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Endophytic Fungi from *Lansium domesticum* Stems as In Vitro Antagonists of *Ceratocystis fimbriata*: Isolation and Identification

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Abstract

Sudden wilt disease caused by *Ceratocystis* has been reported to attack and cause up to 100% mortality in duku plants in South Sumatra. Biological control of this disease in duku plants has not been widely implemented, so it is important to research endophytes to identify microorganisms that live and thrive within plant tissues and can enhance plant resistance to diseases and environmental stress. This study aims to identify endophytic fungi species from duku plant stems and their potential to inhibit the growth of the pathogen *Ceratocystis*, the cause of wilt disease in duku plants. Endophytic fungi were isolated from the stems of duku plants in Ogan Ilir Regency, Ogan Komering Ilir Regency, and Musi Banyuasin Regency. Eleven isolates of endophytic fungi were successfully isolated and fungal identification was conducted by PCR amplification and sequencing of the internal transcribed spacer 1 (ITS1) and ITS4 regions of nuclear ribosomal DNA as *Trichoderma asperelum*, *Phoma* sp. *Fusarium oxysporum*, *Lasiodiplodia theobromae*, *Penicillium citrinum*, *Nigrospora oryzae*, *Nigrospora sphaerica*, *Eutiarosporella* sp. All endophytic fungi isolate exhibited varying levels of inhibitory ability; the isolate with the highest inhibitory ability was SDW 3B (52%), isolates with moderate inhibitory ability were DSPTW 6A, SDMW 7B, SDMW 8A, and SDW 5A (44% to 47%), and the isolate with the lowest inhibitory ability was TRW1B, TRW5, WSA4A and RMIP1 (39-43%). Regarding hyphal interaction mechanisms, six isolates (SDMW 7B, SDW 3B, RMIP 1, TRW 5, TRW 1B, and WSA 4A) caused pathogenic hyphae to lyse. DSPTW 6A Isolate caused pathogenic hyphae to swell, and three isolates (SDW 5A, SDMW 8A, and TRW 1B) caused pathogenic hyphae to coil and lyse.

Keywords – Biological Control – Ceratocystidaceae – Meliaceae – Wilt diseases

Introduction

Lansium domesticum is a tropical fruit plant that belongs to the family Meliaceae (Abdallah et al. 2022). This perennial plant can grow up to 30-40 meters tall. *Lansium domesticum* has seeds of 1-3 segments, each 2.5 cm long and 1.25-2 cm thick (Techavuthiporn 2018). Duku is an important plant in Indonesia and has several varieties, including duku, kokosan, and langsat. Based on micro and macromorphological characterization and identification, the taxonomic status of duku, kokosan, and langsat falls within the same genus, *Lansium*, with the species name *Lansium*

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domesticum. In the infraspecific category, they are divided into two groups: the duku group and the kokosan-langsat group (Hanum et al. 2013a). Duku dominates the Sumatra region and is found in almost all regencies in South Sumatra, while the langsat variety is more dominant in the Kalimantan region (Hanum et al. 2018). The differences in varieties from the various areas are due to differences in anatomical, morphological, and physiological characteristics in the stem, leaves, and fruit of duku (Hanum et al. 2013b, Susilawati et al. 2016).

Duku plantations in South Sumatra are currently managed conventionally, and there is still a lack of knowledge about proper duku maintenance. Maintenance practices are limited to light activities such as sanitation before and after harvest. This light maintenance, which mainly consists of sanitation and is not followed by other maintenance steps, can weaken the plants and make them more susceptible to diseases (Patty et al. 2022). This has also led to low duku production due to pest and disease attacks. Over time, various diseases affecting duku plants have been reported, including duku wilt, branch dieback, and fruit spots. Between 2019 and 2021, a new wilt disease was reported, characterized by the sudden death of duku plants. Suwandi et al. (2021) stated that *Ceratocystis fimbriata* is the cause of the sudden death of duku plants in South Sumatra. This disease has spread across eight regencies in South Sumatra, ranging from mild to severe attacks, with mortality rates reaching up to 100% (Muslim et al. 2022).

Ceratocystis is a pathogen that causes wilt disease and stem canker in several plants in Indonesia. In 2011, this pathogen was reported in Indonesia as the cause of disease in *Acacia mangium*, which belongs to the legume family (Tarigan et al. 2011). This pathogen has also caused sudden wilt in bullet wood (*Mimusops elengi*) (Pratama et al. 2021a), wilt disease in jackfruit (*Artocarpus heterophyllus*) (Pratama et al. 2021b), and wilt disease in soursop (Pratama et al. 2023). The progression of this disease is characterized by the formation of lesions in the form of lines and scratches on the sapwood, followed by discoloration of the xylem, which spreads from the site of inoculation. The discoloration of the xylem is correlated with xylem dysfunction, resulting in a reduced supply of water to the leaves. As the xylem dysfunction spreads, it ultimately leads to plant death (Yakushiji et al. 2019).

Ceratocystis disease is closely related to wounds on the plant. According to Nasution et al. (2022), a strategy to limit the spread of this pathogenic species is to minimize wounds through pruning. One method of biological control for *Ceratocystis* disease is the use of endophytic microorganisms. Endophytes are defined as microorganisms that live and develop within plant tissues and can enhance the plant's resistance to diseases and environmental stress (Mei & Flinn 2009). *Rhodococcus* sp. KB6 from *A. thaliana* plants can control black rot disease on sweet potato leaves caused by the fungal pathogen *Ceratocystis fimbriata*. *Rhodococcus* has become increasingly important in biological control due to its ability to degrade various toxic chemicals and produce bioactive compounds (Hong et al. 2016). Endophytic fungi of *A. mangium* have the potential to be harnessed as anti-Ceratocystis, *Trichoderma* sp. (AC 9R) from *Acacia* root exhibited strong inhibition for *C. fimbriata* between 58.33 to 69.23% (Ahmad et al. 2022). Biological control by exploring endophytic fungi against *Ceratocystis* disease in duku has never been conducted, which is the background of this research aimed at identifying endophytic fungal species in duku plants in South Sumatra and their potential to suppress the growth of *Ceratocystis*, the pathogen causing wilt disease in duku plants.

Materials & Methods

Sample collection and isolation

Sampling was carried out from October 2024 to February 2025. Plant sampling was conducted using a purposive random sampling method in four regencies in South Sumatra: Ogan Komering Ilir (OKI), Ogan Komering Ulu (OKU), Musi Banyuasin (MUBA), and Ogan Ilir (OI). Samples were taken from healthy duku seedlings, with 10 plants per location. The selection of locations was based on the level of *Ceratocystis* disease infestation observed in previous research

(Muslim et al. 2022), categorized as no infestation (OKI and OI), moderate infestation (MUBA), and severe infestation (OKU).

Healthy *L. domesticum* plants aged two to three years were sampled, placed in sterile plastic containers, and transported to the laboratory for subsequent processing. The duku seedlings were first cleaned by rinsing with running tap water to remove debris and soil that usually adheres to the seedling surface. The stem of the samples was then taken. Healthy duku plant stems were cut into three pieces of 1 cm x 1 cm each using sterile scissors. Next, the samples were disinfected with 70% ethanol for 1-3 minutes, followed by 4% sodium hypochlorite (NaClO) solution for 3-4 minutes, and then rinsed with 70% ethanol for 2-5 seconds. In the final step, the samples were rinsed with distilled water twice, each for 1 minute, then dried on sterile filter paper inside a laminar airflow cabinet under sterile conditions (Senanayake et al. 2020). The samples were then planted on potato dextrose agar (PDA) medium (Merck, Germany) with streptomycin sulfate (100 mg/L) (Meiji, Indonesia). The isolation was carried out inside the laminar airflow cabinet, with each petri dish containing 4-5 sample pieces. After inoculation, the dishes were labelled accordingly and incubated on a laboratory bench at a temperature of 28±2°C for 2-3 days. After 2-3 days, the fungi were re-isolated using fresh PDA in the laminar airflow cabinet and then incubated at 28±2°C for 5-7 days (Liao et al. 2025).

Characterization and Identification of Endophytic Fungi

The morphological characteristics of the isolate were examined using both macroscopic and microscopic observations. Macroscopic observations were made by growing all isolates on PDA and MEA media, with five Petri dishes for each isolate. Fungal colony characterization was performed by examining each isolate's colour, shape, and margin. Several colony shapes and margins were used to observe the macroscopic characteristics of the fungi (Aragaw et al. 2023; Huda-Shakirah et al. 2024). The diameter growth of fungal colonies was measured five times at 3-day intervals up to the 15th day. Microscopic characterization was performed using the slide culture method, with one drop of lactophenol blue reagent added. The slides were examined using a light microscope (Olympus CX23). The data on these characteristics were then compared with fungal identification books (Habisukan et al. 2021), such as Larone's Medically Important Fungi (Walsh et al. 2018), Pictorial Atlas of Soil and Seed Fungi (Watanabe 2010), and Illustrated Genera of Imperfect Fungi (Barnett 1998).

DNA extraction and PCR amplification

A total of 100 mg of fungal mycelia harvested from PDB was used for genomic DNA extraction, following the method described by Pratama et al. (2021a) and using the Quick-DNA Fungal/Bacterial Miniprep Kit (California) as per the manufacturer's instructions. The fungal isolates' nuclear ribosomal DNA internal transcribed spacer (ITS) regions were amplified using the ITS1 (5'-CTT GGT CAT TTA GAG GAA GTA A-3′) forward primer and the ITS4 (5'-TCC TCC GCT TAT TGA TAT GC-3′) reverse primer (Muslim et al., 2025). The final reaction volume was 50 µl, containing 25 µl of MyTaq HS Red Mix, 2x (Bioline Reagents Ltd, UK), 1.5 µL of forward and reverse primers, 4 µL of genomic DNA template, and 12 µl sterilized water (ddH2O). The PCR was carried out using C1000 Touch thermal cycler (Bio-Rad, Hercules, CA, USA), programmed for initial denaturation for 1 min at 95°C, 30 cycles for denaturation, annealing, extension for 15s at 95°C, 15s at 52°C, and 10s at 72°C. Final elongation step of 5 min at 65°C. Electrophoresis for PCR products was carried out on 1% agarose gel in TAE buffer (1×). The staining for the amplified DNA fragments was carried out by using 2 µl FloroSafe DNA Stain (1st BASE). A DNA marker (100 bp) was used as a standard. The PCR products were sequenced by 1st BASE (Singapore). The sequences were deposited in NCBI GenBank, and compared with those already deposited in there via BLAST searches.

Sequence and phylogenetic analyses

The DNA sequences were aligned using Gene Studio within MEGA software version 11, then manually trimmed and edited for completeness. Homology searches were performed using the BLAST program against the NCBI GenBank database. A Maximum Likelihood tree was constructed with MEGA version 11, including all positions with gaps and missing data. Clade support was calculated with 1,000 bootstrap replications. 23 related sequences from NCBI GenBank were combined with the 8 endophytic fungal sequences from this study for phylogenetic analysis.

Endophytic Fungal Antagonist Test

The antagonistic test of endophytic fungi against *C. fimbriata* was conducted on PDA medium using the direct opposition method. This method involves growing the *Ceratocystis* fungal isolate and the endophytic fungal isolate facing each other at a distance of 3 cm on a 9 cm diameter petri dish. The antagonistic test was performed by placing a 0.5 mm piece of the antagonistic fungus, cut using a cork borer, opposite a 0.5 mm piece of *Ceratocystis* fungus at a distance of 3 cm. Inoculation was done simultaneously and repeated five times. The cultures were then incubated at room temperature (25-28°C) until the fungi grew to fill the petri dish. The experimental design used was a completely randomized design (CRD) with five repetitions. The analysis results were tested using ANOVA, followed by further testing with BNJ (Honestly Significant Difference) using RStudio. The percentage of inhibition by the endophytic fungi against *C. fimbriata* was calculated using the following formula:
Formula:

$$PI = \frac{R1-R2}{R1} \times 100\%$$

Note:
P1 = Inhibition percentage (%)
R1 = Diameter of *Ceratocystis* fungus in the control without the antagonist
R2 = Diameter of *Ceratocystis* fungi treated with antagonists
T = Antagonistic Fungi

Endophyte Antagonism Interaction against *Ceratocystis fimbriata*

The observation of the antagonistic mechanism was carried out by preparing water agar media, which was then spread on a glass slide using a brush. The microscopic interaction between the hyphae of the endophytic fungus and the pathogen was observed by placing a 0.5 mm piece of the antagonistic fungus, cut using a cork borer, opposite a 0.5 mm piece of *Ceratocystis* fungus at a distance of 3 cm. Inoculation was done simultaneously and repeated five times, lasting for 3 days. The interaction was then observed under a microscope. The observation focused on the mycelium of both the endophytic fungus and the pathogen. During observation, distilled water was added to the glass slide, which was then covered with a cover glass.

Results

A total of 38 isolates were successfully isolated from Ogan Komering Ilir (OKI), Musi Banyuasin (MuBa), Ogan Komering Ulu (OKU), and Ogan Ilir (OI). Among these, 9 isolates with high antagonistic ability were further tested, originating from 4 regencies. From OKI, there were 3 isolates: 1 from Pantai Village (DSPTW 6A) and 2 from Serdang Menang Village (SDMW 7B and SDMW 8A). From MuBa, there were 4 isolates: 2 from Ngulak Village (SDW 5A and SDW 3B) and 2 from Tanjung Raya Village (TRW 1B and TRW 5). From OKU, there were 1 isolate from Kepayang Village (WSA 4A). Lastly, from OI, there was 1 isolate from Sungai Pinang Village (RMIP 1) (Table 1).

Table 1 *Endophytic fungal isolates from* Lansium domesticum *stems.*

Isolates Code	Villages	District	Coordinates Points
DSPTW 6A	Desa Pantai	Ogan Komering Ilir	-3°15'45,786"S 104°53'9,306"E
SDMW 7B	Serdang Menang	Ogan Komering Ilir	3°16'28.3"S 104°52'44.2"E
SDMW 8A	Serdang Menang	Ogan Komering Ilir	3°16'28.3"S 104°52'44.2"E
SDW 5A	Ngulak	Musi Banyuasin	2°46'47.3"S 103°24'02.4"E
SDW 3B	Ngulak	Musi Banyuasin	2°46'47.3"S 103°24'02.4"E
TRW 1B	Tanjung Raya	Musi Banyuasin	02°45.2038'S 103°30.1315'E
TRW 5	Tanjung Raya	Musi Banyuasin	02°45.2038'S 103°30.1315'E
WSA 4A	Kepayang	Ogan Komering Ulu	4°00'09.7"S 104°17'06.3"E
RMIP 1	Sungai Pinang	Ogan Ilir	3°21'30.5"S 104°47'06.7"E

Morphological Characteristics of Endophyte Fungi

Macroscopic observations showed differences in the morphological characteristics of the antagonistic fungi when regrown on potato dextrose agar (PDA) and malt extract agar (MEA) media. On PDA, the colony characteristics of the isolates were as follows: DSPTW 6A (white-black colony, circular shape with entire margin), SDMW 7B (white-red colony, circular shape with entire margin), SDMW 8A (white-green colony, circular shape with entire margin), SDW 5A (white-brown colony, irregular shape with entire margin), SDW 3B (gray-black colony, circular shape with undulate margin), TRW 1B (white-black colony, circular shape with undulate margin), TRW 5 (white colony, circular shape with entire margin), WSA 4A (black colony, circular shape with filiform margin), and RMIP 1 (green colony, circular shape with lobate margin) (Fig.1 and Table 2).

Macroscopic observations revealed differences in the morphological characteristics of the antagonistic fungi re-isolated on PDA and MEA media. On MEA, the colony characteristics of the isolates were as follows: DSPTW 6A (white-black colony, circular shape with entire margin), SDMW 7B (white-red colony, filamentous shape with entire margin), SDMW 8A (white-green colony, circular shape with entire margin), SDW 5A (white-brown colony, circular shape with entire margin), SDW 3B (white-yellowish colony, circular shape with curled margin), TRW 1B (white-black colony, circular shape with curled margin), TRW 5 (white colony, irregular shape with curled margin), WSA 4A (black colony, circular shape with filiform margin), and RMIP 1 (green colony, circular shape with lobate margin) (Figure 2 and Table 4).

As seen in Table 2, on Potato Dextrose Agar (PDA) medium, the endophytic fungal isolates displayed various colors such as white, black, brown, and green with circular shapes (DSPTW 6A, SDMW 8A, SDW 5A, SDW 3B, TRW 1B, WSA 4A, and RMIP 1). The filamentous shape was observed in SDMW 7B, and irregular shapes were seen in TRW 5, with undulate, curled, and entire margins. Rapid fungal growth was noted in SDMW 8A, SDW 5A, WSA 4A, and RMIP 1. Moderate growth was observed in DSPTW 6A, SDW 3B, TRW 1B, and TRW 5, while slow growth was seen in SDMW 7B.

Table 3 shows that the growth of each isolate varies. In the first observation, the growth ranged from 0.30±0.51 to 4.96±0.44. In the second observation, the growth ranged from 2.04±0.69 to 6.70±0.23. In the third observation, the growth ranged from 3.22±0.02 to 7.73±0.67. In the fourth observation, the growth ranged from 4.93±0.02 to 8.81±0.09. In the fifth observation, the growth ranged from 6.56±0.13 to 9.00±0.24. The results of the ANOVA test and the BNJ follow-up test at 5% show that the growth data of each isolate grown on PDA medium were significantly different.

Table 4 shows that on MEA media, the growth of endophytic fungi is faster, with colonies appearing in white, black, gray, and green colors, and a circular shape for isolates DSPTW 6A, SDMW 7B, SDMW 8A, SDW 3B, TRW 1B, TRW 5, WSA 4A, and RMIP 1. There were also irregular shapes for isolates SDW 5A, with entire margins for isolates SDMW 7B, SDMW 8A, and TRW 5.

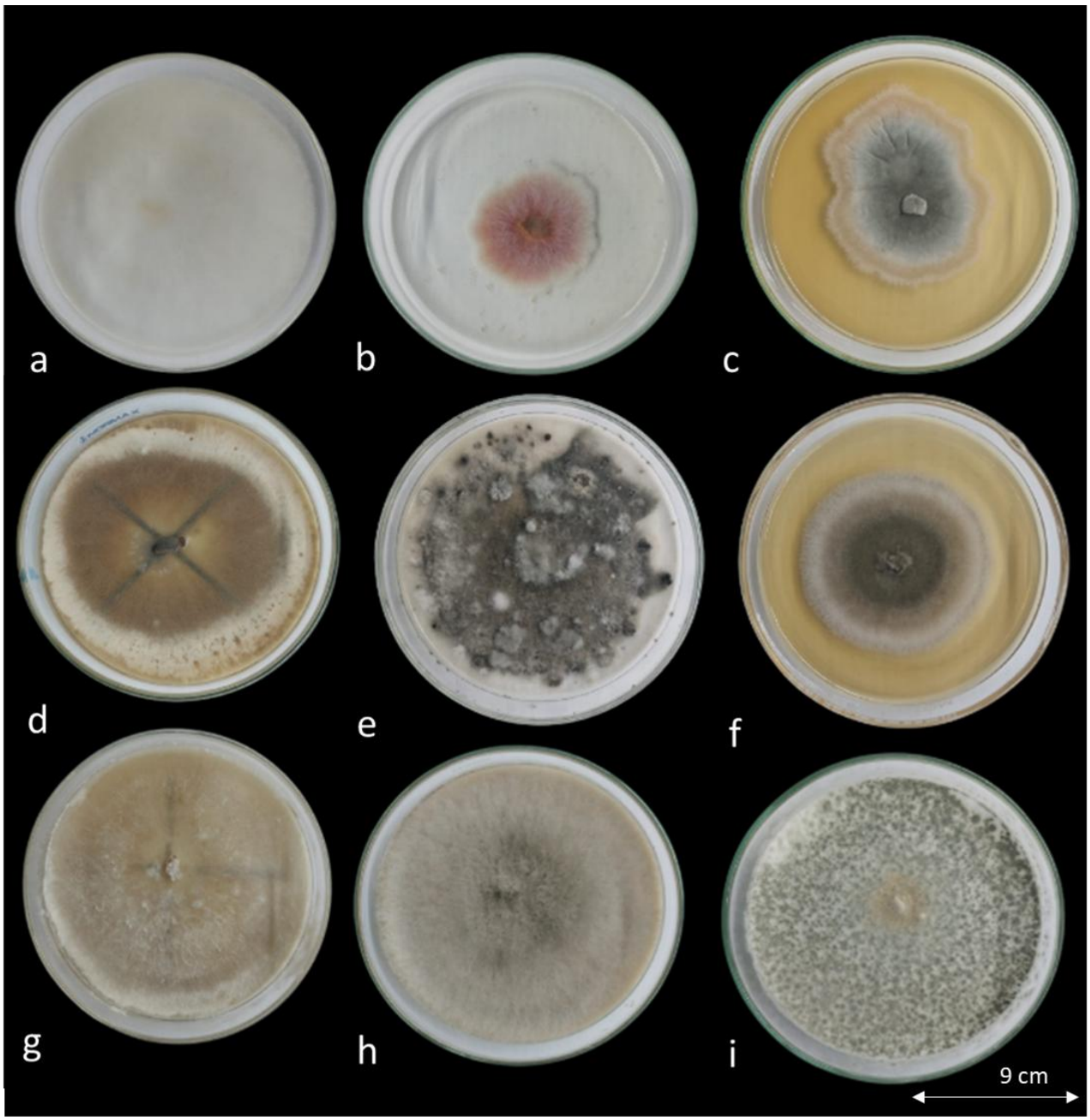

Fig. 1 – Endophytic Fungal Isolates Re-isolated on Potato Dextrose Agar (PDA) Medium. (a) DSPTW 6A (*Nigrospora oryzae*). (b) SDMW 7B (*Fusarium oxysporum*). (c) SDMW 8A (*Penicillium citrinum*). (d) SDW 5A (*Nigrospora sphaerica*). (e) SDW 3B (*Lasiodiplodia theobromae*). (f) TRW 1B (*Phoma* sp). (g) TRW 5 (*Penicillium citrinum*). (h) WSA 4A (*Eutiarosporella* sp). (i) RMIP 1 (*Trichoderma asperellum*).

Table 5 shows that the growth of each isolate varied. In the first observation, the growth ranged from 0.22±0.92 to 4.80±0.46. In the second observation, the growth ranged from 1.68±0.09 to 7.18±0.11. In the third observation, the growth ranged from 3.65±0.65 to 8.56±0.17. In the fourth observation, the growth ranged from 6.72±0.44 to 8.89±0.01. In the fifth observation, the growth ranged from 6.69±0.35 to 9.00±0.00. The results of the ANOVA test and further BNJ 5% test showed that the growth data of each isolate grown on MEA media differed significantly.

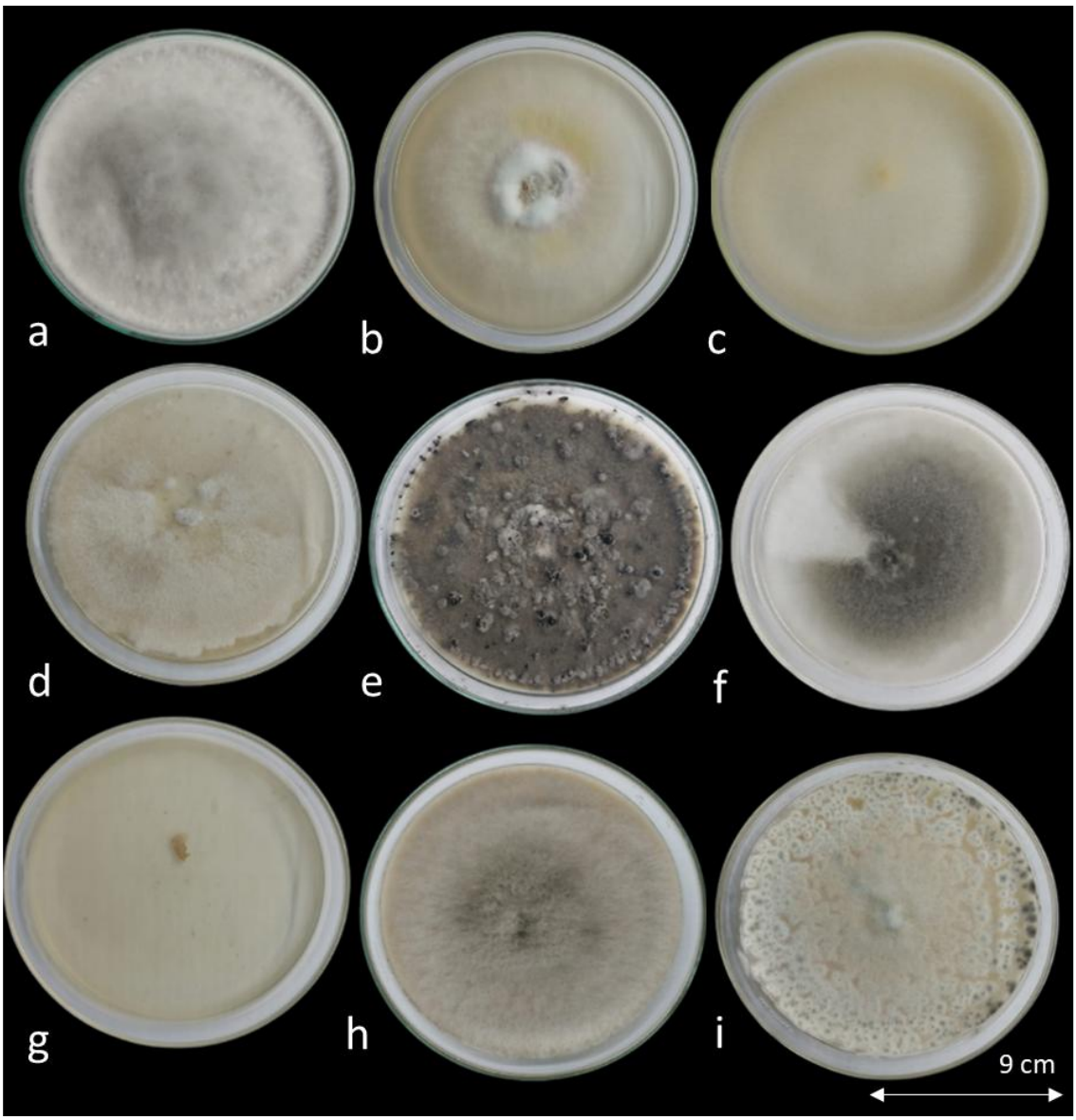

Fig. 2 – Endophytic Fungal Isolates Re-isolated on Malt Extract Agar (MEA) Medium. (a) DSPTW 6A (*Nigrospora oryzae*). (b) SDMW 7B (*Fusarium oxysporum*). (c) SDMW 8A (*Penicillium citrinum*). (d) SDW 5A (*Nigrospora sphaerica*). (e) SDW 3B (*Lasiodiplodia theobromae*). (f) TRW 1B (*Phoma* sp). (g) TRW 5 (*Penicillium citrinum*). (h) WSA 4A (*Eutiarosporella* sp). (i) RMIP 1 (*Trichoderma asperellum*).

Table 2 Morphological characteristics of colony isolates on potato dextrose agar (PDA).

Isolates Code	**Isolates Source**	**Growth**	**Morphological Characteristic**		
			Color	**Shape**	**Margin**
DSPTW 6A	Desa Pantai	++	White-Black	Circular	Entire
SDMW 7B	SerdangMenang	+	White-Red	Filamentous	Entire
SDMW 8A	SerdangMenang	+++	White-Green	Circular	Entire
SDW 5A	Ngulak	+++	White-Brown	Circular	Entire
SDW 3B	Ngulak	++	Gray-Black	Circular	Curled
TRW 1B	Tanjung Raya	++	White-Black	Circular	Curled
TRW 5	Tanjung Raya	++	White-White	Irregular	Curled
WSA 4A	Kepayang	+++	White-Black	Circular	Filiform
RMIP 1	Rami Pasai	+++	Green	Circular	Lobate

Description: + = slow growth, ++ = moderate growth, +++ = fast growth.

Table 3 Growth of endophytic fungal colonies on PDA media.

Isolate Code	Fungal Growth (cm)				
	Observation 1	**Observation 2**	**Observation 3**	**Observation 4**	**Observation 5**
DSPTW 6A	1.91±0.14bc	4.52±0.04b	6.71±0.01b	7.74±0.00b	8.45±0.00b
SDMW 7B	0.30±0.51a	2.04±0.69a	3.22±0.02a	4.93±0.02a	6.56±0.13a
SDMW 8A	5.10±1.09de	6.62±1.56c	7.73±0.67b	8.70±0.59b	9.00±0.24b
SDW 5A	4.95±0.14e	6.43±0.03c	8.33±0.18b	8.81±0.09b	9.00±0.00b
SDW 3B	2.36±0.37bc	5.42±0.37bc	6.76±1.41b	7.98±1.32b	8.45±0.94b
TRW 1B	1.71±0.27ab	3.83±0.37ab	6.62±0.51b	7.70±0.72b	8.28±0.24b
TRW 5	4.44±0.55cd	6.26±0.87bc	6.92±2.08b	8.41±1.42b	8.85±0.90b
WSA 4A	4.96±0.44cde	6.70±0.23bc	7.37±1.30b	8.50±0.98b	8.91±0.47b
RMIP 1	3.51±0.22cde	5.69±0.38bc	7.34±0.52b	8.65±0.24b	9.00±0.00b
P value	0.00	0.00	0.01	0.00	0.00

Table 4 Characteristics of endophytic fungal isolates on MEA media.

Isolate Code	Origin of Isolate	Growth	Morphological characteristics		
			Color	**Shape**	**Margin**
DSPTW 6A	Desa Pantai	++	White-Black	Circular	Undulate
SDMW 7B	Serdang Menang	+	White-Red	Circular	Entire
SDMW 8A	Serdang Menang	+++	White-Green	Circular	Entire
SDW 5A	Ngulak	+++	White-Brown	Irregular	Undulate
SDW 3B	Ngulak	++	Gray-Black	Circular	Undulate
TRW 1B	Tanjung Raya	++	White-Black	Circular	Undulate
TRW 5	Tanjung Raya	++	White-White	Circular	Entire
WSA 4A	Kepayang	+++	White-Black	Circular	Filiform
RMIP 1	Rami Pasai	+++	Green	Circular	Lobate

Description: + = slow growth, ++ = moderate growth, +++ = fast growth.

Table 5 Observation and measurement of fungi on MEA media.

Isolate Code	Fungal Growth (cm)				
	Observation 1	**Observation 2**	**Observation 3**	**Observation 4**	**Observation 5**
DSPTW 6A	2.16±0.08bc	4.52±0.03b	7.26±0.23bc	8.54±0.24bc	8.76±0.41b
SDMW 7B	0.22±0.92a	1.68±0.09a	3.65±0.65a	5.22±0.53a	6.69±0.35a
SDMW 8A	4.60±0.54de	6.30±0.68bc	7.75±1.74d	8.99±1.31c	8.59±0.70b
SDW 5A	4.80±0.46e	7.18±0.11bc	7.88±0.02cd	8.92±0.02c	9.00±0.00b
SDW 3B	2.26±0.09bc	4.88±1.07bc	7.72±0.22bcd	8.49±0.04bc	9.00±0.00b
TRW 1B	0.58±0.16ab	3.79±0.66ab	5.90±1.05bc	7.48±1.24bc	8.47±0.59b
TRW 5	2.84±1.58cd	4.95±1.88bc	8.03±1.04cd	8.84±0.45c	8.98±0.01b
WSA 4A	3.32±0.54cde	5.67±1.38bc	8.56±0.17cd	8.89±0.01c	9.00±0.00b
RMIP 1	3.75±0.56cde	5.78±0.66bc	7.37±0.34cd	8.79±0.27c	8.97±0.04b
P value	0.00	0.0	0.00	0.00	0.00

Table 6 Microscopic endophytic fungi.

Isolate Code	Species	Microscopic characteristics		
		Hyphae	**Conidia/ Chlamydospores**	**Ascospores**
DSPTW 6A	*Nigrospora oryzae*	Septate is divided into compartments. The hyphae are long, tubular, and smooth, often with irregular branching. the hyphae are hyaline.	Conidia are oval to elliptical in shape and dark brown to black color. Chlamydospores are globose to oval. Chlamydospores can vary in color but are often dark brown to black.	Not observed
SDMW 7B	*Fusarium oxysporum*	Septate is divided into compartments and the hyphae are long, tubular, and thread-like. hyphae are hyaline, meaning they are colorless or transparent	Conidia shapes are crescent-shaped to cylindrical and hyaline (transparent) to pale yellow or slightly brown color. Chlamydospores are globose (round) to oval.	Not observed
SDMW 8A TRW 5	*Penicillium citrinum*	Septate is divided by cross walls. Hyphae are hyaline. The hyphae are long, thin, and tubular.	Conidia are greenish to yellowish in color and oval in shape. Chlamydospores are globose to oval.	Not observed
SDW 5A	*Nigrospora sphaerica*	Septate is divided by cross-walls. The hyphae are long, tubular, and typically smooth, with occasional branching. the hyphae are hyaline.	Conidia are spherical to slightly oval in shape. The conidia are dark brown to black. Chlamydospores are globose to oval.	Not observed
SDW 3B	*Lasiodiplodia theobromae*	Hyphae are brownish-black and septate. Septate is divided into compartments and hyphae are long, tubular, and typically exhibit irregular branching.	Conidia shapes are cylindrical to elliptical and dark brown to black.	Not observed
TRW 1B	*Phoma* sp.	Septate have cross-walls that divide the hyphae into individual compartments and hyaline.	Conidia are globose (spherical) to subglobose (almost spherical) or cylindrical and hyaline color.	Not observed
WSA 4A	*Eutiarosporella* sp	Hyphae are septate with a pale to dark color and exhibit irregular branching patterns.	Conidia are elongated and cylindrical. They are hyaline (transparent) to pale yellow or light brown.	Not observed
RMIP 1	*Trichoderma asperellum*	Septate is divided into compartments by cross-walls and hyaline (transparent or translucent). The hyphae are branched, and each branch also has septa.	Conidia shape to oval or ellipsoid and greenish or bluish-green color.	Not observed

Identification of endophytic fungi

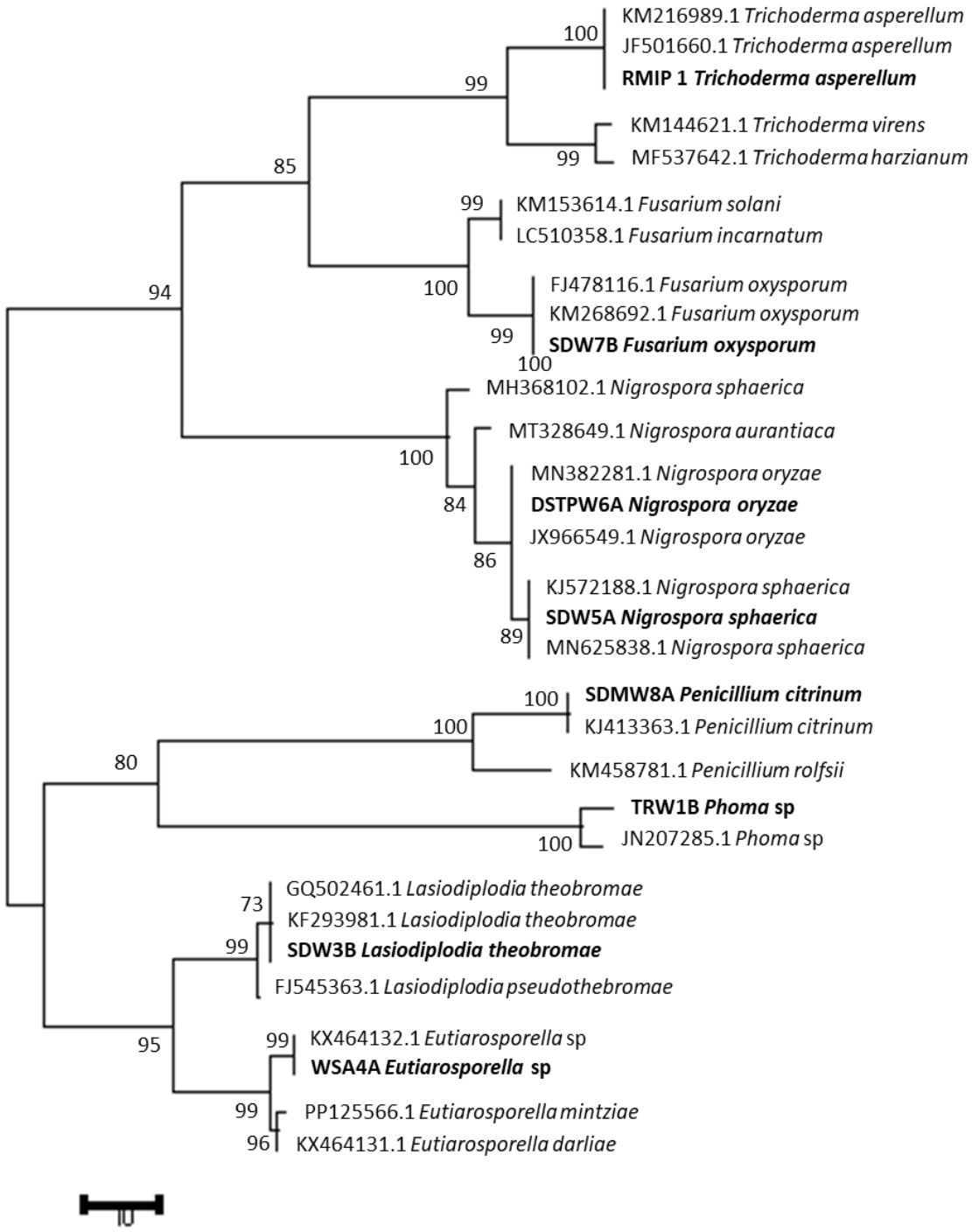

Fig. 3 – Phylogenetic tree generated from maximum parsimony analysis of the internal transcribed spacer (ITS) rDNA genotypes of sequences showing the relationship between fungal endophyte from *Lansium domesticum* (marked in bold) and fungal ITS sequences from the GenBank. The GenBank accession number and species are given for the representatives of each isolate. Bootstrap values greater than 50% obtained after a bootstrap test with 1,000 replications are indicated on the appropriate nodes.

Endophytic Fungal Antagonist Test

The results of the antagonistic test showed that the tested isolates could interact with and inhibit the growth of the *Ceratocystis fimbriata* isolate. This is illustrated in Fig. 4. Table 7 shows

the inhibition levels obtained in the four districts: Ogan Komering Ilir, Ogan Komering Ulu, Musi Banyuasin, and Muara Enim.

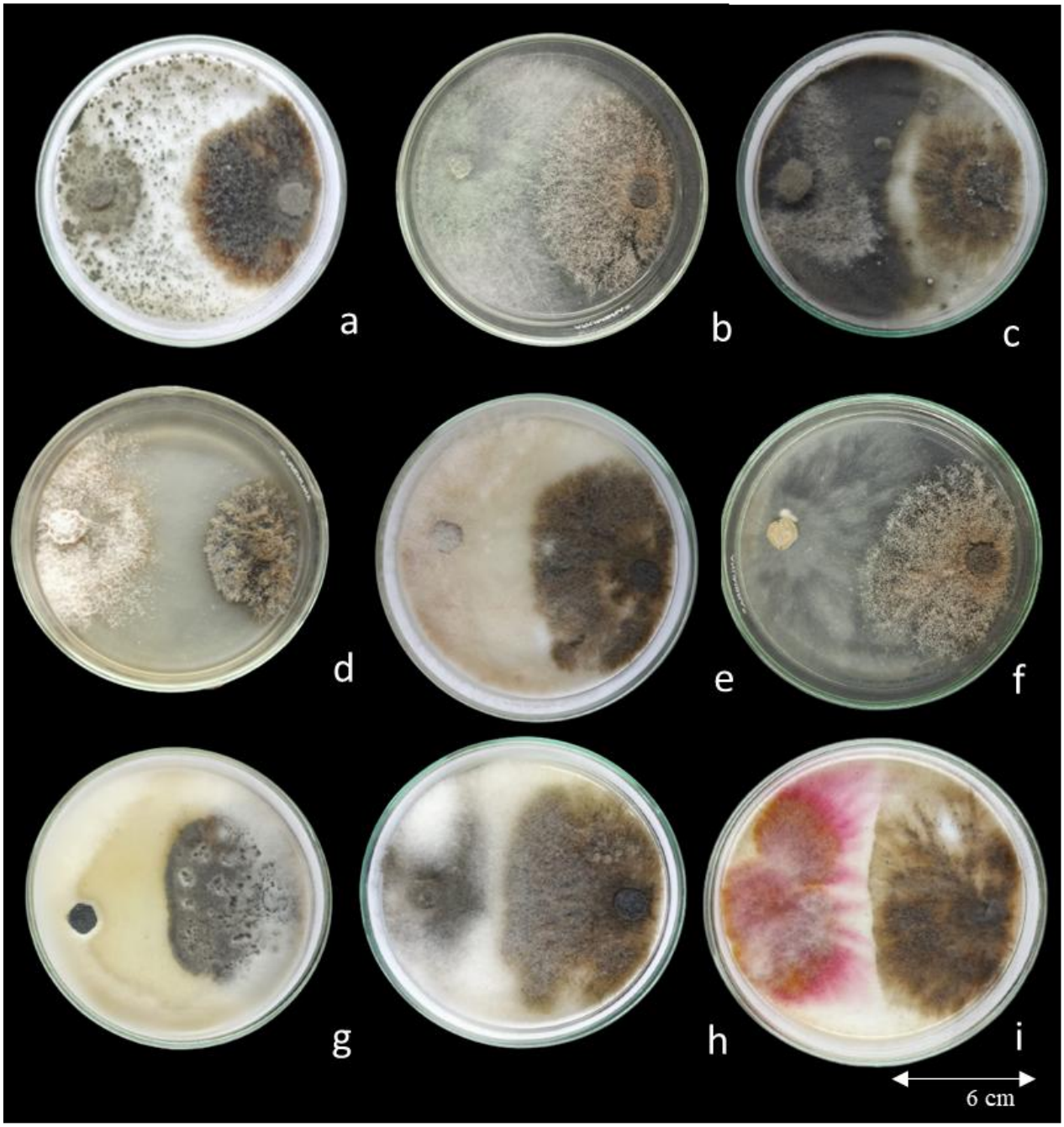

Fig. 4 – Interaction between endophytic fungi and pathogens on culture media: (a) RMIP 1, (b) SDMW 8A, (c) SDW 3B, (d) SDW 5A, (e) TRW 5, (f) TRW 1B, (g) DSPTW 6A, (g) WSA 4A, (i) SDMW 7B.

Antagonistic isolate tests against Ceratocystis isolates showed that all isolates had inhibitory effects, and the ANOVA test results showed a significant difference from the control. The highest inhibitory effect was observed in the SDW 3B isolate (0.52), categorized as moderate for DSPTW 6A, SDMW 7B, SDMW 8A, and SDW 5A (0.44 to 0.47), and the lowest for TRW1B, TRW 5, WSA 4A, RMIP 1 (0.39 to 0.43). Similarly, the inhibition percentages were 52%, moderate between 44% to 47%, and the lowest at 39% to 43%. A follow-up test using BNJ 5% showed significant differences between each isolate.

Table 7 Inhibitory effect test of endophytic fungal isolates.

Isolate Code	Origin of Isolate	Inhibitory (%)	Score
DSPTW 6A	Desa Pantai	44ab	5
SDMW 7B	Serdang Menang	44ab	5
SDMW 8A	Serdang Menang	45ab	3
SDW 5A	Ngulak	47ab	4
RMIP 1	Ngulak	52b	5
TRW 1B	Tanjung Raya	39a	4
TRW 5	Tanjung Raya	42a	4
WSA 4A	Kepayang	43a	3
SDW 3B	Rami Pasai	41a	5

Interactions Between Endophytic Fungi and Pathogens

Endophytic and pathogenic fungal isolates were grown on a medium applied to the surface of glass slides, and after three days, observations were made under a microscope to identify the interaction occurring between the hyphae of the antagonistic and pathogenic fungi. Through the observations (Fig. 5), different interactions were noted. Three types of interactions were observed: hyphal interaction mechanisms. Six isolates (SDMW 7B, SDW 3B, RMIP 1, TRW 5, TRW 1B, and WSA 4A) caused lysis of the pathogenic hyphae. Two isolates (DSPTW 6A and DSPTW 9A) caused swelling of the pathogenic hyphae. Four isolates (SDW 5A, SDMW 8A, TRW 1B, and WPN 4B) caused the pathogenic hyphae to coil and lyse.

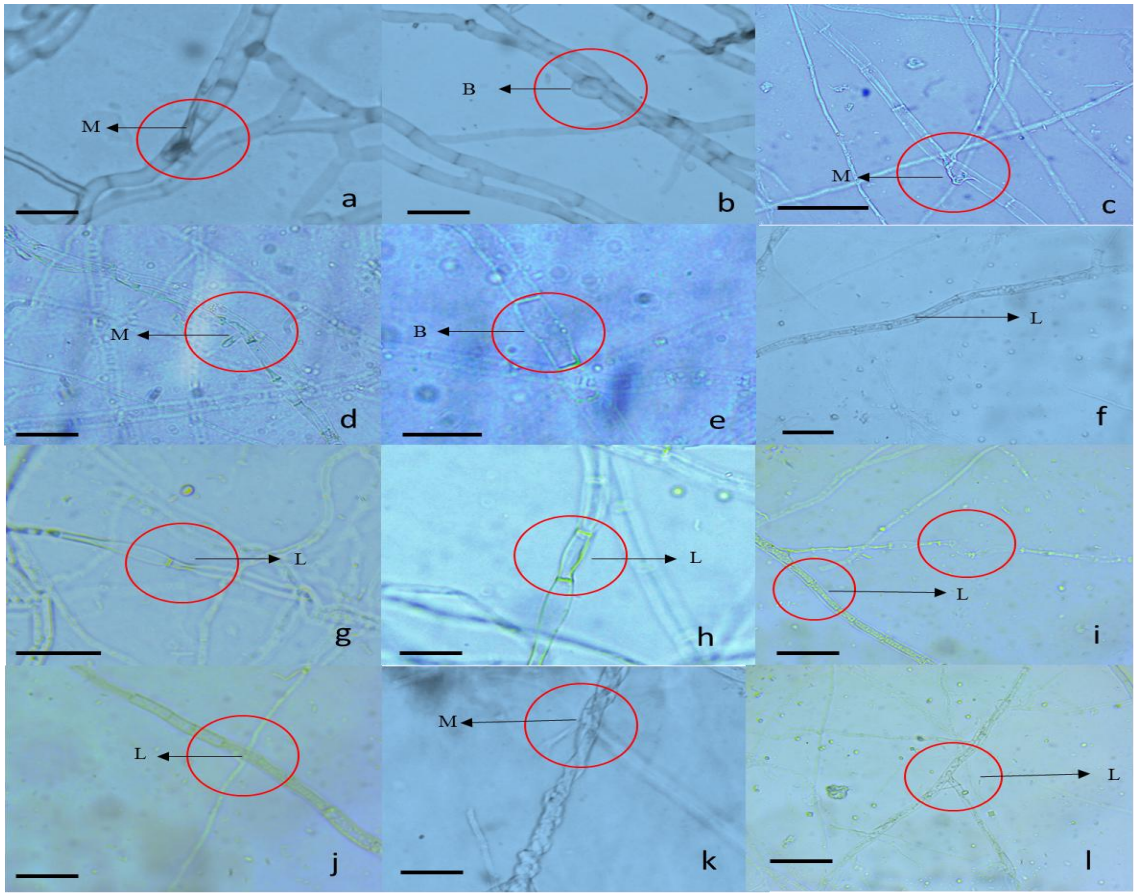

Fig. 5 – Microscopic observation of the antagonistic mechanism of endophytic fungal isolates: (a) SDMW 8A. (b) DSPTW 9A. (c) WPN 4B. (d) TRW 1B. (e) DSPTW 6A. (f) WSA 4A. (g) SDMW 7B. (h) RMIP 1. (i) TRW 5. (j) TRW 5. (k) SDW 5A. (l) SDW 3B. Magnification 400X. Scale bar 20 µm. B = swollen pathogenic hyphae, L = lysed pathogenic hyphae, M = coiling pathogenic hyphae.

Discussion

Thirty-eight isolates of endophytic fungi were successfully isolated from healthy duku plant seedlings. Nine endophytic isolates with the highest inhibitory activity were further tested for their antagonistic potential against *Ceratocystis*. All isolates were identified as *Nigrospora oryzae*, *Fusarium oxysporum*, *Penicillium citrinum*, *Nigrospora sphaerica*, *Lasiodiplodia theobromae*, *Phoma* sp., *Eutiarosporella* sp., and *Trichoderma asperellum*. The results showed that all fungal isolates belonged to the phylum Ascomycota (100%). This phylum is named for its characteristic reproductive structure, the ascus, a sac-like cell where meiosis and spore production occur. Based on a literature review, the isolation of endophytic fungi from the stems and roots and their antagonistic activity against *Ceratocystis* has not been previously conducted. The study by Indrawati et al. (2019) successfully isolated endophytic fungi from the fruit peel of duku, namely *Rhizopus* sp. and *Aspergillus* sp., which have potential antibacterial activity against *Staphylococcus aureus* and *Escherichia coli*. A single plant species can potentially harbor hundreds of endophytic species capable of inhabiting all available tissues, including leaves, petioles, stems, branches, bark, xylem, roots, fruits, flowers, and seeds (Lin et al. 2022, Wang et al. 2022, Asad et al. 2023).

Molecular analysis identified the isolates DSPTW 6A, SDMW 7B, SDMW 8A, SDW 5A, SDW 3B, TRW 1B, TRW 5, WSA 4A, and RMIP as *Nigrospora oryzae*, *Fusarium oxysporum*, *Penicillium citrinum*, *Nigrospora sphaerica*, *Lasiodiplodia theobromae*, *Phoma* sp., *Penicillium citrinum*, *Eutiarosporella* sp., and *Trichoderma asperellum*. *Nigrospora oryzae* (DSPTW 6A) and *Nigrospora sphaerica* (SDW 5A) form circular colonies with a wool-like texture, transitioning from white to black. Their hyphae are hyaline, septate, and the conidia are oval-shaped. Macroconidia are typically falcate (crescent-shaped), while microconidia are abundant, oval to reniform (kidney-shaped), and generally aseptate or occasionally uniseptate (Liu et al. 2024). *Fusarium oxysporum* (SDMW 7B) has colonies ranging from white to purplish-red, with septate, hyaline hyphae. Its conidia are reniform, and crescent-shaped conidia are present. These characteristics align with the description by Singha et al. (2016), stating that *Fusarium* produces crescent-shaped macroconidia and oval microconidia. *Penicillium citrinum* (SDMW 8A and TRW 5) features septate, hyaline hyphae with round conidia. Houbraken et al. (2010) and Akmalasari et al. (2013) describe *Penicillium* species as having septate hyphae, vesicle-forming conidiophores, and conidia that are round or elliptical. *Lasiodiplodia theobromae* (SDW 3B) has dark, septate hyphae. Its mature conidia are often pigmented and exhibit longitudinal striations (de Silva et al. 2019). *Phoma* sp. (TRW 1B) has septate, hyaline hyphae, and colonies that transition from white to olive-gray. The conidia are oval (Bennett et al. 2018). *Eutiarosporella* sp. (WSA 4A) forms colonies ranging from white to gray, with septate, hyaline hyphae. It produces pycnidia as fruiting bodies, and its conidia are oval to ellipsoidal (Li et al. 2023). *Trichoderma asperellum* (RMIP) exhibits greenish colonies with septate, hyaline hyphae, and globose to ovoid conidia (Matas-Baca et al. 2022).

In general, the growth rate of mycelium on PDA and MEA media did not differ significantly; only during the first and second weeks was growth on PDA slightly faster. Potato Dextrose Agar is a preferred medium for cultivating fungi due to its nutrient-rich composition, ease of preparation, slightly acidic pH, and adaptability (Aujla & Paulitz 2017). The isolates SDMW 8A, SDW 5A, RMIP 1, SDW 3B, and WSA 4A exhibited rapid mycelial growth. The isolates DSPTW 6A, SDMW 7B, TRW 1B, and TRW 5 showed moderate growth, while isolate SDMW 7B was categorized as slow-growing. Fungal growth on MEA medium produced thinner mycelium compared to fungi inoculated on PDA medium, where the colonies were thicker. According to a study by Mejía et al. (2008), fungal growth on PDA medium tends to produce abundant and dense colonies due to the availability of complete nutrients in this medium.

The antagonistic test showed that two isolates (SDW 8A and WSA 4A) scored 3, indicating that the growth of the pathogenic fungi stopped upon contact with the antagonistic fungi, and the antagonistic fungi grew beyond the pathogen. Three isolates scored 4 (SDW 5A, TRW 1B, and TRW 5), indicating the presence of an inhibition zone measuring 1 mm. Meanwhile, four isolates scored 5 (DSPTW 6A, SDMW 7B, RMIP 1, and SDW 3B), as they formed inhibition zones larger

than 2 mm. The antagonistic interaction involving competition (WSA 4A) showed that the endophytic fungi and the pathogenic fungi (*Ceratocystis fimbriata*) competed for nutrients and space. The pathogenic fungi's growth halted, while the endophytic fungi grew beyond the pathogen due to colonization and resource utilization (Adeleke et al. 2022, Akram et al. 2023). In addition to competition, the antagonistic test also revealed antibiosis interactions (DSPTW 6A, SDMW 7B, SDMW 8A, SDW 5A, SDW 3B, TRW 1B, TRW 5, and RMIP 1). Clear zones were formed between the pathogenic and antagonistic fungi, indicating that the endophytic fungi could grow effectively and inhibit the growth of the pathogenic fungi. The antibiosis mechanism may involve the direct production of antimicrobial compounds, competition for resources, and induction of plant defense mechanisms (Pathak et al. 2022, Moussa 2024).

The RMIP 1 isolate exhibited a high antagonistic ability in inhibiting the growth of *Ceratocystis*, with an inhibition rate of 52%, which was significantly different from other isolates. The growth rate of this isolate on PDA and MEA media was categorized as rapid. Fast-growing fungi can dominate space and nutrients, ultimately suppressing the growth of competing fungi through competition for nitrogen and carbon (Harman et al. 2008). This aligns with the findings of Weinstock et al. (2016), who stated that biocontrol agents with rapid growth have a greater ability to inhibit pathogen growth due to higher competition for space and nutrients. According to Sunarwati & Yoza (2010), antagonistic fungi with an inhibition rate of 26–50% are classified as having low antagonistic ability because the inhibition capability of antagonistic fungi is influenced by various factors, one of which is their growth rate. Amaria et al. (2013) noted that fungal isolates with high inhibition rates have faster colony growth than the pathogenic colony. Similarly, Octriana et al. (2011) stated that antagonistic fungi can be categorized as having high inhibitory activity against pathogen growth if their inhibition percentage exceeds 60%. However, if the inhibition percentage is only around 30%, the antagonistic fungi are considered to have a low inhibitory effect.

Microscopic observation of the interaction between *Ceratocystis fimbriata* and endophytic fungi was conducted to examine the abnormal growth of pathogenic hyphae compared to the control treatment. According to Sanglard et al. (2009), biocontrol microorganisms exhibit antagonistic mechanisms such as antibiosis by producing antifungal compounds that can cause abnormal or malformed hyphal growth, including lysis, coiling, and swelling. Malformations were observed in cells due to hyphal damage caused by chitinase and saponin enzymes produced by endophytic fungi (Toppo et al. 2024). These enzymes can degrade fungal cell walls, leading to damaged and shrunken hyphae, a process known as lysis. In the interaction between endophytic fungi and pathogens, six isolates (SDMW 7B, SDW 3B, RMIP 1, TRW 5, TRW 1B, and WSA 4A) caused lysis of pathogenic hyphae. Two isolates (DSPTW 6A and DSPTW 9A) caused swelling of pathogenic hyphae, while four isolates (SDW 5A, SDMW 8A, TRW 1B, and WPN 4B) caused coiling and lysis of pathogenic hyphae. According to Habisukan et al. (2021) and Palmieri et al. (2020), endophytic fungi form pointed hyphae around pathogenic hyphae before penetrating or directly entering them. In addition to attachment, some endophytic hyphae exhibit behavior resembling pathogenic hyphae trapping.

Despite their promising potential, the application of endophytic fungi as biocontrol or plant growth–promoting agents faces several limitations. Antagonistic activity observed under in vitro conditions often exaggerates efficacy because nutrient-rich media differ substantially from the heterogeneous and resource-limited environment within plant tissues (Schulz & Boyle 2005). Host genotype and physiology further influence colonization success and metabolite expression, making beneficial effects host-specific and sometimes inconsistent across cultivars (Hartley & Gange, 2009). Colonization stability is another challenge, as many endophytes persist only temporarily and may be outcompeted by native microbiota or suppressed under environmental stress (Mendes et al. 2013). Some taxa can also shift toward pathogenicity under stress, raising biosafety concerns for large-scale deployment (Porras-Alfaro & Bayman 2011). Moreover, inoculation methods such as seed coating or foliar application often result in variable colonization and inconsistent field performance (Murphy et al. 2019). Beyond biological constraints, regulatory and formulation issues

remain, particularly the long-term viability of fungal propagules in bioinoculants (Jaber & Ownley, 2018). These challenges highlight the need for integrating in vitro assays with robust in planta and field validations to ensure reliable application.

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