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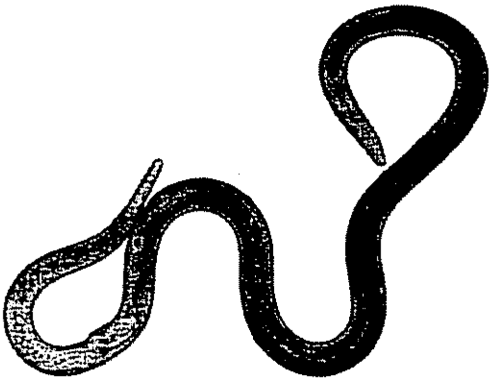
Sustainability of Pine Forests in Relation to Pine Wilt and Decline



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Sustainability of Pine Forests in Relation to Pine Wilt and Decline
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FUNGAL DISEASES OF EXOTIC PLANTATION PINES: A SOUTHERN HEMISPHERE PERSPECTIVE

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Abstract: During the course of this Century, diseases of forest trees have resulted in numerous ecological disasters of immeasurable magnitude. In the case of *Pinus* spp., the best known examples are pine wilt caused by the pine wood nematode and white pine blister rust. In all such cases, the diseases have been caused by pathogens that have been introduced into new but similar environments, where tree species are closely related, yet distinct. In contrast to native pine forests, countries that plant pines as exotics have effectively separated these trees from their natural enemies. However, many pathogens are gradually appearing in these situations, and multiple introductions appear to represent an ongoing event. The movement of a multiplicity of genotypes of *Sphaeropsis sapinea* into new areas and the recent appearance of the wood wasp *Sirex noctilio* into many countries of the Southern Hemisphere are of great concern. They provide excellent examples of the inadequacy of quarantine regulations, aimed at reducing the international spread of pine pathogens. Increasing movement of people and products will undoubtedly lead to the emergence of new and devastating disease problems. In this sense, native pines are seriously threatened. Although plantation forestry, particularly in the Southern Hemisphere will also be seriously affected, increased species diversification, vegetative propagation, hybridization and the application of molecular genetic tools provide outstanding opportunities to deal with these diseases.

INTRODUCTION

The genus *Pinus* is one of the largest groups of conifers and is represented by over 100 species. These trees are native to the Northern Hemisphere where they occupy large areas of land and often comprise the dominant component of the ecosystems in which they occur (Richardson, 1998). *Pinus* has a primary centre of diversity in Central and North America where the greatest number of species occurs. A second area of considerable diversity, although not comparable to the first, is found in East Asia (Price et al., 1998). These trees are thought to have had an association with human development for more than one million years (Le Maitre, 1998). In their native range, they have had a very substantial role in the lives of people from the earliest recorded times and their impact on human existence worldwide remains very substantial. This is both where pines occur in native forests and where they have been propagated intensively in plantations.

Diseases have the potential to cause tremendous damage to forest trees. During the course of this century, diseases of forest trees have resulted in numerous ecological disasters of immeasurable magnitude. Such epidemics are characterised by situations where pathogens have been introduced into new, but similar environments. Here, tree species are native and closely related, yet distinct from those on which the pathogens are native. Perhaps the best known examples of such pandemics are Chestnut blight caused by *Cryphonectria parasitica* and Dutch elm disease caused by *Ophiostoma ulmi* and more recently *Ophiostoma novo-ulmi*. In both these cases, the pathogens are native to Asia and were accidentally introduced into Europe and North America in the early part of this Century (Boyce, 1961; Sinclair et al., 1987).

Accidental cross continental introductions of pathogens into native pine forests have lead to devastating diseases. The best known and first recognised example is white pine blister rust caused by *Cronartium ribicola*. The pathogen is native to Asia (Kaneko, et al., 1995) and was introduced into Europe and then into North America at the beginning of this century (Peterson and Jewell, 1968; Ziller, 1984), where it has subsequently caused tremendous damage. Another example of a pine disease caused by a pathogen introduced into a new, native pine environment is Scleroderris canker caused by *Gremmeniella abietina* (conidial state *Sclerroderris lagerbergii*). This pathogen was introduced into North

America from Europe in the early 1950's and has resulted in a number of serious epidemics (Skilling 1977; Manion and Skilling, 1983). Pine wilt, caused by the pine wood nematode (*Bursaphelenchus xylophilus*) in Japan (Mamiya, 1983; Wingfield, 1987) is causing irrevocable damage to native pine forest in Japan, Taiwan and parts of China. It is in fact the tremendous damage associated with the pine wood nematode that has justified the symposium for which the present account has been produced.

Tree disease epidemics associated with the introduction of pathogens into new and similar native forest environments were first noted at the start of the 20th Century (Harrington and Wingfield, 1998). Their origin has been closely linked to increased levels of cross continental trade. This has chiefly been between countries of the Northern Hemisphere where environments are similar and closely related, but where different tree species occur. Lessons learnt from diseases such as those already mentioned have led to significantly improved quarantine measures to reduce the spread of pathogens. Concurrent with these efforts is the fact that trade between countries has continued to increase dramatically. Thus, new tree disease epidemics continue to emerge. The recent outbreak of pitch canker caused by *Fusarium subglutinans* f.sp. *pini* in California (McCain et al., 1987; Correll et al., 1992; Viljoen et al., 1997), which is thought to be native in Central America, is an example of such a disease.

Many countries plant *Pinus* spp. as exotics in plantations. Some of the most notable are countries in the Southern Hemisphere such as Australia, Brazil, Chile, New Zealand and South Africa. In these countries there has been a dramatic increase in the extent of *Pinus* plantations from virtually zero at the start of the Century, to 1.5 million hectares at present (Le Maitre 1998). Exotic pines have been separated from pests and pathogens that affect them in their native lands (Wingfield, 1990). This situation has provided a window of opportunity for forestry companies who are able to propagate rapidly growing trees, in the absence of problems that affect them in areas where they are native. Gradually, diseases are appearing in these countries, and this is a trend that is likely to continue in the future. Initial introductions are generally from Northern Hemisphere sources, but once established, trans-continental spread in the Southern Hemisphere is more likely.

Diseases that have been introduced into new environments provide excellent examples on which to base a more complete understanding of the factors associated with their introduction and establishment. In this paper, we consider an exotic fungal pathogen and an exotic insect pest that lives in a symbiotic relationship with a fungus, that have been introduced into intensively managed pine plantations in the Southern Hemisphere. We have specifically chosen these examples based on the fact that they have different dispersal strategies, and because they have been the subjects of some considerable study in our laboratories in recent years. The pathogen treated here is the die-back and canker fungus *Sphaeropsis sapinea* (= *Diplodia pinea*) and the insect pest is the wood wasp *Sirex noctilio* with its fungal symbiont *Amylostereum areolatum*. These examples provide considerable information on which to base an extended understanding of procedures used to avoid introduction of new pests and pathogens in the future.

SPHAEROPSIS CANKER AND DIE-BACK

Sphaeropsis sapinea is one of the most common fungi found on *Pinus* spp., throughout the native range of the tree. It is an opportunistic pathogen that results in disease only after trees have been predisposed to infection (Swart and Wingfield, 1991). Stresses associated with disease include environmental factors such as drought, nutrient imbalance and wounding due to insects and hail. Disease is expressed in a wide variety of symptoms that include branch and stem cankers, tip die-back, root disease, seedling death and blue stain (Gibson, 1979; Sinclair, et al., 1987; Swart and Wingfield, 1991).

Where pines are native and growing under natural conditions, *S. sapinea* is generally not considered to be an important pathogen. Although the fungus is commonly found on dead tissue in such circumstances, it is usually not thought of as a primary cause of disease. In contrast, the fungus has been associated with dramatic, episodic disease outbreaks in exotic landscape trees and plantations. The most serious losses associated with *S. sapinea* have been recorded from countries of the Southern Hemisphere such as South Africa, New Zealand, Australia and Chile where the highly susceptible *Pinus radiata* is extensively planted (Swart and Wingfield, 1991).

The most dramatic and serious losses associated with *S. sapinea* are recorded from South Africa, where the fungus was first recorded early this Century (Swart and Wingfield, 1991). In this country, a combination of extensive planting of highly susceptible species such as *P. radiata* and *Pinus patula* and the common occurrence of hail damage has led to dramatic losses annually (Zwolinski et al., 1990). This is ironical given the fact that the fungus is not considered to be amongst the most important pathogens of pine. Nevertheless, it has justified reasonably intensive studies on the possible origin and biology of *S. sapinea*, the results of which are now gradually beginning to emerge.

Origin of *S. sapinea* in South Africa

Pinus species were introduced into South Africa by early European settlers. We surmise that *S. sapinea* was introduced together with the first *Pinus* genotypes brought to this country, although the first record of the fungus was only in 1912 (Waterman, 1943). The first introductions of *S. sapinea* could have been on either plant material or on seed, both of which are now known to commonly harbour propagules of the fungus. Pine seed would certainly have been introduced in the early stages of European settlement and this would have allowed introductions of *S. sapinea*. Although we are not aware of documented evidence of this fact, it is assumed that pine plants were also introduced into South Africa. This would have given rise to the origin of European mycorrhizal fungi which are well established and numerous in the country today.

Sphaeropsis sapinea is known only to reproduce asexually and we feel reasonably convinced that sexual reproduction in this fungus does not occur in nature. This premise is based on the fact that the first author of this paper has actively sought the teleomorph of this fungus, both through careful inspection of naturally infected tissue from many parts of the world and extensive laboratory tests. Our view is thus, that there are limited opportunities for genetic recombination in *S. sapinea* in nature. This has led to our working hypothesis that native populations of *S. sapinea* would be genetically diverse. In contrast, the introduced South African population would be genetically uniform.

Preliminary studies on the genetic diversity of *S. sapinea* in South Africa have led to intriguing and unexpected results. These studies have involved defining the diversity of large hierarchical collections of local isolates of the fungus based on vegetative compatibility (Smith et al., 1998). We have also compared these results with those from similar tests on smaller samples from parts of the world such as Indonesia and Switzerland where *S. sapinea* is most likely native. Suprisingly, in these countries, the fungal population is virtually clonal (authors unpublished). Contrary to expectation, our results, which will now be confirmed using molecular markers, show a tremendously large diversity in the South African *S. sapinea* population.

In the absence of sexual reproduction, *S. sapinea* can rely only on mutation to generate new genetic entities. It is unlikely that the extent of variation observed in South African populations of the fungus could be ascribed to mutation. This is particularly the case, as we would then expect to observe equally large or even greater variability in the pathogen population, where it is native. Our view is rather, that *S. sapinea* has been introduced into South Africa repeatedly during the course of the last 300 years. The onset of intensive pine plantation forestry about 100 years ago, led to the introduction of seed from many parts of the world. This is a trend that has not abated in recent years. Although efforts are made to eliminate fungi from seed, it is likely that infected seed successfully enters South Africa regularly. Thus, the extensive genetic diversity of the fungus in the country is linked to repeated introductions from a wide variety of sources.

Rapid tree death after hail damage

One of the most intriguing aspects of the biology of *S. sapinea* in South Africa, is that it leads to the death of large, established trees of susceptible species, very rapidly after hail damage (Swart and Wingfield, 1991). Mature trees tend to be more severely affected than young trees. Inoculations of established trees with virulent isolates of the pathogen generally result in lesions, but not tree death. These contradictory observations have led us to consider how trees might die so rapidly after hail damage.

Recent studies have shown that *S. sapinea* commonly inhabits healthy asymptomatic pine tissue (Smith et al., 1995; 1998; Blodgett and Stanosz, 1997). In this sense, the fungus is typical of an endophyte, or perhaps more accurately a latent pathogen. The most common source of latent *S. sapinea* infections is found in the pith of pine cones (Smith et al., 1998), where virtually every mature cone will yield an isolate of the fungus. We have found that this is true, not only in South Africa but in isolations from cones from a wide variety of sources including North America, Mexico, Switzerland and Indonesia (authors unpublished).

Observations on hail damaged pine stands has led us to conclude that younger trees generally tend to recover, whereas older trees tend to die dramatically (H. Smith and M.J. Wingfield, unpublished). We believe that this is due to the presence of *S. sapinea* infected cones on older trees. After hail, we believe that trees are physiologically stressed and unable to halt the ingress of *S. sapinea* via the pith of pine cones, into the main stem of trees. This then leads to colonisation of trees and rapid death. Although this explanation of the rapid death of susceptible pines after hail storms is clearly simplistic, it is most consistent with the observations and data at our disposal. Careful studies in the future must focus on the physiology of trees immediately after hail, and how this might influence the movement of *S. sapinea* from the cone pith into the main stems of trees.

SIREX WOOD WASP

The pine saw fly *Sirex noctilio* provides another excellent example of an exotic factor that has led to considerable, and often dramatic damage to exotic pine plantations in the Southern Hemisphere. *Sirex noctilio* is native to Europe and was first recorded in New Zealand early this Century and in Australia around 1950 (Ohmart, 1980). In Australia, the wasp has caused extensive damage, particularly to over mature and unthinned stands of *P. radiata.* This has led to many outstanding studies of the pest and its biology in that country (Neumann et al., 1987; Madden, 1988).

A fascinating aspect of the biology of *S. noctilio* is that the insect lives in a strict symbiosis with the basidiomycete fungus *Amylostereum areolatum* (Morgan, 1968; Talbot, 1977). Propagules of this fungus are carried in mycangial sacs at the base of the ovipositor and these are inoculated into pine tissue when the female insects oviposit. Larvae hatch and proceed to consume wood that is colonised by *A. areolatum*. The presence of the fungus is thought to enhance borrowing activity of the larvae, as well as to provide nutrients and digestive enzymes to the larvae (Kukor and Martin, 1983; Madden and Coutts, 1979). The parasitic nematode *Deladenus siricidicola* has been successfully used in biological control of *S. noctilio* (Neumann and Marks, 1990; Bedding, 1995; Madden, 1998). The life cycle of this nematode includes a phase where it feeds on the fungal symbiont of *S. noctilio* and a parasitic phase where it infests larvae of the insect. Thus, an extremely close relationship exists between *S. noctilio*, its fungal symbiont *A. areolatum* and the parasitic nematode *D. siricidicola.*

Origin of *Sirex* in South Africa

Sirex noctilio has been known as an exotic in the Southern Hemisphere for almost one hundred years. It is interesting to note that it appears to have taken more than 50 years for the insect to move from New Zealand to Australia. Recently, the insect was first reported from South America where it first appeared in Brazil (Reardon et al., 1995). It has subsequently moved to Uruguay and Argentina and its introduction is feared in countries such as Chile where pine plantation forestry is important.

A recently established population of *S. noctilio* was found near Cape Town in South Africa in 1994 (Tribe, 1995). This has led us to question where the South African population might have originated. This could have been from Europe where the pest is native, or from one of the countries where it has been accidentally introduced. The fungal symbiont of *S. noctilio* is intimately attached to the insect and appears to exist as clonal lineages, over large areas (Thomsen and Koch, 1990; Vasiliauskas et al., 1998). Thus, the opportunity to consider the origin of the South African and other *Sirex* populations based on the genetic composition of the fungal symbiont presents a tantalising opportunity.

Using vegetative compatibility tests, we have recently examined large collections of isolates of *A. areolatum* from Brazil and South Africa. We have also examined smaller numbers of isolates from other parts of the world (Slippers et al., 1998). Preliminary results have shown that the fungus associated with wasps in South Africa, represents a single clone. This implies that *S. noctilio* was introduced into South Africa from a reasonably isolated population, and probably with a small number of insects. Similarly, and perhaps not surprisingly, insects collected in Brazil also carry a single clone of *A. areolatum.* Considerably more intriguing is the fact that the *A. areolatum* clone in South Africa is apparently identical to the clone associated with the wasp in Brazil. From these results, we conclude that *S. noctilio* in South Africa originated from the South American population or that the two populations originated separately from the same area. Although the possibility that the pest complex might have been introduced from Europe to Australasia and then into South Africa cannot be ruled out, it seems more probable that the introduction came from South America. We favour the latter hypothesis.

DISEASE TRENDS IN EXOTIC PINE PLANTATIONS

Appearance of pathogens on isolated *Pinus*

One of the most outstanding opportunities linked to the establishment of plantations comprised of exotic *Pinus* spp. in areas where no pines are native, is that these trees are isolated from most pests and pathogens. Such situations occur in many parts of South America, Africa, New Zealand and Australia. Thus, trees can be grown considerably more easily than would be possible in areas where a wide range of pests and pathogens occur on the same, or related species. Although isolation provides forestry companies with considerable opportunity, it is also characterised by substantial risk.

Many pests and pathogens have gradually reached countries that have grown pines in isolation in the past. When such introductions occur, substantial losses can arise. We have already illustrated this point with just two of many possible examples of pests and pathogens known to occur in these situations. However, a noteworthy observation is that the numbers of pests and pathogens of pine that have appeared in these situations is relatively low, when compared with the total number that might be introduced. We expect that, in the longer term, new and damaging pests and pathogens will be introduced into these areas. This will in all likelihood make plantation forestry in Southern Hemisphere considerably more costly and challenging.

Risk due to diseases and pests

The risk of disease causing irrevocable damage to plantation forestry in Southern Hemisphere countries must be closely linked to the nature of forestry in these particular countries. In some situations, whole industries depend largely on a single species such as *P. radiata*. Here risks are considerable and substantially greater than in areas where a wide variety of *Pinus* species are propagated.

While risks associated with the intensive propagation of single species might be great, this needs to be contrasted with the cost of research and development linked to the improvement of a wider variety of species. Where considerable investment can be focussed on a single species, the benefits might outweigh the risks due to disease. The alternative might be to propagate a wide range of species, but not have sufficient research and development capital to focus on any one of these.

Current trends in forestry are to exploit opportunities linked to vegetative propagation of *Pinus* spp. Here it is possible to establish plantations of clones known to be tolerant to diseases. A yet more attractive option is to capitalise on opportunities to develop and exploit hybrids between species that exhibit hybrid vigour and also display a greater range of tolerance to disease. The development of molecular tools such as those that enable marker aided selection will also make it possible to gain the greatest benefits from hybrid clones, including planting of disease and pest tolerant stock.

Quarantine considerations

Exclusion of pests and pathogens from plantations of exotic species initially separated from these debilitating factors, is a crucial component of the long-term sustainability of forestry programmes. This is achieved through quarantine regulations, which are variable in rigor depending on the particular country and usually, its financial capacity to maintain such programmes. Southern Hemisphere pine-growing countries such as New Zealand and Australia are well known for their outstanding quarantine programmes. The fact that these countries are islands without 'land bridges ' to other countries positively influences their capacity to exclude pests and pathogens through quarantine. On continents such as Africa and South America that are comprised of a large number of independent countries, quarantine success in any one of those countries is fully dependant on the quality of quarantine procedures in neighbouring countries. The so-called 'weakest link in the chain' must determine the overall quarantine capacity of the continent as a whole.

Pathogens and pests of pine have continued to enter even those countries with the most rigorous quarantine programmes. While this point is certainly not intended to suggest that quarantine is ineffectual or unnecessary, it does illustrate the difficulty involved in excluding pests and pathogens. The increasing movement of people and products throughout the world will make exclusion of these agents of disease increasingly difficult.

There is much evidence to suggest that seed has been a major vehicle for the movement of pine pathogens to new areas. The example of *S. sapinea* being represented by a very wide variety of genets in South Africa provides a startling example of what appears to have been continuous multiple introductions of a pathogen into a country. It would now be interesting to consider the genetic diversity of the *S. sapinea* population in a country such as New Zealand where rigorous quarantine has been applied for an extended period. Our hypothesis would be that the genetic diversity of the pathogen in that country would be much more limited than it is in South Africa.

The movement of wood and wood products between continents and countries has been closely linked to the movement of important pine pathogens. For example, the pine wood nematode is believed to have entered Japan on pine timber. In recent years, regulations to restrict the movement of untreated pine timber have been significantly strengthened. Nevertheless debates continue as to the advisability of importing logs into countries. The desired importation of conifer timber from Eastern Europe into the United States is one example of such a heated debate. Perhaps one source of timber that has not been carefully scrutinised is freshly sawn untreated timber that is used for the packaging of large appliances and industrial equipment. This is the probable source of the introduction of *S. noctilio* in South Africa. Although it might be most difficult to limit the use of such untreated packing timber, we believe that this is a matter that deserves urgent attention.

Once a new pine pathogen becomes established in a country, the likelihood that it will move to adjacent countries will be greater. For example, the first appearance of the devastating pine needle pathogen, *Dothistroma septospora*, in Africa was followed relatively rapidly by its appearance in South America, New Zealand and Australia (Gibson, 1972; Gibson, 1975). Likewise the introduction of *S. noctilio* in South America appears to have led to an early introduction of the pest into South Africa. Collaboration between adjacent countries in quarantine matters would appear to be an advisable strategy to follow.

CONCLUSIONS

- Many countries in the Southern Hemisphere have histories of exotic pine plantation forestry extending back to the beginning of the Century. These plantations have been highly productive and, in many cases sustain very significant forestry industries. Although diseases and pests have had a serious impact on these plantations, their impact has been alleviated by breeding, selection and the planting of alternative species in areas of high risk.

- New pests and diseases are likely to continue to appear in pine plantations of the Southern Hemisphere. This will lead to new challenges and heightened costs for forestry companies. However, many new opportunities linked to breeding and plant biotechnology will promote opportunities for disease avoidance.

- Risks due to pests and diseases can be substantially reduced through the commercial exploitation of a greater, rather than a smaller number of species. Such reduction in risk will, however, need to be weighed up against the increased costs linked to improvement of additional species.

- Outstanding quarantine measures will slow the appearance of new pests and diseases in exotic pine plantations. Commitment to such programmes is unquestionably worthwhile. Regional efforts and particularly the rather overlooked east/ west continental links should be encouraged. Together with quarantine efforts, diversification of the genetic composition of pine plantations in Southern Hemisphere countries would appear to be most advisable.

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