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Established and new technologies reduce increasing pest and pathogen threats to Eucalypt plantations

Michael J. Wingfield^{a,*}, Jolanda Roux^{a,b}, Bernard Slippers^{a,c}, Brett P. Hurley^{a,d}, Jeff Garnas^{a,d}, Alexander A. Myburg^{a,c}, Brenda D. Wingfield^{a,c}

^a Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Private Bag X20, Pretoria 0028, South Africa

^b Department of Microbiology and Plant Pathology, University of Pretoria, Private Bag X20, Pretoria 0028, South Africa

^c Department of Genetics, University of Pretoria, Private Bag X20, Pretoria 0028, South Africa

^d Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Pretoria 0028, South Africa

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ABSTRACT

Plantation forestry based on Eucalyptus spp. has grown dramatically during the past 100 years, mainly in the tropics and southern hemisphere where these trees are non-native. Early plantations were affected by pests and pathogens, although damage was generally minimal. This is a situation that is changing dramatically with serious pest and pathogen problems now emerging regularly and often times causing very serious damage. Given the growing movement of people and products around the world, this is a trend that is certain to continue and the threat of diseases and insect damage is now seen as one of the most important constraints to the future sustainability of Eucalypt plantation forestry globally. While this is a very troubling situation, there are also reasons to be optimistic. Established technologies such as breeding and selection of disease and insect resistant species and hybrids; enhanced through vegetative propagation have already shown substantial promise to reduce damage. Likewise, biological control is being effectively used to reduce damage due to invasive alien insect pests. New technologies including DNAbased tools for identification, detection and monitoring of pest and pathogens are increasingly valuable. Similarly, the growing availability of genome sequences for Eucalypts and for their pests and pathogens will increasingly add to our capacity to reduce damage. While there are unknown dangers such as the impact of climate change on the damage caused by pests and pathogens, we believe that continual and realistic investment in technology will ensure long term sustainability of Eucalypt plantation forestry. Failure to invest wisely will result in the collapse of plantation enterprises and concomitant loss in investments.

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1. Introduction

Intensive plantation forestry using Eucalypt species (*Eucalyptus* and *Corymbia*) has grown rapidly during the course of the last 30 years, particularly in the tropics and Southern Hemisphere where it has been strongly linked to the production of pulp for paper and viscose. Currently, Eucalypt plantations cover approximately 20 million hectares with planted areas continuing to increase in some areas (Iglesias Trabado and Wilstermann, 2008).

During the early years of plantation development, non-native Eucalypt trees were typically relatively free of pest and disease problems. But with time, insect pests (Fig. 1) and pathogens (Fig. 2) have gradually appeared. These damaging agents are either native and have acquired the capacity to infect/infest Eucalypts or they have been accidentally introduced. In the latter case, they

* Corresponding author. *E-mail address:* Mike.Wingfield@fabi.up.ac.za (M.J. Wingfield). originate either from their areas of origin or from other areas where they have become established. The processes underlying the gradual appearance of insects and pathogens in Eucalypt plantations has been covered in various earlier reviews (Wingfield, 2003; Wingfield et al., 2008) and will not be repeated here.

A general trend in all areas where Eucalypts are being grown in plantations is that pest and pathogen problems are increasing (Wingfield et al., 2008). This is clearly of great concern to plantation growers that rely on these trees to sustain their businesses. The growing numbers of pest and disease problems clearly increases the cost of forestry and in some quarters, the question arises as to whether plantation forestry based on these trees could at some point fail to realise reasonable returns on investment. This is clearly a serious issue and it is one that deserves careful consideration.

Numerous Eucalypt disease and pest problems have been dealt with very effectively in the past. In some cases, these problems have also had a substantial impact on the manner in which these

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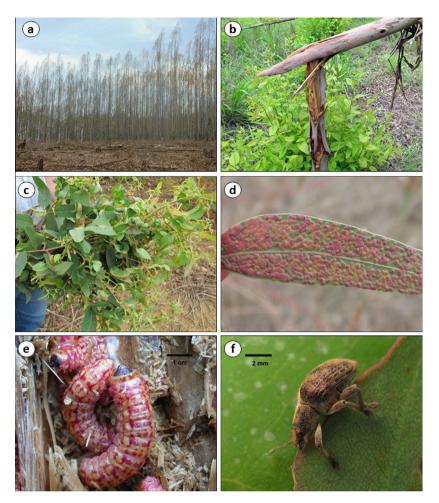


Fig. 1. Insect pests of Eucalypt plantations. (a) Early leaf senescence caused by infestation of *T. peregrinus*; (b) wind break due to tunneling of *Phorocantha* larvae; (c) galling caused by *L. invasa*; (d) leaf galled by *O. maskelli*; (e) larvae of *C. tristis* boring in wood; (f) adult *G. scutellatus* feeding on leaf.

trees are propagated. A classic example here is that concerning Cryphonectria canker (Fig. 2a) caused by various species of *Chrysoporthe* (Wingfield, 2003; Gryzenhout et al., 2006; Gryzenhout et al., 2009). Where this disease first appeared in Brazil in the 1970s (Hodges et al., 1976), it was recognised that some trees in progeny trials were resistant to infection. This prompted the development of vegetative propagation techniques to multiply the resistant individuals, which were natural hybrids of *Eucalyptus grandis* and *Eucalyptus urophylla* (Hodges et al. 1976; Alfenas et al. 1983; Wingfield, 2003). Clonal propagation and the emergence of hybrid Eucalypt forestry, now the basis of most advanced Eucalypt plantation programmes, thus emerged from a solution to a disease problem.

As pest and pathogen problems increasingly challenge Eucalypt plantation forestry, researchers and managers will clearly need to seek innovative new methods to deal with them. Much as vegetative propagation of hybrid clones has been a driving force in dealing with health problems in the past (van Heerden and Wingfield, 2002; Wingfield, 2003; Wingfield et al., 2008), the approach is costly, response time to emerging threats can be long, and sustained success relies on optimizing natural resistance, which may not be present against all pests. Importantly, resistance may ultimately be a trade off with growth, especially when threats from multiple insect and disease organisms must be managed (Potts and Dungey, 2004). Eucalypt growers will need to rely on other approaches to reduce losses. Some of these approaches, such as hybridization between species, are already emerging as important. Others are becoming useful and there will in all likelihood be approaches to pest and disease problems that have not yet even been considered. The focus of this review is to highlight disease and pest management tools that we believe are likely to drive the future of Eucalypt plantation forestry in the future.

2. Breeding and selection: Is there still space for improvement?

Breeding and selection of improved genotypes has formed the basis of Eucalypt plantation programmes for many years. Prior to the widespread utilisation of vegetative propagation and clonal forestry, selection of species, provenances and superior families emerging from breeding played a pivotal role in dealing with disease and to a lesser extent, insect pest problems (Carnegie and Keane, 1994; Dungey et al., 1997; FAO, 2008; King and Alfaro, 2004; O'Reilly-Wapstra et al., 2007; Stukely and Crane, 1994; Van Heerden et al., 2005). Indeed many Eucalypt growers still rely heavily on planting continuously improved seed stock and this approach, while perhaps limited in the case of serious health problems, remains useful. This is particularly true for desirable species that are difficult to propagate vegetatively.

A question that is increasingly raised by forest managers in areas where there has been a long history of breeding and selection of improved Eucalypt genotypes, is how much room (genetic opportunity) remains in the fight to avoid disease and pest problems. For example, in sub-tropical areas (parts of Brazil and South Africa for example) hybrids of *E. grandis* and *E. urophylla* have provided outstanding planting stock and many health problems

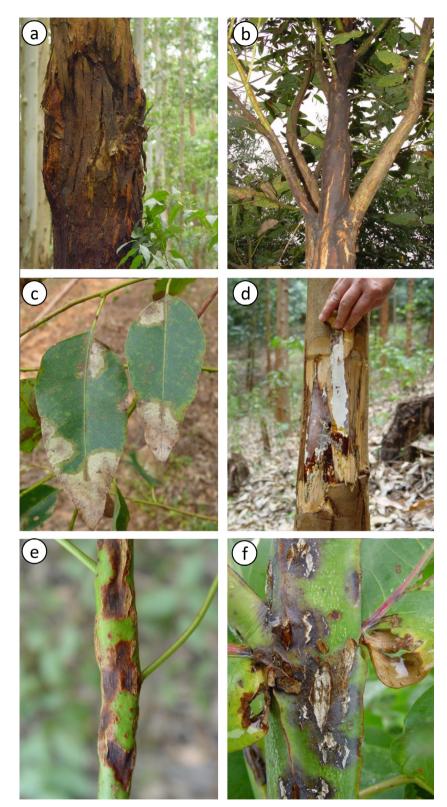


Fig. 2. Diseases of Eucalypts in plantations. (a) Stem canker caused by *Chrysoporthe austroafricana*; (b) Stem canker caused by a fungus in the Botryosphaeriaceae; (c) leaf blight caused by a species of *Calonectria*; (d) white mycelial fan of an *Armillaria* sp. Causing root rot and basal canker; (e) lesions on a young *Eucalyptus grandis* shoot caused by *Teratosphaeria zuluensis*; (f) *Quambalaria eucalypti* causing bark lesions on a *E. nitens* stem.

have been avoided by selecting clones that are resistant to insects and pathogens (van Heerden and Wingfield, 2002; Wingfield, 2003; van Heerden et al., 2005). While it might be argued that there must be limits to using this hybrid combination to deal with health problems, our experience suggests that the diversity in this hybrid still holds substantial opportunity for further improvement. And there are many new hybrid combinations emerging that include species such as *Eucalyptus nitens*, *Eucalyptus globulus*, *Eucalyptus camaldulensis* and their relatives that are well-known in plantation forestry.

An exciting development in Eucalypt clonal forestry is the numerous new hybrid combinations using previously unexplored species. For example, there are many interesting hybrids including species such as Eucalyptus benthamii, Eucalyptus longirostrata, Eucalyptus brassiana and Eucalyptus pellita that are emerging as important in various parts of the world. Very little is known regarding these species in terms of pest and pathogen problems. However, as has been true, for example with *E*. grandis \times *E*. urophylla in the past, these species will certainly contribute many new opportunities to improve tree health. Indeed, substantial diversity within Eucalypt species (>700 species within the native range of Australia and south east Asia, occupying a broad range of habitats and ecological conditions; Henery, 2011) represents an almost inexhaustible source of genetic material for improvement. In countries such as Brazil, where diverse species are being evaluated in hybrid combinations (e.g. Bison et al., 2007) there will be opportunity to combine desirable characteristics such as rapid growth, superior wood quality and disease resistance in multi-species (e.g. three- four-way hybrid combinations). The ability to tag and select for such desirable characteristics derived from different parental genomes using traitlinked molecular markers (Grattapaglia and Kirst, 2008), will create additional opportunities to deal with new disease challenges while exploiting wide segregation in interspecific hybrids.

New and as yet reasonably untested breeding tools will almost certainly also contribute to efforts to deal with pest and pathogen problems in the future. For example, while little is known regarding polyploidy in Eucalypts, there are intriguing early results to suggest that polyploids might offer opportunities for tree improvement (Libby et al., 1969). If this is true, there will likely also be opportunities to seek disease and pest tolerance in polyploids as has been true for many agronomic crops (Ortiz and Vuylsteke, 1994; Osborne et al., 2003).

Opportunities linked to genetic modification and the deployment of GMO Eucalypts are currently tempered by environmental concerns. In this regard, many Eucalypt growers support accreditation systems such as those of the Forestry Stewardship Council (FSC, http://www.fsc.org), which currently does not allow deployment of GMO's. Our view is that this is a situation that is likely to change in the future; probably not the very distant future. We also believe that GM Eucalypts will provide additional opportunities to deal with some of the more serious pest and pathogen problems that are likely to challenge Eucalypts forestry in the future.

Growth in the propagation of selected Eucalypt clones and clonal hybrids during the course of the last two decades has been remarkable and it has had a huge effect on the impact of pests and pathogens. Much has been learned regarding the dangers of planting large areas to single or a few clones, with some dramatic losses having been experienced in various parts of the world (Wingfield, unpublished). The importance of having a clear understanding not only of a safe number of clones to plant but the fact that these clones should not be unduly closely related to each other is now widely recognized. In this regard, molecular genetic tools have provided a very positive influence. Today, companies are able to genetically "fingerprint" clones for easy identification (Faria et al., 2010; Kirst et al., 2005; Myburg et al., 2008a). Likewise, DNA-based technologies have provided information on the relatedness of seed parents and clones and have enabled tree breeders to maintain a broad genetic diversity of planting stock (Poltri et al., 2003; Zelener et al., 2005). This in turn reduces potential losses due to pests and pathogens, many of which are highly host (genotype) specific.

3. Knowing the enemy

While pests and pathogens of Eucalypts have been recognised as a challenge for almost as long as plantation forestry has been practiced with these trees, our capacity to identify them accurately has been relatively poor. This is increasingly being recognised as new DNA-based tools have emerged to identify insects and pathogens. For fungal pathogens this has been particularly evident and it is based on the fact that they have a paucity of morphological characteristics for their identification.

It is somewhat shocking, even for forest pathologists, to recognise that the majority of the most important pathogens of Eucalypts were improperly identified in the past. Indeed, it is only the advent of DNA-based tools for identification that has revealed this problem fully. A vivid example is found in the case of Cryphonectria canker (Fig. 2) mentioned previously and that was believed to be caused by the pathogen Cryphonectria cubensis. Through a series of studies dating back to the late 1980s (Myburg et al., 2002; Gryzenhout et al., 2004; Van der Merwe et al., 2010), it has emerged that the disease is caused by numerous species of the new genus Chrysoporthe. Thus, the fungus treated as *Chrvsoporthe cubensis* is now known to have originated on native woody plants, predominantly Melastomataceae in South and Central America (Van der Merwe et al. 2010). The fungus of the same name in South East Asia is a different species, Chrysoporthe deuterocubensis (Van der Merwe et al. 2010). The fungus in Africa is believed to be native to that area on native Myrtaceae and is known as Chr. austroafricana (Heath et al. 2006; Gryzenhout et al. 2004). Treatment of these very different fungi as a single entity presents an obstacle to biological knowledge and can be hugely misleading. Importantly from a tree health standpoint, breeding and selection of planting stock must logically reflect correct pathogen identification.

DNA-based tools for identification of Eucalypt pests and pathogens has advanced rapidly in recent years and they continue to have an enormous and growing impact on programmes seeking to improve the health of these trees. Virtually every major group of Eucalypt pathogens has been substantially affected by the power and availability of these tools. These for example include the leaf and canker pathogens in the Teratosphaeriaceae (Crous et al., 2006; Hunter et al., 2006; Cortinas et al., 2010; Chen et al., 2011; Taylor et al., 2012), stem canker pathogens in the Botryosphaeriaceae (Fig. 2b) (Slippers et al., 2004; Barber et al., 2005) and Cryphonectriaceae (Gryzenhout et al., 2006), canker and wilt pathogens such as species of Ceratocystis sensu lato (Van Wyk et al., 2012) leaf and root pathogens such as species of Calonectria (Fig. 2c) (Lombard et al. 2010) and Armillaria (Fig. 2d). They have also been used, although to a lesser extent, for the identification of Eucalyptus pests. A superb recent example is where the well-known leaf and shoot feeding weevil, previously believed to be a single taxon Gonipterus scutellatus (Fig. 1) was shown to represent a suite of cryptic species (Mapondera et al., 2012; Garnas et al., in press).

The impact of DNA-based tools for the identification of pathogens and insects will continue well into the future. They will likely become more sophisticated as genome data become available for the organisms of interest. Furthermore, rapid tools for diagnosis are also likely to become increasingly available in the future.

4. Understanding movement and establishment of pests and pathogens

Understanding the pathways by which pests and pathogens move globally makes it possible to reduce the chance of accidental introductions into new areas. For many years, knowledge of this field relied almost entirely on country records and anecdotal evidence. This has changed dramatically with the advent of DNAbased population genetic tools. Using tools such as microsatellite markers, it has thus been possible to track the global movement of important Eucalypt pests and pathogens.

Two important *Eucalyptus* pathogens that have been subjected to substantial study in terms of pathways of introduction are the leaf pathogen *Teratosphaeria nubilosa* (Hunter et al., 2008; Pérez et al., 2009) and the stem canker pathogens *Teratosphaeria zuluensis* (Fig. 2e) (Cortinas et al., 2010; Chen et al., 2011) and *Teratosphaeria gauchense* (Cortinas et al., 2011). *Teratosphaeria nubilosa* was, for example shown to have originated in Australia and most likely moved from that area into South Africa (Hunter et al., 2008; Pérez et al., 2009). Elements of the South African population have evidently moved into other parts of Africa, Spain and Portugal (Hunter et al., 2008). More recently, the pathogen appeared for the first time in Uruguay and Brazil and the source of that invasion appears to have been Spain or Portugal (Pérez et al., 2009).

In a manner similar to that for fungal pathogens, population genetic markers are rapidly becoming important tools to understand the origin and spread of Eucalypt insect pests. These tools have, for example, recently been used to understand the global spread of the important newly-recognised pest *Thaumastocoris peregrinus* (Fig. 1) that has invaded various countries of South America and South Africa (Jacobs and Nesser, 2005; Wilcken et al., 2010; Soliman et al., 2012). Thus, the insect was shown to have invaded South America and South Africa separately (Nadel et al., 2010). Furthermore, good evidence emerged that there was most likely more than one invasion into South Africa. The data emerging from these studies will provide an important foundation for disease management strategies including biological control.

Other than revealing pathways of their movement, population genetic markers have made it possible to understand the genetic diversity of populations of Eucalypt pests and pathogens (Hunter et al., 2008; Ferreira et al., 2011). Such knowledge makes it possible to better understand the likely durability of resistance in selected planting stock (McDonald and Linde, 2002; Graça et al., 2011). For example, the fact that *T. nubilosa* represents a highly diverse population in South Africa (Hunter et al., 2008) suggests that it will more easily overcome resistance in Eucalypt clones than will likely be the case, in for example, Uruguay where the pathogen represents a single clone. The same is true for insect pests such as *T. peregrinus* that represents a very limited genetic base in areas where it is invasive (Nadel et al., 2010).

Data emerging from pathway analyses and population genetic studies are already informing quarantine procedures and other risk-abatement programmes. Markers for population genetic analysis are increasingly being developed for the most important Eucalypt pests and pathogens and these are also becoming increasingly more powerful. They will certainly emerge as increasingly valuable in detecting new invasions of pests and pathogens but importantly also in refining systems to prevent invasions from occurring.

5. Biological control

Biological control represents the most important approach to reduce damage due to non-native insect pests of Eucalypts. This was recognised many years ago when the invasion of *Gonipterus scutellatus* in South Africa was controlled by introducing the parasitoid *Anaphes nitens* (Tooke, 1953). Interestingly, this was one of the first examples of biological control of an insect pest in forestry and it is treated as a classical example of the utility of this approach to dealing with forest pests (Hajek, 2004).

In addition to the *Gonipterus* example, many introduced Eucalypt pests have been controlled through the introduction of biological agents, mainly insect parasitoids. These include biological control programmes for *Phoracantha semipunctata* (Fig. 1), *Trachymella tincticollis, Glycaspis brimblecombei, Ctenarytaina eucalypti, Uraba lugens, Ophelimus maskelii* (Fig. 1) and *Leptocybe invasa* (Tribe, 2000; Hanks et al., 2001; Paine and Millar, 2002; Daane et al., 2005; Prostasov et al., 2007; Kim et al., 2008; Avila and Berndt, 2011). There are currently active programmes to seek improved biological control of some of these and various newly emerging Eucalypt pests such as *Thaumastocoris peregrinus* (Nadel et al., 2012).

Molecular genetic tools are adding substantially to the sophistication of biological control programmes for insect pests and this is likely to be increasingly true in the future. In the past, biological control has been relatively naively applied with little understanding of the structure of the parasitoid populations. Thus, introduced biological control agents could have represented very limited genetic diversity with the risk of failures emerging due to genetic bottlenecks (Roderick and Navajas, 2003). It is now possible to collect biological control agents having known population structure and thus to understand the long term prospects for control.

Biological control of fungal pathogens of trees including Eucalypts is considerably less promising than is the case for insects. While there has been considerable work using mycoparasites such as species of Trichoderma and Gliocladium, there are few examples of biological control being used commercially or effectively. Those examples of effective control are restricted to the nursery environment where the growth media can be sterilised and the biological control fungi favoured over competing strains. There are currently no examples of effective biological control of Eucalypt diseases using biological control fungi at a plantation scale. Although not relevant to Eucalypt plantation forestry, the application of Phlebiopsis gigantea to cut pine stumps to reduce the spread of annosum root rot (Heterobasidion spp.) in western Europe (Holdenrieder and Greig, 1998), shows that some innovative options might be possible. Given that fungi are abundant in the natural environment, it would be necessary for the inoculated strains to compete effectively in the field environment. In this regard, research would need to clearly show that the inoculated strains have survived and are dominant in the field, as well as conferring resistance to the pathogens of interest. Our view is that this approach is likely to hold limited promise.

There has been some interest in using endophytic fungi in trees to increase their resistance to insect pests and pathogens. This approach rests on the notion that trees grown as non-natives have been introduced without the endophytes with which they co-exist in their natural environments. Very little is known regarding the endophytes of trees and this is equally true for Eucalypts. While there might be some opportunity to deal with pests and pathogens using this approach, it is at the very least, a long term prospect. It will clearly rest on our having substantially enhanced knowledge of the diversity of endophytes of Eucalypts, particularly their biology and ecology. Simply finding effective methods to inoculate and maintain a favourable endophytic community in trees under natural conditions promises to be hugely challenging. For the present, while a worthwhile avenue for research, this approach to biological control should be seen as purely experimental and we would urge forest managers to temper expectations in the short term.

6. Genomes and genomics

One of the most exciting developments in terms of Eucalypt forestry is the fact that the first *Eucalyptus* genome (*E. grandis*) has been sequenced to near complete reference quality (http:// www.phytozome.net/euclyptus.php; Myburg et al., 2008b), while others such as *E. camaldulensis* (Hirakawa et al., 2011) and *E. globulus* (Rigault, Tibbits & Spokevicius., unpublished) are also in advanced stages of sequencing. This is clearly just the beginning of an era and as genome sequencing becomes increasingly more affordable, the genomes of many other Eucalypt species will become available. For key commercially grown species such as *E. grandis* and *E. globulus*, next-generation DNA sequencing technologies are already allowing the re-sequencing of the genomes of multiple individuals for genome-wide detection of genetic variation (Rigault et al., unpublished; Myburg et al., unpublished). The availability of the first reference Eucalypt genome is already impacting on research programmes where it is being mined for genes of interest. It also provides a reference for genome-wide analysis of gene expression using next-generation RNA-sequencing in individual trees (Mizrachi et al., 2010) and in populations allowing a systems genetics approach to study complex biological processes in trees (Mizrachi et al., 2012). Furthermore, the genome sequence has supported the development of high-throughput molecular marker resources such as Diversity Arrays Technology (DArT, Sansaloni et al., 2010) and the first demonstration of genomic selection in Eucalypt breeding (Resende et al., 2012).

The impact of genome sequencing and genomics on Eucalypt propagation will increase in the future and it will also impact positively on programmes that seek to deal with insect pests and pathogens. For example, there are already various projects underway to use the genome to identify genes that are involved in resistance to pests and pathogens and these will substantially enhance our understanding of mechanisms of resistance. It is important to note that while some of the basal components of pest and pathogen defence mechanisms may be conserved, it is reasonable to expect that long-lived perennials such as forest trees may have evolved novel approaches to defend themselves over long periods of time against much faster evolving pathogens. Functional genetic studies will promote the discovery of defence mechanisms and genes involved which will eventually make their way into genetically modified Eucalypts or can be used to develop resistance linked DNA markers for use in molecular breeding approaches.

As is true for Eucalypts themselves, the genomes of Eucalypt pathogens and pests are rapidly being sequenced. For example, the genomes of *Teratosphaeria nubilosa*, *Ceratocystis fimbriata* and various species of Botryosphaeriaceae have already been sequenced (authors unpublished). Projects are underway to sequence the genomes of the insect pest *Leptocybe invasa* and numerous other Eucalypt pest and pathogen genomes will surely be sequenced in the relatively near future. The genomes already available are being mined for genes of interest relating to pathogenicity and they are also providing useful tools such as improved markers for identification as well as population genetic studies. The availability of a reference Eucalypt genome as well as that of multiple pathogen and pest genomes will enable powerful new approaches to study tree-pathogen/pest interactions.

Whole-genome expression profiling can be applied in individual genotype interactions (Azaiez et al., 2009; Ralph et al., 2006), but the most informative approaches may result from dissection of biological interactions in segregating tree populations and/or segregating pathogen or pest populations as has been demonstrated in other plant species (Kover et al., 2005; Thabuis et al., 2003). It is the genetic variation segregating in tree populations that is of interest and utility to tree breeders. Genome-wide surveys for resistance-linked markers (e.g. Junghans et al., 2003) will therefore be the priority, while gene expression studies are used to study defence mechanisms, which could in future be used to engineer resistance using GMO technology.

7. Conclusions

While the many new pests and pathogen problems in Eucalypt plantations during the recent past have raised substantial concern amongst forest owners, there is cause for optimism. This is assuming that plantation owners have not over capitalised on limited genetic diversity by the planting of small numbers of clones or clones that are genetically very closely related. There are also growing numbers of technologies that can be used to reduce the impact of pests and pathogens of Eucalypts and investment in these should ensure long term sustainability of plantation forestry based on these remarkable trees.

The growing challenges to deal with disease and insect pests of Eucalypts arise from their introductions into new environments, which are increasing in number annually, arise (Wingfield et al., 2008). Interestingly, there are also growing numbers of unexpected new insects and disease problems that are emerging from new associations linked to host shifts (Gebeyehu et al., 2005). Adding to these problems, there are emerging examples of new pest and disease problems arising from apparent climate change events (Sturrock et al., 2011). Vivid examples are found in the devastation being caused by the mountain pine beetle in western north America (Safranyik and Carroll, 2006), range expansion in Phytophthora cinnamomi in Europe (Jung, 2009) and a serious die-back of native Euphorbia ingens trees in South Africa (Van der Linde et al., 2012). Very little work has been conducted regarding the long term effects of climate change on Eucalypt plantation forestry. Pests and pathogens interact incredibly closely with their hosts and the environment and it is likely that as climate changes in various parts of the world, there will be expansions and contractions in the areas of occurrence of various pests and pathogens. Furthermore, it is clear that trees growing under stressful conditions will be more heavily damaged by pests and pathogens that are positively influenced by predisposition. Yet there is huge opportunity to develop Eucalypt clones that that can withstand changing environments and we feel confident that these are challenges that can be met by dynamic Eucalypt growers.

While it is relatively easy to develop Eucalypt clones that are resistant to damage by pests and pathogens are capable, it is often forgotten that insects and diseases are capable of relatively rapid change. It is, therefore, important to recognise that planting disease or insect resistant genotypes will place a very substantial pressure on the insect or pathogen to adapt. This was rapidly realised with agronomic crops where "refugia" have been established to reduce the dangers of adaptation of insects to genetically modified plants. For Eucalypts, clones known to be resistant to pathogens such as the causal agent of Coniothyrium canker (Fig. 2e) in South Africa have lost this resistance over time (Wingfield, unpublished). Thus reliance on small numbers of clones, clones that are unduly closely related and unreasonable expectations of long term durability of resistance holds great risk. Here, the most promising opportunities lie in having a substantial knowledge of the genetic background of both the trees being planted and the major pests and pathogens that damage them.

Eucalypts have been grown commercially outside their native range for little more than 100 years. From a biological perspective, this is a remarkably short period of time and we are likely to experience many surprises, both positive and negative, in the future. For example, just twenty years ago, the host-shifts where native and relatively host-specific pests and pathogens might adapt to damage Eucalypts were not considered. These appear to be emerging today and we understand very little about them. Where there is substantial concern that native pests or pathogens might adapt to infest/infect Eucalypts in their new environments, little concern has been expressed regarding the dangers of host-specific Eucalypt pests introduced into new environments damaging native trees. For example, the recent report (Pérez et al., 2008) of Quambalaria eucalypti (Fig. 2f), almost certainly a native pathogen in Australia, infecting native Uruguayan Myrtaceae is of great concern. Work on diseases and pests of native trees, particularly in developing world countries where Eucalypt plantation forestry is actively pursued, tends to be very limited. Yet more attention should be paid to diseases and pests of native trees, especially those from the Myrtaceae, and how these might overlap with those on nonnative plantation-grown trees such as Eucalypts.

Huge improvements have been made in commercial Eucalypt forestry during the course of the past 100 years. These remarkable trees with their huge diversity have made it possible to establish productive plantations in areas having vastly different climatic and edaphic characteristics. Improvement of the trees through breeding and selection, more recently vegetative propagation of hybrids has further increased their productivity and adaptability to new and challenging environments. But these trees have also been challenged by pest and disease problems and this is a trend that will grow in the future. New pest and pathogen problems are emerging regularly and the pressure from these biological constraints is growing. Plantation forestry based on non-native trees is prone to "boom and bust' cycles and an ability to sustain these will define the success of forestry enterprises. Belief in simple solutions to complex problems such as those caused by pests and pathogens will surely result in disappointment and loss. A commitment to invest in the scientists and the facilities that will ensure a comprehensive knowledge of the pests and pathogens of Eucalypts and the many and growing technologies to manage them will surely define successful Eucalypt growers of the future.

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