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Increasing threat of diseases to exotic plantation forests in the Southern Hemisphere: lessons from Cryphonectria canker

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Abstract. Plantation forestry in the Southern Hemisphere has grown dramatically in the last hundred years. This has largely been due to the exceptional growth and performance of exotic species, particularly *Pinus*, *Eucalyptus* and *Acacia*. It is generally recognised that the success of these plantations has, at least in part, been due to the separation of the trees from their natural enemies. In this regard, the trees have performed similarly to weeds. Indeed, in some situations, species regarded as highly desirable for forestry are also recognised as noxious weeds. The artificial barrier between exotic plantation species and their pathogens is, however, crumbling. Despite intensive efforts to exclude pests and pathogens from countries now dependent on plantations of exotic trees, new and seriously damaging incursions are occurring with increasing frequency. Cryphonectria canker of *Eucalyptus* caused by *Cryphonectria cubensis* provides an important and interesting example and is used in this paper to illustrate emerging trends. These include evidence to suggest that native pathogens, previously thought to be relatively host specific and non-threatening, are adapting to infect exotic plantation trees. Other than the damage that these pathogens are causing to exotics, they now pose a serious threat to the same or related tree species in their areas of origin. This tremendous threat is only just being recognised and it is little understood. This is, at least in part, due to a poor understanding of the taxonomy and ecology of even some of the better known tree pathogens. Intensive efforts will be required to protect the sustainability of exotic plantation forestry. They will also be needed to ensure that 'new pathogens' do not lead to destruction of the same or related tree species in their areas of origin.

Introduction

Plantation forestry in the Southern Hemisphere has grown dramatically during the course of the last hundred years. This has largely been due to the exceptional growth and performance of exotic species, particularly *Pinus*, *Eucalyptus* and *Acacia*. Thus, in countries such as New Zealand, Australia, South Africa and various countries of South America, large industries have arisen based on exotic plantations. These industries produce both solid wood products, as well as pulp, for local consumption and for export. In many cases, they represent some of the most important products produced by these countries, thus forming pivotal elements of well-established as well as emerging economies.

It is generally recognised that the success of exotic plantation forestry has, at least in part, been due to the separation of the trees from their natural enemies. In this regard, the trees have performed similarly to weeds (Bright 1988). This is most likely attributable to the enemy release hypothesis, which suggests invasive species owe their success to the release from pests and pathogens (Keane and Crawley 2002; Mitchell and Power 2003). Indeed, in some situations, species regarded as highly desirable for forestry and agriculture are also recognised as noxious weeds (Henderson 1999). This has resulted in substantial conflict between forestry enterprises dependent on healthy, rapidly growing plantations and groups keen to eliminate 'weed trees' through biological control.

Plantation forestry based on exotic species in the Southern Hemisphere began towards the end of the 19th Century. The speed at which plantations developed and the motivation for their establishment differed from one country

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to another. But in all cases, it was recognised quite early that disease and pest problems threatened these emerging tree farms.

The artificial barrier between exotic plantation species and their pathogens is crumbling. Despite intensive efforts to exclude pests and pathogens from countries now dependent on plantations of exotic trees, new and seriously damaging incursions are occurring with increasing frequency. For example, when one considers first reports of diseases of *Eucalyptus* in South Africa, it is clear that some diseases were evident early in the history of planting this tree. Indeed, one of the first widely planted species of *Eucalyptus* in this country, *E. globulus*, is known to have failed in plantations due to Mycosphaerella leaf blotch disease (Wingfield 1990). What is also evident is that new records of relatively important diseases are increasing in number and frequency. This increase might, to some extent, be ascribed to increased awareness of diseases and more intensive surveys to determine their occurrence. However, there is little question that new and previously unknown disease problems are arising at an alarming rate.

Countries in the Southern Hemisphere differ in the species they plant and the products produced from plantations. The choice of planting stock is largely related to the environment in the various countries and the species that will grow most effectively under those conditions. Thus, in New Zealand and Chile, *Pinus radiata* is planted almost exclusively. In contrast, plantations in South Africa are made up of more or less equal proportions of a number of species of *Pinus* and *Eucalyptus*. In this case, the country has varied environments and even if desired, it would not be possible to plant only a single tree species.

Despite differences in the trees chosen for planting, concepts relating to disease problems appear to be similar. For the purpose of this paper, I have thus chosen a single disease that I believe aptly illustrates some emerging trends relating to diseases in exotic plantation forestry. This disease is Cryphonectria canker caused by the fungus, *Cryphonectria cubensis* (Bruner) Hodges, which occurs widely in the tropics and Southern Hemisphere.

Taxonomic history of *Cryphonectria cubensis*

Cryphonectria canker was first described from Cuba in 1917 (Bruner 1917). The disease was found on *Eucalyptus* and the causal agent was described as *Diaporthe cubensis* Bruner. Cryphonectria canker remained virtually unknown until Boerboom and Maas (1970) reported a serious canker disease on *E. grandis* and *E. saligna* in Surinam. This disease was attributed to another fungus *Endothia havanensis* Bruner, which was recorded on *Eucalyptus* in Cuba a year prior to the report of *D. cubensis* (Bruner 1916). Having two similar fungi on a single host resulted in some taxonomic confusion and the first outbreaks of cankers on *Eucalyptus* in Brazil were also attributed to *E. havanensis* (Hodges and Reis 1974). However, Hodges and Reis (1974) recognised that the canker pathogen in Brazil and Surinam was the same as *D. cubensis* and not *E. havanesis.* Later research led to *D. cubensis* being transferred to *Cryphonectria* as *C. cubensis* (Bruner) Hodges (Hodges 1980) and this remains the currently accepted name for the fungus (Micales and Stipes 1987).

At the time of discovering Cryphonectria canker in Brazil, the country had developed a thriving industry based on plantations largely of *E. grandis* and *E. saligna* and these trees were severely damaged by Cryphonectria canker (Hodges, personal communication). Some trees in progeny trials and other plantings known as *E*. 'alba' were noted to be free of this disease. These trees that were natural hybrids of *E. grandis* and *E. urophylla* were subsequently multiplied via vegetative propagation. This resulted in an outstanding opportunity for disease avoidance. It might thus be argued that Cryphonectria canker, at least in part, promoted large-scale vegetative propagation of *Eucalyptus* spp. that is widely practised in the tropics and Southern Hemisphere today (Hodges, personal communication).

After its appearance in Brazil in the 1970s, records of *C. cubensis* elsewhere in the world increased rapidly (Old and Davison 2000). These reports do not necessarily imply that the disease was moving rapidly to new areas but rather reflect a growing increase in knowledge and interest in the disease in the 1970s and 1980s. The intriguing question of the probable origin of the disease also arose at this time. In pursuing this question, Hodges *et al.* (1986) recognised the similarity of *C. cubensis* and *Endothia eugeniae* (Nutman & Roberts) Reid & Booth, a canker pathogen of clove (*Syzygium aromaticum*) which, like *Eucalyptus*, is a member of the Myrtaceae. Hodges *et al.* (1986) thus reduced *E. eugeniae* to synonymy with *C. cubensis* and this synonymy has been confirmed in subsequent studies (Micales *et al*. 1987; Myburg *et al*. 1999). The synonymy of the clove and *Eucalyptus* canker pathogens led Hodges *et al.* (1986) to speculate that the *Eucalyptus* pathogen probably had its origin on clove, which is native to the Molucca islands of Indonesia. It could easily have spread from this area together with clove, which has been moved to many parts of the world where *Eucalyptus* spp. are propagated.

The importance of Cryphonectria canker in other *Eucalyptus* growing areas of the world during the 1970s and 1980s, prompted surveys for the disease in South Africa in the mid 1970s (Wingfield, unpublished). Although it was not found at that time, it was discovered in the country in the mid 1980s (Wingfield *et al.* 1989). This discovery was probably partially due to the uniform planting of susceptible clones of *E. grandis*, which would have provided a magnifying effect for the pathogen. At this time, the disease was also thought to represent a new introduction of a *Eucalyptus* pathogen into the country (Wingfield, unpublished).

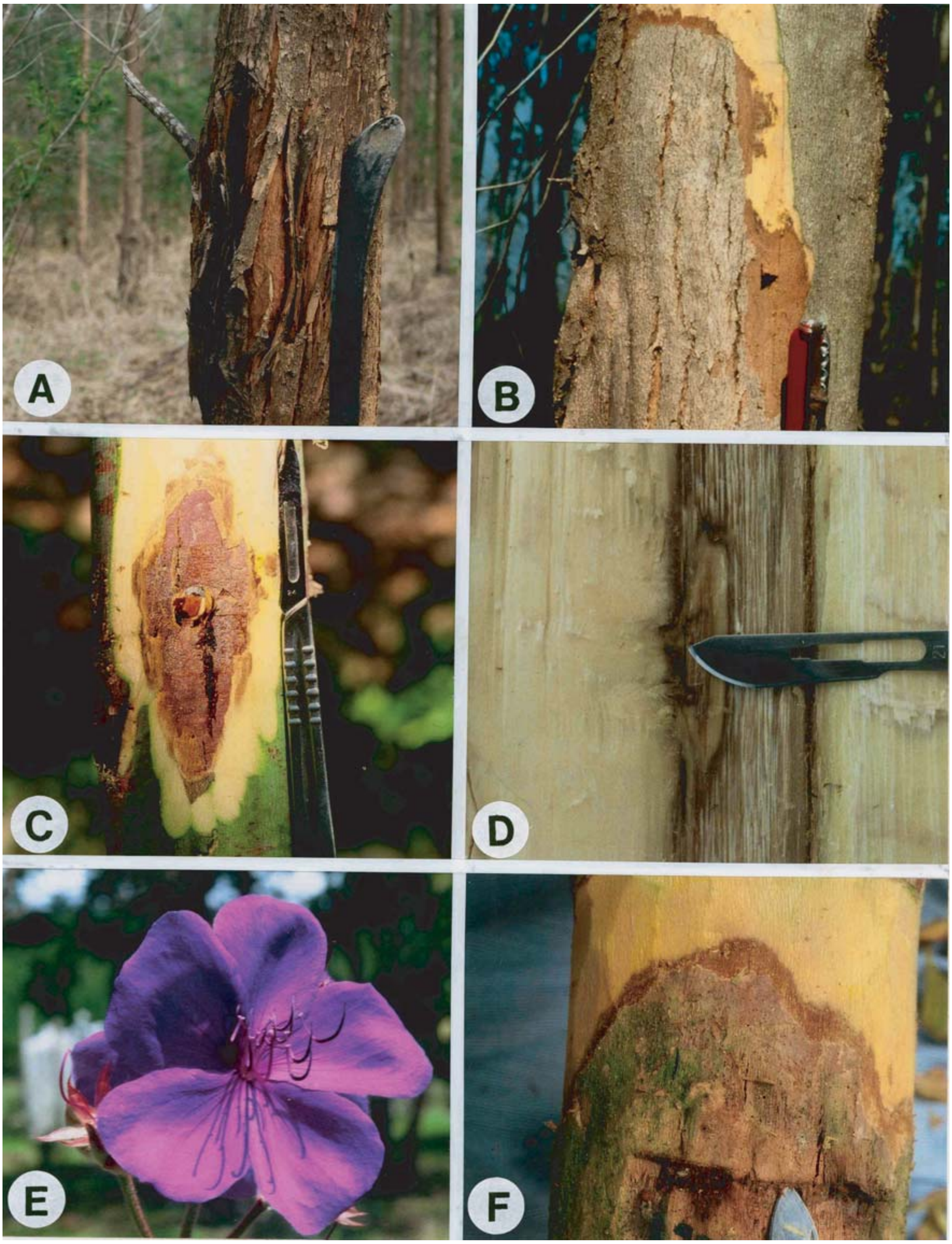

Fig. 1*A–F*. Symptoms of Cryphonectria canker and hosts of *Cryphonectria cubensis*. (*A*, *B*) Stem cankers approximately at breast height on *Eucalyptus grandis* in South America and different from the basal cankers found in South Africa. (*C*) Lesion on the stem of *E. grandis* in South Africa, 6 weeks after inoculation with *C. cubensis*. (*D*) Lesion on *E. grandis* in South America, 6 weeks after inoculation with *C. cubensis*. Note the embedded lesion different from that found after inoculations in South Africa. (*E*) Flower of *Tibouchina urvilleana*. (*F*) Lesion associated with inoculation of *C. cubensis* on *T. lepidota* in Colombia.

Cryphonectria canker on *Eucalyptus* in South Africa

When Cryphonectria canker was first discovered on *Eucalyptus* in South Africa (Wingfield *et al*. 1989), it was considered to be similar to the disease found elsewhere in the world. However, there were some intriguing differences in symptoms. These have become better understood as more thorough comparisons have been made. In South Africa, the disease is most commonly found on young trees, which in the case of highly susceptible planting stock, are generally girdled and killed due to cankers at the tree bases in the first 2 years of growth. Trees that are infected and survive tend to have large basal cankers and they commonly fall over in windstorms or they die gradually during the course of a 5–10 year rotation. These symptoms are distinctly different from those found in South America and South East Asia (Wingfield, unpublished) where cankers can be found at the bases of trees, but they are also common higher up on stems (Fig. 1*A*, *B*), often associated with branch stubs. Stem cankers above the base of the stems have never been seen in South Africa and response to inoculation (Fig. 1*C*, *D*) by the fungi in South Africa and South America is distinctly different.

Another very distinct difference between the Cryphonectria canker in South Africa and the disease found elsewhere in the world concerns the appearance of fungal fruiting structures on the surface of cankers. In South Africa, cankers are typically covered with pycnidia and perithecia are never seen. These structures have been seen only once on *Eucalyptus* trees. This was at the time of the discovery of the disease (Wingfield *et al.* 1989) and the ascocarps occurred on diseased bark tissue collected below the soil surface. This is in contrast to cankers in South America and South East Asia that are typically covered with both perithecia and pycnidia of the pathogen. Inoculations with *C. cubensis* isolates from South Africa give rise to lesions in the cambium that rapidly girdle susceptible trees (Van Zyl and Wingfield 1999; Van Heerden and Wingfield 2002; Wingfield *et al*. 1989). This is in contrast to inoculations with isolates of the fungus from South America and South East Asia (Wingfield, unpublished) that give rise to more limited cankers and the gradual sloughing off of the outer bark.

Differences in the symptoms associated with *C. cubensis* in South Africa, South America and South East Asia have led to a series of studies in which these fungi have been compared based on DNA sequence data. The first of these studies by Myburg *et al.* (1999) used sequences of the ITS regions of the ribosomal DNA operon to consider possible differences between a large set of isolates from different parts of the world. This study showed that isolates from South America and those from South East Asia reside in two clearly resolved, but closely related, groups. Isolates from South Africa were most closely related to those from South America and an isolate from clove resided with isolates of *C. cubensis* from South East Asia.

Cryphonectria canker on *Tibouchina*

One of the most intriguing recent discoveries pertaining to Cryphonectria canker has been the discovery of the disease on native and planted *Tibouchina* spp. (Fig. 1*E*, *F*) in Colombia (Wingfield *et al.* 2001). Although initial reaction to finding structures morphologically similar to those of *C. cubensis* on a non-myrtaceous host was one of surprise, DNA sequence comparisons based on the ITS region of the ribosomal operon showed clearly that isolates of the fungus from *Tibouchina* spp. and *Eucalyptus* were the same. They also were most closely related to those of *C. cubensis* from South America. In addition, pathogenicity tests showed that *Tibouchina* isolates could infect *E. grandis* and *Eucalyptus* isolates caused disease on *Tibouchina* (Wingfield *et al.* 2001).

While the presence of *C. cubensis* on *Tibouchina* in Colombia seemed strange, this has turned out not to be as unusual as it seemed at first. *Tibouchina* spp. reside in the Melastomataceae, which is a family closely related to the Myrtaceace, in the Myrtales (Conti *et al*. 1996, 1997). The common occurrence of *C. cubensis* on *Tibouchina* spp. and other Melastomataceae native to South and Central America (Wingfield, unpublished data) suggests that these plants might represent a source of origin for the canker pathogen of *Eucalyptus*. Although the clove origin of the fungus cannot be discounted, the possibility of the pathogen passing from Melastomataceae to cloves must also be considered. Furthermore, differences based on DNA sequences in the fungus in South East Asia and South America (Myburg *et al*. 1999, 2003; Wingfield *et al*. 2001) might also suggest that the fungus has evolved separately in the two regions.

Many *Tibouchina* spp. have abundant and showy flowers (Fig. 1*E*) and they are easily propagated via cuttings. They have consequently been widely planted along streets and in gardens in countries of South America and in South Africa, Australia and New Zealand. The discovery of *C. cubensis* on *Tibouchina* in Colombia has led to surveys for the fungus on this tree in other parts of the world. These surveys are ongoing, but in South Africa the fungus has recently been found on *Tibouchina* spp. in the same areas where it causes cankers on *Eucalyptus* (Myburg *et al*. 2002*a*). Furthermore, comparisons of DNA sequence data have shown that the fungus from *Tibouchina* in South Africa is most closely related to that on *Eucalyptus* in the country, and more distantly related to isolates from *Tibouchina* and *Eucalyptus* in South America.

Reconsidering the origin of *C. cubensis* in South Africa

As mentioned earlier in this account, symptoms of Cryphonectria canker in South Africa are somewhat different from those found in South and Central America and South East Asia. Indeed, these differences constituted a major portion of the justification for comparing isolates of

C. cubensis based on DNA sequence data (Myburg *et al.* 1999). In this regard, the results of the latter study, based on sequence data for the ITS regions of the ribosomal DNA operon, were rather disappointing. While clear differences could be found between groups of isolates from South America and South East Asia, South African isolates grouped convincingly with those from South America.

More recently, a renewed effort has been launched to compare isolates of *C. cubensis* from various parts of the world. Here, sequence data for both the beta tubulin and Histone *H3* genes have been produced to augment those already available for the ITS regions (Myburg *et al.* 2002*b*). While South East Asian and South American isolates remained related yet nested in two distinct clades, the South African fungus was shown to be distinct from the South East Asian and South American fungus. These data provide strong support for ecological differences previously recognised. They also augment results showing that isolates of *C. cubensis* from *Tibouchina* in South Africa are most closely related to those from *Eucalyptus* in this country. Those from *Tibouchina* in South America are most closely related to isolates from *Eucalyptus* in that part of the world (Myburg *et al*. 2002*a*).

Recognising that *C. cubensis* in South Africa is different from the fungus occurring elsewhere in the world has important implications. If we accept that the fungus in South and Central America might have had its origins on Melastomataceae, and that the fungus in South East Asia either had a similar origin or originated on cloves, we need to consider the question of the origin of the South African fungus. It is with this intriguing question in mind that native Myrtaceae in South Africa have recently become the subject of intensive surveys for Cryphonectria canker. Here the focus has been on the native water berry tree, *Syzygium cordatum*. These surveys have led to the exciting discovery of the same fungus that occurs on *Eucalyptus* and *Tibouchina* on this native plant (Heath *et al.* 2002).

The position of *C. cubensis* in Cryphonectria

Venter *et al*. (2001) undertook a taxonomic study of the *Eucalyptus* canker pathogen known as *Endothia gyrosa* (Schw.:Fr) Fr. This fungus is well known from North America where it is a mild canker pathogen on a wide range of hardwood trees including *Quercus* spp. and *Liquidambar formosana.* This study showed clearly that the fungus on *Eucalyptus* in South Africa and Australia is different from that found on other woody hosts elsewhere in the world. These observations led to a subsequent study using additional DNA sequence data and morphological characteristics (Venter *et al*. 2002), and in which the *Eucalyptus* fungus was transferred to *Cryphonectria* as *C. eucalypti* Venter and M.J. Wingf. Venter *et al*. (2001) also showed clearly that *C. cubensis* in fact resides in a group distinctly apart from that accommodating the chestnut blight pathogen, *Cryphonectria parasitica* (Murill) Barr and *C. eucalypti*.

An unusual aspect of this new generic placement was the fact that *Cryphonectria* had previously been restricted to species with two-celled ascospores, but that spores in *C. eucalypti* are aseptate. However, stromatal morphology in *C. eucalypti* and *C. parasitica* was characteristic and consistent with groupings based on DNA sequences. Stromata in *C. cubensis* were distinctly different and also consistent with the fact that this fungus grouped apart from other species of *Cryphonectria* (Venter *et al*. 2002; Gryzenhout *et al*. 2002).

Although isolates of the fungus that we have known as *C. cubensis* from South Africa and other parts of the world can be distinguished based on DNA sequence data, they are morphologically difficult to tell apart. However, subtle morphological differences do exist between these fungi (Gryzenhout, personal communication; Myburg *et al*. 2002*b*) and these are currently being studied more intensively. Our view (Gryzenhout *et al*. 2002; Venter *et al*. 2002) is now that *C. cubensis sensu lato* should reside in a genus different from that accommodating other species of *Cryphonectria.* The fungus that has been known as *C. cubensis* from South Africa would represent a new species in this genus.

Whether the fungus known as *C. cubensis* in South Africa moved from native *S. cordatum* to *Eucalyptus* and *Tibouchina*, or *vice versa*, must be considered. Early evidence supporting the view that the fungus is native in South Africa arises from the distribution data for the fungus on *S. cordatum*. Here, the fungus has a wide distribution including areas where it is not known to occur on *Eucalyptus* or *Tibouchina* (Heath and Gryzenhout, personal communication). Furthermore, the genetic diversity of a population of *C. cubensis* isolates from *Eucalyptus* in South Africa has been shown to be very limited (Van Heerden and Wingfield 2001). Preliminary comparisons of populations of isolates from the three hosts (Heath *et al*. 2003) also lend credence to the hypothesis that the fungus has a South African origin.

Conclusions

Cryphonectria cubensis is one of the most important pathogens of plantation-grown *Eucalyptus* spp. Yet, when reviewing research on this pathogen during the course of the last three decades, it is clear that we are only just beginning to understand important aspects of its taxonomy, host range and biogeography. For example, a decade ago we believed that this relatively well-known fungus was a newly introduced pathogen in South Africa. This view appears to be incorrect. It also emphasises the fact that other less well-known pathogens of exotic plantation trees are, most likely, even more poorly understood.

Perceived threats relating to diseases such as *Cryphonectria* canker of *Eucalyptus* have clearly been entirely underestimated. This is due to a lack of understanding of the taxonomy and ecology of the fungus. The same is certainly true for many other plant pathogens and a wide range of examples were indeed presented during the congress at which this presentation was made. This lack of knowledge has significant implications for quarantine, where decisions are often being made based on minimal knowledge. It also provides very clear evidence that funding for taxonomic and ecological studies of fungal (and other) plant pathogens is hopelessly inadequate.

Although exotic plantation forestry in the tropics and Southern Hemisphere is more than 100 years old, this might be viewed as relatively young in terms of development of pests and pathogens. Pathogens and particularly those infecting shoots and stems have clearly been introduced into new plantation projects, together with germplasm. However, we know of relatively few examples where host specific pathogens have crossed from native plants to exotic plantation species. Eucalyptus rust caused by *Puccinia psidii* Winter has been considered an unusual and important example (Coutinho *et al.* 1998). Recent research on *Cryphonectria* summarised in this review provides good evidence that native plants, and even those not easily recognised as being related to exotic plantation species, can be the source of important and damaging pathogens of newly established exotics.

In the future, it is reasonable to expect that the cost of exotic plantation forestry will rise due to the appearance of increasing numbers of pests and pathogens. These will not only originate in the areas where the trees are native, but they will also most likely come from trees native to the countries where the exotics have been established. These new pathogens could, in turn, present an even greater threat to trees where these plantation species are indigenous. Certainly the Eucalyptus canker pathogen that has been known as *C. cubensis* in South Africa is substantially more virulent than the fungus of the same name that is found in other parts of the world. It presents a very real threat to *Eucalyptus* and related trees in Australasia. This is, perhaps, a gloomy scenario to consider, but it is sufficiently plausible to justify substantial support for forest pathology research.

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