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EMERGING PATHOGENS OF *EUCALYPTUS* AND *ACACIA* PLANTATION FORESTRY IN INDONESIA

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Emerging pathogens of *Eucalyptus* and *Acacia* plantation forestry in Indonesia

By

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Declaration

I, Mr Marthin Tarigan, hereby declare that this thesis, submitted herewith for the degree of Philosophiae Doctor to the University of Pretoria, contains my own independent work. This work has hitherto not been submitted for any degree at this or any other tertiary institution.

Marthin Tarigan

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Dedication

**I dedicate this thesis to my wife Dr Maria Peratenta Sembiring
my daughter Melisa Phebeyola E. Tarigan
and my son Mikha Daniel L. Tarigan
and in memory of both my late father-in-law
Mr. Meger Sembiring Brahmana (19 Sept 1937 – 25 Nov 2007)
and my late father
Dkn. Em. Sobat Tarigan Silangit (17 Aug 1945 – 8 Oct 2020)**

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PREFACE

Forest plantation areas are expanding rapidly around the world as a result of the global demand for wood-based products such as fibre, plywood, pulp and paper, board and clothing. Non-native tree species such as *Eucalyptus* spp. and *Acacia* spp. have largely been used, particularly in South East Asia, because of their fast growth, wood quality adequate to many different uses, and their ability to reproduce vegetatively. More than seven million hectares of *Acacia* and *Eucalyptus* plantations have been established in SE Asia. These plantations are susceptible to the negative impact of pathogens and a number of disease problems have been reported in plantation-grown *Acacia* spp. and *Eucalyptus* spp. in this region. Despite this fact, relatively little research has been conducted to elucidate the causes of these diseases, or to develop sustainable management plans to reduce the incidence and impact, particularly in Indonesia.

In order to address these needs, a research programme known as the RGE-FABI Tree Health Programme (https://www.fabinet.up.ac.za/index.php/research-groups/rge-fabi-thp) was established in 2018 between RGE (Royal Golden Eagle, https://www.rgei.com/) and FABI (Forestry and Agricultural Biotechnology Institute, http://www.fabinet.up.ac.za). As part of this programme, research has been initiated, particularly on the emerging pathogens in *Eucalyptus* and *Acacia* plantation forestry in Indonesia. The aim of the studies in this thesis has been to address this issue by providing a based of knowledge on emerging diseases of *Acacia* spp. and *Eucalyptus* spp. in Indonesia.

Acacia spp. and *Eucalyptus* spp. are two major tree species established in plantations in South East Asia. Chapter 1 of this thesis provides a review of the literature on diseases of *Acacia* spp. and *Eucalyptus* spp., including leaf, stem and root diseases in South East Asia. The description of the diseases, including causal agents, symptoms, status and impact are discussed, including the disease management strategies where possible.

Chapter 2 of the thesis discusses leaf blight caused by *Calonectria* spp. This disease is a significant problem that causes losses in both production nurseries and plantations. To identify *Calonectria* isolates obtained from diseased *Eucalyptus* seedlings in nurseries and infected leaves in plantations, DNA sequence data based on the translation elongation factor 1-alpha, β-tubulin, calmodulin, and histone H3 gene regions were used. Isolate aggressiveness and clone susceptibility were determined by pathogenicity trials in a greenhouse.

Species of *Chrysoporthe* pose a threat to the rapidly expanding *Eucalyptus* plantation industry in South East Asia, and the canker disease caused by these fungi occurs on several woody plants, including *Eucalyptus* in this region. Such cankers have been observed on *Eucalyptus* trees in Riau and Kalimantan during disease surveys and consequently, Chapter 3 of the thesis describes the collection and isolation and identification of the putative pathogen using the DNA sequence data based on the internal transcribed spacer (ITS) region of the ribosomal DNA and two regions of the β-tubulin gene (TUB1 and TUB2). Field pathogenicity tests were also carried out to assess the aggressiveness of isolates on various *Eucalyptus pellita* clones and their hybrids with *E. grandis*.

Quambalaria species have caused significant damage to *Eucalyptus* plantations and nurseries in various parts of the world. Symptoms of a leaf and shoot blight disease resembling *Quambalaria* have been detected on *Eucalyptus* mother plants during routine disease surveys in Indonesian nurseries. Chapter 4 of the thesis discusses sample collection from nurseries in three regions including North Sumatra, Riau and North Kalimantan, isolation of fungal strains and their identification using the DNA sequence data based on the internal transcribed spacer (ITS) regions 1 and 2, including the 5.8S rRNA region and the large subunit (LSU) of the rRNA. An isolate aggressiveness test was performed to select the most virulent isolates to be used on *E. pellita* clones and their hybrids to assess relative clone susceptibility.

In commercial forestry nurseries, the requirement for high quality and sufficient quantitities of clean water is a necessity. A recent study has shown that the mortality of some *Acacia* seedling plants in Riau is caused by *Pythium myriotylum* infection. Contaminated water was found to be the source of infection. In Chapter 5 of the thesis, the susceptibility of two *Acacia crassicarpa* clones and three *A. mangium* × *A. aurriculiformis* hybrids was tested using the most virulent *P. myriotylum* isolates from the previous study, using a pathogenicity test.

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Chapter 1

Diseases of tropical *Acacia* and *Eucalyptus* in South East Asian forest plantations

1. Introduction

South East Asia (SEA) consists of two geographical regions known as Mainland South East Asia which includes Cambodia, Laos, Myanmar, Peninsular Malaysia, Thailand, and Vietnam; and Maritime South East Asia including Brunei, East Malaysia (Sabah), East Timor, Indonesia, Philippines, and Singapore (Frederick & Leinbach 2020). The climate of South East Asian countries is mainly tropical – hot and humid across the year, with the exception of Northern Vietnam and the mountainous regions of Laos and Myanmar, which have a subtropical climate. These countries typically receive more than 2000 mm of rain per annum, with temperatures ranging between 25°C and 35°C, while the relative humidity ranges between 70% and 90% (Chuan 2020). These climatic factors have favoured the rapid development of tree plantations in SEA (Toledo et al. 2011).

Plantations of fast-growing non-native species have expanded rapidly worldwide over the last thirty years to meet the increasing demand for timber resources and to help reduce pressure on natural forests (Pirard et al. 2016; Messier et al. 2022). *Acacia* spp. and *Eucalyptus* spp. have most commonly been established in plantations in South East Asian countries (Harwood & Nambiar 2014; Healey et al. 2023). The *Acacia* spp. established include *Acacia mangium*, *Acacia crassicarpa*, *Acacia auriculiformis* and *Acacia aulacocarpa,* with *A. mangium* being the main tree species used for plantation development (Cossalter & Nair 2000). However, in recent years, most of the *A. mangium* plantations, particularly in Sumatra and Kalimantan (Indonesia), and Sabah (Malaysia), have been converted to *Eucalyptus* spp. due to widespread damage by monkeys and squirrels that have provided wounds that facilitated vascular wilt disease epidemics caused by *Ceratocystis manginecans* (Tarigan et al. 2011; Nambiar et al. 2018; Wingfield et al. 2023). Planted *Eucalyptus* spp. include *Eucalyptus pellita*, *Eucalyptus grandis* x *E. pellita* hybrid, or *Eucalyptus urophylla* x *Eucalyptus camaldulensis* hybrid, and account for 28% of trees established in plantations (Harwood & Nambiar 2014).

Large areas of single-species plantations, often having a narrow genetic diversity, are particularly vulnerable to damage by pests or pathogens to which they are not tolerant (Wingfield et al. 2008; Wingfield et al. 2010; Wingfield et al. 2015). These pests and pathogens can emerge from the native environment or be accidentally introduced. Furthermore, the risk of new and emerging forest invasive pests and pathogens is increasing over time due to increased trade, the global movement of people, and climate change (Hurley et al. 2017).

Initially exotic *Acacia* and *Eucalyptus* were free from pests and diseases for several decades, but gradually the number of insects and pathogens affecting these trees has increased (Wingfield et al. 2008; Paine et al. 2011; Hurley et al. 2016). Numerous diseases have been recorded on tropical *Acacia* spp. and *Eucalyptus* spp. in plantations in SEA. These include foliar diseases, stem diseases and root diseases. Currently, the threat from fungal diseases in these forest plantations is thought to be greater than that from insect pests (Nair 2001; Wingfield et al. 2011). However, both problems are increasing and control strategies need to be developed to mitigate the risks and to ensure long-term sustainability of the plantations (Wingfield et al. 2011; Wingfield et al. 2015).

There are few studies on the diseases affecting plantations in SEA. Some reports of pathogens are based on herbarium specimens and single incidences, implying that little is known regarding their relevance. Considerable attention has been given to root rot disease caused by *Ganoderma* spp. and Ceratocystis wilt disease caused by *Ceratocystis manginecans* (Tarigan et al. 2011; Wingfield et al. 2023), which are major constraints that reduce the productivity and quality of the timber produced (Lee 2003; Potter et al. 2006; Coetzee et al. 2011; Tarigan et al. 2011). However, several other leaf, stem and root diseases are of importance to the industry. These disease reports are discussed individually in this review. The aim here is to provide as much information as is available in the literature on diseases of *Acacia* spp. and *Eucalyptus* spp. established in plantations in SEA, specifically in Indonesia, Malaysia, Thailand, and Vietnam.

2. Leaf diseases

There are several diseases that affect the foliage of *Acacia* and *Eucalyptus* trees in SE Asian plantations (Figure 1.1). These vary in severity, with some causing little damage and others being more serious, retarding growth and causing mortality. These, as well as some recently

emerging diseases such as Eucalyptus scab and shoot malformation, and Teratospaheria leaf blight, will be discussed in the following section.

2.1. Rust diseases

Rust fungi (Pucciniales, Basidiomycota) are obligate biotrophic pathogens that cause rust diseases on many plant species, including on *Acacia* spp. and *Eucalyptus* spp. (McTaggart et al. 2015a, 2016; Maier et al. 2016; Lelana et al. 2020). There are many species of rust fungi affecting *Acacia* spp. such as *Uromycladium tepperianum* (Morris 1987), *Uromycladium naracoortensis* (Berndt 2010), *Uromycladium falcatarium* (Doungsa-ard et al. 2015) and *Uromycladium acaciae* (McTaggart et al. 2015b). Only two species of rust, *Phakopsora myrtacearum* and *Austropuccinia psidii* (myrtle rust), have been identified from *Eucalyptus* spp. (Maier et al. 2016; McTaggart et al. 2016). This review is limited to those reported from SEA and specifically *Acacia* phyllode rust, and myrtle rust on *Eucalyptus*.

2.1.1. Acacia phyllode rust disease

There are two genera of rust fungi (Pucciniales) known from species of *Acacia* namely *Endoraecium* and *Uromycladium.* It is believed that *Endoraecium* co-evolved with Australian *Acacias* (McTaggart et al. 2015b). Phyllode rust, (Figure 1.1A) caused by *Endoraecium auriculiforme,* formerly known as *E. digitatum* (syn. *Atelocauda digitata* (Basidiomycota: Pucciniales, Pileolariaceae)) is considered the most serious foliar disease of *Acacia* plantations in SEA (Nair & Sumardi 2000; Old et al. 2000; Lee 2003; Lelana et al. 2020).

Occurrence of phyllode rust has been reported from plantations in Indonesia, including Java, Madura, Kalimantan, and Sumatra (Hadi & Nuhamara 1997; Zulfiyah & Gales 1997; Suharti 1980) and Malaysia (Lee 2004). Interestlingly, it has not been reported from Vietnam and other SE Asian countries (Thu et al. 2010). It affects *Acacia auriculiformis, A. aulococarpa, A. 2crassicarpa* and *A. mangium* (Suharti 1980; Santosa & Suharti 1984; Cannon et al. 1997; Zulfiyah & Gales 1997; Nair & Sumardi 2000; Old et al. 2000). The disease is common in native stands in northern Australia, which may be the source of this pathogen (Old 2002; Lee 2003).

Phyllode rust is characterized by the appearance of rust pustules of *Endoraecium auriculiforme* on the phyllodes, shoot tips, petioles, and fruits. Mother plants or garden hedges, seedlings, young and mature trees are all infected by this pathogen (Suharti 1980; Santoso & Suharti

1984; Hadi & Nuhamara 1997; Old et al. 2000). Diseased seedlings become chlorotic and stunted. If material is infected by phyllode rust in the nurseries, this planting stock should not be transferred to new plantation sites to avoid introduction of the disease into new areas (Old et al. 2000). When diseased seedlings are dispatched to the field for planting, the disease is easily established in new plantations (Old et al. 2000). In the field, phyllode rust will continue to develop and cause malformation of the affected parts during early plant growth (Tarigan et al. 2013). Severely infected leaves will drop prematurely, however, phyllode rust rarely causes tree death in the field (Suharti 1980; Old et al. 2000).

The most effective strategy to control phyllode rust is through breeding and selection of tolerant *Acacia* families. It has been shown that there are differences in susceptibility to phyllode rust between different *Acacia* species, provenances and at family level (Old et al. 2000). These differences in susceptibility provide an opportunity for the selection of resistant genotypes to control this disease (Old 1998).

2.1.2. Myrtle rust

The rust fungus *Austropuccinia psidii*, previously known as *Puccinia psidii*, (Basidiomycota; Pucciniales; Sphaerophragmiaceae) causes the disease known most commonly as myrtle rust. Like other rusts, the pathogen is an obligate biotroph, and it infects a variety of hosts within the Myrtaceae, including *Eucalyptus* spp. (Coutinho et al. 1998; Glen et al. 2007). It was found in *Eucalyptus* plantations in Brazil in the 1930s (Joffily 1944) and was first reported to cause significant damage to *Eucalyptus* in nurseries and young plantations in Brazil in 1983 (Fereira 1983). Infected *Eucalyptus* trees showed reduced height and diameter of approximately 25-35% (Silveira & Higashi 2003) and reduced wood volume of 41% (Takahashi 2002). Later it was reported in *Eucalyptus globulus* plantations in Uruguay (Telechea et al. 2003). This pathogen is considered as one of the major threats to commercial *Eucalyptus* plantations in Brazil and in other countries of the world (Coutinho et al. 1998; Santos et al. 2014).

At least two biotypes of *A. psidii* occur outside of its putative native range in Central and South America and that have spread globally (Graça et al. 2013; Roux et al. 2016). The pandemic biotype has been reported from Asia, Australia, Colombia and the Pacific region (Graça 2011; Granados et al. 2017; Machado et al. 2015; McTaggart et al. 2016; Stewart et al. 2017). A second invasive biotype is known only from South Africa and the origin is unknown (Roux et al. 2016).

It is largely accepted that *A. psidii* originated in South America and has since spread to numerous other countries, including the Caribbean such as Cuba, Dominican Republic, Jamaica, Puerto Rico, and Trinidad (Coutinho et al. 1998), Florida and Hawaii (Rayachhetry et al. 2001; Uchida et al. 2006), Japan (Kawanishi et al. 2009), China (Zhuang & Wei 2011), Indonesia (McTaggart et al. 2016), Singapore (du Plessis et al. 2017), South Africa (Roux et al. 2013), Australia (Carnegie et al. 2010), New Caledonia (Giblin 2013) and New Zealand (Large & Galbraith 2017; Ho et al. 2019). In SEA, *A. psidii* can be found on several host species, including *Rhodomyrtus tomentosa* in Singapore and on *Eucalyptus* and *Melaleuca leucadendra* in Indonesia (McTaggart et al. 2016). It is anticipated that this fungus will spread to other Myrtaceae in SE Asian countries given its propensity to do so elsewhere in the world (Large & Galbraith 2017).

One of the main strategies to control myrtle rust is by breeding and selection of genotypes resistant to this disease, as was shown with studies in Brazil where different *Eucalyptus* species exhibited varying susceptibilities to *A. psidii* (Dianese et al. 1984; de Carvalho et al. 1998; Tommerup et al. 2003; Alves et al. 2012; Morin et al. 2012). Likewise, different levels of susceptibility also exist within *Eucalyptus grandis* (Silva et al. 2013), *E. pellita* (Santos et al. 2014), and *E. globulus* (Xavier et al. 2007). These differences provide excellent opportunities to select resistant genotypes to minimize the impact of myrtle rust, especially those within the same biotype. Another strategy used in Brazil, particularly to produce clones with high wood quality, is the application of fungicides (Furtado et al. 2020).

2.2. Eucalypt scab and shoot malformation

Species of *Elsinoe* (Elsinoaceae, Myriangiales) are known to cause scab disease on various economically important hosts, including *Persea americana* (Everett et al. 2011), *Manihot esculenta* (Reeder et al. 2009), *Citrus australasica* and *Simmondsia chinensis* (Miles et al. 2015), *Eucalyptus* (Cheewangkoon et al. 2009), legumes (Mchau et al. 1998), *Mangifera indica* (Condé et al. 1997), and *Proteaceae* (Swart et al. 2001). Several *Elsinoe* spp. also infect *Eucalyptus* spp., including *Elsinoe eucalypti* (Dick 1990; Park et al. 2000), *Elsinoe eucalypticola* and *Elsinoe tectificae* (Cheewangkoon et al. 2009), *Elsinoe eucalyptorum* (Summerell et al. 2006), *Elsinoe eucalyptigena* and *Elsinoe preissianae* (Crous et al. 2016a; Fan et al. 2017). Most recently *Elsinoe necatrix*, a newly described and serious leaf and shoot pathogen, has been reported in *Eucalyptus* plantations, mainly on hybrids of *E. grandis*, *E. urophylla* and *E. pellita,* in North Sumatra, Indonesia (Pham et al. 2021). Currently, only *E.*

necatrix has been found on *Eucalyptus* in the SE Asian region, particularly Indonesia, while other *Elsinoe* spp. have been reported from Australia and New Zealand on this host (Dick 1990; Cheewangkoon et al. 2009; Crous et al. 2016a). Until very recently *E. nectrix* was the only species known to cause serious damage to *Euclayptus* in plantations. A recent report of a closely related species described as *Elsinoe masingae* (Roux et al. 2023) in South Africa has added a second *Elsinoe* sp. that is causing serious damage to plantation-grown *Eucalyptus*.

The disease caused by *E. necatrix* is characterized by black necrotic spots that develop into scab-like lesions over time (Pham et al. 2021). Infections begin on shoots, young leaves, and petioles. Severely infected trees produce multiple shoots with small leaves that appear as feathering leaves (Pham et al. 2021). Tree mortality is rarely observed, but affected trees experience severe growth retardation. In cases where the disease is widespread within and between *Eucalyptus* compartments, where trees are girdled and wrinkled and infected tissues do not recover, the affected compartments must be replanted (Pham et al. 2021). As clones showing tolerance to the pathogen have been identified (Pham et al. 2021), the disease could be managed through breeding and selection of tolerant planting material (Wingfield 2003; van Heerden et al. 2005).

2.3. Leaf and shoot blight

2.3.1. Passalora leaf and shoot blight on *Acacia*

Severe foliar and shoot blight caused by *Passalora perplexa* (Ascomycota: Capnodiales, Mycosphaerellaceae), previously known only as a *Pseudocercospora* species affects *Acacia crassicarpa* plantations (Cannon et al. 1997; Beilharz et al. 2004; Wingfield et al. 2011). The pathogen infects phyllodes, petioles and young shoots (Figure 1.1B). Small, elliptical lesions develop initially on phyllodes and increase in size over time. As the disease progresses, the phyllodes of affected trees begin to curl and leaf malformation occurs when the lesions start from the edges of the phyllodes (Beilharz et al. 2004; Wingfield et al. 2011). As more shoots become infected, apical growth is affected, resulting in new sprouts which affects the growth and shape of the tree (Gafur et al. 2006). The disease can severely affect young trees, but is less severe in trees older than 12 months (Gafur et al. 2006).

In SEA, *Passalora perplexa* is a pathogen of *A. crassicarpa* plantations only in Indonesia (Beilharz et al. 2004). The pathogen has also been reported from plantations and native stands of *A. crassicarpa* in northern Australia. It has therefore been suggested that the fungus is likely

native to Australia. If so, it would most likely have been introduced to Indonesia by seed (Old et al. 1997).

Passalora perplexa has only ever been found on *A. crassicarpa*. This is despite the fact that *A. mangium, A. auriculiformis* and *A. aulococarpa* occur in the same areas as *A. crassicarpa* in Indonesia (Beilharz et al. 2004). This suggests that the fungus is highly host specific, making it very unlikely to infect other *Acacia* spp. In the field, individual *A. crassicarpa* trees show resistance to the disease (Beilharz et al. 2004). Through selection, it has been shown that some *A. crassicarpa* trees have a genetic resistance to Passalora leaf and shoot blight disease (Golani 2006).

2.3.2. Teratosphaeria leaf blight on *Eucalyptus*

Teratosphaeria (Teratosphaeriaceae, Capnodiales) is a genus that causes stem canker and leaf diseases in *Eucalyptus* spp. plantations. Species associated with leaf and shoot blights of *Eucalyptus* that cause severe defoliation known as Teratosphaeria leaf blight (TLB) include *Teratosphaeria nubilosa* and *Teratosphaeria cryptica* in the temperate climatic zones (Mohammed et al. 2003; Hunter et al. 2009; Burgess & Wingfield 2017), and *Teratosphaeria destructans*, *Teratosphaeria eucalypti*, *Teratosphaeria novaehollandiae*, *Teratosphaeria pseudoeucalypti*, *Teratosphaeria viscida* and *Teratosphaeria tiwiana* in tropical and sub-tropical plantations (Burgess & Wingfield 2017; Andjic et al. 2019). *Teratosphaeria epicoccoides* is not an aggressive pathogen causing only minor damage, and is commonly found on older *Eucalyptus* foliage (Crous et al. 1988; Nichol et al. 1992; Andjic et al. 2019; Park et al. 2000). At present, only *T. destructans* and *T. epicoccoides* are known to be present on *Eucalyptus* in SEA.

Teratosphaeria destructans (Figure 1.1E) is one of the most aggressive species causing TLB (Andjic et al. 2019). It was first reported from *Eucalyptus grandis* plantations in North Sumatra, Indonesia (Wingfield et al. 1996a). Since then, the pathogen has been reported on *Eucalyptus* in tropical and subtropical areas of SEA including Thailand, East Timor and Vietnam (Old et al. 2003), and Lao (Barber et al. 2012), and most recently in Sabah, Malaysia (Havenga et al. 2021). The pathogen was found for the first time outside SEA in *Eucalyptus* plantations in China (Burgess et al. 2006a) and on *Eucalyptus grandis* × *E. urophylla* hybrids in South Africa (Greyling et al. 2016). The low population genotypic diversity of the isolates from all these affected countries (Havenga et al. 2020; 2021) suggests that the pathogen has been accidentally

introduced. While the origin of *T. destructans* is not known, there has been speculation that this could be the island of East Timor where *E. urophylla* is native (Andjic et al. 2019).

Currently, the management strategies to control *T. destructans* are based on selection of resistant planting stock emerging from field based observations. Furthermore, efforts are made to avoiding planting trees in unfavourable sites, and minimizing the effects of stress that tends to exacerbate damage due to this disease. Recently a method to categorize host resistance by using artificial inoculations was established that should allow shorter time periods to select individuals for breeding programs (Solis et al. 2022a). Understanding the conditions necessary for spore germination and infection by this pathogen described, including the microscopic and histological observations of the infection process on *Eucalyptus,* will contribute to developing reliable inoculation protocols (Solis et al. 2022a).

2.3.3. Quambalaria leaf and shoot blight on *Eucalyptus*

The genus *Quambalaria* (Quambalariaceae, Microstromatales) includes several species such as *Quambalaria eucalypti* (Simpson 2000; Wingfield et al. 2018), *Quambalaria pitereka* (Simpson 2000), *Quambalaria simpsonii* (Cheewangkoon et al. 2009), *Quambalaria tasmaniae* and *Quambalaria rugosae* (Crous et al. 2019), *Quambalaria coyrecup* (Paap et al. 2008) and *Quambalaria cyanescens* (de Beer et al. 2006). Most of these species are leaf and shoot pathogens of Myrtaceae (De Beer et al. 2006; Pegg et al. 2009), with the exception of *Q. coyrecup,* which is a canker pathogen of *Corymbia calophylla,* and *Q. cyanescens,* an opportunistic pathogen isolated from human skin (Paap et al. 2008; Kuan et al. 2015).

Several *Quambalaria* spp. infect *Eucalyptus,* including *Q. eucalypti*, *Q. simpsonii* (synonym *Quambalaria pusilla*), *Q. rugosae* and *Q. tasmaniae* (Wingfield et al. 1993; Braun 1998; Crous et al. 2019), but *Q. eucalypti* is the most important species causing leaf and shoot blight (Wingfield et al. 2018; Crous et al. 2019). Affected leaves and shoots show symptoms characterised by the appearance of powdery white fungal spore masses (Figure 1.1E). Infected actively growing shoots may die (Wingfield et al. 1993a; Simpson 2000; Roux et al. 2006; Zhou et al. 2007).

Quambalaria eucalypti has a relatively wide global distribution on *Eucalyptus*. It was first described on *Eucalyptus grandis* in South Africa (Wingfield et al. 1993a) and the pathogen was subsequently reported from Brazil (Alfenas et al. 2001), Uruguay (Bettucci et al. 1999), Australia (Pegg et al. 2008), Portugal (Bragança et al. 2016) and China (Chen et al. 2017), and

more recently in Indonesia (Chapter 4, this thesis). In general, *Q. eucalypti* infections affect *Eucalyptus* in nurseries, but the pathogen has also been found to infect established trees in plantations (Alfenas et al. 2004; Roux et al. 2006; Pegg et al. 2008; Chen et al. 2017; Santos et al. 2020).

In the context of SEA, only *Quambalaria simpsonii* in Thailand (Braun 1998) and *Q. eucalypti* in Indonesia (Chapter 4, this thesis) have been found to infect *Eucalyptus*. Given the tendency of *Quambalaria* to spread rapidly, especially *Q. eucalypti* which has already spread widely across many continents (Wingfield et al. 1993; Bettucci et al. 1999; Alfenas et al. 2001; Pegg et al. 2008; Bragança et al. 2016; Chen et al. 2017), it is expected that this pathogen will also spread to susceptible *Eucalyptus* planted in other SE Asian regions (Chen et al. 2017). In addition to wind, rain splash and some insects facilitate the spread of *Quambalaria* (Williams 2013). *Quambalaria* has the potential to cause epidemics where conditions favour the disease, such as in monoculture plantations, especially where seed from single and susceptible provenances is used (McTaggart et al. 2022).

Control of *Quambalaria* infections can be achieved by selecting resistant *Eucalyptus* species and clones. Especially in nurseries, application of fungicides can also be effective. Variation in susceptibility to *Q. eucalypti* has been observed in *Eucalyptus smithii*, *Eucalyptus globulus* x *Eucalyptus urophylla* clones and *Eucalyptus dunni* (Roux et al. 2006) as well as in *Eucalyptus pellita* and *Eucalyptus grandis* x *E. pellita* clones (Chapter 4, this thesis), suggesting the possibility of resistance through breeding and selection. Some fungicides with the active ingredients such as azoxystrobin, epoxiconazole, epoxiconazole+pyraclostrobin, pyraclostrobin and tebuconazole are most effective against *Q. eucalypti* in clonal mini-hedge nurseries (Ferreira et al. 2008).

2.3.4. Pseudoplagiostoma leaf and shoot blight on *Eucalyptus*

Pseudoplagiostoma leaf blight on *Eucalyptus,* caused by *Pseudoplagiostoma* spp. (Dermateaceae, Helotiales), previously known as *Cryptosporiopsis,* is a common disease on *Eucalyptus* leaves in plantations in tropical and temperate regions (Cheewangkoon et al. 2010). Several species have been identified in SEA, including *Pseudoplagiostoma eucalypti*, *Pseudoplagiostoma oldie* and *Pseudoplagiostoma variable* (Crous et al. 2019). *Pseudoplagiostoma eucalypti* is considered the most common pathogen and has been reported on most continents. In Asia it was reported in India (Sankaran et al. 1995), Indonesia, Japan,

Laos, Sri Lanka (Old et al. 2003), Malaysia (Zaiton et al. 2020), Thailand and Vietnam (Old & Yuan 1994). In North America it is only reported from Hawaii (Sankaran et al. 1995), in Oceania it is present in Australia (Sankaran et al. 1995) and New Zealand (Gadgil & Dick 1999), and in South America in Brazil (Ferreira et al. 1998; Zauza et al. 2023) and Venezuela (Crous et al. 2019).

Disease caused by *P. eucalypti* affects both the leaves and shoots of *Eucalyptus*, with infected leaves showing spots on both sides of the leaf, varying in size, shape and colour. *Pseudoplagiostoma eucalypti* is considered to be one of the most damaging foliar pathogens (Old & Mohammed 2003), which can also cause cankers on woody tissues, defoliation, and even tree death (Cheewangkoon et al. 2010). This is often considered a primary pathogen, but it can also be found together with other pathogens such as *Calonectria* spp. and *Pseudocercospora* spp. probably causing secondary infections. Zauza et al. (2023) reported an outbreak of shoot blight and dieback of *Eucalyptus* spp., caused by *P. eucalypti* in Brazil recently, which caused leaf spot, branch cankers, shoot blight, defoliation, and dieback of *Eucalyptus* spp. Further research is needed to understand the role of *P. eucalypti* as a pathogen (Crous et al. 2019) and there is a need to develop a management program, which could include *Eucalyptus* clone resistance screening that has been developed for this pathogen (Singchada et al. 2006).

2.3.5. Calonectria leaf blight on *Acacia* and *Eucalyptus*

Calonectria (Nectriaceae, Hypocreales) is a genus of fungi that infect many important forest plantation tree species including *Acacia* and *Eucalyptus* (Peerally 1974a; Peerally 1974b; Lombard et al. 2015; Li et al. 2017) and causes leaf blight disease (Figure 1.1D) known as Calonectria leaf blight (CLB). The disease is especially well-known on *Eucalyptus* spp. (Marin-Felix et al. 2017; Crous et al. 2019; Liu et al. 2020) but has not been particularly common on *Acacia* spp. These pathogens are common in both nurseries and plantations (Crous et al. 1998; Chen et al. 2011a; Lombard et al. 2015; Li et al. 2017; Pham et al. 2019; Pham et al. 2022). In plantations they are known to cause leaf and shoot blight where in nurseries they also cause root disease and cutting rot (Peerally 1974b; Bertus 1976; Lombard et al. 2010b; Aiello et al. 2020).

Some *Calonectria* species occur on both *Acacia* and *Eucalyptus* spp. such as *Calonectria indusiate*, *Calonecria multiseptata*, *Calonectria pauciramosa* and *Calonectria retaudii*

(Peerally 1974b; Mohanan & Sharma 1988; Polizzi & Catara 2001; Old et al. 2003; Pham et al. 2019; Pham et al. 2022; Tarigan et al. 2023). Only a few species have been recorded solely on *Acacia* with many more recorded on *Eucalyptus*. Those species infecting *Acacia* include *Calonectria brasilensis* (previously known as *Cylindrocladium scoparium*) in Australia, South Africa and India; *Calonectria ilicicola* (=*Calonectria crotalariae*) in India; *Calonectria indusiate* (=*Calonectria theae*) in Sri Lanka and the USA; *Calonectria multiseptata* in Indonesia; *Calonectria pauciramosa* in Italy; and *Calonectria reteaudii* in India and Indonesia (Hageman & Rose 1988; Peerally 1974b; Mohanan & Sharma 1988; Abraham et al. 1996; Polizzi & Catara 2001; Tarigan et al. 2023). Based on the above list, those *Calonectria* reported on *Acacia* spp. in SEA are *C. multiseptata* and *C. reteaudii* in Indonesia.

Several *Calonectria* species have been reported affecting *Eucalyptus* spp. in SEA, including *Calonectria acicola*, *Calonectria eucalypti*, *Calonectria hawksworthii*, *Calonectria lombardiana*, *Calonectria multiseptata*, *Calonectria pseudoretaudii*, and *Calonectria retaudii* (Crous et al. 2006a; Lombard et al. 2010a; Pham et al. 2019; Pham et al. 2022; Tarigan et al. 2023). All of these *Calonectria* spp. are present in Indonesia. Whereas *C. eucalypti* and *C. hawksworthii*, have been reported earlier by Lombard et al. (2010a), the remaining species were only recently discovered in Indonesia (Tarigan et al. 2023; Chapter 2, this thesis). *Calonectria acicola* was previously known only from *Pinus radiata* in New Zealand (Gadgil & Dick 2004) but has recently been found as a pathogen of *Eucalyptus urophylla* in Indonesia (Tarigan et al. 2023; Chapter 2, this thesis). *Calonectria reteaudii* is the only species occurring throughout the SE Asian region, and it has also been reported in Indonesia (Tarigan et al. 2023; Chapter 2, this thesis), Laos, Malaysia, Thailand, and Vietnam (Old et al. 2003; Crous et al. 2006a; Pham et al. 2019; Pham et al. 2022).

Some control measures to manage *Calonectria* leaf and shoot blight include santitation, sterilisation of potting medium, biological control, host resistance and chemical control; all of which should be integrated into nursery management practices (Klinsukon et al. 2021). As these fungi are mainly soil-borne pathogens (Crous 2002; Li et al. 2017; Lopes et al. 2018; Pham et al. 2019), sanitization of the media used in nurseries is the recommended practice (Stapleton & DeVay 1986; Chauhan & Dhruj 2016). Biocontrol agents such as endophytic and free-living *Bacillus* spp., *Trichoderma harzianum*, *Streptomyces* sp. and arbuscular mycorrhizae can reduce the incidence of *Calonectria* infections and enhance plant growth and biomass (Himaman et al. 2016; Paz et al. 2018; Klinsukon et al. 2021). Testing *Eucalyptus* genotypes

for resistance to infection by *Calonectria* spp. have shown differential susceptibility among and within *Eucalyptus* spp. (Alfenas et al. 2016; Wu & Chen 2021; Tarigan et al. 2023; Chapter 2, this thesis). Fungicides that include carbendazim as an active ingredient, showed good efficacy in reducing *Calonectria* incidence in nurseries (Sharma and Mohanan 1991; Ferriera 1994).

2.4. Leaf spots

2.4.1. Pseudocercospora leaf spot on *Eucalyptus*

The genus *Pseudocercospora* (Mycosphaerellaceae, Capnodiales) causes leaf spot symptoms mainly on mature *Eucalyptus* foliage and is, therefore, considered to be of minor importance. However, some species of *Pseudocercospora*, such as *Pseudocercospora eucalyptorum*, can cause conspicuous leaf spot symptoms. In addition, this pathogen causes stem infections on *Eucalyptus* in Italy, but does not infect young seedlings in the nursery (Magnani 1965).

There are 26 *Pseudocercospora* spp. that have been described from *Eucalyptus* spp. and they have been found in South Africa (Crous et al. 1989; Crous 1998; Crous & Wingfield 1996; Hunter et al. 2004; Crous et al. 2013), Madagascar (Crous et al. 2009b), Asia including India, Indonesia, China, Malaysia, Thailand (Crous & Alfenas 1995; Crous 1998; Singh & Bhalla 2000; Cheewangkoon et al. 2008; Hunter et al. 2006; Crous et al. 2013), Dominican Republic (Crous 1998), Italy (Crous et al. 2007), Australia (Crous et al. 2009b; Yuan et al. 2000), New Zealand (Yuan et al. 2000; Braun & Dick 2002), and South America including Paraguay, Peru, Colombia, Cuba and Chile (Crous 1998; Crous et al. 2003).

Several species of *Pseudocercospora* have been reported from SEA, including *Pseudocercopsora gracilis* on *Eucalyptus urophylla* in Indonesia (Crous & Alfenas 1995), *Pseudocercospora basiramifera*, *Pseudocercospora chiangmaiensis*, *Pseudocercospora flavomarginata* in Thailand on *Eucalyptus pellita* and *Eucalyptus camaldulensis* (Crous 1998; Hunter et al. 2006; Cheewangkoon et al. 2008), *Pseudocercospora deglupta* and *Pseudocercospora robusta* in Malaysia on *Eucalyptus deglupta* and *Eucalyptus robusta* respectively (Crous 1998). *Pseudocercospora eucalyptorum* has also been reported to be widespread in SEA (Dell et al. 2012). Records for the region include Malaysia, Thailand and Vietnam. *Pseudocercospora eucalyptorum* is one of the most common causes of leaf spots in the lower crowns of *Eucalyptus camaldulensis* in Thailand and Vietnam (Old et al. 2002). Most of these are likely minor pathogens but very little is known regarding their relative importance.

Pseudocercospora eucalyptorum produces abundant angular spots on infected leaves. The central parts of these lesions are covered with dense clusters of conidiophores bearing needle-like, septate conidia. At present, no control measures are warranted for this or other species of *Pseudocercospora* other than the elimination of any selections showing unusual susceptibility from provenance or clonal trials.

2.4.2. Pestalotiopsis leaf spot on *Acacia* and *Eucalyptus*

Pestalotiopsis (Sporocadaceae, Xylariales) is a genus of fungi that infect many tree species including *Acacia* and *Eucalyptus* as forest plantation tree species (Old et al. 2000; Crous et al. 2019). *Pestalotiopsis* species are widely distributed throughout tropical and temperate regions (Bate-Smith & Metcalfe 1957), including Asia (Thailand, Malaysia, Vietnam, India), Europe, Australia, New Zealand, South Africa, Brazil and Colombia (Yuan, 1996; Old et al. 2000; Carvalho et al. 2019; Crous et al. 2019; Mohanan & Yesodharan 2005; Suwannarach et al. 2012; Morales-Rodríguez et al. 2019).

Pestalotiopsis spp. are generally regarded as endophytic fungi of minor importance, although they can be associated with severe infections in nurseries causing leaf spots and shoot blight as well as severe chlorosis (Suwannarach et al. 2012). In this case, initial symptoms are brown, oval or irregular-shaped lesions on the leaf margin or leaf tips. Lesions can enlarge and coalesce forming large necrotic areas resulting in the diseased leaves becoming blighted and desiccated. These leaf spot diseases can lead to defoliation when severe infection occurs (Sharma & Florence 1997; Suwannarach et al. 2012).

There are only a few records of *Pestalotiopsis* spp. from *Acacia* spp. and these include *Pestalotiopsis acacia* and *Pestalotiopsis neglecta*. Pestalotiopsis leaf spot has been identified from *Acacia* plantations in Indonesia including Kalimantan and Sumatra, Malaysia, and Vietnam (Old et al. 2000; Thu et al. 2010). The occurrence of *Pestalotiopsis* was also reported from *Acacia crassicarpa* seedlings raised in a nursery in Sumatra (Tjahjono 2006), however, in Indonesia and Vietnam they are not considered important (Thu et al. 2010).

Several *Pestalotiopsis* spp. have been recorded on *Eucalyptus* spp. These include *Pestalotiopsis biciliata* (Morales-Rodríguez et al. 2019), *Pestalotiopsis colombiensis* (Maharachchikumbura et al. 2014), *Pestalotiopsis disseminate* (Crous et al. 1989; Crous et al. 2006c), *Pestalotiopsis grandis-urophylla* (Carvalho et al. 2019), *Pestalotiopsis guepinii*, *Pestalotiopsis macrospora*, *Pestalotiopsis maculans*, *Pestalotiopsis mangiferae*, *Pestalotiopsis metasequoiae*,

Pestalotiopsis palustris, *Pestalotiopsis tecomicola*, *Pestalotiopsis uvicola* and *Pestalotiopsis versicolor* (Mohanan & Yesodharan 2005), *Pestalotiopsis neglecta* (Yuan 1996) and *Pestalotiopsis virgatula* (Suwannarach et al. 2012). These fungi are commonly isolated as saprophytes from *Eucalyptus* leaves damaged by other agents, such as herbicide, drought, insects or other fungi (Crous et al. 2019).

Pestalotiopsis spp. are considered minor pathogens, and are successful saprophytes on dead plant tissue. They only appear when trees are stressed and leaves senesce, and are often endophytic in healthy leaf tissue (Watanabe et al. 2010; Maharachchikumbura et al. 2012; Debbab et al. 2013). Apart from good nursery practice, and the avoidance of seedling stress in the nursery and when transporting seedlings or plants derived from cuttings to the field for out planting, no control measures are warranted.

2.4.3. Phyllosticta leaf spots on *Acacia* and *Eucalyptus*

Phyllosticta (Ascomycota: Botryosphaeriales, Botryosphaeriaceae) is a species-rich genus of which many taxa require phylogenetic and taxonomic resolution. *Phyllosticta* spp. are mostly plant pathogens that cause leaf spots and have a wide range of hosts, including *Acacia* spp. and *Eucalyptus* spp. (Old et al. 2000; Crous et al. 2019). Symptoms associated with *Phyllosticta* include a range of fungal spots and tip necrosis. In some cases, a significant proportion of the canopy may be infected, especially the lowermost leaves, but the effects on growth are generally uncertain (Old et al. 2000; Crous et al. 2019).

Several species of *Phyllostica* have been reported from *Eucalyptus,* including *Phyllosticta eucalyptorum* on *Eucalyptus grandis* in Brazil (Crous et al. 1993c), *Phyllosticta eucalyptina* on *Eucalyptus globulus* in Tunisia and Spain, *Phyllosticta eucalypti* on *E. globulus* in Portugal and *Phyllosticta extensa* on *Eucalyptus* sp. in California (van der Aa & Vanev 2002). *Phyllosticta eucalyptorum* was reduced to synonymy with *Phyllosticta capitalensis* (Wikee et al. 2013), which is regarded as a common endophyte, although it is associated with leaf spots on older leaves of different host genera under favourable conditions. There are no records of serious disease symptoms associated with *Phyllosticta* spp. on *Eucalyptus*.

There is currently very little information available on *Phyllosticta* infections on *Acacia* spp. A species was reported on *A. mangium* collected from recently out-planted trees in South Sumatra, Indonesia, and on young *A. aulococarpa* trees in a nursery in Queensland, Australia, following a 1996 survey (Old et al. 1997). This was considered as the first record of the

pathogen on *Acacia* spp. in plantations in Indonesia, although it was noted that the pathogen was already present in the country as it had previously been detected on *A. aulococarpa* herbarium material collected in Indonesia (Cannon et al. 1997). Other reports on *Acacia* spp. include *Acacia crassicarpa* in Thailand (Wikee et al. 2013) caused by *Phyllosticta capitalensis* and *Acacia suaveolens* in Australia caused by *Phyllosticta acaciigena* (Norphanphoun et al. 2020). As there are only a few studies on *Pyllosticta* infections and their damage in SE Asian countries, it appears to be minor pathogen that does not warrant control measures.

2.4.4. Coniella leaf spot on *Acacia* and *Eucalyptus*

The genus *Coniella* (Schizoparmeaceae, Diaporthales) includes several species that cause leaf disease on *Acacia* spp. and *Eucalyptus* spp. (Sutton 1980; van der Walt 2007; Alvarez et al. 2016; Crous et al. 2019). Species of *Coniella* are commonly isolated as endophytes on a wide range of plants. However, they have also been reported as foliar pathogens of *Eucalyptus* including species such as *Coniella eucalyptorum* and *Coniella wangiensis*, which are associated with a range of leaf disease symptoms (Crous et al. 2019).

There are few reports on the incidence of *Coniella* spp. on *Acacia* spp. Only a few species have been reported, including a *Coniella* sp. on *Acacia mellifera* in South Africa (van der Walt 2007) and *Coniella musaiaensis* on *Acacia arabica* in Pakistan (Sutton 1980). *Coniella* spp. were also isolated together with *Calonectria* spp. and *Pestalotiopsis* spp. from *Acacia mearnsii* in a nursery in the state of Rio Grande do Sul, Brazil (Duin et al. 2015).

There are records of *Eucalyptus* spp. being infected by several species of *Coniella.* Three species reported from India including *Coniella eucalypticola* on *Eucalyptus* spp. (Raj 1976), *Coniella minima* on *Eucalyptus citriodora* and *Coniella fragariae* on *Eucalyptus grandis* (Mohanan & Yesodharan 2005). Three species reported from Australia include *Coniella eucalyptorum* on *E. grandis* × *Eucalyptus tereticornis* hybrid, and *Coniella paracastaneicola* and *Coniella wangiensis* on *Eucalyptus* spp. (Alvarez et al. 2016). Other reports include *Coniella africana* on *Eucalyptus nitens* in South Africa (Alvarez et al. 2016), and *Coniella destruens* on *E. grandis* in the USA (Samuel et al. 1993; van Niekerk et al. 2004). Only *Coniella eucalyptorum* has been reported to cause significant disease on *Eucalyptus dunnii* plantations in sub-tropical Australia following periods of high rainfall (Carnegie 2007).

Several species of *Coniella* have been recorded infecting *Eucalyptus* spp. in SEA. *Coniella eucalyptigena* on *E. brassiana* was reported from Malaysia (Crous et al. 2015b; Alvarez et al.

2016). *Coniella fusiformis* on *Eucalyptus* spp. was reported from Indonesia (Alvarez et al. 2016). *Coniella minima* was reported from *E. camaldulensis* in Myanmar (Sutton 1975), *Eucalyptus* spp. in Indonesia (Old et al. 2002), *E. camaldulensis* and *E. urophylla* in Thailand (Pongpanich 1998; Sangwanit 2012), and *E. pellita* in Vietnam (Thu et al. 2010).

Infection by *Coniella* spp. results in leaf spots on both leaf surfaces that are prominent, medium to light brown, with or without significant margins, ranging from small patches with irregularly arranged conidiomata to large conspicuous patches with concentric circles of conidiomata (Crous et al. 2019). The spots appear during the rainy season. The spots are initially greyish-black in the centre, gradually becoming lighter towards the periphery. During the dry season, the spots become light to light brown, and leaves with large areas covered by the spots wilt and drop. In severe cases, the disease can cause extensive premature defoliation of the lower branches. However, there are no data available on the impact of disease caused by *Conniela* spp. It has, however, been observed that the incidence of this disease varies from clone to clone, raising the possibility of selecting planting stock tolerant to this disease (Mohan & Manokaran 2013).

2.4.5. Colletotrichum leaf spot on *Acacia* and *Eucalyptus*

The genus *Colletotrichum* (Glomerellaceae, Glomerellales) is one of the most common fungi found on plants, both those cultivated and in the wild. These fungi are well-known to cause dieback, leaf spots, seedling blight and leaf blight in several hosts, including on tropical *Acacia* and *Eucalyptus* (Mordue 1971; Crous et al. 2019). Disease caused by *Colletotrichum* spp. is generally referred to as anthracnose.

Disease caused by *Colletotrichum gloeosporioides* on *Acacia* spp. has been reported from India (Sharma & Florence 1997). Additionally on *Acacia aulacocarpa, Acacia crassicarpa,* and *Acacia auriculiformis* in Thailand (Pongpanich 1997) and in Florida (Barnard & Schroeder 1984) have been reported. Colletotrichum leaf spot has also been reported on *Acacia auriculiformis* in nurseries and plantations in Vietnam (Sharma 1994).

Several species of *Colletotrichum* have been reported on *Eucalyptus* spp. *Colletotrichum gloeosporioides* (likely a group of cryptic species) associated with leaf spots, twig dieback or lesions on bark and wood, is reported from Australia, Bangladesh, Brazil, Myanmar, South Africa and the USA (Farr & Rossman 2017). *Colletotrichum indonesiense* was isolated from leaf spots developing after herbicide treatment in Indonesia (Damm et al. 2012a).

Colletotrichum karstii has been reported from *Eucalyptus grandis* in South Africa (Damm et al. 2012), and *Colletotrichum theobromicola,* that causes leaf spot and stem girdling, has been found in nurseries of *Eucalyptus urophylla* × *Eucalyptus grandis* hybrid in Brazil (Rodrigues et al. 2014), and in South Africa (Solis et al. 2022b).

The symptoms of anthracnose include limited, often sunken, necrotic lesions on leaves, stems, flowers or fruits, as well as crown and stem rot and seedling blight (Waller et al. 2002; Crous et al. 2019). There have been few studies on *Colletotrichum* infections and their damage, particularly on *Acacia* spp. Various symptoms, including tip necrosis and leaf spots, are produced by *Colletotrichum* sp. on different *Acacia* spp. On *A. mangium* and *Acacia auriculiformis*, antrachnose is first seen as circular to oval reddish-brown spots of variable size with raised margins that coalesce to form larger spots. In severe cases, the phyllodes dry out and crack. This leads to premature defoliation. On *Acacia aulacocarpa*, spots are black, circular to oval, scattered on the lamina regardless of veining. On *Acacia crassicarpa* the spots are dark brown with necrotic centres and darker edges. Given that infections are typically on scenescent plant tissues, and that no economic losses have been associated with these diseases, control measures have not been considered.

2.5. Mildew on *Acacia* and *Eucalyptus*

Both black mildew and powdery mildew, referred to below, are common diseases affecting many plant hosts, including *Acacia* spp. and *Eucalyptus* spp. Black mildew is commonly found in young plantations. Powdery mildew can be found on seedlings in most nurseries and is also occasionally found in humid conditions, on leaves of lower branches or coppice shoots under canopies of established plantations.

2.5.1. Black mildew

Black mildew, caused by *Meliola* spp. (Ascomycota: Melioles, Meliolaceae), is common on *Acacia* spp. and *Eucalyptus* spp. Species of *Meliola* are primarily tropical and are obligate parasites, producing a variety of structures that penetrate into the host cells. These fungi grow on the surfaces of leaves and stems and forms thick, black, radiating, velvety colonies (Old et al. 2000). Lower crown foliage is most commonly infected due to more humid conditions (Old et al. 2000).

Some species of *Meliola* have been reported on *Acacia* spp. such as *Meliola brisbanensis* on *Acacia aulococarpa, Acacia auriculiformis, Acacia dealbata* and *A. mangium* (Cannon et al. 1997; Old et al. 1997; Singh 1980) and *Meliola adenanphererae* on *A. auriculiformis* (Old et al. 2000) in Australia, Indonesia, Malaysia, Myanmar and Vietnam (Old et al. 1997; 2000; Thu et al. 2010). Several *Meliola* spp. have been recorded on leaves of *Eucalyptus* spp., including *Meliola amphitricha* in Queensland and Victoria, Australia (Cooke 1892), *Meliola densa* in Queensland (Simmonds 1966), Papua New Guinea (Shaw 1984) and in Melville Island, Northern Territory of Australia. *Meliola eucalypti* occurs in the Philippines on *Eucalyptus* sp. (Hansford 1962).

Meliola spp. commonly infect leaves, twigs and stems (Old et al. 2000). Black mildew caused by *Meliola* spp. is also common in young plantations, most commonly affecting the lower crown but having little or no effect on tree growth (Figure 1.1C), so the disease is considered to be of minor importance on older trees. If younger seedlings are severely infected, the phyllodes will yellow and abscise prematurely with repeated infection, leading to seedling stunting and growth retardation (De Guzman 1977; Nair & Sumardi 2000; Old et al. 2000). Currently, there is little need to control the disease as it has no serious impact on the host.

2.5.2. Powdery mildew

Powdery mildews that lack sexual states are ascribed to the genus *Oidium* (Ascomycota: Erysiphales, Erysiphaceae). These are obligate pathogens that cause disease on both *Acacia* spp. and *Eucalyptus* spp., as well as many other hosts (Nair & Sumardi 2000; Old et al. 2000; Thu et al. 2010). Powdery mildew mainly affects the lower crowns of young trees by covering the leaf surfaces with powdery white patches of hyphae and spores. Infection leads to yellow spots on the leaves and often results in defoliation. Trees and leaves growing in shade are more susceptible to the disease (Old et al. 2000).

Powdery mildew has been reported on *Acacia aulacocarpa, Acacia auriculiformis*, *Acacia crassicarpa, A. mangium* and other *Acacia* spp. grown in nurseries (Tanaka & Chalermpongse 1990; Boa & Lenné 1994; Cannon et al. 1997; Old et al. 1997) in Australia, parts of Africa, China, Hawaii, India, Indonesia, the Philippines, Malaysia, Myanmar and Thailand (Old et al. 2000). The disease is also common on *Eucalyptus* spp. including *Eucalyptus botryoides, Eucalyptus camaldulensis, Eucalyptus crenulata, Eucalyptus globulus, Eucalyptus gunnii, Eucalyptus muellerana, Eucalyptus perriniana, Eucalyptus tereticornis* and *Eucalyptus*

viminalis (Old et al. 2003) in Argentina, Australia, Brazil, Denmark, Germany, India, Italy, New Zealand, Poland, Portugal, South Africa, UK and USA (Sankaran et al. 1995). Reports from SEA are scarce, although Kobayashi (2001) reported that *Oidium* was common on*Eucalyptus* seedlings in nurseries in the region. There has also been a recent report of powdery mildew on *E. pellita* and *E. camaldulencis* caused by *Erysiphe elevate* in Indonesia and Thailand respectively (Oliveira et al. 2023a).

Powdery mildew is considered of minor importance on older trees (Nair & Sumardi 2000); however, under favorable conditions for the pathogen, severe powdery mildew infection can occur on seedlings in the nursery. Damage to young nursery seedlings can be severe, resulting in abnormal growth of the seedlings, and cases of up to 75% mortality have been reported in Thailand (Tanaka & Chalermpongse 1990). Various control measures have been used for nursery infections, such as prompt removal of infected plants to prevent spread of disease and destruction of fallen leaves to reduce inoculum potential, chemical treatments with sulphur dusting, application of fungicides such as benomyl, chlorothalonil, triademefon, maneb and zineb, including exposing diseased seedlings to direct sunlight for prolonged periods (Old et al. 2000). Increasing leaf wetness was also able to reduce the incidence of powdery mildew on eucalypt mother plants (Oliveira et al. 2023a).

2.6. Bacterial leaf blight on *Acacia* and *Eucalyptus*

Numerous species of bacteria are known to cause leaf blight and dieback symptoms on *Acacia* and *Eucalyptus*. These include *Xanthomonas campestris* on *Acacia crassicarpa* in Indonesia (Tjahjono et al. 2011), and those on *Eucalyptus* spp. include *X. axonopodis* pv. *eucalyptorum* in Brazil and Uruguay (Gonçalves et al. 2008; Ferraz et al. 2018), *Pantoea ananatis* and *Xanthomonas vasicola* in South Africa (Coutinho et al. 2002; Coutinho et al. 2015), *Erwinia psidii* in Brazil (Coutinho et al. 2011; Arriel et al. 2014), and *Xanthomonas perforans* on *Eucalyptus pellita* seedlings in Indonesia (Bophela et al. 2019).

Xanthomonas campestris leaf blight on *Acacia crassicarpa* is the most frequently observed bacterial blight disease in nurseries. It is considered an emerging disease in nurseries (Tjahjono et al. 2011). Initial symptoms of the disease appear as small red streaks on the tip, mid, or basal part of the phyllodes on 5–6-week-old seedlings and within 1-2 weeks the streaks increase in length and width along the veins and later turn brownish red and then develop into blight

(Tjahjono et al. 2011). Affected plants continue to recover after planting in the field. No symptoms have not been observed on other *Acacia* spp. (Tjahjono et al. 2011).

Bacterial blight caused by *Xanthomonas perforans* has become a significant problem on some *Eucalyptus* clones in nurseries and in young plantations in Indonesia and Lao (Dell et al. 2012; Bophella et al. 2019). Affected plants display tip dieback and leaf spots symptoms (Figure 1.1G), where the leaf spots initially have a water-soaked appearance and frequently combine to develop larger lesions (Bophella et al. 2019). The infection seems to move from the leaf petiole into the main leaf vein and then onto the surrounding tissue. As a result, lesions on the leaf frequently cluster along the primary veins. Necrosis of leaf petioles causes premature abscission of the leaves and thus may lead to stunted plants (Bophella et al. 2019).

There are significant differences in susceptibility to Xanthomonas leaf blight between *Acacia crassicarp*a grown from seedlings and cuttings, with cuttings being less susceptible (Tjahjono et al. 2011). Susceptibility to Xanthomonas leaf blight has also been observed between *Eucalyptus* clones. This provides an opportunity for the selection of resistant material through breeding programmes as one of the management strategies to reduce the impact of these diseases (Wingfield 2003; van Heerden et al. 2005).

2.7. Other leaf spots

There are many fungi that have been recorded associated with leaf diseases of *Acacia* spp. and *Eucalyptus* spp. In most cases, they are of minor importance and typically there are no data regarding their ability to cause disease. These are listed in Table 1. 1.

3. Stem diseases on *Acacia* and *Eucalyptus*

There are various diseases affecting the stems of *Acacia* and *Eucalyptus* trees in SE Asian plantations. These vary in importance and in some cases the causal agents are not well understood. They include typical cankers as well as canker wilt diseases such as those caused by species of *Ceratocystis*.

3.1. Pink disease on *Acacia* and *Eucalyptus*

Erythricium salmonicolor (Basidiomycota: Polyporales, Phanerochaetaceae), formerly treated as *Corticium salmonicolor*, is a basidiomycete fungus that infects stems and branches and causes cankers, commonly known as pink disease (Figure 1.2C). The pathogen infects a wide range of hosts including *Acacia* spp. and *Eucalyptus* spp. (Browne 1968; Sharma et al. 1984; Lee 2003). At present, the incidence of this disease on *Acacia* spp. and *Eucalyptus* spp. is rare. This is possibly because the most commonly planted *Acacia* spp. and *Eucalyptus* spp. are tolerant to infection. In addition, the implementation of silvicultural practices, such as tree spacing, also contributes to minimizing infections that are exacerbated by shade and moist conditions.

Pink disease has been common on *Acacia* spp. in Malaysia (Farid et al. 2018), Vietnam (Thu et al. 2010; Dell et al. 2012) and Indonesia (Hadi & Nuhamara 1997; Zulfiyah & Gales 1997), but has not been reported as a significant disease on plantation-grown *Acacia* spp. in Thailand, or Australia. Several *Acacia* spp. have been reported as hosts including *A. mangium, Acacia crassicarpa* and *Acacia aulococarpa* and *Acacia auriculiformis* (Hadi & Nuhamara 1997; Zulfiyah & Gales 1997), with *A. mangium* reportedly the most susceptible (Hadi & Nuhamara 1997).

Pink disease has been reported on *Eucalyptus* spp. in many countries, including India (Seth et al. 1978; Mohanan 1999; Sharma et al. 1999;), Bangladesh (Basak 1993), Costa Rica (de Segura 1970), Brazil (Ferreira & Alfenas 1977) and Vietnam (Sharma 1994), South Africa (Roux et al. 2002), Ethiopia (Gezahgne et al. 2003a). Hosts include *Eucalyptus camaldulensis*, *Eucalyptus grandis*, *Eucalyptus robusta* x *Eucalyptus tereticornis*, *Eucalyptus saligna*, *Eucalyptus diversicolor*, *E. tereticornis*, *Eucalyptus globulus*, *Eucalyptus citriodora* (de Segura 1970; Seth et al. 1978).

Erythricium salmonicolor is especially active in high-rainfall areas, infecting stems and branches causing branch and stem dieback due to the formation of girdling cankers (Hilton 1958). Infection of stems occurs through healthy bark tissue. In the field, the disease is manifested by stem breakage, often high in the canopy. Although infected branches often die, *Acacia* trees are rarely killed (Old et al. 2000), but at least 55% of *Eucalyptus tereticornis* trees have died in one incidence in India (Seth et al. 1978). High density plantations tend to have greater incidences of pink disease because the disease is most likely to develop in shady

conditions (Hadi & Nuhamara 1997; Zulfiyah & Gales 1997). This is linked to the fact that *E. salmonicolor* requires high relative humidity for germination (Seth et al. 1978; Schneider-Chrsitians et al. 1986). Greater levels of spacing, singling and pruning tend to reduce pink disease problems in plantations (Zulfiyah & Gales 1997). Susceptibility to pink disease in different *Acacia* families and among *Eucalptus* clones has been observed (Sharma et al. 1999; Old et al. 2000). Thus planting pink disease-tolerant trees can reduce the occurrence of pink disease in some situations (Lee 1993).

3.2. Stem canker on *Acacia* and *Eucalyptus*

Tree stem cankers are commonly associated with wounds on stems. These wounds can arise from damage due to wind, insect or animal feeding and silvicultural practices such as singling to reduce stem numbers, pruning and mechanical weeding using machetes (Old et al. 2000; Barry et al. 2004; Tarigan et al. 2011b). Trees subjected to environmental stress, such as inadequate soil fertility, extreme climates and improper silvicultural practices are reported to be more susceptible to stem canker diseases than healthy trees (Old et al. 2000). This is especially true in the case of cankers caused by opportunistic fungi in the Botryosphaeriaceae. Fungi in this group are known to be endophytes that are within healthy *Acacia* and *Eucalyptus* trees and to develop under stress conditions (Smith et al. 1996; Roux & Wingfield 1997; Mohali et al. 2007).

3.2.1. Chrysoporthe stem canker on *Eucalyptus*

The genus *Chrysoporthe* (Cryphonectriaceae, Diaporthales) includes numerous economically important pathogens that threaten commercially-grown *Eucalyptus* plantations in tropical and subtropical geographical climate zones (Alfenas et al. 1982; Wingfield 2003). These pathogens cause diseases collectively known as Cryphonectria stem canker and they can result in tree mortality (Wingfield 2003; Rodas et al. 2005; Gryzenhout et al. 2005; 2009). Cryphonectria stem canker can have a significant impact on infected trees including reduced growth rate (Camargo et al. 1991), reduced abilty to coppice (Hodges & Reis 1976; Sharma et al. 1985; Barnard et al. 1987), reduced wood yield (Ferrari et al. 1984), increased mortality (Boerboom & Maas 1970; Hodges et al. 1979) and they can influence plant extractives and lignin which can affect pulp quality (Foekkel et al. 1976; Foekkel et al. 1981).

Cryphonectria stem canker on *Eucalyptus* was initially attributed to the pathogen *Cryphonectria cubensis* (Hodges 1980). Numerous intensive taxonomic studies have been

conducted on this group of pathogens beginning in the mid 1980s and when DNA sequencing technologies became available to better understand species boundaries (Hodges 1980; Gryzenhout et al. 2004; van der Merwe et al. 2010). Currrently, most of the serious *Eucalyptus* pathogens reside in the genus *Chrysoporthe* although there are various others such as *Celoporthe* and *Myrtoporthe* that are also important (Gryzenhout et al. 2004; 2005; Rodas et al. 2005; Gryzenhout et al. 2006a; 2009; van der Merwe et al. 2010; Chen et al. 2011b; Rauf et al. 2020).

Chrysoporthe cubensis and *Chrysoporthe doradensis* were first reported from South and Central America (Hodges et al. 1976; 1979; Gryzenhout et al. 2005); *Chrysoporthe zambiensis* from Central Africa (Chungu et al. 2010); *Chrysoporthe austroafricana* from Southern Africa (Wingfield et al. 1989; Gryzenhout et al. 2004); and *Chrysoporthe deuterocubensis* is primarily found in SEA including Indonesia (Figure 1.2A), Thailand, Vietnam and Malaysia (van der Merwe et al. 2010, Rauf et al. 2020). It is also known that *C. deuterocubensis* was introduced into East Africa, including Kenya, Malawi, Mozambique (Nakabonge et al. 2006) and Republic of Congo (Roux et al. 2003) and Western Australia where it infects *Eucalyptus* (Davison & Coates 1991; van der Merwe et al. 2010). Cankers caused by *C. deuterocubensis* have also been reported in China (Zhou et al. 2008, Chen et al. 2010, Wang et al. 2020) and Hawaii (Hodges et al. 1979; Gryzenhout et al. 2009; Roux et al. 2020a).

In SE Asian countries, *C. deuterocubensis* is thought to be a native fungus having undergone a host shift, most likely from native species of *Melastomataceae* and *Myrtaceae* (Wingfield 2003; Gryzenhout et al. 2009). In Indonesia, *C. deuterocubensis* has been found on *Syzygium aromaticum* on the island of Sulawesi (Hodges et al. 1986; Myburg et al. 2003), on *Melastoma malabathricum* and *Eucalyptus* spp. in North Sumatra (Gryzenhout et al. 2006; van der Merwe et al. 2010), in Malaysia on *S. aromaticum* and *Eucalyptus grandis* (van der Merwe et al. 2010, Rauf et al. 2020), and in Thailand and Singapore on *S. aromaticum* and *Tibouchina urvilleana* (van der Merwe et al. 2010).

Some *Eucalyptus* spp. are highly susceptible to infection by *Chrysoporthe deutrocubensis*, such as *Eucalyptus grandis*, while *E. grandis* x *Eucalyptus urophylla* hybrids are relatively tolerant. Clonal propagation of resistant genotypes has provided effective control of Cryphonectria stem canker disease in Brazil and South Africa (van Zyl & Wingfield 1999; van Heerden & Wingfield 2002). Thus breeding and selection of resistant *Eucalyptus* hybrid clones is currently

the best option for the management of this disease (Old et al. 2003; Wingfield 2003; van Heerden et al. 2005; Gryzenhout et al. 2009).

3.2.2. Teratosphaeria stem canker on *Eucalyptus*

Teratosphaeria (Teratosphaeriaceae, Capnodiales), formerly known as *Coniothyrium,* is a stem canker pathogen of *Eucalyptus* spp. in many countries having subtropical and tropical climates (Gezahgne et al. 2005; Wingfield et al. 1997). The disease is caused by two closely related fungi, *Teratosphaeria zuluensis* and *Teratosphaeria gauchensis*. *Teratosphaeria zuluensis* was first described from South Africa (Wingfield et al. 1997) and is now known in various countries of Southern Africa, Asia, as well as Mexico (Roux et al. 2002b; Cortinas et al. 2006a; Aylward et al. 2019). *Teratosphaeria gauchensis* was first found and described from Uruguay and is also known to occur in Argentina and Portugal (Cortinas et al. 2006b; Crous et al. 2009a; Silva et al. 2015).

Teratosphaeria stem canker was first reported in 1988 on *Eucalyptus grandis* in KwaZulu-Natal in South Africa, identified as *Conithyrium zuluense* and the disease became known as *Conithyrium* canker (Wingfield et al. 1997). The disease was known only in South Africa until the early 2000s (van Zyl et al. 2002) whereafter it was found in plantations in several countries including China, Vietnam and Thailand in Asia (van Zyl et al. 2002; Gezahgne et al. 2003b; Cortinas et al. 2006a), Ethiopia, Zambia, Mozambique, Malawi and Uganda in Africa (Gezahgne et al. 2005; Roux et al. 2005; Muimba-Kankolongo et al. 2009; Jimu et al. 2014), Uruguay, Argentina and Paraguay in South American (Gezahgne et al. 2003a; Cortinas et al. 2006b; Silva et al. 2020) as well as Mexico and Hawaii (Roux et al. 2002b; Cortinas et al. 2004).

Infected trees show small necrotic lesions developing on young green stem tissue. These lesions coalesce to form large resin-exuding cankers. Epicormic shoots develop below the girdling cankers. Although trees die only in severe cases of the disease, the effects of Teratosphaeria canker can be devastating, including a reduction in the quality of the wood due to the staining of the wood with red gum exuding from the cankers and thus rendering it unusable for construction (Gezahgne et al. 2003b; Old et al. 2003), and a reduction in the value of other wood products. Pulping costs and quality are also adversely affected, as cankers impede debarking (Aylward et al. 2019). In highly susceptible clones, trees gradually stop

growing apically and eventually die due to stress and infection by secondary pathogens such as those in the Botryosphaeriaceae.

Considerable work has been done to reduce the impact of Teratosphaeria canker, particularly in South Africa (Cortinas et al. 2010). This has generally been achieved through the selection of disease-tolerant clones. Some *Eucalyptus* spp. are highly susceptible to infection by *Teratosphaeria zuluensis*, such as *Eucalyptus grandis*, while hybrids of *E. grandis* with *Eucalyptus camaldulensis* and *Eucalyptus urophylla* are relatively tolerant (Old et al. 2003). Studies in Uganda also confirm these findings (Syofuna et al. 2021). Thus, breeding and selection of resistant *Eucalyptus* hybrid clones currently offers many opportunities for managing Teratosphaeria canker (Old et al. 2003; Syofuna et al. 2021).

3.2.3. Ceratocystis wilt on *Acacia* and *Eucalyptus*

Ceratocystis (Microascales, Ceratocystidaceae) is a genus of fungus that causes a number of well-known tree diseases such as canker stain caused by *Ceratocystis platani* (Gibbs 1981; Panconesi 1999; Ocasio-Morales et al. 2007) and vascular wilt of many different genera of trees (Upadhyay 1981; Wingfield et al. 1993b). These fungi are also known to cause serious canker and wilt diseases on *Acacia* spp. and *Eucalyptus* spp. (Wingfield et al. 1996b; Ferreira et al. 1999; Roux et al. 2000a; Roux & Wingfield 2009; Tarigan et al. 2011a; Wingfield et al. 2023). Wounds are necessary for infection by *Ceratocystis* spp., and these can either be human-made or linked to feeding damage by animals such as monkeys, elephants and squirrels (Harrington 2007; Tarigan 2011b). Insects such as wood boring beetles can be important vectors and agents of damage and inoculum can be air-borne particularly via frass associated with these insects (Iton 1960; Upadhyay 1981; Hanssen 1993).

Two *Ceratocystis* species are important pathogens of *Acacia* spp. These are *Ceratocystis albifundus* and *Ceratocystis manginecans* (Wingfield et al. 1996b; Tarigan et al. 2011a). *Ceratocystis albifundus* was first found and described causing wilt on *Acacia mearnsii* in South Africa (Wingfield et al. 1996b). Since then, it has been found in Uganda (Roux et al. 2001a; Wingfield et al. 2001), Malawi and Zambia, Kenya and Tanzania (Roux et al. 2005). It can also infect *Acacia caffra*, *Acacia decurrens* and *Acacia nigra* (Roux et al. 2007; Roux & Wingfield 2009). In contrast, *Ceratocystis manginecans* was first isolated and described infecting *A. mangium* in Indonesia (Tarigan et al. 2011a), Malaysia (Brawner et al. 2015; Wingfield et al. 2023) and later in Vietnam (Thu et al. 2012). In addition to *A. mangium*, *C. manginecans* has

also been found infecting *Acacia auriculiformis*, *Acacia crassicarpa* and *A. mangium* x *A. auriculiformis* hybrids (Tarigan et al. 2011a; Thu et al. 2012; Brawner et al. 2015). *Ceratocystis manginecans* is considered to be the most aggressive pathogen affecting *A. mangium* in plantations (Tarigan et al. 2011a; Harwood & Nambiar 2014). Due to rapid tree mortality caused by the pathogen, affected areas have been replanted with more tolerant trees such as *Eucalyptus* spp., particularly in Sumatra and Sabah (Harwood & Nambiar 2014; Nambiar et al. 2018). Infected trees show wilting and canker symptoms (Figure 1.2D, 1.2E, 1.2F) and are commonly observed in young *A. mangium* plantations (Tarigan et al. 2011a). The cankers are discoloured with a black appearance due to gum exudation. The discoloured wood tissue has a streaked appearance that turns a uniform dark brown to dark blue colour with age (Tarigan et al. 2011a).

Ceratocystis wilt is considered as one of the most important diseases affecting *Eucalyptus* spp. in plantations (Alfenas et al. 2009; Mafia et al. 2013; Fernandes et al. 2014;). The disease was first reported in Brazil by Ferreira et al. (1999) and subsequently found in the Republic of Congo (Roux et al. 2000b), Uganda (Roux et al. 2001a), Uruguay (Barnes et al. 2003a), China (Li et al. 2014), Pakistan (Alam et al. 2017) and South Africa (Roux et al. 2020b). The disease causes wilting and death in susceptible trees, reduces volume growth and lower cellulose yields (Mafia et al. 2013).

The *Ceratocystis* spp. causing wilt on *Eucalyptus* was initially treated as *Ceratocystis fimbriata*, which was true for many diseases caused by these fungi prior to the application of DNA sequence-based phylogenetic inference to define species boundaries (Ferreira et al. 1999; Roux et al. 2000a; Barnes et al. 2003a; Li et al. 2014; Fourie et al. 2015; Alam et al. 2017). Currently, *Ceratocystis fimbriata* is a name restricted to the disease known as sweet potato black rot (Marincowitz et al. 2020), where isolates of the fungus represent a single clonal lineage (Li et al. 2016). Several other *Ceratocystis* spp. have been identified infecting *Eucalyptus* spp., including *Ceratocystis chinaeucensis* (Chen et al. 2013), *Ceratocystis eucalypticola* (van Wyk et al. 2012), *Ceratocystis fimbriatomima* (van Wyk et al. 2009), *Ceratocystis manginecans* (Chen et al. 2013), *Ceratocystis neglecta* (Rodas et al. 2008) and *Ceratocystis piriliformis* (Barnes et al. 2003b). Of these, *C. eucalypticola* appears to be responsible for serious tree death of specific *Eucalyptus* clones in South Africa (Roux et al. 2020b), and *C. manginecans* which has recently been reported as the cause of the disease in Vietnam and Indonesia (Oliviera et al. 2022; Trang et al. 2022).

Ceratocystis wilt caused by *Ceratocystis manginecans* is currently the most important disease associated with cankers affecting *Acacia* spp. and *Eucalyptus* spp. in SE Asian countries (Trang et al. 2022; Wingfield et al. 2023). The stems of the affected tree may become deformed, producing coppices and leading to tree death (Tarigan et al. 2018; Oliveira et al. 2022). The selection of disease resistant and tolerant host materials is currently considered the most effective and economic strategy for managing *Ceratocystis* diseases on trees such as *Acacia* spp. and *Eucalyptus* spp. (Kile 1993; Wingfield 2003; van Heerden et al. 2005).

Some tolerance among *A. mangium* populations to infection by *Ceratocystis manginecans* has been detected. For example, populations from Papua New Guinea have a consistently higher survival rate in plantations planted with this host, and shorter lesion lengths, than the populations from Queensland (Brawner et al. 2022). Among the *Acacia* spp., *Acacia auriculiformis* clones were relatively more tolerant to *Ceratocystis* than the *A. mangium* genotype (Trang et al. 2017; Barnes et al. 2023). These differences provide an opportunity to select resistant genotypes or provenances to reduce the impact of the disease.

Susceptibility to *Ceratocystis* spp. was also found to vary significantly between *Eucalyptus* clones (Zauza et al. 2004; Chi et al. 2023). Chi et al. (2023) reported that eighteen *Eucalyptus* genotypes tested against *C. manginecans* showed that three *Eucalyptus* hybrid clones and seven *Eucalyptus urophylla* clones were highly resistant, while the remaining eight clones showed low to moderate resistance. This suggests that there are opportunities to use *Eucalyptus* hybrids and *E. urophylla* clones that are resistant to *C. manginecans* to manage the disease (Chi et al. 2023).

3.2.4. Botryosphaeriaceae stem canker on *Acacia* and *Eucalyptus*

The Botryosphaeriaceae (Dothideomycetes, Botryosphaeriales) is an important and diverse family of latent fungal pathogens of woody plants, including *Acacia* spp. and *Eucalyptus* spp. (Slippers & Wingfield 2007; Phillips et al. 2013; Slippers et al. 2017; Jami et al. 2015; 2022). These fungi live in infected plant tissues for long periods of time without causing symptoms, but emerge to cause severe disease when their hosts are subjected to stress such as drought, freezing, extreme temperatures, defoliation, hail, and wounds caused by insects or other pathogens (Roux et al. 2005; Slippers & Wingfield 2007; Mehl et al. 2013). They cause dieback and canker disease on twigs, branches and trunks of trees (Slippers et al. 2007).

Some *Botryosphaeriaceae* spp. infect both *Eucalyptus* spp. and *Acacia* spp. *Lasiodiplodia theobromae* infects *Acacia* spp. such as *A. mangium* in Indonesia (Tarigan et al. 2011b) and Venezuela (Mohali et al. 2007), *Acacia karoo* in South Africa (Jami et al. 2015) and *Eucalyptus* spp. in Uganda (Roux et al. 2001b), Venezuela (Mohali et al. 2007), Sudan (Khalil 2010), China (Li et al. 2015) and Ethiopia (Admasu et al. 2023). *Lasiodiplodia pseudotheobromae* is a recorded pathogen of *A. mangium* in Venezuela and Costa Rica (Castro-Medina et al. 2014), *Eucalyptus grandis* in South Africa (Pillay et al. 2013) and of *Acacia confusa* and *Eucalyptus* spp. in China (Zhao et al. 2010). *Neofusicoccum australe* and *Neofusicoccum kwambonambiense* occur on *A. karoo* (Jami et al. 2015; 2014) and *E. grandis* (Pillay et al. 2013) in South Africa; *Neofusicoccum vitifusiforme* is found on *A. karoo* in South Africa (Jami et al. 2013) and on *Eucayptus* spp. in Australia (Sutton 1980; Barber et al. 2005; Summerell et al. 2006; Taylor et al. 2009). *Pseudofusicoccum stromaticum* infects *A. mangium* and *Eucalyptus* spp. in Venezuela (Mohali et al. 2006) and *Pseudofusicoccum adansoniae* and *Pseudofusicoccum kimberleyensis* occur on *Acacia synchronica* and *Eucalyptus* spp. in Australia (Pavlic et al. 2008).

Lasiodiplodia theobromae is a widely distributed pathogen that causes cankers on many tree species in tropical areas (Punithalingam 1979). In *Acacia* plantations, it has been isolated from cankered tissue of *A. mangium*, *Acacia auriculiformis* and *Acacia aulococarpa* in Indonesia, Thailand and Vietnam (Hadi & Nuhamara 1997, Pongpanich 1997; Tarigan et al. 2008, Thu et al. 2010; Dell et al. 2012). Symptoms of *L. theobromae* infection include gummosis and severe vertical stem cracking, with no obvious fruiting bodies of the fungus present. The ages of affected trees vary from six months to six-years-old, and the cankers are most common on older trees. Cankers are commonly found at the stem base and at the base of forked branches. It has been noticed that stems also break on trees with canker symptoms (Hadi & Nuhamara 1997).

There are at least 24 species of *Botryosphaeriaceae* reported from *Acacia* spp. (Table 1. 2.) and 41 reported from *Eucalyptus* spp. (Table 1. 3.), including the eight species mentioned above that occur on both species. These reported *Botryosphaeriaceae* spp. are mainly known from China (17), Australia (13) and South Africa (13), where more extensive studies on the *Botryosphaeriaceae* have been carried out. Many of these species are considered new, as our ability to recognise recently diverged but morphologically similar cryptic species in the *Botryosphaeriaceae* has been greatly enhanced by advances in DNA sequencing used for phylogenetics.

The variation in susceptibility of trees to some *Botryosphaeriaceae* species observed in clonal and artificial inoculation trials in the nursery suggests a possible genetic basis for resistance (Chen et al. 2011c; Nakabonge et al. 2020; Li et al. 2022). These results illustrate the potential of using *Eucalyptus* clones to manage canker disease caused by species of *Botryosphaeriaceae*. Furthermore, the possibility of searching for molecular markers of resistance that could be used in breeding programmes should be actively pursued (Slippers et al. 2009).

3.3. Heart rot on *Acacia* species

Heart rot is considered one of the common problems affecting tropical *Acacia* spp. (Old et al. 2000). Several wood decay fungi have been associated with heart rot of *A. mangium* trees in East Kalimantan and Sumatra. They include *Rigidoporus hypobrunneus*, *Phellinus noxius*, *Tinctoporellus epimiltinus* (Lee & Yahya 1999), *Oudemansiella canarii*, *Pycnoporus sanguineus* and *Trametes* spp. (Barry et al. 2006, Glen et al. 2006).

Rigidiporus hypobrunneus is the most frequently associated with heart rot on *A. mangium* in Kalimantan (Lee & Yahya 1999). Based on the sporocarps produced, about 43% of the isolates obtained from *A. mangium* trees with heart rot in Kalimantan were identified as *R. hypobrunneus*. The remaining 57% were identified as *Phellinus noxius*, *Tinctoporellus epimiltinus* and *Oxyporus latemarginatus.* Initially the infected wood turns white, then bleached cream in colour and becomes hard, but light in weight. After some time the infected wood becomes soft in cross sections (Lee & Yahya 1999).

Phellinus noxius is the second most frequently encountered fungus associated with heart rot on *A. mangium* in Kalimantan, Indonesia (Lee & Zakaria 1993; Lee & Yahya 1999; Hood 2006). Fruiting bodies are not always visible, but infected trees can be identified by a characteristic brown mycelium or black mycelial crust that forms on infected roots and develops like a collar around the base of the stem (Hood 2006). The roots and wood of infected trees are pale in colour and the problem can be recognized by characteristic brown zone lines which demarcate the root into pockets, which have a “honey-comb” appearance (Lee & Yahya 1999; Hood 2006).

Tinctoporellus epimiltinus was identified based on only one isolate obtained from *A. mangium* trees with heart rot in Kalimantan. The infected wood was spongy and pale in colour. The fungus produces resupinate and rigid fruiting bodies (Lee & Yahya1999). At present, there is very little information on heart rot caused by *T. epimiltinus* on *A. mangium*, but this fungus is

of greater concern as it has been reported associated with root rot on *A. mangium* in Malaysia (Old et al. 2000). Other fungi that have been identified as being associated with heart rot symptoms include *Oudemansiella canarii*, *Pycnoporus sanguineus* and *Trametes* spp. All were identified from wounding experiments on *A. mangium* trees in Sumatra (Glen et al. 2006). The role of these fungi in heart rot is not clear, but they are likely to have a role in heart rot as enzyme tests showed the presence of laccase and tyrosinase, indicating white rot capabilities (Glen et al. 2006).

In Indonesia, several factors favour the development of heart rot. For example, wounds on stems, branches and roots are infection points for heart rot fungi. Forestry operations such as pruning and singling or slash clearing with machetes are common practice in Indonesian forestry (Barry et al. 2004). In addition, climatic conditions in the country may influence the incidence and occurrence of heart rot, as the absence of a dry season has been reported to reduce the self-pruning ability of *A. mangium* branches, which then provides entry points for heart rot fungi (Lee & Arentz 1997). The fact that some *A. mangium* provenances produce more branches and that they are widely planted is also likely to influence the incidence and occurrence of heart rot. Tree age is another factor influencing heart rot incidence, as six-year-old trees were found to be less susceptible to heart rot than 8-year-old trees (Barry et al. 2004).

Symptoms of heart rot on affected trees are not clearly visible unless stems are sectioned to reveal the rotten centres of the trees (Zulfiyah & Gales 1997; Old et al. 2000; Gales 2002; Barry et al. 2004; Rimbawanto 2006). This destructive assessment is very time consuming and costly. Thus, for survey purposes, the optimal approach is to evaluate heart rot symptoms from logs stacked in plantations following harvest (Barry et al. 2004).

Acacia mangium is known to be higly prone to heart rot, whereas *Acacia auriculiformis* and *A. mangium* x *A. auriculiformis* hybrids are resistant (Ito & Nanis 1997, Mohammed et al. 2006). Different *A. mangium* provenances also differ in their susceptibility to heart rot. This has been demonstrated in two trials in Sumatra, where the incidence of heart rot on *A. mangium* differed significantly between provenances (Barry et al. 2006). This holds promise for the development of breeding programmes to control heart rot on *A. mangium* (Ito & Nanis 1997). Although the incidence of heart rot can be high, the impact of the disease is low, particularly in plantations grown for pulp and paper where rotations are short. Affected trees usually do not die, but the rot in wood causes some volume loss (Old et al. 2000; Gales 2002).

3.4. Bacterial wilt on *Acacia* and *Eucalyptus*

Ralstonia solanacearum and *Ralstonia pseudosolanacearum* cause a disease known as bacterial wilt on many economically important agronomic crops worldwide (Hayward 2000; Elphinstone 2005). They also infect woody plants such as *Acacia* spp. and *Eucalyptus* spp. (Cao 1982; Sudo et al. 1983; Tjahjono et al. 2011; Coutinho & Wingfield 2017), although the cause and effect relationship has not been clearly defined (Supriadi et al. 2001). Bacterial wilt is caused by the blockage of xylem tissue by bacterial growth (Figure 1.2B), resulting in wilt symptoms in the aerial parts of infected plants, which eventually die (Carstensen et al. 2017).

Initially, Fegan & Prior (2005) proposed a classification of the *Ralstonia solanacearum* species complex into four phylotypes, generally related to their geographical origin. Phylotype I includes strains mainly from Asia, Phylotype II contains strains mainly from the Americas, Phylotype III strains typically originate from Africa and nearby islands, while Phylotype IV strains are mainly from Indonesia. Following the work of Safni et al. (2014) and Prior et al. (2016), a division of the *R. solanacearum* species complex into three distinct species was proposed, with phylotype II being *R. solanacearum*, including type strain IBSBF292. Phylotypes I and III were reclassified as *Ralstonia pseudosolanacearum* and phylotype IV as *Ralstonia syzygii.*

There is limited information on the incidence of bacterial wilt on *Acacia* spp. The only information available is from Indonesia, where *A. crassicarpa* was infected by *R. pseudosolanacearum* (Tjahjono et al. 2011, Siregar et al. 2021). Bacterial wilt of *Eucalyptus* was first reported in China (Cao 1982) and Brazil (Sudo et al. 1983). Apart from Brazil (Fonseca et al. 2014), the disease has been recorded in most *Eucalyptus* producing regions worldwide, including China (Wu & Liang 1988), Taiwan (Wang 1992), Australia (Askiew & Tevorrow 1994), Venezuela (Ciesla et al. 1996), South Africa (Coutinho et al. 2000), Thailand (Pongpanich 2000), Vietnam (Thu et al. 2000), the Democratic Republic of Congo and Uganda (Roux et al. 2001b), Paraguay (Santiago et al. 2014) and Ecuador (Romero et al. 2021).

Ralstonia solanacearum (phylotype II) originated from Brazil (Wicker et al. 2012). Only phylotype II has been reported to cause bacterial wilt on *Eucalyptus* in Brazil, but recently *Ralstonia pseudosolanacearum* (phylotype I) has also been found on *E. urophylla* in that country (Freitas et al. 2020). This finding shows that bacterial wilt on *Eucalyptus* in Brazil is caused by both *R. solanacearum* and *R. pseudosolanacearum* indicating possible new spread

or host jump as *R. pseudosolanacearum* has also been found associated with solanaceous crops, such as tomato, aubergine, long pepper and bell pepper (Santiago et al. 2017). Carstensen et al. (2017) reported bacterial wilt disease on *Eucalyptus* in Asia and Africa as *Ralstonia pseudosolanacearum*. This result is consistent with the work of Siregar et al. (2021), who reported *R. pseudosolanacearum* causing bacterial wilt on *Eucalyptus pellita* in Indonesia.

In the nursery, infections by *Ralstonia solanacearum* and *Ralstonia pseudosolanacearum* are characterized by leaf necrosis, which includes darkening of the stem base, complete discolouration of internal tissues, wilting and eventual root death. Symptoms on the shoots are similar to the gradual death of mother plants that have been severely pruned or have a malformed root system (Alfenas et al. 2006). Affected plants show reddening and wilting of the foliage, leaf drop, branch dieback and reduced growth, resembling bacterial wilt symptoms. Bacterial wilt has caused significant economic losses in clonal *Eucalyptus* nurseries (Santiago et al. 2014). Cross-sections of wilted trees in the field show vascular discolouration of the wood and bacterial ooze. Bacterial wilt also causes losses, and can cause a reduction in volumetric growth of 78.6% and 81.7% at 18 and 30 months, respectively, and a reduction in pulp screen yield between 3.2 and 6.4%, with an average of 4.3% (Ferreira et al. 2017).

Eucalyptus species differ in their susceptibility to infection by *Ralstonia* species. Over the last five decades, most research on this disease in *Eucalyptus* has focused on screening for tolerant material (Gan et al. 2004; Li et al. 2007; Wang et al. 2011; Marques et al. 2013; Fonseca et al. 2016). Identifying and deploying this material in plantations is an obvious solution to bacterial wilt. However, screening is challenging and difficult. Biocontrol applications using *Trichoderma harzianum* and *Purpureocillium lilacinum* have also been tested, with results showing the potential to reduce seedling mortality (Gomes et al. 2023). Coutinho & Wingfield (2017) also highlight that one of the most common factors associated with bacterial wilt in *Eucalyptus* is root knotting and planting in highly compacted or dense soils, with trees under extreme stress in both conditions. A recent study by Oliveira et al. (2023b) highlights an integrated disease management approach to control bacterial wilt of *Eucalyptus* in nursery and plantation.

4. Root diseases on *Acacia* and *Eucalyptus*

Root diseases affect the roots and lower stem of the tree and cause the highest tree mortality in comparison to leaf and stem diseases because root diseases affect water and nutrient uptake. They can also remain undetected until the damage becomes visible above ground because it develops in the underground root system. This makes root diseases more difficult to diagnose. Both *Acacia* and *Eucalyptus* trees in SE Asian plantations are affected by root diseases, caused by species of *Ganoderma*, *Armillaria* and *Pythophthora*.

4.1. Ganoderma root rot

Root rot is one of the more important diseases affecting *Acacia* spp. and *Eucalyptus* spp. in plantations. The disease is well known in Indonesia (Coetzee et al. 2011), Malaysia (Lee 2000), Thailand, and Vietnam (Thu et al. 2021), southern Africa (Masuka & Nyoka 1995), India (Bakshi 1974; 1976) and can be caused by several basidiomycetous fungi and oomycetes (Old et al. 2000, Hood 2006, Glen et al. 2009, Dell et al. 2012). These include *Rigidoporus microporus, Fomes lignosus, Junghuhnia vincta* (syn. *Poria vincta* Speg., *Rigidoporus vinctus*), *Phellinus noxius, Ganoderma philippii* (syn. *G. pseudoferreum*), *Ganoderma mastoporum, Ganoderma* aff. *steyaertanum, Ganoderma australe, Amauroderma rugosum, Phytophthora cinnamomi, P. acaciivora* and *Pythium vexans* (Zulfiyah & Gales 1997; Old et al. 2000; Hood 2006; Potter et al. 2006; Glen et al. 2009; Dell et al. 2012; Thu et al. 2021).

Although a number of these fungal pathogens are associated with root rot in SEA, Ganoderma root rot is the most common (Lee 2000, Old et al. 2000, Mohammed et al. 2006, Glen et al. 2009, Coetzee et al. 2011). *Ganoderma* spp. cause red root rot disease, named as such because the roots of infected trees are covered by reddish brown rhizomorphs which can be clearly seen when the roots are washed clean (Old et al. 2000). Various *Ganoderma* spp. have been isolated from infected *A. mangium* and *Eucalyptus* roots in Indonesia (Coetzee et al. 2011) and Malaysia (Glen et al. 2009). DNA-based phylogenetic analyses have shown that *Ganoderma philippii* is the single dominant species causing Ganoderma root rot on *A. mangium* and *Eucalyptus* in Sumatra (Coetzee et al. 2011).

Other than on *A. mangium* and *Eucalyptus, Ganoderma* root rot has been recorded in *Acacia auriculiformis*, *Acacia crassicarpa* and *A. mangium* plantations. Initially the crowns of infected trees turn pale green to yellow (Figure 1.3A), whereafter, the trees wilt completely and eventually tree death follows (Old et al. 2000). In older trees, the fungi produce fruiting bodies

around the bases of the stems after the bark and wood starts to decay (Old et al. 2000). Fruiting bodies are broadly attached (Figure 1.3B, 1.3C), dark reddish or purplish brown with white margins on the upper surfaces with a white or brownish underside (Figure 1.3D, 1.3E) (Hood 2006).

Infection of *Acacia* and *Eucalyptus* trees by *Ganoderma* spp. generally results in tree death (Old et al. 2000). It was reported that root rot diseases cause early losses in subsequent plantings (Nandris et al. 1987b; Eyles et al. 2008). Disease build up from less than 10% of trees in the first rotation, and up to 20 - 40% in the second rotation can die as a result of root rot (Lee 2000; Rimbawanto 2002; Irianto et al. 2006). This figure clearly indicates that root rot disease increases over time as the inoculum builds up. In the second rotation, young trees have been reported to be killed within six months after planting (Old et al. 2000). Due to this inoculum build up, root rot disease caused by *G. philippii* is considered a major threat to forest plantations (Potter et al. 2006).

It is well-known that all root rot diseases spread via root contact between healthy trees and diseased trees (Lee 2000, Old et al. 2000). From the infection point, the numbers of dying and dead trees increase, thus expanding the patch size and increasing the source of inoculum. The incidence of root rot is higher in *A. mangium* and *Eucalyptus* plantations that are planted in ex-hardwood forest areas when compared to plantations that are planted on ex-grasslands. This is due to a higher inoculum source in ex-hardwood forest areas (Lee 1999).

Current management strategies focus on genetic and biological control in the nursery, but genetic screening in the field and artificial inoculation in pot experiments, including biological control, have not shown any exploitable trends in resistance to root rot (Mohammed et al. 2014). Selection of particular tree genotypes for planting and biological control might be useful in large plantations, particularly in SEA, where topography and climate often preclude other management approaches such as stump removal and chemical control (Mohammed et al. 2014).

4.2. Armillaria root rot

The genus *Armillaria* (Basidiomycota, Agaricales, Physalacriaceae) includes serious pathogens that cause root rot of woody plants, including *Acacia* spp. and *Eucalyptus* spp. and they occur in a wide variety of climatic conditions in most forested areas of the world (Gregory et al. 1991; Hood et al. 1991; Kile et al. 1991; Fox 2000). The genus *Armillaria* includes at least 287 species (https://www.mycobank.org) although the taxonomic validity of many of

these names has not been verified. The pathogenicity of these organisms can lead to root and stem rot of *Armillaria* and to what is known as shoestring root rot (Morrison 1992). This disease can cause serious damage to woody plants grown for horticulture, agriculture, as well as those in natural and managed forests across most continents (Guillaumin et al. 1993; Baumgartner & Rizzo 2001, 2002; Labbe et al. 2015).

Several species of *Armillaria* have been reported from *Acacia* spp. (Table 1. 4.) and *Eucalyptus* spp. (Table 1. 5.). There are seven *Armillaria* spp. recorded on both *Acacia* spp. and *Eucalyptus* spp. including *Armillaria fumosa*, *A. gallica*, *A. hinnulea*, *A. limonea*, *A. luteobubalina*, *A. mellea* and *A. novae-zelandiae*. Some species of *Armilaria* have wide global distribution, mainly due to their accidental introduction into new areas, such as in the case of *Armillaria mellea* (Guillaumin et al. 1993; Hosagoudar et al. 2007; Coetzee et al. 2018). Others have limited distributions such as *Armillaria fumosa* and *Armillaria luteobubalina* that are restricted to Australia (Kile & Watling 1988).

There is very little information available on the identity of *Armillaria* in SEA (Hood et al. 1991; Kile et al. 1994). Reports of *Armillaria* in these regions are mostly based on the presence of the characteristic rhizomorphs and basidiocarps in disease centres or typical disease symptoms on infected trees (Kile et al. 1994). Using DNA sequencing analysis, isolates similar to *Armillaria novae-zelandiae* have been identified from *A. mangium* in Malaysia and *Eucalyptus* in Indonesia (Coetzee et al. 2003). However, most reports from Indo-Malaysia attribute Armillaria root rot to *Armillaria mellea sensu lato*, although this identity almost certainly excludes *Armillaria mellea sensu stricto* (Coetzee et al. 2003).

4.3. Phytophthora root rot

The oomycete genus *Phytophthora* (Peronosporales, Peronosporaceae) includes some of the most devastating plant pathogens in the world, where they can destroy crops, trees in planted forests and threaten natural woody ecosystems (Ribeiro 2013; Hansen 2015; Jung et al. 2018). *Phytophthora* spp. are the most important pathogens causing root rot of *Acacia* spp. and *Eucalyptus* spp. (Roux & Wingfield 1997; Kile 2000; Shearer & Smith 2000). There are 17 *Phytophthora* spp. recorded from *Acacia* spp. (Table 1. 6.) and at least 29 species of *Phytophthora* spp. have been reported from *Eucalyptus* spp. (Table 1. 7.) (Burgess et al. 2021; Farr & Rossman 2022).

One of the most aggressive species of *Phytophthora* is *Phytophthora cinnamomi,* which has caused extensive destruction on native *Eucalyptus* populations in Australia (Newhook & Podger 1972; Podger 1972; Davison & Shearer 1989; Cahill et al. 2008; Scott et al. 2009). It has also destroyed other endemic species, threatening the biodiversity of important areas such as the jarrah forest in the south-western of Australia (Shearer et al. 2004; Cahill et al. 2008). In contrast, *Phytophthora cinnamomi* causes little damage to planted forests in Australia or elsewhere. This is probably because the most planted *Eucalyptus* spp. are relatively tolerant to infection (Wingfield & Knox-Davies 1980; Linde et al. 1994; Shearer & Smith 2000; Nagel et al. 2013). However new incidences of *P. cinnamomi* have recently been reported from planted forest, such as in Portugal where it affected *Eucalyptus globulus* (Diogo et al. 2023).

Phytophthora spp., particularly *Phytophthora cryptogea* and *Phytophthora cinnamomi,* are important nursery pathogens in Australasia and Europe (Old et al. 2003; Jung et al. 2016). They are also associated with tree mortality in plantations and native forests. However, Old and Dudzinski (2000), found few significant reports of nursery diseases attributed to this genus in Asia. An exception is Papua New Guinea, where Arentz (1990), considered *Phytophthora* spp. to be the most serious pathogens in nurseries.

Current management strategies focus on genetics, particularly in *Eucalyptus* spp. as variation in susceptibility to *Phytophthora* spp. were noted in this host genus (Tippett et al. 1985; Stukely & Crane 1994; Stukely et al. 2007a). In addition to pathogen aggressiveness and host susceptibility, several other factors, such as climatic stress, including waterlogging or drought, and shallow and compacted soils, are involved in disease expression. All these can act as predisposing factors that reduce the resilience of trees to stress factors (Jurskis 2005; Camilo-Alves et al. 2013).

5. Conclusions

Plantation forestry in SEA is a significant contributor to global wood production. The challenge is to maintain, improve and sustain productivity from the same area of land. Effective plantation management is central to both short and long-term production. The period from harvest to replanting and stand establishment is a critical period where risks and opportunities determine the success of short rotation forestry. There are at least three key areas that need to be addressed to sustain timber production over successive rotations within SEA. These focus on genetic selection and improvement, managing the challenges posed by diseases and pests, and improving site and stand management practices.

A successful plantation forest can only be secured by moving away from potentially unsustainable management practices and by developing and applying integrated, science-based plantation management systems. Evidence from multi-site research shows that with sound management practices, productivity can be increased and sustained over rotations, while maintaining the productive capacity of the land. Initially, unimproved planting stock was used as it was the only material available at the time. This meant that substantial losses occurred, and much of this loss was due to damage by pests and pathogens. But research into tree improvement and pest and disease screening has facilitated the development of uniformly fast-growing genotypes with homogeneous physical properties and disease resistance. In addition, nursery propagation techniques have been improved to provide sufficient material for plantation establishment.

Clonal and family forestry is known to be of great value to the success of plantation forestry as it facilitates the development of uniformly fast-growing genotypes with homogeneous physical properties and disease resistance. *Acacia* and *Eucalyptus* clonal hybrids are used especially for pulp and paper raw material. In the SE Asain contex, for *Acacia*, clones are generated by cross-breeding *Acacia crassicarpa*, *A. mangium* x *Acacia auriculiformis,* and for *Eucalyptus* spp. with three main hybrid clonal groups: *Eucalyptus pellita* clones, *Eucalyptus grandis* x *E. pellita* hybrids, and *E. grandis* x *Eucalyptus urophylla* hybrids. It is anticipated that the successful use of *Acacia* and *Eucalyptus* clones in plantation forestry is capable of reducing timber and wood shortage worldwide (Wingfield et al. 2013; Rezende et al. 2014). However, leaf diseases such as rust disease, *Elsinoe* scab and shoot malformation, Teratosphaeria and Calonectria leaf blights; stem diseases such as Chrysoporthe and Teratosphaeria canker, Ceratocystis wilt and root disease caused by species of *Ganoderma* and *Phythophthora* could threaten successful

establishment. The genetic uniformity of clonal hybrids results in elevated risk due to disease and pest problems where susceptible trees are grown under favourable environmental conditions, at least in comparison to having plantations of species generated from seed (Guimarães et al. 2010).

Other factors contributing to increased plantation health risks include off-site planting, uniform unimproved genetic stock and plantation management practices, such as pruning and weed control, which can cause wounding and phytotoxicity. Several factors may influence pest and disease outbreaks on *Acacia* spp. and *Eucalyptus* spp. These trees have largely been planted and established on the islands of Sumatra and Kalimantan in Indonesia, Malaysia, Vietnam and Thailand, where they do not occur naturally. *Acacia* spp. and *Eucalyptus* spp. are, therefore, non-native and they are not only at risk from the accidental introduction of pathogens, but could also be threatened by pathogens present in the native environment that could undergo host shifts. This has already been seen in the case of, for example, Cryphonectria canker.

This review has attempted to capture the most important background knowledge regarding pathogens of *Eucalyptus* and *Acacia* in SEA. It has not included areas such as China that is not specifically in this region but where *Eucalyptus* spp. are also widely planted. Many of the diseases treated in this review are also found in that country. We have also included a wide diversity of pathogens for which very little knowledge is available. In some cases, pathogenicity tests have not been conducted and the particular fungi may not be of particularly importance. Going forward, there is a great need for in-depth research on many of the fungi already present on *Acacia* and *Eucalyptus* in SEA. This will be the only means to ensure longer term sustainability of the plantation resource. In addition, great effort should be taken to prevent the introduction of new pathogens, particularly via the trade in living plants.

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APPENDIX

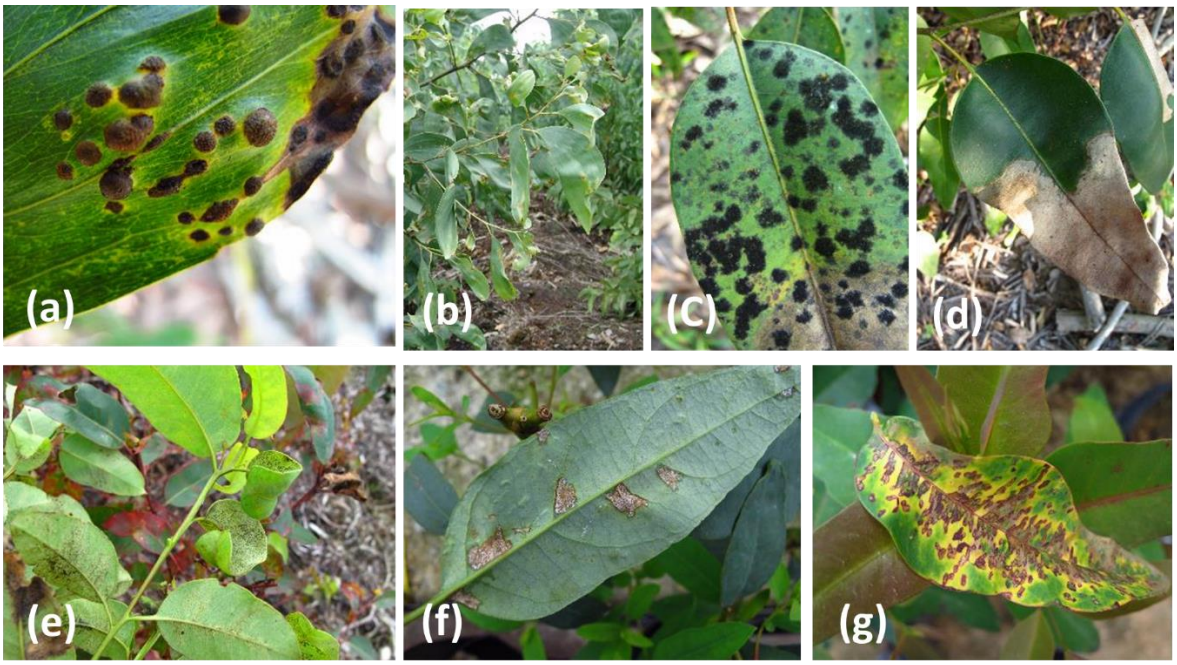

Figure 1. 1. Major leaf diseases on *Acacia* spp. and *Eucalyptus* spp. (a). *Endoraecium auriculiforme* on *A. mangium*, (b). *Passalora perflexa* on *A. crassicarpa*, (c). black mildew caused by *Meliola* spp. on *Eucalyptus*, (d). Calonectria leaf blight on *Eucalyptus*, (e). *Teratosphaeria destructans* on *Eucalyptus*, (f). *Quambalaria eucalypti* on *Eucalyptus*, and (g). *Xanthomonas perforans* on *Eucalyptus*.

Figure 1. 2. Major stem diseases on *Acacia* spp. and *Eucalyptus* spp. (a). stem cankers caused by *Chrysoporthe deuterocubensis* on *Eucalyptus*, (b). bacterial wilt associated with *Ralstonia pseudosolanacearum* on *Eucalyptus*, (c). pink disease caused by *Erythricium salmonicolor*, (d-f). *Ceratocystis manginecans* on *Acacia* (d) and *Eucalyptus* (e) with star-like lesion on cut disc surface (f).

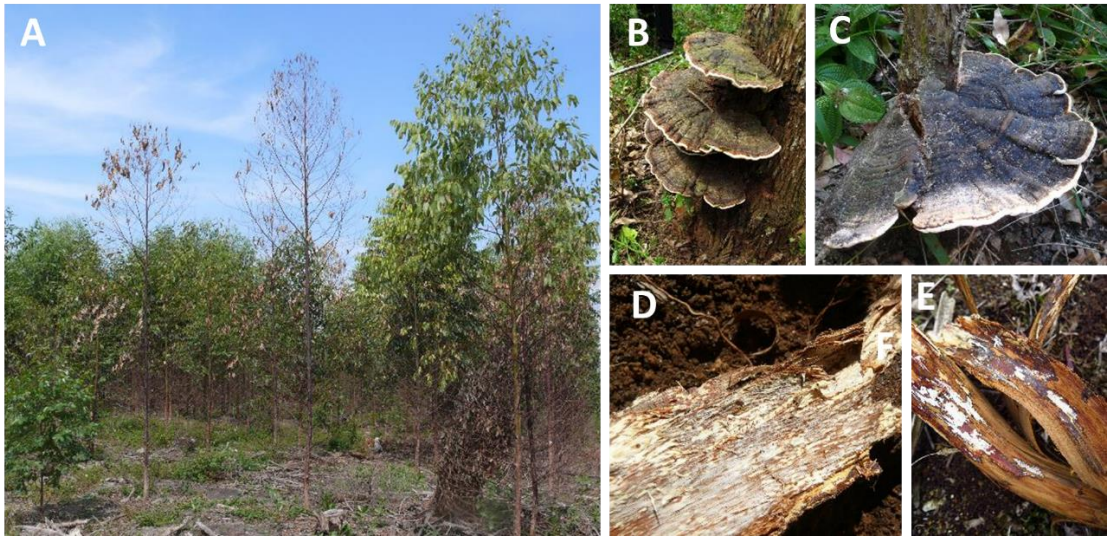

Figure 1. 3. Ganoderma root rot as one major diseases on *Acacia* spp. and *Eucalyptus* spp. caused by *G. philippii,* (a). yellowing canopy and dying trees due to *Ganoderma* infection, (b-c). fruiting bodies of *G. philippii* on basal stem, (d-e). mottled white mycelium under the bark of the root.

Table 1. 1. Minor leaf diseases on *Acacia* spp. and *Eucalyptus* spp. in SEA plantations

Species	Host	Distribution	References
Anthostomella eucalyptorum	*Eucalyptus* sp.	Indonesia	Crous et al. 2006b
Apoharknessia eucalypti	*E. pellita*	Malaysia	Marin-Felix et al. 2019
Apoharknessia eucalyptorum	*E. pellita*	Malaysia	Crous et al. 2017
Castanediella communis	*E. pellita*, *E. brassiana*	Malaysia	Crous et al. 2016a
Castanediella eucalypti	*E. pellita*, *E. brassiana*	Malaysia	Crous et al. 2016a
Castanediella malaysiana	*E. pellita*, *E. brassiana*	Malaysia	Hernandez-Restrepo et al. 2016
Cephaleuros virescens	*Acacia aulococarpa*, *A. crassicarpa*	Thailand, Vietnam	Pongpanich 1997; Dell et al. 2012
Cercospora acaciae-mangii	*A. mangium*	Thailand	Crous et al. 2004
Cercospora spp.	*A. mangium*	Thailand	Pongpanich 1997
Clypeosphaerella quasiparkii	*Eucalyptus* sp.	Thailand	Cheewangkoon et al. 2008
Eucalyptostroma eucalypti	*E. pellita*	Malaysia	Crous et al. 2016a
Leptosphaeria sp.	*A. mangium*	Thailand	Pongpanich 1997
Neoceratosperma eucalypti	*Eucalyptus* sp.	Thailand	Crous et al. 2014; Crous et al. 2004
Parapallidocercospora thailandica	*Eucalyptus* sp.	Thailand	Crous et al. 2014; Crous et al. 2004
Phaeoramularia eucalyptorum	*E. saligna*	Malaysia	Crous et al. 2004
Phomopsis spp.	*A. aulococarpa*, *A. crassicarpa*, *A. auriculiformis*	Vietnam	Thu et al. 2010; Dell et al. 2012
Pseudozasmidium vietnamense	*hybrid E. grandis*	Vietnam	Burgess et al. 2007
Virosphaerella irregularis	*Eucalyptus* sp.	Thailand	Cheewangkoon et al. 2008
Virosphaerella pseudomarksii	*Eucalyptus* sp.	Thailand	Cheewangkoon et al. 2008
Xenosonderhenioides indonesiana	*Eucalyptus* sp.	Indonesia	Videira et al. 2017
Zasmidium eucalyptorum	*E. urophylla*, *E. grandis*	Indonesia	Crous et al. 2006c
Zasmidium xenoparkii	*E. urophylla*, *E. grandis*	Indonesia	Crous et al. 2006c

Table 1.2. The *Botryosphaeriaceae* on *Acacia* spp.

Species	Host	Distribution	References
Botryosphaeria auasmontanum	*Acacia mellifera*	Namibia	Slippers et al. 2014
Diplodia allocellula	*A. karoo*	South Africa	Jami et al. 2012
Dothiorella acacicola	*A. mearnsii*	France	Crous et al. 2016b
Dothiorella brevicollis	*A. karoo*	South Africa	Jami et al. 2012
Dothiorella capri-amissi	*A. erioloba*	South Africa	Slippers et al. 2014
Dothiorella dulcispinae	*A. karoo*	South Africa	Jami et al. 2012
	A. mellifera	Namibia	Slippers et al. 2014
Dothiorella moneti	*A. rostellifera*	Australia	Taylor et al. 2009
Dothiorella oblonga	*A. mellifera*	Namibia, South Africa	Slippers et al. 2014
Dothiorella pretoriensis	*A. karoo*	South Africa	Jami et al. 2012
Dothiorella thripsita	*A. harpophylla*	Australia	Shivas et al. 2009
Lasiodiplodia pseudotheobromae	*A. mangium*	Venezuela	Castro-Medina et al. 2014
Lasiodiplodia pyriformis	*A. mellifera*	Namibia	Slippers et al. 2014
Lasiodiplodia theobromae	*A. mangium,*	Indonesia	Hadi & Nuhamara 1997;
	A. auriculiformis,		Tarigan et al. 2011b
	A. aulacocarpa		
	A. mangium	Venezuela	Mohali et al. 2007
Lasiodiplodia venezuelensis	*A. mangium*	Venezuela	Burgess et al. 2006b
Neofusicoccum australe	*A. karoo*	South Africa	Jami et al. 2015
Neofusicoccum kwambonambiense	*A. karoo*	South Africa	Jami et al. 2014
Neofusicoccum vitifusiforme	*A. karoo*	South Africa	Jami et al. 2013
Neoscytalidium novaehollandiae	*A. synchronica*	Australia	Pavlic et al. 2008
Pseudofusicoccum adansoniae	*A. synchronica*	Australia	Pavlic et al. 2008
Pseudofusicoccum kimberleyensis	*A. synchronica*	Australia	Pavlic et al. 2008
Pseudofusicoccum stromaticum	*A. mangium*	Venezuela	Mohali et al. 2006
Spencermartinsia rosulata	*A. karoo*	Namibia	Slippers et al. 2014
Spencermartinsia viticola	*A. karoo*	South Africa	Jami et al. 2013; 2014
Sphaeropsis variabilis	*Acacia sp*	Namibia, South Africa	Slippers et al. 2014

Table 1.3. The *Botryosphaeriaceae* on *Eucalyptus* spp.

Species	Host	Distribution	References
Aplosporella hesperidica	*Eucalytus camaldulensis*	Ethiopia	Admasu et al. 2023
Botryosphaeria dothidea	*E. grandis*	China	Yu et al. 2009
	E. globulus	Portugal	Barradas et al. 2016
Botryosphaeria fabicerciana	*Eucalyptus* sp.	China	Chen et al. 2011c
Botryosphaeria fusispora	*Eucalyptus* sp.	China	Li et al. 2020
Botryosphaeria pseudoramosa	*Eucalyptus* sp.	China	Li et al. 2018
Botryosphaeria puerensis	*Eucalyptus* sp.	China	Li et al. 2020
Botryosphaeria qingyuanensis	*Eucalyptus* sp.	China	Li et al. 2018
Botryosphaeria ramosa	*E. camaldulensis*	Australia	Pavlic et al. 2008
Botryosphaeria wangensis	*Eucalyptus* sp.	China	Li et al. 2020; 2018
Cophinforma atrovirens	*Eucalyptus* sp.	Thailand	Liu et al. 2012; Li et al. 2018
	E. urophylla	Venezuela	Mohali et al. 2007
	Eucalyptus spp.	Indonesia	Jami et al. 2022
Diplodia corticola	*E. globulus*	Portugal	Barradas et al. 2016
Diplodia seriata	*E. globulus*	Portugal	Barradas et al. 2016
Endomelanconiopsis endophytica	*Eucalyptus* spp.	Indonesia	Jami et al. 2022
Lasiodiplodia brasiliense	*Eucalyptus* hybrid	China	Li et al. 2018
	Eucalyptus spp.	Indonesia	Jami et al. 2022
Lasiodiplodia crassispora	*E. urophylla*	Uruguay, Venezuela	Pérez et al. 2010
Lasiodiplodia laeliocattleyae	*Eucalyptus* spp.	Indonesia	Jami et al. 2022
Lasiodiplodia lignicola	*Eucalyptus* spp.	Indonesia	Jami et al. 2022
Lasiodiplodia pseudotheobromae	*E. grandis*	South Africa	Pillay et al. 2013
	Eucalyptus sp.	China	Li et al. 2020; Chen et al. 2011c; Li et al. 2018
	Eucalyptus spp.	Indonesia	Jami et al. 2022
Lasiodiplodia rubropurpurea	*E. grandis*	Australia	Burgess et al. 2006b
Lasiodiplodia theobromae	*E. urophylla* x *E. grandis*	Widely distributed in tropical and subtropical regions. China	Li et al. 2015; Chen et al. 2011c
	Eucalyptus spp.	Indonesia	Jami et al. 2022
	E. camaldulensis	Ethiopia	Admasu et al. 2023
Lasiodiplodia riauensis	*Eucalyptus* spp.	Indonesia	Jami et al. 2022
Neofusicoccum andinum	*Eucalyptus* sp.	Venezuela	Mohali et al. 2006
Neofusicoccum algeriense	*E. globulus*	Portugal	Barradas et al. 2016
Neofusicoccum australe	*E. grandis*	South Africa	Pillay et al. 2013
	E. globulus	Portugal	Barradas et al. 2016
Neofusicoccum cryptoaustrale	*Eucalyptus sp.*	South Africa	Crous et al. 2013
Neofusicoccum dianense	*Eucalyptus sp.*	China	Li et al. 2020
	Eucalyptus spp.	Indonesia	Jami et al. 2022
Neofusicoccum eucalypticola	*Eucalyptus sp.*	Australia	Burgess et al. 2006b

Table 1.3. (Continue)

Species	Host	Distribution	References
Neofusicoccum eucalyptorum	*Eucalyptus spp.*	South Africa	Smith et al. 2001
		Australia	Slippers et al. 2004
		Uruguay	Pérez et al. 2009
		Mexico	De la Mora-Castaneda et al. 2014
	E. globulus	Portugal	Barradas et al. 2016
Neofusicoccum hongkongense	*Eucalyptus* sp.	China	Li et al. 2018
Neofusicoccum kwambonambiense	*E. grandis*	South Africa	Pillay et al. 2013
	Eucalyptus sp.	China	Li et al. 2020
	Eucalyptus sp.	Uganda	Nakabonge et al. 2020
	E. globulus	Portugal	Barradas et al. 2016
Neofusicoccum macroclavatum	*E. globulus, E. saligna*	Australia	Burgess et al. 2005
Neofusicoccum magniconidium	*Eucalyptus* sp.	China	Li et al. 2020
Neofusicoccum mediterraneum	*Eucalyptus* sp.	Greece	Phillips et al. 2013
Neofusicoccum microconidium	*Eucalyptus* sp.	China	Li et al. 2018
Neofusicoccum ningerense	*Eucalyptus* sp.	China, Indonesia	Li et al. 2020; Jami et al. 2022
Neofusicoccum occulatum	*E. grandis* hybrid	Australia	Sakalidis et al. 2011
	Eucalyptus spp.	Indonesia	Jami et al. 2022
Neofusicoccum parviconidium	*Eucalyptus* sp.	China	Li et al. 2020
Neofusicoccum parvum	*Eucalyptus* sp.	Worldwide, China	Li et al. 2020; Chen et al. 2011c; Li et al. 2018
	Eucalyptus spp.	Indonesia	Jami et al. 2022
	Eucalyptus sp.	Uganda	Nakabonge et al. 2020
	E. globulus	Portugal	Barradas et al. 2016
	E. camaldulensis	Ethiopia	Admasu et al. 2023
Neofusicoccum ribis sensu lato	*Eucalyptus* sp.	China	Chen et al. 2011c
Neofusicoccum sinoeucalypti	*E. urophylla* × *E. grandis*	China	Li et al. 2018
Neofusicoccumursorum	*Eucalyptus* sp.	South Africa	Crous et al. 2013
Neofusicoccum vitifusiforme	*E. corticosa*	Australia	Summerell et al. 2006
	Eucalyptus sp., *E. camaldulensis* , *E. diversicolor* , *E. pauciflora* , *E. marginata* , *E. rubida* , *E. viminalis*	Australia	Barber et al. 2005; Taylor et al. 2009; Sutton 1980
Neofusicoccum yunnanense	*Eucalyptus* sp.	China	Li et al. 2020
Pseudofusicoccum adansoniae	*Eucalyptus* sp.	Australia	Pavlic et al. 2008
Pseudofusicoccum ardesiacum	*Eucalyptus* sp.	Australia	Pavlic et al. 2008
Pseudofusicoccum kimberleyensis	*Eucalyptus* sp.	Australia	Pavlic et al. 2008
Pseudofusicoccum stromaticum	*Eucalyptus* sp.	Venezuela	Mohali et al. 2006
Sphaeropsis eucalypticola	*Eucalyptus* sp.	Thailand	Liu et al. 2012

Table 1.4. List of *Amillaria* spp. on *Acacia* spp.

Species	Host	Distribution	References
Armillaria fumosa	*Acacia dealbata,*	Australia	Kile & Watling 1981
	A. mearnsii,		
	A. melanoxylon		
Armillaria fuscipes	*A. abyssinica*	Ethiophia	Gezahgne et al. 2004
	A. decurrens	India,	Pande & Rao 1998;
		Sri Lanka	Coetzee et al. 2005
Armillaria gallica	*A. kao*	Hawaii USA	Kim et al. 2016
Armillaria heimii	*A. xanthophloea*	Zimbabwe	Gezahgne et al. 2004;
			Mwenje et al. 2003
Armillaria hinnulea	*A. melanoxylon*	Australia	Kile 1983
Armillaria limonea	*A. melanoxylon*	New Zealand	Gadgil 2005
Armillaria luteobubalina	*A. urophylla,*	Australia	Shivas 1989
	A. pulchella,		
	A. browniana,		
	A. saligna		
	A. longifolia	Australia	Cook & Dube 1989
	A. verticillata,	Australia	Kile & Watling 1981
	A. dealbata,		
	A. mucronata,		
	A. mearnsii,		
	A. howittii,		
	A. melanoxylon		
	A. verticillata,	Australia	Sampson & Walker 1982
	A. dealbata		
Armillaria mellea	*A. koa*	Hawaii USA	Bega 1979
	A. mearnsii,	India,	Boa & Lenne 1994
	A. auriculiformis,	South Africa,	
	A. nilotica	Malawi,	
		Tanzania,	
		Indonesia,	
		Zimbabwe,	
		Sri Lanka	
	A. auriculiformis	India	Browne 1968;
			Hosagoudar et al. 2007
	A. baileyana	California USA	French 1989
	A. catechu	India	Pande & Rao 1998
	A. melanoxylon,	Tanzania	Riley 1960;
	A. decurrens,		Spaulding 1961
	A. podalyriifolia,		
	A. dealbata		
	A. melanoxylon	Kenya	Spaulding 1961
	A. pycnantha	Australia	Spaulding 1961
	A. decurrens	East Indies,	Spaulding 1961
		Malawi	

Table 1.4. (Continue)

Species	Host	Distribution	References
Armillaria mellea	*A. mearnsii,*	Zimbabwe	Whiteside 1966
	A. baileyana		
Armillaria novae-zelandiae	*A. melanoxylon*	New Zealand	Gadgil 2005
	A. mangium	Malaysia	Pildain et al. 2009;
			Coetzee et al. 2003
Armillaria sinapina	*A. kao*	Hawaii USA	Gilbertson et al. 2002
Armillaria sp.	*A. truncata,*	Australia	Shivas 1989;
	A. pycnantha		Cook & Dube 1989
	A. kao	Hawaii USA	Gilbertson et al. 2002
	A. melanoxylon	New Zealand	Pennycook 1989
	A. xanthophloea	Zimbabwe	Coetzee et al. 2000
	A. mangium	Malaysia	Coetzee et al. 2003
	A. abyssinica	Ethiopia	Gezahgne et al. 2003c
	A. mearnsii	Kenya	Roux et al. 2005;
			Mwenje & Ride 1996
	A. albida	Zimbabwe	Pildain et al. 2009;
			Mwenje et al. 2003
	A. albida,	Zimbabwe	Mwenje 1996
	A. karroo		

Table 1.5. List of *Amillaria* spp. on *Eucalyptus* spp.

Species	Host	Distribution	References
Armillaria fumosa	*Eucalyptus sp.*	Australia	Pildain et al. 2009; Coetzee et al. 2001
	E. obliqua, *E. ovata,* *E. amygdalina,* *E. rubida*	Australia	Kile & Watling 1983
Armillaria gallica	*E. gunnii*	western Europe	Guillaumin et al. 1993
Armillaria hinnulea	*E. obliqua,* *E. globulus*	Australia	Pildain et al. 2009
Armillaria limonea	*E. delegatensis,* *E. regnans*	New Zealand	Gadgil 2005
Armillaria luteobubalina	*E. regnans*	Australia	Podger et al. 1978; Coetzee et al. 2001
	E. maculata, *E. foecunda*	Australia	Cook & Dube 1989
	E. marginata	Australia	Shearer & Tippet 1988
	E. regnans, *E. obliqua,* *E. baxteri,* *E. macrorhyncha,* *E. dives,* *E. camaldulensis,* *E. melliodora,* *E. globulus,* *E. radiata,* *E. rubida,* *E. viminalis,* *E. ovata*	Australia	Kile & Watling 1981
	E. regnans, *E. obliqua*	Australia	Sampson & Walker 1982
	E. wandoo, *E. megacarpa,* *E. diversicolor,* *E. leucoxylon,* *E. gomphocephala,* *E. marginata,* *E. calophylla*	Australia	Shivas 1989
Armillaria mellea	*Eucalyptus sp.*	California USA	Anonymous 1960
	Eucalyptus sp.	Australia, Kenya	Spaulding 1961; Anonymous 1964
	E. globulus, *E. citriodora*	Tanzania	Riley 1960; Spaulding 1961; Anonymous 1964
	E. paniculata	South Africa	Doidge 1950; Spaulding 1961; Anonymous 1964

Table 1.5. (Continue)

Species	Host	Distribution	References
Armillaria mellea	*E. camaldulensis*	Italy	Anonymous 1964
	E. calophylla	Australia	Anonymous 1964
	E. dalrympleana	western Europe	Guillaumin et al. 1993
	E. microcorys	Malawi	Corbett 1964
	E. polyanthemos,	California USA	Raabe 1965;
	E. sideroxylon,		French 1989;
	E. pulverulenta		Tidwell 1990
	E. robusta	Papua New Guinea	Shaw 1984
Armillaria montagnei	*E. regnans*	Australia	Pildain et al. 2010
Armillaria novae-zelandiae	*E. delegatensis,*	New Zealand	Gadgil 2005
	E. regnans		
	E. grandis	Indonesia	Pildain et al. 2009;
			Coetzee et al. 2003
Armillaria tahescens	*E. dalrympleana,*	western Europe	Guillaumin et al. 1993
	E. gunnii,		
	E. macarthurit,		
	E. pauciflora		

Table 1.6. List of *Phytophthora* spp. on *Acacia* spp.

Species	Host	Distribution	References
Phytophthora acaciae	*Acacia mearnsii*	Brazil	Albuquerque et al. 2019; Alves et al. 2019; Burgess et al. 2020
Phytophthora acaciivora	*A. mangium*	Viet Nam	Burgess et al. 2020
Phytophthora boehmeriae	*A. mearnsii*	South Africa, Brazil	Roux & Wingfield 1997; Dos Santos et al. 2006
Phytophthora cactorum	*Acacia sp.*	Germany	Erwin & Ribeiro 1996
Phytophthora cinnamomi	*A. koa, A. melanoxylon*	Hawai USA	Raabe et al. 1981
	A. dealbata, A. myrtifolia; A. huegelii	Australia	Sampson & Walker 1982; Cook & Dube 1989; Shivas 1989
	A. verticillata	Australia, New Zealand	Sampson & Walker 1982; Pennycook 1989; Gadgil 2005
	A. baileyana	New Zealand	Pennycook 1989; Gadgil 2005
	A. mangium	Vietnam	Dell et al. 2012; Pham et al. 2014
Phytophthora cryptogea	*A. longifolia; A. salicina; A. notabilis*	Australia	Cook & Dube 1989
Phytophthora frigida	*A. mearnsii, A. decurrens*	Brazil, South Africa	Alves et al. 2016; Maseko et al. 2007; Burgess et al. 2020
Phytophthora gibbosa	*A. pycnantha*	Australia	Jung et al. 2011; Aghighi et al. 2012; Yang et al. 2013
Phytophthora gondwanensis	*A. mearnsii*	Brazil	Burgess et al. 2021
Phytophthora meadii	*A. mearnsii*	South Africa	Roux & Wingfield 1997
Phytophthora nicotianae	*A. mearnsii*	South Africa, Brazil	Hall 1993; Erwin & Ribeiro 1996; Crous et al. 2000; Dos Santos et al. 2005
Phytophthora nicotianae var. *parasitica*	*A. mearnsii*	South Africa	Zeijlemaker 1971; Boa & Lenne 1994
Phytophthora niederhauseri	*A. dealbata*	Italy	Faedda et al. 2013; Abad et al. 2014
Phytophthora palmivora	*A. dealbata*	Greece	Pantidou 1973
Phytophthora parasitica	*A. mearnsii*	South Africa	Roux & Wingfield 1997
Phythopthora parvispora	*A. mangium*	Vietnam	Pham et al. 2014
Phytophthora sp.	*A. mangium, Acacia sp.*	Malaysia, India, Thailand, Tanzania, Kenya	Boa & Lenne 1994; Roux et al. 2005

Table 1.7. List of *Phytophthora* spp. on *Eucalyptus* spp.

Species	Host	Distribution	References
Phytophthora alticola	*Eucalyptus badjensis,*	South Africa	Maseko et al. 2007;
	E. macarthurii,		Simamora et al. 2015,
	E. dunnii		Yang et al. 2017
	E. globulus	Portugal	Diogo et al. 2023
Phytophthora arenaria	*E. drummondii*	Australia	Simamora et al. 2015;
			Simamora et al. 2017
Phytophthora boehmeriae	*E. grandis,*	South Africa	Crous et al. 2000
	E. macarthurii,		
	E. dunnii		
	E. pilularis	Australia	Erwin & Ribeiro 1996
Phytophthora boodjera	*Eucalyptus sp.*	Australia	Simamora et al. 2018
Phytophthora cactorum	*Eucalyptus* sp.	California USA	Tidwell 1990; French 1989;
			Erwin & Ribeiro 1996;
			Yakabe et al. 2009
	Eucalyptus sp.,	Australia	Sampson & Walker 1982
	E. risdonii		
	Eucalyptus sp.	Australia	Erwin & Ribeiro 1996
	E. niphophila	Australia	Khaliq et al. 2019
Phytophthora cacuminis	*E. coccifera*	Australia	Khaliq et al. 2019
Phytophthora cambivora	*Eucalyptus* sp.	Australia	Erwin & Ribeiro 1996
Phytophthora captiosa	*E. botryoides,*	New Zealand	Gadgil 2005;
	E. saligna		Dick et al. 2006
	E. saligna	New Zealand	Blair et al. 2008;
			Yang et al. 2014;
			Martin et al. 2014;
			Yang et al. 2017;
			Jung et al. 2017;
			Khaliq et al. 2019
Phytophthora citricola	*Eucalyptus* sp.	California,	Oudemans et al. 1994;
		Australia	Erwin & Ribeiro 1996
	E. deanei,	Australia	Oudemans et al. 1994;
	E. marginata		Burgess et al. 2009
Phytophthora citrophthora	*E. ficifolia*	Australia	Cook & Dube 1989
	Eucalyptus sp.	United States	Tidwell 1990; French 1989;
			Erwin & Ribeiro 1996
Phytophthora condilina	*E. wandoo*	Australia	Burgess et al. 2018
Phytophthora cryptogea	*E. ficifolia,*	Australia	Shivas 1989
	E. rudis		
	E. ficifolia	Australia,	Cook & Dube 1989;
		Japan	Hardy & Sivasithamparam 1988;
			Erwin & Ribeiro 1996
	E. radiata,	Australia	Mills et al. 1991;
	Eucalyptus sp.		Erwin & Ribeiro 1996

Table 1.7. (Continue)

Species	Host	Distribution	References
Phytophthora cinnamomi	*E. marginata,*	Hawaii USA	Raabe et al. 1981;
	E. robusta,		Stukely et al. 2007b
	E. obliqua,		
	E. baxteri,		
	E. calophylla,		
	E. citriodora,		
	E. sieberiana,		
	E. pilularis,		
	E. saligna		
	E. marginata,	Australia	Shivas 1989; Arentz 2017;
	E. gomphocephala,		Stukely et al. 2007b;
	E. occidentalis,		Rea et al. 2010;
	E. Lehmannii		Simamora et al. 2017
	E. obliqua,	Australia	Sampson & Walker 1982;
	E. morrisbyi,		Cook & Dube 1989
	E. amygdalina,		
	E. viminalis,		
	E. globulus,		
	E. regnans,		
	E. delegatensis,		
	E. leucoxylon,		
	E. sieberi,		
	E. baxteri,		
	E. rubida,		
	E. macrandra,		
	E. megacarpa		
	E. citriodora,	South Africa	Crous et al. 2000
	E. lehmannii,		
	E. radiata,		
	E. smithii,		
	E. macarthurii,		
	E. dunnii,		
	E. fastigata,		
	E. fraxinoides		
	E. ficifolia	New Zealand	Pennycook 1989; Gadgil 2005
	E. globulus	France	Jung et al. 2016
	Eucalyptus sp.	California,	Tidwell 1990;
		Brazil,	Mendes al. 1998;
		Spain	Jung et al. 2016
	Eucalyptus sp.	Australia	Spaulding 1961;
			Anonymous 1964;
			Oudemans & Coffey 1991a;
			Erwin & Ribeiro 1996;
			Langrell et al. 2011

Table 1.7. (Continue)

Species	Host	Distribution	References
Phytophthora cinnamomi	*E. marginata,* *E. gummifera*	Australia	Erwin & Ribeiro 1996; Liew et al. 1998; Duran et al. 2010
Phytophthora drechsleri	*E. marginata*	Australia	Shivas 1989
	Eucalyptus sp.	Australia, Papua New Guinea	Sampson & Walker 1982; Erwin & Ribeiro 1996; Shaw 1984
Phytophthora elongata	*E. marginata*	Australia	Rea et al. 2010; Bennett et al. 2017; Burgess et al. 2020
Phytophthora fallax	*E. delegatensis,* *E. fastigata,* *E. nitens,* *E. regnans*	New Zealand	Gadgil 2005; Dick et al. 2006
	E. delegatensis	New Zealand	Yang et al. 2014
	E. delegatensis, *E. fastigata,* *E. nitens*	New Zealand	Yang et al. 2017
	E. fastigata	New Zealand	Blair et al. 2008; Martin et al. 2014; Khaliq et al. 2019
	Eucalyptus sp., *E. regnans*	Australia	Cunnington et al. 2010
Phytophthora frigida	*E. smithii*	South Africa	Maseko et al. 2007; Abad et al. 2011; Crouch & Tomaso-Peterson 2012; Hong et al. 2012; Yang et al. 2017; Rea et al. 2010; Burgess et al. 2020
	Eucalyptus sp., *E. dunnii*	Australia	Simamora et al. 2015; Scarlett et al. 2015
Phytophthora gonapodyides	*E. obliqua*	Australia	Jung et al. 2011; Aghighi et al. 2012
Phytophthora gondwanensis	*E. smithii*	South Africa	Crous et al. 2015a
Phytophthora gregata	*Eucalyptus* sp.	Australia	Jung et al. 2011
Phytophthora heveae	*Eucalyptus pilularis*	Australia	Oudemans & Coffey 1991b; Erwin& Ribeiro 1996; Weir et al. 2015; Scarlett et al. 2015
Phytophthora megasperma	*E. marginata,* *Eucalyptus* sp.	Australia	Shivas 1989; Erwin & Ribeiro 1996

Table 1.7. (Continue)

Species	Host	Distribution	References
Phytophthora multivora	*E. gomphocephala,* *E. marginata*	Australia	Scott et al. 2019; Jung & Burgess 2009
	E. marginata	Australia	Abad et al. 2011; Henricot et al. 2014; Ann et al. 2014; Jung et al. 2017
	E. victrix	Australia	Aldaoud et al. 2016
Phytophthora nicotianae	*Eucalyptus* sp.	Australia, Italy	Erwin & Ribeiro 1996; Hall 1993
	E. smithii, *E. fastigata,* *E. elata,* *E. macarthurii,* *E. nitens, E. dunnii*	South Africa	Maseko et al. 2001
	E. citriodora	Brazil	Erwin & Ribeiro 1996
	E. delegatensis, *E. globulus,* *E. regnans*	Italy	Erwin & Ribeiro 1996
	E. viminalis	Argentina	Erwin & Ribeiro 1996
	E. sieberi	Australia	Hall 1993
Phytophthora nicotianae var. *parasitica*	*E. gomphocephala*	Australia	Shivas 1989.
Phytophthora parasitica	*E. citriodora*	Brazil	Spaulding 1961; Anonymous 1964
	E. viminalis	Argentina	Spaulding 1961; Anonymous 1964
	Eucalyptus sp.	Brazil, United Kingdom, Spain	Erwin & Ribeiro 1996; Jung et al. 2016
Phytophthora polymorphica	*Eucalyptus* sp.	Australia	Gerrettson-Cornell & Simpson 1984
Phytophthora thermophila	*E. marginata*	Australia	Jung et al. 2011; Aghighi et al. 2012; Khaliq et al. 2019; Burgess et al. 2018
Phytophthora sp.	*E. cinerea*	Florida USA	Alfieri Jr 1984
	E. globulus	Mexico	Alvarez 1976
	Eucalyptus sp., *E. lehmannii*	California	Tidwell 1990; French 1989
	Eucalyptus sp.	California, Brazil, Spain	French 1989; Mendes et al. 1998; Jung et al. 2016
	E. marginata	Australia	Rea et al. 2010
	E. niphophila	United Kingdom	Jung et al. 2016

Chapter 2

Calonectria species diversity on eucalypts in Indonesia

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ABSTRACT

Diseases increasingly threaten the rapidly expanding eucalypt plantation industry of Indonesia. Of these, leaf blight caused by *Calonectria* spp. is considered amongst the more important problems, causing losses both in production nurseries and plantations. Using DNA sequence data based on the translation elongation factor 1-alpha, β-tubulin, calmodulin, and histone H3 gene regions, 163 isolates of *Calonectria* spp. obtained from diseased eucalypt seedlings in nurseries and infected leaves in plantations were identified as *Calonectria acicola*, *C. hawksworthii, C. lombardiana, C. multiseptata, C. pseudoreteaudii* and *C. reteaudii.* Of these, *C. lombardiana* was by far the most commonly isolated and accounted for approximately 84% of the isolates. Given the predominance of this fungus, it is interesting that it has not previously been reported from Indonesia. This is also the first report of *C. pseudoreteaudii* and *C. acicola* from the country. All six species of *Calonectria* were found to be pathogenic to eucalypts in artificial inoculation studies. *Calonectria lombardiana* was generally the most pathogenic species and eucalypt genotypes displayed different levels of susceptibility, providing confidence that disease caused by this fungus can be reduced by selecting disease-tolerant planting stock.

Keywords: *Cylindrocladium*, forestry, leaf and shoot blight, multi-gene phylogeny

INTRODUCTION

Calonectria (Nectriaceae, Hypocreales) is a genus that accommodates numerous important pathogens that are widely distributed especially in tropical and sub-tropical regions of the world (Crous 2002; Lombard et al. 2010a; Marin-Felix et al. 2017). These fungi are mainly soil-borne pathogens but infect most plant tissues on susceptible hosts (Crous 2002; Pham et al. 2019; Li et al. 2017; Lopes et al. 2018; Jiang et al. 2019). Liu et al. (2020) produced the most

comprehensive recent taxonomic study on these fungi, defining 120 species based on sequence data for eight gene regions. These included many species known as causal agents of diseases on important forest plantation trees including *Pinus* (Hodges and May 1972; Lombard et al. 2009), *Acacia* (Lombard et al. 2010a) and *Eucalyptus* (Lombard et al. 2015; Li et al. 2017).

Eucalypts are the most widely planted tree used to establish short-rotation plantations globally (Couto et al. 2011; Harwood and Nambiar 2014). Many diseases have been reported on these trees including those caused by a variety of *Calonectria* spp. (Booth et al. 2000; Rodas et al. 2005; Crous et al. 2019). These fungi are amongst the most common pathogens of eucalypts in plantations and nurseries causing *Calonectria* leaf blight (CLB) as well as root disease and cutting rot (Crous 2002; Lombard et al. 2010b). Twenty-seven species of *Calonectria* are currently known to occur on eucalypts worldwide (Crous et al. 2019; Liu et al. 2020). Several of these species were reported to cause serious leaf and shoot blight disease in eucalypt plantations in Southeast Asia (Crous et al. 1998; Old et al. 2003; Chen et al. 2011; Lombard et al. 2015; Li et al. 2017; Pham et al. 2019; Pham et al. 2022).

Industrial forest plantation programs reliant on eucalypts have expanded rapidly in Indonesia and especially in the islands of Sumatra and Kalimantan since the early 1990's (Harwood and Nambiar 2014). Concomitant with this growing industry, there has been an increase in disease problems on these trees (Wingfield et al. 1996; Crous et al. 1998; Gryzenhout et al. 2010; Coetzee et al. 2011; McTaggart et al. 2016; Bophela et al. 2019; Siregar et al. 2020; Pham et al. 2021; Jami et al. 2022). Of these, leaf blight caused by species of *Calonectria* has become increasingly common (Pham et al. 2019; Pham et al. 2022). Particularly in the nursery situation, these pathogens are able to spread rapidly, and losses can seriously hamper nursery production or plantation establishment. The aims of this study were consequently to identify *Calonectria* species causing diseases in eucalypt nurseries and plantations in Indonesia and to assess their relative importance by pathogenicity tests.

MATERIALS AND METHODS

Sample collections and fungal isolations

Leaves and seedlings showing CLB symptoms (Figure 2.1) were collected in both nurseries and plantations in Kalimantan and Sumatra during regular disease surveys in 2018–2019. These

included eight eucalypt nurseries and 26 plantation sites; and two *Acacia crassicarpa* plantation sites in proximity to eucalypt plantations. This resulted in a collection of 61 diseased seedlings and leaves from 102 diseased trees (Table 2.1). Samples were collected from Riau, Central Sumatra including Sei Kebaro (15 leaves and 5 seedlings), Pelalawan (31 leaves and 34 seedlings) and Kuantan Singingi (36 leaves and 8 seedlings); from North Sumatra including Porsea (6 leaves and 4 seedlings); from Kalimantan including East Kalimantan (10 leaves and 2 seedlings) and North Kalimantan (4 leaves and 8 seedlings) (Table 2.1; Figure 2.2). The number of samples collected depended on the disease incidence at the sampling sites.

All collected samples were placed in individual brown paper bags and transported to the laboratory for further study. Pieces (0.5 × 0.5 cm^2) of leaf or shoot tissue were cut from the border of the lesions, surface disinfested in 0.5% sodium hypochlorite for 30 seconds and rinsed three times in sterile distilled water. Surface-disinfested plant segments were placed onto the surface of potato dextrose agar (PDA Acumedia®: 40 g/L) and incubated for 3-4 days at 25 °C. Colonies showing typical morphology of *Calonectria* spp., especially orange-brownish aerial hyphae, were transferred to clean PDA in Petri dishes and all isolates were purified by sequentially transferring hyphal tips to clean PDA. All isolates considered in this study have been stored in the culture collection (CMW) of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa.

DNA extraction, PCR amplification and sequencing

Genomic DNA was extracted from the fungi using Prepman® Ultra Sample Preparation Reagent (Thermo Fisher Scientific, Waltham, MA, USA) from 4-day-old fungal cultures. A fragment of the translation elongation factor 1-α (*TEF1*) gene was amplified using primers EF1-728F (Carbone and Kohn 1999) and EF-2 (O'Donnell et al. 1998), a fragment of the β-tubulin (*TUB2*) gene using primers T1 (O'Donnell and Cigelnik 1997) and CYLTUB1R (Crous et al. 2004), a fragment of the histone H3 (*HIS3*) gene region using primers CYLH3F and CYLH3R (Crous et al. 2004), and a fragment of the calmodulin (*CMDA*) gene using primers CAL-228F (Carbone and Kohn 1999) and CAL-2Rd (Groenewald et al. 2013). Initially, the *TEF1* and *TUB2* gene regions were amplified for all isolates. Based on the preliminary sequencing results, isolates representing the range of genotypes revealed by these two loci were chosen for further study.

Polymerase chain reaction (PCR) amplifications were performed in 12 µL reactions containing 2 µL 5× MyTaq buffer (Bioline, London, UK), 0.1 µL MyTaq DNA polymerases (Bioline), 1 µL DNA, 0.5 µL of each primer (10 mM), and sterile SABAX water. The PCR protocol used included an initial denaturation (94 °C, 5 min), 10 amplification cycles (95 °C, 30 s; 55 °C for *HIS3* and *CMDA*; 52 °C for *TEF1* and *TUB2*), 45 s; 72 °C, 1 min), 30 amplification cycles with auto delta 5s (95 °C, 30 s; 55 °C for HIS3 and CDMA; 52 °C for *TEF1* and *TUB2*, 45 s; 72 °C, 1 min) and a final extension (72 °C, 10 min) (Pham et al. 2019). All the amplicons were purified using ExoSAP-IT PCR Product Cleanup Reagent (Thermo Fisher Scientific, Waltham, MA, USA) and were sequenced in both directions using the BigDye terminator sequencing kit 3.1 (Applied Biosystems, Forster City, CA, USA). Sequences were obtained by running samples on an ABI PRISM 3100 DNA sequencer (Applied Biosystems, Forster City, CA, USA). CLC Main Workbench V20.1 (Qiagen, Hilden, Germany) was used to assemble and edit the raw sequences. All the sequences emerging from this study were deposited in GenBank (http://www.ncbi.nlm.nih.gov/) (Table 2.2. S1).

Phylogenetic analyses

Sequences of previously published *Calonectria* spp. were obtained from GenBank database (http://www.ncbi.nlm.nih.gov/) for comparison with those generated in this study. Alignments of all sequences were assembled using the online version of MAFFT v. 7 (http://mafft.cbrc.jp/alignment/server/) (Katoh and Standley 2013) and then confirmed manually in MEGA v. 7 (Kumar et al. 2016). ML analyses were conducted using RaxML v. 8.2.4 on the CIPRES Science Gateway v. 3.3 (Stamatakis 2014) with default default general time reversible (GTR) substitution matrix and 1,000 rapid bootstraps. Sequences for two isolates of *Curvicladiella cignea* (CBS 109167 and CBS 109168) were used as the outgroup taxa in all phylogenetic analyses. Phylogenetic trees were viewed using MEGA v. 7 (Kumar et al. 2016).

Pathogenicity tests

Preliminary assessment of isolate pathogenicity.

A total of 12 *Calonectria* isolates including two of each species identified were selected for pathogenicity tests. These selections were made specifically to include a diversity of areas of origin and/or host. The isolates were grown on 2% PDA for 10 days at 28 °C. Sporulation was induced using the method described by Alfenas et al. (2013) as follows: 10 ml of sterile distilled

water was poured onto the surface of the cultures in Petri-dishes and the aerial mycelium was scraped from the cultures using a sterile spatula. The remaining colonies on the agar surface were rinsed with sterile distilled water to ensure that all aerial mycelium had been removed. Subsequently, 20 mL of distilled water was added to the Petri-dishes and the sub-surface mycelium was kept submerged for 48 hours. The excess water was then removed, and the colonies were dried using sterile tissue paper. Finally, the colonies were incubated for 48 hours in a laminar air flow cabinet at room temperature (approx. 25 °C) with the Petri dish lids removed. After 48 hours, the conidia forming on the surfaces of the colonies were harvested by pouring 10 mL of sterile distilled water into the Petri-dishes and the inoculum suspension was then diluted to 1×10^6 spores/mL.

Inoculations were conducted on a 14-week-old *E. grandis* x *E. pellita* clone (ECL05). Two mL of a 1×10^6 spore suspension of each isolate was sprayed onto the surface of 30 plants until run-off. After inoculation, a piece of wet cotton was placed at the collar of the plant stem and each plant was covered with a transparent plastic bag to ensure leaf wetness and to maintain a high level of humidity. After 48 hours, the plastic bags were removed, and the plants maintained for 48 hours at room temperature. Control plants were treated in a similar manner, but the inoculum was replaced with sterile distilled water. The trial was arranged in a completely randomized design.

Disease severity was assessed four days after inoculation using a five-level rating scale where 0 = 0%; 1 = 1–25%; 2 = 26–50%; 3 = 51–75% and 4 = 76–100% of the leaves infected on each plant (Figure 2.3). To fulfil Koch's postulates, isolations were made from inoculated tissue and the resulting isolates were identified based on morphology. Data were analysed using Kruskal-Wallis tests to determine whether there were statistically significant differences between the treatments. Pairwise comparisons were then conducted using Wilcoxon rank sum test with continuity correction. All statistical analyses were performed in R statistical software, version 3.2.0 (R Core Team 2020).

Relative tolerance of eucalypt clones.

Five eucalypt genotypes that included three *E. pellita* clones (ECL01, ECL02, and ECL03) and two *E. grandis* x *E. pellita* hybrid clones (ECL04 and ECL05) commonly deployed in plantations were selected to screen against the most aggressive and predominant *Calonectria* species found in this study. Twenty 14-week-old plants of each clone were inoculated as

described above with an equal number of plants used as controls. The trial was arranged in a completely randomized design. Disease severity was assessed four days after inoculation using the same rating scale described for the preliminary inoculation trial. The inoculated fungus was re-isolated from symptomatic tissue and identified based on morphology. Data were analysed in the same manner as the initial inoculation trial.

RESULTS

Isolates

In total, 163 isolates were obtained from diseased leaves and shoots. Most of the isolates (129) were obtained from symptomatic leaves on trees in plantations or seedlings in nurseries in Central Sumatra, Riau as the diisease was most commonly found (Table 2.1; Figure 2. 2.). Of these, five isolates were collected from *A*. *crassicarpa* plantations. In addition, 10 isolates were obtained from North Sumatra and 24 from Kalimantan (Table 2.1; Figure 2.2). The most commonly isolated species accounted for approximately 84% of the isolates (Figure 2.2.; Figure 2.4). The distribution and relative occurrence of *Calonectria* spp. isolated in each region is presented in Figure 2.2 and 2.4.

Phylogenetic analyses

Based on the preliminary sequencing results of the *TEF1* and *TUB2* loci for all 163 isolates, 28 representative isolates were chosen for further sequencing of the *CMDA* and *HIS3* gene regions. Amplicons of approximately 660 bp were generated for the *CMDA* gene region, 430 bp for the *HIS3*, 500 bp for the *TEF1* and 560 bp for the *TUB2*. The combined sequence dataset used in the phylogenetic analyses included 73 ingroup taxa and 2214 characters. The ML tree with bootstrap support values is presented in Figure 2.5. Phylogenetic analyses resulted in the recognition of species residing in two species complexes including the *Calonectria reteaudii* complex and *Calonectria cylindrospora* complex (Figure 2.5).

Of the 28 isolates subjected to four gene region phylogenetic analyses, 26 were in the *C. reteaudii* complex and clustered in five clades. Of these, the majority of the isolates (11) grouped with the ex-type isolate of *C. lombardiana.* In addition, two isolates grouped with *C. pseudoreteaudii,* six with *C. reteaudii*, four with *C. multiseptata* and three with *C. acicola*. The

remaining isolates resided in the *C._cylindrospora* complex, of which two isolates were identified as *C. hawksworthii* (Figure 2.5).

Pathogenicity tests

Preliminary screening. All 12 *Calonectria* isolates representing six species, *C. lombardiana, C. pseudoreteaudii, C. reteaudii, C. acicola, C. multiseptata* and *C. hawksworthi,* were shown to be pathogenic to *Eucalyptus* clone ECL05. Four days after inoculation, all isolates produced severe leaf blight symptoms (Figure 2.6). The Kruskal-Wallis test [H = 282.05, df = 12 and P (p-value) < 2.2e-16] confirmed that there were significant differences among the *Calonectria* isolates. No disease symptoms were observed on the plants inoculated as controls (Figure 2.7; Figure 2.9). Among all six species, *C. hawksworthii* yielded a lower disease severity score and was thus considered less aggressive (Figure 2.9). *Calonectria* spp. were re-isolated from lesions on all inoculated plant and identified as representing the inoculated species. No symptoms appeared on the control plants.

***Relative tolerance of eucalypt clones to* C. lombardiana**.

Four days after inoculation, all five eucalypt clones inoculated with an isolate of *C. lombardiana* (CMW 54860), shown to be the predominant species in this study, displayed extensive symptoms of leaf blight. In some cases, an infected clone (*i.e.* ECL03) showed variation in its level of susceptibility (Figure 2.10). Based on Kruskal-Wallis test results, there were significant differences in susceptibility among the tested clones (H = 80.574, df = 5 and P = 6.365e-16). ECL05 and ECL04 (*E. grandis* x *E. pellita*) were the most susceptible clones to *C. lombardiana*, where they showed significant differences from the other clones and the controls (P < 0.05) (Figure 2.10). ECL01, ECL02 and ECL03 (*E. pellita*) appeared to be more tolerant to infection by *C. lombardiana* than the hybrid clones (Figure 2.8). *Calonectria lombardiana* was re-isolated from lesions on all inoculated plants. No symptoms appeared on the control plants.

DISCUSSION

A total of 163 isolates of *Calonectria* spp. were characterized from diseased eucalypt seedlings in nurseries or leaves in plantations of North and Central Sumatra as well as East and North

Kalimantan, Indonesia. Based on multigene phylogenetic analyses, six species residing in two species complexes were identified. These included *Calonectria lombardiana*, *C. reteaudii, C. acicola, C. multiseptata, C. pseudoreteaudii* and *C. hawksworthii*. An inoculation trial showed that all six *Calonectria* species were pathogenic and that eucalypt genotypes differed in their susceptibility to *C. lombardiana,* which was the most commonly isolated species.

Species in the *C. reteaudii* species complex emerged as the most diverse in this study. Most species in this complex are well-known pathogens associated with leaf and shoot blight on eucalypts and they have predominantly been found in tropical and subtropical regions of Southeast Asia, South China and Australasia (Crous 2002; Old et al. 2003; Crous et al. 2006; Lombard et al. 2010b; Li et al. 2017; Pham et al. 2019; Liu et al. 2020; Wang and Chen 2020; Li et al. 2022; Liu et al. 2022). This is the first report of *C. acicola*, *C. pseudoreteaudii* and *C. lombardiana* from Indonesia.

Calonectria lombardiana was the predominant species in all sampling areas and accounted for approximately 84% of the isolates. Given the predominance of this fungus, it is interesting that it has not previously been reported from Indonesia. This species was first isolated from *Xanthorrhoea australis* in Australia (Crous 2002). *Calonectria lombardiana* was collected from both nursery and plantation in all sampling sites in Central Sumatra, East Kalimantan and North Kalimantan, but was not found in North Sumatra. Besides being the most commonly occurring species, *C. lombardiana* emerged as one of the most aggressive species in pathogenicity tests.

Calonectria hawksworthii was the only species in the *C. cylindrospora* complex found in this study. This species was previously found to cause leaf spots on *Nelumbo nucifera* in Mauritius (Crous 2002) and on eucalypts in Indonesia and China (Lombard et al. 2010b, 2015). In pathogenicity trials, it can cause leaf blight symptoms, however, was less aggressive than the other species tested in the this study.

Pathogenicity tests in this study showed that all six species of *Calonectria* were pathogenic to a single clone of *Eucalyptus*. However, *C. hawksworthii* was clearly less aggressive than the other five species. Of those five species, four species (*C. lombardiana*, *C. multiseptata*, *C. reteaudii* and *C. pseudoreteaudii*) have been previously reported on eucalypts. The remaining species (*C. acicola*) was previously known only from *Pinus radiata* in New Zealand (Gadgil and Dick 2004). This is the first report of *C. acicola* infecting eucalypts.

When an isolate of the most commonly occurring species (*C. lombardiana*) was inoculated on different genotypes of eucalypt, these plants were shown to differ in their susceptibility to infection. In this study, hybrids of *E. pellita* and *E. grandis* were more susceptible to leaf blight than pure *E. pellita* genotypes. This highlights the importance of selecting disease resistant eucalypt genotypes to avoid CLB in the future, similar to the situation with various other eucalypt disease problems that have been resolved through active breeding and selection of disease tolerant planting stock (van Heerden et al. 2005; Wingfield 2003).

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APPENDIX

Figure 2. 1. Symptoms of *Calonectria* infection: (a). on leave of *Eucalyptus* seedlings; (b). on stems of *Eucalyptus* seedlings; (c). on leaves of *Eucalyptus* trees in the field.

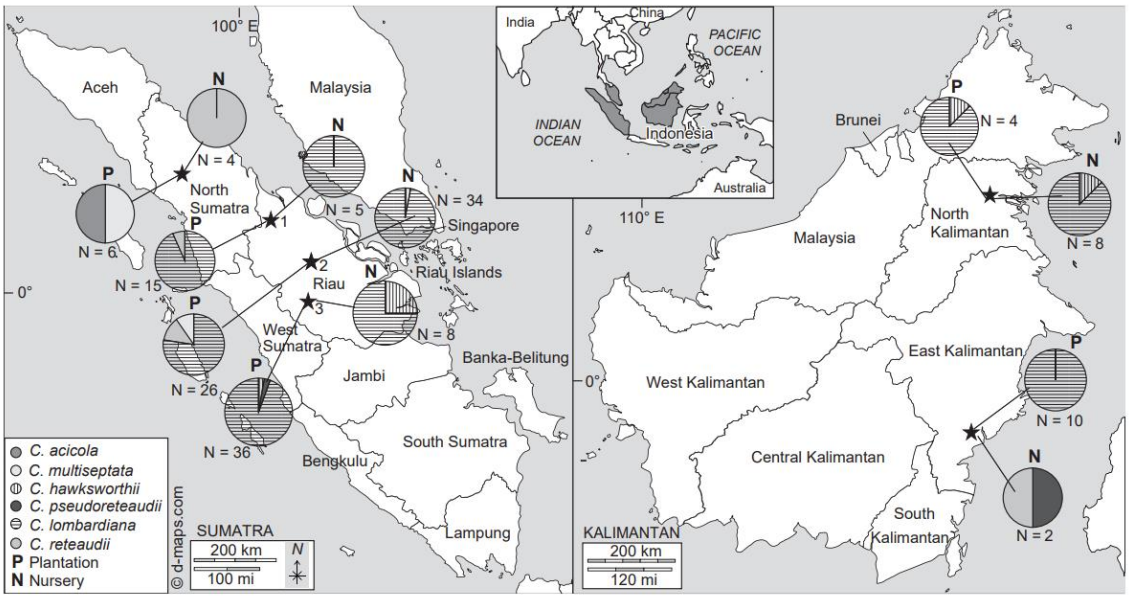

Figure 2. 2. Geographic location of the sampling sites in Indonesia and the diversity of *Calonectria* spp. isolated in each region.

Figure 2. 3. Disease severity scoring chart.

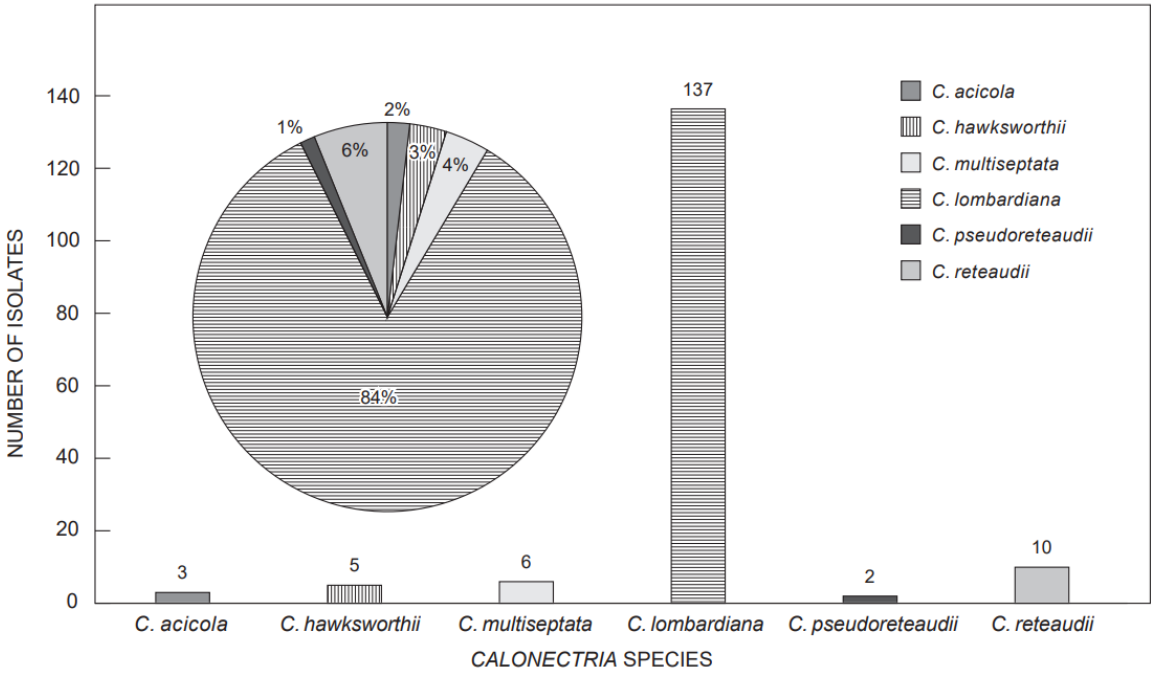

Figure 2. 4. Relative occurrence of the *Calonectria* species from plantations and nurseries in Indonesia. Different species are represented by different patterns.

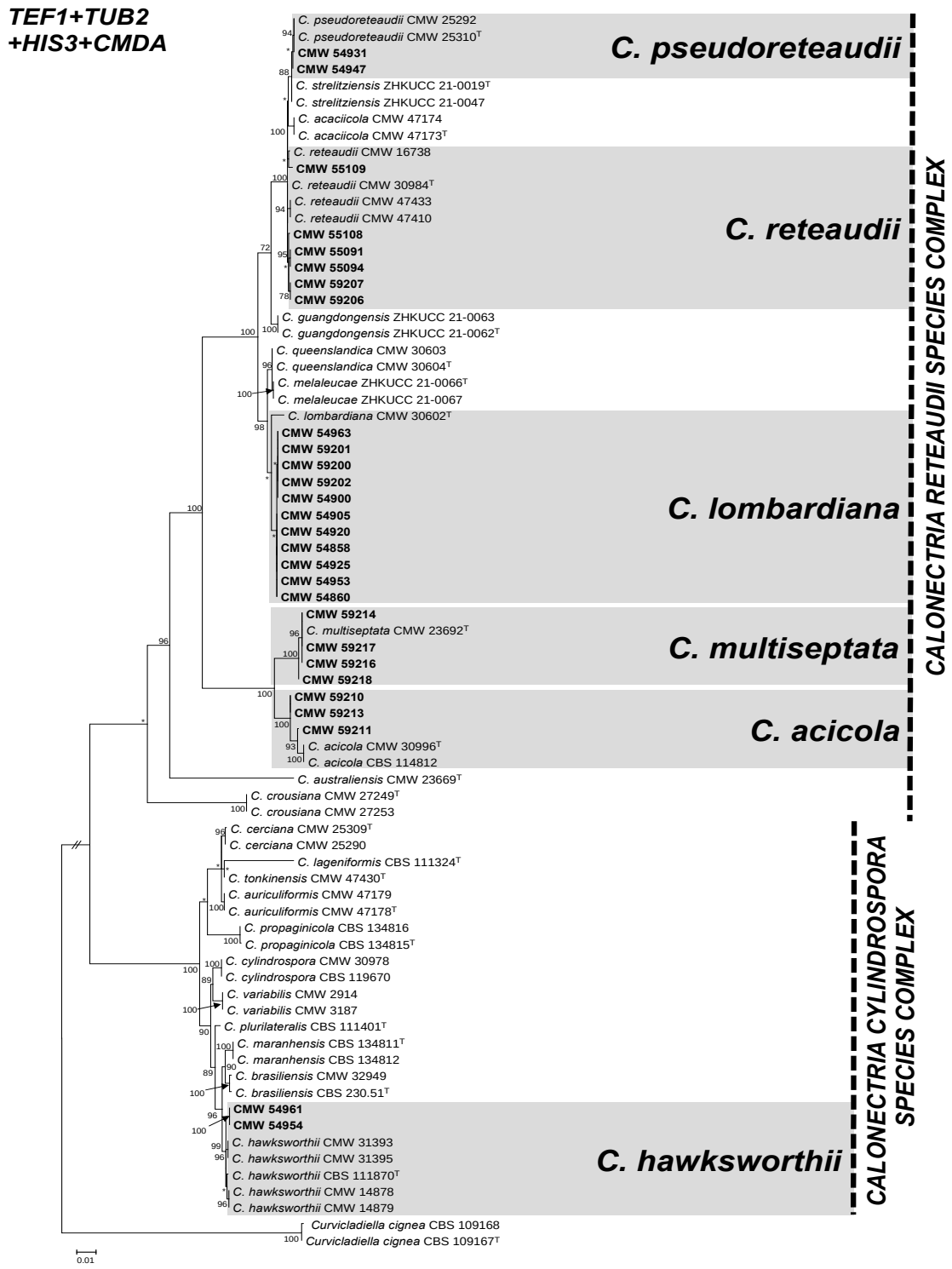

Figure 2. 5. Phylogenetic tree based on maximum likelihood (ML) analysis of a combined data set of *TEF1, TUB2, HIS3* and *CMDA* sequences for *Calonectria* spp. Isolates sequenced in this study are presented in boldface. Bootstrap values of ≥70% for ML analyses are indicated at the nodes. Bootstrap values <70% are marked with "*". Isolates representing ex-type material are marked with "T". *Curvicladiella cignea* (isolate CBS 109167 and CBS 109168) represents the outgroup.

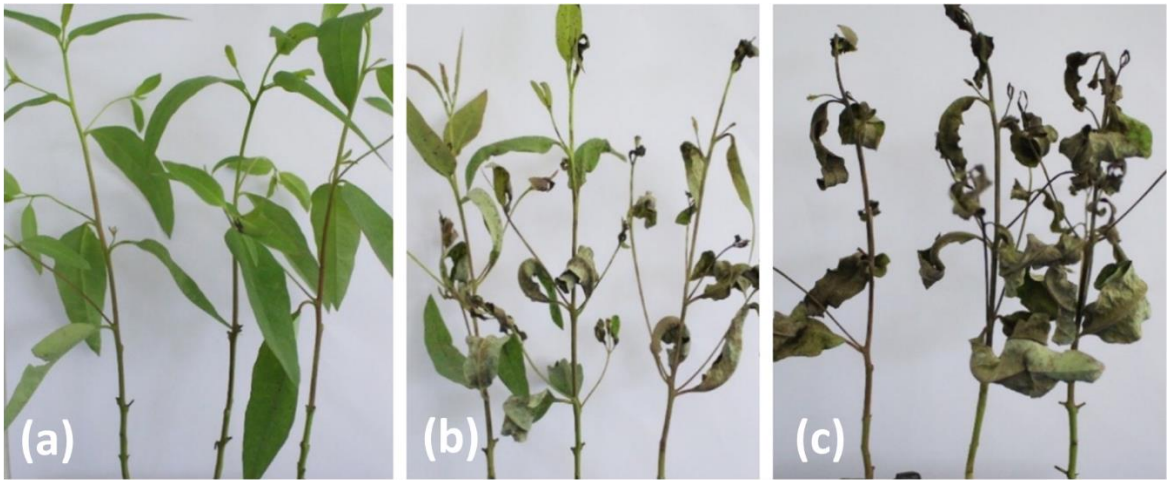

Figure 2. 6. Results of the pathogenicity test on *Eucalyptus* clone ECL05: (a). healthy plants; (b) infected plants 2-d after inoculation (dai) with moderate leaf blight; (c). infected plants at 4-dai with severe leaf blight resulting in plant die-off and defoliation.

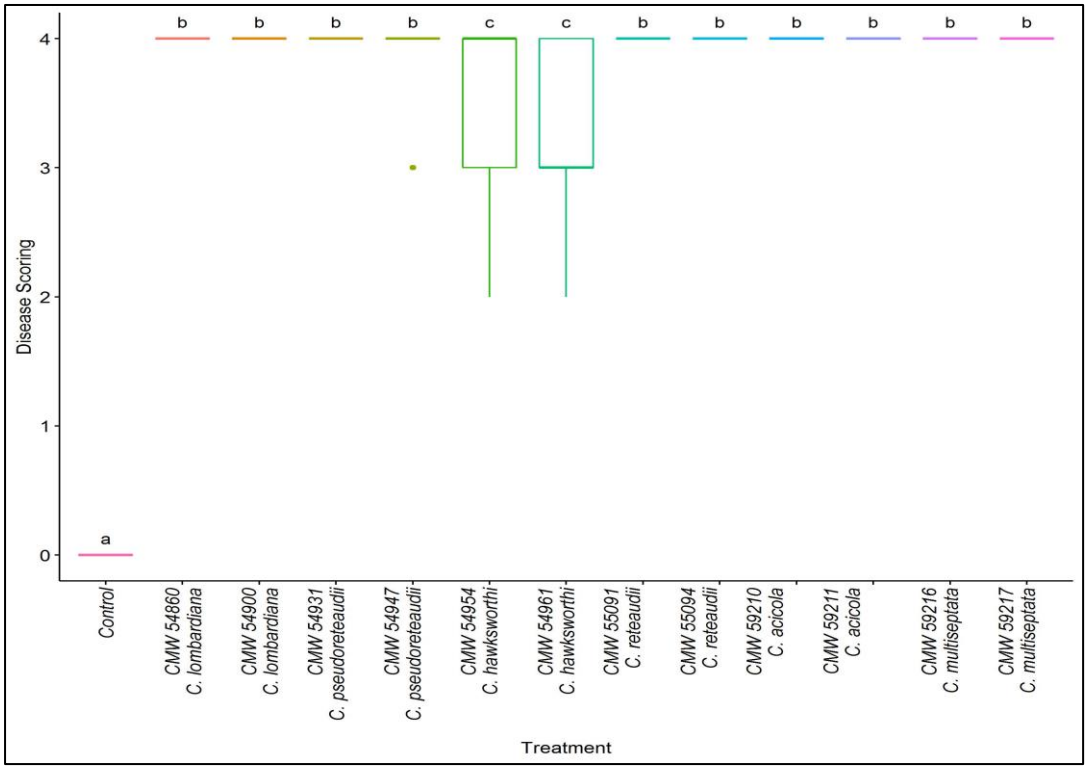

Figure 2. 7. Graphical representations of *Eucalyptus* clone ECL05 pathogenicity trials using 12 different *Calonectria* isolates representing six different *Calonectria* spp. Vertical bars represent the standard error of the means. Different letters indicate statistically significance at $p \leq 0.05$.

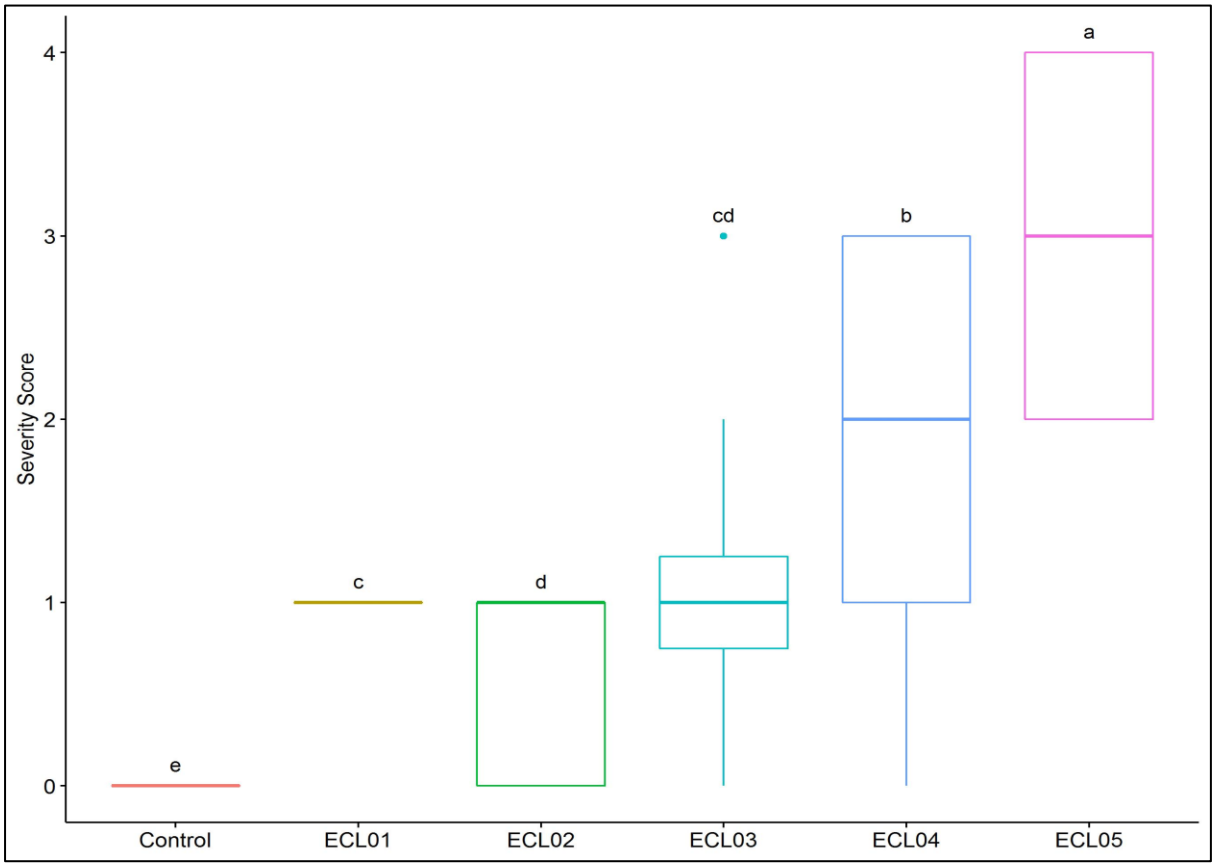

Figure 2. 8. Box plot indicating the severity score resulting from inoculation trials of five eucalypts genotypes inoculated with *C. lombardiana* (CMW 54860) and the controls. Vertical bars represent the standard error of the means. Different letters indicate statistically significance at $p \leq 0.05$.

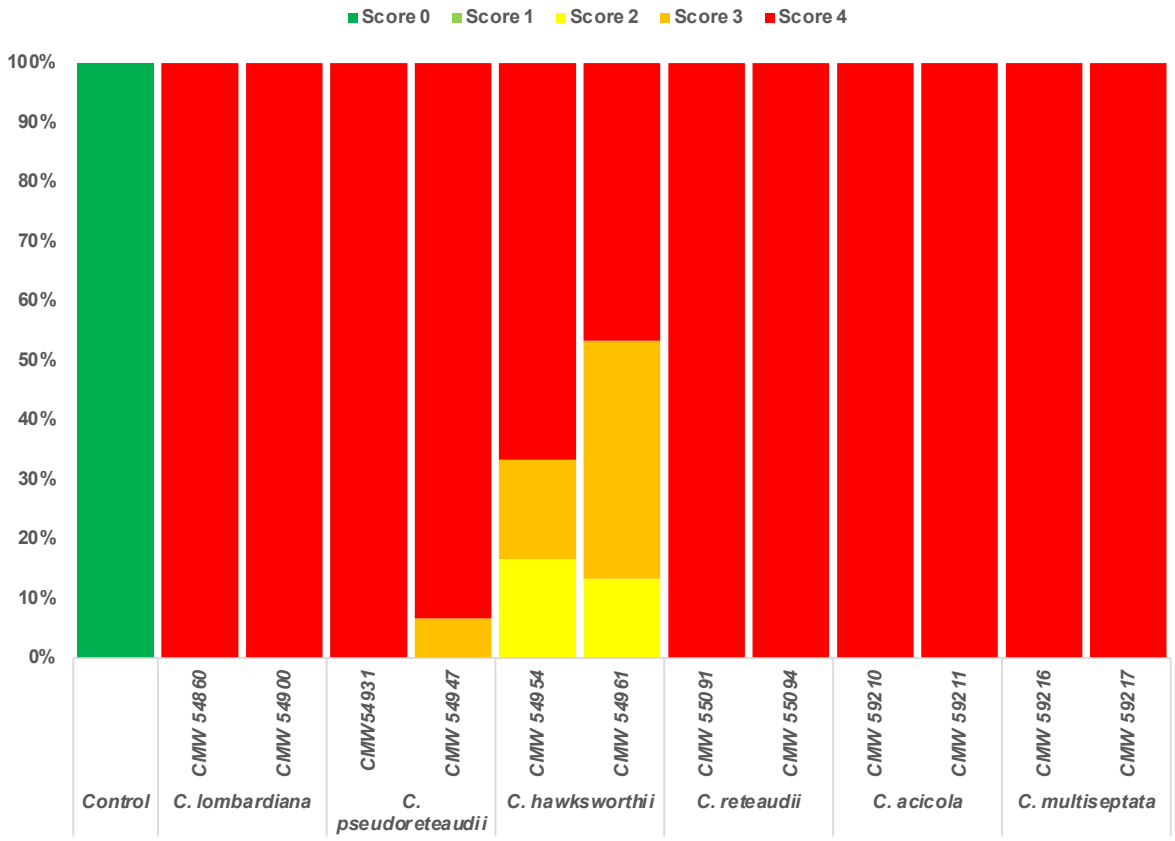

Figure 2. 9. Stack bar graphs representing the aggressiveness of different *Calonectria* spp. on *Eucalyptus* clone ECL05 assessed using 0–4 scale.

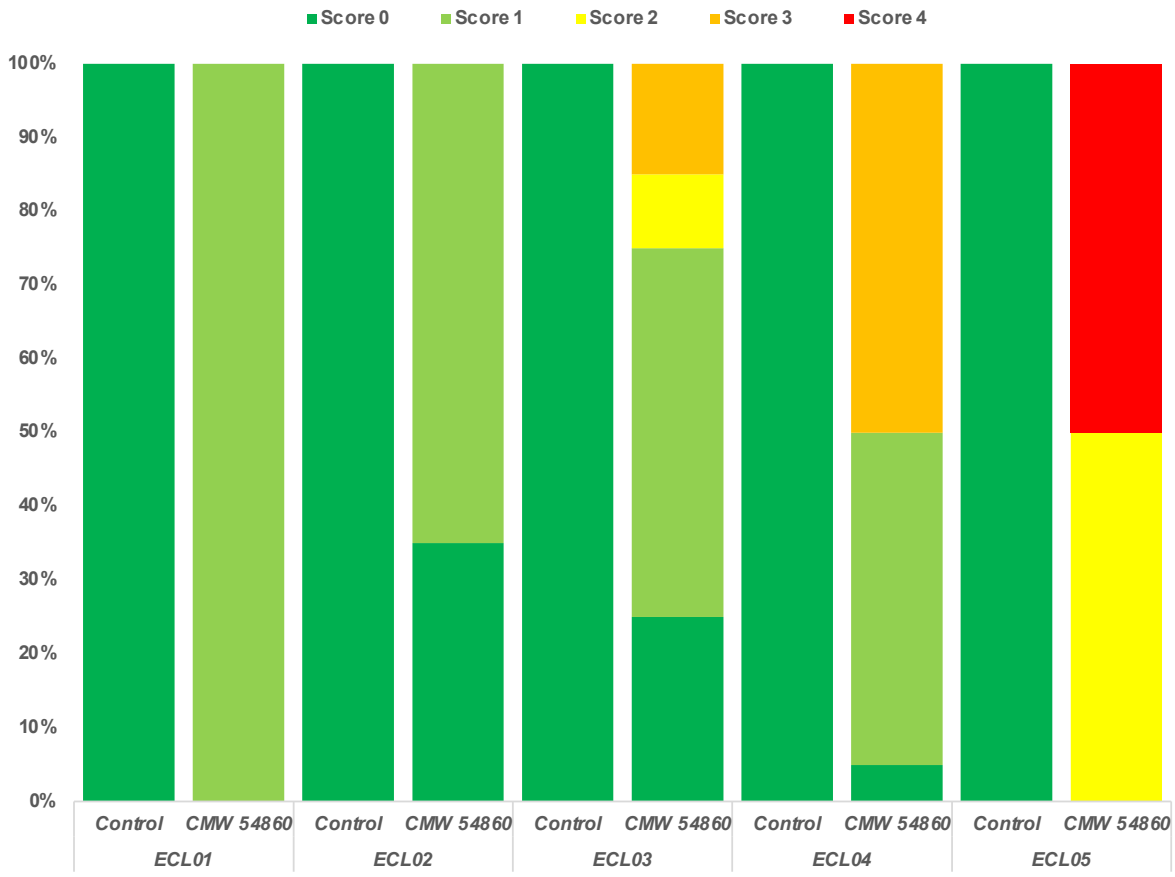

Figure 2. 10. Stack bar graphs representing the aggressiveness of *C. lombardiana* (CMW 54860) on five *Eucalyptus* clones assessed using 0–4 scale.

Table 2.1. Number of samples collected from nurseries and plantations in regions of Sumatra and Kalimantan

Region	Altitude (m.a.s.l.)	Nursery	Plantation	Total
North Sumatra (Porsea)	1 200	4	6	10
Central Sumatra/Riau 1 (Sei Kebaro)	56	5	15	20
Central Sumatra/Riau 2 (Pelalawan)	33	34	31	65
Central Sumatra/Riau 3 (Kuantan Singingi)	52	8	36	44
East Kalimantan (IHM complex)	70	2	10	12
North Kalimantan (AHL complex)	585	8	4	12
Total		61	102	163

Table 2.2. Collection details and GenBank accession numbers of isolates included in the phylogenetic analyses

Species	Isolate number	Host/ substrate	Locality	GenBank accessions				Reference
				CMDA	HIS3	TEF1	TUB	
Calonectria acaciicola	CMW 47173T = CBS 143557	Soil	Vietnam	MT335160	MT335399	MT412690	MT412930	Liu et al. (2020)
Calonectria acaciicola	CMW 47174 = CBS 143558	Soil	Vietnam	MT335161	MT335400	MT412691	MT412931	Liu et al. (2020)
Calonectria acicola	CMW 59210	*E. grandis* x *E. urophylla*	Porsea, North Sumatra, Indonesia	OQ296456	OQ296482	OQ296505	OQ296532	This study
Calonectria acicola	CMW 59211	*E. grandis* x *E. urophylla*	Porsea, North Sumatra, Indonesia	OQ296457	OQ296483	OQ296506	OQ296533	This study
Calonectria acicola	CMW 59213	*E. grandis* x *E. urophylla*	Porsea, North Sumatra, Indonesia	OQ296458	OQ296484	OQ296507	OQ296534	This study
Calonectria acicola	CMW 30996T	*Phoenix canariensis*	New Zealand	MT335162	MT335401	MT412692	MT412932	Liu et al. (2020)
Calonectria acicola	CBS 114812 = CMW 51216	*Phoenix canariensis*	New Zealand	MT335163	MT335402	MT412693	MT412933	Liu et al. (2020)
Calonectria auriculiformis	CMW 47178T = CBS 143561	Soil	Vietnam	MT335190	MT335430	MT412721	MT412944	Liu et al. (2020)
Calonectria auriculiformis	CMW 47179 = CBS 143562	Soil	Vietnam	MT335191	MT335431	MT412722	MT412945	Liu et al. (2020)
Calonectria australiensis	CMW 23669T = CBS 112954 = CPC 4714	*Ficus pleurocarpa*	Australia	MT335192	MT335432	MT412723	MT412946	Liu et al. (2020)
Calonectria brasiliensis	CBS 230.51T = IMI 299576	*Eucalyptus* sp.	Brazil	MT335200	MT335440	MT412731	MT412953	Liu et al. (2020)
Calonectria brasiliensis	CMW 32949 = CBS 114257 = CPC 1944	*Eucalyptus* sp.	Brazil	MT335201	MT335441	MT412732	MT412954	Liu et al. (2020)
Calonectria cerciana	CMW 25309T = CBS 123693	*E. urophylla* × *E. grandis*	China	MT335211	MT335451	MT412742	MT412963	Liu et al. (2020)
Calonectria cerciana	CMW 25290 = CBS 123695	*E. urophylla* × *E. grandis*	China	MT335212	MT335452	MT412743	MT412964	Liu et al. (2020)
Calonectria crousiana	CMW 27249T = CBS 127198	*E. grandis*	China	MT335230	MT335470	MT412761	MT412982	Liu et al. (2020)
Calonectria crousiana	CMW 27253 = CBS 127199	*E. grandis*	China	MT335231	MT335471	MT412762	MT412983	Liu et al. (2020)
Calonectria cylindrospora	CMW 30978 = CBS 110666 = STE-U 497	*Ilex vomitoria*	USA	MT335237	MT335477	MT412768	MT412986	Liu et al. (2020)
Calonectria cylindrospora	CBS 119670 = CMW 51310 = CPC 12766	*Pistacia lentiscus*	Italy	MT335236	MT335476	MT412767	MT412985	Liu et al. (2020)
Calonectria guangdongensis	ZHKUCC 21-0062T	*Heliconia metallica*	China	MZ491127	N/A	MZ491149	MZ491171	Zhang et al. 2022
Calonectria guangdongensis	ZHKUCC 21-0063	*Heliconia metallica*	China	MZ491128	N/A	MZ491150	MZ491172	Zhang et al. 2022
Calonectria hawksworthii	CMW 54954	*E. grandis x E. pellita*	Kalimantan, Indonesia	OQ296459	OQ296485	OQ296508	OQ296535	This study

Table 2.2. (Continue)

Species	Isolate number	Host/ substrate	Locality	GenBank accessions				Reference
				CMDA	HIS3	TEF1	TUB	
Calonectria hawksworthii	CMW 54961	*E. pellita*	Kalimantan, Indonesia	OQ296460	OQ296486	OQ296509	OQ296536	This study
Calonectria hawksworthii	CMW 14878T = CBS 125277	*Eucalyptus* sp.	Indonesia	MT335378	MT335618	MT412909	MT413119	Liu et al. (2020)
Calonectria hawksworthii	CMW 14879 = CBS 125253	*Eucalyptus* sp.	Indonesia	MT335379	MT335619	MT412910	MT413120	Liu et al. (2020)
Calonectria hawksworthii	CMW 31395	*E. urophylla* × *E. grandis*	China	MT335248	MT335488	MT412779	MT412997	Liu et al. (2020)
Calonectria hawksworthii	CMW 31393 = CBS 136641	*E. urophylla* × *E. grandis*	China	MT335247	MT335487	MT412778	MT412996	Liu et al. (2020)
Calonectria hawksworthii	CBS 111870T = CMW 51194 = CPC 2405	*Nelumbo nucifera*	Mauritius	MT335254	MT335494	MT412785	MT413003	Liu et al. (2020)
Calonectria lageniformis	CBS 111324T = CMW 51177 = CPC 1473	*Eucalyptus* sp.	Mauritius	KX784574	N/A	KX784702	KX784632	Marin-Felix et al. 2017
Calonectria lombardiana	CMW 30602T = CBS 112634	*Xanthorrhoea australis*	Australia	MT335395	MT335635	MT412926	MT413133	Liu et al. (2020)
Calonectria lombardiana	CMW 54858	*E. pellita*	Teso, Riau, Indonesia	OQ296461	OQ296487	OQ296510	OQ296537	This study
Calonectria lombardiana	CMW 54860	*E. grandis x E. pellita*	Pelalawan, Riau, Indonesia	OQ296462	OQ296488	OQ296511	OQ296538	This study
Calonectria lombardiana	CMW 54900	*E. pellita*	Teso, Riau, Indonesia	OQ296463	N/A	N/A	OQ296539	This study
Calonectria lombardiana	CMW 54905	*E. pellita*	Pelalawan, Riau, Indonesia	N/A	OQ296489	OQ296512	OQ296540	This study
Calonectria lombardiana	CMW 54920	*E. pellita*	Pelalawan, Riau, Indonesia	OQ296464	OQ296490	OQ296513	OQ296541	This study
Calonectria lombardiana	CMW 54925	*E. grandis x E. pellita*	Teso, Riau, Indonesia	OQ296465	OQ296491	OQ296514	OQ296542	This study
Calonectria lombardiana	CMW 54953	*E. grandis x E. pellita*	Kalimantan, Indonesia	OQ296466	OQ296492	OQ296515	OQ296543	This study
Calonectria lombardiana	CMW 54963	*E. grandis x E. pellita*	Pelalawan, Riau, Indonesia	OQ296467	OQ296493	OQ296516	OQ296544	This study
Calonectria lombardiana	CMW 59200	*E. grandis x E. pellita*	Seikabaro, Riau, Indonesia	OQ296468	OQ296494	OQ296517	OQ296545	This study
Calonectria lombardiana	CMW 59201	*E. grandis x E. pellita*	Seikabaro, Riau, Indonesia	OQ296469	OQ296495	OQ296518	OQ296546	This study
Calonectria lombardiana	CMW 59202	*E. grandis x E. pellita*	Seikabaro, Riau, Indonesia	OQ296470	OQ296496	OQ296519	OQ296547	This study
Calonectria maranhensis	CBS 134811T = LPF142	*Eucalyptus* sp.	Brazil	KM396035	KM396118	KM395861	KM395948	Alfenas et al. (2015)

Table 2.2. (Continue)

Species	Isolate number	Host/ substrate	Locality	GenBank accessions				Reference
				CMDA	HIS3	TEF1	TUB	
Calonectria maranhensis	CBS 134812 = LPF143	*Eucalyptus* sp.	Brazil	KM396036	KM396119	KM395862	KM395949	Alfenas et al. (2015)
Calonectria melaleucae	ZHKUCC 21-0066T	*Melaleuca bracteata*	China	MZ491110	N/A	MZ491132	MZ491154	Zhang et al. (2022)
Calonectria melaleucae	ZHKUCC 21-0067	*Melaleuca bracteata*	China	MZ491111	N/A	MZ491133	MZ491155	Zhang et al. (2022)
Calonectria multiseptata	CMW 59214	*E. grandis* x *E. urophylla*	Porsea, North Sumatra, Indonesia	OQ296471	OQ296497	OQ296520	OQ296548	This study
Calonectria multiseptata	CMW 59216	*Acacia crassicarpa*	Pelalawan, Riau, Indonesia	OQ296472	OQ296498	OQ296521	OQ296549	This study
Calonectria multiseptata	CMW 59217	*Acacia crassicarpa*	Pelalawan, Riau, Indonesia	OQ296473	N/A	OQ296522	OQ296550	This study
Calonectria multiseptata	CMW 59218	*Acacia crassicarpa*	Pelalawan, Riau, Indonesia	OQ296474	OQ296499	OQ296523	OQ296551	This study
Calonectria multiseptata	CMW 23692T = CBS 112682 = CPC 1589	*E. grandis*	Indonesia	MT335299	MT335539	MT412830	MT413044	Liu et al. (2020)
Calonectria plurilateralis	CBS 111401T = CMW 51178 = CPC 1637	Soil	Ecuador	MT335340	MT335580	MT412870	MT413082	Liu et al. (2020)
Calonectria propaginicola	CBS 134815T = LPF220	*Eucalyptus* sp.	Brazil	KM396040	KM396123	KM395866	KM395953	Alfenas et al. (2015)
Calonectria propaginicola	CBS 134816 = LPF222	*Eucalyptus* sp.	Brazil	KM396041	KM396124	KM395867	KM395954	Alfenas et al. (2015)
Calonectria pseudoreteaudii	CMW 54931	*E. grandis x E. pellita*	Teso, Riau, Indonesia	OQ296475	OQ296500	OQ296524	OQ296552	This study
Calonectria pseudoreteaudii	CMW 54947	*E. grandis x E. pellita*	Kalimantan, Indonesia	N/A	N/A	OQ296525	OQ296553	This study
Calonectria pseudoreteaudii	CMW 25310T = CBS 123694	*E. urophylla* × *E. grandis*	China	MT335354	MT335594	MT412885	MT413096	Liu et al. (2020)
Calonectria pseudoreteaudii	CMW 25292 = CBS 123696	*E. urophylla* × *E. grandis*	China	MT335355	MT335595	MT412886	MT413097	Liu et al. (2020)
Calonectria queenslandica	CMW 30604T = CBS 112146 = CPC 3213	E. urophylla	Australia	MT335367	MT335607	MT412898	MT413108	Liu et al. (2020)
Calonectria queenslandica	CMW 30603 = CBS 112155 = CPC 3210	*E. pellita*	Australia	MT335368	MT335608	MT412899	MT413109	Liu et al. (2020)
Calonectria reteaudii	CMW 55091	*E. pellita*	Pelalawan, Riau, Indonesia	OQ296476	OQ296501	OQ296526	OQ296554	This study
Calonectria reteaudii	CMW 55094	*E. pellita*	Pelalawan, Riau, Indonesia	OQ296477	OQ296502	OQ296527	OQ296555	This study

Table 2.2. (Continue)

Species	Isolate number	Host/ substrate	Locality	GenBank accessions				Reference
				CMDA	HIS3	TEF1	TUB	
Calonectria reteaudii	CMW 59206	*E. grandis* x *E. urophylla*	Porsea, North Sumatra, Indonesia	OQ296478	N/A	OQ296528	OQ296556	This study
Calonectria reteaudii	CMW 59207	*E. grandis* x *E. urophylla*	Porsea, North Sumatra, Indonesia	OQ296479	OQ296503	OQ296529	OQ296557	This study
Calonectria reteaudii	CMW 55108	*Acacia crassicarpa*	Pelalawan, Riau, Indonesia	OQ296480	OQ296504	OQ296530	OQ296558	This study
Calonectria reteaudii	CMW 55109	*Acacia crassicarpa*	Pelalawan, Riau, Indonesia	OQ296481	N/A	OQ296531	OQ296559	This study
Calonectria reteaudii	CMW 30984T = CBS 112144 = CPC 3201	*E. camaldulensis*	Vietnam	MT335370	MT335610	MT412901	MT413111	Liu et al. (2020)
Calonectria reteaudii	CMW 16738 = CBS 112143 = CPC 3200	*Eucalyptus* sp.	Vietnam	MT335371	MT335611	MT412902	MT413112	Liu et al. (2020)
Calonectria reteaudii	CMW 47410 = CBS 143563	*E. urophylla*	Vietnam	MT335193	MT335433	MT412724	N/A	Liu et al. (2020)
Calonectria reteaudii	CMW 47433 = CBS 143564	*E. pellita*	Vietnam	MT335194	MT335434	MT412725	MT412947	Liu et al. (2020)
Calonectria strelitziae	ZHKUCC 210019T	*Strelitzia reginae*	China	MZ491105	N/A	MZ491129	MZ491151	Zhang et al. (2022)
Calonectria strelitziae	ZHKUCC 210047	*Strelitzia reginae*	China	MZ491106	N/A	MZ491130	MZ491152	Zhang et al. (2022)
Calonectria tonkinensis	CMW 47430T = CBS 143576	Soil	Vietnam	MT335384	MT335624	MT412915	MT413122	Liu et al. (2020)
Calonectria variabilis	CMW 2914 = CBS 112691 = CPC 2506	*Theobroma grandiflorum*	Brazil	MT335393	MT335633	MT412924	MT413131	Liu et al. (2020)
Calonectria variabilis	CMW 3187T = AR2675 = CBS 114677 = CPC 2436	*Schefflera morototoni*	Brazil	MT335392	MT335632	MT412923	MT413130	Liu et al. (2020)

Note: N/A represents information that is not available. Isolates obtained in this study are indicated in bold. T denotes ex-type strain. AR = Amy Y. Rossman working collection; CBS = The culture collection of Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CMW = culture collection of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa; CPC = Pedro Crous working collection housed at Westerdijk Fungal Biodiversity Institute; IMI = International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, UK; LPF = Laboratório de Patologia Florestal, Universidade Federal de Viçosa, Viçosa, Brazil; STE-U = Department of Plant Pathology, University of Stellenbosch, South Africa; ZHKUCC = Zhongkai University of Agriculture and Engineering Culture Collection. CMDA = calmodulin; HIS3 = histone H3; TEF1 = translation elongation factor 1-alpha; TUB2 = β-tubulin.

Chapter 3

Pathogenicity of *Chrysoporthe deuterocubensis* on *Eucalyptus* in Indonesia

ABSTRACT

Several economically important pathogens, including species of *Chrysoporthe*, pose a threat to the rapidly expanding *Eucalyptus* plantation industry in South East Asia. During 2019, disease surveys in Riau and Kalimantan (Indonesia), cankers were observed on *Eucalyptus* trees and a collection of fungal isolates was obtained from them. The aim of this study was to confirm the identity of the isolates and to evaluate their relative pathogenicity on different *Eucalyptus* clones. Using the DNA sequence data based on the internal transcribed spacer (ITS) region of the ribosomal DNA and two regions of the β-tubulin gene (*TUB1* and *TUB2*), 31 fungal isolates were identified as *Chrysoporthe deuterocubensis*. Pathogenicity trials showed that *C. deuterocubensis* isolates differed in their pathogenicity and that different *Eucalyptus* genotypes differed in their susceptibility to the pathogen. These results will be useful in reducing the importance of stem canker caused by this pathogen in the future.

Keywords: *Cryphonectriaceae*, molecular identification, planted forest, stem cankers, susceptibility

INTRODUCTION

The *Cryphonectriaceae* (*Diaporthales, Ascomycota*) is a globally distributed group of mostly pathogenic fungi of woody plants (Gryzenhout et al. 2006a; 2009). These pathogens cause cankers on stems and branches, which can lead to the tree death (Hodges et al. 1976; 1979; Sharma et al. 1985; Gryzenhout et al. 2009; 2010; Begoude et al. 2010; Chen et al. 2013; 2018; Fan et al. 2013; Rodas et al. 2005; Jiang et al. 2019; Wang et al. 2020). The *Cryphonectriaceae* includes at least 28 genera (Gryzenhout et al. 2009; Chen et al. 2018; Ali et al. 2018; Ferreira et al. 2019; Rauf et al. 2020; Wang et al. 2020; Huang et al. 2022). Amongst the most important pathogen in this group is *Cryphonectria parasitica,* which causes the devastating disease chestnut blight on *Castanea* spp. in Europe and North America (Anagnostakis 1987; Rigling and Prospero 2018).

The *Cryphonectriaceae* have undergone substantial taxonomic revision over the last three decades (Gryzenhout et al. 2004; 2006a; 2009; van der Merwe et al. 2010). This has specifically resulted from extensive surveys, particularly in the tropics and the Southern Hemisphere, and the application of DNA sequence-based phylogenetic inference to define species boundaries (van der Merwe et al. 2010; Hyde et al. 2020; Jiang et al. 2020; Wang et al. 2020). One of the most important of these changes was the recognition that the *Eucalyptus* pathogen previously known as *Cryphonectria cubensis* resides in a distinct genus, *Chrysoporthe*, distantly related to *Cryphonectria parasitica* and its relatives (Gryzenhout et al. 2004; 2009). Species of *Chrysoporthe* are found specifically on trees in the Myrtales, including families such as the Myrtaceae, Melastomaceae and Lythraceae (Wingfield 2003; Rodas et al. 2005; Gryzenhout et al. 2005; 2009; Oliveira et al. 2021).

Nine species of *Chrysoporthe* have been described. Those from South and Central America include *C. cubensis* (Hodges et al. 1976; 1979; Rodas et al. 2005), *C. doradensis* (Gryzenhout et al. 2005), *C. inopina* (Gryzenhout et al. 2006b), *C. hodgesiana* (Gryzenhout et al. 2004) and *C. puriensis* (Oliveira et al. 2021). Species occurring in central and southern Africa include *C. zambiensis*, *C. syzygiicola* (Chungu et al. 2010) and *C. austroafricana* (Wingfield et al. 1989, Gryzenhout et al. 2004). The other species is *C. deuterocubensis,* which is mainly found in South East Asia (Hodges et al. 1986; Myburg et al. 2003; Van der Merwe et al. 2010; Gryzenhout et al. 2006b; Rauf et al. 2022; Suzuki et al. 2022). *Chrysoporthe deuterocubensis* was originally treated as a single taxon together with *C. cubensis* (Hodges 1980). Subsequently, based on multigene phylogenetic analyses, it was later shown to represent a cryptic species and was separated from its close relatives, *C. cubensis* and *C. austroafricana* (Gryzenhout et al. 2004; Van der Merwe et al. 2010). *Chrysoporthe deuterocubensis* has been not only reported from South East Asia (Gryzenhout et al. 2006b; van der Merwe et al. 2010), it has also been reported from other parts of the world, including Kenya, Malawi, Mozambique (Nakabonge et al. 2006), Republic of Congo (Roux et al. 2003), Western Australia (Davison and Coates 1991; van der Merwe et al. 2010), Hawaii (Gryzenhout et al. 2006b; Van der Merwe et al. 2010; Roux et al. 2020), India (Sharma et al. 1985) and China (Zhou et al. 2008; Chen et al. 2010; Wang et al. 2020). In Indonesia, it has been reported from woody plants in the Myrtales, including *Syzygium aromaticum* on the island of Sulawesi (Hodges et al. 1986; Myburg et al. 2003; Van der Merwe et al. 2010) as well as *Melastoma malabathricum* (Gryzenhout et al. 2006b) and *Eucalyptus* spp. on the island of Sumatra (Van der Merwe et al. 2010).

During several disease surveys in 2019, symptoms resembling infection by a *Chrysoporthe* species, including bark cracking and the presence of characteristic fruiting structures, were observed on *Eucalyptus* trees in the clonal trials located in Riau and Kalimantan. The objectives of this study were to verify the identity of these isolates and to evaluate their relative pathogenicity on different *Eucalyptus* genotypes.

MATERIALS AND METHODS

Field incidence, sample collection and fungal isolation

Surveys were conducted in *Eucalyptus* clonal trials situated in Riau and Kalimantan, Indonesia. These trial plots consisted of 20 different *Eucalyptus* genotypes (10 *E. pellita* and *E. grandis* × *pellita*) with a 7 × 7 plant plot established for each clone. The occurrence of cankers resembling infection by a *Chrysoporthe* sp. (Figure 3.1) on individual trees in each plot, was recorded and calculated as a percentage.

Stem and bark samples were collected from cankers (Figure 3.1) on infected trees in eight *Eucalyptus* clonal trials, including seven sites in Riau (Kuansing East = 4, Kuansing West = 1, Kuansing North = 1, and Kuansing South = 1) and one site in East Kalimantan province (Figure 3.2). All samples were placed in separate brown paper bags and then transferred to the laboratory for isolation in culture. Fruiting structures with conidial masses were observed on the samples under a dissecting microscope and these spore masses were lifted from the structures using a sterile needle and transferred to potato dextrose agar (PDA Acumedia®: 40 g/L) in Petri-dishes and incubated at 25 °C for 12-14 days. Pure cultures were obtained by transferring single hyphal tips to clean PDA. All the isolates were then deposited in the culture collection (CMW) of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa (Table 3.1).

DNA extraction, PCR amplification and sequencing

DNA was extracted from mycelium of 14-day-old pure cultures using a Prepman® Ultra Sample Preparation Reagent (Thermo Fisher Scientific, Waltham, MA, USA). DNA sequences of all isolates were generated for three loci, including the internal transcribed spacer (ITS) region of ribosomal RNA using primers ITS-1 and ITS-4 (White et al. 1990) and two regions

of the β-tubulin gene (*TUB1* and *TUB2*) using primers Bt1a/Bt1b and Bt2a/Bt2b, respectively (Glass & Donaldson 1995).

Polymerase chain reaction (PCR) amplification was performed in 13 µL reactions containing 2 µL of 5× MyTaq buffer (Bioline, London, UK), 0.1 µL MyTaq DNA polymerase (Bioline), 1 µL DNA, 0.5 µL of each primer (10 µM), and sterile deionized water. The PCR protocol used was as follows; initial denaturation (96°C, 3 min), 30 cycles of 30 s at 95 °C, 45 s at 55 °C, 1 min at 72 °C, and a final extension (72 °C, 7 min). PCR products were purified using ExoSAP-IT PCR Product Cleanup Reagent (Thermo Fisher Scientific, Waltham, MA, USA) and sequenced using the BigDye Terminator Sequencing Kit 3.1 (Applied Biosystems, Forster City, CA, USA) in both the forward and reverse directions. Sequencing was performed on an ABI PRISM 3100 DNA sequencer (Applied Biosystems, Forster City, CA, USA). CLC Main Workbench V20.1 (Qiagen, Hilden, Germany) was used to assemble and edit the raw sequences. All sequences resulting from this study were deposited in GenBank (http://www.ncbi.nlm.nih.gov/) (Table 3.1).

Phylogenetic analyses

Reference sequences for species closely related to those found in this study were downloaded from the GenBank database (Table 3.1). All sequences were aligned using MAFFT v. 7 (http://mafft.cbrc.jp/alignment/server/) (Katoh & Standley 2013) and, where necessary, manually confirmed using MEGA v. 7 (Kumar et al. 2016). Maximum likelihood (ML) analyses were performed on the combined datasets of the three sequenced regions, using RaxML v. 8.2.4 on the CIPRES Science Gateway v. 3.3 (Stamatakis 2014) with the default GTR substitution matrix and 1,000 rapid bootstraps. Sequences for *Amphilogia gyrosa* (CMW 10469 and CMW 10470) were used as outgroups. The resulting trees were viewed using MEGA v. 7 (Kumar et al. 2016).

Pathogenicity tests

Relative aggressiveness of isolates

Four isolates (CMW 55421, CMW 55433, CMW 55438 and CMW 55446) were selected for inoculation and specifically chosen to represent the range of geographical locations. Inoculations were carried out on 3-year-old *E. grandis* x *E. pellita* hybrid clones (ECL105) with a stem diameter of 130 mm to 140 mm. Twenty trees were used for each isolate and the

same number of trees were inoculated as controls. A sterilised cork borer (10 mm) was used to make a wound in the stems at approximately 1.3 m above ground level, and inoculation was carried out by placing a plug of agar taken from the edges of three-week-old actively growing cultures with the mycelial surface facing the cambium. A sterile 2% PDA plug was used for control inoculations. Inoculation points were sealed with masking tape to reduce desiccation of the agar plugs and wounds.

The length of lesions produced on the stems was measured 12 weeks after inoculation. Re-isolations were made from the lesions to verify the presence of the inoculated fungus. The data were analysed using Kruskal-Wallis tests to determine whether there were statistically significant differences between the treatments. The Wilcoxon rank-sum test with continuity correction was then used for pairwise comparisons. R statistical software, version 3.2.0 (R Core Team 2020) was used for all statistical analyses.

Relative tolerance of **Eucalyptus** *clones*

Five *Eucalyptus* clones, including two of *E. pellita* (ECL101, ECL102) and three of *E. grandis* × *E. pellita* hybrids (ECL103, ECL104, ECL105), were selected to test for susceptibility to the two most aggressive isolates arising from the initial inoculation trial. Inoculation was carried out on 3-year-old *Eucalyptus* trees with stem diameters ranging from 130 mm to 140 mm, at a height of approximately 1.3 m above the ground. Twenty trees of each *Eucalyptus* clone were used for each isolate and the same number of trees were inoculated as controls. Inoculations, lesion length measurements and re-isolations were carried out using the same protocols as for the trial to compare the relative aggressiveness of the isolates. Data were also analysed in the same way as that for the first trial.

RESULTS

Field incidence, sample collection and fungal isolation

Cankers reminiscent of those caused by *Chrysoporthe* species occurred only on two *E. grandis* × *E. pellita* hybrid clones with incidence levels of 30% and 10% respectively on clone ECL105 and clone ECL106. This showed that not all trees in clonal trials, even those of the same clone,

were affected by this disease. A further eight *E. grandis* × *E. pellita* clones and 10 *E. pellita* clones were free of infection.

Thirty-one isolates were obtained from diseased tissues associated with cankers on the stems of trees. Of these, eight isolates were obtained from *E. grandis* × *E. pellita* clone ECL106 in Sumatra (seven isolates) and East Kalimantan (one isolate), and 23 isolates were obtained from *E. grandis* × *E. pellita* clone ECL105 grown in Kuantan Singingi Regency, Riau Province, including Kuansing East (six isolates), Kuansing West (four isolates), Kuansing North (two isolates) and Kuansing South (11 isolates) (Figure 3.2).

Phylogenetic analyses

Amplicons of approximately 490 bp for the ITS, 450 bp for *TUB1* and 345 bp for *TUB2* were generated. The combined sequence data sets used for phylogenetic analyses included 42 ingroup taxa and contained 1292 characters. All isolates sequenced in this study grouped in a well-supported monophyletic clade (ML = 91%), comprised of two sub-clades, with the representative isolates of *C. deuterocubensis* (Figure 3.3). These isolates were, therefore, confirmed as being *C. deuterocubensis.*

Pathogenicity tests

Relative aggressiveness of isolates

Twelve weeks after inoculation, all four *C. deuterocubensis* isolates inoculated on *E. grandis* × *E. pellita* clone (ECL105) caused bark cracking and lesions were observed under the bark (Figure 3.4). Aggressiveness varied between isolates, with mean lesion lengths ranging from 50 to 128 mm (Figure 3.5). Isolate CMW 55446 was the most aggressive with a mean lesion length of 128 mm, followed by CMW 55421, CMW 55438 and CMW 55433 with mean lesion lengths of 87 mm, 80 mm, and 50 mm respectively. The Kruskal-Wallis test gave a value of H = 46.47, df = 4 and P < 1.9e-9 confirming that there were significant differences in aggressiveness between the *Chrysoporthe* isolates. No disease symptoms were observed on the plants inoculated as the controls. *Chrysoporthe deuterocubensis* was re-isolated from lesions on the inoculated trees but never from the controls.

Relative tolerance of* Eucalyptus *clones

Isolates CMW 55421 and CMW 55446, which were the most aggressive in the prior comparison were used in the clone screening test. Twelve weeks after inoculation, the *E. pellita* clone (ECL102) and three of the *E. grandis* x *E. pellita* hybrids (ECL103, ECL104 and ECL105) inoculated with both *C. deutrocubensis* isolates (CMW 55421 & CMW 55446) showed mean lesions ranging from 10 to 55 mm (Figure 3.6). However, no symptoms were observed on the *E. pellita* clone (ECL101) or the control trees. Clone ECL105 was the most susceptible, followed by clones ECL102 and ECL103, while ECL101 and ECL104 were more tolerant to infection. Overall, isolate CMW 55446 produced longer lesions than CMW 55421, which was similar to the results where isolates were screened for aggressiveness. Based on the results of the Kruskal-Wallis test, there were significant differences in susceptibility between the clones tested ($H = 108.4$, $df = 14$ and $P < 2.2e\text{-}16$). *Chrysoporthe deutrocubensis* was re-isolated from lesions on all clones except ECL101 and it was never present in the controls.

DISCUSSION

Cryphonectria canker has been known to occur on *Eucalyptus* for many years (Boerboom & Maas 1970; Hodges et al. 1976; Hodges 1980; Florence et al. 1986; Wingfield et al. 1989), but little is known regarding its relative importance in Indonesia. The results of this study, considering plantation areas in Sumatra and Kalimantan, suggested that the disease is relatively rare. This could be due to the fact that species known to be highly susceptible to infection, such as *E. grandis* (Boeerbomm & Maas 1970; Sharma et al. 1985; Seixas et al. 2004, Mangwanda et al. 2015), have been replaced with species such as *E. urophylla* and *E. pellita* and their hybrids. In this regard, *E. urophylla* (Chen et al. 2010; Mangwanda et al. 2015; Soares et al. 2018) and *E. pellita* (Alfenas et al. 1983; Rauf et al. 2020; Chen et al. 2010) have been recorded to be relatively tolerant to infection by *Chrysoporthe* spp. This is also consistent with our field observations in the present study, where no infection was observed on *E. pellita* clones, whereas hybrids of this species with *E. grandis* were more prone to *Chrysoporthe* infection.

An interesting observation in this study was the fact that individual trees of a clone had cankers while many remained uninfected. This situation is distinctly different to the case where highly susceptible clones are planted and where every tree would be cankered, with infections occurring through natural wounds (Wingfield, unpublished). *Chrysoporthe* spp. require

wounds for infection to occur (Gryzenhout et al. 2009; Seixas et al. 2004) and it is probably that those trees observed with cankers in this study had physical wounds and were sufficiently susceptible to develop disease. It also supports the view that the clones, mainly of hybrids including *E. pellita* and *E. urophylla* are not likely to be threatened by *C. deuterocubensis* infections.

Inoculation trials showed that isolates of *C. deuterocubensis* differed in their relative aggressiveness. This is similar to the results of previous studies with *Chrysoporthe* spp. such as *C. cubensis* (Rodas et al. 2005), *C. austroafricana* (Roux et al. 2003; Chungu et al. 2010), *C. zambiensis*, *C. syzygiicola* (Chungu et al. 2010) and *C. deuterocubensis* (Chen et al. 2010; Rauf et al. 2020). This result is also consistent with the fact that *C. deuterocubensis* is most likely native to South East Asia, where it has undergone a host shift (Slippers et al. 2005) from native woody plants in the Myrtales (Suzuki et al. 2022).

Inoculations on different *Eucalyptus* clones using selected aggressive isolates of *C. deuterocubensis* showed that planting stock being commercially utilised in Indonesia differs in susceptibliy to the pathogen. The results were, however relatively variable, where in the case of *E. pellita*, clone ECL101 was more tolerant compared to clone ECL102. Likewise, in *E. grandis* × *E. pellita* hybrids, clone ECL104 was much less susceptible than clones ECL103 and ECL105. In addition, the lesions developing from the inoculations were relatively short, also suggesting that the clones being deployed for plantation development have only low levels of susceptibility.

An obvious shortcoming of this study is that it did not include clones known to be highly susceptible to infection by *C. deuterocubensis*. Such clones would likely have been of *E. grandis*, which is no longer planted in the area. Replacement of *E. grandis* with species such as *E. urophylla* and particularly *E. pellita*, which are better suited to plantation areas in the humid tropics, appears to have diminished the relative importance of canker caused by *C. deuterocubensis*. It is, however important, to recognise that this pathogen is undergoing sexual reproduction in the background environment and that genotypes having the ability to infect and cause serious disease could easily emerge in the future.

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APPENDIX

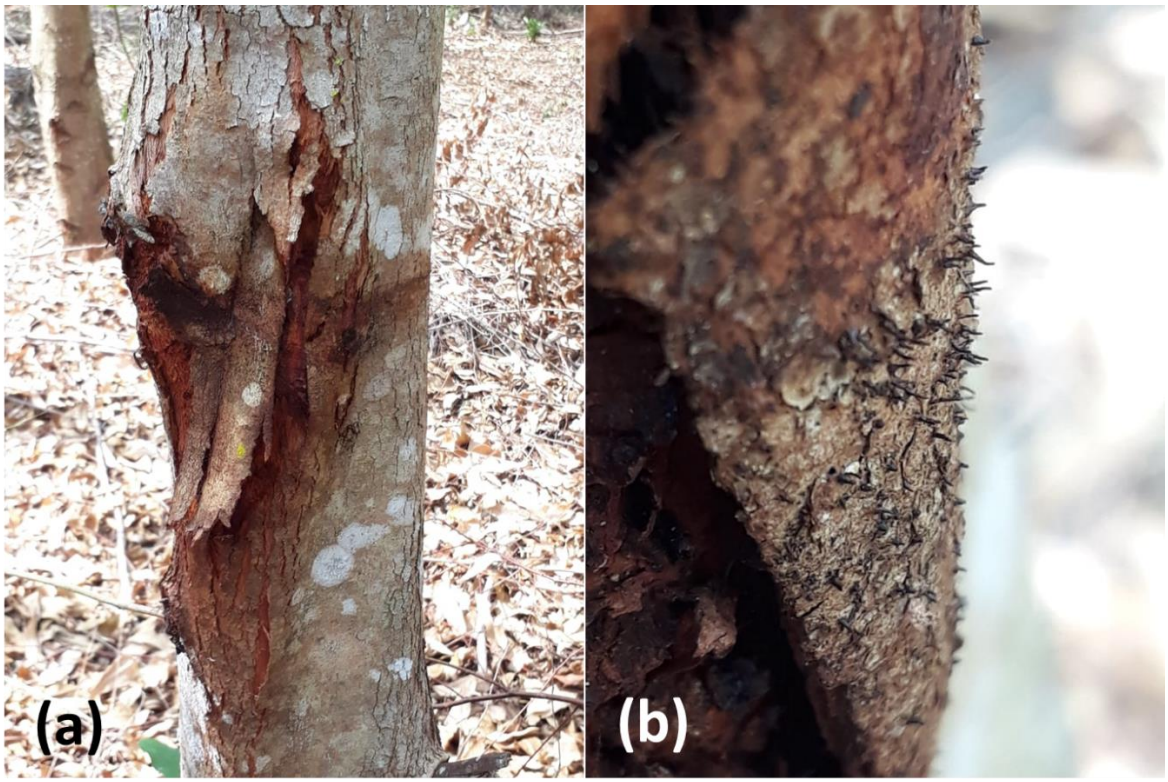

Figure 3. 1. Symptoms of *Chrysoporthe* infection on stem of *Eucalyptus* tree; (a). craking and canker symptoms; (b). fruiting structures observed on the cankers.

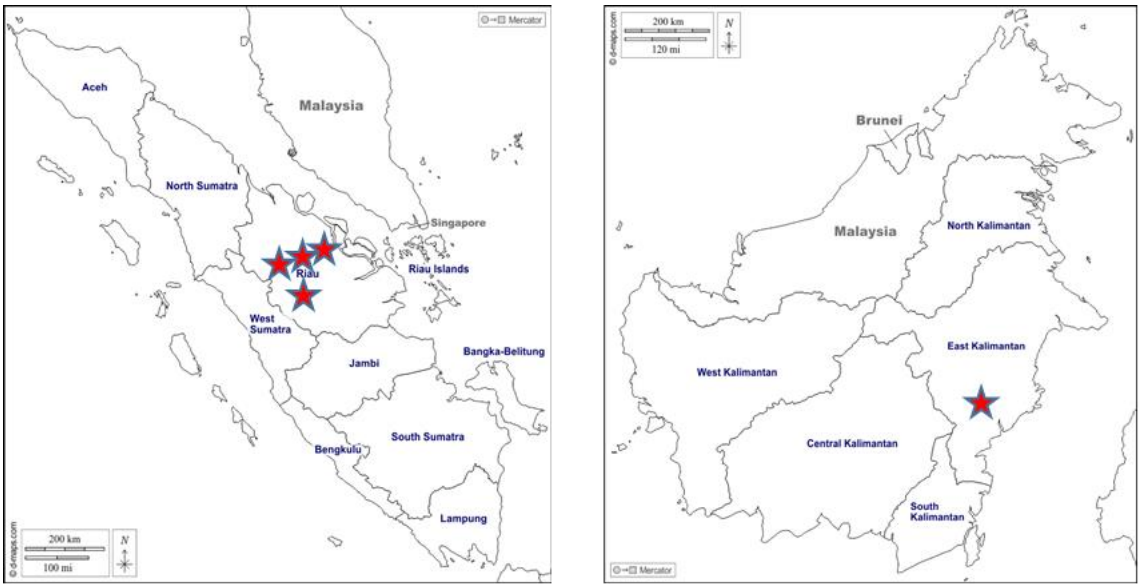

Figure 3. 2. Geographic location of the sampling sites in Sumatra and Kalimantan, Indonesia

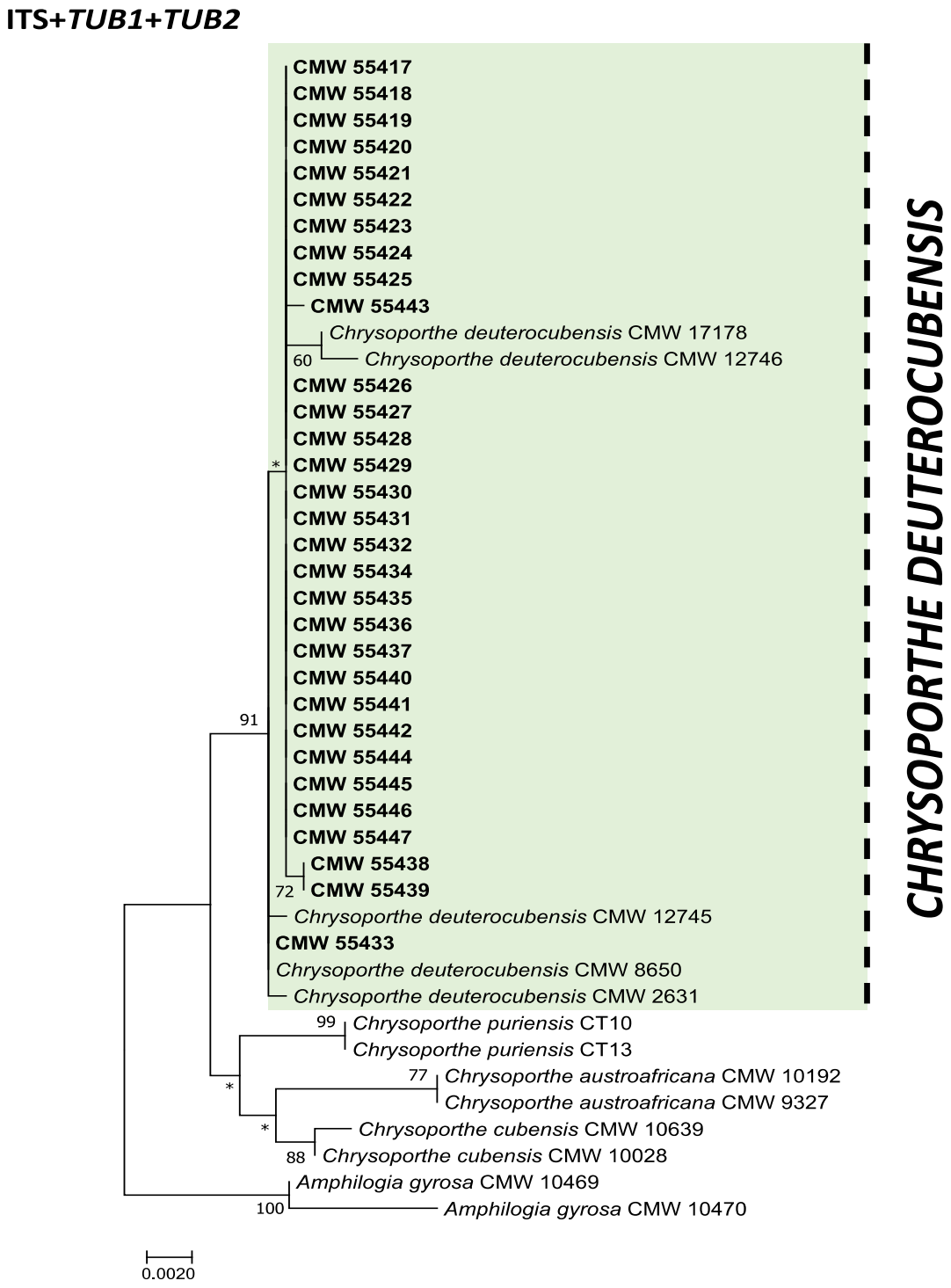

Figure 3. 3. Phylogenetic tree based on maximum likelihood (ML) analysis of a combined data set of ITS, *TUB1* and *TUB2* sequences for *Chrysoporthe* spp. Isolates sequenced in this study are presented in **bold.** Bootstrap values of ≥60% for ML analyses are indicated at the nodes. Bootstrap values 60% are marked with "*". Sequences for *Amphilogia gyrosa* (isolates CMW 10469 and CMW 10470) were used as the outgroup.

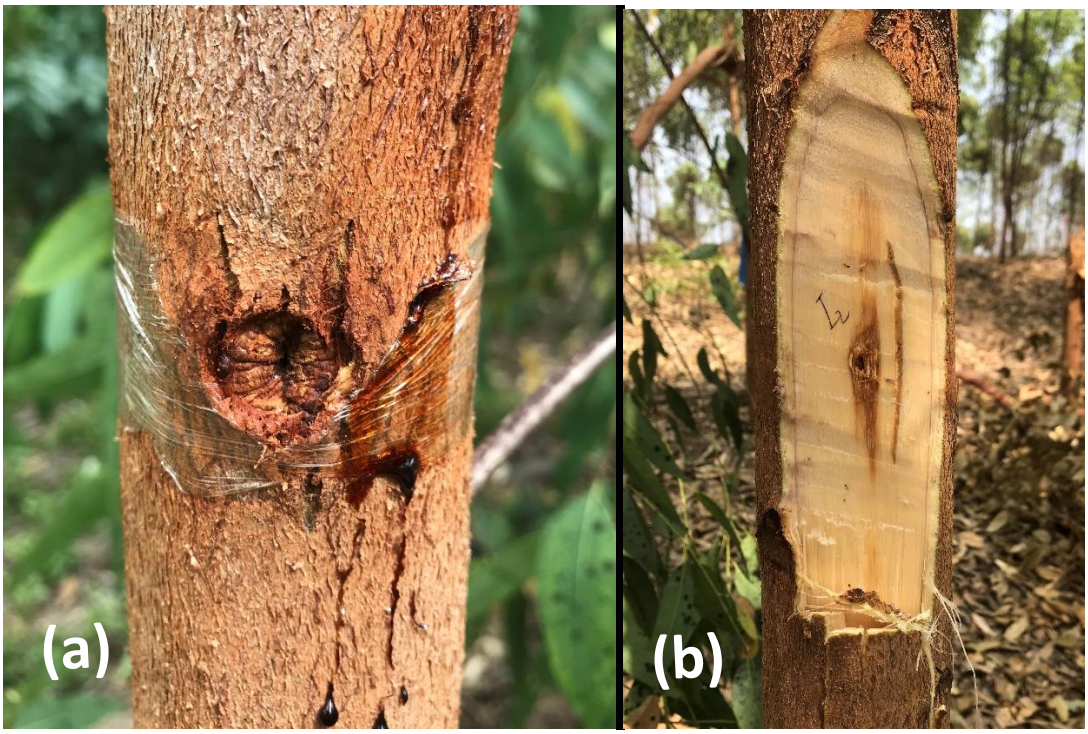

Figure 3. 4. Symptoms of infection by *C. deuterocubensis* 12 weeks after inoculation; (a). overbark with cracking symptom; (b). underbark showing fungus lesions.

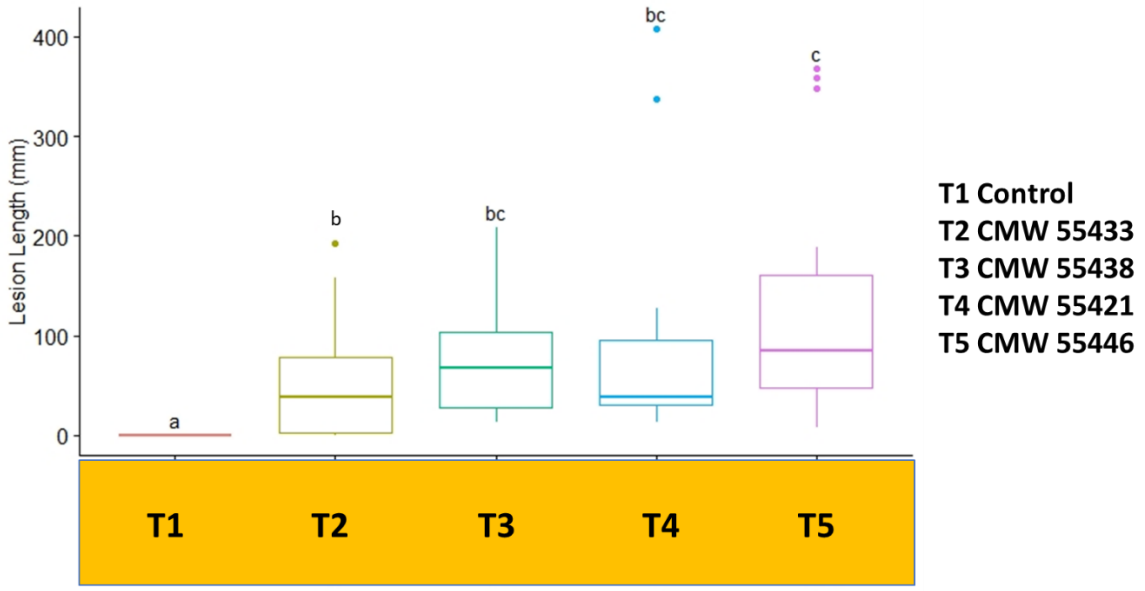

Figure 3. 5 Lesion lengths associated with inoculation of *Eucalytpus* clone ECL105 with four different isolates of *C. deuterocubensis* and a control.

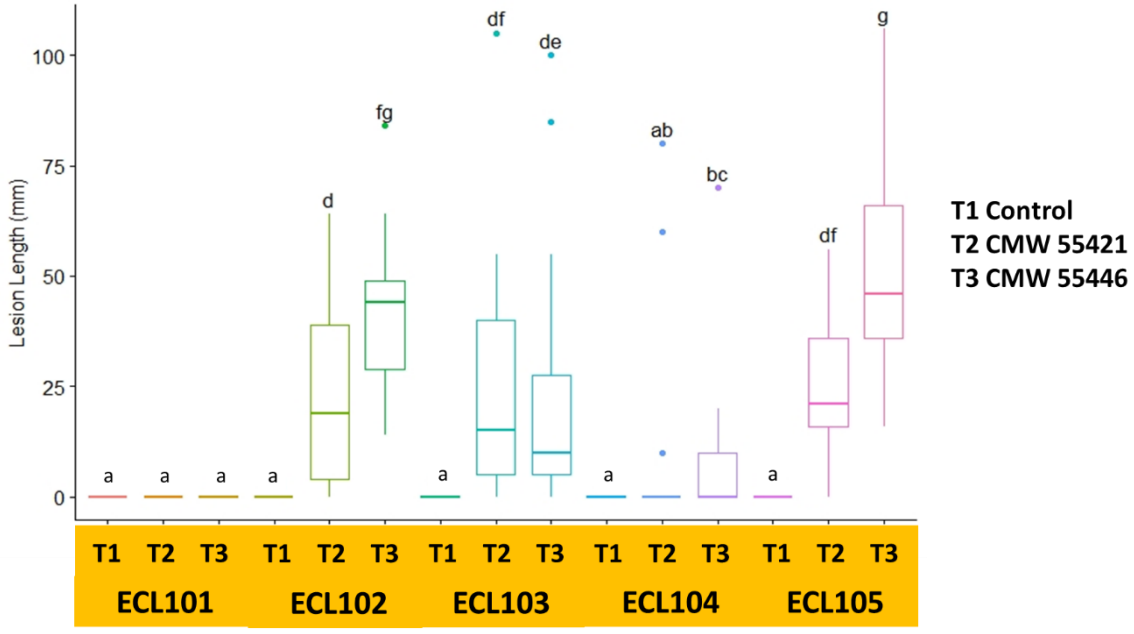

Figure 3. 6. Lesion lengths on five different commercially deployed *Eucalyptus* clones after inoculation with two isolates (CMW 55421 and CMW 55446) of *C. deuterocubensis* and a control. Isolate CMW 55446 consistently produce longer lesion compared to CMW 55421. Clone ECL105 found to be the most susceptible, while ECL101 was the most tolerant.

Table 3.1. Collection details and GenBank accession numbers of isolates included in the phylogenetic analyses

Species	Isolate number	Host	Locality	GenBank accessions			Reference
				ITS	*TUB1*	*TUB2*	
Chrysoporthe austroafricana	CMW 10192	*Syzygium cordatum*	South Africa	AY214299	GQ290176	GQ290187	van der Merwe et al. 2010
	CMW 9327	*Tibouchina granulosa*	South Africa	GQ290158	GQ290185	AF273455	Gryzenhout et al. 2004; van der Merwe et al. 2010
Chrysoporthe cubensis	CMW 10639	*Eucalyptus grandis*	Colombia	AY263421	AY263419	AY263420	Rodas et al. 2005
	CMW 10028	*Miconia rubiginosa*	Colombia	GQ290153	GQ290175	GQ290186	van der Merwe et al. 2010
Chrysoporthe deuterocubensis	CMW 12745	*Tibouchina urvilleana*	Singapore	DQ368764	GQ290183	DQ368781	Gryzenhout et al. 2006b; van der Merwe et al. 2010
	CMW 12746	*Eucalyptus* sp.	China	HM142105	HM142121	HM142137	Chen et al. 2010
	CMW 17178	*Tibouchina urvilleana*	Thailand	DQ368766	AH015649	AH015649	Gryzenhout et al. 2006b; van der Merwe et al. 2010
	CMW 2631	*Eucalyptus marginata*	Australia	GQ290157	GQ290184	AF543825	Gryzenhout et al. 2004; van der Merwe et al. 2010
	CMW 8650	Syzygium aromaticum	Indonesia	AY084001	AY084024	GQ290193	van der Merwe et al. 2010
	CMW 55417	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55418	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55419	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55420	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55421	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55422	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55423	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55424	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55425	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55426	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55427	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55428	*E. grandis* x *E. pellita*	Indonesia				This study

Table 3.1. (Continue)

Species	Isolate number	Host	Locality	GenBank accessions			Reference
				ITS	*TUB1*	*TUB2*	
Chrysoporthe deuterocubensis	**CMW 55429**	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55430	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55431	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55432	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55433	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55434	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55435	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55436	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55437	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55438	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55439	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55440	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55441	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55442	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55443	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55444	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55445	*E. grandis* x *E. pellita*	Indonesia				This study
	CMW 55446	*E. grandis* x *E. pellita*	Indonesia				This study
Chrysoporthe puriensis	CT 10	*Tibouchina granulosa*	Brazil	MN590028	MN590040	MN590040	Oliveira et al. 2021
	CT 13	*Tibouchina granulosa*	Brazil	MN590029	MN590041	MN590041	Oliveira et al. 2021
Amphilogia gyrosa	CMW 10469	*Elaeocarpus dentatus*	New Zealand	AF452111	AF452707	AF452714	Myburg et al. 2004
	CMW 10470	*Elaeocarpus dentatus*	New Zealand	AF452112	AF452708	AF452715	Myburg et al. 2004

Note: Isolates obtained in this study are indicated in bold.

Chapter 4

Quambalaria eucalypti found on *Eucalyptus* in Indonesia

M Tarigan, MJ Wingfield, YMAN Marpaung, A Durán, NQ Pham. 2023. *Quambalaria eucalypti* found on *Eucalyptus* in Indonesia. *Forest Pathology. e12829.* https://doi.org/10.1111/efp.12829

ABSTRACT

The *Eucalyptus* plantation industry in Indonesia has expanded rapidly during the last few decades. During routine nursery disease surveys, symptoms of a leaf and shoot blight disease were detected on *Eucalyptus* mother plants. Isolates were obtained from symptomatic tissues and identified using DNA sequence analyses. Phylogenetic analyses showed that the isolates were those of *Quambalaria eucalypti*. Pathogenicity tests were conducted with isolates of *Q. eucalypti* on clones of *E. pellita* and *E. grandis* x *E. pellita* hybrids. These resulted in symptoms similar to those observed on naturally infected plants. *Eucalyptus* genotypes tested showed variation in their susceptibility, highlighting the potential to select and breed for resistance and thus to manage future outbreaks of the disease. This is the first report of the pathogen in Indonesia as well as in South East Asia.

Keywords: *Eucalyptus* hybrids, fungal pathogen, leaf and shoot blight, mother plants, nursery diseases

INTRODUCTION

Plantation forestry especially utilizing non-native tree species has grown rapidly in many parts of the world during the course of the last three decades, including in South East Asia (SEA) (Payn et al. 2015). Due to pest and pathogen problems, *Acacia mangium* plantations in Indonesia, Malaysia, and Vietnam have declined in relevance, leading to a rise in planting of *Eucalyptus* spp. in these regions (Harwood & Nambiar, 2014; Nambiar et al. 2018; Tarigan et al. 2011). *Eucalyptus pellita* and its hybrids with *E. grandis*, *E. brassiana* and *E. urophylla* are now most widely planted in this region (Hardiyanto et al. 2021). Similar to other non-native trees grown in new environments, the emergence of insect pests and pathogens poses a threat

to the sustainability of these planted forests (Wingfield et al. 1996; Crous et al. 1998; Coetzee et al. 2011; McTaggart et al. 2016; Wingfield 2003; Wingfield et al. 2008; Burgess & Wingfield 2017; Pham et al. 2021).

Diseases that have affected eucalypt plantation forestry in various parts of the world include those caused by species of *Quambalaria*. The genus *Quambalaria* (Quambalariaceae, Microstromatales, Basidiomycota) includes several important pathogens of eucalypts in the tropics and Southern Hemisphere (Wingfield et al. 1993; Braun 1998; Cheewangkoon et al. 2009; Crous et al. 2019). Some of these species cause severe leaf and shoot die-back as well as stem cankers (Alfenas et al. 2004; Roux et al. 2006; Pegg et al. 2008; Chen et al. 2017; Santos et al. 2020). These include *Q. eucalypti* that has caused significant damage to plantations and nurseries in various parts of the world (Wingfield et al. 1993; Bettucci et al. 1999; Simpson 2000; Alfenas et al. 2001; Roux et al. 2006; Pegg et al. 2008).

Quambalaria eucalypti was first described causing a disease of *E. grandis* in South Africa and where the causal agent was named *Sporothrix eucalypti* (Wingfield et al. 1993). The fungus was later transferred to *Quambalaria* and where it was first recognized to be a basidiomycete. Disease problems caused by the pathogen were subsequently reported from Brazil (Alfenas et al. 2001), Uruguay (Bettucci et al. 1999), Australia (Pegg et al. 2008), Portugal (Bragança et al. 2016) and China (Chen et al. 2017). The disease is characterized by the appearance of powdery white fungal spore masses on the surface of infected shoots and leaves (Wingfield et al. 1993; Simpson 2000; Roux et al. 2006; de Beer et al. 2006; Pegg et al. 2009a). *Quambalaria eucalypti* most commonly infects *Eucalyptus* plants in nurseries (Wingfield et al. 1993; Simpson 2000), but it is also known to infect established trees in plantations (Alfenas et al. 2004; Roux et al. 2006; Pegg et al. 2008; Chen et al. 2017; Santos et al. 2020).

Beginning in 2018, symptoms of a leaf and shoot blight disease resembling infection by a *Quambalaria* species were observed in nurseries in North Sumatra, Riau and in North Kalimantan (Indonesia). These infections were mostly on clonal mother plants used to vegetatively propagate *Eucalyptus* for plantation establishment. The objectives of this study were to identify the causal agent of this disease and to test the pathogenicity of the putative pathogen on different *Eucalyptus* genotypes.

MATERIALS AND METHODS

Sample collection and fungal isolation

Symptoms of a leaf and shoot blight disease were observed on the leaves of *Eucalyptus* mother plants in nurseries in three regions, including North Sumatra, Riau and North Kalimantan. The disease was characterized by powdery white fungal spore masses on young leaves, shoots and stems (Figure 4.1). The symptoms were mainly observed on mother plants of *E. pellita* and its hybrids, including *E. pellita* x *E. grandis, E. pellita* x *E. brassiana* and *E. pellita* x *E. urophylla.* Symptomatic leaf and shoot samples (Figure 4.1) were collected from *Eucalyptus* clones in five nurseries in different regions including one in North Sumatra, three in Riau and one nursery in North Kalimantan (Figure 4.2). Each sample was placed in a separate brown paper bag and then transferred to the laboratory for isolation in culture.

White spore masses on the surface of the leaves and shoots were scraped from the samples with a sterile needle and transferred to the surface of potato dextrose agar (PDA Acumedia®: 40 g/L) in Petri dishes. The culture plates were then incubated at 27 °C for 7 days, and single hyphal tips from primary isolations were sub-cultured on clean PDA to obtain pure isolates. The resulting isolates were stored in the culture collection (CMW) of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa.

DNA extraction, PCR amplification and sequencing

DNA was extracted from mycelium of 7-day-old cultures using Prepman® Ultra Sample Preparation Reagent (Thermo Fisher Scientific, Waltham, MA, USA). The internal transcribed spacer (ITS) regions 1 and 2, including the 5.8S rRNA region and the large subunit (LSU) of the rRNA were amplified using primers ITS1F/ITS4 (Gardes & Bruns 1993; White et al. 1990) and LR0R/LR5 (Rehner & Samuels 1994; Vilgalys & Hester 1990), respectively. Polymerase chain reaction (PCR) amplifications were performed in 13 µL reactions containing 1 µL of genomic DNA, 2.5 µL of 5× MyTaq buffer (Bioline, London, UK), 0.25 µL MyTaq DNA polymerases (Bioline), 0.5 µL of each primer (10 µM), and 8.25 µL sterile deionized water. Thermal cycling included an initial denaturation at 95 °C for 5 min, followed by 10 primary amplification cycles of 30 s at 95 °C, 30 s at 55 °C, and 60 s at 72 °C, then 30 additional cycles of the same reaction sequence, with the annealing step increasing by 5 s per cycle. Reactions

were completed with a final extension at 72 °C for 10 min. PCR products were purified using ExoSAP-IT PCR Product Cleanup Reagent (Thermo Fisher Scientific, Waltham, MA, USA) and sequenced using BigDye terminator sequencing kit 3.1 (Applied Biosystems, Forster City, CA, USA) in both the forward and reverse primers. Sequencing was performed on an ABI PRISM 3100 DNA sequencer (Applied Biosystems, Forster City, CA, USA). Geneious Prime 2023.0.3 (https://www.geneious.com) was used to assemble and edit the raw sequences. All the sequences resulting from this study were deposited in GenBank (http://www.ncbi.nlm.nih.gov/) (Table 4.1).

Phylogenetic analyses

Reference sequences for species closely related to those found in this study were downloaded from the GenBank database (Table 4.1). All sequences were aligned using MAFFT v. 7 (http://mafft.cbrc.jp/alignment/server/) (Katoh & Standley 2013), and then manually confirmed in MEGA v. 7 (Kumar et al. 2016) where necessary. Maximum likelihood (ML) analyses were performed on the individual regions as well as on the combined ITS and LSU datasets, using RaxML v. 8.2.4 on the CIPRES Science Gateway v. 3.3 (Stamatakis 2014) with the default GTR substitution matrix and 1,000 rapid bootstraps. Sequences for *Microstroma juglandis* (RB2042) were used as the outgroup. The resulting trees were viewed using MEGA v. 7 (Kumar et al. 2016).

Pathogenicity tests

Relative aggressiveness of isolates

Initially, each isolate was sub-cultured on clean PDA and incubated at 27 ℃ for 21 days. To induce the spore production, 10 mL of sterilized distilled water (SDW) was spread over the surface of the cultures. The water was then removed from the plates, and the cultures were further incubated at 27 ℃ for 48 hours, after which this technique was repeated three times. The spore suspension was then harvested and adjusted to $1x10^6$ spore/ml using a haemocytometer. A drop of Tween 20 (Sigma – Aldrich) was added to the spore suspension prior to the inoculation to facilitate dispersion of the spores.

An initial inoculation trial was conducted using an *E. pellita* clone (clone ECL04) known to be susceptible to infection in the nursery, following the methods described by Mafia et al. (2009) and Bragança et al. (2016) with some modifications. Eight-week-old plants were used in this

test that included nine different isolates chosen to represent the range of collection sites (Table 4.1). Five plants were inoculated with each isolate and where the leaves had either been wounded or not. Wounds were induced using a sterile hypodermic needle (disposable needle 21G, duraSurge) and four 10 mm long scratches on four expanding leaves were made on each plant. The spore suspension was sprayed onto the surface of leaf until run-off. For the controls, an equal number of plants were sprayed with sterilised distilled water. Each plant was then covered with a clear plastic bag to maintain a high relative humidity, and these were incubated at 30 °C for 48 hours. The plastic bags were then removed and the plants maintained at 30 °C for 14 days.

A total of 20 leaves (5 plants x 4 leaves) were evaluated for each treatment. Disease severity of the leaves on each plant was assessed using the rating scale from 0 to 4 (Table 4.2). Isolations were made from inoculated tissue and the resulting isolates were identified based on morphology. Data were analysed using Kruskal-Wallis tests to determine whether there were statistically significant differences between the treatments. Pairwise comparisons were then performed using the Wilcoxon rank sum test with continuity correction. All statistical analyses were performed in R statistical software, version 3.2.0 (R Core Team 2020).

Relative susceptibility of different Eucalyptus *clones*

Six *Eucalyptus* clones, including four of *E. pellita* (ECL01, ECL02, ECL03, and ECL04) and two of a *E. grandis x E. pellita* (ECL05, and ECL06), were selected to test for susceptibility to the most aggressive isolates arising from the prior test. Inoculation was conducted using only the wounding method. Eight-week-old *Eucalyptus* plants generated from cuttings were inoculated with ten plants per treatment and an equal number as controls. A total of 40 leaves (10 plants x 4 leaves) were tested per clone. Inoculations, disease severity assessment and re-isolation were carried out following the protocol described above. The data were analysed in the same way as the initial inoculation trial.

RESULTS

Isolates

A total of 43 isolates were obtained from infected leaf and stem samples, morphologically resembling a *Quamlabaria* species. Of these, eight isolates were obtained from North Sumatra,

31 isolates were obtained from Riau, including Riau 1 (2 isolates), Riau 2 (18 isolates) and Riau 3 (11 isolates), while four isolates were obtained from North Kalimantan.

Phylogenetic analyses

Nine isolates collected across the various sampling regions were selected for further study. Amplicons of approximately 680 bp for the ITS and 870 bp for the LSU were generated. The ITS, LSU and combined sequence data sets used for phylogenetic analyses included 24 ingroup taxa and contained 632, 561, and 1193 characters, respectively. Both the individual tree and combined trees were found to be congruent, having similar topologies. All isolates sequenced in this study were grouped in monophyletic clades with the ex-type and representative isolates of *Q. eucalypti* in all the analyses (Figure 4.3). These isolates were thus identified as *Q. eucalypti*.

Pathogenicity tests

Relative aggressiveness of isolates

No symptoms of *Quambalaria* infection were found on plants inoculated without wounding and there were also no symptoms on the control plants. In the case of the wounded leaves, white spore masses typical of *Q. eucalypti* were found on the most of the inoculated plants 12 days after inoculation (Figure 4.4). The aggressiveness varied between isolates, with disease severity ranging from 0 to 4 (Figure 4.5). Isolate CMW57605 was the most aggressive followed by CMW57602 and CMW57618 where the disease severity ratings were 4, 3.6 and 3.6 respectively. Some isolates produced less infection on the wounds with severity of 1, 0.8, 0.7 and 0.6 for CMW57616, CMW57589, CMW57583 and CMW57609 respectively, while two isolates (CMW57591, CMW57592) failed to induce infection [Kruskal-Wallis test, $H = 589.42$ $df = 9$ and $P < 2.2e\text{-}16$]. *Quambalaria eucalypti* was easily re-isolated from the spore masses on the infected but never the control plants.

Relative susceptibility of different* Eucalyptus *clones

Isolate CMW 57605, found to be the most aggressive in the test where isolates were compared, was used in the clone screening test. Twelve days after inoculation, all inoculated *Eucalyptus* clones showed white spore masses typical of *Q. eucalypti* (Figure 4.4). Disease severity ranged from 1.4 to 3.7 (Figure 4.6), with clone ECL02 (*E. pellita*) as the most tolerant with a severity

of 1.4 compared to other clones of ECL04 (*E. pellita*), ECL06 (*E. grandis* x *E. pellita*), ECL01 (*E. pellita*), ECL03 (*E. pellita*) and ECL05 (*E. grandis* x *E. pellita*) with disease severities of 3.7, 3.5, 3.2, 3.2 and 2.9, respectively (Figure 4.6). Based on the results of the Kruskal-Wallis test, disease tolerance in clone ECL02 was statistically different from the other five clones tested ($H = 1659.7$, $df = 11$, and $P < 2.2e\text{-}16$). Isolates morphologically typical of *Q. eucalypti* were easily recovered from all inoculated plants. No symptoms were observed on the control plants.

DISCUSSION

The results of this study showed that a new leaf and shoot disease emerging on *Eucalyptus* nursery plants in three regions of Indonesia was caused by *Q. eucalypti*. This was determined based on isolations made from symptomatic material, identification of the resulting isolates using DNA sequence analyses as well as pathogenicity tests. This is the first report of the pathogen in Indonesia as well as in SEA.

Several *Eucalyptus* species or genotypes have previously been reported to be affected by *Q. eucalypti* including *E. grandis* and *E. nitens* in South Africa (Wingfield et al. 1993, Roux et al. 2006), *E. globulus* and *E. saligna* × *E. maidenii* hybrids in Brazil (Alfenas et al. 2001), *E. globulus* and *E. grandis* in Uruguay (Bettucci et al. 1999), *E. grandis*, *E. longirostrata*, *E. grandis* × *E. camaldulensis* hybrids, *E. microcorys* and *E. dunnii* in Australia (Pegg et al. 2008), *E. globulus* in Portugal (Bragança et al. 2016) and *E. urophylla x E. grandis* hybrids in China (Chen et al. 2017). However, this is the first time that *Q. eucalypti* has been reported on *E. pellita* and its hybrids including hybrids with *E. grandis*, *E. brassiana* and *E. urophylla.* This is of substantial concern given the growing importance of *E. pellita* as a plantation species in the humid tropics (Brestow et al. 2006; Nambiar et al. 2018).

The pathway of entry of *Q. eucalypti* into Indonesia is unknown. This pathogen is likely native to Australia (Wingfield et al. 1993; Roux et al. 2006; Zhou et al. 2007; Pegg et al. 2009a; de Beer et al. 2006), but has been accidentally introduced into countries in Africa, Asia, Europe and South America (Wingfield et al. 1993; Alfenas et al. 2001; Pegg et al. 2008; Bragança et al. 2016; Chen et al. 2017). Based on DNA sequence analysis, two ITS haplotypes were detected in the *Q. eucalypti* collection in this study. The majority of the isolates, collected in

North Sumatra and Riau, shared the same haplotype as those known in China, while the isolates from Kalimantan shared the same haplotype as that in South Africa, Portugal and Uruguay (Chen et al 2017). Future studies at the population genetic level are planned to understand the likely source of origin of the pathogen in Indonesia.

An inoculation trial showed that wounds were necessary for *Q. eucalypti* to infect leaves. This is an interesting result as the pathogen has previously been shown to easily infect young and unwounded leaf and shoot tissue (Wingfield et al. 1993; Pegg et al. 2009b). In contrast, our results are similar to those of Mafia et al. (2009) who showed that wounds favoured infection by *Q. eucalypti*. These results are intriguing given the fact this pathogen is clearly able to infect leaves via the stomata (Pegg et al. 2009b) and thus typical of a primary pathogen.

Inoculation on *Eucalyptus* leaves of single susceptible genotype with numerous different *Q. eucalypti* isolates showed that these differed markedly in their ability to initiate infections. The most aggressive of the isolates used in an inoculation trial also showed that different *Eucalyptus* genotypes differ in their susceptibility to infection. It should thus be possible to select clones resistant to infection using a relatively simple screening procedure. This approach has been used previously (Pegg et al. 2011, Bragança et al. 2016; Roux et al. 2006) providing an opportunity to manage the problem. Such screening is particularly relevant in the Indonesia situation where mother plant hedges are needed to mass propagate planting stock and leaf or shoot diseases, such as those caused by *Q. eucalypti* can significantly reduce productivity. The results of this study show the potential to manage *Q. eucalypti* in the future by selecting materials tolerant to the disease.

Quambalaria eucalypti appears to be a pathogen of increasing prevalence in many regions of both the Northern and Southern Hemispheres (Wingfield et al. 1993; Bettucci et al. 1999; Simpson 2000; Alfenas et al. 2001; Roux et al. 2006; Pegg et al. 2008; Bragança et al. 2016; Chen et al. 2017). In Indonesia, its incidence is mainly in the nursery and there are currently no reports of the pathogen causing problems on established trees. This situation could easily change, as it has in South Africa (Roux et al. 2006), making it important not to establish susceptible clones in plantations. The pathogen could also undergo a host shift to infect commonly occurring native trees and shrubs in the Myrtaceae, as has been found in Uruguay (Pérez et al. 2008).

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APPENDIX

Figure 4. 1. Symptoms of *Q. eucalypti* infection on leaves and stems of *Eucalyptus* mother plants.

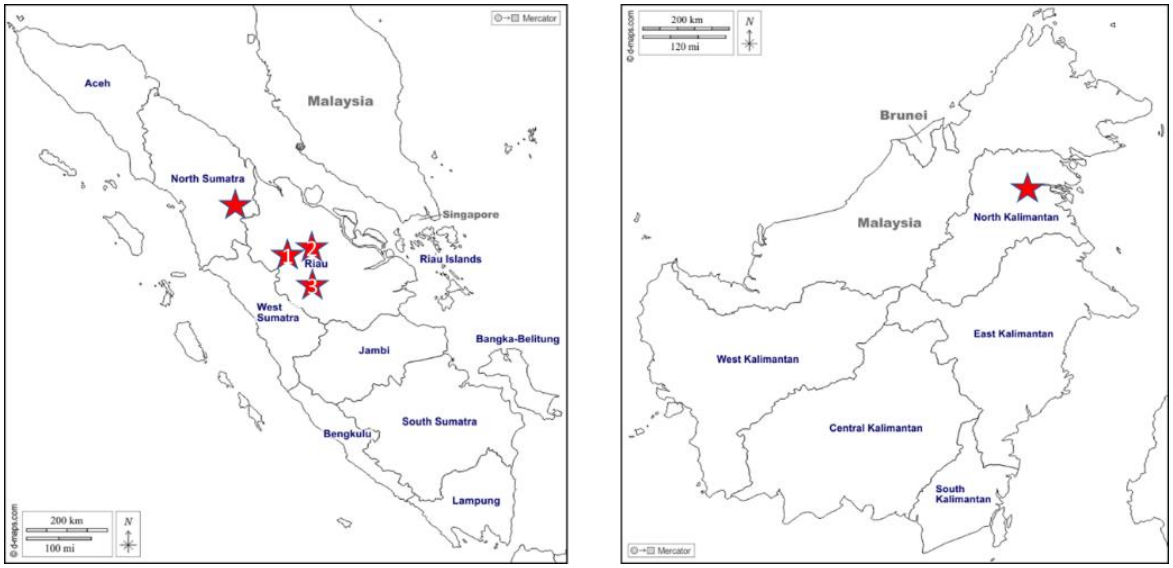

Figure 4. 2. Geographic location of the sampling sites of *Eucalyptus* mother plant affected by *Quamballaria* in Sumatra and Kalimantan, Indonesia.

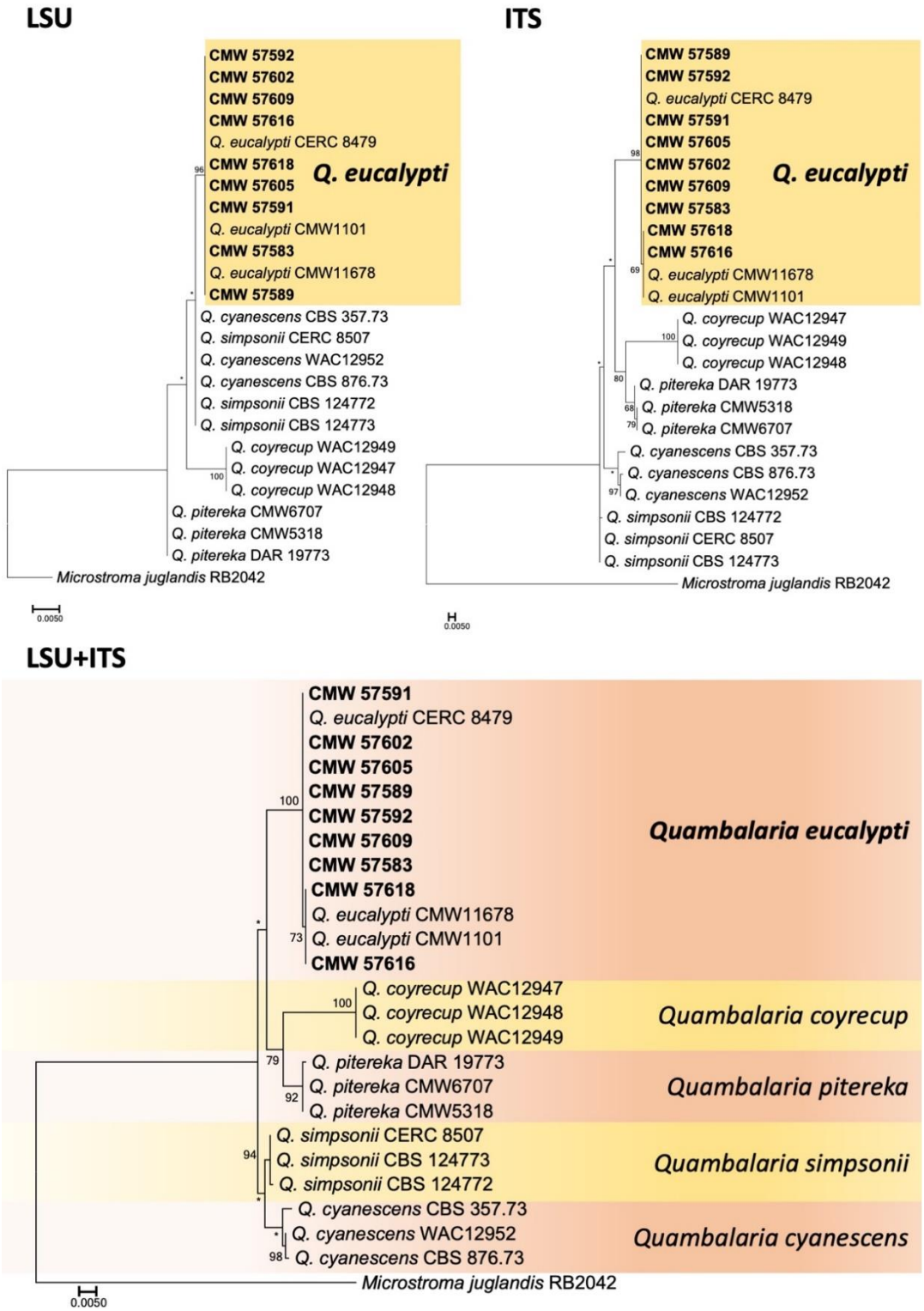

Figure 4. 3. Phylogenetic tree based on maximum likelihood (ML) analyses of ITS, LSU and combined sequences for *Quambalaria* spp. Isolates sequenced in this study are presented in boldface. Bootstrap values of ≥60% for ML analyses are indicated at the nodes. Bootstrap values <60% are marked with "*". *Microstroma juglandis* (isolate RB2042) represents the outgroup.

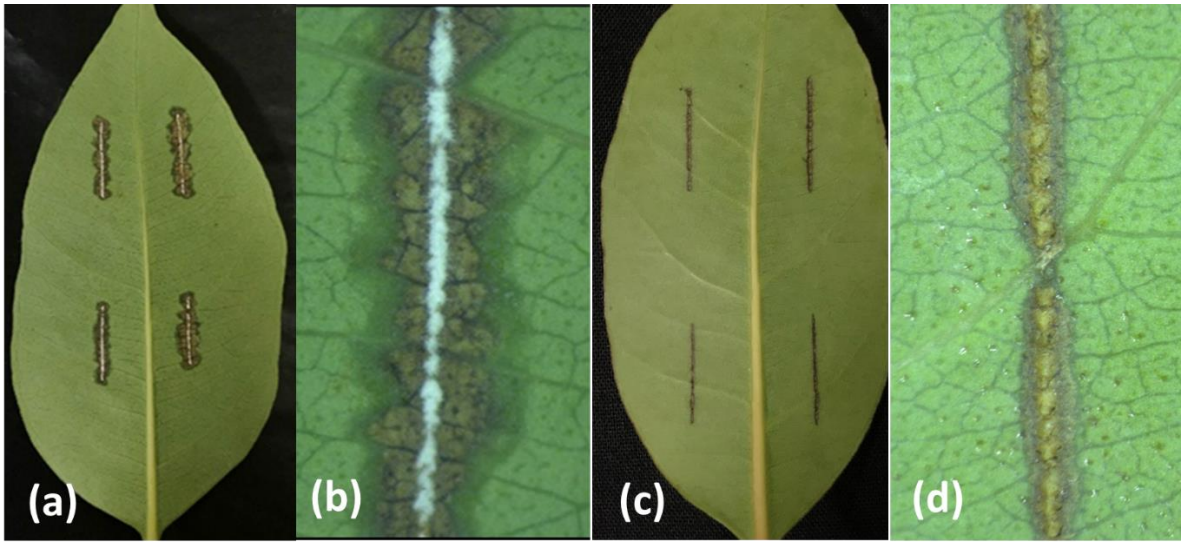

Figure 4. 4. Symptom of *Quambalaria eucalypti* infection on *Eucalyptus* leaves after inoculation showing typical white spore masses of the pathogen (a, b), while control produce no symptom (c, d).

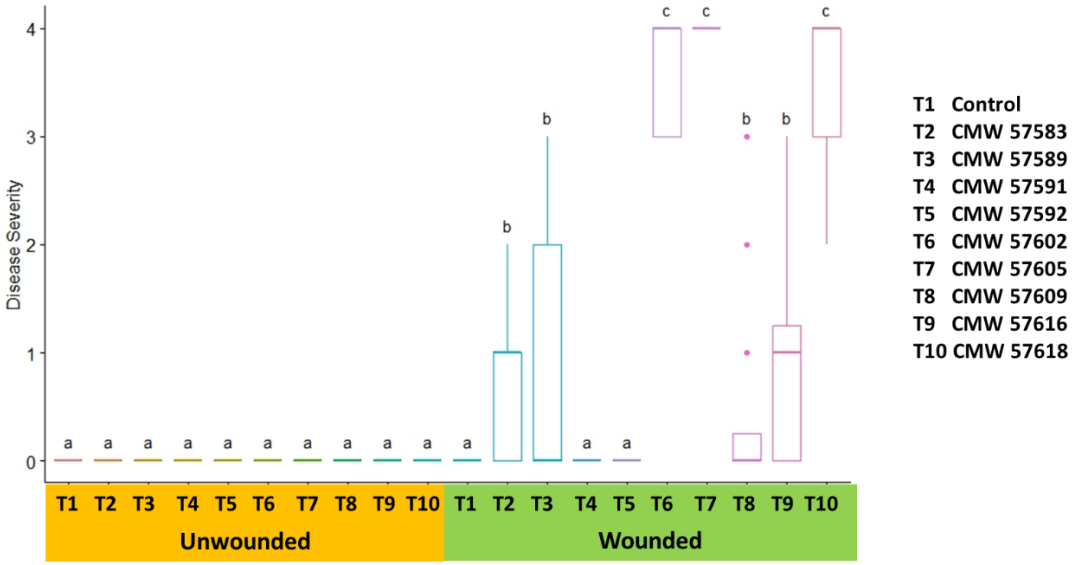

Figure 4. 5. Inoculation with unwounded and wounded methods on *Eucalyptus* clone ECL04 using nine *Quambalaria eucalypti* isolates.

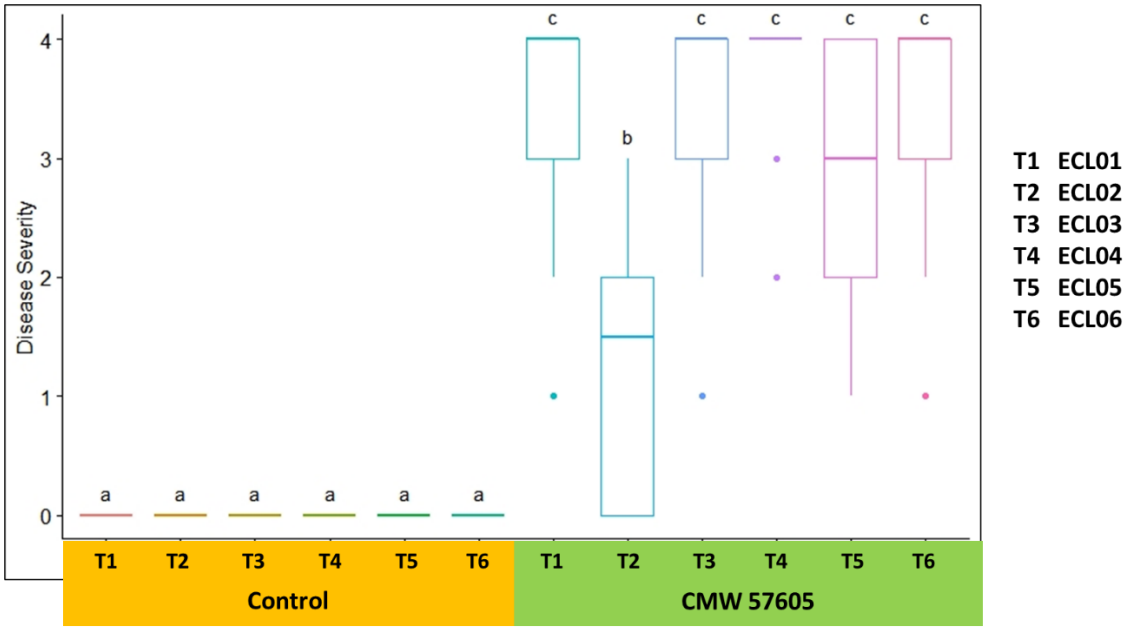

Figure 4. 6. Bar chart indicating the severity score resulting from inoculation trials of six *Eucalyptus* genotypes inoculated with *Quambalaria eucalypti* (CMW 57605) and the controls.

Table 4.1. Collection details and GenBank accession numbers of isolates included in the phylogenetic analyses

Species	Isolate	Host	Locality	GenBank accession		Reference
				ITS	LSU	
Quambalaria coyrecup	WAC12947	*Corymbia calophylla*	Western Australia, Australia	DQ823431	DQ823444	Paap et al. 2008
	WAC12949	*C. calophylla*	Western Australia, Australia	DQ823432	DQ823445	Paap et al. 2008
	WAC12948	*C. calophylla*	Western Australia, Australia	DQ823433	DQ823446	Paap et al. 2008
Quambalaria cyanescens	CBS 357.73 = CMW 5583	human skin	Netherlands	DQ317622	DQ317615	de Beer et al. 2006
	CBS 876.73 = CMW 5584	*E. pauciflora*	New South Wales, Australia	DQ317623	DQ317616	de Beer et al. 2006
	WAC12952	*C. calophylla*	Western Australia, Australia	DQ823419	DQ823440	Paap et al. 2008
Quambalaria eucalypti	CBS 118844 = CMW 1101	*E. grandis*	South Africa	DQ317625	DQ317618	de Beer et al. 2006
	CBS 119680 = CMW 11678	*E. grandis*	South Africa	DQ317626	DQ317619	de Beer et al. 2006
	CERC8479	*E. urophylla* x *E. grandis*	Guangdong, China	KY615012	KY615050	Chen et al. 2017
	CMW 57583	*E. pellita x E. grandis*	Pangkalan Kerinci, Riau, Indonesia			This study
	CMW 57589	*E. pellita x E. grandis*	Pangkalan Kerinci, Riau, Indonesia			This study
	CMW 57591	*E. pellita*	Baserah, Riau, Indonesia			This study
	CMW 57592	*E. grandis x E. pellita*	North Sumatra, Indonesia			This study
	CMW 57602	*E. pellita x E. brassiana*	Baserah, Riau, Indonesia			This study
	CMW 57605	*E. pellita x E. brassiana*	North Sumatra, Indonesia			This study
	CMW 57609	*E. pellita x E. grandis*	Pangkalan Kerinci, Riau, Indonesia			This study

Table 4.1. (Continue)

Species	Isolate	Host	Locality	GenBank accession		Reference
				ITS	LSU	
Quambalaria eucalypti	**CMW 57616**	*E. grandis x E. pellita*	North Kalimantan, Indonesia			This study
	CMW 57618	*E. grandis x E. pellita*	North Kalimantan, Indonesia			This study
Quambalaria pitereka	DAR19773	*C. eximia*	New South Wales, Australia	DQ823423	DQ823438	Paap et al. 2008
	CMW 6707	*C. maculata*	New South Wales, Australia	DQ317627	DQ317620	de Beer et al. 2006
	CBS 118828 = CMW 5318	*C. citriodora* subsp. *variegata*	New South Wales, Australia	DQ317628	DQ317621	de Beer et al. 2006
Quambalaria simpsonii	CBS 124772	*E. tintinnans*	Edith Falls, Australia	GQ303290	GQ303321	Cheewangkoon et al. 2009
	CBS 124773	*Eucalyptus* sp.	Lamphoon, Thailand	GQ303291	GQ303322	Cheewangkoon et al. 2009
	CERC8507	*E. urophylla* x *E. grandis*	Guangdong, China	KY615037	KY615058	Chen et al. 2017

Note: Isolates obtained in this study are indicated in bold. CBS = The culture collection of Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CERC = China Eucalypt Research Centre (CERC), Chinese Academy of Forestry (CAF), ZhanJiang, GuangDong, China; CMW = culture collection of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa; DAR = the plant pathology herbarium for the Department of Agriculture in NSW, Australia; WAC = Department of Agriculture Western Australia Plant Pathogen Collection, Perth, Australia.

Table 4.2. Disease severity scale used to score infections on leaves inoculated with *Quambalaria eucalypti* *

Score	Infection rate	Observation
0	No infection	No typical white spore masses present
1	Low infection	25% of the total wounds infected.
2	Moderate infection	50% of the total wounds infected
3	High infection	75% of the total wounds infected
4	Very high infection	All wounds on inoculated leaves infected.

*Infection determined based on the presence of spore masses typical of *Q. eucalypti*

Chapter 5

Pathogenicity of *Pythium myriotylum* on *Acacia crassicarpa* and *A. mangium* x *A. auriculiformis* clones in Indonesia

ABSTRACT

The oomycete *Pythium myriotylum* is an important pathogen of several crops, causing wilt and damping-off during nursery propagation. This pathogen was recently reported as the causal agent of wilt and damping-off on *Acacia crassicarpa* plants in nurseries located in Riau, Indonesia. The aim of this study was to evaluate the relative pathogenicity of *P. myriotylum* on different clones of *A. crassicarpa* and hybrids of *A. mangium* x *A. auriculiformis*. Based on the results, we observed more tolerance on the *A. mangium* x *A. auriculiformis* hybrids than on the *A. crassicarpa* clones. The *Acacia* clones tested against *P. myriotylum* also displayed different levels of tolerance to infection. At the end of each experiment, the pathogen was re-isolated and confirmed by isolation on selective medium NARP and molecular identification with species-specific primers. Overall the results showed that screening for tolerance to infection by *P. myriotylum* will be important in the *Acacia* breeding program and, especially, make it possible to produce sufficient plantation stock in the nurseries.

Key words: inoculation, molecular markers, nursery disease, oomycetes, selective medium

INTRODUCTION

Pythium is a genus of oomycetes, which based on recent studies, includes more than 140 species (Uzuhashi et al. 2010; Kageyama 2014). *Pythium* species have a cosmopolitan distribution and can be found in a wide range of climatic zones including tropical and polar areas (van der Plaats-Niterink 1981; Levesque & De Cock 2004; Uzuhashi et al. 2010). *Pythium* species can live in soil or water as saprotrophs or parasites (Martin & Loper 1999; Hong & Moorman 2005; Nechwatal et al. 2008), on fish (Miura et al. 2010), red algae (Kawamura et al. 2005) and mammals including humans (Phillips et al. 2008). Some *Pythium* species are also mycoparasitic (Jones & Deacon 1995; Su et al. 2001; Patrice et al. 2005). However, *Pythium* species are best-known as a threat to plant health due to their very wide

diversity of plant hosts. For example, they cause diseases including crown, collar, root and seed rots as well as seedling damping-off (Erwin & Ribeiro 1996).

As plant pathogens, *Pythium* species are mostly disease agents of nursery plants causing wilting and damping-off (Dumroese & James 2005) on many different hosts. Some examples of hosts include *Colodium hortulanum* (Ridings & Hartman 1976), *Eucalyptus* spp., *Pinus* spp. (Linde et al. 1994a; Linde et al. 1994b; Shearer & Smith 2000), and *Pseudotsuga menziesii* (Weiland 2011; Weiland et al. 2013). Although there are few reports of *Pythium* species associated with mortality of mature trees in plantations, there are some examples of *Pythium* species causing disease problems on established trees (Linde et al. 1994a).

Pythium myriotylum Drechsler is one of the species in the genus that has received particular attention as a plant pathogen. This species was first reported affecting tomato seedlings in the USA (Drechsler 1930), and since then it has been shown to have a broad host range worldwide (van der Plaats-Niterink 1981; Farr & Rossman 2012). This is also known as one of the most destructive *Pythium* species in nurseries and green houses (Ben-Yephet & Nelson 1999). This artificial growing environment, coupled with high plant density and intensive irrigation systems, over-watering, as well as poor drainage, can provide favorable environmental conditions for *P. myriotylum* infection (Sutton et al. 2006).

Acacia crassicarpa and hybrids of *A. mangium* x *A. auriculiformis* are currently considered the most commercially important plantation forest trees grown in the lowland tropical regions of Indonesia (Griffin et al. 2011; Nambiar et al. 2018). Over one million hectares of these trees have been planted in the area, mainly to sustain pulp and paper industries (Griffin et al. 2011). To ensure a constant supply of seedlings for these sustainable forests, large-capacity nurseries have been established. One of the most important problems affecting this production system has been a root-collar disease, recently discovered to be caused by *P. myriotylum* (Oliveira et al. 2021). Consequently, the aim of this study was to evaluate the relative aggressiveness of *P. myriotylum* on different clones of *A. crassicarpa* and hybrids of *A. mangium* x *A. auriculiformis*.

MATERIALS AND METHODS

Isolates and inoculum preparation

An aggressive isolate (CMW 55116) of *P. myriotylum* selected in the previous study by Oliveira et al. (2021) was selected for an inoculation test. Prior to inoculation, the isolate was grown in nine cm diameter Petri dishes containing the *Pythium*-specific medium NARP (V8: 8.0 mL/L; CaCO3: 1.0 g/L; Pimaricin: 0.01 g/L; Ampicillin: 0.25 g/L; Rifampicin: 0.01 g/L; PCNB: 0.025 g/L; Agar: 17 g/L), and then incubated at 28 °C. After four days, colonies had covered the plates completely.

The inoculum was prepared by adding a mixture of vermiculite and broken corn (5:1), mixed with 300 ml of distilled water in 1 L Erlenmyer fasks. All the flasks were then plugged with cotton wool and autoclaved. Upon cooling, six agar plugs taken from 4-day-old *P. myriotylum* cultures were inoculated into the medium. After inoculation, the flasks were incubated at room temperature in the dark for four weeks.

Plant material

Acacia clones were prepared by vegetative propagation where cuttings were harvested from mother plants and rooted under misting. Plants were kept in 73 cm^3 containers that were filled with substrate containing coco-peat and rice husk (3:1). Plants were grown in the nursery until seven weeks of age, transplanted into 10 cm (diam) polyethelene bags and then allowed to acclimatise in an inoculation chamber for one week before inoculation.

Five different *Acacia* clones, including two *A. crassicarpa* (CAC001, CAC002), and three *A. mangium* x *A. auriculiformis* (CAH001, CAH002 and CAH003) clones were tested for tolerance to infection by *P. myriotylum*. Sixty eight-week-old plants of each clone were inoculated with isolate CMW 55116 of *P. myriotylum*, and the same number of plants were used as the controls. Inoculation was conducted by making four cavities (2 cm wide and 10 cm deep) in the growing medium around the plants to be tested (Figures 5.1A and 5.1B). Each of these holes was then filled with 5 gr of inoculum (Figure 5.1C). To stimulate the production of sporangia and to release the zoospores from the inoculum source, the planting bags were flooded overnight with sterile distilled water after one day and then again 14 days after inoculation. The control plants were treated in the same way, but instead of inoculum, the cavities around the test plants were filled with sterile vermiculite mixture.

All the plants were maintained in a green house at 28 ±5 °C and arranged in a fully randomized block design. Disease incidence was considered by inspecting plants for wilt symtoms twice a week for four weeks. Plants showing wilt symptoms were taken to a laboratory for re-isolation of the inoculant.

Isolations from infected plants were made on NARP. Colonies emerging from infected plants were identified based on DNA sequencing methods using 5-day-old colonies following the rapid identification protocol using specific primers described by Oliveira et al. (2021).

Statistical analysis

Disease incidence data were analyzed based on plant survival. For this purpose, a survival curve was generated following the Kaplan-Meier method to visualize the survival probability of treatments at each time point (Nesi et al. 2013; Bland & Altman 1998; Schandry 2017). To gain a clear understanding of the differences between clones, Cox proportional hazards models (Therneau 2015; Schandry 2017) were used to analyze the data.

RESULTS

Inoculation of clones

Typical symptoms caused by *P. myriotylum* infection were observed on inoculated plants in all experiments (Figure 5.2). The first symptoms of wilting were observed seven days after inoculation. Re-isolations from the roots of inoculated plants resulted in colonies typical of *P. myriotylum*. Their identity was then confirmed as being of this pathogen with the species-specific primers. No symptoms were seen on the control plants where the roots remained healthy.

Clone tolerance to infection

Disease incidence varied according to the *Acacia* clones tested. The Kaplan-Meier survival probability value of 0.0001 indicates a significant result between treatments, with the survival probabilities for CAC001, CAC002, CAH003, CAH002 and CAH001 being 20%, 25%, 27%, 50% and 80% respectively (Figure 5.3). This result was also supported by the Cox proportional hazards model analysis, which showed that all treatments were significant compared to CAC01

(lowest survival probability) as the reference, with hazard ratios of 0.73, 0.58, 0.32 and 0.13 for CAC002, CAH003, CAH002 and CAH001, respectively (Figure 5.4). For the *A. crassicarpa* clones, the first wilt symptoms were observed on day 7 and both clones CAC001 and CAC002 were considered susceptible. At the end of the experiment, these clones had a disease incidence of 60% and 43% respectively. For the hybrid *A. mangium* x *A. auriculiformis*, both clones CACH002 and CAHC003 showed similar wilt symptoms throughout the experiment, with disease incidences of 23% and 40%, respectively, and were therefore considered susceptible to infection by *P. myriotylum*. Clone CAH001 was moderately tolerant, with only 10% of plants infected at the end of the experiment.

DISCUSSION

The results of this study showed clearly that clones of *A. crassicarpa* have similar levels of susceptibility to infection by *P. myriotylum*. In contrast, clones of the hybrid between *A. mangium* and *A. auriculiformis* differed in their response to the pathogen. These results have important consequences regarding the propagation of *Acacia* clones for plantation establishment.

The fact that *A. crassicarpa* clones did not differ in susceptibility to infection by *P. myriotylum* is broadly relevant to the propagation of this important tree. While every effort is being made to eliminate the pathogen from nurseries, situations arise where contamination of the propagation facilities occurs. Clearly opportunities to produce *P. myriotylum*-tolerant clones appear not to be present. However, relatively small numbers of clones were used in the study. Future plans are to produce much greater numbers of *A. crassicarpa* clones and there are opportunities to test these in a similar way to that used in this study.

The differences observed in the tolerance of the *A. mangium* x *A. auriculiformis* clones to infection by *P. myriotylum* was of interest. A similar situation has been seen in production nurseries where some clones of this hybrid are also less affected by the pathogen. It is also of interest that clones of this hybrid would perform differently to those of *A. crassicarpa*, given that the pathogen has a wide host range beyond *Acacia*. This could provide an opportunity to better understand the biology of *P. myriotylum* in the future.

It is likely that asymptomatic *Acacia* clones have low levels of infection by nursery pathogens such as *P. myriotylum*. If this is the case, it would be reasonable to expect that such infections would affect plantation establishment using such plants. This is a very serious problem for example with fungi such as the pine pitch canker, *Fusarium circinatum*, where infected but asymptomatic plants can fail to become established in plantations (Storer et al. 1998; Wingfield et al. 2008). Future studies will need to consider this issue, where for example *A. crassicarpa* is established on wetlands (Griffin et al. 2011; Nambiar et al. 2018) and where initial growing conditions are stressful.

In plantation forestry, strong breeding programs are focusing on resistance against various important diseases (van Heerden et al. 2005; Wingfield 2003; Rezende et al. 2014). To accomplish this goal, disease tolerance can be evaluated under natural conditions in the field or by artificial inoculations (Guimaraes et al. 2010; Chi et al. 2019). Monitoring of planting stock for disease tolerance under field conditions can be simpler than often complicated inoculation trials, but this approach often suffers from pathogen escape (Raffa et al. 2023). Inoculation trials such as the one used in the study can provide uniform results and these are often achieved more rapidly than waiting for symptoms to appear in plantations. In the present study, we considered a nursery pathogen and thus inoculations under nursery conditions were most appropriate.

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APPENDIX

Figure 5. 1. Inoculation of eight-week-old *Acacia* clones with *Pythium myriothylum*. (a, b) four cavities (2 cm wide and 10 cm deep) were made in the growing medium around the plants with a rod; (c) each of these four holes was then filled with 5 gr of inoculum.

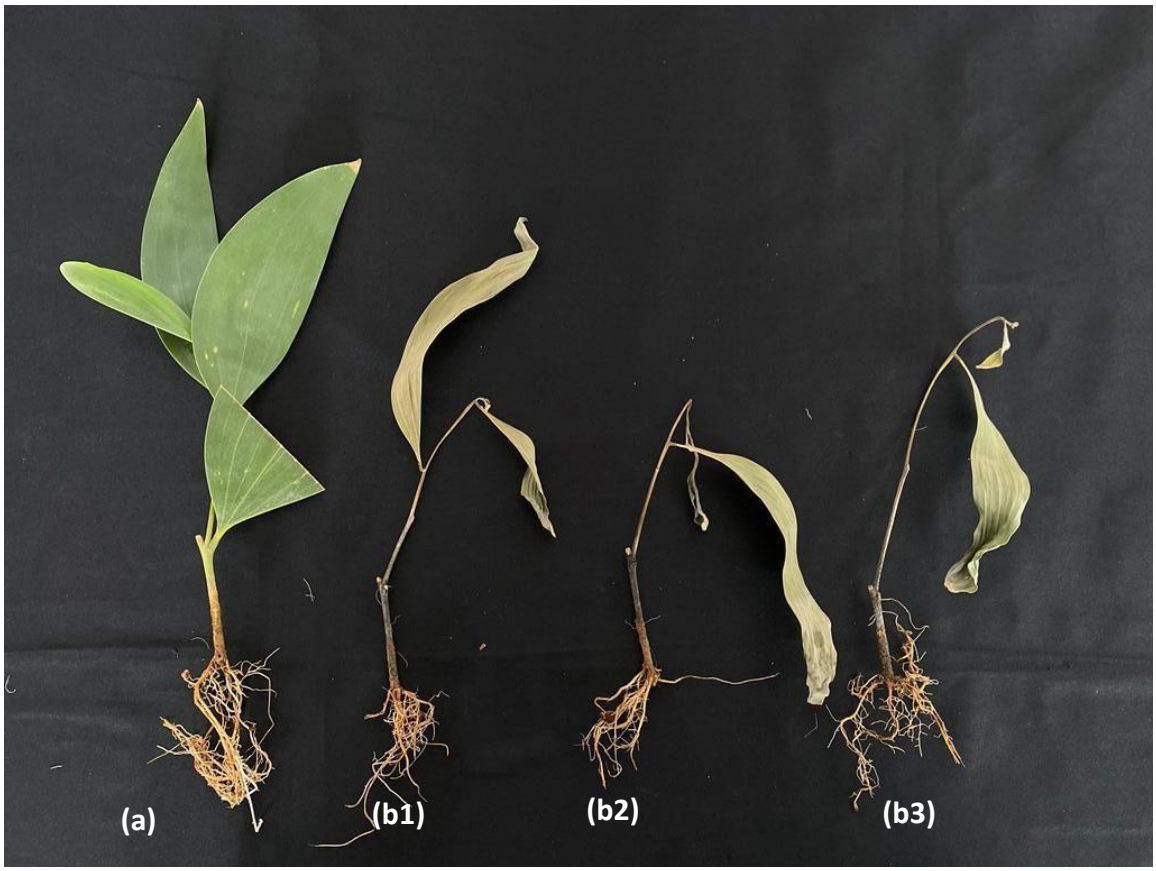

Figure 5. 2. Control plant is healthy (a) and typical symptoms with wilting and dying (b1, b2, b3) caused by *Pythium myriotylum* were observed on inoculated plants.

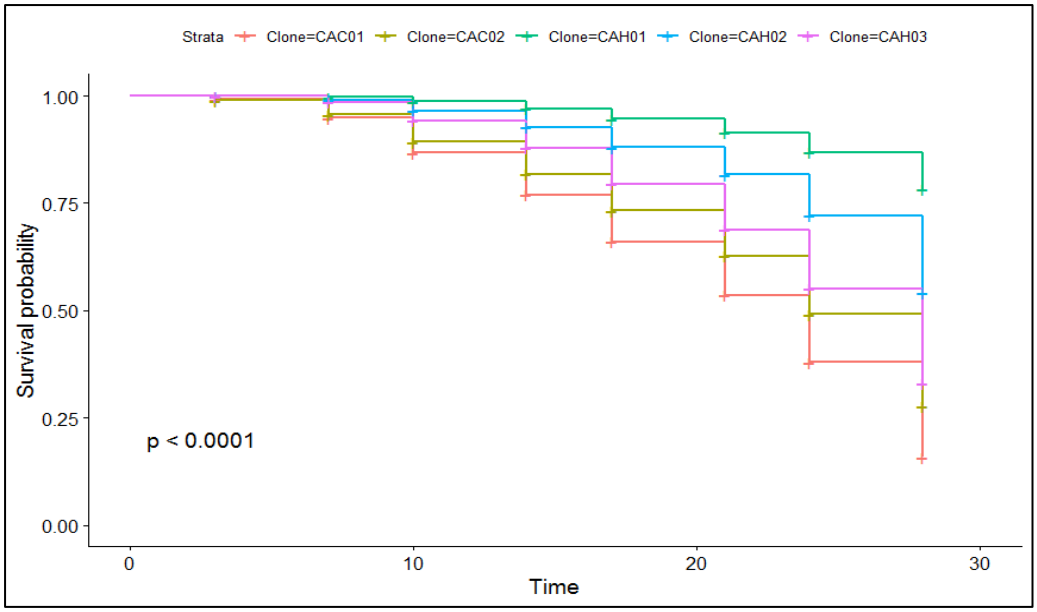

Figure 5. 3. Survival probability over time (days) of *Acacia* clones against *Pythium myriotylum* with the Kaplan Meier Curve. A P-value of 0.0001 indicates a signifant result between the treatments, where the survival probability for CAC001, CAC002, CAH003, CAH002 and CAH001 are 20%, 25%, 27%, 50% and 80% respectively.

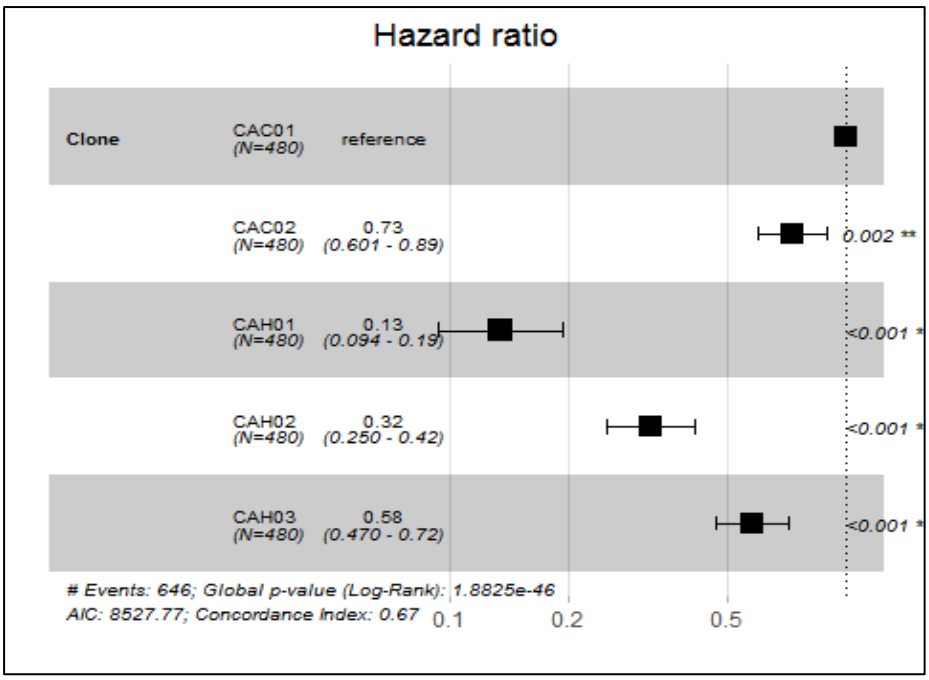

Figure 5 .4. Analysis for genetic resistance of *Acacia* clones against *Pythium myriotylum* with Cox proportional hazard model, with CAC01 (lowest survival probability) as reference. All treatments are significant compared to the reference with hazard ratios of 0.73, 0.58, 0.32, and 0.13 for CAC002, CAH003, CAH002 and CAH001 respectively.

SUMMARY

Plantations of non-native *Eucalyptus* spp. and *Acacia* spp. are expanding rapidly around the world to meet global demand for wood-based products. More than seven million hectares of these trees have been established in South East Asia, where *Eucalyptus* is increasingly replacing *A. mangium*, particularly in Indonesia, Malaysia and Vietnam, due to a vascular wilt disease caused by *Ceratocystis manginecans*. This is an example of how a single disease can result in the failure of one of the most important tree species used to establish plantations.

The first chapter of this thesis presents a review of the literature pertaining to the diseases affecting *Acacia* spp. and *Eucalyptus* spp. plantations in South East Asia. The review clearly shows that both *Acacia* and *Eucalyptus* share many of the same diseases. A recent example is Ceratocystis wilt, caused by *C. manginecans,* which initially affected only *Acacia* spp., but was later found to also infect *Eucalyptus* spp. It was also shown that some of the diseases are caused by native pathogens with wide host ranges such as Ganoderma root rot and others by accidentally introduced pathogesn including leaf diseases, caused by the scab pathogen *Elsinoe necatrix* and the blight pathogen *Teratosphaeria destructans.* Options to manage the impact of these diseases are discussed in detail.

The second chapter of this thesis concerns pathogens in the genus *Calonectria* that are well-known to cause leaf and shoot diseases. Intensive surveys led to the identification of six *Calonectria* species including *C. acicola*, *C. hawksworthii*, *C. lombardiana*, *C. multiseptata*, *C. pseudoreteaudii* and *C. reteaudii*. Of these, *C. lambordiana* was the dominant species, and with the other two species, *C. pseudoreteaudii* and *C. acicola*, they represent first reports on *Eucalyptus* in Indonesia. This study also reported *C. acicola* infecting *Eucalyptus* for the first time. The identification of these fungi was achieved using DNA sequence data based on the translation elongation factor 1-alpha, β-tubulin, calmodulin, and histone H3 gene regions. All six *Calonectria* species were found to be pathogenic to *Eucalyptus* in artificial inoculation studies.

The third research component of this thesis concerned the disease known as Cryphonectria canker. *Chrysoporthe* species were collected from cankers on *Eucalyptus* in Riau and Kalimantan and all isolates were shown to be those of *C. deuterocubensis* using the DNA-based sequence comparisons for multiple gene regions. The aggressiveness of the *C.*

deuterocubensis isolates was tested on *Eucalyptus grandis* x *E. pellita* hybrids under field conditions and showed that they differed in their pathogenicity. *Eucalyptus pellita* clones and their hybrids with *E. grandis,* and different *Eucalyptus* genotypes also differed in their susceptibility to the pathogen, providing options to avoid the disease in the future.

The final two chapters of this thesis concerned nursery disease problems caused by a species of *Quambalaria* and *Pythium myriotylum*. The *Quambalaria* was identified as *Q. eucalypti* using DNA sequence data and isolates were shown to differ in their aggressiveness. Futhermore, different *Eucalyptus* clones were shown to differ in their susceptibility to infection by the pathogen. This is the first report of *Q. eucalypti* as a pathogen of *Eucalyptus* in Indonesia. The study on *P. myriotylum* confirmed the aggressiveness of this oomycete pathogen on two important *Acacia crassicarpa* clones. Both were found to be highly susceptible in contrast *A. mangium* × *A. auriculiformis* hybrids that had various levels of susceptibility.

The studies presented in this thesis provide substantial new knowledge regarding pathogens affecting plantation forestry in Indonesia. They also contribute to management options, particularly through breeding and selection of tolerant planting stock. Furthermore, the results expand the known host and geographical ranges of several previously unknown fungal species such as those in the genera *Calonectria* and *Quambalaria*.While such new knowledge has been aquired, it is also clear that there are many other disease challenges facing plantation forestry in Indonesia and more broadly in South East Asia. Intensive research will be needed to manage them in the future and thus to maintain the sustainability of plantation forestry in the region.

Scientific outputs directly or indirectly emerging from this thesis:

1. Journal publications

Tarigan M, Pham NQ, Jami F, Oliveira LSS, Saha MA, Durán A, Wingfield MJ. 2023. *Calonectria* species diversity on eucalypts in Indonesia. *Southern Forests: a Journal of Forest Science* 85: 56-64. DOI: 10.2989/20702620.2023.2179441

Tarigan M, Wingfield MJ, Marpaung YMAN, Durán A, Pham NQ. 2023. *Quambalaria eucalypti* on *Eucalyptus* in Indonesia. *Forest Pathology*. e12829. https://doi.org/10.1111/efp.12829

Tarigan M, Wingfield MJ, Marpaung YMAN, Durán A, Pham NQ. 2023. Pathogenicity of *Chrysoporthe deuterocubensis* on *Eucalyptus* in Indonesia. Accepted to *Southern Forests: a Journal of Forest Science*.

2. Conference participation and presentation

Tarigan M, Pham NQ, Jami F, Oliveira LSS, Saha MA, Durán A, Wingfield MJ. 2022. *Calonectria* leaf blight and its threat to *Eucalyptus* planting material. Symposium RGE – FABI Tree Health Program. Nov 2022 at the RGE Technology Centre, Pangkalan Kerinci, Indonesia.

Tarigan M, Durán A, Wingfield MJ. 2023. Emerging pathogens of *Eucalyptus* and *Acacia* plantation forestry in Indonesia. Symposium RGE – FABI Tree Health Program. Nov 2023 at the RGE Technology Centre, Pangkalan Kerinci, Indonesia.