction Mini Kit (Intron Bio), followed by quality control and Illumina sequencing. Raw reads were trimmed and quality-assessed using Trimmomatic v3.0 and FastQC v0.12.1. Reads were assembled *de novo* with SPAdes v3.15.5 using default parameters. Genome annotation was performed using the NCBI Prokaryotic Genome Annotation Pipeline (PGAP) and RASTtk (Rapid Annotation using Subsystem Technology).[15] The whole-genome sequence was deposited in DDBJ/ENA/GenBank under accession number JBPQDV010000000. Secondary metabolite biosynthetic gene clusters (BGCs) were predicted using antiSMASH v6.0.[16] Species-level assignment was performed using the Type (Strain) Genome Server (TYGS: https://tygs.dsmz.de/) to construct a phylogenomic tree with default parameters and to calculate digital DNA-DNA hybridization (dDDH) values. Genes implicated in IAA biosynthesis were predicted using RASTtk with thresholds of >30% identity and >50% coverage.

RESULTS AND DISCUSSION

Screening and identification of a bacterial strain with potent antifungal activity

A total of 61 actinomycete strains from a previous study were screened for antifungal activity against *R. solani* using a dual-culture assay. Among the strains tested, VCCM 22715 showed the strongest inhibition of *R. solani* mycelial growth (80.1 ± 5.7%). Therefore, VCCM 22715 was selected for further analyses.

VCCM 22715 grew well on ISP2 agar and formed colonies with dry, rough surfaces (Figure 1A). After 10 days, the vegetative mycelium developed white aerial hyphae and a spore mass (Figure 1B), and no pigment was observed on any of the tested media. These phenotypic characteristics were consistent with assignment to the genus *Streptomyces*.

For species-level identification, a 1,536-bp partial 16S rRNA gene sequence from VCCM 22715 was amplified and sequenced. VCCM 22715 showed 99.7% sequence similarity to *S. albus* NRRL B-1811[T] and *S. albus* NBRC 15415[T]. Phylogenetic analysis based on 16S rDNA sequences further showed that VCCM 22715 clustered with *S. albus*, with *S. albus* NRRL B-1811[T] and *S. albus* NBRC 15415[T] as the closest relatives (Figure 1C). Accordingly, the strain was designated *S. albus* VCCM 22715.

Antifungal potential of the crude extract from *S. albus* VCCM 22715

To determine whether *S. albus* VCCM 22715 exhibits broad antifungal activity, we tested its crude extract against three phytopathogenic fungi: *Magnaporthe oryzae*, *Fusarium solani*, and *Rhizoctonia solani*. The crude extract strongly inhibited mycelial growth of all three fungi, with inhibition ranging from 52.8% to 73.5% (Figure 2). At 150 µg/mL, the highest inhibition was observed for *M. oryzae* (73.5 ± 0.3%), followed by *F. solani* (69.1 ± 2.9%) and *R. solani* (52.8 ± 5.3%).

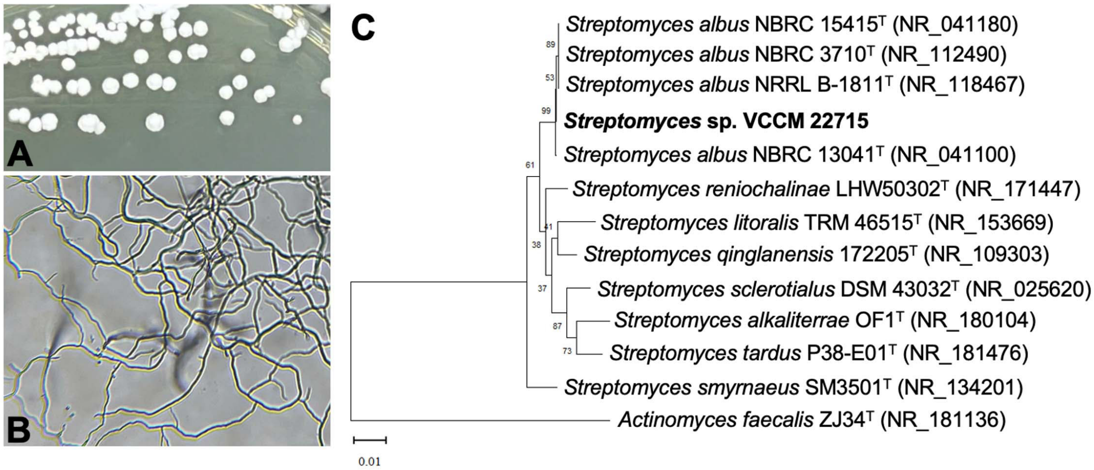

Figure 1. Identification of the strain VCCM 22715. Colonies grown on ISP2 agar plate (A) and aerial hyphae under phase contrast microscopy (B) of the strain VCCM 22715. (C) Phylogenetic tree built from 16S rRNA sequence of the VCCM 22715 and its related type strains

Table 1. Genome characteristics of the VCCM 22715 and its related strains

Attribute	*S. albus* VCCM 22715	*S. albus* N11-50	*S. albus* DSM 40763[T]
Genome size (Mb)	8.0	8.29	8.09
GC content (%)	73.0	72.7	72.6
rRNA genes	17	18	19
tRNA genes	65	62	61
ncRNA genes	3	3	3
CDSs	6796	7010	6888
Predicted genes	6862	7093	6971
GenBank accession	JBPQDV010000000	NZ_BNEJ00000000	NZ_RCIY00000000

Streptomyces spp. can suppress diverse phytopathogenic fungi through the production of secondary metabolites.[17] For example, *Fusarium oxysporum* f. sp. *cubense* Tropical Race 4, *Curvularia fallax, Colletotrichum gloeosporioides, Colletotrichum acutatum,* and *Fusarium graminearum* are strongly inhibited by *Streptomyces* sp. YYS-7, with mycelial growth inhibition ranging from 48.6%-80.9%.[18] In addition, *S. parvulus* VRR3 isolated from green gram exhibits biocontrol activity against *F. solani* under laboratory and greenhouse conditions.[19] These reports are consistent with our findings. Biocontrol mechanisms against phytopathogenic fungi can include antimicrobial metabolites, nutrient competition, and antibiosis. However, the superior performance of VCCM 22715 may also reflect strain-specific genomic features.

In our previous study, *S. albus* RC2 showed strong activity against *Lasiodiplodia theobromae*,

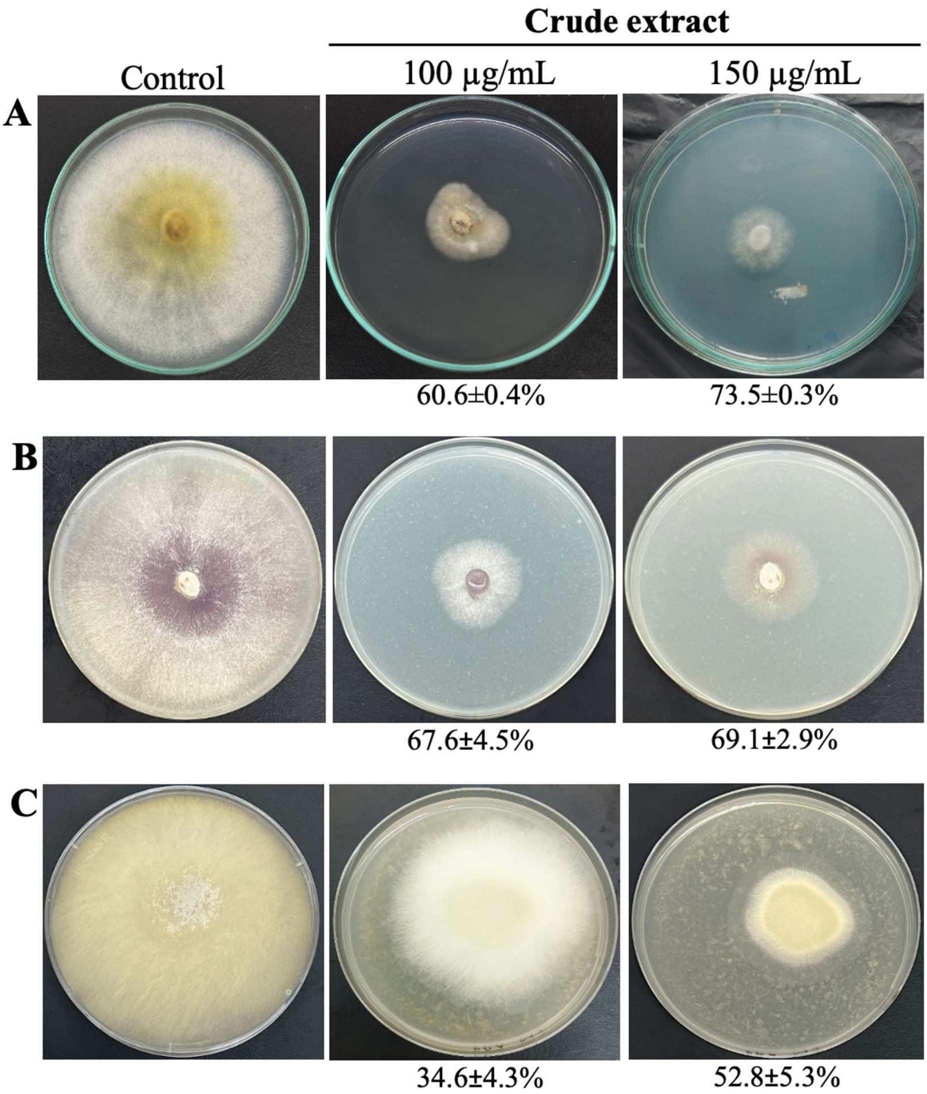

Figure 2. Antifungal activity of the VCCM 22715 extract against *Magnaporthe oryzae* (A), *Fusarium solani* (B), and *Rhizoctonia solani* (C)

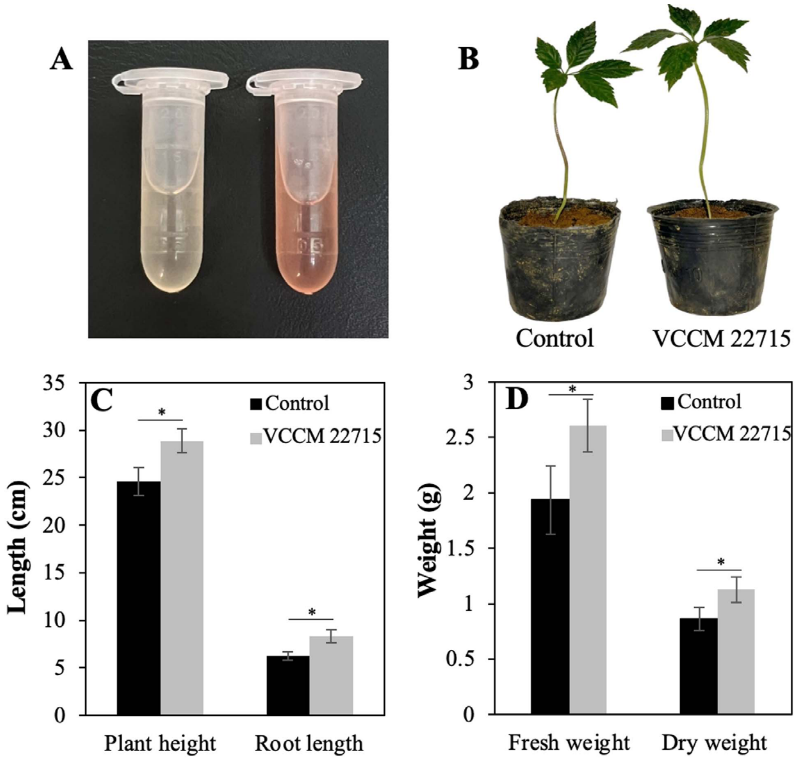

Figure 3. Effects of the VCCM 22715 on growth parameters of *Panax vietnamensis* plants. (A) IAA production by the VCCM 22715 in the ISP2 medium supplemented with 100 µg/mL tryptophan. (B) Representative images of ginseng plants inoculated with and without the VCCM 22715. Plant height, root weight (C) and fresh and dry weights (D) of ginseng in control group and VCCM 22715-treated group. The level *$P < 0.05$ was statistically considered significant using a Student's unpaired two-tailed t-test by the GraphPad Prism 9 software

Table 2. Predicted secondary metabolite biosynthetic gene clusters in *S. albus* VCCM 22715

Region	Size (bp)	Synthetase type	Similar known BGC (similarity)	Biological activity
1.1	35.020	Prodigiosin	Tambjamine BE-18591 (96%)	Antibacteria, antifungi, antitumor
1.3	8.834	NI-siderophore	Legonoxamine A (100%)	Anticancer
2.4	41.239	Nucleoside	Pseudouridimycin (68%)	Antibacteria
2.5	22.715	Lanthipeptide	SapB (75%)	Morphogenetic peptide
3.1	118.266	Lanthipeptide	Xantholipin (81%)	Antitumor, antibacteria
3.2	10.405	Ectoine	Ectoine (100%)	Antioxidant
4.1	26.705	Terpene	Hopene (61%)	Antimicrobial
7.2	48.590	NRPS	Griseobactin (53%)	Iron chelation, anticancer
9.1	69.737	T1PKS	Ibomycin (58%)	Antifungi
15.3	58.331	NRPS	Coelibactin (54%)	-
16.1	24.462	Terpene	Isorenieratene (45%)	-
17.1	10.345	Butyrolactone	A-factor (100%)	-
26.1	33.306	NI-siderophore	Kinamycin (21%)	Antibacteria
39.1	32.093	NRPS	Dudomycin A (65%)	Antibacteria
50.1	14.850	Terpene	Geosmin (100%)	-
57.1	8.407	T1PKS	Griseochelin (53%)	Antibacteria

Fusarium fujikuroi, and *Scopulariopsis gossypii*, which cause serious crop damage in Vietnam.[13] However, *S. albus* RC2 showed no inhibitory activity against *R. solani* in our preliminary screening. This observation supports the view that the antifungal potential of *Streptomyces* spp. depends on both the strain and the target phytopathogen.[17] Collectively, these results indicate that VCCM 22715 is a promising candidate for improving plant growth and controlling disease as a biocontrol agent. However, comprehensive structural elucidation of secondary metabolites produced by VCCM 22715 is required for further studies.

IAA production and effects of VCCM 22715 inoculation on *P. vietnamensis* growth parameters

As IAA regulates diverse plant physiological processes,[20] we evaluated IAA production by VCCM 22715. In the presence of 100 µg/mL tryptophan, VCCM 22715 produced 24.3 ± 2.5 µg/mL IAA after 3 days at 30 °C (Figure 3A). Multiple *Streptomyces* spp., including *S. violaceus*, *S. albidoflavus*, *S. scabies*, *S. coelicolor*, *S. albus*, and *S. lividans*, secrete IAA, with yields varying by medium composition and tryptophan supplementation.[20] Notably, *S. albidoflavus* St-220 produces 30.4 µg/mL IAA in Gause medium containing 500 µg/mL tryptophan, which is higher than that reported for *S. albus* RC2.[9] Together, these findings support the role of tryptophan as an IAA precursor and suggest that VCCM 22715 likely synthesizes IAA via a tryptophan-dependent pathway.

In pot experiments, VCCM 22715 treatment significantly enhanced growth relative to the control (Figure 3B). Plant height and root length increased by 17.3% and 33.5%, respectively ($p < 0.05$) (Figure 3C). Fresh weight and dry weight increased by 34.6% and 30.3%, respectively, in the treated group compared with the control (Figure 3D). These results indicate that VCCM 22715 strongly stimulates root elongation and development, likely through direct or indirect effects of IAA. Consistent with our findings, *S. albidoflavus* St-220 increases root fresh weight, total fresh weight, total dry weight, and root dry weight in *Salvia miltiorrhiza*.[9] Similarly, *S. fradiae* NKZ-259 increases multiple growth parameters in tomato plants under greenhouse conditions.[8]

Wild-simulated cultivation of *P. vietnamensis* typically requires at least 6 years to reach harvest maturity.[21] Extended growth cycles, disease-related replanting, and labor-intensive practices further complicate cultivation. Growth promotion of *Panax ginseng* by bacterial strains such as *Bacillus velezensis* and *Arthrobacter nicotinovorans* has been reported recently.[12,22] *B. velezensis* NT35 promotes ginseng seed

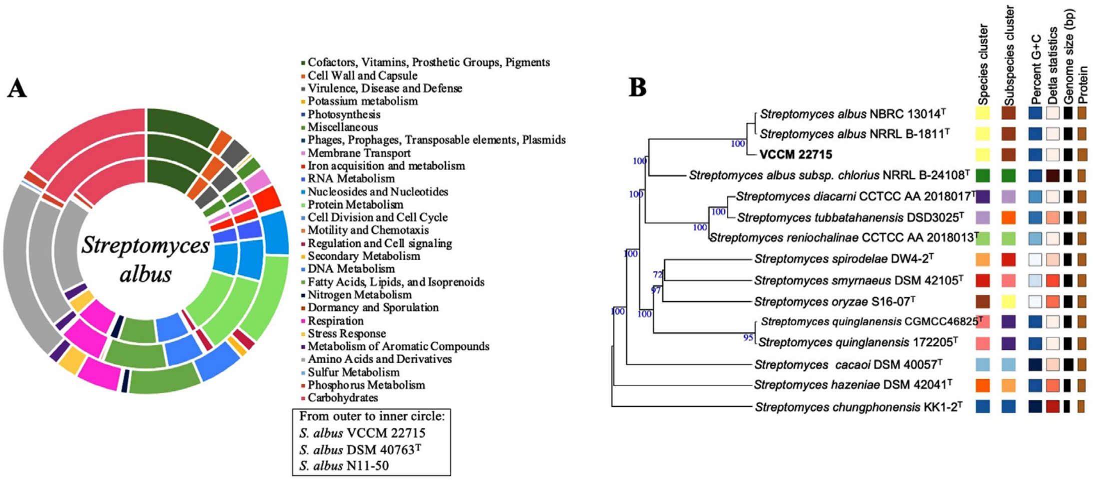

Figure 4. (A) RAST annotations of *S. albus* genomes and (B) Phylogenomic tree constructed for VCCM 22715 and the type strains of Streptomyces data set on TYGS. Tree inferred with FastME 2.1.6.1 from GBDP distances calculated from genome sequences.

germination and controls ginseng rusty root rot under *in vivo* conditions.[12] Treatment with *A. nicotinovorans* JI39 increases plant height, length, and weight of *P. ginseng* after 150 days in the field.[22] To our knowledge, this is the first study demonstrating growth-promoting potential of *Streptomyces* spp. in *P. vietnamensis*, supporting its potential utility for sustainable ginseng cultivation. Nevertheless, the basis for developing VCCM 22715 as an effective biocontrol agent remains unresolved and warrants further investigation.

Genome features of *S. albus* VCCM 22715

To better understand the mechanisms underlying biocontrol and plant growth promotion, the genome of VCCM 22715 was sequenced using the Illumina platform. Sequencing generated 3,392,043 reads and 511,502,970 bases, with an N50 length of 279,269 bp. The draft genome comprised an 8.0 Mb linear chromosome with 85X coverage and 73.0% GC content and was predicted to contain 6,796 coding sequences (CDSs), 17S rRNA genes, 65 tRNA genes, and 3 ncRNA genes (Table 1). The estimated genome completeness was 98.22%. The chromosome sequence of VCCM 22715 was deposited in GenBank under accession number JBPQDV010000000. The genomic characteristics of VCCM 22715 were similar to those of *S. albus* DSM 40763^T and *S. albus* N11-50.

Genome annotation using RAST indicated subsystem and non-subsystem coverage of 18% and 82%, respectively. The top three subsystem categories were Amino Acids and Derivatives (330 genes), Carbohydrate Metabolism (266 genes), and Protein Metabolism (266 genes). Additional categories included Cofactors, Vitamins, Prosthetic Groups, and Pigments (189 genes) and Fatty Acids, Lipids, and Isoprenoids (133 genes). Compared with *S. albus* DSM 40763^T, VCCM 22715 contained higher numbers of genes associated with Cell Wall and Capsule, Phages/Prophages/Transposable Elements/Plasmids, Membrane Transport, and Metabolism of Aromatic Compounds (Figure 4A). These features may contribute to energy conversion efficiency and improved adaptation to the host plant.

Consistent with 16S rRNA based identification, phylogenomic analysis using TYGS showed that *S. albus* VCCM 22715 is closely related to *S. albus* NRRL B-1811^T and *S. albus* NBRC 13014^T, with gene-content formula d4 values of 89.2% and 89.3%, respectively (Figure 4B). These results support assignment of the studied strain to *S. albus*.

Secondary metabolite biosynthetic gene clusters in *S. albus* VCCM 22715

AntiSMASH analysis identified 34 putative BGCs on the VCCM 22715 chromosome, of which 16 showed >21% similarity to known clusters. These included three nonribosomal peptide synthetase (NRPS) clusters, two type I polyketide synthase (T1PKS) clusters, two siderophore clusters, two lanthipeptide clusters, two terpene clusters, and five clusters associated with other secondary metabolites (Table 2). Five BGCs showed >96% similarity to clusters for tambjamine BE-18591, legonoxamine A, ectoine, A-factor, and geosmin. In contrast, the remaining 11 BGCs showed 21%-81% similarity, suggesting potential for production of novel metabolites by *S. albus* VCCM 22715.

With respect to bioactivity, four BGCs were associated with the biosynthesis of compounds reported to have anticancer activity, including tambjamine BE-18591, legonoxamine A, xantholipin, and griseobactin. BGCs linked to pseudouridimycin, hopene, kinamycin, dudomycin A, and griseochelin were associated with antibacterial activity. Notably, only two BGCs, tambjamine BE-18591 and ibomycin, were linked to antifungal activity in *S. albus* VCCM 22715. However, the ibomycin BGC can be silent under standard conditions; for example, co-cultivation of *Streptomyces* sp. WAC2288 with *Cryptococcus neoformans* induces expression of genes involved in ibomycin biosynthesis.[23] Tambjamine produced by *Pseudoalteromonas tunicata* exhibits antifungal activity against *Candida albicans* and *Malassezia furfur*.[24] Microbial co-culture can activate silent BGCs in *Streptomyces* strains by inducing defensive and nutritional metabolite production, thereby promoting synthesis of antifungal compounds.[25]

Accordingly, exposure to phytopathogenic fungi may induce VCCM 22715 to express known or previously uncharacterized antifungal BGCs, which warrants further study.

Identification of genes associated with IAA biosynthesis

To support the observed IAA production, we mined the VCCM 22715 genome for genes involved in IAA biosynthesis. Genes encoding tryptophan monooxygenase IaaM (*orf_1879*) and indole-3-acetamide hydrolase IaaH (*orf_1880*) were identified, consistent with an indole-3-acetamide pathway. In contrast, genes required for the indole-3-acetaldoxime/indole-3-acetonitrile pathway and the indole-3-pyruvate pathway were not detected. In *Streptomyces* sp. AgN23, the complete biosynthetic routes for multiple pathways leading to IAA production have been reported.[7] In pathogenic *Streptomyces* spp. that cause scab disease, the gene encoding IaaM, which is required for IAA biosynthesis, is absent.[26] Collectively, these results suggest that *S. albus* VCCM 22715 produces IAA primarily via a single pathway.

CONCLUSION

In the present study, the bacterial strain exhibiting the strongest antifungal activity against *R. solani* was identified as *S. albus* VCCM 22715. The ethyl acetate extract of VCCM 22715 showed broad-spectrum antifungal activity against *M. oryzae*, *F. solani*, and *R. solani*. Pot experiments further demonstrated that *S. albus* VCCM 22715 significantly enhanced the growth of *P. vietnamensis*, consistent with the IAA concentration measured in the cell-free supernatant. Genome analysis indicated that VCCM 22715 has substantial potential to produce antifungal metabolites and IAA. Collectively, these findings support the use of this strain as a bioinoculant for sustainable agriculture and plant nutrient management. Future studies should evaluate its biocontrol efficacy and elucidate the underlying mechanisms under pot and field conditions.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTION

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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DATA AVAILABILITY

All datasets generated or analyzed during this study are included in the manuscript.

ETHICS STATEMENT

This article does not contain any studies on human participants or animals performed by any of the authors.

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