Asian Journal of Mycology 9(1): 1–19 (2026) ISSN 2651-1339
www.asianjournalofmycology.org

**Article**
**Doi 10.5943/ajom/9/1/1**

# Enhanced Production of Ligninolytic Enzymes by Mangrove Fungal Endophytes Co-cultured with Pathogenic and Beneficial Fungi

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Bitacura JG, dela Cruz TEE 2025 – Enhanced Production of Ligninolytic Enzymes by Mangrove Fungal Endophytes Co-cultured with Pathogenic and Beneficial Fungi. Asian Journal of Mycology 9(1), 1–19, Doi 10.5943/ajom/9/1/1

**Abstract**

Mangrove ecosystems host diverse fungal endophytes with potential ligninolytic activity, yet their functional roles under competitive stress remain underexplored. This study assessed 30 mangrove-derived fungal endophytes (MFE) for their ability to produce key ligninolytic enzymes — laccase (Lac), manganese peroxidase (MnP), and lignin peroxidase (LiP) — in single- and dual-culture with the pathogenic *Fusarium oxysporum* and beneficial *Trichoderma afroharzianum*. Enzyme production was evaluated using qualitative colorimetric assays and quantified through potency index (PI), a measure of enzyme efficiency relative to colony growth. Initial screening revealed that enzyme production was species-specific, with only one isolate, *Schizophyllum commune* RmLE-P12, producing all three enzymes. Notably, *Nigrospora* and *Penicillium* isolates exhibited strong Lac and MnP activity, respectively, and with high PI values designating them as hyper-ligninolytic strains. Under co-culture conditions, enzyme expression and growth rates varied. Some MFE showed enhanced enzyme production in response to competition or antagonistic interaction, while others exhibited reduced or suppressed activity. Interaction assays identified six types of fungal interactions, with growth halts near contact (Type C) and challenge species overgrowth (Type E) being most prevalent. Antagonism indices indicated that *T. afroharzianum* exerted a stronger inhibitory effect than *F. oxysporum*. This comprehensive analysis highlights the species-dependent ligninolytic capabilities of MFE and reveals dynamic enzyme regulation under biotic stress.

**Keywords** – antagonism – beneficial fungi – co-culture – fungal interaction – lignin-degrading enzymes

## Introduction

Fungi are among the most efficient lignin-degrading organisms due to their ability to produce a diverse set of ligninolytic enzymes (LE), including laccase (Lac, EC 1.10.3.2), manganese peroxidase (MnP, EC 1.11.1.13), and lignin peroxidase (LiP, EC 1.11.1.14) (Plácido & Capareda 2015, Kunjadia et al. 2016). Laccase is a copper-containing extracellular enzyme that exists in

Submitted 3 February 2025, Accepted 3 December 2025, Published 20 January 2026
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monomeric to tetrameric glycoprotein forms (Kumar & Chandra 2020), while MnP and LiP are heme-dependent oxidoreductases (Pothiraj et al. 2006). These enzymes are primarily produced by white-rot basidiomycetes (Manavalan et al. 2015), although certain ascomycetes like *Aspergillus* and *Penicillium* have also demonstrated the ability to produce these enzymes (Naraian et al. 2013, Dhakar et al. 2015, Hasanin et al. 2019). Because of their ability to break down complex aromatic polymers, ligninolytic enzymes are being widely explored for their biotechnological applications in industrial processes, including wastewater treatment, pollutant degradation, and food processing (Novotný et al. 2004, Chowdhary et al. 2019, Patel et al. 2022).

Fungal endophytes, which colonize healthy plant tissues asymptomatically (Schulz & Boyle 2006), have also been reported to produce ligninolytic enzymes (Oses et al. 2006). These endophytes play critical ecological roles, including enhancing plant resistance to environmental stress and synthesizing bioactive metabolites (Lunardelli Negreiros de Carvalho et al. 2016). However, endophytes do not exist in isolation within plant tissues but as part of complex fungal communities that constantly interact. These interactions can influence fungal metabolism and may trigger or suppress the production of secondary metabolites, including enzymes. For instance, certain endophytic fungi have been reported to produce antimicrobial compounds in response to competitive interactions with pathogenic fungi (Sornakili et al. 2020). Despite these findings, the effect of such interspecies interactions on ligninolytic enzyme production in fungal endophytes is poorly understood.

Mangrove forests, particularly those in the Philippines, are rich reservoirs of fungal endophytes with potential biotechnological applications. Several studies have reported the diversity, bioactivities and enzyme-producing capacity of fungal isolates from Philippine mangroves (Torres & dela Cruz 2013, Moron et al. 2018, Apurillo et al. 2019, Ramirez et al. 2020, Jacob et al. 2023). One common mangrove species, *Rhizophora mucronata* Lam., is known to harbor diverse endophytic fungi, some of which we previously isolated and identified from its leaves (Bitacura et al. 2024). Although some mangrove-derived fungal endophytes (MFE) isolates from this group have been screened for enzyme activity (Torres & dela Cruz 2013), little is known about their response to antagonistic stimuli, particularly in terms of growth and LE production when challenged by other fungi. In natural ecosystems, fungal interactions, whether competitive or cooperative, can significantly influence microbial behavior (Weiland-Bräuer 2021), yet such dynamics remain unexamined among Philippine mangrove fungal endophytes.

Given these gaps, this study aims to provide a comprehensive analysis of the ligninolytic enzyme production of selected mangrove fungal endophytes (MFE), both in isolation and when co-cultured with other fungi. Specifically, we assessed the ability of MFE isolates to produce Lac, MnP, and LiP individually, evaluated their growth and enzyme production under antagonistic interactions with a known pathogen (*Fusarium oxysporum*) and a beneficial fungus (*Trichoderma afroharzianum*), classified the types of interactions between MFE and the challenge species, and measured and compared the antagonistic strengths of the challenge fungi using computed antagonism indices. We hypothesize that fungal endophytes, being naturally exposed to lignin within plant tissues, are primed to produce ligninolytic enzymes, and that their enzyme production can be positively influenced by their interactions with other fungi. Therefore, we expect the pattern of enzyme expression to differ between single- and dual-cultures.

## Materials & Methods

### The mangrove fungal endophytes

The MFE used in the study were isolated from mature leaves of the host mangrove *R. mucronata*. The detailed description of the isolation and identification of these MFE isolates can be found in Bitacura et al. (2024). For the study, we initially tested 30 MFE for LE production: *Penicillium* sp. (RmLE-D01), *Penicillium commune* (RmLE-D02, -D06, -D07, and -P06), *Diaporthe* sp. (RmLE-D03 and -P25), *Pestalotiopsis* sp. (RmLE-D04), *Aspergillus flavus* (RmLE-D05, -D09, -P05, -P07, -P09, -P14, and -P15), *Cladosporium halotolerans* (RmLE-D10), *Curvularia*

*pseudobrachyspora* (RmLE-P01), *Penicillium citrinum* (RmLE-P02 and -P20), *Diaporthe tectonendophytica* (RmLE-P04), *Aspergillus fumigatus* (RmLE-P11, -P13, and -P17), *Schizophyllum commune* (RmLE-P12), *Nigrospora* sp. (RmLE-P21), *Nigrospora guilinensis* (RmLE-P23), *Fusarium* sp. (RmLE-P24 and -P26), and *Cladosporium* sp. (RmLE-P22 and -P28).

**Individual Ligninolytic Enzyme Production Assay**

Screening for ligninolytic enzyme production of the MFE was done following the method as described by Ali et al. (2012) and Pham et al. (2022) with slight modifications. Laccase and manganese peroxidase were detected using CDA-CHL media supplemented with the indicator dyes 0.005 % (v/v) guaiacol (Sinopharm Chemical Reagent, China) and 0.005% (w/v) phenol red (Loba Chemie Pvt. Ltd., India), respectively. On the other hand, lignin peroxidase was detected by supplementing CDA-CHL media with 0.005 % (w/v) methylene blue (Himedia, USA). Fungal mycelial discs (7 mm in diameter) were taken from colony margin of each MFE isolates (10–15-day old culture initially grown on PDA-CHL agar plates) and inoculated in triplicates onto the LE screening media. CDA-CHL inoculated with only PDA-CHL discs (without fungi) served as negative control. Three replications were employed in this experiment. The inoculated culture plates were then incubated at room temperature (25–28 °C) and observed for enzyme production for seven days. The production of ligninolytic enzymes was determined through zones of color changes in the medium around the fungal colony. The presence of laccase was indicated by the oxidative polymerization of guaiacol into reddish brown while the oxidation of phenol red to yellow would indicate manganese peroxidase production. Lastly, the oxidation of methylene blue to form a green-to-white zone indicates lignin peroxidase enzyme production.

To compare the lignocellulolytic enzyme production efficiency of the mangrove fungal endophytes, the diameter of the colony growth (CG) and the zones of color changes (CC) produced around the colonies on the screening plates were measured with a digital caliper (Ingco HDCP16150, China). From these data, the potency index (PI), which is a measure of the efficiency of the fungi in producing the enzymes, was calculated using the formula below (1).

$$PI = \frac{dCC}{dCG} \qquad (1)$$

where:

*PI* = Potency Index
*dCC* = Diameter of Color Change
*dCG* = Diameter of Colony Growth

Furthermore, the fungal isolates were classified as either hyper-ligninolytic or hypo-ligninolytic strains based on their potency indices following the method described by Kaur et al. (2018). Isolates with PI ≥1 were classified as hyper-ligninolytic strains while isolates with PI <1 were considered as hypo-ligninolytic strains.

**Ligninolytic enzyme production under antagonistic interaction**

To determine the effect of the presence of another microorganism on the ligninolytic enzyme production of the fungal endophytes, select MFE isolates were co-cultured with known pathogenic and beneficial fungi (= challenge fungi). The fungal pathogen used in this study was *Fusarium oxysporum*, an agent of Banana Wilt disease, while *Trichoderma afroharzianum* isolated from the roots of *Saccharum spontaneum* was used as a beneficial fungal species as reported in Cruz & dela Cruz (2024a).

From the 30 MFE isolates, we have chosen twelve MFE for this assay. Each MFE isolate was subjected to the same set of treatments for LE production: MFE isolate alone (control), MFE in co-culture with *Fusarium oxysporum* (a pathogen), and MFE in co-culture with *T. afroharzianum* (a beneficial fungus). The MFE isolates used in the experiment were *Penicillium* sp. (RmLE-D01), *Diaporthe* sp. (RmLE-D03), *Pestalotiopsis* sp. (RmLE-D04), *P. commune* (RmLE-D07), *A flavus*

(RmLE-D09), *C. halotolerans* (RmLE-D10), *D. tectonendophytica* (RmLE-P04), *A flavus* (RmLE-P05), *P. commune* (RmLE-P06), *S. commune* (RmLE-P12), *Nigrospora* sp. (RmLE-P21), and *Fusarium* sp. (RmLE-P26). These twelve strains were selected because of their high Lac, MnP or LiP production and potency indices, production of two or three LE, and/or possible antagonistic properties. The antagonistic interaction was done through the dual culture technique (dela Cruz et al. 2021). This was done by placing mycelial discs (7 mm) of the MFE and the challenge fungal species (pathogen or beneficial) at the opposite edges of 90 mm sterile Petri dishes pre-filled with hardened CDA-CHL supplemented with the respective indicator dyes for the three ligninolytic enzymes. Plates inoculated with only the MFE or only the challenge species served as the control. Following incubation at room temperature (25–28 °C), measurements of the colony growth and color changes expressed as radial growth toward the challenge species or alone (control) were made for two time points. From these data, the rates of colony growth (RCG; 2) and color changes (RCC; 3) were computed using the formula below. Potency index was determined as earlier described, albeit as radial measurements.

$$RCG = \frac{CGD_1 - CGD_2}{T} \qquad (2)$$

where:

*RCG* = Rate of Colony Growth
$CGD_1$ = Radial Measurement of Colony Growth in Day 1
$CGD_2$ = Radial Measurement of Colony Growth in Day 2
*T* = No. of Days between Observations

$$RCC = \frac{CCD_1 - CCD_2}{T} \qquad (3)$$

where:

*RCC* = Rate of Color Change
$CCD_1$ = Radial Measurement of Color Change in Day 1
$CCD_2$ = Radial Measurement of Color Change in Day 2
*T* = No. of Days between Observations

Lastly, the type of interaction (Table 1) between the MFE, designated as the "response species," and the pathogen or beneficial fungus, designated as the "challenge species," was also determined based on the categories described by Morón-Ríos et al. (2017). The challenge species' antagonism index (AI) was determined as their degree of dominance towards the MFE. This index was calculated by multiplying the total number of MFE for each interaction by the assigned score (Table 1), then adding all values to get the final score for each challenge species for every type of media used.

**Experimental Design and Statistical Analysis**

The experiment on individual ligninolytic enzyme production by select MFE was performed in a completely randomized design, while the experiment on ligninolytic enzyme production under antagonistic interaction followed the nested (hierarchical) design. Residual analysis was first performed on the data. The Shapiro-Wilk test was performed to determine the normality of the data, while the Levene test was performed to determine the equality of variances. Analysis of variance (ANOVA) was performed to determine the differences among the treatments considered. For individual ligninolytic enzyme production data, one-way ANOVA was performed to compare the colony growth, color change, and potency indices of the select MFE for the three enzymes studied. For the data on ligninolytic enzyme production under antagonistic interaction, two-stage nested ANOVA was performed for the colony growth, color change, and potency indices to compare all the isolates, treatments within the isolates, potency indices, colony growth rate, and color change rate for the three enzymes studied. Whenever a significant difference among the treatments is found, multiple comparisons of means using Tukey's honestly significant difference (HSD) test were performed. The

significance level considered in the analysis is $\alpha = 0.05$. All the analysis was performed using the free statistical software R version 4.0.2 (Team 2013). Lastly, visualizations were made using Microsoft 365 applications and in R using the ggplot2 package (Wickham 2016).

**Table 1** Categories of fungal interaction and their corresponding scores as adapted from Morón-Ríos et al. (2017).

| Category | Description of Interaction | Score |
|---|---|---|
| **A** | Mutual intermingling of both species. | 0 |
| **$B_1$** | Response species overgrows challenge species, growth of challenge species is reduced. | 1 |
| **$B_2$** | Response species grows up to, on and around challenge species | 1 |
| **C** | Colonies of both species grow until nearly coming into contact and then growth ceases. | 2 |
| **D** | Mutual inhibition at a distance between both species. | 3 |
| **$E_1$** | Challenge species overgrows response species, growth of response species is reduced. | 4 |
| **$E_2$** | Challenge species grows up to, on and around response species | 4 |

## Results

### Ligninolytic Enzyme Production by Individual MFE Isolates

Table 2 shows the ligninolytic enzyme activity of various mangrove fungal endophyte (MFE) isolates based on qualitative assays for laccase (Lac), manganese peroxidase (MnP), and lignin peroxidase (LiP). Lignin peroxidase was the most widely and strongly expressed enzyme, with high activity (++), especially among *Aspergillus flavus*, *Aspergillus fumigatus*, *Fusarium sp.*, and *Penicillium* species. In contrast, laccase and MnP production were limited to a few isolates, notably *Nigrospora*, *Penicillium*, *Diaporthe*, and *Schizophyllum*. Among these, *Schizophyllum commune* RmLE-P12 stood out for producing all three enzymes suggesting its potential as a versatile lignin degrader. Most *Aspergillus* and *Cladosporium* isolates produced only LiP, indicating a likely preference for LiP-dependent ligninolytic pathways.

**Table 2** Qualitative evaluation of the ligninolytic enzyme production by mangrove fungal endophytes.

| MFE Isolates | Lac[a] | MnP | LiP |
|---|---|---|---|
| *Aspergillus flavus* RmLE-D05 | - | - | ++ |
| *Aspergillus flavus* RmLE-D09 | - | - | ++ |
| *Aspergillus flavus* RmLE-P05 | - | - | ++ |
| *Aspergillus flavus* RmLE-P15 | - | - | ++ |
| *Aspergillus flavus* RmLE-P07 | - | - | ++ |
| *Aspergillus flavus* RmLE-P09 | - | - | ++ |
| *Aspergillus flavus* RmLE-P14 | - | - | ++ |
| *Aspergillus fumigatus* RmLE-P11 | - | - | ++ |
| *Aspergillus fumigatus* RmLE-P13 | - | - | ++ |
| *Aspergillus fumigatus* RmLE-P17 | - | - | ++ |
| *Cladosporium halotolerans* RmLE-D10 | - | - | ++ |
| *Cladosporium* sp. RmLE-P22 | - | - | ++ |
| *Cladosporium* sp. RmLE-P28 | - | - | ~ |

**Table 2** Continued.

| MFE Isolates | Lac[a] | MnP | LiP |
|---|---|---|---|
| *Curvularia pseudobrachyspora* RmLE-P01 | + | - | ++ |
| *Diaporthe* sp. RmLE-D03 | - | ++ | + |
| *Diaporthe* sp. RmLE-P25 | - | ++ | + |
| *Diaporthe tectonendophytica* RmLE-P04 | - | - | + |
| *Fusarium* sp. RmLE-P24 | - | - | ++ |
| *Fusarium* sp. RmLE-P26 | - | - | ++ |
| *Nigrospora* sp. RmLE-P21 | ++ | - | + |
| *Nigrospora guilinensis* RmLE-P23 | ++ | - | + |
| *Penicillium citrinum* RmLE-P02 | - | - | ++ |
| *Penicillium citrinum* RmLE-P20 | - | - | ++ |
| *Penicillium commune* RmLE-D02 | - | + | ++ |
| *Penicillium commune* RmLE-D06 | - | + | ++ |
| *Penicillium commune* RmLE-D07 | - | + | ++ |
| *Penicillium commune* RmLE-P06 | - | + | ++ |
| *Penicillium* sp. RmLE-D01 | - | ++ | ++ |
| *Pestalotiopsis* sp. RmLE-D04 | + | - | ++ |
| *Schizophyllum commune* RmLE-P12 | + | + | + |

[a]LE production: (-) no color change, (+) low intensity, (++) high intensity, (~) undetermined

Fig. 1 illustrates the Lac production profiles of selected mangrove fungal endophyte isolates. In Fig. 1A, *Nigrospora* sp. (RmLE-P21) exhibited the largest color change diameter and a high colony growth, indicating strong Lac activity and vigorous growth, followed by *N. guilinensis* (RmLE-P23) and *C. pseudobrachyspora* (RmLE-P01). *Schizophyllum commune* (RmLE-P12), despite having the highest colony growth, showed significantly lower color change, suggesting less ligninolytic activity relative to its biomass. Fig. 1B confirms these observations through potency index values, three isolates were hyper-laccase producing strains with *Nigrospora* sp. (RmLE-P21) showing the highest index, significantly outperforming others ($p < 0.05$), followed by *N. guilinensis*, while *S. commune* had the lowest potency among the hyper-ligninolytic strains. Fig. 1C visually supports these findings, where high and low intensity color halos in *Nigrospora* sp. and *S. commune* plates signify lac activity, respectively, which are absent in the negative control.

Fig. 2 presents a comparative evaluation of the same ligninolytic fungal endophyte isolates, focusing this time on their phenol red-based MnP activity. In Fig. 2A, *Penicillium* sp. (RmLE-D01) showed the highest diameter of color change, indicating strong MnP activity, and ranked significantly higher than all other isolates in both enzyme activity and potency index (Fig. 2B). *Diaporthe* sp. (RmLE-P25 and RmLE-D03) followed closely, with moderate but consistent performance. Several *Penicillium commune* strains and *Schizophyllum commune* (RmLE-P12) showed lower but statistically similar activity levels. The potency index analysis (Fig. 2B) indicated all who tested positive were hyper-MnP producing strains and further confirms *Penicillium* sp. (RmLE-D01) as the most effective peroxidase producer ($p < 0.05$), while the rest of the isolates did not significantly differ from one another. Fig. 2C visually supports these findings, where *Penicillium* sp. (RmLE-D01) produced the most intense yellow halo, followed by *Diaporthe* sp. (RmLE-D03), with the negative control showing no enzymatic reaction.

Fig. 3 illustrates the LiP activity of the same fungal isolates based on methylene blue oxidation on agar plates. We observed no significant differences between diameter of colony growth and color changes, and consequently, the PI among the MFE isolates that tested positive for LiP. However, eight MFE isolates had PI $\geq 1$ and thus, were classified as hyper-ligninolytic strains: *P. commune* (RmLE-D07, -D06, -D02), *A. fumigatus* (RmLE-P13, -P17, -P11), *Pestalotiopsis* sp. (RmLE-D04), and *N. guilinensis* (RmLE-P23).

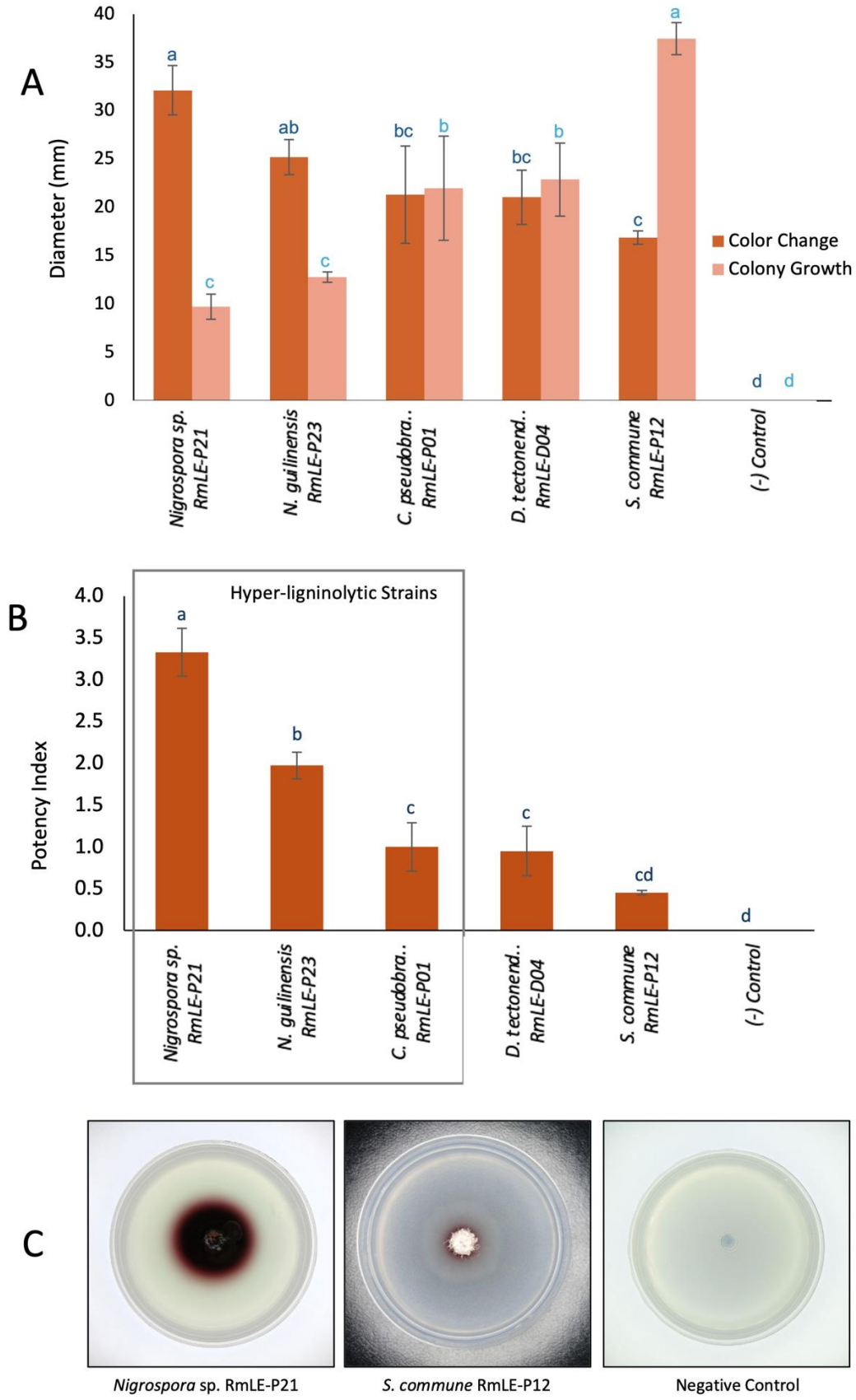



**Fig. 1** – Diameter of colony growth and color changes. A and the potency indices. B of Lac-positive mangrove fungal endophytes. C Representative plates show hyper-ligninolytic (left) and hypo-ligninolytic strains (middle). Mean values not connected by the same letters above the bars are significantly different ($p$<0.05).

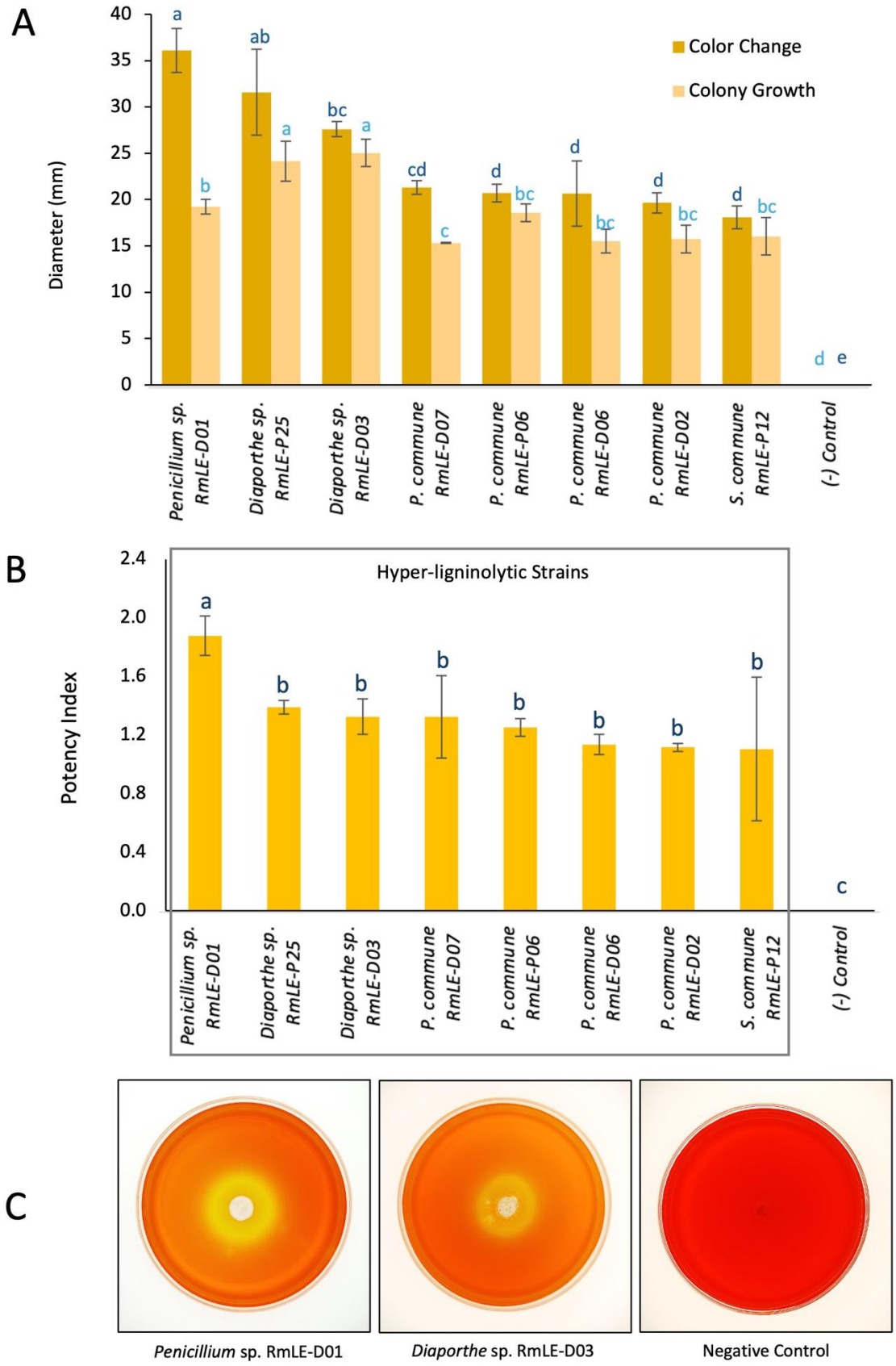



**Fig. 2** – Diameter of colony growth and color changes. A and the potency indices. B of MnP-positive mangrove fungal endophytes. C Representative plates show hyper-ligninolytic (left) and hypo-ligninolytic strains (middle). Mean values not connected by the same letters above the bars are significantly different ($p$<0.05).

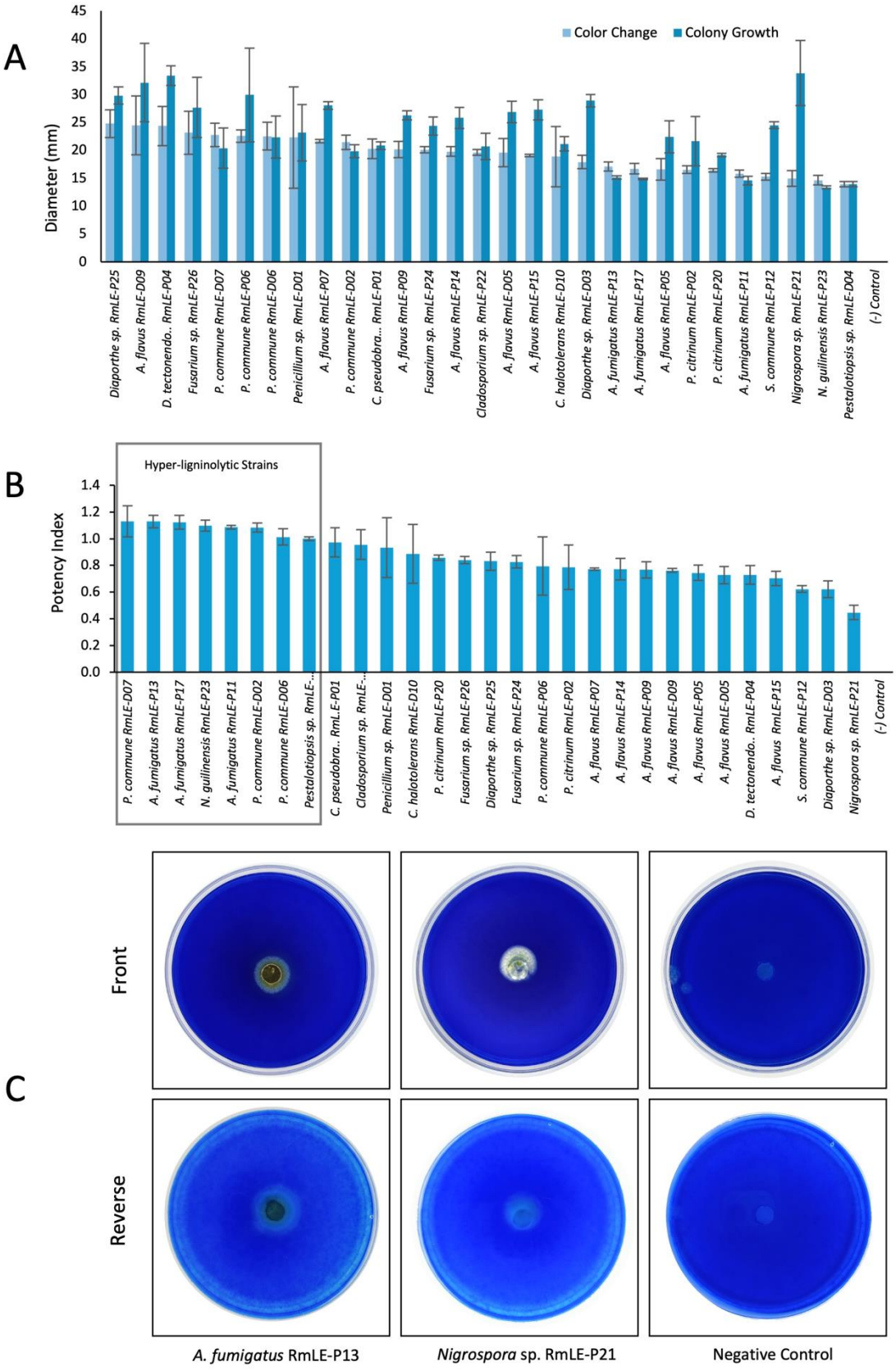



**Fig. 3** – Diameter of colony growth and color changes. A and the potency indices. B of LiP-positive mangrove fungal endophytes. C Representative plates show hyper-ligninolytic (left) and hypo-ligninolytic strains (middle). Mean values not connected by the same letters above the bars are significantly different ($p$<0.05).

**Enzyme Production and Growth Under Antagonistic Conditions**

The growth and Lac production of selected MFE isolates were monitored on the 4th and 6th day on Lac medium. Fig. 4 shows that in general, most isolates grew faster when cultured alone than when co-cultured with either *F. oxysporum* or *T. afroharzianum*. However, *S. commune* (RmLE-P12) showed faster growth when co-cultured with *F. oxysporum*. Only four MFE isolates tested positive for Lac production at varying degrees. *Diaporthe tectonendophytica* (RmLE-P04), *Pestalotiopsis* sp. (RmLE-D04), and *S. commune* (RmLE-P12) gave positive results for Lac production when cultured alone, although *S. commune* (RmLE-P12) and *Pestalotiopsis* sp. (RmLE-D04) also produced Lac enzyme when co-cultured with both challenge species. Interestingly, *Diaporthe* sp. (RmLE-D03) initially did not test positive when co-cultured with *F. oxysporum* but tested positive (albeit reduced) under antagonistic interaction against *T. afroharzianum*. Also, *D. tectonendophytica* (RmLE-P04) exhibited high Lac production during the individual assay but did not produce Lac enzyme during co-culture with both challenge fungi. Lac production efficiency remained largely consistent between Day 4 and Day 6, with only minor variations among isolates.

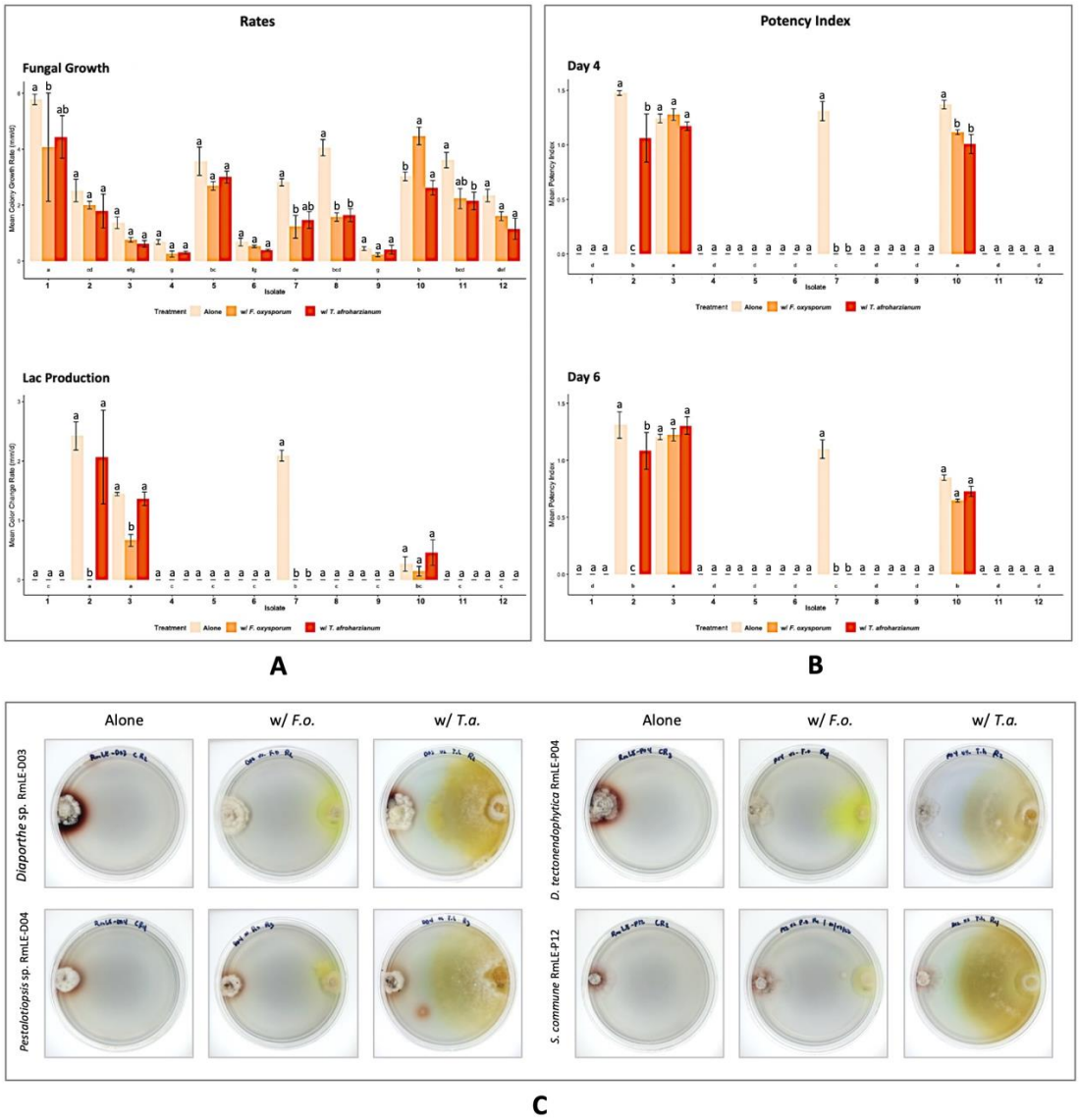



**Fig. 4 –** Colonial growth rates and Lac production expressed as rate of color changes. A and potency indices. B of selected MFE alone and in co-culture with the challenge species. Mean values not connected by the same letters above the bars within the treatments of each isolate are significantly different ($P$<0.05). C Photo inserts are representative plates showing the growth and Lac production (shown as brown pigment production around colonies) of selected MFE alone and in co-culture with

the challenge species on Day 6 of incubation. Test organisms: (1) *Penicillium* sp. (RmLE-D01), (2) *Diaporthe* sp. (RmLE-D03), (3) *Pestalotiopsis* sp. (RmLE-D04), (4) *P. commune* (RmLE-D07), (5) *A. flavus* (RmLE-D09), (6) *C. halotolerans* (RmLE-D10), (7) *D. tectonendophytica* (RmLE-P04), (8) *A. flavus* (RmLE-P05), (9) *P. commune* (RmLE-P06), (10) *S. commune* (RmLE-P12), (11) *Nigrospora* sp. (RmLE-P21), (12) *Fusarium* sp. (RmLE-P26).

Moreover, the results showed that MnP production, efficiency, growth rate, and MnP production rate of the MFE isolates were highly variable under antagonistic interactions (Fig. 5). Only a few isolates exhibited significant changes, indicating that the response to co-culture is strain-specific. For instance, growth responses varied, with *A. flavus* (RmLE-D09) and *S. commune* (RmLE-P12) showing enhanced growth, while *P. commune* (RmLE-P06) and *Pestalotiopsis* sp. (RmLE-D04) exhibited suppressed growth when exposed to the challenge fungi (i.e., either the fungal pathogen *F. oxysporum* or the beneficial fungus *T. afroharzianum*). In terms of MnP production efficiency, *Fusarium* sp. (RmLE-P26) and *S. commune* (RmLE-P12) significantly increased MnP production when co-cultured with *F. oxysporum*, suggesting a possible stimulatory effect of the challenge species. In contrast, *Penicillium* sp. (RmLE-D01) consistently showed reduced MnP production and efficiency, indicating a strong inhibitory response to both *F. oxysporum*. Some isolates, like *Diaporthe* sp. (RmLE-D03) and *C. halotolerans* (RmLE-D10), showed increased MnP efficiency when co-cultured with *F. oxysporum* and *T. afroharzianum*, respectively.

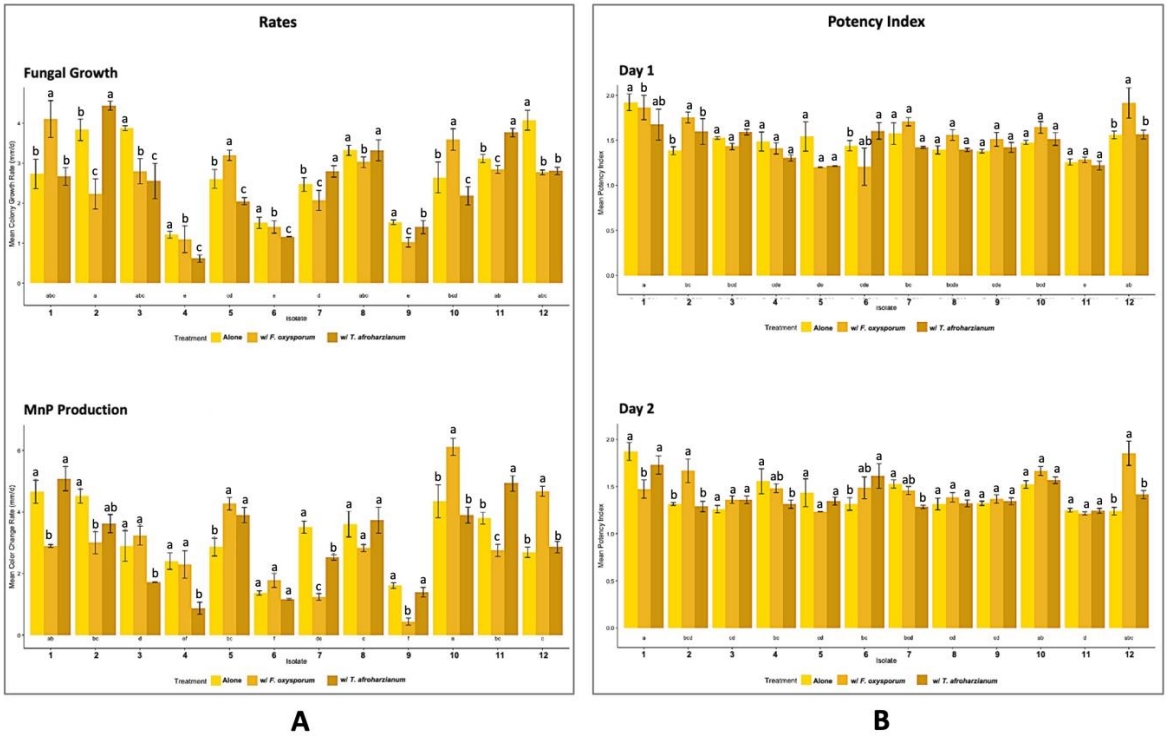
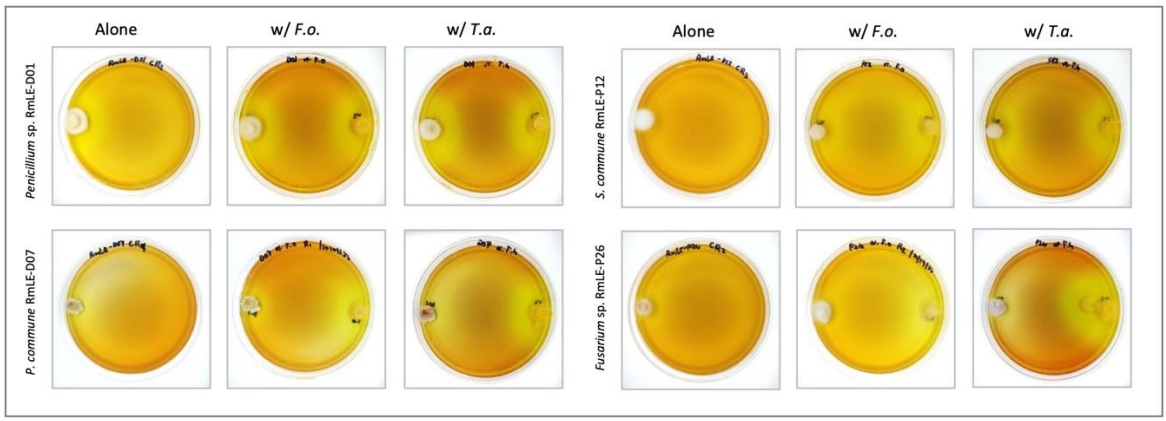



**Fig. 5** – Colonial growth rates and MnP production expressed as rate of color changes. A and potency indices. B of selected MFE alone and in co-culture with the challenge species. Mean values not connected by the same letters above the bars within the treatments of each isolate are significantly different ($P<0.05$). C Photo inserts are representative plates showing the growth and Lac production (shown as brown pigment production around colonies) of selected MFE alone and in co-culture with the challenge species (*F. oxysporum* or *T. afroharzianum*) on Day 2 of incubation. Test organisms: (1) *Penicillium* sp. (RmLE-D01), (2) *Diaporthe* sp. (RmLE-D03), (3) *Pestalotiopsis* sp. (RmLE-D04), (4) *P. commune* (RmLE-D07), (5) *A. flavus* (RmLE-D09), (6) *C. halotolerans* (RmLE-D10), (7) *D. tectonendophytica* (RmLE-P04), (8) *A. flavus* (RmLE-P05), (9) *P. commune* (RmLE-P06), (10) *S. commune* (RmLE-P12), (11) *Nigrospora* sp. (RmLE-P21), (12) *Fusarium* sp. (RmLE-P26).




C

**Fig. 5** – Continued.

Finally, the interaction of mangrove fungal endophytes (MFE) with challenge species on LiP media revealed variable responses in fungal growth, LiP production, efficiency, and rates across different isolates and incubation days. Fig. 6 shows that on Day 6, isolates such as *Nigrospora* sp. (RmLE-P21) and *A. flavus* (RmLE-P05) had significantly higher growth when co-cultured with both challenge fungi, i.e., either *F. oxysporum* or *T. afroharzianum.* LiP production patterns varied, with isolates like *Fusarium* sp. (RmLE-P26) and *A. flavus* (RmLE-D09) showing increased LiP levels when co-cultured with *T. afroharzianum* or *F. oxysporum*, whereas *Penicillium* sp. (RmLE-D01) and *A. flavus* (RmLE-P05) showed reductions when co-cultured with *F. oxysporum*. Efficiency responses were more limited, with *P. commune* (RmLE-P06) and *Fusarium* sp. (RmLE-P26) increasing LiP production efficiency under co-culture, while *C. halotolerans* (RmLE-D10) showed reduced efficiency. Rate analyses further supported these patterns, revealing isolates like *P. commune* (RmLE-D07) and *Diaporthe* sp. (RmLE-D03) had reduced LiP production rates in co-culture, while others like *D. tectonendophytica* (RmLE-P04) and *P. commune* (RmLE-D07) exhibited increased rates under specific challenge conditions.

**Interaction Types and Antagonism Index**

Extended incubation allowed classification of the interactions between MFE isolates and challenge species. Table 3 & Fig. 7 show that among seven known interaction types, only Type A (mutual intermingling) was not observed. The most common interaction with *F. oxysporum* was Type C (growth halts near contact), while Types E1 and E2 (overgrowth by the challenge species) dominated with *T. afroharzianum*. Some MFE isolates exhibited aggressive responses, like *Diaporthe* sp. (RmLE-D03) overgrowing *F. oxysporum* (Type B1), while others like *Pestalotiopsis* sp. (RmLE-D03), *P. commune* (RmLE-D07), and *Penicillium* sp. (RmLE-D01) displayed mutual inhibition (Type D). Finally, antagonism indices confirmed that *T. afroharzianum* was generally more antagonistic than *F. oxysporum*, with nearly double the antagonistic impact across all media types (Table 4).

**Table 3** Types of interactions observed between the selected MFE and the challenge species *F. oxysporum* and *T. afroharzianum* on three LE media. Refer to Table 1 for the description of the interactions.

| Isolates | Types of Interaction | | | | | |
|---|---|---|---|---|---|---|
| | Lac Media | | MnP Media | | LiP Media | |
| | w/ *F. o.*[a] | w/ *T. a.* | w/ *F. o.* | w/ *T. a.* | w/ *F. o.* | w/ *T. a.* |
| *Penicillium* sp. RmLE-D01 | C | $E_2$ | C | D | C | $E_2$ |
| *Diaporthe* sp. RmLE-D03 | C | $E_2$ | $B_1$ | $E_2$ | $B_2$ | C |

**Table 3** Continued.

| Isolates | Types of Interaction | | | | | |
|---|---|---|---|---|---|---|
| | Lac Media | | MnP Media | | LiP Media | |
| | w/ *F. o.*[a] | w/ *T. a.* | w/ *F. o.* | w/ *T. a.* | w/ *F. o.* | w/ *T. a.* |
| *Pestalotiopsis* sp. RmLE-D04 | D | $E_2$ | D | $E_2$ | D | D |
| *P. commune* RmLE-D07 | C | $E_1$ | D | D | C | C |
| *A. flavus* RmLE-D09 | C | $E_2$ | $B_2$ | $E_2$ | $B_2$ | $B_2$ |
| *C. halotolerans* RmLE-D10 | $E_1$ | $E_1$ | $E_2$ | $E_2$ | $E_2$ | $E_1$ |
| *D. tectonendophytica* RmLE-P04 | C | $E_1$ | $E_2$ | $E_1$ | C | $E_2$ |
| *A. flavus* RmLE-P05 | $B_2$ | C | C | C | C | C |
| *P. commune* RmLE-P06 | C | $E_1$ | C | $E_1$ | C | $E_2$ |
| *S. commune* RmLE-P12 | $B_2$ | $E_2$ | $B_2$ | $E_2$ | C | $E_2$ |
| *Nigrospora* sp. RmLE-P21 | $E_2$ | $E_1$ | C | C | $E_2$ | $E_1$ |
| *Fusarium* sp. RmLE-P26 | C | $E_2$ | C | C | C | $E_2$ |

[a]Challenge species: F.o. = *F. oxysporum*; T.a. = *T. afroharzianum*

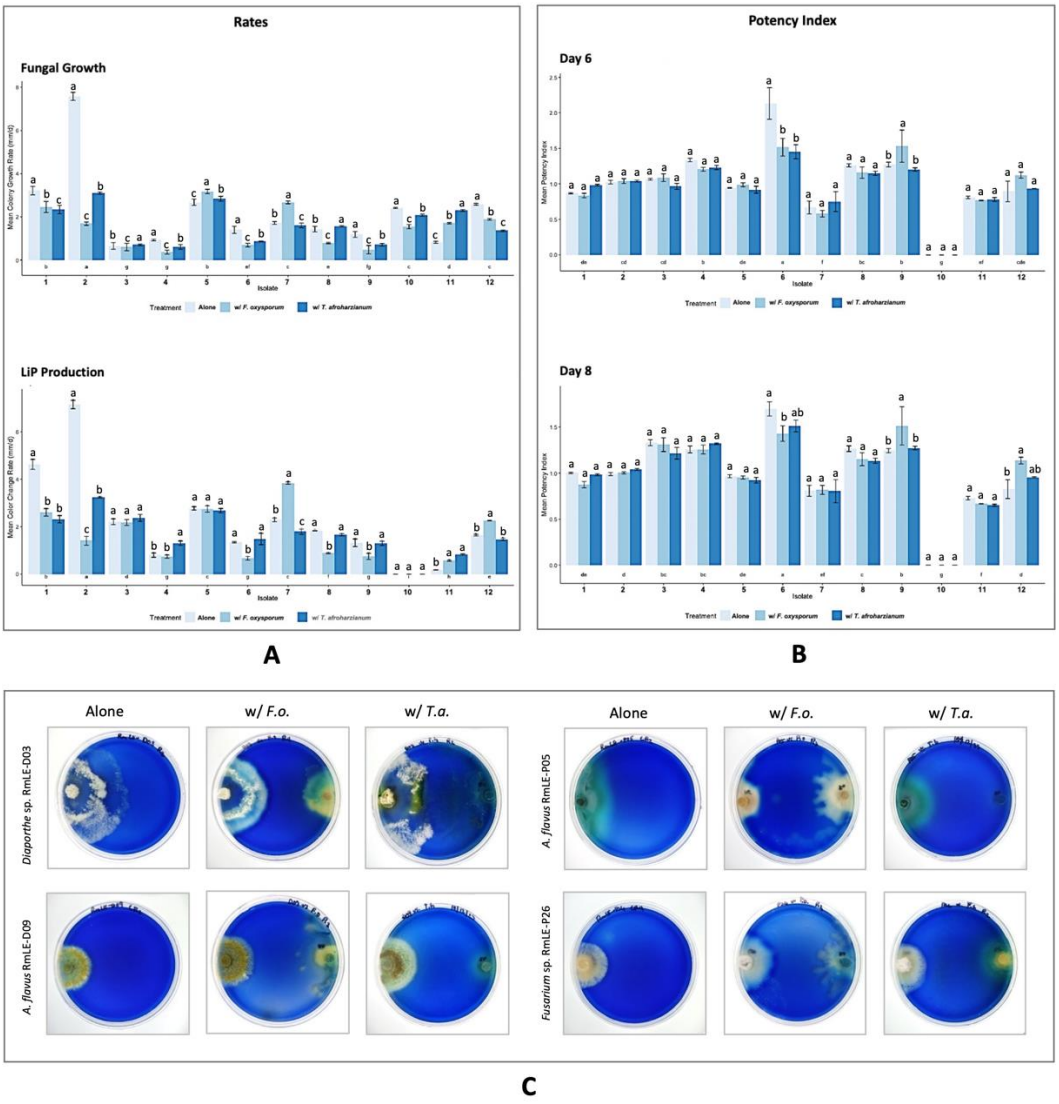



**Fig. 6** – Colonial growth rates and LiP production expressed as rate of color changes (A) and potency indices (B) of selected MFE alone and in co-culture with the challenge species. Mean values not connected by the same letters above the bars within the treatments of each isolate are significantly different ($P$<0.05). C Photo inserts are representative plates showing the growth and Lac production (shown as brown pigment production around colonies) of selected MFE alone and in co-culture with

the challenge species (*F. oxysporum* or *T. afroharzianum*) on Day 8 of incubation. Test organisms: (1) *Penicillium* sp. (RmLE-D01), (2) *Diaporthe* sp. (RmLE-D03), (3) *Pestalotiopsis* sp. (RmLE-D04), (4) *P. commune* (RmLE-D07), (5) *A. flavus* (RmLE-D09), (6) *C. halotolerans* (RmLE-D10), (7) *D. tectonendophytica* (RmLE-P04), (8) *A. flavus* (RmLE-P05), (9) *P. commune* (RmLE-P06), (10) *S. commune* (RmLE-P12), (11) *Nigrospora* sp. (RmLE-P21), (12) *Fusarium* sp. (RmLE-P26).

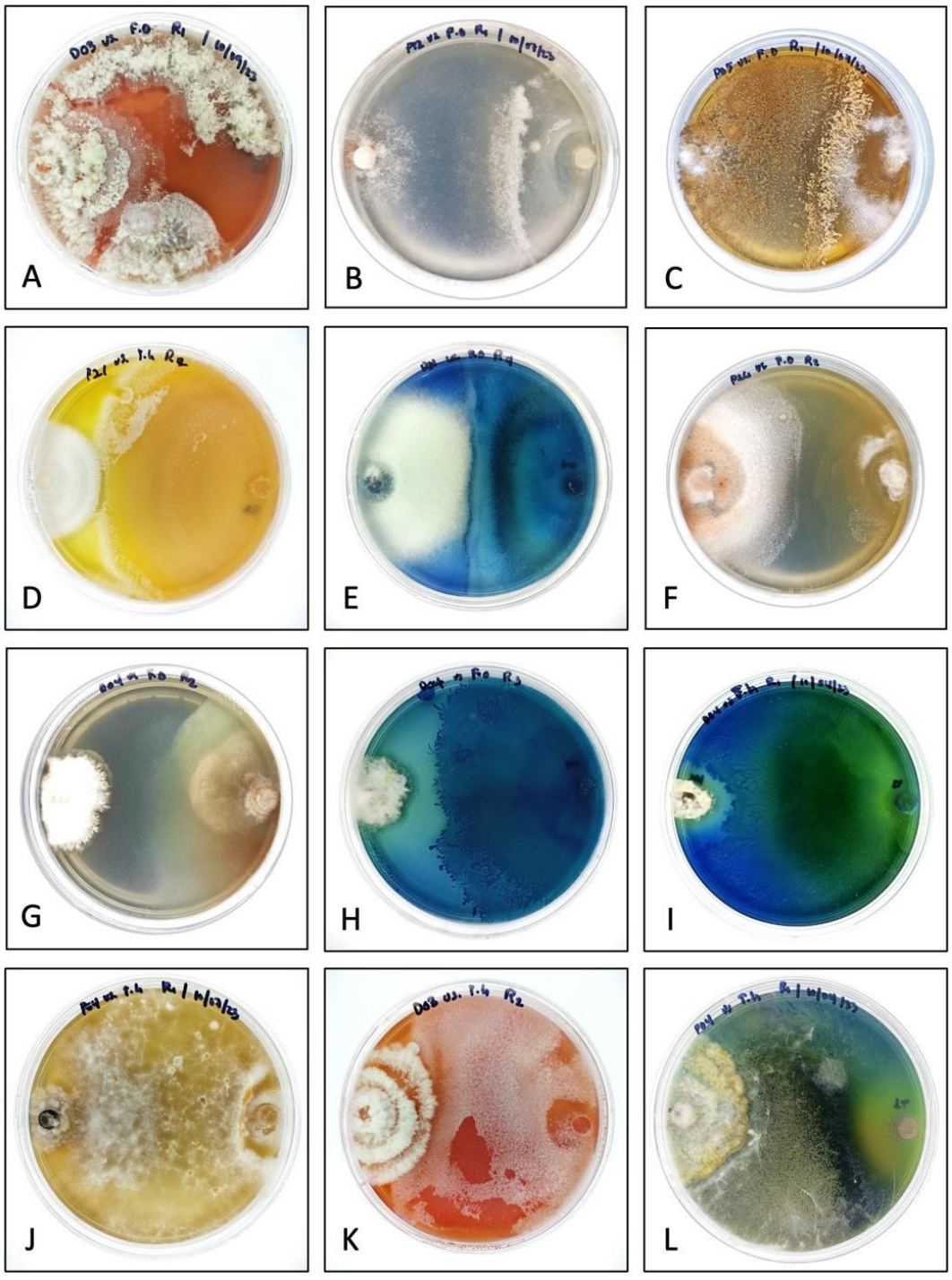



**Fig. 7** – Representative plates showing the different types of antagonistic interaction between the selected MFE and the challenge species (*F. oxysporum* or *T. afroharzianum*). The MFE (response species) are on the left while the challenge species are the right side of the plates. A Type $B_1$. B–C Type $B_2$. D–F Type C. G–I Type D. J Type $E_1$ and K&L Type $E_2$.

**Table 4** Antagonism indices of the challenge species *F. oxysporum* and *T. afroharzianum* during the co-culture assay on three LE media.

| Challenge Species | Media | Types of Interaction | | | | | | | AI[a] |
|---|---|---|---|---|---|---|---|---|---|
| | | A | $B_1$ | $B_2$ | C | D | $E_1$ | $E_2$ | |
| *F. oxysporum* | Lac | - | - | 2 | 14 | 3 | 4 | 4 | **27** |
| | MnP | - | 1 | 2 | 10 | 6 | - | 8 | **27** |
| | LiP | - | - | 2 | 14 | 3 | - | 8 | **27** |
| *T. afroharzianum* | Lac | - | - | - | 2 | - | 20 | 24 | **46** |
| | MnP | - | - | - | 6 | 6 | 8 | 20 | **40** |
| | LiP | - | - | 1 | 6 | 3 | 8 | 20 | **38** |

[a]AI = Antagonism Index

## Discussion

This study confirms that fungal endophytes (MFE) from *Rhizophora mucronata* exhibit ligninolytic enzyme (LE) activity, with several MFE isolates demonstrating the capacity to produce laccase (Lac), manganese peroxidase (MnP), and lignin peroxidase (LiP) individually or in combination with either a pathogenic or a beneficial fungus. These findings align with previous reports on mangrove-derived fungi, such as *Fusarium sambucinum* and *Microsphaeropsis arundinis*, which have been shown to produce significant levels of LEs (Martinho et al. 2019, De Paula et al. 2022). Our study builds on this knowledge by characterizing LE profiles across a broader taxonomic range, including *Nigrospora*, *Penicillium*, *Diaporthe*, *Fusarium*, and *Schizophyllum commune*, and demonstrating their variable enzyme production under both monoculture and dual-culture conditions.

The strong LE production observed, especially the full suite of enzymes by *S. commune* (RmLE-P12), supports its classification as a white-rot basidiomycete and reflects its well-known ligninolytic capabilities (Manavalan et al. 2015, Plácido & Capareda 2015). Interestingly, notable Lac and MnP activities were also detected in ascomycetous genera such as *Nigrospora* and *Penicillium*, which are not traditionally recognized as prolific lignin degraders (Dhakar et al. 2015, Hasanin et al. 2019). These results reinforce earlier suggestions that certain ascomycetes, particularly those from extreme or chemically complex environments like mangroves, may evolve robust ligninolytic systems and bioactivities (Moron et al. 2018, Apurillo et al. 2019). The ecological niche of these fungi, inhabiting plant tissues laden with secondary metabolites, likely exerts selective pressure favoring oxidative enzyme systems, as previously noted by Krishnamurthy & Naik (2017). Corrêa et al. (2014) classified fungal enzymes into hydrolytic and oxidative systems, with the latter well-represented in our isolates. Nutritional factors such as carbon source availability, although not directly assessed here, may also contribute to variability in enzyme expression (Kumar & Prasher 2021).

When subjected to antagonistic interactions with *F. oxysporum* and *T. afroharzianum*, our studied MFE strains exhibited a diverse range of physiological and biochemical responses. While several isolates maintained or even increased enzyme production in dual culture, such as *S. commune* (RmLE-P12) and *Fusarium* sp. (RmLE-P26), others showed suppression, highlighting the strain-specific regulatory complexity of fungal secondary metabolism. These interaction-induced shifts support earlier observations by Sornakili et al. (2020) on the role of competition as a stimulus for enzyme biosynthesis.

In some cases, enzyme suppression was observed. For instance, *D. tectonendophtica* (RmLE-P04) temporarily lost Lac activity in co-culture, which may indicate metabolic trade-offs or competition-induced regulatory inhibition. A similar decline in enzyme activity due to repeated subculturing was reported by Zhao et al. (2022) in *Volvariella volvacea*, emphasizing the need to consider both biological and culture-based variables in evaluating LE production. Moreover, the exclusive appearance of MnP in certain isolates during dual culture implies potential induction by antifungal compounds, supporting the hypothesis of MnP's detoxification role under stress (Čvančarová et al. 2015).

Interaction assays also revealed that most MFE were able to resist overgrowth by *F. oxysporum*, suggesting inherent antagonistic or defensive capabilities, which aligns with reports that endophytes can suppress plant pathogens (Abro et al. 2019, Yang et al. 2023). However, *T. afroharzianum* consistently exhibited stronger antagonistic effects, often overgrowing MFE and significantly altering their enzyme production profiles. This observation corroborates its established role as a potent biocontrol agent capable of mycoparasitism and secondary metabolite secretion (Morón-Ríos et al. 2017, Bouanaka et al. 2021, Cruz & dela Cruz 2024a, 2024b).

Collectively, these findings emphasize the ecological plasticity and metabolic versatility of mangrove-associated fungal endophytes. The observed enzyme dynamics under co-culture conditions highlight the importance of microbial interactions in modulating fungal metabolism, supporting the broader concept that dual-culture systems can activate cryptic metabolic pathways (Schulz & Boyle 2006, Torres & dela Cruz 2013). The ability of certain isolates to sustain or enhance ligninolytic activity under competitive stress suggests their potential applicability in biotechnological processes where microbial consortia are prevalent, such as in bioremediation, biomass conversion, and natural product discovery.

## Conclusions

This study establishes that mangrove fungal endophytes (MFE) from *Rhizophora mucronata* possess diverse and context-dependent ligninolytic enzyme activities, with several isolates capable of producing Lac, MnP, and LiP either individually or in combination with either a pathogenic or a beneficial fungus. The findings demonstrate that enzyme production is not only species-specific but also influenced by ecological interactions, particularly under antagonistic conditions. Notably, some MFE isolates enhanced their enzyme output when co-cultured with competitors, while others showed suppression, underscoring the complexity of fungal metabolic regulation in response to biotic stress. The pronounced activity of *Schizophyllum commune* and the adaptive responses of ascomycetous genera like *Nigrospora* and *Penicillium* further suggest that mangrove endophytes harbor untapped potential for lignin degradation and related biotechnological applications. Future research should focus on the molecular mechanisms underlying enzyme regulation during fungal interactions, including transcriptomic or proteomic analyses to identify key regulatory pathways and stress-responsive genes. Expanding the screening to include additional environmental factors, such as salinity, nutrient availability, and host plant genotype, could provide deeper insights into how these variables shape enzyme expression. Moreover, scaling up co-culture systems and testing MFE in simulated or real-world lignocellulosic waste degradation setups will help evaluate their practical efficacy. Ultimately, integrating ecological, biochemical, and molecular approaches will be critical in harnessing MFE for sustainable biotechnology, especially in the areas of bioremediation, biomass valorization, and green chemistry.

## Acknowledgements

JG Bitacura would like to thank the Department of Science and Technology – Accelerated Science and Technology Human Resource Development Program (DOST-ASTHRDP) for the graduate school scholarship and research dissertation grant. This research is partly supported by a dissertation subsidy grant from the Philippine Society for Microbiology, Inc. The authors also acknowledge Ms. Joannalyn S. Montemayor, UST Fungal Biodiversity, Ecogenomics & Systematics-Metabolomics (FBeS) group, for providing us with mangrove leaf samples used in the isolation of the mangrove-derived fungi, and to Mr. Angel B. Encarmacion of the Bureau of Fisheries and Aquatic Resources (BFAR), Department of Agriculture – Region 2 for the gratuitous permit (No. R02-0003-22) issued to Ms. Montemayor for the collection of mangrove hosts.

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