Pathogens in exotic plantation forestry

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SUMMARY

Exotic plantation trees in the tropics and Southern Hemisphere are highly productive. This can be partly ascribed to the fact that trees have been separated from their natural enemies. Nevertheless, diseases have imparted severe losses to exotic trees in plantations. Pathogens responsible for these diseases include those that are native to the areas where the plantations have been established, as well as introduced pathogens. Substantial success has been achieved in dealing with diseases by planting alternative species and by breeding and selecting disease-tolerant plants. In the future, many new pathogens will be introduced into areas where exotic species are grown in plantations. Some of these pathogens will result is severe losses. However, techniques to avoid the negative impact of diseases are rapidly becoming more sophisticated. This increased capacity to deal with diseases should secure the future of plantation forestry in the tropics and Southern Hemisphere.

Keywords: disease avoidance, clonal hybrids, exotic pathogens, tree improvement.

INTRODUCTION

In order to accommodate the need for fibre and solid wood products, there has been a world-wide trend towards the establishment of plantations of exotic tree species. Thus, many millions of hectares of plantations of exotic species have been established, particularly in the tropics and Southern Hemisphere. In many situations, these plantations play an important role in the provision of employment, concomitant with wealth creation and the production of export capital for resource-poor countries. Perhaps more importantly, they help to alleviate the exploitation and destruction of native, old growth, forests.

Many different genera and species of trees have been selected for plantation development in the tropics and Southern Hemisphere. The most widely planted are species of Acacia, Eucalyptus, Populus and Pinus. In many situations, these plantations have been remarkably productive and major industries producing solid wood, fuelwood, as well as pulp products have arisen in association with them. One of the important reasons for the unusually high productivity and success of these plantations is the fact that the trees have been separated from the pests and pathogens which reduce their productivity where they are native (Bright 1998). These trees have also been substantially improved through extensive breeding programmes. In recent years, there has also been substantial focus on vegetative propagation of high yielding individuals of single species, but particularly of hybrids between species.

The aim of this paper is to briefly consider the role that pathogens have played in the development of plantations of exotic tree species, particularly in the tropics and Southern Hemisphere. It should not be seen as a review but rather as a commentary on a topic that has not been extensively treated in the recent past. The focus is on *Pinus* and *Eucalyptus*, which are the most extensively planted trees in the tropics and Southern Hemisphere. There are many examples of diseases that have caused serious losses to this category of plantation, and some excellent general reviews are available (Ferreira 1989, Gibson 1974,1979, Ivory 1987). It is beyond the scope of this commentary to treat specific diseases in detail and I will rather concentrate on small number of examples that illustrate trends. Hopefully, these will also illustrate how we might might learn from past experience.

ORIGIN OF PATHOGENS

Two distinct categories of pathogen cause disease on exotic plantation trees. These include those that are native to the country where the exotic tree species are being established, and those that are introduced from elsewhere in the world. Introduced pathogens generally originate from areas where the host trees are native. However, interesting trends are emerging where native pathogens, not known in the areas of origin of the trees, have become adapted to the exotics. These are now available for introduction into new areas. They threaten not only exotic plantation forestry, but also these species in their native environments.

Knowledge pertaining to the origin of causal agents of disease has traditionally been based on whether these

pathogens are known on trees in their areas of origin. The accuracy of this knowledge is, therefore, generally based on the extent of information available on the diseases of trees where they are native. In native situations, pathogens would be subjected to strong ecological pressures. Thus, even though the pathogens are present, they would be difficult to detect, and in many cases their presence would not be known. In the case of some diseases, it is not clear whether the causal agents are native or introduced. Here the application of powerful molecular techniques has in recent years made it possible to analyse pathogen population diversity (Leslie 1993, McDonald 1997). Knowledge emerging from such studies can provide good evidence as to whether a pathogen is native or introduced. It is also useful in developing management strategies aimed at reducing the impact of pathogens.

The following two sections focus on a small number of diseases of exotic plantation *Eucalyptus* and *Pinus* grown in the tropics and Southern Hemisphere. Their selection is based on the fact that they are amongst the most important pathogens in these situations and that they have been relatively fully treated in the scientific literature. Their designation as native or exotic is based on good evidence to this effect, or in some cases, such as in Cylindrocladium blight of *Eucalyptus*, a degree of supposition. Brief comments on management strategies to reduce the impact of these pathogens are provided.

Native pathogens

Exotic plantations of *Eucalyptus* spp. and *Pinus* spp. have been severely damaged by a wide number of pathogens that are thought to be native. These pathogens include those that cause root, stem and foliage diseases. In general, they have appeared in the early stages of plantation development and before the onset of diseases caused by exotic pathogens (for examples see Gibson 1974, 1979).

One of the best-studied examples of disease in the tropics and Southern Hemisphere is Armillaria root rot caused by various species of Armillaria (Hood et al. 1991). Armillaria spp. occur on the root systems of native woody plants and become a problem where native trees are clear-felled to provide land for plantation development. The pathogen then moves from stumps of felled trees and new infection centres arise in stands of the exotic species. The impact of Armillaria root rot has been significantly reduced by stump removal, but more importantly by the modern trend not to clear-fell native stands of trees (Shaw and Kile 1991).

Leaf diseases caused by native pathogens have also had a severe impact on plantations of exotic species. One of the best examples is that of *Cylindrocladium* leaf blight on *Eucalyptus*. This disease is caused by various *Cylindrocladium* spp. and these species tend to be different, in different countries. In some cases, such as that of *Cylindrocladium multiseptatum* (Crous *et al.* 1998), species have been found in only one very limited area. This finding also supports the view that the disease is probably caused

by a native pathogen. Although damage due to *Cylindrocladium* leaf blight has been very severe in some countries, excellent disease avoidance has been achieved through the deployment of disease tolerant clones and hybrids (Crous, Phillips and Wingfield 1991, Crous and Wingfield 1994).

One of the most interesting examples of a native pathogen causing disease on an exotic plantation tree is that of Eucalyptus rust caused by Puccinia psidii (Coutinho et al. 1998). In this case the pathogen has its origin in South and Central America where it occurs on native Myrtaceae. The pathogen has moved from these plants to exotic Eucalyptus and has caused serious disease in some cases. Good progress has been made in avoiding this disease through the deployment of disease tolerant hybrids and clones. What is of great concern, however, is the fact that this disease might be introduced into other parts of the world. A particularly threatened area would be Australia, which has a rich diversity of Myrtaceae and where native plant populations could be severely damaged. Various threat abatement strategies are underway to reduce this risk including an international effort launched by the CSIRO in Australia which involves partners in Brazil and South Africa.

Exotic pathogens

Many pathogens of exotic *Pinus* and *Eucalyptus* species have followed the introduction of these trees into new areas. Some of them appeared very early in the process of plantation development. It is assumed that these were introduced with planting stock, which in most cases was seed. Thus, pathogens such as *Mycosphaerella* spp. that infect *Eucalyptus* and *Sphaeropsis sapinea* on *Pinus* were amongst the first pathogens reported on these trees grown as exotics. In many countries, there has also been a gradual appearance of new and obviously exotic pathogens. Despite thorough quarantine programmes in most countries, this is a trend that seems likely to continue.

Perhaps the best known introduced pathogen of exotic pines is Sphaeropsis sapinea that causes shoot blight and sometimes death of trees (Gibson 1979, Swart and Wingfield 1991). The fungus is known on pines wherever they are native and has been recorded from most countries where these trees are grown as exotics (Gibson 1979, Gilmour 1966, Marks and Minko 1969, Peterson and Wysong 1968). Sphaeropsis sapinea owes its notoriety to the South African situation where a combination of susceptible species (P. radiata and P. patula) and hail damage results in extensive tree death every year (Swart and Wingfield 1991). The pathogen is known to exist as an endophyte in healthy trees (Smith et al. 1996, Stanosz et al. 1997) and some combination of stress to trees after hail and its presence in cones appears to lead to rapid tree death. Disease avoidance is achieved through planting tolerant species as well as through promoting silvicultural practices that reduce stress (Brookhauser and Peterson 1971, Chou 1977, Swart and Wingfield 1991). Substantial progress is also being made in the development of pine hybrids that are able to withstand hail damage and that are not susceptible to *S. sapinea* infection (Wingfield unpublished data).

Dothistroma needle blight, caused by *Dothistroma* septospora, is by far the most important pathogen of exotic pines (Gibson 1972). This is due to the damage that it causes to *P. radiata* and the fact that this tree is one of the most widely planted exotic species (Gibson 1972, Harrington and Wingfield 1998). Considerable progress has been made in reducing the impact of Dothistroma needle blight. This has been achieved through outstanding efforts in breeding for disease tolerance and the judicious use of fungicide sprays in areas where infections are severe (Carson and Carson 1989, Ivory and Paterson 1969, Gibson 1972, 1979).

There are many Eucalyptus pathogens that are believed to be introduced into areas where these trees are grown as exotics (Ferreira 1989. Gibson 1979). Perhaps the best known of these is Cryphonectria canker caused by Cryphonectria cubensis (Conradie, Swart and Wingfield 1990). This pathogen has seriously damaged plantations. particularly of E. grandis in South and Central America and Africa (Alfenas, Jeng and Hubbes 1983, Wingfield, Swart and Abear 1989). There is good evidence to suggest that the pathogen is native to Indonesia (Hodges, Alfenas and Ferreira 1986, Myburgh, Wingfield and Wingfield 1999). However, recent studies on the genetic diversity of populations of the pathogen in South America (van Zyl et al. 1998) would support the view that it has been present in that part of the world for an extended period. Considerable success has been achieved at reducing the impact of Cryphonectria canker through selection of disease tolerant clones and hybrids (Alfenas, Jeng and Hubbes 1983, Conradie, Swart and Wingfield 1992). Furthermore, ds RNA infections associated with hypovirulence have recently been found in the pathogen and there is promise that biological control of the pathogen will be possible in some situations (van Zyl et al. 1999).

FUTURE PROPECTS FOR PATHOGENS

Exotic plantation forestry is associated with tremendous success in the tropics and southern hemisphere. In my view, the level of success is closely linked to the fact that these trees have been separated from the majority of their natural enemies. I do not wish to imply that diseases have not been important in these situations. This is certainly not the case and some pathogens have caused very serious damage to plantations (Gibson 1979, Harrington and Wingfield 1998. Ivory 1987). Indeed, in many areas, diseases and insect pests have had a very marked influence on the choice of species or clones that are planted (Wingfield 1990). What is evident, however, is that the majority of pathogens that occur on pines, eucalypts and wattles in their areas of origin have not, as yet reached countries where they are grown as exotics.

In time, many new pathogens must be expected to move from their areas of origin to trees that are grown as exotics elsewhere in the world. Although considerable efforts are made to control the movement of pests and pathogens through quarantine, the increasing movement of people and products between countries will render these efforts increasingly difficult. Ultimately, many new pathogens will emerge in new environments. The recent new invasions of pests and pathogens in countries with outstanding quarantine programmes emphasise this view (Bright 1998). Clearly strategies to minimise risks due to new diseases will need to be devised and supported.

The outstanding success achieved in dealing with debilitating diseases in the past raises hope for overcoming similar problems in the future. One of the best examples of successfully overcoming the impact of a disease in exotic plantation forestry in the southern hemisphere is that of Dothistroma needle blight. The disease was first noted in Tanzania in the late 1950's and developed rapidly, making successful P. radiata establishment impossible (Gibson 1972). The disease then appeared and began to threaten P. radiata plantings in New Zealand in the early 1960's, and it later spread to Australia. South America and Asia (Gibson 1979). A large number of outstanding studies of the biology of D. septospora were conducted in the two decades subsequent to its first appearance in Africa (see references in Gibson 1972). These have made it possible to overcome the most serious impact of this disease in countries such as Australia, New Zealand and Chile where P. radiata is extensively grown. Thus, practical chemical control measures, closely linked to the biology of the pathogen (Gadgil 1976, Gibson 1974) were successfully implemented and continue to be used today. Outstanding progress has also been made in breeding for disease tolerance (Carson and Carson 1989, Ivory and Paterson 1969) and today, Dothistroma tolerant planting stock is generally deployed. Dothistroma needle blight remains an important disease. particularly in Australia, New Zealand and Chile. However. losses can be managed and this achievement represents an impressive success in exotic plantation forestry.

DISCUSSION

Forest managers have many tools at their disposal to minimise risks due to new and emergent diseases. This resource is also increasing rapidly with the emergence of new technologies. These include methods that make it possible to propagate hybrids between species using vegetative propagation, molecular marker aided selection of desirable planting stock as well as opportunities linked to the production of transgenic trees.

One of the simplest means to reduce the impact of disease is to plant a number of different species of trees. Thus, when a disease does appear, timber would remain available during the time when alternative planting stock is being sought. While this approach is logical and relatively simple, it is also associated with disadvantages. Modern tree improvement is costly. Thus, where research and development funds might be focused on a single species, spreading this resource across a wider base clearly restricts the extent of programmes to improve trees of interest.

Exotic plantation forestry has changed dramatically during the course of the last century. Techniques for tree improvement including those linked to selection and breeding have been significantly refined and are increasingly well understood. Thus, outstanding breeding programmes have been established in many countries that have significant exotic plantation resources (Zobel and Talbert 1984). Planting stock is of an increasingly higher quality and many disease problems have already been overcome through effective selection and breeding.

Perhaps one of the most exciting developments in contemporary plantation forestry has been the development of methods for vegetative propagation of trees (Ahuja and Libby 1993). Currently, methods for vegetative propagation are available for most genera and a wide range of species. Admittedly, some species are much easier to propagate than are others. Yet methods are continuously being improved and this trend is likely to continue in the future. Forestry companies are now presented with the advantages of being able to select and deploy clones with outstanding properties which often include disease tolerance.

The relatively recent emergence of clonal hybrid stock now available in some species of pine and a large number of *Eucalyptus* species is an exciting development. Fast growing hybrids with a wide array of desirable traits can now be selected and multiplied through vegetative propagation. Certainly, this approach has already led to the development of *Eucalyptus* planting stock that is tolerant to important diseases such as Cryphonectria canker (Alfenas, Jeng and Hubbes 1983, Conradie, Swart and Wingfield 1992, van Zyl and Wingfield 1999) and Coniothyrium canker caused by *Coniothyrium zuluense* (Wingfield, Crous and Coutinho 1997). It is reasonable to expect that many other diseases, including those that are likely to appear in new environments in the future, will be resolved through the selection of clonal hybrids that display high degrees of tolerance to them.

Because of relatively long rotations, tree diseases have traditionally been considered difficult or even impossible to resolve through traditional breeding. This situation has changed substantially in recent years. Rotation lengths for exotic plantation species have been significantly reduced through the selection of fast growing clones and hybrids. Thus, five to seven year rotations in *Eucalyptus* grown for pulp are common today and, although not as short, pine rotations for both pulp and solid wood production have been significantly reduced. A consequence is that disease problems can be more easily and rapidly avoided than was possible in the past.

Exotic plantation forestry is rapidly being influenced through the application of molecular genetics (Robinson 1999). Thus, accelerated breeding linked to genetic marker aided selection is already being used by various groups. Traits of interest include diseases and it is reasonable to expect that these developments will lead to significant improvements in disease avoidance. It must be anticipated that significant linkage maps will become available for most plantation species in the future. These will have a very positive impact on programmes linked to tree improvement

and selection of disease tolerant planting stock.

The field of gene discovery is advancing rapidly and various genes linked to disease tolerance are already known. Transgenic eucalypts and poplars containing new and desirable genes have been planted in trials. Although a number of hurdles have yet to be crossed, there seems little doubt that such trees will reach the commercial markets in coming years. These will include those transformed with a variety of desirable genes, including disease tolerance.

The biology and genetics of exotic forest tree pathogens is becoming increasingly well understood. Here, molecular biology techniques have significantly influenced our ability to unravel questions pertaining to the genetic diversity of pathogens. Such knowledge makes it possible to determine the origin of pathogens. This in turn is useful when searching for biological control agents or where it is necessary to refine quarantine measures to reduce the introductions of new pathogens.

Knowledge pertaining to the genetic diversity of pathogen populations should be an essential component of programmes aimed at breeding for disease tolerance. Where pathogen populations are genetically diverse, durability of disease tolerance in planting stock can be expected to be limited. In contrast, introduced pathogens represented by genetically uniform populations should be more easily managed through breeding and selection.

Many successes have been recorded in the field of biological control of insect pests found in exotic forest plantations. Successes linked to biological control of fungal pathogens included outstanding work on the biological control of the root pathogen Heterobasidion annosum in European plantations (Harrington and Wingfield 1998. Rishbeth 1951). In the tropics and Southern Hemisphere. biological control successes are limited to nursery situations. This is likely to change in the future. For example, as viral infections of fungal pathogens linked to hypovirulence (Nuss 1992) are better understood, it should become possible to produce isolates of fungal pathogens infected with viruses or partial viral genomes that confer hypovirulence, and that are also able to spread effectively through pathogen populations. Such a development would significantly enhance our ability to reduce the impact of pathogens.

CONCLUSIONS

There are many examples of hugely successful forestry operations based on exotic plantation development. The fact that these successes have been built on the foundations of many decades of research, including intensive breeding and selection, is commonly overlooked. New forestry ventures, based on the perceived ease of establishing plantations of exotic trees, have in many cases led to disappointing outcomes. Failures during the early phase of development of exotic plantations have commonly been linked to serious problems with pests and diseases. These include diseases caused by both native and exotic pathogens. The fact that there are few alternatives to the relatively slow process of

establishing species and provenance trials for the selection of desirable planting stock is often not considered. This work must be followed by breeding programmes and ultimately high-yielding, disease tolerant trees including clones and hybrids can emerge.

Diseases have had a tremendous impact on plantations of exotic forest trees in every part of the tropics and Southern Hemisphere where such plantations have been established. In most cases, through many years of intensive breeding and study, these problems have been overcome, or significantly reduced. It is certainly true to say that, as yet, a relatively small number of pathogens of *Pinus* spp., *Eucalyptus* spp. and *Acacia* spp. have entered countries where these trees are grown as exotics. This is in comparison to the large numbers of pathogens known on these trees in their native ranges. Some of these pathogens will never find a conducive environment in which to develop in the exotic situations. However, there certainly will be some that will have a debilitating impact.

Opponents of exotic plantation forestry commonly argue for the establishment of plantations of native trees. From a pathology standpoint, this view is naïve and tends to overlook the complexities of pathogen biology. Where native species are established in plantations, pests and diseases often devastate them. These plantations are generally represented by planting stock that is, genetically, more uniform than that in native stands. Huge numbers of pests and pathogens are also present on the native relatives of these plantation trees and they usually cause very heavy losses in the plantation trees. The genetic diversity of pathogens is usually great in native stands and thus, the durability of disease tolerance in plantations of these trees is much more limited than in the exotic situation. Thus tremendous opportunities are gained from separating desirable plantation species from their natural enemies.

In many parts of the world, plantation development is seen as an alternative to logging of native forest. Plantations are also desirable due to the role that they can play as carbon sinks. From a pathology standpoint, the most productive and healthy plantations are likely to be those of exotic species. While capitalising on the opportunities to grow relatively disease free trees, responsible forestry groups should carefully consider negative aspects of selected species, such as their ability to escape from plantations as weeds.

The ability to avoid diseases through planting exotic species will be greater in the early years of plantation development. They will diminish as pathogens are gradually introduced into these exotic situations. This fact might sound an alarm for some prospective plantation developers. What is perhaps more important to recognise is the fact that tremendous opportunities exist whereby disease problems can be overcome. Deployment of a reasonably broad diversity of species and planting stock should ensure that crippling losses do not occur. Furthermore, the development of local land races of desirable species, hybridisation and cloning and the development of transgenic plantation trees, will all help to overcome problems such as those associated with disease.

Exotic plantation forestry has a great deal to offer human kind. Contemporary plantation development based on exotic species is reliant on intensive research and development. Successful programmes are technologically sophisticated and demand significant financial inputs to overcome problems such as damage due to disease. Yet with the necessary inputs, these problems can be overcome. There is thus every reason to feel positive about exotic plantation forestry and to promote it strongly.

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REFERENCES

- Ahuja, M.R. and Libby, W.J. (eds.) 1993 Clonal forestry, I. Genetics and biochemistry, II. Conservation and application. Springer-Verlag. Berlin.
- ALFENAS, A.C., JENG, R. and HUBBES, M. 1983 Virulence of Cryphonectria cubensis on Eucalyptus species differing in resistance. European Journal of Forest Pathology 13: 179-205.
- Bright, C. 1998 Life out of bounds. Bioinvasion in a borderless world. W.W. Norton, New York, 287 pp.
- BROOKBAUSER, L.W. and PETERSON, G.W. 1971 Infection of Austrian. Scots and Ponderosa pines by *Diplodia pinea*. *Phytopathology* **61**: 409-414.
- CARSON, S. and CARSON, M.J. 1989 Breeding for resistance in forest trees – a quantitative genetic approach. Annual Review of Phytopathology 27: 373-395.
- CHOU, C.K.S. 1977 Effect of tree age on *Diploida pinea* infection of *Pinus radiata*, *Plant Disease Reporter* **61**: 101-103.
- CONRADIE, E., SWART, W.J. and WINGFIELD, M.J. 1990 Cryphonectria canker of *Eucalyptus*, an important disease in plantation forestry in South Africa. *South African Forestry Journal* 152: 43-49.
- CONRADIE, E., SWART, W.J. and WINGFIELD, M.J. 1992 Susceptibility of Eucalyptus grandis to Cryphonectria cubensis. European Journal of Forest Pathology 22: 312-315.
- COUTINHO, T.A., WINGFIELD, M.J., ALFENAS, A.C. and CROUS, P.W. 1998 Eucalyptus rust: a disease with a potential for serious international implications. *Plant Disease* 82: 819-825.
- CROUS, P.W. and WINGFIELD, M.J. 1994 A monograph of Cylindrocladium including anamorphs of Calonectria. Mycotaxon LI: 341-435.
- CROUS, P.W., WINGFIELD, M.J., MOHAMMED, C. and YUAN, Z.K. 1998 New foliar pathogens of *Eucalyptus* from Australia and Indonesia. *Mycological Research*: 527.
- CROUS, P.W., PHILLIPS, A.J. and WINGFIELD, M.J. 1991 The genera Cylindrocladium and Cylindrocladiella in South Africa, with special reference to forestry nurseries. South African Forestry Journal 157: 69-85.

- FERREIRA, F.A. 1989 Patalogia Florestal. Pricipais Doencas Florestais no Brasil Vicosa Sociedade de Investigacoes Florestais. 570 pp.
- GADGIL, P. 1976 Effect of environment on infection of *Pinus radiata* by *Dothistroma pini*. Proceedings of Working Party S6.02.04, XVI IUFRO World Congress, Oslo.
- Gibson, I.A.S. 1972 Dothistroma needle blight of *Pinus radiata*. Annual Review of Phytopathology 10: 51-72.
- Gibson, I.A.S. 1974 Impact and control of Dothistroma blight of pines. European Journal of Forest Pathology 4: 89-100.
- GIBSON, I.A.S. 1979 Diseases of forest trees widely grown as Exotics in the Tropics and Southern Hemisphere. Part II. The genus Pinus. Kew: Commonwealth Mycological Institute, and Oxford: Commonwealth Forestry Institute. University of Oxford.
- GILMOUR, J.W. 1966 The pathology of forest trees in New Zealand. The fungal, bacterial and algal pathogens. New Zealand Forest Service, Forest Research Institute Technical Paper Number 48.
- HARRINGTON, T.C. and WINGFIELD, M.J. 1998 Diseases and the ecology of indigenous and exotic pines. *In*: Richardson, D.M.
 (ed.) *Ecology and biogeography of* Pinus. Cambridge University Press, Cambridge, pp. 381-404.
- HODGES, C.S., ALFENAS, A.C. and FERREIRA, F.A. 1986 Conspecificity of Cryphonectria cubensis and Endothia eugeniae. Mycologia 78: 542-548.
- HOOD, I.A., REDFERN D.B. and KILE, G.A. 1991 Armillaria in planted hosts. In: Shaw III. C.G. and Kile, G.A. (eds.) Armillaria root disease. U.S.D.A. Forest Service. Agriculture Handbook No. 691. Washington D.C.
- IVORY, M.H. 1987 Diseases and disorders of pines in the tropics. Oxford Forestry Institute, Overseas Research Publication Number 31.
- IVORY, M.H., and PATERSON, D.N. 1969. Progress in breeding *Pinus radiata* resistant to Dothistroma needle blight in East Africa. Silvae Genetica 19: 38-42.
- LESLIE, J.F. 1993 Fungal vegetative compatibility. Annual Review of Phytopathology 31: 127-150.
- MARKS, G.C. and MINKO, G. 1969 The pathogenicity of Diplodia pinea to Pinus radiata D. Don. Australian Journal of Botany 17: 1-12.
- McDonald, B.A. 1997 The population genetics of fungi. Tools and techniques. *Phytopathology* 87: 448-453.
- Myburg, H., Wingfield, B.D. and Wingfield, M.J. 1999 Phylogeny of *Cryphonectria cubensis* and allied species inferred from DNA analysis. *Mycologia* 91: 243-250.
- Nuss, D.L. 1992. Biological control of chestnut blight. An example of virus-mediated attenuation of fungal pathogenesis. *Microbiological Reviews* 56: 561-576.
- PETERSON, G.W. and Wysong, O.S. 1968 Diplodia tip blight of pines in the central Great Plains; Damage and control. *Plant Disease Reporter* 52: 359-360.
- RISHBETH, J. 1951 Observations on the biology of *Fomes annosus*, with particular reference to East Anglian pine plantations. II. Sport production, stump infection, and saprophytic activity in stumps. *Annals of Botany* (London) 15: 1-22.
- ROBINSON, C. 1999. Making forest biotechnology a commercial reality. *Nature Biotechnology* 17: 27-30.
- Shaw, C.G. and Kile, G.A. (eds.) 1991 Armillaria root disease. United States Department of Agriculture, Forest Service Handbook No. 691. Washington D.C., 233 pp.
- SMITH, H., WINGFIELD, M.J., CROUS, P.W. and COUTINHO, T.A. 1996 Sphaeropsis sapinea and Botryosphaeria dothidea endophytic in Pinus spp and Eucalyptus spp. in South Africa. South African Journal of Botany 62: 86-88.

- STANOSZ, G., SMITH, D.R., GUTHMILLER, M.A. and STANOSZ, J.C. 1997. Persistence of *Sphaeropsis sapinea* on or in asymptomatic stems of red pine nursery seedlings. *Mycologia* 89: 525-530.
- SWART, W.J. and WINGFIELD, M. J. 1991. Biology and control of Sphaeropsis sapinea on Pinus species in South Africa. Plant Disease 75: 761-766.
- VAN ZYL, L.M. and WINGFIELD, M.J. 1999. Wound response of Eucalyptus clones after inoculation with Cryphonectria cubensis. European Journal of Forest Pathology 29: 161-167.
- VAN ZYL, L.M., WINGFIELD, M.J., ALFENAS, A.C. and CROUS, P.W. 1998 Population diversity amongst Brazilian isolates of Cryphonectria cubensis. Forest Ecology and Management 112: 41-47.
- Van Zyl, L.M., Wingfield, M.J., Alfenas, A.C. and Crous, P.W. 1999 Hypovirulence detected in Brazlian isolates of Cryphonectria cubensis. Plant Pathology 48: 267-272.
- WINGFIELD, M.J. 1990. Current status and future prospects of forest pathology in South Africa. South African Journal of Science 86: 60-62.
- WINGFIELD, M.J., CROUS, P.W. and COUTINIO, T.A., 1997 A serious canker disease of *Eucalyptus* in South Africa caused by a new species of *Coniothyrium*. *Mycopathologia* 136: 139-145.
- WINGFIELD, M.J., SWART, W.J. and ABEAR, B., 1989. First record of Cryphonectria cankerof *Eucalyptus* in South Africa. *Phytophylactica* 21: 311-313.
- ZOBEL, B. and Talbert, J. 1984 Applied forest tree improvement. John Wiley & Sons, New York, 505 pp.