Worldwide Movement of Exotic Forest Fungi, Especially in the Tropics and the Southern Hemisphere

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Plantations of forest trees have been established throughout the world, primarily to provide structural timber and fiber for pulp. In the Northern Hemisphere, plantations tend to be of native species generated from seedlings in nurseries. Over the last century, however, extensive plantations of exotic species have been established in many parts of the tropics and the Southern Hemisphere. In these areas, trees were initially established in provenance trials to identify superior seed sources and genetic material. Subsequent selection of desirable trees from the best performing provenances led to the establishment of seed orchards and sophisticated breeding programs. In some cases, these breeding programs have included hybridization of species and large-scale vegetative propagation of desirable genotypes.

In both the tropics and the Southern Hemisphere, the most widely established tree species in plantations are *Pinus* Linnaeus, *Eucalyptus* L'Heritier, and *Acacia* Miller. Local land races—many of them natural hybrids resulting from early progeny tests, others the result of artificial hybridization between species (and land races) in all three genera—have emerged in countries with long histories of exotic plantation forestry. This hybridization, both natural and artificial, coupled with vegetative propagation, has made it possible to produce highly productive clones with a wide range of desirable traits. Based on the development of these species hybrids, large international companies have emerged and become important contributors to world timber and pulp production. Most of these companies also contribute to international efforts to reduce the logging of old-growth native forests.

Exotic plantation forestry in the tropics and in the Southern Hemisphere is not trouble free. For example, fungal diseases caused by native fungal pathogens, as well as pathogens introduced with planting stock, have had a significant impact on this industry (Gilmour 1967, Gibson 1979, Florence et al. 1986, Hodges et al. 1986, Conradie et al. 1990, Wingfield et al. 1991, 1995). More attention has been given lately to quarantine issues, but new pests and diseases continue to appear in exotic plantations, posing a serious threat to the productivity of plantations and thus to the industries that rely on them. The importance of the impact on, and threats to, native plants have been little recognized.

THIS ARTICLE EXAMINES THE IMPACT OF FUNGAL PATHOGENS INTRODUCED IN PLANTATION FORESTRY

In this article we look at the impact of pathogens on exotic plantation forestry in the tropics and in the Southern Hemisphere. We describe the means of spread and the possible origins of several pathogens to illustrate emerging trends, such as conflicts of interest between conservation groups and forestry companies. We also discuss the relatively

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poor capacity of researchers to adequately evaluate the magnitude of risks linked to the introduction of pathogens.

Origin of exotic pathogens

Natural and introduced pathogens are present in exotic plantations. Exotic pathogens commonly enter new areas via germ plasm. Root pathogens, which tend to require soil and plant roots for their spread, have traveled less frequently between continents because of long-standing and strict quarantines on the movement of soil. However, many species of stem, leaf, and shoots pathogens have been introduced into new areas with seeds and plant debris associated with seed.

Figure 1. The root pathogen of pine,* Rhizina undulata, *which was probably introduced into the Southern Hemisphere with contaminated soil.

Root pathogens. Root diseases in exotic plantations are caused predominantly by native pathogens. Nevertheless, there are some intriguing examples of root diseases of exotic plantation trees caused by pathogens that are in all likelihood also introduced. One of these is Rhizina root disease, caused by *Rhizina undulata* (Figure 1), which can be extremely damaging in southern Africa (Gibson 1979, Germishuizen 1984). This pathogen is specific to conifers and is thought to be native to boreal regions (Booth and Gibson 1972). It is generally accepted that *R. undulata* was introduced into plantations in southern Africa via contaminated soil, perhaps when the area was first colonized by Europeans, who introduced pine trees together with their mycorrhizal associates. Exotic *Pinus* and *Eucalyptus* plantation forestry would not have been possible in South Africa without the accidental introduction of mycorrhizae. Clearly, there was a concomitant introduction of pathogens, of which *R. undulata* is most likely only one example.

Pathogens of aboveground tree parts. A number of diseases appeared during the early stages of establishment of exotic species in the tropics and in the Southern Hemisphere. The pathogens were most likely introduced with early planting stock, seeds, or cones, when very little attention was given to risks associated with disease.

Many needle- and leaf-infecting pathogens were recognized relatively early in the establishment of exotic plantations. Early reports of needle diseases on pine included species of *Lophodermium, Cyclaneusma,* and the important pathogen *Dothistroma septospora* (Gibson et al. 1964, Gilmour 1967, Edwards and Walker 1978, Gibson 1979, Millar and Minter 1980, Roux 1984). For example, in the last century *D. septospora* caused millions of dollars' worth of losses in the *P. radiata* industry in New Zealand, Australia, Chile, Kenya, and other countries where this tree is planted as an exotic. Some possibly exotic pathogens of *Eucalyptus* species that appeared early in the process of plantation establishment were *Mycosphaerella* (Doidge et al. 1953, Park and Keane 1982, Crous and Wingfield 1996, Crous 1998), *Phaeophloeospora* (Heather 1967, Chipompha 1987, Crous et al. 1989, 1997), and *Aulographina eucalypti* (Doidge et al. 1953, Wall and Keane 1984). These pathogens have also been found in Australia, where *Eucalyptus* is native, indicating that they were most likely introduced from that country.

Sphaeropsis sapinea is one example of an introduced pathogen of exotic trees with a now cosmopolitan distribution. In many countries this opportunistic pathogen is considered relatively unimportant, of significance only where pines are growing under stress (Van der Byl 1933, Minko and Marks 1973, Wingfield and Knox-Davies 1980, Brown et al. 1981, Swart and Wingfield 1991). In South Africa, however, where highly susceptible species (*Pinus patula* and *P. radiata*) are planted, regular hail damage to trees and the ubiquitous occurrence of *S. sapinea* as an endophyte in healthy trees (Swart and Wingfield 1991, Smith et al. 1996, Stanoz et al. 1997) has led to millions of dollars' worth of losses each year (Figure 2; Zwolinski et al. 1990). Obviously, the significance of a pathogen in its natural range has little predictive value as to its aggressiveness in exotic situations.

Pathogens of timber products. Little is known about the intercontinental spread of pathogens that infect solid wood products. Sapstain fungi, which cause discoloration of timber (Figure 3), include pathogens such as *S. sapinea*, which is widespread throughout areas where exotic pine is grown. Other sapstain fungi, such as *Ophiostoma* species, also have spread from native pine-growing areas to exotic plantations. Four species (*Orthotomicus erosus, Ips grandicollis, Hylastes angustatus,* and *H. ater*) of pine-infesting bark beetles have appeared in plantations outside the native range of pines and are vectors for sapstain fungi (Wingfield and

Marasas 1980,1983,Stone and Simpson 1987, Wingfield et al. 1988, Schowalter and Filip 1993).

One of the most fascinating wood decay fungi that infect exotic pine plantations in the Southern Hemisphere is *Amylostereum areolatum*. This fungus is an obligate symbiont of the wood wasp *Sirex noctilio* (Figure 4), which was first introduced to New Zealand around 1900 (Gourley 1951, Gilmour 1965, Chou 1991). The wasp appeared in Australia in 1961 (Gaut 1970, Talbot 1977, Neumann and Minko 1981, Madden 1988) and subsequently became established in Brazil (1980s), Argentina (1985), Uruguay (1980), and South Africa (1994) (Baxter et al. 1995, Tribe 1995). It is likely that new introductions of *S. noctilio* and *A. areolatum* have occurred with the transport of wood products. It is particularly interesting that *S. noctilio* remained in Australia and New Zealand for an extended period of time without becoming established in other Southern Hemisphere countries. Yet the time span between its appearance in South America and South Africa was very short, suggesting a multiplicative effect whereby a greater distribution and an increase in international trade accelerated the spread.

The recent discovery of the wilt pathogen *Ceratocystis fimbriata* on *Eucalyptus* (Figure 5) in the Republic of the Congo and in Brazil (Roux et al. 2000) and on *Acacia mearnsii* in South Africa (Roux et al. 1999) provides another example of a pathogen that may have traveled on wood products or perhaps on sap-feeding insects associated with wood products. This view is supported by the fact that an isolate of the fungus from *A. mearnsii* in South Africa is more closely related to isolates from South America than it is to isolates from the Congo. Congolese isolates of *C. fimbriata* are also closely related to isolates from a wide range of hosts in South America.

Figure 2. Die-back of pine in South Africa following hail damage, caused by the opportunistic pathogen* S. sapinea, *which has been repeatedly introduced into the country on seed.

Exclusion of pathogens through quarantine

Because devastating tree diseases—for example, Dutch elm disease (caused by *Ophiostoma ulmi* and *O. novo-ulmi*), chestnut blight (from *Cryphonectria parasitica*), and pine wilt (caused by the nematode *Bursaphelenchus xylophilus*)—inflict great costs, both financially and in terms of their impact on ecosystems, governments have instituted quarantine measures to minimize outbreaks. Furthermore, international plant quarantine measures have been considerably refined and improved during the course of the last century, although efforts to facilitate international trade have probably increased the risks (Campbell 2001). Despite bold attempts to prevent the spread of fungal pathogens, new diseases continue to appear and quarantine regularly fails to exclude tree pathogens.

There are many possible reasons for the failure of plant quarantine measures to exclude pathogens. Clearly, developed countries with outstanding quarantine regulations, strictly monitored borders, and the capacity to control ports of entry have the best chances of excluding pathogens. If they share borders with countries with poorer border control, however, they have little hope of effective quarantine. The so-called weakest-link-in-the-chain concept applies—that is, whole continents might be negatively affected by poor quarantine measures in a small number of countries.

One step in assessing risk and developing appropriate quarantine strategies is to find out whether a particular pathogen is already present in a country. This approach ensures that no new pathogens are introduced into a country but overlooks the fact that pathogens are represented by populations of individuals. The introduction of additional genotypes of a pathogen could have undesirable consequences, as is the case with *S. sapinea*, which consists of three morphotypes (De Wet et al. 2000). Morphotype C is much more virulent than morphotypes A and B, but even morphotype A is responsible for large-scale losses in South Africa (De Wet et al.2000). The introduction of a more virulent morphotype should be avoided at all costs. Greater numbers of pathogen genotypes will vitiate the durability of disease tolerance in selected trees and, where sexual reproduction occurs, lead to greater genetic diversity of the pathogen (McDonald and McDermott 1993), which would complicate disease control.

Recent studies of *S. sapinea* in South Africa have yielded intriguing information on the genetic diversity of this pathogen. Contrary to expectation for an introduced fungus, the population of this asexual pathogen in South Africa has a high level of genetic diversity (Smith et al. 2000). In contrast, genetic diversity was very limited in the population of *S. sapinea* from Indonesia, where pines—and thus probably the pathogen—are native (Smith et al. 2000). The only reasonable explanation for the genetically diverse population of *S. sapinea* in South Africa is that the fungus has been introduced into the country repeatedly and from a wide range of countries during the past century. Imported pine seed was most likely the vehicle for these introductions. In terms of quarantine, the presence of the fungus in the country would have reduced the significance of *S.sapinea* as a priority. The consequence of lower perceived risk is the introduction of large numbers of genotypes of the pathogen and a significantly heavier burden in terms of disease management strategies.

The advent of molecular tools to identify pathogens is already increasing the capacity to evaluate risks. There are many examples of pathogen species previously believed to represent single taxa that are now known to comprise more than one and sometimes large numbers of species (O'Donnell et al. 1997, Harrington and Wingfield 1998, Nirenberg and O'Donnell 1998, Witthuhn et al. 1998). Such information is crucial in developing meaningful strategies for pathogen exclusion. Without the aid of molecular tools, scientists would be unable to correctly identify many species, which would mean that pathogens might be allowed into countries where they did not previously occur. The need to use such sophisticated tools to identify pathogens complicates the process of quarantine implementation, but in the long run the benefits of the tools—more accurate pathogen identification at the species and population levels—will far outweigh any such complications.

Figure 3. Evidence that various species of sapstain fungi have spread outside their native ranges together with associated insects, such as bark beetles, and now cause considerable losses to softwood industries.

Conflicts of interest

Although the establishment of exotic tree plantations can confer many economic and ecological benefits, these trees can also have negative effects on environments. Many species of exotic trees used for plantation development have the capacity to become serious weeds that damage sensitive native ecosystems. For example, *Pinus radiata, P. contorta*, and *P. pinaster*, which were introduced as plantation trees,are considered to be serious invaders in various parts of the world (Kay 1994, Richardson and Higgins 1998). Their invasiveness can be reduced through the introduction of seed-invading pests and pathogens (Kay 1994, Brockerhoff and Kay 1998), yet this approach presents a conflict of interests between the forestry industry and environmentalists. Resolving such conflicts will be difficult, given that little information is available about how to evaluate risks associated with the introduction of biological control agents. Increased knowledge and multiparty commitment to sustainability of plantations,as well as the environment, will be demanded in the future.

Biological control of weeds in general has many positive aspects, but it can also have serious negative consequences. These problems usually emerge because of incomplete knowledge of the biology of target species, of the biological control agent, and of the environment in which control is desired.

A recent study on biological control of the *Sirex* wood wasp in the Southern Hemisphere highlights the complicated nature of this form of control (Slippers et al.2001). Populations of *S.noctilio* were significantly reduced with the use of the parasitic nematode *Deladenus siricidicola* (Taylor 1978, Neumann et al.1987, Haugen 1990, Bedding 1995). In addition to being a parasite of *Sirex* larvae, this nematode feeds on the *Amylostereum areolatum* fungal symbiont of the wasp during a mycetophagous part of its life cycle (Bedding and Akhurst 1974, Bedding 1995). Researchers recently reported, however, that the introduction of *D. siricidicola* to South Africa and to countries in South America led to the accidental introduction of a genotype of *A. areolatum* that is different from the one carried by the wasp (Slippers et al. 2001). This new genotype of the fungus was apparently in-

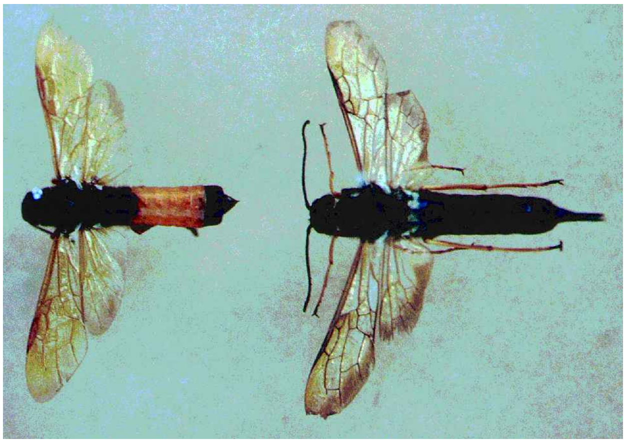

Figure 4. Male (left) and female (right) **Sirex noctilio** *woodwasps which, together with their symbiotic fungus* **Amylostereum areolatum,** *have been introduced into various countries in the Southern Hemisphere on wood products.*

troduced into Australia with the nematode during the development of the biological control program for *Sirex*, and it was not recognized that it differed from the fungus genotype introduced with the insect. The significance of this oversight is difficult to assess because the fungal symbiont of *S. noctilio* is not a primary pathogen. However, it may be linked to poor establishment of the nematode in South Africa and to other negative consequences that cannot yet be predicted (Slippers et al. 2001).

Future threats to exotic plantations

Exotic plantation forestry has benefited from high productivity, which is linked primarily to the absence of pests and pathogens in native ranges (Bright 1998). Although many pathogens have gradually appeared in these plantations, losses have been small relative to what they might have been. New diseases, caused by exotic and apparently native pathogens, continue to appear. All indications are that they will continue to do so. For example, three of the four most important pathogens of *Eucalyptus* in South Africa were unknown or very rare only a decade ago (Wingfield et al. 1989, Smith et al. 1994, Wingfield et al. 1997).

Compared with the number of pathogens found with forest tree species in their native ranges, relatively few pathogens have reached their host trees in their exotic situations. Of course, some pathogens might not be suited to areas where trees have been planted as exotics. Tree selection, and particularly hybridization between species, will also have an impact on the susceptibility of trees to some pathogens. Nonetheless, it is reasonable to expect that new pathogens will continue to appear over time and that profitability of plantations will be significantly affected.

In addition to introduced pathogens in the Southern Hemisphere, various native pathogens infecting exotic tree species have emerged over the last century. An important example is Eucalyptus rust, caused by *Puccinia psidii*, also known as guava rust fungus (Knipscheer and Crous 1990, Coutinho et al. 1998). This pathogen is native to Central and South America, where it is found on a wide range of native Myrtaceae, and it has recently also infected exotic *Eucalyptus* species in South America (Dianese et al. 1984, Coutinho et al. 1998). *Puccinia psidii* now threatens exotic eucalypt plantings elsewhere in the world. Perhaps of greater concern is the threat to native Myrtaceae in Australia, which represents a center of diversity for this important plant family (Coutinho et al. 1998).

Native pathogens affecting exotic trees and exotic pathogens introduced to new areas often have no apparent impact initially (Bright 1998). Such low levels of disease could reflect either low levels of susceptibility in planting stock or an environment that is unfavorable to pathogens' establishment. Another explanation, however, is that initial low levels of disease might reflect an establishment or incubation period for the pathogen during which it is subject to natural selection, followed by multiplication of virulent genotypes. As Bright (1998, p. 26) commented, "An exotic may spend decades as an innocuous good citizen in its new home before some subtle adaptation or shift in the ecological dynamic triggers an explosive invasion." Bright suggested also that exotic weeds in the United States may not be discovered until about 30 years after their introduction or after they have spread about 4000 hectares. The threat of new and exotic pathogens is therefore likely to be underestimated, which could create a false sense of security among foresters.

Conclusions

All available assessments show that the movement of plant material and their associated pathogens is a trend that shows no signs of abating. Rather, the introduction of new pathogens and pests appears to be increasing despite efforts to improve quarantine guidelines. Clearly, the increased movement of people and products throughout the world is the major factor influencing this trend (Bright 1998).

The worldwide trend in forestry has been to establish plantations of rapidly growing trees with desirable properties. Such plantations have the advantage of reducing the highly undesirable practice of logging native and old-growth forests that still too often supply timber and pulp mills. To satisfy the need for wood, many millions of hectares of plantation trees have been established, particularly in the tropics and in the Southern Hemisphere, largely through the introduction of exotic species and genotypes. The need for timber has also significantly increased the movement of logs and other wood products between countries and continents.

Although the justification for establishing plantations of exotic tree species has generally been based on positive principles, there have been significant negative consequences—namely, the introductions of pests, pathogens, and weed plants into new areas. The use of molecular tools

Figure 5. Sequence data suggesting that **Ceratocystis fimbriata,** *a serious wilt pathogen of* **Eucalyptus** *spp. and* **Acacia mearnsii,** *has been introduced into South Africa and Congo from South America.*

has provided new insights into the movement of such pests and diseases and the influence that this movement has on local populations of these organisms. For example, well-known diseases thought to be associated with a single pathogen introduction now appear to be caused by large numbers of genotypes. This high diversity in introduced pathogen populations illustrates the inefficiency of quarantine efforts. Moreover, there is evidence of increasing numbers of pathogens of native plants that have become adapted to related plantation tree species. These "new" pathogens now threaten plantation tree species where these trees are native. In addition, well-intentioned efforts to establish biological control of insect pests of trees have led to the accidental introduction of new pathogen genotypes. Finally, efforts to implement effective biological control of plantation trees that have also become weeds are giving rise to conflicts of interest between forestry and environmental organizations. The risks that are associated with the introduction of pests and pathogens of these plants are virtually impossible to assess.

The need to promote greater understanding of the impact of introduced pests and pathogens of plantation trees is urgent. Efforts to achieve that understanding should address not only the losses that might accrue to forest industries but also the fact that plantation forestry is associated with the evolution of new pathogens and an increased movement of forest fungi between continents.

References cited

Baxter AP, Rong IH, Schutte AL. 1995. *Amylostereum areolatum* (Aphyllophorales:Stereaceae) in South Africa. South African Journal of Botany 61:352-354.

Bedding RA. 1995. Biological control of *Sirex noctilio* using the nematode *Deladenus siricidicola.* Pages 11-20 in Bedding RA, Akhurst RJ, Kaya H, eds. Nematodes and Biological Control of Insect Pests Melbourne, Australia:CSIRO.

Bedding RA, Akhurst RJ. 1974. Use of *Deladenus siricidicola* in the biological control of *Sirex noctilio* in Australia. Journal of the Australian Entomological Society 13: 129–135.

Booth C, Gibson IAS. 1972. *Rhizina undulata.* CMI Descriptions of Pathogenic Fungi and Bacteria. Surrey (UK): Commonwealth Mycological Institute, Kew. Report no. 324.

Bright C. 1998. Life Out of Bounds. Bioinvasion in a Borderless World. New York: W. W. Norton.

Brockerhoff EG, Kay M. 1998. Prospects and risks of biological control of wilding *Pinus contorta* in New Zealand. Proceedings of the 51st New Zealand Plant Protection Conference; 11–13 August 1998; Hamilton, New Zealand.

Brown BN, Bevege DI, Stevens RE. 1981. Site stress and Diplodia induced dieback and death of hail damaged slash pine. Paper presented at the XVII IUFRO Congress; September 1981; Japan. Joint Meeting P2.01/P2.03.

Campbell FT. 2001. The science of risk assessment for phytosanitary regulation and the impact of changing trade regulations. BioScience 51: 148–153.

Chipompha NWS. 1987. *Phaeoseptoria eucalypti*: A new pathogen of *Eucalyptus* in Malawi. South African Forestry Journal 142: 10–12.

Chou CKS. 1991. Perspectives of disease threat in large-scale *Pinus radiata* monoculture—the New Zealand experience. European Journal of Forest Pathology 21: 71–81.

Conradie E, Swart WJ, Wingfield MJ. 1990. *Cryphonectria* canker of *Eucalyptus*, an important disease in plantation forestry in South Africa. South African Forestry Journal 152: 43–49.

Coutinho TA, Wingfield MJ, Alfenas AC, Crous PW. 1998. Eucalyptus rust: A disease with the potential for serious international implications. Plant Disease 82: 819–825.

Crous PW. 1998. *Mycosphaerella* spp. and their anamorphs associated with leafspot diseases of *Eucalyptus*. Mycological Memoir no. 21. St. Paul (MN): APS Press.

Crous PW, Wingfield MJ. 1996. Species of *Mycosphaerella* and their anamorphs associated with leaf blotch disease of *Eucalyptus* in South Africa. Mycologia 88:441–458.

Crous PW, Knox-Davies PS, Wingfield MJ. 1989. A summary of fungal leaf pathogens of *Eucalyptus* and the diseases they cause in South Africa. South African Forestry Journal 149: 9–16.

Crous PW, Ferreira FA, Sutton BC. 1997. A comparison of the fungal genera *Phaeophleospora* and *Kirramyces* (Coelomycetes). South African Journal of Botany 63: 111–115.

De Wet J, Wingfield MJ, Coutinho TA, Wingfield BD. 2000. Characterization of *Sphaeropsis sapinea* isolates from South Africa, Mexico, and Indonesia. Plant Disease 84: 151–156.

Dianese JC, Moraes TS, DeA, Silva AR. 1984. Response of *Eucalyptus* species to field infection by *Puccinia psidii.* Plant Disease 68: 314–316.

Doidge EM, Bottomley AM, van der Plank JE, Pauer GD. 1953. A revised list of plant diseases in South Africa. Union of South Africa: Department of Agriculture. Science Bulletin no. 346.

Edwards DW, Walker J. 1978. Dothistroma needle blight in Australia. Australian Forest Research 8: 125–137.

Florence EJM, Sharma JK, Mohanan C. 1986. A stem canker disease of *Eucalyptus* caused by *Cryphonectria cubensis* in Kerala. Kerala Forest Research Institute Scientific Paper 66: 384–387.

Gaut IPC. 1970. Studies of siricids and their fungal symbionts. PhD thesis. University of Adelaide, Australia.

Germishuizen PJ. 1984. *Rhizina undulata*—A pine seedling pathogen in Southern Africa. Proceedings of the IUFRO Symposium on site and productivity of fast growing plantations; 30 April–11 May; Pretoria and Pietermaritzburg, South Africa.

Gibson IAS, Christensen PS, Munga RM. 1964. First observations in Kenya of a foliage disease of pines caused by *Dothistroma pini* Hulbary. Commonwealth Forestry Review 43: 31–48.

Gibson IAS. 1979. Diseases of Forest Trees Widely Planted as Exotics in the Gropics and Southern Hemisphere. Kew, Surrey (UK): Commonwealth Mycological Institute.

Gilmour JW. 1965. The life cycle of the fungal symbiont of *Sirex noctilio*. New Zealand Journal of Forestry 10: 80–89.

———. 1967. Distribution, impact and control of *Dothistroma pini* in New Zealand. Rotorua, New Zealand: New Zealand Forest Service. Reprint no. 340.

Gourlay ES. 1951. Notes on insects associated with *Pinus radiata* in New Zealand. Bulletin of Entomological Research 42: 21–22.

Harrington TC, Wingfield MJ. 1998. The *Ceratocystis* species on conifers. Canadian Journal of Botany 76: 1446–1457.

Haugen DA. 1990. Control procedures for *Sirex noctilio* in the Green Triangle: Review from detection to severe outbreak (1977–1987). Australian Forestry 53: 24–32.

Heather WA. 1967. Susceptibility of juvenile leaves of *Eucalyptus bicostata* Maiden et al. to infection by *Phaeoseptoria eucalypti* (Hansf.) Walker. Australian Journal of Biological Sciences 20: 769-775.

Hodges CS, Alfenas AC, Ferreira FA. 1986. The conspecificity of *Cryphonectria cubensis* and *Endothia eugeniae*. Mycologia 78: 343–350.

Kay M. 1994. Biological control for invasive tree species. New Zealand Forestry 39: 35–37.

Knipscheer N, Crous PW 1990. First record of a rust disease on *Eucalyptus*. Forestry News 2/90: 22–23.

Madden JL. 1988. Sirex in Australasia. Pages 407–429 in Berryman AA, ed. Dynamics of Forest Insect Populations: Patterns, Causes, Implications. New York: Plenum Press.

McDonald BA, McDermott JM. 1993. Population genetics of plant pathogenic fungi. BioScience 43: 311–319.

Millar CS, Minter DW. 1980. *Naemacyclus minor* CMI Descriptions of Pathogenic Fungi and Bacteria no. 659. Kew, Surrey (UK): Commonwealth Mycological Institute.

Minko G, Marks GC. 1973. Drought index and the sensitivity of *Pinus radiata* to *Diplodia pinea* infection. Research Activity 72. Victoria, Australia: Forests Commission.

Neumann FG, Minko G. 1981. The *Sirex* wood wasp in Australian radiata pine plantations. Australian Forestry 44: 46–63.

Neumann FG, Morey JL, McKimm RJ. 1987. The *Sirex* wood wasp in Victoria. Victoria (Australia): Department of Conservation, Forest and Lands. Bulletin no. 29.

Nirenberg HI, O'Donnell K. 1998. New *Fusarium* species and combinations within the *Gibberella fujikuroi* species complex. Mycologia 90: 434–458.

O'Donnell K, Cigelnik E, Nirenberg HI. 1997. Molecular systematics and phylogeography of the *Gibberella fujikuroi* species complex. Mycologia 90: 465–493.

Park RF, Keane PJ. 1982. Leaf diseases of *Eucalyptus* associated with *Mycosphaerella* species. Transactions of the British Mycological Society 79: 101–115.

Richardson DM, Higgins SM. 1998. Pines as invaders in the Southern Hemisphere. In Richardson DM, ed. Ecology and Biogeography of *Pinus*. Cambridge (UK): Cambridge University Press.

Roux C. 1984. The morphology of *Dothistroma septospora* on *Pinus canariensis* from South Africa. South African Journal of Botany 3: 397–401.

Roux J, Harrington TC, Wingfield MJ. 1999. Genetic variation of *Ceratocystis albofundus* in South Africa. Proceedings of the IXth International Congress of Mycology; 16–20 August; Sydney, Australia.

Roux J, Wingfield MJ, Wingfield BD, Bouillett JP, Alfenas AC. 2000. A serious new disease of *Eucalyptus* caused by *Ceratocystis fimbriata* in Central Africa. European Journal of Forest Pathology 30: 175–184.

Schowalter TD, Filip GM. 1993. Beetle-pathogen interactions in conifer forests. San Diego (CA): Academic Press.

Slippers B, Wingfield MJ, Coutinho TA, Wingfield BD. 2001. Population structure and possible origin of *Amylostereum areolatum* in South Africa. Plant Pathology. Forthcoming.

Smith H, Kemp GHJ, Wingfield MJ. 1994. Canker and die-back of *Eucalyptus* in South Africa caused by *Botryosphaeria dothidea*. Plant Pathology 43: 1031–1034.

Smith H, Wingfield MJ, Crous PW, Coutinho TA. 1996. *Sphaeropsis sapinea* and *Botryosphaeria dothidea* endophytic in *Pinus* spp. and *Eucalyptus* spp. in South Africa. South African Journal of Botany 62: 86–88.

Smith H, Wingfield MJ, De Wet J, Coutinho TA. 2000. Genotypic diversity of *Sphaeropsis sapinea* from South Africa and Northern Sumatra. Plant Disease 84: 139–142.

Stanoz G, Smith DR, Guthmiller MA, Stanoz JC. 1997. Persistence of *Sphaeropsis sapinea* in asymptomatic stems of red pine nursery seedlings. Mycologia 89: 525–530.

Stone C, Simpson JA. 1987. Influence of *Ips grandicollis* on the incidence and spread of bluestain fungi in *Pinus elliottii* billets in northeastern New South Wales. Australian Forestry 50: 86–94.

Swart WJ, Wingfield MJ. 1991. Biology and control of *Sphaeropsis sapinea* in South Africa. Plant Disease 75: 761–766.

Talbot PHB. 1977. The *Sirex-Amylostereum-Pinus* association. Annual Review of Phytopathology 15: 41–54.

Taylor KL. 1978. Evaluation of the insect parasitoids of *Sirex noctilio* (Hymenoptera: Siricidae) in Tasmania. Oecologia 32: 1–10.

Tribe G. 1995. The wood wasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), a pest of *Pinus* species, now established in South Africa. African Entomology 3: 215–217.

Van der Byl PA. 1933. Annual Report of the Stellenbosch College of Agriculture: Farming in South Africa 8: 516.

Wall E, Keane PJ. 1984. Leaf spot of *Eucalyptus* caused by *Aulographina eucalypti*. Transactions of the British Mycological Society 82: 257–273.

Wingfield MJ, Knox-Davies PS. 1980. Observations of diseases in pine and *Eucalyptus* plantations in South Africa. Phytophylactica 12: 57–63.

Wingfield MJ, Marasas WFO. 1980. *Ceratocystis ips* associated with *Orthotomicus erosus* (Coleoptera: Scolytidae) on *Pinus* spp. in the Cape Province of South Africa. Phytophylactica 12: 65–69.

———. 1983. Some *Verticicladiella* species including *V. truncata* sp. nov., associated with root diseases of pine in New Zealand and South Africa. Transactions of the British Mycological Society 80: 231–236.

Wingfield MJ, Capretti P, McKenzie M. 1988. *Leptographium* spp. as root pathogens of conifers: An international perspective. Pages 113–128 in Harrington TC, Cobb FW, eds. Leptographium Root Diseases on Conifers. St. Paul (MN): American Phytopathological Society Press.

Wingfield MJ, Swart WJ, Abear B. 1989. First record of Cryphonectria canker of *Eucalyptus* in South Africa. Phytophylactica 21: 311–313.

Wingfield MJ, Swart WJ, Kemp GHJ. 1991. Pathology considerations in clonal propogation of *Eucalyptus* with special reference to the South African situation. Pages 811–820 in Proceedings of the IUFRO International Symposium on Intensive Forestry: The role of *Eucalyptus*; 2–6 September; Durban, South Africa.

Wingfield MJ, Wingfield BD, Coutinho TA. 1995. Management of *Eucalyptus* diseases in subtropical areas of South Africa. Pages 171–172 in Proceedings of the IUFRO Conference on Silviculture and Improvement of Eucalypts; Salvador, Bahia, Brazil.

Wingfield MJ, Crous PW, Coutinho TA. 1997. A serious canker disease of Eucalyptus in South Africa caused by a new species of *Coniothyrium*. Mycopathologia 136: 139–145.

Witthuhn RC, Wingfield BD, Wingfield MJ, Wolfaardt M, Harrington TC. 1998. Monophyly of the conifer species in the *Ceratocystis coerulescens* complex based on DNA sequence data. Mycologia 90: 96–101.

Zwolinski JB, Swart MJ, Wingfield MJ. 1990. Economic impact of post-hail outbreak of die-back induced by *Sphaeropsis sapinea*. European Journal of Forest Pathology 20: 405–411.