BIODIVERSITAS
Volume 27, Number 1, January 2026
Pages: 12

ISSN: 1412-033X
E-ISSN: 2085-4722
https://doi.org/10.13057/biodiv/d270109

Cellulolytic bacteria as biocontrol agents of chili basal stem rot disease caused by *Phytophthora capsici*

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Manuscript received: 2 July 2025. Revision accepted: 15 January 2026.

Abstract. *Dwinugroho FF, Giyanto, Tondok ET, Nawangsih AA. 2026. Cellulolytic bacteria as biocontrol agents of chili basal stem rot disease caused by* Phytophthora capsici. *Biodiversitas 27 (1): d270109. https://doi.org/10.13057/biodiv/d270109. Phytophthora capsici* is a major pathogen that causes severe yield losses in chili cultivation. Its cellulose-rich cell wall presents an opportunity for biocontrol using cellulolytic bacteria capable of degrading cellulose. This study aimed to isolate cellulolytic bacteria with antagonistic activity against *P. capsici* and to evaluate their effectiveness in managing basal stem rot in chili. A total of 279 bacterial isolates were collected from diverse natural sources, of which 72 exhibited cellulolytic activity, with cellulolytic indices ranging from 0.22 to 10.42. Pathogenicity screening through hypersensitivity and hemolysis assays identified 26 non-pathogenic isolates. These isolates inhibited *P. capsici* growth by 8.15 to 79.81%. Selection of promising isolates was conducted using the Analytical Hierarchy Process (AHP), which considered both inhibition rate and plant growth-promoting traits (volatile organic compound [VOC] production, phosphate solubilization, nitrogen fixation, indole-3-acetic acid [IAA] production, and siderophore production). Based on this evaluation, five isolates were selected: S55, S61, K15, S80, and FS28, with inhibition rates of 79.81, 69.26, 57.78, 46.85, and 40.37%, respectively. In vivo greenhouse assays showed that S55 and K15 provided the highest plant survival rates (86.67 and 75.56%, respectively), compared to 50% in the control. Molecular identification revealed that S55 and S61 were closely related to *Pseudomonas aeruginosa*, K15 to *Proteus penneri*, FS28 to *Bacillus altitudinis*, and S80 to *Brevundimonas* sp. These findings demonstrate the potential of cellulolytic bacteria as biocontrol agents against *P. capsici*, while also highlighting the functional diversity of isolates with plant growth-promoting traits. This diversity expands the pool of candidates for sustainable and targeted disease management strategies in chili cultivation.

Keywords: *Brevundimonas* sp., cellulolytic index, growth inhibition, Oomycota, *Proteus penneri*

INTRODUCTION

The genus *Phytophthora* is a group of plant pathogens that cause significant damage and have a considerable economic impact on important crops worldwide. This genus was initially classified under the family Pythiaceae in the phylum Oomycota, but recent analyses using large subunit (LSU) or small subunit (SSU) rDNA sequences have shown that *Phytophthora* is more closely related to downy mildew and white rust in the family Peronosporaceae (Jayawardena et al. 2020). The phylum Oomycota is biologically distinct from the main fungal group within the kingdom Fungi. Their cell walls are primarily made of cellulose, as opposed to chitin found in fungi, and they are unable to synthesize β-hydroxysterols, which are essential for the production of hormones regulating sexual reproduction in fungi (Hyde 2020). *Phytophthora* attacks plants by killing tissues, causing necrosis in leaves, stems, collar, and roots. Differences between species can lead to varied symptoms, even multiple symptoms in a single host (Jayawardena et al. 2020).

Phytophthora capsici Leonian is a highly destructive plant pathogen from the phylum Oomycota that causes significant yield losses in chili plants worldwide. This wind-spread pathogen infects all parts of the plant, including roots, stems, leaves, and fruits, leading to a range of symptoms such as stunted growth, sudden wilt, and dark lesions on the stem near the soil surface. These lesions spread along the stem, ultimately causing the plant to wilt and die (Majid et al. 2016; Irabor and Mmbaga 2017; Wan and Liew 2020). The disease has become one of the most severe threats to chili production, affecting both the vegetative and reproductive stages of growth.

Phytophthora species are characterized by the presence of cellulose-based cell walls, a key feature that distinguishes them from true fungi, which typically contain chitin in their cell walls (Hyde 2020). This characteristic makes *P. capsici* an ideal target for biological control strategies involving cellulolytic bacteria. These bacteria produce cellulase enzymes—Endo-β-1,4-glucanase, Exo-β-1,4-glucanase, and β-glucosidase—that break down cellulose into glucose, which can then be utilized by the microorganisms for energy and carbon (Behera et al. 2017; Faizah et al. 2020). The ability to degrade cellulose in the pathogen's cell wall not only limits the growth and survival of *P. capsici* but also weakens its structural integrity, thereby increasing the antagonistic potential of cellulolytic bacteria in biological control applications.

Biological control is considered a promising alternative for managing plant diseases, particularly as an environmentally friendly substitute for chemical pesticides. Over the past few decades, various microbial biological control agents (BCAs) have been developed to control fungal pathogens. Among the most extensively studied bacterial genera with biocontrol potential are *Streptomyces*, *Pseudomonas*, and *Bacillus* (Bonaterra et al. 2022), along with *Azospirillum* (Pedraza 2015), *Azotobacter* (Dey et al. 2017), *Flavobacterium* and *Cytobacillus* (Bashizi et al. 2025), also *Rhizobium*, and *Bradyrhizobium* (Nakei et al. 2024). This study aims to isolate various bacterial strains capable of producing cellulase enzymes and to evaluate their potential as biological control agents against *P. capsici*. The isolates were assessed for their ability to inhibit the growth of *P. capsici* both in vitro and under greenhouse conditions, as a potential environmentally safe alternative to chemical control methods.

MATERIALS AND METHODS

Rejuvenation of *Phytophthora capsici*

The rejuvenation of isolates was carried out by culturing *Phytophthora capsici* isolates on corn meal agar (CMA), potato dextrose agar (PDA), and vegetable-8 agar (V8 agar) media. V8 agar contain: V8 juice 100 mL/L, $CaCO_3$ 10 g/L, glucose 2 g/L, yeast extract 2 g/L and agar 20 g/L. *P. capsici* isolate used in this experiment, *P. capsici* CKM1, is a collection from the Plant Mycology Laboratory, Department of Plant Protection, Institut Pertanian Bogor, Bogor, Indonesia.

Isolation of cellulolytic bacteria

Isolation of cellulolytic bacteria was carried out from various samples with high cellulose content. The samples and isolate code consisted of organic waste (S), termite intestines (R), rotten wood (K), soil (T), also feces from cow (FS), goat (FKa), and horse (FKu). Isolation was performed using the serial dilution and quadrant streak methods on nutrient agar (NA) medium. Selection of cellulolytic bacteria is carried out by spotting bacterial colonies from the isolation into 1% carboxymethylcellulose (CMC) agar medium with a toothpick. The CMC medium contain: $(NH_4)_2SO_4$ 1 g/L, $MgSO_4 \cdot 7H_2O$ 1 g/L, MnSO4 1 g/L, yeast extract 1 g/L, agar 30 g/L and carboxymethylcellulose sodium salt 10 g/L (Ruhimat et al. 2024). Bacteria that show clear zone formation are continued to the next test.

Measurement of cellulolytic index

Cellulolytic index measurements were carried out according to the modified method (Chantarasiri et al. 2015). The clear zone formed around the bacterial colony after being poured by 0,5% (w/v) Congo red indicates cellulolytic activity. Calculation of cellulolytic index (CI) value based on the equation:

$$CI = \frac{(TD - CD)}{CD}$$

Where:
CI : Cellulolytic Index
TD : Total Diameter (colony and clear zone)
CD : Colony Diameter

Potential test as a plant and mammal pathogen of cellulolytic bacteria

The test was conducted using hypersensitivity reaction test and haemolysis test. The hypersensitivity reaction test was conducted by infiltrating 1 mL of cellulolytic bacterial suspension into 24-hour-old Luria Broth (LB) 10^8 cfu/mL media on the underside of tobacco leaves and incubating for 24 hours. The tobacco variety used is the burley variety. Haemolysis test is carried out by inoculating cellulolytic bacterial colonies on blood agar media. Bacteria that are not pathogenic to plants and mammals will be tested further.

Growth inhibition of *Phyotphthora capsici* by cellulolytic bacteria

The growth inhibition of *P. capsici* by cellulolytic bacteria was assessed using the disc diffusion method (Meena et al. 2024). Cellulolytic bacteria were cultured in CMC broth for 48 hours. Circular discs (5 mm in diameter) of Whatman No. 42 filter paper were placed 2 cm inward from the periphery of PDA plates at four equidistant points, with the pathogen inoculum positioned at the center. Each disc was inoculated with 10 µL of bacterial suspension. The plates were incubated for 7 days, after which observations were recorded. The test was performed in triplicate. Mycelial growth inhibition of *P. capsici* was calculated using the following formula:

$$IP = \frac{(D2 - D1)}{D2} X\ 100$$

Where:

IP : Inhibition Percentage (%)
D2 : Diameter of *P. capsici* control (cm)
D1 : Diameter of *P. capsici* in the disc diffusion test (cm)

Physiological characterization of cellulolytic bacterial

The physiological characterization carried out in this study included: nitrogen fixation, phosphate solubilization, indole-3-acetic acid (IAA), siderophore, and volatile organic compound (VOC) production. The methods for nitrogen fixation, phosphate solubilization, and IAA production followed Batista et al. (2021). Siderophore production was assessed according to the procedure described by Prihatiningsih et al. (2017), while VOC production was evaluated based on the method outlined by Ávila-Oviedo et al. (2024). Phosphate and siderophore dissolution tests were measured quantitatively using index values, while IAA, VOC and nitrogen fixation production tests were carried out qualitatively.

Selection of potential isolates using Analytical Hierarchy Process (AHP)

The selection of potential cellulolytic bacterial isolates as biocontrol agents against *P. capsici* was conducted using the Analytic Hierarchy Process (AHP), based on a modified approach by Saaty (2008). AHP provides a systematic framework for evaluating complex decisions by comparing multiple criteria (Table 1).

Table 1. Analytical hierarchy process criteria and weights for bacterial isolate selection

Criteria	Analytical hierarchy process weight
Inhibition zone	9
VOC production	7
Siderophore production	5
Phosphate solubilization	3
Nitrogen fixation	3
IAA production	3

Phytotoxicity test of cellulolytic bacteria on chili seed germination

The test was conducted using the rolled paper method, modified from Ramdan and Risnawati (2018). A suspension of cellulolytic bacteria was prepared at an optical density (OD) of 1.0. Chili seeds were soaked in the bacterial suspension for 12 hours and then air-dried. Thirty chili seeds were placed on each sheet of rice straw paper. Each treatment was replicated six times, with three replications observed on day 7 and the remaining three on day 14. Observation parameters included root length, shoot height, seed germination percentage, and vigor index. The control treatment consisted of seeds soaked in sterile distilled water.

The effectiveness of cellulolytic bacteria in suppressing basal stem rot in chili seedlings

Preparation of cellulolytic bacterial isolates was carried out by inoculating each isolate into LB medium and incubating it on a shaker for 48 hours. Surface-sterilized chili seeds were then soaked in a suspension of cellulolytic bacteria adjusted to an optical density (OD) of 1.0 for 12 hours. The seeds were air-dried for 60 minutes before sowing. The inoculum of *P. capsici* used for stem rot suppression tests consisted of a zoospore suspension prepared following Trinidad-Cruz et al. (2021), with minor modifications. The in vivo experiment was conducted using a randomized block design with three replications and seven treatments: control, fungicide, bacterial isolate 1, bacterial isolate 2, bacterial isolate 3, bacterial isolate 4, and bacterial isolate 5. All treatments were inoculated with *P. capsici* and applied when the seedlings were 18 days old. Each treatment included three seedling trays, each containing 30 chili plants. To evaluate the effect of cellulolytic bacteria on chili growth in the greenhouse, agronomic parameters including shoot height, root length, number of leaves, fresh weight, and dry weight were measured. Measurements were taken 10 days after application, at the end of the in vivo test. Plant survival percentage was calculated using the following formula:

$$\text{Survival (\%)} = \frac{30 - \text{No.of dead plants}}{30} \text{ x } 100$$

Molecular identification of cellulolytic bacteria based on 16S rRNA

Bacterial DNA extraction was performed according to the GeneJET Genomic DNA Purification protocol. The extracted DNA was subjected to PCR using universal 16S rRNA primers 27F (5'-AGAGTTGATCCTGGTCCAG3') and 1492R (5'-CGGTTACCTTGTTACGACTT-3') (Weisburg et al. 1991). The total PCR volume was 50 µL consisting of 25 µL master mix, 4 µL 16S rRNA primers (10 pmol), 2 µL template DNA, and 19 µL NFW. The PCR program used: pre-denaturation at 95°C for 5 minutes, denaturation at 95°C for 30 seconds, annealing at 55°C for 30 seconds, extension at 72°C for 60 seconds for 35 cycles, and a final extension at 72°C for 10 minutes. The PCR product was electrophoresed using 1% agarose gel at 100 V for 30 minutes and visualized using a UV transilluminator. A 30 µL PCR product was sent to the First Base Asia Laboratory for nucleotide sequencing. The nucleotide sequencing results were analyzed using BioEdit and MEGA 11 software and homology analysis using BLAST-N on the NCBI website.

Data analysis

Data obtained from this study were analyzed by One-way analysis of variance (ANOVA) using R Studio and Microsoft Excel. For each treatment, generated data were presented as arithmetic means±S.D. Significantly different means were separated using Tukey Honestly Significant Difference at 5% level of significance.

RESULTS AND DISCUSSION

Bacterial isolate and cellulolytic index

A total of 279 bacterial isolates were obtained from seven environmental sources: organic waste, termite guts, rotten wood, soil, and the feces of goat, cow, and horse. The number of isolates from each source is presented in Figure 1, showing the variation in bacterial abundance across samples. Of these, 72 isolates were identified as cellulolytic based on the formation of clear zones around colonies grown on carboxymethyl cellulose (CMC) agar after staining with 0.5% (w/v) Congo red solution. The presence of a clear zone indicated cellulase activity, reflecting cellulose hydrolysis in the medium. To assess the cellulolytic potential of these isolates, the cellulolytic index (CI) was calculated as the ratio of the clear zone diameter to the colony diameter. The CI values are shown in Figure 2, demonstrating variability in enzymatic activity among the isolates. These findings provide a foundation for exploring the biochemical mechanisms underlying the observed cellulolytic activity.

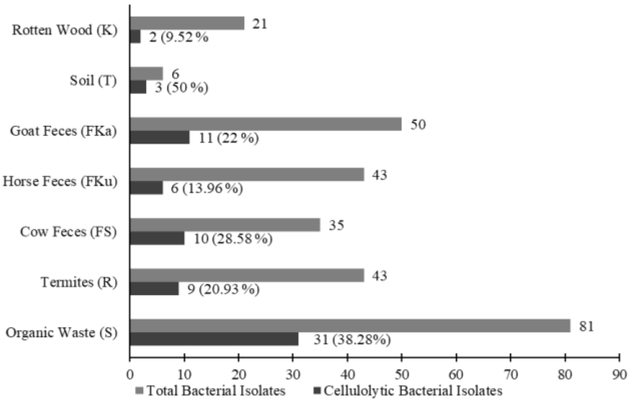

Figure 1. Total bacterial isolates and cellulolytic bacterial isolates

Growth inhibition of *Phytophthora capsici* by non-pathogenic cellulolytic bacteria

The results of the hypersensitivity reaction and hemolysis tests indicated that 36 isolates were non-pathogenic to both plants and mammals. Of these, 26 isolates exhibited growth inhibition against *P. capsici* (Figure 3), with inhibition levels ranging from 8.15 to 79.15% (Figure 4). The strongest inhibition was observed in isolate S55 (79.15%), followed by S61 (69.25%) and S54 (62.22%). These findings suggest that isolates such as S55, S61, and S54 may produce potent antimicrobial compounds, potentially including lytic enzymes. Conversely, isolates showing lower inhibition may either lack effective antagonistic mechanisms or be less competitive under in vitro conditions. The observed variation in inhibition could also be influenced by the nutrient composition of the growth medium, as bacterial growth and secondary metabolite production are strongly affected by culture conditions (Shi et al. 2024).

Physiological characteristic of cellulolytic bacterial isolate

The 26 tested isolates exhibited a variety of physiological characteristics, as shown in Table 2. These isolates demonstrated diverse abilities, including the production of volatile organic compounds (VOCs), phosphate solubilization, nitrogen fixation, indole-3-acetic acid (IAA) production, and siderophore production.

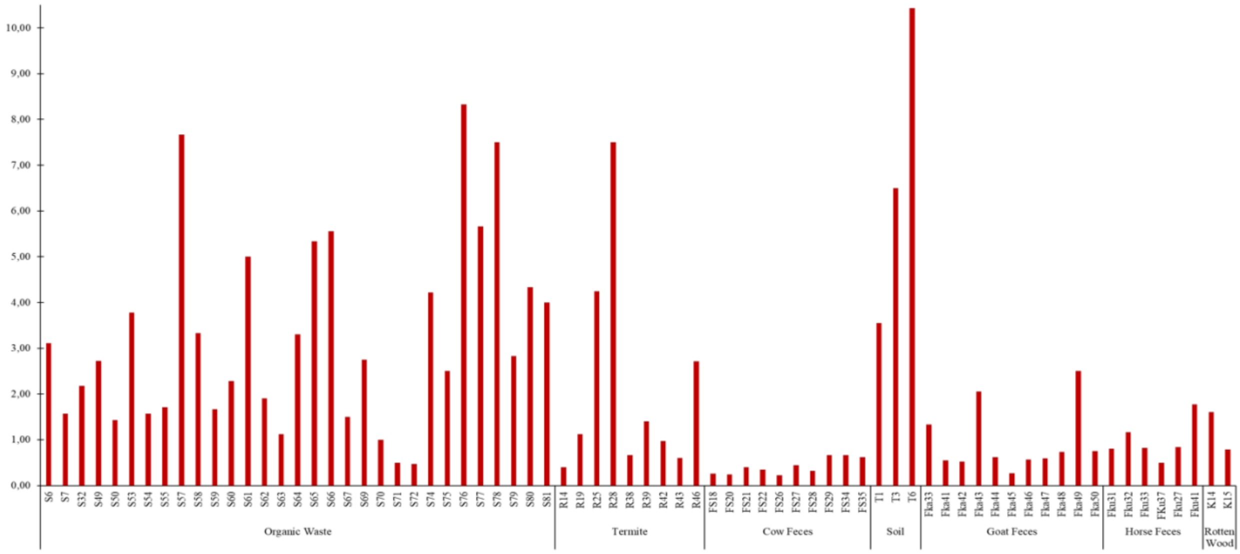

Figure 2. Cellulolytic index of cellulolytic bacteria from various sample

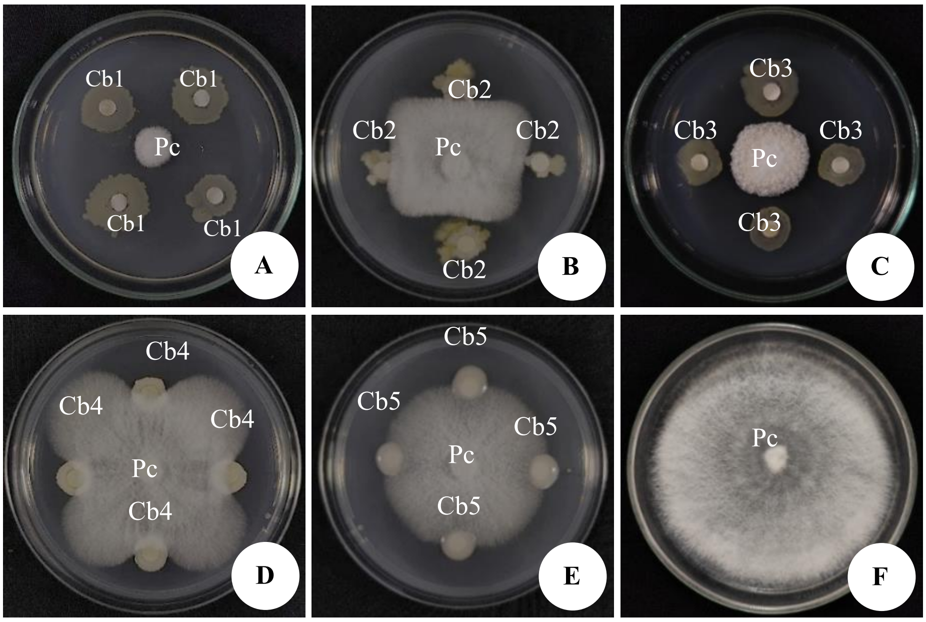

Figure 3. Growth of *Phytophthora capsici* with different cellulolytic bacterial isolates at day 7. Pc: *P. capsici*. A. Cb1: Isolate S55, B. Cb2: Isolate K15, C. Cb3: Isolate S61, D. Cb4: Isolate FS28, E. Cb5: Isolate S80, F. *P. capsici* only

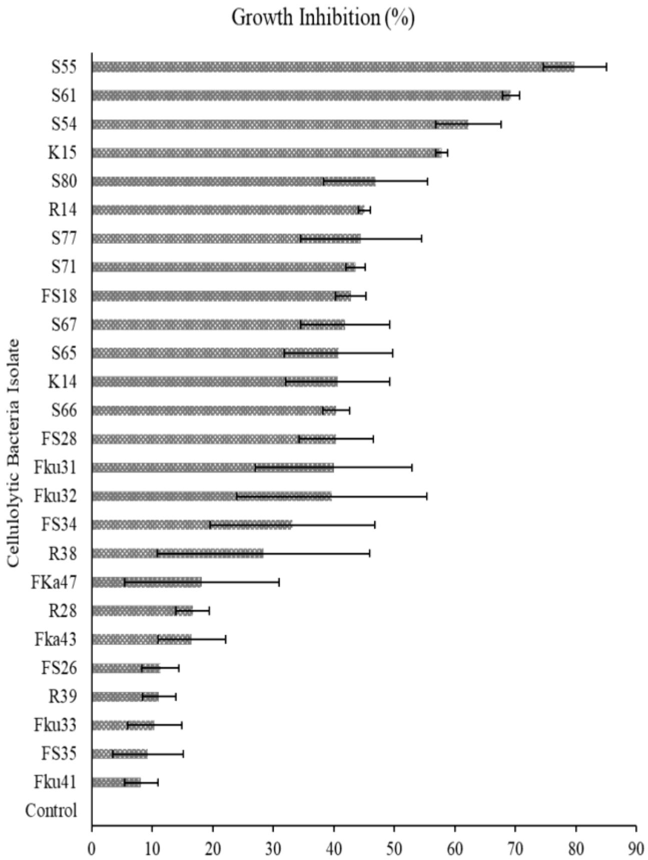

Figure 4. Effect of cellulolytic bacteria on the growth inhibition of *Phytophthora capsici*

Table 2. Physiological characteristic of cellulolytic bacteria

Bacterial isolate	Volatice organic compounds production	Phosphate solubility index	Nitrogen fixation	IAA production	Siderophore production index
S54	-[a]	0.60[b]	+	-	4.27
S55	+	0.42	-	-	3.04
S61	+	0.76	+	-	6.84
S65	-	0.47	+	-	2.18
S66	-	0.91	+	-	0.00
S67	-	1.09	+	-	3.66
S71	-	0.44	+	-	4.53
S77	-	0.00	+	+	0.00
S80	-	0.00	+	+	0.00
R14	-	0.00	-	+	0.00
K14	-	0.00	-	+	0.00
K15	-	1.16	+	+	0.00
R28	-	0.00	+	+	0.00
R38	+	0.00	+	+	0.00
R39	-	0.00	+	+	0.00
FS18	-	1.50	+	-	0.00
FS26	-	0.26	+	+	1.90
FS28	-	3.61	+	+	0.00
FS34	-	1.71	-	-	0.00
FS35	-	0.21	+	-	2.47
Fka43	-	0.23	+	+	0.00
Fka47	-	0.21	+	+	3.34
Fku31	+	0.00	+	-	1.25
Fku32	-	0.85	+	-	5.23
Fku33	-	1.22	+	-	3.24
Fku41	+	1.07	+	-	0.00

Note: [a]Qualitatively measured, (+): positive, (-): negative, [b]Quantitatively measured using index values

Volatile organic compounds production by cellulolytic bacterial isolates

From the results in Table 2, five out of twenty-six tested cellulolytic bacterial isolates produced VOCs. These VOCs can cause abnormalities in the mycelium of *P. capsici*, preventing its normal growth without direct contact. These isolates include S55, R38, FKu41, S61, and FKu31.

Phosphate solubilization by bacterial cellulolytic isolates

The ability of cellulolytic bacterial isolates to solubilize phosphate is shown in Table 2. Among the 26 tested isolates, 18 demonstrated the ability to solubilize phosphate. Phosphate solubilization activity was indicated by the formation of clear zones around the colonies on Pikovskaya medium. Isolate FS28 exhibited the highest phosphate solubilization index, with a value of 3.61.

Nitrogen fixation by bacterial cellulolytic isolates

Twenty-two out of 26 cellulolytic bacteria were able to fix nitrogen (Table 2). Nitrogen-fixing bacteria produced exopolysaccharide (EPS) polymers that form a gel structure, facilitating the formation of a pellicle.

IAA production by cellulolytic bacterial isolates

The ability of cellulolytic bacterial isolates to produce IAA is shown in Table 2. Twelve out of 26 isolates were able to produce IAA, as indicated by the color change in the test medium from clear to pink or deep red.

Siderophore production by cellulolytic bacterial isolates

The ability of cellulolytic bacterial isolates to produce siderophores is shown in Table 2. Twelve isolates were able to produce siderophores, as indicated by the color change in the medium from blue around the colonies to yellow-green.

Phytotoxicity test of cellulolytic bacteria on chilli seedling

Phytotoxicity tests on chili seedlings were conducted using 12 of the 26 bacterial isolates, selected through the Analytical Hierarchy Process (AHP). The evaluation was based on agronomic responses, including shoot height, root length, germination rates on days 7 and 14, and the vigor index (Table 3). The results showed that one isolate exhibited phytotoxic effects, inhibiting seedling growth at both early and later developmental stages. In contrast, several isolates, including S80, FKu31, S65, K15, and FS28, positively influenced multiple parameters. Isolates that negatively affected more than two parameters were classified as potentially phytotoxic to chili seedlings.

Effectiveness of cellulolytic bacteria in suppressing basal stem rot of chili

Cellulolytic bacteria that were previously tested for phytotoxicity were further selected based on morphological differences. The five selected isolates, S55, K15, S61, FS28, and S80, were evaluated for their ability to suppress basal stem rot of chili caused by *P. capsici*. The survival percentage of chili seedlings treated with these isolates and inoculated with *P. capsici* is presented in Table 4, with observations recorded on the 10th day after bacterial application. Agronomic parameters, including shoot height, root length, and germination rate, were also assessed on day 10. The control consisted of chili seedlings inoculated with *P. capsici* but without bacterial treatment. Among the bacterial treatments, isolate S55 showed the highest survival rate, which was significantly greater than the control. In contrast, isolate S80 exhibited the lowest survival rate, also differing significantly from the control. A fungicide treatment was included for comparison to assess the relative effectiveness of cellulolytic bacteria against conventional management practices.

Molecular identification of cellulolytic bacteria based on 16S rRNA gene sequences

The five isolates were identified molecularly based on the 16S rRNA gene sequence and multiple alignment on Genbank. It was found that the isolates were similar to *Pseudomonas aeruginosa* (S55), *Proteus penneri* (K15), *P. aeruginosa* (S61), *Brevundimonas* sp. (S80), and *Bacillus altitudinis* (FS28) (Figure 5).

Discussion

The cellulolytic potential of various bacterial isolates was assessed through this method across a range of samples. The highest number of isolates (31) was obtained from organic waste, which is consistent with the findings of Gautam et al. (2012), who noted that organic waste, due to its high cellulose content, provides an ideal environment for cellulolytic bacteria. Cellulolytic isolates were also recovered from goat, cow, and horse feces, which supports the idea that microbial communities in the digestive tracts of mammals contribute significantly to cellulose breakdown and energy utilization (Froidurot and Julliand 2022). Additionally, nine isolates were obtained from termite samples, further confirming the association between termite gut microbiota and cellulolytic bacteria (Boontanom and Chantarasiri 2021). In contrast, fewer cellulolytic isolates were recovered from soil and rotten wood, with only three isolates obtained from soil and two from rotten wood. This finding contrasts with studies that report abundant cellulolytic bacteria in these environments due to their roles in organic matter decomposition (Shamshitov et al. 2022; Bautista-Cruz et al. 2024). The lower number of isolates from soil may be attributed to the dry conditions of the sampled soil, which could have negatively impacted microbial diversity. Similarly, the reduced number of isolates from rotten wood contradicts earlier studies that identify it as a rich source of cellulolytic bacteria, likely due to its high microbial diversity and cellulose content (Ma et al. 2020).

Table 3. Agronomic parameters at day 7 and day 14 on different bacterial treatments

Treatment	Agronomic parameter at day 7				Agronomic parameter at day 14		
	Shoot height (cm)	**Root length (cm)**	**Germination (%)**	**Vigor index**	**Shoot height (cm)**	**Root length (cm)**	**Germination (%)**
Control	1.48±0.15*^{ab}	4.24±0.17^{a}	83.33±16.67^{a}	479.0±112.4^{a}	2.33±0.40^{cde}	4.75±1.25^{b}	85.56±1.92^{abc}
S55	1.17±0.1^{abc}	2.76±0.3^{bc}	83.33±3.33^{a}	328.67±67^{abc}	2.86±0.16^{bcde}	3.29±0.26^{b}	78.33±7.07^{abc}
S61	1.72±0.3^{a}	2.92±0.46^{b}	56.67±5.7^{ab}	263.10±48.14^{abc}	2.67±0.24^{cde}	4.61±1.26^{b}	98.89±1.92^{a}
S54	0.71±0.47^{bc}	1.47±0.86^{cd}	35.56±1.92^{ab}	79.10±49.37^{bc}	2.54±0.32^{cde}	3.69±0.38^{b}	95.56±3.84^{ab}
K15	1.92±0.05^{a}	3.23±0.33^{ab}	87.78±13.47^{a}	454.13±93.60^{a}	2.22±0.24^{de}	3.90±0.35^{b}	98.89±1.92^{a}
S80	1.41±0.24^{ab}	2.86±0.4^{b}	75.56±13.87^{a}	328.0±104.8^{abc}	3.15±0.13^{abc}	7.83±0.94^{a}	100.00±0^{a}
R14	1.14±0.29^{abc}	2.00±0.45^{bcd}	65.56±11.7^{ab}	209.78±75.08^{abc}	2.87±0.38^{bcde}	4.75±1.60^{b}	88.89±5.09^{ab}
S77	1.37±0.32^{ab}	2.74±0.56^{bc}	71.11±22.19^{a}	302.87±150.73^{abc}	2.61±0.19^{cde}	4.01±0.41^{b}	93.33±9.42^{ab}
S71	1.27±0.06^{ab}	2.60±0.18^{bc}	43.33±30.5^{ab}	166.5±114.09^{abc}	3.00±0.42^{abcd}	5.21±1.0^{b}	75.56±16.77^{bc}
FS18	0.44±0.06^{c}	0.82±0.15^{d}	11.11±5.09^{b}	14.45±7.65^{c}	2.02±0.33^{e}	3.00±0.35^{b}	66.67±11.54^{c}
FS28	1.68±0.15^{a}	3.18±0.17^{ab}	83.33±10^{a}	406.96±74.98^{a}	2.80±0.13^{bcde}	4.64±0.26^{b}	98.89±1.92^{a}
Fku31	1.32±0.18^{ab}	3.02±0.22^{ab}	80.00±12^{a}	349.95±81.72^{ab}	3.64±0.31^{ab}	8.00±0.34^{a}	95.56±3.84^{ab}
S65	1.30±0.58^{ab}	2.87±0.67^{b}	46.67±47.2^{ab}	321.0±254.55^{abc}	3.81±0.24^{a}	8.45±0.73^{a}	97.78±3.84^{a}

Note: *Mean values within a column followed by the same letters are not significantly different at $p<0.05$ according to Tukey Honestly Significant Difference

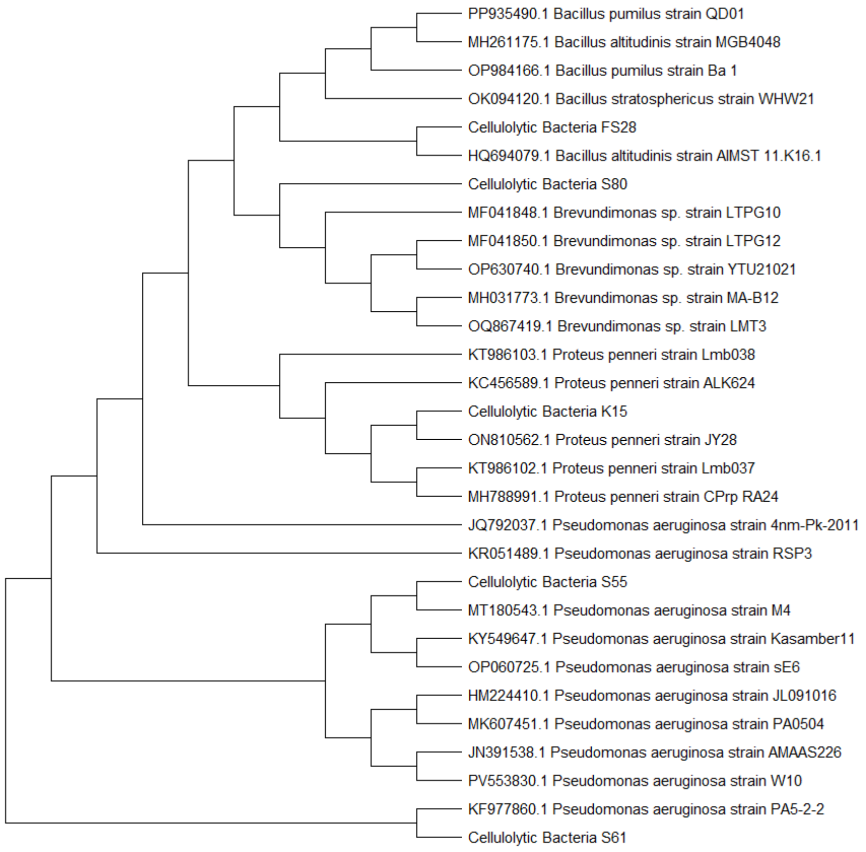

Figure 5. Phylogenetic tree of 5 isolates of cellulolytic bacteria using Neighbor-Joining method with 1000 bootstrap replication

Table 4. Effectiveness of cellulolytic bacteria on plant survival percentage and agronomic parameters of chilli seedling under greenhouse conditions on 10th day after application

Treatment	**Survival (%)**	**Agronomic parameter**				
		Shot height (cm)	**Root length (cm)**	**Number of leaves**	**Wet weight (g)**	**Dry weight (g)**
Control	50±20,81^{abc*}	17.30±0.40^{a}	5.42±0.26^{ab}	8.37±0.47^{a}	12.09±2.10^{a}	0.91±0.16^{a}
Fungicide	61.11±15.75^{abc}	16.50±0.22^{ab}	5.18±0.75^{ab}	7.8±0.20^{ab}	9.42±2.52^{ab}	0.66±0.18^{ab}
S55	86.67±10^{a}	14.98±1.18^{bc}	5.24±0.46^{ab}	7.37±0.11^{b}	8.14±0.39^{ab}	0.33±0.06^{c}
K15	75.56±11.7^{ab}	14.70±0.62^{c}	4.39±0.46^{ab}	8.13±0.35^{ab}	10.07±1.02^{ab}	0.57±0.05^{bc}
S61	46.67±18.55^{abc}	15.23±0.40^{bc}	5.20±0.53^{ab}	7.97±0.50^{ab}	10.06±1.88^{ab}	0.53±0.10^{bc}
FS28	37.78±3.84^{bc}	14.80±0.15^{bc}	5.86±0.66^{a}	7.87±0.11^{ab}	8.38±0.30^{ab}	0.58±0.02^{bc}
S80	31.11±16.77^{c}	14.73±0.49^{bc}	3.86±0.51^{b}	7.37±0.05^{b}	7.09±0.06^{b}	0.47±0.00^{bc}

Note: *Mean values within a column followed by the same letters are not significantly different at $p < 0.05$ according to Tukey Honestly Significant Difference

Bacterial isolates were considered cellulolytic if they produced clear zones after Congo red staining, followed by rinsing with NaCl. Although Congo red staining is a standard method for identifying cellulase-producing microorganisms, it does not always directly correlate with actual enzyme production (Liang et al. 2014). This is because Congo red binds to intact β-D-glucans, creating a stable red complex in the medium. However, when cellulolytic microorganisms produce β-D-glucanase, the carboxymethyl cellulose (CMC) is hydrolyzed into smaller oligosaccharides that bind Congo red less effectively. After rinsing with NaCl, the unbound or weakly bound dye is removed, leaving only the dye bound to the intact CMC (Zulaika et al. 2022).

The interaction between bacteria and fungal pathogens, such as *P. capsici*, involves several mechanisms, including the production of antibiotics, cell-wall-degrading enzymes, nutrient competition, and volatile organic compounds (VOCs). Each of these factors contributes to the bacterial ability to inhibit fungal growth in the controlled conditions of the in vitro test. Antagonistic bacteria can produce antibiotics that directly target and inhibit the growth of *P. capsici* and other competing microorganisms. These antibiotics act as a natural defense mechanism, limiting the spread of the pathogen. Several bacterial species have been identified to produce a range of antibiotics, which play a crucial role in suppressing the growth of *P. capsici*, thereby inhibiting its ability to cause infection and spread (Li et al. 2020).

Additionally, bacteria produce a variety of cell-wall-degrading enzymes that break down the structural components of fungal cell walls, contributing to the inhibition of *P. capsici*. These enzymes, including cellulases, hemicellulases, chitinases, amylases, degrade polysaccharides, and glucanases, in the fungal cell wall (Chater et al. 2010), weakening the pathogen and hindering its growth. In this study, cellulolytic bacterial isolates were grown in CMC broth to induce cellulase production, and a paper disc diffusion test was performed on PDA media inoculated with *P. capsici*. This test aimed to evaluate the cellulase activity of the bacterial isolates. Mulya and Harmen (2003) demonstrated that cellulase enzyme extracts from *Trichoderma harzianum* were capable of hydrolyzing cellulose in the rough preparation of *P. capsici* cell walls. This hydrolysis was indicated by the glucose released, which was measured spectrophotometrically at a wavelength of 575 nm, providing evidence of cellulase activity in the interaction between *P. capsici* and microorganisms.

Beyond producing antibiotics and cell-wall-degrading enzymes, bacteria are also capable of generating volatile organic compounds (VOCs) that play a significant role in inhibiting pathogen growth. These VOCs, including acetoin, L-lactic acid, and 2,3-butanedione, have been shown to exhibit antimicrobial properties, specifically inhibiting the growth of *P. capsici* (Ávila-Oviedo et al. 2024). VOCs are small, low molecular weight compounds released by bacteria into the surrounding environment. These compounds can have a direct toxic effect on fungal pathogens or can alter their growth and behavior by disrupting key cellular processes such as metabolism, spore germination, and hyphal development.

Phosphorus, an essential nutrient for plants, plays a crucial role in nucleic acid synthesis, cell division, new tissue growth, photosynthesis, carbohydrate metabolism, and signaling (Elhaissoufi et al. 2022). While phosphorus is abundant in nature, most of it exists in insoluble forms that cannot be directly absorbed by plants. Phosphate-solubilizing bacteria play a critical role in converting insoluble phosphorus into soluble forms, such as HPO_4^{2-} and $H_2PO_4^-$, which plants can absorb and use effectively (Pan and Cai 2023). Similarly, nitrogen is an essential macronutrient for plant growth. Although nitrogen gas constitutes 78% of the atmosphere, plants cannot directly utilize it. Instead, they absorb nitrogen in the forms of nitrate (NO_3^-) or ammonium (NH_4^+). Biological nitrogen fixation, facilitated by prokaryotes like *Cyanobacteria*, *Rhizobium*, *Azospirillum*, and *Azotobacter*, is a key process in converting atmospheric nitrogen into forms that plants can use (Alomari et al. 2024).

IAA, a natural auxin, plays a pivotal role in regulating cell division and elongation, vascular differentiation, gravitropism, and phototropism in plants (Zhang et al. 2021). While plants can synthesize IAA, microbes can also produce it through both tryptophan-dependent and independent pathways, with L-tryptophan being the most efficient precursor (Lata et al. 2024). Bacteria that produce IAA can accelerate plant growth, enhance lateral root development, and increase root hair density, thereby improving nutrient uptake and plant development. Siderophore production was notably highest in isolate S61 (Table 2). Siderophores are low-molecular-weight compounds that have a high affinity for iron (Fe^{3+}) ($Kf > 10^{30}$). These compounds are crucial for improving the availability of iron in environments where it is limited. Siderophores can bind iron from Fe-binding proteins such as ferritin, transferrin, and lactoferrin, facilitating iron absorption by plants, especially under iron-deficient conditions. By synthesizing siderophores, bacteria can enhance iron availability and promote plant growth in iron-limited environments (Raymond et al. 2003; Kell et al. 2020).

Building upon the observed growth-promoting effects, it is crucial to also assess the potential phytotoxicity of bacterial isolates, as some strains may produce compounds that inhibit plant growth. Phytotoxicity tests are important for determining whether bacterial isolates, while potentially beneficial in some aspects, could negatively impact plant health through the production of harmful metabolites or secondary compounds. In the phytotoxicity test, isolate FS18 exhibited significantly lower shoot height, root length, germination rate on day 7, and vigor index compared to the control. These findings suggest that FS18 may produce specific compounds or metabolites that hinder the early growth of chili seedlings, potentially suppressing their overall development. On the other hand, several bacterial isolates demonstrated positive effects on seedling growth compared to the control, highlighting their potential as growth enhancers. Isolates such as S80, FKu31, S65, K15, and FS28 showed high germination rates, a strong vigor index, and enhanced root length and shoot height compared to the control. Notably, S80 exhibited the highest seed germination rate on day 14, reaching 100%, and had a significantly longer root length than the control. Isolate K15 displayed the highest vigor index, indicating its strong potential to promote seedling development. In addition to S80, FKu31 and S65 also promoted root elongation by day 14, surpassing the control group. Among these isolates, S80, K15, and S65 were identified as indole-3-acetic acid (IAA) producers, which may explain the observed improvements in seedling performance. IAA, a plant growth-promoting phytohormone, facilitates root elongation and lateral root formation, thus enhancing the plant's ability to absorb water and nutrients through its root system (Matthews et al. 2024). This suggests that IAA production by these isolates plays a key role in the improved growth of chili seedlings.

The mode of action of bacteria in controlling plant pathogens can occur both directly and indirectly in the environment. Direct interactions include antibiosis through antimicrobial secondary metabolites, inactivation of pathogen virulence factors, and degradation of pathogen cell walls by enzymes (Köhl et al. 2019). Cellulolytic bacteria produce cellulase enzyme complexes, such as endoglucanase, exoglucanase, and β-glucosidase, which break down cellulose into glucose. Since *P. capsici* has a cell wall composed of cellulose, it is hypothesized that cellulolytic bacteria can directly control *P. capsici* by using cellulase enzymes to degrade its cell wall. Cellulase is a cell wall-degrading enzyme that consists of a protein complex, which includes between 100 and 1000 amino acids, and catalyzes specific substrates into distinct products (Palmer and Bonner 2011). The function of this enzyme depends not only on its amino acid sequence but also on its complex tertiary structure (Iyer and Ananthanarayan 2008).

In the case of isolates FS28 and S80, plant survival rates were lower than those of the control, although the differences were not statistically significant. This outcome may be linked to interactions between nitrogen fixed by the bacteria and the pathogen. Mestas et al. (2023) reported that while nitrogen fertilization can enhance root development, it increases symptoms caused by *Phytophthora cinnamomi* and *P. plurivora*. A similar interaction may explain the reduced survival observed with isolates FS28 and S80 in the presence of *P. capsici*.

Microbial interactions in the rhizosphere play a crucial role in soil ecosystem dynamics and can take various forms, including neutral, synergistic, or antagonistic relationships. *Phytophthora* species, though recognized as aggressive plant pathogens, often rely on interactions with other microorganisms to fully express their pathogenic potential. In natural environments, the inoculum density of *Phytophthora* is typically low, and its ability to initiate infection may be limited without microbial interactions that support its growth, survival, or virulence (Kong and Hong 2016). Research by Frey-Klett et al. (2011) showed that certain bacterial associations can influence the growth, physiology, and pathogenicity of Oomycota. In a similar vein, a study by Larousse et al. (2017) demonstrated that a specific phylotype of *Pseudomonas* sp. exhibited antibiosis against *Phytophthora parasitica* in vitro. However, in vivo testing revealed that it significantly increased the symptom severity in treated plantlets, suggesting that the bacterium enhanced the pathogenicity of *P. parasitica* toward its host. In the present study, isolate S80 displayed a similar pattern, where it increased the pathogenicity of *P. capsici* in chili plants, as evidenced by a significantly reduced survival rate in treated plants.

In the phytotoxicity assay, isolate S80 showed no significant difference in shoot height compared to the control, but it significantly increased root length and achieved a 100% germination rate. Isolate S80 exhibited an in vitro inhibition rate of 46.85% against *P. capsici*. However, this result did not align with the in vivo assay on chili seedlings, where S80 treatment led to reduced seedling growth and increased pathogen virulence, ultimately resulting in a lower plant survival rate. A similar unexpected outcome was reported in a study by Raya-Hernández et al. (2023), where the co-application of *Azospirillum brasilense* (a plant growth-promoting bacterium) with *P. capsici* unexpectedly led to stunted development and aggravated disease symptoms in vivo. These findings highlight the complexity of bacterial interactions with pathogens, where certain bacteria may show beneficial effects under controlled conditions but lead to negative outcomes when exposed to more natural or stressful environments.

The molecular identification in this study revealed several bacterial isolates with potential biocontrol activity, including *P. aeruginosa*, *P. penneri*, *B. altitudinis*, and *Brevundimonas* sp. Among them, *P. aeruginosa* has been extensively reported for its antagonistic effects against various plant pathogens. It has demonstrated strong inhibitory activity against *P. capsici*, the causal agent of stem rot disease in chili, as well as other fungal pathogens such as *Sclerotinia sclerotiorum*, *Pyricularia oryzae*, *Diaporthe citri*, *Botrytis cinerea*, *Fusarium graminearum*, and *Penicillium simplicissimum* (Li et al. 2024). *P. aeruginosa* is widely recognized for its ability to produce a diverse array of lytic enzymes including cellulases.

Bacillus altitudinis has emerged as a promising candidate in the development of biological control strategies for plant disease management. This species has been isolated from diverse environments and is known to exhibit plant growth-promoting traits (Gopalakrishnan et al. 2011). Previous studies reported that *B. altitudinis* inhibited the growth of *Macrophomina phaseolina* (Gopalakrishnan et al. 2011). Moreover, *B. altitudinis* was shown to suppress mycelial growth and zoospore germination of the pathogenic oomycete *Phytophthora sojae*, a destructive pathogen responsible for significant yield losses in soybean. In addition, it was found to enhance the production of reactive oxygen species (ROS) and callose deposition in soybean leaves (Lu et al. 2017). Given these attributes, *B. altitudinis* may also hold potential in suppressing *P. capsici*, making it a promising biocontrol agent. In contrast, research on *P. penneri* and *Brevundimonas* sp. as biocontrol agents remains limited. However, *P. penneri* has been reported to possess antibacterial activity against *Aeromonas hydrophila* (Fitriadi et al. 2023), suggesting its potential to produce antimicrobial compounds that may also be effective against plant pathogens. Meanwhile, although studies on *Brevundimonas* are rare, *Brevundimonas naejangsanensis* has been identified as a biocontrol agent capable of suppressing *Fusarium redolens* (Bekkar and Zaim 2024), indicating preliminary biocontrol potential within the genus.

However, this study has limitations that must be acknowledged. The antagonistic activity was confirmed under in vitro and greenhouse conditions, but environmental factors such as soil heterogeneity, microbial competition, moisture availability, and climatic variability may influence the performance of these isolates in the field. Furthermore, while the use of cellulolytic microbes offers a more environmentally friendly alternative to chemical fungicides, their introduction into agricultural systems requires careful consideration of potential non-target effects. For example, excessive cellulolytic activity could impact soil organic matter turnover or alter native microbial communities in ways that may not always be beneficial. Future research should therefore integrate ecological assessments and field trials to validate the consistency and stability of biocontrol performance under diverse agricultural conditions. Additionally, exploring the molecular mechanisms of antagonism and developing safe, efficient formulations will be essential to translate the promising laboratory and greenhouse results into sustainable disease management strategies.

ACKNOWLEDGEMENTS

The authors are thankful to the Directorate General of Research and Development, Indonesian Ministry of Higher Education, Science, and Technology, for supporting this research and publication through the National Competitive Regular Fundamental Research scheme in 2025 with the Research Implementation Contract Number: 006/C3/DT. 05.00/PL/2025.

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