Quarantine is important in restricting the spread of exotic seed-borne tree pathogens in the southern hemisphere

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SUMMARY

The lack or destruction of indigenous forests in the southern hemisphere has in some cases led to extensive afforestation with exotic softwoods that subsequently developed into large successful forestry industries. *Pinus radiata* is the predominant softwood species in the southern hemisphere, with over 3 million ha planted. In its natural environment on the West coast of the United States, *P. radiata* has been decimated by an epidemic outbreak of pitch canker caused by *Fusarium circinatum*. The potential devastation of softwood industries in the southern hemisphere, as a consequence of introducing this pathogen, has resulted in strict quarantine regulations. However, this may be too little, too late. *F. circinatum* is already present in South Africa and it appears that only the lack of an insect vector that has prevented its movement from seedlings to mature trees in plantations. This review considers the risk of introducing new pathogens into the southern hemisphere softwood plantations. The pine pathogen *Sphaeropsis sapinea* is used as a model to assess future risks, particularly of introducing seed-borne pathogens.

The genotypic diversity observed in the pine endophyte *S. sapinea*, is consistent with historical records of the frequency and quantity of seed and germplasm importation to and within the southern hemisphere. The diversity in South Africa is high, moderate in New Zealand and low in Australia. Many of the genotypes observed were probably introduced before the advent of quarantine. However, new introduced genotypes may be more pathogenic than existing genotypes, potentially leading to more severe disease outbreaks. In pathogens capable of sexual reproduction such as *F. circinatum*, newly introduced genotypes crossing with existing genotypes would allow for more gene diversity and a greater risk of the pathogen overcoming the trees' resistance. Thus, quarantine is now more important than ever, as limiting the genetic diversity of an exisiting introduced pathogen can be as important as excluding new pathogens.

Keywords: Pinus radiata, Sphaeropsis sapinea, afforestation, quarantine, southern hemisphere

INTRODUCTION

Exotic pine forestry commenced in the southern hemisphere at the end of the 19th Century (Burgess and Wingfield 2001a, Legat 1930, Rodger 1946, Turner 1932). Initially the areas under afforestation were small; however, the forestry industry expanded rapidly and today large areas in countries such as South Africa, Australia, New Zealand, Brazil and Chile are planted to exotic pines. Early in the establishment of exotic pine plantation industries, the trees were relatively free of pests and diseases (Laughton 1937, Wingfield 1999). However, as the industries expanded, so did the incidence of pests and diseases.

In response to the appearance of pests and diseases in southern hemisphere plantations, quarantine regulations were implemented to prevent incursions (Burgess and Wingfield 2001a). Effective quarantine relies on surveillance of all entry points into a country. This is extremely difficult when there are land borders between countries, such as between South Africa and other Southern African countries. With island countries such as Australia and New Zealand, exclusion of pests and diseases through quarantine is more realistic. However, in spite of these regulations, the number of incursions of forest pests and diseases has increased over the past 25 years (Eldridge and Simpson 1987, Old and Dudzinski 1998, Walker 1987, Wingfield 1999, Wylie 1989). Recent globalization of markets through International treaties, such as the General Agreement on Tariff's and Trade (GATT), have facilitated the movement of agricultural and forestry products around the world by the removal of tariffs and quotas. This has also increased the risk of introducing pests and pathogens into new areas (Bright 1998, Palm 1999, Wingfield 1999).

The lack of or ineffective quarantine, resulting in the introduction of new fungal pathogens, has often led to the destruction of indigenous and exotic tree hosts (Old and Dudzinski 1998, Palm 1999). Examples of diseases leading to mass destruction of indigenous forests include chestnut blight caused by *Cryphonectria parasitica* (Murrill) Barr (Anagnostakis 1987), Dutch elm disease caused by *Ophiostoma ulmi* (Buisman) Nannfeldt and *O. novoulmi* in Europe and North America (Hubbes 1999) and jarrah dieback caused by *Phytophthora cinnamomi Rands* in Western Australia (Shearer and Tippett 1989). Introduced pathogens causing destruction in exotic plantations include *Dothistroma septospora* (Dotoguine) Morelet, the causal agent of *Dothistroma* needle blight in pines (Gibson 1972, Old and Dudzinski 1998). Another example, *Cryphonectria cubensis* (Bruner) C. S. Hodges, a pathogen of tropical and subropical eucalypts, can result in the death of up to 80% of susceptible trees under favourable conditions (Wingfield 1999). These and other diseases have increased the pressure on legal agencies to address potential risks before damaging introductions occur. This is predominantly through the implementation of more effective quarantine strategies.

One disease currently of great importance to both native and exotic pine forestry is pitch canker caused by Fusarium circinatumi Nirenberg and O'Donnell (= Fusarium subglutinans f. sp. pini Correll, Gordon, McCain, Fox, Koehler, Wood and Schultz). This pathogen has recently emerged as the causal agent of a devastating disease of Pinus radiata D. Don in its natural environment in California (Devev et al. 1999). The area of P. radiata plantations in the southern hemisphere now exceeds 3 million ha and the threat of pitch canker to industries based on this species is of great concern (Devey et al. 1999, Storer et al. 1998, Viljoen et al. 1997). South Africa was the first country in the southern hemisphere to report the presence of F circinatum, where it was associated with severe disease of P. patula Schl. et Cham. seedlings in commercial nurseries (Viljoen et al. 1994). The disease has not, as yet, spread into mature plantations (Wingfield et al. 1999). In response to the findings of a risk assessment workshop held in Monterey, California during 1998 (Devey et al. 1999), Australia prohibited by legislation the importation of pine seed from North and Central America, Chile, Haiti, Iraq, Italy, Spain, Tanzania, Philippines, Japan and South Africa (Australian Quarantine and Inspection Service 2001). Similar measures have been implemented in Chile and New Zealand. It is hoped these restrictions will be sufficient to exclude E circinatum from these countries.

This review evaluates the efficacy of quarantine pertaining to Pinus in the southern hemisphere. The pine pathogen, Sphaeropsis sapinea (Fr:Fr) Dyco and Sutton (= Diplodia pinea (Desm.) Kickx, Petrak and Sydow), has been chosen as a model on which to base the evaluation. This choice is based on knowledge of various characteristics of the pathogen. Firstly, S. sapinea is an introduced pathogen occurring in all southern hemisphere countries where Pinus are grown as exotics (Burgess et al. 2001, Gibson 1979). It was one of the first pathogens to be recorded in most southern hemisphere countries and was most likely introduced early in the development of exotic pine forestry (Gibson 1979). Furthermore, the biology of S. sapinea is well understood and it is the only pathogen of exotic pines in the southern hemisphere that has been thoroughly studied in terms of genetic diversity (Burgess et al. 2001, de Wet et al. 2000, Smith et al. 2000). The genotypic diversity of native and introduced populations of this pathogen, as influenced by the movement of exotic conifer germplasm, in particular P. radiata, into the southern hemisphere, is discussed.

PINUS RADIATA: INTRODUCED EARLY INTO THE SOUTHERN HEMISPHERE

P. radiata (Monterey pine) is native to California and two islands in the Gulf of Mexico (Figure 1), where less than 7 000 ha now exists in five discrete populations (Lavery 1986a; Libby 1997; Moran *et al.* 1988). These indigenous populations are currently under threat from pitch canker (Devey *et al.* 1999). On mainland California, there are three populations of *P. radiata var radiata*; approximately 450 ha at Point Año Nuevo, 5 000 ha at Monterey and 1 200 ha at Cambria. The two small populations on Guadalupe (400 trees) and Cedros Island (130 ha) are of *P. radiata var bicostata* and *P. radiata* var cedrosensis, respectively. In its native range *P. radiata* is not an impressive timber species.



FIGURE 1 Natural distribution of Pinus radiata. After Moran et al. (1988)



FIGURE 2 Post-hail dieback of Pinus patula (on left) in sub-tropical South Africa caused by Sphaeropsis sapinea.

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Planted as an exotic in the southern hemisphere, however, *P. radiata* has been extremely successful, with 3.4 million ha of commercial plantations in South Africa, Australia, New Zealand and Chile (Figure 2). This accounts for 60% of all softwoods planted in these countries (Balocchi *et al.* 1998). The native population of *P. radiata* thus represents only 0.2% of the area currently under afforestation with this species in other parts of the world.

Conservation of the genetic diversity of *P. radiata* is important because of its limited natural distribution and the economic importance of this species in exotic plantation forestry. This can be achieved by protecting the tree in its natural habitat and by the planting and maintenance of appropriate genetic material in countries where the species is exotic. *P. radiata* has high interpopulation genetic diversity (Moran *et al.* 1988) and it is, therefore, important to conserve genetic material from all populations. The threat of pitch canker to *P. radiata* in its natural environment thus makes it extremely important that experimental plantings, such as the Eldridge provenance trials established in all regions where P. radiata is grown commercially, are maintained (Eldridge 1978, Eldridge 1997).

P. radiata is the most site demanding of all commercial pine species, and can only be grown in a limited climatic range on good quality, well-drained sites. However, it is also the species giving maximum financial yield in most areas (Grey and Taylor 1983) and thus attempts have been made to grow *P. radiata* in many sub-tropical climatic regions, even though it is a species best adapted to a Mediterranean climate. Boundaries to the expansion of *P. radiata* plantations are largely determined by the tree's susceptibility to fungal pathogens, including *S. sapinea*, when planted off-site (Marks and Minko 1969, Poynton 1977b).

South Africa: multiple seed importations

In 1857, fertile seed of P. radiata was collected from mature trees at the 'Oaks of Caledon' in the Western Cape (Lister 1957). P. radiata takes at least 7 years to produce mature cones (Poynton 1977a); therefore the trees must have been planted prior to 1850. Trees were also planted in the Botanical gardens in Cape Town and in 1883 Joseph Storr-Lister, the Conservator of Forests for the Western Cape, collected seed from these trees and planted them at Tokai, also in the Western Cape. This was the commencement of afforestation in South Africa and by 1900, extensive plantations were established in the Cape (Poynton 1977a). Subsequently, large quantities of seed have been imported for commercial planting, mainly from cultivated trees in New Zealand, but also from seed merchants in Europe, Australia, Japan and the United States (Poynton 1977a). The importation of seed from the Cambria population in 1959 was the first seed imported directly from a known population in California (Poynton 1977a).

The origin of seed imported into South Africa before 1925 is unknown. However, as the Monterey district in California is the most accessible, it is assumed this area is primary the source of *P. radiata* in South Africa (Poynton 1977a). In 1939, elite trees were identified and by 1961there were grafted clonal seed orchards providing 50 kg of seed annually. In 1925, 150 kg of seed were received from Nelson, New Zealand (Shepherd 1990b) and again in 1965, seed from New Zealand elite trees was obtained. In 1971, *S. sapinea* resistant collections of *P. radiata* were imported from Australia. In 1970, 300 seed lots were obtained from an international gene pool scheme and in 1977. Five provenance trials based on seed from the Eldridge collection were planted in the Western and Eastern Cape (Eldridge 1978).

Australia: few seed importations

P. radiata may have arrived in Australia before 1850, but the first record (1857) of its importation is of a few seedlings from Kew Gardens in London for the Sydney and Melbourne Botanical gardens (Fielding 1975). The original source of these seedlings is most likely the collections of the Scottish explorer David Douglas in 1833 in the Monterey region of California. This seed had been grown by the Horticultural Society of London at Chiswick, and would have produced seed by 1857 (Lavery 1986b, Shepherd 1990a). An alternative source might have been seed collected by William Lobb in 1850, also at Monterey, and grown by J. G. Veitch in Devon, England. These trees, however, would not have produced cones by 1857 and it is unlikely they were the original source of seed in Australia.

In 1859, the director of the Melbourne Botanical Garden distributed seedlings to landowners around Melbourne. The source of the seed used to raise the seedlings is not known, but it almost definitely came from England probably from J. G. Veitch in Devon (Shepherd 1990b). Trees felled during World War II in Doncaster, Victoria were found to be over 80 years old, indicating they were planted around 1860 (Simpfendorfer 1966). The Hobart Botanical garden also has *P. radiata* in its species list for 1857. In 1865, cones from these trees were sent to Melbourne (Shepherd 1990a). In 1866, an avenue of *P. radiata* was planted in the Adelaide Botanic gardens, South Australia (Lavery 1986b). In 1869, the Inspector of state forests in Victoria recommended the purchase of Monterey Pine seed from Europe (Brown 1883).

The first commercial plantings of *P. radiata* in the southern hemisphere were in South Australia in 1876, with seed collected from trees in a local park. In 1881, the Woods and Forests Department of South Australia acquired P. radiata seed from Lawson Seed merchants in Edinburgh (Brown 1883). When afforestation commenced seriously in South Australia in 1907, all the seed was collected locally. By 1925, all the southern states (except Western Australia) were planting locally collected *P. radiata* as the sole exotic pine species. A number of experimental plantings of *P. radiata* seed collected in California have been established, the most extensive being the Eldridge provenance trials (Eldridge 1978). There has been some exchange of breeding material with New Zealand over the past 40 years.

P. radiata was not planted extensively in Western Australia until late 1960's. Initially seed was collected at Mt Burr in South Australia, although some seed lots from New South Wales and Victoria were also obtained (Butcher pers comm.). During the 1970's a small amount of seed was also imported from Nelson, New Zealand. All the seed currently used for commercial plantings has been collected within Western Australia. There have been no commercial plantings based on seed from California, but four provenance trials from the Eldridge collection were planted in 1977 (Eldridge 1978).

New Zealand; moderate seed importations

P. radiata was well established in New Zealand by 1865 with the first seed provided by J. G. Veitch in 1859. As with the first seed to arrive in Australia in 1857, the trees planted by J. G. Veitch in Devon in 1850 could not have produced seed by then. Thus, the seed source was either from the trees at Chiswick or seed collected in California and brought to New Either way, as with other early Zealand via England. introductions into Australia and South Africa, the source of this seed was Monterey, California. There were a few more consignments of seed from England before 1870 and seedlings were also brought from Australia. New Zealand, unlike Australia, is known to have received seed directly from California. There were at least six consignments of this seed between 1865 and 1972 (Shepherd 1990a). This seed came from suppliers in San Francisco and was from unknown origins in California. All these importations prior to 1870 were very small, consisting of a few seedlings or small quantities of seed.

Large quantities of seed were imported in the 1870's to supply a land settlement scheme in New Zealand. (Lavery 1986b, Shepherd 1990a). There was no state forest service at that time and this seed was distributed by the New Zealand Geological Survey (Shepherd 1990a). About 25 kg of P. radiata seed was received and the resulting half a million trees were distributed throughout New Zealand. Some seed may also have been distributed in Australia. Thereafter, local seed became available in New Zealand and there were no more importations of seed for large-scale afforestation. Thus, seed distributed by the Geological Survey predominantly formed the basis of genetic stocks for commercial plantings in New Zealand. Interestingly, the main source of this seed seems to be Point Año Neuvo (Shepherd 1990b). Consequently, this population dominates genetic stocks in New Zealand, whilst in Australia and South Africa, the Monterey population of P. radiata is predominant.



selection of elite trees (Empire Forestry Association 1958). By the 1960's there were large quantities of high quality seed available for planting. All further importations of seed from California or Australia, including the Eldridge collection have been for experimental purposes only although it is probable that some of this seed was planted out into the forest.

Science and Australian regional forest agreements

Tree breeding in New Zealand started in 1951 with the

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SPHAEROPSIS SAPINEA: INTRODUCED WITH EXOTIC PINES

S. sapinea is one of the best-known pathogens of P. radiata (Laughton 1937; Swart et al. 1985; Zwolinski et al. 1990). It is considered an endophyte in all Pinus and is thus found wherever pines grow (Gibson 1979, Smith et al. 1996). S. sapinea is an opportunistic pathogen causing disease only in stressed trees (Swart et al. 1987, Zwolinski et al. 1990).

In South Africa, the most serious S. sapinea outbreaks are after hail damage in summer rainfall areas (Laughton 1937) (Figure 3). By 1930 afforestation with P. radiata in these areas was abandoned in preference for the more resistant P. elliottii Engelm. and P. patula (Poynton 1977a). Even in the winter rainfall areas of South Africa, P. radiata growing on poor or badly drained sites, susceptible to water logging and drought, were also vulnerable to damage by S. sapinea (Laughton 1937). This phenomenon was also evident in New Zealand where P. radiata was planted across a broad climatic range in the late 1920's and 30's. In 1934, there was a severe drought and large areas of plantations on unsuitable sites were lost to S. sapinea (Empire Forestry Association 1934, Thomson 1969). These outbreaks altered management strategies and subsequently greater attention was paid to site selection.

The northern expansion of P. radiata in Australia was halted because of susceptibility to S. sapinea (Wright and Marks 1970). As a result, P. elliottii and P. caribaea Morelet. are planted in Queensland. In Western Australia, a severe drought in the late1960's resulted in S. sapinea outbreaks



FIGURE 3 Growth of afforestation with Pinus radiata in the southern hemisphere during the 20th century

FIGURE 4 A graft union between P. pinaster rootstock from Western Australia and scions imported from South Africa. Many of the grafts failed and fruiting bodies of Sphaeropsis sapinea were observed at the graft union. Reproduced with permission of Mr Allan Wills.

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Location	Source	Host	No. isolates	Genotypic Diversity (%)
Western Australia	Burgess et al. (2001)	P. radiata	113	1.6
South Australia	Burgess et al. (2001)	P. radiata	26	4.8
South Africa	Burgess et al. (2001)	P. radiata	54	71.4
New Zealand	Burgess et al. (2001)	P. radiata	29	28.2
South Africa	Smith et al. (2000)	P. patula	107	30.5
California, USA	Burgess et al. (2001)	P. radiata	22	26.2
Switzerland	Wingfield (unpubl.)	P. sylvestris P. nigra	. 22	18.2
Mexico	De Wet et al. (2000)	P. patula P. greggii	26	9.2
Michigan, USA	Burgess (unpubl.)	P. sylvestris P. nigra	30	15.5
Indonesia	Smith et al. (2000)	P. patula	83	1.5

TABLE 1 Precent maximum genotypic diversity of different Sphaeropsis sapinea populations estimated from vegetative compatibility tests

in unthinned stands of young *P. radiata* (Butcher pers. comm.). Plantings in Zimbabwe between 1928 and 1934 were also abandoned due to their susceptibility to S. sapinea (Poynton 1977b).

S. sapinea could have been introduced into the southern hemisphere in or on seed or seed chaff (Anderson et al. 1984, Fraedrich et al. 1994), with breeding material (Figure 4), on timber or even with soil introduced to provide mycorrhizal fungi. Phytosanitary and certification certificates were not required for seed traded prior to the 1950's (Burgess and Wingfield 2001a, Empire Forestry Association 1948). Thus, seed and seed chaff was the most likely source of S. sapinea introductions. S. sapinea is not known to show host specificity and, therefore, it is assumed S. sapinea moves between host species. However, this discussion is restricted to P. radiata, because it was one of first pine species introduced into a wide range of countries across the southern hemisphere. S. sapinea reproduces asexually (Sutton 1980) and despite intensive efforts to do so, a sexual state has never been found for this fungus. Thus, it is assumed each separate genotype of this introduced fungus in the southern hemisphere reflects a separate incursion or introduction event. Consequently, the diversity within an introduced population of S. sapinea provides a good indication of the number of introductions of the fungus. Likewise, this reflects the efficacy of quarantine measures to reduce the spread of pathogens.

GENOTYPIC DIVERSITY OF SPHAEROPSIS SAPINEA

Genotypic diversity of *S. sapinea* isolates collected around the world has been assessed using vegetative compatibility (VC) tests (Burgess et al. 2001, de Wet et al. 2000, Smith et al. 2000) (Figure 5). Smith et al. (2000) observed high genotypic diversity among introduced *S. sapinea* isolates collected from *P. patula* in South Africa (Table 1). More recently, Burgess et al. (2001) have estimated the genotypic diversity of introduced *S. sapinea* isolates collected from *P. radiata* across the southern hemisphere. Genotypic diversity of isolates from South and Western Australia was extremely low at 4.8 and 1.6% respectively. This is in contrast to the genotypic diversity of isolates from South Africa that was unusually high at 71.4%. New Zealand had an intermediate genotypic diversity of 28% (Table 1).

Genotypic diversity also has been estimated for a number of native populations of *S. sapinea* (Burgess et al. 2001, de Wet *et al.* 2000, Smith *et al.* 2000). Diversity among *S. sapinea* isolates collected from *P. radiata* in California was 26%, diversity for isolates collected in Mexico from *P. patula* and *P. greggii*. Engelmann was 9%, whilst diversity of isolates from the northern USA was 15%, Switzerland 18% and Indonesia 1.5% (Table 1). The diversity of these native populations is, in general, higher than the diversity observed for introduced populations in Australia, and lower than the diversity of introduced populations in South Africa.

South Africa: high genetic diversity

The genotypic diversity observed in an introduced population of *S. sapinea* in South Africa was greater than the highest diversity observed for isolates in native populations (Table 1). The high diversity in South Africa is most likely due to repeated introductions from many sources, as isolates from



FIGURE 5 Sphaeropsis sapinea vegetative compatibility tests on oatmeal agar. Each letter represents a different isolate. In this test each isolates belonged to different compatibility groups.

different native populations have been found to belong to different VC groups (Burgess et al. 2001). South Africa was colonised in 1649, much earlier than Australia in 1788 and New Zealand in 1792. P. pinaster Aiton, P. pinea L. and P. sylvestris L, were present in South Africa for at least 100 years before these other countries were colonized (Legat 1930). Prior to 1935, large consignments of seed were imported from a variety of sources. Poynton (1977a) refers to quantities of 7 t for P. radiata and approximately 400 t for P. pinaster. Less seed of P. patula and P. elliottii was imported, as there was not the supply available from either their natural origin or from plantations. Since 1935, the majority of seed for afforestation has been collected in South Africa, but there has been exchange of seed from breeding programs elsewhere in the world (CAMCORE 2000). Prior to the 1950's this seed would not have been certified and new genotypes of S. sapinea could have entered South Africa.

Australia: low genotypic diversity

In contrast to South Africa, diversity among isolates of S. sapinea in Western Australia is extremely low. The isolates used in the genetic diversity study we collected from throughout the range of P. radiata in Western Australia and a single genotype accounted for over 80% of the isolates, further strengthening the observation of extremely low diversity in this region (Burgess et al. 2001). P. radiata was present in Western Australia from the turn of the 20th century, although commercial softwood plantations in this state were predominantly comprised of P. pinaster (Butcher, pers. comm.). It was not until the 1950's that P. radiata was planted extensively. By this time, phytosanitary certificates were required for all seed imported into the state. The seed was also certified. Thus, unlike nearly all other areas where P. radiata is planted, the origin of all seed in Western Australia is known. The majority of seed was bought in from South Australia with some seed lots from other Australian states and New Zealand, Conditions in Western Australia differed from

those in other growing regions and an extensive breeding program was established. Consequently, most seed for plantation establishment was derived from seed orchards within the state. The only seed from California was planted in the experimental Eldridge provenance trials.

Genotypic diversity in South Australian isolates of *S. sapinea* is as low as that found in isolates from Western Australia. This is surprising, as *P. radiata* has been grown commercially in South Australia since 1876, only 40 years after the first settlements in the region. There has also been exchange of breeding material and a number of experimental plantings of seed from California. The cones for the study on which these data are based were, however, collected from a plantation established in 1918 (Burgess *et al.* 2001). At this time, all seed was collected in South Australia and the observed genotypic diversity probably reflects the diversity existing in 1918. A South Australian collection from a seed orchard or a current plantation would perhaps better reflect the diversity in the region today.

New Zealand, moderate genotypic diversity

The genotypic diversity of *S. sapinea* isolates from New Zealand lies between that observed for Australia and South Africa. This also reflects the history of seed importation into New Zealand. Since the 1930's, the majority of seed for commercial plantations in New Zealand has been collected locally, although a number of importations of seed in Europe and America were made before then. These imports were prior to the implementation of phytosanitary requirements and it can be assumed the new genotypes of *S. sapinea* were introduced with the seed. Interestingly, the New Zealand collection of *S. sapinea* comes from a seed orchard of trees selected from across the country. As such, a large proportion of genotypic diversity present in New Zealand is probably represented in this seed orchard.

CONCLUSIONS

Overall, the genotypic diversity observed in the pine endophyte and latent pathogen *S. sapinea*, is consistent with historical records of the frequency and quantity of seed and germplasm importation to and within the southern hemisphere (Figure 6). Large quantities of seed of different pine species from different locations have been imported into South Africa over a long period of time and a high diversity of *S. sapinea* is found there. In contrast, a small amount of seed has been imported into Western Australia, the exotic pine industry there is the youngest in the southern hemisphere and the genotypic diversity of *S. sapinea* is the lowest. In the early days of afforestation in New Zealand, seed was imported from a variety of locations, and although this importation was subsequently stopped, it appears many genotypes of *S. sapinea* were introduced in those early years.

The high genotypic diversity of *S. sapinea* in South Africa indicates that the fungus has been introduced repeatedly into the country from different sources. This would also imply that



FIGURE 6 Known movements of Pinus radiata seed to and around the southern hemisphere countries of Australia, New Zealand and South Africa since it's introduction in the mid 19th century. Grey (seed directly from native populations in California) and white (seed from trees grown in the southern hemisphere) lines represent known movements of P. radiata seed with the thickness of the line representing the quantity. The black lines represent importations of seed of other pine species. These movements are reflected in the observed genotypic diversity (percentage values) of Sphaeropsis sapinea isolates from Australia and New Zealand and South Africa.

the risk of having introduced other pathogens is also high. The diversity of *S. sapinea* in New Zealand almost certainly reflects past events. The current quarantine practices in New Zealand are probably the best in the world and consequently their chances of excluding pathogens is also the best (Australian Quarantine and Inspection Service 1999). Australia has been both fortunate and vigilant with their quarantine practises. Good fortune is reflected in the fact that little seed was ever imported into Australia. However, despite restrictive quarantine practices, incursions in both Australia and New Zealand have occurred (Old and Dudzinski 1998). Once a new incursion of a forest pathogen has occurred, there is little chance of eradication. This is especially true in forestry due to the vast areas of plantations and isolation of forest estates.

High diversity of *S. sapinea* equates to multiple incursions, low diversity to few incursions. This should provide a caveat to all countries with exotic forests to carefully consider the import and export of timber. Failure to do so could easily result in the loss of valuable industries. Although the example of *S. sapinea* provided in this review may largely reflect past history prior to quarantine regulations, there are certainly areas where quarantine is not particularly effective. The introduction of the pitch canker fungus into South Africa (Wingfield *et al.* 1999), and numerous eucalypt diseases into various countries of the southern hemisphere (Burgess and Wingfield 2001b, Wingfield 1999) does not indicate effective quarantine practices.

Effective quarantine relies on two key principals. These are firstly understanding the risk and secondly an ability to accurately assess risk. Identifying the risk is extremely difficult. For example, pests and pathogens of pine, such Sirex wood wasp (Sirex noctilio F.) and Dothistroma needle blight (Dothistroma septospora), both extremely damaging to plantations in new environments, were not a problem in their native environment (Eldridge and Simpson 1987). Assessment of risk is also difficult, as the chain of quarantine can be broken at many points. New introduced genotypes may be more pathogenic than existing genotypes potentially leading to more severe disease outbreaks. In pathogens capable of sexual reproduction, newly introduced genotypes crossing with existing genotypes would allow for more gene diversity and a greater risk of the pathogen overcoming a tree's resistance. Breeding for disease resistance in trees takes many years. Thus, limiting the genetic diversity of an exisiting introduced pathogencan be as important as excluding new pathogens.

Effective quarantine is essential to protect a valuable resource such as forestry, which contributes substantially to the economies of countries such as South Africa, New Zealand and Australia. Although governments decide on quarantine regulations, they cannot afford to be the sole enforcers of these rules. The public, government and industry must ultimately join forces to ensure pests and pathogens do not impact negatively on the prosperity of countries. Poor quarantine threatens not only the exotic plantation industry, but also indigenous forests.

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REFERENCES

- ANAGNOSTAKIS, S.L. 1987 Chestnut blight: the classical problem of an introduced pathogen. Mycologia 79: 23-37.
- ANDERSON, R.L., BELCHER, E., and MILLER, T. 1984 Occurrence of seed fungi inside slash pine seeds produced in seed orchards in the United States. Seed Science and Technology 12: 795-799.
- AUSTRALIAN QUARANTINE AND INSPECTION SERVICE 2001 Import Case details. Pinus spp., http://www.aqis.gov.au/icon/asp/ex_casecontent.asp?intN odeld=318426&intCommodityId=5761
- AUSTRALIAN QUARANTINE AND INSPECTION SERVICE 1999 National Stakeholder Timber Pest Conference, Canberra, AQIS.
- BALOCCHI, C., AHUMADA, R., and RAMIREZ, O. 1998 Present and future of Radiata pine In: Chile. In: DEVEY, M., MATHESON, C., and GORDON, T.E. (eds.) Current and Potential Impacts of Pitch Canker in Radiata Pine. proc. IMPACT Monterey Workshop, Monterey, CA, USA, 30 Nov. to 3 Dec. 1998, CSIRO Australia. pp. 1-4.
- BRIGHT, C. 1998 Life out of Bounds. Bioinvasions in a Borderless World. New York, WW Norton.
- BROWN, J.E. 1883 Annual Progress upon State Forest Administration of South Australia. 1882-1883. Adelaide, South Australia, Wood and Forests Department, Government Printer.
- BURGESS, T., WINGFIELD, B.D., and WINGFIELD, M.J. 2001 Comparison of genotypic diversity in native and introduced populations of *Sphaeropsis sapinea* isolated from *Pinus radiata*. *Mycological Research*. (in press).
- BURGESS, T., and WINGFIELD, M. 2001a Exotic pine forestry in the Southern hemisphere: A brief history of establishment and quarantine practices. *South African Forestry Journal* 192: 79-84.
- BURGESS, T., and WINGFIELD, M.J. 2001b Impact of fungi

in natural forest ecosystems. In: SIVASITHAMPARAM, K., and DIXON, K.W. (eds.) *Microorganisms in Plant Conservation and Biodiversity* (in press).

- CAMCORE 2000 Conservation and Testing of Tropical and Subtropical Forest Tree Species by the CAMCORE Cooperative. College of Natural Resources, NCSU, Raleigh, NC, USA, Grow Graphics, South Africa.
- DE WET, J., WINGFIELD, M.J., COUTINHO, T.A., and WINGFIELD, W.D. 2000 Characterization of Sphaeropsis sapinea isolates from South Africa, Mexico and Indonesia. *Plant Disease* 84: 151-156.
- DEVEY, M., MATHESON, C., and GORDON, T.E. 1999 Current and Potential Impacts of Pitch canker in Radiata Pine. Proc. IMPACT Monterey Workshop, Monterey, CA, USA, 30 Nov. to 3 Dec. 1998, CSIRO, Australia, 120 pp.
- ELDRIDGE, K.G. 1978 Refreshing the genetic resources of radiata pine plantations. Detailed Internal report of seed collections of Pinus radiata from its 5 natural populations, Feb and March 1978. 7. Canberra, CSIRO Division of Forest Research, Genetics Section.
- ELDRIDGE, K.G. 1997 Genetic resources of Radiata Pine in New Zealand and Australia. IUFRO' 97 - Genetics of Radiata Pine, 1-4 December, Rotorua, New Zealand, New Zealand Forest Research Institute. pp. 26-40.
- ELDRIDGE, R.H., and SIMPSON, J.A. 1987 Development of contingency plans for use against exotic pests and diseases of trees and timber. 3. Histories of control measures against some introduced pests and diseases of forests and forest products in Australia. *Australian Forestry* 50: 24-36.
- EMPIRE FORESTRY ASSOCIATION 1934 New Zealand: report of the state forest service for the year ended 31st march 1934. Empire Forestry Journal 13: 294-296.
- EMPIRE FORESTRY ASSOCIATION 1948 Review of 5th Empire Forestry Conference, 1947: 5. Forest Practice. Empire Forestry Journal 27: 97-103.
- EMPIRE FORESTRY ASSOCIATION 1958 The Seventh British Commonwealth Forestry Conference; Summaries and reviews of some papers submitted. Application of tree breeding to New Zealand forestry by I. J. Thulin. Commonwealth Forestry Review 37: 96-97.
- FIELDING, J.M. 1975 The introduction of Monterey pine into Australia. Australian Forestry 21: 15-16.
- FRAEDRICH, S.W., MILLER, T., and ZARNOCH, S.J. 1994 Factors affecting the incidence of black seed rot in slash pine. Canadian Journal of Forest Research 24: 1717-1725.

- GIBSON, I.A.S. 1972 Dothistroma needle blight of Pinus radiata. Annual Review of Phytopathology 10: 51-72.
- GIBSON, I.A.S. 1979 Diseases of forest trees widely planted as exotics in the tropics and southern hemisphere. Part 2. The genus Pinus., Commonwealth Mycological Institute, Kew, Surrey and Commonwealth Forestry Institute, University of Oxford, England. 135 pp.
- GREY, D.C., and TAYLOR, G.I. 1983 Site requirements for commercial afforestation in the Cape. South African Forestry Journal 127: 35-38.
- HUBBES, M. 1999 The American elm and Dutch elm disease. The Forestry Chronicle 75: 265-273.
- LAUGHTON, E.M. 1937 The incidence of fungal diseases of

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timber trees in South Africa. South African Journal of Science 33: 337-382.

- LAVERY, P.B. 1986a Pinus radiata an introduction to the species. In: LAVERY, P.B. (ed.) Plantation Forestry with Pinus radiata-Review Papers No. 12, School of Forestry, University of Canterbury, Christchurch, New Zealand: 5-12.
- LAVERY, P.B. 1986b Status and prospects as an exotic. In: LAVERY, P.B. (ed.) Plantation Forestry with Pinus
 radiata-Review Papers No. 12, School of Forestry, University of Canterbury, Christchurch, New Zealand: 13-40.
- LEGAT, C.E. 1930 The cultivation of exotic conifers in South Africa. Empire Forestry Journal 9: 32-63.
- LIBBY, W.J. 1997 Native origins of domesticated Radiata Pine. IUFRO '97 - Genetics of Radiata Pine, 1-4 December, Rotorua, New Zealand, New Zealand Forest Research Institute. pp. 9-21.
- LISTER, M.H. 1957 Joseph Storr Lister, the first chief Conservator of the South African Department of Forestry. *The Journal of the South African Forestry Association* 29: 10-18.
- MARKS, G.C., and MINKO, G. 1969 The pathogenicity of Diplodia pinea to Pinus radiata D. Don. Australian Journal of Botany 17: 1-12.
- MORAN, G.F., BELL, J.C., and ELDRIDGE, K.G. 1988 The genetic structure and the conservation of the five natural populations of *Pinus radiata*. *Canadian Journal of Forest Research* 18: 506-514.
- OLD, K.M., and DUDZINSKI, M. 1998 Forest pathogen introductions to Australia: Experiences, threats and counter measures. Present and future of Radiata pine in Chile. In: DEVEY, M., MATHESON, C., and GORDON, T.E. (eds.) Current and Potential Impacts of Pitch Canker in Radiata Pine. proc. IMPACT Monterey Workshop, Monterey, CA, USA, 30 Nov. to 3 Dec. 1998, CSIRO Australia, pp. 11-19.
- PALM, M.E. 1999 Mycology and world trade: a view from the front line. *Mycologia* 91: 1-12.
- POYNTON, R.J. 1977a Establishment and trial of pine species in Southern Africa. In: Report to the South African regional Commission for Conservation and Utilization of the Soil (SARCCUS) on Tree Planting in Southern Africa. Vol. 1 The Pines, South African Forestry Research Institute: 9-13.
- POYNTON, R.J. 1977b Pinus radiata D. Don. In: Report to the South African regional Commission for Conservation and Utilization of the Soil (SARCCUS) on Tree Planting in Southern Africa. Vol. 1 The Pines, South African Forestry Research Institute.
- RODGER, C.J. 1946 Softwoods in Australian Forestry. Empire Forestry Journal 25: 180-187.
- SHEARER, B.L., and TIPPETT, J.T. 1989 Jarrah Dieback: The Dynamics and management of Phytophthora cinnamomi in the jarrah (Eucalyptus marginata) Forests of South-western Australia. 3. Perth, Australia, Department of Conservation and Land Management.

SHEPHERD, R.W. 1990a Early importations of Pinus radiata

to New Zealand and distribution in Canterbury to 1885: Implications for the genetic makeup of *Pinus radiata* stocks. Part 1. *Horticulture in New Zealand Volume 1 Number 1 Summer 1990* 1: 33-38.

- SHEPHERD, R.W. 1990b Early importations of Pinus radiata to New Zealand and distribution in Canterbury to 1885: Implications for the genetic makeup of Pinus radiata stocks. Part 11. Horticulture in New Zealand Volume 1 Number 2 Winter 1990 1: 28-35.
- SIMPFENDORFER, K. 1966 History of Pinus radiata D. Don. Forestry Technical Papers No. 17: 5-14. Victoria, Forests Commission.
- 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.
- SMITH, H., WINGFIELD, M.J., DE WET, J., and COUTINHO, T.A. 2000 Genotypic diversity of Sphaeropsis sapinea from South Africa and Northern Sumatra. Plant Disease 84: 139-142.
- STORER, A.J., GORDON, T.R., and CLARK, S.L. 1998 Association of the pitch canker fungus, *Fusarium subglu*tans F sp. pini, with Monterey pine seeds and seedlings in California. *Plant Pathology* 47: 649-656.
- SUTTON, B.C. 1980 Coelomycetes. Kew, Surrey, England, Commonwealth Mycological Institute.
- SWART, W.J., WINGFIELD, M.J., and KNOX-DAVIES, P.S. 1985 Sphaeropsis sapinea, with special reference to its occurrence on Pinus spp. in South Africa. South African Forestry Journal 35: 1-8.
- SWART, W.J., WINGFIELD, M.J., and KNOX-DAVIES, P.S. 1987 Factors associated with Sphaeropsis sapinea infection of pine trees in South Africa. Phytophylactica 19: 505-510.
- THOMSON, A.P. 1969 New Zealand's expanding forest resources. Commonwealth Forest Review 48: 289-301.
- TURNER, E.P. 1932 A retrospective of forestry in New Zealand 1894-1931. Empire Forestry Journal 11: 198-212.
- VILJOEN, A., WINGFIELD, M.J., and MARASAS, W.F.O. 1994 First report of Fusarium subglutinans f.sp. pini in South Africa. Plant Disease 79: 309-312.
- VILJOEN, A., WINGFIELD, M.J., MARASAS, W.F.O., and COUTINHO, T.A. 1997 Pitch canker of pines - A contemporary review. South African Journal of Science 93: 411-413.
- WALKER, J. 1987 Development of contingency plans for use against exotic pests and diseases of trees and timber. 1. Problems with the detection and identification of exotic plant pathogens of forest trees. *Australian Forestry* 50: 5-15.
- WINGFIELD, M.J. 1999 Pathogens in exotic plantation forestry. International Forestry Review 1: 163-168.
- WINGFIELD, M.J., WINGFIELD, B.D., COUTINHO, T., VILJOEN, A., BRITZ, H., and STEENKAMP, E. 1999 Pitch Canker: A South African perspective. In: DEVEY, M., MATHESON, C., and GORDON, T.E. (eds.) Current and Potential Impacts of Pitch Canker in Radiata Pine.

proc. IMPACT Monterey Workshop, Monterey, CA, USA, 30 Nov. to 3 Dec. 1998, CSIRO Australia. pp. 62-67.

- WRIGHT, J.P., and MARKS, G.C. 1970 Loss of merchantable wood in radiata pine associated with infection by *Diplodia pinea*. Australian Forestry 34: 107-119.
- WYLIE, F.R. 1989 Recent trends in plant quarantine policy in Australia and New Zealand and their implications for forestry. New Zealand Journal of Forestry Science 19: 308-317.
- ZWOLINSKI, J.B., SWART, W.J., and WINGFIELD, M.J. 1990 Intensity of die-back induced by Sphaeropsis sapinea in relation to site conditions. European Journal of Forest Pathology 20: 167-174.