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23 years of research on Teratosphaeria leaf blight of *Eucalyptus*

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ABSTRACT

In Australia, during the course of the last two decades, plantation area of *Eucalyptus* has expanded dramatically. One of the most important threats to these trees, and to the forest industries they sustain, is a complex of fungal diseases broadly treated as Teratosphaeria Leaf Blight. The aim of this review is to summarise some of the most important findings relating to *Teratosphaeria* spp. (previously *Kirramyces*) associated with leaf and shoot blight of *Eucalyptus.* The review spans a period of 23 years since the description of the aptly named *Teratosphaeria destructans*. Six species of *Teratosphaeria* are associated with leaf and shoot blights of *Eucalyptus* and these are *T. destructans*, *T. eucalypti*, *T. novaehollandiae*, *T. pseudoeucalypti*, *T. viscida* and *T. tiwiana*. With the exception of *T. destructans,* all of these species have been found in Australia. Based on the damage they cause, the most significant of these fungi are *T. destructans*, *T. pseudoeucalypti* and *T. viscida*. *Teratosphaeria viscida* has been found only in the tropics of eastern Australia, while *T. destructans* and *T. pseudoeucalypti* have spread globally; *T. destructans* throughout Asia and South Africa and *T. pseudoeucalypti* into South America. Factors driving the development of these diseases have included the establishment of plantations adjacent to native eucalypt forests in Australia and planting on sites not favourable to the growth of the host trees. These factors, in conjunction with a lack of selection for resistance to emerging pathogens, lack of resilience to disease in monocultures, and the movement of pathogens with planting stock and seeds around the globe have led to substantial losses. Based on the Teratosphaeria leaf blight example, it is clear that more effective forest management and more stringent biosecurity measurements will be a required to sustain eucalypt plantations globally.

1. Introduction

More than 600 species of *Eucalyptus* are endemic to Australia, with only a few native to Papua New Guinea, some parts of Indonesia and Mindanao in the Philippines (Brooker and Kleinig, 1990; Potts and Pederick, 2000). They are highly favoured plantation species because they are easy to cultivate and are fast growing (Turnbull, 2000). These trees have a wide range of desirable wood properties, they are genetically diverse, and include species adapted to a wide range of climates and soil fertility conditions across Australia. These properties have contributed to their suitability for pulpwood, timber and fuel wood production, as well as for stabilising degraded lands (King, 1943; Doughty, 2000; Turnbull, 2000). Outside of Australia, *Eucalyptus* are some of the most important trees planted by forestry companies for the production of wood and pulp products sustaining more than 20 million ha of commercial plantations globally (Iglesias Trabado and Wilstermann, 2008).

Prior to 1995, most *Eucalyptus* plantations in Australia were either established for long rotations or were experimental (Dargavel and Semple, 1990; Carnegie, 2007a) with areas planted amounting to approximately 45, 000 ha. The industry grew rapidly together with the expansion in Managed Investment Schemes (MIS) in the late 1990′s and 2000′s to meet world demands for wood chips, and to supply new domestic pulpwood and engineered timber mills. This was concurrent with reductions in the harvesting of native forest due to Regional Forest Agreements (http://www.agriculture.gov.au/forestry). From 1998 to

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2008, new plantings in Australia averaged at about 70,000 ha a year and in 2010 the total commercial *Eucalyptus* plantation area was 770 000 ha (ABARES, 2013). Most of *Eucalyptus* plantations were in the temperate regions of southern Australia (Western Australia, Tasmania, Victoria) and were mostly comprised of *Eucalyptus globulus* and *E. nitens* (Dickinson et al., 2004; Carnegie et al., 2005).

Plantation forestry expanded in the tropics and sub-tropics following the initial growth of plantations in temperate Australia. The North Coast of New South Wales (NC-NSW) led the way in sub-tropical plantation forestry in Australia. There had been experimental and commercial plantings in this region since the 1960′s of which the majority utilized *E. grandis*, *E. saligna* and *E. pilularis* grown mainly for saw logs (Dreilsma et al., 1990). These experimental plantings and taxa trials were established from NC-NSW to far north Queensland (FNQ). Expansion of the sub-tropical plantation industry followed the southern states in the 1990 s, but different species were used; for example *Corymbia* spp., *E. dunnii*, *E. grandis, E. pilularis, E. cloeziana* and clones of *E. grandis* × *E. camaldulensis* developed in South Africa and Brazil were planted (Florence, 1996; Dickinson et al., 2004; Carnegie et al., 2005; Lee, 2007). These were established in NC-NSW and South East Queensland (SE-QLD) (ABARES, 2013). During the initial stages of the sub-tropical plantation industry expansion, the region was in the throes of the millennium drought (1996–2010) and thus weather conditions were not favourable for the development of leaf and shoot diseases. When the drought came to an end, diseases began to emerge, in particular Teratosphaeria leaf blight (TLB) (Andjic et al., 2010; ABARES, 2013; Burgess and Wingfield, 2017).

Many fungi have been described from eucalypt foliage in Australia (Sankaran et al., 1995), but most were considered to be endemic. Consequently they were not of great concern for forest management, because they predominantly caused diseases on eucalypts in native forests where their impact was low (Park et al., 2000). This was due to the balanced co-evolution (genetic homeostasis) between the eucalypt trees and their pathogens and genetic and age diversity (Burgess and Wingfield, 2002, 2017).

2. Teratosphaeria species associated with leaf blight diseases of *Eucalyptus*

The most common pathogens associated with *Eucalyptus* leaf diseases are members of *Mycosphaerellaceae* and *Teratosphaeriaceae* (Crous, 1998; Crous et al., 2004). These fungi cause diseases known as Mycosphaerella leaf diseases (MLD) and Teratosphaeria leaf blight diseases (TLB) (Hunter et al., 2011). There are more than 150 species associated with MLD and TLD (Hunter et al., 2011). Most of those species are apparently facultative pathogens and are not significant causal agents of disease (Maxwell et al., 2003). However, there is one group of closely related *Teratosphaeria* species responsible for all major leaf and shoot disease problems (Fig. 1). These include *Teratosphaeria nubilosa* and *T. cryptica* (not the focus of this review) on *E. nitens* and *E. globulus* in the temperate climatic zone (Mohammed et al., 2003; Hunter et al., 2009; Burgess and Wingfield, 2017), and a group of species that have emerged as the most significant foliar pathogens of tropical and sub-tropical plantations where they causing leaf and shoot blight on *E. grandis*, *E. camaldulensis* and *E. urophylla* and their hybrids. These related species, formerly grouped by their typical spore morphology in *Kirramyces*, include *T. destructans, T. eucalypti*, *T. pseudoeucalypti,* and *T. viscida* (Andjic et al., 2007; Andjic et al., 2010; Andjic et al., 2011).

In this review, we consider this group of species and discuss disease emergence, disease impact and species recognition in chronological order of their appearance. We include unpublished information from more recent surveys, and also consider the potential for hybridisation between these species and disease management.

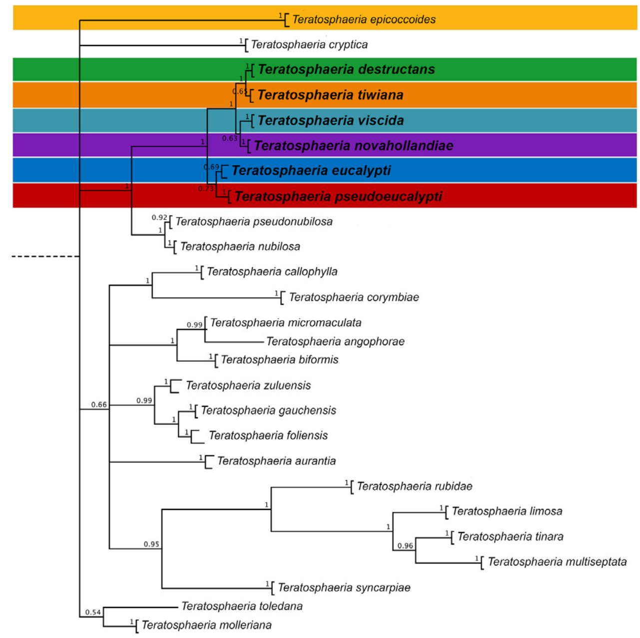

Fig. 1. Phylogenetic tree of concatenated ITS, EF and TUB sequence data of *Teratosphaeria* species commonly encountered on *Eucalyptus* highlighting the clustering of the highly pathogenic species with *Kirramyces*-like anamorph spores which Teratosphaeria leaf blight diseases (TLB). T. epiccocoides is included here to show its phylogenetic placement, but it is not considered to cause TLB.

3. Prior to 1996

Prior to 1996, the only known kirramyces-like leaf and shoot blight pathogen of *Eucalyptus* was *T. eucalypti* (formerly *Kirramyces eucalypti*). *Teratosphaeria eucalypti* was first described from senescing leaves of a *Eucalyptus* sp. collected from Victoria, Australia in 1884 (Cooke, 1889). It is known as a leaf pathogen of several native *Eucalyptus* species in Australia (Park et al., 2000; Hood et al., 2002a; Hood et al., 2002b) This pathogen has caused severe damage on *E. dalrympleana* and *E. viminalis* in temperate NSW (Heather, 1961), and reported in plantations of *E. nitens* and *E. globulus* in southern NSW, Victoria (Gippsland) and Tasmania (Yuan et al., 1999) (Table 1). *Teratosphaeria eucalypti* was accidentally introduced into New Zealand via infected nursery stock, where it caused complete defoliation of juvenile leaves of *E. nitens* (Dick, 1982) and is now considered a the major pathogen of *Eucalyptus* plantations (Hood et al., 2002a).

Teratosphaeria eucalypti mostly infects juvenile foliage with symptoms first appearing in spring and ultimately leading to defoliation. Symptoms caused by *T. eucalypti* include blotchy, necrotic lesions, round or delimited by veins, initially pale yellow turning carmine red before becoming necrotic, often with a carmine-red halo surrounding the necrotic spot (Fig. 2) (Heather, 1961; Dick, 1982; Gadgil and Dick, 1983). Although causing damage in New Zealand, *T. eucalypti* was not considered a problem in Australia prior to the expansion of *E. nitens* plantations.

Surveys of the expanding eucalypt plantation estate in Tasmania in the late 1990 s identified *T. eucalypti* amongst the most prevalent foliar fungi on *E. nitens* (Yuan et al., 1999). Similarly, *T. eucalypti* was common but not damaging on *E. nitens* in the expanding plantation estate in Victoria (D. Smith pers. comm.) and southern NSW (Carnegie 2007b) in the late 1990 s. In the mid-2000′s, several plantations of *E. nitens* and hybrids of *E. nitens* × *E. nobilis* in northern NSW were severely defoliated by *T. eucalypti.* Repeated defoliation resulted in infection by canker pathogens leading to dieback and tree mortality (Carnegie, 2007b). Similar damage was observed in *E. nitens* on the northern tablelands of NSW (temperate climate) in the late 2000′

Table 1
Known hosts of the *Teratosphaeria* species considered in this review.

	Known hosts	Hosts found in plantations
T. eucalypti	*E. aggregata, E. aromaphloia, E. camaldulensis, E. cephalocarpa, E. cinerea, E. cordata, E. cypellocarpa, E. dalrympleana, E. dunnii, E. grandis, E. glaucescens, E. globoidea, E. globulus, E. gunnii, E. kitsoniana, E. longirostrata, E. macarthuri, E. moluccana, E. nicholii, E. nitens, E. obligua, E. perriniana, E. sideroxylon, E. urnigera, E. ovata, E. punctata, E. platypus, E. parvula, E. tereticornis, E. viminalis E. grandis × E. urophylla, E. scorparia* and *E. smithii*	*E. nitens* (Dick, 1982; Hood et al., 2002b), *E. nitens × E. nobilis* (Carnegie, 2007b)
T. epicoccoides	Numerous over 200 reported hosts	*E. camaldulensis, E. grandis, E. grandis × E. camaldulensis, E. grandis × E. urophylla, E grandis × E. tereticornis, E. tereticornis* (Carnegie, 2007b)
T. destructans	*E. camaldulensis, E. grandis, E. grandis × E. urophylla, E. urophylla*	*E. camaldulensis, E. grandis, E. urophylla* (Wingfield et al., 1996; Burgess et al., 2006a; Greyling et al., 2016)
T. viscida	*E. grandis, E. grandis × E. camaldulensis*	*E. grandis × E. camaldulensis* (Andjic et al., 2007)
T. pseudoeucalypti	*E. botryoides, E. camaldulensis, E. grandis, E. grandis × E. camaldulensis, E. grandis × E. tereticornis, E. globulus, E. macarthurii, E. maidenii, E. tereticornis*	*E. grandis × E. camaldulensis, E. grandis × E. tereticornis, E. globulus × E. maidenii* (Andjic et al., 2010; Pérez et al., 2016)
T. novaehollandiae	*E. camaldulensis, E. grandis × E. camaldulensis, E. victrix*	
T. tiwiana	*E. camaldulensis, E. grandis × E. camaldulensis, E. grandis × E. urophylla, E. pellita, E. robusta, E. urophylla* hybrids	

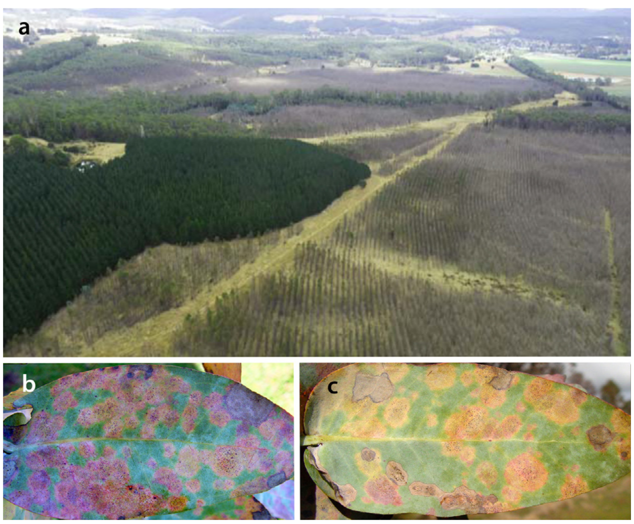

Fig. 2. *Teratosphaeria* eucalypti (a) defoliation of *Eucalyptus nitens* plantation in northern Tasmania, adjacent *Pinus radiata* (image T. Wardlaw). Early leaf symptoms on (b) adaxial and (c) abaxial surface of *E. nitens* leaf.

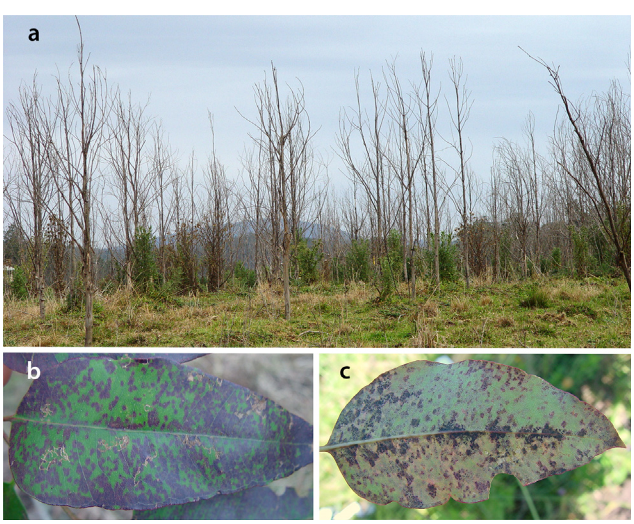

Fig. 3. *Teratosphaeria epicoccoides.* (a) tree mortality of *Eucalyptus grandis* in northern NSW due to repeated defoliation (b) typical vein delimitated symptoms on older leaves on (b) adaxial and (c) abaxial surface.

resulting in extensive mortality. After very wet summers in 2010 and 2011, *T. eucalypti* emerged as a major pathogen of *E. nitens* in Victoria and northern Tasmania, with severe repeated defoliation resulting in extensive tree mortality (David Smith and Tim Wardlaw pers comm.) (Fig. 2). The *T. eucalypti* inoculum load has accumulated in these areas to the point where its impact now surpasses that of the previously dominant *T. nubilosa* (David Smith and Tim Wardlaw pers comm.).

Eucalyptus nitens is propagated in plantations in cool temperate regions of the world including Australia (Tasmania, Victoria, parts of NSW), New Zealand, Chile and South Africa. It is an increasingly popular plantation timber species because it is fast-growing with desirable wood properties suitable for both pulpwood and veneer production and it is relatively tolerant to low winter temperatures (Vega Rivero, 2016). Currently, *T. eucalypti* is restricted to Australia and New Zealand. With the increased importance of *E. nitens* plantations worldwide, the threat of this pathogen is rising. Given the documented global movement of related species (see section on *T. pseudoeucalypti*), there is a substantial risk of this pathogen spreading to new countries where *E. nitens* plantations are increasingly important.

4. 1996–2000; the emergence of *Teratosphaeria destructans*

Teratosphaeria destructans was first described from 1 to 3 year-old *E. grandis* from Northern Sumatra, Indonesia (Wingfield et al., 1996). This highly aggressive and devastating pathogen causes distortion of infected leaves and blight of young leaves, buds and shoots (Wingfield et al., 1996). The symptoms caused by *T. destructans* include large subcircular light brown leaf spots with diffuse borders and red-brown margins, which are present on both leaf surfaces (Fig. 4). The leaf blight associated with *T. destructans* is not known from the native range of *Eucalyptus* or any other area outside of Sumatra. Because *Eucalyptus* is not native to Sumatra, it was thought the pathogen might have been introduced from Timor where *E. urophylla* is native (Wingfield et al., 1996), from native Myrtaceae in Sumatra, or from an as yet unknown host in Australia.

5. 2000–2009; *Teratosphaeria destructans* spreads throughout South East Asia

In 2000, *T. destructans* was found in eastern Thailand where it caused severe defoliation of susceptible clones of *E. camaldulensis* (Old et al., 2003a). In 2002, the pathogen was discovered at several locations in south, central and northern Vietnam, on *E. camaldulensis, E. urophylla* and hybrid clones (Old et al., 2003a). Because *T. destructans* was spreading rapidly throughout South-East Asia, the source of infection was thought to be via the movement of infected planting stock.

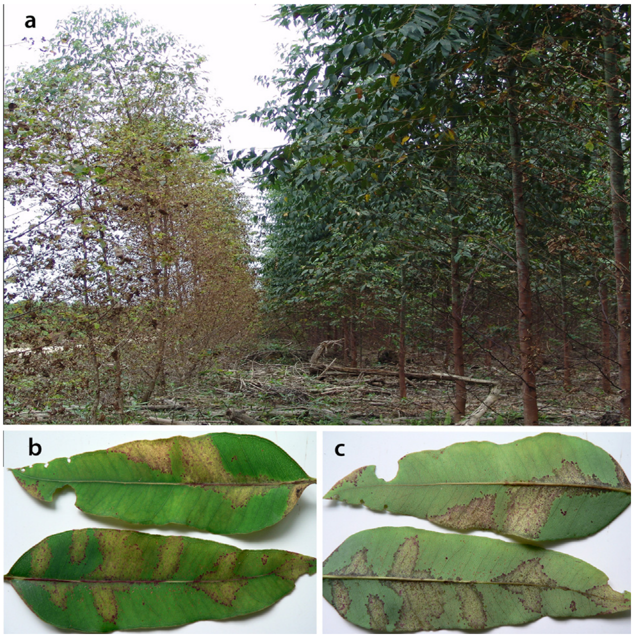

Fig. 4. *Teratosphaeria destructans* (a) comparison of a susceptible (left) and tolerant *Eucalyptus* clone (right). Early leaf symptoms on (b) adaxial and (c) abaxial surface of *E. urophylla* leaves.

Between November 2003 and July 2004, production nurseries in China were inspected for the incidence of foliar pathogens in four eucalypt-growing regions (Burgess et al., 2006a). Leaf blight was observed in all inspected nurseries in regions. Many leaves had fallen from the trees, and early symptoms similar to those of *T. destructans* were observed. Morphological examination and DNA sequencing confirmed presence of *T. destructans* in China (Burgess et al., 2006a). In 2009, *T. destructans* was detected in Laos causing widespread severe defoliation of plantations (Barber et al., 2012). This was not surprising as Laos is surrounded by other countries where *T. destructans* is present (China, Thailand, Vietnam) and the origin of planting stock was from those countries.

The severe impact of disease and the rapid movement of *T. destructans* throughout South-East Asia prompted a study of the genetic diversity and movement of the pathogen (Andjic et al., 2011). In this case, multi-gene phylogenies and microsatellite markers were used to determine whether the initial disease outbreak in Indonesia was the result of introduction of the pathogen into the region. Furthermore, whether Indonesia might have been the source of the subsequent introductions in South-East Asia and China. Four microsatellite markers and five gene regions were used to analyse 60 representative *T. destructans* isolates from a range of geographical locations and hosts. Surprisingly, the genetic diversity of *T. destructans* across the regions was extremely low. This led to the conclusion that *T. destructans* is not native to the region (Andjic et al., 2011). Subsequently, DNA was extracted from lesions present on two leaves of *E. urophylla* collected in Timor. These isolates were identical to *T. destuctans* based on molecular phylogeny, but in a microsatellite analysis they differed from each other and from all other isolates from the region (Andjic et al., 2011). Because *E. urophylla* is native to Timor, this island is now considered as the most likely origin for *T. destuctans.*

6. *Teratosphaeria destructans,* a pathogen of biosecurity concern to Australia

Because *T. destructans* had not been found in Australia, it was considered to be a pathogen of considerable biosecurity concern both for plantation forestry and natural ecosystems (Old et al., 2003a; Plant Health Australia, 2007). In 2004, a research project involving most of the authors of this review commenced to investigate new and emerging pathogens threatening the biodiversity of Australian forests and productivity of eucalypt plantations (Murdoch University, ARC Discovery DP0343600, DP0664334). Sentinel plantings were established with 20 *Eucalyptus* species at five locations; northern Vietnam, central Thailand, Tiwi Island and two in southern China. Additionally, eucalypt species trials previously established throughout Australia to test the suitability of different environments for growing eucalypts were surveyed. Some of these trials have been planted in the east coast tropics in FNQ and NC-NSW (Dickinson et al., 2004; Lee, 2007) where the climate is similar to parts of South-East Asia. The *Eucalyptus* species being tested in these trials included *E. grandis*, *E. camaldulensis, E. dunnii, E. pellita* and various hybrids between those species, which are commonly used in tropical plantation forestry worldwide (Turnbull, 2000). These plantations effectively served as sentinel plantings and were close to native forests.

During the course of monitoring in northern Australia, leaf blight caused by a fungus similar to *T. destructans* was encountered on two occasions. The first of these was found in taxa trials at Mareeba in FNQ, however detailed molecular analysis resulted in the description of a new species, *T. viscida* (Fig. 5) (Andjic et al., 2007). In the second case, juvenile eucalypt leaves with symptoms resembling those of *T. destructans* were collected in July 2006 from a clonal taxa trial on Melville Island, 50 km off the coast from Darwin. Based on conidial morphology and sequence data, the pathogen was identified as *T. destructans* (Burgess et al., 2007). As a consequence, *T. destructans* was removed from the Northern Australia Quarantine Strategy (NAQS) surveillance target list for exotic invasive plant pathogens. However, subsequent inclusion of additional isolates from across the north of Australia and more detailed DNA sequence comparisons subsequently resulted in the description of two new species; *Teratosphaeria tiwiana* (Fig. 6) and *Teratosphaeria novaehollandiae* (Andjic et al., 2016). The isolates from Melville Island initially considered to be *T. destructans* have now been described as *T. tiwiana,* and *T. destructans* is again recognised as absent from Australia.

7. Teratosphaeria leaf blight in sub-tropical *Eucalyptus* plantations in Australia

In Australia, most tropical *Eucalyptus* plantations were established in NC-NSW and SE-QLD, with the industry in NSW predating that in QLD. The Forestry Corporation of NSW initiated a forest health surveillance program in 1995 following expansion of their eucalypt plantation program (Carnegie et al., 2008). This surveillance program also included several private plantation companies whose properties were not routinely surveyed for pests and diseases (Carnegie et al., 2018). Most plantations were located on previously cleared ex-agricultural land (improved pasture), and mostly planted with multiple *Eucalyptus* species per plantation. Carnegie (2007b, 2007a) presented the findings of the first 10 years of surveillance. A number of foliar pathogens

Fig. 5. *Teratosphaeria viscida* (a) symptoms of complete defoliation of *Eucalyptus grandis* × *camaldulensis.* (b) Early leaf symptoms on adaxial surface of leaves.

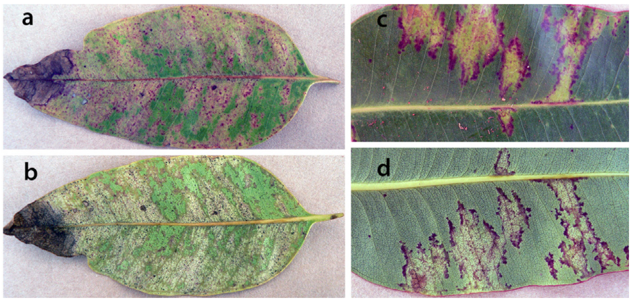

Fig. 6. *Teratosphaeria tiwiana.* Early leaf symptoms on (a) adaxial and (b) abaxial surface of a *E. pellita* leaf and (c) adaxial and (d) abaxial surface of a *E. robusta* leaf.

causing significant damage were found, but the most significant were those caused by *Teratosphaeria* spp., such as *T. nubilosa*, *T. epicoccoides* and *T. eucalypti* (Carnegie, 2007b). While *T. epicoccoides* is commonly found on older foliage causing minor damage (Box 1), this fungus was found causing significant and widespread damage to *E. grandis* and *E. grandis* × *E. camaldulensis* clones in plantations in northern NSW. Due to severe and repeated infection by *T. epicoccoides,* more than 300 ha were classed as 'failed' plantations (Box 1) (Carnegie, 2007b). *T. epicoccoides* continued to cause significant damage to *E. grandis,* especially in lower-lying plantations, and more broadly to *E. grandis* × *E. camaldulensis,* resulting in further plantation failures.

During surveys of eucalypt plantations in SE-QLD in the mid-2000 s, severe outbreaks and damage caused by species of *Teratosphaeria* were reported. This was initially observed in August 2005 from a trial site west of Brisbane on *E. grandis* × *E. camaldulensis* hybrid clones originating from Brazil and South Africa and then from samples sent from Mackay region north of Brisbane. Although the symptoms and the severe blight damage resembled those caused by *T. destructans*, the causal agent was identified as *T. eucalypti*. This was based on conidia size and morphology. *T. eucalypti* had been recorded in Queensland since 1971 (Australian Plant Pest Database), but it was not considered a pathogen of concern. However, the symptomatology and impact of the disease in Queensland differed to that observed for *T. eucalypti* elsewhere in Australia. In Queensland, infection resulted in leaf blight and total defoliation while elsewhere infection was characterized by discrete lesions and minimal leaf loss. Molecular systematic studies were conducted using isolates collected in eastern Australia and New Zealand and it became clear that the causal agent of a serious leaf disease of eucalypts in Queensland was not *T. eucalypti.* This resulted in the description of the new species *T. pseudoeucalypti* (Fig. 7) (Andjic et al., 2010). *T. pseudoeucalypti* was later found at a production nursery in central NSW on *E. grandis* × *E. camaldulensis* seedlings derived from QLD. More recently, *T. pseudoeucalypti* was the primary pathogen associated with severe defoliation to *E. grandis* × *E. camaldulensis* hybrid clones in NC-NSW (Fig. 7), the first record of significant impact from this species in NSW. Previously, only *T. epicoccoides* was associated with defoliation in these plantations. In Australia, *T. pseudoeucalypti* is limited to regions with sub-tropical and tropical climate, whilst *T. eucalypti* is found in both temperate and sub-tropical areas (Andjic et al., 2010).

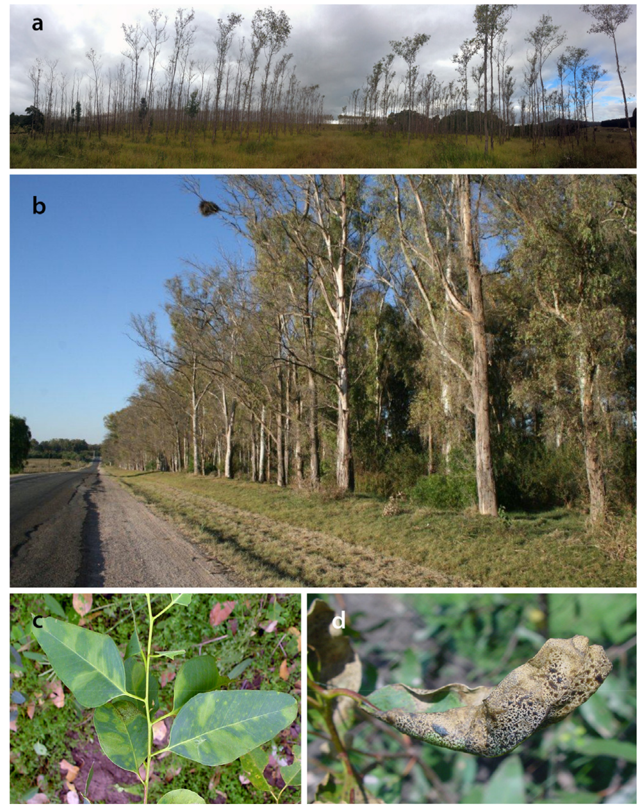

Fig. 7. *Teratosphaeria pseudoeucalypti.* (a) defoliation of *E. grandis* × *E. camaldulensis* hybrid clones in NC-NSW (b) defoliation of *Eucalyptus camaldulensis* amenity plantings in Uruguay. (c) Early leaf symptoms on adaxial leaf surface (d) blighting symptoms showing prolific sporulation.

The impact of disease caused by *T. pseudoeucalypti* in central Queensland increased annually. Initially older trees and some hybrid eucalypts were more resistant to TLB (Box 2). However, as the inoculum load increased, these trees also succumbed to disease. Significant areas of plantation were severely defoliated by *T. pseudoeucalypti*, and as a consequence, the companies decided to disinvest from the region (McKenzie, 2010). Similarly in NC-NSW, plantations of *E. grandis* × *E.*

Box 1
Teratosphaeria epicoccoides; leaf blight or minor leaf pathogen?

Teratosphaeria epicoccoides is known to be endemic to eastern Australia (Hansford, 1957; Heather, 1965; Walker et al., 1992; Taole et al., 2015) and was introduced into Western Australia (Jackson et al., 2008; Taole et al., 2015) and many parts of the world including Africa, South America, South East Asia, India and Europe (Park et al., 2000). This pathogen primarily occurs on species of sub-genus *Symphyomyrtus,* but has a very wide host range (Table 1). The symptoms caused by *T. epicoccoides* are variable and depend on host species and stage of development of infection, but most common are purple spots on the upper surfaces of leaves, necrotic lesions delimited by veins and the presence of spore masses and tendrils of conidia on the undersides of leaves (Dick, 1982; Walker et al., 1992). In general, *T. epicoccoides* is considered to be a minor pathogen causing disease on older leaves or on the leaves of stressed trees (Crous et al., 1988; Nichol et al., 1992; Park et al., 2000) without having any major impact on growth or vigour. However, when inoculum levels are high, and plantations are planted off-site or poorly managed and conditions are conducive for infection, T. epicoccoides can cause significant damage resulting in defoliation and tree death, especially *E. grandis* and *E. grandis* x *E. camaldulensis* (Knipscheer et al., 1990; Carnegie, 2007b). This has been observed in *Eucalyptus* plantations in Australia (Fig. 3) and plantations of non-native *Eucalyptus* spp. in other parts of the world including South Africa (Nichol et al., 1992), India (Brown, 2000) and Indonesia (Old et al., 2003b).

Box 2
Monocultures drive epidemics.

In natural ecosystems, including eucalypt forests, mixed species and age ranges within a species promotes resilience to epidemics (Burgess and Wingfield, 2017). Monocultures are more susceptible than heterogeneous systems to disease epidemics (Garrett and Mundt, 1999; Thor et al., 2005; Guyot et al., 2015). This is based in theoretical models (Segarra et al., 2001) and supported by observational (Pautasso et al., 2005) and experimental studies (Zhu et al., 2000). Observational evidence from plantation eucalypt forestry demonstrates how homogeneity, in terms of genetics and even aged stands, play a role in the development of favourable conditions for foliar disease epidemics. Over the past 20 years in Australia where plantations and native eucalypt forests occur in close proximity, new diseases and the pathogens associated with them are often first detected in plantations (Maxwell et al., 2003; Burgess and Wingfield, 2017). Similarly disease epidemics are more commonly recorded in plantations than in native forest (Burgess and Wingfield, 2017). This proximity provides a selection pressure that drives host shifts of endemic pathogens towards exotic plantation trees (Burgess et al., 2006b).

The polycyclic rate of disease expansion caused by *T. cryptica* is related to the repeated production of asexual kirramyces-type spores throughout the epidemic (Park, 1988). Similarly other *Teratosphaeria* species with kirramyces-type spores have caused devastating epidemics in plantations of eucalypts. Plantations in southern and central Queensland were established in the early 2000s with predominantly *E. grandis*, *E. dunnii*, and *E. camaldulensis*. Initially TLB occurred only at low levels However, post 2009 TLB became very common in this region. In 2009, existing taxa trials and newly established trials were rated for their tolerance to TLB, and some hybrids appeared to be tolerant. However, within a year, even the putatively tolerant hybrids had collapsed because of the accumulation of inoculum from species causing TLB, and the plantations were abandoned (Andjic et al., 2010).

camaldulensis severely damaged by *T. epicoccoides* and *T. pseudoeucalypti* are now being abandoned and returned to pasture for grazing cattle.

8. The global Teratosphaeria leaf blight situation post 2010

In a global context, there have been two major events since 2010; *T. destuctans* has spread beyond Asia and *T. pseudoeucalypti* has been introduced and spread in South America. In early 2015, *T. destructans* was found on leaves of one year old *E. grandis* × *E. urophylla* hybrids in the Zululand region, South Africa (Greyling et al., 2016). The DNA sequences of South African isolates were identical to those from Asia and clearly represents a recent introduction, most likely on germplasm.

Since its first discovery in Australia in 2010*, T. pseudoeucalypti* has been detected in Argentina (Ramos and Perez, 2015), Brazil (Cândido et al., 2014) and Uruguay (Soria et al., 2014). The detection of this pathogen in the three countries more or less at the same time suggests it was recently introduced, and encountered suitable conditions for disease establishment resulting in rapid regional spread. In Argentina, *T. pseudoeucalypti* was detected on clonal *E. grandis* × *E. camaldulensis* hybrid trials in Entre Ríos province in September 2013 (Ramos and Perez, 2015). In Uruguay, it was first detected on both juvenile and adult leaves of *E. globulus* and *E. maidenii* in forestry plantations in the South–East region (Soria et al., 2014), confirmed later on *E. botryoides, E. camaldulensis, E. dunnii, E. grandis,* hybrids *E. grandis* × *E. tereticornis, E. macarthurii,* and *E. tereticornis* (Simeto et al., 2005). In Brazil, it was found on *E. globulus*, *E. urophylla* × *E. globulus* and *E. nitens* × *E. globulus* (Cândido et al., 2014). In all these regions, disease impact has been severe.

Teratosphaeria pseudoeucalypti is currently devastating *E. camaldulensis* and *E. tereticornis* in Uruguay. Repeated foliar infections and defoliation resulting in tree death is having a significant impact on *Eucalyptus* plantations used for livestock shade and shelter, solid wood products and firewood sources. It is also a valued ornamental species in urban parks (Pérez et al., 2016), thus, having significant economic and social impact. In addition, the identification of *T. pseudoeucalypti* on *E. globulus* has led to substantial concern from the forestry industry given the impact is similar to that previously caused by *T. nubilosa* in Uruguay, with crown damage caused by *T. nubilosa* being the main reason for *E. globulus* virtually being abandoned. Interestingly, in Australia *T. pseudoeucalypti* is found only in sub-tropical regions; whereas in South America it is causing disease in cooler areas.

There is a growing concern regarding the possible introduction of *T. pseudoeucalypti* into other countries in South America where *E. globulus* is planted extensively, for example Chile, Colombia, Ecuador and Peru (Cândido et al., 2014). Further exacerbating the problem, *Eucalyptus* plantations in South America, and especially in Brazil, have large planting areas of the same genetic material potentially increasing the risk of significant production losses.

9. Future concerns and solutions

Some isolates from Melville Island in Northern Australia were not included in the description of *T. tiwiana* and *T. novaehollandiae* (Andjic et al., 2016) because the DNA sequences were incongruent with those of other isolates. For this review, we included them in a multilocus dataset consisting of ITS2, β-tubulin *(tub2)* and translation elongation factor 1-α *(tef1)* gene regions and included the sequence data from the flanking regions of three microsatellites markers. Although in phylogenetic analysis *T. viscida* is more closely related to *T. novaehollandiae,* in the resultant haplotype network (Fig. 8) isolates of *T. viscida* and *T. tiwiana* are connected. This could be indicative of hybridization between the species, as has been observed for other ascomycetes (Cruywagen et al., 2017). This is of great concern because the hybridization of closely related *Teratosphaeria* species could lead to emergence of more aggressive species capable of colonizing new hosts (Brasier, 2001) and negatively impacting on native and plantation forestry.

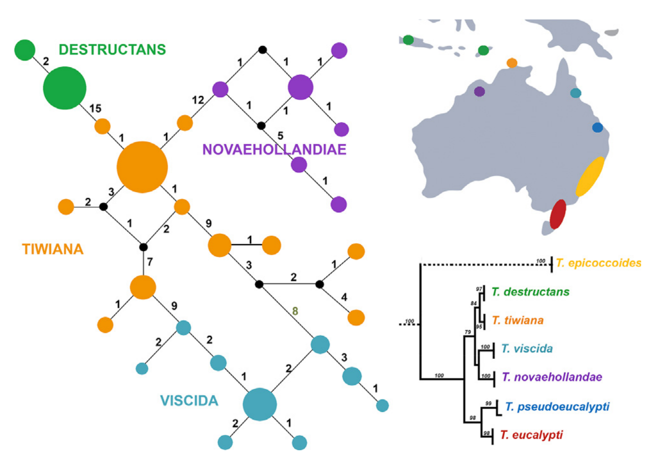

Fig. 8. Network analysis showing relationship between the four closely related *Teratosphaeria* species. Although in phylogenetic analysis *T. viscida* is more closely related to *T. novohollandae* (Fig. 1), in the network analysis *T. viscida* and *T. tiwiana* are closer suggesting these two species may hybridize as their natural ranges overlap.

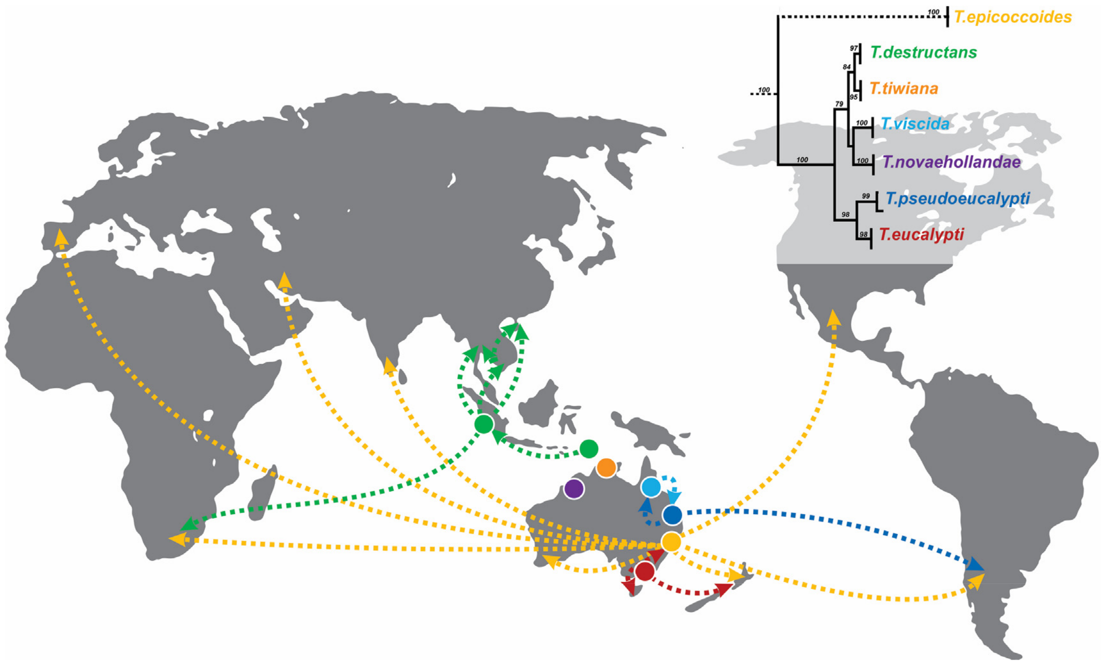

Fig. 9. Global movement of species associated with Teratosphaeria leaf blight diseases.

The global distribution of *T. epicoccoides*, the spread of *T. destructans* across Asia and its introduction into South Africa, and the introduction of *T. pseudoeucalypti* into South America suggests these species have been moved with infected plants and possibly seeds *via* international trade. The presence of *Eucalyptus* pathogens including stem canker *T. zuluensis* in seed and seed capsules has been recently demonstrated using metabarcoding (Jimu et al., 2015). Other members of the *Teratosphaeriaceae* and *Mycosphaerellaceae* were also detected in the same study confirming the potential for *Eucalyptus* pathogens to be spread *via* global seed trade. Many of these pathogens grow slowly in culture and in the case of seed, they would easily escape quarantine (Burgess et al., 2016). This suggests the need for much more sophisticated and more stringent biosecurity measures (McTaggart et al., 2016), such as the routine use of metabarcoding approaches to test seedlots under quarantine.

One solution to slow the global spread of *Teratosphaeria* spp. would be implementation of biosecurity measures such as those used in Australia (Eschen et al., 2015). In this case, imported *Eucalyptus* species for use as nursery stock must be inspected at the border (import permit, phytosanitary certificate/declaration required), confirmed free of pests and diseases, and forwarded to post entry quarantine facilities for disease screening for two years. Alternatively, plants can be imported as tissue culture where the cuttings are produced from a clean mother stock (BICON, Department of Agriculture and Water Resources, bicon.agriculture.gov.au 21 March 2018). This would not prevent these pathogens from entering on seed but it would at least reduce the rate of accidental pathogen introductions. Management strategies to mitigate the disease risk from imported seed include mandated import conditions of freedom from trash (including leaf, stem and capsule); phytosanitary certification with declarations of area freedom or pathogen testing; and seed treatment with fungicides.

Currently the host range of three most devastating pathogens, *T. destructans*, *T. viscida* and *T. pseudoeucalypti* is limited to certain species of *Eucalyptus* such as *E. grandis*, *E. urophylla*, *E. camaldulensis, E. tereticornis* and their hybrids, with *T. pseudoeucalypti* being less specific. The most appropriate strategy to manage disease caused by TLB must lie in breeding and the selection of resistant or tolerant clones. Inter- and intra-specific variation in susceptibility to *Teratosphaeria* spp. has been observed across multiple *Eucalyptus* spp. × *Teratosphaeria* spp. pathosystems eg. (Nichol et al., 1992; Carnegie et al., 1994; Dungey et al., 1997; Hood et al., 2002b). A range of leaf traits have been identified in resistant families that Smith et al. (2017) identify as potential mechanisms employed by eucalypts resist infection by *Teratosphaeria* spp. Furthermore, it is important to deploy planting stock on sites optimal for growth and were stress is minimized (Box 2).

10. Conclusions

The expansion of eucalypt plantation forestry into the sub-tropics of Australia has led to the discovery of many new *Teratopshaeria* species. Some of these have become the dominant cause of foliar disease in tropical and sub-tropical plantations, with the severity of their impact leading to the abandonment of plantations in some areas. Over the past twenty years a much greater understanding of the taxonomy of these species has developed, with sequence data and ex-type cultures are now available for eight *Teratosphaeria* species with kirramyces-like asexual morphs described from *Eucalyptus*.

With the exception of *T. destructans*, which is likely to have originated in Indonesia or East Timor, all other species are thought to have originated in Australia from whence they have now spread to other *Eucalyptus* plantation growing regions globally (Fig. 9). *Teratosphaeria epicoccoides* has been spread world-wide, *T. destructans* has expanded throughout Asia and now occurs in South Africa, *T. pseudoeucalypti* has been introduced into South America; and *T. eucalypti* into New Zealand. Currently only *T. viscida, T. tiwiana* and *T. novaehollandiae* are known exclusively from Australia. The global movement of *Teratosphaeria* species causing leaf and shoot blight, demonstrates the anthropogenic movement of pathogens *via* the world-wide trade in germplasm indicating the need for more stringent biosecurity measures to manage the risk of pest introductions associated with *Teratosphaeria* species. Countries wanting to stay free of exotic TLB pathogens should introduce stringent quarantine regulations.

The Australian experience demonstrates the importance of breeding and selection of tolerant/resistant clones for the future management of TLB. This must be done in conjunction with selection of species, hybrids and clones adapted to the climatic and geographic area and planted on sites optimal for growth in order to promote tree health and reduce stress related disease impacts. Of paramount concern is the need for more sophisticated and stringent biosecurity measures to reduce the introduction of new pathogens and pathotypes.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.04.013.

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