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SPECIAL ISSUE: HUMAN-MEDIATED INTRODUCTIONS OF AUSTRALIAN ACACIAS—A GLOBAL EXPERIMENT IN BIOGEOGRAPHY

Insect pests and pathogens of Australian acacias grown as non-natives – an experiment in biogeography with far-reaching consequences

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ABSTRACT

Aims To highlight the increasing importance of pests and pathogens to Australian *Acacia* species, where they are planted as non-natives in commercial plantations and in their native environment.

Location Africa, Asia, Australia, South America.

Methods Existing literature and results of unpublished surveys on pests and pathogens of Australian acacias are reviewed. These are discussed within the context of a growing importance of invasive alien insects and pathogens including novel encounters and host jumps.

Results Australian acacias planted as non-natives in various parts of the world are increasingly threatened by pests and pathogens. These include those that are accidentally being introduced into the new environments as well as 'new encounter' pests and pathogens that are undergoing host shifts to infect non-native acacias. Furthermore, insects and pathogens for biological control of invasive Australian acacias present substantial challenges for plantation forestry.

Main conclusions Pests and pathogens will seriously challenge plantation forestry based on non-native Australian acacias. In the longer term, new encounter pests and pathogens will also threaten these trees in their native environments.

Keywords

Biological invasions, fungal tree pathogens, new encounter diseases, novel host–pathogen interactions.

INTRODUCTION

Forests are amongst the most sensitive ecosystems on earth, and they are increasingly threatened by invasive alien pests and pathogens (Wingfield *et al.*, 2010). The reality of this threat first arose early in the last century with devastating insect and disease problems such as those caused by the gypsy moth and the chestnut blight pathogens appearing in North America. It is unfortunate that new invasive alien pest and pathogen problems have continued to appear in native woody ecosystems and forests and that there is no evidence of this trend abating. The primary driving force behind these invasions is anthropogenic, with major pathways of introduction linked to the movement of people and products globally (Mattson *et al.*, 2007; Wingfield *et al.*, 2010). A more recently emerging and compounding factor is found in the emergence of novel associations between pests, pathogens and trees planted, for example, to sustain plantation forestry (Wingfield, 2003; Wingfield *et al.*, 2010, 2011). These so-called new encounter pests and pathogens now threaten the same trees in their native environments. In this sense, planting non-native trees in new environments represents an interesting and important experiment, the results of which have yet to be realized.

Similar to species of *Eucalyptus* and *Pinus*, Australian *Acacia* species have been widely established in the tropics and Southern Hemisphere as non-natives in intensively managed plantations. While many Australian *Acacia* spp. have been tested for this purpose, the three species most extensively planted and that have been most widely exposed to pests and pathogens are *A. crassicarpa*, *A. mangium* and *A. mearnsii*.

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Of these, *A. mearnsii*, suited to growing in temperate environments, has been managed in plantations in South Africa for more than 140 years. This species thus provides an example of an *Acacia* species that has been grown over large areas outside its native range for an extended period of time and in which interesting examples of pest and disease problems have been able to emerge (Fig. 1; Table 1). Large-scale plantation forestry with *A. crassicarpa* and *A. mangium* has developed more recently in tropical environments where these trees are best suited to grow. In this case, pest and disease problems are of a more recent nature. Yet, intriguing patterns are emerging that are likely to strongly influence the future of plantation forestry in those parts of the world.

The appearance of pest and pathogen problems in plantations of non-native *Acacia* spp. has followed patterns that are similar to those for non-native species of *Eucalyptus* and *Pinus*. Eucalypts have been planted more extensively as non-natives, and for longer, than have *Acacia* spp. Consequently, this group serves as an interesting and appropriate base for comparisons. For example, early plantations of pines and eucalypts outside their native ranges were relatively free of disease and insect problems. Their success has been attributed to the fact that they had been separated from their natural enemies and thus 'enemy escape' (Jeffries & Lawton, 1984; Keane & Crawley, 2002; Mitchell & Power, 2003; Wingfield *et al.*, 2008), although other factors such as browsing and the genetic plasticity of the species might also contribute to their success. Disease and pest problems were typically those caused by native pathogens or insects with wide host ranges, for example defoliating Lepidoptera (Tooke, 1938; Van V Web, 1974) and root pathogens such as species of *Armillaria* (Coetzee *et al.*, 2000) and *Ganoderma* (Irianto *et al.*, 2006; Eyles *et al.*, 2008). A number of important leaf and shoot pathogens also appeared relatively early, for example, *Diplodia pinea* on *Pinus* spp. (Swart *et al.*, 1985) and *Teratosphaeria nubilosa* on *Eucalyptus* spp. (Doidge, 1950; Wingfield, 1990; Hunter *et al.*, 2004); these were most likely introduced together with the first planting stock or seeds.

The first serious problem to affect *A. mearnsii* in South Africa was root disease caused by a *Phytophthora* sp. (Van Der Byl, 1914; Sherry, 1971; Zeijlemaker, 1971) and defoliation by native insects such as the wattle bag worm (Van V Web, 1974; Kirsten *et al.*, 2000) (Fig. 2a,b). Likewise, plantations of *A. mangium* and *A. crassicarpa* in South-east Asia have been seriously affected by root rot caused by native *Ganoderma* (Fig. 2c,d) as well as being damaged by a number of native insects such as the shoot damaging *Helopeltis* spp. and defoliation by Lepidopteran larvae such as *Plusia* sp. (Nair, 2001).

While Australian *Acacia* spp. have been increasingly established outside their native range for plantation forestry, various species of these trees occupy large areas where they occur as invasive weeds (Richardson & Rejmánek, 2011). The most notable examples are found in South Africa where species such as *A. cyclops* and *A. longifolia* were introduced in the 1830s to stabilize the coastal sands on the Cape flats (Roux, 1961). While these trees are not the focus of this study, they do provide an example of Australian *Acacia* species that have been exposed to pests and pathogens outside their native range for a long period of time. Because of their negative impact on the native environment (Le Maitre *et al.*, 2011), these trees have also been the subject of intensive biological control initiatives using both insects and fungal pathogens (Morris, 1991; Impson *et al.*, 2008; Post *et al.*, 2010; Wilson *et al.*, 2011). These studies thus provide interesting perspectives on how pest

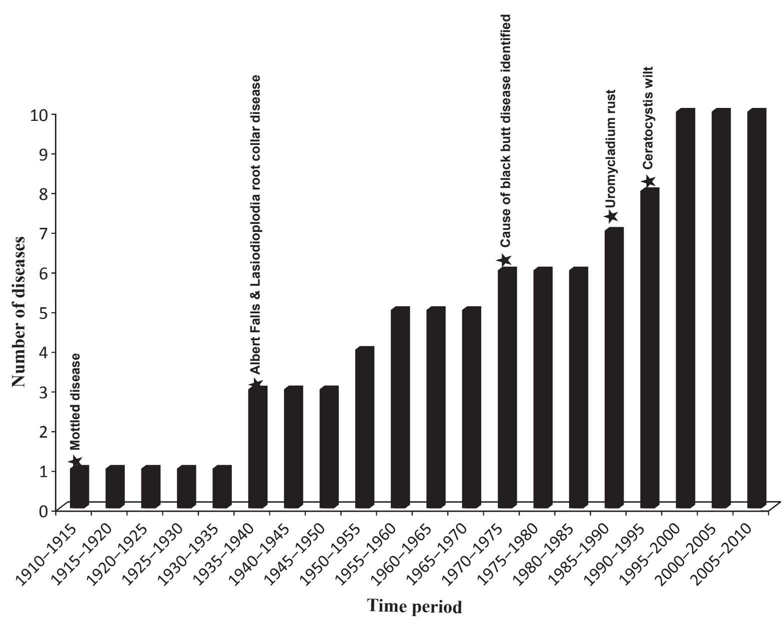

Figure 1 Cumulative appearance of diseases of *Acacia mearnsii* in South Africa from the time of first establishment of the tree in the country. Annotations on the bars relate to key milestones listed in Table 1. Regular disease monitoring of *A. mearnsii* has taken place since the first half of the previous century and most disease problems are not likely to have been overlooked.

Table 1 Important milestones relating to the propagation of *Acacia mearnsii* in South Africa with special emphasis on pests, pathogens and the introduction of biological control agents.

Date	Event	Reference
1860s	First plantings of *A. mearnsii* in South Africa	Sherry (1971)
1914	First disease reported – Mottled disease	Van Der Byl (1914)
1937	Root disease caused by *Lasiodiplodia theobromae*	Laughton (1937)
1938	Albert Falls disease and root collar rot reported	Stephens & Goldschmidt (1938)
1947	Establishment of Wattle Research Institute (WRI)	
1957	First list of fungi in *A. mearnsii* plantations compiled	Roberts (1957)
1971	Cause of black butt disease confirmed as *Phytophthora nicotianeae*	Zeijlemaker (1971)
	Cutworms, *Agrotis* spp., reported from *A. mearnsii*	Sherry (1971)
	Termites reported as problem on *A. mearnsii*	Sherry (1971)
	Wattle semi-looper, *Achaea* sp. reported from *A. mearnsii*	Sherry (1971)
1980s	Introduction of *Melanterius maculatus* for biological control of *A. mearnsii*	Dennill *et al.* (1999)
1984	Institute for Commercial Forestry Research (ICFR) constituted out of the WRI	
1988	First rust disease caused by *Uromycladium alpinum* reported	Morris *et al.* (1988)
1990	Establishment of the Tree Protection Co-operative Programme (TPCP) to deal with pathogen problems of plantation grown tree species in South Africa	
1993	First official report of wilt disease caused by a *Ceratocystis* sp., then named *C. fimbriata*	Morris *et al.* (1993)
1996	Description of *C. albifundus*, a species new to science, as the cause of wattle wilt disease	Wingfield *et al.* (1996)
1997	Publication of results of a disease survey of plantation grown *A. mearnsii* in South Africa, listing several new reports of fungi on these trees in the country	Roux & Wingfield (1997)
2008	Gall midge, *Dasineura rubiformis* introduced as a biological control agent for *A. mearnsii*	Impson *et al.* (2008)
2009	First report of insect associates of the wattle wilt pathogen, *C. albifundus,* from *A. mearnsii*	Heath *et al.* (2009)

and disease problems might emerge in plantations in the future.

The aim of this review is not to provide lists of insects and pathogens that have been recorded on Australian *Acacia* species growing outside their native range. The focus is rather to interrogate trends relating to changes in the biogeography of selected Australian acacias by exposing these non-native trees to new environments where they have initially been released from the insect pests and diseases that control their populations naturally. Examples illustrating emerging trends are taken largely from experiences in South Africa with *A. mearnsii* and in South-east Asia with *A. crassicarpa* and *A. mangium*.

GRADUAL APPEARANCE OF PESTS AND PATHOGENS

As has been the case for other plants grown as non-natives in new environments, there has been a gradual appearance of pest and pathogen problems in plantations of *A. mearnsii* (Fig. 1), *A. crassicarpa* and *A. mangium* over time. This is consistent with the fact that the trees were separated from the majority of their natural enemies. Increasing levels of trade and tourism, however, are providing opportunities for pests and pathogens to 'catch up' with their original hosts (Clay, 2003; Mitchell & Power, 2003). All indications are that forestry companies will have to contend with greater numbers of biotic problems in the future (Wingfield, 2003; Wingfield *et al.*, 2008).

Not all insects and pathogens that are introduced into new environments will become successfully established. Thus, it is only those organisms that are suited to the new environments in which *Acacia* spp. are planted that will ever be recognized as having been introduced. Introduced invasive organisms can remain undetected for many years before they eventually reach levels that are noticeable. For some invasive aliens, the establishment phase before problems emerge can last decades or more (Crooks, 2005). Thus, when an alien pest or disease appears in a plantation area, the causal organism could have been present for many years/decades.

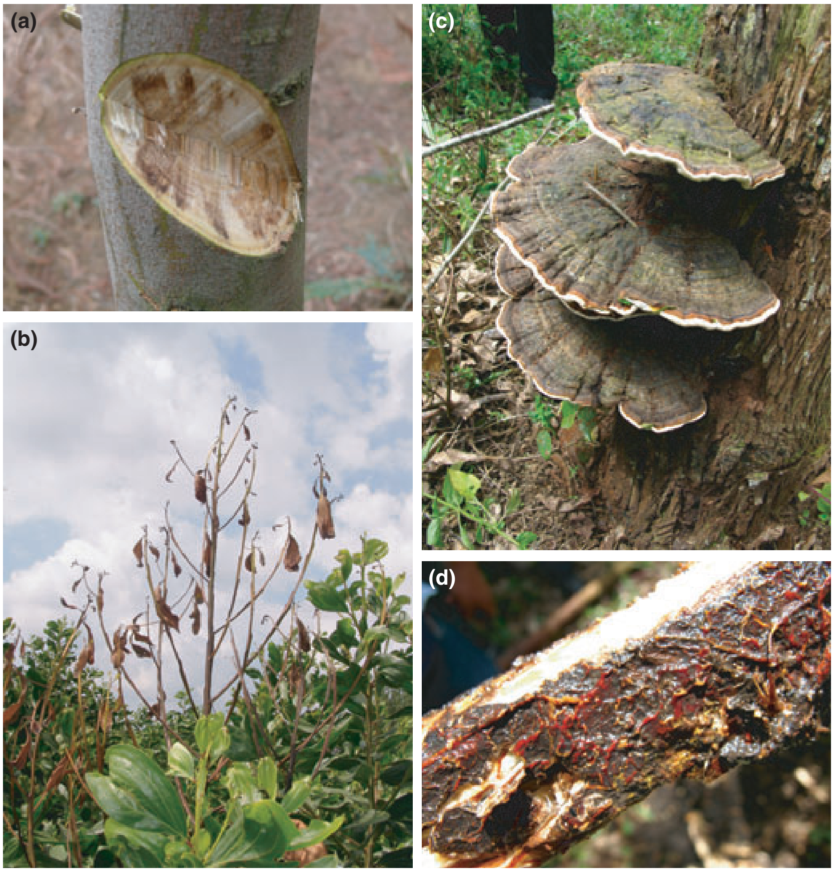

Figure 2 Diseases of non-native plantation-grown *Acacia* spp. caused by native fungi (a) Xylem discouloration caused by *Ceratocystis albifundus* on *A. mearnsii* in South Africa, (b) die-back of *A. mangium* in Indonesia caused by *C. acaciivora*, (c) *Ganoderma* fruiting bodies on the stem of a *A. mangium* tree in Indonesia, (d) red rhizomorphs of *Ganoderma philipii* on the root of a diseased *A. mangium* tree.

Acacia mearnsii in South Africa has been affected by very few pathogens that are known on the tree where it is native in Australia. These include two foliar pathogens, the Ascomycete *Camptomerris albizzae* and the rust *Uromyces alpinum* (Sherry, 1971; Morris *et al.*, 1988). Both of these pathogens were only discovered relatively recently but are relatively minor and might well have been present from the very early days of planting this tree in South Africa. Interestingly, there have been no accidental introductions of serious insect pests of *A. mearnsii* from Australia. However, the seed-feeding weevil *Melanterius maculatus* and a gall midge, *Dasineura rubiformis*, have been introduced into the country as part of biological control programmes aimed to reduce the invasive nature of the tree (Impson *et al.*, 2008).

Very few diseases caused by accidentally introduced pathogens have affected the large-scale establishment of *A. crassicarpa* and *A. mangium* in South-east Asia. Rust caused by *Atelocauda digitata*, a disease well known on native *A. mangium* (Fig. 3a), appeared relatively soon after these trees were established as non-natives (Old *et al.*, 2000). This suggests that the pathogen was probably brought into the area with seed or possibly even plants used to establish the first plantations. More recently, *A. crassicarpa* plantations in South Sumatra were seriously damaged (Fig. 3c,d) by the leaf and shoot pathogen *Passalora perplexa* (Beilharz *et al.*, 2004) that spread rapidly throughout the region. As is true for many pathogens and pests of trees established in plantations outside their native range, *P. perplexa* was not known on *A. crassicarpa* where it is native in Australia, south-western Papua New Guinea and south-western Irian Jaya (Indonesia). Thus, discovery of this new pathogen included the need to identify it and to provide a name for it for the first time. Unlike the case with fungi, no seriously damaging introduced insect pests have appeared on *A. mangium* or *A. crassicarpa* where these trees are being grown as non-natives in plantations.

NEW ENCOUNTER DISEASES

The most serious disease of *A. mearnsii* in South Africa is wilt caused by the pathogen *Ceratocystis albifundus* (Roux & Wingfield, 1997; Roux, 2002). This disease (Fig. 2a) was first discovered in invasive stands where the trees were being cut and harvested for firewood and where the fungus was found entering the wounds made to the trees (Morris *et al.*, 1993). The pathogen was first identified as the closely related *Ceratocystis fimbriata*. Studies based on DNA comparisons,

Figure 3 Diseases of non-native plantation-grown *Acacia* spp. caused by introduced fungi and insects (a) Rust of *A. mangium* caused by *A. digitata* in Indonesia, (b) Gals caused by the leaf rust pathogen *Uromycladium tepperianum* on *A. longifolia* in South Africa, (c) Leaf spot caused by *Passalora perplexa* on *A. crassicarpa* in Indonesia, (d) Leaf blight caused by *P. perplexa*, (e) *Trichilogaster acacialongifolia* on *A. longifolia* in South Africa.

however, showed that it represented a distinct species (Wingfield *et al.*, 1996). It was later shown to be the same fungus, also incorrectly identified as *C. fimbriata*, found on *Protea* spp. in the 1970s (Roux *et al.*, 2007).

Ceratocystis albifundus is a pathogen native to Africa. This has become evident from population studies showing that the fungus is genetically diverse in the region (Nakabonge, 2002; Barnes *et al.*, 2005; Heath *et al.*, 2008) and the fact that it commonly infects wounds on native trees (Roux *et al.*, 2007). Moreover, infections on native trees seldom result in disease, whereas those on *A. mearnsii* cause rapid wilt and death. It is intriguing that *C. albifundus* has undergone a host shift to cause disease on a tree unrelated to those on which it occurs as a native. The fungus has a wide host range on native woody plants in South Africa, including trees in more than seven genera (Roux *et al.*, 2007). These include native hosts in the family Fabaceae, to which the genus *Acacia* belongs. Yet there is no easy explanation as to why it should cause a serious disease on *A. mearnsii* and *A. decurrens* and it has not been found causing disease on any other non-native woody plants in the country.

Many *Ceratocystis* spp. in the *C. fimbriata* species complex are virulent tree pathogens (Van Wyk *et al.*, 2007; Roux & Wingfield, 2009; Tarigan *et al.*, 2010). These fungi require wounds to infect their hosts, and they are most commonly carried by casual insects such as Nitidulidae that visit freshly made wounds. Thus, various species of Nitidulidae have been found to carry *C. albifundus* (Heath *et al.*, 2009), and they will have moved this fungus from native African trees to *A. mearnsii*.

Interestingly, a new and serious canker wilt disease has recently appeared on *A. mangium* in South Sumatra (Fig. 2b). This disease is caused by a *Ceratocystis* sp. recently described as *Ceratocystis acaciavora* (Tarigan *et al.*, 2010). Very little is known regarding the infection biology of *C. acaciavora* but the main sites of infections appear to be wounds made to the trees during pruning. These wounds are visited by nitidulid beetles that appear to carry the pathogen. There is also a close association between the fungus and wood-boring ambrosia beetles, which is also typical of many *Ceratocystis* spp. The origin of *C. acaciavora* is not known but it is closely related to *C. manginecans* that is associated with the wood-boring beetle

Hypocryphalus mangifera and that kills mango trees in Oman (Al Adawi *et al.*, 2006; Van Wyk *et al.*, 2007). Isolates identical to *C. manginecans* have also been collected from wounds on *A. mangium* although they appear to be less pathogenic to these trees than *C. acaciavora*. This complex situation requires substantially more study but available evidence suggests that *C. acaciavora* is a native fungus in Indonesia and that it has undergone a host shift (Slippers *et al.*, 2005) to infect *A. mangium*.

An as yet unknown threat relating to new encounter diseases is that pathogens are effectively new to the trees and thus do not occur where the trees are native. Thus, these 'new' pathogens (Wingfield *et al.*, 2010, 2011) of *Acacia* now threaten these trees in their native environments. This, for example, accounts for the concern that the new encounter disease, Eucalyptus rust, caused by *Puccinia psidiii* (Coutinho *et al.*, 1998), a fungus native to Myrtaceae but that has undergone a host shift to *Eucalyptus* in South America, might enter Australia (Glen *et al.*, 2007). The recent appearance of a serious Eucalyptus rust disease in Australia and apparently caused not by *P. psidii* but by the relatively poorly known yet similar pathogen *Uredo rangelii* (Carnegie *et al.*, 2010) is clearly of great concern. It is not unlikely that new encounter pathogens such as *C. albifundus* will eventually move to Australia and could cause serious damage to native *Acacia* spp. in that country.

INSECTS VERSUS PATHOGENS

Pathogens appear to have caused greater damage to plantations of *A. mearnsii*, *A. crassicarpa* and *A. mangium* than insects. The question thus arises as to whether pathogens are able to move to new environments more easily than insects or whether native pathogens are likely to cause more serious problems than native insects exposed to new tree species. There is no clear answer to this question but certainly, when considering plantations of non-native *Eucalyptus* and *Pinus*, the impact of pests and pathogens can be equally serious (Wingfield *et al.*, 2008).

One of the most common pathways of movement of alien pests and pathogens is via germplasm used to establish plantation programmes (Burgess & Wingfield, 2002; Wingfield *et al.*, 2008). In this regard, seed provides an avenue to move unwanted organisms such as fungi and insects. Because it is easier to eliminate insects from seed lots, fungi appear to be most commonly moved, and this probably accounts for many non-native pathogens that have appeared in plantations of pines, eucalypts and acacias.

While insects might move on seed less easily than fungi, many insects native to pines and eucalpts have been introduced into areas where these trees are grown as non-natives in plantations (Wingfield *et al.*, 2008). Some of these insect pests complete their life cycles in dead wood, and they have moved globally in wood products and wood packaging material. Other insects such as the Hemiptera have most likely moved globally on plants linked to the nursery trade with so-called plants for planting. These pathways of movement provide ample opportunities for the introduction of seriously damaging insect pests and pathogens into areas where they do not presently occur.

CONFLICTS RELATING TO BIOLOGICAL CONTROL

While Australian *Acacia* species grow rapidly and have proven to be exceptional sources of fibre for plantation forestry, they capture new sites very easily, and many species have emerged as serious weed problems damaging pristine natural ecosystems (Matthews & Brand, 2004; Richardson & van Wilgen, 2004; Richardson & Rejmánek, 2011). This has led to conflicts of interest between those groups that seek to grow *Acacia* spp. effectively and others that seek to eliminate these trees (De Wit *et al.*, 2002; Kull *et al.*, 2011). In the case of the latter group, biological control using host-specific pests and pathogens presents a highly desirable option (Wilson *et al.*, 2011). The only insect pest that has been introduced into a new environment for the biological control of an *Acacia* species that is also grown commercially in plantations is *Melanterius maculatus* for the control of Australian *A. mearnsii* (Impson *et al.*, 2008). This is a seed-destroying insect specific to *A. mearnsii* that was introduced into South Africa to reduce the seed load of this tree. Clearly, the insect is viewed as undesirable by companies that rely on *A. mearnsii* as a product but given that the damage is to the seeds only, the insect does not threaten industry.

Various insect pests and a pathogen have been introduced into South Africa for the biological control of weed *Acacia* spp. that are not grown in plantations. Most notable are the gall wasp *Trichilogaster acacialongifoliae* (Dennill, 1985) and the rust fungus *Uromycladium tepperianum* (Fig. 3b,e) that damages the flowers and reduces seed production in *Acacia longifolia* (Dennill, 1985; Morris, 1991). Both the insect and the pathogen have been introduced into South Africa, and they have imparted severe damage on the target host (Dennill, 1985; Morris, 1991). These biological control agents are host specific, and there is little chance that they will ever affect native *Acacia* spp. in South Africa or *A. mearnsii* grown in plantations. Yet their distribution and population levels have been increased significantly, and they consequently have a greater opportunity to move to other areas of the world and cause problems that cannot be anticipated at the present time.

THE ROLE OF ENDOPHYTIC FUNGI

The fact that large numbers of fungi live within the tissues of healthy, asymptomatic trees was recognized only relatively recently (Carroll, 1988; Petrini, 1991; Smith *et al.*, 1996a,b). These fungi were discovered based on isolations on agar from surface disinfested plant tissue. New generation sequencing has, however, been used to show that there are orders of magnitude more fungi in healthy plant tissue than those that can be cultured (Tedersoo *et al.*, 2010). Yet the role that these fungi play in the biology of trees is in most cases very poorly understood. Some might function to produce compounds toxic to defoliating insect pests as has for instance been shown for some grasses (Siegel *et al.*, 1987), others are latent pathogens that cause disease under stressful conditions (Smith *et al.*, 1996a,b). It is possible that some of these fungi play a role in leaf and branch abscission, and there could well be many that have particular importance.

There have been few studies dealing with the endophytic fungi in *Acacia* spp. Most of these have been on native Southern African *Acacia* species (Van der Walt *et al.*, 2007; Van der Linde *et al.*, 2009, 2010), and there is almost nothing known regarding endophytic fungi in Australian *Acacia* species. However, various die back and stress-related diseases are caused by fungi that are known to be latent pathogens that live as asymptomatic endophytes in healthy tissue. This is similar to the situation with *Eucalyptus* where some of the most important stress-related pathogens are members of the Botryosphaeriaceae, a well-known group of plant endophytes (Smith *et al.*, 1996a,b; Slippers & Wingfield, 2007). Thus, Botryosphaeria canker and die back can result in very severe disease on Australian *Acacia* species in plantations (Roux & Wingfield, 1997; Roux, 2002). In South Africa, these diseases are well known on *A. mearnsii,* and serious die-back is likewise found on *A. mangium* and to a lesser extent *A. crassicarpa* in South-east Asia (Hadi & Nuhamara, 1997; Old *et al.*, 2000).

An intriguing hypothesis is that a loss of endophytic fungi could account for the invasiveness of Australian acacias in non-native environments. Certainly, there is emerging evidence to show that trees grown as non-natives have far fewer endophytic fungi than occur in these trees in their native environment (Hoffman & Arnold, 2008; Shipunov *et al.*, 2008). Preliminary studies in South Africa have also shown that *A. mearnsii* has relatively few endophytic Botryosphaeriaceae than are found in native South African *Acacia* spp. These studies provide ample justification to investigate the relationship between endophytic fungi, invasiveness and disease in Australian *Acacia* species grown in plantations outside their native range.

FUTURE THREATS AND CONCLUSIONS

The global spread of seriously damaging forest pests and pathogens appears to increase in momentum with time. Once a non-native species has become established in a new and genetically uniform environment such as that found in intensively managed plantations, the pest or pathogen appears to have an increased opportunity to spread to new environments. Thus, populations of the pest or pathogen rise to levels seldom found in natural forests, and they gain added opportunity to spread. This is generally referred to as a 'beachhead' effect where increasingly robust bases of 'power' enable a pest or pathogen to move yet again. Thus, as *Acacia* plantation forestry increases and as new pests and disease build up in various parts of the world, the sustainability of plantations elsewhere in the world will likely increasingly be threatened. Likewise, similar 'beachheads' of 'new encounter' pests and pathogens arising from often unexpected or difficult to predict host shifts will increasingly threaten native *Acacia* ecosystems.

Pathogens and pests that are introduced into new environments represent a founder effect and thus generally have a limited genetic diversity. In this regard, the invasives are vulnerable to attack by their own natural enemies that might also be introduced at some time. For example, failures in biological control programmes often result from the introduction of hyperparasites of the biological control agents (Sullivan, 1987). Invasive pests and pathogens could also be seriously damaged by native organisms that might undergo host shifts to damage them. Thus, while introduced pests and pathogens might present a serious threat to non-native *Acacia* plantations in the short term, these invasives are also likely to face threats in the future.

It is relevant to recognize that plantation forestry using non-native Australian *Acacia* species or for that matter other non-natives such as species of *Eucalyptus* and *Pinus* is a relatively new practice. The halcyon days of inexpensive forestry benefiting from the separation of trees from their natural enemies are clearly going to change as new pests and pathogens appear. Biological control programmes will, for example, help to reduce the impact of the pests and pathogens. But in the longer term, they too will face the reality of natural enemies of biological control agents being damaged. This is clearly a dynamic situation, and one that will likely swing back and forth in the favour of the trees and the pests and pathogens that feed on them. In this regard, human nature tends towards a short-term view, whereas these situations might rather be considered over many decades or even centuries.

The dramatic growth of non-native *Acacia* species in plantations might be strongly linked to a separation of the trees from their natural enemies. However, an equally important factor relates to the technologies that have been applied to plantation forestry. This initially begins with the selection of species best suited to the environments in which they are required. Breeding and selection follows as does hybridization and cloning of rapidly growing genotypes. These techniques are likewise used to choose planting stock that is not vulnerable to the ravages of pests and pathogens. These approaches are increasingly being aided by molecular techniques to accelerate breeding and selection. In the future, it is most likely that genetic modification will be used to avoid damage because of pests and pathogens.

Clearly, plantation forestry based on non-natives is dynamic. From a pest and disease perspective, it is little different to agriculture, and it will most likely always represent a continuous battle for improved tree growth. The battle will be won by those groups that embrace new and emerging technologies to beat off pests and pathogens.

In terms of pests and diseases, planting Australian acacias in new environments represents a fascinating experiment in biology and biogeography (Richardson *et al.*, 2011). This experiment is young; the long-term outcomes are largely unpredictable and are likely to hold surprises, some of which will not be favourable for the natural environment or for commercial forestry. Yet there are positive actions that can be taken, perhaps the most important of which is investment in research and new technologies that will enable the useful exploitation of Australian acacias in non-native environments while protecting these trees in their natural ecosystems.

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