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RESEARCH ARTICLE

Bioprospecting endophytic *Bacillus* spp. from tomato for antagonistic potential against tomato leaf curl virus (ToLCV)

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Abstract

Tomato leaf curl virus (ToLCV) is one of the most destructive viral pathogens of tomato, causing severe yield losses and posing significant management challenges because of its persistent transmission by *Bemisia tabaci* and the rapid emergence of viral variants. In search of sustainable alternatives to chemical control, the present study investigated the antiviral potential of endophytic *Bacillus* spp. isolated from wild and cultivated tomato germplasm. A total of twenty-four bacterial endophytes were isolated from surface-sterilized root, stem and leaf tissues, of which six representative isolates were identified as *Bacillus subtilis*, *B. safensis*, *B. pumilus* and *B. cereus* through morphological traits and 16S rRNA gene sequencing. Greenhouse-based evaluation of antiviral activity was conducted using seed priming and foliar application of bacterial culture filtrates. Seed priming with *Bacillus* isolates showed limited protection, with high percent disease incidence (PDI) values (90-100 %), indicating poor suppression of ToLCV. In contrast, culture filtrates demonstrated strong isolate-specific antiviral effects. Notably, *B. subtilis* isolates GSB1 and HLB1 recorded the lowest PDI (46.67 %), significantly delaying symptom onset and reducing disease severity, followed by moderate activity from *B. safensis* (HSB2). The remaining isolates showed minimal efficacy. The superior performance of culture filtrates suggests that bioactive metabolites produced by certain *Bacillus* strains may induce systemic resistance and/or interfere with viral infection processes. Overall, the study highlights the potential of tomato-associated endophytic *Bacillus* spp. particularly *B. subtilis* as promising candidates for developing environmentally safe biocontrol strategies against ToLCV.

Keywords: antiviral activity; *Bacillus* spp.; culture filtrate; endophytes; germplasm; seed priming

Introduction

Tomato (*Solanum lycopersicum* L.) is one of the world's most widely cultivated vegetable crops and an important source of vitamins, antioxidants and income for both small- and large-scale farmers. Despite considerable advancements in breeding and crop protection, viral diseases particularly tomato leaf curl disease caused by tomato leaf curl virus (ToLCV) (1, 2) belonging to the genus Begomovirus (family *Geminiviridae*) continue to rank among the most destructive constraints to tomato production globally (3, 4).

ToLCV is transmitted by the whitefly *Bemisia tabaci* persistently, making its management exceptionally challenging under field conditions (1, 5). Infected plants typically show severe leaf curling, vein thickening, chlorosis, yellowing, stunting and significant yield losses (6). The virus remains a major threat in tropical and subtropical regions, where warm climates favor rapid vector multiplication (7). Despite the use of resistant varieties, vector management, cultural practices and chemical control, integrated disease management remains ineffective mainly due to rapid viral evolution, vector adaptability and the continual emergence of new ToLCV variants. Additionally, heavy reliance on chemical insecticides raises environmental and health concerns, prompting an urgent need for safer, sustainable alternatives.

Biological control using microbial antagonists offers an eco-friendly and promising approach, providing multiple mechanisms of action while reducing chemical inputs. Among microbial biocontrol agents, endophytic *Bacillus* spp. has gained considerable attention due to their remarkable ability to colonize internal plant tissues, promote plant health and produce a wide array of bioactive secondary metabolites (8, 9). Gram-positive, spore-forming bacteria in this group are widely distributed in the rhizosphere and endosphere of crop and wild plants and are known for synthesizing bioactive lipopeptides, including surfactin, fengycin and iturin, which confer antifungal, antibacterial, antiviral, insecticidal and plant defense-inducing effects (10).

Over the last decade, several *Bacillus* species including *B. subtilis*, *B. amyloliquefaciens*, *B. velezensis* and *B. pumilus* have

demonstrated significant antagonistic effects against major phytopathogens through mechanisms like antibiosis, siderophore production, hydrolytic enzyme secretion, ISR (induced systemic resistance) and competitive colonization (11).

In recent years, growing evidence suggests that *Bacillus*-derived metabolites also possess antiviral properties, with several studies reporting suppression of plant viruses through mechanisms involving ISR, production of antiviral lipopeptides and interference with virus replication or movement (12, 13). For example, formulations of *Bacillus amyloliquefaciens* have shown activity against cucumber mosaic virus (CMV), tobacco mosaic virus (TMV) and tomato spotted wilt virus (TSWV), largely through the induction of host defense pathways and accumulation of antiviral compounds in treated plants (14-16). Such findings highlight the potential of endophytic *Bacillus* strains as alternative tools for managing agriculturally important viral diseases such as ToLCV.

The present study aimed to isolate and characterize endophytic *Bacillus* species from ToLCV-resistant cultivars, confirm their taxonomic identity through morphological traits and 16S rRNA-based molecular analysis and evaluate their antagonistic and antiviral potential against ToLCV under controlled glasshouse conditions.

Materials and Methods

Maintenance of ToLCV culture in tomato seedlings

The ToLCV culture used in this study was obtained from tomato plants exhibiting characteristic symptoms of tomato leaf curl disease (leaf curling, puckering, yellowing, stunting and reduced leaf size) collected in 2025 from the GKVK campus, Bengaluru Urban district. Symptomatic plants were molecularly confirmed as tomato leaf curl Bangalore virus (isolate: BGU-1) using two sets of primers: (i) begomovirus universal primers (Deng primers) targeting the conserved coat protein (CP) gene region (17, 18) and (ii) strain-specific primers designed for precise identification of ToLCV isolates (2). The ToLCV culture was maintained under controlled glasshouse conditions to ensure a consistent and reliable source of inoculum. Plants were grown at 28 ± 2 °C, with a relative humidity of 60-70 %. Seeds of the susceptible tomato cultivar Arka Vikas were sown in sterilized soil and farmyard manure mixture within insect-proof cages to raise healthy, virus-free seedlings, which served as host plants for ToLCV maintenance.

A laboratory culture of the whitefly vector, *Bemisia tabaci* (Gennadius), was simultaneously reared on healthy brinjal plants grown in polyethylene bags under insect-proof conditions to provide a continuous supply of non-viruliferous insects. To establish and maintain the virus culture, ToLCV-infected tomato plants exhibiting characteristic leaf curl symptoms were collected from research plots at the University of Agricultural Sciences, GKVK, Bengaluru and the presence of the virus was confirmed using PCR with universal and specific primers. Adult *B. tabaci* were allowed an acquisition access period (AAP) of 24 hr on infected tomato twigs, followed by a 24 hr inoculation access period (IAP) on healthy 15-day-old tomato seedlings (approximately 15 adults per seedling) to facilitate virus transmission. After inoculation, the insects were removed and the newly infected plants were maintained under insect-proof cages to prevent cross-contamination. Periodic re-inoculation of healthy seedlings with viruliferous whiteflies was conducted to sustain the ToLCV isolate, ensuring the consistent availability of uniform and well-characterized viral material for subsequent experiments (19).

Maintenance of whitefly *Bemisia tabaci* culture

A laboratory culture of the whitefly vector, *Bemisia tabaci* Gennadius, was maintained to facilitate transmission of ToLCV. The insect colony was reared on healthy brinjal plants, which served as the maintenance host. Brinjal seedlings were raised in polyethylene bags (4 × 6 cm) containing sterilized soil and farmyard manure mixture and subsequently introduced into insect-proof rearing cages housed within a controlled glasshouse environment. To sustain the colony, fresh brinjal plants were periodically supplied by replacing senescent or infested plants with healthy, newly grown plants. To ensure a continuous and reliable source of non-viruliferous whiteflies, multiple cages containing brinjal host plants were maintained concurrently under strict insect-proofing conditions to prevent vector escape and cross-contamination.

Collection and raising of tomato germplasm

ToLCV resistant tomato cultivars *viz*., *Nandi* (TLB-130), *Sankranthi* (TLB-111) and *Vybhav* (TLB-182) (20), were selected for endophyte isolation. Seeds of Nandi, Sankrathi and Vybhav were obtained from the Department of Plant Pathology, University of Agricultural Sciences (UAS), Bangalore. Before sowing, seeds were surface sterilized by sequential treatment with 70 % ethanol for 1 min and 1 % sodium hypochlorite for 1 min, followed by 5 thorough rinses with sterile distilled water. Sterilized seeds were then sown in autoclaved soil and maintained under greenhouse conditions at a temperature of 28 ± 2 °C for 30 to 40 days until sampling.

Sample collection and surface sterilization for endophytes isolation

Healthy, asymptomatic tissues (roots, stems and leaves) were collected from 40-day-old tomato plants. Three plants per genotype were sampled, the plants were collected. Later, the plants were carried in individual polybags to the laboratory and washed under running tap water to remove adhering soil and debris. Under aseptic conditions inside a laminar air flow cabinet, surface sterilization was performed to eliminate epiphytic microbes. Plant tissues were treated with 70 % ethanol for 1 min, followed by 1 % sodium hypochlorite for 30 sec and then treated with 70 % ethanol for 30 sec. Further, tissues were rinsed thoroughly three times with sterile distilled water (21). To verify the efficacy of surface sterilization, 100 µL from the final rinse water was plated on nutrient agar (NA) and incubated at 30-35 °C for 24-48 hr for bacterial growth. Plates showing no microbial growth after 24-48 hr were considered sterile, confirming the effectiveness of the surface sterilization procedure (22).

Isolation of bacterial endophytes

For bacterial isolation, plant tissues (2 g) were macerated in 1 mL sterile potassium phosphate buffer (pH 7.2) using a sterilized pestle and mortar. The resulting suspensions were serially diluted up to 10^5 and aliquots from appropriate dilutions were plated on nutrient agar (NA), Luria-Bertani agar (LBA) and King's B medium (KBM) (Fig. 1). Plates were incubated at 30-35 °C for 24-48 hr for bacterial growth. Morphologically distinct colonies were subcultured on NA within 2 days of bacterial growth to obtain a pure culture for further use (23).

Nomenclature and coding system for endophytic operational taxonomic units (OTUs)

Pure cultures of bacterial endophytes were categorized into different Operational Taxonomic Units (OTUs). A lab-wide culture tracking system with unique alphanumeric IDs for every isolate and subculture was implemented. IDs encode: tomato genotype code,

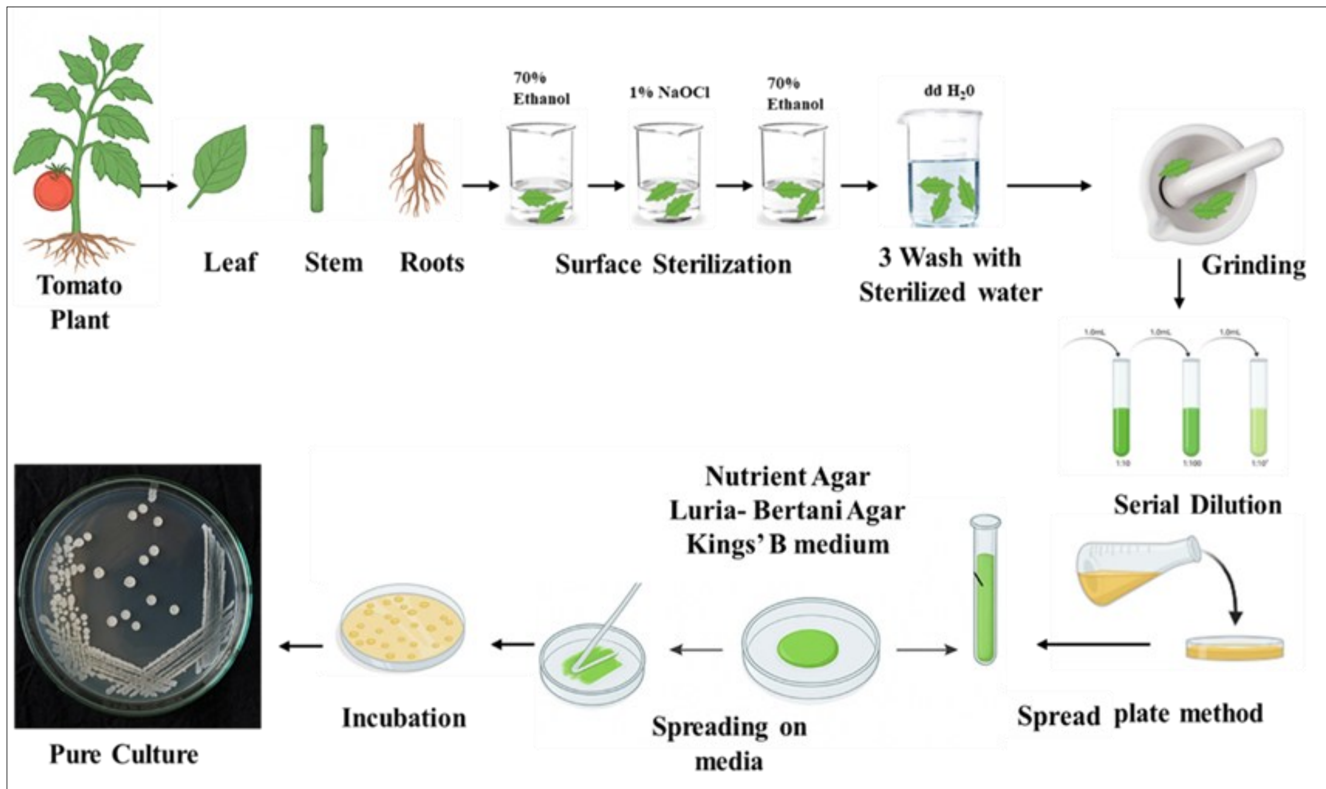

Fig. 1. Flow chart represents the isolation of bacterial endophytes from tomato plants.

part of plant, endophyte code and isolate sequence number (format: tomato genotype code (G-*Nandi*, H-*Sankrathi*, I-*Vybhav*); Part of plant (L-Leaf, S-Stem and R-Root); endophyte code (B-Bacteria); Numerical isolate sequence (1,2,3,. . .n).

Morphological and molecular identification of bacterial endophytes

Bacterial isolates were characterized based on colony morphology, including colony colour, form, elevation, margin and surface features, along with Gram reaction. For molecular identification, genomic DNA was extracted from bacteria using a modified CTAB-based protocol (24, 25). 1.5 mL of a 24 hr old bacterial culture was transferred into an Eppendorf tube and centrifuged at 10000 rpm for 10 min at 4 °C. The supernatant was discarded and the pellet was washed with 1.5 mL of sterile distilled water. The pellet was then resuspended in 600 µL of genomic DNA lysis buffer containing 564 µL of 1X Tris-HCl–EDTA buffer, 30 µL of 10 % SDS and 6 µL of Proteinase K (10 mg/mL), followed by incubation at 37 °C for 1 hr. After incubation, 100 µL of 5 M NaCl and 80 µL of preheated (65 °C) CTAB were added and the mixture was further incubated at 65 °C for 15 min. An equal volume of chloroform:isoamyl alcohol (24:1) was added, mixed thoroughly and centrifuged at 10000 rpm for 10 min at room temperature. The aqueous phase was carefully transferred to a fresh tube and DNA was precipitated by adding an equal volume of phenol:chloroform:isopropyl alcohol (25:24:1), followed by centrifugation at 10000 rpm for 10 min. The resulting supernatant was transferred to a new tube and DNA was further precipitated by adding 0.6 volumes of isopropanol and incubating the mixture for 15 min at room temperature. The sample was then centrifuged at 10000 rpm for 10 min to obtain a DNA pellet, which was washed twice with 70 % ethanol and air-dried for 30 min. Finally, the dried pellet was dissolved in 50 µL of TE buffer (10 mM Tris, 1 mM EDTA, pH 8) containing 10 µg/mL RNase and the DNA samples were stored at -20 °C.

The quality and concentration of DNA were assessed by agarose gel electrophoresis and Nanodrop spectrophotometry. DNA was diluted to a final concentration of 50 ng/µL and used as a template for all the PCR reactions. PCR amplification of the 16S rRNA gene was performed using universal primers 27F (5'-AGAGTTTGATCCTGGCTCAG-3') and 1492R (5'-TACGGYTACCTTGTTACGACTT-3') (26). PCR reactions were performed in a 25 µL reaction volume containing 12.5 µL of 2X PCR master mix (Takara, PCR Master Mix, Japan), 10 pmol of each forward and reverse primer and approximately 50-100 ng of template DNA. The thermal cycling conditions were as follows: initial denaturation at 95 °C for 5 min, followed by 35 cycles consisting of denaturation at 95 °C for 60 sec, annealing at 57 °C for 90 sec, extension at 72 °C for 60 sec and a final extension at 72 °C for 10 min (26). Amplified PCR products were visualized on a 1 % agarose gel, purified and sequenced commercially at Barcode Bioscience Limited, Bengaluru.

Sequence and phylogenetic analysis of bacterial endophytes

PCR-amplified products of the bacterial endophytes were submitted for bidirectional Sanger sequencing at a commercial sequencing facility (Barcode Biosciences, Bengaluru, India). The raw chromatogram files obtained were carefully inspected, quality-trimmed and assembled into consensus sequences using BioEdit version 7.2.6 (27). The resulting sequences were subjected to BLASTn analysis against the NCBI GenBank nucleotide database to identify closely related *Bacillus* species and determine sequence similarity. For comparative analysis, multiple sequence alignment of the obtained sequences along with representative reference sequences of related *Bacillus* spp. (Table 1) was performed using the ClustalW algorithm integrated within MEGA X software (28). Reference sequences of *Bacillus* and other phylogenetically related taxa were retrieved from GenBank and included for phylogenetic reconstruction. A phylogenetic tree was generated using the Maximum Likelihood method based on the Tamura-Nei nucleotide substitution model and the robustness of the resulting clades was evaluated through 1000 bootstrap replications.

Table 1. NCBI GenBank accession numbers of reference sequences of *Bacillus* spp. used in phylogenetic analysis

Sl. No.	Bacterial species	NCBI GenBank accession number
1.		OQ954758
2.		PP930724
3.	*Bacillus subtilis*	OQ504779
4.		HQ441254
5.		OR091483
6.		KX350055
7.		KX363807
8.	*Bacillus pumilus*	KU950739
9.		KP454005
10.		KR560043
11.		MW699631
12.		LC602960
13.	*Bacillus safensis*	PP325789
14.		OM535932
15.		OR062360
16.		MW530459
17.		MT052656
18.	*Bacillus cereus*	OP001792
19.		OP329213
20.		MW281811
21.	*Clavibacter michiganensis* (Outgroup)	NR_118300

Evaluation of isolated *Bacillus* spp endophytes against ToLCV

Isolated endophytic *Bacillus* spp. isolated from different ToLCV-resistant tomato germplasm were subsequently evaluated for their efficacy against ToLCV. The screening was conducted under controlled glasshouse conditions at 28 ± 2 °C, with a relative humidity of 60-70 % using the susceptible tomato cultivar Arka Vikas. The experiment employed *in vivo* (*in planta*) assays, in which the isolates were applied to plants before virus challenge to assess their potential to mitigate infection and reduce symptom expression.

Preparation of endophytic bacterial cell suspension

Bacterial isolates were cultured in nutrient broth (NB) medium and incubated overnight in a rotary shaker at 30-35 °C to obtain actively growing cultures. Following incubation, the bacterial density was standardized to 1 × 10^8 CFU/mL by measuring the optical density (OD) at 600 nm using a spectrophotometer. An OD value of approximately 0.1 at 600 nm was considered equivalent to 1 × 10^8 CFU/mL (29). The standardized bacterial suspension was subsequently used for seed treatment and in planta assays to evaluate their efficacy against ToLCV.

Evaluation of isolated endophyte through seed priming against tomato leaf curl virus (ToLCV)

Tomato seeds of the susceptible cultivar Arka Vikas were surface-sterilized using 70 % ethanol, rinsed three times with sterile double-distilled water and soaked for 24 hr in suspensions of endophytic bacterial cultures (1 × 10^8 CFU/mL) before sowing. The bio-primed seeds were sown under insect-proof glasshouse conditions and healthy seedlings were transplanted 15 days after sowing (DAS) into polyethylene bags filled with sterilized soil. Each treatment consisted of three replicates with ten plants per replicate, arranged in a completely randomized design (CRD). Plants received regular irrigation with sterile water and no fertilizers were applied throughout the experimental period. At the 2–3 leaf stage (30 DAS), seedlings were inoculated with *Bemisia tabaci* carrying ToLCV. Adult whiteflies were allowed a 24 hr acquisition access period (AAP) on PCR-confirmed ToLCV-infected plants (17, 30), followed by a 48 hr inoculation access period (IAP) on healthy bio-primed seedlings. After inoculation, whiteflies were eliminated by spraying imidacloprid (0.3 mL/L; Bayer CropScience) and plants were maintained under insect-proof conditions (Fig. 2). Seedlings were regularly monitored for symptom development, including leaf curling, yellowing and stunting which typically appear 10-14 days post-inoculation (31).

Preparation of bacterial endophytes culture filtrates

Culture filtrates of bacterial endophytic strains were prepared using actively growing bacterial isolates maintained on nutrient agar (NA) plates, which served as the source of inoculum. From the margin of 24-48 hr old bacterial colonies, a single well-isolated colony was

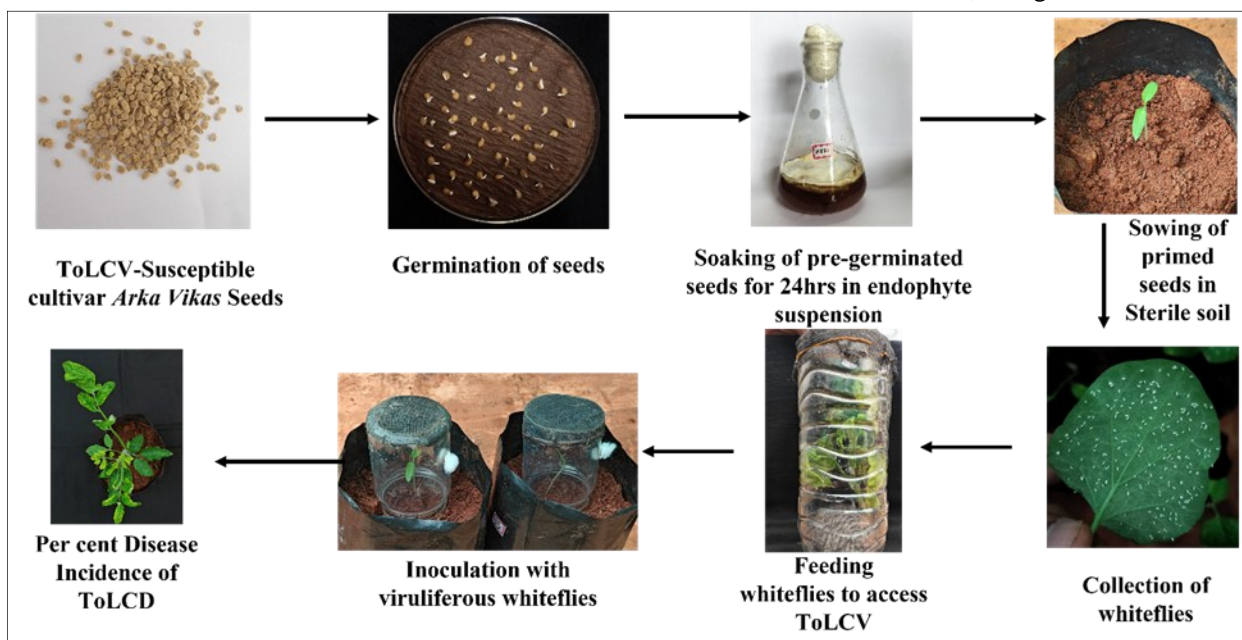

Fig. 2. Flow chart represents the *in planta* screening of seeds primed with endophytes against ToLCV.

aseptically picked and transferred into 50 mL of nutrient broth (NB) contained in a 250 mL sterile Erlenmeyer flask. The cultures were incubated at 30-35 °C on a rotary shaker at 180 rpm for 48 hr to promote active growth and metabolite secretion into the medium. After incubation, the bacterial cells were separated from the broth by centrifugation at 8000 rpm for 10 min at 4 °C. The resulting cell-free supernatants were carefully collected and passed through sterile syringe-driven membrane filters (0.22 µm pore size) to ensure complete sterility. The sterile bacterial culture filtrates thus obtained were stored at 4 °C until further use in antiviral screening assays (32).

Evaluation of isolated endophyte culture filtrates against tomato leaf curl virus (ToLCV)

For the antiviral assay, 15-day-old tomato plants of the susceptible cultivar Arka Vikas were sprayed once with sterile culture filtrates of individual bacterial endophytes using a hand-held atomizer until runoff, ensuring uniform foliar coverage. Plants treated with sterile nutrient broth served as controls (Fig. 3). After foliar application, the plants were kept under insect-proof conditions for 24 hr to facilitate absorption of bacterial metabolites and activation of potential defense responses. Subsequently, the plants were challenged with *Bemisia tabaci* adults carrying ToLCV. Disease progression was monitored regularly in both treated and control plants to evaluate the protective efficacy of metabolites derived from the bacterial endophytes against ToLCV infection.

Assessment of disease parameters

Tomato plants subjected to endophyte-mediated seed priming and subsequently inoculated with ToLCV *via* viruliferous *Bemisia tabaci* were monitored for 30 days post-inoculation to record symptom development. Characteristic ToLCV symptoms leaf curling, puckering, vein thickening and stunting were assessed as described in earlier reports (30). Disease incidence was calculated as the percentage of symptomatic plants in each treatment (33) allowing comparison of disease intensity among treatments.

Statistical analysis

Quantitative data on disease incidence collected from both field and glasshouse experiments were subjected to analysis of variance (ANOVA) to determine the significance of differences among treatments and cultivars. Mean comparisons were carried out using Tukey's Honest Significant Difference (HSD) test at 5 % significance level, as implemented in the OPSTAT statistical analysis software (34).

Results and Discussion

Tomato plants exhibiting characteristic symptoms of tomato leaf curl disease (ToLCD) such as upward leaf curling, vein thickening, yellowing and stunted growth were observed in the experimental fields at GKVK, Bengaluru Urban district (Fig. 4). The symptomatic viral isolate collected from these plants was designated as BGU1 and selected for molecular characterization. These observed symptoms are consistent with previous descriptions of ToLCD reports (2, 35, 36). Symptomatic leaf tissues were collected and total genomic DNA was extracted using the CTAB method, yielding intact DNA bands on agarose gel, indicating good quality for downstream molecular analyses. PCR amplification using begomovirus-specific primers and tomato leaf curl Bangalore virus (ToLCBV) strain-specific primers produced clear amplicons of approximately 520 bp and 1020 bp, respectively.

Fig. 4. Typical leaf curling symptoms of ToLCD, observed in fields of GKVK, Bengaluru Urban district isolate BGU-1.

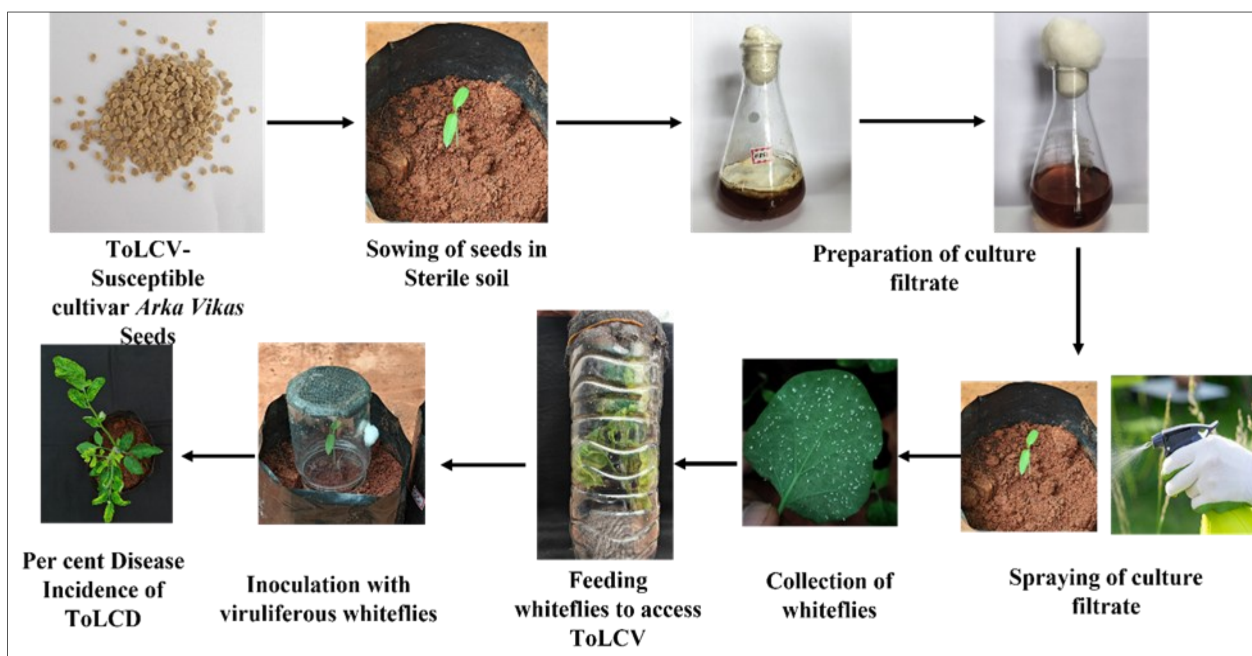

Fig. 3. Flow chart represents the *in planta* screening of culture filtrate of endophytes against ToLCV.

Isolation and identification of bacterial endophytes

Endophytic bacteria were successfully isolated from surface-sterilized root, stem and leaf tissues of all tomato genotypes. A total of twenty-four bacterial isolates were obtained, displaying diverse colony morphologies and growth characteristics on nutrient agar (Fig. 5). Based on preliminary morphological characterization, including colony shape, colour, margin type, elevation and Gram staining, six representative bacterial isolates were tentatively assigned to the genus *Bacillus*. These isolates consistently exhibited phenotypic traits typical of *Bacillus* spp., such as cream to off-white pigmentation, irregular or rough colony surfaces and Gram-positive rod-shaped cells. Such morphological characteristics are well documented as diagnostic features for *Bacillus* (37, 38). Detailed morphological characteristics of the selected *Bacillus* isolates are presented in Table 2. Similarly, previous reports suggest that diverse endophytic bacteria isolated from the root, stem and leaf tissues of healthy tomato plants using nutrient media, providing a consistent reservoir of culturable endophytes with plant growth-promoting (PGP) potential (39). Further molecular characterization was performed to confirm their taxonomic identity and assess phylogenetic relationships among the isolates. The isolation of six *Bacillus* spp. from tomato root, stem and leaf tissues highlights the prevalence and potential functional role of *Bacillus* as a common endophytic bacterial genus in tomato and other crop plants.

For molecular identification, the bacterial isolates were subjected to PCR amplification and sequencing of the 16S rRNA gene using universal bacterial primers (27F and 1492R) (37, 40, 41). The resulting sequences were analyzed using BLASTn searches against the NCBI GenBank database to determine their closest taxonomic affiliations. BLASTn analysis of the 16S rRNA sequences revealed that all representative isolates showed high sequence similarity (≥97 %) with authenticated *Bacillus* species available in the NCBI GenBank database, confirming their placement within the genus *Bacillus*. The isolates were identified as *B. subtilis*, *B. safensis*, *B. pumilus* and *B. cereus*. Phylogenetic analysis based on 16S rRNA sequences further supported the BLASTn-based identifications, confirming the close evolutionary relationships of the isolates with their respective reference taxa (Fig. 6) and these sequences were submitted to NCBI GenBank and obtained accession numbers (Table 3).

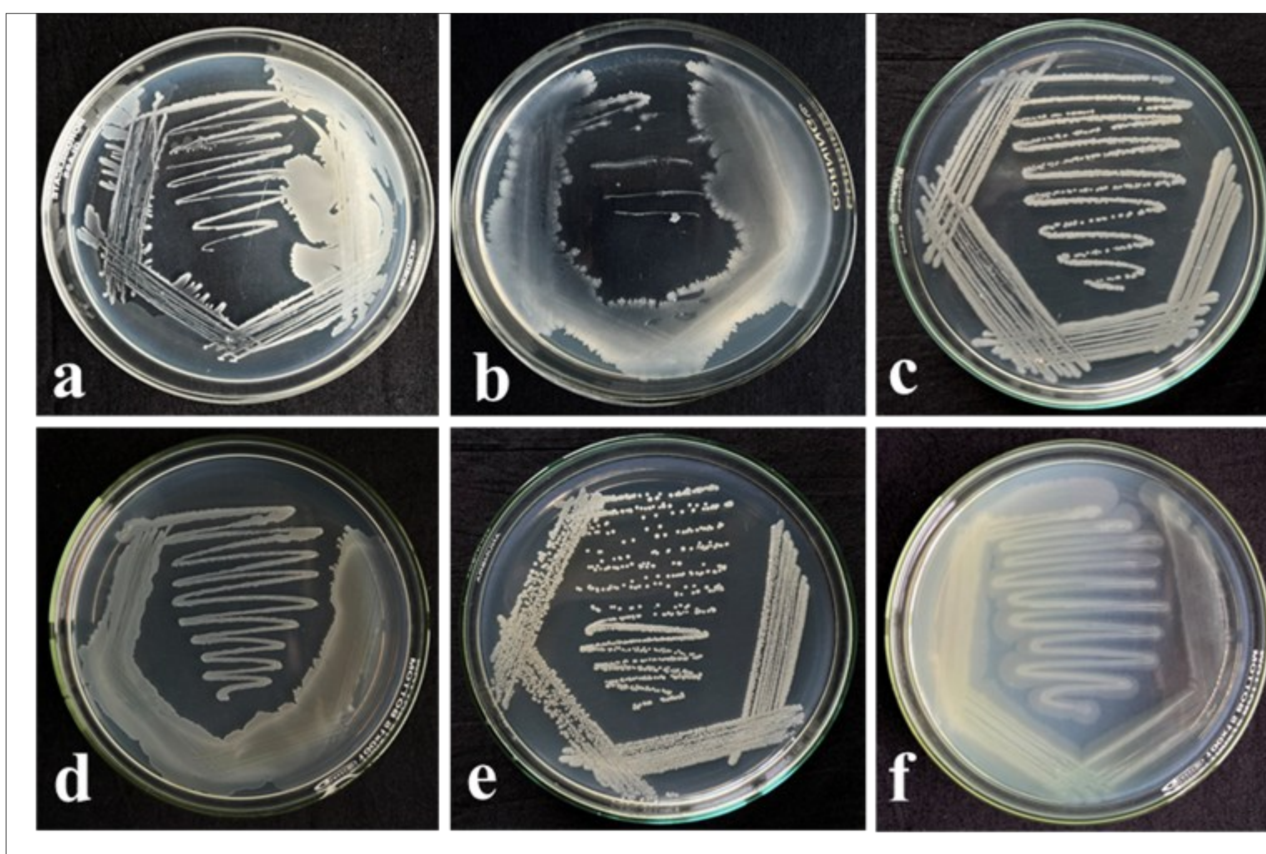

Fig. 5. Cultural and colony characteristics of isolated endophytic *Bacillus* spp. on nutrient agar. (a) GSB1, (b) HLB1, (c) HSB1, (d) HSB2, (e) HSB4, (f) IRB4.

Table 2. Cultural and morphological characters of isolated endophytic *Bacillus* spp.

Isolate	Bacterial endophytes	Color	Form	Elevation	Margin	Surface	Gram reaction
GSB1	*Bacillus subtilis*	White to cream	Irregular	Flat/dry	Lobate/undulate	Wrinkled/dry	Gram +
HLB1	*Bacillus subtilis*	White to cream	Irregular	Flat/dry	Lobate/undulate	Wrinkled/dry	Gram +
HSB1	*Bacillus pumilus*	White, opaque	Circular	Raised	Entire	Smooth	Gram +
HSB2	*Bacillus safensis*	White	Circular	Convex	Entire	Smooth	Gram +
HSB4	*Bacillus pumilus*	White, opaque	Circular	Raised	Entire	Smooth	Gram +
IRB4	*Bacillus cereus*	Creamy/white	Circular	Raised/convex	Entire	Smooth	Gram +

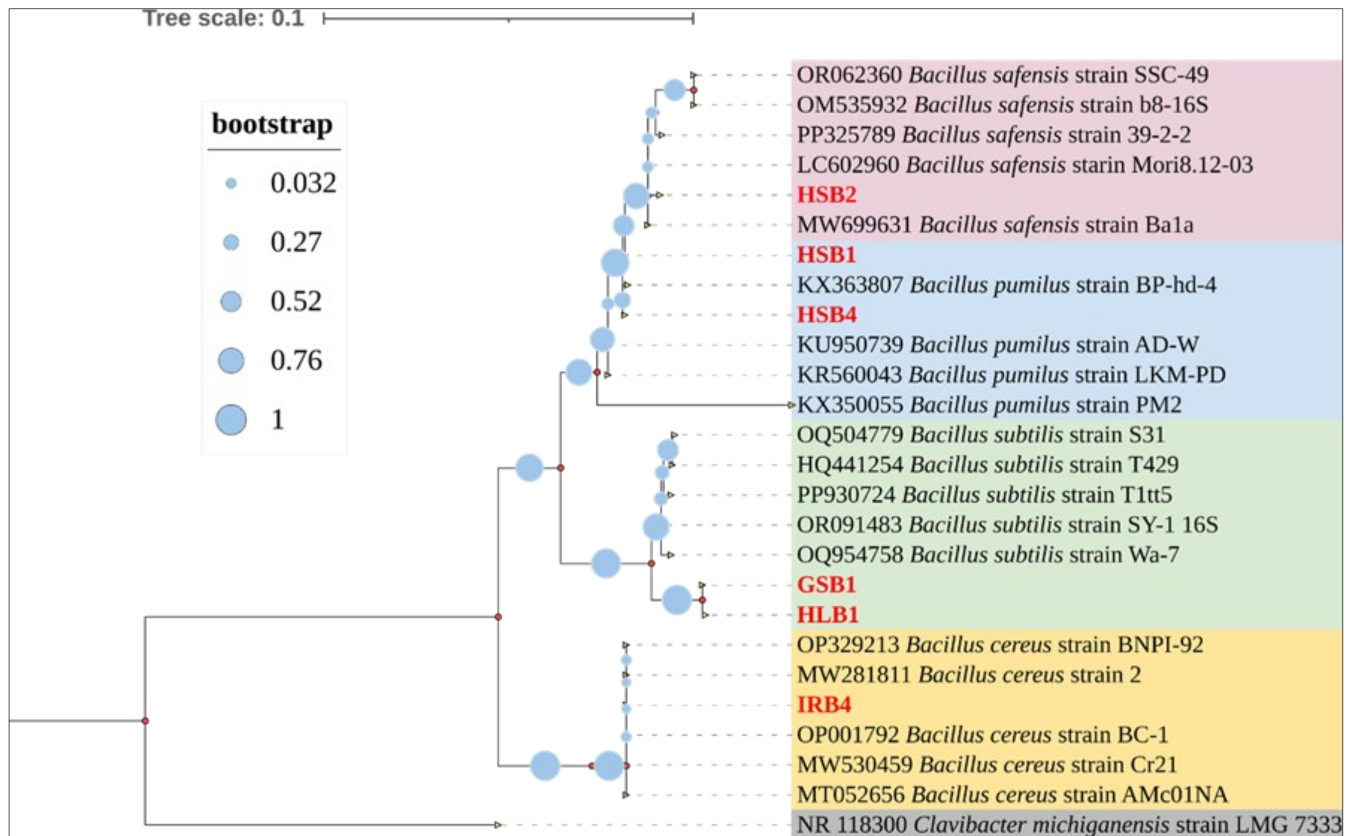

Fig. 6. Phylogenetic analysis of different *Bacillus* spp. constructed using the maximum likelihood method with 1000 bootstrap replicates.

Table 3. NCBI GenBank accession number of isolated endophytic *Bacillus* spp.

Sl. No.	Tomato genotype	Plant part	Isolate code	Bacterial endophytes	NCBI GenBank accession number
1.	Nandi	Stem	GSB1	*Bacillus subtilis*	PV876467
2.	Shankrathi	Leaf	HLB1	*Bacillus subtilis*	PV876475
3.	Shankrathi	Stem	HSB1	*Bacillus pumilus*	PV876476
4.	Shankrathi	Stem	HSB2	*Bacillus safensis*	PV876477
5.	Shankrathi	Stem	HSB4	*Bacillus pumilus*	PV876479
6.	Vybhav	Root	IRB4	*Bacillus cereus*	PV876509

The wide morphological and biochemical heterogeneity observed among the bacterial endophytes in this study reflects the substantial ecological and functional diversity commonly associated with tomato and other crop hosts. The broad spectrum of colony characteristics and physiological traits supports the presence of multiple bacterial lineages coexisting within tomato tissues, in line with earlier findings from plant endophyte diversity studies. Tissue-specific colonization patterns were also evident, likely shaped by variations in tissue physiology, nutrient availability and microenvironmental conditions (42). The diverse assemblage of endophytic *Bacillus* and other bacterial species documented here suggests a complex network of ecological interactions ranging from competition and niche specialization to metabolic cooperation providing a strong foundation for future functional screening aimed at identifying strains with promising biocontrol potential.

Screening of endophytes against ToLCV through seed priming

A total of six *Bacillus* endophytic isolates obtained from different tomato genotypes were evaluated through seed priming to assess their effect on ToLCV incidence under greenhouse conditions. Seed priming with standardized bacterial suspensions of each *Bacillus* isolate supported good germination and uniform seedling establishment across treatments. After transplantation, all plants showed normal growth and vigor before viral inoculation. Following exposure to viruliferous whiteflies carrying ToLCV, untreated control plants began expressing typical symptoms upward leaf curling, vein clearing, yellowing and stunted growth between 15-30 days post-inoculation. In contrast, plants primed with *Bacillus* isolates showed delayed symptom expression, though the level of protection varied among isolates.

The bio-priming of tomato seeds with different *Bacillus* isolates resulted in measurable differences in ToLCV disease incidence under greenhouse conditions (Table 4). Among the six isolates tested, GSB1 (*B. subtilis*) recorded a percent disease incidence (PDI) of 96.67 %, while HLB1 (*B. subtilis*) showed a slightly lower PDI of 90 %. HSB2 (*B. safensis*) and HSB4 (*B. pumilus*) exhibited PDI of 93.33 %. The isolates HSB1 (*B. pumilus*) and IRB4 (*B. cereus*) showed the highest PDI values of 100 %. Overall, all the *Bacillus* isolates tested through seed priming demonstrated high disease incidence values, indicating that they were comparatively ineffective in reducing ToLCV severity or significantly delaying symptom onset under greenhouse conditions.

The observed outcome underscores that the success of endophyte-conferred resistance is multifactorial. Key determinants include the mutual compatibility between the host and endophyte, the mode of inoculation and the chemical nature of the metabolites elaborated by the endophyte. Although seed priming is known to stimulate early vigor and foundational defense mechanisms by pre-activating systemic resistance pathways (43), the marginal antiviral efficacy in this study is likely a consequence of a compressed host-

Table 4. Percent disease incidence of ToLCD in tomato plants treated with bacterial endophytes (seed primed and culture filtrate)

Sl. No.	OTUs	Bacterial endophytes	Mean PDI (%)	
			Seed primed	Culture filtrate spray
1	GSB1	*Bacillus subtilis*	96.667[a]	46.667[c]
2	HLB1	*Bacillus subtilis*	90[a]	46.667[c]
3	HSB1	*Bacillus pumilus*	100[a]	93.333[a]
4	HSB2	*Bacillus safensis*	93.333[a]	63.333[b]
5	HSB4	*Bacillus pumilus*	93.333[a]	93.333[a]
6	IRB4	*Bacillus cereus*	100[a]	96.667[a]
		C.D.	N/A	10.385
		SE(m)	2.357	3.333
		SE(d)	3.333	4.714
		C.V.	4.272	7.873

endophyte interaction period before viral inoculation, or inadequate endophyte establishment through the seed priming approach. These findings parallel earlier reports that biological agents, while effective against mycotic and bacterial diseases, exhibit constrained activity against viral infections (44). This suggests that effective viral containment necessitates either the presence of potent antiviral secondary metabolites or a greater induction of host-mediated signaling, specifically involving pathways dependent on salicylic acid or jasmonic acid, which seed priming alone does not sufficiently trigger.

Instead of relying on colonization, the focus shifted to examining the potential of culture filtrates from the Bacillus endophytes for disease suppression. This was based on the idea that secondary metabolites secreted into the growth medium might possess antiviral activity even without the bacteria directly colonizing the plant. Accordingly, the filtrates were applied to tomato plants to assess their ability to reduce the incidence of ToLCD, providing an alternative means of evaluating the antiviral potential of the endophytes.

Screening of endophytes against ToLCV through culture filtrate

Culture filtrates obtained from *Bacillus* endophytic isolates were evaluated for their antiviral activity against ToLCV under controlled greenhouse conditions using the susceptible tomato cultivar Arka Vikas. Foliar application of sterile culture filtrates at 20 days after sowing (DAS) was well tolerated by the plants, with no visible phytotoxic effects or growth abnormalities. After a 24 hr incubation period, treated plants were inoculated with ToLCV through viruliferous whiteflies to assess the protective potential of the bacterial metabolites.

Control plants sprayed with sterile broth developed typical ToLCD symptoms upward leaf curling, vein clearing, yellowing and stunted growth within 15-30 days post-inoculation. In contrast, plants treated with *Bacillus* culture filtrates showed noticeable variation in symptom onset and disease severity, indicating isolate-specific differences in antiviral activity. Some filtrates delayed the onset of symptoms or reduced their severity, indicating that metabolites produced by certain *Bacillus* isolates may enhance plant defense responses or interfere with virus infection and replication.

The foliar application of culture filtrates from different *Bacillus* isolates resulted in distinct differences in ToLCV disease incidence under greenhouse conditions. Percent disease incidence (PDI) among treatments ranged from 46.67 % to 96.67 %, demonstrating varying levels of antiviral efficacy (Table 4). Among the six isolates tested, GSB1 and HLB1 (*B. subtilis*) recorded the lowest PDI values (46.67 %), indicating strong suppression of ToLCV infection. HSB2 (*B. safensis*) exhibited moderate PDI (63.33 %), showing partial antiviral activity. In contrast, HSB1 and HSB4 (*B. pumilus*) showed higher PDIs of 93.33 %, while IRB4 (*B. cereus*) exhibited the highest PDI (96.67 %), reflecting limited effectiveness. Overall, culture filtrates from GSB1 and HLB1 were the most effective in reducing disease incidence and delaying symptom development compared to the control.

The percent disease reduction over control among tomato plants treated with endophytic *Bacillus* spp. through seed priming and foliar application of culture filtrates is presented in Fig. 7. Culture filtrates produced markedly stronger antiviral effects than seed priming, especially in GSB1 and HLB1, which achieved the highest reduction in ToLCV incidence. HSB2 also showed a moderate response under culture-filtrate treatment, while the remaining isolates exhibited only minimal reduction. Seed priming produced uniformly low reductions across all isolates, indicating limited efficacy. Overall, the visual pattern highlights that metabolite-rich culture filtrates offer far superior antiviral protection compared to seed-based treatments.

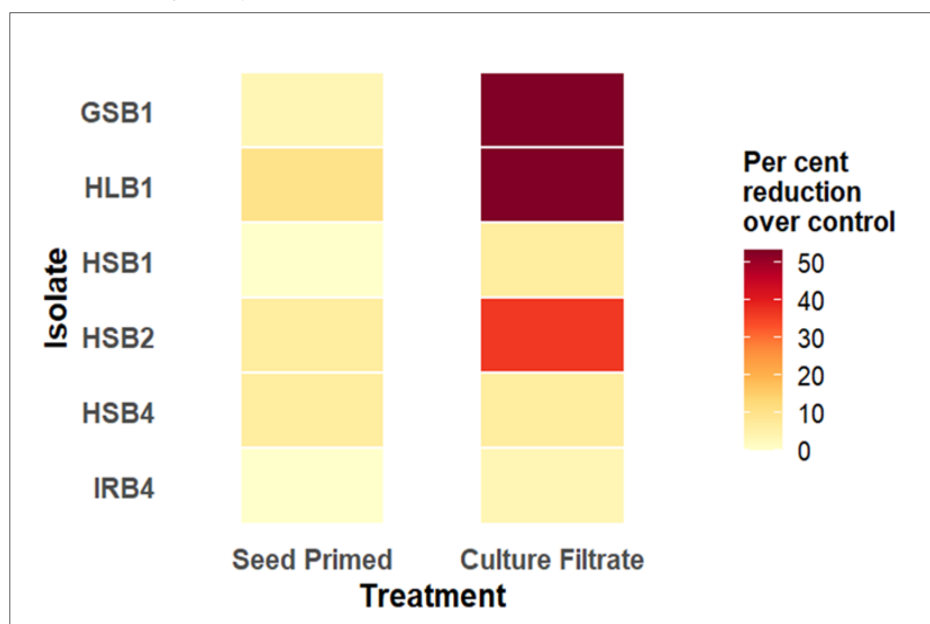

Fig. 7. Percent disease reduction over control of ToLCD in tomato plants treated with endophytes (seed primed and culture filtrate).

The observed variation in percent disease reduction among the six endophytic *Bacillus* spp. culture-filtrate treatments underscores the isolate-specific nature of antiviral efficacy in the greenhouse screening of ToLCV. The two *B. subtilis* isolates (GSB1, HLB1) that showed the highest reduction illustrate strong protective potential, delaying symptom onset and reducing severity compared to the control. These findings align with earlier reports demonstrating that endophytic *Bacillus* spp. can function as antiviral agents by inducing systemic resistance and/or producing bioactive metabolites (45-47). For instance, foliar application of a *B. subtilis* culture filtrate has been reported to enhance tomato resistance to viral infection by inducing defense-related gene expression and reducing viral accumulation. The differential performance of isolates likely reflects variations in metabolite production, colonization efficiency or elicitation of host immunity. Overall, the experiment suggests that certain endophytic *Bacillus* isolates may be promising components of integrated management strategies for ToLCV in tomato. Furthermore, metabolites of endophytic bacteria *Bacillus* spp. can induce systemic resistance in plants by triggering the production of defense-related proteins and phytohormones. This induction of systemic resistance is often associated with the activation of salicylic acid (SA)-mediated pathways, leading to the upregulation of pathogenesis-related (PR) proteins and other defense mechanisms. Among the isolates evaluated, *B. subtilis* emerged as a strong bioinoculant candidate due to its ability to colonize plant tissues, form biofilms, produce volatile compounds and activate host defense responses (48-50).

Conclusion

The present investigation highlights the potential of endophytic *Bacillus* species as promising biocontrol agents against ToLCV in tomato. A diverse set of endophytic *Bacillus* spp. isolates was successfully recovered from ToLCV-resistant tomato cultivars and confirmed through morphological characterization and 16S rRNA gene sequence analysis. Although seed priming with these isolates produced limited antiviral effects, foliar application of their culture filtrates reduced ToLCV incidence under greenhouse conditions. Among the isolates tested, *B. subtilis* strains GSB1 and HLB1 consistently exhibited the strongest antiviral activity, significantly reducing disease incidence and delaying symptom development, likely due to the presence of potent bioactive metabolites capable of inducing host defense pathways. Collectively, these findings underscore that metabolite-based delivery through culture filtrates is more effective than seed-based inoculation for managing viral diseases. This study provides valuable insights into the antiviral potential of tomato-associated endophytic *Bacillus* spp. It lays a strong foundation for future research aimed at metabolite characterization, defense-gene expression profiling and field-level validation to develop sustainable ToLCV management strategies.

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Authors' contributions

DC contributed to conceptualization, data curation, formal analysis, investigation, methodology, project administration, supervision, visualization and writing of the original draft as well as review and editing. KBS contributed to conceptualization, formal analysis, methodology, supervision, visualization and writing of the original draft and review and editing. A contributed to formal analysis, supervision, visualization and writing-review and editing. NN and CNLR contributed to conceptualization, supervision and visualization. RC and HPG contributed to writing-review and editing. AS and SC contributed to formal analysis. SGK and TMN contributed to conceptualization and supervision. All authors have read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no competing interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical issues: None

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