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# Biocontrol potential of rice endophytic fungi against phytopathogens in East Kalimantan, Indonesia

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**Abstract.** *Sopialena, Mujiono K, Syakhril, Nurhasanah. 2025. Biocontrol potential of rice endophytic fungi against phytopathogens in East Kalimantan, Indonesia. Biodiversitas 26: 5737-5754.* Endophytic fungi are increasingly recognized for their potential as eco-friendly biocontrol agents in sustainable agriculture. This study aimed to isolate, identify, and evaluate the antagonistic potential of rice endophytic fungi across diverse agroecosystems in Penajam Paser Utara, Samarinda, and Kutai Kartanegara, East Kalimantan, Indonesia. Endophytic fungi were isolated from healthy rice plants and screened for antagonism against five pathogens using dual-culture assays. A total of six fungal genera were identified, including *Aspergillus niger*, *Penicillium* sp., *Rhizopus* sp., *Trichoderma* sp., *Gliocladium* sp., and *Paecilomyces* sp., with *A. niger*, *Penicillium* sp., and *Rhizopus* sp. being the most frequently isolated. Morphological characterization revealed distinct colony and microscopic traits supporting genus-level identification. Results of antagonistic assays against the five major rice pathogens *Magnaporthe oryzae, Fusarium* sp., *Cercospora* sp., *Rhizoctonia solani*, and *Curvularia* sp. demonstrated that endophytic fungi employed mechanisms, such as competition, parasitism, and antibiosis to suppress pathogen growth. The inhibitory activity of endophytic fungal isolates varied significantly, with inhibition rates ranging from 36.25% to 85%. The highest levels of inhibition were recorded against *Fusarium* sp. (81.11%), *Cercospora* sp. (85.00%), *Rhizoctonia solani* (85.00%), and *Curvularia* sp. (76.44%), while moderate inhibition was observed against *M. oryzae* (54.18%). Among the isolates, *Rhizopus* sp. and *Gliocladium* sp. consistently demonstrated the strongest antagonistic activity across multiple pathogens. The variability in inhibition rates highlights the importance of strain specificity, pathogen susceptibility, and host-endophyte compatibility in determining biocontrol efficacy. These fungi offer eco-friendly alternatives to chemical pesticides.

**Keywords:** Dual culture assay, endophytic fungal diversity, rice pathogens, *Rhizopus* sp., sustainable agriculture

## INTRODUCTION

Endophytic fungi are microorganisms that live asymptomatically within plant tissues, forming beneficial symbiotic relationships that enhance plant growth, nutrient acquisition, and stress tolerance (Alam et al. 2021; Corbu et al. 2023). They play an important role in sustainable agriculture, by offering eco-friendly alternatives to chemical fertilizers and pesticides (Rana et al. 2020; Jana et al. 2022; Parveensumaiya and Rashtrapal 2024), and improving the health and productivity of crops such as rice (Watts et al. 2023; Hu et al. 2024). Rice-associated endophytic fungi contribute to several critical plant functions, including phytohormone production (Baron and Rigobelo 2021), facilitation of nutrient uptake, and induction of systemic resistance to both biotic (Akram et al. 2023) and abiotic stresses (Fontana et al. 2021; Ganie et al. 2022).

Numerous studies have demonstrated the antagonistic potential of endophytic fungi against major rice pathogen, such as *Pyricularia oryzae* (rice blast) (Putri et al. 2022; Motlagh et al. 2023), *Rhizoctonia solani* (sheath blight) (Khunnamwong et al. 2020; Motlagh et al. 2022; Deb et al. 2022), *Curvularia lunata* and *Helminthosporium oryzae* (seedling root) (Limtong et al. 2020), *Bipolaris oryzae* (brown spot) (Lalngaihawmi et al. 2019), as well as other rice diseases, not only caused by fungal but also bacterial and viral diseases (Nayak et al. 2021; Grabka et al. 2022). Beyond their role in disease suppression, endophytic fungi have shown entomopathogenic effects (Sopialena et al. 2024), functioning as biocontrol agents against insect pests including rice planthopper (*Nilaparvata lugens*) (Peng et al. 2020; Zhao et al. 2020; Trizelia et al. 2023) and rice stem borer (*Sesamia calamistis*) (Bancole et al. 2020), as well as plant-parasitic nematodes (Grabka et al. 2022). These fungi are known to produce diverse bioactive secondary metabolites with antimicrobial properties (Ancheeva et al. 2020; Fan and Shi 2024), further reinforcing their potential as biocontrol agents in rice protection (Fadiji and Babalola 2020; Hu et al. 2024; Wang et al. 2024). Moreover, certain endophytic fungi have demonstrated plant growth-promoting effects (Parveen et al. 2023; Jena et al. 2024), enhancing rice resilience to various abiotic stresses including salinity (Sodhi and Saxena 2023; Airin et al. 2023), drought (Saddique et al. 2018), and other abiotic stresses such as high temperature, elevated $CO_2$ levels, and heavy metal stress (Verma et al. 2022).

The diversity of rice-associated endophytic fungi is shaped by plant genotype, environmental factors, and agricultural practices (Ji et al. 2022; Su et al. 2023; Liu et al. 2024). Host genetic background strongly influences

fungal community composition (Ali et al. 2021), with different rice genotypes hosting distinct fungal populations. Hybrid rice varieties with varying disease resistance harbor unique fungal communities (Nunna and Balachandar 2024), while wild rice species often maintain greater diversity than cultivated rice (Tian et al. 2021; Wang et al. 2024). Environmental factors such as soil type, climate, and stress conditions also influence endophytic fungi diversity (Hidayah et al. 2021; Ganie et al. 2022). Agricultural practices can either suppress or enhance diversity; conventional methods involving chemical fertilizer and pesticide tend to reduce fungal diversity (Dincă et al. 2022), whereas organic and low-input promote more diverse and beneficial endophytic communities (Rana et al. 2020).

In East Kalimantan Province, Indonesia, the variety and functional activities of endophytic fungi associated with rice plants have not been fully investigated. Rice cultivars grown in this region are believed to harbor unique fungal communities that may offer significant benefits to crop health and productivity. In addition, evaluation of endophytic fungi antagonistic activity against major rice pathogen in tropical countries is very limited. Therefore, it is crucial to understand these fungal communities and their important role in promoting sustainable rice production. The aim of this study was to isolate and identify endophytic fungi associated with rice plants in East Kalimantan and to assess their diversity. Additionally, their antagonistic potential against key rice pathogens was evaluated to explore their role in biological disease control.

## MATERIALS AND METHODS

### Sampling and collection of endophytic fungi

Endophytic fungi were sampled at three rice cultivation sites in each research region in East Kalimantan, Indonesia, Samarinda, Kutai Kartanegara, and Penajam Paser Utara Regencies; as these regions are key rice-producing areas and exhibit distinct agroecological characteristics. Samples were collected from five healthy rice plants per variety exhibiting no visible disease or physiological stress symptoms. Plant tissues were sampled from three distinct parts (roots, leaves, and young stems) to ensure a comprehensive representation of endophytic fungal diversity.

Sampling was performed using sterile techniques to minimize contamination, and carefully excised from each plant using sterilized scissors or scalpel blades. The collected tissues were placed into sterile polyethylene bags, labeled with site and plant part information, and transported in a cooler to the laboratory for further processing.

### Isolation of endophytic fungi from plant parts

Plant samples were washed thoroughly with distilled water to remove any adhering debris. The surface of each sample was further sterilized by sequentially immersing them in 5% sodium hypochlorite (NaOCl) solution for 5 minutes, followed by 70% ethanol for 1 minute. This sterilization process was repeated twice for thorough decontamination. The samples were rinsed twice with sterile distilled water to remove residual chemicals. Sterilized plant tissues were blotted dry using sterile tissue paper and cut into 1 cm segments under aseptic conditions in a laminar air flow cabinet. These segments were prepared for subsequent fungal isolation.

The sterilized tissue pieces (roots, stems, and leaves) of ~0.5 cm were plated onto Potato Dextrose Agar (PDA) media under aseptic conditions. To ensure sterility of the procedure, a control was included by plating 1 mL of the final rinse water from the sample sterilization process onto PDA media. The inoculated plates were incubated at 25-30°C for 5-7 days or until fungal colonies fully developed. Daily observations were conducted to monitor the growth of endophytic fungi, documenting colony morphology and other growth characteristics.

### Purification of endophytic fungi

Purification was performed for each fungal colony that exhibited distinct macroscopic morphology based on visible characteristics, such as color, shape, and colony distribution patterns. Fungal colonies were carefully separated using a sterile inoculating needle or syringe, then transferred onto fresh PDA media under aseptic conditions. The inoculated plates were incubated at 25-30°C, and the growth of each isolate was monitored daily. This process was repeated to ensure that each fungal isolate exhibited uniform colony morphology, confirming its purity. The purified isolates were maintained for further identification and analysis.

### Identification of endophytic fungi

The identification of isolated endophytic fungi was conducted morphologically following the guidelines of Barnett and Hunter (1998), at both macroscopic and microscopic levels to ensure accurate classification of the fungal isolates. Macroscopic observations focused on key morphological characteristics of the fungal colonies grown on PDA, including colony color, which highlighted pigmentation differences, colony shape, which distinguished concentric or non-concentric growth patterns, and colony texture, which described the surface appearance as smooth, velvety, or rough. The growth rate of colonies was also measured as radial expansion in centimeters per day (cm/day), providing a quantitative assessment of fungal growth dynamics. Microscopic examination included, growth pattern of hyphae (septate or non-septate and branched or unbranched), pigmentation, and conidial size.

### In vitro antagonistic test of endophytic fungal

The antagonistic potential of endophytic fungi against five pathogenic fungi, *Magnaporthe oryzae, Fusarium* sp., *Cercospora* sp., *Rhizoctonia solani*, and *Curvularia* sp., was evaluated in vitro. The pathogenic fungi were isolated from the infected rice plants and then identified by culturing symptomatic plant tissues on PDA media. Pure cultures of pathogenic fungi were paired with selected purified endophytic fungal isolates to assess their inhibitory effects. For each test, a small portion (approximately 0.5 cm in diameter) of endophytic fungal colony was transferred using a sterile inoculating needle and inoculated onto a Petri dish containing PDA media. Endophytic fungus and pathogenic fungus were placed opposite each other on the

same plate, separated by 3 cm between the inocula. A 9 cm diameter Petri dish was used for each pairing, with three replications for each treatment.

The inoculated plates were incubated at room temperature (28-30°C) and observed daily. The pathogenic fungi were allowed to grow until they nearly filled the Petri dish. Observations were conducted 4-7 days after inoculation to assess the interaction between the fungal colonies. The growth inhibition of pathogenic fungi by endophytic isolates was determined by measuring the colony radius and calculating the percentage of inhibition. Additionally, antagonistic mechanisms of endophytic fungi, such as competition, mycoparasitism, or production of inhibitory compounds, were recorded.

The antagonistic effect of endophytic fungi was evaluated by measuring the radial growth of pathogenic fungi *M. oryzae*, *R. solani*, and *F. oxysporum*. Observations were made by determining each pathogen's colony radius in the presence of the endophytic fungi. The percentage of inhibition of radial growth (PIRG) was calculated to quantify the antagonistic activity. PIRG was determined using the following formula:

$$\text{PIRG (\%)} = \frac{(\text{R1} - \text{R2})}{\text{R1}} x\ 100\%$$

Where: R1: the radial growth of the pathogen in the control plate (without endophytic fungi) and R2: the pathogen's radial growth in the presence of the endophytic fungi.

**Data analysis**

Quantitative data were analyzed using Analysis of Variance (ANOVA) following a Completely Randomized Design (CRD) framework. Mean differences were assessed through the Least Significant Difference (LSD) test at a 5% level of significance. Meanwhile, qualitative data, including morphological characteristics and observations of antagonistic interactions, were evaluated descriptively.

## RESULTS AND DISCUSSION

**Diversity of endophytic fungi in rice**

Endophytic fungi were successfully isolated from rice plants sampled across 11 sites in Penajam Paser Utara (PPU), Samarinda, and Kutai Kartanegara. A total of six fungal genera were identified, including *Aspergillus niger*, *Penicillium* sp., *Rhizopus* sp., *Trichoderma* sp., *Gliocladium* sp., and *Paecilomyces* sp. (Table 1). Among these, *Aspergillus niger, Penicillium* sp., and *Rhizopus* sp. were the most frequently encountered, suggesting their broad adaptability and stable endophytic association with rice plants across diverse locations. In contrast, genera, such as *Trichoderma* sp., *Gliocladium* sp., and *Paecilomyces* sp. were detected only occasionally. These findings indicate that both geographic location and host variety may influence the composition and diversity of endophytic fungal communities in rice.

In Penajam Paser Utara (PPU) district, six fungal genera were isolated from healthy rice plants, namely *Trichoderma* sp., *Paecilomyces* sp., *A. niger*, *Penicillium* sp., *Gliocladium* sp., and *Rhizopus* sp. (Table 1). Three genera of endophytic fungi, *A. niger*, *Penicillium* sp., and *Rhizopus* sp., were successfully isolated from healthy rice plants in Samarinda (Table 1). Four fungal genera of endophytic fungi were successfully isolated from healthy rice plants collected from several sites in Kutai Kartanegara. Based on their morphological characteristics, they were identified as *Trichoderma* sp., *Penicillium* sp., *A. niger*, and *Rhizopus* sp. All these isolates displayed diverse macroscopic and microscopic features, including variation in colony color, texture, and growth pattern. Microscopic observation showed taxonomic distinctions among the genera, particularly in the morphology of conidia, conidiophores, and hyphal structures (Figures 1, 2, and 3). Morphological characterization revealed distinct features among the isolates. *A. niger* exhibited black, clustered colonies with a rough, sand-like texture and unbranched conidiophores bearing dark green conidia. *Penicillium* sp. produced green colonies with a pinkish reverse surface, moderate smoothness, and branched conidiophores with phialides. *Rhizopus* sp. was characterized by its rapid radial growth, dense white-to-cream colonies, and sporangia borne on rhizoid-supported hyphae. All isolates exhibited hyaline hyphae, with variation in septation patterns across genera.

**Antagonistic potential**

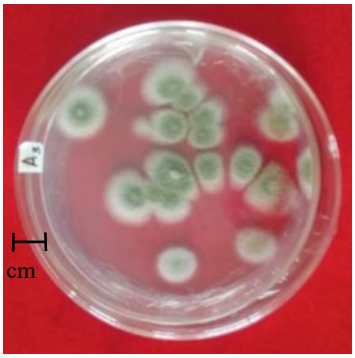
The antagonistic potential of six endophytic fungal species, *Paecilomyces* sp., *A. niger*, *Trichoderma* sp., *Gliocladium* sp., *Rhizopus* sp., and *Penicillium* sp., was evaluated against five major rice pathogens, namely *M. oryzae, Fusarium* sp., *Cercospora* sp., *Rhizoctonia solani,* and *Curvularia* sp. The primary mechanisms observed were competition, parasitism, and antibiosis (Table 2 and Figure 4). Competition for space and nutrients was the most commonly exhibited antagonistic mechanism and was observed in all fungal isolates against all tested pathogens. Parasitism was observed less frequently and was limited to specific combinations, particularly in *Trichoderma* sp., *Gliocladium* sp., and *Rhizopus* sp., which showed parasitic activity against *Fusarium* sp., *Cercospora* sp., *R. solani,* and *Curvularia* sp. Notably, *Penicillium* sp. exhibited parasitism only against *R. solani*, suggesting a more specialized mode of interaction.

Antibiosis, inferred through inhibition zones and altered pathogen growth patterns, was less prevalent but notable in specific interactions. *Paecilomyces* sp. showed antagonistic effects through antibiosis against *Fusarium* sp., *Cercospora* sp., and *R. solani*, whereas *A. niger* exhibited antibiosis against *Cercospora* sp. only. *Trichoderma* sp. and *Gliocladium* sp. demonstrated broad-spectrum antagonistic response through both competition and parasitism, particularly against *Fusarium* sp., *Cercospora* sp., and *R. solani*. Among the tested fungi, *Trichoderma* sp. and *Gliocladium* sp. consistently exhibited the strongest antagonistic activity across multiple pathogens and mechanisms. In contrast, *Penicillium* sp. showed limited antagonistic diversity, with its activity confined primarily to competitive exclusion and selective parasitism.

**Table 1.** Characteristics of endophytic fungi isolated from healthy rice plants in PPU, Samarinda, and Kutai Kartanegara Districts, Indonesia

| Rice varieties | Endophytic fungi | Plant parts | Macroscopic observation | | | Microscopic observation | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Colony color | Growth pattern / direction | Colony texture | Conidia / sporangium shape | Conidia / sporangium color | Conidiophore / sporangiophore | Hyphal type | Hypha color |
| Penajam Paser Utara Regency Location 1, Desa Gunung Makmur, Babulu Darat (GPS -1.5328692, 116.4224936) | | | | | | | | | | |
| Inpari 32 | *Paecilomyces* sp. | Root | Grayish-white to green or cream-brownish | Rapid spreading, flat smooth colony | Smooth, sometimes slightly hairy | Round to oval | Transparent | Branched, with 2–7 phialides | Septate | Hyaline |
| | *Penicillium* sp. | Root, Stem, Leave | Green with pinkish reverse surface | Spreads in all directions | Moderately smooth | Round | Green | Branched, with phialides | Septate | Hyaline |
| | *Aspergillus niger* | Root, Stem | Black | Spreads in all directions, forming clustered colonies | Rough, sand-like texture | Dark brown-black | Dark green | Unbranched | Aseptate | Hyaline |
| | *Rhizopus* sp. | Root | White to cream | Rapid radial spreading | Smooth and dense | Round or oval | Brown to blackish | Hyphae supporting the sporangium | Rhizoid | Hyaline |
| | *Gliocladium* sp. | Root | White to green | Spreads in all directions | Smooth | Round | Dark green | Branched | Septate | Hyaline |
| Penajam Paser Utara Regency Location 2, Desa Sebakung, Babulu Darat (GPS -1.5470657, 116.3872541) | | | | | | | | | | |
| Inpari 42 | *Aspergillus niger* | Root | Black | Spreads in all directions, forming clustered colonies | Rough, sand-like texture | Dark brown-black | Dark green | Unbranched | Aseptate | Hyaline |
| | *Penicillium* sp. | Root | Green with pinkish reverse surface | Spreads in all directions | Moderately smooth | Round | Green | Branched, with phialides | Septate | Hyaline |
| | *Gliocladium* sp. | Root | White to green | Spreads in all directions | Smooth | Round | Dark green | Branched | Septate | Hyaline |
| Penajam Paser Utara Regency Location 3, Desa Gunung Makmur, Babulu Darat (GPS -1.5371374, 116.4150790) | | | | | | | | | | |
| Mekongga | *Trichoderma* sp. | Root, Leave | White to dark green | Spreads laterally and vertically, forming circular colonies | Smooth | Round | Green | Branched | Septate | Hyaline |
| | *Rhizopus* sp. | Root | White to cream | Rapid radial spreading | Smooth and dense | Round or oval | Brown to blackish | Hyphae supporting the sporangium | Rhizoid | Hyaline |
| Samarinda Location 1 Betapus, Lempake (GPS -0.4165575, 117.1765598) | | | | | | | | | | |
| Mekongga | *Aspergillus niger* | Root, Leave | Black | Spreads in all directions, forming clustered colonies | Rough, sand-like texture | Dark brown to black | Dark green | Unbranched | Aseptate | Hyaline |
| | *Rhizopus* sp. | Root | White to cream | Rapid radial spreading | Smooth and dense | Round or oval | Brown to blackish | Hyphae supporting the sporangium | Rhizoid | Hyaline |
| Samarinda Location 2, Desa Giri Rejo, Lempake (GPS -0.4114353, 117.1819755) | | | | | | | | | | |
| Inpari 32 | *Rhizopus* sp. | | White to cream | Rapid radial | Smooth | Round or | Brown to | Hyphae | Rhizoid | Hyaline |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | spreading | and dense | oval | blackish | supporting the sporangium | | |
| | *Penicillium* sp. | Root, Leave | Green with a pinkish reverse surface | Spreads in all directions | Moderately smooth | Round | Green | Branched with phialides | Septate | Hyaline |
| | *Aspergillus niger* | Leave | Black | Spreads in all directions, forming clustered colonies | Rough, sand-like texture | Dark brown to black | Dark green | Unbranched | Aseptate | Hyaline |
| Samarinda Location 3, Sempaja Selatan (GPS -0.4409773, 117.1635092) | | | | | | | | | | |
| Mayas | *Aspergillus niger* | Root | Black | Spreads in all directions, forming clustered colonies | Rough, sand-like texture | Dark brown to black | Dark green | Unbranched | Aseptate | Hyaline |
| Kutai Kartenegara Regency Location 1, Desa Bukit Raya, Tenggarong Seberang (GPS -0.4060468, 117.0837480) | | | | | | | | | | |
| Inpari 32 | *Penicillium* sp. | Root, Leave | Greenish with a pinkish reverse surface | Spreads in all directions | Moderately smooth | Round | Green | Branched with phialides | Septate | Hyaline |
| | *Aspergillus niger* | Root, Leave | Black | Spreads in all directions, forming clustered colonies | Rough, sand-like texture | Dark brown-black | Dark green | Unbranched | Aseptate | Hyaline |
| | *Rhizopus* sp. | Root | White to cream | Rapid radial spreading | Smooth and dense | Round or oval | Brown to blackish | Hyphae supporting sporangium | Rhizoid | Hyaline |
| Kutai Kartenegara Regency Location 2, Desa Bukit Raya, Tenggarong Seberang (GPS -0.4153431, 117.0596034) | | | | | | | | | | |
| Inpari 42 | *Penicillium* sp. | Root, Leave | Greenish with a pinkish reverse surface | Spreads in all directions | Moderately smooth | Round | Green | Branched with phialides | Septate | Hyaline |
| | *Aspergillus niger* | Leave, Stem | Black | Spreads in all directions, forming clustered colonies | Rough, sand-like texture | Dark brown-black | Dark green | Unbranched | Aseptate | Hyaline |
| | *Rhizopus* sp. | Root | White to cream | Rapid radial spreading | Smooth and dense | Round or oval | Brown to blackish | Hyphae supporting sporangium | Rhizoid | Hyaline |
| Kutai Kartenegara Regency Location 3, Pulau Atas, Makroman (GPS -0.5637383, 117.2285863) | | | | | | | | | | |
| Mayas | *Penicillium* sp. | Root, Leave | Greenish with a pinkish reverse surface | Spreads in all directions | Moderately smooth | Round | Green | Branched with phialides | Septate | Hyaline |
| | *Aspergillus niger* | Stem | Black | Spreads in all directions, forming clustered colonies | Rough, sand-like texture | Dark brown-black | Dark green | Unbranched | Aseptate | Hyaline |
| | *Rhizopus* sp. | Root | White to cream | Rapid radial spreading | Smooth and dense | Round or oval | Brown to blackish | Hyphae supporting sporangium | Rhizoid | Hyaline |
| Kutai Kartenegara Regency Location 4, Desa Bukit Raya, Tenggarong Seberang (GPS -0.4191219, 117.0607427) | | | | | | | | | | |
| Mekongga | *Aspergillus niger* | Root, Stem | Black | Spreads in all directions, forming clustered colonies | Rough, sand-like texture | Dark brown-black | Dark green | Unbranched | Aseptate | Hyaline |
| | *Trichoderma* sp. | Root, Stem, Leave | White to dark green | Lateral and vertical, forming circular colonies | Smooth | Round | Green | Branched | Septate | Hyaline |

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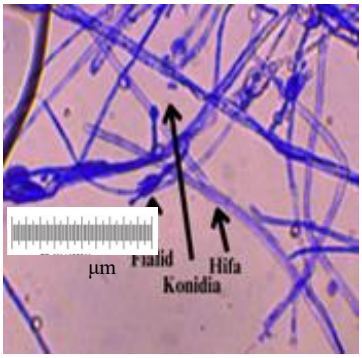


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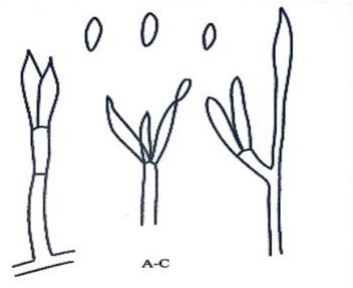


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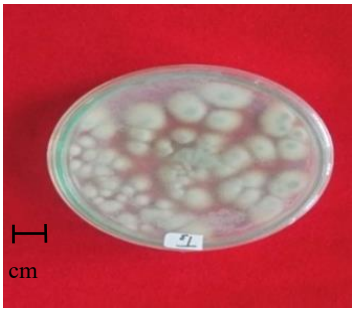


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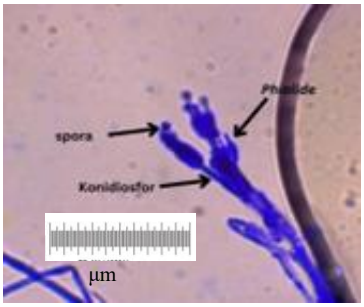


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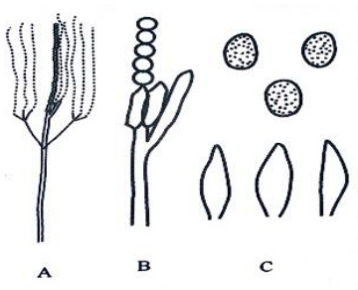


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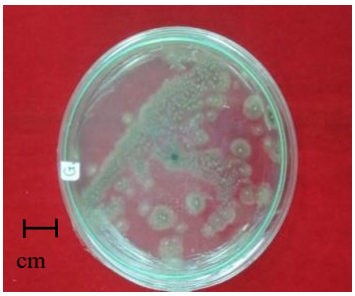


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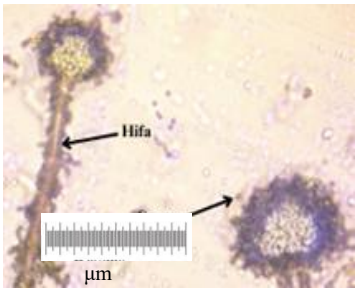


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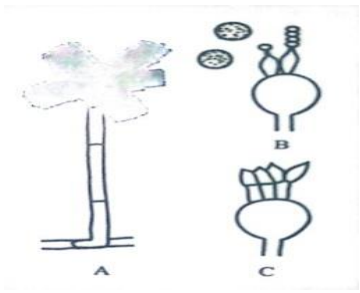


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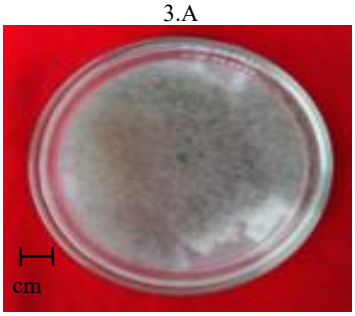


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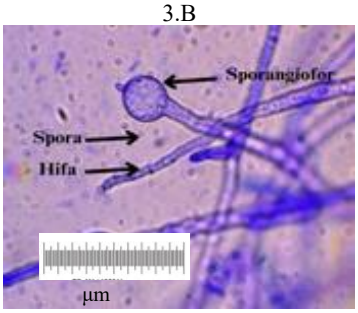


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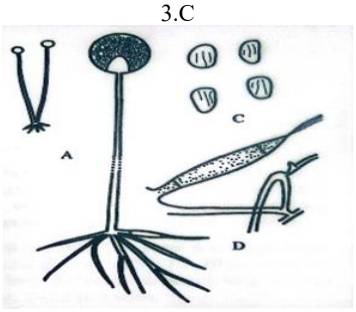
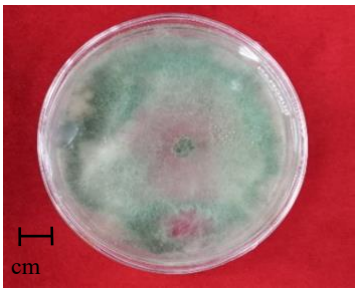
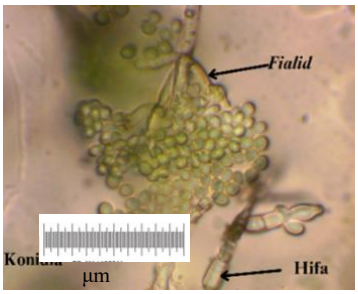



4.C




5.A

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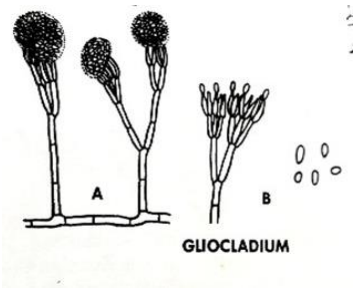


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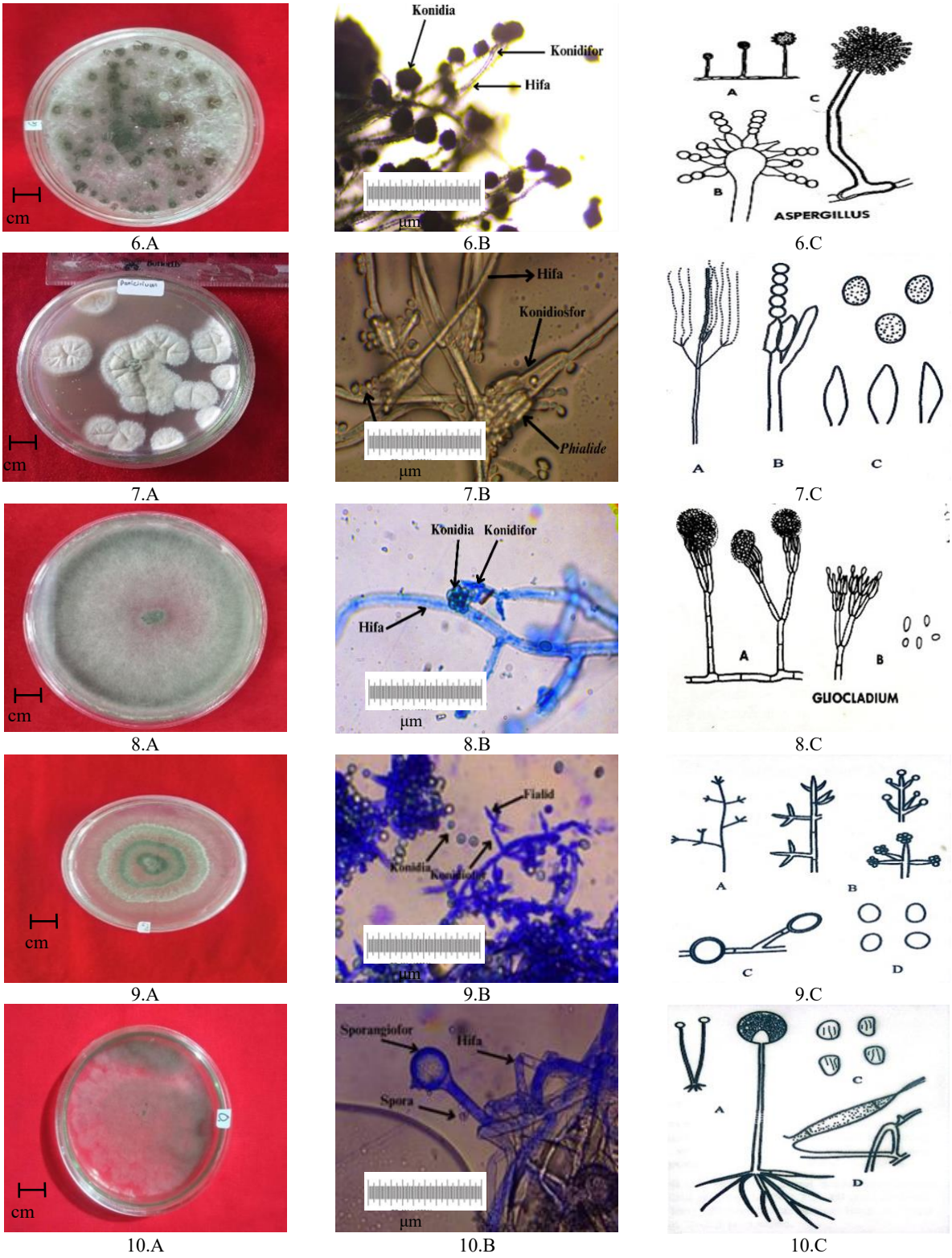



**Figure 1.** Endophytic fungi diversity in rice isolated from PPU Regency. PPU 1: 1. *Paecilomyces* 2. *Penicillium* 3. *Aspergillus niger* 4. *Rhizopus* sp.; PPU 2: 5. *Gliocladium* sp. 6. *Aspergillus niger* 7. *Penicillium* 8. *Gliocladium* sp. PPU 3: 9. *Trichoderma* sp. 10. *Rhizopus* sp. A. Macroscopic observation/Colony B. Microscopic observation

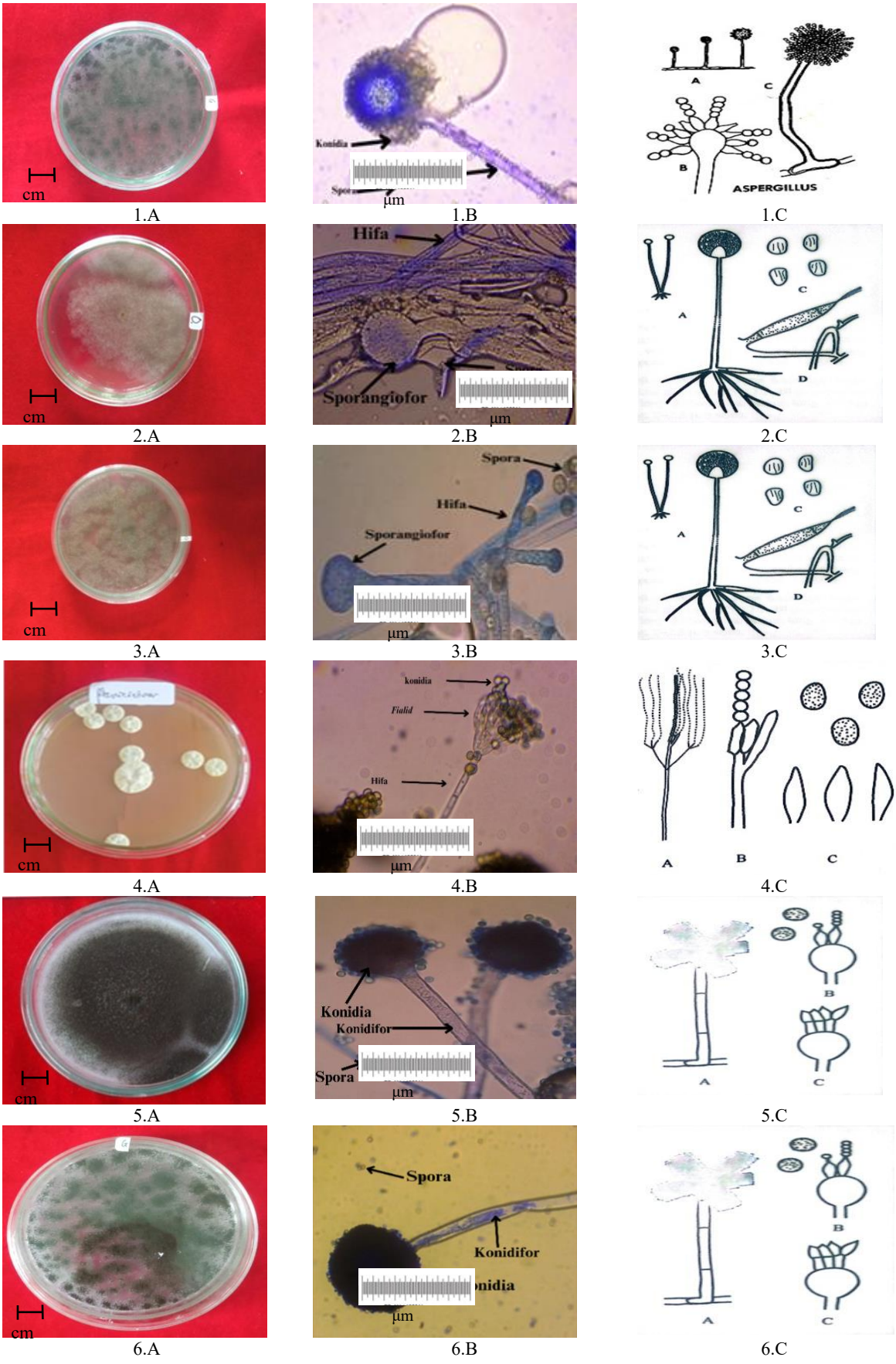
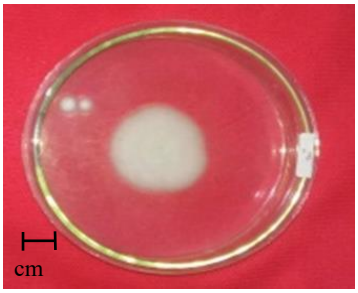



**Figure 2.** Endophytic fungi diversity in rice isolated from Samarinda region. Samarinda 1: 1. *Aspergillus niger* 2. *Rhizopus* sp.; Samarinda 2: 3. *Rhizopus* sp. 4. *Penicillium* 5. *Aspergillus niger*; Samarinda 3: 6. *Aspergillus niger*. A. Macroscopic observation/Colony B. Microscopic observation

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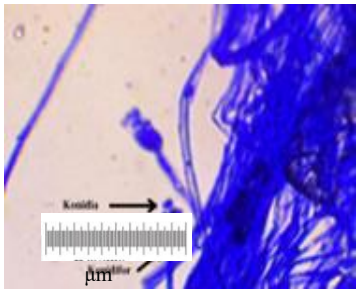


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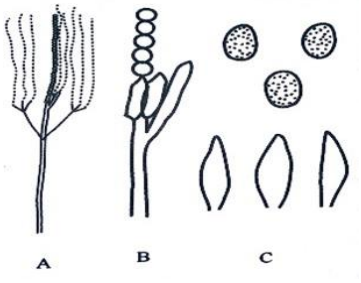


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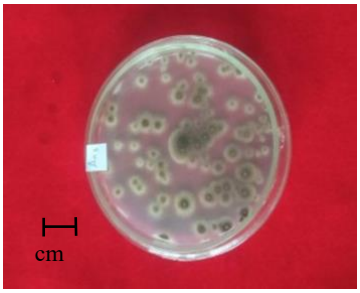


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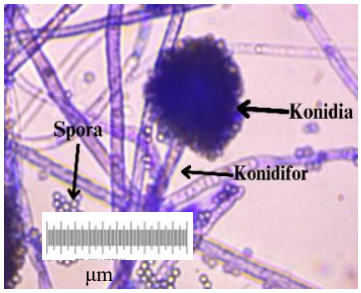


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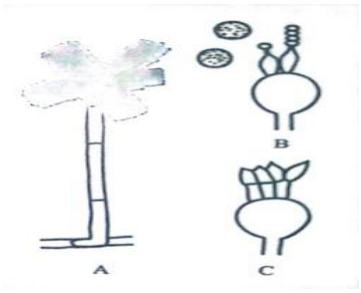
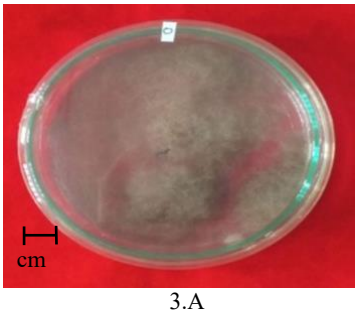



2.C

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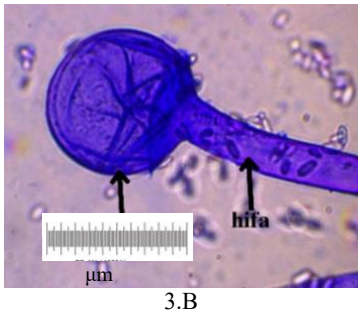
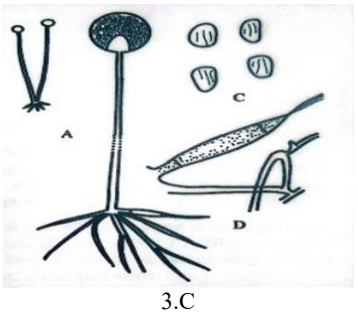
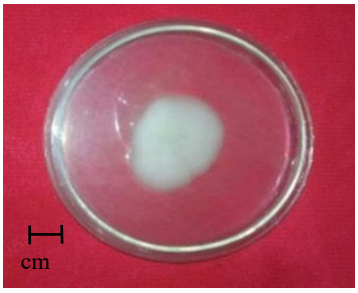


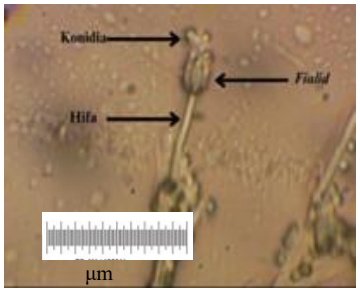

3.B



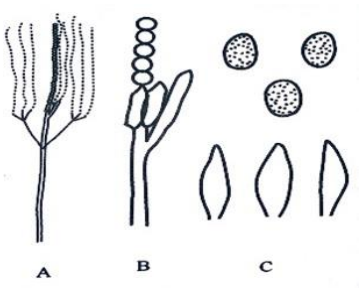

3.C




4.A




4.B

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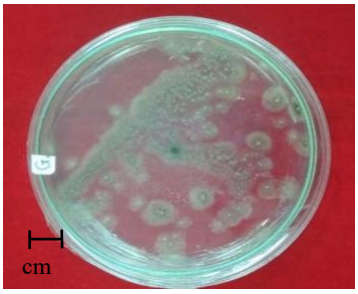


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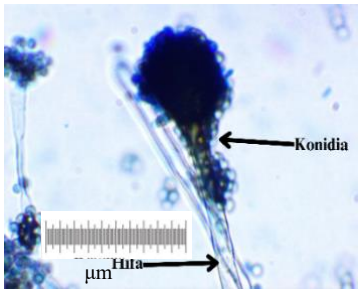
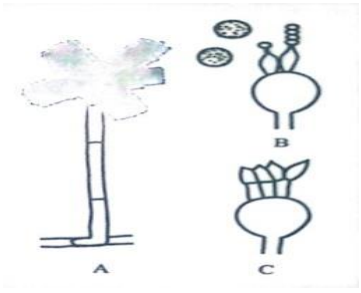
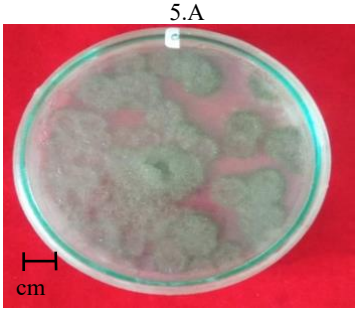



5.B

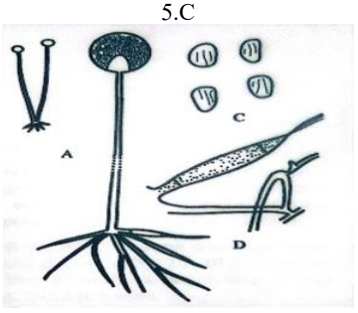



5.C

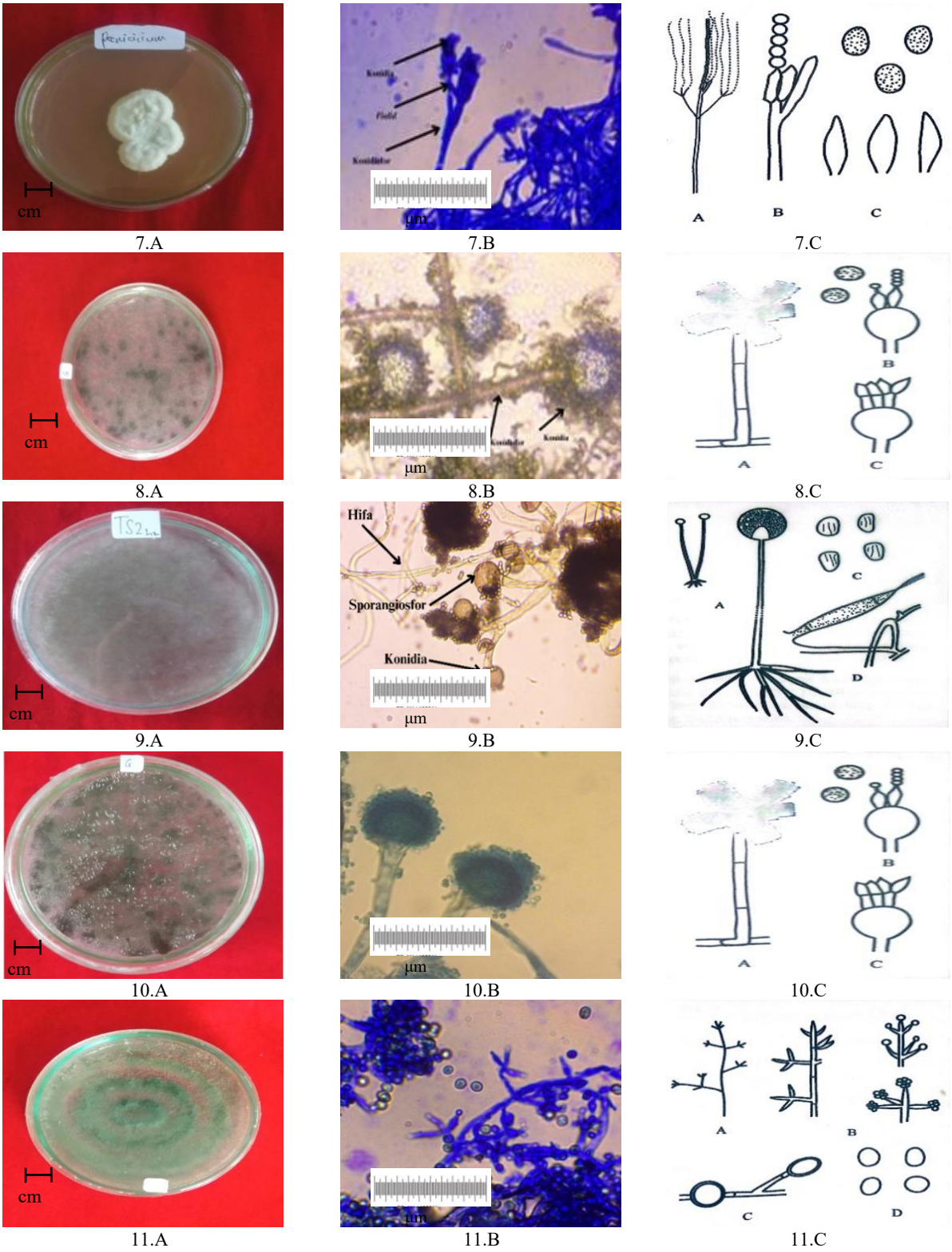



6.A


6.B

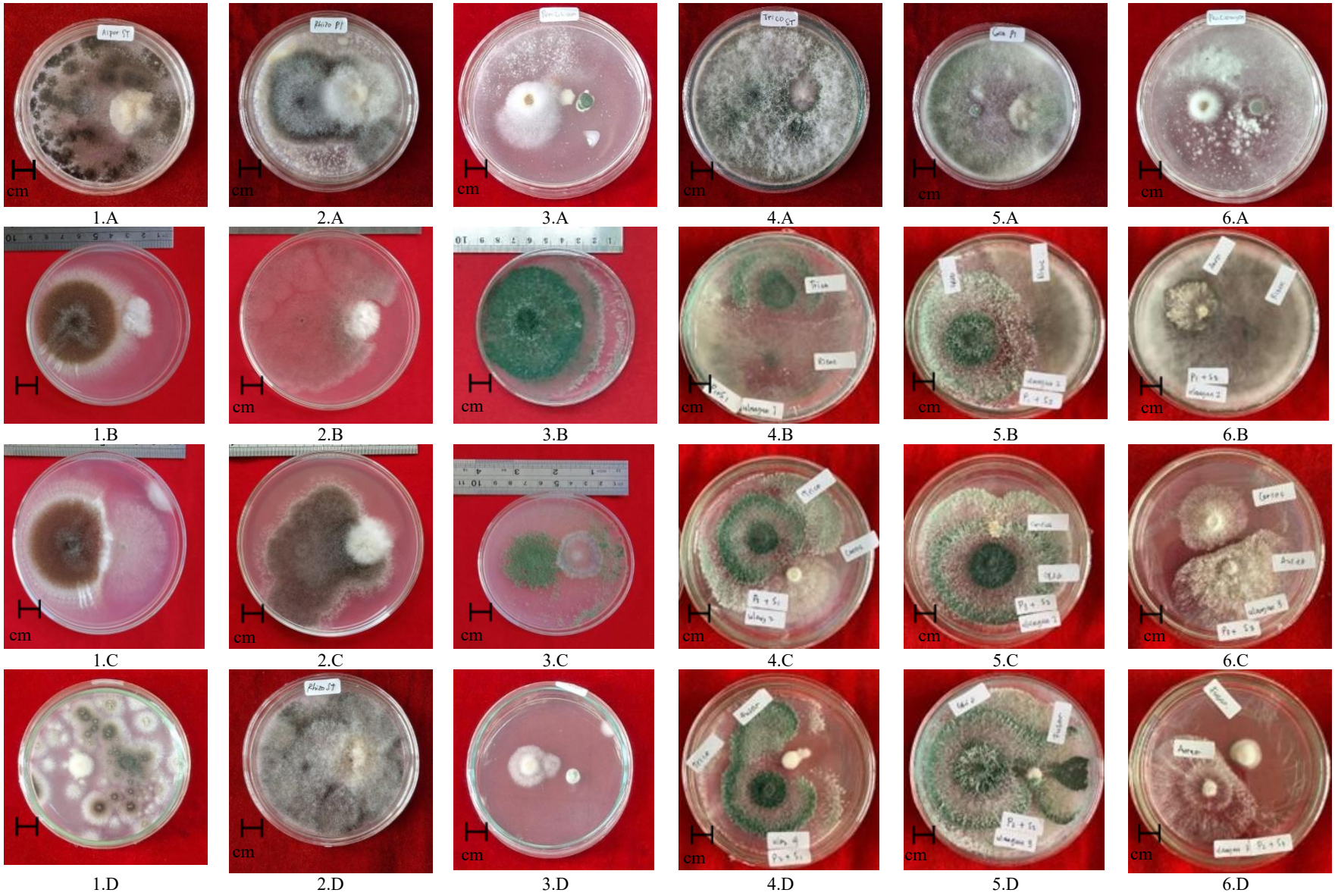



6.C




7.A 7.B 7.C
8.A 8.B 8.C
9.A 9.B 9.C
10.A 10.B 10.C
11.A 11.B 11.C

**Figure 3.** Endophytic fungi diversity in rice isolated from Kutai Kartanegara Regency. Kutai Kartanegara 1: 1. *Penicillium* 2. *Aspergillus niger* 3. *Rhizopus* sp. Kutai Kartanegara 2: 4. *Penicillium* 5. *Aspergillus niger* 6. *Rhizopus* sp. Kutai Kartanegara 3: 7. *Penicillium* 8. *Aspergillus niger* 9. *Rhizopus.* Kutai Kartanegara 4: 10. *Aspergillus niger* 11. *Trichoderma* sp. A. Macroscopic observation/Colony B. Microscopic observation


cm
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2.A
3.A
4.A
5.A
6.A
1.B
2.B
3.B
4.B
5.B
6.B
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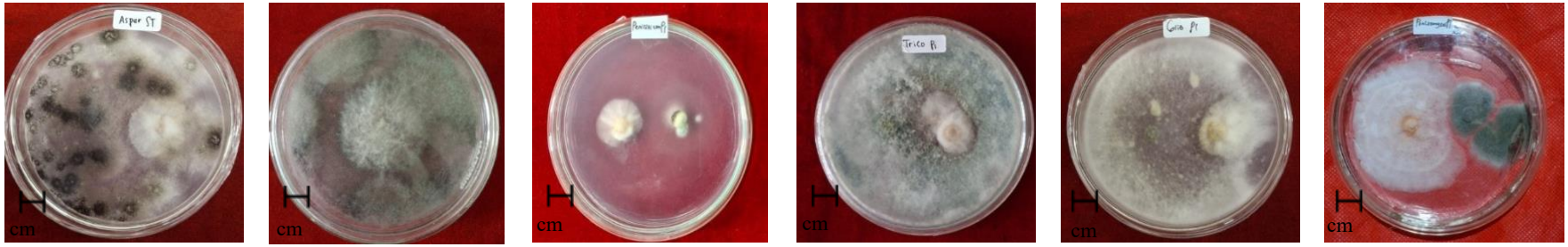
1.D
2.D
3.D
4.D
5.D
6.D




1.E 2.E 3.E 4.E 5.E 6.E

**Figure 4.** Antagonistic mechanism of rice endophytic fungi. 1. *Aspergillus niger*; 2. *Rhizopus* sp.; 3. *Penicillium* sp.; 4. *Trichoderma* sp.; 5. *Gliocladium* sp.; 6. *Peacylomyces* sp.; A. *Magnaporthe oryzae*; B. *Rhizoctonia solani*; C. *Cercospora* sp.; D. *Fusarium oxysporum*; E. *Curvularia* sp.

**Inhibitory activity**

The inhibitory activity of six endophytic fungal isolates against the five major rice pathogens *M. oryzae, Fusarium* sp., *Cercospora* sp., *R. solani,* and *Curvularia* sp. showed statistically significant differences ($p<0.05$) (Table 3). Among the isolates, *Rhizopus* sp. consistently showed the highest antagonistic activity, with inhibition rates of 81.11% against *Fusarium* sp., 85.00%, against both *Cercospora* sp. and *R. solani*, and 71.33% against *Curvularia* sp. *Gliocladium* sp. also exhibited strong inhibitory effects, particularly against *Cercospora* sp. (73.92%), *R. solani* (82.82%), and *Curvularia* sp. (76.44%).

In contrast, *Paecilomyces* sp., *Trichoderma* sp., and *A. niger*, exhibited moderate inhibition across most pathogens, with inhibition percentages ranging from 36.25% to 62.78%. *Penicillium* sp. showed the lowest overall activity, although it reached 55.83% inhibition against *Curvularia* sp. Notably, the weakest inhibitory effects were generally observed against *M. oryzae*, all isolates exhibiting inhibition rates around or below 50%, with *Gliocladium* sp. and *Penicillium* sp. showing the lowest values of 41.67% and 43.75%, respectively.

**Discussion**

*Endophytic fungal diversity*

The isolation results showed that a total of six endophytic fungal genera, namely *A. niger, Penicillium* sp., *Rhizopus* sp., *Trichoderma* sp., *Gliocladium* sp., and *Paecilomyces* sp. were found associated from rice plants across various sites in Penajam Paser Utara (PPU), Samarinda, and Kutai Kartanegara. The diverse fungal communities are associated with rice and intricate relationships between fungi, their host varieties, and the surrounding environment (Sudová et al. 2020; Baron and Rigobelo 2021; Farrer et al. 2025). The frequent occurrence of *A. niger, Penicillium* sp., and *Rhizopus* sp. across multiple sampling sites indicates their strong ecological adaptability and consistent association with rice plants. Similar findings have been reported on the widespread presence of these fungal genera in various rice-growing environments (David et al. 2023; Trizelia et al. 2023; Tripathy et al. 2023; Hu et al. 2024).

The differences in fungal diversity observed in the current study are consistent with previous reports emphasizing the influence of environmental factors, host plant variation, and geographic location on the composition of endophytic communities (Huang 2020; Baron and Rigobelo 2021; Wang et al. 2022). Such spatial variations have been documented in other studies, suggesting that local environmental conditions and agricultural practices, such as soil characteristics (Lin et al. 2020), climate (Siddique et al. 2023), and plant genotype (Nunna and Balachandar 2024; Liu et al. 2024), shape the diversity and composition of endophytic communities in rice. In addition, dynamic nature of these communities throughout the plant's life cycle suggests a complex interplay between the host and its associated endophytes (Orozco-Mosqueda and Santoyo 2021; Sehrish et al. 2023; Danso Ofori et al. 2024).

Most of the endophytic fungi observed were identified only to the genus level, as the morphological characterization methods employed were insufficient for species-level identification. *A. niger* was an exception, as its distinct microscopic features allowed for accurate identification at the species level. Morphological characterization remains a fundamental approach for fungal identification. Accurate identification of endophytic fungi is crucial for understanding their ecological roles and potential applications. Distinct morphological characteristics observed in the fungal isolates, such as differences in colony color, surface texture, growth behavior, and microscopic traits like conidia and hyphal structure, offered valuable taxonomic clues that supported accurate identification at the genus level (Houbraken et al. 2020). These results align with earlier research reporting a wide range of endophytic fungi associated with rice, including genera like *Aspergillus, Penicillium, Trichoderma,* and *Fusarium*.

**Table 2.** Antagonistic mechanism of endophytic fungi

| Treatments | Antagonistic mechanisms | | |
|---|---|---|---|
| | C | P | A |
| *Peacylomyces* sp. vs. *Magnaporthe oryzae* | + | - | - |
| *Aspergillus niger* vs. *Magnaporthe oryzae* | + | - | - |
| *Trichoderma* sp. vs. *Magnaporthe oryzae* | + | - | - |
| *Gliocladium* sp. vs. *Magnaporthe oryzae* | + | - | - |
| *Rhizopus* sp. vs. *Magnaporthe oryzae* | + | + | - |
| *Penicillium* sp. vs. *Magnaporthe oryzae* | + | - | - |
| *Peacylomyces* sp. vs. *Fusarium* sp. | + | - | + |
| *Aspergillus niger* vs. *Fusarium* sp. | + | - | - |
| *Trichoderma* sp. vs. *Fusarium* sp. | + | + | - |
| *Gliocladium* sp. vs. *Fusarium* sp. | + | + | - |
| *Rhizopus* sp. vs. *Fusarium* sp. | + | + | - |
| *Penicillium* sp. vs. *Fusarium* sp. | + | - | - |
| *Peacylomyces* sp. vs. *Cercospora* sp. | + | - | + |
| *Aspergillus niger* vs. *Cercospora* sp. | + | - | + |
| *Trichoderma* sp. vs. *Cercospora* sp. | + | + | - |
| *Gliocladium* sp. vs. *Cercospora* sp. | + | + | - |
| *Rhizopus* sp. vs. *Cercospora* sp. | + | - | - |
| *Penicillium* sp. vs. *Cercospora* sp. | + | - | - |
| *Peacylomyces* sp. vs. *Rhizoctonia solani* | + | - | + |
| *Aspergillus niger* vs. *Rhizoctonia solani* | + | - | - |
| *Trichoderma* sp. vs. *Rhizoctonia solani* | + | + | - |
| *Gliocladium* sp. vs. *Rhizoctonia solani* | + | + | - |
| *Rhizopus* sp. vs. *Rhizoctonia solani* | + | - | - |
| *Penicillium* sp. vs. *Rhizoctonia solani* | - | + | - |
| *Peacylomyces* sp. vs. *Curvularia* sp. | + | + | - |
| *Aspergillus niger* vs *Curvularia* sp. | + | + | - |
| *Trichoderma* sp. vs. *Curvularia* sp. | + | - | - |
| *Gliocladium* sp. vs. *Curvularia* sp. | + | - | - |
| *Rhizopus* sp. vs. *Curvularia* sp. | + | + | - |
| *Penicillium* sp. vs. *Curvularia* sp. | + | - | - |

Note: C: Competition, P: Parasitism, A: Antibiosis, (+): Presence of antagonistic mechanism occurs; (-): Absence of antagonistic mechanism

**Table 3.** Percentage of inhibition of endophytic fungi against several rice pathogens (%)

| Fungi | Pathogens | | | | | | | | | | Mean |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | *M. oryzae* | | *Fusarium* sp. | | *Cercospora* sp. | | *R. solani* | | *Curvularia* sp. | | |
| | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | |
| *Peacylomyces* sp. | 50.00 a | 4.20 | 50.00 bc | 3.10 | 52.14 b | 3.50 | 61.25 b | 6.50 | 45.83 c | 6.50 | 51.84 |
| *Aspergillus niger* | 50.00 a | 4.30 | 50.00 bc | 4.60 | 50.00 b | 5.10 | 50.00 bc | 4.50 | 48.33 bc | 4.50 | 49.67 |
| *Trichoderma* sp. | 50.00 a | 3.20 | 50.00 bc | 4.40 | 36.25 bc | 3.30 | 62.78 b | 4.50 | 50.42 bc | 4.50 | 49.89 |
| *Gliocladium* sp. | 41.67 ab | 3.10 | 65.59 ab | 3.60 | 73.92 a | 3.70 | 82.82 a | 5.60 | 76.44 a | 5.60 | 68.09 |
| *Rhizopus* sp. | 54.18 a | 3.20 | 81.11 a | 4.30 | 85.00 a | 4.60 | 85.00 a | 4.20 | 71.33 ab | 4.20 | 75.32 |
| *Penicillium* sp. | 43.75 ab | 4.50 | 43.64 cd | 5.10 | 37.33 bc | 6.10 | 50.10 bc | 4.70 | 55.83 abc | 4.70 | 46.13 |
| Mean | 48.27 | 3.55 | 56.72 | 4.25 | 55.77 | 4.38 | 65.33 | 5.20 | 58.03 | 5.20 | 48.27 |
| ANOVA | * | | * | | * | | * | | * | | |
| LSD | 14.47 | | 18.17 | | 20.69 | | 17.24 | | 24.99 | | |

Note: *ANOVA test significant at 95%; SD: Standard Deviation; LSD: Least Significant Different Value

*Antagonistic potential*

The antagonistic potential of endophytic fungal isolates against several major rice pathogens, including *M. oryzae, Fusarium* sp., *Cercospora* sp., *R. solani,* and *Curvularia* sp., was evaluated in terms of competition, parasitism, and antibiosis mechanisms. Among these, competition for nutrients and space emerged as the most frequent antagonistic mechanism. This finding aligns with earlier studies that describe resource competition as a central mechanism in microbial antagonism within plant-pathogen-endophyte systems (Akram et al. 2023; Priyashantha et al. 2023). Competitive dominance in vitro may indicate strong rhizospheric adaptability, allowing these fungi to suppress pathogens in nutrient-rich or resource-limited conditions (Grabka et al. 2022). However, in vivo relevance depends on host-microbe compatibility and environmental factors, which should be further explored through greenhouse or field-based assays.

Parasitism, particularly mycoparasitism, was evident in interactions involving *Trichoderma* sp., *Gliocladium* sp., and *Rhizopus* sp., as characterized by coiling around pathogen hyphae, penetration structures, and degradation zones. *Trichoderma* spp. are well-documented mycoparasites, producing hydrolytic enzymes such as chitinases and glucanases that degrade pathogen cell walls (Matas Baca et al. 2023; Stange et al. 2024). Similarly, *Gliocladium* spp. have demonstrated direct parasitism against pathogens like *Sclerotium rolfsii* and *Botrytis cinerea* (Hassine et al. 2022; Nagaraj and Kolanthasamy 2025). It showed parasitism against *Fusarium* sp., *Rhizoctonia solani* and *Cercospora* sp. Interestingly, while *Rhizopus* spp. are commonly recognized for their ecological role in decomposing organic matter, serving primarily as saprophytes in soil systems. Recent studies suggest that *R. oryzae* may also influence plant development through the production of indole-3-acetic acid (IAA), hormone essential for root development and cell elongation (Parvez et al. 2023). Because of this, *R. oryzae* has been identified as a potential candidate for use in biofertilizer formulations. In addition, *R. microsporus* has also been found to have antagonism against nematode, supporting the idea that members of this genus may contribute positively to plant stimulator and anti-nematodes (Attia et al. 2023). However, definitive mycoparasitic activity in *Rhizopus* remains underreported and requires further validation using microscopy and enzyme profiling.

Antibiosis is indicated by inhibition of pathogen growth and development through the secretion of secondary metabolites, including antibiotics, hydrolytic enzymes, and volatile organic compounds (Tyśkiewicz et al. 2022; Leetanasaksakul et al. 2024). In this study, *Paecilomyces* sp. exhibited antibiosis against *Fusarium* sp., *Cercospora* sp., and *R. solani*, while *A. niger* demonstrated antibiosis specifically against *Cercospora* sp. *Paecilomyces* species. A previous study has shown that *Paecilomyces lilacinus* possesses notable antifungal properties, achieving inhibition rates of 66.3% against *Cladosporium* spp. and 52.53% against *R. solani* (Constantin et al. 2022). In addition, *Paecilomyces variotii* has demonstrated effectiveness as a biocontrol agent against a range of both foliar and soil-borne fungal diseases, suggesting a broad antifungal spectrum (Moreno-Gavíra et al. 2021). These observations highlight the potential of *Paecilomyces* species to suppress pathogenic fungi through the synthesis of bioactive compounds. Similarly, *A. niger* is known to produce a wide array of secondary metabolites (Yu et al. 2023) with potential antimicrobial properties (Wei et al. 2022), including pyridone derivatives, polyketides and alkaloids, and terpenoids (Niazi et al. 2023). A consortium of endophytic fungi exhibiting comprehensive antagonistic mechanisms, encompassing competition for space and nutrients, mycoparasitism, and the production of antifungal metabolites, could provide multi-faceted and sustainable protection against rice pathogens under real agricultural conditions.

*Inhibitory activity*

In this study, the ability of rice-derived endophytic fungi to inhibit pathogen growth was considerably varied, with suppression rates ranging from 36.25% to 85% depending on the targeted pathogen. This reflects the complex and dynamic nature of the interactions between endophytes, plant hosts, and specific pathogens involved. Several critical factors, such as fungal strain specificity (Gao et al. 2025), pathogen susceptibility diversity (Ji et al. 2022), and host-endophyte compatibility (Fontana et al. 2021), collectively influence biocontrol outcomes (Grabka et al. 2022; Ul Haq et al. 2024).

Among the isolated endophytic fungi, *Rhizopus* sp. and *Gliocladium* sp. demonstrated the highest inhibition rates against most tested rice pathogens, reaching up to 85% suppression of *Cercospora* sp., *R. solani*, and *Fusarium* sp. (Table 3). Their strong antagonistic performance suggests potent biocontrol potential, likely mediated through rapid colonization, nutrient competition, and the production of antifungal metabolites (Attia et al. 2023; Fardhani et al. 2024). The ability of *Rhizopus* sp. to inhibit multiple pathogens aligns with previous findings that members of this genus can suppress diverse fungi through competition and secretion of organic acids (Parvez et al. 2023), while *Gliocladium* spp. employ mycoparasitism and enzymatic degradation of pathogen hyphae, reinforced by antifungal compounds such as gliotoxin, providing effective control of soil and seed-borne pathogens (Fardhani et al. 2024).

Concurrently, *Paecilomyces* sp., *Trichoderma* sp., and *A. niger* displayed moderate efficacy, whereas *Penicillium* sp. was the least effective among the isolates tested (Table 3). *Paecilomyces* spp., has an average of 51.84% inhibitory effects against rice pathogen, especially against *R. solani* and *Cercospora* sp. This fungi combine antifungal compound production with direct parasitism of spores and hyphae, and can also target plant-parasitic nematodes, offering multifunctional crop protection (Giri et al. 2022). *Trichoderma* sp. exhibited antagonistic activity, though generally lower than *Rhizopus* and *Gliocladium*. Its inhibitory effects, particularly against *R. solani* and *Curvularia* sp., are consistent with its established mechanisms of mycoparasitism and secretion of cell wall–degrading enzymes and secondary metabolites (Sopialena et al. 2018; Matas Baca et al. 2023; Chen et al. 2024). In addition, *A. niger* produces a wide range of extracellular enzymes (e.g., cellulases, chitinases, β-1,3-glucanases) and organic acids (oxalic, citric) that degrade pathogen cell walls and alter pH (Alam et al. 2021; Tong et al. 2024). *Penicillium* spp. generate diverse antimicrobial metabolites, including penicillin-like compounds and volatile organic compounds, and can induce systemic resistance (Bhardwaj et al. 2023; Murad et al. 2024). Although in this study *Penicillium* sp. displayed the lowest inhibition values compared to others; however, many studies reveal its potential role in producing bioactive secondary metabolites and inducing systemic resistance remains noteworthy (Bhardwaj et al. 2023; Murad et al. 2024).

Pathogen susceptibility also plays a crucial role in determining the extent of fungal inhibition. Some pathogens are highly responsive to antagonistic compounds or resource competition, while others might appear more resistant, showing limited suppression (Khaskheli et al. 2020). A notable finding was that relatively weak inhibition was observed against *M. oryzae*, a major pathogen in cultivated rice. This suggests that additional factors, such as complex infection strategies or structural defenses of the pathogen, may reduce the effectiveness of certain endophytes (Mapuranga et al. 2022; Bhardwaj et al. 2023). Therefore, further mechanistic studies are warranted to elucidate the specific modes of action employed by effective endophytic strains and to identify those with broad or targeted pathogen specificity.

The fungal strain plays a major role in antagonistic performance. Different strains can exhibit distinct levels of antifungal activity due to variations in their genetic makeup and secondary metabolite profiles (Xu et al. 2021; Putri et al. 2022). These differences highlight the need to select fungal strains for specific disease targets (Sopialena et al. 2018). The variability in inhibition also supports the use of consortia-based approaches in which combinations of fungal strains are deployed to improve disease control breadth and consistency (Djatmiko et al. 2023). Such combinations can reduce variability and increase the overall efficacy of disease suppression. These findings support the integration of endophytic fungi as eco-friendly alternatives to chemical pesticides in sustainable rice disease management.

In conclusion, this research highlights the rich diversity and promising biocontrol capacity of endophytic fungi inhabiting rice plants cultivated across various agroecological regions in East Kalimantan, Indonesia. From four distinct rice varieties, six fungal genera were successfully isolated, including *Aspergillus niger, Penicillium* sp*., Rhizopus* sp*., Trichoderma* sp*., Gliocladium* sp*.,* and *Paecilomyces* sp. The dominance of *A. niger, Penicillium* sp*.,* and *Rhizopus* sp. across multiple sites suggests their ecological stability and broad adaptability as endophytes in rice ecosystems. The antagonism assays demonstrated that *Rhizopus* sp. and *Gliocladium* sp. exhibited strong inhibitory effects across multiple pathogens, including *M. oryzae, Fusarium* sp*., Cercospora* sp*., R. solani,* and *Curvularia* sp., indicating their potential for broad-spectrum biocontrol applications. A notable finding was that relatively weak inhibition was observed against *M. oryzae*, the major pathogen in cultivated rice. Practically, the integration of these potent endophytic fungi into rice cultivation systems provides a promising strategy for reducing reliance on chemical fungicides. Their application as biocontrol agents can support the development of eco-friendly, sustainable pest and disease management programs. This aligns well with Integrated Pest Management (IPM) approaches by enhancing biological control components, reducing environmental impact, and contributing to long-term agricultural resilience in East Kalimantan and similar agroecosystems. However, further research is needed to elucidate the fungi identity into species level using molecular characterization, and evaluate their performance under field conditions. As well as policy recommendations include providing targeted subsidies for biofungicides to encourage farmer adoption of environmentally friendly disease management practices.

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