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Metabolite-mediated antagonism of *Achromobacter xylosoxidans* against *Curvularia lunata* in banana

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Curvularia lunata (MLP-01; Gen Bank accession ON246070) is an important phytopathogen that causes leaf spot disease in *Musa paradisiaca*, resulting in significant yield losses. In the present study, one potent plant growth-promoting endophytic bacterium, *Achromobacter xylosoxidans* (MRH-11; Gen Bank accession ON955872) was isolated from healthy *Musa* sp. root tissues and transmission electron microscopy as well as confocal microscopic images were also taken to locate *A. xylosoxidans* within the root tissue of *Musa paradisiaca. A. xylosoxidans* was evaluated for antifungal activity against *C. lunata*. Dual culture assay showed strong antagonism, with *A. xylosoxidans* inhibiting 83% of mycelial growth. Extracellular metabolites were extracted with chloroform, ethyl acetate and analysed by gas chromatography–mass spectrometry (GC–MS) and Fourier transform infrared (FT-IR) spectroscopy. GC–MS profiling revealed a diverse range of bioactive metabolites, including phenolic compounds, fatty acids, long-chain hydrocarbons, esters and nitrogen-containing heterocycles. FT-IR analysis confirmed the presence of hydroxyl, aliphatic, alkene, ester, ether and amine functional groups, strongly supporting GC–MS-based compound identification. Nuclear Magnetic Resonance (NMR) was also used to identify the compounds. The integrated analytical approach highlights the biocontrol potential *of A. xylosoxidans* and demonstrates the role of endophytic bacterial metabolites as eco-friendly alternatives for the management of *C. lunata* in banana.

Keywords : *Curvularia lunata*, *Achromobacter xylosoxidans,* Metabolite mediated antagonism, GC–MS, FT-IR, NMR, Confocal, TEM

INTRODUCTION

Banana (*Musa* spp.) is one of the most important fruit crops worldwide; however, its productivity is severely constrained by fungal diseases. Leaf spot disease, caused by *Curvularia lunata*, is an emerging threat that leads to necrotic lesions, reduced photosynthetic efficiency and yield loss (Chowhan *et al.* 2023a). Prolonged use of chemical fungicides results in environmental contamination, pathogen resistance and health hazards. Plant growth-promoting endophytic bacteria have gained considerable attention as sustainable biocontrol agents because they can colonise plant tissues and produce antifungal secondary metabolites.

Merve and Soylu (2022) reported endophytic bacterial isolates from healthy banana plants which have antagonistic activities against crown rot disease caused by *Fusarium verticillioides*. Many endophytes produce a range of antibiotics, such as coronamycin, ecomycins, kakadumycins, munumbicins, pseudomycins and xiamycins (Christina *et al.* 2013). These endophytes are also resistant to various fungal infections. Studies have shown that endophytes can help mitigate diseases like *Fusarium* wilt in plants, particularly in pepper, tomato and banana (Sundaramoorthy *et al.* 2012). Bacterial endophytes that support plant growth can also prevent the spread of plant diseases (Morales-Cedeño *et al.* 2021). These bacteria can control many harmful fungi that cause diseases in vital crops. Some of these fungi include *Rhizoctonia, Sclerotium, Fusarium, Sclerotinia*, *Verticillium, Pythium* and *Phytophthora* (Cui *et al.* 2022). Among these, *Achromobacter xylosoxidans* has recently been reported as an endophyte in *Musa* root tissues with promising antifungal activity

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(Chowhan *et al.* 2023b; 2023c; Chowhan and Chakraborty, 2024).

Although the antifungal activity of *Achromobacter xylosoxidans* has been reported, comprehensive metabolite-level characterisation and correlation of chemical functionality with antifungal efficacy against *C. lunata* remain limited. Therefore, the present study aimed to (i) evaluate the antagonistic potential of *A. xylosoxidans* against *C. lunata*, (ii) characterise their extracellular metabolites using GC–MS and FT-IR and (iii) correlate functional groups with compound-wise biological significance to explain antifungal activity.

MATERIAL AND METHODS

Isolation and Identification of Microorganisms

The pathogen *Curvularia lunata* (MLP-01) was isolated from leaf-spot-infected banana leaves and identified by morphological characteristics and 18S rRNA sequencing (Chowhan *et al.* 2023a). *Curvularia lunata* (MLP-01) was used as the test pathogen. *Achromobacter xylosoxidans* (MRH-11) was isolated as endophytic bacterium from surface-sterilised healthy *Musa* root tissues and maintained on nutrient agar (Chowhan *et al.* 2023b). Molecular identification using 16S rRNA gene sequencing confirmed MRH-11 as *Achromobacter xylosoxidans* (Gen Bank accession ON955872). The rRNA sequencing results and datasets are submitted in NCBI GENBANK with accession numbers ON246070 and ON955872; the datasets are available at https://www.ncbi.nlm.nih.gov/nucleotide/

Antagonistic Assay

Antifungal activity was evaluated using the dual culture technique on potato dextrose agar plates. Percentage inhibition of mycelial growth was calculated relative to control plates without bacteria (Chowhan *et al.* 2023b).

Extraction of Extracellular Metabolites

Bacterial isolates were cultured in nutrient broth under shaking conditions. After incubation, cultures were centrifuged and the cell-free supernatant was extracted separately with chloroform and ethyl acetate. The organic phases were concentrated under reduced pressure and used for GC–MS and FT-IR analyses. The cell-free culture supernatants were extracted separately with chloroform and ethyl acetate. The organic phases were concentrated and used for chemical analysis.

GC–MS Analysis

Gas chromatography–mass spectrometry (GC–MS) analysis was performed to identify volatile and semi-volatile metabolites. Compounds were tentatively identified by comparing mass spectra with the NIST library. GC–MS analysis was performed using a capillary column-equipped GC–MS system. The GC–MS analysis was carried out by Environcheck in a private laboratory in West Bengal. The two solvents used in the GC–MS analysis were chloroform and ethyl acetate for MRH-11. A 10 ml amber vial was filled with a 2 ml sample of sterile culture filtrate obtained after centrifuging the broth culture media. The material was then combined with 2 ml of ethyl acetate/chloroform. The mixture was extracted until the two layers were distinct. The chloroform/ethyl acetate layer (1:1) was pipetted after the anhydrous sodium sulphate layer was used as an inert drying agent to remove water from organic solutions. The chloroform and ethyl acetate layer (1:1) was filtered using a syringe filter before being subjected to GC–MS. To find the toxic metabolites, the AGILENT 7890B System was utilised for gas chromatography mass spectrometry (GC–MS).The initial temperature (hold time zero) was 75 °c, and the input temperature was 225°c. The temperature ranges for Ramps 1 and 2 were 25 °c/min to 150 °c and 10 °c/min to 280 °c (Hold time 10 min), respectively (Chowhan and Chakraborty, 2024).

FT-IR Analysis

Fourier Transform Infrared spectroscopy (FT-IR) was used to identify functional groups in crude extracts. Spectra were recorded over the range 4000–400 cm^{-1}. FT-IR spectra of dried extracts were recorded using the KBr pellet method over the same range. Functional groups were assigned using standard IR reference data. ATR-FTIR spectra of the sample were recorded using a

Perkin-Elmer Spectrum Two with a Universal ATR FT-IR spectrometer equipped with an ATR accessory. Samples were dissolved in a minimal amount of methanol, and a thin film was deposited onto the ATR crystal by pipeting ~2–3 µL and allowing the solvent to evaporate, or the solid was placed directly onto the crystal and gently pressed with the ATR clamp to ensure good contact. Spectra were acquired from 4000–400 cm^{-1} at 4 cm-1 resolution, averaging 32 scans per sample. A background spectrum was recorded before each set of measurements. Spectra were baseline-corrected and normalised to the band at 1450 cm^{-1} using Spectrum 10 software (Spectrum 10.5.2.636). Spectra were then exported as a spectrum between wave number (cm-1) vs transmittance (%). FT-IR analysis was done from Heredity Bioscience, Bhubaneswar, Odisha (Gong *et al.* 2024).

¹H NMR methodology

¹H Nuclear Magnetic Resonance (NMR) analysis was performed on bacterial isolate MRH-11, using a BRUKER ASCEND™ 400 NMR spectrometer with a 400 MHz superconducting magnet at the Presidency University, Kolkata. Spectral acquisition and processing were performed using TopSpin software version 3.5, and detailed spectral interpretation, integration and peak assignment were further supported using MestReNova software. Samples were prepared from cell-free broth extracts, dissolved in appropriate deuterated solvents and transferred to standard 5 mm NMR tubes. Chemical shifts (ä) were reported in parts per million (ppm) relative to the residual solvent signal and signal multiplicity and proton integration values were used to infer the structures of the dominant metabolites in each extract (Hays, 2005).

Transmission Electron Microscopy (TEM)

To determine the presence of endophytic bacteria within banana root cells, control and treated banana plants were sampled and root samples (1–2 mm) were fixed in 2.5% glutaraldehyde and 2% paraformaldehyde in 0.1 M phosphate buffer (pH 7.4) following standard TEM protocols (Graham and Orenstein, 2007; Hayat, 2012; Karanja *et al.* 2021). Fixation was performed at room temperature, followed by post-fixation at 4 °C. Samples were washed with phosphate buffer and dehydrated through a graded ethanol series (30–100%). Resin infiltration was carried out with LR White resin, followed by polymerisation at 56 °c. Ultrathin sections were cut using a Leica EM UC7 ultra microtome, mounted on grids and examined under a CRYO-TEM (TALOS S, Thermo Scientific) at AIIMS, New Delhi.

Confocal microscopy

To localise the endophytic bacterium MRH-11 within banana root tissues, both treated (bacteria broth–inoculated) and control (uninoculated) samples were subjected to fluorescence-based confocal microscopy. Banana seedling root segments were thoroughly washed, surface-sterilised (by 0.1% $HgCl_2$) and incubated with bacterial broth suspensions of MRH-11 for 48 hrs to allow colonisation. Following incubation, root tissues were gently rinsed to remove loosely attached cells and stained with propidium iodide (PI) and DAPI (42 ,6-diamidino-2-phenylindole) a nucleic acid–binding fluorochrome that emits red fluorescence upon intercalation with DNA. Stained samples were mounted on glass slides and visualised using a Leica SP8 Confocal Laser Scanning Microscope at AIIMS, New Delhi. Appropriate excitation and emission settings were used to detect PI and DAPI fluorescence and optical sectioning (z-stacks) was performed to distinguish internalised bacterial signals from surface-associated fluorescence (Thomas and Reddy, 2013).

RESULTS AND DISCUSSION

Antifungal activity against Curvularia lunata

Achromobacter xylosoxidans exhibited strong antagonistic activity against *C. lunata*. *A. xylosoxidans* showed significantly higher inhibition of 83%, indicating its biocontrol potential (Fig. 1).

GC–MS Profiling of Bacterial Metabolites

GC–MS analysis revealed that extracts contained a complex mixture of bioactive compounds (Chowhan *et al.* 2025; Chowhan *et al.* 2023c).

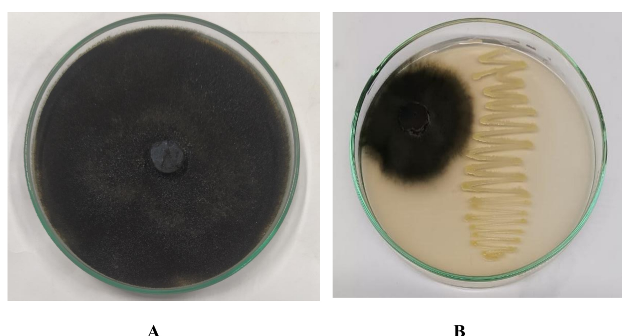

Fig 1: *Curvularia lunata* growth alone (A); *In vitro* antagonistic activity of *Achromobacter xylosoxidans* against *C. lunata* (B)

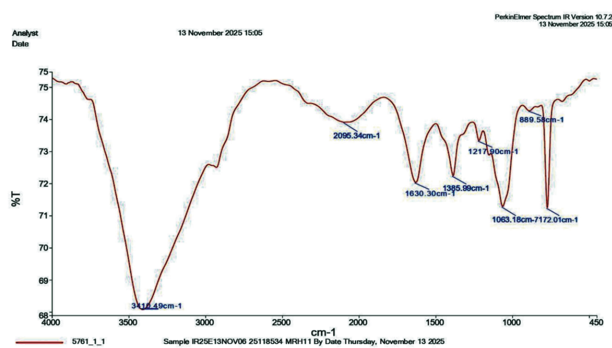

Fig. 2: ATR-FTIR Spectral Interpretation of *Achromobacter xylosoxidans*

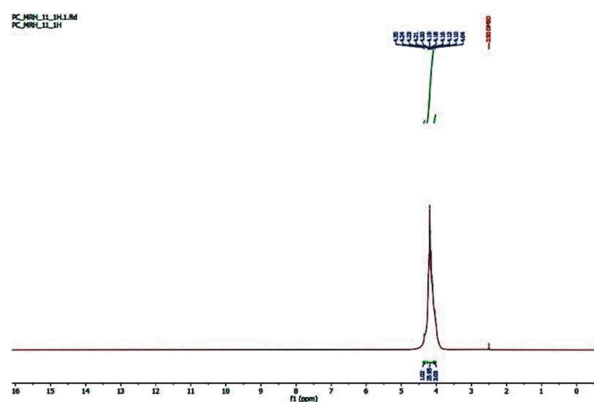

Fig 3: ^{1}H NMR analysis of culture filtrate of *Achromobacter xylosoxidans* showing 30 protons

Major chemical classes included long-chain alkanes and alkenes (cyclododecane, octadecene, nonadecene), fatty acids (n-hexadecanoic acid), esters (diethyl phthalate, long-chain acetates), phenolic compounds (2,4-di-tert-butylphenol) and nitrogen-containing heterocycles such as pyrrol [1,2-a] pyrazine derivatives. These compounds have been widely reported to possess antifungal, antibacterial and antioxidant activities.

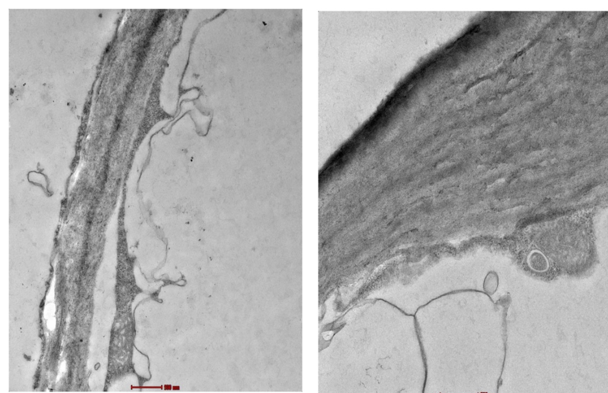

Fig 4 : TEM images of untreated banana root

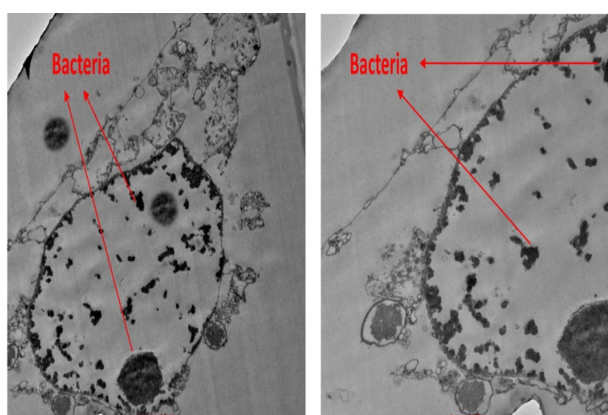

Fig 5: Presence of *Achromobacter xylosoxidans* inside the banana root tissue, observed through TEM

GC–MS profile of metabolites produced by Achromobacter xylosoxidans

GC–MS analysis of chloroform and ethyl acetate extracts of *Achromobacter xylosoxidans* (ON955872) revealed a broad spectrum of extracellular metabolites with varying polarity and biological relevance. The chloroform extract predominantly contained non-polar and weakly polar compounds, including long-chain alkanes and alkenes (cyclododecane, 1-decene, tetradecene isomers, cetene), aldehydes, fatty alcohols and high-molecular-weight hydrocarbons (tritetracontane). In contrast, the ethyl acetate extract was enriched in moderately polar compounds, including phenolics, nitriles, esters, nitrogen-containing heterocycles and fatty acids. This diversity indicates that *A. xylosoxidans* employs multiple chemical strategies for antagonism, combining membrane-active lipophilic molecules with polar bioactive secondary metabolites (Chowhan *et al.* 2023c; 2025).

FT-IR spectral interpretation of Achromobacter xylosoxidans

FT-IR analysis of the crude extracts revealed distinct absorption bands corresponding to functional groups associated with the GC–MS-identified compounds (Fig. 2). The broad band at 3410.49 cm^{-1} corresponds to N–H stretching vibrations, indicating the presence of primary amines and nitrogen-containing heterocycles. The absorption at 2095.34 cm^{-1} is characteristic of cumulenes or highly unsaturated carbon systems, supporting the detection of unsaturated hydrocarbons. The band at 1630.30 cm^{-1} represents N–H bending and C=C stretching vibrations typical of amides, alkenes and aromatic systems (Dehnavi *et al.* 2021; Coates, 2000). Bands observed at 1385.99 cm^{-1} are attributed to aldehydic C–H bending, while strong absorptions at 1217.90 and 1063.18 cm^{-1} correspond to C–O stretching of esters and ethers. Peaks at 889.58 and 772.01 cm^{-1} confirm the presence of alkene C=C bending and substituted aromatic rings, respectively.

Integrated GC–MS and FT-IR correlation analysis of Achromobacter xylosoxidans

Correlation of GC–MS and FT-IR data provides mutual validation of metabolite identification. Nitrogen-associated FT-IR bands strongly support the detection of pyrrolo [1,2-a] pyrazine-1,4-dione derivatives and diazabicyclic compounds in ethyl acetate extracts. Aliphatic C–H stretching and bending vibrations correspond with the abundance of long-chain hydrocarbons, fatty alcohols and alkenes identified by GC–MS. Ester and ether-associated C–O stretching bands corroborate the presence of carbonic acid esters, acetate esters and phthalate derivatives. Importantly, aromatic C–H bending vibrations are consistent with phenolic compounds such as 2,4-di-tert-butylphenol and dimethoxyphenols, which are well known for antifungal activity. Unlike isolated compound identification, this integrated spectroscopic approach confirms that the antagonistic activity of *A. xylosoxidans* is likely due to the combined action of chemically diverse metabolites rather than a single dominant compound. To establish a robust chemical validation of metabolites produced by *Achromobacter xylosoxidans*, GC–MS-identified compounds from chloroform and ethyl acetate extracts were correlated with FT-IR spectral understanding. The FT-IR functional group assignments closely matched the chemical classes detected by GC–MS, confirming the presence of alkenes, long-chain hydrocarbons, phenolics, esters, alcohols, amines and nitrogen-containing heterocycles. (Table 1) presents a direct correlation between FT-IR absorption bands and GC–MS-identified metabolites along with literature-supported functional relevance.

Nuclear Magnetic Resonance (NMR)

The ^1H NMR spectrum of *A. xylosoxidans* was dominated by a large aliphatic proton envelope integrating to approximately 30 protons (Fig. 3), indicative of a long-chain fatty alcohol, tentatively identified as 2-tetradecanol. Long-chain aliphatic alcohols generally display intense upfield signals between ä 0.8–1.6 ppm corresponding to terminal methyl and methylene groups and are commonly reported microbial metabolites involved in membrane modulation and antibacterial activity (Schwob *et al.* 2006). Overall, the ^1H NMR data corroborate GC–MS findings, demonstrating that *A. xylosoxidans* is rich in lipid-derived metabolites, highlighting distinct metabolic signatures and biological roles among the studied pathogens.

Solvent-Dependent Distribution of Bioactive Compounds

The FT-IR spectral features of *A. xylosoxidans* underscores the importance of solvent polarity in metabolite recovery. Chloroform preferentially extracted hydrophobic compounds, including wax alcohols, alkenes and phenolic antioxidants, which are known to disrupt fungal membranes. Ethyl acetate efficiently recovered phenolic, esterified and nitrogenous metabolites associated with enzyme inhibition and oxidative stress induction in fungal cells. This complementary solvent behaviour ensures comprehensive metabolite profiling and strengthens the reliability of the analytical results. Ethyl acetate favoured extraction of moderately polar antifungal metabolites, including fatty acids, nitrogen-containing compounds and phenolics.

Table 1: Correlation of FT-IR bands with GC–MS-identified metabolites from *Achromobacter xylosoxidans*

FT-IR wavenumber (cm?^{1})	Functional group assignment	Representative GC–MS compounds	Chemical / biological relevance	Literature support
3410.49	N–H stretching (primary amine)	Pyrrolo[1,2-a]pyrazine-1,4-dione derivatives; diazabicyclo compounds	Antimicrobial, antifungal, quorum-sensing inhibition	Dehnavi *et al.* 2021
2095.34	C=C=C stretching (allene/alkyne-related)	Unsaturated hydrocarbons (1-decene, tetradecene isomers)	Membrane-disrupting antifungal activity	Annamalai and Kasilingam, 2024
1630.30	N–H bending / C=C stretching	Phenolic compounds; alkenes	Protein interaction; inhibition of fungal enzymes	Coates, 2000
1385.99	Aldehyde C–H bending	E-15-heptadecenal; hexenal derivatives	Antifungal volatile signaling molecules	Strobel and Daisy 2003
1217.90	C–O stretching (vinyl ester/ether)	Carbonic acid esters; acetate esters	Cell wall permeability alteration	Silverstein *et al.* 2014
1063.18	Alkyl aryl ether C–O stretching	Dimethoxyphenols; phenyl sulfides	Antioxidant and antifungal roles	Stuart, 2004
889.58	Alkene C=C bending	1-octadecene; nonadecene; cetene	Disruption of fungal lipid bilayers	Desbois and Smith , 2010
772.01	1,3-disubstituted aromatic C–H bending	2,4-di-tert-butylphenol; dimethoxyphenols	Strong antifungal and antioxidant activity	Padmavathi *et al.* 2015

Chloroform extracts of *A. xylosoxidans* were dominated by non-polar hydrocarbons, long-chain alkenes, fatty alcohols and aldehydes, whereas ethyl acetate extracts showed a higher abundance of phenolics, esters, nitriles and nitrogenous heterocycles. This solvent-dependent variation confirms the differential solubility of bioactive metabolites and highlights the importance of using multiple solvents for comprehensive metabolite profiling.

Biological and antifungal relevance against Curvularia lunata

Phenolic compounds such as 2,4-di-tert-butylphenol and 3,5-dimethoxyphenol are well-known bacterial secondary metabolites with broad-spectrum antifungal activity, mediated by oxidative stress induction and membrane destabilisation. Nitrogen-containing heterocycles, including pyrrolo [1,2-a]pyrazine-1,4-dione derivatives, play a vital role in microbial antagonism by inhibiting fungal growth and signalling pathways. Long-chain alkenes, alcohols and fatty acids disrupt fungal plasma membranes, causing leakage of cellular contents and growth inhibition. Phenolic metabolites identified in the ethyl acetate extract interfere with fungal cell wall synthesis and induce oxidative stress. Nitrogen-containing heterocycles disrupt fungal metabolic pathways and signalling systems. Long-chain fatty acids, aldehydes and alkenes compromise membrane integrity, leading to cytoplasmic leakage and growth inhibition. The coexistence of these compound classes suggests a synergistic antifungal mechanism, explaining the strong antagonistic activity of *A. xylosoxidans* against *C. lunata*. Several metabolites identified in this study have documented antifungal properties. 2,4-Di-tert-butylphenol is known to inhibit fungal growth by inducing membrane damage and oxidative stress (Sundar and Arunachalam, 2025). Fatty acids such as n-hexadecanoic acid and dodecanoic acid interfere with fungal lipid metabolism (Guimaraes and Venancio, 2022). Pyrrolo-pyrazine derivatives are recognised as microbial antibiotics with broad-spectrum antifungal activity.

Localization of A. xylosoxidans within the root tissue of Musa paradisiaca observed thorough transmission electron microscopy

Transmission electron microscopic images revealed clear differences between treated and

control banana root tissues. No bacteria were observed in control root tissue (Fig. 4). In roots treated with *A. xylosoxidans*, the presence of endophytic bacteria was observed within banana root cells (Fig. 5), confirming successful colonisation of *A. xylosoxidans* within the plant tissue.

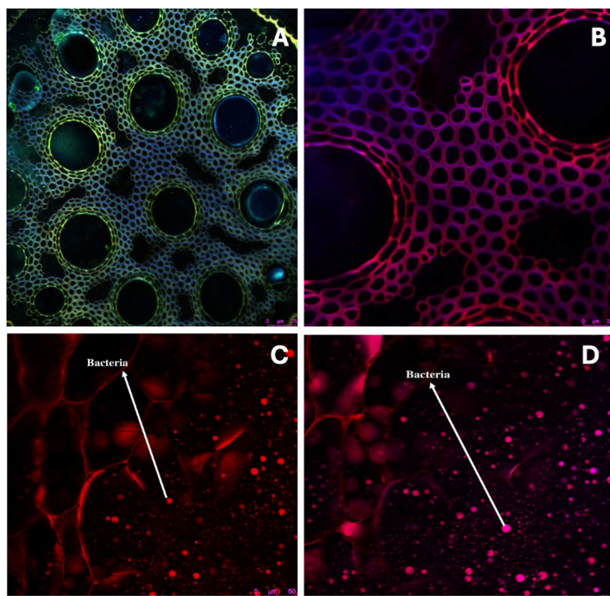

Fig 6 : Confocal images of untreated banana root (A&B); Presence of *Achromobacter xylosoxidans* inside the banana root tissue, observed through confocal images (C&D).

Confocal microscopy

Confocal laser scanning microscopy revealed clear differences between treated and control banana root tissues. In roots treated with *A. xylosoxidans* broth cultures, confirming successful colonisation of endophytic bacteria within the plant tissue (Fig. 6 A&B). These signals were absent or negligible in control roots, indicating the absence of bacteria (Fig. 6 C&D). The internal localisation pattern suggests that *A. xylosoxidans* can penetrate root tissues and establish endophytic associations rather than remaining as surface contaminants. Similar use of confocal microscopy has been widely reported for tracking bacterial colonisation in plant tissues. Previous studies have demonstrated that effective endophytic colonisation is closely linked to enhanced plant growth promotion and biocontrol efficacy, particularly in banana and other monocotyledonous crops. The observed contrast between treated and control tissues in the present study therefore provides strong microscopic evidence supporting the endophytic nature of *A. xylosoxidans* and its potential functional role in host–microbe interactions.

From the above results, in a nutshell, FT-IR spectra showed strong absorption bands corresponding to O–H stretching of alcohols and phenols, N–H stretching of amines and heterocycles, aliphatic C–H stretching of long hydrocarbon chains, C=C stretching of unsaturated compounds, and C–O stretching of esters and ethers. These functional groups confirm the chemical diversity observed in GC–MS analysis. The presence of hydroxyl groups correlates with phenolic compounds and fatty alcohols identified by GC–MS. Aliphatic C–H vibrations support the abundance of long-chain hydrocarbons, while ester-related C–O stretching corresponds to fatty acid esters and phthalates. Nitrogen-related FT-IR bands validate the detection of heterocyclic compounds. This strong agreement confirms the reliability of the integrated analytical approach. Phenolic compounds such as 2,4-di-tert-butylphenol are known to disrupt fungal cell membranes and inhibit spore germination. Fatty acids and long-chain alcohols interfere with membrane integrity and energy metabolism. Nitrogen-containing heterocycles may inhibit fungal enzymatic pathways and quorum sensing. The higher inhibition observed for *A. xylosoxidans* is attributed to its richer and more diverse metabolite profile. The results of NMR also support the GC–MS profile and TEM and confocal microscopy images confirm the presence of endophytic bacteria inside the root tissue of banana, which act as plant growth-promoting endophytic bacteria.

CONCLUSION

The present study demonstrates that *Achromobacter xylosoxidans* produces diverse antifungal secondary metabolites effective against *Curvularia lunata*. *Achromobacter xylosoxidans* exhibited antagonistic activity (83%). GC–MS and FT-IR analyses provided complementary evidence for the presence of bioactive compounds responsible for antifungal activity. These findings highlight the potential of endophytic bacteria as sustainable biocontrol agents for managing leaf spot disease in banana.

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DECLARATION

Conflict of interest .There are no competing interests among the authors.

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