Southern Forests: a Journal of Forest Science
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t911320171

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Online publication date: 12 November 2009

To cite this Article Roux, J. and Wingfield, MJ(2009) '*Ceratocystis* species: emerging pathogens of non-native plantation *Eucalyptus* and *Acacia* species', Southern Forests: a Journal of Forest Science, 71: 2, 115 — 120
To link to this Article: DOI: 10.2989/SF.2009.71.2.5.820
URL: http://dx.doi.org/10.2989/SF.2009.71.2.5.820

Southern Forests 2009, 71(2): 115–120
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SOUTHERN FORESTS
ISSN 2070–2620 EISSN 2070–2639
doi: 10.2989/SF.2009.71.2.5.820

Ceratocystis species: emerging pathogens of non-native plantation *Eucalyptus* and *Acacia* species

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The fungal genus *Ceratocystis* includes many economically important tree pathogens. Until the 1980s, this genus of plant pathogens was not known from non-native plantation-grown forestry species. However, during the course of the last 20 years, a number of reports have been made of *Ceratocystis* spp. causing death of non-native plantation-grown forestry species from several locations worldwide. Affected trees include both Australian *Acacia* spp. and *Eucalyptus* spp. The first report of disease caused by a *Ceratocystis* sp. on *Eucalyptus* was made less than 10 years ago from Central Africa and, shortly thereafter, the disease was reported from Brazil. Subsequently, a number of other reports of *Ceratocystis* diseases have emerged from Africa, South America and Asia. These diseases are characterised by rapid wilt and death of trees and they have been reported to affect coppice stems as well as mature trees. In many cases, infection is associated with pruning wounds or other mechanical damage. The causal agent has been reported as *Ceratocystis fimbriata s.l.*, but the *Eucalyptus* pathogen most likely represents a number of previously undescribed species. *Ceratocystis* spp. are vectored by wood- and bark-associated insects and typically those that visit fresh wounds, which act as infection courts. The fungi infect woody tissue and produce fruity aromas, which are attractive to insects. In this way, they can easily spread between countries and continents, thus posing a considerable quarantine threat. The biology of *Ceratocystis* spp. is such that diseases caused by this group of fungi are likely to become more common in the future.

Keywords: fungal pathogens, insect vectors, wilt diseases, wound infecting

Introduction

The genus *Ceratocystis* was first described in 1890, with the description of *C. fimbriata* Ellis and Halsted causing rot of sweet potatoes (*Ipomoea batatas* (L.) Lam.) in the USA (Halsted 1890, Halsted and Fairchild 1891). Subsequently, this genus has emerged as one of the most important groups of plant, and especially tree, pathogens known. Species of *Ceratocystis* cause canker stain and wilt diseases of trees and rot of root crops such as sweet potato. Tree hosts include oak (*Quercus* spp.; Henry et al. 1944), plane (*Platanus* spp.; Walter 1946, Panconessi 1981, Tsopelas and Angelopoulos 2004), rubber (*Hevea* sp.; Olson and Martin 1949), coffee (*Coffea arabica*; Pontis 1951, Marin et al. 2003) and various others that are less well known (Kile 1993, CAB International 2001).

Ceratocystis species are well adapted for dispersal, relying on several different strategies. In their sexual state, they produce ascomata with long necks that give rise to sticky masses of spores at their apices (Ingold 1961, Upadhyay 1981). These sticky spores attach to the bodies of insects that are then responsible for spreading the fungus to new hosts (Iton 1960, Upadhyay 1981). Some species of *Ceratocystis* also produce fruity aromas that attract insects, thereby ensuring the presence of insects that can spread them to new areas (Hunt 1956, Lanza et al. 1976, Lanza and Palmer 1977, Hanssen 1993). Many *Ceratocystis* spp. produce thick-walled conidia that can survive in the soil for extended periods of time (Nag Raj and Kendrick 1975, Upadhyay 1981, Paulin-Mahady and Harrington 2002). In this manner, *Ceratocystis* spp. can also be spread through contaminated soil (Rossetto and Riberio 1990, Moutia and Saumtally 1999, Marin et al. 2003). *Ceratocystis* spp. can also spread through the air, in rain-splashed water and in contaminated insect frass, which is easily blown in the wind (Iton 1960).

During the course of the last two decades, *Ceratocystis* spp. residing in the *Ceratocystis fimbriata s.l.* species complex have emerged as important pathogens of plantation-grown forest tree species. Prior to 1996, these fungi were all assigned to the single species *C. fimbriata*, which, since its first discovery in 1890 (Halsted 1890), has been recognised as an important pathogen with a wide host range. It is currently recognised that there are many cryptic species accommodated in the *C. fimbriata s.l.* species complex. Strictly, *C. fimbriata* refers to a pathogen of sweet potato tubers. Many of the other species in the *C. fimbriata s.l.* species complex are important pathogens that have been assigned names (Wingfield et al. 1996, van Wyk et al. 2004, Johnson et al. 2005, van Wyk et al. 2006a). Others,

although also recognised as representing phylogenetically discrete groups, have not been described as separate species and for the purpose of this paper they are referred to as *C. fimbriata s.l.*

The aim of this review is to summarise current knowledge regarding plantation forestry diseases caused by *Ceratocystis* spp. Furthermore, factors that are likely to lead to increased numbers of diseases caused by these fungi are considered.

Plantation forestry diseases caused by *Ceratocystis* species

The first reports of *Ceratocystis* spp. causing disease and death of plantation-grown forestry species was in the 1980s. In this case, *C. fimbriata s.l.* was identified as the cause of cankers and death of non-native *Acacia decurrens* in Brazil (Ribeiro et al. 1988). Shortly thereafter, there was a report of *C. fimbriata s.l.* causing wilt and death of non-native plantation-grown *A. mearnsii* in South Africa (Morris et al. 1993). As knowledge began to emerge that *C. fimbriata* represents a complex of cryptic species, the pathogen responsible for wilt of *A. mearnsii* was found to be a novel species, which was given the name *C. albifundus* (Wingfield et al. 1996).

The first report of a *Ceratocystis* sp. causing disease and death of non-native plantation-grown *Eucalyptus* spp. emerged late in the 1990s, when *C. fimbriata s.l.* was reported from *Eucalyptus* clones in the Republic of Congo (Roux et al. 2000) and, shortly thereafter, from Brazil (Ferreira et al. 1999, Laia et al. 1999, Roux et al. 2000). Subsequently, a number of other reports have been made of *Ceratocystis* spp. on both *Acacia* spp. and *Eucalyptus* spp. grown in plantations (van Wyk et al. 2007, Rodas et al. 2008, Heath et al. 2009b, van Wyk et al. 2009).

Diseases of Acacia *species*

Canker and wilt diseases of plantation-grown *Acacia* spp. caused by species of *Ceratocystis* have been reported from Africa and South America (Ribeiro et al. 1988, Morris et al. 1993, Roux et al. 2001a; Figure 1 and 2). Several species of *Ceratocystis* have been associated with these diseases, including *C. fimbriata s.l.* and *C. albifundus* (Ribeiro et al. 1988, Wingfield et al. 1996). Of these, *C. albifundus* and the disease that it causes on *A. mearnsii* and *A. decurrens* in South Africa has been studied most intensively (Morris et al. 1993, Wingfield et al. 1996, Roux and Wingfield 1997, Roux et al. 1999, 2001b, Barnes et al. 2005, Roux et al. 2007, Heath et al. 2009b). In all cases, infection results in stem cankers, wilting and death of trees. Ceratocystis wilt of commercially grown *A. mearnsii* in South Africa is considered the most important disease of these trees in the country (Roux and Wingfield 1997; Figure 3a and b).

Ceratocystis wilt of *A. mearnsii* in Africa was first reported from South Africa after trees were found dying in the KwaZulu-Natal Midlands of the country (Morris et al. 1993). All the infected trees had been wounded through the pruning of branches. Later reports of the disease caused by *C. albifundus* were also associated with hail damage, singling of trees and where branches had been harvested for fuel wood (Roux and Wingfield 1997, 2001). Recent studies by Heath et al. (2009b) have shown that *C. albifundus* also commonly infects *A. mearnsii* stumps after harvesting. *Ceratocystis albifundus* can infect trees as young as one year old as well as trees of 20 years or older (Roux and Wingfield 1997). It has also been shown that infection of susceptible one-year-old *A. mearnsii* can lead to tree death within six weeks of infection (Roux et al. 1999).

Since its first report from non-native *Acacia* spp. in South Africa, *C. albifundus* has been reported from *A. mearnsii* in Uganda (Roux and Wingfield 2001), Kenya and Tanzania (Roux et al. 2005, Heath et al. 2009b). It has also been found on various native African tree species in South Africa (Gorter et al. 1977, Roux et al. 2007), Malawi and Zambia (Roux et al. 2004b). Population diversity studies on collections of *C. albifundus* from *A. mearnsii* in South Africa and Uganda, together with the occurrence of this fungus on native species in the absence of disease, suggest that the fungus is native to Africa (Roux et al. 2001b, Nakabonge et al. 2002, Barnes et al. 2005).

Recent investigations of *Ceratocystis* spp. infecting the stumps of recently harvested *A. mearnsii* trees in southern and eastern Africa has resulted in the discovery of a number of species previously unknown to science. Heath et al. (2009b) recently described *C. tanganyicensis* from Tanzania and *C. oblonga, C. polyconidia* and *C. obpyriformis* from wounds in South Africa. In artificial inoculation trials under greenhouse conditions, all four species produced significant lesions on young *A. mearnsii* trees, suggesting that they could be pathogens of this tree (Heath et al. 2009b).

Diseases of Eucalyptus *species*

Several *Ceratocystis* spp. have been associated with *Eucalyptus* trees during the course of the last 10 years. However, only some of these have been associated with disease and death of trees. *Ceratocystis eucalypti* (Kile et al. 1996), *C. moniliformis* (Roux et al. 2004a), *C. moniliformopsis* (Yuan and Mohammed 2002), *C. atrox* (van Wyk et al. 2007), *C. neglecta* (Rodas et al. 2008), *C. zombamontana*, *Thielaviopsis ceramica* (Heath et al. 2009b) and *C. fimbriatomima* (van Wyk et al. 2009) were all isolated from wounds and stain but they are not known to cause disease on *Eucalyptus* trees. Another recently described species, *C. pirilliformis*, which was first discovered in Australia (Barnes et al. 2003a) but is now also known in South Africa (Roux et al. 2004a, Kamgan Nkuekam et al. 2009), is capable of causing extensive lesions on young inoculated *E. grandis* clones (Roux et al. 2004a). It has, however, not been associated with disease under plantation conditions (Roux et al. 2004a, Kamgan Nkuekam et al. 2009).

The first report of a *Ceratocystis* sp. causing disease and death of *Eucalyptus* spp. was from the Republic of Congo in Africa (Roux et al. 2000). Infection was found on trees of differing ages, including young coppice shoots and older trees approximately 10 years of age. Affected coppice stems showed rapid wilting and death, while death of older trees occurred more slowly. At approximately the same time as the discovery of a *Ceratocystis* disease on *Eucalyptus* in Africa, a *Ceratocystis* sp. was also found associated with diseased *Eucalyptus* trees in Brazil (Laia et al. 1999). Roux et al. (2000) included the Brazilian isolates in their study

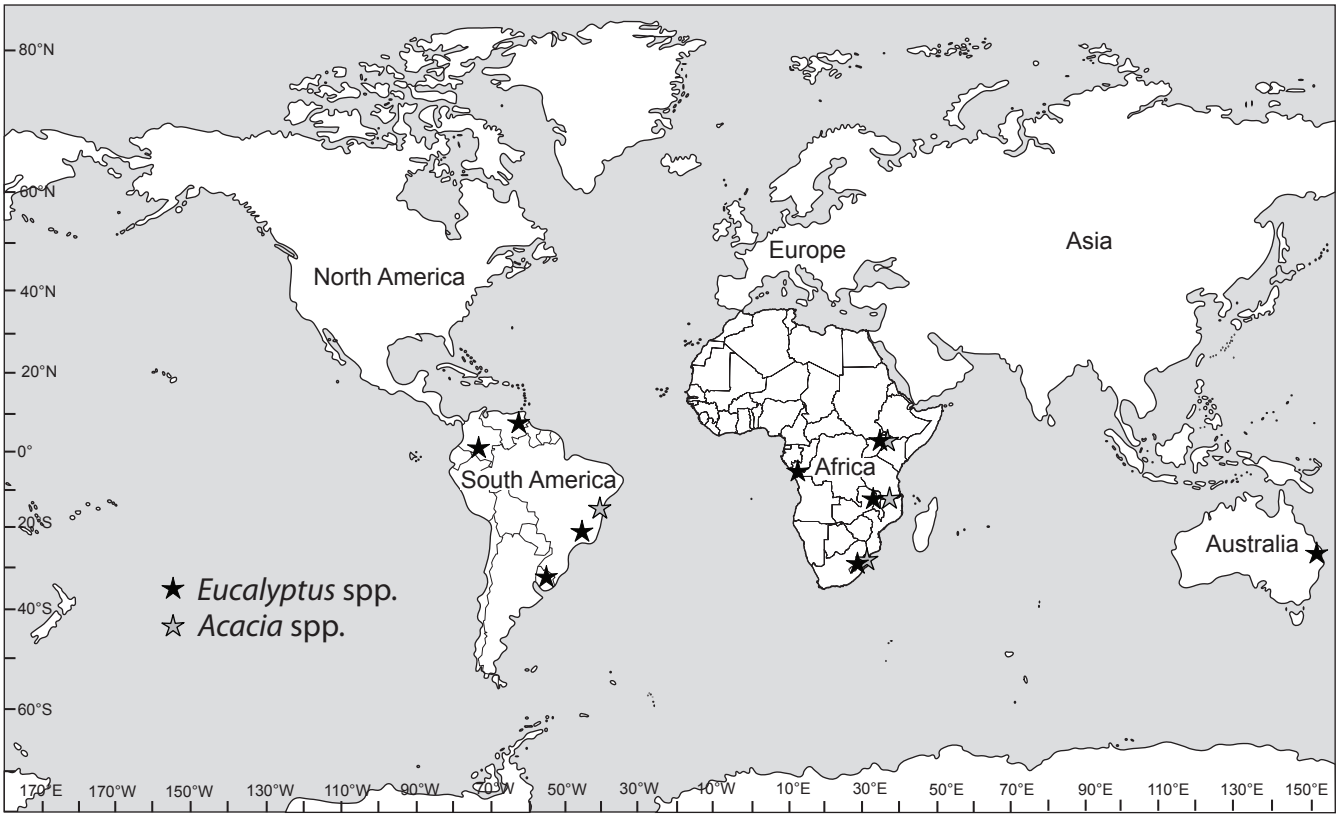

Figure 1: Areas from which *Ceratocystis* species have been reported from plantation-grown *Eucalyptus* species and *Acacia* species

and confirmed that they represented *C. fimbriata s.l.*, the same fungus responsible for *Eucalyptus* mortality in the Congo. Later reports of *C. fimbriata s.l.* causing disease or death of *Eucalyptus* trees have been from Uganda (Roux et al. 2001a) and Uruguay (Barnes et al. 2003b). In Uruguay, disease and death was associated with pruning wounds on *E. grandis* trees. Typical symptoms of *C. fimbriata* infection of *Eucalyptus* trees include dark brown streaking of the cambium and wood, wilting and death of trees (Roux et al. 2000, Barnes et al. 2003b).

Ceratocystis fimbriata s.l. was recently reported from *E. grandis* and *E. grandis* × *E. camaldulensis* trees in South Africa (Roux et al. 2004a; Figure 3c and d). In this instance, the fungus was not associated with tree mortality or disease and the only symptom was xylem discolouration. The fungus was found to be abundant in South African plantations. However, population diversity studies using microsatellite markers showed that the fungus on *Eucalyptus* in South Africa is clonal, with a very low genotypic diversity (van Wyk et al. 2006b). Results of these studies imply that the fungus was likely introduced into South Africa. Further studies using populations from other countries are required to determine a possible origin and route of spread for this fungus.

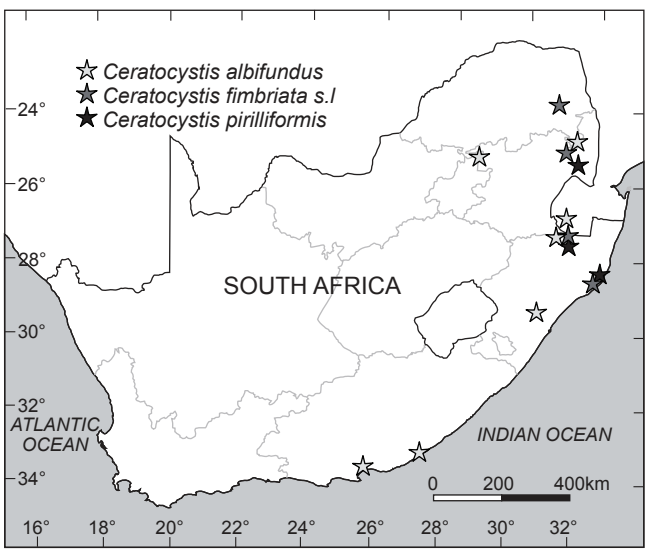

Figure 2: Distribution of *Ceratocystis* species in South Africa. Data for *C. albifundus* included reports on both native tree species and plantation-grown Australian *Acacia* species

Spread and infection of *Ceratocystis* species

Several factors contribute to *Ceratocystis* spp. being ideally suited to long-distance spread and being serious constraints to plantation forestry. These include their association with wood and bark inhabiting insects and their ability to infect wounds on trees. The former characteristic affords them easy spread between trees, countries and also continents,

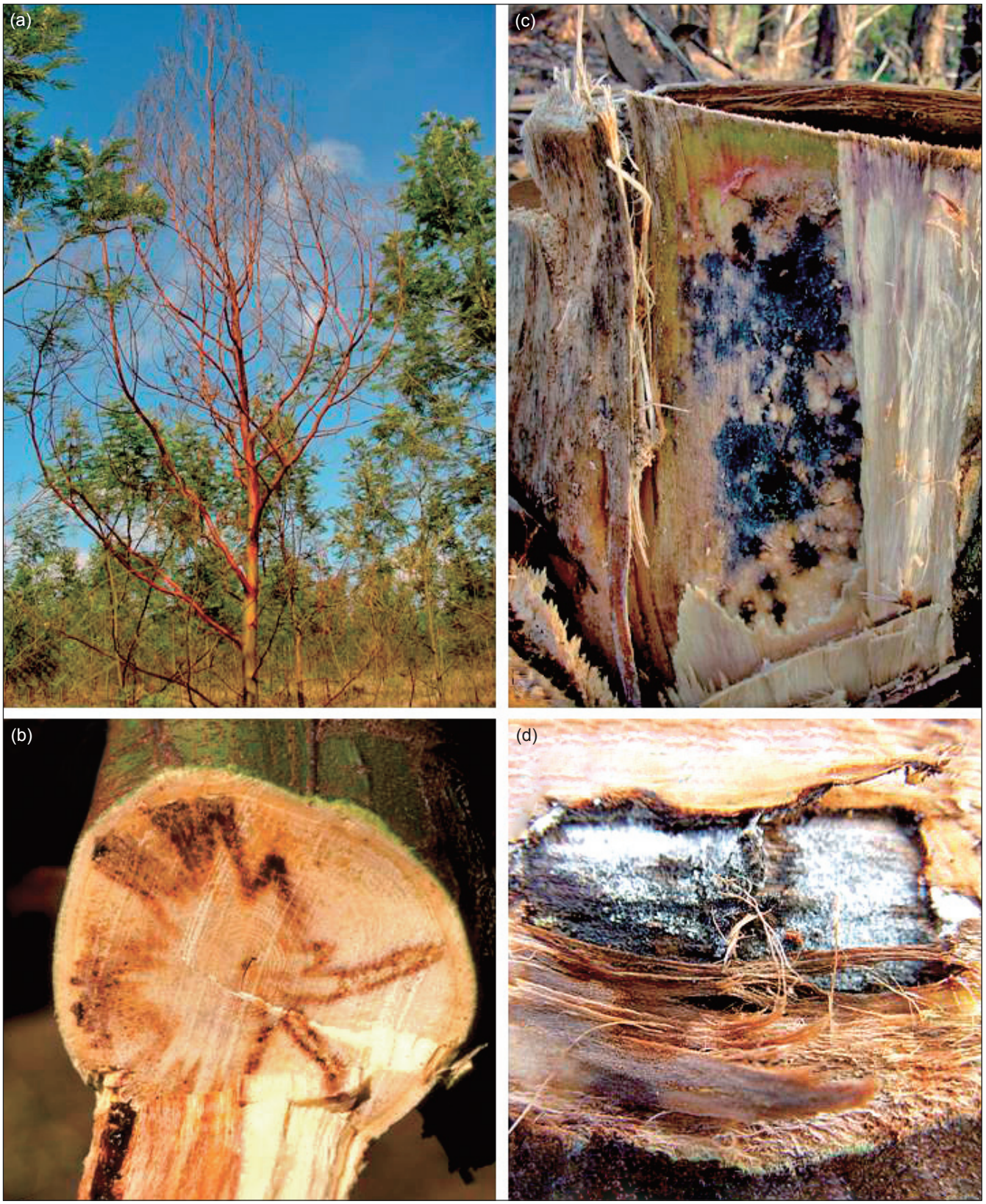

Figure 3: Symptoms caused by *Ceratocystis* species on plantation forestry species. (a) Wilt and death of *Acacia mearnsii*, (b) roseatte pattern of discolouration in the stem of a dying *A. mearnsii*, (c) infection of a *Eucalyptus* stump by *Ceratocystis* species after harvesting and (d) *Ceratocystis* species growing on a hail wound on *E. nitens*

while their ability to infect wounds provides them infection courts on trees.

Ceratocystis fimbriata s.l. has been associated with nitidulid beetles, flies and mites (Crone and Bachelder 1961, Moller and DeVay 1968). Recent work has shown that *C. albifundus*, the cause of wattle wilt, is closely associated with nitidulid beetles in South Africa (Heath et al. 2009a). *Ceratocystis* spp. in the *C. fimbriata* species complex that are pathogens of *Acacia* and *Eucalyptus* have various modes of dispersal. In plantations, their primary means of spread is via casual insects that visit freshly made wounds on trees. This relationship represents an elegant form of coevolution where the fungi produce fruity odours that are attractive to flies (Diptera) and picnic beetles (Coleoptera: Nitidulidae) (Lanza et al. 1976). These insects pick up the sticky *Ceratocystis* spores from infected wounds and transmit them to fresh wounds that they visit to feed on the sweet sap (Teviotdale and Harper 1991).

Ceratocystis spp. are known to require wounds for infection of trees (Walter 1946, DeVay et al. 1968, Teviotdale and Harper 1991, Wingfield et al. 1993; Figure 3c and d). Species of *Ceratocystis fimbriata s.l.*, for example, infect stone fruit trees through harvesting wounds (Teviotdale and Harper 1991). Likewise, coffee trees in Colombia become infected through wounds created by the boots of plantation workers that use the bases of trees to secure themselves when working with trees growing on steep slopes (Marin et al. 2003). In plantation forestry, *C. fimbriata s.l*. infects pruning wounds on *E. grandis* in Uruguay (Barnes et al. 2003b) as well as stumps and wounds in South Africa (Roux et al. 2004a), Malawi, Tanzania (Heath et al. 2009b), Colombia (Rodas et al. 2008) and Venezuela (van Wyk et al. 2009). In a similar manner, *C. albifundus* infects pruning and hail wounds in South Africa (Roux and Wingfield 1997).

Ceratocystis spp. can clearly spread and infect trees on their own or with the help of several different types of insects. Those reported from plantation forestry trees use generalist insects as vectors. This increases their chances of spread, in comparison to species that are reliant on specific insect species for survival and spread. Quarantine agencies and importers of timber should be concerned with regards to the movement of fungal mycelium in infected wood, fungal propagules on the bodies of insects that have hidden in the timber, or under the bark, in soil or on equipment.

Future prospects

Evidence clearly shows that the incidence of *Ceratocystis* spp. as pathogens of plantation forestry tree species is increasing. It is also clear that considerable research is still required to fully understand the species involved in disease development, as well as their origins. However, their association with insects and their ability to infect wounds poses important constraints to plantation forestry. Management of disease caused by *Ceratocystis* spp. must thus rely on an integrated approach. Careful selection and breeding of disease-tolerant material will be required to produce planting stock that is resistant to infection by *Ceratocystis* spp. This route has already been shown to provide good results in South Africa (Roux et al. 1999) and in Brazil (Zauza et al. 2004). Furthermore, great care will have to be taken to minimise the creation of wounds on trees during silvicultural and other operations. The reduction of wound size and the timing of wounding to occur during periods when the insect vectors are less active will also reduce the occurrence of disease (Heath et al. 2009a).

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