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RESEARCH ARTICLE

Efficacy of biocontrol agents in suppressing *Fusarium oxysporum* f. sp. *cubense* TR4, the causal pathogen of *Fusarium* wilt of banana in Bihar

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Abstract

The present study was conducted at the Department of Plant Pathology and Nematology, RPCAU, Pusa, during the year 2022–2023. It demonstrates the *in vitro* antagonistic effect of native *Trichoderma* isolates and fungal endophytes, as well as the inhibitory effects of volatile organic compounds (VOCs) from four selected bacterial endophytes against *Fusarium oxysporum* f. sp. *cubense* (Foc TR4). The results revealed that *Trichoderma* isolates, i.e. T1-1723; T2-1723; T3-1723, in which T-3-1723 and *Trichoderma asperellum* showed maximum per cent mycelium inhibition of 88.89 and 88.92 respectively, whereas fungal endophytes LfFE1 exhibited inhibition per cent of 44.78 %. In addition, bacterial endophytes (GNBEF-14) have shown an inhibition of 40.13 % over control. Overall, it was found that among all biocontrol agents, only *Trichoderma* isolates showed best antagonistic effect against pathogen. Thus, it can be used further to test their efficacy and develop consortia to manage this devastating pathogen at the field level.

Keywords: endophytes; *Fusarium oxysporum* f. sp. *cubense* TR4; pathogen; *Trichoderma*; volatile organic compounds

Introduction

Fusarium wilt is one of the most lethal diseases of banana, posing a significant threat to global banana production, causing substantial economic losses to growers. *Fusarium oxysporum* f. sp. *cubense* Tropical Race 4 (Foc TR4), a new variant, is projected to reduce production by approximately 36 million tonnes and incur losses exceeding US$10 billion by 2040, potentially affecting up to 17 % of the world's banana-growing regions (1). The pathogen is soil-borne, hemibiotrophic, broad host range with no known teleomorph, producing macroconidia, microconidia and chlamydospores for colonization and dispersal. Macroconidia (27–55 × 3.3–5.5 µm) are falcate to nearly straight, thin-walled and typically 3-septate, borne singly on phialides. Microconidia (5–16 × 2.4–3.5 µm) are aseptate, oval to kidney-shaped and formed abundantly in false heads on short monophialides. Chlamydospores (7–11 µm) are produced abundantly in hyphae, singly or in pairs (2). Fusarium wilt, a serious and destructive disease in banana caused by a soil-borne *Fusarium oxysporum* f. sp. *cubense* (Foc) threatens 15 % of the global banana production and approximately 47 % of the total banana cultivation area of the world (3). In India, the Fusarium wilt incidence in cv. Grand Naine (Cavendish group) have been reported in most of the major banana growing areas, including Bihar, having Purnea and Kathiar with an incidence of 6–65 % and was also reported in Faizabad district of Uttar Pradesh with an incidence of 30–45 % (4, 5).

The perennial nature of the pathosystem, the polycyclic nature of the fungus, the ability of the fungus to survive in soil as chlamydospores for several years or in the non-hosts as asymptomatic endophytes, systemic nature of the disease, dissemination of the

fungus by contaminated planting material, soil, water, contaminated tools, farm equipment, clothes and footwear make conventional contact-based control measures ineffective, hence making the management of the disease difficult (6). Even though most of the chemical fungicides have been widely used in the management of various fungal diseases, in the case of Foc TR4 it has been found to be either non-efficacious or limited control efficiency (7). Efficient long-term management of Fusarium wilt disease is still challenging and involves the development of novel management approach (8). Numerous studies have shown that biocontrol strategies based on the selection of effective native endophytes and *Trichoderma* spp. provide promising results against FocTR4 under both *in vitro* and *in vivo* conditions. These endophytes produce a diverse range of secondary metabolites with broad-spectrum activity, which directly or indirectly contribute to plant growth promotion and enhance plant resistance to various biotic and abiotic stresses.

Among all the endophytic microbes, bacteria are the most dominant ones, followed by fungi (9). Endophytes have a myriad of biocontrol mechanisms to obstruct the growth and reproduction of pathogens in direct or indirect way. Direct mechanisms include antibiosis, lytic enzyme secretion, phytohormone production, phosphate solubilisation, siderophore production, Indole Acetic Acid production, 1-aminocyclopane-1-carboxylic acid (ACC) deaminase activity and competition for food and space. Likewise, indirect mechanisms include induction of plant resistance (ISR), stimulation of plant secondary metabolites, promotion of plant growth, hyper parasitism and predation (10). The endophytic fungi belonging to genera including non-pathogenic *Fusarium, Trichoderma*, *Serendipita,* etc. have been reported from different banana cultivars to manage Fusarium wilt, sigatoka disease and many other diseases (11). In addition, the comprehensive studies on fungal endophytes to manage FocTR4 through *in vitro* have been published by several workers (11–18). Several studies have reported the antagonistic potential of *Trichoderma* spp. in suppressing the growth of Foc TR4 under *in vitro* conditions and reducing disease severity under controlled greenhouse environments (19–21). A recent study showed that both *Trichoderma asperellum* strains, TRC900 and T34, inhibited Foc TR4 growth by ~40 % *in vitro*. TRC900 significantly reduced Fusarium wilt symptoms and induced systemic resistance in 'Valery' but not in 'Grand Naine'. Both strains promoted growth in 'Valery', while TRC900 reduced growth in 'Grand Naine'. Higher root colonisation by TRC900 in 'Valery' is correlated with its superior biocontrol efficacy (22). Similarly, another study on *Trichoderma virens* XZ11-1 produced 79.45 % siderophores (hydroxamate and carboxylate types) under optimised conditions and exhibited strong antagonism against Foc TR4 and ten other phytopathogenic fungi.

To date, there are no commercially available banana varieties that are resistant to Foc TR4. In addition, Foc TR4 is insensitive to some fungicides and long-term application of chemical pesticides causes pollution of soil ecology (23). In this context, the use of Trichoderma as a biological control agent (BCAs) offers a useful alternative for the management of Fusarium wilt of banana (24). *Trichoderma* species are fast-growing fungi that compete with pathogenic fungi for nutrition and living space, thereby limiting the growth of pathogenic fungi. They can parasitise the hyphae of pathogenic fungi and produce cell wall-degrading enzymes, ultimately leading to the death of the pathogenic fungi. Additionally, *Trichoderma* can also inhibit the growth of plant pathogens by producing secondary metabolites and volatile organic compounds that have antagonistic activity (25). Several authors have demonstrated the ability of certain *Trichoderma* species to reduce Foc growth (mainly Foc-TR4) under *in vitro* conditions and, in some cases, the severity of the disease under controlled greenhouse conditions (26). Pot experiments confirmed its root colonisation in banana plants, enhancing resistance to FocTR4 and improving iron uptake and growth through siderophore secretion (27). To be used as a BCA, bacterial VOCs must elicit specific detrimental effects on fungal pathogens, which show inhibition of conidia germination, damage fungal cell walls, alter hyphae morphology and even kill fungal pathogens (28). The antifungal efficacy of select bacterial endophytes viz.,*Brachybacterium paraconglomeratum* YEBPT2 (MK263736), *Brucella melitensis* YEBPS3 (MN022548), *Bacillus velezensis* YEBBR6 (MT372157), *Bacillus amyloliquefaciens* YEBFL3 (MT326231) and *Myroides odaratimimus* YEBRT3 (MN082530), in which *Brachybacterium paraconglomeratum* YEBPT2 exhibited the highest antifungal activity, suppressing Foc mycelial growth by 61.56 % and producing multiple bioactive compounds, such as Fluorouracil, Azetidine, Hydroxysulfonyl-3,4,4-trimethyl-2-azetidinone (29). Several endophytic bacteria producing antifungal VOCs against FocTR4 have been well characterised by several workers (30–32). The aim of this study was to screen out the best antagonistic isolates from the respective isolates against FocTR4 under *in vitro* assay to make their bioformulation for the management of Fusarium wilt of banana. Further evaluation for testing their efficacy and consortium development at field level can proceed to manage this devastating pathogen.

Materials and Methods

Collection isolation and identification of pathogen from wilt infected banana rhizome cv. Grand Naine

Samples of naturally Fusarium wilt infected banana plants cv. Grand Naine was collected from Kajha village of Purnea district in Bihar. During the collection process, cultivar Grand Naine displayed typical external and internal symptoms of wilting, having reddish brown discolouration around the inner corm that was used for the isolation process.

Half-strength Potato Dextrose Agar (PDA) media was used for isolation of the pathogen as per protocol (2). Using a sterilised razor blade, small pieces (2–3 mm) of infected diseased samples were cut. After sterilisation, the tiny pieces were washed with 1 % NaCl solution for 3 to 5 min, followed by thorough washing three times in sterile distilled water and then the samples were transferred to sterilised blotter paper to remove excess moisture. Under aseptic conditions, these pieces were then placed in petri plates (90 mm) containing PDA medium and incubated for 5 to 7 days at 26±2 °C. Various morphological characteristics, such as microconidia, macroconidia, septation and chlamydospores produced terminally or intercalary in single or chain forms, were used to identify pathogens (33). Additionally, cotton blue and lactophenol were used to make a slide of diseased sample and examined under compound microscopes (*Nikon Ci-L)* (40X and 100X) and photographs were taken. Purified cultures of the pathogen were obtained through the single hyphal tip technique (34). For further experiments, pure cultures were maintained on PDA slants in a refrigerator at 4 °C. Sufficient care was taken to maintain the genetic purity of isolates throughout the study. The fungus was identified using universal primer internal transcribed spacer (ITS) and race specific primer

secreted in xylem (SIX) genes followed by submitting the sequence to the NCBI site and obtaining accession number of FBGN8501 isolates (OQ999335.1; OR020890.1; OQ804372.1). The *SIX* genes used for race-specific identification of FocTR4, STR4, R1 and R4 of Foc (35). Specific *SIX* genes and their unique sequence variations/presence are used for the race-specific identification and differentiation of FocTR4.

Isolation of *Trichoderma* from rhizospheric soil from wilt infected banana field

The rhizospheric soil of 10 randomly selected plants was collected from wilt infected banana field in Purnra district (Bihar, India). Isolation of *Trichoderma* spp. was carried out using *Trichoderma*-Selective Medium (TSM) following the method described previously (36). One gram of rhizospheric soil from different banana cultivars was transferred into a 250 mL conical flask containing 100 mL of sterile distilled water and agitated on a rotary shaker at 120 rpm for 10 min to obtain a uniform suspension. The supernatant was serially diluted up to 10^{-5} and 1 mL aliquots from 10^{-3}, 10^{-4} and 10^{-5} dilutions were pipetted into sterile petri plates. Sterile medium was then poured and gently rotated to ensure even distribution. Plates were incubated at 28 ± 1 °C for 48 hr and emerging *Trichoderma* colonies were purified using the hyphal tip technique. Morphologically distinct colonies were sub cultured onto fresh PDA to obtain pure isolates and purified cultures were incubated at 28 ± 1 °C for 5–7 days and preserved in 50 % glycerol at -80 °C for long-term storage. In addition, the cultural and morphological characteristics features of *Trichoderma* isolates were observed.

Isolation, purification and maintenance of fungal endophytes from banana plant cv. Grand Naine

The protocol for the isolation of endophytes from banana plant with slight modification (cv. Grand Naine) was given by previous researchers (37). Following thorough washing with tap water, samples were chopped into tiny fragments and then treated with surfactants i.e. Tween-20 at 0.01 % followed by disinfected with 4 % NaCl for 20 min and rinsed three times with sterilised distilled water (SDW) then after 70 % ethanol for 1 min followed by rinsing 8 times with SDW and kept over the sterilised blotter paper to remove the excess moisture. Using a mortar and pestle, the sample was crushed in peptone salt water. The homogenate was serially diluted up to 10^{-3} dilutions. Aliquots (100 µL) from 10^{-1} and 10^{-3} dilutions were pipetted and plated onto petri plates containing PDA and TSM for the isolation of fungal endophytes. After plating, the plates were kept in an incubator at 25 °C for 48 –72 hr for colony appearance and any new colonies were immediately taken out and sub-cultured to the fresh medium. The culture was preserved in 20 % glycerol stock (v/v) and stored at -20 °C under refrigerator for further studies.

In vitro antagonistic effect of native *Trichoderma* and fungal endophytes isolates against *Fusarium oxysporum* f. sp. *cubense* TR4

To screen out the antagonistic effect of fungal endophytes and *Trichoderma* isolates against FocTR4 under *in vitro* conditions, a dual culture method elucidated by previous researchers was used (38). The 7-day-old culture of the pathogen was taken. Using a sterilised cork borer, the mycelial disc (5 mm) of both pathogen and *Trichoderma* isolates was cut from the margin of the culture plate and it was inoculated at 3 cm from the edge of the plate. Control plates containing only Foc were used and incubated at 28 ± 2 °C. Triplicates of the experiment were maintained. After ten days of incubation, observations were taken and the antifungal activity of the endophytes using per cent inhibition (PI) over control was computed by the formula as given by previous researchers (39).

Per cent Inhibition (PI) = (C-T/C) X 100 (Eqn. 1)

Where,

C = Growth in the control plate

T= Growth in the treated plate.

In vitro antagonistic effects of volatile organic compound (VOCs) of bacterial endophytes on mycelial growth of *Fusarium oxysporum* f. sp. *cubense* TR4

An antagonistic effect of VOCs produced by the four selected endophytic bacteria (GNBEF-4; GNBEF-9; GNBEF-12 & GNBEF-14) over the pathogen was carried out by adopting the procedure given by a previous researcher (40). Petri dishes with nutrient agar medium inoculated with the selected endophyte were covered with Petri dishes with PDA medium inoculated with a 6 mm diameter plug of Foc. Then, a double-plate chamber was fashioned by sealing the two petri plates tightly with parafilm. The average distance of 1.5 cm between the nutrient agar media surface and the PDA surface were maintained. Over the course of seven days, the double-plate chamber was incubated at 26±2 °C. A control chamber was made without bacterial strains. Three times the experiment was repeated. The bacterial endophytes were identified based on 16S r-DNA sequencing. The sequence was submitted to NCBI site and got accession numbers of respective endophytes GNBEF-4 (*Alcaligens faecalis*); GNBEF-9 (*Stenotrophomonas maltophilia*); GNBEF-12 (*Staphylococcus warneri*); GNBEF-14 (*Bacillus subtilis* of OR004594; OQ780907; OQ780918; OQ780887respectively.

Data analysis

All experiments were conducted in a CRD design. The generated data was statistically analysed by subjecting them to an analysis of variance (ANOVA) and means were compared using Duncan's Multiple Range Test ($p < 0.05$) using SPSS version 26.0 software.

Results

Cultural and morphological characteristics of *Trichoderma* isolates

The research work was conducted on different isolates of *Trichoderma* spp isolated from Foc-infected soil for testing their antagonistic potential against FocTR4. In the present investigation, the isolation of *Trichoderma* isolates from Foc infected field from Purnea district in Bihar and their cultural and morphological characteristics were studied on PDA medium. The data presented in (Table 1) showed that the isolates T-1-1723, T-2-1723, T-3-1723 and *T. asperellum* showed different cultural characteristics. The colony colour varied from buff white, dark green to brownish colour and the margin was regular, texture was fluffy to cottony, elevation was convex and pigmentation was shown to be dull white, pinkish to grey. As a morphological point of view, the *Trichoderma* was tentatively identified under a microscopic picture at 100X, the isolates (T-1-1723) was identified as *T. viride* based on the presence of conidia on phialids and isolates (T-2-1723) were identified as *T. harzianum* and isolates (T-3-1723) was identified as *T. asperellum* and one *Trichoderma* spp was molecularly identified as a *T. asperellum,* as shown in (Fig. 1).

Table 1. Cultural and morphological characteristics of *Trichoderma* spp.

Sl.No.	Isolates name	Colony colour	Margin	Texture	Elevation	Pigmentation
1	T-1-1723	Buff white with greenish	Regular	Fluffy to cottony	Convex	Dull white & pinkish in centre
2	T-2-1723	Dark green	Regular	Fluffy to cottony	Convex	Dull white & light pink in centre
3	T-3-1723	Light green & later brownish	Regular	Fluffy	Convex	Light pink
4	*T. asperellum*	Dark green	Regular	Fluffy	Convex	Dull white to grey

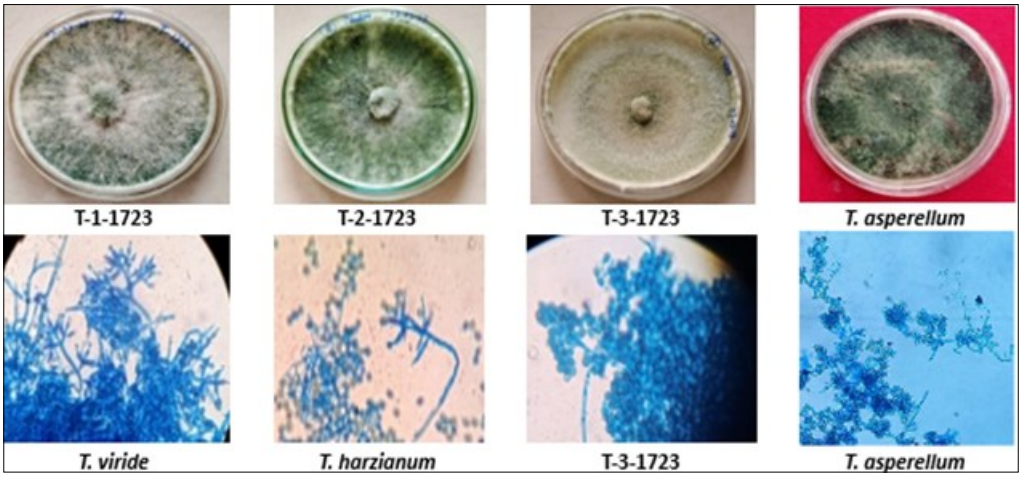

Fig. 1. Cultural and morphological characteristics of *Trichoderma* spp.

In vitro antagonistic effect of *Trichoderma* spp against *Fusarium oxysporum* f. sp. *cubense* TR4

The data presented in Table 2 showed that the isolates T-1-1723 and T-2-1723 showed 83.33 and 83.84 % inhibition of pathogen mycelial growth respectively. Isolates T-3-1723 and *Trichoderma asperellum* showed per cent mycelium inhibition of 88.89 and 88.82 mm respectively after 120 hr of incubation over control (Fig. 2).

In vitro antagonistic effect of fungal endophytes against *Fusarium oxysporum* f.sp. *cubense* TR4

Similarly, the antagonistic effect of five fungal endophytes against FocTR4 was presented in Table 3. The maximum inhibition of pathogen was found in the case of LfFE1 with 44.78 % followed by RzFE with 42.18 % inhibition over control, which was non-significant with each other. The endophyte i.e. PtFE2 and PsdFE, were also found to be non-significant with each other but significant to RzFE and LfFE1. The lowest 25.67 % mycelial growth inhibition was observed in PtFE1 (Fig. 3).

Effect of volatile organic compounds (VOCs) of most effective antagonistic bacterial endophytes against *Fusarium oxysporum* f. sp. *cubense* TR4

After testing their antagonistic effect against FocTR4 under dual culture assay, four potent bacterial endophytes were selected for VOCs production. The endophytes were used to determine the production of VOCs which have an inhibitory effect on the growth of the pathogen. The data presented in Table 4 showed that the highest per cent inhibition of mycelium growth of the pathogen over control was observed in GNBEF14 with 40.13 % followed by GNBEF-12 with 34.16 % and GNBEF-9 with 24.16 %. The lowest inhibition per cent of mycelium growth was recorded by GNBEF-4 with 17.50 % over control. The inhibitory effect of GNBEF-14 has shown a significant effect over GNBEF-9, GNBEF-12 and GNBEF-4. All fungal endophytes showing inhibition per cent of their respective value, are not statistically at par with respect to GNBEF-14 (Fig. 4).

Discussion

Cultural and morphological features of Trichoderma isolates

A taxonomically useful characteristic of *Trichoderma* is its growth rate, colony colour and colony appearance (41). In the present investigation the colony colour was initially observed as whitish to light green but later become dark green except isolates T-3-1723 which showed brownish colour colony along with yellowish colony reverse as shown in (Fig. 1). Similar results were obtained in various studies with pale to yellowish colour of colony reverse and many *Trichoderma* isolates grew rapidly at 25 °C to 30 °C but did not grow at 35 °C (41–43). After 48 hr, the colonies turned intense green because of the high number of spores produced in the mycelium, until eventually acquiring the colour of red wine (44). Several species of the genus *Trichoderma* show conidiophores with a tuft-like conidial mass of fertile conidia, arising from a conidiophore having 1 to 4 phialides and conidia are globose or ellipsoidal at the apex (45). Similar result for isolates T-2-1723, were reported earlier (46–48). The research finding of isolates T-1-1723 agrees with finding of previous

Table 2. *In vitro* antagonistic effect of *Trichoderma* spp. against *Fusarium oxysporum* f.sp. *cubense* TR4

Sl. No.	Trichoderma isolates	Colony diameter (mm)	Inhibition over control (%)
1	T-1-1723	15.14±0.61	83.33±0.69
2	T-2-1723	15.13±0.59	83.84±0.65
3	T-3-1723	10.23±0.62	88.89±0.69
4	*T. asperellum*	10.25±0.86	88.82±0.96
5	Control	90.00±0.00	0.00±0.00
	SEm±	0.35	0.39
	CD (p=0.05)	1.12	1.25
	CV (%)	1.40	1.31

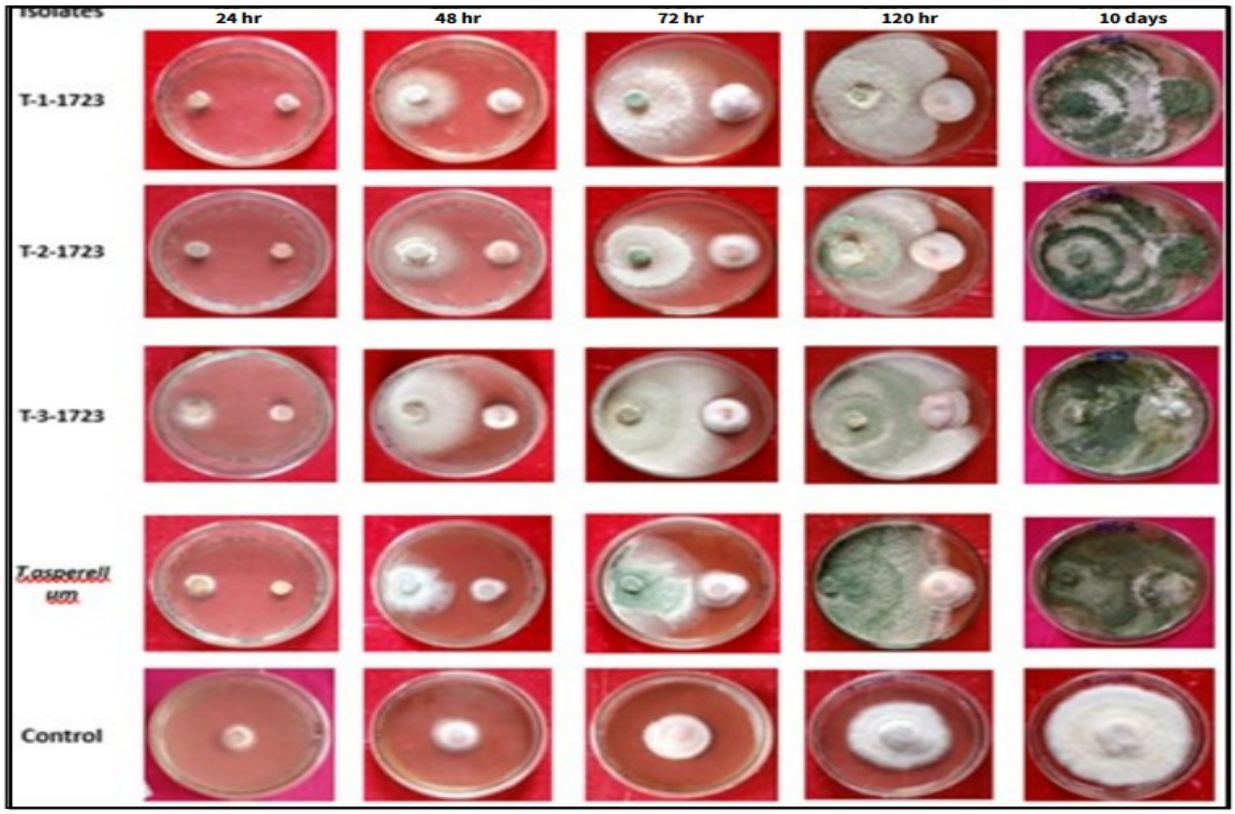

Fig. 2. *In-vitro* antagonistic effect of bacterial endophytes isolated from different parts of banana cv. Grand Naine against *Fusarium oxysporum* f. sp. *cubense* TR4.

Table 3. *In vitro* antagonistic effect of fungal endophytes against *Fusarium oxysporum* f.sp. *cubense* TR4 (FocTR4)

Sl. No.	Fungal endophytes	Colony diameter (mm)	Inhibition over control (%)
1	RZFE	52.50±3.33^{a}	42.18±4.66^{a}
2	PtFE1	67.00±5.33^{b}	25.67±7.36^{b}
3	PtFE2	60.00±4.77^{ab}	32.33±6.64^{ab}
4	PsdFE	56.51±6.32^{ab}	36.11±6.92^{ab}
5	LfFE1	49.50±0.87^{a}	44.78±0.96^{a}
6	Control	90.00±0.0^{c}	0.00±0.0^{c}
	SEm±	1.77	3.33
	CD (p=0.05)	7.59	8.67
	CV (%)	6.99	6.03

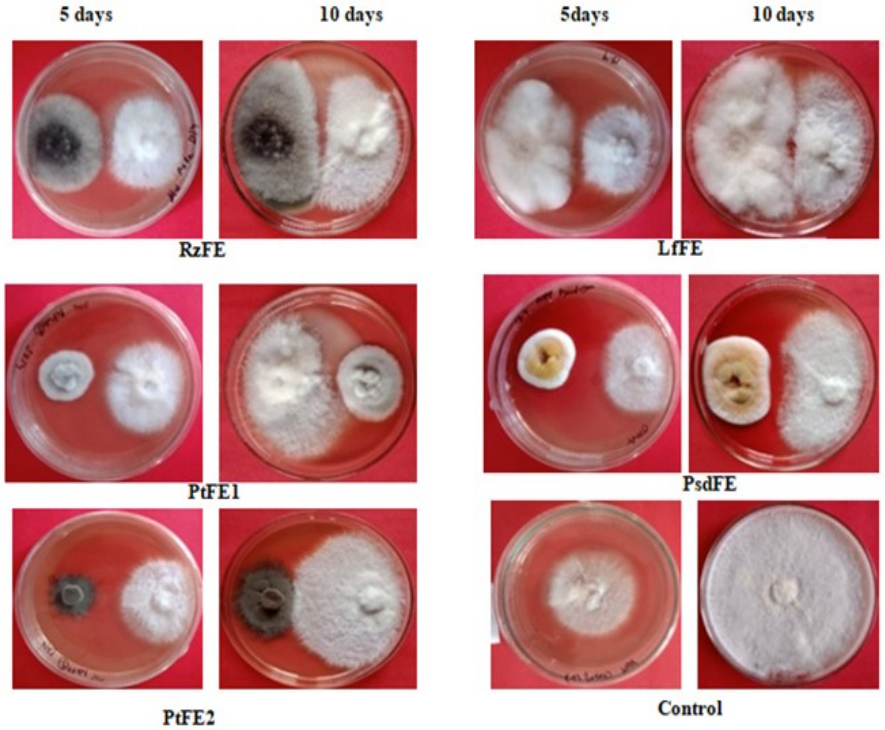

Fig. 3. *In-vitro* antagonistic effect of bacterial endophytes isolated from different parts of banana cv. Grand Naine against *Fusarium oxysporum* f. sp. *cubense* TR4.

Table 4. *In-vitro* effect of volatile organic compounds (VOCs) of most effective antagonistic bacterial endophytes against *Fusarium oxysporum* f. sp. *cubense* TR4 (FocTR4)

Sl.No.	Endophyte isolates	*Colony diameter (mm)	Inhibition over control (%)
1	GNBEF-4	49.50±0.44[b]	17.50±0.49[c]
2	GNBEF-9	45.50±0.62[c]	24.16±0.69[c]
3	GNBEF-12	39.50±1.18[d]	34.16±1.31[b]
4	GNBEF-14	36.00±1.23[c]	40.13±1.37[a]
5	Control	60.00±0.00[a]	0.00±0.00[d]
	SEm±	0.48	0.54
	CD (p=0.05)	1.54	1.72
	CV (%)	1.26	3.59

Fig. 4. Effect of volatile organic compound (VOCs)of bacterial endophytes isolated from different parts of banana cv. Grand Naine against *Fusarium oxysporum* f. sp. *cubense* TR4.

researchers who reported that conidiophores of *T. harzianum* were smooth or rounded, wide near the base (41). Phialides were arising from conidiophores having whorls of 2–6 phialides on the terminal branches. Conidia were sub-globose to ellipsoidal in shape, the apex was broadly rounded and base was narrowly rounded. The research findings are consistent with the previous work done on cultural and morphological characterisation of *T. viride* and *T. harzianum* (49).

In vitro antagonistic effect of *Trichoderma* spp. against *Fusarium oxysporum* f.sp. *cubense* TR4

To manage a diverse range of phytopathogens, *Trichoderma* spp produce a variety of bioactive secondary metabolites with antifungal, antibacterial and toxic properties like *Alternaria alternata, Fusarium* spp., *Pythium* spp., *Rhizoctonia solani* and *Sclerotinia sclerotiorum* and are reported as a bottomless source of antibiotic derivatives like terpenes, polyketides, isocyanide derivatives, piperacines and complex families of peptaibols (50). Furthermore, *Trichoderma* spp TRC-54 were earlier reported to show strong biocontrol activity against Foc race 1 through the direct action of enzymes and metabolites produced by plant growth-promoting Rhizobacteria (PGPR) (51). The most crucial hydrolytic enzyme endo-β-1,6-glucanase is one of the crucial hydrolytic enzymes for myco -parasitic activity of *Trichoderma* sp, which catalyses cell wall degradation by attacking β-1,6 linkages internally and mycoparasitism through hyphal coiling and conidiation (52, 53). In the present study all *Trichoderma* isolates showed mycelium inhibition ranging from 80–90 % as shown in (Fig. 2). The research findings of the present study is in agreement with the previous work on *Trichoderma* spp (11). It was reported that 3 *Trichoderma* isolates i.e. *T. reesei* (CSR-T-3), *T. koningiopsis* (CSR-T-2) and *T. asperellum* (CSR-T-4) against FocTR4 and among all strains the CSR-T-3 exhibited maximum inhibition of mycelium growth (85.19 %) after 120 hr followed by CSR-T-2 with 62.65 % and the lowest in CSR-T-4 with 50.00 %. Similar studies have reported the efficacy of *Trichoderma* spp. against *Fusarium oxysporum* f. sp. *cubense* tropical race 4 (FocTR4) (20, 21). In addition, numerous investigations have extensively reported the antagonistic potential of different *Trichoderma* species against FocTR4 (19, 51, 54–57). *T. viride* and *T. harzianum* have been evaluated under *in vitro* conditions and demonstrated significant antagonistic activity against Foc race 1 (FocR1), race 2 (FocR2) and FocTR4 (49). However, a recent *in vitro* study of *Trichoderma harzianum* D-LD and *T. asperelloides* G-BT against FocTR4 revealed a per cent inhibition of 87.4 % and 84.2 % respectively over control through the production of cell wall degrading enzymes, notably chitinase and protease (58).

In vitro antagonistic effect of fungal endophytes against *Fusarium oxysporum* f.sp. *cubense* TR4

In the case of fungal endophytes, 5 isolates were tested against FocTR4. All the isolates showed less than 50 % inhibition of the pathogen's mycelial growth. The highest inhibition was observed with LfFE1 (42.75 %), followed by RzFE (42.18 %). The difference between these 2 isolates was not statistically significant. The endophytes PtEF2 and PsdFE showed a non-significant difference from each other but were significantly inferior to RZEF and LfEF1. The lowest mycelial growth inhibition was observed in PtFE1 with 26.67 % as shown in (Fig. 3). Earlier, 3 *Trichoderma* isolates, *T. reesei* (CSR-T-3), *T. koningiopsis* (CSR-T-2), and *T. asperellum* (CSR-T-4), were tested against Foc TR4 using the dual culture method. The results showed that strain CSR-T-3 exhibited the highest inhibition of mycelial growth (85.19 %) after 120 hr, followed by CSR-T-2 (62.65 %), while the lowest inhibition was observed in CSR-T-4 (50.00 %) (11). Similarly, another study reported that two fungal endophytes *Trichoderma reesei* (UH EF), *Rigidoporus vinctus* (AAU EF) and one bacterial endophyte, *Sphingobacterium tabacisoli* (UHEB) exhibited significantly higher antagonistic potential against Foc, with inhibition of 72.33 %, 70 % and 65.5 % respectively (12). Other studies of fungal endophytes against FocTR4 were reported by several researchers (13, 58).

Effect of volatile organic compounds (VOCs) of native bacterial endophytes against *Fusarium oxysporum* f. sp. *cubense*TR4

Pathogens are controlled by antagonists through the production of antimicrobial compounds. These compounds may be formed either in volatile or non-volatile forms (59). Bacterial VOCs apparently have the potential to act as antifungal compounds (59). The issue of direct versus indirect effects of bacterial volatile compounds on pathogens arises from the fact that bacterial volatile compounds can directly inhibit pathogen growth (60). Furthermore, brown spores and abnormal mycelia could be due to dissolved volatile compounds in the culture medium, which may have impacted the fungal physiological traits (61). In the present investigation highest

inhibition of mycelium growth of the pathogen was observed in GNBEF-14 with 40.13 % followed by GNBEF-12 with 34.16 % and GNBEG-9 with 24.16 %. The lowest inhibition of mycelium growth was recorded in endophyte GNBEF-4 with 17.50 %. Thus, the higher production of VOCs was recorded in endophytes GNBEG-14 rather than other as shown in (Table 4 & Fig. 4). Previous researchers reported that out of 144 endophytic actinomycetes, *Streptomyces malaysiensis* 8ZJF-21 was found to be effective against FocTR4 which inhibited mycelial growth and spore germination under *in vitro* condition through production of 19 VOCs as confirmed by GC-MS (62). Similarly, the VOCs activity on the mycelial growth of FocTR4 was suggested in earlier reports which indicate that the strain CSR-D4 of *Bacillus licheniformis* showed highest mycelial growth inhibition (77.59 %) of the Foc TR4 through production of a diverse array of VOCs, including iturin, fengycin, surfactin and bacillomycin, confirmed by LC-MS (63). In addition, the effect of VOCs against FocTR4 was reported as confirmed by GC-MS assay (64). Furthermore, dual culture assay revealed that endophytes *Alcaligens* sp. showed maximum mycelial inhibition (75.18 %), followed by *S. maltophilia* (71.90 %) and *Staphylococcus wameri* (70.69 %), while lowest in *B. subtilis* (61.07 %) over control (65). Antagonistic activity of *Alcaligenes faecalis* against *Fusarium oxysporum* due to siderophore production in which 75 µL siderophore-broth gave the best inhibition of *F. oxysporum* (66). Likewise, *Alcaligenes faecalis* subsp. *Faecalis* S18 gave the highest suppression of *Fusarium* wilt of tomato due to chitinolytic, pectinolytic and hydrogen cyanide production (67). Similarly, the current study on endophytes B. *subtilis* PLLF2 against Foc exhibited significant inhibitory activity (58.66 %) over control through production of a broad spectrum of metabolites like nonanol and organic acids like hippuric acid and mucic acid (68). *Bacillus* spp. emits different VOCs, including organic acids, aldehydes, alcohols, ketones, esters, phenols, N-containing compounds, S-containing compounds and other hydrocarbons that have the potential for antifungal activity (69). Some of the VOCs include primary amines and organic acids such as 3-methyl butanoic acid and 2-methylbutanoic acid (69, 70). These antifungal VOCs can disrupt the hyphal morphology and lower the cell membrane stability, which causes desiccation and cell invasion by water-soluble toxins, due to increased cell membrane permeability (71). This antagonist activity of VOCs reduces the spore germination and mycelial growth of phytopathogenic fungi, which, in turn, lowers the rate of infection and plant damage (69).

The best antagonistic effect of *Trichoderma* isolates T-3-1723 against FocTR4 might be due to the presence of secondary metabolites, antibiosis, secretion of hydrolytic enzymes like chitinase, β-1,3 gluconase and mycoparasitism. In addition, the potent endophytic bacteria (GNBEF-14) against the pathogen might be due to the release of a diverse array of volatile organic compounds. However, the fungal endophytes (LfFE1) exhibited a per cent inhibition of 44.78 % only. This might be due to the rapid growth of pathogen or nutrient and niche competition or due to the standard PDA media or other media used in dual cultures, which might not favour the endophyte's optimal production of specific antifungal secondary metabolites or lytic enzymes (e.g., chitinases, glucanases) that are effective against FocTR4.

Conclusion

Our findings demonstrate the *in vitro* antagonistic potential of 4 native *Trichoderma* isolates including *T. asperellum* against FocTR4 obtained from wilt infected banana field. The results suggest that all *Trichoderma* isolates (04) showed per cent mycelial inhibition ranging from 80–90 % over the control followed by per cent mycelial inhibition in case of fungal endophytes ranging from 25-45 % over control and least mycelial inhibition through release of VOCs in case of bacterial endophytes (05) was ranged from 17–40 % over control. Overall, it was concluded that maximum antagonistic activity against the FocTR4 was found towards *Trichoderma* isolates and the least antagonistic activity towards bacterial endophytes. The future research should focus on validating the combined efficacy of promising all *Trichoderma* isolates, fungal & bacterial endophytes under field conditions after testing their compatibility. Efforts should also be directed towards optimising formulations and application strategies to sustain high inoculum levels and stable biocontrol activity in agricultural environments. Furthermore, genomic investigations of highly inhibitory *Trichoderma* strains and endophytes could reveal novel genes and pathways involved in biocontrol, paving the way for the development of improved or genetically enhanced biocontrol agents.

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Authors' contributions

MKP carried out the experiment, collected the data, and performed the analysis. SKS and AJ guided the research by formulating the research concept, while DKC and AS approved the final manuscript. PK and MC participated in the study design and conducted the statistical analysis. SC, PP and RW contributed to conducting the experiment and assisted in editing, summarizing and revising the manuscript. SAB and BSM helped with summarizing and revising the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

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

Ethical issues: None

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