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The Potential of Cellulolytic Bacteria to Control Heart Rot Disease (*Phytophthora nicotianae*) on Pineapple

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ABSTRACT

Pineapple (*Ananas comosus*) is a high-value horticultural commodity whose productivity is frequently reduced by heart rot disease caused by the soil-borne pathogen *Phytophthora* sp., which can lead to severe infections and yield losses of up to 100%. Cellulolytic bacteria, known for producing hydrolytic enzymes, volatile compounds, and antimicrobial metabolites, are promising biological control agents. This study aimed to isolate and evaluate cellulolytic bacteria from the rhizosphere of Bromeliaceae plants with the potential to inhibit *Phytophthora* sp. Research activities included rhizobacterial isolation, pathogen identification, cellulolytic screening, biosafety assessment, antagonistic assays (in vitro and semi-in vivo), and molecular characterization of promising isolates. Molecular identification of the pathogen using ITS1/ITS4 primers confirmed its close similarity to the *Phytophthora nicotianae* strain BG4K3b. Nineteen cellulolytic were obtained, exhibiting diverse cellulolytic indices. Dual culture assays identified A45 (47.11%) and FTA22 (40.99%) as the most effective isolates, whereas volatile compound assays revealed the highest inhibition by FT57 (55.18%) and K5 (44.98%). Semi-in vivo assays on five isolates selected through the Analytic Hierarchy Process demonstrated that all isolates could inhibit lesion development, with FT57 and A45 showing the highest reductions of 73.74% and 71.81%, respectively. Both isolates also produced indole-3-acetic-acid, solubilized phosphate, and exhibited cellulolytic index of 1.83 and 1.18. Molecular identification using 16S rRNA gene amplification (27F/1492R) indicated that FT57 was similar to *Bacillus subtilis* MS7, whereas A45 was similar to *Stenotrophomonas maltophilia* Y042. Overall, the isolates FT57 and A45 exhibited strong potential for development as biological control agents to manage heart rot disease in pineapple.

Keywords: *Bacillus subtilis*, biological control agents, *Stenotrophomonas maltophilia*

INTRODUCTION

Pineapple (*Ananas comosus*, Bromeliaceae) is a major tropical fruit widely cultivated in Indonesia and is valued for its flavor, nutritional content, and dietary fiber, which provides various health benefits (Rikawati *et al.* 2018). In addition to the fruit, pineapple leaves have economic importance as raw materials for paper and textile production. National pineapple production reached 3.157 million tons in 2023 but declined by 13,18% to 2,74 million tons in 2024 (BPS 2025), partly due to diseases caused by pathogenic infections. Heart rot disease, caused by *Phytophthora* sp., is one of the most destructive diseases in pineapple and has been reported to cause severe yield losses of up to 100% (Jasper *et al.* 2019). This soil-borne pathogen can persist for long periods, infecting plants from the vegetative to the generative stages. Early symptoms include water-soaked lesions and soft rot at the base of young leaves, which become easily detached, followed by wilting and plant death (Shen *et al.* 2013). The pathogen spreads through zoospore chemotaxis, electrotaxis, and water or soil movement (Jeon *et al.* 2016). Current disease management relies on good drainage, resistant cultivars, destruction of infected plants, raised bed systems, crop rotation, and chemical fungicides. Although fungicides offer rapid control, their repeated use can drive pathogen resistance, leave harmful residues, and disrupt soil health by reducing soil respiration, microbial biomass, and key enzyme activities (Wang *et al.* 2025). Consequently, eco-friendly alternatives, particularly biological control, are required. Cellulolytic bacteria are promising biocontrol agents because they produce cellulase and other hydrolytic enzymes, as well as antimicrobial compounds, such as siderophores and antibiotics, which collectively inhibit pathogen growth (Ryu *et al.* 2004). Previous studies have shown the efficacy of cellulolytic bacteria, such as *Pseudomonas fluorescens* 4RS1 and *Bacillus subtilis,* in suppressing soil-borne pathogens, including *Phytophthora palmivora* (Suriani and Muis 2016). However, information on cellulolytic bacteria associated with Bromeliaceae plants as biocontrol agents against *Phytophthora* sp. in pineapple remains limited. Therefore, this study aimed to explore and isolate cellulolytic bacteria and evaluate their potential as biological control agents against *Phytophthora* sp.

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METHODS

Place and Time of Research

The study was conducted the Plant Mycology Laboratory, Department of Plant Protection, Faculty of Agriculture, Bogor Agricultural University.

Rejuvenation and Pathogenicity of *Phytophthora* sp.

The isolate of *Phytophthora* sp. was obtained from the culture collection of PT Great Giant Pineapple Laboratory Lampung (PPL1). The isolate was rejuvenated on ISP-2 (International Streptomyces Project No. 2) medium supplemented with ampicillin to prevent contamination. A pathogenicity test was performed using the detached leaf method on pineapple leaves to assess pathogen virulence (Shen *et al*. 2013).

Identification of *Phytophthora* sp.

The pathogen was identified based on its morphological and molecular characteristics. Morphological identification was performed based on macroscopic and microscopic characteristics following the guidelines of Illustrated Genera of Imperfect Fungi by Barnett and Hunter (1972). Molecular identification was performed using universal primers ITS1 (5′-TCCG-TAGG-TGAA-CCT-GCGG-3′) and ITS4 (5′-TCCT-CCGC-TTAT-TGAT-ATGC-3′), as described by Cooke and Duncan (1997).

Isolation of Rhizobacteria from Bromeliaceae Plants

Cellulolytic bacteria were isolated from the rhizosphere of healthy Bromeliaceae plants with no visible pests or disease symptoms. Soil samples were collected using purposive sampling from two sites: Sukamantri Village and the yard area of IPB Dramaga, Bogor, Indonesia. Isolation was carried out using a serial dilution method from 10^{-1} to 10^{-6}. A 50 µL aliquot from the last three dilution levels was spread onto nutrient agar (NA) medium and incubated at room temperature for 48 hours. Distinct, well-separated bacterial colonies exhibiting different morphological characteristics were selected and purified using the quadrant streak method on fresh NA medium plates. The purified isolates were cultured on NA slants and stored as stock cultures for subsequent analyses.

Screening of Bacterial Isolates from Bromeliaceae Plants

Bacterial isolates obtained from Bromeliaceae plants were screened on Carboxymethyl Cellulose (CMC) medium to assess cellulolytic activity. Clear zone formation around the colonies was observed after flooding the medium with 2 mL of 0.1% Congo Red solution, following the method of Shaikh *et al.* (2013). Isolates that displayed clear zones were subsequently subjected to biosafety testing, including a hypersensitivity reaction (HR) assay on tobacco leaves (Schaad *et al.* 2001), and a hemolysis assay on blood agar medium (Manns *et al*. 1994). These tests were conducted to determine the potential pathogenicity of cellulolytic isolates in plants and mammals.

Assessment of the Cellulolytic Potential of Rhizobacterial Isolates

Cellulase Activity Test

Cellulase activity was evaluated as described by Teather and Wood (1982). Clear zones surrounding the bacterial colonies were observed, and the diameters of both colonies and clear zones were measured on the seventh day of incubation using digital calipers. These data were used to calculate the cellulolytic activity index using the following formula:

$$\text{Cellulolyic index} = \frac{\text{Clear zone diameter} - \text{diameter colony}}{\text{diameter colony}}$$

Inhibition Test

The antagonistic ability of the cellulolytic bacteria against *Phytophthora* sp. was assessed using the dual culture method. The radius of the fungal colony in the control plate (R1) and the radius of the fungal growth toward the bacterial colony (R2) were measured. The percentage of inhibition was calculated using the following formula:

$$\text{Relative inhibition} = \frac{\text{R1} - \text{R2}}{\text{R1}} + 100\%$$

Volatile Organic Compound (VOC) Production Test

The ability of cellulolytic bacteria to produce VOCs that inhibit *Phytophthora* sp. without direct contact was assessed. The relative inhibition level was determined by comparing the diameter of the control fungal colony (D1) to that of the treated fungal colony (D2). The percentage of inhibition was calculated as follows:

$$\text{Relative inhibition} = \frac{D1-D2}{D1} + 100\%$$

Characterization of Cellulolytic Bacterial Isolates

The selected isolates were characterized using Gram staining with 3% KOH, an indole-3-acetic acid (IAA) production test, and a phosphate solubilization assay to evaluate additional plant growth-promoting traits.

Analytic Hierarchy Process (AHP)

AHP analysis was performed to select the five most promising cellulolytic isolates for semi-in vivo testing, following the method described by Saaty (2008). The criteria used for AHP evaluation were the cellulolytic index, dual culture inhibition, VOC

inhibition ability, IAA production, and phosphate solubilization.

Semi in-vivo Assay of Cellulolytic Bacterial Potential

Five selected cellulolytic isolates were evaluated for antagonistic activity under semi-in vivo conditions, following a modified method described by Ngo *et al*. (2020). Cellulolytic bacteria and pathogens were suspended. Bacterial cultures were incubated in a shaker for 48 h, while pathogen cultures were incubated under alternating light and dark conditions to induce zoospore formation. Surface-sterilized pineapple leaves were wounded and dipped into the bacterial suspensions for 1 hour, and then air-dried. Leaves were placed in sterile containers and inoculated with a Phytophthora sp. zoospore suspension 24 h after. The experiment used a completely randomized design (CRD) with eight treatments and three replicates: five selected isolates, a fungicide treatment, and positive and negative controls. Disease severity was observed for seven days by measuring the lesion length and width. The lesion inhibition percentage was determined by comparing the lesion length of the control sample (Lc) with the lesion length of the treatment sample (Lt), using the following formula:

$$\text{Lesion inhibiton} = \frac{Lc - Lt}{Lc} x100\%$$

Molecular Identification of Promising Cellulolytic Isolates

The two most promising isolates based on semi-in vivo assays were molecularly identified using PCR amplification of the 16S rRNA gene with primers 27F (5′-AGAG-TTTG-ATCM-TGGC-TCAG-3′) and 1492R (5′-TACG-GYTA-CCTT-GTTA-CGAC-T-3′) (Weisburg *et al.* 1991). Genomic DNA was extracted, and the PCR products were sequenced. The resulting nucleotide sequences were assembled and edited using BioEdit, and sequence similarity was determined using BLAST analysis against the NCBI GenBank database.

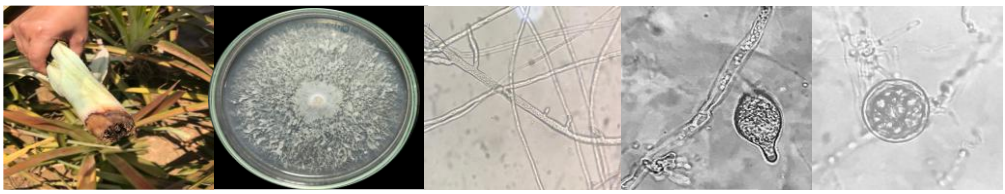
Analysis Data

All observation data were tabulated using Microsoft Excel 2010 and analyzed using analysis of variance (ANOVA) with a 95% confidence level in the RStudio. Treatments that showed significant differences were further analyzed using Tukey's test at a 95% confidence level.

RESULTS AND DISCUSSION

Pathogenic *Phytophthora sp.*

The pathogen, *Phytophthora* sp. (PPL1) was propagated on ISP-2 medium, and the required growth period was 10 days until the surface of the medium was fully colonized. The pathogen exhibits hyaline, non-septate, and filamentous mycelia with smooth texture and wavy colony surface. Concentric ring-like structures were formed in the central region, and the mycelium grew perpendicularly. This pathogen reproduces asexually through sporangia and sexually through oospores (Figure 1). The pathogenicity test confirmed necrotic symptoms in pineapple leaves. Soft rot was clearly visible at the leaf bases, whereas control leaves remained healthy (Figure 2). Infected tissues exhibited wet rot and discoloration, which are characteristic of *Phytophthora* sp. infections (Shen *et al.* 2013). Sequence analysis



(A) (B) (C) (D) (E)

Figure 1 *Phytophthora* sp. pathogen. (A). Disease symptoms on pineapple plants; (B). *Phytophthora* sp. isolate grown on ISP-2 medium; (C). Hyphae of P. nicotianae; (D). Asexual reproduction showing lemon-shaped sporangia; (E). Sexual reproduction showing oval-shaped oospores.

(A) (B)

Figure 2 Results of the pathogenicity test of *P. nicotianae*. (A). Control; (B). Pathogen treatment.

using ITS1 and ITS4 primers, compared with GenBank data, showed that the pathogen isolate had the highest homology with *Phytophthora nicotianae* strain BG4K3b isolated from the rhizosphere of citrus plants in Tunisia, with 100% query coverage and 99,98% identity (Figure 3).

Rhizobacteria from Bromeliaceae Plants

A total of 550 bacterial isolates were obtained from the rhizosphere of Bromeliaceae family plants in Bogor, West Java. Isolates were selected based on their distinct macroscopic morphological characteristics. Each isolate was purified by quadrant streaking to obtain a single colony for further analysis. From the cellulolytic screening, 93 isolates were able to grow on CMC medium containing cellulose as the sole carbon source, and clear zones were observed around the colonies after the application of 0,1% Congo red solution (Figure 4A). The formation of these clear zones occurred due to the interaction of β-1,4-glycosidic bonds with sodium benzidinediazo-bis-1-naphthylamine-4-sulfonate present in the CMC medium (Arifin *et al.* 2019). The hypersensitivity assay indicated that 78 isolates were non-pathogenic to plants, as shown by the absence of necrotic lesions on tobacco leaves following infiltration of the bacterial suspension using a sterile needleless syringe (Figure 4B). Furthermore, hemolysis testing identified 19 isolates as non-pathogenic to mammals, as indicated by the absence of clear or green halos around the bacterial colonies. These biologically safe cellulolytic isolates were selected as potential biological control agents (Figure 4D).

Potential and Characteristics of Cellulolytic Bacteria from Bromeliaceae Plants

The ability of the bacterial isolates to hydrolyze cellulose was assessed based on their cellulolytic activity index. Cellulolytic isolates that passed the biosafety evaluation were further examined for their cellulolytic potential. Each isolate exhibited a distinct cellulolytic activity index (Table 1). Among the 19 isolates, A45, FT23, and FK14C showed the highest activity, with values of 1.83, 1.62, and 1.60, respectively. According to Choi *et al.* (2005), a high cellulolytic index was defined as a value ≥ 2. The index obtained from the Bromeliaceae rhizosphere bacteria in this study were relatively low compared with the findings of Puspawati *et al.* (2018), who reported a cellulolytic index of 7.3 for isolate B6 obtained from organic waste in Denpasar, Bali. This difference may be attributed to the greater abundance of cellulose-rich substrates in environments dominated by decomposing organic matter such as agricultural residues and livestock waste. The antagonistic potential of the selected cellulolytic bacteria against *P. nicotianae* was evaluated using the dual-culture method, resulting in varying levels of inhibition. The highest inhibition was recorded for isolate A45, which suppressed pathogen growth by 47.11%, whereas the lowest inhibition was observed for isolate K30 (2.13%) (Table 2). The inhibition of *P. nicotianae* growth is likely due to antimicrobial compound production, as indicated by shortened mycelia, the presence of a clear inhibition zone between the pathogen and bacterial colony, and deformation of hyphal structures, including cell lysis

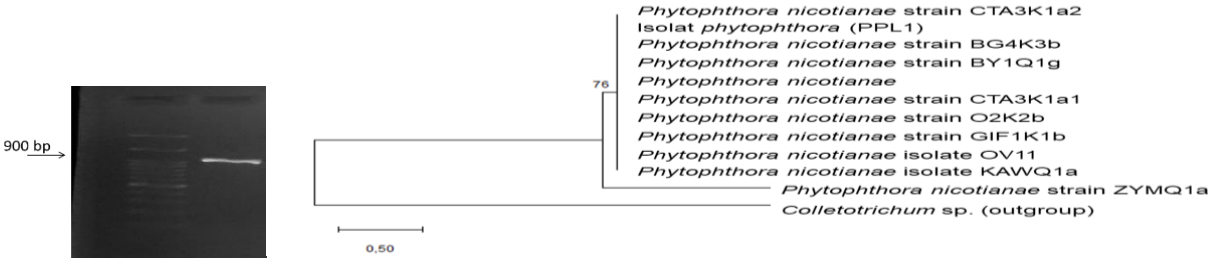


Figure 3 Gene visualization and phylogenetic tree of the *P. nicotianae* isolate amplified with universal primers ITS1 and ITS4.

(A) (B) (C) (D) (E)

Figure 4 Results of cellulolytic bacterial screening. A. Cellulolytic activity test on CMC medium indicated by a clear zone; B. Hypersensitivity test (control); C. Hypersensitivity test (treatment); D. Positive hemolysis test; E. Negative hemolysis test.

Table 1 Cellulolytic bacterial potential based on cellulolytic activity index, dual culture assay, and VOC assay

Isolate	Cellulolytic activity index	Percentage inhibition	
		Dual culture (%)	VOC (%)
A45	1.83^{a}	47.11 ± 2.32^{a}	33.61 ± 1.03^{cde}
FT23	1.62^{ab}	39.57 ± 0.33^{ab}	31.83 ± 0.04^{cde}
FK14C	1.60^{ab}	25.37 ± 0.37^{def}	36.28 ± 0.21^{bcd}
FT31	1.25^{abc}	31.03 ± 0.22^{bcd}	30.52 ± 0.17^{cde}
K67	1.19^{abcd}	15.67 ± 3.08^{fgh}	28.62 ± 0.29^{cde}
FT57	1.18^{abcd}	35.89 ± 4.64^{bcd}	55.18 ± 0.39^{a}
FTA 29	0.89^{bcde}	4.30 ± 0.50^{ij}	29.11 ± 1.45^{cde}
FTA22	0.75^{cdef}	40.99 ± 0.11^{ab}	32.02 ± 4.46^{cde}
AB 21	0.52^{def}	10.63 ± 0.12^{hij}	25.34 ± 0.34^{e}
K30	0.44^{ef}	2.13 ± 0.37^{j}	31.81 ± 0.02^{cde}
K5	0.42^{ef}	3.72 ± 2.62^{ij}	44.98 ± 3.76^{b}
FTA 20	0.38^{ef}	4.96 ± 4.12^{hij}	37.29 ± 2.31^{bc}
FK9C	0.34^{f}	15.27 ± 0.93^{fgh}	29.64 ± 0.34^{cde}
FTC 8	0.32^{f}	15.27 ± 0.00^{efg}	30.41 ± 2.17^{cde}
AB 3	0.18^{f}	27.30 ± 166^{cde}	25.96 ± 0.96^{e}
EM21	0.16^{f}	14.17 ± 0.07^{ghi}	36.43 ± 0.21^{bcd}
FTC2	0.12^{f}	37.09 ± 0.02^{bc}	27.71 ± 0.06^{de}
EM19	0.09^{f}	24.48 ± 0.53^{efg}	34.07 ± 0.11^{cde}
K29	0.09^{f}	14.14 ± 1.76^{ghi}	25.91 ± 0.33^{e}

Note: Values within the same column followed by the same letter are not significantly different according to Tukey's test at α = 5%.

Table 2 Characterization of cellulolytic bacteria isolated from plants of the Bromeliaceae family using KOH, IAA hormone production, and phosphate-solubilization tests

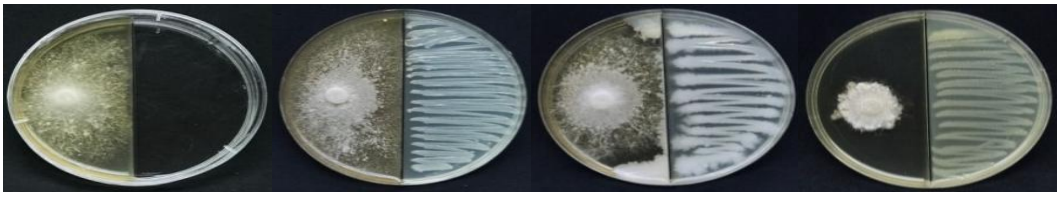
Isolate code	KOH	IAA^{a}	Phosphate S^{b}
A45	-	+	2.08 ± 0.03^{f}
FT23	-	++	4.46 ± 0.28^{bc}
FK14C	-	+++	0.00 ± 0.00
FT31	+	+	2.47 ± 0.05^{ef}
K 67	-	+++	4.30 ± 0.09^{bc}
FT 57	+	++	2.38 ± 0.16^{ef}
FTA 29	+	+++	2.80 ± 0.22^{def}
FTA 22	+	+++	2.46 ± 0.03^{ef}
AB 2.1	-	+	4.58 ± 0.50^{bc}
K 30	-	++	3.37 ± 0.23^{cdef}
K5	-	+	3.68 ± 0.54^{cde}
FTA 20	-	+++	2.50 ± 0.07^{ef}
FK 9C	-	-	0.00 ± 0.00
FTC 8	-	+++	3.35 ± 0.07^{cdef}
AB 3	-	+++	5.70 ± 0.49^{ab}
EM 21	+	++	4.12 ± 0.29^{cd}
FTC 2	-	+++	4.50 ± 0.46^{bc}
EM 19	+	++	6.55 ± 1.25^{a}
K 29	+	+	5.61 ± 0.10^{ab}

Note: a (–) no color; (+) pale pink; (++) light orange; (+++) deep orange; b Values within the same column followed by the same letter are not significantly different according to Tukey's test at α = 5%.

and tapered hyphal tips (Figure 5). Raaijmakers *et al.* (2010) reported that members of the genus *Bacillus* exhibit antibiosis mechanisms that contribute to pathogen suppression. The cellulolytic isolates also demonstrated the ability to produce volatile compounds capable of inhibiting *P. nicotianae*, with the highest inhibition percentage reaching 55.18% (Table 1). The reduced diameter of pathogen hyphal growth in the treatments compared to the control confirmed the suppressive effect of bacterial volatiles. Growth inhibition was associated with disrupted metabolic activity, resulting in shrunken hyphae and curled hyphal tips (Figure 6). Gram staining revealed that the cellulolytic isolates consisted of seven gram-positive and the remaining gram-negative bacteria (Table 2). All isolates tested positive for qualitative IAA production, as indicated by color changes in the reaction mixture, with the strongest responses observed for isolates K67, FTA29, FTA22, FTA20, FTC8, AB3, and FTC2 (Table 2). Additionally, the phosphate-solubilizing assay showed that 17 isolates could solubilize phosphate, as evidenced by clear zones surrounding the colonies, whereas two isolates did not exhibit solubilization. Rodriguez and Fraga

(A) (B) (C) (D)

Figure 5 Dual culture assay of cellulolytic bacteria showing varying levels of inhibition against *P. nicotianae,* from low to high. (A). Control; B. Isolate K67; C. Isolate FT23; D. Isolate A45.



(A) (B) (C) (D)

Figure 6 VOC assay of cellulolytic bacteria against P. nicotianae, showing inhibition levels from relatively low to relatively high. (A). Control; (B). Isolate AB21; (C). Isolate A45; (D). Isolate FT57.

(1999) reported that *Bacillus* and *Pseudomonas* species are among the dominant groups known to produce IAA and solubilize phosphates.

Selection of the Best Cellulolytic Bacterial Isolates as Biological Control Agents

Based on the Analytical Hierarchy Process (AHP), five isolates, FT23, FT31, AB3, FT57, and A45, were identified as the most promising cellulolytic bacteria. The ranking was performed by multiplying the eigenvector values of the criteria and sub-criteria, resulting in final AHP scores of 0.24, 0.23, 0.20, 0.19, and 0.19, respectively.

Potential of Cellulolytic Bacteria in Inhibiting *P. nicotianae* on Pineapple Leaves

Semi-in vivo assays demonstrated that all cellulolytic bacterial treatments, along with the metalaxyl-based fungicide, effectively reduced heart rot symptoms in pineapple leaves compared with the untreated control. Isolates FT57 and A45 exhibited the highest symptom inhibition, with percentages of 73.74% and 71.81%, respectively, and were significantly more effective than the other isolates tested (Table 3).

Characteristics and Identity of Potential Cellulolytic Bacteria

Based on lesion inhibition levels, isolates FT57 and A45 were identified as the most effective c ellulolytic bacteria capable of suppressing *P. nicotianae* symptom development. The KOH Gram test showed that isolate FT57 is Gram-positive, whereas isolate A45 is Gram-negative. Sequence alignment of the 16S rRNA gene with GenBank data revealed that isolate FT57 shared 91.96% similarity with *Bacillus subtilis* MS7 from Mexico, whereas isolate A45 showed 97.94% similarity to *Stenotrophomonas maltophilia* strain Y042 from Sri Lanka. The phylogenetic relationships among these isolates are illustrated in the constructed phylogenetic tree (Figure 7). As shown in the phylogeny, isolates A45 and FT57 belong to two distinct genera, indicating substantial taxonomic diversity among the tested cellulolytic bacterial isolates.

Members of the *Bacillus* group are commonly found in the rhizosphere and are recognized as Plant Growth Promoting Bacteria (PGPB). They possess multiple plant beneficial traits, including the ability to produce phytohormones such as indole-3-acetic acid (IAA), gibberellic acid, cytokinins, and ethylene; synthesize siderophores; fix atmospheric nitrogen; produce antibacterial compounds; suppress plant pathogens; and solubilize phosphate (Hashem *et al*. 2019). Similarly, Tang *et al.* (2020) reported that cellulolytic *Stenotrophomonas* species, categorized as Plant Growth-Promoting Rhizobacteria (PGPR), can produce IAA and solubilize phosphate, further supporting the potential of isolate A45 as a biological control agent.

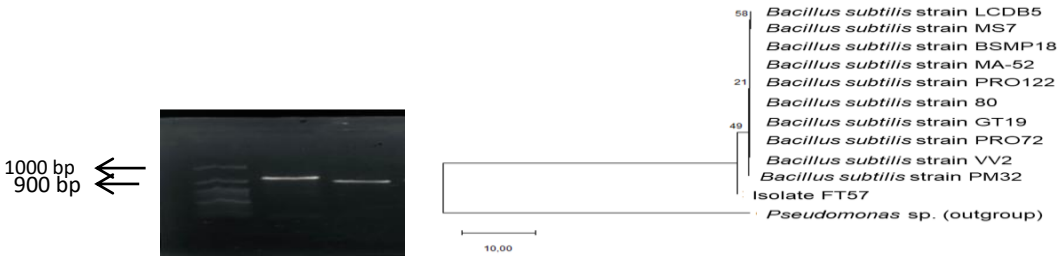
CONCLUSION

Cellulolytic bacteria isolated from the rhizosphere of Bromeliaceae plants showed strong potential to suppress *P. nicotianae*, with isolates FT57 and A45 exhibiting the highest inhibition in semi–in vivo assays. Molecular analysis identified isolate FT57 as closely related to *Bacillus subtilis* strain MS7 and isolate A45 as closely related to *Stenotrophomonas maltophilia* strain Y042. Both isolates produced IAA

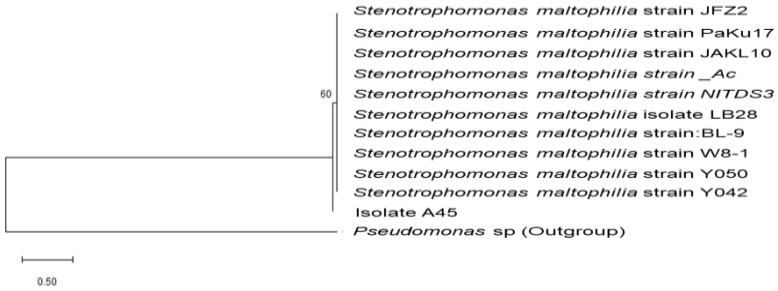
Table 3 Potential of cellulolytic bacteria as biological control agents under semi–in vivo conditions

Isolate	Percentage of Inhibition %
FT57	73.74 ± 4.37[a]
A45	71.81 ± 2.03[ab]
AB3	67.14 ± 0.33[abc]
FT31	64.32 ± 1.98[bc]
FT23	62.01 ± 2.26[c]
Metalaxyl	68.50 ± 1.66[abc]
*Kontrol (+)	0.00 ± 0.00[d]
**Kontrol (-)	0.00 ± 0.00[d]

Note: Values within the same column followed by the same letter are not significantly different according to the HSD test at α = 5%, (*) only *P. nicotianae*, (**) without *P. nicotianae*.



a) A dendrogram of isolate FT57 and reference isolates retrieved from GenBank was constructed using MEGA XII with 1,000 bootstrap replicates.



b) A dendrogram of isolate A45 and reference isolates retrieved from GenBank was constructed using MEGA XII with 1,000 bootstrap replicates.

Figure 7 Gene visualization and phylogenetic tree based on 16S rRNA amplified with primers 27F and 1492R for cellulolytic bacterial isolates FT57 (a) and A45 (b).

and solubilized phosphate, indicating their dual potential as biocontrol agents and plant growth-promoting rhizobacteria.

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