

MICROBIOME INTERACTIONS, PATHOGENICITY AND DISEASE RESISTANCE IN OIL PALM (*ELAEIS GUINEENSIS* JACQ.)

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Microbiome Interactions, Pathogenicity and Disease Resistance in Oil Palm (*Elaeis guineensis* Jacq.)

Abiodun Abeeb Azeez

ACADEMIC DISSERTATION

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Cover images: Healthy oil palm tree and oil palm tree killed by *Thielaviopsis paradoxa* disease (upper left); healthy oil palm frond and frond exhibiting leaf spot disease symptoms (upper right). *T. paradoxa*–inoculated oil palm seedlings (lower left I); oil palm seedling being inoculated with *T. paradoxa* using a hypodermic syringe (lower left II); seedlings displaying disease symptoms three weeks post-inoculation (lower centre). Pure culture of *T. paradoxa* (lower right I); dual culture of *T. paradoxa* and *Simplicillium lamellicola* (lower right II); microscopic image showing alterations in *T. paradoxa* hyphal morphology following inhibition by the biocontrol agent *S. lamellicola* (lower right III).

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To my loving wife and beloved children

ABSTRACT

Oil palm (*Elaeis guineensis*) production is increasingly threatened by fungal diseases, among which *Thielaviopsis paradoxa*, a widespread and economically significant pathogen, poses a major constraint. This pathogen infects a broad range of hosts, predominantly monocots and exhibits substantial variation in pathogenicity across tropical and subtropical regions, suggesting a strong influence of climatic conditions on disease development. This thesis examines the ecological, physiological and molecular determinants of *T. paradoxa* biology and oil palm disease development using an integrated, multi-scale approach.

Genetic diversity and phylogenetic relationships among *T. paradoxa* isolates from Nigeria and Papua New Guinea (PNG) were analyzed using nuclear ribosomal DNA markers, together with comparative assessments of growth responses across temperature gradients. Pronounced isolate-specific variation in growth performance and thermal tolerance was observed, including the identification of thermotolerant isolates, highlighting adaptive potential with relevance under climate change. However, phylogenetic clustering showed limited correspondence with temperature-dependent growth patterns, indicating the need for broader population-level analyses.

The fungal communities associated with oil palm leaf spot disease were characterized using ITS2 metabarcoding of leaf, root and soil compartments from symptomatic and asymptomatic trees. Disease status was associated with distinct mycobiome compositions and taxonomic signatures across compartments. Network analyses revealed highly modular community structures and identified rare taxa as keystone species, underscoring their potential importance in maintaining microbial community stability and mediating disease-associated interactions. Amplicon sequence variants (ASVs) correspond to putative fungal pathogens, including *Thielaviopsis*, *Neopestalotiopsis*, *Pseudopestalotiopsis* and *Colletotrichum* were detected in apparently healthy trees. Notably, the relative abundance of *Thielaviopsis*, together with *Trichoderma* and an unassigned member of the Ascomycota, reached approximately 6% in asymptomatic samples, representing at least a one-third increase compared with symptomatic samples.

Antagonistic interactions between *T. paradoxa* and the endophytic fungus *Simplicillium lamellicola* were investigated using dual-culture assays combined with comparative transcriptomic analyses, with *Heterobasidion annosum* included as a reference necrotrophic pathogen. *S. lamellicola* strongly inhibited pathogen growth through antibiosis and induced extensive transcriptional reprogramming related to stress responses, membrane remodeling, detoxification and nutrient competition, supporting its potential as a biological control agent.

Pathogenicity assays and host-induced transcriptome profiling further revealed that interactions between oil palm and sugarcane derived *T. paradoxa* isolates and different oil palm cultivars were highly isolate- and cultivar-dependent. Resistant cultivars displayed more coordinated and metabolically efficient defence responses than susceptible cultivars, resulting in reduced disease severity.

Overall, this thesis demonstrates that oil palm disease outcomes are governed by the interplay between pathogen diversity, microbial community structure, environmental adaptation, antagonistic fungi and host defence mechanisms. These findings provide a foundation for microbiome-informed disease management strategies and the development of resilient oil palm cultivars.

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I. Gorea, E. A., Tokilala, E. T., Esiegbuya, O. D., **Azeez, A. A**., Siang, C. S., & Jaber, E. H. (2023). Oil palm tree diseases. *In Forest Microbiology*, Volume 3 "Tree Diseases & Pests". Eds Asiegbu FO & Kovalchuk A. Elsevier publishers, ISBN 9780443186943 pp. 339–373. https://doi.org/10.1016/B978-0-443-18694-3.00004-3

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III. **Azeez, A. A**., Esiegbuya, D. O., Lateef, A. A., & Asiegbu, F. O. (2024). Mycobiome analysis of leaf, root and soil of symptomatic oil palm trees (*Elaeis guineensis* Jacq.) affected by leaf spot disease. *Frontiers in Microbiology*, *15*, 1422360. https://doi.org/10.3389/fmicb.2024.1422360

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II. Lateef, A. A., **Azeez, A. A**., Ren, W., Hamisu, H. S., Oke, O. A., & Asiegbu, F. O. (2024). Bacterial biota associated with the invasive insect pest *Tuta absoluta* (Meyrick). *Scientific Reports*, *14*(1), 8268. https://doi.org/10.1038/s41598-024-58753-w

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Activity	Study I	Study II	Study III	Study IV	Study V
Study conception	FOA	FOA	FOA, **AAA**	FOA	FOA, **AAA**
Experimental design & execution	–	**AAA**; FOA	**AAA**; FOA	**AAA**; ZW; FOA	**AAA**; FOA
Field sampling	–	–	**AAA**; DOE	–	–
Data collection & curation	–	**AAA**; DOE; EJ; WR; AO	**AAA**; DOE	**AAA**; ZW	**AAA**; DOE; EJ
Data analysis, visualization & interpretation	–	**AAA**; AAL	**AAA**; AAL	**AAA**; ZW	**AAA**
Original draft	–	**AAA**	**AAA**	**AAA**	**AAA**
Review & editing	**AAA**; DOE; EAG; ETK; CSS; EJ	**AAA**; DOE; EJ; WR; AO; AAL; FOA	**AAA**; DOE; AAL; FOA	**AAA**; ZW; FOA	**AAA**; DOE; EJ; FOA

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ABBREVIATIONS

ABC	ATP-binding cassette
AKR	Aldo-keto reductase
APX	Ascorbate peroxidase
Bp	Base pairs
BGC	Biosynthetic gene cluster
CAZymes	Carbohydrate-active enzymes
CoA	Coenzyme A
DEG	Differentially expressed genes
DNA	Deoxyribonucleic acid
ETI	Effector-triggered immunity
FPKM	Fragments per kilobase of transcript per million mapped reads
GO	Gene Ontology
GST	Glutathione S-transferase
ITS	Internal transcribed spacer
KEGG	Kyoto Encyclopedia of Genes and Genomes
M or MD	Malaysian compact (semi-dwarf)
MAMP	Microbe-associated molecular pattern
MAPK	Mitogen-activated protein kinase
MFS	Major facilitator superfamily
NB-LRR	Nucleotide-binding leucine-rich repeat
NGS	Next-generation sequencing
PAMP	Pathogen-associated molecular pattern
PCA	Principal component analysis
PCR	Polymerase chain reaction
PR	Pathogenesis-related protein
PTI	PAMPs-triggered immunity
Q30	Phred quality score ≥ 30
rDNA	Ribosomal DNA
RNA	Ribonucleic acid
RNA-Seq	RNA sequencing
ROS	Reactive oxygen species

INTRODUCTION

1.1 Forest Disturbances and Biotic Stressors in Global and Tropical Forests

Forests worldwide are increasingly affected by natural and anthropogenic disturbances that compromise ecosystem health, productivity and the sustained provision of forest goods and services (Sánchez *et al*., 2021). Global assessments indicate that fire, insect pests, plant diseases and extreme weather events collectively disturb vast forest areas each year (van Lierop *et al*., 2015), contributing substantially to forest degradation and net forest loss. Although less conspicuous than fire or storm damage, forest diseases are increasingly recognized as important drivers of long-term canopy degradation and forest health decline yet remain comparatively underrepresented in global monitoring efforts.

Tropical forests occupy only less than one-fifth of Earth's land area, yet rank among the most biodiverse ecosystems, harboring approximately 62% of the world's terrestrial vertebrate diversity (Dinerstein *et al*., 2017; Pillay *et al*., 2022). They render essential ecological services, including carbon sequestration, soil protection and regulation of water cycles and support the livelihoods of millions of people in developing regions. Within these regions, plantation forestry contributes substantially to national economies and rural development, with crops such as oil palm, rubber and coconut forming core components of the agricultural landscape. However, tropical trees are continually exposed to biotic stress from pests and pathogens that can impair their health, hinder productivity and jeopardize the long-term sustainability of these plantation systems. Tropical tree diseases are predominantly caused by bacterial and fungal pathogens whose development and spread are strongly influenced by environmental and ecological factors. Favorable hot and humid climatic conditions, high nutrient availability and exceptional biodiversity promote pathogen persistence and transmission, while also facilitating coevolution with hosts and other associated organisms. During unfavorable dry seasons, many of these pathogens survive by forming resistant structures such as cysts, chlamydospores and oospores, which enable long-term persistence under adverse conditions (Renard, 2001). Therefore, a robust understanding of the ecological, epidemiological and molecular processes that shape tree–pathogen interactions is therefore critical for designing effective and sustainable disease management strategies in tropical forestry (Velásquez *et al*., 2018).

1.2 Palms (Arecaceae): Diversity, Distribution and Economic Importance

Palms (Arecaceae) are widely cultivated plantation crops distributed across diverse habitats, including tropical forests, savannahs and grasslands (Ribeiro *et al*., 2008). They generally thrive in warm climates where the mean temperature of the coldest month is at least 18 °C and the annual temperature range does not exceed 10 °C (Reichgelt *et al*., 2018). Several palm species, particularly fan palms such as *Hyphaene petersiana* (real fan palm), *Roystonea regia* (royal palm) and *Livistona australis* (cabbage tree palm), are extensively cultivated as ornamentals for landscaping and avenue planting (https://en.wikipedia.org/wiki/Fan_palm; Ulfa Adzkia *et al*., 2020). Some species, including *Trachycarpus fortunei* (chusan palm), are well suited for outdoor decoration in temperate regions, whereas others, such as *Dypsis lutescens* (golden cane palm), *Chamaedorea elegans* (parlour palm) and *Howea forsteriana* (kentia palm), are popular indoor potted ornamentals (Reichgelt *et al*., 2018). The family also includes economically important tree crops such as oil palm, coconut and date palm. Palms exhibit a comparatively high capacity for carbon assimilation, which enhances their

competitiveness in tropical rainforests (Ma *et al*., 2015). Consequently, they are often used as indicators for reconstructing the biogeographical history of these ecosystems (Couvreur *et al*., 2011).

1.3 Oil Palm: Cultivation, Production and Economic Importance

Within the cultivated palms, *Elaeis guineensis* (the African oil palm) is particularly significant because of its exceptionally high oil yield, contributing about 40% of global vegetable oil production (M.P. Evans Group PLC., 2025; Swaray *et al*., 2020). The Latin American species *E. oleifera* is the second, though far less widely cultivated. *E. guineensis* is native to West Africa, where its earliest cultivation occurred along the West and Central African coastal belt, spanning present-day Guinea/Liberia to northern Angola (Corley & Tinker, 2015). The African oil palm was introduced to the Americas in the 15th century, first to Brazil via the transatlantic slave trade facilitated by Portuguese explorers and later reached Colombia in 1932 (Syed, 1984). Its cultivation expanded markedly across Africa from the 1930s onward. Today, oil palms are extensively cultivated across tropical and subtropical regions, including West Africa, Southeast Asia and parts of South America. Although oil palm is cultivated across many tropical countries, palm oil production is highly uneven, with Southeast Asia accounting for most of the global output. Indonesia and Malaysia dominate global palm oil production, contributing approximately 58% (≈45.5 million metric tons) and 25% (≈19.4 million metric tons) of world's production, respectively. Outside Southeast Asia, Thailand and Colombia rank ahead of Nigeria, while Nigeria remains the leading palm oil producer in Africa, with an estimated 1.5 million metric tons annually (USDA, 2025).

The expansion of oil palm cultivation has driven significant land-use changes globally. In Southeast Asia, approximately 45% of new plantations have replaced forests, with large areas also established on peatlands, contributing to highly significant carbon emissions and biodiversity loss (Purnomo *et al*., 2019; Abdullah *et al*., 2025). In South America, about 31% of plantations replaced forests, while in Africa, only around 7% of plantations replaced forested areas. According to the European Space Agency (ESA, 2022), global suitability maps show that large areas of tropical Africa and South America are biophysically suitable for oil palm cultivation (Fig. 1), highlighting the potential vulnerability of Africa's extensive intact forests to future deforestation under continued expansion (Vijay *et al*., 2016; Hamdani & Ningsih, 2025).

Oil palm is primarily valued for its two major products, palm oil and palm kernel oil, which are among the most widely traded vegetable oils globally. Beyond these globally traded commodities, nearly every part of the plant is utilized, enhancing its overall economic value. The fronds serve as building materials in rural communities; the roots and trunks have ethnomedicinal uses; and the seed residues are applied as fertilizer. These diverse benefits make oil palm an indispensable crop, supporting job creation, income generation and significant foreign exchange earnings in producer countries.

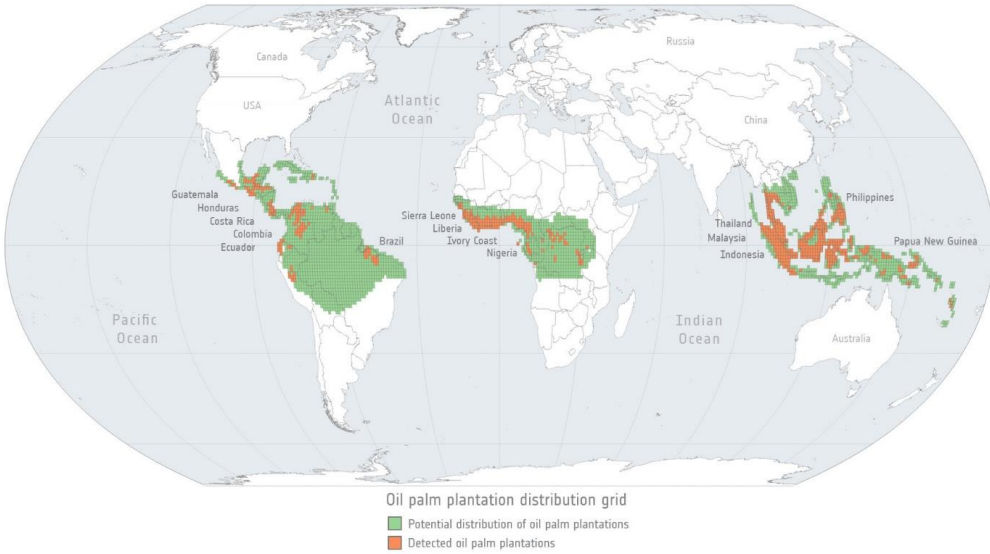


Fig. 1: Global distribution of oil palm plantations and potential cultivation areas (The European Space Agency, 2022).

1.4 Oil Palm Leaf Spot Disease: Pathogen Diversity and Research Gaps

Despite its considerable economic importance, oil palm productivity is constrained by several diseases, among which leaf spot represents a widespread and persistent problem in both nursery and field-grown palms. Leaf spot disease is predominantly fungal in origin and is most severe at the seedling and juvenile stages. Symptoms typically initiate as discrete necrotic lesions and may progress into leaf blight when individual spots coalesce, leading to extensive tissue damage, reduced photosynthetic capacity and premature leaf senescence.

The etiology of oil palm leaf spot disease is characterized by high pathogen diversity and marked geographical variability (Turner, 1981; Kittimorakul *et al*., 2013). Leaf spot and leaf blight symptoms have been associated with multiple fungal taxa, predominantly within the Ascomycota, including *Colletotrichum*, *Pestalotiopsis*, *Curvularia*, *Cercospora* and *Botryodiplodia* (Rajagopalan, 1973; Aderungboye, 1977; Elliott, 2006, 2009). The recurrent involvement of different taxa across studies suggests that no single pathogen is universally responsible for leaf spot disease across all environments. Instead, multiple fungi may act as independent causal agents under specific ecological and geographical conditions. For example, *Pestalotiopsis* spp. are widely distributed across palm-growing regions and can colonize multiple leaf tissues, while *Cercospora elaeidis* remains a common foliar pathogen of nursery seedlings and juvenile palms in West Africa (Rajagopalan, 1973; Kittimorakul *et al*., 2013; Elliott, 2009; Betancourt-Ortiz *et al*., 2023).

Moreover, inferring disease causality based solely on presence or isolation frequency is inherently problematic because fungi recovered from symptomatic tissues may not fulfill Koch's postulates. Rather, some may exist as non-pathogenic endophytes whose presence only influence disease expression (Kuo *et al*., 2014; Kashyap *et al*., 2025). Others may act as

opportunistic pathogens that colonize already stressed, weakened, or damaged tissues rather than serving as primary causal agents**.**

Importantly, leaf spot symptoms are not always attributable to a single, host-specific pathogen. Ecologically versatile fungi may induce similar foliar disease phenotypes across different monocot hosts; for example, *Thielaviopsis paradoxa*, best known for causing stem and fruit diseases, has been reported as the causal agent of leaf spot disease in pineapple (Hewajulige & Wijesundera, 2014). Such cross-host expressions of comparable symptoms highlights the limitations of pathogen-centric interpretations and suggests that disease expression may reflect the combined influence of multiple microbial taxa, host physiology and environmental conditions.

Despite extensive documentation of fungi associated with leaf spot symptoms, critical gaps remain regarding their relative pathogenic roles, variation in virulence and the microbial interactions governing disease progression from localized lesions to severe blight. Consequently, reconsidering oil palm leaf spot disease within a community-level framework is warranted. Microbiome-based approaches, particularly analyses of leaf-associated mycobiomes, offer a powerful means to identify context-dependent contributors to disease development, including latent pathogens, opportunistic fungi and microbial interactions that may exacerbate or suppress symptom expression.

1.5 Ceratocystidaceae: A Diverse Family Encompassing *Thielaviopsis* and Related Genera

The genus *Ceratocystis* was first described in 1890 to include *C. fimbriata*, the causal agent of black rot in sweet potatoes in the USA (Halsted, 1890). Over time, *Ceratocystis* sensu lato became taxonomically problematic due to the dual nomenclature system and an overreliance on morphological characters that lack robustness. In particular, classification was complicated by reliance on spore stages and shared asexual morphological features, including phialidic conidiogenous mechanisms, which obscured clear species and genus boundaries (Paulin-Mahady *et al*., 2002; De Beer *et al*., 2014; Dharmaraj *et al*., 2022). In recent decades, the genus *Ceratocystis* has been reclassified from a genus to the rank of a family (Ceratocystidaceae), with the modern concept of *Ceratocystis* now largely restricted to its type species, *C. fimbriata* (De Beer *et al*., 2014; Mayers *et al*., 2020).

Members of the Ceratocystidaceae are filamentous ascomycetous fungi that undergo both asexual and sexual reproduction, characteristic of the Ascomycota (Fig. 2). The asexual cycle is predominant, producing haploid (1n) conidia or endoconidia mitotically. These propagules disperse effectively and quickly establish haploid mycelia, especially in wounded or stressed host tissues. Sexual reproduction occurs through plasmogamy between compatible haploid hyphae, followed by the development of dikaryotic hyphae within ascomata. Within the ascus, karyogamy and subsequent meiosis, often accompanied by a post-meiotic mitosis, generates haploid ascospores. This balance between frequent asexual multiplication and intermittent sexual recombination facilitates rapid colonization while preserving genetic variability and adaptive capacity (Naidoo *et al*., 2013).

The Ceratocystidaceae family encompasses phylogenetically diverse fungi of economic significance, including destructive plant pathogens, insect-associated symbionts and agents of

timber discoloration and degradation (De Beer *et al*., 2014). In agricultural and forestry systems, members of this family cause a wide range of diseases, such as stem cankers, vascular wilts, rots of roots and fruits and trunk-neck bending disease (Engelbrecht *et al*., 2007; Esiegbuya *et al*., 2022).

Phylogenetic reconstructions based on multigene datasets, together with morphological and ecological evidence, have clarified generic boundaries within this formerly heterogeneous group, resulting in the recognition of 15 well-defined and phylogenetically coherent genera. These include *Ambrosiella, Berkeleyomyces, Bretziella, Ceratocystis, Chalaropsis, Davidsoniella, Endoconidiophora, Huntiella, Meredithiella, Phialophoropsis and Thielaviopsis* (De Beer *et al*., 2014; Nel *et al*., 2018; Mayers *et al*., 2020; Harrington *et al*., 2024).

Following the designation of *C. fimbriata* as the type species, 43 *Ceratocystis* species have been described. These species exhibit a broad spectrum of pathogenicity, ranging from weak wound-associated colonizers of trees to highly aggressive pathogens causing cankers, vascular wilts and postharvest rots in forest and fruit crop (Holland *et al*., 2019; Harrington *et al*., 2024). Phylogenetic studies further recognize four major geographic clades within *Ceratocystis*: North American (7 species), Asian–Australasian (15 species), African (5 species) and Latin American (16 species). Among these, the Latin American clade is the most economically significant and genetically homogeneous (Johnson *et al*., 2005; Mbenoun *et al*., 2014; Li *et al*., 2017; Holland *et al*., 2019).

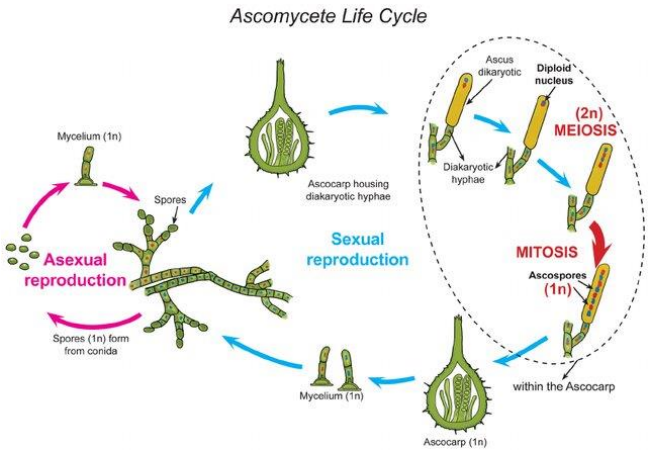


Fig. 2 Schematic illustration of the life cycle of *Ceratocystis* species, representing a typical ascomycete life cycle (Naidoo *et al*., 2013).

1.6 *Thielaviopsis paradoxa*: Biology, Host Range and Disease Associations

The ascomycete genus *Thielaviopsis* was established based on its type species *Thielaviopsis ethacetica* Went (Raj & Kendrick, 2006) which was later synonymized with *T. paradoxa* (Paulin-Mahady *et al*., 2002). Six species of *Thielaviopsis* namely, *T. paradoxa, T. ethacetica, T. euricoi , T. cerberus, T. musarum and T. punctulata,* are recognized as *Ceratocystis paradoxa* complex (De Beer *et al*., 2014)**.** These synonymizations were largely based on shared morphological characteristics and the similarity of disease symptoms caused by these taxa

(Mbenoun *et al*., 2014). For instance, black seed rot of oil palm caused by *Thielaviopsis* spp. was considered synonymous with black seed rot of *Raphia hookeri* attributed to *Chalara paradoxa* (Esiegbuya *et al*., 2013).

Since the first discovery of *T. paradoxa* in *Ananas comosus* (pineapple) in 1886 by France De Seynes, several hosts have been reported. *T. paradoxa* is a cosmopolitan, soil- and wound-borne pathogen with a broad host range, primarily infecting monocots like palms, pineapple, banana, sorghum, cocoa, sweet potato, corn and sugarcane, where it causes severe rots and postharvest losses (Hewajulige & Wijesundera, 2014). Its polyphagous nature and ecological plasticity allow infection of diverse hosts. Historically, *T. paradoxa* has been described under multiple names, including *Sporochisma paradoxum*, *Chalara paradoxa* and *Ceratocystis paradoxa*, most now considered synonyms, with *C. paradoxa* representing the sexual stage. Molecular studies further distinguish *T. paradoxa* from other members of the genus, including *T. musarum*, *T. ethacetica*, *T. euricoi* and the homothallic *T. Cerberus* (De Beer *et al*., 2014; Mbenoun *et al*., 2014).

In Pineapple, *T. paradoxa* is popular with three diseases: basal rot, butt rot and leaf spot disease (Hewajulige & Wijesundera, 2014). Similar diseases have been documented in several palm species, including oil palm. However, unlike basal and trunk-related rots, leaf spot symptoms have rarely been attributed to *T. paradoxa* in palms, with its association in oil palm leaf spot only recently reported (Azeez *et al*., 2024). In this context, *T. paradoxa* was detected as a constituent member of the oil palm leaf spot pathobiome rather than as a sole causal agent.

In accordance with the One Fungus–One Name (1F1N) principle and the International Code of Nomenclature (ICN), *Thielaviopsis* is retained as a distinct genus, comprising taxa closely allied to *T. paradoxa sensu stricto* (De Beer *et al*., 2014). These revisions also revealed substantial genetic and reproductive diversity within the genus, distinguishing homothallic and heterothallic species previously grouped under *T. paradoxa* sensu lato (Mbenoun *et al*., 2014).

1.6.1 Infection Biology and Disease Development of *T. paradoxa*

Like many *Ceratocystis* species, *Thielaviopsis paradoxa* is an opportunistic necrotrophic fungus that initiates infection primarily through fresh wounds in non- or lightly lignified tissues , with direct penetration of intact tissues being uncommon (Py *et al*., 1987; Elliott, 2019). Such wounds may arise from agricultural practices, environmental stress, or insect activity and they play a central role not only in facilitating pathogen entry but also in shaping subsequent disease dynamics (Py *et al*., 1987). Wounded tissues release volatile compounds, including ethyl acetate and ethanol–like substances, which attract sap-feeding insects such as flies (Diptera) and nitidulid beetles (Coleoptera: Nitidulidae). These insects act as vectors, transferring sticky conidia between hosts, a transmission strategy comparable to that described for other Ceratocystidaceae, including *Ceratocystis fagacearum* and *C. manginecans* (Teviotdale & Harper, 1991; Cease & Juzwik, 2001; Roux & Wingfield, 2009).

Once inside the host, endoconidia germinate and produce hyphae that rapidly colonize surrounding tissues, leading to progressive necrosis (Gaitán-Chaparro *et al*., 2021). This colonization results in diseases such as dry basal rot and neck bending in palms, as well as black rot in pineapple. In addition to vector-mediated spread, *T. paradoxa* is soil-borne and persists as an important inoculum reservoir, contributing to infection and disease recurrence in

susceptible hosts. The pathogen can infect multiple plant parts, including roots, trunks, leaves, inflorescences and fruits, as well as sugar cane, pineapple and other tropical crops (Streets, 1933; Hewajulige & Wijesundera, 2014; Gaitán-Chaparro *et al*., 2021; Yu *et al*., 2026). Consequently, diseases caused by *T. paradoxa* pose a significant threat and can result in extensive damage in oil palm plantations. Infected palms often remain asymptomatic during the initial stages of infection while internal tissue degradation progresses gradually (Elliott, 2019). Visible symptoms typically emerge only at advanced stages when extensive structural weakening leads to trunk bending or sudden crown collapse (Elliott *et al*., 2004). Disease outbreaks are favoured by conditions that increase tissue damage or physiological stress, such as intensive cultivation, mechanical injury, insect infestation and poor postharvest handling in pineapple production systems.

1.6.2 Asexual Spore Dimorphism and Its Role in Infection and Survival of *T. paradoxa*

The fungus produces two functionally distinct asexual spore types. Endoconidia are small, hyaline, cylindrical propagules (approximately 8.5–12.7 × 2.5–4.7 μm) that are readily produced in chains from phialidic conidiophores and serve as the primary infective units, germinating rapidly on wounded host tissues to drive active colonization and necrotrophic spread. In contrast, thick-walled, pigmented chlamydospores (macroconidia) act as durable survival structures, persisting for extended periods in soil, plant debris and contaminated planting material (Hewajulige & Wijesundera, 2014). These resting spores constitute a stable inoculum reservoir capable of initiating new infections when susceptible tissues are exposed through wounding (Elliott, 2019; Hewajulige & Wijesundera, 2014). This dimorphic spore system underpins *T. paradoxa*'s opportunistic biology, with endoconidia enabling acute outbreaks via wound entry and insect dispersal, while chlamydospores sustain chronic reservoirs that fuel recurring epidemics in stressed plantations. The brown macrospores impart the characteristic blackening seen in rots of palm trunks, pineapple fruit, sugar cane and other hosts during late-stage tissue decay.

1.6.3 Management Strategies for *T. paradoxa*

The management approaches published in our literature review on oil palm diseases (Paper I: page 364-366), follows an established integrated framework prioritizing prevention through wound minimization during cultural operations and strict sanitation via tool disinfection and infected material removal. In addition, chemical controls, including systemic fungicides like triazoles and strobilurins, prove effective alongside postharvest treatments, while biological agents offer sustainable alternatives where chemical restrictions apply. Recent UF/IFAS advancements, including three-day detached leaflet assay for trunk rot susceptibility, enhance resistance screening across palm species, supporting tailored breeding and rapid evaluation in high-incidence oil palm areas (Mederos, 2025).

1.7 Microbiomes: Diversity, Function and Host Associations

Microorganisms are ubiquitous across the Earth's ecosystems and constitute a substantial proportion of global biomass, highlighting their central role in ecosystem functioning and planetary processes (Bien *et al*., 2021; Mo *et al*., 2023). Yet, despite their essential functions,

most microbes in soils, oceans, the atmosphere and host-associated environments remain poorly understood (Turner *et al*., 2013). Early microbiome research was largely descriptive, relying on sequencing technologies to reveal microbial diversity far beyond the limits of culture-based methods. While initial studies focused primarily on plant physiology and genomics, contemporary studies have shifted toward uncovering the mechanisms that govern microbiome structure and function (Ren *et al*., 2024). This functional perspective seeks to explain why microbes colonize specific hosts and how their interactions influence host biology, health and disease outcomes.

Advances in high-throughput amplicon and metagenomic sequencing have accelerated this transition by enabling cost-effective, high-resolution profiling of complex microbial communities across diverse ecosystems (Sunagawa *et al*., 2015; Bahram *et al*., 2018; McDonald *et al*., 2018). Contemporary microbiome surveys mostly rely on conserved marker genes, particularly the 16S rRNA, 18S rRNA and internal transcribed spacer (ITS) regions, to generate standardized abundance units such as operational taxonomic units (OTU) or amplicon sequence variants (ASV) (Callahan *et al*., 2016; Bien *et al*., 2021). These analytical steps ensure accurate taxonomic assignment, robust phylogenetic reconstruction and meaningful comparative ecological analyses (Chaudhary *et al*., 2015; Bien *et al*., 2021) and also support the integration of microbiome ecology into broader questions of host evolution, ecosystem functioning and disease biology.

While culture-based approaches remain essential for mechanistic and functional validation of individual taxa, molecular techniques allow the *in situ* characterization of entire microbial assemblages and their collective ecological roles (Turnbaugh *et al*., 2007; Gilbert *et al*., 2010). This shift has challenged the traditional one-pathogen–one-disease paradigm, originally established through Koch's postulates, as microbiome-wide association studies increasingly demonstrate the role of polymicrobial interactions in disease outcomes (Gilbert *et al*., 2016). Extending this framework, emerging evidence suggests that disease severity and host resilience in both plants and animals are shaped not by single causal agents alone, but by the structure and function of entire microbial communities.

Host's identity strongly shapes associated forest microbiomes (Baldrian, 2016), a principle that extends to oil palm where roots selectively recruit diverse bacterial, fungal, archaeal and viral communities from bulk soils, shaped by environmental factors, developmental stage, genotype and land-use practice (Hunter *et al*., 2014; Doehlemann *et al*., 2017; Taffner *et al*., 2018; Khan *et al*., 2022). These microbiota fulfill essential functions in palm nutrition, growth promotion, productivity and ecosystem resilience by facilitating nutrient cycling, antagonizing pathogens and bolstering abiotic stress tolerance (Kirkman *et al*., 2022; Azeez *et al*., 2024; Rosid *et al*., 2025).

Among the various palm hosts, oil palm, date palm and coconut palm are the most extensively investigated in microbiome research, with oil palm clearly leading in rhizosphere and endosphere studies and date palm increasingly prominent in fruit and sap microbiome work. Across these systems, high-throughput 16S rRNA and ITS amplicon sequencing dominate, often generating hundreds of thousands of reads per study and revealing communities typically dominated by Proteobacteria, Firmicutes, Actinobacteria and Ascomycota, with statistically significant shifts in diversity and composition driven by compartment, plantation age and management.

Although microbiome research has highlighted the diversity and functional significance of host-associated microbial communities, ecological disturbances can restructure these communities in ways that undermine host health. Shifts in community composition, interaction networks, or environmental conditions may reconfigure microbe–microbe and host–microbe relationships to favor disease development. Framing such dysbiotic assemblages as pathobiomes enables a systems-level understanding of disease, emphasizing the collective behavior of microbial communities and their interactions with host and environmental contexts.

1.8 Pathobiomes: The Paradigm from the One-Pathogen–One-Disease Concept

The pathobiome concept originated from human microbiome research, where disease development was linked to disruptions in stable and beneficial microbial communities (Defazio *et al*., 2014; Krezalek *et al*., 2016). These disease-associated shifts were initially described as dysbiosis to reflect reductions in microbial diversity and changes in community metabolic function that favour pathogen establishment and disease progression (Brüssow, 2020). However, as microbiome research advanced, dysbiosis was increasingly recognized as a descriptive rather than mechanistic term, limiting its ability to explain how specific microbial interactions actively modulate pathogenesis (Hooks & O'Malley, 2017; Brüssow, 2020). In response to these limitations, the pathobiome framework was developed to shift microbiome research from a predominantly descriptive focus toward a functional understanding of how microbial communities modulate disease processes. Rather than concentrating on isolated pathogen–host interactions, this approach simply revisits Koch's postulates at the level of microbial communities to emphasize that disease outcomes emerge from interactions among multiple microorganisms and the host, rather than from single causal agents alone (Defazio *et al*., 2014; Vayssier-Taussat *et al*., 2014; Kashyap *et al*., 2025). These assemblages usually encompass diverse host-associated organisms, including prokaryotes, eukaryotes and viruses, whose collective interactions with each other and with the host contribute to reduced health status and disease expression. Importantly, pathobiomes are not defined solely by organismal presence but by the nature of their interactions (Kashyap *et al*., 2025), which are moderated by host physiology and the surrounding biotic and abiotic environment. Consequently, pathobiomes are host- and compartment-specific, context dependent and may vary temporally across disease stages, reflecting dynamic host–microbe–environment interactions (Bass *et al*., 2019). Empirical examples to support this framework include the olive knot disease, where quorum-sensing–mediated cooperation between pathogenic *Pseudomonas savastanoi* and non-pathogenic *Erwinia toletana* enhances disease expression (Morris *et al*., 2012; Passos da Silva *et al*., 2014; Derome *et al*., 2016) and bleaching disease in the red alga *Delisea pulchra*, which arises from the combined activity of multiple bacterial lineages rather than a single pathogen (Zozaya-Valdés *et al*., 2017). Our studies on oil palm leaf spot disease have demonstrated that disease development is best understood within the framework of the pathobiome concept, where multiple interacting microorganisms collectively influence disease expression (Azeez *et al*., 2024), This perspective moves beyond the traditional single-pathogen paradigm, highlighting the importance of microbial consortia in shaping host health and disease outcomes. Furthermore, this concept was reinforced by network interaction analyses, which revealed complex relationships among microbial taxa, including potential synergistic and antagonistic interactions that may drive disease progression (Azeez *et al*., unpublished).

Although defining a universal healthy microbiome baseline remains challenging, this systems-based perspective offers a more robust explanation for disease emergence than the traditional reductionist models. Therefore, understanding interactions among pathogens, the surrounding microbiota and the host within a pathobiome framework could provide deeper mechanistic insight into disease development and new opportunities for improving disease prediction, prevention and management in complex host-associated systems.

1.9 Molecular and Ecological Foundations of Plant Immune Responses to Fungal Pathogens

Plant–pathogen interactions are regulated by multilayered immune systems that determine whether infection results in disease or resistance (Peyraud *et al*., 2017; Zhou & Zhang, 2020). Plant defense operates through constitutive barriers, such as the cuticle and cell wall and inducible immune responses activated upon pathogen perception. Inducible immunity is initiated by the recognition of conserved pathogen-associated molecular patterns (PAMPs) or microbe-associated molecular patterns (MAMPs), such as β-glucans and chitin, by pattern-recognition receptors, leading to PAMP-triggered immunity (PTI) (Jones & Dangl, 2006; Rojas *et al*., 2020; Zhou & Zhang, 2020). PTI activates broad-spectrum defenses such as cell wall reinforcement, antimicrobial compound production and oxidative signaling, providing effective basal resistance against diverse pathogens (Jones & Dangl, 2006).

To establish successful infection, many pathogens secrete effector proteins that suppress PTI, resulting in effector-triggered susceptibility (De Wit *et al*., 2009; Todd *et al*., 2022). In response, plants deploy intracellular resistance (R) proteins, predominantly nucleotide-binding leucine-rich repeat (NB-LRR) receptors, which recognize specific effectors or effector-induced host perturbations and activate effector-triggered immunity (ETI). ETI is typically associated with stronger defense outputs, including detoxification responses, activation of wall-associated kinases, reinforcement of structural barriers and localized hypersensitive cell death that restricts pathogen spread (Elmore *et al*., 2011; Hurni *et al*., 2015; Xu *et al*., 2022). The effectiveness of these responses depends on tight regulation of resistance-associated genes, as excessive or dysregulated defense can impose metabolic costs and reduce fitness.

Pathogenesis-related (PR) proteins are key components of inducible defense and serve as widely used molecular markers of immune activation. Multiple PR families, including chitinases, β-1,3-glucanases, thaumatin-like proteins, defensins and protease inhibitors, are consistently induced during fungal infection and contribute to pathogen restriction through enzymatic degradation of fungal cell walls and inhibition of pathogen growth (Han *et al*., 2023; Upadhyay, 2024). In oil palm, molecular studies of defense responses have been dominated by work on *Ganoderma boninense*, the causal agent of basal stem rot (Zakaria, 2023), although defense-related genes and immune pathways have also been reported in response to other fungal challenges. Collectively, these studies have revealed extensive activation of pathogenesis-related (PR) genes and associated defense mechanisms, including antimicrobial proteins, redox regulation and cell wall–associated defenses (Alizadeh *et al*., 2011; Naher *et al*., 2011; Yeoh *et al*., 2012; Tan *et al*., 2013; Tee *et al*., 2013; Yeoh *et al*., 2013; Rosli *et al*., 2018). Resistance to *G. boninense* has been linked to sustained peroxidase activity, lignin biosynthesis and laccase-mediated cell wall reinforcement, whereas susceptibility is often

associated with enhanced expression of detoxification-related genes, reflecting distinct molecular strategies underlying compatible and incompatible interactions (Faizah *et al*., 2022).

In contrast, comparatively little is known about the molecular and physiological defense responses of oil palm to *Thielaviopsis paradoxa*, despite its broad host range and increasing recognition as an important pathogen in tropical agroecosystems. This knowledge gap limits our understanding of whether defense mechanisms characterized in *G. boninense* pathosystems are conserved, modified, or distinct in interactions involving *T. paradoxa*.

Reactive oxygen species (ROS) also play dual roles in plant immunity as antimicrobial agents and signaling molecules. Effective defense requires tight control of ROS accumulation by antioxidant enzymes, including glutathione peroxidase (GPX) and ascorbate peroxidase (APX), to maintain redox homeostasis and prevent cellular damage (Liu *et al*., 2018; Jiang *et al*., 2023). Enzymes such as laccases contribute to lignin polymerization and cell wall fortification, enhancing structural barriers against pathogen invasion (Ahlawat *et al*., 2024).

1.10 Fungal–Fungal Interactions and Disease Ecology in Oil Palm Systems

Beyond direct plant–pathogen interactions, fungal–fungal interactions introduce a critical layer of ecological complexity that shapes disease dynamics in tropical agroecosystems such as oil palm plantations. *Thielaviopsis paradoxa* occupies multiple ecological niches, persisting in soilborne reservoirs and associating with insect vectors, notably *Rhynchophorus palmarum*. On the insect carapace, the pathogen coexists with saprotrophic, phytopathogenic and entomopathogenic fungi (Eliziario, 2024), facilitating long-distance dispersal and highlighting the multifactorial nature of the oil palm pathobiome.

Across these shared ecological niches, interactions with endophytic and co-occurring fungi are likely to influence pathogen persistence, colonization dynamics and disease expression (Van Bael *et al*., 2017; Akram *et al*., 2023; Baltruschat *et al*., 2025). Increasing evidence suggests that such microbial assemblages can modulate pathogen behavior indirectly by shaping resource availability, niche occupancy and overall community structure (Akram *et al*., 2023; Bandara *et al*., 2006; Grabka *et al*., 2022). As a result, fungal–fungal interactions are increasingly recognized as integral components of disease ecology rather than peripheral phenomena. This perspective is particularly relevant in perennial cropping systems such as oil palm, where the establishment of stable, long-term microbial associations can significantly influence disease dynamics and underpin the development of sustainable disease management strategies.

1.11 *Thielaviopsis paradoxa* as a Model for Integrative Host–Pathogen and Genomic Studies

Within this broader immunological and ecological framework, *T. paradoxa* represents a powerful model for investigating both host-dependent defense responses and interspecific fungal interactions. Variation in pathogenicity among *T. paradoxa* isolates, together with differential susceptibility across hosts including oil palm (*E. guineensis*), could be explored to examine how host genetic background, pathogen diversity and defense-related pathways

jointly determine infection outcomes. These biological insights are further enhanced by the availability of the *T. paradoxa* genome and those of closely related species, including *T. punctulata*, *Chalara longipes* and *Bretziella fagacearum*, which facilitate comparative genomic analyses aimed at deciphering effector repertoires, virulence strategies and evolutionary relationships within this group of plant-pathogenic fungi.

At the host level, the publication of the oil palm genome has markedly advanced the identification of genes associated with key agronomic traits, including disease tolerance (Singh *et al*., 2013; Rosli *et al*., 2018). However, despite this genomic resource, pinpointing the most functionally relevant candidates within large and often redundant gene families remains a major challenge for effective deployment in resistance breeding. In this context, integrative approaches that combine genomic information with functional and ecological analyses, such as pathogen challenge assays and interactions with antagonistic endophytic fungi like *Simplicillium lamellicola*, could enable the characterization of stress- and defense-related transcriptional responses linked to antibiosis. Collectively, these strategies provide a systems-level perspective on *T. paradoxa* biology, host resistance mechanisms and ecologically informed avenues for sustainable disease management.

2. AIM, OBJECTIVES AND HYPOTHESES

The study aimed to elucidate the molecular and ecological interactions between *Thielaviopsis paradoxa* and one of its major hosts, *Elaeis guineensis* (oil palm), with the goal of identifying mechanisms that can inform disease management strategies.

The specific objectives were as follows:

(i) To document an exhaustive and up-to-date literature review covering oil palm diseases, including those caused by *T. paradoxa*.

(ii) To characterize and establish the phylogenetic relationships among diverse *T. paradoxa* isolates originating from Nigeria and Papua New Guinea (PNG).

(iii) To unravel the fungal communities constituting the oil palm leaf spot pathobiome and assess their potential ecological interactions with *T. paradoxa*.

(iv) To investigate antifungal interactions and transcriptional responses of *T. paradoxa* during interaction with *Simplicillium lamellicola*, thereby elucidating mechanisms underlying its potential as a biological control agent, with *Heterobasidion annosum* included as a comparative necrotrophic phytopathogen.

(v) To evaluate the pathogenicity and host-induced transcriptional responses of oil palm and sugarcane-derived *Thielaviopsis paradoxa* isolates during interactions with different oil palm cultivars.

The hypotheses were as follows:

(i) *T. paradoxa* isolates from Nigeria and Papua New Guinea form distinct phylogenetic clades correlating with geographic origin or environment, driving virulence variation.

(ii) Oil palm leaf spot–affected tissues harbor a structured fungal pathobiome in which *T. paradoxa* represents a key fungal taxon exhibiting significant ecological interactions.

(iii) *S. lamellicola* inhibits *T. paradoxa* through antifungal activity and induces specific transcriptional reprogramming in the pathogen.

(iv) Oil palm-derived *T. paradoxa* isolates exhibit higher pathogenicity and trigger stronger transcriptional defense responses in oil palm cultivars than sugarcane host-derived isolates.

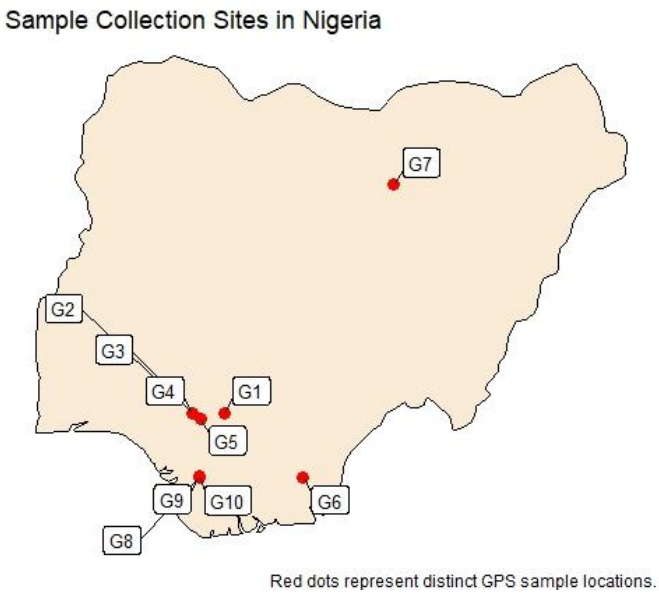
3. MATERIALS AND METHODS

The fungal isolates, plant materials, sampling procedures and analytical methods employed in the study are summarized in Table 1, Fig. 3 and Table 2. Detailed protocols and methodologies are described in the associated publications.

Table 1: Fungal isolates and plant materials used for the experiments

Fungal Isolates and Plant materials	**Publications**
Thielaviopsis paradoxa isolates (41)	II
Simplicillium lamellicola (1)	IV
Heterobasidion annosum	IV
Oil palm seedlings (Tenera & Malaysian compact (semi-dwarf))	V
Oil palm leaf, root and soil samples	III

(a)



(b)

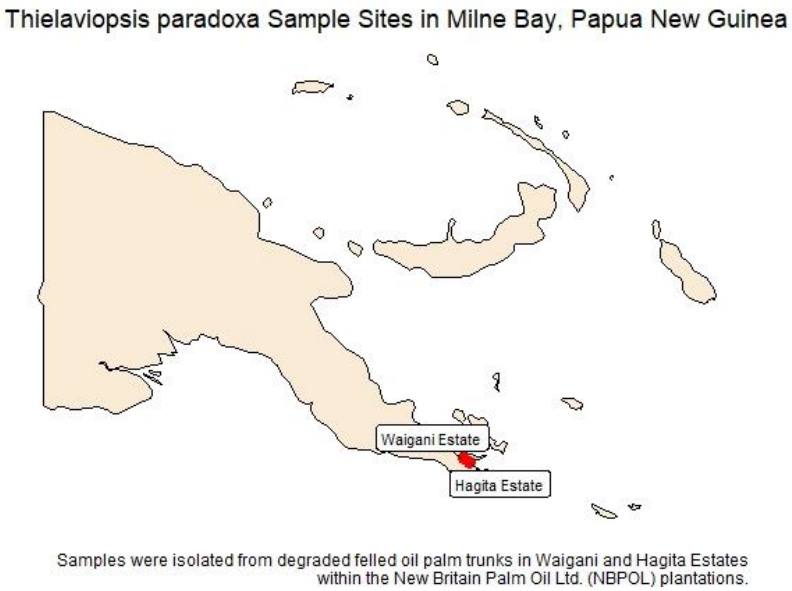


Fig. 3 Map showing sources of *T. paradoxa* isolates in (a) Nigeria and (b) Papua New Guinea

Table 2: Various methods employed in the study

Methods	**Publications**
Bioinformatics and statistical analysis	II, III, IV, V
DNA extraction	II, III
Fungal isolates	II, IV, V
Functional annotation of DEGs	IV, V
Microscopy	II, IV
Microbiome analysis	III
Network Analysis	III
Pathogenicity test on oil palm seedlings	V
PCR amplification of ITS	II, III, IV
Phylogenetic analysis	II, IV
Radial growth studies	II
RNA extraction	IV, V
Sequencing and library preparation	III, IV, V
Sample collection	II, III, IV, V
Seedling establishment and nursery management	V
Transcriptomic analyses	IV, V

4. RESULTS AND DISCUSSION

4.1 Thermal Tolerance, Growth Responses and Phylogenetic Relationships among *T. paradoxa* Isolates

Forty-one fungal isolates of *T. paradoxa* collected from Nigeria and PNG were used in this study. Nigerian isolates were obtained from oil palm trunks showing dry basal rot and neck bending disease, as well as from associated soil samples, sugar cane stems and a rotten date palm fruit collected across Edo, Delta and Jigawa states, while PNG oil palm isolates were obtained from PNG Oil Palm Research Association (PNGOPRA) herbarium. These isolates were subjected to temperature-dependent growth assays and molecular characterization and phylogenetic analysis based on internal transcribed spacer (ITS) rDNA sequences.

4.1.1 Influence of Temperature on Isolate Growth Rate

Radial growth of *T. paradoxa* isolates was evaluated three days post-inoculation on potato dextrose agar (PDA) pre-covered with a membrane across a temperature gradient of 22, 25, 30, 32, 34 and 35 °C (Paper II: Table 2). Most isolates exhibited a maximum growth rate of 2.93 cm day^{-1}, whereas sugarcane-derived isolates AA034 and AA036 showed comparatively lower maxima of 2.07 and 2.23 cm day^{-1}, respectively. In general, optimal growth occurred between 25 °C and 32 °C, consistent with previous studies reporting similar temperature optima for *T. paradoxa* (Liu & Cortés-Monllor, 1972; Bachiller, 1998; Tzeng *et al*., 2010; Sikder *et al*., 2021). At 22 °C, growth rates ranged from 0.53 to 2.93 cm day^{-1}; all oil palm isolates from PNG grew at this temperature, whereas only a subset of Nigerian isolates exhibited measurable growth, indicating potential geographic variation in thermal adaptation (Liu & Cortés-Monllor, 1972).

Most isolates reached peak growth between 25 °C and 30 °C, although some displayed reduced growth at 32 °C, suggesting isolate-specific thermal responses. Growth declined markedly at 34 °C and was minimal at 35 °C, where no sugarcane isolates grew and only limited growth was observed in the oil palm isolate DA029 (0.97 cm day^{-1}). This reduction at elevated temperatures aligns with studies demonstrating that temperatures above 32 °C suppress vegetative growth and pathogenicity in sugarcane-associated isolates (Alvarez *et al*., 2012). However, this contrasts with reports indicating broader optimal growth ranges extending up to 35 ° (Sikder *et al*., 2021), likely reflecting differences in isolate origin and experimental conditions.

Statistical analyses revealed significant differences in growth rates among isolates at all tested temperatures, with particularly strong effects at 30 °C [$F(40,41) = 275{,}700$, $p < 0.001$] and 32 °C [$F(40,41) = 214{,}215$, $p < 0.001$], underscoring substantial intraspecific variability in thermal tolerance. Notably, oil palm and date palm isolates exhibited greater tolerance to elevated temperatures than sugarcane isolates, likely reflecting host–pathogen co-adaptation in tropical environments (Liu & Cortés-Monllor, 1972). Such physiological variability has important implications for predicting disease dynamics under climate change (Paterson, 2020) and may inform strain selection for biological control. Nevertheless, the relationship between in vitro growth performance and field pathogenicity remains unclear (McConnell & Balci, 2015; Ouedraogo *et al*., 1997).

4.1.2 Phylogenetic Analysis of ITS Sequences

PCR amplification of ITS region from genomic DNA of the 41 isolates produced fragments of 516–528 bp, showing 99.02–100% identity with *T. paradoxa* reference sequences in GenBank, thereby confirming species identity. These sequences, together with references of *Ceratocystis fimbriata* and *T. thielavioides* used as outgroups, were analyzed using Bayesian inference (Paper II: Fig. 2), yielding a phylogeny with moderate to high node support (posterior probabilities >60%), consistent with the utility of ITS markers in fungal systematics and population studies (Samson *et al*., 2010; Op De Beeck *et al*., 2014; Saeed *et al*., 2016).

Five clades were resolved, but no clear clustering by geographic origin, host, or substrate was observed. A dominant clade comprised most Nigerian isolates from oil palm, date fruit and sugarcane, along with several oil palm isolates from Papua New Guinea, while four smaller clades contained the remaining isolates. This lack of phylogeographic or host-associated structure indicates high genetic similarity among isolates and supports previous reports of largely clonal *T. paradoxa* populations (Alvarez *et al*., 2012), potentially influenced by vegetative reproduction and the movement of infected planting material.

ITS-based phylogenetic relationships did not align with temperature-dependent growth responses, as isolates exhibiting contrasting thermal tolerances clustered within the same groups. This suggests that thermal adaptation is not captured by variation in the ITS region alone. Although multiple clades were identified, they reflect only limited ITS polymorphism within *T. paradoxa* populations, a factor that remains relevant for molecular diagnostics. A more comprehensive understanding of population structure and thermal adaptation will require expanded sampling and the use of additional genetic markers beyond the ITS region.

4.2 Mycobiome community associated with Leaf spot Disease of Oil palm

In this study, ITS2 rRNA gene metabarcoding was applied to compare the structure and composition of fungal communities associated with leaf, root and soil compartments of asymptomatic and leaf spot–symptomatic oil palm trees under natural field conditions. High-throughput sequencing captured a broad spectrum of fungal taxa, including putative pathogens, endophytes and saprotrophs, providing a comprehensive view of the oil palm mycobiome across asymptomatic (AS) and symptomatic (SS) samples.

4.2.1 Fungal Diversity Patterns and Community Organization

Alpha- and beta-diversity analyses revealed no significant differences between AS and SS samples across tissues and locations (Paper III: Fig. 7; Supplementary Figure 4a), although overall diversity tended to be higher in AS samples. This pattern is typical of plantation systems with simplified microbial assemblages shaped by land-use history and management practices (Wang & Foster, 2015). Similarly, ordination analyses showed no clear clustering by symptom status or sampling site, consistent with previous oil palm microbiome studies (de Assis Costa *et al*., 2018; Kirkman *et al*., 2022).

4.2.2 Dominant Taxonomic Groups and Community Composition

Across all samples, Ascomycota and Basidiomycota dominated the fungal communities (Paper III: Fig. 2) consistent with previous reports on oil palm and other perennial crops (Guo *et al*., 2001; de Assis Costa *et al*., 2018; Kirkman *et al*., 2022). The increased relative abundance of Basidiomycota in symptomatic samples may reflect successional shifts following tissue colonization and disease development. At the order level, Hypocreales and Pleosporales were prevalent across compartments, supporting their ecological versatility as endophytes, saprotrophs and pathogens (Kruys & Wedin, 2009; Wong *et al*., 2021).

4.2.3 Evidence for a Pathobiome in Oil Palm Leaf Spot Disease

Several genera previously associated with oil palm leaf spot and other foliar diseases, namely *Neopestalotiopsis*, *Pseudopestalotiopsis*, *Colletotrichum*, *Ceramothyrium* and *Lasiodiplodia*, were detected in both asymptomatic (AS) and symptomatic (SS) samples (Paper III: Fig. 3; Fig. 4). Overall, their relative abundance across sample categories was higher in AS tissues than in SS tissues. Combinations of these genera, particularly *Neopestalotiopsis* and *Pseudopestalotiopsis*, have previously been implicated in oil palm leaf spot disease (Suwannarach *et al*., 2013; Ismail *et al*., 2017; Yurnaliza *et al*., 2021). Additionally, *Pestalotiopsis*, together with two of these genera, has been linked to other foliar diseases in oil palm (de Assis Costa *et al*., 2018). Notably, *Colletotrichum* spp. and *Trichoderma asperellum* were more abundant in asymptomatic samples, consistent with reports describing these taxa as endophytes in other plant systems. This pattern suggests that their roles may be context-dependent, influenced by host physiological status, microbial interactions, or environmental conditions. In contrast, symptomatic leaves were enriched with *Oxydothis*, *Pseudocercospora* and an unassigned member of the family Sporormiaceae, all of which have documented associations with foliar diseases in palms and other crops (Ávila *et al*., 2005; Fröhlich & Hyde, 1999; Chomnunti *et al*., 2012; Hongsanan *et al*., 2015). The concurrent presence of multiple disease-associated taxa supports the hypothesis that oil palm leaf spot disease is driven by a consortium of interacting fungi, a pathobiome rather than a single causal agent (de Assis Costa *et al*., 2018).

4.2.4 Network Structure and Putative Keystone Taxa

Despite broadly similar taxonomic composition, network analyses revealed distinct interaction patterns between AS and SS communities (Paper III: Fig. 8). Symptomatic samples showed greater connectivity and a higher number of putative keystone taxa (Paper III: Table 2), indicating intensified microbial interactions under disease conditions. Rare taxa identified as network hubs may play disproportionate roles in community stability and disease progression (Berry & Widder, 2014; Wood *et al*., 2017).

Most group-level networks exhibited high modularity (Paper III: Table 2), reflecting stable and compartmentalized community structures. Reduced modularity in symptomatic root samples (Paper III: Table 2) may indicate ecological disturbance or weakened host control over microbial assembly (Burgos *et al*., 2007; Ding *et al*., 2015). The overall similarity in network

structure likely reflects the close geographical proximity of the sampled agroecosystems (Kreimer *et al*., 2008).

4.2.5 Implications for Disease Ecology and Management

The enrichment of *Trichoderma asperellum* in asymptomatic roots is consistent with its well-documented disease-suppressive and biocontrol potential (Boari, 2008; John & Mathew, 2017). (Boari, 2008; John & Mathew, 2017). Collectively, the coexistence of pathogenic and beneficial fungi, stable diversity patterns and contrasting network organization support a pathobiome-based framework for oil palm leaf spot disease, underscoring the critical role of microbial interactions in disease development.

4.3 Antagonistic interactions and transcriptional responses of *T. paradoxa* and *Heterobasidion annosum* during interaction with *Simplicillium lamellicola*

4.3.1 Antagonistic Interactions Assessed by Dual-Culture Assays and Microscopy

S. lamellicola exhibited strong antibiosis against *T. paradoxa* (Tp) and *H. annosum* (Ha) in dual-culture assays, forming distinct inhibition zones that prevented pathogen colony expansion. Microscopy of interaction zones revealed pronounced hyphal deformations in both pathogens, including irregular hyperbranching, apical swelling, anomalous fusions and cytoplasmic lysis, which are absent in their respective monoculture hyphae (Paper IV: Fig. 1). These structural disruptions indicate pronounced *S. lamellicola*–induced stress, providing direct evidence of antagonism (González *et al*., 2020) and supporting its biocontrol potential against necrotrophic pathogens affecting oil palm and forest systems.

4.3.2 Transcriptomic Responses under Dual-culture Interaction

4.3.2.1 RNA-seq Data Overview

RNA-seq analysis of monocultures (*T. paradoxa* and *H. annosum*) and dual cultures (TpSl and HaSl), each with three biological replicates (12 libraries total), detected 6,508 and 7,922 expressed genes, respectively. In TpSl, 452 genes were upregulated and 884 downregulated, whereas HaSl showed 193 upregulated and 248 downregulated genes. Principal component analysis and hierarchical clustering clearly separated monoculture and dual-culture samples (Paper IV: Fig. 2), indicating robust and pathogen-specific transcriptional responses to antagonism.

4.3.2.2 Shared transcriptomic Responses by *T. paradoxa* and *H. annosum*

Both pathogens exhibited marked transcriptional reprogramming in response to combined chemical and physical antagonistic pressure (Paper IV: Fig. 3; Fig. 4). Genes involved in ROS detoxification, transmembrane transport and hydrolytic enzyme function were widely regulated, indicating active control of redox balance and nutrient acquisition (Paper IV: Table

S4). Chitinases showed varied expression patterns in the two fungi and are essentially linked to pentose and glucuronate interconversion pathway in *T. paradoxa* which could be due to species specificity or temporal roles (Paper IV: Fig. 5; Fig. 6).

Previous studies have shown that chitinases are central to fungal recognition and mycoparasitic defense (Latgé, 2007; Seidl-Seiboth *et al*., 2014). Fatty acid desaturases were consistently induced in both fungi (Paper IV: Fig. 5; Fig. 6) consistent with reinforcement of membrane integrity under stress, whereas cytochrome P450 monooxygenases displayed contrasting regulation (Paper IV: Fig. S5; Fig. S11), pointing to divergent detoxification pathways. Differential expressions of MAPK-associated kinases and carbohydrate-binding C-type lectins further underscores their importance in signaling and partner recognition during antagonistic interactions.

4.3.2.3 Distinct Response of *T. paradoxa* to *S. lamellicola*

T. paradoxa responded primarily through structural reinforcement and transporter-mediated defense. Strong induction of ABC and MFS transporters (Paper IV: Fig. 7; Fig. S7) suggests active efflux of inhibitory compounds, while upregulation of glycerophospholipid metabolism and aquaporins indicates membrane remodeling under stress. Increased expression of carbohydrate-active enzymes (Paper IV: Fig. 5) including chitin-related genes, further supports cell wall reinforcement. In contrast, central carbon metabolism (Paper IV: Table S3b), including glycolysis and the pentose phosphate pathway (Paper IV: Fig. S3; Fig. S4), together with redox-associated enzymes, was broadly downregulated, consistent with reduced metabolic investment in favour of defense. Limited induction of aspartyl proteases and sub-set of secondary metabolism genes points to cellular reorganization rather than an aggressive chemical counter-response.

4.3.2.4 Distinct Response of *H. annosum* to *S. lamellicola*

H. annosum adopted a chemically oriented defense strategy against *S. lamellicola*, featuring fatty acid metabolism, xenobiotic degradation and secondary metabolite biosynthesis (Paper IV: Fig. 6; Fig. S11). Key induced genes encompassed terpenoid synthases, laccases, flavonoid monooxygenases and 4-coumarate-CoA ligase, aligning with metabolite-based countermeasures to antagonistic compounds. This response was further supported by the induction of cytochrome P450 monooxygenases, NADPH dehydrogenases and acetyl-CoA C-acyltransferases, reflecting a coordinated activation of redox-dependent detoxification pathways. Concurrent downregulation of signal transduction (Paper IV: Fig. S13) and transcription-associated genes (Paper IV: Fig. S14) indicate a reallocation of cellular resources toward chemical defense rather than structural reinforcement. This contrasts with the predominantly structural and transporter-mediated defense strategy observed in *T. paradoxa*, highlighting species-specific survival responses among necrotrophic fungi.

Previous studies on interspecific fungal interactions emphasized extracellular enzymes, particularly laccases and mRNA differential display to identify antagonism-related genes (Boddy, 2000; Iakovlev & Stenlid, 2000; Iakovlev *et al*., 2004). The upregulation of laccases was moderate but accompanied by broad activation of secondary metabolism genes, indicating a shift toward chemically mediated antagonism. Unlike saprotrophic systems where oxidative

enzymes can dominate responses (Olson *et al*., 2012), this coordinated induction suggests multifunctional metabolite deployment rather than reliance on a single antagonistic enzyme.

Unlike *T. paradoxa*'s transporter reliance, *H. annosum* prioritized oxidative stress mitigation via aldo-keto reductases (AKRs) and alcohol dehydrogenases for redox homeostasis (D'Autréaux & Toledano, 2007; Montibus *et al*., 2015; Liu *et al*., 2022). Minimal ABC/MFS transporter and aquaporin regulation, plus repression of MAPK, GTPases, transcription factors, cell cycle and cell wall genes, reflected energy conservation for chemical defense. Selective upregulation of lectins and peptidases suggests localized recognition and defense signaling at the fungal interaction interface, despite global transcriptional repression. Downregulation of β-1,6-N-acetylglucosaminyltransferases suggests reduced exposure of immunogenic glycans, while suppressed hydrophobins indicate limited investment in hyphal sealing or barrage formation (Wösten *et al*., 1999; Adomas *et al*., 2006; Ujor *et al*., 2012; Fesel & Zuccaro, 2016). Concurrent repression of ferric reductases points to a strategic shift from iron acquisition toward oxidative stress management.

These enrichment patterns are well supported by KEGG and GO analyses (Paper IV: Fig. 3; Fig. 4) confirming enrichments in ribosome processes, fatty acid metabolism, amino acid degradation, oxidoreductase activity and cofactor binding. Together, these enrichments depict a metabolically streamlined yet chemically aggressive defense program, delineating *H. annosum*'s metabolite-driven strategy, elucidating fungal antagonism at the molecular level and reinforcing *S. lamellicola*'s potential as a biocontrol agent against necrotrophic pathogens.

4.4 Pathogenic variability of *T. paradoxa* and differential transcriptomic responses of oil palm cultivars to isolates of contrasting virulence

4.4.1 Pathogenicity test

Pathogenicity assays revealed pronounced isolate- and cultivar-specific differences in *T. paradoxa* virulence. In Tenera, disease severity varied by isolate, with DA002 identified as the most aggressive and AA034 among the least virulent. In contrast, Malaysian compact (semi-dwarf) remained asymptomatic throughout the three-week experimental period, indicating strong resistance at the early to intermediate stages. However, a few Malaysian compact seedlings developed symptoms six months after the experiment.

Based on these contrasting responses, four cultivar–isolate combinations were selected for transcriptomic profiling: DA002- and AA034-inoculated Tenera (T2, T34) and Malaysian compact (M2, M34), along with their respective controls (TC, MC), representing high- and low-virulence interactions (Paper V: Fig. 1).

4.4.2 Transcriptomic studies

4.4.2.1 RNA-seq Overview of Cultivar-Specific Transcriptomic Responses to *T. paradoxa*

RNA-seq analysis generated high-quality data across 18 libraries, with ~92 million reads per sample and >96% of bases above Q30. Reads were evenly distributed between pairs and strands, consistent with non–strand-specific libraries and mapped efficiently to the *Elaeis guineensis* genome (83% total, 81% unique), with ~94% aligning to exonic regions (Paper V: Table S1). Transcriptomic responses mirrored pathogenicity patterns: the highly virulent isolate DA002 induced extensive differential expression in both cultivars, particularly in Tenera, whereas the weakly virulent AA034 elicited comparatively modest changes. Tenera exhibited broader transcriptional reprogramming, while Malaysian compact responses were more restrained and dominated by gene induction. PCA, Venn analysis and hierarchical clustering confirmed clear separation between treatments and controls and highlighted cultivar- and isolate-dependent transcriptional variation (Paper V: Fig. 3; Fig. S2).

4.4.2.2 Transcriptomic Reprogramming in Tenera Following *T. paradoxa* Infection

In Tenera, transcriptional responses closely reflected the pathogenicity of *T. paradoxa* isolates. T2, which caused severe disease in pathogenicity assays, induced extensive reprogramming, including activation of PR proteins such as PR1, PR4 and PR-like, multiple R-gene homologs such as RGA, RPM1-like, RPP8 and Lr10-like (Paper V: Fig. 5), receptor-like kinases, chitinases (Paper V: Fig. 8) and stress-associated transcription factors particularly WRKY, MYB, ERF, NAC and bHLH (Paper V: Table S8). Secondary metabolic pathways were strongly engaged, with induction of phenylpropanoid-, lignin-, flavonoid- and alkaloid-associated genes such as C4H, CCoAOMT, CHS, F3′5′H, PODs and laccases (Paper V: Fig. 6; Tables S5–S7), supporting cell-wall reinforcement and antimicrobial metabolite diversification (Besseau *et al*., 2007; Van Acker *et al*., 2017; Wen *et al*., 2022). Redox-related genes, including glutathione-, ascorbate- and polyamine-associated enzymes namely GPX, APX, GS, IDHs and GSTs (Paper V: Fig. 7) and cysteine-rich RLKs were upregulated (Paper V: Fig. 8), reflecting intensified ROS detoxification (Hasanuzzaman *et al*., 2019; Ushio-Fukai *et al*., 2021; Do Carmo Santos *et al*., 2025). By contrast, T34 elicited limited transcriptional changes, with minimal induction of defense, secondary metabolism and redox genes (Paper V: Fig. 6; Fig. 7) and photosynthesis remained largely unaffected (Paper V: Table S4). These results indicate that Tenera's host responses scale with isolate aggressiveness rather than reflecting cultivar-level tolerance or susceptibility.

4.2.2.3 Transcriptomic Responses of Malaysian Compact (Semi-Dwarf) to *T. paradoxa*

In Malaysian compact transcriptomic patterns also aligned with isolate virulence. M2, which caused more pronounced pathogenicity in assays, elicited a coordinated defense program characterized by induction of PR proteins (MLP423, A70, PTI5), resistance genes (RPM1, RGA3/4) (Paper V: Fig. 5), cysteine-rich RLKs (Paper V: Fig. 8) and stress-associated transcription factors particularly HSFB1 and SAP1 (Paper V: Table S8) (Sayhan *et al*., 2017; Sahebi *et al*., 2018). The phenylpropanoid–lignin–flavonoid network was broadly activated

viz. PALs, 4CLs, CCR, TTMT, C3H, CHI and DFR alongside cytochrome P450s, laccases (Paper V : Fig. 6; Table S5; Table S6) and chitinases (Paper V: Fig. 8), supporting cell-wall reinforcement and diversification of defense metabolites (Besseau *et al*., 2007; Govender *et al*., 2017; Dong & Lin, 2021). Redox modulation was selective, with upregulation of specific GSTs and RDRM2 (Paper V: Fig. 7), indicating efficient ROS management without excessive metabolic cost (Hasanuzzaman *et al*., 2019; Ushio-Fukai *et al*., 2021). In contrast, M34 triggered minimal transcriptional activation, with few defense or secondary metabolism genes induced, weak redox engagement and limited transcription factor activity (Paper V: Fig. 6–8; Tables S5–S8). These findings demonstrate that, as also observed in Tenera, Malaysian compact scales transcriptional investment according to isolate virulence rather than intrinsic cultivar susceptibility.

5. SUMMARY AND CONCLUSIONS

This study provides a multi-scale analysis of *Thielaviopsis paradoxa* biology and oil palm disease ecology by integrating physiological assays, phylogenetics, mycobiome profiling, fungal–fungal interaction studies and host–pathogen transcriptomics. Together, the findings demonstrate that disease outcomes in oil palm are shaped by isolate-level variability, microbial community interactions and host genotype–dependent defense strategies rather than by single pathogens or conserved genetic lineages alone.

Thermal tolerance assays revealed substantial intraspecific variability among *T. paradoxa* isolates, with most showing optimal growth between 25–32 °C but differing markedly in tolerance to higher temperatures. Isolates from oil palm and date palm exhibited greater heat tolerance than those from sugarcane, consistent with host-associated adaptation in tropical environments. However, ITS-based phylogeny showed limited genetic resolution and no association with thermal performance, host, or geographic origin. This decoupling indicates that adaptive variation in *T. paradoxa* is not captured by standard barcoding markers, highlighting the need for higher-resolution genomic approaches to resolve population structure and functional diversity.

Mycobiome profiling of asymptomatic and leaf spot–symptomatic oil palm tissues revealed similar alpha and beta diversity, with *Ascomycota* and *Basidiomycota* dominating across compartments. The lack of pronounced diversity shifts suggests that disease is not driven by large-scale community disruption. Instead, differences in taxon abundance and, more notably, network structure between health states support a pathobiome framework, where disease emergence reflects altered microbial interactions rather than a single causal agent. Enrichment of disease-associated genera in symptomatic tissues, alongside beneficial taxa such as *Trichoderma asperellum* in asymptomatic roots, further underscores the role of microbial balance and interaction dynamics in disease suppression and progression.

Dual-culture assays and transcriptomic analyses demonstrated that *Simplicillium lamellicola* exerts strong antagonistic effects on both *T. paradoxa* and *Heterobasidion annosum*, causing pronounced hyphal damage and extensive transcriptional reprogramming. While both pathogens activated general stress responses, they employed contrasting defense strategies: *T. paradoxa* reinforced cell walls and membranes and relied on transporter-mediated detoxification, downregulating central metabolism, whereas *H. annosum* mounted a chemically driven defense involving secondary metabolism, fatty acid turnover and oxidative stress mitigation, alongside repression of signaling and growth processes. These results highlight species-specific survival strategies and provide molecular support for *S. lamellicola* as a promising biocontrol agent against necrotrophic fungi.

Pathogenicity assays and transcriptomics further showed that disease severity depends on isolate aggressiveness and host–isolate interactions rather than cultivar identity alone. In both *Tenera* and Malaysian compact, highly virulent isolates triggered extensive transcriptional responses, including activation of resistance genes, PR proteins, secondary metabolism and redox pathways, whereas less virulent isolates elicited minimal responses. The apparent resistance of Malaysian compact was linked to an efficient, restrained defense, suggesting tolerance via targeted activation rather than constitutive or broad-scale transcriptional investment.

In conclusion, this thesis demonstrates that oil palm diseases associated with *T. paradoxa* emerge from the interplay of pathogen variability, microbial community dynamics, antagonistic fungal interactions and host-specific defense strategies. The findings emphasize the limitations of single-gene diagnostics and single-pathogen disease models, advocating instead for integrated, systems-level approaches to disease management. By linking physiological traits, microbiome ecology and transcriptomic responses, this work provides a robust framework for predicting disease behavior under changing environmental conditions and for developing microbiome-informed and biologically based disease control strategies in oil palm and forest ecosystems.

6. FUTURE PERSPECTIVES

Future research will build directly on the findings of this thesis to advance a mechanistic and ecologically grounded understanding of *Thielaviopsis paradoxa*–oil palm interactions across scales of biological organization. By providing the first integrated analysis of pathogen diversity, host responses, microbial interactions and associated transcriptomic dynamics, this work establishes a foundation for predictive and intervention-oriented research on oil palm disease systems.

A key priority will be the expansion of *T. paradoxa* isolate collections beyond Nigeria and Papua New Guinea to encompass additional oil palm–growing regions in Africa, Southeast Asia and Latin America, where the pathogen causes recurrent and severe disease outbreaks. These expanded collections will enable more comprehensive assessments of pathogen diversity, adaptive potential and population structure using multi-locus and whole-genome sequencing approaches. Integrating phylogenomic data with temperature-dependent growth assays and standardized pathogenicity tests will facilitate the identification of thermotolerant and highly aggressive lineages, thereby improving projections of disease emergence and severity under future climate scenarios.

To resolve the ecological context of disease development much better, future studies will adopt integrative multi-omics frameworks that combine transcriptomics, metabolomics and proteomics to functionally characterize oil palm–associated fungal communities. Emphasis will be placed on rare microbial taxa identified as keystone species, whose disproportionate influence on community stability and pathogen suppression warrants experimental validation. Elucidating the functional contributions of these taxa will provide critical insight into how microbiome structure and function modulate disease outcomes.

Building on *in vitro* interaction assays, *in planta* co-inoculation experiments involving *T. paradoxa* and the antagonistic endophyte *Simplicillium lamellicola* will be conducted to assess biocontrol efficacy under field and biologically realistic conditions. These experiments will enable direct evaluation of disease suppression, pathogen colonization dynamics and host responses during simultaneous microbial interactions. Time-resolved pathogenicity assessments coupled with transcriptomic and metabolomic profiling will capture dynamic molecular responses across early, intermediate and late stages of infection and microbial competition. Integrating metabolite profiles with biosynthetic gene cluster (BGC) predictions generated using tools such as antiSMASH will support the identification of secondary metabolite pathways associated with virulence, antagonism and stress adaptation. Functional validation of candidate effectors, regulatory genes and BGC-associated pathways will be pursued using CRISPR–Cas–mediated genome editing.

While this study examined host responses at the cultivar level, future work will extend pathogenicity and interaction assays to full- and half-sib oil palm populations to better capture heritable variation in disease resistance. Integrating pedigree-based analyses with genome-wide association studies (GWAS) will enable finer resolution of quantitative resistance traits and their links to pathogen virulence. Ultimately, combining host–pathogen interaction data with greenhouse and field validation of antagonistic microorganisms, tested as single strains and designed consortia, will support the development of resilient planting materials and microbiome-informed disease management strategies that reduce reliance on chemical control.

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